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Differentiation diversity of Argentine cacti and its relationship to environmental factors

Mourelle, Cristina & Ezcurra, Exequiel

Centro de Ecología, UNAM; Apartado Postal 70-275; 04510 - Mexico, D.F.; Mexico;
E-mail: eezcurra@miranda.ecologia.unam.mx

Abstract. We studied the differentiation diversity (β-diversity or species turnover) patterns of the three main cactus growth forms (columnar, opuntioid and globose) in 318 ($1° \times 1°$) squares covering Argentina. We analysed the degree of association between species turnover of each growth form with the spatial variation of a set of 15 environmental variables.

Species turnover was estimated in two ways: (1) by calculating species turnover along latitudinal and longitudinal gradients and (2) by evaluating the species turnover between each square and its eight surrounding neighbouring grid cells.

For the three growth forms, species turnover in latitudinal transects was mostly related to the mean within-transect values of certain environmental variables, while in longitudinal transects it was related to the variation of some environmental variables within the transect rather than to their mean values. For columnar species, transect species turnover was mainly associated with variation in temperature, confirming the temperature-sensivity of this growth form. For opuntioid species, turnover along transects was mainly related to topographic variables. In the case of globose cacti, transect turnover was associated with variation in temperature and rainfall.

For the three growth forms, areas of high turnover coincided with marked transitions between different biogeographic provinces, while the areas with lowest species turnover coincide with topographically and climatically uniform plains. Species turnover between individual squares was positively associated with the proportion of summer rainfall in globose cacti, the variation of mean annual temperature in columnar cacti and was negatively related to mean annual temperature in opuntioid cacti. Compared to the other growth forms, globose cacti presented a much larger proportion of squares with a high species turnover.

In general, differentiation diversity was lower for the opuntioid and the columnar species, two growth forms with higher dispersal ability and was highest for the globose cacti, which have the lowest dispersal capacity. Environmentally heterogeneous areas, where large-scale transitions between biomes occur, have exceptionally high species turnover, and are important target areas for the conservation of biodiversity.

Keywords: Dispersal capacity; Environmental variable; Growth form; Species turnover.

Introduction

The concept of biological diversity has been subdivided into two main components: (1) local richness or inventory diversity and (2) differentiation or β-diversity, also known as replacement or turnover between species assemblages. Both components apply to a wide range of scales. The first concept has been commonly labelled as α-diversity, when applied within a community or a homogeneous habitat, but has also been defined as γ-diversity when applied to the landscape level and as ε-diversity at a regional level (Whittaker 1977). The second component has received a large array of names from many authors, such as (1) internal β-diversity or pattern diversity, (2) β-diversity, between-habitat diversity or between-site diversity and (3) γ-diversity, geographic differentiation or δ-diversity (Whittaker 1960, 1972, 1977; MacArthur 1965; Cody 1975, 1986, 1993; Magurran 1988; Cowling et al. 1989; Cornell et al. 1992; Colwell & Coddington 1994). This terminological heterogeneity arises mostly from the application of essentially the same concept at different scales in which different biological processes may operate.

Local and regional diversity, or species richness at a local or regional scale, have long been major topics in the ecological and biogeographical literature, focusing on their definition and measurements (Pielou 1975; Magurran 1988; Begon et al. 1990; Sánchez & López 1988) and on its biological determinants (MacArthur 1965; Pianka 1966; Huston 1979; Brown 1981, 1988; Shmida & Wilson 1985; Begon et al. 1990; Rhode 1992; Rosenzweig & Abramsky 1993). Differentiation diversity, usually approached as species turnover, has received less systematic analysis (for remarkable exceptions see Whittaker 1972; Cody 1975, 1986; Routledge 1977; Wilson & Shmida 1984; Shmida & Wilson 1985; Magurran 1988; Harrison et al. 1992). Yet, turnover of species between areas is as important as local richness in determining diversity at any scale.

In this paper, we will focus on the analysis of differentiation diversity for three growth forms of the *Cactaceae* in Argentina: (a) columnar and barrel cacti,
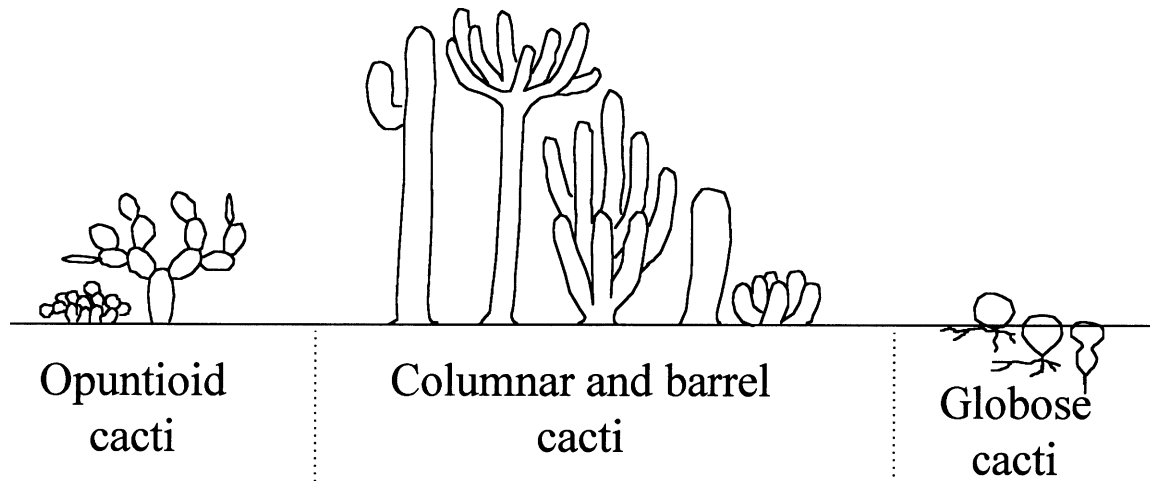
Fig. 1. Schematic representation of the three cactus growth forms studied. The columnar group also includes barrel cacti, which are short-stemmed but not globose. Columnar and globose growth forms belong to the subfamily *Cactoideae*; most of the columnar genera belong to the tribes *Trichocereeae* and *Cereeae* while the globose genera belong mostly to the tribe *Notocacteae*. All opuntioid species belong to the subfamily *Opuntioideae* (Mourelle & Ezcurra 1996).

(b) globose cacti and (c) opuntioid cacti (Fig. 1). Columnar species have cylindrical stems with ribs, formed by an arrangement of the areoles in longitudinal rows. We also included the short-stemmed barrel cacti in this category. Globose cacti, the smallest growth form, are more or less spherical in shape. Opuntioid species are non-ribbed, with stems formed by flat or cylindrical cladodes (for a detailed description of cactus growth forms see Mourelle & Ezcurra 1996). In Argentina, species of the globose growth form present a high level of endemism and are restricted in both habitat and range; opuntioid species are the most widespread and less specific in habitat requirements, and columnar species are chiefly limited by low temperatures (Mourelle & Ezcurra 1996).

The main purpose of our study was to evaluate the degree of association between species turnover and a set of environmental variables that were assumed to be potentially significant determinants of biological variation. We used a pixel resolution of ca. 100 km, as smaller scales cannot be used with the current collection intensity of the data set (see Mourelle & Ezcurra 1996). This scale is within an order of magnitude of some other studies on species turnover (e.g. Harrison et al. 1992). In terms of scale, our measurement of species turnover or differentiation diversity is intermediate between the concept of β-diversity or between-habitat diversity and the concept of δ-diversity or geographic differentiation (e.g. Cody 1975, 1993; Ricklefs & Schluter 1993).

Few studies have analysed the influence of the different environmental factors affecting species turnover. Most of these investigations (Retuerto et al. 1990; Meave

1991; Tueller et al. 1991; Harrison et al. 1992; Cody 1993; Kadmon et al. 1993; Wolf 1993; Scheiner & Rey-Benayas 1994) have evaluated the association between species turnover and direct environmental factors (e.g. mean annual temperature, mean altitude), or a measure of their temporal variability (e.g. the standard deviation of mean monthly temperature, the standard deviation of total monthly precipitation). None of the studies mentioned above related species turnover to the spatial variation of environmental variables; that is, they did not attempt to relate the difference in species composition between two or more sites (species turnover) with the difference in the values of the environmental variables between the same sites (spatial environmental heterogeneity).

Methods

To analyse species turnover, we used a database containing 3395 records from 228 species of the *Cactaceae* occurring in Argentina. Data on the distribution of the species were taken from herbarium labels in seven Argentine herbaria, and supplemented by Kiesling and Ferrari's unpublished field data and with published sources (see Mourelle & Ezcurra 1996). We subdivided the *Cactaceae* into three main growth forms: (1) columnar cacti, including the shorter-stemmed barrel cacti, (2) globose cacti and (3) opuntioid cacti, with 50, 109 and 50 species respectively (for a complete species list, see Mourelle & Ezcurra 1996). All the analyses were carried out for each growth form separately. We excluded from our analysis the five pereskioid species and the 14

epiphytic species known to occur in Argentina, as the low number of species in these two growth forms does not allow for robust statistical tests of hypotheses. Introduced species and species with either dubious distribution records or non-valid names (totalling 10 species) were also excluded. The map of Argentina was divided into a grid of 318 cells of $1° \times 1°$. For each species we digitised the grid squares from where it had been collected. These cartographic cells are not equal in area, they range from around 11 000 km^2 in the North of Argentina, to ca. 9000 km^2 in the southernmost latitudes with registered cactus species (an analysis of the potential sources of error introduced by units with variable area was presented by Mourelle & Ezcurra 1996).

Species richness and species turnover

In this study, species richness is defined as the local number of cactus species contained in a square of $1° \times 1°$. Differentiation diversity was calculated in two different ways: (1) by estimating turnover along geographical gradients following latitudinal or longitudinal transects one degree wide and (2) by evaluating, for each individual square, the turnover between the cell and its eight surrounding squares.

Species turnover along geographical transects

For the analysis of transects, we used both Whittaker's and Wilson and Shmida's measures of species turnover or β-diversity (Magurran 1988). Firstly we calculated Whittaker's measure $\beta_w = k / \ln2$, where k is a parameter derived from the negative exponential function $S = e^{-kx}$, which predicts how between-square similarity (S) decreases with distance (x) along a transect (Whittaker 1972). The negative exponential model is derived from the differential equation $(1 / S) (\partial S / \partial x) = -k$; where the parameter k is the intrinsic rate of change of biological similarity per unit distance, which can also be rewritten as $(\partial \ln S / \partial x) = k$. Thus, β_w (a transform of k) is a turnover rate in a $\log_2$ scale – with 'octaves' as intervals; it measures turnover rates in 'half-changes' per unit distance. To estimate β_w, all possible between-square similarities were calculated for each transect, together with the corresponding between-square distances. The negative exponential parameter (k) was estimated by non-linear regression, fitting Whittaker's model to the set of similarity vs. distance data points. The significance of the fit was evaluated by an approximate F-test (as variances are not always additive in non-linear models, an exact ANOVA is not strictly possible, see Draper & Smith 1981). Similarities (S) were calculated using Sørensen's Coefficient of Community (Whittaker 1960, 1972; Pielou 1979; Wilson et al. 1983; we also tried Jaccard's Index and obtained qualitatively similar results, though its fit to

the negative exponential model was somewhat lower). The resulting measure of species turnover is given in half-changes per unit grid cell.

We also used Wilson and Shmida's index corrected by the size of the transect: $\beta_t = (g + l) / [2\alpha (n - 1)]$, where g is the cumulative number of species that are gained following successive squares from one extreme of the transect to the opposite, l is the cumulative number of species that are lost, α is the mean number of species per square (mean species richness) and n is the number of squares in the transect. β_t measures, for the whole transect, the mean relative turnover between adjacent squares (Wilson & Shmida 1984; Shmida & Wilson 1985). Like Whittaker's measure, β_t is also a turnover rate, estimated in an arithmetic rather than in a logarithmic scale. Additionally, because it only takes into consideration changes between adjacent squares, Wilson and Shmida's approach emphasises local species turnover and hence better reflects the effects of short-distance environmental heterogeneity, while Whittaker's measure emphasises species turnover along extensive distances and better reflects the effects of distributional amplitude of the species in the group.

For both methods, we estimated turnover rates along 15 longitudinal transects (less for some growth forms) and 15 latitudinal transects of different length (both ranging from 3 to 13 squares). We only analyzed those transects containing more than three squares with five or more species. Squares with fewer than three species were discarded from the analysis.

Species turnover between individual squares

For this analysis we calculated the similarity between each individual square and its eight adjacent neighbouring squares by means of Sørensen's Coefficient of Community. As similarity decreases exponentially with distance (see previous section), we corrected the similarities of the corner squares (which are farther away from the central square and hence are more likely to show lower similarities) by elevating their values to the power $(1 / \sqrt{2})$, where the value $\sqrt{2}$ is the diagonal distance between squares one unit in size. This correction can be deduced from Whittaker's negative exponential model described in the previous section. Thus, the species turnover between the central square and any one of its neighbours is simply $\beta_i = 1 - S_i$, where S_i is the corrected similarity between the central square and the neighbouring square i.

It can be seen that, if Sørensen's Coefficient of Community is used to measure similarity, then $\beta_i = 1 - [2c / (q + s_i)]$, where c is the number of species shared between both squares, q is the number of species in the central square, and s_i is the number of species in the

neighbouring square i. This equation can be rewritten as $\beta_i = (g + l) / 2\,\alpha$, where g is the number of species which are present in the neighbouring square and absent in the central square, l is the number of species which are present in the central square and absent in the neighbouring square and α is the mean species richness in both squares. This last form is identical to the index of Wilson & Shmida introduced in the previous section. Thus, the mean species turnover between a square and its neighbours (β_q) was simply measured as the average of n values of floristic turnover with the neighbouring squares, where $0 < n \leq 8$ is the number of neighbours with registered species. Measured in this manner, β_q is the mean turnover rate from a given square with respect to its n neighbours. The resulting values were mapped for the whole country in three categories: squares with high species turnover (0.661 - 1.0), squares with intermediate turnover (0.331 - 0.66) and squares with low turnover (0 - 0.33).

Latitudinal and longitudinal trends in transect species turnover

To test if there were spatial trends in species turnover, we evaluated the relationship between species turnover in longitudinal transects and their latitudinal position by means of time-series analysis of long-term linear trends; and we also evaluated the relationship between species turnover in latitudinal transects with respect to their position along the east-west gradient.

Species turnover and environmental predictors

16 environmental variables were digitised for the whole country on a $1° \times 1°$ scale: two geographic, 11 climatic and three topographical – aimed at estimating small-scale environmental heterogeneity as discussed in Palmer & Dixon (1990):

Latitude;
Longitude;
Mean annual temperature;
Mean annual precipitation;
Mean annual minimum temperature;
Proportion of annual rain falling in summer;
Mean number of frost-free days;
Mean annual water deficiency measured as the ratio of the net annual radiation to the heat energy required to evaporate the mean annual precipitation;
Mean actual evapotranspiration;
Mean July temperature;
Mean December temperature;
Difference between Mean July and Mean December temperature;
Annual primary productivity calculated from Lieth's (1975) index of evapotranspiration;
Altitudinal range calculated as the difference between maximum and minimum altitude within a square;
Topographic variability calculated as the standard deviation of the altitude of nine points selected systematically within each square;
Mean altitude calculated as the average of the nine within-square

points.

To estimate the spatial heterogeneity of the climatic and topographic variables we calculated (1) the mean and the variance of each variable between the squares of the latitudinal and longitudinal transects described in the previous section and (2) the mean squared difference between the value of each cartographic cell and the values of its eight neighbouring squares (i.e. the variance with respect to the central value). For the analysis of transects, the mean and variance of each environmental variable in that transect were regressed against both Whittaker's and Wilson and Shmida's species turnover estimates for the transect (β_w and β_t respectively). For the analysis of individual squares, the values of the environmental variable in that particular square and of its spatial variation were regressed against the species turnover of the square (β_q). Regression analysis was performed with the GLIM package, following an additive stepwise procedure (Payne 1986; McCullagh et al. 1989; Yee et al. 1991). To increase parsimony in our analysis, we previously did a Principal Component Analysis (PCA) of the environmental variables in order to identify groups of correlated variables. In order to decrease the probability of Type I errors, once a variable had entered the regression model, we avoided testing the inclusion of new variables showing significant collinearity with the first one. We also performed the regressions directly against the PCA axes, but in no case did a composite axis show a better predictive value than the best individual variable.

The effect of data collection intensity

The number of species detected in a given area is a function of the number of herbarium specimens that were collected (Soberón & Llorente 1993). Based on the properties of accumulation functions (Mourelle & Ezcurra 1996), we incorporated the logarithm of the number of voucher specimens registered per square in our regression models (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 undercollection in our study of species turnover. 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 gaps in the collection effort. As with the environmental variables, the potential effect of undercollection on the estimates of species turnover was evaluated both for transects and for individual squares, and the effect of spatial variation in the collection effort was also included as a predictor. That is, we evaluated how much of the estimated species turnover could be attributable to the fact that some squares were more collected than others.

Table 1. Best predictors of species turnover in latitudinal transects for the three cactus growth forms in Argentina. In all growth forms only one best predictor was found (i.e. once the first stepwise variable entered into the model all other predictors became non-significant). The variances of the variables estimate variation between grid-cells within each transect (see Methods).

Growth forms	Dependent variable	Best predictors	r^2	Sign	P
Columnar	β_w	Mean actual evapotranspiration	0.60	–	0.001
	β_t	Variance of mean minimum annual temperature	0.63	+	< 0.001
Opuntioid	β_w	Mean altitudinal range	0.39	+	0.003
	β_t	Mean number of frost-free days	0.43	+	0.002
Globose	β_w	Mean percentage of summer rainfall	0.57	+	< 0.001
	β_t	Mean minimum annual temperature	0.55	+	0.001

Results

Species turnover along transects

In all growth forms and in all transects, the non-linear fit of Whittaker's exponential model to transect data was always highly significant, and in all cases the residuals fitted adequately the required assumptions of independence and randomness (Draper & Smith 1981).

Latitudinal transects

Different significant predictors resulted from the regression analysis with species turnover (the dependent variable) calculated as Whittaker's measure (β_w) or as Wilson and Shmida's index (β_t). For the columnar species, Whittaker's measure of species turnover was significantly higher in N-S transects where actual evapotranspiration was low, i.e. in arid habitats (Table 1). β_t, on the other hand, was higher in transects where minimum annual temperature varied considerably between grid cells. For opuntioid cacti, β_w increased in transects where within-square altitudinal variation was high, while β_t was associated with transects with a high number of frost-free days. Finally, for globose cacti, β_w was higher in transects where rainfall was concentrated in summer,

while β_t was associated with transects where mean minimum annual temperature was high, i.e. transects with mild winters. For all three growth forms, species turnover in transects was unrelated to the mean collection effort, or with its within-transect variation.

Longitudinal transects

In contrast to latitudinal change, longitudinal turnover for the three growth forms was always related to the between-squares variation of the environmental factors, rather than to the factors themselves (Table 2). For the columnar species, the strongest predictor for β_w was the variance in the number of frost-free days. Transects with high variation in the number of frost-free days had, generally, a higher turnover than transects with little variation in this environmental factor. The best predictor of β_t was thermal variation (a variable obviously related to the number of frost-free days), but the fit of the regression model was not significant. For the opuntioid species, both measures of species turnover were best predicted by altitudinal variation between squares, although in this case the fit of the model to β_w was not significant. Finally, in globose cacti β_w was strongly related to variations in the mean annual water defficiency, an index of aridity; and β_t was significantly related to variations in altitude, a

Table 2. Best predictors of species turnover in longitudinal transects, for the three cactus growth forms in Argentina. In all growth forms, only one best predictor was found. The variances of the variables estimate the variation between grid-cells within each transect (see Methods).

Growth forms	Dependent variable	Best predictors	r^2	Sign	P
Columnar	β_w	Variance of number of frost-free days	0.33	+	0.04
	β_t	Variance of mean annual temperature	0.18	+	0.15
Opuntioid	β_w	Variance of mean altitude	0.18	+	0.15
	β_t	Variance of mean altitude	0.49	+	0.0008
Globose	β_w	Variance of mean annual water deficiency	0.59	+	0.004
	β_t	Variance of mean altitude	0.67	+	0.003

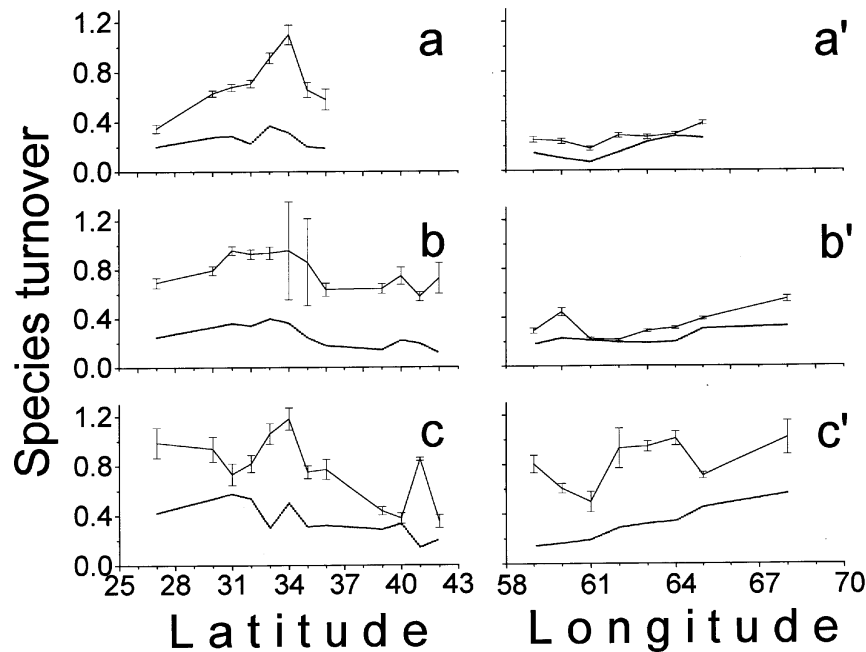**Fig. 2.** Turnover rates in longitudinal (°W) transects plotted against latitude (°S) (*a, b, c*); and turnover rates in latitudinal transects plotted against longitude (*a', b', c'*), for columnar species (*a, a'*); opuntioid species (*b, b'*), and globose species (*c, c'*). In all cases, β_w is plotted with continuous lines and β_t with broken lines.

complex measure of environmental heterogeneity. As with the longitudinal transects, species turnover in latitudinal transects was not significantly related for any growth form, neither the mean collection effort, nor with its between-square variation.

Latitudinal and longitudinal trends in transect species turnover

The values of β_w and β_t for each longitudinal transect were plotted against latitude (Fig. 2). As a general rule, species turnover tended to increase towards the tropics, but the trend was significant only for β_t in the globose cacti (Table 3; because the analysis involved 12 non-independent tests, we used a Bonferroni correction on the probability values, and only accepted the existence

of a trend when $P < 0.01$). A similar result was found when species turnover in latitudinal transects was plotted against the longitude of the transect. Species turnover tended to increase towards the Andes (i.e. towards the West), but the trend was significant (at $P < 0.001$) only for β_t in the globose cacti.

Species turnover in individual squares

Columnar species (Fig. 3a) showed high values of square species turnover towards the Northwest, an area of marked transitions between different biogeographic provinces (Puna, Prepuna, Monte, Yungas and dry Chaco; see map in Mourelle & Ezcurra 1996). Species turnover was also high in the centre-east of the country,

Table 3. Spatial trends in species turnover (correlation coefficients) for latitudinal and longitudinal transects, for the three cactus growth forms in Argentina.

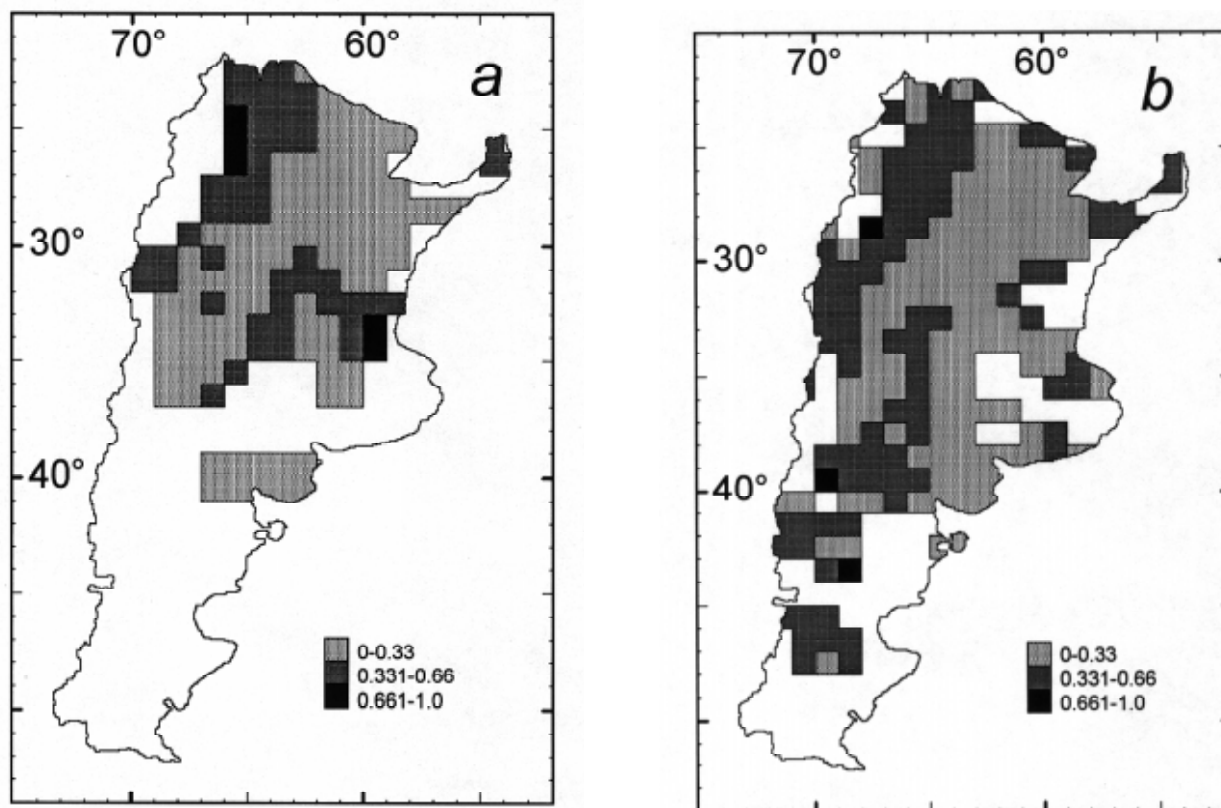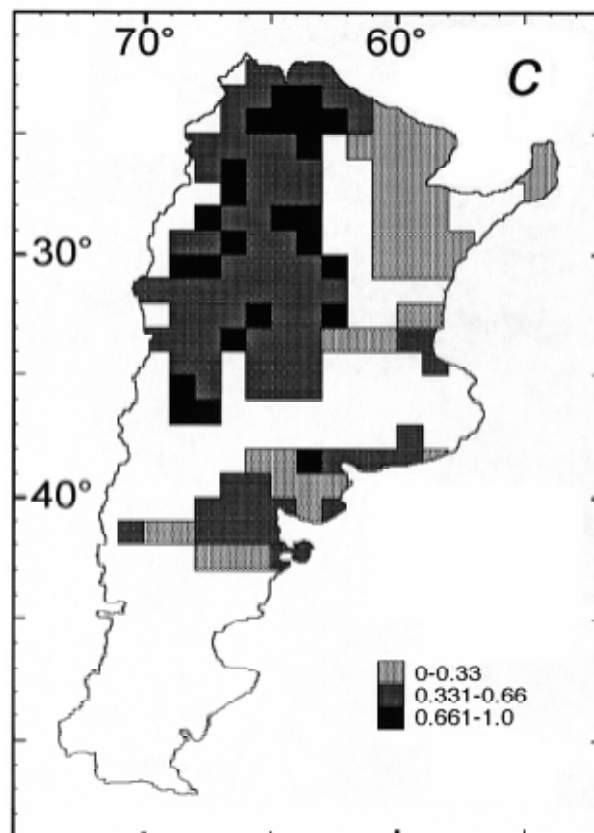| Growth forms	Species turnover measure	Latitudinal trend along longitudinal transects		Longitudinal trend along latitudinal transects	
		r	*P*	*r*	*P*
Columnar	β_w	− 0.06	0.84	0.52	0.18
	β_t	− 0.36	0.22	0.57	0.08
Opuntioid	β_w	− 0.15	0.53	0.31	0.38
	β_t	− 0.53	0.02	0.51	0.09
Globose	β_w	− 0.67	0.02	0.55	0.16
	β_t	− 0.77	0.003	0.99	< 0.001

Fig. 3. Maps of Argentina showing areas of low, intermediate and high species turnover in individual grid-cells: (*a*) columnar; (*b*) opuntioid, and (*c*) globose species. Blank cells contain less than three species, and were not included in the analyses.

in the transition between the Pampean Province (a temperate grassland) and Espinal (a xerophyllous woodland). The lowest species turnover values were found in topographically and climatically uniform plains, e.g. the Pampas, the Chaco and the southern Monte Desert.

In opuntioid species (Fig. 3b), relatively high values of species turnover occurred mostly in the Northwest (as in the columnar group), in the central mountain ranges of Córdoba, and in the North and West of the Patagonian Plateau. All these areas of high or intermediate values of species turnover coincide with biogeographic transitions. In the Northwest, high turnover values occur in areas between the high-altitude Puna and the neighbouring lower-altitude ecosystems, as discussed for the columnar group. The central squares with higher turnover values coincide with the transition between the Pampean Province and the central mountain ranges, and between the latter and the Monte Desert. The Patagonian squares with high species turnover occur either in the transition between the Monte Desert and the Patagonian Steppe, or between the steppe and the Andean-Patagonian Forests. As in the columnar group, low turnover values
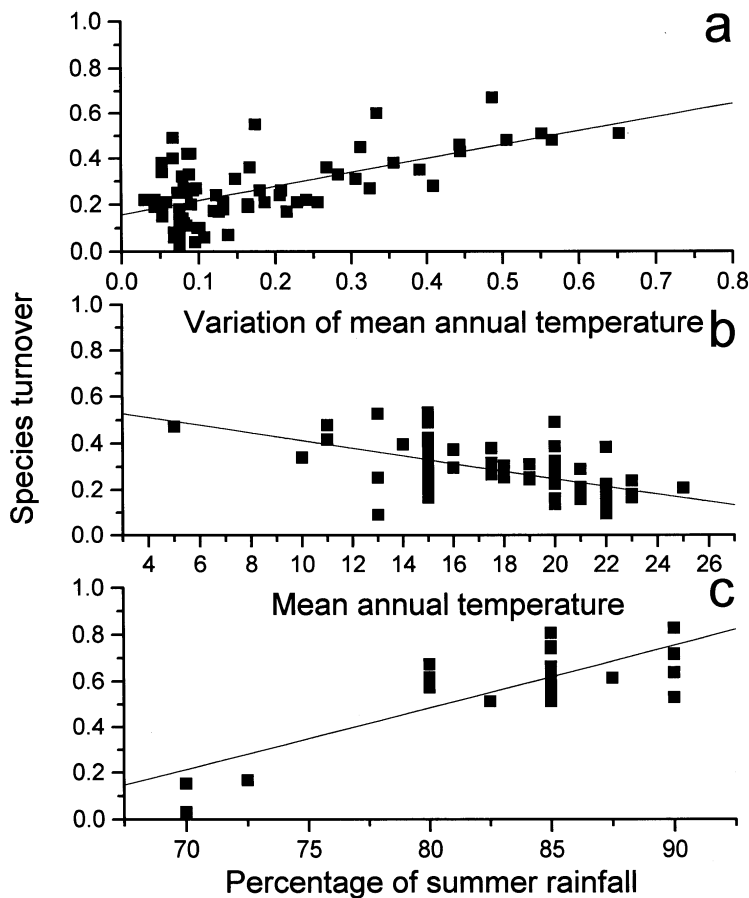
Fig. 4. Regressions between species turnover in grid cells and their best predictors for (*a*) columnar; (*b*) opuntioid, and (*c*) globose species (see Table 4).

occurred in plains with high topographic and climatic homogeneity, e.g. the Pampas, the Chaco, and the southern Monte Desert.

The globose species (Fig. 3c) presented a different trend compared with the opuntioid and columnar groups. Medium and high turnover squares occupied 75.7% of all the analysed squares. The high-species-turnover area was concentrated in the northwestern part of the country, from 62° - 63° W westwards, and northwards from 35° - 36° S. It occupied a north-south corridor comprising many phytogeographic provinces: in the north, the High-Andean, the Puna and the Prepuna and further south, the northern Monte Desert, the Espinal and part of the dry western Chaco. A secondary centre of high turnover was found in northeastern Patagonia, in an area where the Monte Desert becomes replaced by the Patagonian Steppe.

Environmental predictors of species turnover in individual squares

Neither latitude nor species richness showed a significant association with species turnover between individual squares for any of the growth forms. The globose

cacti (Fig. 4c) showed the growth form in which the species turnover in individual cells was most highly related to environmental factors; 65% of the variance in species turnover was explained by the proportion of annual rain falling in summer (Table 4). That is, species turnover increased towards regions where monsoon-type rains are highly concentrated in summer. For columnar cacti (Fig. 4a), the spatial heterogeneity in the mean annual temperature explained 63% of the variability in square species turnover and was positively correlated with it. That is, the more different the mean annual temperature the higher the species turnover. The species turnover of opuntioid species was negatively associated with the mean annual temperature, i.e., species turnover increases towards cooler environments. Opuntioid species turnover (Fig. 4b) also was significantly associated with the spatial heterogeneity in mean annual precipitation, i.e., species turnover also tends to increase in regions where the precipitation gradient is steep. For all three growth forms, a small, but significant, part of the residual species turnover was attributable to spatial heterogeneity in the collection effort (Table 4).

Table 4. Best predictors of species turnover (β_q) in individual grid-cells for the three cactus growth forms in Argentina. The variation in environmental variables represents the degree of change of the variables between each grid-cell and its neighbours (i.e. the between-cell variation, see Methods).

Growth forms	Best predictors	r^2	Sign	P
Columnar	Variation in mean annual temperature	0.63	+	< 0.001
	Variation in collection effort	0.08	+	0.01
Opuntioid	Mean annual temperature	0.47	–	< 0.001
	Variation in mean annual precipitation	0.16	+	0.0004
	Variation in collection effort	0.03	+	0.04
Globose	Mean percentage of summer rainfall	0.65	+	< 0.001
	Variation in collection effort	0.05	+	0.05

Discussion

Species turnover along transects

Differences in turnover rates between longitudinal and latitudinal transects were related to different variables for the same group. Species turnover in latitudinal transects was mostly related to the mean values of certain environmental variables within the transect, while in longitudinal transects it was always related to the between-squares variation of certain environmental variables, rather than to the mean values. The reason for this possibly lies in the distribution of the environmental variables in Argentina, and especially in the subtropical northern part of Argentina where most of the squares with cacti are found. In this region, there is a marked gradient from the eastern plains, which are more humid and have deep fertile soils, to the western pre-Andean areas, which are more arid, topographically heterogeneous, more continental in their temperature regime and with strict summer-type rains.

The latitudinal transects run parallel to this east-west gradient, while the longitudinal transects intersect it. That is, longitudinal transects cut across widely different ecosystems, while latitudinal transects run through more homogeneous biomes. Thus, the best predictors of species turnover in longitudinal transects are variables that measure the intensity of environmental change within the transect from east to west (e.g. within-transect variation in mean altitude, in water deficiency, in the number of frost-free days or in mean annual temperature). In contrast, the best predictors of species turnover within latitudinal transects are mostly variables that measure the relative position of the north-south transect on the east-west gradient (e.g. actual evapotranspiration, percentage of summer rainfall, mean minimum annual temperature or number of frost-free days).

In the specific case of columnar cacti, it is interesting to note that, with the exception of β_w in latitudinal transects, species turnover along transects was associated with variations in temperature (e.g. variation in the number of frost-free days, variation in mean minimum temperature). It has been well documented that columnar cacti are extremely sensitive to freezing temperatures (see Gibson & Nobel 1986 for a review).

Latitudinal and longitudinal trends in transect species turnover

There was a feeble trend of increased species turnover towards the tropics and towards the west, although the trend was significant only for the globose growth form. Whittaker (1977) predicted that species turnover should increase towards the tropics, and this prediction has been confirmed for several groups such as birds (MacArthur 1965,1967), insects and the plants they feed on (Janzen & Schoener 1968), bryophytes (Wolf 1993) and mammals (Willig & Sandlin 1991). This prediction, however, did not clearly hold for our cacti.

Species turnover in individual squares

No association was found between species richness and species turnover. For all growth forms, the squares with high species turnover tended to occur in areas where there are transitions between different biogeographic provinces, or where the physical environment varies between squares. In particular, the northwestern part of Argentina, a topographically and climatically heterogeneous region where the boundaries of different biogeographic provinces converge, appeared in all cases as an area of high species turnover. In contrast, the environmentally uniform large plains of the Pampas, the Chaco and the southern Monte Desert appeared in all cases as regions of low species turnover. The behaviour of the columnar and the opuntioid species was quite similar. Both showed high values in the northwest, in the transition between the Pampas grasslands and the surrounding, more arid ecosystems. The opuntioid spe-

cies also showed high species turnover in the transitions between the different biogeographic provinces of northern Patagonia, a geographic trend not shown by the more frost-sensitive columnar group, which does not prosper at these temperate latitudes. The globose species presented relatively high turnover rates in a much larger proportion of the country. This suggests that regions which are relatively uniform for the species with larger individuals, are markedly heterogeneous for the more poorly-dispersed globose group. In particular, the globose species showed high species turnover in all the central and northwestern squares, a region occupied by valleys and pre-Andean ranges with heterogeneous soils and a more pronounced topography. This trend in individual squares confirmed the tendency observed in the analysis of transects, in that species turnover increased both towards the tropics and towards the west.

The best predictors of species turnover between grid cells followed the tendency discussed above. The best predictor of columnar turnover (variation in mean annual temperature) is highest in the pre-Andean ranges of the northwest, where the pronounced topography induces abrupt changes in mean temperature. The best predictor of opuntioid species turnover (mean annual temperature) is low in the Patagonian squares and in the mountainous ranges of the northwest, the two main areas where opuntioid turnover is high (the relationship between the predictor and opuntioid turnover). The best predictor of globose species turnover, percentage of annual rain falling in summer, is associated with areas with summer rain. Again, this summer-precipitation pattern is more marked throughout central-northwest Argentina, where both the Andes and the central mountain ranges originate rainshadows that impede the arrival of winter rains from the Atlantic or the Pacific. It is important to note, however, that no causal conclusions should be drawn from these regressions. Comparing the species-turnover maps with the biogeographic map of Argentina (see Mourelle & Ezcurra 1996) it seems obvious that the highest turnover rates coincide with certain biogeographic boundaries where both biological and environmental changes are pronounced.

In the case of columnar species, variation in mean temperature is the best predictor of species turnover. This is in agreement with our previous report (Mourelle & Ezcurra 1996), in which we found that a temperature variable (the number of frost-free days) was the best predictor of species richness. Although high sensivity to low temperatures has been extensively reported (e.g. Nobel 1981, 1982; Gibson & Nobel 1986) high temperature damage is difficult to find in the field (Gibson & Nobel 1986). We may conclude then, that columnar species turnover is related to temperature change in as much as this variable reflects varying degrees of frost risk.

Finally, it is noticeable that the collection effort was only weakly related to species turnover. This result strongly contrasts with our previous study (Mourelle & Ezcurra 1996) for species richness, where the collection effort explained a much higher proportion of the residual variation.

General trends in species turnover

Species turnover is mainly influenced by two group of factors: the characteristics of the habitat (especially environmental heterogeneity), and the characteristics of the intervening species (chiefly the range of tolerance to environmental variation; Whittaker 1972, 1977; Schluter & Ricklefs 1993). In particular, habitat breadth and dispersal capacity have been singled out as important determinants of turnover (e.g. Shmida & Wilson 1985; Westoby 1985; Harrison et al. 1992). With respect to specialisation in habitat (a measure of niche breadth), the three growth forms may be ranked as: globose > columnar > opuntioid, while their dispersal ability can be ranked as: opuntioid > columnar > globose (including both seed-dispersal and cladodes as vegetative propagules; see Steenbergh & Lowe 1977; Barthlott & Hunt 1993; Mourelle & Ezcurra 1996). It is known that opuntioid cacti are dispersed by small and large mammals (Janzen 1986; Vargas-Mendoza & Gonzalez-Espinosa 1992) and by lizards (Valido & Nogales 1994), columnar cacti are mostly dispersed by birds and mammals (Steenbergh & Lowe 1977; Barthlott & Hunt 1993, Valiente-Banuet et al. 1996) and globose cacti are chiefly dispersed by insects, lizards and small mammals (Barthlott & Hunt 1993; Figueira et al. 1994). In agreement herewith, species turnover in our data set was lower in the opuntioid and columnar groups and it was highest in the globose cacti.

Species turnover in individual squares showed clear geographical trends in all growth forms: it tended to increase towards the northwest, and was especially high in squares where different biogeographic provinces converge. This yields a somewhat expected but none the less important generalization: the spatial component of species diversity is likely to be higher in heterogeneous regions or in the ecotonal transition between large biomes.

The results presented here have important implications for conservation biology. As a general rule, environmentally heterogeneous regions, together with regions where large-scale transitions between biomes occur, have an exceptionally high species turnover, and can be targeted for conservation purposes. In the case of Argentine cacti, such regions occur in the northwest of the country, in the transition between the Monte Desert, the Prepuna, the dry western Chaco, and other surrounding biogeographic provinces.

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