The influence of shrubs on herb diversity in an Andean semidesert, the Prepuna

Teresa Ortuño
Herbario Nacional de Bolivia/Museo Nacional de Historia Natural

Introduction

In arid and semi-arid regions, shrubs and trees (known as nurses) create different levels of heterogeneity. In contrast to open spaces, a more mesic microclimate and improved nutrient conditions are found below the shrubs' crowns. Sometimes, the undercanopies of shrubs and trees offer protection from some herbivores as well. All this promotes the establishment of a particular herb flora (beneficiaries) associated to these microenvironments below shrubs. This positive interaction is known as facilitation. Thus, woody species help to increase community diversity. But the importance of shrubs or trees for herb species varies from region to region, and it may be different according to the spatial or temporal scale of analysis.

The knowledge about the role of woody species in the arid Andes of Bolivia and Argentina is extremely scarce. With this study, I want to assess how important are shrub species for herb diversity in the arid Andes at different spatial scales: locally and regionally. A regional analysis of this kind has not been attempted before. By gaining insight into the strength and characteristics of the interaction between these two growth forms, we will get information that will likely be important for conservation, restoration, and good management of arid zones in the Andes.

Methods

The study was conducted in eight sites located in the Bolivian Prepuna biogeographical region (Table 1). In each site, 50 below shrub and 50 open spaces were sampled sistematically. Both microhabitats were selected from points located 10 meters apart along sampling lines randomly located. Those shrubs > 1m diameter closest to the points were chosen, as well as the open spaces adjacent to those shrubs. In each sampling point, a 40x20 cm frequency quadrat was placed and the presence of each herb species was recorded.

Table 1. The study sites

Locality	Coordinates (lat, long)	Altitude (m)
Alto Impora	21º23.239 S, 65º17.993 W	3150
Tomayapo	21º21.119 S, 65º03.268 W	3000
Villa Abecia	21º 04.624 S, 65º 13.141 W	2350
San Pedro	20º44.017 S, 65º12.266 W	2700
Cruz Huasa	20º46.878 S, 65º13.860 W	2400
Parinolqui I	20º41.813 S, 65º29.333 W	3000
Parinolqui	20º43.645S, 65º34.146W	3100
Cascabel	20º45.052S, 65º37.857W	3140

Three increasingly larger spatial scales were considered. The first scale considered the individual patches, i.e., the 40x20 cm quadrats (**individual patch**

scale). Here, the average species number per quadrat was calculated. The second scale considered the cumulative richness values in a given locality, i.e., the sum of species from all quadrats (**patch type scale**). This separation in the analysis is important because the species turnover in the two patch types may be different. Hence, we obtained observed species lists for patch type. However, as the observed species lists may not adequately represent their respective communities in terms of richness, I employed rarefaction tests based on samples, with the Chao 2 richness estimator. For the rarefactions, the program *Estimates 8.0.0* was used.

The third scale corresponds to the region (**regional scale**). For the regional analysis, I was interested in comparing if the patterns in different localities were different from one another, in order to evaluate if they had to do with peculiar phenomena or were consistent among localities. The latter would mean greater generality to the findings. Thus, for the present study, the patterns in the eight localities were compared. Moreover, for the regional scale, I compared the floristic composition of the localities employing ordination methods.

Results and discussion

At the quadrat scale, more herb species were found below shrubs than in open areas (Tables 2 and 3). However, in one locality this relationship was reversed and in two there was the same number of species (this is shown by the significant interaction term microhabitat x place; Table 3). The analysis also shows that the number of herb species differs among sites (significant between subjects term).

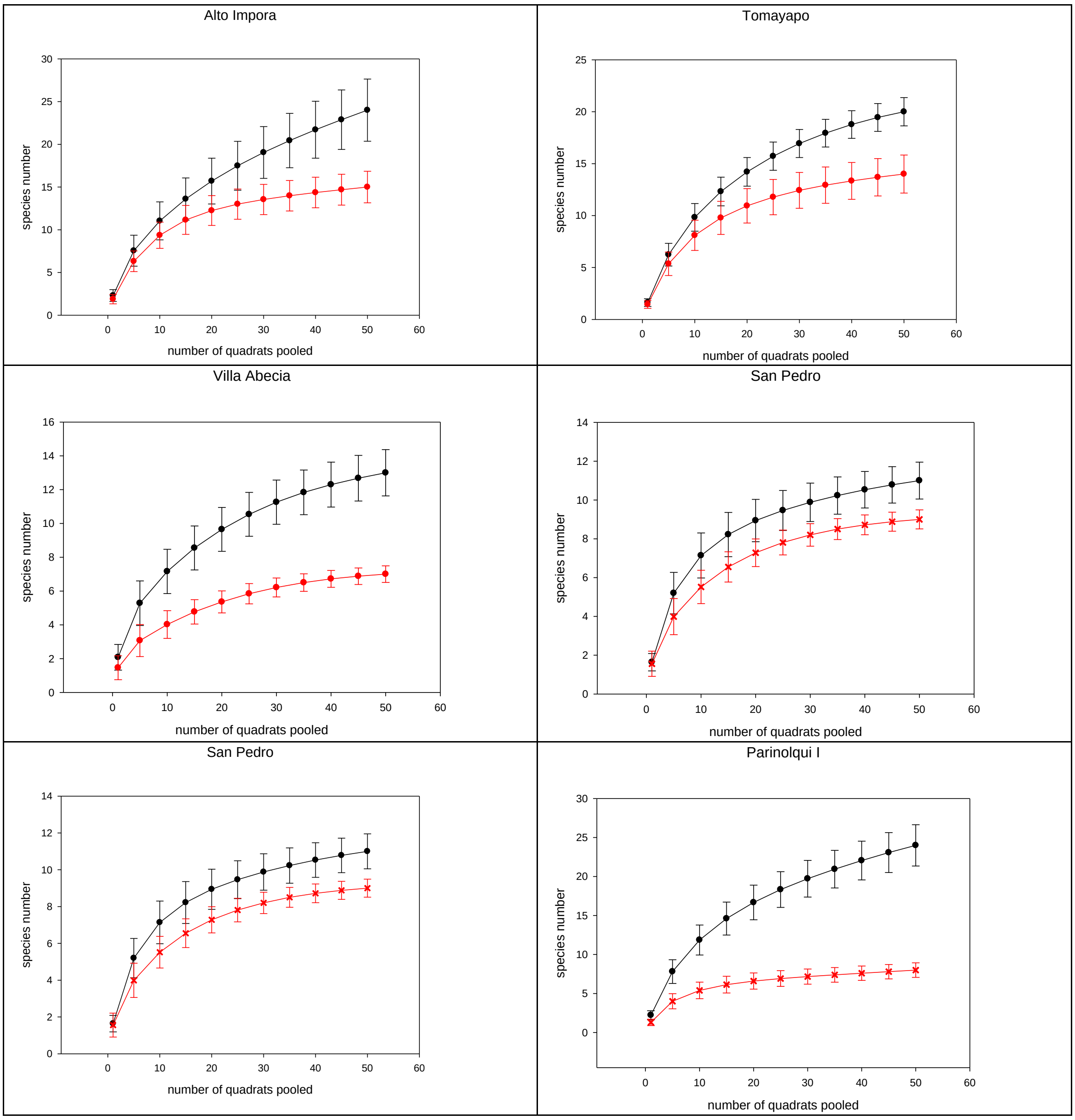
Table 2. Average number of species per quadrat.

Locality	Shrubs	Open
Alto Impora	2.3	1.5
Tomayapo	1.1	1.0
Villa Abecia	1.9	1.2
San Pedro	1.3	1.3
Cruz Huasa	1.6	1.9
Parinolqui I	2.5	0.9
Parinolqui	2.6	0.7
Cascabel	2.7	1.9
Overall average	1.9175	1.3025

Table 3. Repeated measures analysis of variance

Source of variation	df	F	Significance
Total	799		
Subjects (bloks)	399		
Site	7	8.575	<<0.01
Error	392		
Within subjects	400		
Microhabitat	1	54.833	<< 0.01
Microhabitat x site	7	9.629	<<0.01
Error	392		

The influence of shrubs at the patch scale follows a similar trend (Figure 1). In general, more herb species are found associated to the shrub undercanopies, but in some localities (Cascabel, and even in Cruz Huasa), open spaces seem to have as many species as those present beneath shrubs. In Parinolqui, there is even a tendency in open spaces towards more species (species-area curve does not show signs of reaching the asymptote). Thus, for Parinolqui, I employed the Chao 2 richness estimator to determine its potential species number, and the index indicates that there should be more species in the open (43) than in the open (26). It is interesting to compare these results with those obtained for the same zone the year before. In 2007, a humid year too, more species were found below shrubs (26) than in the open (only eight). This shows that there may be important differences from year to year in the relative importance of patch types.



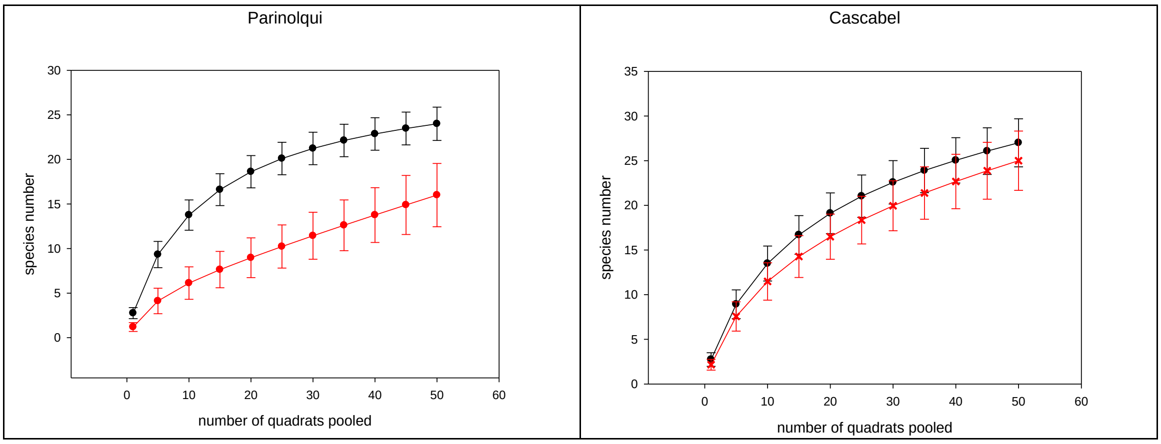


Figure 1. Rarefaction curves showing the number of species as a function of cumulative quadrat number. In all cases, the lower (red) curve represents the open spaces patch type.

The more frequent species were *Anthericum* sp. (Liliaceae), *Allionia incarnata* (Nyctaginaceae), and *Aristida adscensionis* (Graminae), which were found in 15, 14, and 14 communities (considering that each microhabitat in each locality is a community; thus, we had eight localities each with two microhabitats = 16 communities). Also quite abundant were *Euphorbia* sp. (Euphorbiaceae; 10 communities) and *Stipa ichu* (Graminae; nine communities), as well as *Heterosperma nana* (Compositae), *Polygala* sp. (Polygalaceae), *Pappophorum* sp. (Graminae) and *Mastigostyla* sp. (Iridaceae), each present in nine of the 16 communities (see Appendix). The last one could be a new species that is being described.

Of the 70 species recorded, Gramineae were by far the most speciose family (25 species). Compositae (6) and Convolvulaceae (5) were also important (see Appendix).

López & Ortuño (2008), studying four different Prepuna localities, found a consistent trend of more species at the patch scale below shrubs than in open areas. This indicated that the phenomenon was of regional importance, since in all sites the same pattern prevailed. In this study we found a similar trend, but it was more complicated. At the individual patch and the patch type levels, there were usually more species associated with the shrub undercanopies, but there were localities were this was not the case, and more species were associated to the open spaces or there were equal numbers in both microhabitats. Nonetheless, even there the contribution of shrubs was important in terms of increasing herb species richness, as some species were exclusively associated with shrubs and some were more abundant there. Those species growing only in the more mesic microhabitat conditions underneath shrubs may possess a physiology that does not enable them to establish in open areas. The populations of those species less abundant in the open might be sustained by the populations growing below shrubs, in a sort of source-sink dynamics. It may be inferred, then, that the absence of shrubs would imply the disappearance of those species present only in the shrubs' undercanopies. At least one may imagine that their abundance would be greatly reduced. In the interpretation of these results, it must be considered that this was a very rainy period. It is supposed that shrubs become more important nurse species when there is more aridity. We could expect, hence, a greater positive influence in very dry years. However, here we documented the positive role of shrubs even in good years. At least, this could be the case in summer rain semi-deserts.

The ordination of the 16 communities separates the different communities, along axis one (which describes most of the variation in the data), according to their altitude (Figure 2). In the far left are those from the lower belts (Cruz Huasa and Villa Abecia, < 2500 m) and at the other extreme are those from higher altitudes (> 2800 m). Between both groups is San Pedro, which is located at intermediate altitudes (2700 m). The fact that shrubs have a greater spread along axis one of the ordination suggests that shrubs have a more diverse herb assemblage, and thus contribute significantly also to regional diversity.

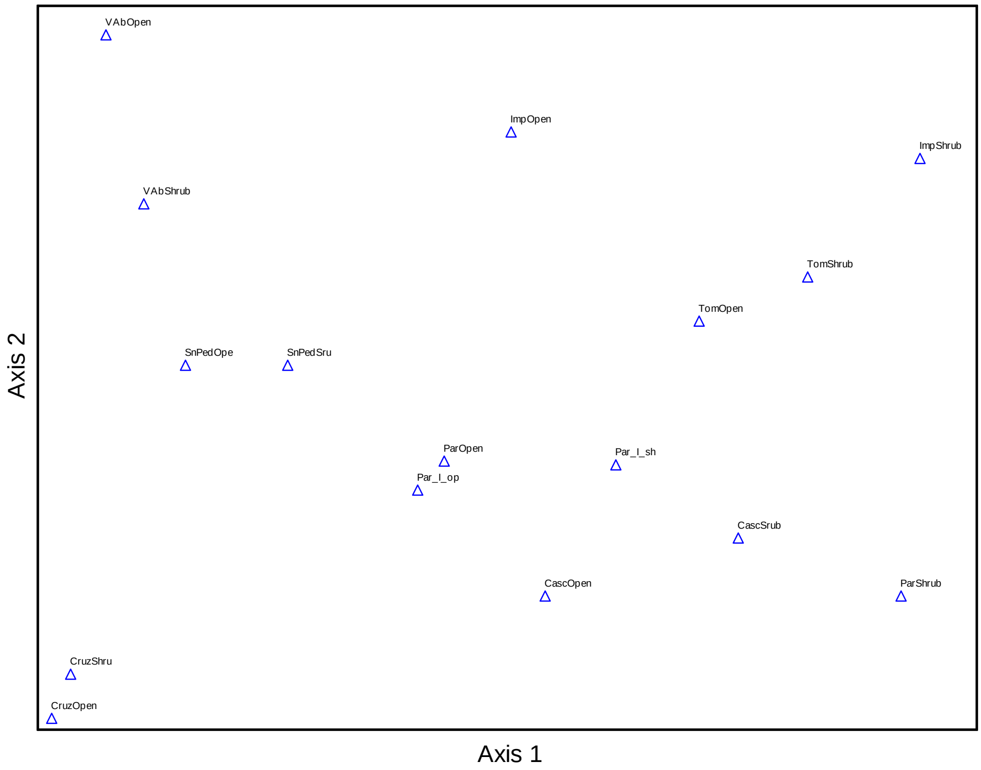


Figure 2. Ordination graph of the 16 herb communities (eight from below shrubs and eight from open spaces). Casc = Cascabel; Par = Parinolqui; Par_I = Parinolqui I; Imp = Alto Impora; Tom = Tomayapo; SnPed = San Pedro; VAb = Villa Abecia; Cruz = Cruz Huasa.

Conclusions

Shrubs placed an important role in increasing herb species richness in the Bolivian Prepuna. This effect seems to be important at different spatial scales. This finding is all the more important since this positive influence was detected in a humid year. Theory and several studies indicate that this effect should be especially pronounced in dry years, and of less importance in humid years. This could explain the fact that in a few localities as much or even more species were found in the open.

There may be important differences from year to year in the relative importance of patch types.

Different herb communities were found from locality to locality, especially along the altitudinal gradient. However, some species occurred in practically all study sites and in both microhabitats, though they were more important in one of these microhabitats.

Appendix. The species found in the study sites. The numbers indicate the number of occurrences out of 50 quadrats. Casc = Cascabel; Par = Parinolqui; Par_I = Parinolqui I; Imp = Alto Impora; Tom = Tomayapo; SnPed = San Pedro; VAb = Villa Abecia; Cruz = Cruz Huasa.

Family	Species	CascSrub	CascOpen	ParShrub	ParOpen	Par_I_shrub	Par_I_open	ImpShrub	ImpOpen	TomShrub	TomOpen	SnPedSrub	SnPedOpen	VAbShrub	VAbOpen	CruzShrub	CruzOpen
Amaranthaceae	*Gomphrena phaeotrichia*	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Amaranthaceae	*Gomphrena tomentosa*	1	2	7	10	0	0	0	0	0	0	0	0	3	0	0	0
Amaranthaceae	*Guilleminea* cf. *densa*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amaranthaceae	*Guilleminea* sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Boraginaceae	*Heliotropium abbreviatum*	0	0	4	2	2	0	4	6	7	3	0	0	0	0	0	0
Boraginaceae	*Heliotropium campestre*	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2	5
Caryophyllaceae	*Drymaria* sp.	1	0	9	0	5	0	15	0	0	0	0	0	0	0	0	0
Chenopodiaceae	*Chenopodium graveolens*	0	0	21	0	0	0	0	0	1	0	0	0	0	0	0	0
Compositae	*Coniza* sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Compositae	*Heterosperma nana*	33	7	22	1	13	0	20	2	4	0	0	0	0	0	0	0
Compositae	*Parthenium hysterophorus*	0	0	6	0	0	0	16	8	0	0	2	0	0	0	0	0
Compositae	*Pectis sessiliflora*	1	4	0	0	0	0	0	0	2	3	0	0	0	0	29	42
Compositae	*Schkuhria* sp. 1	1	3	0	0	0	0	0	0	11	16	0	0	0	0	0	0
Compositae	*Schkuhria sp. 2*	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Convolvulaceae	*Dichondra argentea*	4	1	0	0	0	0	4	5	0	0	0	0	0	0	0	0
Convolvulaceae	*Evolvolus sericeus*	4	8	0	1	14	19	0	0	0	0	12	4	0	0	0	0
Convolvulaceae	*Evolvolus* sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Convolvulaceae	*Ipomoea minuta*	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
Convolvulaceae	*Ipomoea* sp. 2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cruciferae	*Lepidium aletes*	3	0	17	1	0	0	0	0	5	2	0	0	0	0	0	0
Euphorbiaceae	*Euphorbia* sp.	1	1	3	0	1	0	4	10	10	9	0	0	0	0	3	1
Gramineae	*Aristida adscensionis*	14	18	7	1	24	19	1	7	3	7	0	0	19	1	22	32
Gramineae	*Aristida* sp.	0	0	0	0	0	0	0	0	0	0	5	7	3	2	7	3
Gramineae	*Bothriochloa* sp.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Gramineae	*Bouteloa curtipendula*	2	3	2	1	0	0	0	0	2	4	0	0	0	0	0	0
Gramineae	*Enneapogon desvauxii*	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1
Gramineae	*Eragrostis* sp.	0	0	3	1	5	0	3	0	16	11	0	0	0	0	0	0
Gramineae	*Eragrostis* sp. 2 (Impora)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Gramineae	*Eragrostis* sp. 3 (CruzHuasa)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Gramineae	*Erioneuron avenaceum*	0	0	0	0	2	4	0	1	0	0	0	0	0	0	0	0
Gramineae	*Leptochloa dubia*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Gramineae	*Microchloa* sp.	0	4	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Gramineae	*Munroa* sp.	0	0	0	0	0	0	1	1	2	4	0	0	27	23	0	0
Gramineae	Pappophoreae 1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gramineae	Pappophoreae 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Gramineae	*Pappophorum* sp. 1	12	21	2	0	5	6	0	0	0	7	1	2	0	0	0	0
Gramineae	*Pappophorum* sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Gramineae	*Sporobolus* sp.	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0
Gramineae	*Stipa ichu*	17	2	2	0	2	0	19	7	1	0	8	3	0	0	0	0
Gramineae	*Stipa sp.* 1 (h pubescent)	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gramineae	*Stipa sp.* 2 (plana)	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Gramineae	*Stipa* sp. 3 (ramif)	4	0	4	0	8	0	0	0	2	0	0	0	0	0	0	0
Gramineae	*Tripogon* sp.	5	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Gramineae	Indeterminate 1	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
Gramineae	Indeterminate 2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Gramineae	Indeterminate 3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hydrophyllaceae	*Nama dichotomun*	0	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0
Iridaceae	*Mastigostyla* sp.	0	0	0	0	6	1	0	0	4	3	6	1	3	4	0	0
Leguminosae	*Neocracca heterantha*	0	0	0	0	0	0	0	6	0	0	0	0	2	3	0	0
Liliaceae	*Anthericum* sp.	6	1	3	5	1	6	3	4	1	1	6	2	3	0	5	1
Malvaceae	*Sida argentina*	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0
Malvaceae	*Tarasa* sp.	4	2	6	1	0	0	1	0	0	0	2	0	0	0	0	0
Nyctaginaceae	*Allionia incarnata*	4	13	3	19	4	9	1	28	0	0	19	36	31	38	8	9
Oxalidaceae	*Oxalis* sp.	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Polygalaceae	*Poylgala* sp.	0	0	0	0	0	0	1	0	1	0	20	18	8	2	6	6
Portulacaceae	*Portulaca oleracea*	6	1	4	0	0	0	0	0	0	1	0	5	0	0	0	0
Portulacaceae	*Portulaca* sp. 2 (h ancha)	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Portulacaceae	*Portulaca* sp. 3	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solanaceae	*Solanum* cf. *radicans*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Solanaceae	*Solanum physalifolium*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Solanaceae	*Solanum tripartitum*	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0
Solanaceae	*Solanum* sp. (urticating)	2	0	8	0	1	0	0	0	0	0	0	0	0	0	0	0
Sterculiaceae	*Ayenia boliviana*	0	0	0	0	2	0	0	0	0	0	0	0	0	0	6	1
Verbenaceae	*Verbena scrobiculata*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Zygophyllaceae	*Tribulus terrestris*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	Indeterminate 4 (h fl lila)	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
	Indeterminate 5 (h gr_lk)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

	Indeterminate 6 (Oenothera-lk)	0	0	0	0	0	0	1	0	4	1	0	0	0	0	0	0
	Indeterminate 6 (Sclerophyllax?)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Indeterminate 7 (Galinsoga_lk)	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0