

Variation in Insect Assemblage and Functional Groups along a Grazing Gradient in an Arid Environment

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Abstract

Exotic livestock may affect plant and pollinator composition as well as their interactions. Changes in pollinator assemblage (e.g. composition) may alter pollination process and, therefore, plant reproduction. This study examined seven independent paddocks environmentally similar but with increasing livestock densities, in Patagonian Monte Desert. This allows investigating the response of different insect groups to livestock effect on vegetation along a grazing gradient. Water traps was used to capture insects (focusing on pollinators) and pollinator visitation frequencies were measured in five of the most abundant native plant species of the region. Regressions between livestock density and insect richness and abundance of the different functional groups of insects (dipterans, herbivores and pollinators) were performed. Insect assemblage was mostly composed, in decreasing order, by hymenopterans, coleopterans, dipterans and lepidopterans. Ordination analysis of insect composition showed a high correlation between the first axis and livestock density ($r=0.95$). In the first year of sampling, pollinators significantly decreased in richness and wasps increased in abundance with livestock density. In the second year of sampling, pollinator abundance increased and herbivores decreased as livestock density increased. Unimodal ordination analyses showed that plant species were significantly associated to insect composition and livestock density marginally explained the variation in insect composition that visited the five studied plant species across paddocks.

Interacting factors such as livestock density and climatic conditions may partially explain the patterns observed in this work. Disturbances may alter the ecological scenarios, impoverishing the composition and abundance of flora and fauna. This study describes that changes in the density of exotic livestock can affect insect assemblage associated to pollination process differently through the years. Changes through time may determine population dynamic and their response to anthropogenic disturbances.

Keywords: Composition; Insect richness; Livestock density; Monte desert; Native plant; Water traps; Wild pollinators

Introduction

Spatial and temporal changes in abundance, diversity and/or distribution of flowering plants may strongly affect pollinator populations that depend on them, and vice versa [1–3]. Therefore, habitat changes that affect the composition and abundance of flowering plants and/or pollinators might have strong consequences on their interactions [4]. Previous works showed that the disturbances generated by human activity caused pollinator and plant diversity declines worldwide [5–11]. One of the main human-disturbance that may affect plant-pollinator interactions is the introduction of livestock for grazing in natural areas [12–15].

Livestock may alter pollinator populations by trampling decreasing both the quality and quantity of nesting sites and/or destroying the nests already settled [16–20]. This may affect some species and alter pollinator assemblage in unpredicted ways. For example, in natural pollinator populations, it is frequent that dominant species displace rarer ones by competing for food resources [21]. However, intermediate levels of disturbances may decrease the abundance of dominant species increasing rarer ones through reduced competition, leading to a higher contribution to plant pollination [22–25]. Furthermore, not all pollinator species are equally efficient therefore

any change in pollinator assemblage may also modify their foraging behavior (e.g. visitation frequency) and pollination efficiency affecting plant reproduction [3,26–28].

Livestock may also decrease plant and/or flower abundance, leading to insufficient food resources to maintain pollinator populations and enhancing their migration to more resource-rich locations [21,29]. Both the physical habitat modifications (e.g. trampling) and the decrease in native pollinator populations may also enhance invasions by opportunistic exotic species [30,31], potentially affecting plant reproduction [32,33]. Therefore, understanding the effect of livestock on pollinator assemblage is important to determine the impact on plant-pollinator interactions. Monte Desert, Argentina, is characterized by a shrubby xeric vegetation that serves as food resource for feeding a wide variety of exotic livestock - usually, sheep, goats, cattle and horses [34]. This study examined seven paddock treatments environmentally similar but with increasing livestock densities providing a natural experimental condition to study how pollinator assemblage vary along a disturbance gradient, (i.e., a gradient of livestock density). Pollinator assemblage was estimated both by water traps and by visitation frequency measured on five of the most abundant native plant species of the region, present in all the paddocks.

Materials and methods

Study site and plant species

The study area was located in Patagonia, Argentina, within the phytogeographic region of Monte Desert in Neuquén province (39°17'S, 68°55'W). The region has a mean annual precipitation of 180 mm spread throughout the year and a mean annual temperature of 15°C, with cold winters and warm summers [34]. Samplings were carried out during two spring-summer seasons (2003-2004) in seven paddocks with different grazing intensities, (i.e., livestock ha⁻¹) but within the same habitat and therefore similar in climatic features and plant physiognomy [34]. Paddocks varied in size from 4000 to 21000 ha and had been grazed for more than 5 years. Livestock composition was a mixture of goats, sheep, cattle, and horses. Stocking densities were standardized using animal unit equivalents and expressed as cattle ha⁻¹ (1 cow=1.25 horse, 0.17 goat, 0.3 sheep) [35].

The negative association of livestock density and plant cover, density and richness was previously tested in this region [34]. The sampling area in each paddock was located at least 300 m away from the main road and 3 km from the house-farms. The most abundant plant species in Patagonian Monte Desert were selected to study pollinator visitation frequency [34]. Plant species were: *Grindelia chiloensis* (Asteraceae); *Gutierrezia solbrigii* Cabrera (Asteraceae); *Larrea cuneifolia*, *L. divaricata* (Zygophyllaceae) and *Monttea aphylla* (Miers) Griseb. (Scrophulariaceae).

Insect assemblage

Insect abundance was determined using yellow water traps that were placed along transects during the spring of 2003 and 2004. Trap yellow color was chosen because most of the plant species in the region have yellow flowers. Twenty traps were placed every 30 m along two parallel transects spaced at a distance of 100 m (10 traps/transect/paddock, a total of 140 traps in 2003 and 420 in 2004).

Sampling efforts during 2003 was lower than in 2004 as it was a very dry year with a scarce blooming and consequently with low pollinator abundance. Transects were randomly located within each paddock and traps were left during the period of pollinator activity from 11am to 2pm (see Visitation frequency section). Captured insects were preserved in 70% alcohol for taxonomic identification at the laboratory.

Visitation frequency

Direct observations during periods of 10 min per plant were carried out to determine visitation frequencies for each plant species at each paddock. Pollinator activity was measured from 8am to 6pm during a month in the first year of sampling to determine their activity period. As their activity period was restricted between 11am to 2pm all subsequent observations were done during that period. Twenty plants per species were marked within the study area and sampled periodically. Additionally, random plants were sampled once. The number of visitors was recorded during each period to estimate the visitation frequency per plant, (i.e., visits/plant x time). Only those insect species that contacted plant sexual organs were recorded and considered pollinators.

Samplings were conducted weekly during the flowering season each year. In each sampling, a minimum of three individuals per plant species was observed in each paddock. A total of 489 periods of

observation, (i.e., 815 hours) were performed (133 in 2003 and 356 in 2004). Live pollinators were captured when possible, for taxonomic identification by an expert. Insect assemblage composition was determined both by traps and visitation observations.

Statistical analysis

Insects were separated in four main categories: dipterans (variated group including some pollinators), herbivores (coleopterans), pollinators (hymenopterans and lepidopterans) and wasps (predators). Simple regressions were performed to evaluate the association between the percentages of each insect group (response variable) in each paddock and livestock density (independent variable). Unimodal ordination methods (Correspondence Analysis, CA, and Canonical Correspondence Analysis, CCA) were performed to describe pollinator composition among paddocks. The statistical significance of each selected environmental variables (i.e., livestock density, plant species) was judged by a Monte Carlo permutation test. The data was transformed using logarithms ($y = \log y + 1$). Two matrices were constructed; the first depicts insect composition by paddock with the mean abundance of each insect species in each paddock (7 paddocks x 92 insect species) and the second summarizes pollinator composition with a site-specific matrix in which each "sample" corresponds to the mean visitation frequency of each pollinator species to each plant species in each paddock. CCA were performed using livestock density and/or plant species identity as "environmental variable" when corresponded.

Results

Insect assemblage sampled by water traps

The insect assemblage, sampled by water traps, was mostly composed of hymenopterans (>50%), followed by coleopterans (~10-15%), dipterans (~5-10%) and lepidopterans (<5%). The CA performed for water traps explained 77.2% of the variance along the first four axes, the first axis explaining 23.8% and the second 19.6% (Figure 1a).

The CCA for water traps, with livestock density included as environmental variable, explained 75% within the first four axes; the first axis explained 17.6% and the second 21.2% (Figure 1e). Livestock density was not significant as environmental variable ($\lambda = 0.17$, $F = 1.07$, $P = 0.27$), however, the first axis was canonical and it was highly correlated with livestock density ($r = 0.95$). For water traps, the group of pollinators showed a decreased richness with livestock density in the first year of sampling and an increase in abundance in the second year of sampling (Table 1).

Herbivores showed a decrease in abundance in the second year of sampling as livestock density increased (Table 1 and Figure 2).

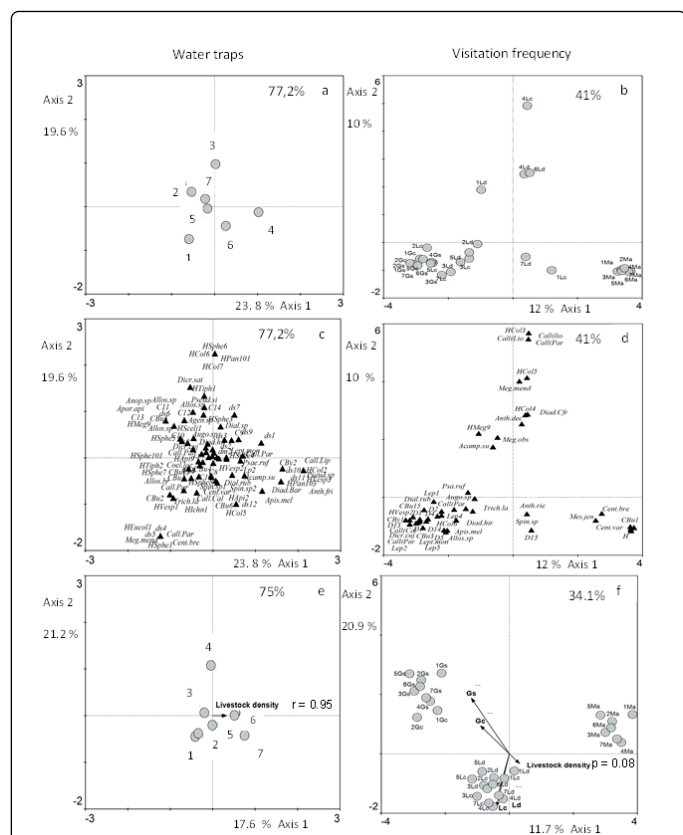


Figure 1: Unimodal ordination graphs (CA and CCA) of pollinator abundance sampled by traps (a,c,e) and visitation frequency samplings (b,d,f). Data from water traps was analysed using livestock density as explanatory variable (CCA, e). Data from visitation frequency was evaluated using livestock density and plant species identity as explanatory variables (CCA, f). Only the dispersion of samples (paddocks and plant species-paddocks) is represented in the first line of graphs (a, b), for clarity. The numbers from 1 to 7 represent the paddocks with increasing livestock densities (from 1= 0.002 to 7 = 0.038 cow ha⁻¹). Plant species were represented as: Ld = *Larrea divaricata*, Lc = *L. cuneifolia*, Ma = *Monttea aphylla*, Gs = *Gutierrezia solbrigii*, Gc = *Grindelia chiloensis*.

Year	Variable	Insect group	R	R ²	F	Df	P
2003	Abundance	D	-0.55	0.30	2.2	1.5	0.20
		H	0.23	0.06	0.29	1.5	0.61
		P	0.05	0.003	0.01	1.5	0.91
	Richness	D	-0.40	0.16	0.98	1.5	0.37
		H	-0.22	0.05	0.25	1.5	0.64
		P	-0.81	0.65	9.5	1.5	0.03
2004	Abundance	D	-0.06	0.004	0.008	1.5	0.90
		H	-0.76	0.58	7.01	1.5	0.046

	P	0.77	0.60	7.46	1.5	0.04
Richness	D	-0.13	0.02	0.09	1.5	0.78
	H	-0.38	0.14	0.83	1.5	0.40
	P	0.40	0.01	0.06	1.5	0.82

Table 1: Regression analyses between livestock density (cattle Ha⁻¹) as independent variable and: abundance (%) and richness (%) of insect groups (D: dipterans, H: herbivores, P: pollinators) sampled in water traps.

Visitation frequency

The pollinator assemblage observed visiting the five plant species studied during both years (2003-2004) was mostly composed by hymenopterans in similar proportions than in water traps hymenopterans: (63±9.4%), dipterous: (19.5±4.3%), coleopterans: (10.5± 6.3%), lepidopterans: (6.9±4%); all expressed as mean percentage ± SD). Different groups of pollinators visited the studied plant species, although some visitors were common to more than one plant species (Figure 1 b, d, f).

The CA for visitation frequency explained 41% of the variance within the first four axes; the first axis explaining 12.2% and the second 10.7% (Figure 1 b). The CCA, for the same data, using species identity and livestock density as environmental variables, explained 34.1% of the variance (the first four axes), from which 20.9% was explained by the first axis and 11.7% by the second, all axes being canonical (Figure 1 f; Trace=3.45, F=2.1, P=0.002). Plant species were all statistically significant (all P≤0.01, λ1=0.39- 0.61) and livestock density was marginally significant (λ1= 0.32, F=1.48, P=0.08). Wasps was the only group that showed a significant increase with livestock density for the first years of sampling (2003), the rest of the groups (dipterans, herbivores and pollinators) did not show any association (Table 2, Figure 2).

Year	Insect group	R	R ²	F	Df	P
2003	W	0.81	0.66	9.5	1.5	0.03
	D	-0.34	0.12	0.67	1.5	0.45
	H	0.16	0.03	0.14	1.5	0.72
	P	-0.27	0.07	0.38	1.5	0.56
2004	W	0.58	0.34	9.5	1.5	0.16
	D	-0.16	0.03	0.13	1.5	0.73
	H	-0.47	0.22	1.4	1.5	0.29
	P	0.28	0.07	0.42	1.5	0.55

Table 2: Regression analyses between livestock density (cattle Ha⁻¹) as independent variable and abundance (%) of insect groups (W: wasps, D: dipterans, H: herbivores, P: pollinators) sampled in visitation frequency.

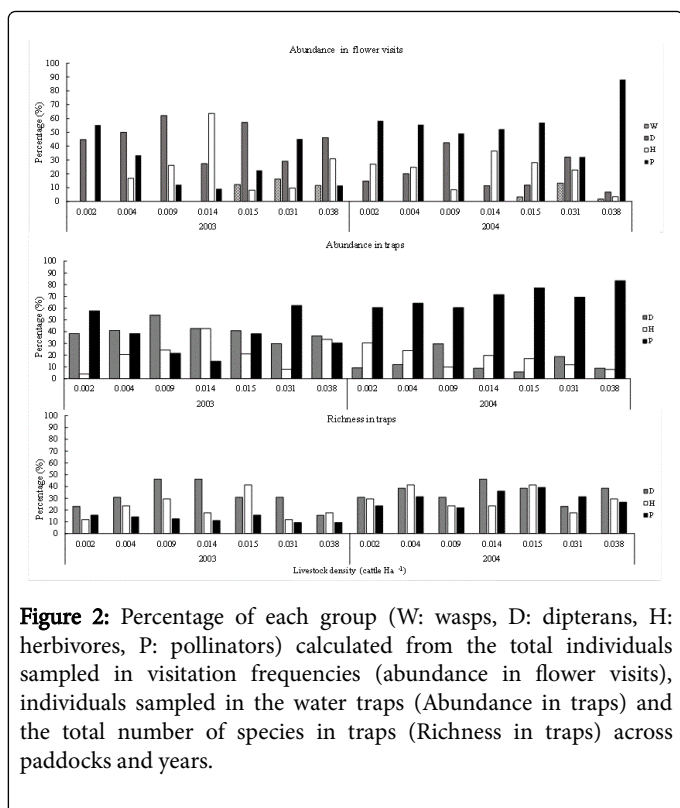


Figure 2: Percentage of each group (W: wasps, D: dipterans, H: herbivores, P: pollinators) calculated from the total individuals sampled in visitation frequencies (abundance in flower visits), individuals sampled in the water traps (Abundance in traps) and the total number of species in traps (Richness in traps) across paddocks and years.

Discussion

This study investigated how changes in livestock density affected pollinator assemblage. Insect composition determined by water traps and visitation frequency varied across paddock and years. In general paddocks with intermediate livestock density showed more insect richness and abundance [36]. Livestock density may affect pollinator assemblage in a complex way, as the pattern observed in this work was not consistent through the years studied. Probably combination of many factors are determining insect assemblage across paddocks.

There was a high species turnover between paddocks probably attributed to livestock density [36]. The species turnover between paddocks suggests that habitat degradation caused by livestock may particularly affect certain groups of insects. For instance, those insects that nest on the ground, such as solitary bees, may be more affected by this kind of disturbance [18,19]. The hymenopterans observed in this study were mainly solitary bees, of which several are cavity-nesting [36,37]. Therefore, livestock may be affecting nesting sites through changes in soil characteristics such as desiccation, increase in bare soil and/or soil compactness. For example, the study area presented a drastic increase in bare soil along the grazing gradient [34] which might have increased desiccation affecting nesting sites [16,38]. Nonetheless, the hymenopterans showed higher richness and abundance in intermediate livestock densities than in the extreme grazing intensity treatments [36]. Livestock may be reducing the abundance of some dominant bee species, releasing inter-specific competition and enhancing the abundance of more rare species. This is consistent with the result that, in 2004, the percentage of pollinator abundance increased with no changes in their richness and the opposite trend was observed in 2003, pollinator richness significantly decreased but abundance did not change with livestock density (Figure

2). Possibly, the combination of climate and disturbance (i.e. livestock) were determining pollinator richness those years [36]. The climatic conditions in the years of sampling were very different, 2003 was extremely dry with scarce blooming, whereas in 2004 climatic condition were relatively better, with higher precipitation [36]. Therefore, the high species turnover between years might also be partially explained by climatic influence.

Ordination diagrams also showed that pollinator assemblage was determined by food resource (i.e., plant/flower abundance) as insect composition was highly associated with the plant species they visited. A previous work, in the same study area, showed that food resource showed a negative effect on pollinator richness but a positive effect on their abundance suggesting an increase in competition between pollinator species [36]. This implies the dominance of a few species with increased abundance, partially supported by the results presented in this work that showed a decrease of richness one year without changes in the abundance (2003) and the opposite trend the next year (Table 1). If livestock enhanced the dominance of less efficient pollinator species, it could have indirectly affected plant reproduction through reduced pollination quality [39,40]. Changes in pollinator composition (e.g., specialists by generalists) and species abundance may lead to variations in pollinator foraging behavior through alterations in inter-species competition for resources [26]. Additionally, the group of herbivores showed a significant decreased with livestock density during the second year. Note that herbivores sampled in this work may also act as pollinators, since they were mostly found feeding on flowers (personal observation). The consequences of their presence on plant reproduction still needs further investigation. More studies of variations in insect assemblages through time are needed to better understand its net consequences on plants.

Ecological context helps to understand inter-species relationships and are highly variable across time and space, making plant-animal interactions very dynamic [41]. However, disturbances may alter those ecological scenarios, impoverishing flora and fauna composition and abundance. This study described how changes in exotic livestock density might affect insect assemblage associated to pollination process evidencing variation between years. This temporal variation may have strong consequences on species ecology and are important to determine their responses to anthropogenic disturbances.

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