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Species richness of Argentine cacti: A test of biogeographic hypotheses

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Abstract. Patterns of species richness are described for 50 columnar, 109 globose and 50 opuntoid cacti species in 318 grid cells ($1^\circ \times 1^\circ$) covering Argentina. Biological richness hypotheses were tested by regressing 15 environmental descriptors against species richness in each group. We also included the collection effort (estimated as the logarithm of the number of herbarium specimens collected in each cell) to estimate the possible error induced by underrepresentation in certain cells. Log-linear regression models accounted for a large portion of the variation in richness of columnar species, opuntoid species, globose species and all forms combined. Opuntoid and globose species richness was associated with percentage summer rainfall. Columnar species richness was associated with the number of frost-free days. The distribution of columnar cacti seems to be limited by freezing temperatures. The results are consistent with the climate favourableness and climatic variation hypotheses, but do not support the hypothesis that energy flow limits regional species richness.

Altitudinal range (a measure of habitat heterogeneity) was related to richness of globose cacti. A floristic affinity analysis between geographic provinces and the distribution of the different growth forms confirmed the high degree of endemism of globose cacti and the cosmopolitanism of the opuntoid ones. Two cells in the Prepuna and northern Monte Provinces showed species richness values that were significantly higher than those predicted by the log-linear model. This is interpreted in terms of Quaternary historical events having affected the main South American biomes.

Keywords: *Cactaceae*; Growth form; Phytogeographic province; Plant-environment relationship.

Nomenclature: Hunt (1992) and Kiesling (in press).

Introduction

Members of the family *Cactaceae* exhibit a remarkable variety of growth forms (Gibson & Nobel 1986), possibly as a result of different environmental selective pressures throughout the distributional range and the evolutionary history of the family. Within the *Cactaceae*, five main growth forms can be recognized: (a) columnar cacti, (b) globose cacti, (c) opuntoid cacti, (d) epiphytic

cacti and (e) pereskoid cacti. Columnar species have column-like stems with ribs, formed by an arrangement of the areoles in longitudinal rows. These species have parallel vascular bundles, separated by succulent parenchyma, sometimes fusing towards a woody base in the adults. We broadly considered as columnar cacti: candelabriform arborescent species, unbranched erect stems (or solitary columnar arborescent cactus), branched cacti, shrub-like forms with ascending or pendent branches, and shorter barrel cacti.

Globose cacti are small, more or less spherical in shape and have a high density of areoles in their stems. Columnar and globose growth forms belong to the subfamily *Cactoideae*. Most of the columnar genera belong to the tribes *Trichocereae* and *Cereae*, while the genera of the globose species belong mostly to the Tribe *Notocactae* (Gibson & Nobel 1986). Opuntoid species do not form ribs. Their vascular bundles are fused into a netlike, reticular structure. The stem consists of one or more flat or cylindrical cladodes. Each cladode is an independent unit with definite growth that may clone into a complete individual if detached from the mother plant. All opuntoid species belong to the subfamily *Opuntioideae*. Epiphytic cacti are anatomically similar to the columnar species. Their growth habit, however, is quite different. They are mostly herbaceous plants (Gibson & Nobel 1986) with decumbent or prostrate growth, and generally showing a few shallow ribs.

Most of the genera of the epiphytic cacti belong to the Tribe *Hylocereae* of the subfamily *Cactoideae*. The pereskoid cacti show many ancestral anatomical characters of the family. They are leaf-bearing trees and shrubs with a woody, almost non-succulent stem, and belong to the subfamily *Pereskioideae*. The adults of this group are C3 plants while the adults of the other groups show CAM metabolism (Rayder & Ting 1981; Gibson & Nobel 1986; Nobel 1988).

As in other studies (e.g. Cody 1986, 1989; Brown 1988; Major 1988;) species richness is considered a main constituent of species diversity. Many historical, evolutionary and ecological hypotheses have been proposed to explain species richness patterns (e.g. Simpson

1964; MacArthur 1965; Pianka 1966; Cook 1969; Schall & Pianka 1978; Shmida & Wilson 1985; Silvertown 1985; Currie 1991) and geographic variation in growth forms (e.g. Raunkiaer 1934; Box 1981). Palmer (1994) identified at least 120 plausible hypotheses on species richness patterns published in the literature. Attempts to classify these hypotheses (Giller 1984; Brown 1988; Begon et al. 1990; Zobel 1992; Eriksson 1993; Palmer 1994; van der Maarel et al. 1995) have not been very successful as many are not mutually exclusive, and are frequently based on the same theoretical mechanisms, such as the competitive exclusion principle (Palmer 1994).

The aim of our work was to describe the patterns of geographic distribution of the main growth forms of Argentine cactus species: how does the number of species in each growth form vary geographically, and what is the relationship between environmental variables and the richness of the different cactus growth forms. We tested the following hypotheses: (1) environmental favourableness, (2) temporal climatic variation, (3) habitat heterogeneity and (4) limited energy and productivity. We did not explore other hypotheses, such as interspecific interactions, due to the more local scale of their effect. Disturbances such as fire, and speciation and extinction processes were taken into account in the interpretation of patterns but were not directly evaluated. We analyzed the different cactus growth forms separately, as the species in each life form may correspond to different structural niches, and the overall diversity of perennial plants is largely determined by the coexistence of different growth forms (Cody 1986, 1989).

The environmental favourableness hypothesis states that extreme environmental conditions should support fewer species than intermediate environments, as costly adaptive mechanisms are needed (Brown 1988; Begon et al. 1990). Thus, this hypothesis examines the relationship between mean values of the environmental variables (e.g. mean annual rainfall or temperature) and diversity (Giller 1984). As a general rule, a heterogeneous environment may offer more opportunities for the establishment of species with different tolerances.

The climatic variation hypothesis is based on the temporal heterogeneity of the environment. More species may be expected to coexist in seasonal environments (Brown 1988; Begon et al. 1990). Unpredictable, non-seasonal climatic variation is a form of disturbance and species diversity may be highest at intermediate levels (Hutchinson 1961; Connell 1978; Richerson & Lum 1980; Giller 1984).

The habitat heterogeneity hypothesis is based on the spatial variation of the environment. A heterogeneous habitat may offer more by way of microhabitat differences. Thus more niches may be available and more

species or growth forms may co-occur (Simpson 1964; Giller 1984; Auerbach & Shmida 1987; Aarsen 1992).

According to the limited energy hypothesis the amount of energy available will support a restricted number of species. Under certain conditions and at a biogeographic scale species richness is related to primary productivity – a measure of energy flow – (e.g. Abramsky & Rosenzweig 1984; Rosenzweig 1984, 1992; O'Brien 1993). However, productivity is dependent on other factors such as climatic stability (Giller 1984) and at high levels of productivity diversity decreases again (e.g. Pausas 1994). A review of the complex relationship between productivity and species richness is found in Rosenzweig (1995).

Methods

223 cactus species, known to occur in Argentina, were included – five low-frequency pereskioid species, some introduced species and species with either dubious distribution records or non-valid names were omitted (App. 1). Data on the distribution of the species were taken from herbarium labels in eight Argentine herbaria (SI, LIL, LP, BA, BACP, BAB, BAF and MERL, acronyms as in *Index Herbariorum*) and supplemented by Kiesling and Ferrari's unpublished field data (Kiesling in press), and with various published sources (a list is available upon request). A total of 3395 records were elaborated. For each species, we mapped the sites where it had been collected; for this purpose the map of Argentina was divided into a grid of 318 cells of 1° latitude × 1° longitude. We superimposed the grid onto the maps with the records for each species and digitized the species occurrences.

We also digitized climatic descriptors on a 1° × 1° scale; data were taken from published maps from the Servicio Meteorológico Argentino and from Hoffman (1975). The Centro Biometeorológico Argentino provided us with an unpublished map showing the proportion of annual rain falling in summer. Topographic data were taken from Anon. (1981). We assigned to each cell values of mean annual temperature, mean annual precipitation, mean minimum annual temperature, proportion of annual rain falling in summer, number of frost-free days, average annual water deficiency (defined as the ratio of the net radiation to the heat energy required to evaporate the mean annual precipitation), mean annual potential evapotranspiration, mean July temperature, mean December temperature, the difference between the last two measures, and annual primary productivity calculated from Lieth's model (Lieth 1975). Finally, we also recorded the cell's latitude and three topographic variables considered relevant to species

distribution: (a) altitudinal range, calculated as the difference between the maximum and the minimum value from nine systematically chosen elevations within each cell; (b) topographic variation, measured as the standard deviation of the same nine elevations per cell, and (c) mean elevation, obtained as the average of the nine elevations. Table 1 summarises the environmental variables and the hypotheses put to test with each variable.

Species richness patterns and environmental variables

Statistical analyses were performed for the three dominant growth forms: columnar, globose and opuntoid cacti ($n = 50, 109, \text{ and } 50$ species, respectively). Due to the small number of epiphytic cacti ($n = 14$), species of this growth form were mapped, but not analyzed. We used log-linear models in all cases, since species numbers are frequencies (a discrete variable) which can be assumed to have a Poisson error distribution (Crawley 1993). Standard regression models cannot be applied in this case since (1) the variance of frequency counts is usually not constant, and (2) the error is frequently not normally distributed, especially when the observed frequencies are low. Log-linear models ensure that the predicted values are always positive; the assumption of a Poisson error distribution takes into account the fact that the data include integer values and have variances that increase with the mean. For our log-linear models we used the GLIM package (Anon. 1986, Crawley 1993), and evaluated the fit of the model by means of the G -statistic as a measure of goodness-of-fit (McCullagh & Nelder 1989). As in standard regression, we tested the residuals of the model to evaluate their compliance with the assumptions of the Poisson error distribution. Generalized linear models are frequently used in biological surveys (e.g. Nicholls 1989, Austin et al. 1990, Bojórquez-Tapia et al. 1995), as their statistical approach allows the analysis of data that frequently do not conform to the assumptions of standard regression and analysis of variance.

Regression against latitude

For each growth form, we counted the number of species in each cell of the grid, and used this information to map species richness. The relationship between species richness and latitude was determined by log-linear regression. Strictly speaking, latitude is not an environmental factor directly affecting the distribution of plants; rather, it is a variable related to a complex set of environmental factors that co-vary from the tropics to the temperate zones. By using latitude as an independent variable, we tried to evaluate its power as a single predictor of species richness.

Table 1. Environmental variables tested as predictors of species richness, and the main hypothesis tested with each variable.

Hypothesis	Variable	Symbol
Climate severity or climate favourableness	Number of frost-free days	FFD
	Average minimum annual temperature	AMT
	Mean annual temperature	MAT
	Mean annual precipitation	MAP
	Average annual water deficiency	AWD
	Mean July temperature	MJT
	Mean December temperature	MDT
	Mean elevation	MEL
Climatic variation	Actual evapotranspiration	AEV
	Difference between the mean July and December temperatures	DIF
	Proportion of annual rain falling in summer	PRS
	Latitude	LAT
Habitat heterogeneity	Altitudinal range	ALR
	Topographic variation	STD
Energy	Actual evapotranspiration	AEV
	Primary productivity	APP
History	Residuals of the models	
Disturbance	Fires (discussed, but not included in the model)	

Regression against environmental variables

In a second regression model, we tried to identify more precisely those variables that could be more directly affecting plant distribution. For this purpose, we determined the relationship between species richness in each growth form and the environmental variables through an additive stepwise log-linear regression model. Because the data were collected from natural conditions, the multiple regression log-linear model did not follow an orthogonal design for the independent variables. Some of these predictors were significantly correlated between themselves (Table 2) and their explanatory power, as indicated by the partial r^2 -value, may depend on the order in which they were introduced into the model. In the stepwise procedure we used, the most significant predictor was introduced into the model at each step and the resulting sequential r^2 -value was registered with that criterion.

The effect of collection intensity

The number of species detected in a given area is non-linearly related to the number of herbarium specimens that have been collected (Soberón & Llorente 1993). At first, new specimens will frequently incorporate new species, but once the collection is large, most new specimens will belong to species that have already been collected. The incorporation of new species into a collection is a 'diminishing returns function' of the number of specimens (Fisher et al. 1943; Efron & Thisted 1976). The mathematical equations that predict this relationship are often called 'accumulation functions'. Soberón & Llorente (1993) have made a detailed review

Table 2. Correlations between environmental variables. Only the significant values ($P \leq 0.01$) are shown. The symbols for each variable are given in Table 1. The variable productivity is not included in the matrix because it is a linear function of the actual evapotranspiration.

	LAT	ALR	FFD	PRS	MAP	MAT	AMT	STD	MEL	DIF	MDT	JUL	AEV
ALR	-0.77	1											
FFD	0.21	-	1										
PRS	-0.71	0.52	-	1									
MAP	-0.38	0.41	-	-	1								
MAT	-	-	-	-	0.49	1							
AMT	-	-	-	-	-0.20	-0.22	1						
STD	0.58	-	-	-0.63	-	-	-	1					
MEL	-	-	-0.93	-	-	-	-	-	1				
DIF	-0.42	0.49	-	-	-	-	0.33	-	-	1			
MDT	-	-	-	-	-	-	0.36	-	-	-	1		
JUL	-	-	-	-	-	-	-0.59	-	-	0.33	-0.68	1	
AEV	-	-	-	-	-	-0.39	-	-0.19	-	-	-	-	1
AWD	-	-	-	-	0.05	0.33	-0.21	-	-	-	-	-	0.48

of various accumulation functions. Their study, based on theoretical models fitted to field data, has shown that both variables (specimens and species) should exhibit an approximately linear behaviour on a log-log scale (the functional relationship of logarithmic accumulation functions is not exactly linear since the number of species eventually reaches an asymptote while the number of collected individuals can increase indefinitely with time (see Efron & Thisted 1976; Williams 1995). Based on this property, we incorporated to our log-linear models the logarithm of the number of voucher specimens registered per cell (we previously added one to the number of specimens, to avoid the indetermination of log-zero) as an additional predictor, with the objective of evaluating the potential effect of under-collection in our study (we also tried the non-transformed data, but the log-transformed values were in all cases significantly better predictors). Thus, once the final model based on environmental predictors had been fitted, we added the logarithm of the number of specimens (our estimation of collection intensity), in order to evaluate the proportion of the model's error that could be attributed to spatial heterogeneity in the collection effort. Once this last effect had been fitted, we analysed the residual χ^2 deviance of the log-linear model (i.e. the model's error) for significance. If the residual variation was significantly higher than could be expected by chance, we then proceeded to analyse the residuals of the model as explained in the next section.

Analysis of the residuals

In Poisson frequency data the standardized residuals

$$(\text{observed} - \text{expected}) / \sqrt{[\text{expected}]} \quad (1)$$

follow asymptotically a normal distribution (Everitt 1977). Thus, for each cell the standardized residuals can be used as a measure of the fit of that particular cell to the complete model (any residual higher than a certain

critical normal deviate can be regarded as not fitting adequately to the model). Because the number of cells was 318, we followed the Bonferroni criterion of using a lower probability threshold ($P \leq 0.0002$) in each individual test of residuals, in order to obtain a global probability of a type-I error of 0.05 (Cook & Weisberg 1982; Miller 1965). We also followed Pearson's rule for the expected values, and did not analyse residuals in cells where the frequencies predicted by the log-linear model were lower than five.

All cells with residuals departing significantly from the model, and with predicted values higher than five, were marked on the map in order to analyse the distribution of sites where species richness was significantly higher than would be expected from the present environmental conditions. In this way, we could identify areas where the differences between the predictions of the model and the actual floristic richness could not be attributed to random variation. We also tested the standardized residuals for independence, following Draper & Smith (1981).

Floristic affinities between regions

In order to analyse floristic affinities between regions, we chose three base cells of relatively high cactus richness. Each base cell was located in the central part of one of the three most cactus-rich phytogeographic provinces of Argentina: the Prepuna, Monte and Chaco Provinces (Cabrera & Willink 1980; Fig. 1). We then calculated, for each cell on the map, the number of species shared with the base cells. We then plotted maps of equiprobabilistic contour lines showing the similarity of all cells with the chosen centre of comparison (i.e. the base cell). These curves have been used to predict species barriers and corridors for different taxa (Rapoport 1975, 1982; Rapoport & Ezcurra 1979). This analysis was repeated for the three main growth forms: opuntoid, columnar and globose cacti.

The distribution of geographic ranges

The geographic range of each species was estimated by adding the number of cells in which the species was present. The frequency distribution of species ranges in each growth form was then calculated, together with the median of the distribution. This procedure allows evaluation of the proportion of endemic species in each growth form (i.e. the number of species below a given low number of cells). As predicted by previous biogeographic research, the data were log-normally distributed (Rapoport 1975, 1982). Thus, the mean and the standard deviation of the distributions of ranges were calculated on the log-transformed data, and these values were used to test for differences in the ranges of the three growth forms.

Results

Species richness patterns

When the whole group was considered (Fig. 2), areas in the NW of the country showed the highest species richness: Prepuna Province, northern Monte Desert and Chaco dry forest. The number of species in the peaks of the first two regions double that of the richest cells in the Chaco. The Andean-Patagonian and Pampean provinces showed the lowest levels of cactus species richness. The columnar cacti (Fig. 3a) followed a pattern similar to that of the whole group. In both cases, the number of species decreased from north to south, and from west to east. Both groups showed a marked decline above 34–36° S. The globose cacti (Fig. 3c) did not fit this pattern, although their southern limit was similar to that of the columnar group. They reach their highest species richness in the Prepuna Province and the Monte Desert, and in two isolated ranges: the *Sierras* of Córdoba and San Luis, and the hills of Entre Ríos. This growth form has a strikingly low species richness in the Chaco dry forest compared to either the columnar growth form or the whole family. The opuntoid form (Fig. 3b), more widespread than the others, spanned a large altitudinal and latitudinal range. Although its species richness decreased in regions such as Patagonia and the high Andes, plants in this group reach colder habitats than those generally tolerated by the other growth forms. In spite of the low number of species, the species richness pattern of the epiphytic cacti (Fig. 3d) was quite conspicuous. Two areas of high species richness appeared, both in the most humid parts of Argentina: the Yungas Province, a cloud forest in the NW, and the Parana Province, a wet tropical forest in the NE linked to the Brazilian *Mata Atlántica* (coastal cloud forests).

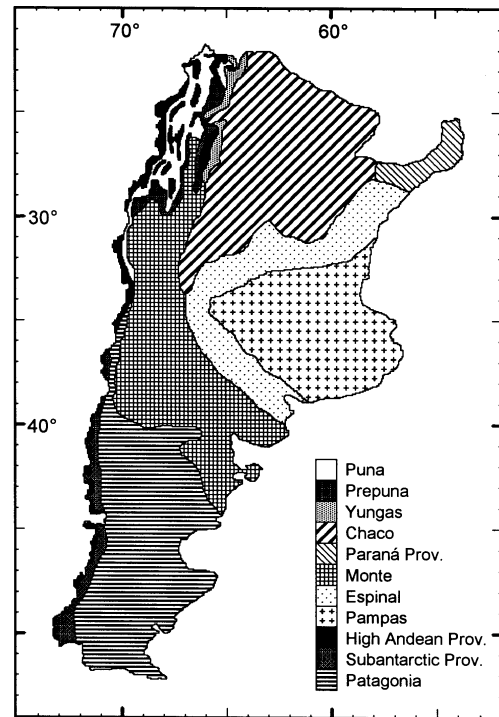


Fig. 1. Phytogeographic provinces of Argentina, after Cabrera & Willink (1980). The main biome in each province is given in parentheses: Puna Province (high-altitude cold semidesert), Prepuna Province (sarcocaulous scrub), Yungas Province (cloud forest), Chaco Province (dry subtropical forest), Parana Province (humid savannah), Monte Province (warm desert), Espinal Province (xerophyllous woodland), Pampas Province (temperate grassland), High-Andean Province (high-altitude cold grassland), Subantarctic Province (temperate humid forest), Patagonia Province (steppe).

Species richness and environmental variables

Regression against latitude.

The growth forms showed a significant negative association between species richness and latitude (whole group: $r^2 = 0.46$, $P < 0.0001$; opuntoid cacti: $r^2 = 0.27$, $P < 0.0001$; globose cacti: $r^2 = 0.24$, $P < 0.0001$; columnar cacti: $r^2 = 0.54$, $P < 0.0001$). Species richness increased in all cases towards tropical, low latitude cells. However, in the opuntoid and globose growth forms, as well as in the whole family, latitude was not the best individual predictor, as the specific environmental variables were more significantly associated with species richness. In contrast, in the columnar growth form latitude showed a higher association with species richness than any other single environmental variable (Fig. 4).

Regression against environmental variables

Globally, the environmental variables selected by the multiple regression procedure, together with the

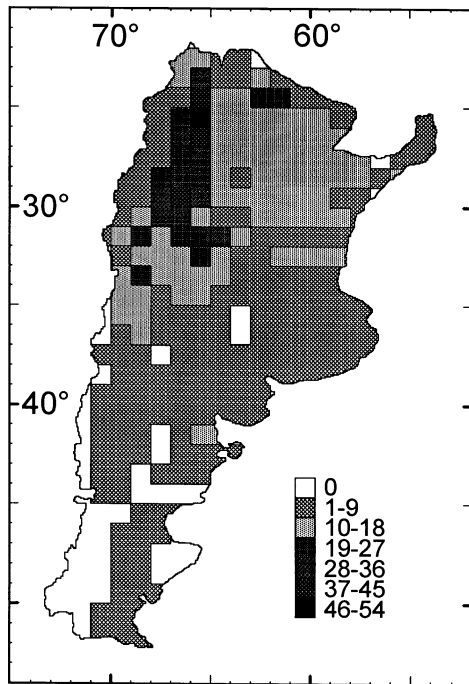


Fig. 2. Species richness – numbers per $1^\circ \times 1^\circ$ cell – for all cacti in Argentina (excluding Pereskioidei species).

estimate of the collection effort, accounted for a large proportion of the total variation in species richness for the whole group, and for the individual growth forms (Table 3). For the whole group, the proportion of summer rainfall was the strongest predictor ($P < 0.0001$; Fig. 5a). The pooled set was also significantly associated with the number of frost-free days ($P < 0.0001$), the altitudinal range ($P < 0.0001$) and the mean annual temperature ($P < 0.0001$).

In the globose and opuntoid forms the best predictor of species richness was the proportion of annual rain falling in summer ($P < 0.0001$ for both growth forms; Figs. 5c, 5d and Table 3). Additionally, in the globose cacti the mean minimum annual temperature and the altitudinal range explained a significant ($P < 0.0001$), albeit lower, proportion of the residual variation. In short, the globose species tend to occur in regions where rain falls mainly in summer, but which are at the same time relatively warm and topographically heterogeneous. Besides the proportion of annual rain falling in summer, the species richness of the opuntoid group was also significantly ($P < 0.0001$) associated with the aridity index and with the mean annual temperature.

The number of frost-free days was the strongest predictor for the columnar growth form ($P < 0.0001$; Fig. 5b). As the number of frost-free days increases, the species richness increases as well. This result seems to confirm the high sensitivity to freezing temperatures of

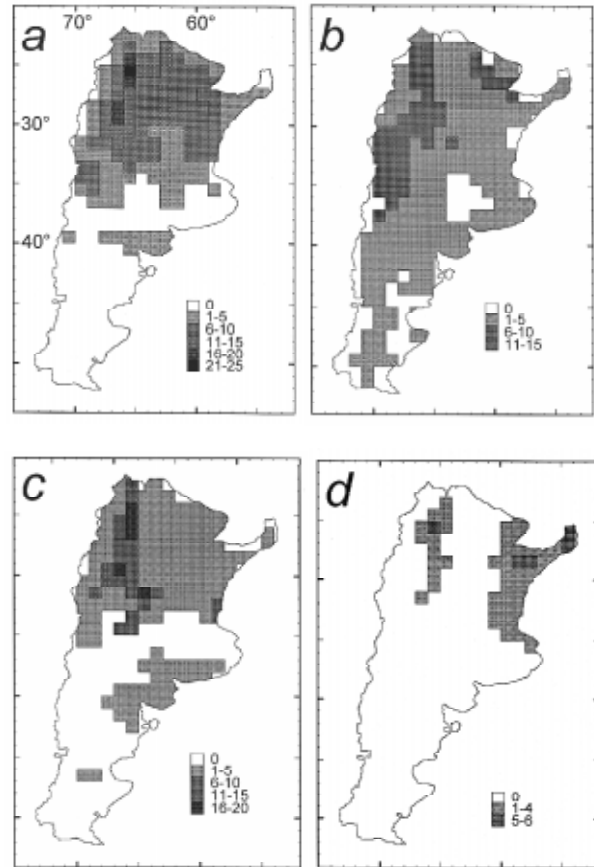


Fig. 3. Species richness for (a) columnar, (b) opuntoid, (c) globose, and (d) epiphytic cacti in Argentina.

the columnar growth form (Gibson & Nobel 1986). The columnar species were also significantly associated with altitudinal range ($P < 0.0001$), although the variation explained by this second variable was lower.

The effect of collection intensity

In all growth forms the intensity of collection explained a highly significant ($P < 0.0001$) proportion of the residual variation of the models, although in no case was it more important than the first environmental predictor (Table 3).

Analysis of the residuals

As can be seen in Figs. 4 and 5, the dispersion of the data increased with the mean values of species richness, and with the predicted values of the model. For example, for the whole cactus family it can be seen that in the low-latitude regions the mean species richness is higher, but the dispersion of the data is also higher (Fig. 5a). This should be expected in frequency data, as a Poisson error distribution predicts that the variance of randomly-varying frequency values should be equal to the mean

(i.e. the expected value). The standardized residuals followed the assumptions of the regression model (Poisson error and independence) in all growth forms separately ($G = 235.7$, d.f. = 303 for the opuntoid species; $G = 303.0$, d.f. = 303 for the columnar species; $G = 297.7$, d.f. = 303 for the globose species), but the whole group did show a significant residual variation ($G = 407.0$, d.f. = 302, $P < 0.0001$) that suggested non-random departures from the model in some cells.

When the residuals that departed significantly from the Poisson error distribution were analysed for the whole group, it was found that a cell in the Prepuna and another in the northernmost tip of the Monte Desert showed significantly higher species richness than was predicted by the regression model (Fig. 6). Three cells also appeared with significant negative residuals, showing areas where species richness is lower than could be expected following the model's predictions. These three cells corresponded to the three most collected grid cells in Argentina. While on average the number of specimens per cell was 14.3 for the whole country and 25.2 for the subtropical northern section, these three sites had well above 100 specimens each.

The effect of cell size

As the size of the cells used in this study covaries with latitude (the area of each cell decreases with latitude), we could ask whether the area *per se* can explain the observed latitudinal patterns of species richness. In order to analyse the effect that decreasing cell size may have on species richness, we followed Preston's species-area equation ($s = k A^z$, where s is species richness, A is the sampled area, z is the exponential parameter, and k is a scale coefficient; see Preston 1960, Palmer & White 1994). For a more conservative analy-

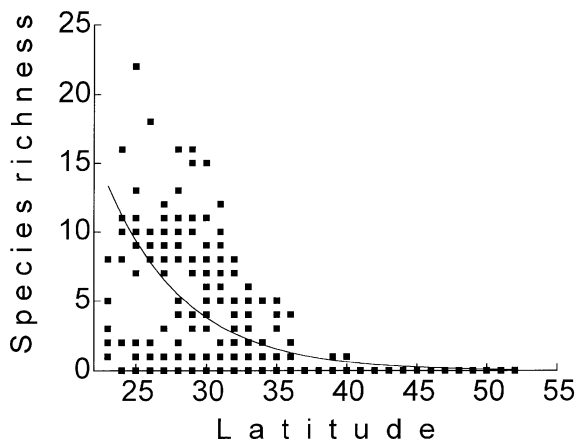


Fig. 4. Relationship between species richness of the columnar growth form and latitude.

Table 3. Proportion of the variation accounted by the best predictors of the linear regression models, excluding latitude. The sign of the coefficient explains the relationship between the predictor and species richness.

Growth Form	Variable	r ²	Sign
Columnar and barrel cacti	Number of frost-free days per year (FFD)	0.50	+
	Proportion of rain falling in summer (PRS)	0.17	+
	Altitudinal range (ALR)	0.02	+
	Collection effort	0.15	+
	Total	0.74	
Opuntoid cacti	Proportion of rain falling in summer (PRS)	0.37	+
	Average annual water deficiency (AWD)	0.05	+
	Mean annual temperature (MAT)	0.03	+
	Collection effort	0.27	+
	Total	0.72	
Globose cacti	Proportion of rain falling in summer (PRS)	0.33	+
	Average minimum annual temperature (AMT)	0.07	+
	Altitudinal range (ALR)	0.03	+
	Collection effort	0.32	+
	Total	0.75	
Whole group	Proportion of rain falling in summer (PRS)	0.50	+
	Number of frost-free days per year (FFD)	0.07	+
	Altitudinal range (ALR)	0.05	+
	Mean annual temperature (MAT)	0.03	+
	Collection effort	0.21	+
	Total	0.86	

sis, we set the z value to 0.4, much higher than Preston's 'canonical' value ($z = 0.23$). Preston's model predicts that a difference in cell area of 17% between northern Argentina and southern Patagonia may result in a reduction in species richness not higher than 6%. As the observed reduction in species number was almost 100% in all growth forms, only a minor part of this change in species richness can be attributed to the latitudinal reduction of cell size. Another possible bias in cell area may result from the fact that some cells are located on a seacoast, peninsula or in border areas. To analyse the significance of the effect of incomplete cells on species richness, these cells were identified with a statistical factor (a dummy variable) in the regression analyses. It was found that the effect of incomplete cells was not significantly associated with species richness. Thus, the effect of cell size on the observed patterns of cactus richness can be safely ignored for all practical purposes.

Floristic affinities between regions

Prepuna

In general, a remarkable level of endemism was found in this region. Of all the opuntoid species present in the Prepuna, only 40% are shared with a small part of the High-Andean province (Figs. 7a'). Less than 20% of the columnar and globose species present in the Prepuna occur outside this province (Figs. 7a and 7a'').

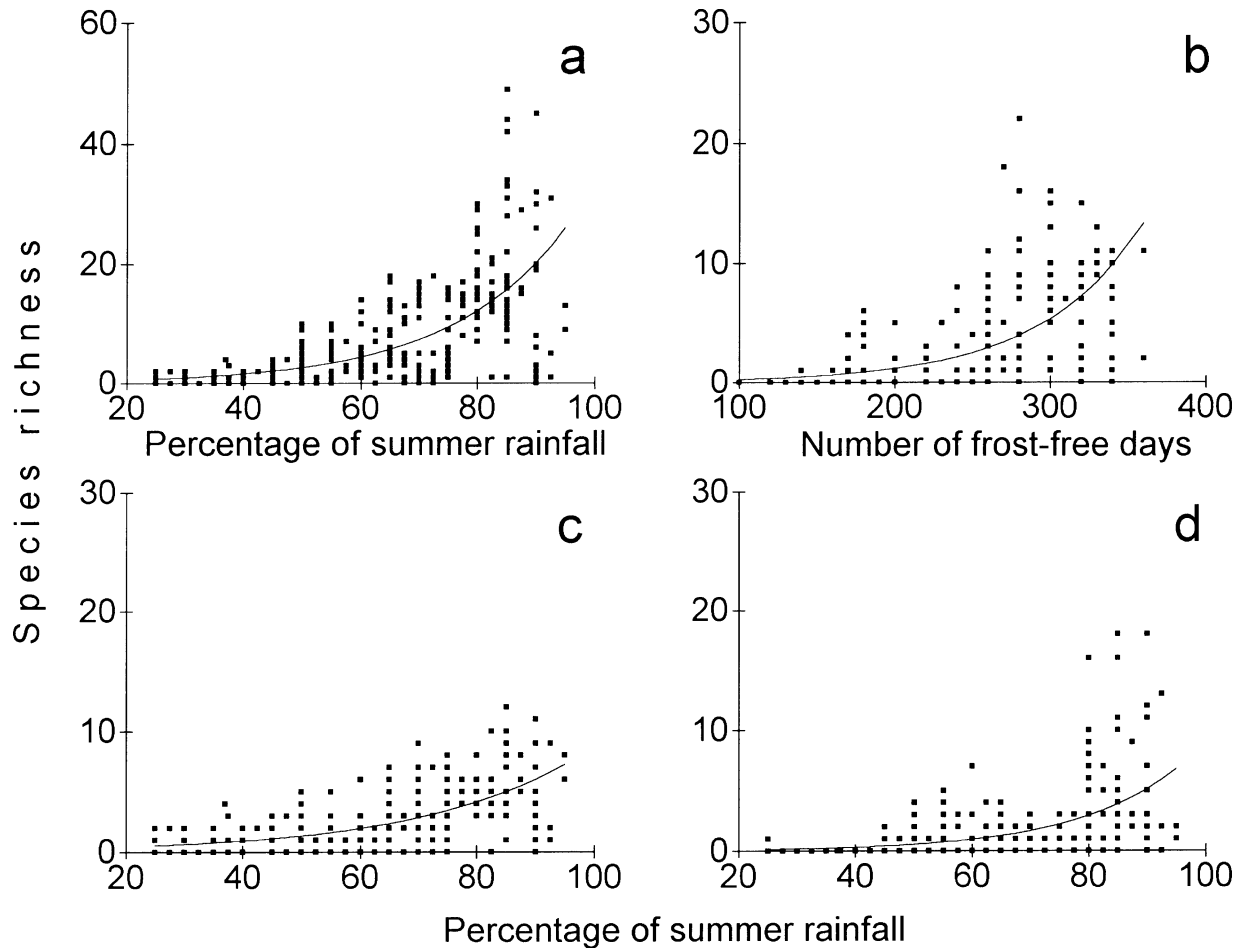


Fig. 5. Relation between species richness per growth form and its best predictor: (a) all species; (b) columnar species; (c) opuntoid species; (d) globose species. Regression line indicates the log-linear function predicted by the stepwise regression analysis.

The Monte Desert

With the central Monte Desert as the base cell, a strong southern barrier appeared in all three groups with a western barrier on the Andes. For the opuntoid growth form a corridor of high affinity running northwards was observed (Fig. 7b'). The columnar species in this region showed a high number of shared species with the northern Monte Desert and Prepuna, while the globose forms presented a corridor of shared species with the northern Monte Desert and the northern Espinal province (a xerophyllous woodland; Figs. 7b and 7b').

The Chaco dry forest

Most opuntoid species present in the Chaco also occur in the Prepuna and in the northern Monte Desert (Fig. 7c'). In the case of columnar cacti, this trend is less marked and only 60% of the species were found to be shared with the western arid zones (Fig. 7c). Most of the globose cacti in the dry Chaco (more than 50%) are also shared by the Prepuna and northern Monte provinces

(Fig. 7c''). The existence of cells with a floristic similarity of 100% in these last provinces, as well as the general pattern of isolines, suggest a biogeographic corridor for all globose species in the dry Chaco, allowing their dispersion into the northern Monte and the Prepuna, and also into the wet Chaco.

The distribution of geographic ranges

The globose group exhibited the highest number of species with restricted distribution: 77.06% of the globose species occupied five cells or less, compared to 33.33% for the columnar species and 34% for the opuntoid form (Fig. 8). In increasing order, the median range of the globose group was the lowest ($Me = 3.65$), followed by the columnar and the opuntoid forms ($Me = 9.33$ and $Me = 11.00$ respectively). There were also significant differences between the mean log-range of globose cacti ($\bar{x} = 1.86$; S.E. = 0.11) with the opuntoid species ($\bar{x} = 3.35$; S.E. = 0.21; $P < 0.001$) and with the

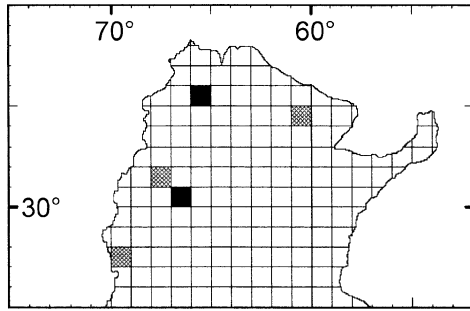


Fig. 6. Standardized residuals of the log-linear regression models for the whole cactus group. Black squares correspond to significantly positive residuals (cells having significantly more species than predicted by the Poisson error distribution), the grey squares correspond to significantly negative residuals.

columnar species ($\bar{x} = 3.29$; $se = 0.23$; $P < 0.001$). No significant difference was found between the mean log geographic ranges of opuntoid and columnar cacti. Additionally, the globose form included a relatively high number of strongly localized species: 10% of the globose species were restricted to only one cell while none of the opuntoids and only 2 % of the columnars displayed such highly restricted ranges.

Discussion

The biodiversity patterns found for Argentine cacti showed significant variation between the different growth forms. Environmental factors operating at a regional scale – mostly linked to climatic favourableness and climatic variation – accounted for a large proportion of the geographic variation observed in the species richness of all growth forms. Variables related to habitat heterogeneity or energy interception levels were poorer predictors of species richness in general, although habitat heterogeneity was a significant predictor for the globose growth form.

The columnar and globose growth forms, as well as the combined group, showed the highest species richness in the Prepuna and the northern Monte Desert. The ubiquity of the opuntoid form was noticeable in the high-diversity corridors found linking the Chaco with the Prepuna and the northern Monte. The opuntoid cacti are the only group reaching the Patagonian steppe in the southernmost province of Santa Cruz, a fact that underscores their wider climatic tolerances. The broad tolerances of opuntoid cacti may be related to the modular growth and the morphological plasticity of this form, as suggested by Gibson & Nobel (1986) and

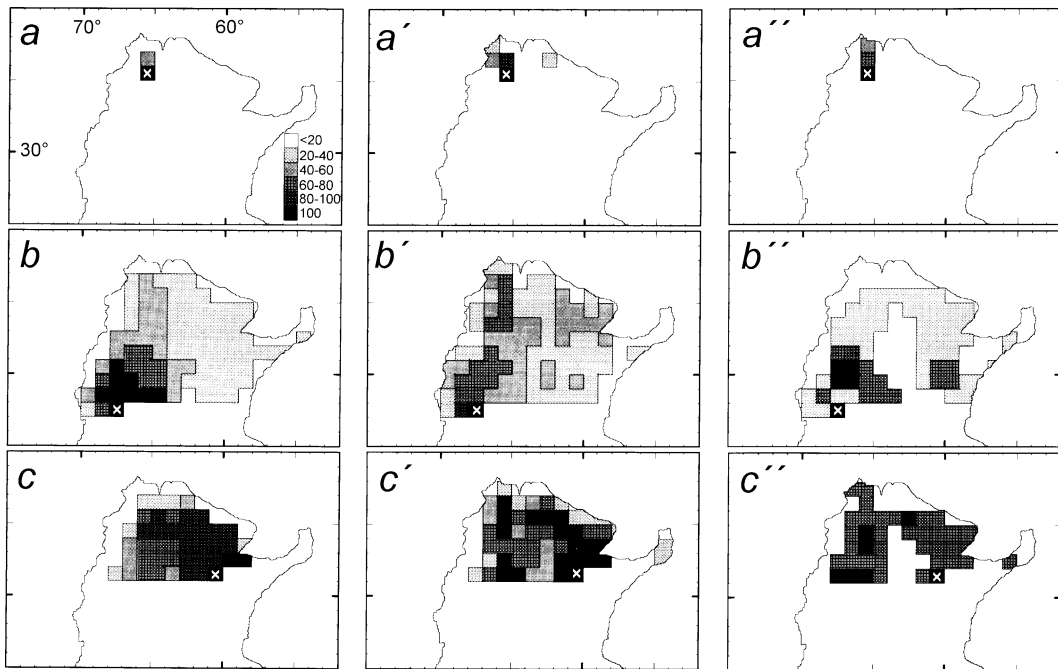


Fig. 7. Floristic similarity centred in three selected cells representing different Provinces: (a-a'-a'') Prepuna; (b-b'-b'') Monte, and (c-c'-c'') Chaco. The shading represents the percentage floristic similarity from a central point of comparison (base cell representing a 100% of species), marked by a cross. Maps to the left (a-b-c) correspond to columnar species, maps in the middle (a'-b'-c') to opuntoid species, maps to the right (a''-b''-c'') to the globose species.

Nobel (1982a, b, 1985). The adaptive advantage of the terminal orientation of the flat cladodes according to the latitude and to specific environmental conditions, may be the base of the higher success of opuntoid cacti in extreme environments. Gibson & Nobel (1986) have also attributed the higher temperature tolerance of opuntoid species to the shifting of the temperature response for net nocturnal CO₂ uptake as the environmental temperature changes. In spite of their wider tolerances, the opuntoid species were statistically associated with the proportion of annual rain falling in summer, the aridity index and the mean annual temperature. This group thus seems to be mainly associated with warm areas with concentrated summer rains.

The distribution of columnar cacti appears to be severely constrained by low temperatures. The northern, subtropical biogeographic regions showed little floristic similarity with the southern, more temperate regions, and the maps of floristic affinity suggest the existence of a barrier south of the Chaco and Prepuna Provinces. Additionally, species richness decreases abruptly above latitude 34 °S and above altitudes of 3000 m. An exception is the genus *Oreocereus* (with two species in Argentina), which can be found at elevations of 4000 m. Their stems are completely covered with white long spines and hairs, which seem to thermally insulate the plant from frost, supplying freezing resistance and mechanical protection in stressful habitats. The number of frost-free days was the best predictor for columnar species richness, explaining a significant proportion of the variation (50 %). It is necessary to note here that all cells in Argentina have some level of frost danger in winter, ranging from fewer than five freezing days in the north to more than 250 days in Patagonia. This result confirms a trend described by Burgess & Shmida (1988): Cactoid vegetation does not occur in areas where freezing occurs frequently. It has also been reported (Gibson & Nobel 1986) for the

saguaro (*Carnegiea gigantea*, a columnar species) in North America, that frost damage may cause a reduction in stem growth and often leads to substantial constriction in stem diameter. In short, columnar species seem to respond to the climate favourableness hypothesis.

Apart from their strong association with the amount of the precipitation falling in summer, the distribution of the globose species seems to be linked also to substrate characteristics (e.g. microsites and soil rockiness), which are basically independent of the large-scale variables used in this study. In general they do not occur in areas lacking rocky substrates (e.g. the Chaco plains), where other cactus groups are common. This substrate preference may explain the high species richness of the group in the rocky Prepuna and the striking level of endemism they show in the mountainous ranges of central Argentina (Córdoba and San Luis) and in the rocky hills of Entre Ríos in the mesic northeast of the country. In general, the species richness pattern of this growth form at our scale of study seems to follow the climatic variation hypothesis, as the percentage of summer rainfall explained a significant proportion of their variation in species numbers. For columnar and barrel cacti, it has been shown that the key environmental factor affecting survival during the seedling stage is the availability of water, until the plant can reach a larger size and a lower surface/volume relationship (Steenbergh & Lowe 1977). To survive an ensuing drought, the seedling must develop sufficient water storage tissue during the preceding wet season. More studies of seedling microhabitats and requirements for germination and establishment (e.g. the length of the summer wet season) are needed for opuntoid and globose cacti.

The altitudinal range of the cells explained a significant, but low, proportion of the variation in species numbers for all groups with the exception of opuntoid cacti ($r^2 = 0.03$, $P < 0.0001$ for the globose form; $r^2 = 0.02$, $P < 0.0001$ for the columnar species, and $r^2 = 0.05$, $P < 0.0001$ for the whole group). Our results, unlike those of Richerson & Lum (1980), are not completely consistent with the habitat heterogeneity hypothesis as a major determinant of species richness; the analysed variables only explained a small proportion of the observed variation.

Latitude, as an indirect environmental factor, was the single best predictor only for columnar species richness, but it is difficult to use this relationship in order to test any specific hypothesis on the causes of species richness. As it is strongly correlated to variables such as the number of frost-free days and the proportion of summer rainfall, latitude can be interpreted as a composite indicator of both climatic favourableness and climatic variation, and consequently it cannot be used to discriminate between the two hypotheses.

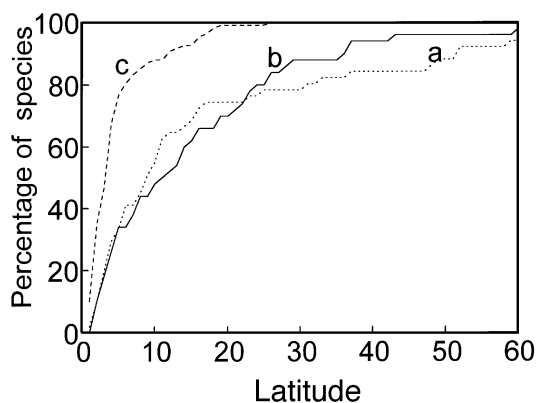


Fig. 8. Geographic range of the different growth forms: (a) columnar; (b) opuntoid and (c) globose.

The species richness patterns of the whole group, and of the opuntoid and the globose growth forms, turned to be more consistent with the climatic variation (seasonality) hypothesis, with the proportion of summer rainfall appearing as the best predictor in all the regression analyses. According to Burgess & Shmida (1988), cactoids preferentially thrive in warm semi-desert areas where rainfall ranges from 150 to 400 mm/yr. While cacti are not restricted to climates with summer rainfall, they are rarer where winter rain is common and summer rain lacking. A salient feature of the observed relationships between species richness and climatic variables is that the mean values of the variables were not as strongly related to species richness as seasonality indices or other measures of variation in climatic favourableness (i.e. number of frost-free days).

In agreement with other authors (Whittaker 1965; Richerson & Lum 1980) and at odds with the findings of Currie (1991) and Rosenzweig (1992), productivity was not related to species richness, nor did variables such as evapotranspiration, mean temperature and mean precipitation (two main elements of productivity) show a strong relationship with species numbers. This may result from the fact that productivity obtained as a function of evapotranspiration showed little variation within the distributional range of cacti in Argentina. Additionally, cacti are mainly found in low-productivity environments, the exception being the epiphytes which were not included in the regression analyses. Potential productivity could also be measured from estimates of incoming solar energy; it is possible that if such an estimate of productivity was used it would more closely correlate with species richness.

Although we did not explicitly test the incidence of fire as a predictor of cactus species richness, it has been reported that cacti tolerate fire poorly (e.g. Thomas & Goodson 1992; McLaughlin & Bowers 1982). The central pampas, which are distributed along a moisture gradient from a humid prairie in the east to an arid wooded grassland in the west, have been for centuries the areas with the highest fire intensity in Argentina. It is interesting to note that for all growth forms, these formations have a relatively low number of species. Fire may be partially responsible for these low-richness areas.

For all growth forms, the significant association found between collection intensity and the residual variation of the models suggests that undercollection is possibly biasing the observed distribution of species presences, as some cells are much better collected than others. This also suggests that, for the present intensity of botanical exploration in Argentine cacti, the use of cells one degree in size is an adequate scale, as in smaller cells the error introduced by spatial gaps in the botanical collection would be more important than the

variation associated with environmental factors.

Remarkable differences were found between the three growth forms in the area covered by their distributional ranges. Globose species showed a striking level of microendemism, consistent with the idea previously discussed that factors operating at a more local scale, such as substrate type and topographic heterogeneity, are significantly associated with the distribution of this group. The distribution of rocky soils and mountainous ranges in central Argentina is highly discontinuous; this in turn gives rise to a fragmented distribution of the globose cacti, the group most associated to these types of habitats. The distributional ranges of opuntoid and columnar cacti were significantly larger than those of the globose species, although they were not significantly different between themselves. In particular, many opuntoid species do not only occupy large continuous geographic areas (e.g. *Opuntia quimilo*, endemic to the Chaco phytogeographic province or *O. sulphurea*, endemic to the Monte province), but many of them (e.g. *O. brasiliensis*, *O. monacantha*, *O. nigrispina*, *O. pentlandii* and *O. soehrensii*) also inhabit more than one phytogeographic region.

For the whole group, significantly low residuals were found in three cells that are the most collected areas in Argentina. This result is quite likely an artefact of the model: as the number of species was positively associated with the number of collected specimens, in cells with an extraordinarily high number of specimens the model will predict a very high number of species. In practice, however, most accumulation functions will tend to reach an asymptote at some level (Soberón & Llorente 1993; Williams 1995).

Similarly, significantly high residuals in the regression model were observed in the Prepuna and the northern Monte Desert, indicating that these two cells have more species than can be attributed to random change. It could be that the climatic maps used, which were obtained by smoothing data points from weather stations, failed to adequately represent the real environmental conditions at these sites. We have found no reason for an artefact of this sort to occur in this region more than others, but the possibility cannot be completely ruled out. In some cases, high species richness areas have been associated with oversampling (Nelson et al. 1990), as plant collecting is subject to several sources of biases: (a) some regions are more accessible than others, and the collection efforts may be heterogeneous and (b) many experts prefer rarities, and common species may be poorly represented in collected samples. In our case, however, undercollection was controlled by including our measure of collection effort into the model. Additionally, the collection intensity in these two sites (82 and 61 specimens) was well above the average. An

alternative explanation can be found in the environmental history of these cells. Present environmental conditions may not explain the extraordinarily high species richness of these sites because past events may be responsible for the present species density. Possibly the Prepuna and northern Monte functioned as a refuge for cacti during Pleistocene glacial events; this may still be reflected in their present high species richness. It has been suggested that the central Monte, as opposed to the Puna and the Chaco Provinces, experienced periods of high humidity during the Quaternary (Axelrod 1958; Tricart 1970; Vuilleumier 1971; see further Markgraf 1983, 1985, 1989 on South-American paleoclimates).

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App. 1. List of Argentine cactus species included in this study.

COLUMNAR CACTI

Cereus aethiops Haworth
Cereus argentinensis Br. et Rose (Britt. and Rose)
Cereus chalybaeus Hauman (non Otto)
Cereus dayami Speg.
Cereus forbesii Haworth
Cereus hankae Web.
Cereus stenogonus K. Sch.
Cleistocactus baumannii (Lem.) Lemaire
Cleistocactus ferrarii R. Kiesling
Cleistocactus jujuyensis (Backbg.) Backbg.
Cleistocactus smaragdiformis (Web.) Britton et Rose
Denmoza rhodacantha (SD) Britton et Rose
Echinopsis leucantha (Gill.) Walp.
Echinopsis rodoltricha R. Mey
Harrisia bonplandii (Parmentier) Britton et Rose
Harrisia martinii (Labouret) Britton et Rose
Harrisia pomanaensis (Weber) Britton et Rose
Harrisia tortuosa (Forbes) Britton et Rose
Lobivia chrysochete Werdermann
Lobivia ferax Britton et Rose
Lobivia formosa (Pfeiff.) Britton et Rose
Lobivia koretroides (Werd.) Backbg.
Lobivia walteri R. Kiesling
Monvillea cavendishii (Monville) Britton et Rose
Monvillea spegazzini (Weber) Britton et Rose
Notocactus shumannianus Berger
Oreocereus celsianus (Lemaire) Riccobono
Oreocereus trollii Kupp
Pyrrhocactus umadeave (Werd.) Backbg.
Stetsonia coryne (Salm-Dyck) Britton et Rose
Soehrensia brucchi (Br. et Rose) Backbg.
Trichocereus andalgalensis (Web.) Hosseus
Trichocereus angelesii R. Kiesling
Trichocereus cabrerai R. Kiesling
Trichocereus candicans (Gillies) Britton et Rose
Trichocereus fabrisii R. Kiesling
Trichocereus huascha (Web.) Britton et Rose
Trichocereus lampochlorus (Lemaire) Britton et Rose
Trichocereus pasacana (Web.) Britton et Rose
Trichocereus pseudocandicans (Backbg.) ex R. Kiesling
Trichocereus rowleyi (Friedr.) R. Kiesling
Trichocereus schickendantzii (Web.) Britton et Rose
Trichocereus smirzianus (Backbg.) Backeberg
Trichocereus spachianus (Lem.) Ricc.
Trichocereus strigosus (Salm-Dyck) Britton et Rose
Trichocereus tarijensis (Vpl.) Werdermann
Trichocereus terscheckii (Parm.) Britton et Rose
Trichocereus thelegonoides (Speg.) Britton et Rose
Trichocereus thelegonus (Web.) Britton et Rose
Trichocereus vatteri Kiesling

OPUNTIOID CACTI

Austrocylindropuntia shaferi (Britton et Rose)
Austrocylindropuntia verschaffeltii (Cels. & Web.) Backbg.
Austrocylindropuntia vestita (Salm-Dyck) Backbg.
Cylindropuntia tunicata (Lehm.) Knuth
Maihueiopsis boliviana (S.-D.) R. Kiesling
Maihueiopsis darwinii (Hensl.) Ritter
Maihueiopsis minuta (Backbg.) R. Kiesling
Maihueiopsis nigrispina (K. Schum.)
Maihueiopsis ovata (Pfeiff.) Ritter
Maihueiopsis pentlandii (S.-D.) R. Kiesling
Opuntia arechavaletae Speg.
Opuntia aurantiaca Lindl.
Opuntia brasiliensis (Will.) Haw.
Opuntia brunescens Britt. et Rose
Opuntia chakensis Speg.
Opuntia cordobensis Speg.
Opuntia corrugata Salm-Dick
Opuntia delaetiana Web.
Opuntia discolor Britton et Rose
Opuntia halophila Speg.
Opuntia penicilligera Speg.
Opuntia quimilo Schumann
Opuntia retrorsa Speg.
Opuntia salagria Castellanos
Opuntia salmiana Parm. ex Pfeiff.
Opuntia schickendantzii Weber
Opuntia soehrensii Britton et Rose
Opuntia subsphaerocarpa Speg.
Opuntia sulphurea Salm-Dick
Opuntia wetmorei Britton et Rose
Pterocactus araucanus Castellanos
Pterocactus australis (Weber) Backbg.
Pterocactus fisherii Britton et Rose
Pterocactus gonjianii R. Kiesling
Pterocactus hickenii Britton et Rose

Pterocactus kuntzei K. Schumann
Pterocactus meglioni R. Kiesling
Pterocactus pumilus Britton & Rose
Pterocactus reticulatus R. Kiesling
Pterocactus valentini Spegazzini
Puna clavarioides (Pfeiff.) Kiesling
Puna subterranea (R. E. Fries) R. Kiesling
Tephrocactus alexanderi (Br. & Rose) Backbg.
Tephrocactus aoracanthus (Lem.) Lem.
Tephrocactus articulatus (Pfeiff.) Backbg.
Tephrocactus articulatus (Pfeiff.) Backbg.
Tephrocactus geometricus (Cast.) Backbg.
Tephrocactus halophilus (Speg.) Backbg.
Tephrocactus molinensis (Speg.) Backbg.
Tephrocactus weberi (Speg.) Backbg.

GLOBOSE CACTI

Acanthocalycium glaucum Ritter
Acanthocalycium thionathum (Speg.) Backbg.
Acanthocalycium violaceum (Werd.) Backbg.
Austrocactus bertinii Britton et Rose
Austrocactus dusseii Speg.
Austrocactus patagonicus Hoss.
Blossfeldia liliputana Werd.
Echinopsis ancistrophora Speg.
Echinopsis aurea Br. et Rose
Echinopsis eyriesii (Turp.) Zucc.
Echinopsis mamillosa Gürke
Echinopsis obrepanda (S.-D.) K. Schumann
Echinopsis silvestrii Speg.
Echinopsis tubiflora (Pfeiff.) Zucc.
Frailea castanea Backbg.
Frailea cataphracta Britton et Rose
Frailea grahliana Britton et Rose
Frailea mamnifera Buining et Brederoo
Frailea pygmaea Britton et Rose
Frailea shilinzkyana (HGE. jr.) Britton et Rose
Gymnocalycium andreae Krainz
Gymnocalycium asterianum Castellanos
Gymnocalycium baldianum Speg.
Gymnocalycium brucchi (Speg.) Hoss.
Gymnocalycium brucchi Hoss.
Gymnocalycium calochlorum (Bödek.) Y. Ito
Gymnocalycium capillaense (Schick) Backbg.
Gymnocalycium capillense Hoss.
Gymnocalycium castellanii Backbg.
Gymnocalycium denudatum Pazout
Gymnocalycium ferrarii Rausch
Gymnocalycium gibbosum Backbg.
Gymnocalycium glaucum Ritter
Gymnocalycium horridispinum Frank
Gymnocalycium huachinensis Schütz
Gymnocalycium hybopleurum Backbg.
Gymnocalycium kieslingii Ferrari
Gymnocalycium marsoneri Y. Ito
Gymnocalycium mazarense Backbg.
Gymnocalycium mesopotamicum R. Kiesling
Gymnocalycium mihanovichii Britton et Rose
Gymnocalycium mostii Britton et Rose
Gymnocalycium multiflorum (Hook)
Gymnocalycium nidulans Backbg.
Gymnocalycium parvulum Speg.
Gymnocalycium patense (Speg.) Britton et Rose
Gymnocalycium pugionacanthum Backbg.
Gymnocalycium quehlianum Vaupel.
Gymnocalycium ragonesei Castell.
Gymnocalycium ritterianum Rausch
Gymnocalycium saglionis Britton et Rose
Gymnocalycium sanguiniflorum Werderm.
Gymnocalycium schickendantzii (Web.) Britton et Rose
Gymnocalycium schroederianum v. Osten
Gymnocalycium spegazzini Backbg.
Gymnocalycium stuckertii Britton et Rose
Gymnocalycium tanigaensis Pilz.
Gymnocalycium triacanthum Backbg.
Gymnocalycium valnicekianum Jajó
Gymnocalycium vatteri Buin.
Gymnocalycium wessianum Backbg.
Lobivia cachensis Britton et Rose
Lobivia chrysantha (Backbg.) Rausch
Lobivia densispina Werdermann
Lobivia einsteinii M. Fric
Lobivia famatimensis (Speg.) Britton et Rose
Lobivia haemathanta (Spegazzini) Britton et Rose
Lobivia iridescens Backbg.
Lobivia jajotiana Backbg.
Lobivia kieslingii Rausch
Lobivia pygmaea (R.E.Fr.) Backbg.

Lobivia saltensis (Spegazzini) Britton et Rose
Lobivia sanguiniflora Backbg.
Lobivia schreiteri Castell.
Lobivia shaferi Britton et Rose
Lobivia steinmannii (Solms-Laub.) Backbg.
Lobivia stilowiana Backbg.
Lobivia walteri R. Kiesling
Neowerdermania vorwerkii Fric
Parodia auricentra Backbg.
Parodia chrysacanthion (Schum.) Backbg.
Parodia faustiana Backbg.
Parodia linkii (Lehm.) R. Kiesling
Parodia maasii (Heese) Berg.
Parodia microsperma (Web.) Speg.
Parodia nivosa Backbg.
Parodia ottonis (Lehmann) N.P. Taylor
Parodia penicillata Fescher et Van der steeg
Parodia schuetziana Jajó
Parodia setifera Backbg.
Parodia stuemeri (Werd.) Backbg.
Parodia submannulosa R. Kiesling
Parodia tureckianus R. Kiesling
Pyrrhocactus andreaeus (Backbg.) Ritter
Pyrrhocactus atroviridis Ritter
Pyrrhocactus bulbocalix (Werderm.) Backbg.
Pyrrhocactus pachacoensis Rausch
Pyrrhocactus sanjuanensis (Speg.) Backbg.
Pyrrhocactus straussianus Berger
Pyrrhocactus villicumensis Rausch
Rebutia calliantha Bewerunge
Rebutia einsteinii Fric
Rebutia fiebrigii (Gürke) Britton et Rose
Rebutia margaretae Rausch
Rebutia minuscula Schumann
Rebutia pseudominuscula Spegazzini
Setiechinopsis mirabilis (Speg.) De Haas
Weingartia neumanniana (Backbg.) Werd.
Wigginsia tephroacantha (Speg.) D.M.Porter

EPIPHYTIC CACTI

Epiphyllum phyllanthum (L.) Haworth
Pfeiffera ianthothele (Monv.) Web.
Rhipsalis aculeata Weber
Rhipsalis baccifera (Mill.) Stearn
Rhipsalis cereuscula Haworth
Rhipsalis cruciformis Vell.
Rhipsalis houlettiana Lemaire
Rhipsalis linearis Schumann
Rhipsalis lorentziana Grisebach
Rhipsalis lumbricoides (Lem.) Lem.
Rhipsalis monacantha Grisebach
Rhipsalis shaferi (Britton et Rose)
Rhipsalis tucumanensis Weber
Selenicereus setaceus (S-D) Berger

PERESKIOID SPECIES (not included in the analyses)

Pereskia aculeata Miller
Pereskia sacharosa Griseb.
Pereskia nemorosa Rojas Acosta
Quiabentia pflanzii (Vaup.) Berger
Quiabentia chacoensis Backeberg