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THE EFFECTS OF LAND USE ON THE STRUCTURE OF GROUND-FORAGING ANT COMMUNITIES IN THE ARGENTINE CHACO[1]

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Abstract. We examined the responses of a ground-foraging ant community to a gradient of land-use intensity in a grazing agroecosystem in the Chaco of northern Argentina. The gradient extended from a highly degraded condition characteristic of traditional grazing practices, through an area of less severe disturbance where grazing was less concentrated, to two areas in which grazing had been managed for 3 and 18 yr, respectively. Ground cover changed along this gradient from bare to litter-covered, ground-layer vegetation changed from sparse to a structurally complex mixture of grasses and forbs, and canopy cover increased in areas of intermediate grazing intensity and then decreased. Community diversity varied among the sites depending on both season and scale of analysis. Site-scale ant species richness was slightly higher in sites of intermediate disturbance in the summer–wet season but was much greater in the least disturbed site in the winter–dry season. The same dry-season pattern was evident in both species richness and diversity at the scale of transects within sites, whereas species richness at the scale of individual traps within transects was significantly lower at sites of intermediate disturbance than at either highly restored or highly degraded sites. Abundances of individual ant species and functional groups also changed along the land-use gradient. Litter-inhabiting cryptic species and specialized predators responded positively to grazing management, whereas opportunists and the hot-climate specialist *Forelius nigriventris* were prevalent in highly disturbed areas. Other functional groups exhibited redundancy and species turnover along the gradient. Detrended correspondence analysis (DCA) revealed that the ant faunas at the extremes of the land-use gradient were more similar than expected. We hypothesize that the interaction of local-scale habitat features with historical and biogeographic influences may determine the responses of this ant community to land use, and that highly degraded areas may have conservation value because they are regional sources of arid-adapted ants.

Key words: ants; Argentina; biodiversity; biogeography; Chaco; conservation; disturbance by grazing; Formicidae; functional groups, ants; semiarid ant habitats.

INTRODUCTION

Increasingly, ecologists are asked to evaluate the effects of anthropogenic change on the structure and function of communities and ecosystems (Lubchenco et al. 1991, Primack 1992, Solbrig 1992). With rapidly expanding human economies, it is apparent that few areas will escape the impacts of resource extraction, agriculture, and pollution (Wilson 1989, Ojima et al. 1991). In many regions, however, ecosystems can be managed for grazing or harvest of natural products such that some or all of the original components and function of the ecosystem are preserved. This "semi-natural matrix" (J. H. Brown, *unpublished manuscript*) dominates many inhabited regions of the world and may contain most of the world's biological diversity (Pimentel et al. 1992), yet it has been largely ignored by ecologists (Franklin 1993).

This fact is especially apparent in the dry neotropics, which have received little attention compared to moist neotropical forests. Nevertheless, dry regions dominate the South American continent (Mares 1992), harbor considerable biological diversity, and are extensively exploited through resource extraction, grazing, and agriculture (Schofield and Bucher 1986). The Gran Chaco of south-central South America examined here is one such dry neotropical region where most areas may be characterized as a "semi-natural matrix" used primarily for grazing and timber harvest.

Any attempt to assess and manage anthropogenic effects in these systems must, of necessity, focus on certain subsystems or taxa that may reveal the broader consequences of those effects (Kimball and Levin 1985, van der Ploeg 1986, Kremen 1992). For a number of reasons, ant communities (Hymenoptera: Formicidae) in neotropical environments may be useful in evaluating biotic responses to ecosystem change, and they have been used as such in Australia (Andersen 1993, Lobry de Bruyn 1993, Scougal et al. 1993), in the southern USA (Anthony et al. 1991), in Costa Rica (Roth et al. 1994), and in Brazil (Castro et al. 1990,

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Majer 1991). Ants are relatively sedentary and responsive to changes occurring at relatively small scales in space and time (cf. Kremen et al. 1993). Most ants are easily sampled and observed, and the ecology of the group is comparatively well understood (Hölldobler and Wilson 1990, Andersen 1995). In tropical and subtropical zones, ant communities contain many species and are often numerically dominant (Pisarski 1978, Hölldobler and Wilson 1990).

The success of ants in these regions may be attributed to the wide variety of life-styles they exhibit (Wilson 1987). As a consequence, ants may also play important roles in ecosystem processes. In the neotropics, ants have radiated to occupy foraging niches ranging from herbivores (leaf-cutting Attini) to highly mobile carnivores (ecitonine army ants). They are often the predominant predators and scavengers (Jeanne 1979) and the principal herbivores in these systems (Cherrett 1986, Fowler et al. 1986), and may also be important as soil modifiers (Bucher and Zuccardi 1967) and as pest-control agents (Risch and Carroll 1982) in agroecosystems. The responses of different functional groups of ants to environmental changes may therefore have important consequences in neotropical systems and may parallel the responses of a wide array of invertebrate taxa (Majer 1983, Andersen 1987, 1990).

Habitat modification resulting from natural and anthropogenic disturbances and succession may have strong effects on ant community diversity and organization. Reduced vegetative structure may lead to lower diversity and increased dominance in ant communities (Room 1975, Greenslade and Greenslade 1977, Risch and Carroll 1982, Majer 1985, Castro et al. 1990, Gallé 1991, Mackay et al. 1991; but see Brian et al. 1976, Briese and Macauley 1977). This relationship supports the hypothesis that diversity is positively related to vegetative complexity, which increases the possibilities for niche diversification (MacArthur 1972, Rosenzweig 1973).

Reductions in vegetative structure due to disturbance may also enhance ant diversity by increasing habitat heterogeneity (Wisdom and Whitford 1981) or microclimate favorability (Torres 1984, Punttila et al. 1991) or by reducing the activity of dominant species (Gallé 1981, Andersen and Yen 1985, Majer 1985, Anthony et al. 1991). These patterns relate closely to the notion that diversity peaks at intermediate levels of disturbance (Huston 1994). The prevailing explanation of this pattern emphasizes local processes: with low disturbance or high productivity, a few species can attain competitive dominance and exclude other species, reducing community diversity, whereas at high disturbance or low productivity, only a few stress-tolerant or generalist species can survive.

Here we report on the effects of two land-use methods on communities of ground-foraging ant species in a subtropical Chacoan savanna in Argentina. On the one hand, traditional land-use methods in which livestock grazing is uncontrolled result in moderate to severe degradation of vegetation. Alternatively, if an area is subdivided with fences, and livestock activity rotated among subdivisions, a more natural habitat (as well as greater beef production) results (Bucher 1987). We assessed the degree of habitat modification produced by these different land-use patterns and then asked the question, how do the different land-use practices affect ant community structure?

THE STUDY AREA

The Gran Chaco is a large sedimentary plain spanning the Tropic of Capricorn over northern Argentina, western Paraguay, eastern Bolivia, and part of southeast Brazil (Adámoli et al. 1990). Although characterized as a biogeographic province (Cabrera and Willink 1973), vegetation formations vary widely, favoring either arid or wet tropical elements (Sarmiento 1972). The western Chaco of Salta Province is semiarid, receiving about 500 mm of precipitation annually, mostly in the summer wet season (December to April). The vegetation is xerophyllous subtropical forest with a ground cover of cacti and grasses (Bucher 1982). Canopy species include *Schinopsis, Aspidosperma,* and *Zysiphus,* and shrub species are dominated by *Capparis, Prosopis, Acacia,* and *Celtis* (C. Saravia Toledo, *personal communication*). The area has little topographic relief; elevation is ≈300 m.

This study was conducted on four sites located ≈20 km east of puesto Santo Domingo, located on Ruta Provincial 13 in the province of Salta, Argentina (Fig. 1). The area was colonized by settlers from 1920 to 1960, and has been used primarily for grazing and timber production (C. Saravia Toledo, *personal communication*). Typically, goats and cattle are free-ranging and grazing is unmanaged. The elimination of fire-starting indigenous cultures (with subsequent fire suppression) and overgrazing have resulted in the encroachment of woody shrubs and the virtual elimination of grasslands from the vegetation mosaic (Bucher 1987), as well as poor re-establishment of valuable tree species (e.g., *Shinopsis quebracho*) (Morello and Saravia Toledo 1959). Variation in grazing intensity and land-management practices has produced areas differing in the level of degradation that can be qualitatively distinguished based upon the type and amount of vegetative cover.

The *puestos* (or posts) that the settlers inhabit are located adjacent to deep artesian wells. Cattle and goats concentrate their grazing within ≈2 km of the puesto and leave little vegetative cover. One of our sites was located adjacent to the puesto Campo Grande, which has existed for ≈60 yr. This site was classified as "highly degraded" (HD) and was characterized by the presence of few shrubs and trees, scattered low unpalatable forbs, and no grass (Fig. 2). Soil compaction due to grazing in this area may be significant (Adámoli et al. 1990). A second site was located ≈2–4 km from the puesto, where few goats forage and cattle graze in lower densities. This area had more shrub cover and litter development and grasses were restricted to small patches under thorny shrubs. This site was classified as "moderately degraded" (MD), and represents the dominant land-use type in the region (Adámoli et al. 1990).

Adjacent to Campo Grande is fenced land (Los Colorados) owned by Carlos Saravia Toledo that has been managed under a structured grazing/timber cutting system that allows natural restoration of heavily used areas (Saravia Toledo 1987). At the periphery of Los Colorados, reduced grazing pressure for 3 yr has resulted in heavy thorn-scrub growth, light forb growth under the shrubs, and some grass growth. This situation is characteristic of an initial recovery from intense grazing pressure, and was designated "moderately restored" (MR) (Fig. 2). The interior of Los Colorados has been managed for ≈18 yr, has been ungrazed for ≈6 yr, and is characterized by lighter thorn-scrub cover and greatly increased cover of tall grasses and forbs; it was designated as "highly restored" (HR). These land-use types represent points along a gradient of decreasing grazing disturbance ranging from HD to HR (Fig. 2), over which we examined differences in ant communities.

METHODS

Ant surveys

Ants were sampled using pitfall traps. Although pitfall traps do not provide an unbiased estimate of true forager abundance, they have been found to give an adequate representation of the relative abundance and composition of ground ant faunas in savannas similar to that studied here (Andersen 1991*a*). At each of the four sites, four transects of 5 traps each (10-m spacing) were located at random along seldom-used paths (i.e., 20 traps/site). Transects were placed a minimum of 200 m apart within a site and at least 20 m away from trail-associated disturbances. The pitfall traps were plastic ice-cream buckets 22 cm in diameter and 21.5 cm deep. The mouth of each trap was bordered with a 1-cm wide lip that extended across discontinuities between the trap and the surrounding surface and facilitated the capture of smaller ant species, especially when sprinkled with sand or detritus. Traps were placed in the ground to settle for ≈1 mo prior to operation, thus avoiding the "digging-in" effect noted by Greenslade (1973). Traps were filled to a depth of 1.5 cm with a 70% solution of an ethylene glycol/ethanol mixture as a preservative. Ethanol preservatives are not known to attract ant species differentially (Greenslade and Greenslade 1971). All traps were operated simultaneously for three consecutive days in early March 1992 (mid-wet season) and for 8 consecutive days in late July 1992 (mid-dry season). The dry season trapping period was extended 5 d because unusually cold weather ensued the day after the traps were set, reducing ant activity greatly. This sampling inequity may bias a seasonal comparison of species diversity (Magurran 1988), but should not bias the within-season land-use comparisons addressed here. No precipitation occurred during the trapping periods; air temperatures ranged from 15° to 37°C in March and −7° to 18°C in July.

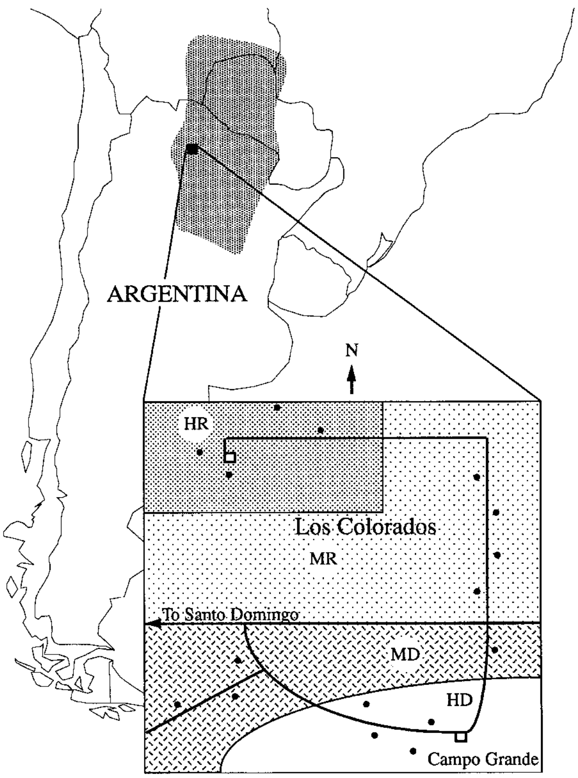

FIG. 1. Location of the study area and sites in the Los Colorados reserve and the adjacent puesto Campo Grande in Salta province, Argentina (HR = highly restored, MR = moderately restored, MD = moderately degraded, and HD = highly degraded). The approximate extent of the Chaco region is shown. Thick lines are roads, and dots are transect locations. The height of the square is ≈10 km.

Ants were sorted and identified to species or to morphologically defined taxonomic groups (Appendix). Identifications were validated by Roy R. Snelling of the Natural History Museum of the County of Los Angeles, Los Angeles, California (where voucher specimens are stored).

Vegetation measurements and analysis

Vegetation measurements were taken during the wet season. At each trap, three points were located 90° apart on a 1.5 m radius circle centered on the trap. This point-placement protocol was chosen to avoid the disturbed area around the trap. At each point, the ground cover was recorded according to four categories: bare ground, leaf litter, moss, or *Selaginella,* a low-lying lycopod. Foliage height profiles (FHP) were measured at each point with a thin, 1.5 m long rod. The rod was placed

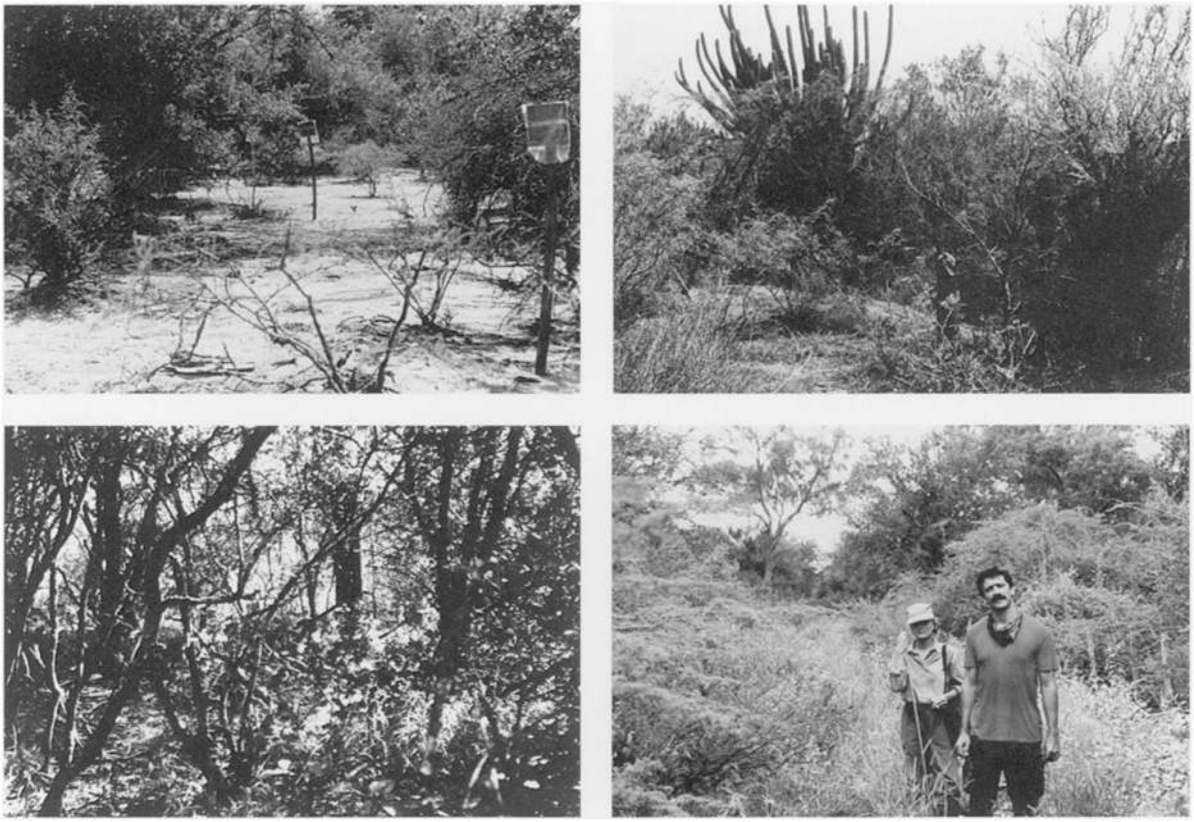

FIG. 2. Photographs of representative areas on the grazing-intensity gradient: highly degraded (upper left), moderately degraded (upper right), moderately restored (lower left), and highly restored (lower right).

vertically at each point and the number of contacts with plants within each 50-cm height increment was recorded (cf. Rotenberry and Wiens 1980). FHPs provide a basis for comparison among sites of the vertical density of vegetation at different heights above ground. Proportion of canopy cover was estimated using a right ascension prism in which cross-hairs divided the field of view into four sections. The prism was held 1.5 m above the ground at each point and the number of sections in which vegetation was observed was recorded. FHP was compared between sites using MANOVA (SYSTAT; Wilkinson 1990) and canopy cover was compared using ANOVA.

Diversity analysis

Two diversity measures were compared among sites across the land-use gradient: species richness (*S*) and logseries-α. *S* was selected because it is commonly used and relatively simple to interpret, but it makes no adjustments for commonness or rarity of species (Magurran 1988). Logseries-α is a parameter of the log-series distribution that incorporates both species richness and abundance. Even when samples do not follow a log-series distribution, the logseries-α has good discriminating ability between samples (Taylor 1978) and is relatively insensitive to sample size. Furthermore, values of logseries-α are most strongly influenced by species of intermediate abundance (Magurran 1988). Because disproportionately large numbers of ants may be captured when traps are near nests (producing inflated high-abundance classes) and some ant species are poorly sampled by pitfall trapping due to arboreal or hypogaeic habits (inflating the low-abundance classes), logseries-α may be an especially appropriate diversity measure for ant communities (see also Caldas and Moutinho 1993). Richness and diversity were analyzed using ANOVA. The "protected" least significant difference test was used to separate means when the overall *F* test indicated significant land-use effects (e.g., Andelt et al. 1991).

Analyses of ant species richness (*S*) were conducted at both per-trap and per-transect levels. Trap-level ANOVA models included the transect term nested within land-use type, and transect was treated as a random effect. The *F* tests for the effect of land use on trap reported here employ the mean square of transect in the denominator, not the mean square error (see Zar 1984). Because abundances of ants are sensitive to trap location, however, logseries-α (which includes an abundance component) was analyzed only at the transect level. In these analyses, transects were treated as independent samples and trap contents were summed within transects.

Because transects were located at least 200 m from one another, it is unlikely that foragers from single ant nests (excepting nomadic army ant species) were sampled in more than one transect. Within transects, foragers from colonies of wide-ranging species may have been captured in more than one trap, which may have resulted in some non-independence of captures in the trap-level richness analyses. Microhabitat variation at the trap level due to land use, however, may have important effects on forager behavior and, ultimately, on the functional characteristics of the ant community. A slight loss of independence among samples is unlikely to affect the analyses of such functional characteristics.

Samples of community diversity measures may not satisfy assumptions of parametric statistics, however, so we also used a community randomization procedure for transect-level analyses that tends to be conservative with reference to ANOVA (Solow 1993). The procedure first pools species abundances from two samples to obtain a combined species-abundance distribution. The combined distribution is then randomly partitioned into two samples of individuals so that each random sample has the same number of individuals as the observed sample. A diversity index is calculated for the two randomized samples obtained from each random partition. The observed difference in diversity can then be compared to a null distribution of differences obtained from a large number of randomizations.

We extended Solow's (1993) procedure from a two-sample to a multisample test to examine the effect of land use on diversity measures (see Wiens et al. 1996). Capture data from each of the 16 transects across four sites were used to obtain species-abundance distributions. We first combined the species abundances obtained from the 16 transects and randomly partitioned them into 16 species-abundance distributions such that the total counts of each transect and each species in the randomized distributions equalled those in the observed distributions. We performed 1000 random partitions, and from each randomization we calculated the species richness and logseries-α of each transect. These randomized diversity measures were then grouped by land-use type and 1000 F values were calculated by ANOVA (df = 3, 12). The observed F value could then be placed within the ranking of the 1000 randomized F values to obtain a probability for the observed F value to the nearest 0.001.

Functional groups

Ant species were assigned a priori to functional groups based upon independent field observations of behavior at baits (B. T. Bestelmeyer, *unpublished manuscript*) and previously published accounts of the behavior of some species groups (Kusnezov 1963, Levins et al. 1973, Bucher 1974, Levings and Franks 1982, Levings 1983, Torres 1984, Andersen 1987, Castro et al. 1990; R. Snelling, *personal communication*). We used the decision tree presented in Fig. 3 (see also the Appendix). The criteria for functional-group membership follow those developed by Greenslade (1978) and modified by Andersen (1987) for Australian communities. Functional groups provide a means of evaluating ant responses to the land-use gradient using easily observed, broad ecological characteristics without requiring detailed knowledge of natural history or species designation. In almost all cases, we followed others (Andersen 1990, 1991*b*, Lobry de Bruyn 1993) in assigning entire genera to functional groups. Exceptions here include the diverse genera *Pheidole, Solenopsis, Dorymyrmex,* and *Forelius,* which contributed species to two or more groups.

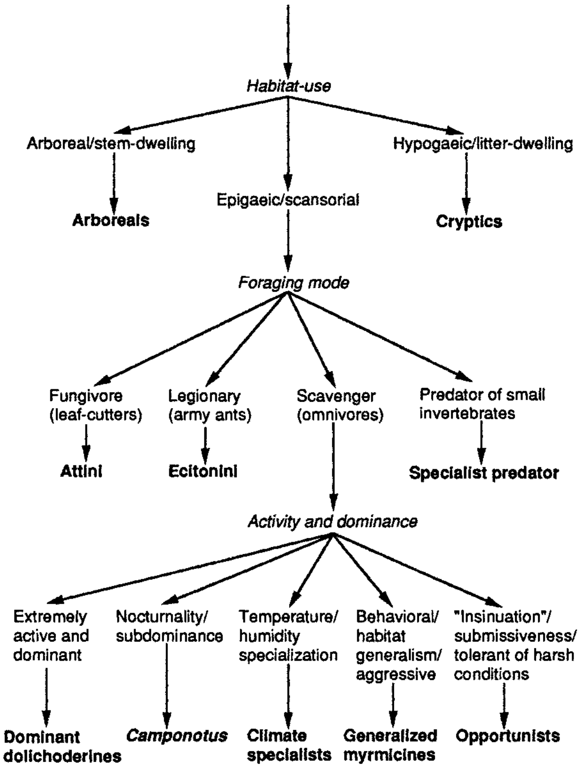

FIG. 3. Decision tree used for assignment of species and morphologically defined taxa to functional groups using broad-level ecological characteristics. See *Methods: Functional groups* for a more detailed description.

We designated functional groups as follows (see Fig. 3). Ants were first divided into groups based upon broad differences in habitat use. Arboreals included ants that nest and forage exclusively in trees or shrubs (e.g., *Zacryptocerus* and *Pseudomyrmex).* These ants are not adequately sampled by pitfall traps and seldom interact with ground-dwelling ant species. Cryptic species included one *Forelius* sp., small *Solenopsis* spp., two small *Pheidole* spp., *Wasmannia auropunctata,* and *Brachymyrmex* spp. These ants forage mainly in the soil and leaf litter although they may (as in the case of *Brachymyrmex*) be dominant above the litter in interactions with epigaeic species.

Epigaeic and/or scansorial (tree-climbing) species were subdivided based upon diet and foraging behavior.

In general, these groups do not compete for food. Attini were fungus-culturing ants including leaf-cutting *Atta* and *Acromyrmex* and detritus-collecting *Trachymyrmex, Mycetophylax,* and *Cyphomyrmex.* Ecitonini were nomadic army ants, including *Eciton* and *Neivamyrmex.* Predators, including *Odontomachus* and *Pachycondyla,* specialized on small invertebrates. The latter two functional groups may prey upon other ant species.

Scavenging species are usually omnivorous and will prey upon small invertebrates, scavenge animal/plant materials, or collect homopteran exudates. Members of this group are frequently recorded in tuna-bait studies. Extremely aggressive and dominant species, such as the *Iridomyrmex* and *Oecophylla* species found in Australian communities (Greenslade 1978), were absent from the Chaco area. Species of *Camponotus* were virtually absent in the dry season but were abundant during the wet season. Though active throughout the day, *Camponotus* achieved extreme dominance at night. *Forelius nigriventris* is a hot-climate specialist and was most active when soil-surface temperatures exceeded 38°C. Few other species were active at these temperatures, so *F. nigriventris* dominated food sources easily. Generalized myrmicines comprised the genus *Crematogaster,* most *Pheidole,* and two *Solenopsis* spp. Although generalized myrmicine genera exhibit a variety of lifestyles, they have in common world-wide distributions and relatively flexible habitat requirements when compared to other ant groups (Andersen 1987). The small-bodied foragers of generalized myrmicines recruit quickly and effectively defend food resources, although in this system they were usually subordinate to *Camponotus* and *Brachymyrmex.* Opportunists are unspecialized, compete poorly with other groups, and are generally unable to recruit effectively to food sources. They typically function as "insinuators" (sensu Wilson 1971) that often escape notice of more dominant mass-recruiting competitors while foraging. Opportunists included a number of *Dorymyrmex* species, *Ectatomma,* and *Gnamptogenys.* The larger size of the latter two genera enables them to remove large quantities of food quickly and may impart an exploitative advantage.

Overall abundances and functional-group abundances were compared among sites within seasons using MANOVA. Abundance values were ln-transformed to homogenize sample variances.

Multivariate analysis

Species composition and abundance (ln-transformed) among sites were analyzed for each season separately by detrended correspondence analysis (DCA; detrended by segments; CANOCO 2×; ter Braak 1988). DCA uses the weighted averages of species abundance to generate species–site joint plots in which sample scores in the ordination diagram lie at the centroids of the positions of species that occur in them. Sites close to a particular species are likely to have a high abundance of that species and those farther away a lower abundance, although DCA cannot distinguish whether species positions occurring between site positions represent uni- or bimodal response functions (Jongman et al. 1987). To simplify presentation, sample scores for transects were plotted as minimum-space polygons including all four transects in each land-use type superimposed with the positions of the 10 most abundant ant species in either season (15 species total). The effect of land-use type on species abundance in each season was assessed by comparing sample scores and species scores in the first two DCA dimensions. Units of ordination length in DCA are standardized as an average standard deviation (SD) of species turnover, where 1 SD represents ≈50% turnover and 4 SD is 100% turnover; hence, it is valid to compare different data sets directly (Gauch 1982).

RESULTS

Vegetation measurements

The sites subjected to different land use clearly differed in the vertical complexity of vegetation occurring at different strata (Wilks' $\lambda = 0.177$; $F = 2.89$; df = 9, 24; $P = 0.02$; Fig. 4A). Over all strata, density of vegetation declined from HR to HD, but the decline was not consistent across strata. Foliage-height profiles at the 0–50 cm stratum ($F = 3.55$; df = 3, 12; $P = 0.048$) and at the 100–150 cm stratum ($F = 3.66$; df = 3, 12; $P = 0.044$) were affected by land use; at the 50–100 cm stratum the effect was only marginally significant ($F = 2.73$; df = 3, 12; $P = 0.09$). There was little vertical density in HD; MD and MR tended to be intermediate, and there was considerably greater vertical density in HR. Differences between HD and HR were most apparent at the 0–50 cm stratum (due mostly to increases in grasses and forbs) and the 100–150 cm stratum (woody shrubs). The proportion of bare ground was great in the HD site, whereas litter dominated all other sites (Fig. 4B). The proportion of canopy cover was also affected by land use ($F = 5.44$; df = 3, 12; $P = 0.016$; Fig. 4C). The HD site had much less canopy cover than either the MD or MR sites, and the HR site was intermediate.

Ant abundance and diversity measures

Overall, 104 ant species (or morphologically recognizable taxa) from 34 genera were recorded from the study area (Appendix). The richest genera (accounting for 53% of all species) were *Pheidole* (18 species), *Solenopsis* (13), *Camponotus* (9), *Dorymyrmex* (7), *Zacryptocerus* (6), and *Forelius* (5). Across all sites, the number of individuals captured by pitfall traps varied seasonally. In the wet season, the pitfall traps yielded 28.5 ants·trap^{-1}·d^{-1}, whereas only 6.5 ants·trap^{-1}·d^{-1} were captured in the dry season. The numerically dominant species also differed between the seasons (Table 1). In the wet season, the 10 most abundant species

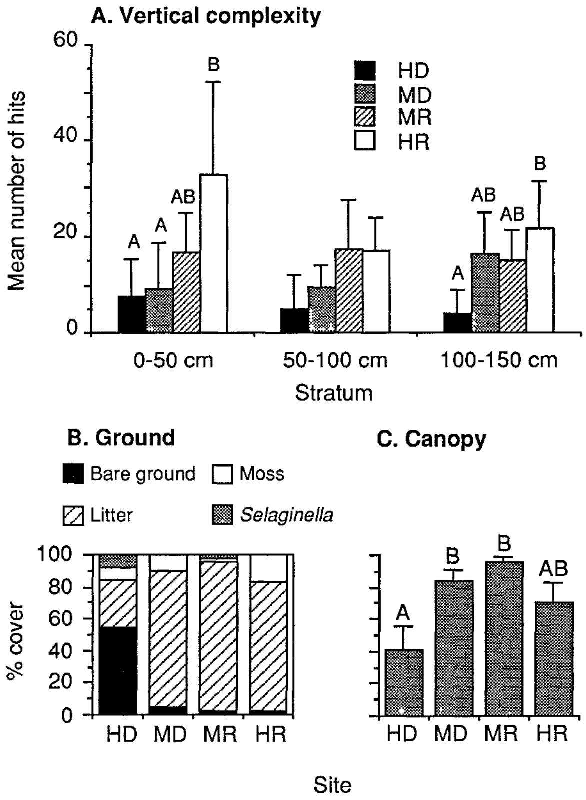

FIG. 4. (A) Mean number of hits (hits = contacts of a vertical rod with vegetation) in different strata in each site; (B) mean proportions of different ground cover types in each site; and (C) proportion of canopy cover in each site. Measurements were recorded in the wet season. Bars with different letters are significantly different at $P < 0.05$. HD = highly degraded; MD = moderately degraded; MR = moderately restored; HR = highly restored.

TABLE 1. Percentage of total individuals captured for the 15 most abundant species in this study.

Subfamily Species	Percentage of total individuals captured Wet season (n = 6680)	 Dry season (n = 4131)
Ponerinae		
Ectatomma quadridens	3.3	1.2
Myrmicinae		
Acromyrmex aspersus	6.8	3.9
Mycetophylax emeryi	1.5	1.9
Pheidole oxyops	15.3	29.5
Pheidole triconstricta	7.3	14.3
Pheidole sp. D	0.5	4.1
Pheidole sp. G	0.8	2.9
Pheidole sp. I	0.7	12.5
Solenopsis electra	2.8	0.1
Wasmannia auropunctata	9.0	3.5
Dolichoderinae		
Dorymyrmex exsanguis	3.5	7.6
Dorymyrmex sp. C	0.3	3.7
Forelius nigriventris	17.7	0.1
Formicinae		
Brachymyrmex sp. A	1.9	1.2
Camponotus sp. A	2.8	1.0

accounted for 70.3% of the 6680 individuals captured; in the dry season, the 10 most abundant species contributed 84.1% of 4131 individuals captured.

The number of ants captured was influenced by land-use type in both seasons (see Appendix). Captures were greater at the extremes of the land-use continuum than in either the MD or MR sites in the wet season, but in the dry season the HD site and the MR site did not differ significantly. In both seasons the HD and HR sites and the MD and MR sites were similar.

Species richness was consistently greater during the wet season than the dry season at all sites and at all levels of analysis (Fig. 5). The total number of species recorded throughout each site was greater in the MD and MR sites than in either HD or HR sites in the wet season. In the dry season, however, more species were found in the HR site than in the others. When analyzed at the scale of transects within sites, species richness did not differ significantly among the sites during the wet season (ANOVA: $F = 0.838$, df = 3, 12, $P = 0.499$), but was greater at the HR site in the dry season (ANOVA: $F = 7.692$, df = 3, 12, $P = 0.004$) (Fig. 5). At the scale of individual trap locations, however, there was a strong pattern of reduction of species richness at the sites subjected to intermediate levels of grazing disturbance (MR and MD) (ANOVA; transect nested within site): wet season: $F = 4.95$, df = 3, 12, $P = 0.018$; dry season: $F = 9.79$, df = 3, 12, $P = 0.0015$). Much the same pattern was evident in the transect-scale analyses of variations in logseries-α: diversity was significantly lower in the MR site than in the HD and HR sites during the wet season (ANOVA: $F = 3.854$, df = 3, 12, $P = 0.038$) and lowest in the MR and MD sites during the dry season (ANOVA: $F = 6.274$, df = 3, 12, $P = 0.008$) (Fig. 5). ANOVAs generated from Solow's procedure revealed no effect of land use on either richness or logseries-α in the wet season, but S was significant ($P = 0.05$) and α was marginally significant ($P = 0.08$) in the dry season.

Functional groups

Land use had significant effects on the abundances of functional groups in both the wet season ($\lambda = 0.005$; $F = 3.18$; df = 24, 15; $P = 0.01$) and the dry season ($\lambda = 0.005$; $F = 3.24$; df = 24, 15; $P = 0.01$). In the wet season, the hot-climate specialist, *Forelius nigriventris,* was more abundant at the HD site than in all other areas ($F = 22.69$; $P = 0.000$) and constituted 41% of ants captured in that site (Fig. 6). Cryptic species were more abundant in restored sites (MR and HR, 44 and 27% of records, respectively) than in degraded sites (HD and MD, 6 and 19%, respectively; $F = 7.20$; $P = 0.005$). Predators occurred in very low densities throughout the study area, but were abundant in HR ($F = 7.79$; $P = 0.004$). *Camponotus,* opportunists, generalized myrmicines, Attini and Ecitonini did not reveal

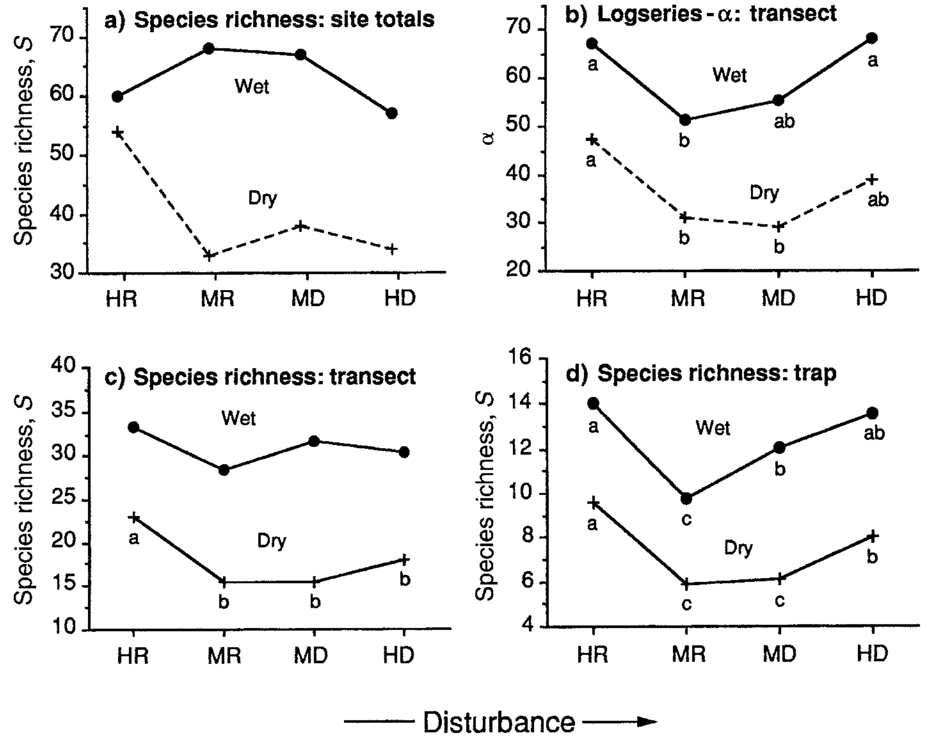

FIG. 5. (a) Species richness totals ($n = 1$), (b) logseries-α values by transect ($n = 4$), (c) richness by transect ($n = 4$), and (d) richness by traps ($n = 20$) in each site in each season along the land-use (disturbance) gradient. Pairwise contrasts were analyzed using protected least significant difference tests (df = 12 for transects, df = 64 for traps). Symbols with different letters within a season are significantly different at $P < 0.05$. HR = highly restored; MR = moderately restored; MD = moderately degraded; HD = highly degraded.

significant responses to land use (Fig. 6). Generalized myrmicines, however, made up a large proportion of the ant fauna (between 22 and 55% of the records among sites).

In the dry season, *F. nigriventris* was virtually absent from all sites (Fig. 6). *Camponotus* was more abundant in HD than in either MD or MR but not HR, although the relationship was only marginally significant ($F = 2.83$; $P = 0.08$). One species, *Camponotus* sp. A, accounted for nearly all *Camponotus* records. Opportunists were more abundant in the HD site (32% of records) than in all other sites (2–8% of records; $F = 12.85$; $P = 0.001$) except HR. Again, cryptic species were more abundant in the restored sites than in the degraded sites ($F = 7.42$; $P = 0.005$), although they were much less abundant overall than in the wet season. Predators were more abundant in the HR site than in all other sites ($F = 7.89$; $P = 0.004$), as in the wet season. Attines occurring in the MR site were less abundant than in either the HD or MD site ($F = 3.43$; $P = 0.05$). Again, generalized myrmicines and Ecitonini were unaffected by land use. Generalized myrmicines constituted an even larger proportion of ants in the dry season than in the wet season: from 53% in the HD site to ≈73% in all other sites.

Multivariate analysis

Detrended correspondence analysis revealed relatively high similarity in species composition and abundance among transects occurring in the HD and HR sites, whereas transects in the MD and MR sites were more variable, especially along axis 2 (Fig. 7). Axis 1 corresponded with the land-use gradient. The HD transects were well separated from most other transects along axis 1, especially in the dry season, and they showed greater similarity to both MD and HR transects than to MR transects in either season. The eigenvalue for axis 1 was 0.348 in the wet season and 0.293 in the dry season, indicating considerable variation in the conditions within sites. Season did not greatly alter the positions of the other site clusters with respect to one another.

Of the 15 species examined with DCA, *Forelius nigriventris, Pheidole triconstricta, Mycetophylax emeryi,* and *Dorymyrmex* sp. C were abundant in the HD site in both seasons. *Dorymyrmex exsanguis* was highly associated with the HD transects, and showed a lesser affinity to HR transects in either season. *Camponotus* sp. A was also associated with both HD and HR sites in the dry season, although in the wet season it was most abundant in the HR site. *Brachymyrmex* A was

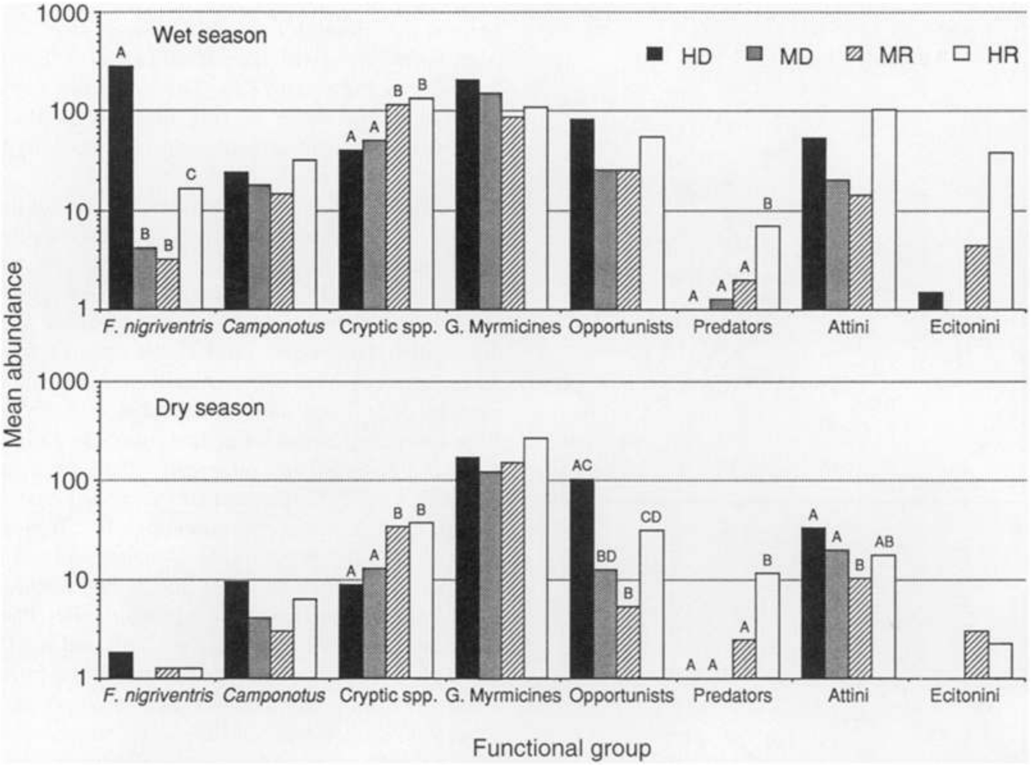

FIG. 6. Mean abundances of functional groups in wet and dry seasons. Note that the y axis is log-scaled. Bars with different letters within functional groups are significantly different at $P < 0.05$.

most associated with the HR transects, and *Wasmannia auropunctata* was associated with MD, MR, and HR sites. *Pheidole* sp. D reversed its affinity from the HD transects in the wet season to the HR and MR sites in the dry season. *Solenopsis electra* was also abundant in the HD site in the wet season, but was represented in the dry season by only six individuals (most occurring in the MR site). *Pheidole oxyops, Pheidole* sp. I, *Acromyrmex aspersus,* and *Ectatomma quadridens* were well represented throughout the study area (B. T. Bestelmeyer, *personal observation*), although in the wet season they were relatively less abundant in the HD sites. *Pheidole* sp. G had very high counts in a few transects in MD and MR, hence its distant positions on the ordination diagrams (Jongman et al. 1989).

DISCUSSION

Variations in land use were associated with several measures of ant community structure, from diversity and abundance to the composition of functional groups to the abundance of particular species. The greater number of ant captures observed near the puesto may be a consequence of the reduced vegetational complexity at ground level relative to the more heavily littered sites. Of the three sites with a nearly continuous litter layer, the highly restored site had greater overall ant density. These differences between sites did not reveal much sensitivity to seasonality, except in the general reduction in ant activity in the dry season. Such reductions are a common phenomenon in ants occurring in subtropical climatic regimes because cold and dry conditions are generally unfavorable to ants (Levings 1983, Andersen, 1995).

Diversity

The relationship between land use and ant diversity differed depending on the season and the scale of analysis. The area with the least grazing impact (HR) showed dramatically greater total species richness only in the dry season; in the wet season, this pattern was not apparent. It is possible that increased litter development and greater overall productivity in this area buffered the ant fauna against general declines in habitat suitability, and hence in ant activity, that occurred during the dry season in the more degraded sites. Greater insolation in the highly restored site relative to intermediate sites may have created conditions more suitable to cold-sensitive species, such as *Solenopsis* (Torres 1984). The positive effects of high insolation around the puesto in the dry season were likely outweighed by the lack of litter, exposure to wind, and low productivity.

Although the total number of species recorded during the wet season was greatest at the sites with intermediate levels of disturbance, this pattern disappeared or was reversed when species richness or diversity was

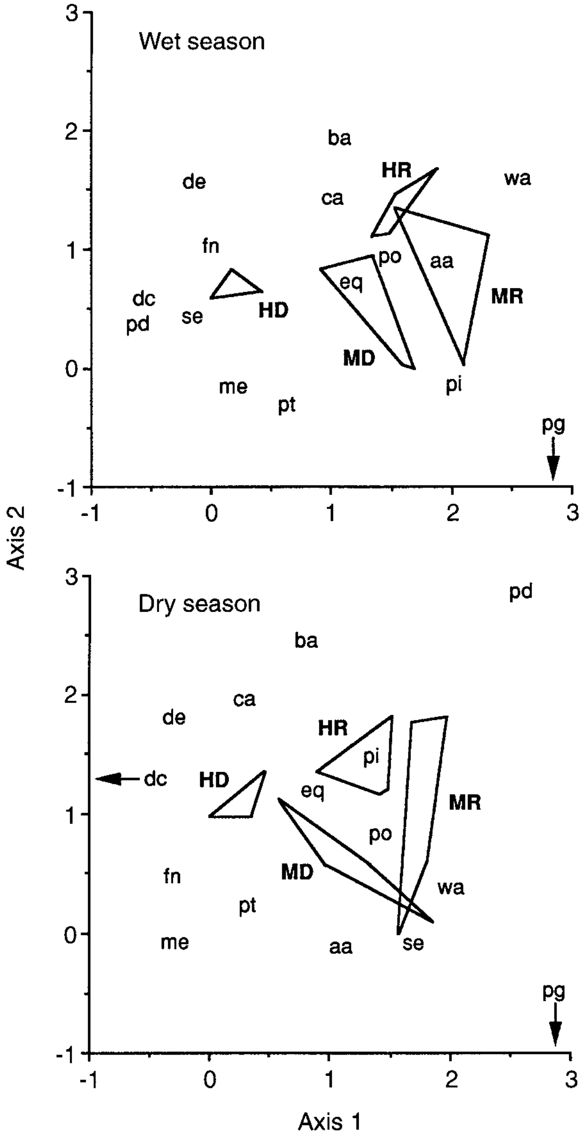

FIG. 7. Detrended correspondence analysis (DCA) ordination of transects and species positions of the 15 most important ant species according to species composition and abundance (see *Methods: Multivariate analysis* for details). Boldface letters indicate site polygons that include all four transect positions. aa = *Acromyrmex aspersus,* ba = *Brachymyrmex* sp. A, ca = *Camponotus* sp. A, dc = *Dorymyrmex* sp. C, de = *Dorymyrmex exsanguis,* eq = *Ectatomma quadridens,* fn = *Forelius nigriventris,* me = *Mycetophylax emeryi,* pd = *Pheidole* sp. D, pg = *Pheidole* sp. G, pi = *Pheidole* sp. I, po = *Pheidole oxyops,* pt = *Pheidole triconstricta,* se = *Solenopsis electra,* wa = *Wasmannia auropunctata.*

evaluated at the scale of replicate transects or individual traps within sites. Species numbers were reduced during the dry season, but the pattern of relatively high richness or diversity at the HR site and (to a lesser extent) the HD site and lower values at the intermediate sites persisted. This pattern of "intermediate depression" does not agree with MacArthur's (1972) suggestion that diversity should increase with vegetative complexity, from which we would expect relatively low diversity in the puesto site. The lower diversity in the areas of intermediate grazing intensity is also inconsistent with the intermediate disturbance hypothesis (Huston 1994).

The failure of these hypotheses to explain the intermediate depression pattern we observed may be due to their emphasis on local-scale explanations (Ricklefs and Schluter 1993). Denslow's (1980) suggestion that local diversity patterns are determined by the abundance of habitat types (and of the species adapted to them) at a regional scale is consistent with the intermediate depression pattern. In addition to the typically Chacoan complement of species such as *Pheidole oxyops* and *Ectatomma quadridens,* the extremes of the land-use gradient are enriched by species that are well represented in adjacent biogeographic regions. The highly degraded puesto area is structurally similar to regions of low productivity and harsh abiotic conditions, such as occur in the Monte desert, Patagonia, and mountainous regions to the south and west (Mares et al. 1985). Species that characterized the puesto site, such as *Forelius nigriventris, Dorymyrmex exsanguis, Mycetophylax emeryi,* and *Pheidole triconstricta* (Fig. 7), are well represented in these regions (Kusnezov 1963, Kempf 1972, Bestelmeyer, *in press*). Species that are widely distributed in mesic subtropical and Amazonian regions, such as *Odontomachus chelifer, Ectatomma tuberculatum,* and *Wasmannia auropunctata* (Kempf 1972), were best represented in the highly restored site, where the lush undergrowth and heavy litter development may have approximated conditions found in more mesic regions.

In a similar vein, Andersen (1992, 1995) suggested that diversity patterns in Australian ant communities may also be influenced by their regional context. Diversity may decline in more shaded habitats in Australian semi-arid zones because the regional ant fauna consists largely of open-adapted taxa. In contrast, ant diversity in tropical forests declines sharply with structural simplification of vegetation (e.g., in agricultural settings: Room 1975, Greenslade and Greenslade 1977, Castro et al. 1990, MacKay et al. 1991, Roth et al. 1994). The regional species pool of tropical faunas, however, may harbor few species that are adapted to open conditions and that are therefore able to colonize deforested patches. Roth et al. (1994) suggested that declines in ant diversity along gradients of increasing agricultural disturbance in wet Costa Rican forests were mediated by the proximity of source populations in undisturbed forest patches. It seems clear from these studies that it is necessary to consider regional, biogeographic influences as well as local factors to develop an understanding of the controls of local ant community structure (Ricklefs and Schluter 1993).

Attempts to fit our observations of ant-community patterns to conventional diversity/disturbance theories may also be complicated by the nature and scale of "disturbance." Intermediate frequencies or intensities of disturbance are thought to produce maximum habitat heterogeneity (Levin and Paine 1974). The heterogeneity that is important to ants, however, may be greater at the extremes of the land-use gradient than in areas of intermediate grazing intensity. In the highly restored site, heterogeneity with respect to well-insolated and shaded, well-littered habitats may be important in maintaining high diversity. In the puesto area, patches of moss, cryptogamic soil and *Selaginella* occurring at small scales may permit many cryptic species to tolerate the otherwise harsh and dry conditions (B. T. Bestelmeyer, *personal observation*).

Functional groups

The puesto fauna was characterized by a hot-climate specialist, *Forelius nigriventris,* in the wet season, and in the cooler, dry season by opportunists (mostly *Dorymyrmex* spp.) (Fig. 6). Few studies employing ant functional groups have been performed, but in structurally similar Australian savannas and forests, Andersen (1991*b*) observed increases in hot-climate specialists and opportunist species in response to increased fire frequency, and Scougall et al. (1993) documented an increase in thermophilic *Iridomyrmex* in grazed forest fragments. In general, structural simplification of habitats appears to favor hot-climate specialists and opportunists (Greenslade 1978).

Differences among the less degraded site and the two managed sites were less dramatic. Both managed sites favored litter-inhabiting cryptic species (as occurs also in relatively undisturbed Australian systems; Scougall et al. 1993) and also harbored specialized predators such as *Odontomachus chelifer,* which was absent from the highly degraded site. The well-developed litter layer in managed sites provided nest sites and foraging areas for cryptic and predaceous species (B. T. Bestelmeyer, *personal observation*).

In contrast to the situation in Australia, however, generalized Myrmicinae in the Chaco study area were apparently unaffected by land use. The Chaco lacks an analogue to the ubiquitous Australian *Iridomyrmex,* which is extremely dominant and is an important structuring force in ant communities, yet reacts negatively to shading and litter cover (Greenslade 1978). In Australia, disturbances that generated conditions similar to those of the highly degraded Chaco site resulted in reductions in generalized myrmicines due to competition from *Iridomyrmex.* The effects of dominant competitors on the responses of functional groups to land use do not appear to be as important in the Chaco system, although generalized myrmicines may benefit from reduced competition in the dry season (B. T. Bestelmeyer, *unpublished data*).

The apparent stability of some functional groups in the face of environmental change masks changes in the abundance and characteristics of component species (e.g., Steneck and Dethier 1994). The composition of the consistently abundant generalized myrmicines changed considerably as a function of land use, shifting from *Solenopsis electra* and *Pheidole triconstricta* in the degraded sites to *Pheidole* sp. I and *Pheidole oxyops* in the restored sites. Such species substitutions across environmental gradients may provide stability to functional groups and resilience in ecosystem functions (Walker 1992). The responses of the herbivorous Attini to land use illustrate this concept. As a group, attines were not adversely affected in the highly degraded site (Fig. 6). *Mycetophylax emeryi* was favored in the puesto site (Fig. 7); they have small-bodied workers, small colony sizes, and use detritus as fungal substrate (Hölldobler and Wilson 1990). *Acromyrmex aspersus* was associated with less degraded sites; they have relatively large-bodied workers, large colony sizes, and utilize freshly cut leaves as fungal substrate. The association of *A. aspersus* with less degraded areas may be related to increases in grasses and forbs, which provide a relatively concentrated and abundant substrate to support their large colonies. *M. emeryi* fills the attine role in the vegetation-impoverished puesto site where detrital matter is available but in lower densities. In addition, extremely large colonies of *Atta sexdens* were present only in the highly degraded site. These ants require large open spaces in which to nest and may forage >100 m from nest sites to find suitable quantities of vegetation (E. H. Bucher 1974 and *personal observations*). Despite important changes to the nature of resources and the ecology of the species consuming them, the functional role of attines was maintained across the land-use gradient. This result highlights the importance of linking functional and taxonomically based approaches in studies of community structure.

The DCA revealed that the area restored the longest became more similar to the pre-restoration state (HD) with respect to ant composition and abundance (Fig. 7). Open-adapted ants such as hot-climate specialists and opportunists were abundant in both the most degraded and most restored sites (Fig. 6). These similarities may be related to the relatively open canopy and insolation in the two sites (Figs. 2 and 4C). The increase in the cover of grasses and forbs and the reduction of canopy cover in the highly restored site mark a return to the more open character of historical grassland-mosaic conditions (Bucher 1987). This observation suggests that the highly degraded puesto site may harbor species that were more common in pre-colonization Chacoan environments.

Conclusions

Traditional notions of "biological simplification" due to human land use suggest that biodiversity is diminished in disturbed areas. This is often the case in tropical rainforests (Myers 1984). In the case of ant communities at this Chaco site, however, the structural simplification of the puesto apparently provided habitat for a suite of ant species and functional groups that were not well represented in other land-use types. In this region, puestos may be regional sources of arid-adapted ant species that provide resilience to diversity and associated ant functions in Chacoan ecosystems. The maintenance of puesto networks may provide dispersal centers for many ant species and maintain local diversity in disturbed habitats (Roth et al. 1993). On the other hand, the establishment of the Los Colorados reserve has fostered habitat regeneration from heavy grazing disturbance, and many components of the ant fauna that are underrepresented or absent elsewhere have been favored inside the reserve.

These observations suggest that ant biodiversity at both local and regional scales might be enhanced if both puestos and reserves were well represented in the Chaco. These considerations shift our attention to the landscape, regional, biogeographic contexts of local communities (Ricklefs and Schluter 1993). The proximity of other biogeographic regions may interact with local habitat and microhabitat characteristics in determining community patterns. Clearly, conservation and resource management must consider the interactions among elements in entire landscape mosaics that include differing intensities of human land use rather than focussing on local areas alone (Noss 1983, Risser 1985, Franklin 1993, Wiens 1994).

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APPENDIX

Ants recorded during the study, functional group designation, and presence (+) or absence (0) in each site and season. Species ,identifications by Roy R. Snelling, Los Angeles County Museum of National History.

Subfamily Species	Group†	Sites			
		HD‡ S/W	MD‡ S/W	MR‡ S/W	HR‡ S/W
Ponerinae					
Acanthoponera mucronata (Roger)	Op	+/0	+/0	0/0	+/0
Anochetus neglectus Emery	Cr	+/0	+/+	+/+	+/+
Ectatomma edentatum (Roger)	Op	0/0	0/0	0/0	0/+
Ectatomma quadridens (Fabricius)	Op	+/+	+/+	+/+	+/+
Ectatomma ruidum (Roger)	Op	+/0	0/0	0/0	0/0
Ectatomma tuberculatum (Olivier)	Op	0/0	0/0	+/0	+/+
Gnamptogenys regularis Mayr	Op	0/0	0/0	+/0	0/0
Gnamptogenys striatula Mayr	Op	0/0	+/+	+/+	+/+
Gnamptogenys sulcata (Fr. Smith)	Op	0/0	+/0	+/0	+/0
Hypoponera sp. A	Cr	0/0	0/0	+/+	0/+
Odontomachus chelifer (Latreille)	Pr	0/0	0/0	+/+	+/+
Pachycondyla harpax (Fabricius)	Pr	0/0	0/0	+/0	0/0
Pachycondyla marginata (Roger)	Pr	0/0	0/0	+/+	+/0
Pachycondyla rostrata Emery	Pr	0/0	+/0	+/0	0/0
Ecitoninae					
Eciton quadriglume (Haliday)	Ec	+/0	0/0	+/0	+/0
Labidus coecus (Latreille)	Ec	0/0	0/0	+/+	0/0
Neivamyrmex pertyi (Shuckard)	Ec	0/0	0/0	+/0	+/0
Neivamyrmex pseudops (Forel)	Ec	0/0	0/0	+/0	0/0
Nomamyrmex esenbecki (Westwood)	Ec	0/0	0/0	0/0	0/+
Pseudomyrmicinae					
Pseudomyrmex denticollis Emery	Ar	+/0	+/0	+/+	+/0
Pseudomyrmex pallida group	Ar	0/0	+/0	0/0	0/0
Pseudomyrmex gracilis (Fr. Smith)	Ar	0/0	+/0	+/0	0/0
Myrmicinae					
Acromyrmex aspersus (Fr. Smith)	At	+/+	+/+	+/+	+/+
Acromyrmex sp. A	At	0/0	0/0	0/0	+/0
Acromyrmex striatus (Roger)	At	+/0	+/0	+/0	0/0
Apterostigma steigeri Santschi	At	0/0	0/0	+/0	+/0
Atta sexdens (Linnaeus)	At	+/+	+/+	0/0	0/0
Crematogaster sp. A	Gm	+/0	+/0	0/0	+/0
Crematogaster sp. B	Gm	+/+	+/+	+/+	+/+
Crematogaster sp. C	Gm	+/0	0/0	0/0	0/0
Crematogaster sp. D	Gm	+/0	+/0	0/0	0/0
Cyphomyrmex cochunae Kusnezov	At	+/0	+/+	+/+	+/+
Cyphomyrmex lilloanus Kusnezov	At	0/0	0/+	+/0	0/0
Cyphomyrmex sp. A	At	+/0	0/0	+/+	+/0
Leptothorax spininodis Mayr	Cr	0/0	0/0	0/0	+/0
Leptothorax sp. A	Cr	0/0	0/0	+/0	+/0
Megalomyrmex sp.	?	0/0	0/0	0/+	0/0
Mycetophylax emeryi Forel	At	+/+	+/+	+/+	+/+
Mycetophylax sp. A	At	+/+	+/0	0/0	0/0
Pheidole cornutula Emery	Cr	+/0	0/0	0/0	+/0
Pheidole oxyops Forel	Gm	+/+	+/+	+/+	+/+
Pheidole scapulata Santschi	Gm	+/+	+/0	0/0	0/+
Pheidole sp. C	Gm	+/0	0/0	0/0	0/0
Pheidole sp. D	Gm	+/+	+/0	0/+	0/+
Pheidole sp. E	Gm	+/0	+/0	+/0	0/0
Pheidole sp. F	Gm	+/+	0/0	+/0	+/+
Pheidole sp. G	Gm	0/0	+/+	+/+	0/0
Pheidole sp. H	Gm	0/+	+/+	+/+	+/+
Pheidole sp. I	Gm	+/+	+/+	+/+	+/+
Pheidole sp. J	Cr	+/+	+/0	+/+	+/+
Pheidole sp. L	Gm	0/0	+/0	0/0	0/0
Pheidole sp. M	Gm	0/0	0/0	+/0	0/0
Pheidole sp. N	Gm	0/0	+/0	0/0	0/0
Pheidole triconstricta Forel	Gm	+/+	+/+	+/+	+/+
Pogonomyrmex cunicularius Mayr	Gm	+/0	+/0	+/0	+/0
Rogeria sp. A	Cr	0/0	0/0	0/0	+/0
Smithistruma sp. A	Cr	0/0	0/0	0/0	+/0
Solenopsis electra Forel	Gm	+/+	+/0	+/+	+/+
Solenopsis sp. A	Gm	+/0	0/0	+/0	0/0

APPENDIX. Continued.

		Sites			
Subfamily Species	Group†	HD‡ S/W	MD‡ S/W	MR‡ S/W	HR‡ S/W
Solenopsis sp. B	Cr	+/+	+/0	0/0	0/0
Solenopsis sp. C	Cr	+/0	+/0	+/0	+/0
Solenopsis sp. D	Cr	+/0	+/0	+/+	+/0
Solenopsis sp. E	Cr	0/+	+/+	+/+	+/+
Solenopsis sp. F	Cr	+/0	+/0	+/0	+/+
Solenopsis sp. G	Cr	0/0	+/+	+/0	0/0
Solenopsis sp. H	Cr	+/0	+/0	+/0	0/0
Solenopsis sp. I	Cr	0/+	+/+	+/0	0/+
Solenopsis sp. J	Cr	0/+	0/0	+/0	0/0
Solenopsis sp. K	Cr	+/0	+/0	0/0	0/0
Solenopsis tridens Forel	Cr	0/0	+/0	+/0	+/+
Trachymyrmex sp. A	At	0/0	+/+	+/0	+/+
Trachymyrmex sp. B	At	0/0	0/0	0/0	+/0
Wasmannia auropunctata (Roger)	Cr	0/+	+/+	+/+	+/+
Zacryptocerus fiebrigi (Forel)	Ar	0/0	0/0	0/0	+/0
Zacryptocerus eduarduli (Emery)	Ar	0/+	0/0	0/0	0/0
Zacryptocerus jheringi (Emery)	Ar	+/0	+/+	0/0	+/0
Zacryptocerus prodigiosus (Santschi)	Ar	0/0	+/0	+/0	0/0
Zacryptocerus pusillus (Klug)	Ar	+/0	+/+	+/+	+/0
Dolichoderinae					
Dorymyrmex bitubera Santschi	Cr	+/+	+/0	+/+	+/0
Dormyrmex ensifer Forel	Op	+/+	0/0	0/0	0/+
Dorymyrmex exsanguis Forel	Op	+/+	+/+	+/+	+/+
Dorymyrmex sp. A	Op	+/+	+/0	+/0	0/0
Dorymyrmex sp. B	Op	+/+	+/0	+/0	+/+
Dorymyrmex sp. C	Op	+/+	+/+	0/0	+/+
Dorymyrmex sp. D	Op	+/+	+/+	+/+	+/+
Forelius nigriventris Forel	Cl	+/+	+/0	+/+	+/+
Forelius sp. A	Cr	+/+	0/0	0/0	+/0
Forelius sp. B	?	+/0	0/0	0/0	0/0
Forelius sp. C	?	+/0	+/0	+/0	+/0
Forelius sp. D	?	0/0	+/0	0/0	0/0
Linepithema sp. A	?	0/0	0/+	0/0	0/0
Formicinae					
Acropyga sp. A	?	0/0	0/0	0/+	0/0
Brachymyrmex sp. A	Cr	+/+	+/+	+/+	+/+
Brachymyrmex sp. B	Cr	0/0	+/0	+/0	+/0
Camponotus blandus (Fr. Smith)	Ca	+/0	+/0	0/0	0/0
Camponotus borelli Emery	Ca	+/+	+/+	+/0	+/+
Camponotus cameranoi Emery	Ca	+/+	+/+	+/+	+/+
Camponotus crassus Mayr	Ca	0/0	+/0	0/0	+/0
Camponotus leydigi Forel	Ca	0/0	+/0	+/0	+/0
Camponotus sp. A	Ca	+/+	+/+	+/+	+/+
Camponotus sp. B	Ca	+/0	0/0	+/0	+/0
Camponotus sp. C	Ca	+/0	0/0	+/0	+/0
Camponotus sp. D	Ca	0/0	+/0	0/0	0/0
Total: 104					

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† Cl = climate specialists, Ca = *Camponotus*, Gm = generalized myrmicines, Cr = cryptic species, Op = opportunists, Pr = predators, At = Attini, Ec = Ecitonini, Ab = Arboreal. Question mark indicates rare species about which too little is known to assign to a functional group.

‡ HD = highly degraded; MD = moderately degraded; MR = moderately restored; HR = highly restored. S = summer; W = winter.