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FLORISTIC AND DIVERSITY CHANGES IN THE PHANEROPHYTIC VEGETATION OF COPACABANA WATERSHED (CENTRAL ARGENTINA) AS A RESPONSE TO DISTURBANCE*

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Abstract. Changes in phanerophytic vegetation in a mountain woodland of Central Argentina are analyzed. Floristic composition, disturbance factors (logging and grazing) and some physical variables are recorded in sampling plots located along a gradient of use intensity. Multivariate analysis shows that the main trend of variation in floristic composition is related to an alteration gradient rather than to physical factors. This gradient is significatively correlated with logging. Diversity parameters are used in order to study spatial organization. Species diversity decreases from slightly to highly disturbed sites. Spatial heterogeneity and average spatial niche width decreases as disturbance intensity increases. The behaviour of diversity parameters applied to highly disturbed woody vegetation is discussed.

Introduction

Potential natural vegetation of the upper Copacabana watershed is a low xerophytic woodland (Sayago, 1969; Luti *et al.*, 1979). At present, the vegetation is predominantly bushy as a consequence of anthropogenic activities. No relictual units were observed in this part of the watershed. According to Díaz *et al.* (1987), the watershed has been subjected to intensive logging carried out in the late XIX century and throughout the mid XX century. This activity is still going on though with less intensity. Anthropogenic preassure has been concentrated on the bottom and mid and low slopes which, according to Luti *et al.* (1979), lie within the Mountain woodland belt.

The present vegetation is a mosaic of units with different levels of alteration. The principal trends of variation are subjected to study. The analysis of phanerophytic vegetation was approached from a structural and diversity viewpoint. Diversity has been applied by various authors to the analysis of vegetation subjected to disturbance. Dayton (1975) and Grime (1977) found low diversity in highly disturbed sites. Mc Naughton and Wolf (1977) related intense alteration and low diversity to the predominance of generalist species. Dealing with herbaceus vegetation, Pineda *et al.* (1981) found that spatial heterogenity increases as secondary succession advances. Interestingly, Peco *et al.* (1983) reported that heterogeneity is low during early and advanced stages with a maximum in intermediate stages. Based on different diversity parameters, Facelli *et al.* (1987) reported no increase in spatial heterogeneity as succession advances.

The aim of this paper is to study the phanerophytic vegetation of the upper Copacabana watershed from the points of view of floristic composition and spatial distribution of species, in order to determine trends of variation related to the intensity of disturbance. The following hypothesis were stated:

1. The present vegetation displays a range of conditions with different intensities of use, that may be reflected through changes in the relative abundance of shared species or through floristic composition. It is possible to detect species specific to different intensities of disturbance.
2. The main disturbance factor has been logging, namely the removal of the upper vegetation strata.
3. The alteration process mentioned above may lead to a progressive floristic and structural homogeneity of the ligneous vegetation. This is reflected by diversity parameters: a progressive decrease in the divérsity of phanerophytes in the spatial segregation and also in the number of specialist species.

Study area

Copacabana watershed is located approximately at 30°35'S and 64°34'W, in the Ischilín Departament of Province of Córdoba, Central Argentina. The upper sector comprises of a valley limited by two mountains ranges. Two levels of pedimentation can be noticed: a first level composed of relicts or control peaks (cretacious sediments), severely eroded by fluvial action, and a second level formed by modern deposits. Mean annual

* There is not a published flora from Central Argentina. The nomenclature follows Cabrera (1963, 1965a, 1965b, 1967, 1968 and 1970). Complete list of recorded species in the study area is available upon request.

rainfall is 500-600 mm and mean annual temperature is 16°C; the annual hydric deficit is 300 mm (Capitanelli 1979). The area is placed within the montane woodland belt (Luti *et al.* 1979), which extends in the study area approximately from 600 m up to 1000 m above sea level. When lightly disturbed, the montane woodland appears as a low woodland between 6 and 9 m high, closed in favourables sites and sparse in damaged and exposed areas. *Schinopsis haenkeana, Lithraea ternifolia, Ruprechtia apetala* and *Fagara coco* are the most abundant species (Sayago 1969; Luti *et al.* 1979). However, the present vegetation mainly comprises a shrubland with few montane woodland relicts.

Methods

Sampling design

In order to identify units representative of different use intensities (grazing and logging) a transparent square gride of 1 cm sides was laid on aerial photographs (1:20,000 scale). The degree of anthropogenic influence was recorded in each quadrat using the following indicators: path density, percentage of surface uncovered by upper strata of vegetation, vecinity to yards, roads, dwellings, and water reservoirs. Tree disturbance degrees were distinguished: 1 (low), 2 (intermediate), and 3 (high). In order to minimize variability due to factors other than range, a stratified sampling was designed, with strata defined as follows:
1. Woodland-shrubland from flood plains at two different altitudinal sites: 700 to 800 m and 800 to 900 m.
2. Orophyllous woodland-shrubland form first level of local pedimentation, with two strata: sunny slopes (facing North) and shaded slopes (facing South). On these basis, gride units were selected, rejecting those traversed by water courses. Within each of the selected quadrat units, starting from a random point, two per pendicular 10 m long transect (S-N and E-W orientation) were drawn. In the case of slopes, the mid-slope area was sampled. Intersection frequency of phanerophytes along the lines were recorded.

Within each quadrat alteration degree was determined by means of two variables: alteration by logging (*i.e.*, percentage of tree canopy cover 4 m high or more); alteration by grazing (*i.e.*, percentage of bare soil and percentage of herbaceous cover). Altitude and slope percentage were measured. The recording (54 samples comprising two transects) was carried out during the spring-summer seasons (October-February, 1986 and 1987).

Data analysis

Floristic data were analyzed by Detrended Correspondance Analysis or DCA (Hill 1979). Since the alteration degree is a complex of several variables, a correlation assay was applied (Engelman 1981) to the main variables quantitatively registered. This test consists of determining correlation coefficients among the values of these variables for each sample plot and the values of the coordinates on Axes I and II of DCA (Olsvig-Whittaker *et al.* 1982). Diversity analysis was carried out according to Pielou (1975, 1977) and Pineda *et al.* (1981). These authors suggest that diversity could be partitioned into two components: uncertainty about the richness and evenness of species *H (E)*, and uncertainty about spatial distribution in the community, known as spatial diversity, *H (P/E)*. Total diversity is defined as $H (E.P) = H (E) + H (P/E)$. The expression $A = H (P/E)/log_2 N$, *N* the number of sampling plots considered, is interpreted by De Pablo *et al.* (1982) as the

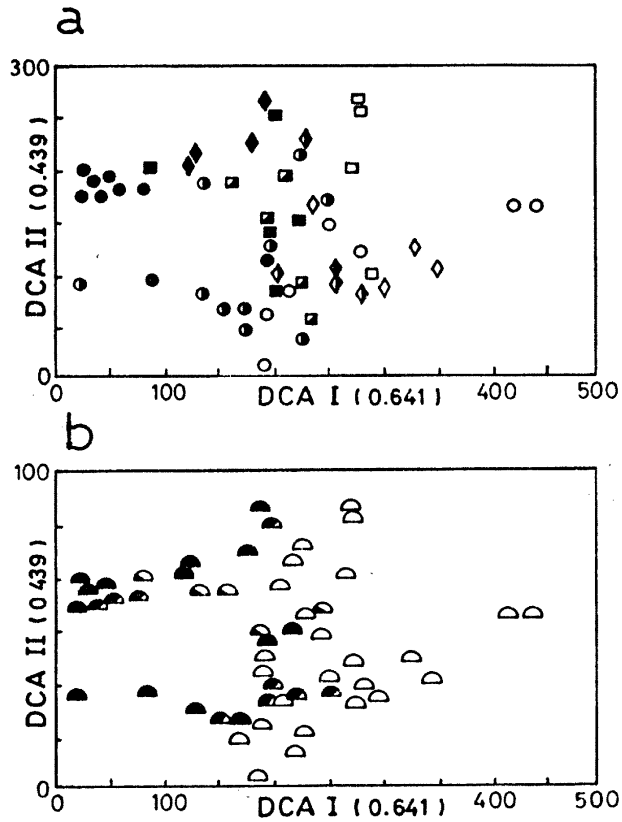
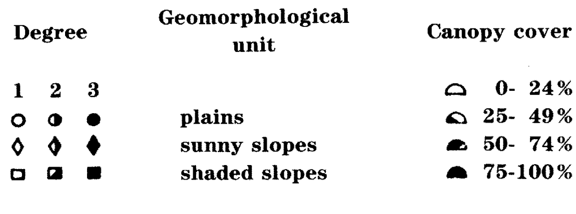


Fig. 1. Copacabana watershed valley vegetation ordination (DCA) of sampling units. The eigenvalue of each axe is indicated in brackets. Fig. 1a shows the sampling unit projections on the plane of DCA axes I and II with corresponding alteration degree and geomorphological unit identified. Fig. 1b displays percentage canopy cover.



mean width of spatial niche, and is similar to the niche width *(W)* proposed by Pielou (1977). Both *H (P/E)* and *A*, its standarized expression, may be defined for a whole community, just for a part, or for each individual species. In this case, low uncertainty species and high uncertainty species can be differentiated as specialists and generalists respectively, in relation to their spatial distribution.

Results and discussion

Floristic analysis

Fig. 1 shows the sample plots' projection on the plane defined by Axes I and II of DCA. Fig. 1a shows the surveyed sample plots and their corresponding alteration degree. The analysis does not discriminate between sunny or shaded slopes. However, whenever plots with degree I of alteration occured, the differentiation between plains and slopes is clear, but not for degrees 2 and 3. Fig. 1b displays the most evident trend corresponding to increasing alteration degree, rather than geomorphological differences. The results of the correlation analysis among altitude, slope percentage, tree canopy cover percentage, bare soil percentage, herbaceous cover percentage, and plot coordinates over Axes I and II of DCA are shown in Table 1.

Table 1. Correlation analysis among values of five variables and coordinates over axes I and II of DCA for each sampling unit. Asterisk* indicates correlation significant at $p=0.01$.

Variable	Correlation coefficient (r)	
	DCA I	DCA II
Tree canopy cover (%)	–0.6372*	0.2084
Bare soil (%)	0.5944*	–0.2841
Herbaceous cover (%)	–0.2632	0.2985
Altitude	˙0.0544	0.4021*
Slope (%)	0.3828	0.300

Tree canopy cover (as indicator of logging) is the most important variable. Next comes percentage of bare soil. The influence in tree canopy cover on light availability and water balance is so strong that it may mask the variability found in the vegetation as a response to different geomorphological features. Fig. 1b shows the sample plot projection indicating their percentage canopy cover. This variation, as it was expected, fits the general variation trend showed in Fig. 1a.

Relating groups of sample plots and associated species, the principal trend of variation may be interpreted as an alteration gradient. On one extreme plots presenting relatively undisturbed areas, patches of woodland with high percentage of tree canopy cover and with medium-large size individuals are found. The dominant species are *Schinopsis haenkeana* on slopes and *Prosopis alba, P. nigra* and *Aspidosperma quebracho-blanco* on plains. Herbaceous cover is higher than 50%. The low percentage of bare soil is characteristic. *Croton sarcopetalus* and *Ephedra triandra* are associated species. The other extreme of the gradient is occupied by plots with severe alteration, open shrublands with low herbaceous cover, high percentage of bare soil and evidences of water erosion. The associated species are *Monnina dictyocarpa* and *Acalipha communis* var. *guaranitica. Baccharis rufescens* is characteristic on slopes and *Larrea divaricata* on plains.

Between the extremes, a wide range of intermediate conditions is found corresponding to degree 2 of alteration, usually with shrublands, mixed shrubland-woodland or patches of woodland with highly disturbed understory and severe overgrazing. These conditions are caracterized by *Ruprechtia apetala* and *Lippia integrifolia* for slopes and *Trithrinax campestris, Cestrum parqui* and *Celtis tala* for plains. We mention that *Flourensia campestris, Acacia caven* and *Aspidosperma quebracho-blanco* are widely distributed over the whole study area, with high frequency values and showing no clear relation to any geomorphological unit or degree of alteration. Most of the *Aspidosperma quebracho-blanco* and *Schinopsis haenkeana* individuals recorded during sampling are shrub-like young trees and do not effect the physiognomy. This is especially evident for *Schinopsis haenkeana* growing on slopes with high frequency values but as dwarfed trees, strongly damaged by browsing. The original woodland has been replaced by a shrubland dominated by *Flourensia campestris* and *S. haenkeana* individuals, strongly deformed by browsing.

Further analysis of vegetation in the area should consider high tree individuals and shrubby or dwarf trees as separate entities, although they may belong to the same species. Their ecological significance within the community appears to be significantly different.

Diversity analysis

Slightly disturbed sites appear more affected by geomorphological variation than highly disturbed sites (Fig. 1a). This evidence, added to the progressive reduction in the number of species found as alteration increases, may be interpreted as follows: most disturbed areas with vegetation in the early stages of secondary succession tend to be occupied by generalist species, with wide spatial distribution and tolerance ranges. This may lead to a fairly homogeneous distribution of species among the different geomorphological units involved. Where vegetation is in more advanced successional stages specialist species tend to predominate. They have much narrower tolerance ranges, and therefore a more restricted distribution reflected by a wider spatial segregation.

In order to test these, an analysis of diversity was

Table 2. Diversity analysis. For each alteration degree the following values are given: *H (E.P)* = total diversity; *H (E)* = species diversity; *H (P/E)* = spatial diversity; *A* = mean width of spatial niche; *E/G* = ratio of number of specialist species/number of generalist species; *N* = number of species; *FT* = total frequency of species.

	DEGREE 1	DEGREE 2	DEGREE 3
H (E.P)	6.840	6.430	5.883
H (E)	4.214	3.760	3.709
H (P/E)	2.626	2.670	2.174
A	0.651	0.631	0.567
E/G	34	36	30
FT	696	600	296

performed. Results are summarized in tables 2 and 3. In table 3 it can be noticed that out of 44 recorded species, only 7 occur exclusively at one extreme of the alteration gradient. There are 18 species that, being typical for one extreme and for the intermediate situations of the gradient, are absent at the opposite extreme. This fact indicates that differences between conditions with distinct alteration degrees are a result of species relative abundances more than foristic changes. Table 2 shows that species diversity *H (E)*, such as proposed by the hypothesis, diminishes as alteration increases. This causes a decrease in total diversity *H (E.P)*. Specific diversity *H (E)* values agree with Mc Naughton and Wolf (1970), Dayton (1975), and Grime (1977). However, contrary to expected results, *H (P/E)* and A disminish, whereas the ratio specialist/generalist rises as alteration increases. These facts are contrary to those reported by Pineda *et al.* (1981) and Mc Naughton and Wolf (1970). According to the results of Mc Naughton and Wolf (1970) low specific diversity is not related to

Table 3. Specialist (low uncertainty) and generalist (high uncertainty phanerophytic species recorded in Copacabana watershed. In the case of specialists, the symbol on the left corresponds to the degree of alteration.

SPECIALIST SPECIES	GENERALIST SPECIES
● Croton sarcopetalus	Abutilon cfr. terminale
● Glandularia hookeriana	Acacia atramentaria
● Lepechinia floribunda	Acacia caven
● Prosopis alba	Aloysia gratissima
○ Monnina dictyocarpa	Aspidosperma quebracho blanco
○ Acalipha communis var. guaranitica	Cestrum parqui
○ Baccharis rufescens	Condalia microphylla
○ Proustia cuneifolia	Flourensia campestris
○ Vernonia incana	Geoffroea decorticans
	Lippia turbinata
	Porlieria microphylla
	Prosopis nigra
	Ximenia americana
	Schinopsis haenkeana
	Schinus praecox

a larger number of generalists, but to a higher spatial heterogeneity and larger rate of species considered as specialists. These results agree with those obtained by Peco *et al.* (1983). A possible explanation lies in the spatial distribution of the phanerophytes surveyed: sites with the maximum degree of alteration are characterized by a low frequency of individuals and a high percentage of bare soil. Phanerophytes have not yet colonized the disturbed areas, or if present, they are remnant individuals, which survived the disturbance. Particularly evident in those species which were selectively removed, namely trees, is that their spatial distribution, specifically their absence, does not indicate environmental limitations inherent to the species. Therefore, having in mind the local frequency of individuals of all species, most of the differences among plots are not a consequence of the environmental selectivity of species, but of persistence phenomena in some instances, and for impossibility of colonization due to disturbance intensity in others. It is important to consider these aspects when analyzing spatial diversity in highly disturbed areas, especially in ligneous vegetation where individuals may persist for a long time in protected sites. Neglecting this issue may lead to erroneous conclusions regarding the spatial generalist or specialist species behaviour.

Conclusions

With respect to the hypotheses postulated, it is pointed out that:

1. Phanerophytic vegetation of the upper Copacabana valley is in different states related to the intensity of anthropogenic disturbance. When disturbance has been severe, the variability of vegetation related to geomorphological features is blurred.
2. Variation among different disturbed conditions mainly affects the relative abundances of species and there are also differences in floristic composition. There are phanerophytic species closely associated with specific alteration regimes. These species are considered as ''indicators''.
3. Logging with consequent simplification of vertical vegetation structure is the main disturbance factor in the region, strongly determining the most important variational trend, *i.e.*, alteration intensity.
4. As alteration increases, floristic empoverishment as well as progressive indifferentiation among the geomorphological units are noticed, but the spatial heterogeneity of phanerophytic vegetation increase. This may be caused by the persistence of a small number of individuals of certain species under intense disturbance. This results is high spatial segregations.
5. From all of the above, the importance of distinguishing between the ecological significance of high spatial segregation in low-disturbed situations and high-disturbed ones is clear.

6. When considering diversity behaviour over severely disturbed sites, the methods applied allow an interpretation of the main trends in a scarcely studied vegetation of a heterogeneous areas such as the upper Copacabana valley.

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