



Diversity and guild structure of insect assemblages under grazing and exclusion regimes in a montane grassland from Central Argentina

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Abstract. The effects of grazing disturbance on insect communities were examined at a montane grassland in Central Argentina, by comparing two grazed sites differing in cattle load (heavy and continuous or moderate and discontinuous) and two cattle exclusions differing in age (7 and 19 years). Two aspects of insect diversity (taxonomic and guild structure) and two levels of taxonomic resolution (family and species) were considered. Four monthly samples were taken with a suction sampler in two 1 m² areas at each site. Collected specimens were counted, identified to family (all insects) or species (Coleoptera) level, and allocated to trophic guilds. Abundance, richness, diversity and biomass of the insect assemblages had minimum values in the most intensely grazed habitat, which also differed from the other sites in terms of insect families and Coleoptera species composition. It also showed a distinct guild structure, with fewer secondary consumers, and chewers replacing suckers as the most abundant herbivore group. According to these observations, intense grazing in montane grasslands in Central Argentina could result in taxonomic and guild changes in the associated insect communities, but such effects would not be noticeable with less intensive use. Moreover, using family taxonomic level could be as or even more appropriate than species level in order to characterize insect communities in the studied habitats under varying disturbance regimes.

Key words: Argentina, cattle grazing, diversity, guild structure, insects

Introduction

Cattle introduction is a frequent practice in habitats unsuitable for agriculture (Collins and Glenn 1990). The disturbance imposed by grazing can affect plant diversity (Milchunas and Lauenroth 1993; Fleischner 1994), vegetation structure (Díaz et al. 1992; Fleischner 1994; Pucheta et al. 1998) and even ecosystem processes (Fleischner 1994; Chapin III et al. 1996). Grazing-induced changes in the plant community can in turn affect diversity and composition of the associated invertebrate communities (Morris 1978; Gibson et al. 1992).

Insect diversity and/or abundance have been reported to decrease (Welch et al. 1991; Fahrig and Jonsen 1998) or increase (Collins and Glenn 1990; Wettstein and

Schmid 1999) following grazing or cutting disturbance. The insect habits and the environmental features being altered could condition the response to disturbance (Gibson et al. 1992; Dennis et al. 1998). Thus, while phytophagous Coleoptera might be affected by changes in floristic composition, but not by changes in structural vegetation parameters (Brown and Hyman 1986; Gibson et al. 1992), other groups such as spiders (Dennis et al. 1998), Homoptera (Morris 1981; Brown 1991; Dennis et al. 1998) Hemiptera (Morris 1979; Brown 1991; Gibson et al. 1992) and Orthoptera (Wettstein and Schmid 1999) seem to respond mainly to pasture structural characteristics.

In the mountain grasslands of Central Argentina, a long history (over 300 years) of cattle grazing has altered plant communities by increasing their diversity, while reducing both their structural complexity and the frequency of tall grasses (Pucheta et al. 1998). The accepted position of these grasslands as a district of the Chaco Phytogeographic Province has been recently challenged (Cabido et al. 1998), due to their richness in Andean species and highly restricted endemisms. Despite the biogeographic value of the area, the effects of grazing on the scarcely studied fauna associated with these pastures has not yet been evaluated.

The present paper aims to examine the effects of cattle grazing disturbance on the taxonomic and guild diversity of the associated insect communities in one of these grasslands. A comparison of results from two levels of taxonomic identification (species vs. families) is also provided. The use of higher taxonomic hierarchies such as Family could be advantageous in biodiversity assessments (Williams and Gaston 1994), although the trade-off between economy and accuracy implicit in this approach has been much debated (Gaston 2000).

Study area

The study was done at the granitic high plane of Pampa de Achala (31°30' S, 64°45' W), at an altitude of about 2100 m in the mountains (Sierras Grandes) of Córdoba province, Argentina. The climate in the area is cold-temperate, with average temperatures of 5 °C in winter and 11.4 °C in summer, and frosts being frequent. Rainfall is concentrated between November and March, reaching an annual mean of 850 mm, with some snowfall in winter and spring (Capitanelli 1979).

The vegetation in the region consists of a mosaic of patches dominated by tall tussock grasses alternating with lawn patches (Cabido et al. 1999). These pastures are currently grazed (traditional extensive farming) by cattle and horses, which represent the most important vertebrate herbivores in the region (Díaz et al. 1992).

Methods

Sampling design

Samples were taken in four sites representing different degrees of intensity and frequency of grazing disturbance. Two of them were selected within the general grassland matrix: at one side of a stone wall, a heavily grazed site (HG) continually exposed to cattle for at least 30 years at a moderate-to-high stocking rate 0.25 horse and 0.5 cows/ha; and at the opposite side a site of low grazing (LG), with discontinuous exposure and lower stocking rate (about a quarter of the values in HG). Two smaller areas (ca. 25 × 25 m) from which cattle had been excluded for 7 years (young enclosure, YE) and 19 years (old enclosure, OE) respectively, were also sampled. Therefore two disturbance gradients were involved: one of decreasing grazing intensity (from HG through LG to both enclosures), and one of decreasing frequency (HG–LG–YE–OE).

The enclosures, with records of their original state and known history of disturbance, are unique in the montane grasslands of Central Argentina. Sipowicz et al. (1978) reported close similarities in vegetation and conditions between the grazed sites and protected areas before the establishment of the enclosures. Although not solving the absence of true replication, this information increases the likelihood that significant differences between sites are due to grazing influence (Díaz et al. 1992; Pucheta et al. 1998).

In the study area, neither noticeable changes in plant species composition nor invasion by exotics which could be attributable to grazing have been observed, but the latter has been associated with a change in species frequency, higher plant species richness, smaller photosynthetic structures and concentration of plant biomass closer to the ground (Pucheta et al. 1998).

The heavily grazed site presented a lawn structure with concentration of biomass in the first 5 cm, vegetation composed mainly by turf species like *Alchemilla pinnata*, *Muhlenbergia peruviana* and *Relbunium richardianum*, and few sparse, short tussocks (Figure 1, HG). The low grazing site (Figure 1, LG) had a matrix of medium to tall grass species like *Deyeuxia hieronymi*, *Festuca tucumanica* and *Poa stukertii* interspersed with lawn patches similar to the vegetation found in HG. The old enclosure (OE) was dominated by tall tussock grasses like those found at LG, with large amounts of litter and standing dead plant biomass accumulating among them (Figure 1, OE). At the young enclosure (Figure 1, YE) litter and standing dead biomass were at most a quarter of the quantity found in OE, with smaller grasses and an increase of dicots cover (Cabido and Acosta 1986; Pucheta et al. 1998; Cabido et al. 1999).

Monthly samples were taken in late spring and summer (November 1996–February 1997). Insects were collected using a modified ‘Blow and Vac’ machine (Stewart and Wright 1995), by passing it repeatedly across the vegetation for 60 s in two 1 m² areas at each site. Suction samplers are the standard equipment for

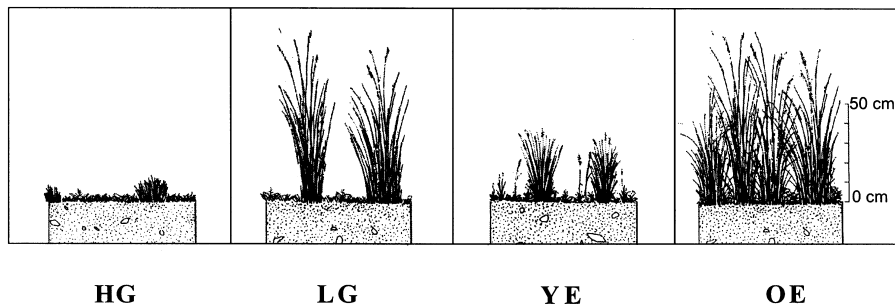


Figure 1. Vegetation profiles of the study sites, at a montane grassland in Central Argentina. (HG) Heavy Grazing; (LG) low grazing; (YE) young exclosure (7 years old); (OE) old exclosure (19 years old). Courtesy of Marcelo Cabido and Diana Aval.

quantitative sampling in grasslands, though it has been noted that their efficiency can vary for different arthropod groups and according to vegetation structure (Stewart and Wright 1995).

Sorting and identification

All collected insects were counted and identified to family level (or to the nearest possible taxonomic category), and to species (or morphospecies) in the case of Coleoptera specimens. This order was selected for a more detailed analysis due to its variety of guilds (the widest within the insects) and to the possibility of further comparisons with information on ground-dwelling insects in the same sites, for which preliminary data have been presented by Cabido et al. (1999).

Insects were grouped into feeding guilds (following Borror et al. 1989) to allow the consideration of functional aspects of the studied communities. The following guilds were considered: herbivores, predators, scavengers, and parasites (including parasitoids). Herbivores were in turn partitioned as chewers, suckers or scrapers, depending on their mouth parts. Some immature specimens of known feeding habits (though not taxonomically identifiable) were included in this analysis; however, ants were excluded due to their variety of feeding habits and the difficulty in ascertaining them. Biomass for insects in each feeding guild was calculated by using Hódar's (1996) formula, based on group-specific body length/weight correlations.

Data analysis

Family (for insects in general) and species (for Coleoptera) richness (S), their abundance (N), diversity (H') and evenness (J) were estimated for each site. Non-parametric analysis of variance (Friedman test, with monthly samples as blocks) and the Mann-Whitney U test were used to test for statistically significant differences in the aforementioned variables among sites. Given the overlap in the studied disturbance

gradients, they were considered simultaneously for the statistical analyses. A multivariate analysis was used to assess changes in family/species assemblages among the different grazing situations. Matrices of monthly frequencies of families/species at each site were ordinated through detrended correspondence analysis (DCA, Hill 1979). The relationship between the number of insect families and Coleoptera species in each habitat was analyzed by the Spearman rank correlation. The frequency distribution of the main insect families, as well as frequencies of insects in each feeding guild were checked for independence among habitats by means of the χ^2 test. The α -values were corrected for the multiple tests by using the Bonferroni correction ($\alpha/\#$ tests) (Vitenbroek 1997). The Friedman and Mann–Whitney U tests were used to compare insect biomass (total and for each guild) in the studied sites.

Results

Grazing vs. taxonomic composition of insect communities (family level)

A total of 16 971 insects belonging to 90 families were collected in the grassland at Pampa de Achala (Table 1A). Family richness was significantly lower at the most intensely grazed site (HG), and highest at the moderately grazed habitat LG (Table 1A). Diversity decreased with increasing grazing pressure, though only the most disturbed habitat differed significantly from the rest (Table 1A). Evenness and abundance did not differ among sites when monthly data were considered (Table 1A). However, intense grazing was associated with lower cumulative insect abundance ($\chi^2 = 506.4$, $df=3$, $P < 0.001$), with at least 6% more insects being collected in the sites with low or no cattle pressure (Table 2).

Table 1. Monthly averages (\pm SE) of richness (S), abundance (N), diversity (H') and evenness (J) of insect families (A) and Coleoptera species (B) assemblages in four sites under different grazing regimes and age of exclusion from cattle at a montane grassland in Central Argentina.

| | HG | LG | YE | OE | Total | χ_r^2 | P |
|----------|---------------------|--------------------|----------------------|----------------------|-------|------------|-----|
| A | | | | | | | |
| S | 24.75 \pm 2.86 a | 49.5 \pm 4.15 b | 45 \pm 3.24 c | 47 \pm 4.63 bc | 90 | 9.9 | * |
| N | 747.3 \pm 296.4 a | 1172 \pm 273.3 a | 1049.3 \pm 176.3 a | 1208.3 \pm 262.4 a | 16971 | 5.4 | NS |
| H' | 1.935 \pm 0.27 a | 2.435 \pm 0.13 b | 2.571 \pm 0.13 b | 2.632 \pm 0.33 b | 2.736 | 8.4 | * |
| J | 0.608 \pm 0.1 a | 0.625 \pm 0.04 a | 0.677 \pm 0.04 a | 0.685 \pm 0.09 a | 0.608 | 2.7 | NS |
| B | | | | | | | |
| S | 4.5 \pm 1.7 a | 8.25 \pm 3.9 a | 6.5 \pm 1.91 a | 7.25 \pm 1.25 a | 46 | 6.6 | NS |
| N | 9 \pm 1.47 a | 14.3 \pm 3.37 a | 14.3 \pm 1.93 a | 15 \pm 2.48 a | 210 | 3.71 | NS |
| H' | 1.322 \pm 0.4 a | 1.86 \pm 0.34 b | 1.575 \pm 0.36 b | 1.788 \pm 0.09 b | 3.011 | 7.8 | * |
| J | 0.902 \pm 0.09 a | 0.919 \pm 0.06 a | 0.858 \pm 0.11 a | 0.88 \pm 0.05 a | 0.786 | 1.5 | NS |

(HG) heavy grazing; (LG) low grazing; (YE) 7 years of exclusion; (OE) 19 years of exclusion. The last two columns on the right are the results of Friedman analysis ($df=3$, (*) $P < 0.05$), (NS): not significant). Different letters denote significant differences between sites at $P < 0.05$, Mann–Whitney U test.

Table 2. Number of insects in the main families (representing over 1% of the total) collected in four sites under different grazing regimes and age of exclusion from cattle, at a montane grassland in Central Argentina.

| | HG | LG | YE | OE | EV | Total | χ^2 | P |
|----------------------|------|------|------|------|---------|-------|----------|---|
| Entomobryidae | 341 | 1574 | 976 | 1608 | 1124.75 | 4499 | 955.8 | * |
| Sminthuridae | 1141 | 324 | 658 | 148 | 567.75 | 2271 | 1008 | * |
| Ciccadellidae | 4 | 441 | 525 | 567 | 384.25 | 1537 | 523.2 | * |
| Formicidae | 449 | 228 | 288 | 377 | 335.5 | 1342 | 84.6 | * |
| Delphacidae | 7 | 59 | 395 | 346 | 201.75 | 807 | 577.2 | * |
| Fulgoridae | 3 | 628 | 42 | 25 | 174.5 | 698 | 1575.9 | * |
| Thripidae | 346 | 115 | 103 | 130 | 173.5 | 694 | 230.7 | * |
| Phlaeothripidae | 321 | 8 | 61 | 276 | 166.5 | 666 | 433.1 | * |
| Liposcellidae | 1 | 171 | 125 | 131 | 107 | 428 | 151.7 | * |
| Coccoideae | 31 | 97 | 127 | 160 | 103.75 | 415 | 87.1 | * |
| Miridae | 12 | 83 | 164 | 106 | 91.25 | 365 | 129.9 | * |
| Scelionidae | 4 | 65 | 74 | 60 | 50.75 | 203 | 59.5 | * |
| Empididae | – | 60 | 50 | 90 | 50 | 200 | 84 | * |
| Cecidomyiidae | 11 | 75 | 53 | 27 | 41.5 | 166 | 57.7 | * |
| Chironomidae | 137 | 59 | 23 | 33 | 63 | 252 | 126.9 | * |
| Chloropidae | 7 | 62 | 24 | 69 | 40.5 | 162 | 65.8 | * |
| Sciaridae | 7 | 63 | 24 | 61 | 38.75 | 155 | 59.6 | * |
| Aphididae | 7 | 68 | 42 | 17 | 33.5 | 134 | 66.8 | * |
| Ephydriidae | 1 | 47 | 54 | 39 | 32.25 | 141 | 196.2 | * |
| Coniopterygidae | – | 28 | 47 | 53 | 32 | 128 | 53.3 | * |
| Reduviidae | – | 35 | 36 | 51 | 30.5 | 122 | 46 | * |
| Others (69 families) | 296 | 470 | 328 | 492 | 396.5 | 1586 | – | – |
| Total | 3126 | 4760 | 4219 | 4866 | 4242.75 | 16971 | 506.4 | * |

(HG) heavy grazing; (LG) low grazing; (YE) 7 years of exclusion; (OE) 19 years of exclusion, (EV) expected value from a habitat independent distribution. $df=3$, (*) $P < 0.001$ ($\alpha = 0.002$ after Bonferroni's adjustment), χ^2 test.

The OE showed the highest number (7) of exclusive (i.e. not found at any other site) families, as well as the lowest number of missing families (18), with the opposite being found in HG (2 exclusive, 46 missing families). Taxonomic composition of insect assemblages varied among sites (Table 2); the most distinctive assemblage was the one associated to HG, where Sminthuridae replaced Entomobryidae (both Collembola) as the dominant group. Most families were rarer in that habitat (Table 2), but Chironomidae (Diptera), Formicidae (Hymenoptera), Thripidae (Thysanoptera) and the already mentioned Sminthuridae reached their highest abundance there. Supporting these observations, the samples corresponding to HG were distinctly separated from the rest, towards the right of the principal axis (Figure 2A) in the ordination analysis (DCA).

Grazing vs. Coleoptera assemblages

Only 210 Coleoptera specimens were collected on the vegetation at Pampa de Achala, which belonged to 16 families and 46 species and represented just 1.5% of all insects

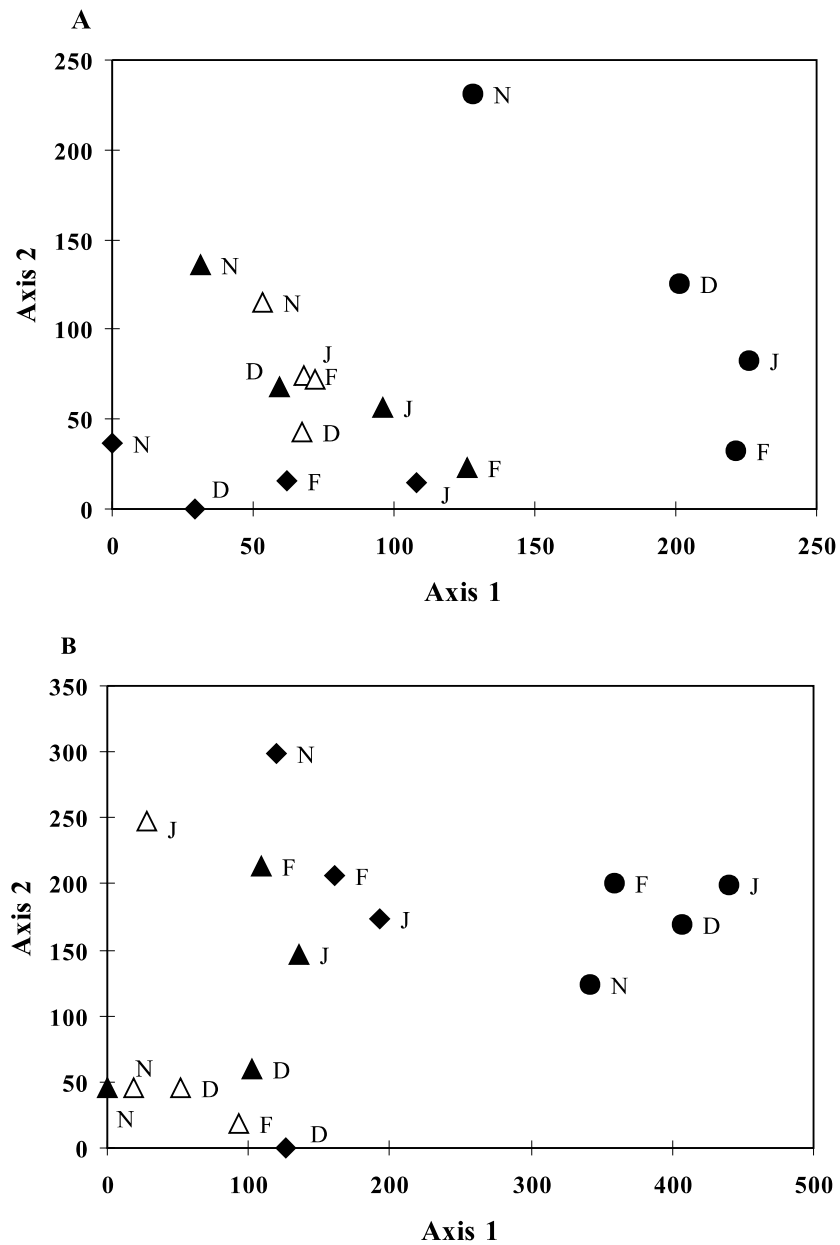


Figure 2. DCS based on the matrix of insect families \times sites (A) and Coleoptera species \times sites (B) at a montane grassland in Central Argentina. (●) heavy grazing (HG); (◆) low grazing (LG); (△) young enclosure (7 years old) (YE); (▲) old enclosure (19 years old) (OE); (N) November; (D) December; (J) January; (F) February.

Table 3. Number of Coleoptera specimens collected in four sites under different grazing pressure and age of exclusion from cattle at a montane grassland in Central Argentina.

| | HG | LG | YE | OE | Total |
|------------------------------|----|----|----|----|-------|
| <i>Anthicidae</i> sp. 2 | – | 15 | 20 | 19 | 54 |
| <i>Lathrididae</i> sp. 1 | – | 6 | 11 | 6 | 23 |
| <i>Eumolpinae</i> sp. 2 | 14 | – | 2 | – | 16 |
| <i>Staphylinidae</i> sp. B | – | 5 | – | 9 | 14 |
| <i>Carboniella platensis</i> | – | 5 | 4 | 1 | 10 |
| <i>Staphylinidae</i> sp. 4 | 6 | 4 | – | – | 10 |
| <i>Bradycellus</i> sp. 2 | 8 | – | – | – | 8 |
| Others (39 species) | 8 | 22 | 20 | 25 | 75 |
| Total | 36 | 57 | 57 | 60 | 210 |

Only species reaching at least 1% of the total Coleoptera collected have been included. (HG) heavy grazing; (LG) low grazing; (YE) 7 years of exclusion; (OE) 19 years of exclusion.

sampled (Tables 1B and 3). Diversity was significantly lower in the most intensely grazed habitat. Species richness showed the same trend though no significant differences were observed among sites, either for this variable or for evenness (Table 1B). Coleoptera were also less abundant in HG, which yielded half as many specimens as any of the less disturbed sites (Table 3). The number of Coleoptera species in each site was highly correlated to the number of insect families ($r = 0.67$, $n = 16$, $P < 0.006$, Spearman rank correlation).

Although the low number of specimens collected did not allow for statistical testing, intense grazing seemed to be associated to changes in the species composition of Coleoptera (Table 3). The three species which made up to 80% of the beetles in HG (*Eumolpinae* sp. 1; *Bradycellus* sp. 2; *Staphylinidae* sp. 4) had little or no representation at the other sites, while the most abundant species in the latter were absent in HG. This difference in taxonomic composition is reflected in Figure 2B, where samples from the most disturbed habitat appear clearly separated from the rest. No obvious differences were detected among Coleoptera assemblages from sites with moderate or no cattle pressure.

Grazing and guild composition of insect communities

Most of the insects collected in the studied grassland were either herbivores or scavengers, together accounting for 92% of the specimens. Trophic guilds varied in abundance ($\chi^2 = 3300.8$, $df = 15$, $P < 0.001$) among sites, particularly regarding predators and parasites (Figure 3A) for which approximately a fifth of the expected numbers were found at the most heavily grazed site ($\chi^2 = 188.2$ and $\chi^2 = 156.6$ respectively, $df = 3$, $P < 0.008$). Furthermore, the abundance of suckers in the latter habitat was an order of magnitude lower than in any of the other sites ($\chi^2 = 1112.6$,

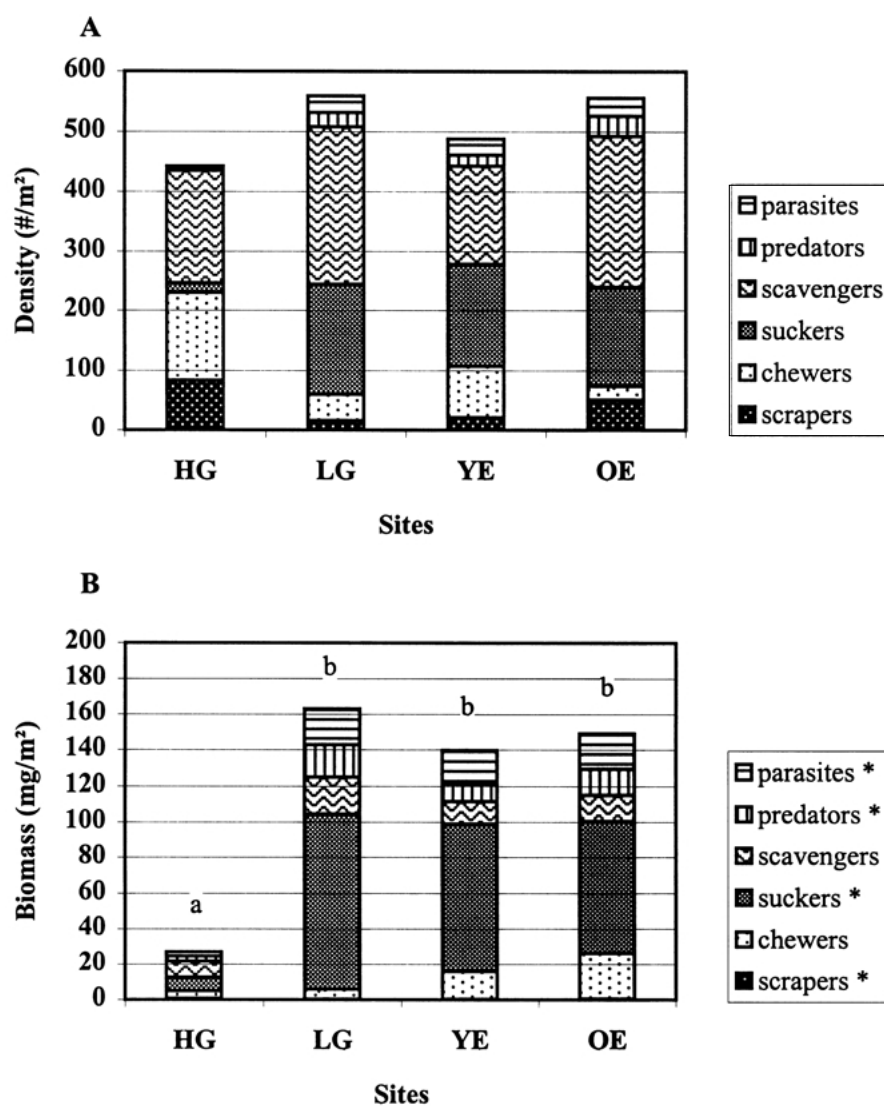


Figure 3. Density (A) and biomass (B) of insects in each trophic guild, collected at four sites under different grazing regimes and age of exclusion from cattle, at a montane grassland in Central Argentina. (HG) Heavy grazing; (LG) low grazing; (YE) young exclosure (7 years old); (OE) old exclosure (19 years old). Different letters above bars denote significant differences in biomass (total and for (*) marked guilds) among sites; $P < 0.05$, Mann-Whitney U test.

$df=3$, $P < 0.008$), while chewers doubled the expected value for that habitat ($\chi^2 = 405.4$, $df=3$, $P < 0.008$) (Figure 3A).

Considerably less insect biomass ($x_r^2 = 18.04$, $df=3$, $P = 0.0004$) was collected at HG than at any other site. Biomass distribution in feeding guilds (Figure 3B) also

varied among sites, most noticeably for suckers ($\chi_r^2 = 17.62$, $df = 3$, $P = 0.0005$) but also for parasitoids ($\chi_r^2 = 14.95$, $df = 3$, $P = 0.01$), predators ($\chi_r^2 = 8.541$, $df = 3$, $P = 0.04$), and marginally for scrapers ($\chi_r^2 = 6.95$, $df = 3$, $P = 0.07$).

Discussion

In the grassland studied at Pampa de Achala, a sustained, high-density cattle presence was associated with a noticeably poorer insect community, for two hierarchies of taxonomic organization (families and species). No consistent differences were detected between insect assemblages in sites either currently (but lightly) grazed or after 7 or 19 years of cattle exclusion, suggesting that grazing intensity rather than its frequency could have a strong influence on this system.

Several studies have shown insect diversity to be related to vegetation characteristics such as plant diversity (Siemann et al. 1998) and/or structural complexity (Lawton 1983, 1986; Brown 1991; Gardner et al. 1995; Wettstein and Schmid 1999). In the present case, cattle presence seems to have resulted in highly diverse but structurally simpler vegetation (Pucheta et al. 1998). Although hard evidence is lacking, the impoverishment of the insect assemblage in the most heavily grazed site could therefore reflect reduced availability of food, refuges, oviposition sites or particular microclimates, due to the lower structural complexity of the habitat.

Cattle exclusion was related to a higher number of 'exclusive' families. Perhaps a higher environmental stability resulting from absence of cattle disturbance might save insect groups normally occurring at low densities in the area, from becoming locally extinct due to stochastic events (Denslow 1985; Collins and Glenn 1990; Fahrig and Jonsen 1998). The lack of baseline data collected when grazing rates were similar at all sites, prevents any inference about the source of those additional taxa. On the other hand, more families were missing at the site under strong cattle pressure than at any of the others, indicating that many insect groups would not be able to tolerate such conditions. Nevertheless, none of the studied sites yielded much more than half of the total number of families found in the grassland, suggesting that the coexistence of patches like the ones here considered could be advisable from a conservation viewpoint (Morris 1991; Dennis et al. 1998).

Besides the above-mentioned trend regarding insect diversity, a strong cattle grazing pressure was also related to lower abundance and biomass of both insect families and Coleoptera species. This could result from a reduced availability of trophic and non-trophic resources, because plant biomass is mainly consumed by livestock and the vegetation structure is simplified (Hutchinson and King 1980; Welch et al. 1991).

The assemblages of insect families or Coleoptera species found in the habitat with sustained high density cattle presence, differed markedly in their taxonomic composition from those found under lighter or no grazing. This would result from a differential response to grazing, as a combination between insect lifestyles and

requirements, with the particular aspects of vegetation being affected (Dennis et al. 1998). Thus, while most insect groups might be unable to cope with the conditions created by HG, others (e.g. Sminthuridae, Thripidae, Phlaeothripidae, Formicidae, Chironomidae; Eumolpinae sp. 2; *Bradicellus* sp. 2; Staphylinidae sp. 4) seem to benefit under the same conditions. The replacement of one family of Collembola (Entomobryidae) as the dominant group at the lightly or non-grazed sites, by another family of the same order (Sminthuridae) in the heavily grazed site, added to their great abundance in the area, deserves further study in a context of grazing disturbance indicators in this grassland.

While sites under either little or no cattle grazing pressure shared a similar trophic composition, the insect community associated to the heavily grazed habitat showed a distinct guild structure, clearly impoverished in secondary consumers (parasites and predators) and with chewers replacing suckers as the dominant herbivore group. Suckers were represented mainly by Homoptera, a strongly grass-associated group (Tscharntke and Greiler 1995). This could explain the poor representation of suckers in the most intensively disturbed site, where the tall tussock grasses dominating the vegetation under low or no grazing disturbance were scarce (Pucheta et al. 1998). On the other hand, a decrease in secondary consumers could result from reduced niche availability in a simplified habitat (Gibson et al. 1992; Thomas et al. 1992) or from a reduced plant biomass, as a cascade effect of restricted energy flow to higher trophic levels (Paine 1966). Furthermore, secondary consumers such as parasitoids seem to be more sensitive to environmental disturbance than their herbivore hosts (LaSalle 1993). Low numbers of secondary consumers could enhance the possibility of herbivore population explosions (Scholwater 1985; Thomas et al. 1992), therefore decreasing the system sustainability (Chapin III et al. 1996).

Less insect biomass, both total and for most individual feeding guilds, was found in relation to a stronger grazing pressure. From a comparison of Figures 3A and B, biomass of the insect assemblages appeared to be much more dramatically affected than their density. However, the numerical dominance of chewing herbivores at the highly grazed site was not reflected in the biomass analysis. This could be due to the small body size of Sminthuridae, the group accounting for such dominance; a population increase of these insects would have little effect in terms of biomass.

The main trends discussed above seem to be consistent, at least regarding taxonomic composition (the heavily grazed site showing lower diversity and a more differentiated composition), whether insect families or Coleoptera species are considered. Using the number of higher taxa as surrogate for species richness has many advantages and disadvantages (Gaston 2000). In the present study, the high correlation between both variables suggests that family level could act as a reasonable predictor of species richness, with lower costs in terms of time and resources. The use of family level shows a further advantage in this case, since for the same sampling effort it allowed a broader analysis (including functional aspects) than the lower level of taxonomic resolution. On the other hand, this approach could be weakened

when dealing with endemism-rich faunas (Samways et al. 1996), as sensitive endemic species might be affected without a noticeable effect at higher taxon levels.

Conservation efforts are directed at preserving species that humans assess as valuable, and insects are frequently overlooked. However, because of their diverse behaviors and ecological interactions they provide essential functions for the long-term survival of other species populations and species assemblages (Fisher 1998). Even though methodological constraints (e.g. lack of true replicates, the inferential rather than experimental approach) might limit the extent of extrapolations from our results, we found markedly impoverished, and taxonomically as well as functionally different insect assemblages developing under intensive cattle grazing pressure, in comparison with their counterparts from less disturbed sites. In terms of management, it is important to note the strong resemblance among the insect communities associated with a lighter cattle pressure, and those inhabiting sites from which cattle had been excluded for either 7 or 19 years. This suggests that the practice found at the former site (LG) might be an adequate option to allow exploitation of the grazing resource while preserving insect communities of high diversity in this grassland.

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References

- Borror DJ, Triplehorn CA and Johnson NF (1989) *An Introduction to the Study of Insects*. Saunders College Publishing, Florida
- Brown VK (1991) The importance of habitat structure in the maintenance of insect's species diversity. In: Pineda FD, Casado MA, de Miguel MJ and Montalvo J (eds) *Diversidad biológica*, pp 49–55. Editorial Centro de Estudios Ramón Areces S.A., Madrid
- Brown VK and Hyman PS (1986) Successional communities of plants and phytophagous Coleoptera. *Journal of Ecology* 74: 963–975
- Cabido M and Acosta A (1986) Variabilidad florística a lo largo de un gradiente de degradación en céspedes de la Pampa de Achala, Sierras de Córdoba, Argentina. *Documents Phytosociologiques* 10: 289–304
- Cabido M, Funes G, Pucheta E, Vendramini F and Díaz S (1998) A chorological analysis of the mountains from Central Argentina. Is all what we call Sierra Chaco really Chaco? Contribution to the study of the flora and vegetation of the Chaco. XII. *Candollea* 53: 321–331
- Cabido M, Molina S, Perez Harguindeguy N, Valladares G, Pucheta E and Gardner S (1999) Uso de la tierra, estructura del hábitat y biodiversidad en ecosistemas del centro de Argentina. In: Matteucci SD, Solbrig OT, Morello J and Halffter G (eds) *Biodiversidad y uso de la tierra. Conceptos y ejemplos de Latinoamérica*, pp 421–442. Editorial Universitaria de Buenos Aires, Buenos Aires
- Capitanelli R (1979) Clima. In: Vázquez J, Miatello R and Roqué M (eds) *Geografía física de la provincia de Córdoba*, pp 45–138. Editorial Boldt, Buenos Aires

- Chapin III FS, Torn MS and Tateno M (1996) Principles of ecosystem sustainability. *American Naturalist* 148: 1016–1037
- Collins SL and Glenn SM (1990) A hierarchical analysis of species abundance patterns in grassland vegetation. *American Naturalist* 135: 633–648
- Dennis P, Young MR and Gordon IJ (1998) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology* 23: 253–264
- Denslow JS (1985) Disturbance-mediated coexistence of species. In: Pickett STA and White PS (eds) *The Ecology of Natural Disturbance and Patch Dynamics*, pp 307–323 Academic Press, Orlando, Florida
- Díaz S, Acosta A and Cabido M (1992) Morphological analysis of herbaceous communities under different grazing regimens. *Journal of Vegetation Science* 3: 689–696
- Fahrig L and Jonsen I (1998) Effects of habitat patch characteristics on abundance and diversity of insects in an agricultural landscape. *Ecosystems* 1: 197–205
- Fisher BL (1998) Insect behavior and ecology in conservation: preserving functional species interactions. *Annals of the Entomological Society of America* 91: 155–158
- Fleischner TL (1994) Ecological costs of livestock grazing in Western North America. *Conservation Biology* 8: 629–644
- Gardner SM, Cabido M, Valladares G and Díaz S (1995) The influence of habitat structure on arthropod diversity in Argentine semi-arid Chaco forest. *Journal of Vegetation Science* 6: 349–356
- Gaston KJ (2000) Biodiversity: higher taxon richness. *Progress in Physical Geography* 24: 117–127
- Gibson CWD, Brown VK, Losito L and McGavin G (1992) The response of invertebrate assemblages to grazing. *Ecography* 15: 166–176
- Hill MO (1979) DECORANA: A FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging. Cornell University Press, Ithaca, New York
- Hódar JA (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica* 17: 421–433
- Hutchinson KJ and King KL (1980) The effect of sheep stocking level on invertebrate abundance, biomass and energy utilization in a temperate sown grassland. *Journal of Applied Ecology* 17: 369–387
- LaSalle J (1993) Parasitic Hymenoptera, biological control and biodiversity. In: LaSalle J and Gauld ID (eds) *Hymenoptera and Biodiversity*, pp 197–215. Redwood Books, Trowbridge
- Lawton JH (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review Entomology* 28: 23–39
- Lawton JH (1986) Surface availability and insect community structure: the effects of architecture and fractal dimension of plants. In: Juniper BE and Southwood TRE (eds) *Insects on Plant Surfaces*, pp 317–331. Edward Arnold, London
- Milchunas DG and Lauenroth WK (1993) A quantitative assessment of the effects of grazing on vegetation and soils over a global range environments. *Ecological Monographs* 63: 327–366
- Morris MG (1978) Grassland management and invertebrate animals, a selective review. *Scientific Proceedings of the Royal Society, Dublin* A6: 247–257
- Morris MG (1979) Responses of grassland invertebrates to management by cutting I. Species diversity of Hemiptera. *Journal of Applied Ecology* 16: 77–98
- Morris MG (1981) Responses of grassland invertebrates to management by cutting. III Adverse effects on Auchenorrhyncha. *Journal of Applied Ecology* 18: 107–123
- Morris MG (1991) The management of reserves and protected areas. In: Spellerberg IF, Goldsmith FB and Morris MG (eds) *The Scientific Management of Temperate Communities for Conservation*, pp 323–348. Blackwell Scientific Publications, Oxford
- Paine RT (1966) Food web complexity and species diversity. *American Naturalist* 100: 850–860
- Pucheta E, Cabido M, Díaz S and Funes G (1998) Floristic composition, biomass, and aboveground net plant production in grazed and protected sites in a mountain grassland of Central Argentina. *Acta Oecologica* 19: 97–105
- Samways MJ, Caldwell PM and Osborn R (1996) Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agriculture, Ecosystems and Environment* 59: 19–32
- Scholwalter TD (1985) Adaptation of insects to disturbances. In: Pickett STA and White PS (eds) *The Ecology of Natural Disturbance and Patch Dynamics*, pp 235–252. Academic Press, Orlando, Florida

- Siemann E, Tilman D, Haarstad J and Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist* 152: 738–750
- Sipowicz DI, Luti R and Morlans C (1978) Productividad primaria de la estepa de altura de las Sierras Grandes, Córdoba. *Ecología Argentina* 3: 117–123
- Stewart AJA and Wright AF (1995) A new inexpensive suction apparatus for sampling arthropods in grassland. *Ecological Entomology* 20: 98–102
- Thomas MB, Wratten SD and Sotherton NW (1992) Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predators densities and species compositions. *Journal of Applied Ecology* 29: 524–531
- Tscharntke T and Greiler HJ (1995) Insect communities, grasses and grasslands. *Annual Review of Entomology* 40: 535–558
- Vitenbroek DG (1997) Binomial SISA (<http://home.clara.net/sisa/binomial.htm>). Accessed 1 March 2001
- Welch JL, Redak R and Kondratieff BC (1991) Effect of cattle grazing on the density and species of grasshoppers (Orthoptera: Acrididae) of the Central Plains Experimental Range, Colorado: a reassessment after two decades. *Journal of the Kansas Entomological Society* 64: 337–343
- Wettstein W and Schmid B (1999) Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. *Journal of Applied Ecology* 36: 363–373
- Williams P and Gaston K (1994) Measuring more of biodiversity: can higher – taxon richness predict wholesale species richness? *Biological Conservation* 67: 211–217