ANTS AS INDICATORS OF EXPOSURE TO ENVIRONMENTAL STRESSORS IN NORTH AMERICAN DESERT GRASSLANDS

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Abstract. The relative abundance of ant species was measured by pit-fall trapping at 44 sites in southern New Mexico and southeastern Arizona, U.S.A.. Sites were selected for study based on documentation of a history of disturbance or protection from disturbance, exposure to varying intensities of livestock grazing, dominance by an exotic species of plant and vegetation change resulting from disturbance or restoration efforts. Ant community composition, relative abundances of species, and species richness were the same on disturbed and undisturbed sites. None of the metrics based on hypothesized responses of ants to disturbance clearly distinguished between disturbed and undisturbed sites. Ant communities on sites where restoration efforts have resulted in distinct differences in vegetative cover and composition were similar to the ant communities on degraded unrehabilitated sites on the same soil type. Ant communities in riparian cottonwood gallery forests in Arizona and New Mexico were similar but differed from the assemblages in exotic salt cedar and native ash riparian woodlands. Ant species exhibited remarkable resistance to human-induced disturbances in these rangeland areas. In grasslands dominated by the South African grass, *Eragrostis lehmanniana* Nees, large seed harvesting ants, *Pogonomyrmex* spp., were greatly reduced in abundance compared to native grasslands. Other ant metrics were not different in *E. lehmanniana* grasslands and native grasslands. We conclude that ants cannot be used as indicators of exposure to stress, ecosystem health or of rehabilitation success on rangeland ecosystems. Ants are also not useful indicators of faunal biodiversity in rangeland ecosystems.

Key words: environmental stressors, exposure indicators

1. Introduction

Ants are among the most ubiquitous invertebrates of terrestrial ecosystems. They occupy habitats from the driest deserts to sub-alpine regions. Diversities of ants are high even in human-modified habitats (Holldobler and Wilson, 1990; Nuhn and Wright, 1979; Talbot, 1953; Torres, 1984; Van Pelt, 1963; Whitcomb et al., 1972). Assemblages of ant species include species with different life history characteristics and trophic relationships. Ants fill most kinds of consumer trophic levels as predators, omnivores, detritivores (including species that culture fungi), granivores, and sugar feeders. The complex interrelationships between ant species and their physical and biological environment should make ants sensitive indicators of environmental stress. These complex interrelationships may also make ants good indicators of the characteristics of environmental stressors.

Indicators of ecosystem stress should be easily linked to essential ecosystem processes. Ants play many clearly identifiable, important roles in ecosystems.

Most species of ants make nests in the soil and as soil animals they are important modifiers of the chemical and physical nature of the soil (Lobry de Bruyn and Conacher, 1990). These modifications of soil properties have effects on ecosystem processes such as water infiltration, nutrient cycling and nutrient distribution. Some species are keystone predators (Bradley, 1973). Some species are pollinators, some disperse seeds, and some regulate the abundance of insects living on plants (Banks, 1962; Beattie et al., 1979; Levin and Anderson, 1970; Post and Jeanne, 1982; Way, 1963; Wilson, 1971). Rissing (1986) and Risch and Carroll (1986) showed that seed predation by ants altered local plant species composition. Thus ants may affect many important ecosystem processes and the structure of some ecosystems.

Their effects on ecosystem structure and function led Majer (1983) to propose ants as indicators of impacts of human disturbances on natural ecosystems. He listed a number of attributes that were valuable in using ants as bioindicators of disturbance in natural ecosystems by various kinds of human activities such as recreation, reclaimed mine sites, and farming practices. Those attributes included: (1) they are extremely abundant, (2) there is a relatively high species richness, (3) there are many specialist species, (4) they occupy higher tropic levels, (5) they are easily sampled, (6) they are easily identified, and (7) they are responsive to changing environmental conditions. Although Majer (1983) was referring to Australia, these attributes characterize North American ants and should apply to the ant communities that we studied. Thus ant species and ant communities may provide signals about environmental quality.

The abundance of ant colonies remains relatively constant from year to year because of the tendency of social insects not to respond dramatically to short-term fluctuations in climate (Whitford, 1978). This feature of the biology of ants should make them particularly suitable as indicator organisms for a wide variety of ecosystem stressors. Indicators of ecosystem stress should be (1) clearly interpretable, i.e. consistently responsive to the stress, (2) easily measured, (3) quantitative, (4) repeatable, and (5) easily communicated. Based on the literature, we hypothesized that ant communities meet the criteria for indicators of exposure to ecosystem stress. Our study was designed to evaluate the potential of ants as indicators of ecosystem health, their potential as indicators of biodiversity, and their potential as indicators of disturbance and recovery. We selected a range of sites that were exposed to different intensities of grazing by domestic livestock. We also selected sites that had been subjected to a variety of treatments in attempts to restore desert grassland in shrub-dominated areas. These treatments included bulldozing, root-plowing, herbicide application and introduction of an exotic grass species. Sites were selected based on the availability of detailed management records covering at least the past 20 years and reliable information on land use and vegetation for the past century.

Multi-metric indices have been developed to track condition of aquatic ecosystems (Fore and Karr, 1996). Most biological indices have been adapted from the index of biological integrity (Karr, 1981). Testing of multimetric indices involves

examining richness and composition of taxa, tolerant and intolerant species (with respect to environmental change), changes in the feeding ecology structure of the taxa and dominance and abundance (Fore and Karr, 1996). We utilized the strategy of Fore and Karr (1996) to examine the potential of ants to provide a multi-metric index of the condition of southwestern rangelands, an index of restoration, and an index of the condition of southwestern riparian woodlands.

We hypothesized that exposure to chronic stress such as livestock grazing would result in marked differences in ant species composition, species richness and diversity, and relative abundance. We hypothesized that ant communities on sites exposed to an acute stress such as soil disturbance or herbicide application would recover at the same rate as the vegetation. We also hypothesized that ant communities at sites dominated by exotic plant species would exhibit low species richness and diversity and large differences in species abundances and composition when compared to ant communities at sites with native vegetation.

2. Study Sites

Sites were selected for study based on the availability of historical records of management and where long-term grazing studies were being conducted. The sites selected for riparian comparisons were based on permission to access the sites and on availability of documented management history. Thirty-six of the study sites were located on the Jornada Experimental Range and the Chihuahuan Desert Rangeland Research Center which are approximately 40 km N and NE of Las Cruces, NM. Two rangeland sites were at the Empire Cienega Ranch, which is approximately 80 km NW of Sierra Vista, AZ and two were at the Santa Rita Range Reserve located approximately 40 km S of Tucson, AZ. Two riparian sites were at Percha State Park on the Rio Grande river approximately 20 km south of Truth or Consequences, NM. Two riparian sites were located in the San Pedro river valley: a native cottonwood gallery forest in the San Pedro Riparian Reserve approximately 10 km E of Sierra Vista, AZ and a salt cedar thicket at St. David, AZ approximately 40 km downstream of the San Pedro Riparian Reserve.

Studies were conducted at 2 sites during the summer, 1993 and 42 sites during the summer, 1994. A one hectare grid of 100 traps was established at each site (Table I). The list of rangeland sites and the characteristics of the vegetation and soil at those sites are presented in Table I. All of the riparian sites were protected from grazing and used primarily by bird watchers and hikers.

2.1. Grazing gradients. exclosures and desertified sites

The three grazing intensity gradients and three exclosure pairs were in pastures that are dominated by black grama grass (*Bouteloua eriopoda* (Torr.) Torr.) with bunch grasses, *Aristida* spp. and *Sporobolus* spp. and mesquite shrubs, *Prosopis*

Table I

Characteristics of 44 rangeland sites where ant communities were sampled. Vegetation characteristics are percent cover of perennial grass and shrubs. Average size of unvegetated patches is reported as average bare diameter in cm.

Site code	Disturbance/ Grazing History	Grass (%)	Shrub (%)	Bare (cm)	Soil
Grazing intensity gradients					
WW0	Winter–Spring	0.88	15.9	197.6	Sandy-loam,
WW1	Winter–Spring	3.3	21.7	139.2	indurated
WW2	Winter–Spring	8.9	13.7	133.1	caliche at
WW3	Winter–Spring	27.6	5.1	50.9	40–100 cm
CW0	Winter–Spring	0.47	5.7	396.2	Sandy-loam,
CW1	Winter–Spring	2.4	8.6	126.0	indurated
CW2	Winter–Spring	4.5	5.5	126.9	caliche at
WW3	Winter–Spring	20.8	4.3	68.5	40–100 cm
MW0	Continuous	1.2	6.8	296.4	Sandy-loam,
MW1	Continuous	4.1	17.2	96.9	indurated
MW2	Continuous	5.7	10.9	90.2	caliche at
MW3	Continuous	23.7	6.7	62.6	40–100 cm
Exclosure-grazed comparisons					
EXW	Exclosed 1946	47.9	0.66	54.1	Sandy-loam,
EWC	Continuous	6.7	17.5	125.1	
EXE	Exclosed 1946	41.6	1.1	56.6	Sandy-loam
EEC	Summer	2.2	3.0	171.1	
EXN	Exclosed 1946	53.4	4.0	50.2	Sandy-loam,
ENC	Continuous	5.7	10.9	90.2	
Desertification series					
LTG	Winter grazed	46.2	4.5	53.3	Sandy-loam, indurated caliche 40–100cm
LTT	Grazed-variable	28.5	28.4	57.7	Fine silty-loam, argyllic layer, 40–70 cm
LTP	Grazed-variable	5.1	26.9	110.1	Silty-loam, Sandy-loam
LT2	Grazed	26.4	8.8	47.4	Patchy sandy loam, silty loam
LTM	Exclosed	1.6	36.1	313.7	Sandy-loam, indurated caliche 40–100 cm
MTX	Ungrazed	0.0	26.0	ND	Patchy sandy loam, silty loam
LTC	Eclosed 1971	20.8	20.1	86.2	Coarse loamy-sand, indurated caliche at 40–100 cm
Herbicide – untreated pairs					
TCC	Untreated	13.5	23.5	208.8	Fine sandy-loam,
TCE	Treated 1971/2	33.8	8.6	82.0	Fine sandy-loam
TCH	Treated 1971/2	20.2	20.1	77.7	Fine sandy-loam
MHJ	Treated 1979	10.2	12.9	ND	Sandy-loam, indurated
EMS	Untreated	2.3	33.3	ND	caliche 20–70 cm

Table I
Continued.

Site code	Disturbance/ Grazing History	Grass (%)	Shrub (%)	Bare (cm)	Soil
Bulldozed – untreated pair					
BMD	Bulldozed 1975/6	4.2	5.8	99.9	Sandy-loam,
BMC	Untreated	1.8	24.8	311.9	indurated caliche
Root-plowed – untreated comparisons					
GRE	Eclosure – not plowed	31.1	17.4	102.3	Sandy-clay-loam
GR2	Exclosure – not plowed	14.5	31.0	311.9	Sandy-clay-loam
GR1	Grazed – not plowed	9.7	19.7	108.6	Sandy-clay-loam
GRP	Root plowed	30.4	9.1	54.7	Sandy-clay-loam
Exotic grass (*Eragrostis lehmanniana*) – native grassland comparisons					
SNG	Native	5.4	10.4	50.9	Loamy-sand
SRL	Established 1978	15.3	27.7	41.9	Loamy-sand
ECG	Native	37.9	2.2	21.9	Loamy-sand
ECL	Established 1978	19.1	11.9	31.7	Loamy-sand

Riparian comparisons	Dominant tree	Stem density No./ha		Grass-herbaceous cover (%)	
RGC	Cottonwood gallery	112		37.4	
RGA	Ash, closed canopy	ND		21.9	
SPC	Cootonwood gallery	ND		11.0	
SPT	Salt cedar thicket	1409		0.8	

glandulosa Torr., varying in abundance and cover depending upon distance from water points and other factors. The grazing exclosures were approximately 1 ha in size and were located 150 m from livestock watering points. The grazing intensity gradient plots were located at fixed distances from water points starting at 10 m and the most distant plot starting at 1000 m (Table I). The most distant plot at each of the grazing intensity gradients was in a *B. eriopoda*-dominated grassland. All of these sites were on the same soil series (USDA Soil Concervation Service, 1980).

There is a well documented history of vegetation change from desert grassland in 1858 to a variety of shrub-dominated ecosystems that now characterize much of the Jornada Basin (Buffington and Herbel, 1965; Gibbens and Beck, 1988). Some areas that were shrub-dominated in 1858 have exhibited little change since the 1858 survey. We selected a series of sites based on the historical vegetation records that provided a gradient from minimal vegetation change (perennial grassland – LTG and tarbush shrubland – LTT, Table I) through intermediate change (open mesquite shrubland with clump grasses – LTP, mixed shrubs and perennial grasses – LT2, Table I) to maximum change (mesquite coppice dunes LTM and MTX;

creosotebush shrubland – LTC, Table I). This series of sites represents stages in desertification (conversion of productive areas to desert condition) and is identified as a desertification series (Table I). Mesquite coppice dunes are sand dunes that vary from 1–4 m in height and from 10 m to more than 300 m in diameter. The sand is held by the dense coppice of stems of one or more mesquite plants. Stem heights vary from 0.2 to 0.5 m above the sand surface. The LTM site is in a 259 ha exclosure that was established in 1934 following the removal of existing mesquite. The characteristics of the coppice dunes inside that exclosure and the grazed dune sites are very similar (Table I). The coppice dunes on the Jornada Experimental Range began to form during the drought of the early 1930s and the area dominated by coppice dunes increased during the drought of the 1950s and now cover more than 14 500 ha. The coppice dune sites are on the same soil series or a closely related soil series to the grassland site (USDA Soil Conservation Service, 1980).

2.2. RESTORATION SITES

Various attempts at restoring grassland on sites that had been degraded to shrubland or mesquite coppice dunes were made during the 1970's. These efforts included aerial application of herbicides, bulldozing coppice dunes to remove the mesquite and to level the soil, and root-plowing to kill shrubs. We selected paired (treated and untreated) sites for comparisons of ant communities (Table I). In the herbicided tarbush comparison and the root-plowed comparison we selected additional plots that were inside grazing exclosures for comparison with the treated plots and the grazed untreated plots. Several sites (TCC, TCE, TCH, Table I) were located in areas that were dominated by tarbush, *Flourensia cernua* DC, and burro grass, *Scleropogon brevifolius* Phil. These pastures are grazed annually at variable stocking rates and the season during which the pastures are grazed varies depending upon forage availability.

The root plowed comparisons were made on four sites located on a piedmont slope of the San Andres Mts. The vegetation is predominately creosotebush, *Larrea tridentata* (DC) Cov., with bush muhly, *Muhlenbergia porteri* Scribn, under many of the shrub canopies. The exclosure in which GRE was located is 259 ha and was constructed in 1934. The grass cover in the root plowed area, GRP, includes several grasses not native to the area including Lehmann's love grass, *Eragrostis lehmanniana* Nees, and little blue stem, *Bothriochloa laguroides* (DC) Herter. These pastures are grazed at variable rates and duration depending upon forage availability.

2.3. RIPARIAN SITES

Two riparian sites were chosen in the San Pedro river valley in southeastern Arizona. The native cottonwood site was in the San Pedro Riparian Reserve approximately 10 km east of Sierra Vista, Arizona. The density of cottonwoods (*Populus fremontii* S.

Wats.) at this site was 112/ha comprised mostly of large trees of 1 m stem diameter or larger. There was a sparse understory (average 11.0% cover) of willows, and grasses (*Sporobolus giganteus* Nash, *Aristida* spp. and *Cynodon dactylon* (L.) Pers. The cottonwood forest produced an essentially closed canopy. The salt-cedar (*Tamarix (pendantra) ramosissima* Lebed.) site was located at St. David, Arizona, approximately 40 km downstream from the San Pedro Riparian Reserve. This site had a dense stand of salt cedar, (1409 stems/ha) and no herbaceous or grass vegetation in the understory. In the Rio Grande valley in southern New Mexico, we sampled a cottonwood gallery forest and an ash forest at Percha State Park, 20 km south of Truth or Consequences, NM. These were essentially closed canopy forest patches with a sparse grass, forb, and sapling understory.

3. Methods

Pit-fall trapping is rapid, repeatable, and quantitative, and provides a relatively unbiased sample of the ants in the community (Andersen, 1990). Pit-fall traps (38 mm × 70 mm tall plastic vials) were placed in 100-trap grids of ten lines of traps with 10 m spacing between traps. Each vial was filled to a depth of 30 mm with a mixture of 70% ethanol and 30% glycerol (Greenslade and Greenslade, 1971). Vials were carefully placed in holes in the soil which were back-filled to make the soil surface level with the lip of the vial. Traps were left in place for 24 hours, retrieved, labeled and stored.

Vegetation cover and species composition was measured at each rangeland site by 10, 100 m intercept lines (Canfield, 1941) adjacent to the pit-fall trap grid lines.

All ants in a vial were identified to species or to an operational taxonomic unit (*Pheidole* spp. with no major workers). The data used in the analyses were (a) the average number of species per vial, (b) a relative abundance based on the sum of the number of ants of a species in a vial divided by the total number of ants of all species in all traps at the site, and (c) abundance rankings obtained by assigning a relative abundance value to the number of ants of a species in a trap, i.e. 0–5 ants = 1, 6–10 ants = 2, 11–20 ants = 3, 21–30 ants = 4 ... > 50 ants = 7 summed for all traps with that species for a site. Because our studies were based on various land management practices, grazing exclosures in different pastures etc., there were few replicates of exposure to stressors. Therefore we used clustering techniques and principal components analysis to search for consistent patterns in the data (Ludwig and Reynolds, 1988; Ray, 1982).

A large number of metrics based on the ant communities were examined by plotting the values against the disturbance gradient. In addition to species richness (S) and Shannon–Weaver diversity index (H′), we examined all of the hypothesized responses of rangeland ants to disturbance (Table II) and as indicators of rehabilitation. We developed a list of hypothesized responses of ants to disturbance, vegetation change resulting from drought and overgrazing, and/or exposure to

Table II

Hypothesized responses of ants to exposure to grazing by domestic livestock and to vegetation and soil changes resulting from desertification

< species richness of *Pheidole* spp.

< species richness of *Pognonomyrmex* spp.

< species richness of all ant taxa

> species richness of small body size generalists (*Conomyrma, Forelius, Solenopsis, Monomorium*)

> Species richness of *Solenopsis* spp.

< Species richness of *Myrmecocystus* spp.

> relative abundance of *Solenopsis* spp.

< relative abundance of *Pogonomymex* spp.

< relative abundance of *Pheidole* spp.

> relative abundance and species richness of tolerant species *Forelius pruinosus Solenopsis xyloni, Paratrechina terricola*)

< relative abundance and species richness of intolerant species *Aphaenogaster cockerelli, Myrmecocystus* spp., *Pogonomyrmex rugosus*)

< dominance

chronic stress by livestock grazing. The hypothesized responses of southwestern rangeland ants were based on the available literature and our experience with these species (Holldobler and Wilson, 1990; Whitford and Ettershank, 1975; Whitford et al., 1980; Whitford et al., 1981). Other features of ant communities that should be seen in ecosystems under stress were derived from Rapport et al. (1985, Table II). Indicator metrics of the status of restoration should be the reverse of the hypothesized responses to disturbance and degradation (Table II). Relative abundances of groups of ant species and species diversity measures were plotted against a disturbance gradient from least disturbed to most disturbed. The numerical values for this gradient were derived by setting the values for grass cover, shrub cover and bare patch size of grazing exclosures equal to zero (data in Table I). The difference in values of grass cover, shrub cover, and bare patch size expressed as a percent for all of the other plots was summed and used to set the values for the gradient. The exclosures were assumed to be the least disturbed sites available based on historical records. The values of grass and shrub cover and bare patch size are measures of changes in ecosystem structure resulting from the interaction of grazing stress and climatic disturbance. The gradient for recovery of restoration sites was obtained in a similar fashion using the values of the unmanipulated sites as the reference and calculating the departure from the unmanipulated disturbed site as a measure of recovery. This approach provided an objective way of assigning sites on a disturbance gradient from minimal disturbance and/or change to maximum change.

Ant communities at selected pairs of sites were compared by calculating Sorenson's index of similarity (Krebs 1989).

4. Results

4.1. HYPOTHESIZED RESPONSES: EXPOSURE TO LIVESTOCK GRAZING

For some of the most abundant species, e.g. *Conomyrma* spp. and *Forelius* spp., our knowledge of basic history was rudimentary. However, despite this shortcoming, we were relatively confident that our hypothesized responses (Table II) were reasonable and likely to occur. However, none of the hypothesized responses were confirmed by the data.

Although the two measures of relative abundance (percent of traps in which a species was captured and abundance categories based on numbers of ants of a species in a trap) produced different patterns in the principal components analysis (Figure 1), there was no separation of undisturbed, moderately disturbed and severely disturbed (changed) sites. The principal components analyses suggest that ant communities are not responsive to grazing stress nor to structural changes in the rangeland ecosystems.

We present a selected sub-set of the figures that provide the graphical analysis of the hypothesized responses of ants to grazing stress and vegetation change and to restoration efforts because of similarities in the patterns of those presented here and those not presented. The measures of species diversity (species richness and H') produced similar patterns over the disturbance gradient (Figure 2). The range of values for H' for the sites exhibiting intermediate change from the least disturbed was larger than the range for the least disturbed sites. The most disturbed site had values of S and H' that were higher than those for some of the sites that had experienced minimal change (Figure 2). The patterns of species richness of feeding generalists and specialists were very similar (Figure 3) with no differentiation in the least to most disturbed sites. The Shannon-Weaver diversity index (H') produced a pattern very similar to that of species richness for this group of species. The eveness metric calculated as $E = H'/\ln S$ produced a pattern that was similar to that of species richness and H' (Figure 3). There were no clear disturbed sites in any of these analyses. Species richness patterns of selected genera that were hypothesized to be tolerant also showed no patterns that were related to disturbance or vegetation-soil change (Figure 4).

The patterns of relative abundance of ants exhibited similarities for all of the hypothesized responses for selected species and groups of species. For all of the hypothesized responses, the relative abundances were lower in the least disturbed sites than at most of the intermediate disturbed sites (Figures 5 and 6). The highest values were predominately at intermediate disturbed sites but some of the highest values were recorded at some of the most disturbed sites, e.g. small generalists and *Pheidole* spp. (Figures 5 and 6). There was no pattern in the relative abundances of species hypothesized to be tolerant of disturbance. Some probably tolerant species like *Forelius foetidus* (Buckley) were abundant at some intermediate disturbed sites and only marginally present at others (Figure 7). The relative abundances
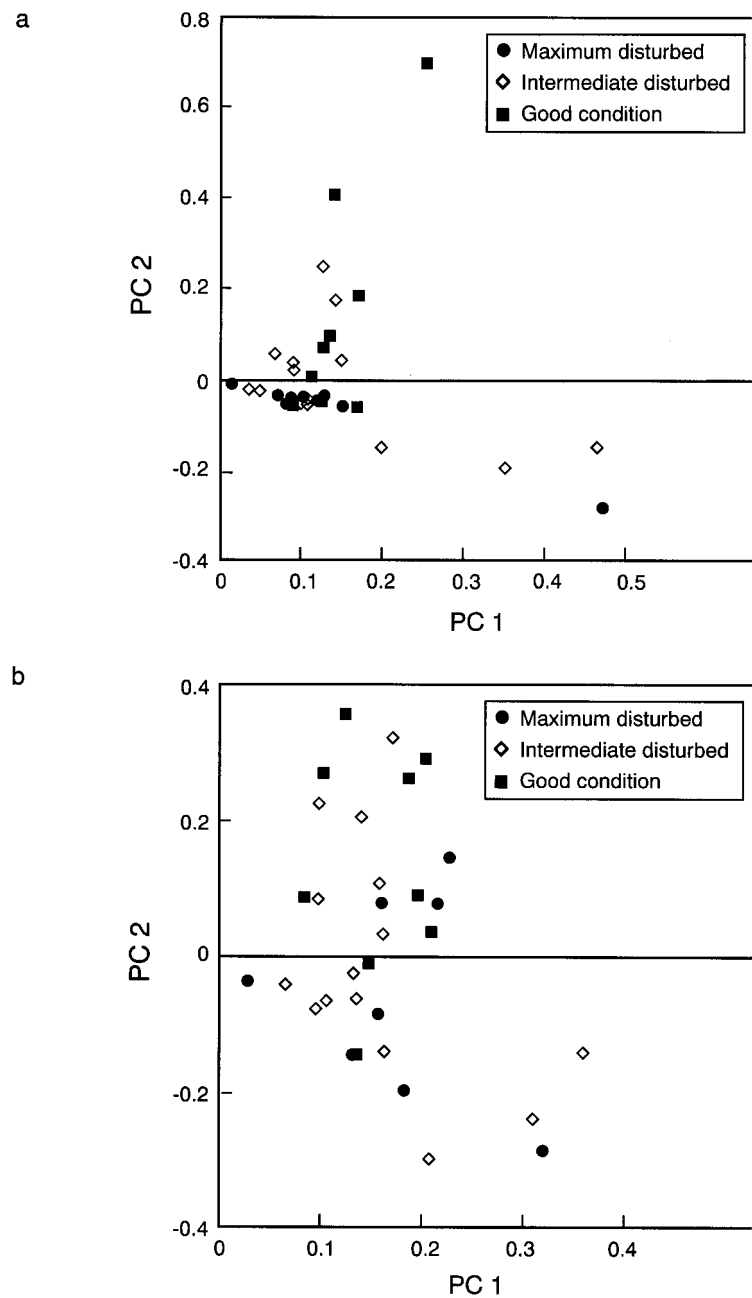
Figure 1. Principal components analysis of ant communities, based on the percentage of traps in which a species was captured (a) and based on abundance categories (b) on rangeland sites documented to be free from exposure to grazing by domestic livestock or minimally impacted by domestic livestock (good condition) and ant communities on rangeland sites with documented histories of disturbance and degradation (intermediate and maximum disturbed).
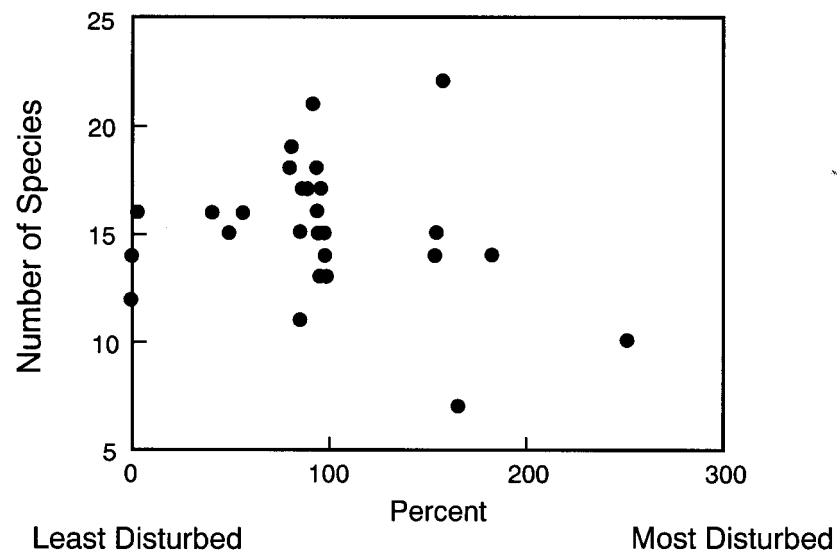
a
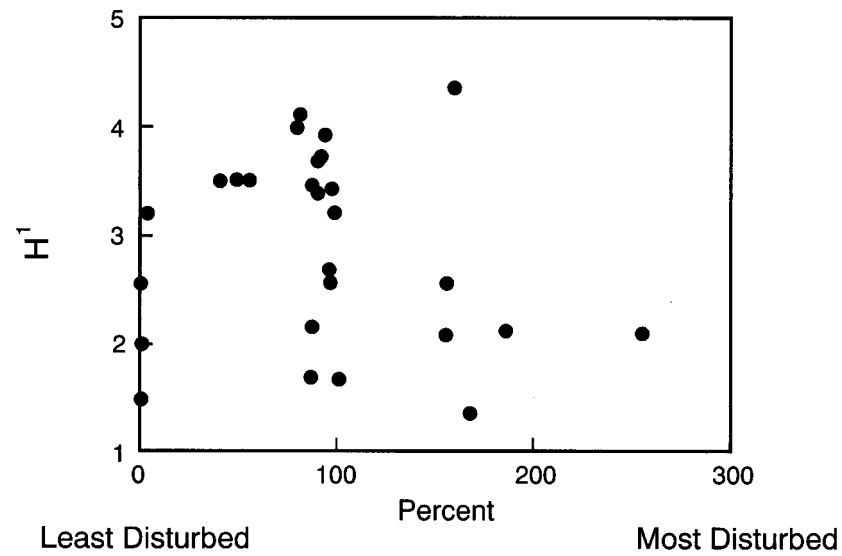
b

Figure 2. The Shannon-Weaver diversity index (H$'$) (a) and species richness (b) on rangeland sites with varying histories and characteristics of disturbance. The percent on the abscissa is the sum of percent change in grass cover, shrub cover, and bare patch intercept from the average values of these measures for reference sites that have changed minimally (based on 1995 site measurements of cover and data in Buffington and Herbel, 1965, and Gibbens and Beck, 1988).

a

Small Generalists
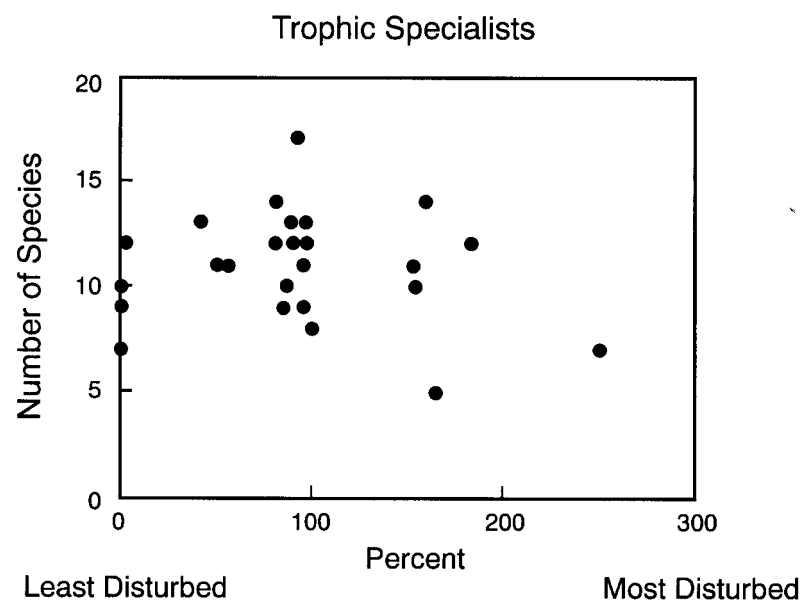

b

Trophic Specialists
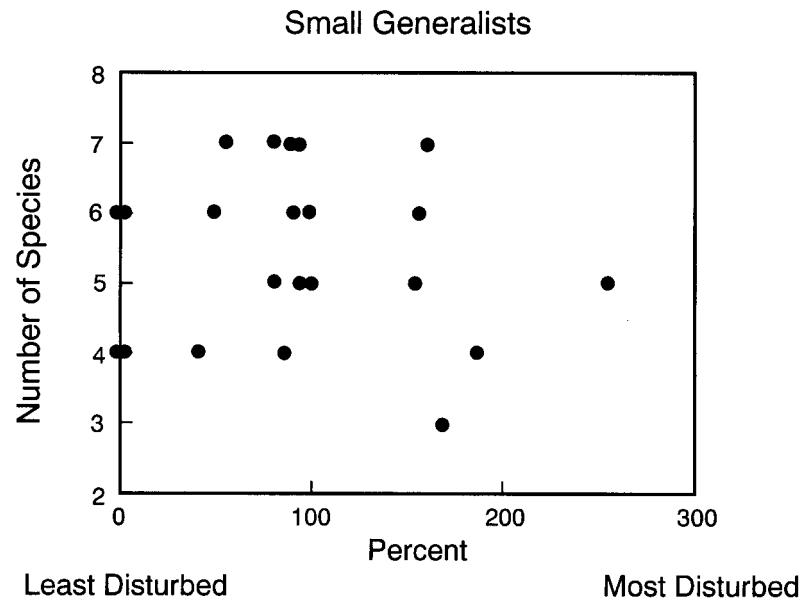
Figure 3. Species richness of small generalist feeding ants (a) and ant species that are trophic specialists (b) on rangeland sites with varying histories of disturbance. Method of presentation same as Figure 2.
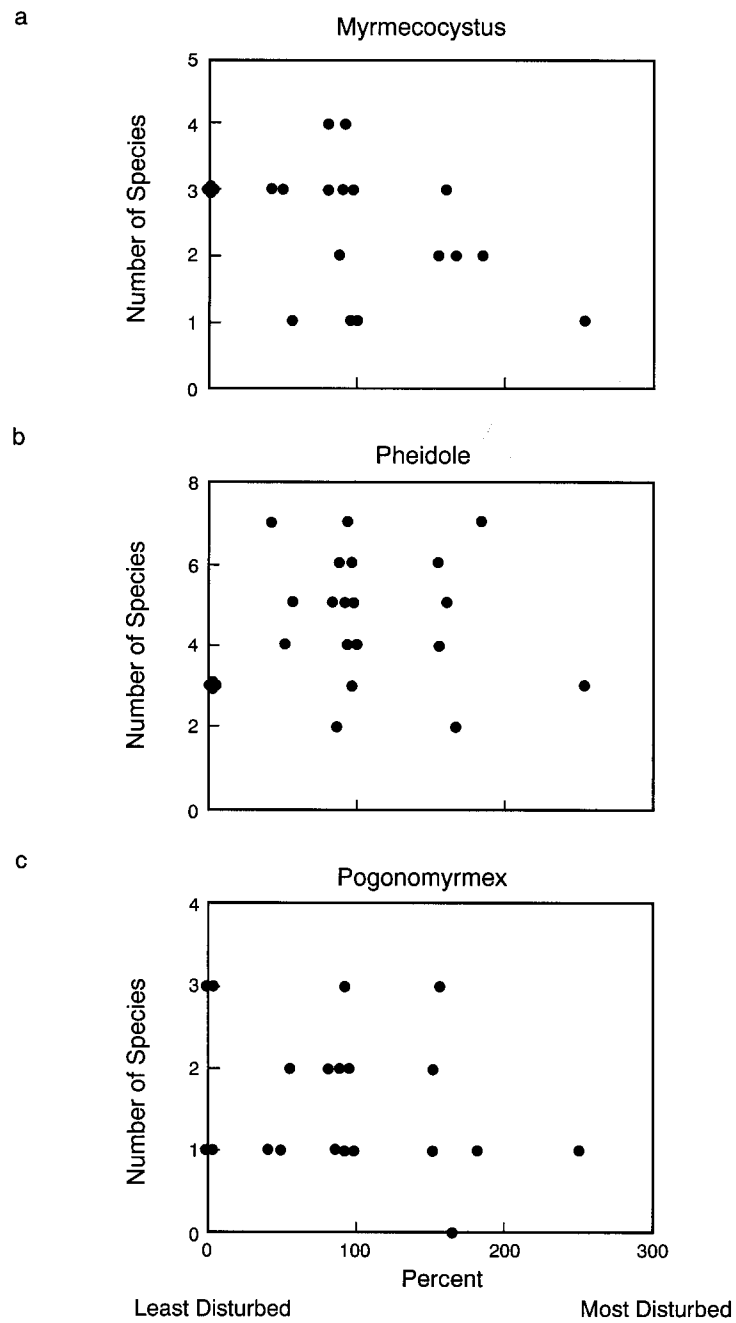
a

Myrmecocystus

c

Pogonomyrmex

Figure 4. Species richness of selected genera of ants on rangeland sites with varying histories of disturbance. Method of presentation same as Figure 2.
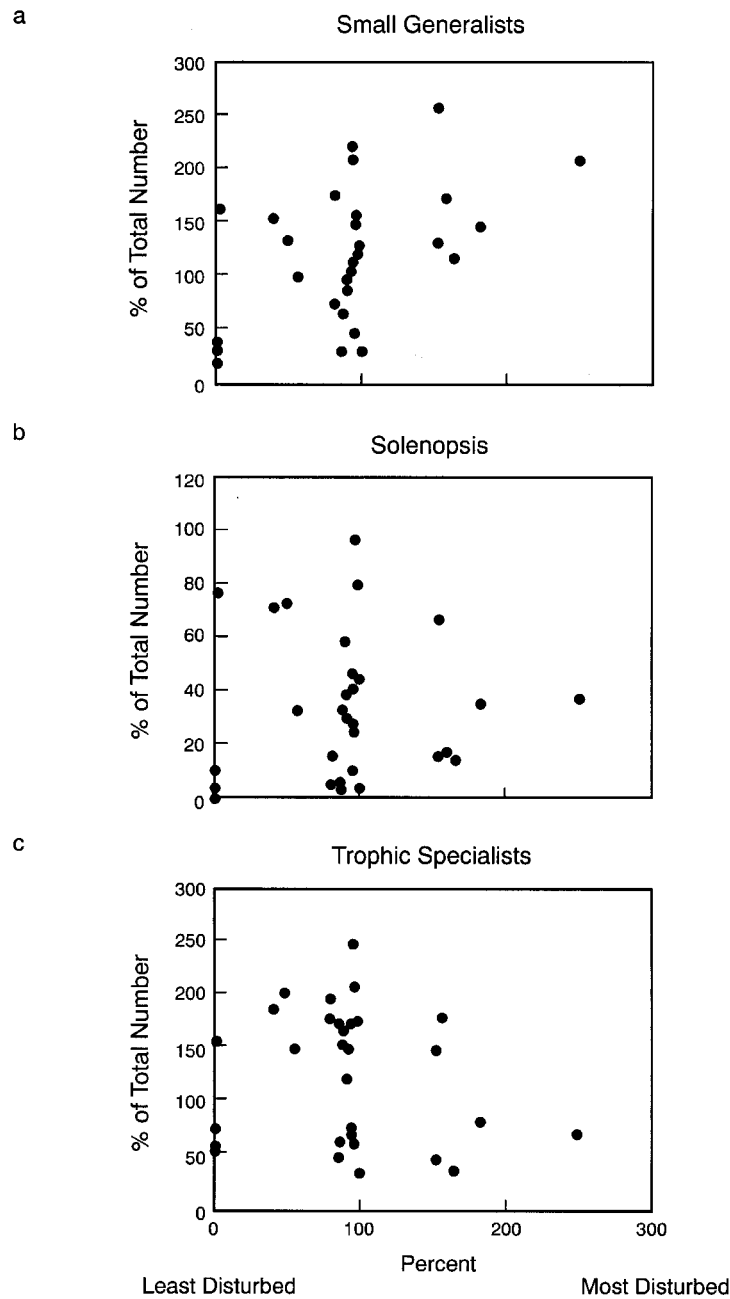
Figure 5. Relative abundances of ant species that are feeding generalists (a), species of *Solenopsis* (b) and feeding specialists (c) on rangeland sites with varying histories of disturbance. Percent of total number refers to the percent of traps in which a species was captured. Abscissa is percent departure from reference sites calculated as the difference in the sum of percent change in grass covers, shrub cover, and mean bare patch intercept.
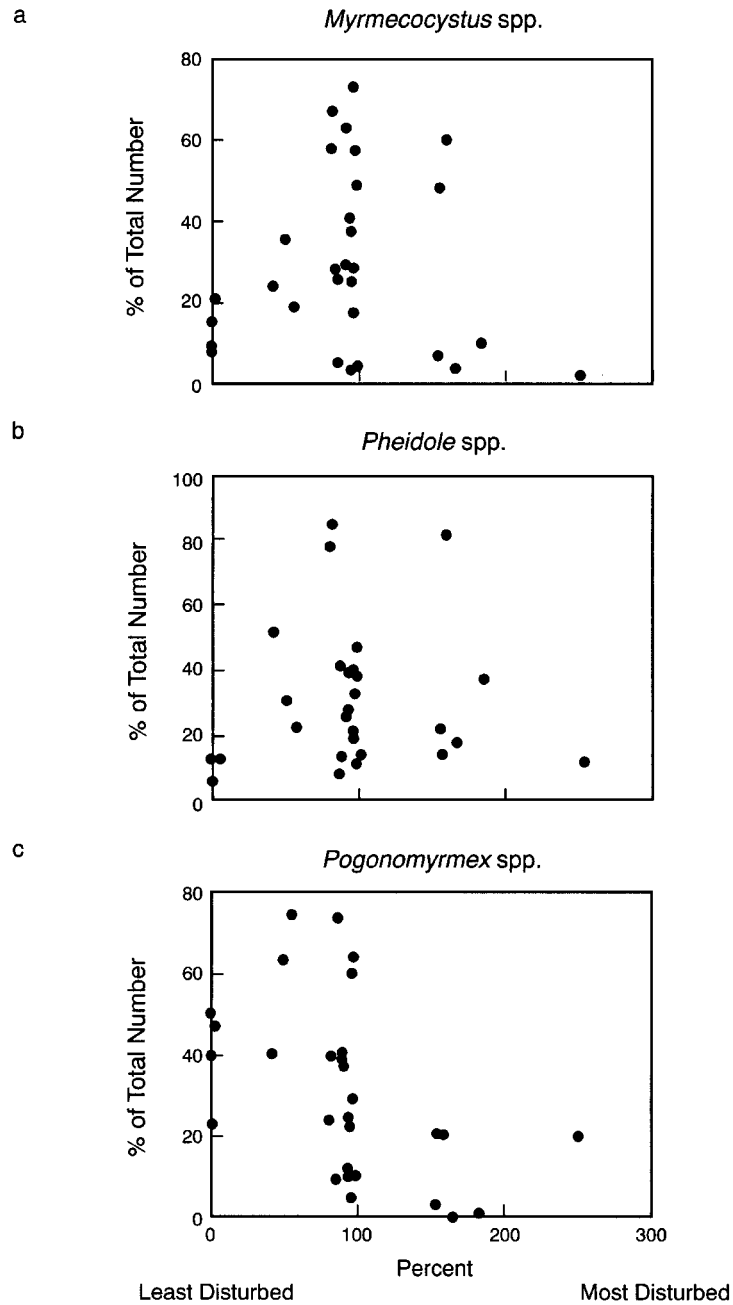
a

Myrmecocystus spp.

b

Pheidole spp.

c

Pogonomyrmex spp.

Figure 6. Relative abundances of selected genera of ants on rangeland sites with varying histories of disturbance. Method of presentation same as Figure 5.

of *Solenopsis xyloni* McCook and *F. pruinosus* (Roger) were highest at some intermediate disturbed and maximally disturbed sites but were of low abundance at some of the least disturbed and intermediate disturbed sites. The lack of a pattern in the relative abundances of those genera that we hypothesized to be intolerant of disturbance or change in vegetation and soils is clear (Figure 7) but obviously unexpected.

The absence of reliable patterns in relative abundances of groups of species of ants and the absence of clear patterns of species diversity across a gradient of sites that encompasses more than a 200% change in vegetation cover-composition and size of bare patches is solid evidence that ants do not respond to disturbance or stress resulting fom the activities of domestic livestock.

4.2. RESTORATION SITES

The hypothesized responses of ants to ecosystem restoration efforts were not observed (Figure 8). This result was unexpected especially since there were clear differences in vegetational composition and cover between the degraded references sites and the restored sites (Table I). Several of the restoration efforts involved soil movement. At the bulldozed site and the herbicided coppice dune site, the soil was leveled resulting in a relatively homogeneous distribution of grass clumps. Soil surface stability in untreated coppice dune areas is greatly reduced as evidenced by casual observation on windy days and historical data on net soil redistribution from interdune areas to dunes (Gibbens et al., 1983) and subsequent changes in soil stability. Despite this, the ant species composition and abundances on the treated and untreated sites were very similar. This was reflected in the high level of similarity among the paired restoration sites in the multivariate clustering analysis (figures not shown). There were no differences among the species groups that were hypothesized to respond to changes resulting from restoration efforts. Species richness was highest in the tarbush shrubland and communities but there was little difference in the species richness of ants in areas restored to grassland and the degraded areas (Figure 8). Species richness at other sites subjected to restoration also showed no differences resulting from soil and vegetation changes. In addition, the species richness of specialist and generalist feeders was not different in restoration areas and degraded areas (Figure 8). The relative abundances of selected species groups also did not differ among degraded and restoration sites (Figure 8).

4.3. RIPARIAN SITES

There were some differences in the limited number of riparian comparisons. Species richness and diversity in the cottonwood gallery forests of the Rio Grande and San Pedro ($S = 13$, $H^{'} = 1.94$ and 1.91, respectively) were higher than in the San Pedro tamarisk forest ($S = 9$, $H^{'} = 1.03$) or the Rio Grande ash grove ($S = 3$, $H^{'} = 0.30$). The dominant species in the tamarisk woodland was *Formica gnava*
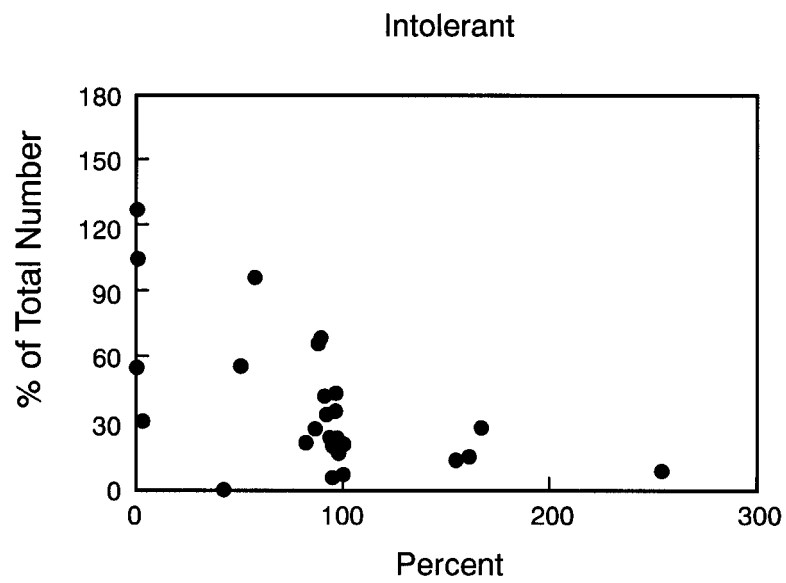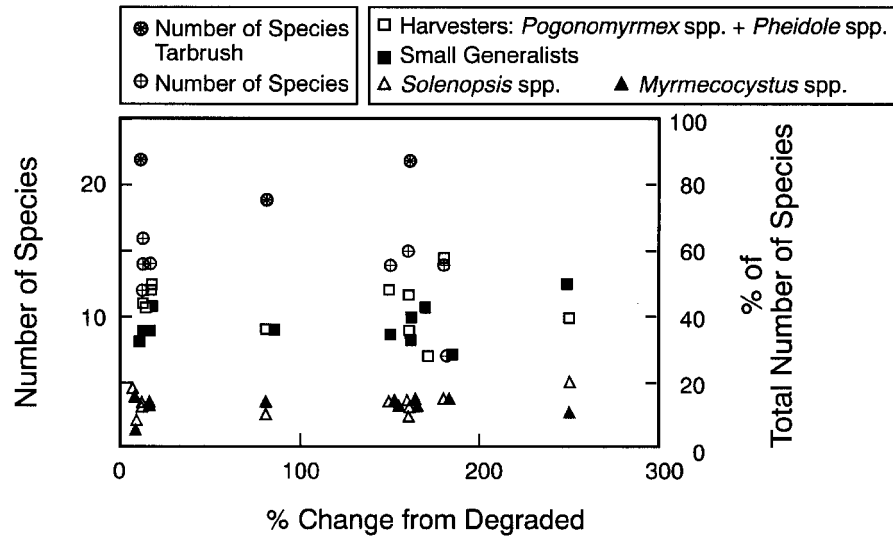
a

Tolerant

b
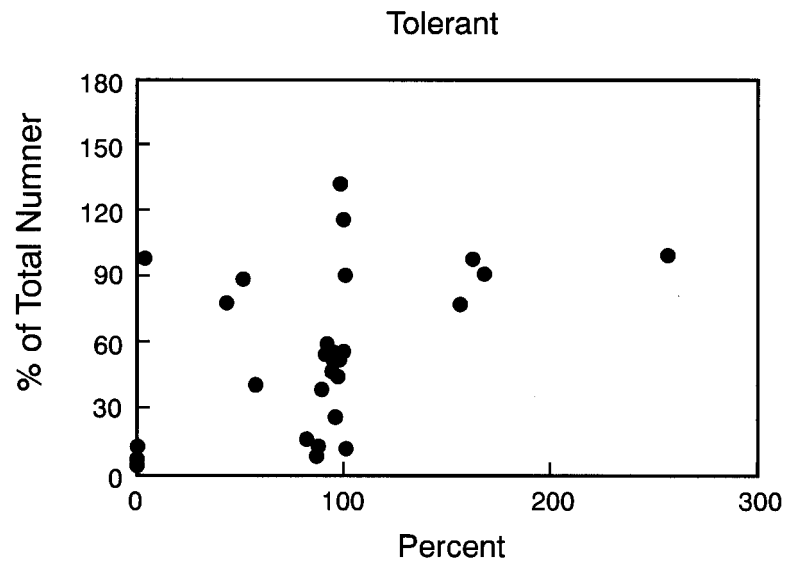
Intolerant

Figure 7. Relative abundances of ant species hypothesized to be tolerant to disturbance (a) and intolerant to disturbance (b) on rangeland sites with varying histories of disturbance. Method of presentation same as Figure 5.

a

b
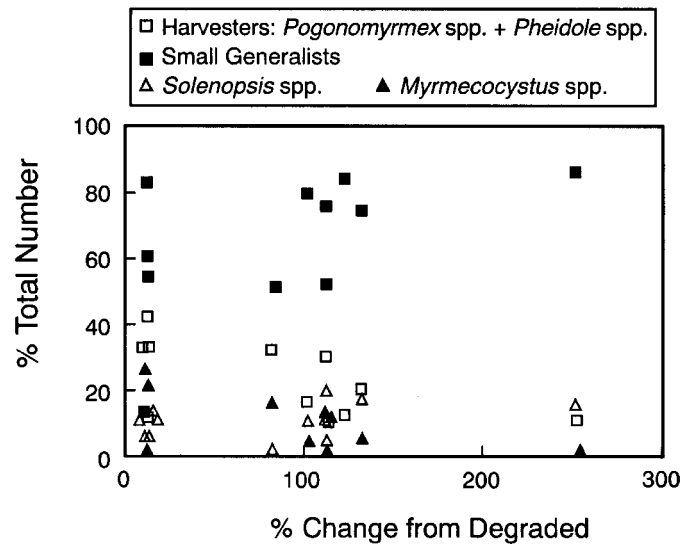
Figure 8. Species richness and percent composition of selected species on sites subjected to restoration efforts. Abscissa is percent change from degraded which was calculated as the departure of the sum of grass cover, shrub cover, and bare patch intercept from the sum of those values for the untreated control sites. Species richness (left ordinate) and percent of total number of species (right ordinate) of seed harvesters, small generalists, species of *Solenopsis* and *Myrmecocystus* (a). Relative abundances of seed harvesters, small generalists, species of *Solenopsis* and *Myrmecocystus* (b) on sites subjected to restoration efforts. Relative abundances are the percent of traps in which a species was captured.

Buckley, d = 62%, which accounted for less than 0.2% of the ants in the cottonwood gallery forest. In the San Pedro cottonwood gallery forest, the dominant species was *Tapinoma sessile* Say (d = 65%) and in the Rio Grande cottonwood gallery forest the dominant species was *Pheidole hyatti* Emery (d = 34%). In the Rio Grande cottonwood forest *T. sessile* was the second most abundant species accounting for 14% of the ant population. Ant species composition was similar in the San Pedro cottonwoods and tamarisk woodlands (Sorenson's Index = 0.64). Ant species composition was fairly similar in the Rio Grande and San Pedro cottonwood gallery forests, Sorenson's Index = 0.5. The ants in riparian woodlands dominated by an exotic tree (tamarisk) had higher ant species diversity and more similar species composition to the cottonwood gallery forest than to the native ash dominated riparian woodland on the Rio Grande.

4.4. DOMINANCE

The Berger-Parker dominance index (d) is the proportion of the most abundant species in a community (Roth et al., 1994). We calculated dominance on the proportion of traps in which a species was taken. The dominance index varied between 16.1% in a tarbush-creosotebush community in which the dominant species was *Myrmecocystus depilis* Forel to 48% in a tarbush community in which the dominant ant species was *Forelius pruinosus*. We also examined the sum of the proportion of the three most abundant species in each ant community. This value of dominance ranged between 34.1% in a grazing axclosure to 78.0% in a tarbush area. The three most abundant species accounted for more than 50% of the total abundance except at two sites. The dominant species was different in each of the grazing exclosures (*F. pruinosus, Aphaenogaster cockerelli* Andre *and C. insana*). The dominant species was also different in the mesquite coppice dune sites (*F. pruinosus, D. insana*, and *Formica perpilosa* Wheeler), and in the areas of greatest and least disturbance on the grazing intensity gradients (*S. xyloni* and *Pogonomyrmex desertorum* Wheeler – maximum disturbance) (*C. insana, S. xyloni*, and *A. cockerelli* – minimum disturbance). There were no interpretable patterns in the dominance index in any of the comparisons.

4.5. EXOTIC SPECIES – LEHMANN'S LOVEGRASS SITES

The comparisons of ant communities in rangelands dominated by the South African grass, *Eragrostis lehmanniana* (Lehmann's lovegrass), and native grasslands produced some results that suggest that ants may be a useful indicator in rangelands invaded by exotic species. Species richness was equal (S = 20) in the Santa Rita comparison. At the Empire Cienega Ranch, ant species richness was higher (S = 16) in the Lehmann's lovegrass grassland than in the native grassland (S = 12). However, species diversity was nearly equal in each of the ranches and grasslands (SRN – $H^{'}$ = 1.16, SRL – $H^{'}$ = 1.06, ECN – $H^{'}$ = 0.82, ECL – $H^{'}$ = 0.87). The

Table III

Sorensen's Similarity Indices comparing ant communities at pairs of sites. Index is a percent similarity. Site codes are the same as in Table I

BMC – BMD	64.3	BMC – MHJ	60.9	SRL – SRG	76.9
CWO – CW3	73.3	MWO – MW3	87.5	WWO – WW3	87.5
EEC – EXE	89.7	EWC – EXW	80.0	ENc – EXN	81.5
LTG – MTX	48.3	LTG – LTM	71.0	TCH – TCC	85.7
GRP – GRE	66.7	GRP – GR2	78.8	GRP – GR1	69.0
TCE – TCH	82.9	LTG – CE3	62.5	LTG – MW3	64.5
LTG – WW3	62.5	LTG – EXE	60.0	LTG – EXN	57.1
LTG – EXW	60.0	LTG – LTP	74.3	LTG – LTC	58.1
LTG – LTT	43.8	LTG – LT2	58.5	–	–

ant communities in areas dominated by Lehmann's lovegrass had fewer large seed-harvesting *Pogonomyrmex* spp.: SRL = 4%, SRN = 13%, ECL = 0.5%, ECN = 6% of the total population. At Santa Rita, *A. cockerelli* accounted for 11% of the ant population in the native grassland had only 1% in the Lehmann's lovegrass. *Aphaenogaster cockerelli* did not occur at the Empire Cienega grasslands. In these comparisons there were no differences in the species richness or relative abundance (% of total population) of small seed harvesters (*Pheidole* spp.), small generalists, tolerant genera or intolerant genera except as noted above.

4.6. GENERAL HABITAT RELATIONSHIPS

Chihuahuan Desert habitats are dominated by small dolichoderine ants, *Forelius* spp. and *Conomyrma* spp. (Table IV). Other species that occurred in all of the Chihuahuan Desert rangeland habitats included: *Myrmecocystus depilis, M. mexicanus* Wesmel, *Pogonomyrmex californicus* Buckley, *P. desertorum, Solenopsis krockowi* Wheeler, and *S. xyloni*. There were marked reductions in the relative abundances of *A. cockerelli, Acromyrmex versicolor* (Pergande), *Pogonomyrmex rugosus* Emery and *P. californicus* in the Lehmann's lovegrass sites compared to the native grasslands in southeastern Arizona. However, species richness was higher in Lehmann's lovegrass sites than in the native grasslands (Table IV). Ant species richness was lower in creosotebush shrublands and mesquite coppice dune shrublands than in the black-grama grasslands, tarbush shrublands and shrub-grass mosaic habitats (Table IV).

4.7. SORENSEN'S SIMILARITY COEFFICIENTS

In most of the paired comparisons, species compositions were similar at > 50% (Table III). The similarities in species composition were between 73% and 87.5% in comparisons of the plots at the water points and plots at more than 1 km from the water points. Similarities in species composition were even higher in the

Table IV

The mean relative abundance of ant species of ants in Chihuahuan Desert habitats. S and a number following a generic name denotes species that were unidentified because only minor workers were present. The mean relative abundance was calculated as the percentage of the total traps at a site containing a species averaged for all of the sites within habitat

Species	Arizona		Riparian wood- land	Black grama grass	Creosite- bush shrubland	Mesquite copice dune	Shrub- grass mosaic	Tarbush shrub- land
	Lehman's love	Native grass grass						
Acromyrmex versicolor	1.0	7.5	–	–	–	–	–	–
Aphaenogaster cockerelli	1.0	17.0	–	26.5	3.8	–	17.6	–
Camponotus noveboracensis	–	–	3.8	–	–	–	–	–
Camponotus SO1	0.5	–	–	–	–	–	–	–
Conomyrma bicolor	–	–	–	0.3	–	24.8	1.5	–
Conomyrma insana	37.0	40.5	3.3	26.7	20.5	54.6	69.2	47.1
Crematogaster dentinodis	0.5	14.5	–	–	–	–	–	–
Crematogaster depilis	–	–	–	–	1.8	–	6.3	1.5
Crematogaster hespera	–	–	2.8	–	–	–	–	–
Crematogaster opuntiae	3.0	10.0	–	–	–	–	–	–
Crematogaster punctulata	0.5	–	–	–	–	–	12.0	–
Forelius foetidus	–	–	–	3.1	6.6	0.2	0.5	46.8
Forelius gnava	7.5	–	16.8	–	–	–	–	–
Forelius perpilosa	–	–	5.9	–	–	10.8	–	–
Forelius pruinosus	47.5	47.5	0.3	19.1	75.6	52.6	84.7	41.7
Leptothorax pergandei	–	–	–	–	–	–	–	3.0
Monomorium cyaneum	2.5	11.0	5.0	–	–	–	–	–
Monomorium minimum	–	–	7.3	0.8	0.6	1.1	–	7.0
Myrmecocystus depilis	–	–	–	13.2	15.0	20.8	81.6	58.4
Myrmecosystus mexicanus	–	–	–	2.5	1.8	2.5	5.6	7.4
Myrmecocystus mimicus	34.0	5.5	–	13.4	–	0.4	0.5	17.3
Myrmecocystus placodops	0.5	–	–	1.4	–	–	–	–
Myrmecocystus romainei	–	–	–	0.1	–	1.0	1.0	–
Neivamyrmex nigrescens	1.5	–	–	–	–	–	–	0.3
Neivamyrmex SO1	–	–	–	–	–	–	0.5	–
Odontomachus clavatus	1.5	–	–	–	–	–	–	–
Paratrechina hystrix	1.0	–	–	–	–	–	4.7	–
Paratrechina terricola		–	–	–	–	–	–	0.8
Pheidole crassicornis	4.5	7.5	–	5.3	2.2	–	6.7	11.9
Pheidole militicida	–	–	–	7.7	–	1.5	3.1	–
Pheidole nevadensis	–	–	–	0.1	–	–	–	–
Pheidole rugulosa	–	–	–	2.3	1.0	–	–	3.5
Pheidole SO1	–	–	0.9	–	1.8	–	–	–
Pheidole SO2	13.0	15.5	17.4	4.8	6.6	3.9	–	34.3
Pheidole SO4	–	–	–	1.5	1.4	1.7	–	0.5
Pheidole SO6	2.0	5.5	–	–	0.6	–	–	–
Pheidole SO8	–	–	–	–	–	1.3	0.5	–
Pheidole SO9	–	–	–	0.1	2.7	–	0.5	–

Table IV
Continued.

Species	Arizona		Riparian wood-land	Black grama grass	Creosite-bush shrubland	Mesquite copice dune	Shrub-grass mosaic	Tarbush shrub-land
	Lehman's love	Native grass grass						
Pheidole S11	–	–	0.3	–	–	–	–	–
Pheidole S12	0.5	0.5	3.8	–	–	–	–	–
Pheidole S13	–	–	0.3	–	–	–	–	–
Pheidole S14	1.0	4.0	0.4	–	–	–	–	–
Pheidole S18	–	–	–	–	–	–	1.6	0.3
Pheidole S19	–	–	–	–	0.8	3.4	0.5	–
Pheidole S21	–	–	4.0	–	–	–	–	–
Pheidole S23	–	–	–	–	0.4	–	–	–
Pheidole sciophila	1.0	2.0	–	1.9	–	1.4	14.1	7.5
Pheidole sitarches-soritis	–	–	–	0.1	1.4	0.9	1.5	–
Pheidole spp	–	–	–	0.1	–	1.0	–	0.8
Pheidole tucsonica	–	–	–	–	–	–	–	9.8
Pheidole xerophila	–	–	0.3	5.0	11.0	1.4	–	2.6
Pogonomyrmex apache	2.0	–	–	–	1.0	–	11.5	–
Pogonomyrmex barbatus	–	–	–	–	–	0.2	–	–
Pogonomyrmex californicus	1.5	7.5	–	1.6	0.6	5.7	17.8	19.8
Pogonomyrmex desertorum	0.5	0.5	–	36.3	0.4	7.8	39.6	8.5
Pogonomyrmex imberbiculus	–	–	–	0.1	6.2	–	7.8	2.8
Pogonomyrmex maricopa	–	–	–	–	–	2.3	0.5	0.3
Pogonomyrmex rugosus	–	17.0	–	1.9	–	–	0.5	0.3
Pseudomyrmex pallidus	–	–	0.4	–	–	–	–	–
Solenopsis aurea	3.5	13.5	0.3	4.3	–	2.5	13.6	1.8
Solenopsis krockowi	–	–	3.5	6.8	1.2	2.7	8.8	1.3
Solenopsis molesta	1.5	3.5	2.9	–	–	–	–	–
Solenopsis xyloni	4.5	3.0	–	26.8	15.5	27.5	4.7	10.5
Tapinoma sessile	–	–	19.6	–	–	–	–	–
Tetramorium spinosum	12.5	9.5	–	–	3.4	–	1.6	5.8
Trachymyrmex smithii-neomexicanus	–	–	–	0.3	–	2.3	–	–

grazed–exclosure paired comparisons (Table IV). The lowest similarities in species composition were in the desertification sequence comparisons of the blackgrama grassland (LTG) site with mesquite coppice dunes (MTX) and tarbush shrubland (LTT). There was a 76.9% similarity in ant species in the comparison of the Santa Rita native grassland (SRG) and the Lehmann's lovegrass site at the Santa Rita (SRL). Species compositions were very similar in the undisturbed and soil disturbed site (bulldozed and root-plowed). Differences in species composition were primarily due to presence or absence of rare species in all of the site comparisons.

4.8. INDICATOR SPECIES

Although there were no consistent patterns in ant comunities exposed to chronic or acute disturbance, there appeared to be consistent differences in two species of ants (*Aphaenogaster (Novomessor) cockerelli and Myrmecocystus depilis/mimicus*) in the exclosure-grazed comparisons and in the grazing intensity comparisons. The abundances of these species were compared by two tailed t-tests to examine the hypothesis that the relative abundance in the grazed compared to the exclosure was zero. The relative abundances of these species were not sgnificantly different in the grazed plots and exclosures at $p < 0.05$. The relative abundances of these species were significantly different only at $p < 0.20$. We also examined the relationship between perennial grass cover and relative abundance aof *A. cockerelli*. The regression showed that grass cover accounted for only 50% of the variance in abundance of *A. cockerelli*.

5. Discussion

The results of this study show that ants of southwestern rangelands are resistant to ecosystem stress resulting from the concentrated activity of livestock at water points and to long-term changes in vegetation and soil stability. This result leads to the question: what are the characteristics of desert rangeland and species that make them resistant to chronic stress and to changes in vegetation and soil properties? The ant fauna of desert rangelands has evolved with recurrent climatic stress (drought) and the resultant decreases in food availability. Vegetation, soil erodibility and climate have changed considerably over the past 12 000 years (Van Devender, 1995). Many species of southwestern rangeland ants store food in their nests (*Pogonomyrmex* spp., *Pheidole* spp., *Myrmecosystus* spp., *Aphaenogaster* spp.) which buffers these species against food shortage during droughts. Although seed harvesting ants prefer certain seeds, these are primarily seeds of annual plants, not perennials (Whitford, 1978). Despite the large differences in vegetational cover and soil stability in the grasslands and desertified, shrub-dominated ecosystems, there are no large differences in densities and species composition of annual plants on degraded sites and sites protected from disturbance (unpublished data). Thus food availability for harvester ants is not compromised by loss of grasses and increases in shrubs. In addition, nest construction appears not to be adversely affected by soil compaction resulting from concentrated activity of domestic livestock.

In tropical Costa Rica, and diversity was higher in abandoned cacao and banana plantations than in actively managed plantations (Roth et al., 1994). In their study there was a good correlation between several measures of ant species diversity and intensity of disturbance. In a related study, Perfecto and Snelling (1995) reported that several ant diversity measures decreased with reduction in vegetational diversity in coffee plantations. In southwestern rangelands, vegetational structural

diversity is greatest in the shrub-grass mosaic habitats and lowest in the coppice dune habitats. The shrub-grass mosaic habitats are those that fit the intermediate disturbed site category and two of those sites had the highest species richness of the 44 sites sampled, including the riparian sites. However, not all of the grass–shrub mosaic habitats had high species diversity measures and some were lower than the maximally disturbed and minimally disturbed sites.

Our study demonstrates that unlike stream invertebrates (Fore and Karr, 1996), ants are not good indicators of ecosystem condition for southwestern desert rangelands nor are they good indicators of the relative success of restoration activities. One advantage of faunal indicators of biotic integrity is that the indices provide data on faunal biodiversity. We predicted that ants would serve as good indicators of faunal biodiversity changes resulting from exposure to stress (grazing by domestic livestock) and disturbance (soil erosion). However, since the data demonstrate that ants are not good indicators of biodiversity in southwestern rangelands, we will have to examine other groups of animals for potential indicators.

Indicators of exposure to environmental stress and indicators of ecosystem health must be consistent in direction and magnitude for all types of sites in a region and for a particular stressor. In hot desert rangelands, ant communities do not meet those criteria. There were no consistent patterns in ant communities exposed to grazing stress, soil disturbance, herbicide application or dominance by exotic plant species. Majer and Beeston (1996) found that their index of biological integrity based on ant species richness failed in the rangelands because ant species richness was maintained at high levels in grazed rangeland.

General textural characteristics of soils appeared to be more important in structuring the ant communities in the rangeland ecosystems that we studied than were vegetative cover and composition or disturbance intensity. Soil texture has been shown to influence the distribution of desert seed-harvester ants (Johnson, 1992). Although soil texture affects variables such as water-holding capacity and thermal characteristics of a soil as well as the structural integrity of nests constructed in that soil, it is surprising that soil texture was more important than vegetative cover and composition in structuring the ant community. In our studies, the grazing intensity gradients, exclosure comparisons and the mesquite coppice dune sites were all on the same sandy-loam textured soils of the same soil series. Despite the vegetational cover and composition differences, there were no significant differences in the species composition and abundances of the ants on our study sites. The principal components analysis also clustered sites that were on the same soil without regard to disturbance. The findings of Catangui et al. (1996) support our conclusion that soil properties appear to be more important than vegetational cover or disturbance history as determinants of the distribution of rangeland ant species.

Despite the very large differences in vegetative cover and composition, most ant species were obviously able to obtain sufficient food to maintain colonies even on those sites that were nearly devoid of perennial vegetation. Thus the results of our study do not support the conclusions of studies that found a close relationship

between vegetation and density, diversity, and species richness of ant communities (Bhatt and Soni, 1992; Burbidge et al. 1992; Roth et al., 1994). These studies report on vegetation and ant communities but not on soil textural characteristics which limits their value for comparison with our study. Catangui et al. (1996) also reported that the spatial distribution of ant species was related to combinations of soil properties. The principal factors were soil texture and soil drainage.

None of the indices calculated for the ant communities were consistent in comparisons of disturbed and relatively undisturbed sites or on disturbance gradients. In the southwestern United States, grazing by domestic livestock is the most widespread and consistent environmental stressor. However, the comparisons of ant communities at sites that had not been grazed in more than 40 years with adjacent areas that had been grazed at the same intensity and season of grazing for more than 40 years were more similar than other grazed-exclosure community comparisons. Also, there were no consistent patterns in the ant communities at varying distances from water points along gradients of grazing disturbance from bare-trampled areas near water to relatively high cover perennial grassland. The resistance of rangeland ant species to acute stress was reported by Catangui et al. (1996). They found that the abundances of ant species in mixed-grass rangelands was not significantly reduced by aerial applications of several types of chitin synthesis inhibitor insecticides.

These results suggest that soil and vegetation differences are more important than either chronic or acute disturbance in the structuring of the ant community. Microclimate and vegetation have been shown to affect the species composition and relative abundance of the ant community in evergreen woodland in southeastern Arizona (Chew and Chew, 1980). Our data suggest that soil textural characteristics are more important than exposure to chronic or acute exposure to ecosystem stressors and the resulting changes in vegetative cover and composition.

The desertification sequence and the piosphere comparisons showed that species richness, index of relative frequency and species diversity indices were highest at sites with an intermediate level of exposure to grazing. The shrub-grass mosaic site (LTT) had patchy soil distribution, i.e. discontinuous patches of sandy loam and silty loam. The vegetation on that site was patchily distributed also with clumps of grass and clumps of shrubs within bare patches or patches of a rhizomatous grass. The other shrub-dominated sites had a relatively uniform distribution of shrubs. The heterogeneity of this site appears to be the most important factor affecting the species abundance and diversity indices.

The presence of and/or abundance of *A. cockerelli* was thought to be a good indicator of exposure to intense grazing and of the history of degradation of grassland to shrubland. In a long-term study of ants on a site that was degraded to shrubland when his study was initiated, Chew (1995) reported that *A. cockerelli* had become locally extinct outside of a grazing exclosure that was constructed in the 1950s but had exhibited no significant change in colony densities within the exclosure. Chew's data suggest that the exposure to grazing was the primary

factor causing the local extinction outside the exclosure. However, the variability in presence of *A. cockerelli* in grassland habitats and its presence in some degraded shrubland ecosystems (Whitford, 1978) severly limits its usefulness as an indicator species. Chew (1995) also reported an 11-fold increase in densities of *M. mexicanus* within his exclosure but no change in abundances of other *Myrmecosystus* spp. At the Jornada sites, *M. depilis/mimicus* increased in abundance on the sites most disturbed by livestock. Chew (1995) attributed the increase in *M. mexicanus* to a decrease in canopy cover at his site. A decrease in canopy cover is related to the increase in *Myrmecocystus* in our study and may be the factor affecting that increase. *Myrmecocystus* abundance may be a useful indicator of the health of a desert rangeland ecosystem, but some history of the vegetation must be considered before making an assessment based on the abundance of these ants.

This study demonstrated that exposure to both chronic disturbance such as continuous or seasonal grazing and to acute disturbance such as root plowing, bulldozing and herbicide application had little effect on the ant communities. Because the acute disturbances occurred twenty or more years prior to our study, the ensuing time allowed the ant communities to completely recover. However, the differences in vegetative cover and composition on the disturbed sites compared with the untreated controls remained very large. In a study comparing a grassland ant community with the ant community in mesquite, *Prosopis glandulosa*, coppice dunes, Wisdom and Whitford (1981) found that the only species that was really different was *Trachymyrmex smithii* Buren, which occurred only at the edges of the mesquite canopy on the coppice dunes. That species collects mesquite leaves as a substrate for culturing fungi that are its food source and apperars to be limited to areas where there are leguminous shrubs.

The data on ant communities in riparian woodlands produced equivocal results. Species diversity and composition is obviously affected by the structure or dominant tree species in the riparian woodland. The low diversity and abundance of ants in the Rio Grande ash grove may have been the result of the dense canopy and virtual absence of sunlit patches on the soil surface. All of the other riparian woodlands had canopies that created patches of shade at the soil surface. The dominance of *F. gnava* in the tamarisk woodland suggests that this species may be a good indicator of degradation of southwestern riparian ecosystems. However, because of the variability in the ant communities in the four riparian areas that we sampled, it will be necessary to examine a larger number of riparian woodlands with different levels of disturbance or degradation before a decision can be made on the adequacy of ants as indicators of the status of riparian woodlands.

The best indicator of the impact of invasion of grassland sites by the exotic Lehmann's lovegrass is the marked reduction in the abundance of *Pogonomyrmex* spp. harvester ants. Lehmann's lovegrass-dominated grasslands produce few spring annual plants (unpublished data, M. McClaran, pers. comm.) and the seeds of this grass are vary small. The reduction in abundance of *Pogonomyrmex* spp. is probably the result of the lack of suitable seeds (Inouye et al., 1980). Small seed harvesting

ants, *Pheidole* spp., exhibited no differences in abundance in native grasslands and lovegrass grasslands.

This study demonstrates that ants are not good indicators of exposure to chronic stress, or of disturbance. However, these data apply only to the desert grassland rangelands of the southwestern United States and northern Maxico. In this region ants are also not useful as indicators of changes in biodiversity resulting from anthropogenic changes in ecosystem structure and function. We conclude that most desert ant species are remarkably resistant to disturbance and environmental stress.

Acknowledgements

References

Andersen, A. N.: 1990, 'The Use of Ant Communities to Evaluate Change in Australian Terrestrial Ecosystems: A Review and a Recipe', *Proceedings of the Ecological Society of Australia* **16**, 347–357.

Banks, C. J.: 1962, 'Effects of the Ant *Lasius niger* (L.) on Insects That Prey on Small Populations of *Aphis fabae* Scop. on Bean Plants', *Annuals of Applied Biology* **50**, 660–679.

Bhatt, V. and P. Soni: 1992, 'Revegetation and Ant Colonization Relationships in Reclaimed Rock Phosphate Mines', *Tropical Ecology* **33**, 223–230.

Beattie, A. J., Culver, D. C. and Pudlo, R. J.: 1979, 'Interactions Between Ants and the Diaspores of Some Common Spring Flowering Herbs in West Virginia', *Castanea* **44**, 177–186.

Bradley, G. A.: 1973, 'Effect of *Formica obscuripes* (Hymenoptera:Formicidae) on the Predator–Prey Relationship Between *Hyperaspis congressis* (Coleoptera:Coccinellidae) and *Toymeyella nuimismaticum* (Homoptera:Coccidae)', *Canadian Entomologist* **105**, 1113–1118.

Buffington, L. C. and Herbel, C. H.: 1965, 'Vegetational Changes on a Semidesert Grassland Range From 1858 to 1963', *Ecological Monographs* **35**, 139–164.

Burbidge, A. H., Leicester, K., McDavitt, S. and Majer, J. D.: 1992, 'Ants as Indicators of Disturbance of Yanchep National Park, Western Australia', *Journal of the Royal Society, West Australia* **75**, 89–95.

Canfield, R. H.: 1941, 'Application of the Line Interception Method in Sampling Range Vegetation', *Journal of Forestry* **39**, 388–394.

Catangui, M. A., Fuller, B. W., Walz, A. W., Boetel, M. A. and Brinkman, M. A.: 1996, 'Abundance, Diversity, and Spatial Distribution of Ants (Hymenoptera:Formicidae) on Mixed-grass Rangelands Treated with Diflubenzuron', *Environmental Entomology* **25**, 757–766.

Chew, A. E. and Chew, R. M.: 1980, 'Body Size as a Determinant of Small-scale Distributions of Ants in Evergreen Woodland Southeastern Arizona', *Insectes Sociaux, Paris* **27**, 189–202.

Chew, R. M.: 1995, 'Aspects of the Ecology of Three Species of Ants (*Myrmecocystus* spp., *Aphaenogaster* spp.) in Desertified Grassland in Southeastern Arizona, 1958–1993', *The American Midland Naturalist* **134**, 75–83.

Fore, L. S. and Karr, J. R.: 1996, 'Assessing Invertebrate Responses to Human Activities:Evaluating Alternative Approaches', *Journal of the North American Benthological Society* **15**, 212–231.

Gibbens, R. P., Tromble, J. M., Hennessy, J. T. and Cardenas, M.: 1983, 'Soil Movement in Mesquite Dunelands and Former Grasslands of Southern New Mexico from 1933–1980', *Journal of Range Management* **36**, 145–148.

Gibbens, R. P. and Beck, R. F.: 1988, 'Changes in Grass Basal Area and Forb Densities Over a 64-year Period on Grassland Types of the Jornada Experimental Range', *Journal of Range Management* **41**, 186–192.

Greenslade, P. J. M. and Greenslade, P.: 1971, 'The Use of Baits and Preservatives in Pitfall Traps', *Journal of the Australian Entomological Society* **10**, 253–260.

Holldobler, B. and Wilson, E. O.: 1990, *The Ants.* Harvard University Press, Cambridge, MA.

Inouye, R. S., Byers, G. S. and Brown, J. H.:1980, 'Effects of Presation and Competition on Survivorship, Fecundity, and Community Structure of Desert Annuals', *Ecology* **61**, 1344–1351.

Johnson, R. A.: 1992, 'Soil Texture as an Influence on the Distribution of the Desert Seed-Harvester Ants', *Pogonomyrmex rugosus* and *Messor pergandei, Oecologia* **89**, 118–124.

Karr, J. R.: 1981, 'Assessment of Biotic Integrity Using Fish Communities', *Fisheries* **6**, 21–27.

Krebs, C. J.: 1989, *Ecological Methodology*. Harper and Row, N.Y.

Levin, D. A. and Anderson, W. W.: 1970, 'Competition for Pollinators Between Simultaneously Flowering Species', *The American Naturalist* **104**, 455–467.

Lobry de Bruyn, L. A. and Conacher, A. J.: 1990, 'The Role of Termites and Ants in Soil Modification: A Review', *Australian Journal of Soil Research* **28**, 55–93.

Ludwig, J. A. and Reynolds, J. F.: 1988, *Statistical Ecology*. John Wiley & Sons. New York, N.Y.

Majer, J. D.: 1981, 'Ants: Bio-Indicators of Minesite Rehabilitation, Land Use, and Land Conservation', *Environmental Management* **7**, 375–383.

Majer, J. D. and Beeston, G.: 1996, 'The Biodiversity Integrity Index: An Illustration Using Ants in Western Australia', *Conservation Biology* **10**, 65–73.

Nuhn, T. P. and Wright, C. G.: 1979, 'An Ecological Survey of Ants (Hymenoptera:Formicidae) in a Landscaped Surburban Habitat', *The American Midland Naturalist* **102**, 353–362.

Perfecto, I and Snelling, R.: 995, 'Biodiversity and the Transformation of a Tropical Agroecosystem: Ants in Coffee Plantations', *Ecological Applications* **5**, 1084–1097.

Post, D. C. and Jeanne, R. L.: 1982, 'Rate of Exploitation of Aboreal Ants in the Old-Field Habitat in Wisconsin', *The American Midland Naturalist* **108**, 88–95.

Rapport, D. J., Regier, H. A. and Hutchinson, T. C.: 1985, 'Ecosystem Behavior Under Stress', *The American Naturalist* **125**, 617–640.

Ray, A. A. (ed.): 1982, *SAS User's Guide:Statistics*. SAS Institute Inc., Carey, N.C.

Risch, S. J. and Carroll, C. R.: 1986, 'The Ecological Role of Ants in two Mexican Agroecosystems', *Oecologia* **55**, 114–119.

Rissing, S. W.: 1986, 'Indirect Effects of Granivory by Harvester Ants: Plant Species Composition and Reproductive Increase Near Ant Nests', *Oecologia* **68**, 231–234.

Roth, D. S., Perfecto, I. and Rathcke, B.: 1994, 'The Effects of Management System on Ground-foraging Ant Diversity in CostaRica', *Ecological Applications* **4**, 423–426.

Talbot, M.: 1953, 'Ants of an Old Field Community on the Edwin S. George Reserve, Livingstone County, Michigan', *Contributions of the Laboratory of Vertebrate Biology, University of Michigan* **63**, 1–13.

Torres, J. A.: 1954, 'Diversity and Distribution of Ant Communities in Puerto Rica', *Biotropica* **16**, 296–303.

USDA Soil Concervation Service: 1980, *Soil of Dona Ana County Area, New Mexico*.

Van Devender, T. R.: 1995, 'Desert Grassland History: Changing Climates, Evolution, (Biogeography, and Community Dynamics, In McClaran, M. P. and T. R. Van Devender (eds.). *The Desert Grassland*. University of Arizona Press, Tucson, pp. 68–99.

Van Pelt, A. F.: 1963, 'High Altitude Ants of the Southern Blue Ridge', *The American Midland Naturalist* **69**, 205–223.

Way, M. J.: 1963, Mutualism Between Ants and Honeydew Producing Homoptera', *Annual Review of Entomology* **8**, 307–344.

Whitcomb, W. H., Denmerk, H. A., Bhatkar, A. P. and Greene, G. L.: 1972, 'Preliminary Studies on Ants of Florida Soybean Fields', *Florida Entomologist,* **55**, 129–142.

Whitford, W. G.: 1978, 'Structure and Seasonal Activity of Chihuahuan Desert Ant Communities', *Insectes Sociaux, Paris* **25**, 79–88.

Whitford, W. G. and Ettershank, G.: 1975, 'Factors Affecting Foraging Activity in Chihuahuan Desert Harvester Ants', *Environmental Entomology* **4**, 689–696.

Whitford, W. G., De Pree, E. and Johnson, P.: 1980, 'Foraging Ecology of Two Chiluahuan Desert Ant Species: *Novomessor and Novomessor albisetosus', Insectes Sociaux, Paris* **27**, 148–156.

Whitford, W. G., DePree, D. J., Hamilton, P. and Ettershank, G.: 1981, 'Foraging Ecology of Seed-Harvesting Ants, *Pheidole* spp. in a Chihuahuan Desert Ecosystem', *The American Midland Naturalist* **105**, 159–167.

Wilson, E. O.: 1971, *The Insect Societies*. Harvard University Press, Cambridge, MA.

Wisdom, W. A. and Whitford, W. G.: 1981, 'Effects of Vegetation Change on Ant Communities of Arid Rangelands', *Environmental Entomology* **10**, 893–897.