

## Some factors determining species diversity of prepuna and puna vegetations in a Bolivian Andes region

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**Background and aims** – The only semi-arid plant formations that occur in Andean Bolivia are prepuna with its associated dry valleys and puna. A quantitative ecological study was conducted in the district of Apillapampa, which is situated on the transition between the latter vegetation types.

**Methods** – Vegetation was sampled in twenty-nine 50 × 2 m<sup>2</sup> transects, yielding a total of 280 different plant taxa.

**Key results** – Floristic and ecological findings correspond well with comparable studies in prepuna and puna vegetations in Bolivia and significantly contribute to the still severely understudied Bolivian flora. Our research suggests that a significant part of the variation in species abundances in the sampled transects is explained by a combination of some of the natural and anthropogenic variables we measured. The latter include altitude, travel time (as a measure of site accessibility), proximity to a (temporal) river or stream, and evidence of firewood harvesting. Furthermore, we detected an inverse relationship between diversity of plants in transects and altitude. Of the anthropogenic disturbance variables, only cultivation of exotic tree or shrub species had a negative impact on plant diversity in transects.

**Conclusions** – Vegetation in Apillapampa is highly fragmented and of secondary nature, mainly as a consequence of past and present human activities.

**Key words** – altitudinal gradient, Andean flora, anthropogenic disturbance, diversity.

### INTRODUCTION

Arid and semi-arid plant formations in South America consist of ‘monte’, ‘prepuna’ and associated dry valleys, and the coastal desert of Peru-Chile (hot desert) on the one hand and ‘puna’ and ‘patagonia’ (cold deserts) on the other (López 2003b). Of these, only the prepuna with its associated dry valleys and the puna ecoregions occur in Bolivia. Both are situated in the Tropical Andes, which has been identified as the leading biodiversity hotspot worldwide with an estimated 20,000 endemic plant species (Myers et al. 2000). Puna stretches out from central Peru to northern Argentina, whereas contrasting concepts have been proposed referring to the geographical distribution and differential characteristics of the prepuna ecoregion. According to one concept, the prepuna would represent a dry naturally non-forested region in Southern Bolivia and Northern Argentina that can be distinguished from the ecoregion of the interandean dry forests (Ibisch et al 2003a). In the view of other authors, the prepuna represents a subdivision of the interandean valleys located in the southern part of Bolivia (López 2003b, García & Beck

2006). Navarro (2002) on the other hand, uses the term prepuna in his detailed phytosociological classification system to refer to vegetation of the altitudinal zone of the interandean valleys situated between 2,100–2,300 and 3,000–3,200 m a.s.l. Throughout the rest of this paper we have used the classification proposed by Navarro (2002) for characterising puna and prepuna vegetation.

According to Navarro (2002), the prepuna is a transitional vegetation zone and considered to be the upper part of the Bolivian dry interandean valleys *sensu lato*. The Bolivian interandean valleys (fig. 1) represent a regionally important centre of endemism (Antezana & Navarro 2002, Ibisch et al. 2003a, López 2003a). Harbouring around 16–18% endemic plant species, the flora of this ecoregion is mainly composed of locally evolved species derived from a southern-central South American stock (López 2003a & 2003b). Therefore, the plant species of the dry interandean valley regions between 1,300 and 3,200 m a.s.l. are more related to those present in southern-central South America than to the flora of northern South America that ranges southwards to Peru

(López 2003b). In terms of species, arid and semi-arid Andean plant formations are dominated by Andean elements, whereas in terms of genera, a dominance of genera with widespread distribution occurs (cosmopolitan and subtropical genera). Probably more than 2,000 species of vascular plants occur in the Andean dry valleys of Bolivia (López 2003b; Larrea-Alcazar & López 2005). Cacti and thorny leguminous trees are a more or less conspicuous characteristic of the landscape, at least in secondary vegetation.

To the west and at higher altitudes, the dry interandean valleys continue into the puna (López 2003b), termed by Ibsch et al. (2003) as the semi-humid puna bioregion. In accordance with the trend that floristic diversity decreases with rising levels of aridity, diversity in the puna region is lower than in other major Bolivian vegetation formations. Nevertheless, total species number remains high when considering the difficult habitat conditions that prevail for plant growth (García & Beck 2006). Unfavourable factors include high radiation (particularly UV-B), low temperatures, and alkaline and saline soils. In spite of limitations imposed by altitude and the extreme climatic conditions prevailing there, puna harbours about 1,500 different plant species and about forty endemic genera. Tree line in the tropical Andes generally occurs around 3,200–3,500 m (Rivas-Martínez & Tovar 1982) but tends to be slightly higher in the more subtropical Bolivian Andes (Davis et al. 1997). For example, *Polylepis* trees are known to occur up to altitudes of 4,400–5,000 m (Kessler 2006).

Various authors have argued that current low vegetation cover in the interandean valleys and puna ecoregions is consequence of a severe degradation process of various centuries of human occupation (Ellenberg 1979, Kessler & Driesch 1993, Ibsch & Rojas 1994, Ibsch 1994a, 1994b, 2002 & 2003, Ibsch et al. 2003b, Paduano et al. 2003). The highlands of the central Andes have been inhabited for at least 15,000 years (Dollfus 1984). According to Ibarra (1986), colonisation of the Bolivian Andes might even have started as early as 30,000 year ago. Overexploitation of natural resources by man has restricted remaining relicts of the original climax vegetation mainly to sites with low accessibility (Kessler & Driesch 1993, Ibsch & Rojas 1994, Ibsch et al. 2003b, Thomas et al. 2009b).

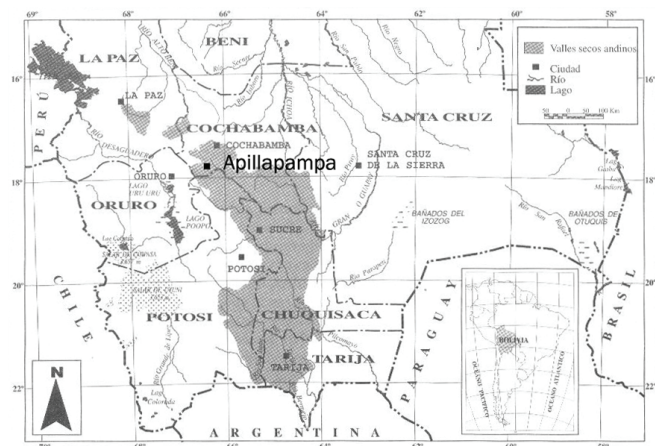


Figure 1 – Dry interandean valleys according to Lopez (2003a & b).

The aim of this paper is to describe the current, mainly secondary vegetation from the district of Apillapampa that is situated on the transition between puna and prepuna, in accordance with Navarro's (2002) classification system. Based on transect data, it is verified whether the altitudinal delimitation between both vegetation zones as described by Navarro (2002) is also valid for our research area. Next, the dominant species and families in both vegetation zones are presented. Finally, the impact of a number of measured (natural and anthropogenic) environmental variables on the actual floristic composition and diversity in transects is examined.

## MATERIAL AND METHODS

### Research area

The present study was conducted in the district of Apillapampa (Capinota province, department of Cochabamba, Bolivia), named after the principal Andean community of subsistence farmers it harbours. The community of Apillapampa is situated at about 3,250 m a.s.l. and 17° 51' S, 66° 15' W, along

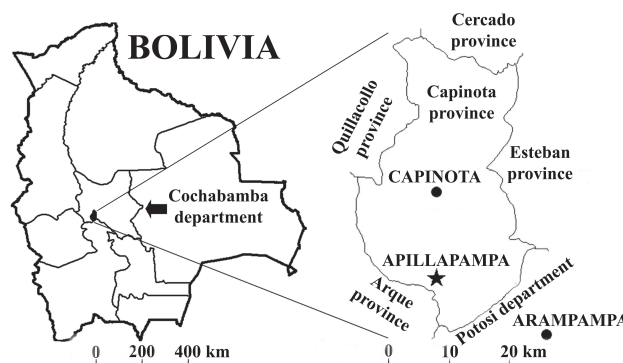


Figure 2 – Location of the study area within Bolivia and Capinota province, respectively. The city of Cochabamba is situated just north of Capinota province (map elaborated with DIVA-GIS (www.diva-gis.org)).

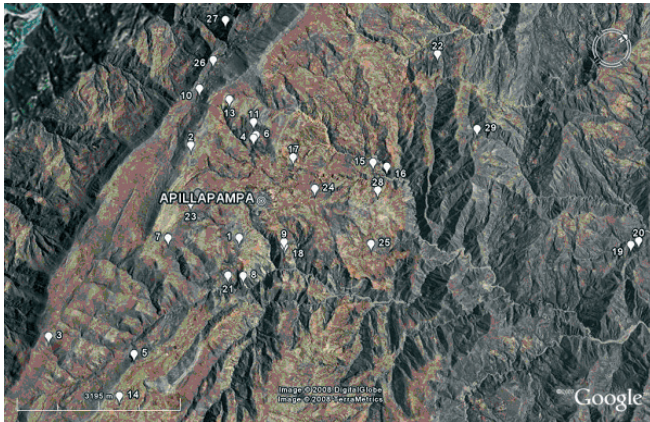
the road connecting Capinota with Arampampa (fig. 2). No on-site climate data are available, but the nearest village of Capinota (2,400 m a.s.l.) is characterized by a semi-arid bioclimate with a mean annual temperature of 17.8°C and mean annual precipitation of 447 mm (Navarro 2002). Hence, a somewhat lower temperature and higher precipitation can be expected for Apillapampa. Rainfall is concentrated in a rainy season; there is a pronounced dry season with 6–8 arid months (Ibsch et al. 2003a).

Vegetation in the study area is highly fragmented and degraded as a result of past and present human activity (Pedrotti et al. 1988, Navarro 2002, Ibsch et al. 2003a, García & Beck 2006, Thomas et al. 2009b). People in Apillapampa make exhaustive use of the wild flora (Thomas et al. 2008, 2009a & 2009b). At present, agriculture, animal husbandry and firewood harvesting are among the most important factors causing fragmentation, since most households own agricultural fields at different altitudes along the vertical vegetation gradient (Pedrotti et al. 1988, Thomas 2009). Relicts of climax vegetations are mainly situated on soils with limited

agricultural potential and/or in areas that are more or less safeguarded from harvesting of firewood and intensive grazing by livestock.

### Field sampling

Ecological and botanical data of the herbaceous and (sub-) woody flora of the study area were collected between December 2002 and May 2003 by means of twenty-nine 0.01-ha transects of  $50 \times 2 \text{ m}^2$  (fig. 3). All sites were reached after walks in the presence of the land owner or a relative. At each site, transects were constructed in areas that had not been visibly influenced by agricultural practices over the last years. However, due to severe landscape fragmentation, it was impossible to find sites with completely undisturbed vegetation. All sites had at least partly been subjected to harvesting of firewood or grazing by livestock. In some cases, there was evidence of (recent) burning, or cultivation of exotics such as *Pinus radiata*, *Eucalyptus globulus* or *Spartium junceum*. Under custody of the local N.G.O. FEPADE (1998), people started planting these species in the remaining wild vegetation in very low densities. Following the advice of Bonham (1989), individual transects were separated by horizontal distances of a minimum of one hundred meters. To guarantee comparison between transects that are constructed on different slopes (Roberts-Pichette & Gillespie 1999), a horizontal transect surface of  $100 \text{ m}^2$  was set standard. In each transect, slope corrections were performed for all different sections with noticeable slope change separately (up to five different sections).



**Figure 3** – Distribution of transects sampled in the vicinities of Apillapampa (source: Google Earth accessed 19/3/2008).

For every transect, the following environmental parameters were measured: (1) mean altitude of transect (range: 2,850–3,750 m a.s.l.); (2) travel time from Apillapampa village centre to transect (on foot; range: 22 min to 3 h 25 min); (3) mean transect slope (range: 5.7–40.8°); (4) exposition (measured as compass bearing parallel to dominant site slope, downhill side; range: 15–355°); (5) whether or not exotics (*E. globulus*, *P. radiata* or *S. junceum*) had been planted in or nearby the transect; (6) whether or not a (periodical) river occurred in direct vicinity (< 10 m away) of the transect; (7) whether or not there was evidence of fire-

wood harvesting; (8) whether or not there was evidence of grazing; (9) whether or not there was evidence of vegetation burning; and (10) whether or not there were paths crossing the transect. Travel time was taken as a proxy for site accessibility. Altitude and slope were measured with a Suunto X6 altimeter.

However, it is proper to point out some potential bias in these environmental data. Whereas mean altitude, transect slope and exposition were sampled more or less evenly over the entire spectrum, repetitions of long travel times were fewer than for short travel times. The presence-absence variables ‘firewood’, ‘grazing’ and ‘fire’ may also be subjected to bias. They represent only a limited number of observations (taken at the time of sampling) whereas an absence status may have been assigned erroneously to transects when evidence had already vanished.

Also important to note here is that the measured variables are clearly insufficient to characterize all possible environmental and anthropogenic impacts on local vegetation. Important anthropogenic variables that have not been taken into account are, for example, (past and present) local land use and ownership (Ibisch 1994b). The attitude of individual land owners towards conservation and sustainable use of existing vegetation strongly influences the presence or absence of specific (relict) vegetations in the study area (Ibisch 1994b, Thomas 2009). Examples of important environmental variables that have not been considered are hydrological (e.g. water level, flow, frequency...) and physicochemical (e.g. soil texture and structure) characteristics of sample sites.

In each transect, all non-Poaceae individuals of plant species with a height or length of  $\geq 0.1 \text{ m}$  at maturity were systematically counted. The reason for excluding Poaceae from our sampling related to the practical difficulties of counting individual plants in this family, whereas this was relatively straightforward for species in all other plant families. Small crawling herbs rooting at their nodes with internodes of less than 0.1 m were not included. When it was not possible to separate individual shrubs from one another, we treated each different clump as an individual, following the advice of Roberts-Pichette & Gillespie (1999). Only those plant individuals of which more than half of the number of ramets were on the inside of the transect-line were counted. Every individual was recorded as a unique ‘morphospecies’. Subsequently, a voucher collection was made according to botanical standards if the taxon was encountered for the first time or in case its botanical identification was uncertain. Collected specimens were identified by the first author in the Herbario Nacional Forestal “Martín Cárdenas” of Cochabamba and by international taxonomical specialists (see acknowledgements). Cronquist’s (1988) taxonomy was followed for reasons of comparison with relevant literature, as well as for practical reasons since Bolivian herbaria adopted this classification. Authors of plant names in the text are only given when a taxon is not included in the electronic appendix. Fabaceae-Caesalpinioideae, Fabaceae-Mimosoideae, and Fabaceae-Papilionoideae were pooled together into Fabaceae. Voucher specimens were deposited in the Bolivian herbaria of Cochabamba (BOLV) and La Paz (LPB).

### Data analysis

Diversity in transects is expressed as Alpha diversity (i.e. species number or richness) and Shannon-Wiener diversity (H, hereafter called Shannon diversity). Shannon diversity is calculated as  $H = -\sum p_i \times \log(p_i)$ , whereby  $p_i$  is the proportional abundance of species  $i$  on the total abundance of all species. Therefore, Shannon diversity considers both species richness and evenness (i.e. equality in the abundances of each species).

To determine whether the sampled transects are representative for the flora of Apillapampa, a species-area curve was constructed by means of the BioDiversity-Pro program (McAleece 1997). It plots the number of new species accumulating as the transect samples are randomly pooled.

We used correspondence analysis (CA) to assess the hypothetical border between prepuna and puna vegetation in our research area. Canonical correspondence analysis (CCA) was applied to identify which of the environmental variables measured during the present study explain the variation in abundance of species best. The use of these unimodal response models (CA and CCA) is justified because the lengths of gradients were larger than two standard deviations (2 s.d.) (Jongman et al. 1996). Lengths of gradients were determined by means of detrended correspondence analysis (DCA). Ordination analyses were performed in PC-Ord 4.0 (McCune & Mefford 1999). The main matrix consisted of rows with transect data and columns with species data. Cells contained the number of individuals by which species were represented in transects. In the second matrix, rows also represented transect data while columns were environmental variables. Transect scores were centred and normalized such that the mean was zero and the variance one. Following the recommendation of Ter Braak (1994), scores for rows in the main matrix (i.e. transects) were calculated as linear combinations of the columns in the second matrix (i.e. environmental variables). The existence of a relationship between main and second matrix was tested by means of a Monte Carlo test, which investigates how the observed eigenvalues and species-environment correlations compare with those from randomized runs (McCune & Mefford 1999). The significant contribution of environmental variables to the ordination axes was examined by means of intraset correlations,

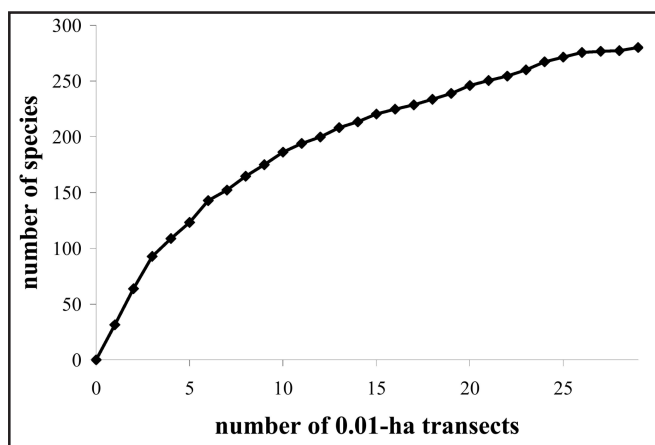


Figure 4 – Species-area curve of 29 transects.

whereby it was assumed that only values  $> |0.5|$  contribute substantially to the axis.

Pearson and Kendall correlations, linear regressions and t-tests were performed in SPSS 12.0.

## RESULTS AND DISCUSSION

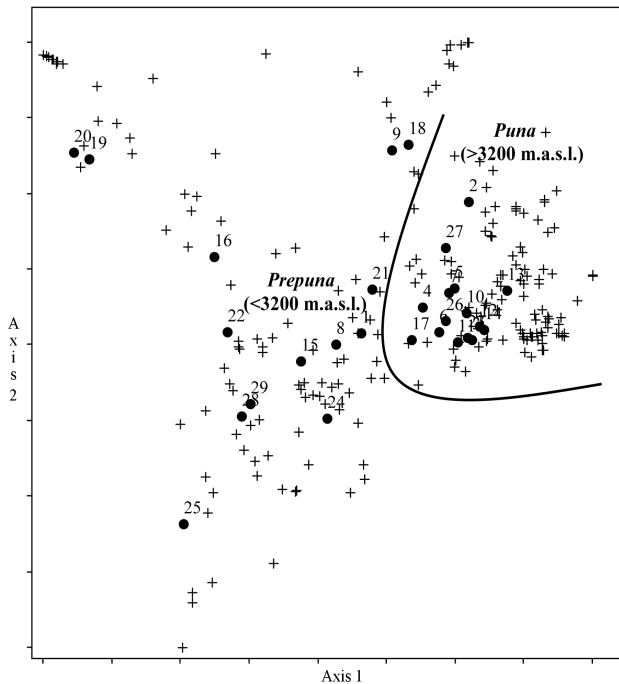
### Floristic composition and sampling effort

The 29 transects that were sampled contained a total of 280 taxa, belonging to 68 families (see Appendix). The ten plant families that were best represented by number of species are: Asteraceae (31%), Fabaceae (8.5%), Solanaceae (5.3%), Asclepiadaceae (3.6%), Lamiaceae (3.6%), Verbenaceae (2.9%), Cactaceae (2.5%), Apiaceae (2.1%), Convolvulaceae (2.1%) and Scrophulariaceae (2.1%). Pteridophyta were represented by ten species (3.9%) and four families. The non-Poaceae vegetation consisted principally of herbs (59.3% of all species), followed by shrubs (i.e. (sub-)woody and  $\leq 4$  m high; 26.9% of all species). Trees represented only 3.3% of all collected plant species. In our complete plant inventory of Apillapampa (441 taxa, including species found outside of transects; see Thomas 2009), Poaceae represent 6% of species.

The floristic composition at family level of the plants sampled in the study area corresponds well with data from literature. According to Moraes & Beck (1992), the flora of the interandean valleys and the high Andes, which covers our research area, is characterized by a more or less constant presence of 18–28% Asteraceae, 15–19% Poaceae, 4–7% Fabaceae, 3% Scrophulariaceae, 3% Apiaceae and  $\leq 5\%$  Pteridophyta. Based on all collections that are deposited in Bolivia's national herbarium (LPB), López (2003a), calculated that the most species-rich botanical families for the interandean dry valleys are Asteraceae (16%), Cactaceae (9%), Poaceae (9%), Fabaceae (8%), Solanaceae (5%), Bromeliaceae (4%), Pteridophyta (4%), Malvaceae (3%), Euphorbiaceae (3%), Verbenaceae (2%), Lamiaceae (2%), Asclepiadaceae (2%). Similar results are presented by Antezana and Navarro (2002). Finally, also the largest families recorded by Ibisch and Rojas (1994) in a study of the flora of neighbouring Arque province (fig. 2) are quite similar to those of the present study, despite some significant proportional differences: Asteraceae (17.5%), Poaceae (12%), Fabaceae (5.5%), Solanaceae (4%), Cactaceae (3.8%), Caryophyllaceae (3.4%), Scrophulariaceae (2.9%), Bromeliaceae (2.6%), Apiaceae (2.1%), Pteridaceae (2.2%) and Lamiaceae (2.2%).

As our calculations do not include Poaceae, they give a slight overestimation of non-Poaceae families, compared to results from other studies in literature. It is, however, clear that similar patterns are observed at very different scales and that the dominant families given in literature largely coincide with the families that are best represented in this study, although actual proportions may differ.

Alpha diversity in the sampled transects varied between 12 and 67 species (mean  $41 \pm 13$ ), whereas Shannon diversity varied between 1.64 and 3.61 (mean  $2.54 \pm 0.39$ ). The number of individual plants in transects ranged between 115 and 4,949 (mean  $1,506 \pm 950$ ). Thirty-three percent of all sampled plant species occurred in only one transect.



**Figure 5** – Ordination diagram of a Correspondence Analysis (CA). Dots (●) with numbers represent transects and crosses (+) mark the points where species abundance is highest, with (imaginary) concentric circles away from the species position indicating lower abundance of a species (Kindt & Burn 2002). Scores of transects with high numbers of individuals for a given species tend to be close to the score of that species in the diagram. Hence, the closer together transects are represented, the more their species compositions will correspond. For clarity species names are not given.

There exists a positive correlation between the diversity of a transect and the number of species that were found exclusively in that transect ( $R = 0.58$ ;  $p = 0.001$  for Alpha diversity and  $R = 0.63$ ;  $p < 0.001$  for Shannon diversity; Pearson correlation).

To determine whether the 29 sampled transects are representative for the flora of Apillapampa, a species-area curve was constructed. Figure 4 shows that the slope of the curve declines as the sample area increases. The curve clearly starts to level off after 29 transects and enlarging the sample area would probably have yielded only a few more species.

#### Determining the border between prepuna and puna vegetation

Correspondence analysis was applied to detect whether groupings of transects can be distinguished on the basis of species composition and abundance. The eigenvalues of the first two ordination axes are higher than 0.5 (0.79 and 0.63, respectively; explaining 17% of total variance in data), indicating a good dispersion of species scores (Jongman et al. 1996).

Figure 5 shows how transects cluster together more or less according to their altitudinal zoning. Transects that were sampled in puna vegetation (i.e.  $> 3,200$  m a.s.l.) form a rather dense group whereas prepuna transects (i.e.  $< 3,200$

m a.s.l.) occur much more dispersed. Hence, transects in the puna vegetation seem to be much more alike floristically than transects from the prepuna area. Of course, the dividing line between in fig. 5 is hypothetical and solely based upon our data. The transition from one ecological zone to another will not occur abruptly but rather gradually extend over 100–200 altitudinal meters (Navarro 2002, García & Beck 2006). Transect scores that are situated near to the dividing line in fig. 5 (especially 1 and 21) are located in this transition zone and contain elements that are characteristic for both prepuna and puna. By contrast, transects 9 and 18 had a rather distinct floristic composition as compared to other transects. Both were sampled on a site consisting of giant rocks, thus creating a peculiar sort of microclimate with apparently reduced evaporation throughout the dry season.

Altitude above sea level seems to be the environmental variable with the greatest influence on the species composition of a transect and is most likely significantly correlated with the first axis in fig. 5. Altitude increases from left to right on axis 1. The lowest sampled transects are 19 and 20, situated at 2,850 m a.s.l., followed by transects 16 (2,910 m a.s.l.) and 25 (2,960 m a.s.l.). Transects with highest locations are transects 2 (3,750 m a.s.l.), followed by 13 (3,670 m a.s.l.), 14 (3,630 m a.s.l.) and 10 (3,610 m a.s.l.). Species overlap between the highest and lowest transects is almost zero.

**Table 1** – Dominance for the twenty most common families in the sampling area. Values represent percentages of individuals.

Family	Entire area	Prepuna	Puna
Asteraceae	34.4	29.8	36.2
Fabaceae	17.0	16.4	17.4
Oxalidaceae	6.1	-	9.3
Apiaceae	5.9	1.1	8.6
Lamiaceae	5.5	4.4	6.6
Verbenaceae	4.2	6.4	3.0
Convolvulaceae	3.9	7.0	2.3
Solanaceae	3.4	5.0	2.5
Plantaginaceae	3.1	3.4	2.9
Rhamnaceae	1.5	4.1	-
Amaranthaceae	1.2	2.8	-
Araceae	1.2	3.2	-
Geraniaceae	1.1	-	1.8
Scrophulariaceae	1.1	1.0	1.2
Ranunculaceae	1.0	0.9	1.1
Berberidaceae	0.9	-	1.4
Cheilanthaceae	0.7	0.9	0.6
Adiantaceae	0.5	-	0.5
Malvaceae	0.4	1.2	-
Cactaceae	0.4	1.1	-
Total other families	5.9	10.6	4.3
Total number of species	280	212	153
Total number of families	68	59	50

### Dominant species and families in puna and prepuna vegetation

As demonstrated by the outcomes of ordination analyses, transects are separated in two main groups representing prepuna and puna vegetation, respectively, whereby 3,200 m a.s.l. can be used as an approximate dividing limit. In the following, the latter limit will be used as a simplified interpretation of reality to discuss the dominant families and species of both zones. Thirteen and sixteen transects were sampled in prepuna and puna, respectively.

The number of species encountered in the puna zone was considerably lower than in the prepuna zone. Two hundred and twelve (212) plant species were encountered in prepuna transects as opposed to 153 for puna. Also, the number of families that was represented by at least one individual was higher for prepuna transects than for puna transects (59 versus 50).

The best-represented families in terms of total number of individuals in all sampled transects were Asteraceae, Fabaceae, Oxalidaceae, Apiaceae, Lamiaceae and Verbenaceae

**Table 2 – Most abundant species in all 29 transects sampled.**

Absolute density represents the total number of individuals per plant species counted in all 29 transects. Relative density is the proportion of individuals of a species from the total number of individuals in all transects. Relative frequency is the proportion of the frequency of a species from the sum of frequencies of all species. Note that fifteen of the twenty most abundant species have herbaceous growth forms.

	Absolute density (#ind)	Relative density (%)	Relative frequency (%)
<i>Trifolium amabile</i>	2,659	5.6	1.2
<i>Eryngium nudicaule</i>	2,562	5.4	0.6
<i>Oxalis eriolepis</i>	2,192	4.6	1.2
<i>Viguiera tucumanensis</i>	1,790	3.7	1.9
<i>Bidens andicola</i>	1,741	3.6	1.2
<i>Cologania broussonetii</i>	1,292	2.7	0.9
<i>Minthostachys andina</i>	1,196	2.5	1.5
<i>Glandularia aristigera</i>	1,108	2.3	0.9
<i>Plantago tomentosa</i>	918	1.9	1.1
<i>Stevia galeopsidifolia</i>	880	1.8	0.8
<i>Melilotus indicus</i>	865	1.8	1.0
<i>Solanum acaule</i>	799	1.7	1.2
<i>Salvia haenkei</i>	769	1.6	1.2
<i>Stevia</i> aff. <i>bangii</i>	707	1.5	0.5
<i>Kentrothamnus weddellianus</i>	706	1.5	0.7
<i>Cosmos peucedanifolius</i>	702	1.5	0.7
<i>Adesmia miraflorensis</i>	670	1.4	0.8
<i>Stevia boliviensis</i>	663	1.4	0.8
<i>Stevia tunariensis</i>	629	1.3	0.5
<i>Lantana balansae</i>	555	1.2	0.4
Total of other species	24,206	50.6	80.9
Total	47,799	100	100

(table 1). Asteraceae and Fabaceae dominated the overall prepuna and puna floras, representing 46% and 54% of total number of individual plants, respectively. The (sub-)woody flora was dominated by Lamiaceae, Verbenaceae, Rhamnaceae and Asteraceae in the prepuna zone. These four families alone embodied 71% of all sampled (sub-)woody prepuna plants. Rhamnaceae and Verbenaceae representatives largely disappeared in the (sub-)woody puna flora which was dominated by Asteraceae and Lamiaceae (accounting for 64% of all plants). Asteraceae granted its overall dominance in the research area to the high number of species by which it was represented, rather than to high abundances of a few species (Thomas 2009).

In table 2, plants are ranked according to decreasing abundances. Species with the highest abundances in the overall flora were small herbs, such as *Trifolium amabile*, *Eryngium nudicaule* and *Oxalis eriolepis* (represented by > 2000 individuals each). Most frequent species were *Viguiera tucumanensis* (in 83% of transects), *Baccharis dracunculifolia* (83%), *Ophryosporus heptanthus* (76%) and *Minthostachys andina* (66%). Even though (sub-)woody species might be more evenly distributed over the landscape, as evidenced by higher frequencies, these data suggest that in terms of abundance the vegetation in the wet season in Apillapampa is dominated by herbaceous plants. Most abundant (sub-)woody plants were *Minthostachys andina*, *Salvia haenkei*, *Kentrothamnus weddellianus*, *Adesmia miraflorensis*, *Lantana balansae* and *Baccharis dracunculifolia*.

In table 3, the twenty most abundant species are listed for the prepuna and puna ecological zones, separately. An immediate eye-catcher is that absolute densities of these species in the puna zone are almost consistently 1.5–2 times higher than in the prepuna zone. This is in accordance with our finding presented further on in table 5 that the number of individuals in transects correlates positively with altitude. As shown in table 3, the most abundant species in both zones were quite distinct and only five genera and three species overlapped: *Cologania broussonetii*, *Viguiera tucumanensis* and *Plantago tomentosa*.

*Cologania broussonetii*, *Kentrothamnus weddellianus* and *Stevia* aff. *bangii* were the most abundant species in the prepuna transects, whereas *Viguiera tucumanensis* (in 85% of prepuna transects), *Baccharis dracunculifolia* (77%) and *Tagetes terniflora* (77%) were the most frequent ones. In terms of vegetation cover, other authors have likewise identified *K. weddellianus* as the most dominant woody species in comparable prepuna sites (see Navarro 2002). In the puna zone, the most abundant species were *Trifolium amabile*, *Eryngium nudicaule* and *Oxalis eriolepis*. *Ophryosporus heptanthus* (sampled in all (100%) puna transects), *Minthostachys andina* (88%) and *Baccharis dracunculifolia* (88%) were the most frequent species.

According to the phytosociological classification of Navarro (2002), two main ecological zones can be distinguished in the prepuna flora (roughly between 2,300 and 3,200 m a.s.l.). The first ranges from 2,300–2,400 to 2,700–2,900 m a.s.l. and is characterized by a combination of the climax vegetation species *Schinopsis haenkeana* and *Aspidosperma quebracho-blanco* Schltdl., often being replenished with

**Table 3 – Most abundant and most frequent species in prepuna and puna transects.**

Species are ranked in order of decreasing density, species density is expressed here as the mean number of individuals per transect (i.e. 100 m<sup>2</sup>).

<i>Prepuna</i>				<i>Puna</i>			
	dens (# ind/ 100 m <sup>2</sup> )	rel dens (%)	rel freq (%)		dens (# ind/ 100 m <sup>2</sup> )	rel dens (%)	rel freq (%)
<i>Cologania broussonetii</i>	69	5.2	1.2	<i>Trifolium amabile</i>	165	8.5	2.1
<i>Kentrothamnus weddellianus</i>	54	4.1	1.4	<i>Eryngium nudicaule</i>	159	8.2	1.1
<i>Stevia aff. bangii</i>	50	3.8	0.8	<i>Oxalis erirolepis</i>	132	6.8	1.4
<i>Lantana balansae</i>	43	3.2	0.8	<i>Bidens andicola</i>	104	5.4	1.8
<i>Spathantheum orbignyana</i>	42	3.2	0.9	<i>Viguiera tucumanensis</i>	78	4.0	2.1
<i>Viguiera tucumanensis</i>	42	3.2	1.7	<i>Minthostachys andina</i>	66	3.4	2.2
<i>Dalea boliviana</i>	42	3.2	0.3	<i>Stevia galeopsidifolia</i>	55	2.8	1.6
<i>Medicago lupulina</i>	35	2.6	0.3	<i>Glandularia aristigera</i>	55	2.8	0.6
<i>Zinnia peruviana</i>	34	2.6	1.4	<i>Melilotus indicus</i>	50	2.6	1.4
<i>Solanum acaule</i>	32	2.4	1.2	<i>Cosmos peucedanifolius</i>	44	2.3	1.4
<i>Onoseris alata</i>	30	2.3	0.6	<i>Salvia haenkei</i>	42	2.2	1.6
<i>Eupatorium clematideum</i>	24	1.8	0.9	<i>Adesmia miraflorensis</i>	41	2.1	1.3
<i>Conyza bonariensis</i>	24	1.8	0.6	<i>Stevia boliviensis</i>	39	2.0	1.3
<i>Gnaphalium gaudichaudianum</i>	24	1.8	1.1	<i>Plantago tomentosa</i>	39	2.0	1.4
<i>Plantago tomentosa</i>	23	1.7	0.8	<i>Stevia tunariensis</i>	33	1.7	0.8
<i>Crotalaria sagittalis</i>	22	1.6	0.2	<i>Geranium soratae</i>	30	1.5	0.8
<i>Hypochaeris chillensis</i>	20	1.6	1.2	<i>Gnaphalium melanosphaeroides</i>	30	1.5	1.1
<i>Glandularia aristigera</i>	18	1.4	1.2	<i>Amicia cf. andicola</i>	26	1.4	0.3
<i>Proustia cuneifolia</i>	14	1.1	1.4	<i>Ophryosporus heptanthus</i>	25	1.3	2.5
<i>Salpichroa tristis</i> var. <i>tristis</i>	14	1.1	0.5	<i>Cologania broussonetii</i>	25	1.3	0.5
Total of other species (all transects)	8,746	50.2	81.8	Total of other species (all transects)	10,421	35.1	72.1
Total	17,275	100	100	Total	30,524	100	100

*Vasconcellea quercifolia* (also see Ibsch 1994b). The second zone ranges from 2,600–2,700 to 3,100–3,200 m a.s.l. and has a potential climax vegetation dominated by *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnst., *Kageneckia lanceolata* and *Schinus molle*. In eroded soils or intermittently burned zones, this vegetation is substituted by shrubs, including *Dodonaea viscosa* and *Baccharis dracunculifolia* (Pedrotti et al. 1988). According to our transect data and observations most of the characteristic species of the climax vegetation have a low to extremely low abundance in current vegetation.

In line with Ibsch (1994b), Navarro (2002) and our own observations, potential climax vegetation of the puna ecological zone between 3,100–3,200 and 3,900–4,000 m a.s.l., is formed by *Polylepis besseri* and *Berberis commutata*. *Berberis rariflora* and *Schinus microphyllus* are among the associated species. Although there still are some limited relict areas with puna climax vegetation in the study area, most of it has been replaced by shrub- or grassland with very few individual trees. Apart from the study of Ibsch & Rojas (1994) and Ibsch (1994a & 1994b), which does, however, not distinguish between prepuna and puna vegetation, no representative inventories were found in literature for puna vegetation. Nonetheless, most characteristic genera for this ecological zone mentioned by Navarro (2002) were also represented in our floristic data. These include: (1) the woody

genera *Berberis*, *Schinus*, *Dunalia*, *Barnadesia* and *Mutisia*; (2) the herbaceous genera *Bowlesia*, *Bomarea*, *Thalictrum*, *Solanum* and *Bartsia*; and (3) the Pteridophyta genera *Adiantum* and *Asplenium*. Pestalozzi (1998) performed a study of the high Andean vegetation. Although his study area was situated at a higher altitudinal range (3,800–4,500 m a.s.l.) as ours (2,850–3,750 m a.s.l.), the author collected many species that are also represented in our inventory.

Hence, in spite of some local differences, our data seem to correspond fairly well with floristic inventories from other biographical prepuna and puna areas. It is also clear that the currently remaining vegetation in Apillapampa is largely secondary. The degraded state of vegetation is reflected in the floristic composition and structure we recorded from our prepuna and puna samples. Abundance of several poisonous species (e.g. *Astragalus garbancillo*, *Heterophyllaea lycioides*) and spiny plants belonging to genera and families such as *Tetraglochin*, *Barnadesia*, *Adesmia*, *Berberis*, *Acacia*, *Prosopis*, *Proustia*, Cactaceae and Rhamnaceae are an (in)direct effect of overgrazing (Ibsch & Rojas 1994, Ibsch 1994b & 2003). Other species with pioneering characteristics such as *Satureja boliviana*, *Senecio pampeanus*, *Nicotiana glauca* and many species from the genus *Baccharis* (notably *B. dracunculifolia*, the second-most frequent species in all transects) indicate considerable alteration of the natural potential of soil and vegetation (Pedrotti et al. 1988, Ibsch

**Table 4 – Intraset correlations.**

Indicates the relations between environmental variables and ordination axes for fitted site scores (CCA). Only values > |0.5| contribute substantially to the axis.

Variable	Axis 1	Axis 2
Travel time	-0.281	<b>0.784</b>
Altitude	<b>0.939</b>	0.152
Slope	-0.358	0.061
Compass	-0.200	0.185
Firewood	0.020	<b>0.601</b>
Path	-0.039	-0.256
River	-0.148	<b>-0.544</b>
Plantation	-0.249	-0.476
Fire	-0.005	-0.152

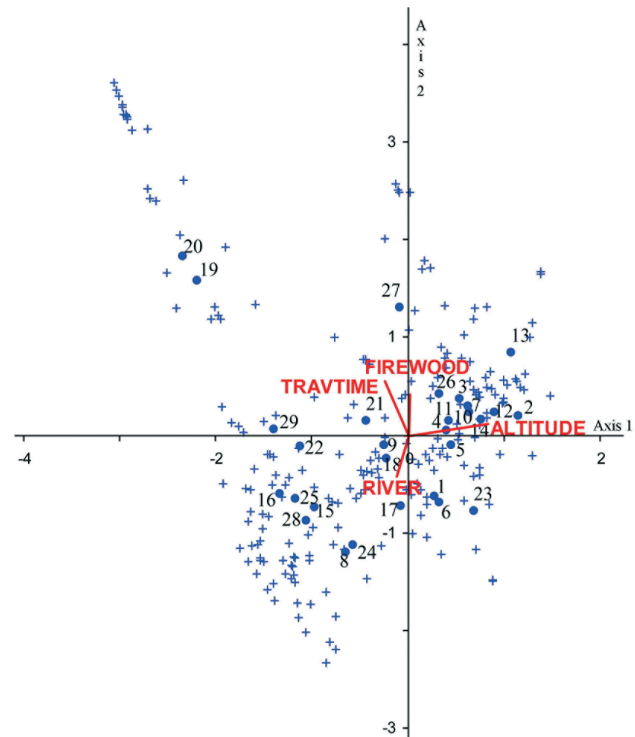
1994b). Likewise, the in the research area relatively common fire-tolerant shrub *Dodonaea viscosa* typically establishes on degraded soils (Pedrotti et al. 1988, Ibsch 1994b, Navarro 2002). Finally, also a number of introduced Old World species (16 – mainly weeds; see appendix) were found in transects. Since most of these typically flourish in disturbed habitats (Ibsch 1994b, Ibsch 2003), their presence in natural vegetation points to the degraded state of the latter. Based on abundance data, some of these species could even be considered as invasive (e.g. *Melilotus indica*, *M. lupulina*).

A number of species identified by Pedrotti et al. (1988), Ibsch (1994b), Navarro (2002) and Wood (2005) as characteristic for the vegetation of our research area, such as *Escallonia millegrana* Griseb., *Zanthoxylum coco* Gill. ex Hook. & Arn., *Tipuana tipu*, *Prosopis laevigata*, *Erythrina falcata* Benth., *Acacia visco* Griseb. or *Jacaranda mimosifolia* D.Don, *Aspidosperma quebracho-blanco*, *Salix humboldtiana* Willd. and *Alnus acuminata* Kunth were only sampled during fieldtrips (in some cases only as cultivated species) but not in transects (Thomas 2009). As argued before, it is highly likely that the scarce abundance of these species is mainly determined by past and present anthropogenic pressure that led to their depletion (Ibsch 1994b). In order to gain more insight into some of the factors that contribute to determining the current distribution of species in the research area, in the following paragraphs we will evaluate the impact of some environmental variables (anthropogenic and natural) on species composition in transects.

**Which of the measured environmental variables explain the variation in species abundance data best?**

An appropriate technique to answer this question is CCA (Ter Braak 1986). Eigenvalues of the first two axes (explaining 15.5% of total variance in data) are higher than 0.5 (0.771 and 0.514, respectively), which indicates a good dispersion of species scores over the ordination axes. Monte Carlo test results revealed that correlations between species and environmental parameters are significant for the first two axes ( $p < 0.01$  in both cases). Altitude correlates best with the first axis, whereas travel time, firewood harvest and proximity to a river correlate with the second axis (table 4).

Figure 6 shows a picture that is largely similar to fig. 5. Dispersion of transects over the first ordination axis is similar for both CA and CCA (Kendall's  $t_b = -0.95$ ;  $p < 0.001$ ), since eigenvalues of the first two axes are only slightly lower for CCA as compared to CA. These data confirm our initial impression that the first CA axis correlates with altitude. Division of transects based on altitude is even more apparent in the CCA diagram (fig. 6) than for CA (fig. 5). Transect scores of the prepuna zone are situated on the left side of the second axis (the only exception being transect 27). Correspondence between CA and CCA is much lower for dispersion of



**Figure 6** – Ordination diagram representing the first two axes of a canonical correspondence analysis (CCA). Crosses (+) and dots (•) with numbers represent species and transects, respectively. Transects with high abundance of a species tend to be close to the point of that species. The position of species scores (i.e. +) indicates where species abundance is highest, with (imaginary) concentric circles away from the species score indicating lower abundance of a species (Kindt & Burn 2002). Environmental variables are represented by vectors that determine additional axes in the diagram and species scores must be projected onto these axis. The overall mean of all environmental variables is represented by the origin of the plot. The inferred weighted average of a species or a transect is higher than average if the projection point (of species or transects) lies on the same side of the origin as the vector-tip and is lower than average if the origin lies between the projection point and the end-point of the vector line. For example, transects 19 and 20 are situated at the largest measured travel times, whereas transect 23 is situated closest to Apillapampa in terms of travel time. Environmental variables with long vectors are more strongly correlated with the axes than those with short vectors (Jongman et al. 1996). Altitude is correlated with the first axis and travel time, firewood harvest and proximity to a river with the second axis. Units on both ordination axes correspond to multiples of variance.



**Table 5 – Pearson correlations between diversity indices and environmental variables.**

\* = correlation is significant at the 0.05 level (2-tailed).

		Travel time	Altitude	Slope	Compass bearing
<b>Alpha diversity</b>	Pearson Correlation	0.187	<b>-0.408*</b>	0.294	-0.017
	Sig. (2-tailed)	0.331	<u>0.028</u>	0.121	0.931
<b>Shannon diversity</b>	Pearson Correlation	0.270	<b>-0.371*</b>	0.233	0.005
	Sig. (2-tailed)	0.157	<u>0.047</u>	0.223	0.978
<b>Number of individuals</b>	Pearson Correlation	-0.006	<b>0.380*</b>	<b>-0.408*</b>	-0.132
	Sig. (2-tailed)	0.976	<u>0.042</u>	<u>0.028</u>	0.495

transects along the second ordination axes in both diagrams (Kendall's  $t_b = -0.61$ ;  $p < 0.001$ ). Hence, the combination of travel time, firewood harvesting and proximity to a river can only partly explain the variation accounted by the best fit scenario provided by the second CA axis (fig. 5). Other anthropogenic and environmental variables that were not taken into account (cf. material and methods section) such as land use, land ownership, soil texture and structure, hydrologic profile, etc. are also expected to have an important impact on species composition.

The fact that neither vegetation burning, nor grazing activity were selected as significant variables in ordination analysis probably relates to the temporary aspect of our observations for these variables. Most likely, all transect sites had been subjected to grazing and the majority of transects to vegetation burning. The negative effect of fire on vegetation is well-documented (Veach et al. 2003, Ibsch 2003). Kessler & Driesch (1993) have argued that frequent burning of the vegetation is responsible for reducing forest cover in the high Andes. The main objective of burning is to promote grass regrowth and improve fodder quality, but in the past burning was probably also a part of hunting practices. Although mature trees are often able to survive fire, this is not the case for seedlings and young trees (Kessler & Driesch 1993). The negative impact of fire is intensified by grazing, which is particularly detrimental for natural succession and the reproduction of native tree species and practiced in most parts of the Andes with livestock densities well above the ecosystem's carrying capacity (Bentley & Valencia 2003, Ibsch & Rojas 1994, Ibsch 1994b, Ibsch et al. 2003b, García & Beck 2006, Kessler 2006).

In sum, CCA suggests that a significant part of the variation in current species abundances and distributions is explained by a combination of some of the limited natural and anthropogenic variables we measured. These variables are altitude, travel time, proximity to a (temporal) river or

**Table 6 – Numbers of transects sampled with observed incidence of firewood harvest, grazing activity, crossing paths and nearby (seasonal) rivers or streams.**

	Observed	Not observed
Firewood harvest	11	18
Grazing activity	24	5
Vegetation burning	4	25
Presence of path	12	17
Presence of river	5	24

stream, and evidence of firewood harvest. Of the measured anthropogenic variables, travel time from the village centre (a measure of accessibility) appears to be the dominant human factor to explain variation in species abundance data, but also firewood harvest contributes significantly.

### Predicting diversity in transects based on measured environmental variables

Now that the measured environmental variables that best explain variation in the transect abundance data have been identified, it will be explored to what extent diversity in transects can be predicted from these and other measured variables. We therefore exposed our data to various statistical techniques (correlation and regression analysis, t-tests) to investigate several null hypotheses that test the contribution of each environmental predictor variable to the observed diversity in transects.

**Ho = diversity in transects is random with respect to height above sea level, travel time, slope and compass direction** – Although travel time, as a measure of transect accessibility, explains a statistically significant part of the variation in abundance of different species in transects, it does not explain variation of plant species diversity in transects. When only (sub-)woody plant species are considered, there does, nonetheless, seem to exist a negative relation between plant diversity (measured as Alpha or Shannon diversity or as the number of individuals in transects) and travel time (see Thomas et al. 2009b). A possible explanation for this is that, in terms of transect diversity, herbaceous species might be more resilient to human disturbance than (sub-)woody species, for which transect diversity tends to decrease with increasing accessibility. In this context, 'more resilient' does not mean that individual herbaceous plant species would not be impacted by human disturbance. It is possible that the structure and composition of herbaceous plant communities change with increasing human pressure (e.g. replacement of native species by (invasive) New World species), while overall transect diversity remains equal. Further research is needed to corroborate or refute this hypothesis.

The only variables that correlate with diversity are altitude and site slope. Alpha and Shannon diversity significantly decrease with altitude, while density of all individual plants in transects increases (table 5). The decrease in diversity on the altitude gradient is essentially linear (Alpha diversity =  $-0.019 \times \text{altitude} + 104.135$  ( $R^2 = 0.17$ ;  $p = 0.028$ ) and Shannon diversity =  $-0.001 \times \text{altitude} + 4.337$  ( $R^2 = 0.11$ ;

$p = 0.047$ )) and hence corroborates the findings of Gentry (1988). The latter author uncovered a linear trend of decreasing diversity for plants  $\geq 2.5$  cm dbh with increasing altitude for the South American Andes as a whole. Similarly, Galindo et al. (2003) found that species richness (for plants  $\geq 1$  cm dbh) was inversely related to altitude in the Colombian Andes.

Higher numbers of individuals in transects at higher altitudes might be explained by a combination of several underlying factors. For example, at higher altitudes precipitation is higher and evapotranspiration lower, whereas more plants are able to grow per square meter because of their smaller size. Furthermore, results show that the total number of individuals in transects correlates negatively with site slope (table 5). Since such a trend is not observed when only (sub-)woody species are considered (Thomas et al. 2009b), lower numbers of plant individuals on sites with steeper slopes might be related to the fact that herbaceous plants establish less easily on steeper slopes. Generally, they have less extended roots systems and are more susceptible to erosive forces as compared to (sub-)woody plants. Ibisch (1994b) presents a similar reasoning by arguing that graminoids generally dominate in relatively deep soils whereas shrubs perform better in more degraded, shallow and coarse soils (characteristic for soils of steep slopes).

**Ho = diversity in transects is random with respect to plantation or cultivation of exotic species in transects** – In five of 29 sampled transects, exotic tree (*Eucalyptus globulus* and *Pinus radiata*) or shrub (*Spartium junceum*) species had been planted. An independent sample t-test showed that Alpha diversity is significantly lower ( $t = 2.1$ ;  $p = 0.046$ ) in transects with planted exotic species ( $31.2 \pm 13.5$  (s.d.)) than in transects without plantations ( $43.4 \pm 11.5$  (s.d.)). One could ask whether this result is not more a consequence of the fact that exotics are cultivated at higher altitude sites with lower natural species richness, than of the negative influence of exotics. However, transects with planted or cultivated exotics are relatively evenly distributed over the altitudinal interval we sampled (2,960–3,530 m a.s.l.). The total number of individuals and Shannon diversity are equal for both groups.

The negative impact on species number of exotic trees and shrubs in Apillapampa is not a real surprise. The negative allelopathic impacts of *Eucalyptus globulus* and *Pinus radiata* on understory vegetation are well known and studied (Molina et al. 1991, Mahboubi et al. 1997, Souto et al. 2001, Ibisch 2003). People from Apillapampa are aware of this problem and know that these trees do not combine well with agriculture because they deteriorate soil quality. In Andean Ecuador (3,000–4,000 m), Hofstede et al. (2002) observed regeneration of Andean woody species in some pine (*Pinus radiata*) plantations, while understory was completely lacking in other sites. This made the authors conclude that the impact of pine plantations cannot be generalized but should be evaluated case by case. Results from the present study would suggest that the impact of exotic species on the diversity of native species is rather negative.

**Ho = diversity in transects is random with respect to firewood harvest, grazing activity, vegetation burning, paths crossing transects and presence of nearby (seasonal) river** – The null hypothesis is accepted for all of the above binary environmental variables. The number of transects where firewood harvest, grazing activity, crossing paths or the vicinity of a (temporary) river or stream have been observed, are given in table 6.

The previous analyses show that variables that explain most variation in species abundance data (identified by CCA), do not necessarily overlap with statistically significant predictor variables for diversity, such as Alpha, Shannon and the number of individuals in transects. Firewood harvest and presence of a river were identified as significant environmental variables by CCA, but they do not explain differences in diversity (i.e. Alpha, Shannon and number of individuals) between transects. On the other hand, plantation of exotic species and site slope were not selected by CCA but do explain significant variation in diversity between transects.

## CONCLUSIONS

Qualitative and quantitative floristic data from the district of Apillapampa presented here correspond well with other studies conducted at comparable sites in the Bolivian Andes, and significantly contribute to the still severely understudied Bolivian flora. From literature (Navarro 2002), it is known that Apillapampa is situated on the transition between prepuna and puna vegetations, the occurrence of which is controlled by an altitudinal gradient. We have been able to confirm this for our own transect data by means of different statistical techniques which allowed us to establish the hypothetical border between prepuna and puna in our research area at about 3,200 m a.s.l.

We agree with other authors that the secondary nature of vegetation in the research area is mainly the consequence of a severe degradation process of various centuries of human occupation that continues until today. The negative impact of anthropogenic disturbance on local vegetation is corroborated by the ecological findings of the present study. We have demonstrated that apart from altitude, which is the predominant ecological variable in the Andes, other variables associated with anthropogenic pressure influence species abundance data in the sampled transects. In particular, site accessibility (measured as travel time from the village centre), proximity to a river or stream, and/or evidence of firewood harvesting are factors that significantly explained part of the abundance data of species.

In addition, analysis of the impact of environmental variables on the local flora in terms of species richness, Shannon diversity and/or the number of individual plants, revealed that diversity in transects is mainly controlled by altitude. Of all measured anthropogenic disturbance variables, we only detected lower species richness in transects where exotic tree or shrub species had been planted. It is, however, clear that the variables we measured are insufficient to characterize all possible (past and present) environmental and anthropogenic impacts on local vegetation.

## SUPPLEMENTARY DATA

Supplementary data is available at *Plant Ecology and evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consists of the following: plant species identified in twenty-nine 50 × 2 m<sup>2</sup> transects in the district of Apillapampa, Capinota province, Bolivia (pdf file).

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## REFERENCES

- Antezana C., Navarro G. (2002) Contribución al análisis biogeográfico y catálogo preliminar de la flora de los valles secos interandinos del centro de Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 12: 3–38.
- Bonham C.D. (1989) Measurements for terrestrial vegetation. New York, Wiley-Interscience.
- Cronquist, A. (1988) The evolution and classification of flowering plants. 2nd ed. New York, The New York Botanical Garden.
- Davis S.D., Heywood V.H., Herrera-Macbride O., Villa-Lobos J., Hamilton A.C. (1997) Centres of plant diversity. Volume 3: The Americas. Oxford, Information Press.
- Dollfus O. (1984) Desarrollo de la formas del aprovechamiento de tierras en los Andes Centrales. In: Baker P.T. (ed.) Población humana e interacciones con la biosfera en los Andes Centrales: 55–69. MAB 2, Informe sobre los conocimientos actuales de los ecosistemas andinos.
- FEPADE (Fundación Ecueménica Para el Desarrollo) (1998) Diagnostico del distrito de Apillapampa Cochabamba, Bolivia. Cochabamba, Bolivia, Unpublished Report.
- Galindo R.T., Betancur J., Cadena-M. J.J. (2003) Estructura y composición florística de cuatro bosques Andinos del Satuario de flora y fauna Guanentá-Alto río Fonce, Cordillera oriental Colombiana. *Caldasia* 25: 313–335.
- García E.E., Beck, S.G. (2006) Puna. In: Moraes M., Ollgaard B., Kvist L.P., Borchsenius F., Balslev H. (eds), *Botánica económica de los Andes Centrales*: 51–76. La Paz, Bolivia, Universidad Mayor de San Andres.
- Gentry A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 1–34.
- Hofstede R.G.M., Groenendijk J.P., Coppus R., Fehse J.C., Sevink J. (2002) Impact of pine plantations on soils and vegetation in the Ecuadorian High Andes. *Mountain Research and Development* 22: 159–167.
- Ibarra, G.D.E. (1986) 30.000 años de prehistoria en Bolivia. Bolivia, Editorial Los Amigos del Libro, Werner Guttentag.
- Ibisch P.L., Rojas P.N. (1994) Flora y vegetación de la provincia Arque, departamento Cochabamba, Bolivia: I. Flora. *Ecología en Bolivia* 22: 1–41.
- Ibisch P.L. (1994a) Flora y vegetación de la provincia Arque, departamento Cochabamba, Bolivia: II. Situación fitogeográfica de la flora de la provincia Arque. *Ecología en Bolivia* 22: 43–52.
- Ibisch P.L. (1994b) Flora y vegetación de la provincia Arque, departamento Cochabamba, Bolivia: III. Vegetación. *Ecología en Bolivia* 22: 53–92.
- Ibisch P.L. (2002) Evaluation of a rural development project in southwest Cochabamba, Bolivia, and its agroforestry activities involving *Polylepis besseri* and other native species – a decade of lessons learned. *Ecotropica* 8: 205–218.
- Ibisch P.L. (2003) Degradación y pérdida de la biodiversidad por cambios de la calidad de los hábitats. In: Ibisch P.L., Mérida G. (eds), *Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación*: 231–263. Santa Cruz de la Sierra, Bolivia, Editorial FAN.
- Ibisch P.L., Beck S.G., Gerkmann B., Carretero A. (2003a) Ecoregiones y ecosistemas. In: Ibisch P.L., Mérida G. (eds), *Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación*: 47–88. Santa Cruz de la Sierra, Bolivia, Editorial FAN.
- Ibisch P.L., Carretero A., Beck S.G., Cúellar S., Espinoza S.D., Araujo N.V. (2003b) Estado de conservación de la biodiversidad: El caso de los bosques andinos. In: Ibisch P.L., Mérida G. (eds), *Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación*: 272–285. Santa Cruz de la Sierra, Bolivia, Editorial FAN.
- Jongman R.H.G., Ter Braak C.J.F., Van Tongeren O.F.R. (1996) Data analysis in community and landscape ecology. Cambridge, Cambridge University Press.
- Kessler M., Driesch P. (1993) Causas e historia de la destrucción de bosques altoandinos en Bolivia. *Ecología en Bolivia* 21: 1–18.
- Kessler M. (2006) Bosques de *Polylepis*. In: Moraes M., Ollgaard B., Kvist L.P., Borchsenius F., Balslev H. (eds), *Botánica económica de los Andes Centrales*: 110–120. La Paz, Bolivia, Universidad Mayor de San Andres.
- Kindt R., Burn R.W. (2002) The Biodiversity Analysis Package. Resources and guidelines for the analysis of biodiversity and ecological information. CD-ROM, version 1. World Agroforestry Centre.
- Larrea-Alcazar D., López R.P. (2005) An estimation of the floristic richness of Bolivia's Andean dry valleys. *Biodiversity and conservation* 14: 1923–1927.
- López R.P. (2003a) Diversidad florística y endemismo de los valles secos bolivianos. *Ecología en Bolivia* 38: 27–60.

- López R.P. (2003b) Phytogeographical relations of the Andean dry valleys of Bolivia. *Journal of Biogeography* 30: 1659–1668.
- Mahboubi P., Gordon A.M., Stoskopf N., Voroney R.P. (1997) Agroforestry in the Bolivian Altiplano: evaluation of tree species and greenhouse growth of wheat on soils treated with tree leaves. *Agroforestry Systems* 37: 59–77.
- McAleece (1997) BioDiversity professional version 2. The Natural History Museum & The Scottish Association for Marine Science.
- McCune B., Mefford M.J. (1999) PC-ORD version 4.0: Multivariate analysis of ecological data. Glenden Beach, Oregon, US, MjM Software.
- Molina A., Reigosa M.J., Carballeira, A. (1991) Release of allelochemical agents from litter, throughfall, and topsoil in plantations of *Eucalyptus globulus* Labill in Spain. *Journal of Chemical Ecology* 17: 147–160.
- Myers N., Mittermeier R.A., Mittermeier C.G., Da Fonseca G.A.B., Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Navarro G. (2002) Vegetación y unidades biogeográficas. In: Navarro G., Maldonado M. (eds), *Geografía ecológica de Bolivia: vegetación y ambientes acuáticos*: 1–500. Cochabamba, Bolivia, Centro de Ecología Simón I. Patino - Departamento de Difusión.
- Moraes M. & Beck S.G. (1992) Diversidad florística de Bolivia. In: Marconi M. (ed.) *Conservación de la diversidad biológica en Bolivia*: 75–111. La Paz, Bolivia, CDC (Centro de datos para la conservación).
- Paduano G.M., Bush M.B., Baker P.A., Fritz S.C., Seltzer G.O. (2003) A vegetation and fire history of lake Titicaca since the last glacial maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 194: 259–279.
- Pedrotti F., Venanzoni R., Suarez Tapia E. (1988) Comunidades vegetales del valle de Capinota. *Ecología en Bolivia* 11: 25–45.
- Pestalozzi H.U. (1998) Flora ilustrado altoandina. la relación entre hombre, planta y medio ambiente en el Ayllu Majasayu Mujlli (Prov. Tapacari, Dpto. Cochabamba, Bolivia). Cochabamba, Bolivia, M&C Editores.
- Rivas-Martínez S., Tovar. O. (1982) Vegetatio Andinae, I. Datos sobre las comunidades vegetales altoandinas de los Andes Centrales del Perú. *Lazarroa* 4: 167–187.
- Roberts-Pichette P., Gillespie, L. (1999) Terrestrial vegetation monitoring protocols. Ontario, Canada, EMAN Occasional Paper Series Report No. 9.
- Souto X.C., Bolano J.C., González L., Reigosa M.J. (2001) Allelopathic effects of tree species on some soil microbial populations and herbaceous plants. *Biologia Plantarum* 44: 269–275.
- Ter Braak C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- Ter Braak C.J.F. (1994) Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience* 1: 127–140.
- Thomas E., Vandebroek I., Goetghebeur P., Sanca S., Arrazola S., Van Damme P. (2008) The relationship between plant use and plant diversity in the Bolivian Andes, with special reference to medicinal plant use. *Human Ecology* 36: 861–879.
- Thomas E. (2009) Quantitative ethnobotany in Bolivia: knowledge, use and diversity of plants in Quechua, Yuracaré and Trinitario communities from the Andes and Amazon. Saarbrücken, Germany, VDM Verlag Dr. Müller.
- Thomas E., Vandebroek I., Sanca S., Van Damme P. (2009a) Cultural significance of medicinal plant families and species among Quechua farmers in Apillapampa, Bolivia. *Journal of Ethnopharmacology* 122: 60–67.
- Thomas E., Vandebroek I., Van Damme P., Goetghebeur P., Douterlungne D., Sanca S., Arrázola S. (2009b) The relation between accessibility, diversity and indigenous valuation of vegetation in the Bolivian Andes. *Journal of Arid Environments* 73: 854–861.
- Veach R., Lee D., Philippi T. (2003) Human disturbance and forest diversity in the Tansa valley, India. *Biodiversity and Conservation* 12: 1051–1072.
- Wood J. (2005) La guía “Darwin” de las flores de los valles Bolivianos. Santa Cruz, Bolivia, Sirena.

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