Hypogaeic and epigaeic ant (Hymenoptera : Formicidae) assemblages of atlantic costal rainforest and dry mature and secondary Amazon forest in Brazil : Continuums or communities

HAROLD G. FOWLER[1], JACQUES H.C. DELABIE[2] & PAULO R.S. MOUTINHO[3]

[1]*Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, São Paulo, Brazil (e-mail: hgfowler@rc.unesp.br);* [2]*CEPEC, CEPLAC, Caixa Postal 7, Itabuna, Bahia, Brazil;* [3]*Departamento de Psicologia Experimental, Universidade Federal de Pará, Belém, Pará, Brazil*

Abstract: Meat, flour and sugar baits were used on the soil surface and buried to examine species composition of the ant fauna in three separate tropical forests in Brazil, and to control for the effect of the regional faunal pool. Compositional mosaic diversities were comparable among areas, bait types and foraging strata. Mosaic diversity was independent of mean assemblage size. The number of unique species per sampling unit was correlated with mean assemblage size. Canonical correspondence analysis ordered species first by foraging substrate, second by geographic location, and third by diet. The first axis was significantly correlated with mean similarity and affinity. Mean Mahanalobis distances between centroids of groups based upon foraging strata were significantly larger than between localities, indicating local ecological pressures stronger than regional species pool constraints. As most species foraged in only one stratum in one geographical position and were not omnivorous, the response of species to environmental gradients (continuums) showed a lower coherency with these patterns than did communities, structured around guilds based upon foraging strata and diet.

Resumen: Se usaron cebos de carne, harina y azúcar en la superficie del suelo y enterrados para observar la composición de especies de la fauna de hormigas en tres selvas tropicales en Brasil y para controlar el efecto de la fauna regional. Las diversidades del mosaico composicional fueron comparables entre areas, tipos de cebo y estratos de forrajeo. La diversidad del mosaico fue independiente del tamaño promedio de la agrupación. El número de especies únicas por unidad de muestra se correlacionó con el tamaño promedio de la agrupación. Un análisis de correspondencia canónica ordenó a las especies primero por sustrato de forrajeo, en Segundo lugar por localización geográfica y en tercero por la dieta. El primer eje estuvo significativamente correlacionado con la similitud media y afinidad. Las distancias medias de Mahanolabis entre centroides de grupos basadas en los sustratos de forrajeo, fueron significativamente más grandes que entre las localidades lo cual indica presiones ecológicas locales mas fuertes que las restricciones regionales para éste grupo de especies. La mayoría de las especies forrajearon en sólo un sustrato en una posición geográfica y no fueron omnivoras. La respuesta de las especies a los gradientes ambientales (continuo), mostró una baja coherencia con éstos patrones más que con las comunidades, estructurando gremios basados en el sustrato de forrageo y la dieta.

Resumo: Para examinar a composição específica da fauna de formigas em três florestas tropicais distintas usaram-se iscos de carne, farinha e açúcar à superfície do solo e enterradas. A diversidade da composição do mosaico foi comparada entre áreas, tipos de isco e estrato alimentar. A diversidade do mosaico era independente da dimensão media das construções. O

número de espécies únicas por unidade de amostragem estava correlacionado com a dimensão media da construção. A análise canónica de correspondências ordenou as espécies em primeiro lugar pelo substrato alimentar, em segundo pela localização geográfica e em terceiro pela dieta. O primeiro eixo encontrava-se significativamente correlacionado com a similaridade media e a afinidade. As distâncias médias de Mahanalobis entre os centroides dos grupos, baseados de acordo com o substrato alimentar, foram significativamente maiores entre localidades, indicando pressões ecológicas locais mais fortes do que os constrangimentos regionais da pool de espécies. Dado que a maior parte das espécies se alimentam somente num único estrato numa posição geográfica e não eram omnivores, a resposta das espécies aos gradients ambientais (*continua*) mostrou uma pequena coerência com estes padrões do que mostraram as comunidades, estruturadas segundo associações baseadas no estrato de colheita alimentar e dieta. posição geográfica e não eram omnivores, a resposta das espécies aos gradients ambientais (*continua*) mostrou uma pequena coerência com estes padrões do que mostraram as comunidades, estruturadas segundo associações baseadas no estrato de colheita alimentar e dieta.

Introduction

In species-rich tropical ground ant communities, resources are exploited through interference competition (Andersen 1991; Fowler & Delabie 1995; Delabie & Fowler 1995). Competition for food resources results in specialized sizes or types of food exploited (Samways 1990), and divergence in foraging strata (Torres 1984). These characteristics allow comparison of the continuum and community concepts (Austin 1985). Are species assemblages ephemeral, non-stationary phenomena along regional gradients (continuums)? Or, are species assemblages discrete, replicable entities in discrete habitats with inherent intrinsic properties (communities)? The continuum concept is implicitly accepted by most researchers, which refer to species assemblages and not communities. If the community concept is valid, a full set of environmental parameters must be characterized which constrain and structure it. If the continuum concept is valid, the biotic component of species' environmental responses must be characterized.

The biotic component of the landscape can be characterized by the relationship between the distribution patterns of individual species and their abundance and distribution within landscape features. This leads to a complementation of continuum and community concepts (Austin 1985). However, the species richness is the result of the interaction of regional biogeographical and local

ecological factors (Ricklefs 1987). Regionally, landscape characteristics and individual species distributions, constrained by interspecific interactions, along environmental gradients produce assemblages. Are regional faunal pool, or biogeographical, constraints more important than local environmental heterogeneity, or local ecological interactions ? An analysis of landscape heterogeneity at the scale of an ant may reveal environmental gradients and patterns which differ than those perceived by man (Wiens 1989; Wiens & Milne 1989). However, recognition of spatial and temporal scales (Allen & Starr 1982; Wiens 1989; Schneider 1994) is highly dependent upon the spatial variation of the data. Assemblage organization is consequently hierarchial and controlled by different processes at different temporal and spatial scales.

The continuum concept can be described by three alternative models of individual species distributions : (1) individually distributed with no apparent pattern; (2) dominant species are regularly distributed along complex environmental gradients with other species individually distributed; or (3) species stratification divides the environmental gradient regularly but individual strata vary independently (Austin 1985; Austin & Smith 1989). Ant assemblages structured through the exploitation of particular food resources can be considered as feeding guilds (Root 1967), which are considered as hypothesis 2 and 3 (Austin 1985).

Here, we examine sequentially whether ant assemblages are dominated by few species (hypothesis 2) (Austin 1985; Risch & Carroll 1982), characterized by multiple independent species (hypothesis 1) (Austin 1985), or are organized by guilds (hypothesis 3) (Austin 1985). To do this we use differing food types in differing foraging strata in different geographic areas.

Materials and methods

Studies were conducted in three separate sites. The first site was located in the Cocoa Research Center (CEPLAC) in Ilhéus, Bahia (14o45 S, 39o13 W) situated in a relict fragment of the South American Atlantic Coastal Rainforest. The climate is tropical humid, with two seasons characterized by temperature, rather than rainfall, variation. We used an old cocoa (*Theobroma cacao* L.) plantation which had received no pesticide treatment for 20 years. Overstory shading was heterogeneous, composed of second-growth trees, 10 to 20 m tall, established in podzols (Leite 1987). The other two sites were located approximately 7 km from Paragominas, Pará (3o15 S, 47o30 W). The first of these was a regenerating secondary forest, while the other was a mature dry-land Amazonian forest. Seasonality is marked by rainfall and not temperature, and soils are principally kaolinitic oxicols (Ritcher & Babbar 1991). Further details of these sites can be found in Uhl *et al.* (1988) and Nepstad *et al.* (1991).

Baits were used to characterize the feeding habits of the ant species. Within a 1000 m² area of the Bahian cocoa plantation, we marked 40 plots each of 5 x 5 m. Small piles of dry sugar, meat, and manioc flour were placed on separate 6 cm diameter ceramic dishes (one of each type per plot), and were either buried at 5 to 15 cm depth in the soil or placed on the soil surface (one of each type per plot), each replicated 5 times. In the Paragominas sites, 40 surface baits were placed on toilet paper in both secondary and mature forests, along transects at 10 m intervals, with 4 transects per site. We additionally placed 40 buried baits in 5 cm long perforated plastic vials at a depth of 5 to 15 cm at each surface baiting station. In all sites, baits were exposed for 8 h, from dusk to dawn, during the summer (January). Bait stations were collected into plastic bags, and species identified in the laboratory. These data provide feeding habits of ant species as well as their ability to explore food resources through recruitment (Holldobler & Wilson 1980).

Dietary and vertical niche dimensions were estimated using bait visitation frequencies, divided into superficial and subterranean strata for each bait type. These dimensions form a dissimilarity matrix (Cody 1974). Jaccard's (1901) similarity, a suitable index for diversity (Wilson & Schmida 1984), was calculated between sites, strata and bait type, as were their corresponding affinities (Scheiner & Istock 1987). Affinities have been shown to be higher order measures of affinities (Istock & Scheiner 1987). Affinities and similarities were regressed on each other to estimate compositional mosaic diversity (Scheiner 1992), or an estimate of landscape complexity from the patterning of the ant assemblages. A jack-knife estimate of mosaic diversity was generated by the software AA4.3 (Scheiner 1992). For this, we used all data, as well as their separation into locality, site and bait strata exploited, to determine large breaks of pattern based upon spatial scope (Schneider 1994) of foraging strata, diet and geography.

Cannonical correspondence analysis (Gauch 1985; Digby & Kempton 1987) was used to examine combinations of bait type, foraging strata, and geographic locations. This method was chosen over methods of nonmetric multidimensional scaling (Austin 1976) as it provided direct comparison with mosaic diversity. Species as well as bait type, foraging strata, and geographic location were used for ordination (Pielou 1984: Gauch 1985). The number of foraging strata, geographic locations, and bait types exploited by each species were correlated with species loadings using Kendall's correlation ( ) coefficient (Siegel 1956) to examine their relative importance in species and site ordination (Johnson & Wichern 1982). Pearson product-moment correlations (Sokal & Rohlf 1981) were used to examine site ordination characteristics with respect to mean affinities and diversities (Gauch 1985). The interpretation of the cannonical correlation ordination was based upon the types and numbers of baits foraged as well as foraging strata and geographic location (Digby & Kempton 1987). Regional versus local influences were tested with the Mahalanobis distance from centroids which separated groups. As groupings resulted from foraging strata and geography, we examined which distance was more significant (Johnson & Wichern 1982). The relative Mahala-

nobis distance can be used to infer which factor is more important (Johnson & Wichern 1982).

Ant taxonomy follows Kempf (1972) and Brandão (1992). Voucher specimens are deposited in the collections of the senior and secondary authors. A complete listing of species can be obtained upon request from the authors.

Results

Seventy four ant species were recorded, with 49 found in Bahia and 48 found in Pará. Within Pará, 40 species were found in secondary growth forest and 31 species in mature forest. Almost all species were exclusively hypogaeic or epigaeic, with only a small percentage found using both foraging strata (Fig. 1). Using all major combinations of foraging strata and bait types with geography, all assemblages were similar in estimated mean species richness (Table 1). Local assemblag-

es based upon bait type and foraging stratum ranged from 5 to 22 species (Table 2), with the number of unique species per grouping being higher for Bahia than for Pará (t = 2.278, P<0.05). Higher mean similarities and affinities were found for hypogaeic than for epigaeic assemblages (Table 2). A smaller relative proportion of species occurred at only one geographic location, with a larger percentage present in two and three sites (Fig. 2). Bait types exploited were more uniform, with a gradient of highest to lowest ranging from 1 to 3 bait types (Fig. 3). Sugar and meat baits attracted significantly more species than manioc flour baits (t = 4.291 and t = 2.577, P<0.05, respectively), but did not differ between themselves (Table 1).

Mosaic diversity was independent upon mean assemblage size (r = 0.01), but the number of unique species was dependent upon mean assemblage size (r = -0.60) (Table 1). Surprisingly, mosaic diversity was smaller when all sampling stations in both regions were analyzed together (Table 1), and no significant differences were found between these regions (Table 1). Nevertheless, meat and sugar baits, as well as ant assemblages from Bahia, had non-significantly larger mean numbers of unique species than did flour baits or sites from Pará (Table 1). Bait types and foraging strata all produced a similar jack-knifed estimates of mosaic diversity (Table 1).

Cannonical correspondence analysis grouped ant assemblages by both geography and foraging strata, and much less by bait type (Table 2, Fig. 4). The first dimension was significantly correlated with mean similarity (r = -0.67) and affinity (r =
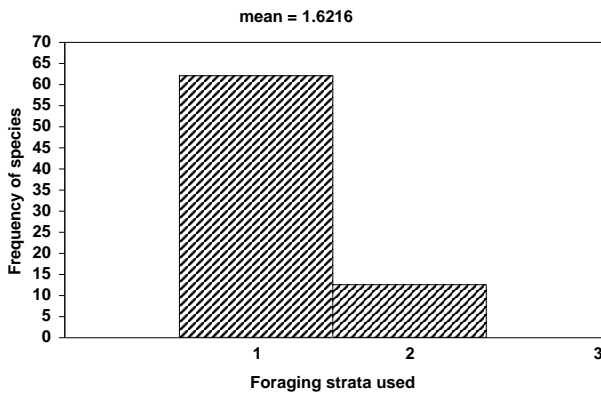

Fig. 1. The distribution of the number of foraging strata in which all species were active in Bahia and Pará.
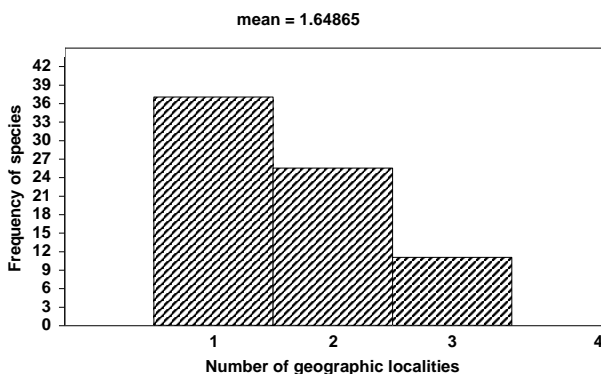

Fig. 2. The distribution of geographic locations of the epigaeic and hypogaeic ant fauna in Bahia and Pará.
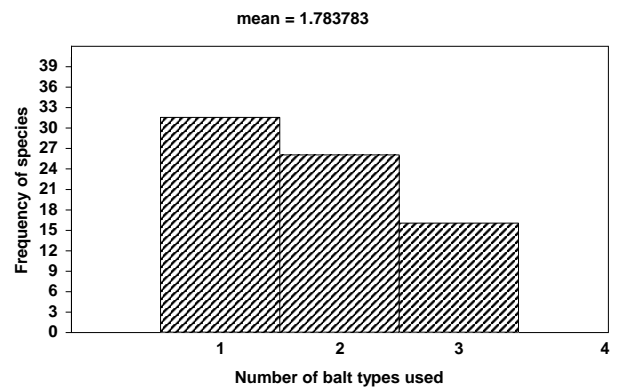

Fig. 3. The distribution of the number of bait types used by the epigaeic and hypogaeic ant fauna in Bahia and Pará.

Table 1. Changes in mosaic (m) and jack-knifed mosaic [E (m)] diversities with respect to geographic location, bait type and foraging stratum. S = number of species.

Scale	N	m	R^2	E(m) (+ S.D.)	Mean S	Unique S
All sites and baits	18	3.200	0.940	3.240 + 0.184	13.1 + 5.68	1.3 + 1.71
Pará: all sites	12	3.969	0.902	4.032 + 0.794	11.5 + 5.04	1.4 + 1.78
Bahia: all sites	6	3.950	0.754	4.484 + 1.046	16.0 + 5.51	4.3 + 3.20
Subterranean baits: all sites	9	4.098	0.957	4.329 + 0.318	9.9 + 3.26	1.0 + 1.22
Surface baits: all sites	9	4.130	0.957	4.323 + 0.511	16.7 + 5.32	2.4 + 2.40
Flour baits: all sites	6	3.949	0.953	4.685 + 1.273	9.7 + 2.16	2.7 + 1.63
Meat baits: all sites	6	2.647	0.581	4.122 + 1.030	13.5 + 5.35	4.3 + 3.50
Sugar baits: all sites	6	3.954	0.767	4.516 + 1.353	16.7 + 5.39	4.2 + 3.37

0.71). Species loadings were polarized on this axis by foraging strata (Kendall's = -0.2743, P <0.05), as well as by site loadings (Fig. 4). The second axis was significantly correlated with the number of unique species (r = 0.50), standard deviation of affinity (r = -0.61), and the number of geographic locations in which a species was present (Kendall's = -0.1615, P <0.05). On the second axis, species loadings were polarized by geography, with sites from Pará having lower values than their respective counterparts in Bahia (Fig. 1). The third cannonical correspondence axis was only significantly correlated with the standard deviation of similarity (r = 0.50) and the number of bait types exploited (Kendall's = -0.2743, P <0.05). This axis was thus polarized by diet, or type of bait exploited. Mean Mahanalobis distances between centroids of groups based upon foraging strata were larger than between localities (Fig. 4) (P <0.05). [A full listing of species, their loadings, diet, localities and feeding specialization is available from the senior author].

Discussion

Local ant assemblage composition depends to a large extent upon the distribution of individual species. Interpretation of assemblage composition relies on an understanding of individual species distributions along regional gradients. The vast majority of species were found at only one foraging stratum (Fig. 1). *Pheidole* sp. 4 was a codominant in the epigaeic and assemblage of Bahia, and was also highly frequent in the hypogaeic ant assemblage, using all three bait types. The other codominant species, the fire ant *Solenopsis geminata* (Fabr.), also used all bait types, and especially more intensively in the hypogaeic assemblage than in the epigaeic assemblage. The dominance of

these two species was much more than that of other species in Pará, in spite of the fact that most species were found in only one geographic locality (Fig. 2). The little fire ant, *Wasmannia auropunctata* (Roger), was the most widespread species, attaining higher levels of resource usage in Pará than in Bahia, although flour baits were not used as intensively. Although numerous species were omnivorous (Fig. 3), these were restricted by foraging stratum (Fig. 1), and often enforced by geography (Fig. 2). Consequently, *W. auropunctata* was an intermediate species in ordination (Fig. 4), as it was present in both Pará and Bahia as well as in all bait types (Fig. 4). In all sites, for species attracted to baits, the hypogaeic fauna was less than the epigaeic fauna (Table 2). However, many of the hypogaeic species have highly specialized ecologies
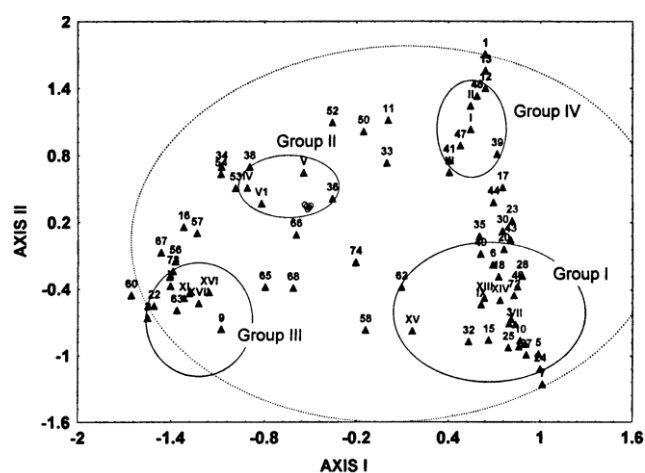

Fig. 4. Cannonical correspondence ordination of epigaeic and hypogaeic ant assemblages sampled with three bait types in two foraging strata in Bahia and Pará. Major feeding groups and guilds (Roman Numerals) are given in Table 2. Species ordination (numbers) is available from the senior author.

(Fowler & Delabie 1995), and are generally collected only by soil core sampling (Delabie & Fowler 1995). Preliminary estimates suggest that this fauna is almost twice as species rich as the epigaeic ant fauna (Delabie & Fowler 1995), and the small numbers of species sampled may represent the opportunists of this fauna.

Estimates of mosaic diversity were all large, irrespective of the type or location of the baits and their geographic location (Table 1). All values were much higher than those obtained for Neotropical arboreal and other epigaeic ant assemblages (Fowler *et al.* 1991). All estimated mosaic diversity values were representative of extremely complex landscapes (Scheiner 1992), indicating high turnovers in local assemblages as functions of both foraging strata and diet, in accordance with Austin's (1985) third hypothesis, and can, thus, be considered as ecological communities. The effect of the regional species pool on each assemblage apparently was continuous, although Pará and Bahia separated on the second cannonical axis (Fig. 4). In spite of the fact that the regional species pool is very rich for Bahia (>500 species) (Fowler & Dela-

bie 1995; Delabie & Fowler 1995), no comparable estimates exist for Pará, a dry Amazonian forest, which we suspect to have a poorer regional species contribution than found in the mesic Atlantic Coastal Rainforest of Bahia. Additionally, local assemblages are generally highly speciose in Neotropical ground ant faunas (Levings 1983; Levings & Franks 1984; Torres 1984; Delabie & Fowler 1995). However, the number of species collected by baiting is generally much less than the total fauna (Fowler 1997, 1998; Fowler & Delabie 1995).

Foraging strata was a more decisive factor in ordination than was geography (Figs. 1 and 2). No clear separation was found between secondary and mature Amazonian dry forest in Pará (Fig. 4), for either epigaeic or hypogaeic faunas (Table 2). Thus, the hierarchy of species ordination was foraging strata > geography > diet, based upon the relative Mahalanobis distance differences among the centroids of each grouping of the cannonical correspondence analysis. Scale was, thus, different, but based upon jack-knifed estimates of mosaic diversities, the landscape, estimated by its taxonomic compositional diversity, was equivalent

Table 2. Cannonical correspondence ordination of epigaeic and hypogaeic ants with respect to bait type, foraging stratum (surface or subterranean), habitat and geographic location. Groups and reference guilds are those shown in Fig. 4. Also shown are mean faunal similarities and affinities as well as total number (S) and unique (U) species for the combination. Species ordination is available from the senior author. Second growth and mature forest Amazonian sites in Pará. Cocoa is the site in Bahia.

Group/ Guild		Habitat/Site	Foraging Stratum	Bait Type	Similarity (+S.D.)	Affinity (+S.D.)	S	U
Group I	XII	Second Growth Pará	Subterranean	Flour	0.185 + 0.1708	0.538 + 0.1197	8	0
	X	Second Growth Pará	Subterranean	Sugar	0.213 + 0.1891	0.629 + 0.1018	11	0
	XI	Mature Forest Pará	Subterranean	Meat	0.203 + 0.1604	0.639 + 0.1211	8	1
	XVIII	Mature Forest Pará	Subterranean	Flour	0.171 + 0.1522	0.479 + 0.1368	6	0
	XVII	Mature Forest Pará	Subterranean	Meat	0.149 + 0.1430	0.529 + 0.1503	5	0
	XVI	Mature Forest Pará	Subterranean	Sugar	0.189 + 0.1503	0.479 + 0.1367	9	1
Group II	IV	Cocoa Bahia	Subterranean	Sugar	0.193 + 0.1409	0.570 + 0.1326	17	3
	VI	Cocoa Bahia	Subterranean	Flour	0.215 + 0.1365	0.666 + 0.0833	11	1
	V	Cocoa Bahia	Subterranean	Meat	0.191 + 0.1213	0.580 + 0.1202	11	0
Group III	VIII	Second Growth Pará	Surface	Meat	0.156 + 0.1419	0.467 + 0.1544	17	3
	VII	Second Growth Pará	Surface	Sugar	0.141 + 0.1420	0.401 + 0.1258	22	4
	XIV	Mature Forest Pará	Surface	Meat	0.160 + 0.1348	0.529 + 0.1503	16	0
	XIII	Mature Forest Pará	Surface	Sugar	0.184 + 0.1485	0.600 + 0.1423	17	0
	IX	Second Growth Pará	Surface	Flour	0.129 + 0.0864	0.395 + 0.1428	10	0
	XV	Mature Forest Pará	Surface	Flour	0.153 + 0.0804	0.487 + 0.1367	9	0
Group IV	I	Cocoa Bahia	Surface	Sugar	0.126 + 0.1076	0.387 + 0.1099	23	4
	II	Cocoa Bahia	Surface	Meat	0.126 + 0.1111	0.386 + 0.1129	23	5
	III	Cocoa Bahia	Surface	Flour	0.091 + 0.0762	0.261 + 0.0634	12	2

at all scales, a result not expected (Schneider 1994).

Data were insufficient to characterize intra-assemblage species distributions or predictions of individual species occurrences. Species loadings in cannonical correspondence analysis were largely noninformative, as some species did unpredictable things, such as the leaf-cutting ant, *Atta sexdens* (L.), occurring at meat baits and a number of species occurring at flour baits, in both foraging strata. This fact calls into question the use of "standardized" bait stations (Chew 1977) to study ant community organization, as well as our general ignorance of ant nutritional ecology (Fowler *et al.* 1991). What use flour would have for a colony is unknown, except for, perhaps, the fungus-growing attines. However, for the comparisons in our study at the assemblage level, compositional mosaic diversities are as good an indicator of complexity as are more formal models of indirect gradient analysis, such as cannonical correspondence analysis. Only the Bahia ant assemblages were dominated by few species (hypothesis 2, Austin 1985). Overall, assemblages had multiple independent species (Gleason 1925) (hypothesis 1, Austin 1985), possibly confounded by diffuse competition (Davidson 1980), and were organized into guild structures (Root 1967; Cody 1974) (hypothesis 3, Austin 1985), based principally upon foraging stratum and secondarily upon diet. Omnivory, assessed by bait types exploited (Fig. 3), was not the dominant strategy in our assemblages, unlike other studies (Marsh 1985). Bait sizes are known to affect the sampling of assemblages (Fowler 1988). However, omnivory may be a consequence of bait size and not type (Fowler *et al.* 1991). Bait size may induce a behavioral response, and not as a nutritional response of component species.

All of these evidences suggest that the community concept was favored over species continuums. The regional species pool was important, but apparently not the determinant factor structuring local ant assemblages (Ricklefs 1987). Spatial scale, examined from the size of an ant (Levin 1992), has indicated that processes are comparable in spite of differing faunas. This highlights Samway's (1990) caevats that management of individual species may be, at best, an impossible feat. Community structure remains fairly constant, however, in spite of the differing spatial and temporal patterning present in our data.

Acknowledgements

References

Allen, T.F.H. & T.B. Starr. 1982. *Hierarchy: Perspectives in Ecological Complexity*. University of Chicago Press, Chicago.

Andersen, A.N. 1991. Parallels between ants and plants : implications for community ecology. pp. 539-558. *In*: C.R. Huxley & D.F. Cutler (eds.) *Ant-Plant Interactions*. Oxford University Press, Oxford.

Austin, M.P. 1976. On non-linear species response models in ordination. *Vegetatio* **33**: 33-41.

Austin, M.P. 1985. Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics* **16**: 39-61.

Austin, M.P. & T.M. Smith. 1989. A new model for the continuum concept. *Vegetatio* **83**: 35-47.

Brandão, C.R.F. 1991. Adendos ao catálogo abreviado das formigas da região neotropical (Hymenoptera : Formicidae). *Revista Brasileira de Entomologia* **33**: 319-412.

Chew, R.M. 1977. Some ecological characteristics of the ants of a desert-scrub community in southeastern Arizona. *American Midland Naturalist* **98**: 33-49.

Cody, M.L. 1974. *Competition and the Structure of Bird Communities*. Princeton University Press, Princeton.

Davidson, D.W. 1980. Some consequences of diffuse competition in a desert ant community. *American Naturalist* **116**: 92-105.

Delabie, J.H.C. & H.G. Fowler. 1995. Soil and litter cryptic ant assemblages in Bahiain cocoa plantations. *Pedobiologia* **39**: 423-433.

Digby, P.G.N & R.A. Kempton. 1987. *Multivariate Analysis of Ecological Communities*. Chapman & Hall, New York.

Fowler, H.G. 1988. A organização das comunidades de formigas no estado de Mato Grosso, Brasil. *Anais del Museo de Historia Natural de Valparaiso* **19**: 35-42.

Fowler, H.G. 1997. Foraging, diet and community structure in an epigaeic ant (Hymenoptera: Formicidae) assemblage: the role of recruitment. *Ciência e Cultura* **49**: 199-202.

Fowler, H.G. & J.H.C. Delabie. 1995. Resource partitioning among epigaeic and hypogaeic ants (Hymenoptera: Formicidae) of an abandoned Brazilian cocoa plantation. *Ecologia Austral* **5**: 117-124.

Fowler, H.G., L.C. Forti, C.R.F. Brandão, J.H.C. Delabie & H.L. Vasconcelos. 1991. Ecologia nutricional de formigas. pp. 131-223. *In*: A.R. Panizzi & J.R.P. Parra (eds.) *Ecologia Nutricional de Insetos*. Editora Manole, São Paulo.

Gauch, H.G., Jr. 1985. *Multivariate Analysis in Community Ecology*. Cambridge University Press, London.

Gleason, H.A. 1925. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**: 7-26.

Istock, C.A. & S.M. Scheiner. 1987. Affinities and high-order diversities within landscape mosaics. *Evolutionary Ecology* **1**: 11-29.

Holldobler, B. & E.O. Wilson. 1990. *The Ants*. Harvard University Press, Cambridge.

Jaccard, P. 1901. Distribución de la flore alpine dans le Bassin des Dranses et dans quelques régions voisines. *Bulletin de la Societé de Science Naturelle* **37**: 241-272.

Johnson, R.A. & D.W. Wichern. 1982. *Applied Multivariate Analysis*. Prentice Hall, New York.

Kempf, W.W. 1972. Catálogo abreviado das formigas da região neotropical (Hymenoptera: Formicidae). *Studia Entomologica* **15**: 33-44.

Leite, J. de O. 1987. Caractéristicas do manto detrítico e sua relação com a fertilidade da camada superficial do solo em plantações de cacau. *Revista Brasileira das Ciências do Solo* **11**: 42-49.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**: 1942-1968.

Levings, S.C. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest : some causes of patchy species distributions. *Ecological Monographs* **53**: 432-455.

Levings, S.C. & N.R. Franks. 1984. Patterns of nest dispersion in a tropical ground ant community. *Ecology* **54**: 331-344.

Marsh, A.C. 1985. Forager abundance and dietary relationships in a Namib Desert ant community. *South African Journal of Zoology* **20**: 197-203.

Neptstad, D.C.C., C. Uhl & E.A.S. Serrão. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. *Ambio* **20**: 248-255.

Pielou, E.C. 1984. *The Interpretation of Ecological Data*. Wiley Interscience, New York.

Risch, S.J. & C.R. Carroll. 1982. Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. *Ecology* **62**: 1971-1983.

Ritcher, D.D. & L. Babbar. 1991. Soil diversity in the tropics. *Advances in Ecological Research* **21**: 315-389.

Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**: 317-350.

Ricklefs, R.E. 1987. Community diversity : relative roles of local and regional processes. *Science* **235**: 161-171.

Samways, M.J. 1990. Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. *Oecologia* **84**: 482-490.

Scheiner, S.M. 1992. Measuring pattern diversity. *Ecology* **73**: 1860-1867.

Scheiner, S.M. & C.A. Istock. 1987. Affinity analysis: methodologies and statistical inference. *Vegetatio* **72**: 89-93.

Schneider, D.C. 1994. *Quantitative Ecology: Spatial and Temporal Scaling*. Academic Press, New York.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw Hill, New York.

Sokal, R.R. & F.J. Rohlf. 1981. *Biometry*. 2nd ed. W.H. Freeman, San Francisco.

Torres, J.A. 1984. Niches and coexistence of ant communities in Puerto Rico: repeated patterns. *Biotropica* **16**: 284-295.

Uhl, C., R. Buschbacher & E.A.S. Serrão. 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *Journal of Ecology* **76**: 663-681.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**: 385-397.

Wiens, J.A. & B.T. Milne. 1989. Scaling of `landscapes' in landscape ecology, or landscape ecology from a beetle's perspective. *Landscape Ecology* **3**: 87-96.

Wilson, M.V. & A. Schmida. 1984. Measuring beta diversity with presence - absence data. *Journal of Ecology* **72**: 1055-1064.