UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

INSTITUTO DE ECOLOGÍA

BIODIVERSIDAD EN LA FAMILIA CACTACEAE: UN ENFOQUE BIOGEOGRÁFICO

TESIS
QUE PARA OBTENER EL GRADO DE
DOCTOR EN ECOLOGÍA
PRESENTA:
CRISTINA MOURELLE DE BATTISTI

DIRECTOR DE TESIS: DR. EXEQUIEL EZCURRA REAL DE AZÚA

MÉXICO, D.F. **JUNIO DE 1997**

ÍNDICE

Agradecimientos

Debo agradecer ante todo, la paciencia y las ideas tan heterodoxas de mi tutor, Exequiel Ezcurra. Exequiel elaboró todos los programas de esta tesis, sin los cuales, ésta nunca se hubiese realizado. Gracias a su gran ayuda, estímulo y amistad este trabajo llegó FINALMENTE a su término. Gracias también a Bárbara, que "soportó" con infinita paciencia, a todos los alumnos de Exequiel.

A mis queridísimas amigas Paty Balvanera y Pilar Rodríguez, por las largas discusiones centradas en la diversidad beta y en otros temas no tan académicos, pero muy **enriquecedores** y entretenidos. Al Dr. Jorge Soberón, por contribuír de manera crítica al divague teórico de la diversidad beta y por sus valiosas observaciones al capítulo 3 de la tesis.

A todos los miembros del jurado (Héctor Arita, Exequiel Ezcurra, Miguel Martínez, Jorge Meave, Daniel Piñero, Jon Rebman y Jorge Soberón) que criticaron constructivamente el manuscrito de esta tesis. Jorge Meave hizo acertados comentarios y meticulosas contribuciones.

A la Negrita, Liz Izquierdo, una gran amiga, siempre dispuesta con muy buen humor y solidaridad, a dar una mano en lo que necesitaba. A mis compañeros de laboratorio, Santiago Arizaga, ErnestoVega, Fernando Ramírez de Arellano, Eduardo Peters, Arturo Flores, Oscar Briones, Leopoldo Valiente y Alfonso Valiente por las múltiples discusiones, ayuda en la programación y manejo de algunos programas. A César Rodríguez, por su incondicional ayuda en la construcción y análisis de la base de datos de cactáceas columnares de México.

Al Morocho, por su gran apoyo ; la lista sería innumerable.

A mis compañeros de generación, Luma, Arturo, Consuelo, Lalo, Fabián, Víctor y Coro por brindar un ambiente de gran camadarería y solidaridad.

A Mercedes Sanders y a Francisca García, por cuidar tan cariñosamente de mi hijo Matías y permitirme de esta manera, terminar la tesis. Al locólogo, Guillermo Pruneda por soportarme en los momentos depresivos y de desencanto; a Guillermo, mil gracias.

Agradezco al personal del Centro de Ecología, muy particularmente a Elena, Chelito, Carolina, Gloria, Alicia, Virgi y Ernesto. Finalmente debo agradecer muy especialmente al Dr. Daniel Piñero y al Dr. Jorge Soberón por otorgarme una beca para llevar a cabo mis estudios de doctorado en México. El Programa de Medio Ambiente de la UNAM (PUMA), PADEP y la Comisión Nacional de Biodiversidad (CONABIO) ofrecieron una importante ayuda económica para el cuarto capítulo de la tesis.

Y a manera de dedicatoria…

dedico con mucho cariño este trabajo

al Morocho

a Matías

a Francoise

y

a la memoria de Pepe

Junio de 1997

RESUMEN

Este trabajo comprende el estudio de tendencias biogeográficas en una escala regional, para la familia Cactaceae, en los dos centros de mayor diversidad de su área de distribución, distinguiendo los diferentes elementos en los que se ha definido la diversidad biológica a esta escala. Los tres artículos que se incluyen en esta tesis analizan los patrones de distribución de la diversidad de tres formas de crecimiento de la familia Cactaceae. En particular, se describen los patrones biogeográficos para las cactáceas de Argentina y de México.

En el primer trabajo titulado "*Species richness of Argentine cacti: a test of some biogeographic hypotheses*", se analizan los patrones de la riqueza de especies (o diversidad alpha) de tres formas de crecimiento (columnar, opuntioide y globosa) y de todas las formas combinadas en función de 15 descriptores ambientales. Para el morfo columnar se confirmó una particular sensibilidad a las bajas temperaturas y a las heladas acotando su distribución al norte de los 34 °S y por debajo de los 3000 m de altitud. Las opuntioides presentaron áreas de distribución más grandes que el resto de los morfos y, al igual que las globosas, una relación significativa con el porcentaje de lluvias en verano, una variable de estacionalidad. En los tres morfos se detectó una asociación estadística significativa con el esfuerzo de colecta.

En el segundo manuscrito titulado "*Differentiation diversity patterns of Argentine cacti and their relationship to environmental factors*", se estudia el recambio de especies (diversidad β) entre sitios y a lo largo de transectos latitudinales y longitudinales de las tres formas de crecimiento (columnar, opuntioide y globosa). Se analiza el grado de asociación entre la diversidad β de cada forma de crecimiento y la heterogeneidad espacial de un conjunto de 15 variables ambientales. Comparado con las otras formas, las globosas presentaron los valores más altos de recambio de especies. En la forma de crecimiento columnar, el recambio de especies estuvo relacionado con la variación espacial de los predictores térmicos. En las opuntioides, la diversidad β de los transectos se asoció significativamente con las variables topográficas, mientras que la diversidad β entre cuadros lo hizo con la temperatura media anual. Las globosas, presentaron una correlación significativa con variaciones en la temperatura y en la precipitación. Las regiones más heterogéneas, donde confluyen distintos biomas geográficos, concentraron el mayor recambio de especies.

El tercer manuscrito "*Rapoport´s rule: a comparative analysis between South and North American columnar cacti*" analiza de manera comparativa los intervalos latitudinales de distribución de las cactáceas columnares entre norte y sudamérica, en particular para las especies de México y de Argentina. En México, la media de los intervalos latitudinales de las especies se correlacionó positivamente con la latitud media, confirmando la Regla Rapoport, aunque el ámbito latitudinal de las especies argentinas no se relacionó con la latitud. Sin embargo, en los dos hemisferios la riqueza de especies aumenta hacia los trópicos.

En síntesis, la riqueza (diversidad α) y el recambio de especies (diversidad β) en la familia Cactaceae responden a diferentes factores evolutivos a lo largo de su rango de distribución en el continente americano. Diferentes patrones de distribución de especies se observan para las distintas formas de crecimiento. Acorde a su fisiología, las especies de cada forma de crecimiento presentan determinados rangos de tolerancia a variables del ambiente. De las tres formas, las opuntioides son las más euriecas, las columnares están fuertemente restringidas por las bajas temperaturas y las globosas por el tipo de sustrato rocoso.

Variables ambientales hasta ahora poco consideradas en estudios biogeográficos, como el ancho del continente, pueden condicionar el carácter universal de reglas biogeográficas como la Regla Rapoport.

ABSTRACT

This thesis comprises the study of biogeographic trends in a regional scale for the Cactaceae family in two of the centers with highest diversity within its distribution, distinguishing the different components of the biological diversity. The three articles included in this thesis analyse the diversity distribution patterns of three different cactus life-forms. In particular, I described the biogeographical patterns for the Argentine and the Mexican columnar cacti.

In the first article, entitled "*Species richness of Argentine cacti: a test of some biogeographic hypotheses*", I analyzed the patterns of species richness of three main cactus life-forms (columnar, opuntioid and globose) and the pattern for all forms combined. Species richness in each group was regressed on fifteen environmental descriptors. A particular sensitivity to low and freezing temperatures was confirmed for the columnar growth-form confining their distribution north of 34°S and below 3000 m. The opuntioid species present the largest range of distribution compared with the other life-forms. Species richness for both, globose and opuntioid was closely associated with a seasonality variable, namely the percentage of summer rainfall. Species richness of the three growth-forms showed a significative association with the collection effort.

In the second manuscrit entitled "*Differentiation diversity patterns of Argentine cacti and their relationship to environmental factors*" I studied the species turnover (β diversity) between different sites and along latitudinal and longitudinal transects. I analysed the degree of correlation between β-diversity for each growth-form and the spatial heterogeneity of 15 environmental variables. Compared with the other growth-forms, the globose species showed the highest β-diversity. For the columnar growth-form species turnover was significantly related to the spatial variation of thermal predictors. For the opuntioids, transect-β diversity was significantly associated with topographic variables while quadrat-beta diversity was significantly related to the mean annual temperature. The globose species presented a significant correlation with temperature and rainfall variations. Environmentally heterogeneous areas, where different biomes occur, concentrated the highest species turnover.

The third manuscrit entitled "*Rapoport´s rule: a comparative analysis between south and north american columnar cacti*" compared the latitudinal ranges between South and North American cacti found respectively in Argentina and Mexico. In Mexico, the mean latitudinal range was positively correlated with the mean latitude, confirming Rapoport´s rule, but the geographical range of Argentine species was not related to latitude. In both hemispheres, however, species richness increases towards the tropics.

Summing-up our conclusions, species richness (or α diversity) and turnover (or β diversity) in the Cactaceae family respond to different evolutionary factors in the whole range of distribution in the American continent. Different species distribution pattern is observed for each growth form. Depending on their physiological characteristics, the species of every growth form show distinct tolerance ranges to environmental variables. Of the three growth-forms, opuntioids are the most widespread and the less especific in

habitat requirements, while the columnar cacti are strongly constrained by low temperatures and the globose by the rocky soils.

Environmental variables that have so far received little or no attention in biogeographical studies, such as the continental width, can modify the universal character of certain biogeographical rules like Rapoport's Rule.

I. INTRODUCCIÓN

INTRODUCCION

La familia Cactaceae en el continente americano presenta una gran diversidad de especies y de forma de crecimiento (Gibson y Nobel 1986) que han estado presumiblemente sujetas a diferentes presiones de selección en su enorme área de distribución geográfica. Destacan en particular, la forma de crecimiento columnar, la globosa, la opuntioide, la epífita y las arbóreas con hojas verdaderas.

Las especies de la forma de crecimiento columnar poseen tallos o troncos con costillas formadas por el arreglo longitudinal de las areolas. Estas especies tienen haces vasculares paralelos separados por tejido suculento parenquimatoso. En nuestro trabajo, incluímos dentro de las especies columnares desde las arborescentes candelabriformes, profusamente ramificadas, hasta columnas solitarias sin ramificación alguna, incluyendo las barriliformes. Las cactáceas globosas son las de tamaño más pequeño y de forma esférica. La alta densidad de espinas en el tallo es su rasgo más característico. Columnares, barriles y globosas pertenecen a la subfamilia Cactoideae (Buxbaum 1958, Gibson y Nobel 1986). En contraste, las areolas de las especies opuntioides no se organizan en costillas. Sus haces vasculares forman una estructura reticular y su tallo consiste en uno o más cladodios planos o cilíndricos que pueden desprenderse de la planta madre y dar lugar a otro individuo. Todas las especies opuntioides pertenecen a la subfamilia Opuntioideae. Las especies opuntioides tienen una mayor capacidad de dispersión que las columnares y éstas, a su vez, mayor que las globosas (Steenbergh y Lowe 1977, Barthlott y Hunt 1993). Las dos últimas formas de crecimiento, es decir las cactáceas epífitas y las arbóreas con hojas verdaderas, son las más raras desde el punto de vista de su riqueza de especies.

La amplísima diversidad de formas de crecimiento y de hábitos en esta familia, la cual le ha permitido conquistar diversos ambientes (selváticos, áridos, semi-áridos y fríos), la dota de singulares mecanismos adaptativos en todo su área de distribución geográfica. En particular, para plantas del desierto, Cody (1986, 1989) sugiere que diferentes formas de crecimiento corresponden a nichos estructurales diferentes y que la diversidad de plantas perennes es determinada en gran parte por la coexistencia de esas diferentes formas de crecimiento. En este contexto, nos preguntamos cuáles son las características del medio físico que desencadenaron determinados mecanismos de adaptación en cada forma de crecimiento.

La hipótesis central es que distintos factores, ecológicos y evolutivos, determinan patrones de distribución diferenciales de especies y formas de crecimiento. Dada la escala espacial del estudio que sustenta esta tesis, los factores evolutivos juegan un papel central. Para entender la importancia de estos factores, es necesario analizar cómo los patrones de distribución de las cactáceas se asocian a factores ambientales relativamente estables en el tiempo evolutivo (aunque posiblemente cambiantes en el tiempo geológico), tales como el clima y la topografía. El análisis de la relación entre distribución de las especies y el ambiente físico nos puede permitir evaluar el valor adaptativo de las distintas formas e interpretar sus patrones de distribución a gran escala.

Las preguntas "¿por qué las regiones de un continente varían en riqueza de o número de especies?" o "¿cuáles son las causas de la variación en la riqueza de especies?" han sido importantes a lo largo de toda la historia de la ecología. Dado que la variación en la riqueza de especies se distingue significativamente del azar (Palmer 1987, 1991, Wilson et al. 1987) sin duda existen patrones en la diversidad de especies (MacArthur 1965). Más relevante aún y ya señalado en numerosos textos (Crawley 1986, Ricklefs 1987, Begon et al. 1990, entre otros), esos patrones se relacionan de manera predictiva con gradientes ambientales, tales como altitud (Stevens 1992), área (Gleason 1925, Nilsson et al. 1988), biomasa (Grime 1973), disturbio (Connell 1978), diversidad en el hábitat (Harman 1972), fertilización (Silvertown 1980), latitud (Connell y Orias 1964, Pianka 1966, Rhode 1992), precipitación (Brown y Davidson 1977) y depredación (Lubchenco 1978). Los intentos para explicar los gradientes latitudinales y longitudinales en el número de especies, la coexistencia de éstas o la variación temporal y espacial en el número de especies dieron lugar a múltiples hipótesis sobre los mecanismos a nivel ecológico, evolutivo e histórico (Zobel 1992). Von Humboldt (1855), Wallace (1878) y otros naturalistas del siglo XIX pensaron que el clima era el factor regulador de las diferencias geográficas en la riqueza de especies y en la diversidad de forma de crecimiento. Recientemente, Palmer (1994) identificó por lo menos 120 hipótesis publicadas sobre los patrones de diversidad e intentó clasificarlas basándose en el paradigma de la exclusión competitiva. Si bien se conocen otros sistemas de clasificación para este tipo de hipótesis (Zobel 1992, Eriksson 1993, Brown 1988, Crawley 1986, Giller 1984, Begon et al. 1990), muchas de estas hipótesis no son mutuamente exclusivas y se basan en los mismos principios teóricos. Además, a diferentes escalas espaciales, el mismo fenómeno puede ser explicado por diferentes hipótesis (Palmer 1994). Por ejemplo, a pequeña escala, las especies pueden coexistir temporalmente dentro de un parche perturbado, pero a una escala mayor, pueden coexistir permanentemente en muchos parches si éstos están frecuentemente perturbados. Este constituiría un ejemplo de diferenciación de nicho o de hábitat, a dos escalas, bajo determinadas condiciones de perturbación.

Biodiversidad o diversidad biológica es un término que comprende distintos niveles jerárquicos que han sido reconocidos con diferentes nombres por distintos autores. A nivel individual y poblacional, se distingue la diversidad genética, a nivel de la comunidad, diversidad ecológica o taxonómica y a nivel geográfico, la diversidad biogeográfica (Huston 1994, Halffter y Ezcurra 1992). La diversidad genética está dada por la variabilidad genotípica y fenotípica a nivel de una sola especie. La diversidad ecológica o taxonómica puede descomponerse en el número o riqueza de especies y en la dominancia relativa de cada una de ellas (Huston 1994). La diversidad biogeográfica se define en función de la diversidad de ecosistemas en una región determinada. Esta tesis estudia dos niveles de la diversidad: la biogeográfica y la ecológica o taxonómica. Dentro de esta última, se consideró unicamente la riqueza o el número de especies en un sitio dado, no tomando en cuenta la abundancia relativa de cada una de ellas. A partir de aquí, cuando se mencione diversidad α , me referiré sólo a la riqueza de especies.

Los principales procesos determinantes de la diversidad taxonómica dependen de la escala de estudio (Shluter y Ricklefs 1993, Shmida y Wilson 1985, Whittaker 1972). A nivel local predominan los ecológicos mientras que a nivel regional, los evolutivos juegan un papel predominante (Rickleffs 1987). Dada la escala continental de este estudio, se destacan los evolutivos, y aunque los factores ecológicos son señalados, éstos no son puestos a prueba. Si bien la diversidad puede definirse a distintas escalas, procesos como la especiación, la inmigración, la colonización y la extinción de especies en un área dada se aplican en todas las escalas generando zonas o parches de mayor o menor número de especies (Rickleffs 1987, Cornell 1993). En síntesis, a cualquier escala de estudio, la riqueza de especies está determinada por procesos que ocurren dentro y fuera de la comunidad (Palmer 1994, Brown y Kodrick-Brown 1977, Shmida y Wilson 1985).

Hasta el presente, no se han analizado de manera cuantitativa y predictiva los patrones biogeográficos de la diversidad de las cactáceas a gran escala (es decir, en estudios que incluyan comparativamente varias regiones biogeográficas), aunque existen estudios a escala intra-regional (por ejemplo, Hernández y Bárcenas 1994). La diversidad α, definida como la riqueza de especies, es decir el número de especies distintas en un sitio dado (Whittaker 1972) y la diversidad β, definida como el recambio espacial (entre sitios o a lo largo de un gradiente) de las especies (Whittaker 1977, Magurran 1988), son los componentes de mayor importancia de la diversidad biológica a gran escala. Las diferencias en abundancia relativa entre especies o la variación genética, no son cuantificables a esa escala para una familia completa.

Aunque las relaciones ambiente-riqueza y ambiente-diversidad-α a una escala local y a una escala regional han sido desde principios de siglo ampliamente estudiados (O´Brien 1993), el otro componente de la diversidad, la diversidad de diferenciación (o diversidad-β, Colwell y Coddington 1994), ha recibido menos atención y discusión teórica (Harrison et al. 1992). Desde Whittaker (1972), se reconocen dos componentes causales de esta diversidad que han sido muy difíciles de estudiar por separado: las características de las especies, en particular los ámbitos de tolerancia a determinadas condiciones ambientales, y la heterogeneidad en las características del hábitat o ambiente donde se encuentran estas especies. Schluter y Ricklefs (1993) consideran dentro de la diversidad-β al efecto del hábitat (o de la tolerancia ambiental) como una función inversa del número de localidades o hábitats que ocupan las especies dentro de una determinada región, y al efecto de la heterogeneidad regional como el número de hábitats totales en la región. En el mismo sentido, Westoby (1993) estima globalmente la diversidad-β como la proporción de la diversidad regional que es contenida en distintas localidades. Aunque tanto las características del hábitat como las de las especies dependen de la escala espacial y temporal del estudio, cuanto más heterogéneo sea un sitio, como regla general presentará un mayor valor de diversidad-β. El problema es cómo definir la heterogeneidad a distintas escalas espaciales. En una primera aproximación, a una escala regional, la heterogeneidad ambiental y el recambio de especies están relacionados con grandes diferencias climáticas, geológicas, geomorfológicas e históricas (O´Brien 1993, Whittaker 1972). En una escala más local, la heterogeneidad puede estar asociada a microtopografía, microclimas (por ejemplo, Shmida y Wilson 1985), tipos de suelo (por ejemplo, Orians y Solbrig 1977) y regímenes de disturbio (por ejemplo, Meave 1991), entre otros factores. Las características de las especies - el otro componente de la diversidad-β - están principalmente relacionadas con la amplitud del hábitat y, a su vez, determinadas por tres factores: la capacidad de dispersión, de colonización y la susceptibilidad a la extinción en un determinado sitio (Schluter y Ricklefs 1993, Holt 1993, Cody 1993).

Con el propósito de explicar las grandes tendencias biogeográficas de las cactáceas en el continente americano es necesario diferenciar los patrones de los diferentes elementos que componen la diversidad de estas especies. Para ello, esta tesis integra el estudio de la diversidad en tres aspectos: la riqueza de especies o diversidad-α, el recambio de especies o diversidad-β, y la variación de la riqueza en un gradiente latitudinal que abarca los dos hemisferios. Para cada uno de estos aspectos, se plantean hipótesis y objetivos específicos.

La primer etapa de este estudio comprendió el análisis de los patrones de la riqueza de especies o de la diversidad-α. Este análisis se describe en el segundo capítulo de esta tesis titulado "*Species richness of Argentine cacti: a test of some biogeographic* *hypoteses*". En este artículo se ponen a prueba algunas hipótesis de la distribución de la diversidad biológica con respecto a descriptores ambientales, y se evalúa también el efecto del esfuerzo de colecta con el fin de detectar las áreas sobre y sub colectadas. Las hipótesis que se ponen a prueba en este trabajo son: (a) la benignidad o favorabilidad ambiental o climática, (b) la variación climática, (c) la heterogeneidad del hábitat, y (d) la energía y la productividad primaria. No se exploraron otras hipótesis como las referentes al papel de las interacciones bióticas, dada la escala local de sus efectos. La hipótesis de la benignidad (o "favorabilidad") climática establece que los ambientes extremos sostienen un menor número de especies que los ambientes más favorables ya que las especies requieren de mecanismos adaptativos más costosos para su supervivencia (Brown 1988, Begon et al. 1990). Esta hipótesis relaciona los valores promedio de las variables ambientales, tanto de las medias anuales como de los valores extremos (por ejemplo, temperatura media anual, precipitación media anual y temperatura mínima anual) con la riqueza de especies (Giller 1984).

La hipótesis de la variación climática se basa en la heterogeneidad temporal del ambiente es decir la heterogeneidad dada por la variación en estaciones. Esta hipótesis predice que el número de especies aumenta con la estacionalidad del ambiente. No consideramos la variación climática como un tipo de perturbación o ruido a corto plazo. En este caso, si la variación no es estacional ni predecible, la diversidad de especies puede ser mayor en los niveles intermedios de esta perturbación, dado que niveles extremos de variación ambiental pueden hacer difícil el desarrollo de todas las especies (Giller 1984, Hutchison 1961, Connell 1978, Richerson y Lum 1980).

La hipótesis de la heterogeneidad del hábitat se origina en la variación espacial del ambiente. Si bien el concepto de heterogeneidad es muy amplio, consideramos un hábitat heterogéneo como aquél que ofrece un gran número de micrositios distintos; es decir, un mayor número de microhábitats y de recursos que pueden ser usados por distintas formas de crecimiento (Aarsen 1992, Begon et al. 1990, Auerbach y Shmida 1987).

La hipótesis de la energía predice que una determinada cantidad de energía soportará un número finito de especies. La energía puede traducirse en productividad primaria y como tal, se ha demostrado que la productividad se relaciona significativamente con el número de especies (Currie y Paquin 1987, Currie 1991, Rosenzweig y Abramsky 1993). En la práctica, ha sido en ciertas circunstancias, difícil aislar la productividad de otras hipótesis biogeográficas como por ejemplo, la estabilidad climática. De hecho, una mayor productividad no conduce necesariamente a una mayor diversidad (Giller 1984). Rosenzweig (1995) discute las múltiples funciones que relacionan productividad y riqueza en distintos taxa.

El tercer capítulo de esta tesis, titulado "*Differentiation diversity patterns of Argentine cacti and their relationship to environmental factors*", describe los patrones de recambio de especies en Argentina. Este artículo aborda el otro gran componente de la diversidad, la llamada diversidad de diferenciación o diversidad-β (Whittaker 1960, 1972, Cody 1986). Según la escala, este parámetro ha recibido también otras denominaciones como diversidad delta (Whittaker 1977), o gamma (Cody 1993), y ha sido conceptualmente asociada a la heterogeneidad ambiental.

Para independizarnos de las discusiones de nomenclatura, en este segundo capítulo se define operativamente la diversidad-β como el recambio espacial de especies, ya sea entre sitios, a través de hábitats o de gradientes geográficos (Westoby 1993, Magurran 1988). Dado que a mayor heterogeneidad ambiental, ocurre en general un mayor recambio de especies (Shmida y Wilson 1985, Williamson 1988), la pregunta central de esta sección es "¿Qué tipo de heterogeneidad ambiental es determinante de los recambios de especies observados?" En este artículo se pone a prueba si el recambio de especies está significativamente asociado a valores absolutos de las variables ambientales y de esfuerzo de colecta o a la variación espacial de estos valores. Esta hipótesis nos condujo a explorar distintos métodos para calcular la diversidad-β y se usaron, en cada uno de ellos, índices diferentes para medirla. El método más ortodoxo de análisis, el de gradientes, se complementa con el método de recambio entre cuadros vecinos, una técnica de análisis que no ha sido hasta ahora descrita en la literatura. Al analizar las relaciones entre hábitat y reemplazo de especies, se discuten en este capítulo las características diferenciales de cada forma de crecimiento.

En el tercer trabajo, titulado "*Rapoport´s rule: a comparative analysis between South and North American columnar cacti*" se comparan los patrones latitudinales de la riqueza de especies columnares en norte y Sudamérica. Uno de los fenómenos biogeográficos más conocidos pero explicados menos satisfactoriamente es el de los patrones globales en la riqueza de especies, en particular los gradientes latitudinales en la riqueza de plantas, descritos por primera vez por von Humboldt hace 200 años (Brown 1988).

Dado que procesos histórico-evolutivos similares en ambos continentes derivaron en una convergencia de estructuras y forma de crecimientos en las comunidades áridas y semiáridas, discuto en este capítulo si la mayor riqueza de especies columnares se concentra hacia los trópicos en los dos hemisferios y las posibles causas de esta tendencia biogeográfica. Según la "Regla de Rapoport" (Stevens 1989, basado en el fenómeno descrito por Rapoport 1982), los ámbitos latitudinales de las especies decrecen hacia los trópicos. Stevens (1989) señala una correlación entre esta regla biogeográfica y la regla general de que para la mayoría de los taxa, la riqueza específica aumenta hacia los trópicos. Esto indicaría que áreas geográficas pequeñas permiten un mayor compactamiento de especies, y por ende, mayor riqueza. Dado que, según la Regla de Rapoport los individuos de climas templados son más euriecos en sus tolerancias a los factores climáticos que los individuos de climas tropicales, Stevens concluye que es esta tolerancia la que permitió a las especies de altas latitudes extender su área geográfica más ampliamente que a las especies de bajas latitudes, y que este fenómeno en su conjunto sería el principal mecanismo causal de la mayor diversidad en los trópicos. En el cuarto capítulo de esta tesis se investigó la hipótesis de Stevens, analizando si los ámbitos latitudinales de las cactáceas columnares decrecen efectivamente hacia los trópicos en ambos continentes.

REFERENCIAS

Auerbach, M. y Shmida, A. 1987. Spatial scale and the determinants of plant species richness. *Trends in Ecology and Evolution* **2**: 238-242

Aarssen, L. W. 1992. Causes and consequences of variation in competitive ability in plant communities. *Journal of Vegetation Science* **3**: 165-174.

Barthlott, W. y Hunt, D. R. 1993. Cactaceae. In: Kubitzki, K. (ed.) *The families and genera of vascular plants,* pp. 161-197. Springer-Verlag, Berlin, Heidelberg.

Begon, M. Harper, J. L. y Townsend C. R. 1990. *Ecology: individuals, populations and communities*. Blackwell, Boston.

Brown, J. H. 1988. Species diversity. In: Myers, A.A. y Giller, P.S.(eds.) *Analytical biogeography*, pp. 57-89. Chapman and Hall, New York..

Brown , J. H. y Davidson, D. W. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* **196**: 880-882.

Brown, J. H. y Kodrick-Brown, A. 1977. Turnover rates in insular biogeography: effect of inmigration on extinction. *Ecology* **58**: 445-449.

Buxbaum, F. 1958. The phylogenetic division of the subfamily Cereoideae, Cactaceae. Madroño **14**: 177-206.

Cody, M. L. 1986. Diversity, rarity and conservation in Mediterranean-climate regions. In: Soulé, M. E. (ed.) *Conservation biology: the science of scarcity and diversity*, pp. 123-152. Sinauer Associates, Sunderland, Mass.

Cody, M. L. 1989. Growth-form diversity and community structure in desert plants. *Journal of Arid Environments* **17**: 199-209.

Cody, M. L. 1993. Bird diversity components within and between habitats in Australia in Species diversity In: Ricklefs, R. y Schluter, D. (eds.) *Species diversity in ecological communities: historical and geographical perspectives*, pp.147-158. The University of Chicago Press. Chicago and London.

Colwell, R. K. y Coddington, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transaction Royal Society, London* **345**: 101-118

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-1309.

Connell, J. H. y Orias, E. 1964. The ecological regulation of species diversity. *American Naturalist* **98**: 399-414.

Cornell, H. V. 1993. Unsaturated patterns in species assemblages: The role of regional processes in setting local species richness. In: Ricklefs, R. y Schluter, D.(eds.) *Species diversity in ecological communities: historical and geographical perspectives*, pp.243-252. The University of Chicago Press. Chicago and London.

Crawley, M. J. 1986. *The structure of plant communities.* In: Crawley, M. J. (ed.):Plant Ecology, Blackwell, Oxford, pp. 1-50.

Currie, D. J. y Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* **329**: 326-327.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant- species richness. *American Naturalist* **137**: 27-49.

Eriksson, O. 1993. The species pool-hypothesis and plant community diversity. *Oikos* **68**: 371-374

Gibson, A. y Nobel. P. S. 1988. *The Cactus Primer*. Harvard University Press, Cambridge, MA:

Giller, P. S. 1984. Community structure and the niche. Chapman and Hall, London.

Gleason, H. A. 1925. Species and area. *Ecology* **6**: 66-74.

Grime, J. P. 1973. Control of species density in herbaceous vegetation. *Journal of Environmental Management* **1**: 151-167.

Halffter, G. y Ezcurra, E. 1992. Qué es la biodiversidad? En: Halffter, G. (comp.) *La Diversidad Biológica en Iberoamérica I,* pp. 3-24. Instituto de Ecología. Jalapa. Veracruz.

Harman, W. N. 1972. Benthic substrates: their effect on freshwater molluscs. *Ecology* **53**: 271-272

Harrison, S., Ross, S. J. y Lawton, J. H. 1992. Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology* **61**: 151-158.

Hernández, H. M. y Bárcenas, R. T. 1994. Endangered cacti in the Chihuahuan desert: I. Distribution patterns. *Conservation Biology* **9**: 1176-1188

Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs, R. y Schluter, D.(eds.) *Species diversity in ecological communities: historical and geographical perspectives*, pp.77-88. The University of Chicago Press. Chicago and London.

Humboldt, A. von. 1855. Géographie botanique raisonnée: ou, expositions des faits principaux et des lois concernant la distribution géographique des plantes de l´époque actuelle. V. Masson, Paris.

Huston, M. A. 1994. Biological Diversity: The coexistence of species on changing landscapes. Cambridge University Press. Cambridge, Great Britain.

Hutchinson, G. E. 1961. The paradox of the planton. *American Naturalist* **95**: 37-146.

Lubchenco, J. 1978. Plant species diversity in marine intertidal community:importance of herbivore food preference and algal competitive abilities. *American Naturalist* **112**: 23-39.

MacArthur, R. H. 1965. Pattern of species diversity. *Biological Review.* **40**: 510-533.

Magurran, A. E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey.

Meave, J. A. 1991. Maintenance of tropical rainforest plant diversity in riparian forests of tropical savannas. Tesis doctoral, York University, Toronto, Canadá.

Nilsson, S.G., Bengtsson J. y As S. 1988. Habitat diversity or area per se? Species richness of woody plants, carabid beetles, and land snails on islands. *Journal of Animal Ecology* **57**: 685-704.

O´Brien, E. M. 1993. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa´s woody flora. *Journal of Biogeography* **20**: 181-198.

Orians, G. H. y Solbrig, O. T. 1977. *Convergent evolution in warm deserts*. Dowden, Hutchinson y Ross. Stroudsberg, Pa.

Palmer, M. W. 1987. Variability in species richness within Minnesota oldfields: a use of the variance test. *Vegetatio* **70**: 61-64.

Palmer, M. W. 1991. Patterns of species richness among North Carolina hardwood forests: tests of two hypotheses. *Journal of Vegetation Science.* **1**: 57-65

Palmer, M. W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobot. Phytotax., Praha*, **29**: 511-530.

Pianka, E. R. 1966. Latitudinal gradients in species richness: a review of concepts. *American Naturalist* **100**: 33-46.

Rapoport, E. H. 1982. *Aerography: Geographical strategies of species*. Pergamon Press. New York.

Rhode, K. M. 1992. Latitudinal gradients in species diversity : the search for the primary cause. *Oikos* **65**: 514-527.

Richerson, P. J. y Lum, K-W. 1980. Patterns of plant species diversity in California: relation to weather and topography. *American Naturalist* **116**: 504-536.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**: 167-171.

Rosenzweig, M. L y Abramsky, Z. 1993. How are diversity and productivity related? In: Ricklefs, R. y Schluter, D.(eds.) *Species diversity in ecological communities:historical and geographical perspectives*, pp.52-65. The University of Chicago Press. Chicago and London.

Rosenzweig , M. .L. 1995. *Species diversity in space and time*. Cambridge University Press. Cambridge. 436 pp.

Schluter, D. y Ricklefs, R. 1993. Species diversity: an introduction to the problem. In: Ricklefs, R. y Schluter, D.(eds.) *Species diversity in ecological communities:historical and geographical perspectives*, pp.1-10. The University of Chicago Press. Chicago and London.

Shmida, A. y Wilson, M. V. 1985. Biological determinants of species diversity. *Journal of Biogeography* **12**: 1-20.

Silvertown, J. 1980. The dynamics of a grassland ecosystem: botanical equilibrium in the park grass experiment. *Journal of Applied Ecology* **17**: 491-504.

Steenbergh, W. F. y Lowe, C. H. 1977. Ecology of the saguaro.II: Reproduction, germination, establishment, growth, and survival of the young plant. National Park Service Scientific Monograph Series, no. 8, U.S. GPO, Washington, D.C.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how many species coexist in the tropics. *American Naturalist* **133**: 240-256.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport´s latitudinal rule to altitude. *American Naturalist* **140**: 893-911

Wallace, A. R. 1878. Tropical nature and other essays. Macmillan, London.

Westoby, M. 1993. Biodiversity in Australia compared with other continents. In: Ricklefs, R. y Schluter, D.(eds.) *Species diversity in ecological communities:historical and geographical perspectives*, pp.147-158. The University of Chicago Press. Chicago and London.

Whittaker, R. M. 1960. Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs* **30**: 279-338.

Whittaker, R. M. 1972. Evolution and measurement of species diversity. *Taxon* **21**: 213-251.

Whittaker, R. M. 1977. Evolution of species diversity in land communities. *Evolutionary Biology* **10**: 1-67.

Williamson, M. 1988. Relationship of species number to area, distance and other variables. In: Myers, A. A. y Giller, P. S. (eds.) *Analytical Biogeography: An integrated approach to the study of animal and plant distributions*, pp. 91-115. Chapman y Hill, London.

Wilson, J. B. , Gitay, H. y Agnew, A. D. Q. 1987. Does niche limitation exist? *Functional Ecology* **1**: 391-397.

Zobel, M. 1992. Plant species coexistence: the role of historical, evolutionary and ecological factors. *Oikos* **65**: 314-320.

II. SPECIES RICHNESS OF ARGENTINE CACTI: A TEST OF SOME BIOGEOGRAPHICAL HYPOTHESES.

Species richness of Argentine cacti: A test of some biogeographic hypotheses

Abstract.. We described patterns of species richness of three main cactus growth-forms (50 columnar, 109 globose and 50 opuntioid species) and of all forms combined in 318 (1°×1°) quadrats covering Argentina. We tested biological richness hypotheses 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 quadrat) to estimate the possible error induced by undercollection in some quadrats. Log-linear regression models accounted for a large portion of the variation in columnar species numbers (r^2 = 0.84), in opuntioid species (r^2 = 0.72), in globose species (r^2 = 0.75) and in all forms combined (r^2 = 0.86). Opuntioid and globose species richness was closely associated with the percentage of summer rainfall (a measure of climatic variation). Columnar species richness was positively associated with the number of frost-free days. A strong distribution limit marked by freezing temperatures seems to exist for columnar cacti. As the percentage of summer rainfall and the number of frost-free days were good predictors for all the growth-forms considered, the results are consistent with the climate favourableness and the climatic variation hypotheses as determinants of species richness. Our results do not support the hypothesis that energy flow limits regional species richness. Altitudinal range (a measure of habitat heterogeneity) was also related to the species richness of globose cacti. A floristic affinity analysis between geographic provinces and the distribution of geographic ranges for the different growth-forms confirmed the high degree of endemicity of the globose cacti and the cosmopolitanism of the opuntioid growth form. For the pooled group, two quadrats in the Prepuna and northern Monte Provinces showed species richness values that were significantly higher than those predicted by the log-linear model. The existence of these high-diversity regions is possibly a result of the way Quaternary historical events affected the main South American biomes.

Keywords: species richness; Cactaceae; growth-forms; Argentina; phytogeographic provinces; plant-environment relationships.

Running head: Biogeographic patterns of Argentine cacti.

Nomenclature: Nomenclature follows 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 along the evolutionary history of the family. Within the Cactaceae, five main growth-forms can be recognised: (a) columnar cacti, (b) globose cacti, (c) opuntioid cacti, (d) epiphytic cacti, and (e) pereskioid 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 in this paper as columnar cacti the candelabriform arborescent species, the unbranched erect stems (or solitary columnar arborescent cactus), the branched cacti, shrub-like forms with ascending or pendent branches, and the shorter barrel cacti. Globose cacti, the smallest growth-form, are more or less spherical in shape. Their small size, rounded shape, and the high density of areoles in the stem are the most striking features in this growth-form. Columnar and globose growth-forms belong to the subfamily Cactoideae. Most of the columnar genera belong to the Tribes Trichocereeae and Cereeae while the genera of the globose species belong mostly to the Tribe Notocacteae (Gibson & Nobel 1986). Opuntioid 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 opuntioid 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 low number of shallow ribs. Most of the genera of the epiphytic cacti belong to the Tribe Hylocereeae of the Subfamily

Cactoideae. The pereskioid 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 a CAM metabolism (Rayder & Ting 1981; Gibson & Nobel 1986; Nobel 1988).

As in other studies (Owen 1989; Arita 1993; Brown 1988; Major 1988; Cody 1986, 1989) we consider species richness as a main constituent of species diversity. The aim of our work was to describe the patterns of geographic distribution of the main growth-forms of the Argentine cactus species. Specifically, we tried to answer (a) how does the number of species in each growth-form vary geographically, and (b) what is the statistical relationship between selected environmental variables and the richness of the different cactus growth-forms. Answering these questions we also tried to evaluate if there are distinct environmental requirements among the different growth-forms, and to discuss the observed patterns in terms of the adaptive characteristics and the geographic ranges of each growth-form, the floristic affinities between regions, the published hypotheses on the causes of species diversity, and the history of the region.

Numerous historical, evolutionary and ecological hypotheses have been proposed to explain species richness patterns (*e.g.* Simpson 1964; MacArthur 1965, 1969; Pianka 1966; Cook 1969; Schall & Pianka 1978; Shmida & Wilson 1985; Silvertown 1985; Currie & Paquin 1987; Begon *et al.* 1990; Currie 1991) and geographic variation in growth-forms (*e.g.* Raunkier 1934; Box 1981). In a recent review, Palmer (1994) identified at least 120 plausible hypotheses on species richness patterns published in the literature. Although there have been attempts to classify these hypotheses (for reviews see Palmer 1994, Zobel 1992, Eriksson 1993, Brown 1988, Crawley 1986, Giller 1984, Begon *et al.* 1990), it is a difficult task as many of them are not mutually exclusive, and are frequently based on the same theoretical mechanisms, such as the competitive exclusion principle (Palmer 1994).

In this paper, we tested the following hypotheses : (a) environmental favourableness, (b) climatic variation, (c) habitat heterogeneity, and (d) 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. In short, we concentrated on the relationship between species richness and different abiotic variables at a regional scale. We did our analysis for the different cactus growth-forms separately, as the species in each life form may be considered as sharing at large a similar adaptive morphology. Cody (1986, 1989) has suggested that the different growth-forms of desert plants correspond to different structural niches, and that the overall diversity of perennial plants is largely determined by the coexistence of the different growth forms.

The environmental favourableness hypothesis states that extreme environmental conditions should support fewer species than mild environments, as extreme environments demand costly adaptive mechanisms for survival (Begon *et al.* 1990, Brown 1988). 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 (Begon *et al.* 1990, Brown 1988). Unpredictable, non-seasonal, climatic variation is a form of disturbance and species diversity may be highest at intermediate levels (Giller 1984, Richerson & Lum 1980, Hutchinson 1961, Connell 1978). 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 occur together (Aarsen 1992, Giller 1984, Begon *et al.* 1990, Auerbach & Shmida 1987, Simpson 1964). Finally, as energy is limited, it may be hypothesised that the amount of energy available will support a restricted number of species. It has been shown that in some ecosystems primary productivity (a measure of energy flow) is associated with species richness (Connell & Orias 1964; Brown & Davidson 1977; Abramsky & Rosenzweig 1984; Rosenzweig 1984, 1992, O'Brien 1993). However, it is difficult in practice to isolate productivity from other factors, such as climatic stability, and often increasing productivity does not lead to increasing diversity (Giller 1984). A review of the complex relationship between productivity and species richness is found in Rosenzweig (1995).

Methods

We included in the analysis a total of 223 cactus species whose distribution is known to occur in Argentina (Appendix 1). We discarded five pereskioid species, as their low number does not allow the testing of statistical hypotheses. We also discarded introduced species and species with either dubious distribution records or non-valid names. 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 (Appendix 2). We gathered a total of 3395 records for this study. For each species, we mapped the sites where it had been collected. The map of Argentina was divided into a grid of 318 quadrats of 1° latitude × 1° longitude. We superimposed the grid on the maps with the records for each species and we digitised the quadrats where each species had been observed into a data-base.

We also digitised the climatic descriptors of the environment on a 1° × 1° scale. The 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 with the proportion of annual rain falling in summer. Topographic data were taken from CEAL (1981). Digitising the values from these maps, we assigned to each quadrat 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 actual 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 quadrat'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 quadrat; (b) topographic variation, measured as the standard deviation of the same nine elevations per quadrat, 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 associated environmental variables

We made all the statistical analyses for the three dominant growth-forms: columnar, globose and opuntioid cacti (*n* = 50, 109, and 50 species, respectively). Due to the small number of species within the group of epiphytic cacti (*n* = 14), we did not perform statistical analyses for this growth-form although we mapped the species richness pattern. We used log-linear models in all cases, as 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, as the variance of frequency counts is usually not constant, and as 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, and the assumption of a Poisson error distribution, instead of normal errors, takes into account the fact that the data are integer and have variances that increase with the mean. For our log-linear models we used the GLIM package (NAG 1986, Crawley 1993), and we evaluated the fit of the model by means of the *G* statistic as a measure of goodness-of-fit (MacCullagh & 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. Generalised 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 quadrat 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.

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 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; 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 quadrat (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 (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 X^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 standardised residuals ([*observed* - *expected*] / √[*expected*]) follow asymptotically a normal distribution (Everitt 1977). Thus, for each quadrat the standardised residuals can be used as a measure of the fit of that particular quadrat 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 quadrats 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 quadrats where the frequencies predicted by the log-linear model were lower than 5.

All quadrats 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 standardised residuals for independence, following Draper & Smith (1981).

Floristic affinities between regions

In order to analyse floristic affinities between regions, we chose three base quadrats of relatively high cactus richness. Each base quadrat 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 quadrat in the map, the number of species shared with the base quadrats. We then plotted maps of equiprobabilistic contour lines showing the similarity of all quadrats with the chosen centre of comparison (*i.e.* the base quadrat). These curves have been used to predict species barriers and corridors for different taxa (Rapoport 1975, 1982; Rapoport & Ezcurra 1979). Again, this analysis was made on the three main growth-forms: opuntioid, columnar and globose cacti.

The distribution of geographic ranges

The geographic range of each species was estimated by adding the number of quadrats 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 to evaluate the proportion of endemic species in each growth form (*i.e.* the number of species below a given low number of quadrats).

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), the areas of highest species richness appeared towards the NW of the country, corresponding, in decreasing order, to the Prepuna Province, the northern Monte Desert and the Chaco dry forest. The number of species in the peaks of the first two regions double that of the richest quadrats in the Chaco. The Andean-Patagonian and the Pampean provinces showed the lowest levels of cactus species richness. The columnar cacti (Fig. 3a) followed a similar pattern 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 the pattern described above, although their southern limit was similar to that of the columnar group. Their highest species richness areas, in decreasing order, were the Prepuna Province, and the Monte Desert, together with two isolated ranges: the *Sierras* of Córdoba and San Luis, and the hills of Entre Ríos. A striking feature was the low species richness of this growth-form in the Chaco dry forest when compared to either the columnar growth-form or the whole family. The opuntioid form (Fig. 3b), more widespread than the rest, 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).

Species richness and environmental variables

Regression against latitude.

The whole group, and all three growth forms separately, showed a significant negative association between species richness and latitude (whole group: $r^2 = 0.46$, $P < 0.0001$; opuntioid 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 quadrats. However, in the opuntioid 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 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 opuntioid forms the best predictor of species richness was also the proportion of annual rain falling in summer ($P < 0.0001$ for both growth forms; Figs. 5c and 5d, and Table 3). Additionally, in the globose cacti the mean minimum annual temperature and the altitudinal range explained a significant ($P < 0.0001$) but 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 opuntioid 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 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 it was in no case 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 standardised 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 opuntioid 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 quadrats.

When the residuals that departed significantly from the Poisson error distribution were analysed for the whole group, it was found that a quadrat 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 quadrats also appeared with significant negative residuals, showing areas where species richness is lower than could be expected following the model's predictions. These three quadrats corresponded to the three most collected grid cells in Argentina. While on average the number of specimens per quadrat 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 quadrat sizes

As the size of the quadrats used in this study co-varies with latitude (the area of each quadrat 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 quadrat 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 analysis, 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 quadrat 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 quadrat size. Another possible bias in quadrat area may result from the fact that some quadrats are located on a seacoast, peninsula or in border areas. To analyse the significance of the effect of incomplete quadrats on species richness, these quadrats were identified with a statistical factor (a dummy variable) in the regression analyses. It was found that the effect of incomplete quadrats was not significantly associated with species richness. Thus, the effect of quadrat size on the observed patterns of cactus richness can be safely ignored for all practical purposes.

Floristic affinities between regions

The Prepuna

In general, a remarkable level of endemism was found in this region. Of all the opuntioid 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").

The Monte Desert

When the central Monte Desert was chosen as the base quadrat, a strong southern barrier appeared in all three groups with a western barrier on the Andes. For the opuntioid 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 opuntioid 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 quadrats 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 quadrats or less, compared to 33.33% for the columnar species and 34% for the opuntioid 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 opuntioid forms ($Me = 9.33$ and $Me = 11.00$ respectively). There were also significant differences between the mean log-range of globose cacti ($\bar{x} = 1.86$; $se = 0.11$) with the opuntioid species ($\bar{x} = 3.35$; $se = 0.21$; $P < 0.001$) and with the columnar species ($\bar{x} = 3.29$; $se = 0.23$; $P < 0.001$). No significant difference was found between the mean log geographic ranges of opuntioid and columnar cacti. Additionally, the globose form included a relatively high number of strongly localised species: 10% of the globose species were restricted to only one quadrat while none of the opuntioids and only 2% of the columnars presented 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, and 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 opuntioid form was noticeable in the high-diversity corridors found linking the Chaco with the Prepuna and the northern Monte. The opuntioid 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 opuntioid cacti may be related to the modular growth and the morphological plasticity of this form, as suggested by Gibson & Nobel (1986) and Nobel (1982a, 1982b, 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 opuntioid cacti in extreme environments. Gibson & Nobel (1986) have also attributed the higher temperature tolerance of opuntioid species to the shifting of the temperature response for net nocturnal CO_2 uptake as the environmental temperature changes. In spite of their wider tolerances, the opuntioid species were statistically associated with the proportion of annual rain falling in summer, the aridity index and the mean annual temperature. This group seem thus 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 quadrats 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 also linked 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 opuntioid and globose cacti.

The altitudinal range of the quadrats explained a significant, but low, proportion of the variation in species numbers for all groups with the exception of opuntiod 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.

The species richness patterns of the whole group, and of the opuntioid 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 per year. 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 (1987, 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 fires 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 areas with the highest fire intensity in Argentina have been for centuries the central pampas, that are distributed along a moisture gradient from a humid prairie in the east to an arid wooded grassland in the west. It is interesting to note that for all growth-forms, these formations have a relatively low number of species. Fires 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 quadrats are much better collected than others. This also suggests that, for the present intensity of botanical exploration in Argentine cacti, the use of quadrats one degree in size is an adequate scale, as in smaller quadrats 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, like 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 opuntioid and columnar cacti were significantly larger than those of the globose species, although they were not significantly different between themselves. In particular, many opuntioid 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. soehrensii, O. pentlandii, O. monacantha, O. brasiliensis, O. nigrispina*) also inhabit more than one phytogeographic region.

For the whole group, significantly low residuals were found in three quadrats 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 quadrats 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 quadrats 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 the these two sites (82 and 61 specimens) was well above the average. An alternative explanation can be found on the environmental history of these quadrats. 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. It is possible that the Prepuna and the northern Monte functioned as a refuge for cactus species during Pleistocene glacial events, and that this fact is still reflected in their present high species richness. It has been suggested that the central Monte, as opposed to the Puna and the Chaco Provinces, reached periods of high humidity during the Quaternary (Axelrod 1958; Tricart 1970; Vuilleumier 1971). Literature on South-American paleoclimates based on pollen and lake-levels data (*e.g.* Markgraf 1983, 1985, 1989) may give further clues on this subject.

Acknowledgements

The authors thank the enthusiastic support received from Roberto Kiesling and Omar Ferrari during C. Mourelle's travels in Argentina. This paper is part of the first author's doctoral research at UNAM, supported by a scholarship from the Noyes-Smith Sciences Foundation. The research received finantial support from the National Council of Science and Technology (CONACyT). A first version of this paper was greatly improved by constructive criticism from Dr. Michael Palmer.

References

Aarsen, L. W. 1992. Causes and consequences of variation in competitive ability in plant communities. *Journal of Vegetation Science* 3: 165-174.

Abramsky, Z. & Rosenzweig, M. L. 1984. Tilman's predicted productivity-diversity relationship shown by desert rodents. *Nature* 309: 150-151.

Arita, H. T. Riqueza de especies de la mastofauna de México. In: Ceballos,G. & Medellín, R.A. (eds.) *Avances en el estudio de los mamíferos mexicanos.* Asociación Mexicana de Mastozoología, A.C. México. (in press).

Auerbach, M. & Shmida, A. 1987. Spatial scale and the determinants of plant species richness. *Trends in Ecology and Evolution* 2: 238-242.

Austin, M. P. , Nicholls, A. O. & Margules, C. R. 1990. Measurement of the realized qualitative niche of plant species: examples of the environmental niches of five *Eucalyptus* species. *Ecol. Monogr.* 60: 161-177.

Axelrod, D. I. 1958. Evolution of the Madro-Tertiary geoflora. *Bot.Rev.* 24: 433-509.

Begon, M., Harper, J. L. & Townsend, C. R. 1990. *Ecology: Individuals, populations and communities.* 2nd ed. Blackwell Scientific, Boston.

Bojórquez-Tapia, L. A., Azuara, I. & Ezcurra E. 1995. Identifying conservation priorities in Mexico through geographic information systems and modeling. *Ecological Applications* 5: 215-231.

Box, E. O. 1981. *Macroclimate and plant forms: an introduction to predictive modeling in phytogeography.* Dr. W. Junk Publishers, The Hague.

Brown, J. H. 1988. Species diversity. In: Myers, A. A. & Giller, P. S. (eds.) *Analytical Biogeography:an integrated approach to the study of animal and plant distribution,* pp. 57-89. Chapman and Hall, London.

Brown, J. H. & Davidson, D. W. 1977. Competition between seed-eating rodents and ants in desert ecosysytems. *Science* 196: 880-882.

Burgess, L. T. & Shmida, A. 1988. Succulent growth forms in arid environments. In: Whitehead, G. G., Hutchinson, C. F., Timmermann, B. D. & Varady, R. G. (eds.) *Arid Lands Today and Tomorrow.* Proceedings of an International Research and

Development Conference at Tucson, Az., pp. 383-395. Westview Press, Boulder, Colorado & Belhaven Press, London.

Cabrera, A. L. & Willink, A. 1980. *Biogeografía de América Latina.* Serie de Biología, Monografía no.13. Organization of American States, 2nd ed. Washington, D. C.

CEAL. 1981. *Atlas Físico de la República Argentina.* Centro Editor de América Latina, Buenos Aires.

Cody, M. L. 1986. Diversity, rarity and conservation in Mediterranean-climate regions. In: Soulé, M. E. (ed.) *Conservation biology: the science of scarcity and diversity*, pp. 123-152. Sinauer Associates, Sunderland, Mass.

Cody, M. L. 1989. Growth-form diversity and community structure in desert plants. *Journal of Arid Environments* 17: 199-209.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Connell, J. H. & Orias, E. 1964. The ecological regulation of species diversity. *Am. Nat.* 98: 399-414.

Cook, R. D. & Weisberg, S. 1982. *Residuals and influence in regression.* Chapman and Hall. London.

Cook, R. E. 1969. Variation in species density of North American birds. *Syst.Zool.*18: 63-84.

Crawley, M. J. 1986. The structure of plant communities. In: Crawley, M. J. (ed.) *Plant Ecology*, pp1-50. Blackwell, Oxford.

Crawley, M. J. 1993. *GLIM for ecologists*. Blackwell Scientific Publ., Oxford. 379 pp.

Currie, D. J. & Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* 329: 326-327.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.* 137: 27-49

Draper, N. R. & Smith, H. 1981. *Applied Regression Analysis*, 2nd ed. Wiley & Sons, New York, NY.

Efron, B. & Thisted, R. 1976. Estimating the number of unseen species: How many words did Shakespeare know? *Biometrika* 63:435-447.

Eriksson, O. 1993. The species-pool hypothesis and plant community diversity. *Oikos* 68: 371-374

Everitt, B. S. 1977. *The analysis of contingency tables*. Chapman and Hall, London.

Fisher, R. A., Corbett, A. S. & Williams, C. B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12: 42-58.

Gibson, A. & Nobel, P. S. 1986. *The Cactus Primer*. Harvard University Press, Cambridge, MA.

Giller, P. S. 1984. *Community structure and the niche*. Chapman and Hall. London.

Hoffman, J. A. 1975. *Atlas climático de América del Sur. Mapas de temperatura y precipitaciones medias*. WHO, UNESCO, Cartographia.

Hunt, D. 1992. *CITES Cactaceae Checklist*. Royal Botanical Gardens. Kew. London. 167 pp.

Hutchinson, G. E. 1961. The paradox of the plankton. *Am.Nat.* 95: 37-146.

Kiesling, R. *Cacti on the rocks: cacti of Argentina, Paraguay and Uruguay.* Vasquez-Mazzini, Buenos Aires (in press)

Lieth, H. 1975. Modeling the primary productivity of the world. In: Lieth, H. & R. H. Whittaker (eds.) *Primary Productivity of the Biosphere*, pp.237-263. Springer Verlag, Berlin & New York.

MacArthur, R. H. 1965. Patterns of species diversity. *Biol. Rev.* 40: 510-533.

MacArthur, R. H. 1969. Patterns of communities in the tropics. *Biol. J. Linn. Soc.* 1: 19-30.

Major, J. 1988. Endemisms: a botanical perspective. In: Myers, A. A. & Gillers, P. S. (eds.) *Analytical Biogeography,* pp.116-146. Chapman and Hall, London.

Markgraf, V. 1983. Late and postglacial vegetational and paleoclimatic changes in subantartic, temperate, and arid environments in Argentina. *Palinology* 7: 43-70

Markgraf, V. 1985. Paleoenvironmental history at the last 10,000 years in the northwestern Argentina. *Zentralbl. Geol. Paläontol.* 11-12: 1739-1749

Markgraf, V. 1989. Paleoclimates in Central and South America since 18,000 BP based on pollen and lake-level records. *Quat. Sci. Rev.* 8: 1-24.

McCullagh, P. & Nelder, J. A. 1989. *Generalized Linear Models. 2nd ed.* Chapman and Hall, London.

McLaughlin, S. P. & Bowers, J. E. 1982. Effects of wildfire on a Sonoran Desert plant community. *Ecology* 63: 246-248.

Miller, R. 1965. *Simultaneous inference*. McGraw Hill. New York. NY.

NAG 1986. *The Generalised Linear Interactive Modelling System Release 3.77 Manual*. Numerical Algorithms Group, Oxford.

Nelson, B. W., Ferreira, C. A. C., da Silva, M. F & Kawasaki M. L. 1990. Endemism centres, refugia and botanical collection density in Brazilian Amazonia. *Nature* 345: 714-715.

Nicholls, A. O. 1989. How to make biological surveys go further with Generalised Linear Models. *Biol. Conserv.* 50: 51-75.

Nobel, P. S. 1982a. Orientations of terminal cladodes of platyopuntias. *Bot. Gaz.* 143: 219-224.

Nobel, P. S. 1982b. Orientation, PAR interception, and nocturnal acidity increases for terminal cladodes of a widely cultivated cactus, *Opuntia ficus-indica*. *Amer. J.Bot.* 69: 1462-1469.

Nobel, P. S. 1985. Form and orientation in relation to PAR interception by cacti and agaves. In: Givnish, T. J. (ed.) *On the Economy of plant form and function*, pp. 83-103. Cambridge University Press, Cambridge.

Nobel, P. S. 1988. *Environmental Biology of Cacti and Agaves*. Cambridge University Press, Cambridge.

O'Brien, E .M. 1993. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *J.Biogeogr.* 20: 181-198.

Owen, J. G. 1989. Patterns of herpetofaunal species richness: relation to temperature, precipitation, and variance in elevation. *J. Biogeogr.* 16: 141-150.

Palmer, M. W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobot. Phytotax. Praha* 29: 511-530.

Palmer, M. W. & White P. S. 1994. Scale dependence and the species-area relationship. *Am. Nat.* 144: 717-740.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *Am.Nat.* 100: 33-46.

Preston, F. W. 1960. Time and space and the variation of species. *Ecology* 41: 611-627.

Rapoport, E .H. 1975. *Areografía.* Fondo de Cultura Económica. Mexico.

Rapoport, E. H. 1982. *Areography, geographical strategies of species.* Pergamon Press, Oxford.

Rapoport, E. H. & Ezcurra, E. 1979. Natural and man-made biogeography in Africa: a comparison between birds and phytopathogens. *J. Biogeogr.* 6: 341-348.

Raunkier, O. 1934. *The life-forms of plants and statistical plant geography.* Clarendon Press. Oxford.

Rayder, L. & Ting, Y. P. 1981. Carbon metabolism in two species of *Pereskia* (Cactaceae). *Plant Physiology.* 68: 686-688

Richerson, P. J. & Lum, K-W. 1980. Patterns of plant species diversity in California: relation to weather and topography. *Am. Nat.* 116: 504-536.

Rosenzweig, M. L. 1984. On continental steady states of species diversity. In: Cody, M. L & Diamond, J. M (eds.) *Ecology and the evolution of communities*, pp. 121-137. Harvard University Press, Cambridge, Mass.

Rosenzweig, M. L. 1992. Species diversity gradients: we know more and less than we thought. *J. Mamm.* 73: 715-730.

Rosenzweig , M. .L. 1995. *Species diversity in space and time*. Cambridge University Press. Cambridge. 436 pp.

Schall, J. J. & Pianka, E. R. 1978. Geographical trends in the numbers of species. *Science* 201: 679-686.

Shmida, A. & Wilson, M. V. 1985. Biological determinants of species diversity. *J. Biogeogr.* 12: 1-20.

Silvertown, J. J. 1985. History of a latitudinal diversity gradient: woody plants in Europe 13,000-1000 years B.P. *J. Biogeogr.* 12: 519-525.

Simpson, G. G. 1964. Species diversity of North American recent mammals. *Syst. Zool.* 13: 57-73.

Steenbergh, W. F. & Lowe, C. H. 1977. *Ecology of the saguaro II: Reproduction, germination, establishment, growth, and survival of the young plant*. National Park Service Scientific Monograph Series, No. 8. 242 pp.

Soberón, J. & Llorente, J. 1993. The use of species accumulation functions for the prediction of species richness. *Conserv. Biol.* 7: 480-488.

Thomas, P. A. & Goodson, P. 1992. Conservation of succulents in desert grasslands managed by fire. *Biol. Cons.* 60: 91-100.

Tricart, J. 1970. Actions éoliennes dans la pampa deprimida (Rep. Argentine). *Rev. Géomorphol. Dyn.* 19: 178-189.

Vuilleumier, B. S. 1971. Pleistocene changes in the fauna and flora of South America. *Science* 173: 771-780.

Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* 147: 250-260.

Williams, M. R. 1995. An extreme-value function model of the species incidence and species-area relations. *Ecology* 76: 2607-2616.

Zobel , M. 1992. Plant species coexistence - the role of historical, evolutionary and ecological factors. *Oikos* 65: 314-320

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

HYPOTHESES	VARIABLES	SYMBOLS
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 defficiency	AWD
	Mean July temperature	MJT
	Mean December temperature	MDT
	Mean elevation	MEL
	Actual evapotranspiration	AEV
Climatic variation	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 qualitatively, not included in the model)	

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

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	VARIABLES	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	0.84	
Opuntioid cacti	Proportion of rain falling in summer (PRS)	0.37	+
	Average annual water defficiency (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	

APPENDICES

SPECIES LIST & LITERATURE ON COLLECTION SITES

APPENDICES

Appendix 1: Species List

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 hankeanus Web.
Cereus stenogonus K. Sch.
Cleistocactus baumannii (Lem.) Lemaire
Cleistocactus ferrarii R. Kiesling
Cleistocactus jujuyensis (Backbg.) Backbg.
Cleistocactus smaragdiflorus (Web.) Britton et Rose
Denmoza rhodacantha (SD) Britton et Rose
Echinopsis leucantha (Gill.) Walp.
Echinopsis rodotricha R. Mey
Harrisia bonplandii (Parmentier) Britton et Rose
Harrisia martinii (Labouret) Britton et Rose
Harrisia pomanensis (Weber) Britton et Rose
Harrisia tortuosa (Forbes) Britton et Rose
Lobivia chrysochete Werdermann
Lobivia ferox 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 cabrerae R. Kiesling
Trichocereus candicans (Gillies) Britton et Rose
Trichocereus fabrisii R. Kiesling
Trichocereus huascha (Web.) Britton et Rose

Trichocereus lamprochlorus (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 verschafeltii (Cels. & Web.) Backbg.
Austrocylindropuntia vestita (Salm-Dyck) Backbg.
Cylindropuntia tunicata (Lehm.) Knuth
Maihueniopsis boliviana (S.-D.) R. Kiesling
Maihueniopsis darwinii (Hensl.) Ritter
Maihueniopsis minuta (Backbg.) R. Kiesling
Maihueniopsis nigrispina (K. Schum.)
Maihueniopsis ovata (Pfeiff.) Ritter
Maihueniopsis pentlandii (S.-D.) R. Kiesling
Opuntia arechavaletai 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 & 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 meglioli R. Kiesling
Pterocactus pumilus Britton & Rose
Pterocactus reticulatus R. Kiesling
Pterocactus valentinii Spegazzini
Puna clavarioides (Pfeiff.) Kiesling
Puna subterránea (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 dussenii 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 mammifera 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 brucchii (Speg.) Hoss.
Gymnocalycium brucchii Hoss.
Gymnocalycium calochlorum (Bödek.) Y. Ito
Gymnocalycium capillaense (Schick) Backbg.
Gymnocalycium capillensis Hoss.
Gymnocalycium castellanosii 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 mazanense 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 platense (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 iridiscens Backbg.
Lobivia jajoiana 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 submammulosa R. Kiesling
Parodia turecekianus R. Kiesling
Pyrrhocactus andreanus (Backbg.) Ritter
Pyrrhocactus atroviridis Ritter
Pyrrhocactus bulbocalix (Werderm.) Backbg.
Pyrrhocactus pachacoensis Rausch
Pyrrhocactus sanjuanensis (Speg.) Backebg.
Pyrrhocactus straussianus Berger
Pyrrhocactus villicumensis Rausch
Rebutia calliantha Bewerunge
Rebutia einstenii Fric
Rebutia fiebrigii (Gürke) Britton et Rose
Rebutia margaretae Rausch
Rebutia minuscula Schumann

Rebutia pseudominuscula Spegazzini
Setiechinopsis miriabilis (Speg.) De Haas
Weingartia neumanniana (Backbg.) Werd.
Wigginsia tephracantha (Speg.) D.M.Porter

EPIPHYTIC CACTI
Epiphyllum phyllantum (L.) Haworth
Pfeiffera ianthothele (Monv.) Web.
Rhipsalis aculeata Weber
Rhipsalis baccifera (Mill.) Stearn
Rhipsalis cereuscula Haworth
Rhipsalis cruciformis Vell.
Rhipsalis houlletiana 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

Appendix 2: Literature consulted to verify collection sites

Ambrosetti, J. A., Del Vitto L. A. & Méndez, E. 1983. *Esquema de la vegetación desde Mendoza a las Cuevas por Villavicencio y Paso de Uspallata.* IADIZA. Mendoza. Argentina.

Ambrosetti, J. A., Del Vitto, L. A. & Roig, F. 1986. La vegetación del Paso de Uspallata, Provincia de Mendoza, Argentina. *Veroff.Geobot.Inst.ETH*, Stiftung Rübel, Zürich 91: 141-180

Anderson, D., Del Aguila, J. & Bernardón, D. E. 1970. Las formaciones vegetales de San Luis. *Rev. Inv. Agr. Serie Biol. y Prod. Veg.* VII: 153-183.

Backeberg, C. & Knuth, F. 1935. *Kaktus-ABC.* Denmark

Backeberg, C. 1958-1962. *Die Cactaceae.* 6 Bände. Fischer Verlag, Jena

Backeberg, C. 1977. *Cactus-lexicon (1966-1973).* Blandford Press. Poole. Dorset

Britton N. L. & Rose J. N. 1919-1922. *The Cactaceae I-IV*, Carnegie Institution, Washington.

Burkart, A. E. 1963. Noticia sobre algunos herbarios argentinos en Gran Bretaña y su interés fitogeográfico. *Darwiniana* 12: 533-558.

Buxbaum, F. 1950-1955. *Morphology of Cacti I (root and stems); II (the flower); III (fruits and seeds)*. Pasadena. California.

Buxbaum, F. 1968. Gattung *Gymnocalycium*. In: Krainz H. (ed.) *Die Kakteen*. CVI. pp.38-9.

Buxbaum, F. 1969. Die Entwicklungswege Der Kakteen In Sudamerika. In: Fittkau, E.J., Illies, J., Klinge, H., Schwabe, G.H. & Sioli, H. (eds.) *Biogeography and ecology in South America,* pp. 583-623. Dr. W. Junk N.V., Publishers. The Hague.

Cabrera, A. L. 1957. La vegetación de la Puna Argentina. *Rev. Invest. Agric.* 11: 317-412.

Cabrera, A. L. 1971. Fitogeografía de la Rep. Argentina. *Bol. Soc. Arg. Bot.* 16: 1-50.

Cabrera, A. L. 1976. Regiones fitogeográficas argentinas. In: *Enciclopedia Argentina de Agricultura y Jardinería*. 2nd.ed. Ed. Acme, Buenos Aires.

Cabrera, A. L. 1976. La vegetación de Argentina. In: *Enciclopedia Argentina de Agricultura y Jardinería*. 2nd ed. Ed. Acme, Buenos Aires.

Castellanos, A. 1952. El género *Quiabentia*. *Lilloa* 25: 595-603.

Castellanos, A. 1964. Revisión de las cactáceas argentinas, II *Pterocactus*. *Revista Fac. Cienc. Agr.* 8: 3-14.

Gibson, A. 1977. Vegetative anatomy of *Maihuenia* (Cactaceae) with some theoretical discussions of ontogenetic changes in xylem cell types. *Bull. Torrey Club* 104: 35-48.

Gibson, A. 1977. Wood anatomy of Opuntias with cylindrical to globular stems. *Bot. Gaz.* 138: 334-351.

Hunt, D. R. 1967. Cactaceae In: Hutchinson (ed.) *The genera of Flowering plants*. Oxford.

Hunt, D. R. & Taylor, N. P. 1986. The genera of the Cactaceae:towards a new concensus. *Bradleya* 4: 65-78.

Hunziker, J. 1952. Las comunidades vegetales de la cordillera de la Rioja. *Rev. Invest. Agric.* 6 : 167-196.

Kiesling, R. 1971. Dos nuevas especies de *Pterocactus*. *Boletín de la Sociedad Argentina de Botánica* XIV: 111-116.

Kiesling, R. 1972. *Alberto Castellanos:Recopilación de sus publicaciones sobre Cactáceas*. Ed. Círculo de Coleccionista de Cactus y Crasas de La República Argentina.

Kiesling, R. 1972. Los géneros de Cactaceae de Argentina. *Bol. Soc. Arg. Bot.* 16: 197-227.

Kiesling, R. 1975. *Recopilación, en edición facsimilar de todos los trabajos o referencias sobre cactáceas publicadas por el D. Carlos Spegazzini*. Ed. LibroSur. Buenos Aires. Argentina.

Kiesling, R. 1976. Novedades en *Trichocereus* (Cactaceae). *Hickenia* 1: 29-34.

Kiesling, R. 1976. Una nueva especies de *Lobivia* (Cactaceae). *Hickenia* 1: 35-38.

Kiesling, R. 1978. El género *Trichocereus* (Cactaceae): Las especies de la República Argentina. *Darwiniana* 21: 263-330

Kiesling, R. 1980. *Gymnocalycium mesopotamicum* sp. nov. *The Cactus and Succulent Journal of Great Britain* 42: 39-42.

Kiesling, R. 1982. Nota sobre *Gymnocalycium platense* (Speg.) Br. et Rose (Cactaceae). *Darwiniana* 24 : 437-442.

Kiesling, R. 1982. Problemas nomenclaturales en el género *Cereus* (Cactaceae). *Darwiniana* 24: 443-453.

Kiesling, R. 1982. *Puna*, un nuevo género de Opuntioideae. *Hickenia* 1: 289-292.

Kiesling, R. 1982. The genus *Pterocactus*. *Cactus and Succulent Journal Great Britain* 44: 51-56.

Kiesling, R. 1984. Estudios en Cactaceae de Argentina:*Maihueniopsis*, *Tephrocactus* y Géneros afines. *Darwiniana* 25: 171-215.

Kiesling, R. 1984. Una nueva especies de *Cleistocactus* (Cactaceae). *Hickenia* II: 37-40.

Kiesling, R. 1985. *Gymnocalycium kieslingii*, a new species from La Rioja, Argentina. *Cactus and Succulent Journal (US)* 57: 244-246.

Kiesling, R. 1986. Cold resistant cacti of Argentina. *Cactus and Succulent Journal (USA)* 58: 18-25

Kiesling, R. 1987. Two new subspecies of *Gymnocalycium schroederianum*. *Cactus and Succulent Journal* (U.S.) 59: 44-49.

Kiesling, R. 1988. Cactus de la Patagonia. In: Correa, M.N. (ed.) *Flora Patagónica.* Parte V. (Dicotiledóneas dialipétalas) (Oxalidaceae a Cornaceae). pp. 218-243. INTA. Bs.As. Argentina.

Kiesling, R. 1990. *Parodia* sensu strictu in Argentina, Part I. *Cactus and Succulent Journal (US)* 62: 194-198.

Kiesling, R. 1990. *Parodia* sensu strictu in Argentina, Part II. *Cactus and Succulent Journal (US)* 62: 244-250.

Kiesling, R. *Cacti on the rocks: Cactaceae of Argentina, Paraguay and Uruguay.* Ed. Vasquez-Mazzini. Buenos Aires (in press)

Martínez Carretero, E. 1985. La vegetación de la Reserva Natural del Divisadero Largo (Mendoza, Argentina). *Documents phytosociologiques* IX: 25-49.

Martínez Carretero, E. 1986. Ecología, fitogeografía y variación intraespecífica en *Cercidium praecox* (Ruiz et Pavon) Harms. (Leguminosae) en Argentina. *Documents phytosociologiques* X: 319-329.

Morello, J. 1951. El bosque de algarrobo y la estepa de jarilla en el Valle de Santa María (Provincia de Tucumán). *Darwiniana* 9: 315-347.

Morello, J. 1958. La provincia fitogeográfica del Monte. *Opera Lilloana* 2: 5-115.

Morello, J. 1967. Bases para el estudio fitoecológico de los grandes espacios:el Chaco Argentino. *Ciencia e Investigación* 23: 252-267.

Morello, J. & Adamoli, J. 1967 . Vegetación y Ambiente del NE del Chaco Argentino. *Boletín de la EEA Colonia Benítez* 3: 1-75.

Morello, J. & Adamoli. J. 1968. *Las grandes unidades de vegetación y ambiente del Chaco Argentino. Parte I: Objetivos y Materiales.* INTA. Serie fitogeográfica 10: 1-125.

Rausch, W. 1985. *Lobivia 85.* Verlag R. Herzig. Wien.

Ritter, F. 1979. *Kakteen in Sudamerika I.* Spangenberg.

Ritter, F. 1980. *Kakteen in Sudamerika II.* Spangenberg.

Roig, F. A. 1969. Descripción de un viaje botánico del viaje de Mendoza a Uspallata por los Paramillos. *X Jornadas Argentinas de Botánica*, pp. 1-62. Mendoza.

Roig, F. A. 1972. Bosquejo fisionómico de la provincia de Mendoza. *Bol. Soc. Arg. Bot.* 13: 40-80.

Roig, F. A. 1976. Las comunidades vegetales del piedemonte de la precordillera de Mendoza. *Ecosur* 3: 1-45

Roig, F. A. 1982. Cuyo. In: Grassi M. (ed.) *Conservación de la vegetación natural de la República Argentina.* Simposio. XVIII. Jorn. Arg. Bot., pp. 61-100. Fund. Miguel Lillo y Soc. Arg. Bot., Tucumán, Argentina.

Rowley, D. G. 1958. Reunion of the genus Opuntia. *The Nat. Cact. Succ. J.*13: 3-6.

Ruiz Leal, A. 1951. La ruta de la quebrada de Horcones hasta el Aconcagua. *Actas XV semana de Geografía.* pp. 99-131. Mendoza. Argentina.

Ruiz Leal, A. 1965. Breve reseña de las cactáceas mendocinas. *Soc. Arg. de Hort.* 23: 91-96

Ruiz Leal, A. 1969. Guía botánica del viaje desde Uspallata hasta el Cristo Redentor. *X Jorn. Arg. Bot.* Mendoza. Argentina.

Ruiz Leal, A. 1972. Los confines Boreal y Austral de las provincias Patagónicas y Central respectivamente. *Bol. Soc. Arg. Bot.* XIII:90-118.

Ruthsatz B. & C. P. Movia. 1975. *Relevamiento de las estepas andinas del NE de la provincia de Jujuy.* INTA. Argentina.

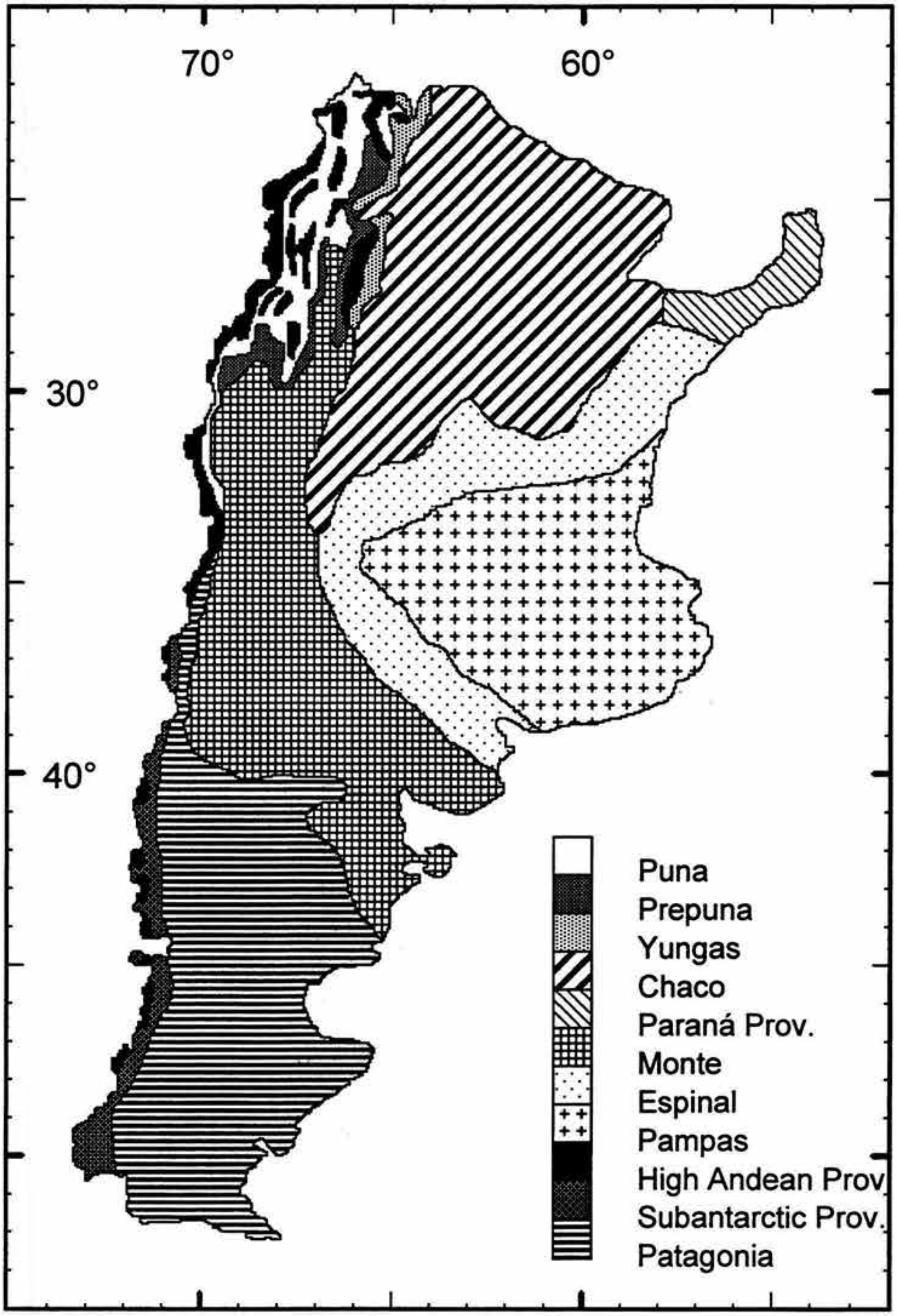

Figure 1. Phytogeographic provinces of Argentina, after Cabrera (1980). The main biome n each province is given in parentheses: Yungas Province (cloud forest), Parana Province (humid savannah), Chaco Province (dry subtropical forest), Espinal Province (xerophyllous woodland), Monte Province (warm desert), Prepuna Province (sarcocaulescent scrub), Pampean Province (temperate grassland), High-Andean Province (high-altitude cold grassland), Puna Province (high-altitude cold semidesert), Patagonian Province (steppe), Subantartic Province (temperate humid forest).

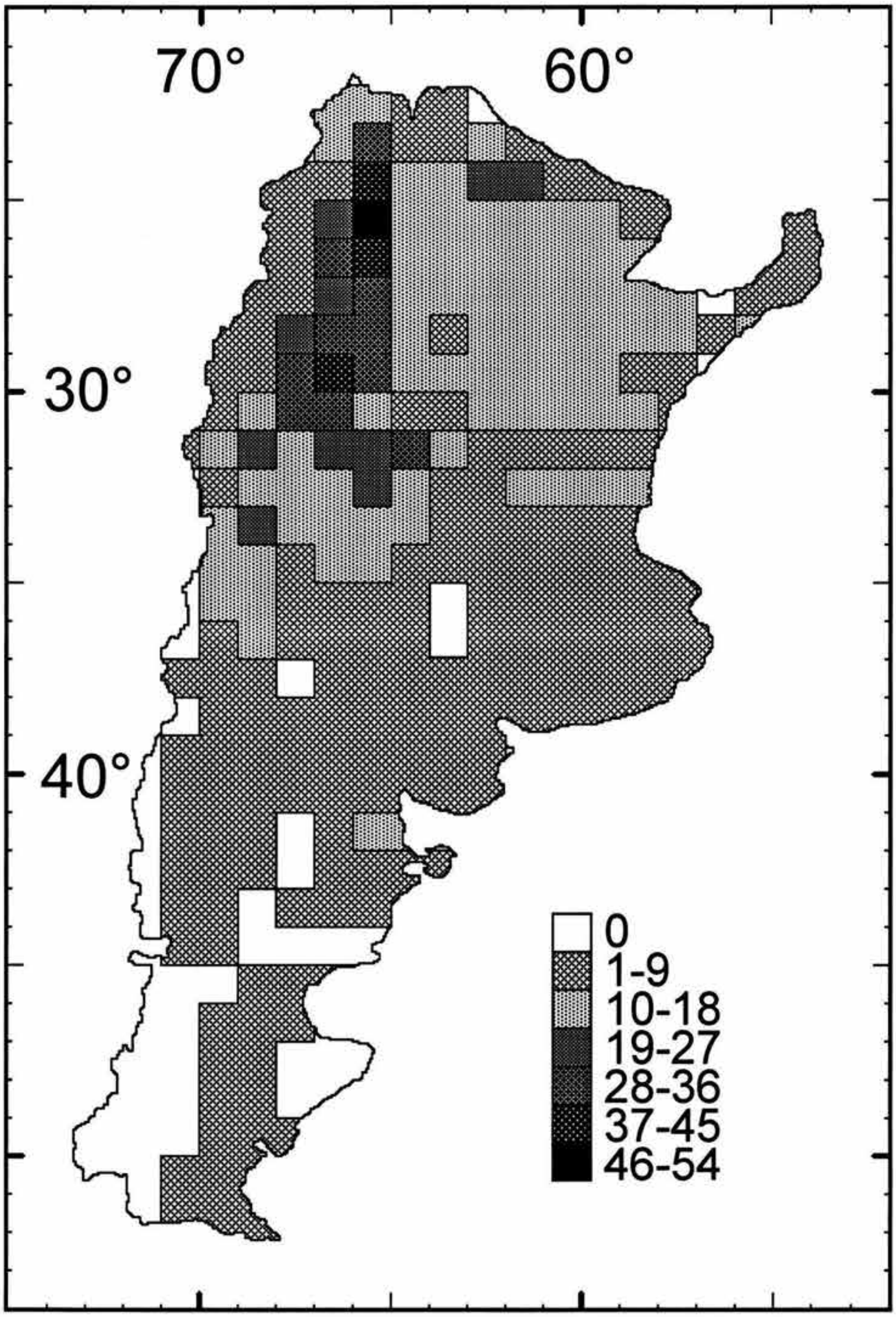

Figure 2. Species richness for the whole cactus family in Argentina (excluding the Pereskioid species). The texture filling the quadrats represent different number of species. Each square represents a 1°x1° quadrat.

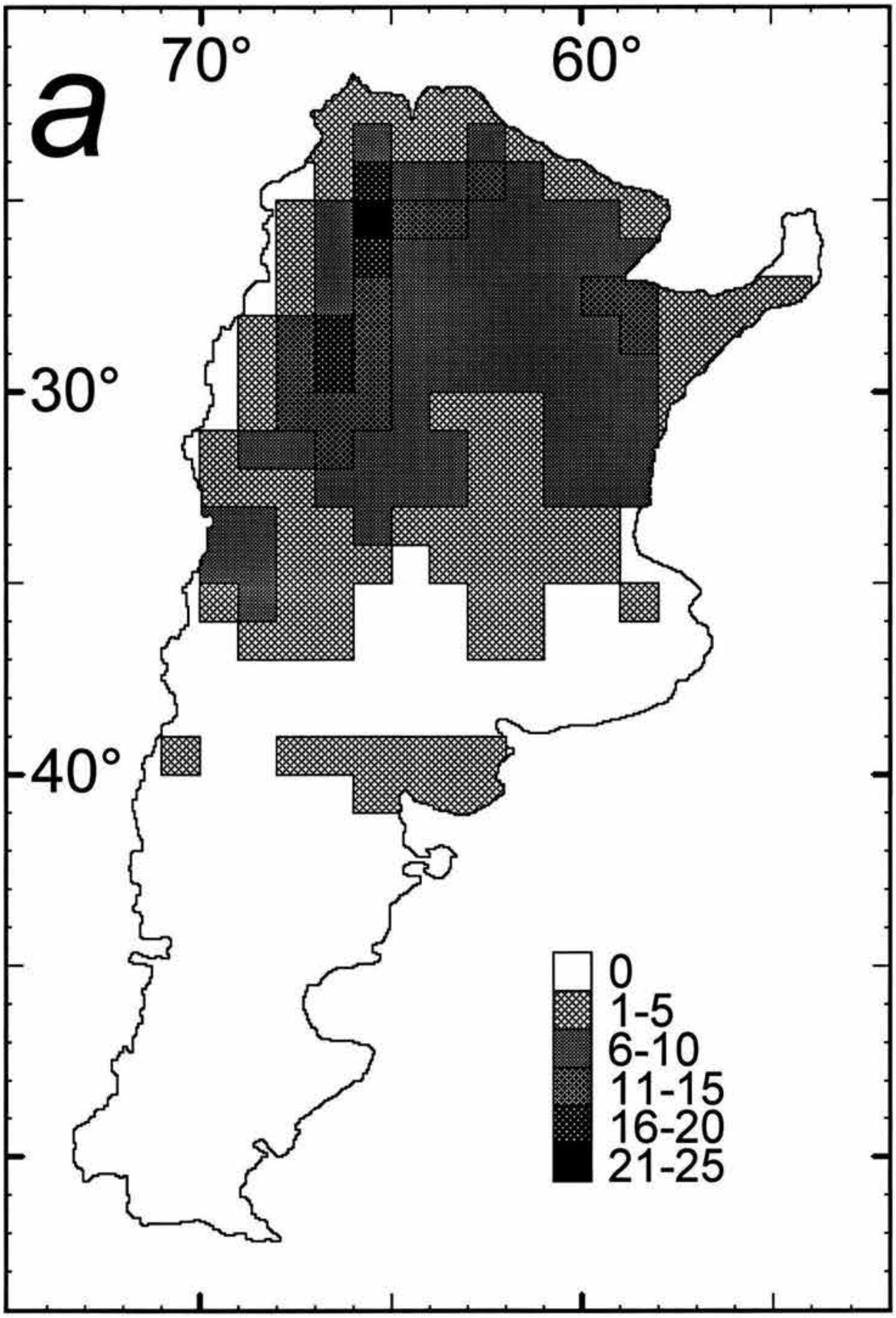

Figure 3. Species richness for columnar cacti

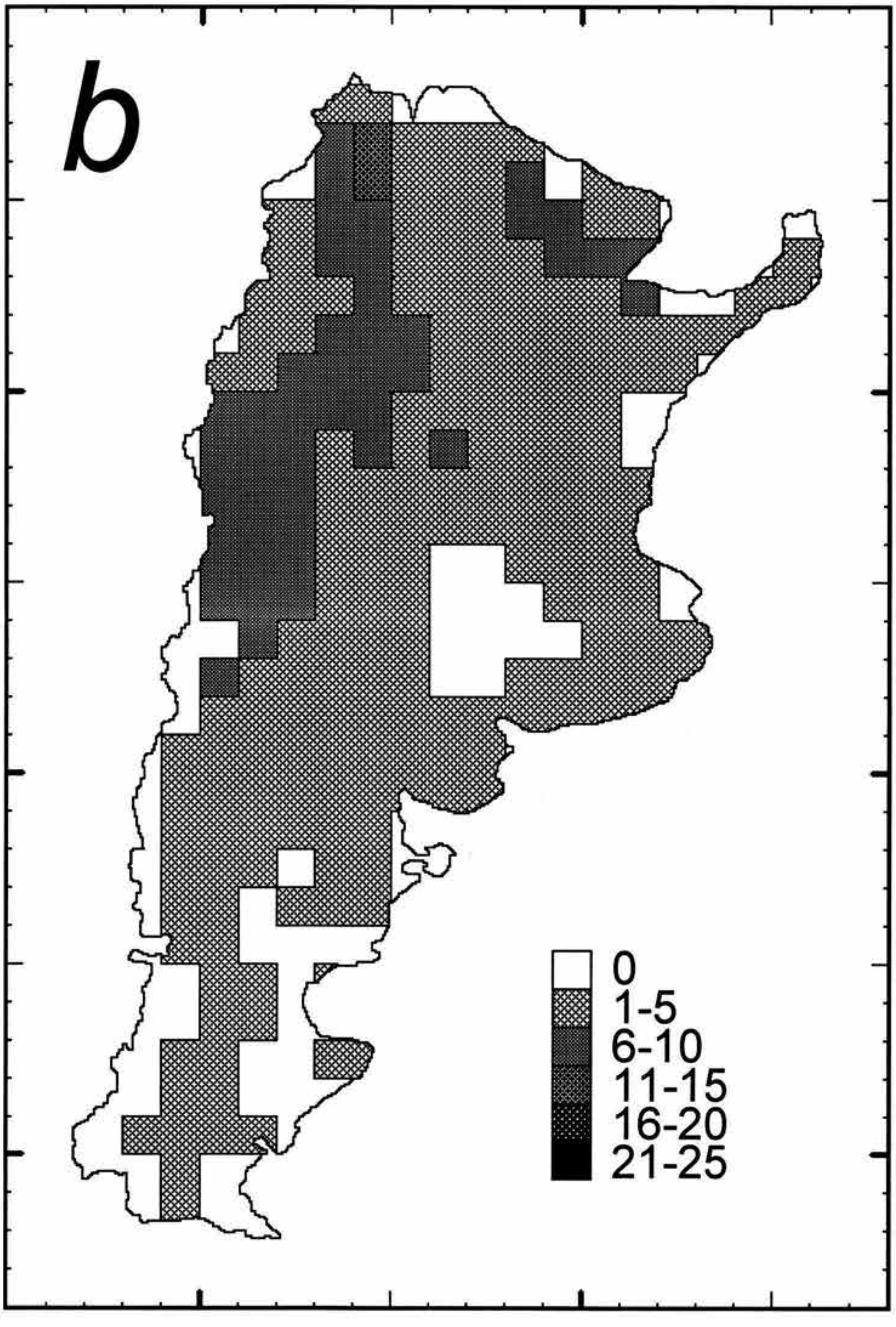

Figure 3. Species richness for opuntioid cacti

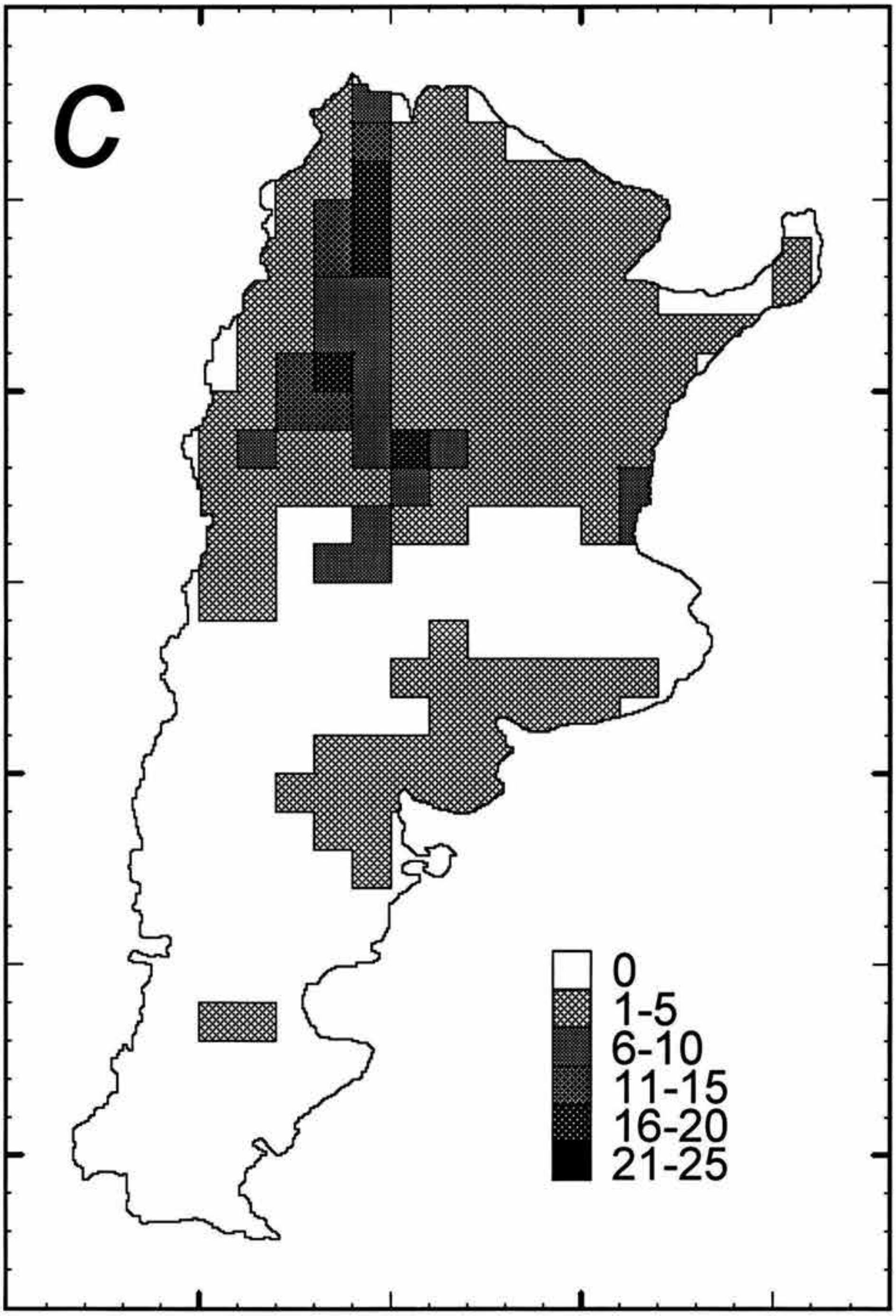

Figure 3. Species richness for globose cacti

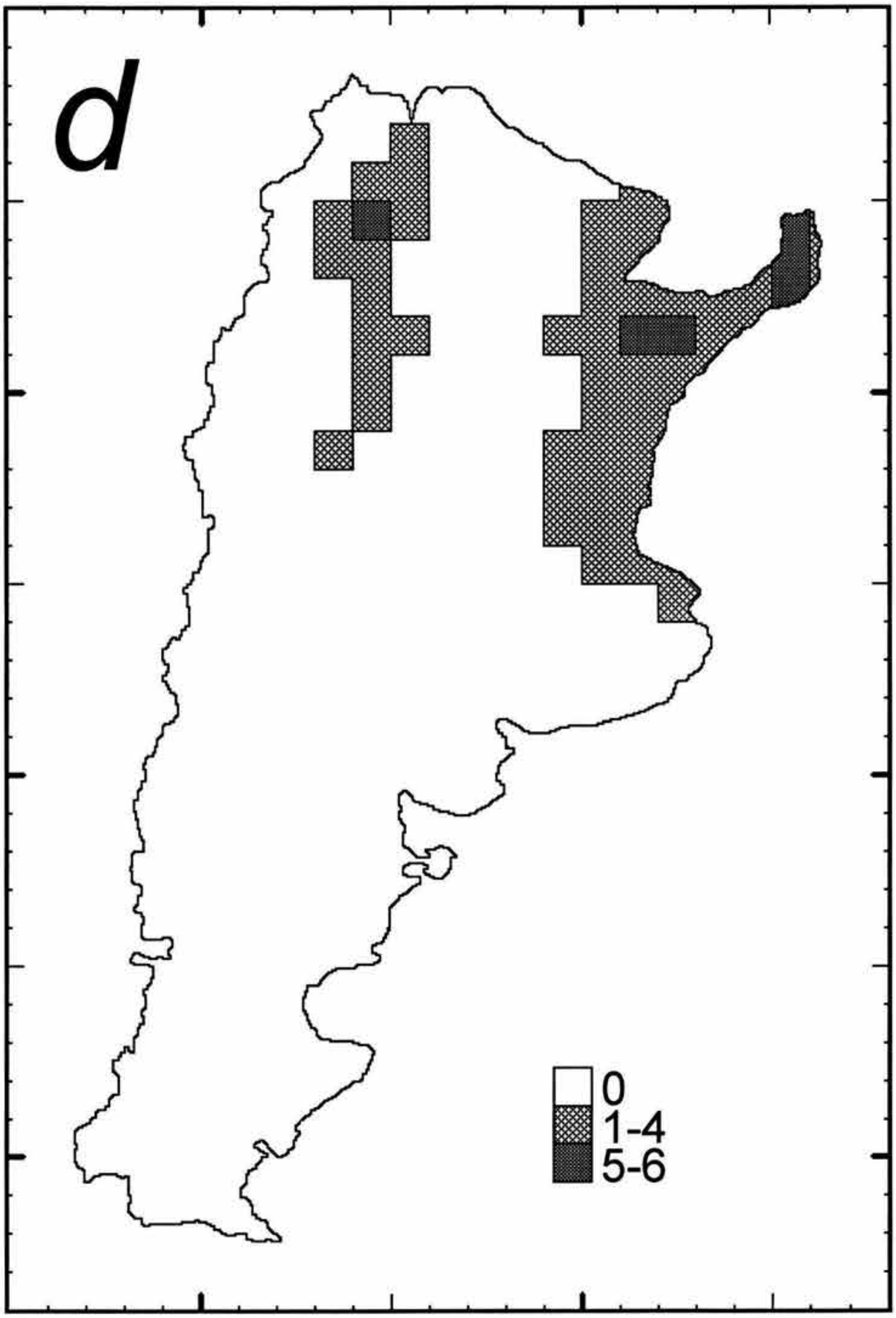

Figure 3. Species richness for epiphytic cacti

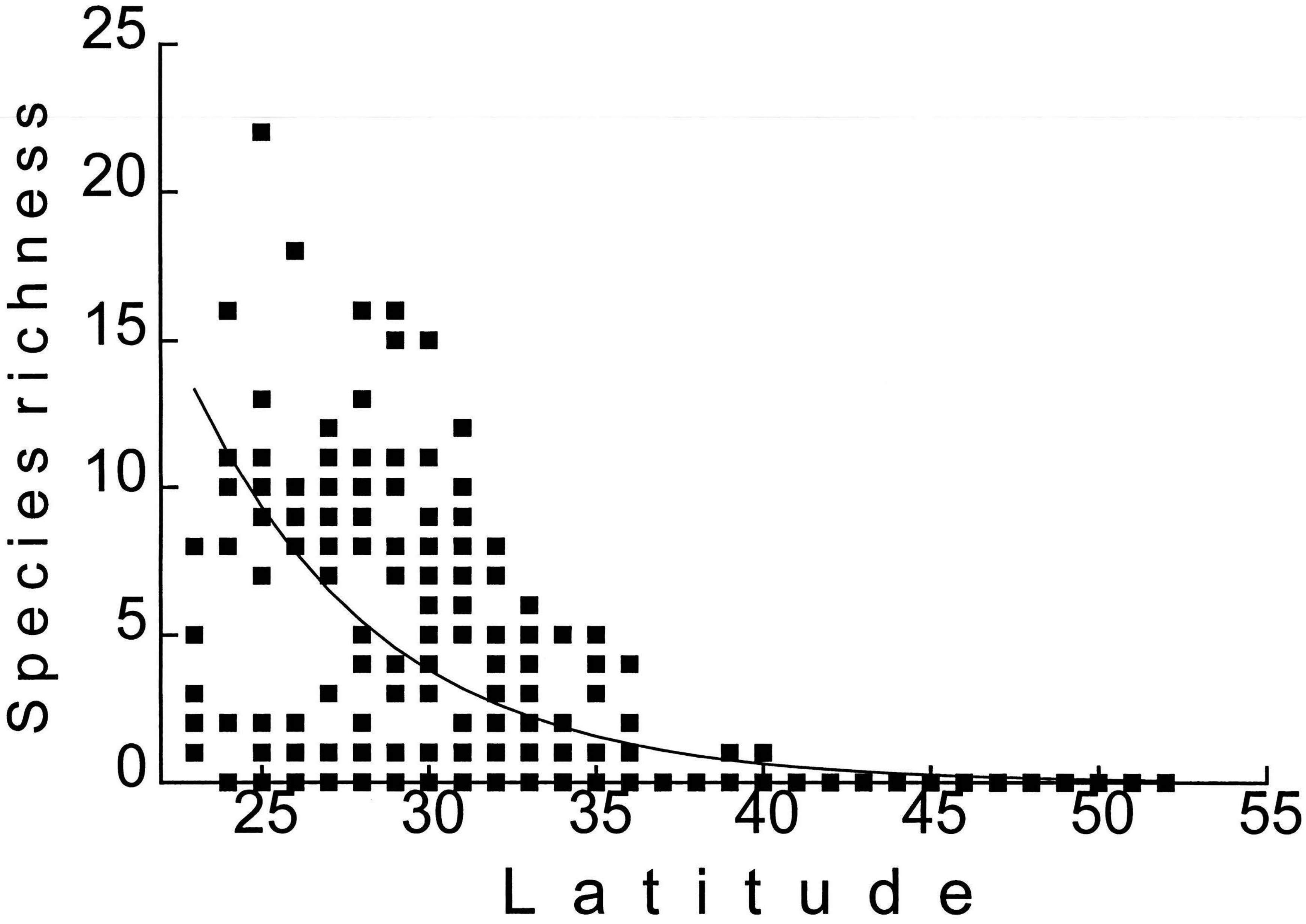

Figure 4. Relationship between species richness of the columnar growth-form and latitude

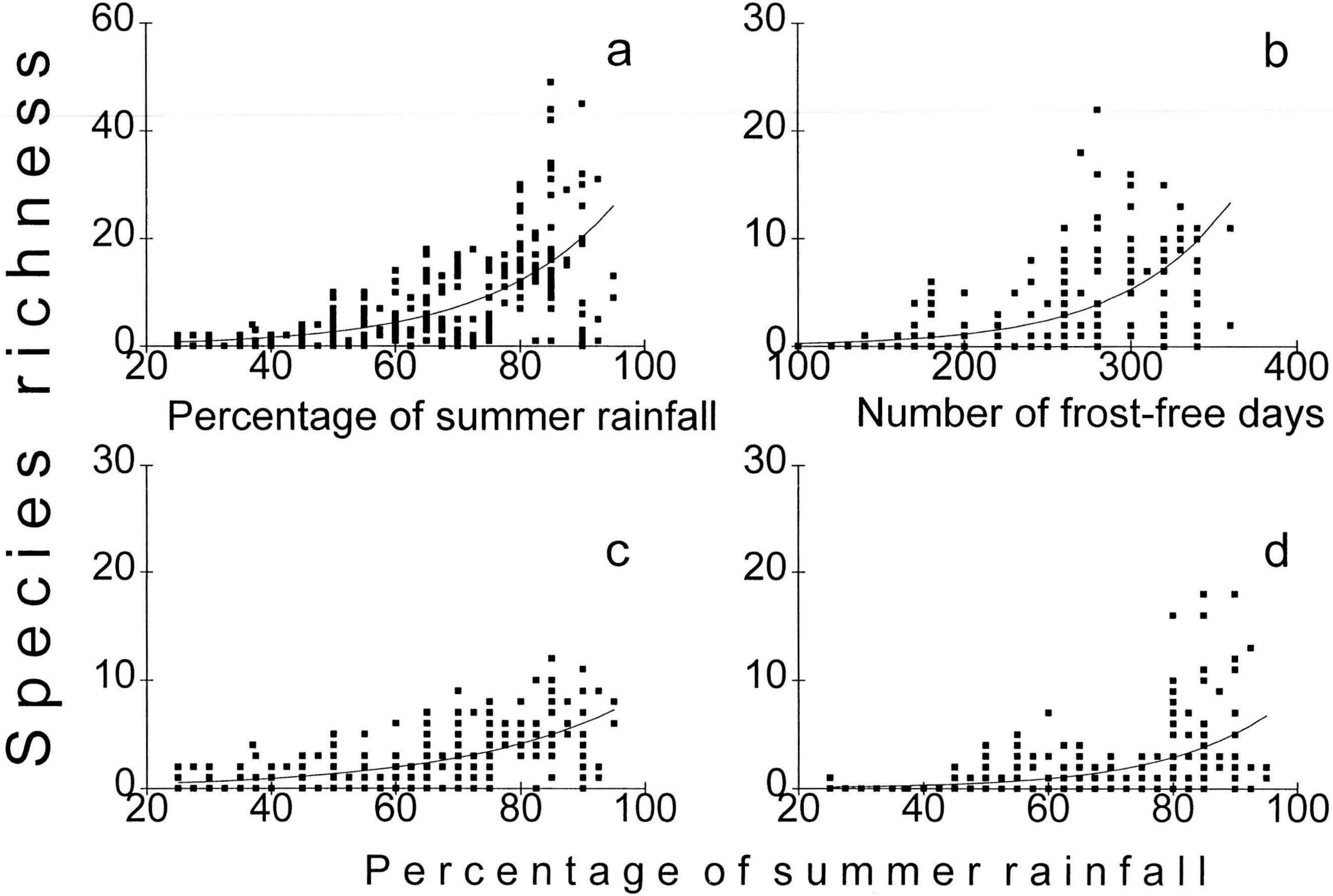

Figure 5. Relationship between the species richness of each growth-form and its best predictor: (*a*) whole family, (*b*) columnar species, (*c*) opuntioid species, and (*d*) globose species. The continuous line indicates the log-linear function predicted by the stepwise regression analysis.

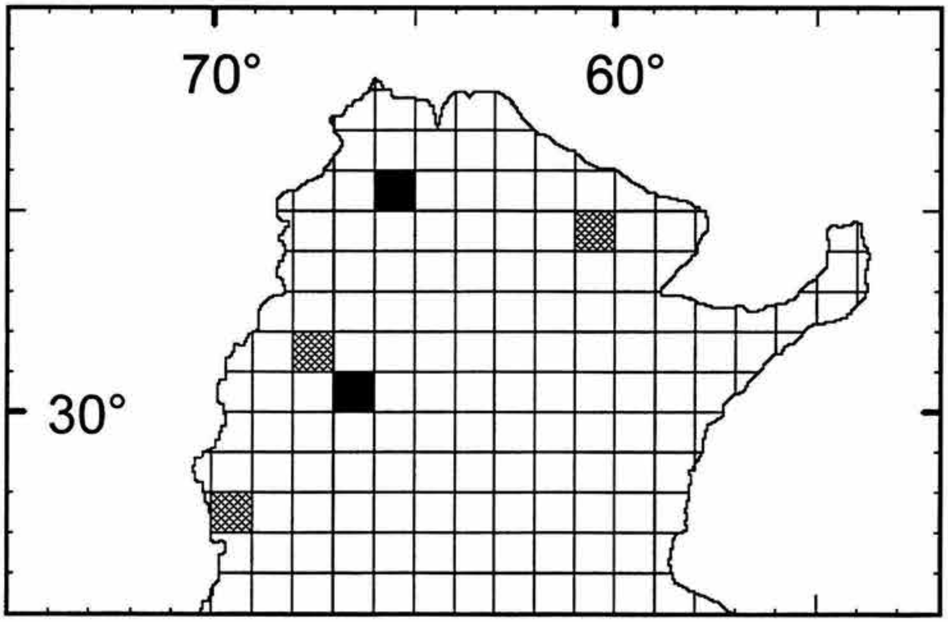

Figure 6. Standardised residuals of the log-linear regression models for the whole cactus group. The black squares correspond to significantly positive residuals (quadrats having significantly more species than predicted by the **Poisson** error distribution), the grey squares correspond to significantly negative residuals.

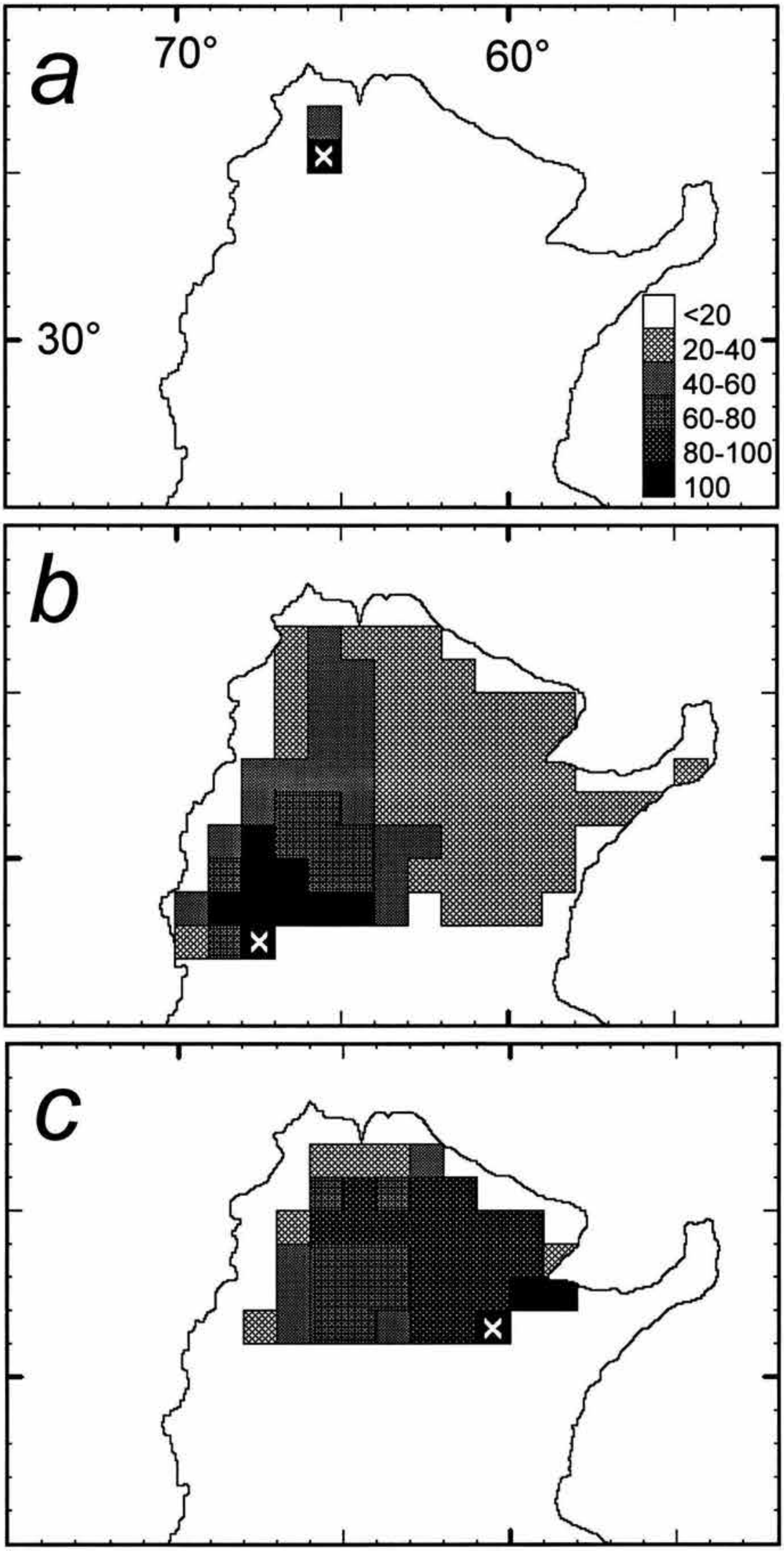

Figure 7. Floristic similarity in columnar cacti centred in three selected quadrats representing different Provinces: (*a*) Prepuna, (*b*) Monte and (*c*) Chaco. The shading represents the percentage of floristic similarity from a central point of comparison (base quadrat representing 100% of species), marked by a cross.

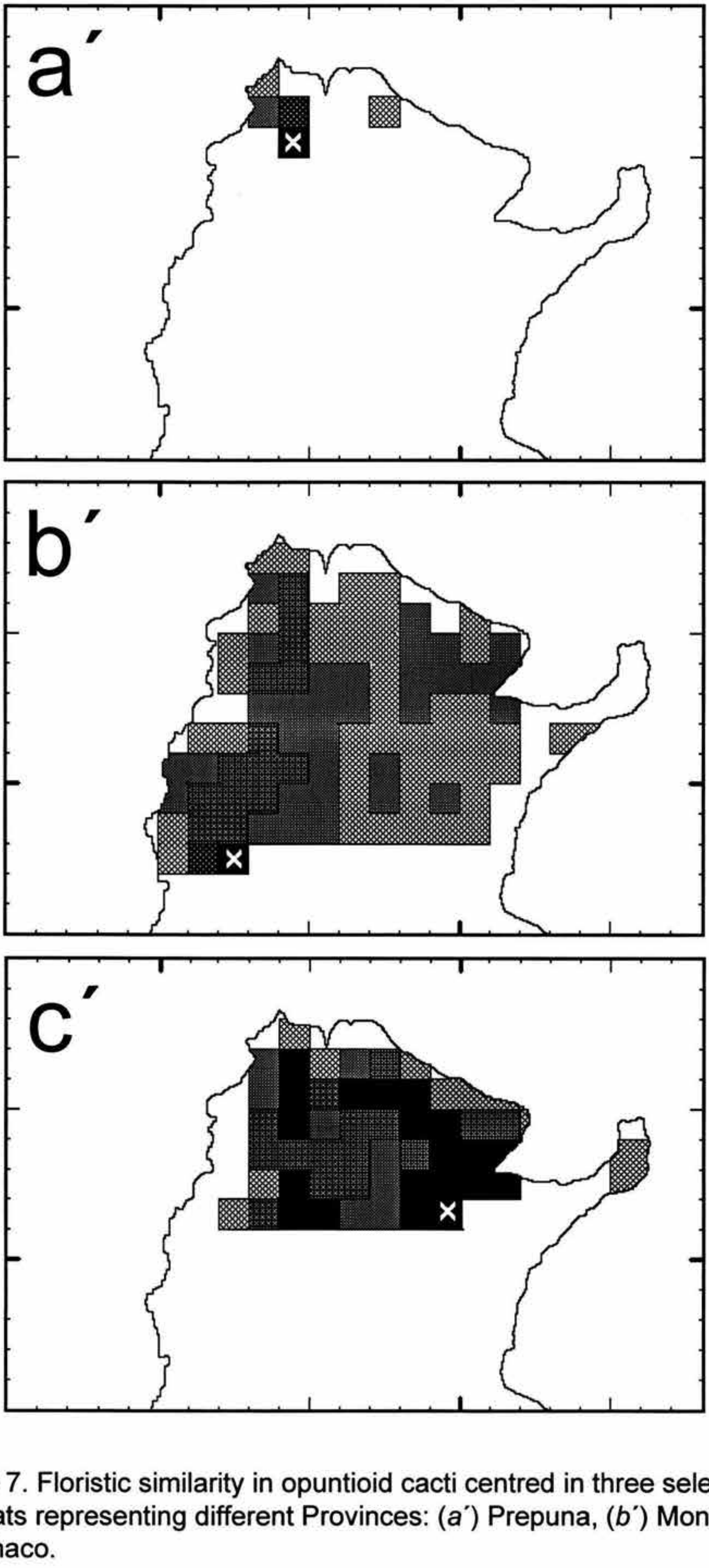

Figure 7. Floristic similarity in opuntioid cacti centred in three selected quadrats representing different Provinces: (*a´*) Prepuna, (*b´*) Monte, and (*c´*) Chaco.

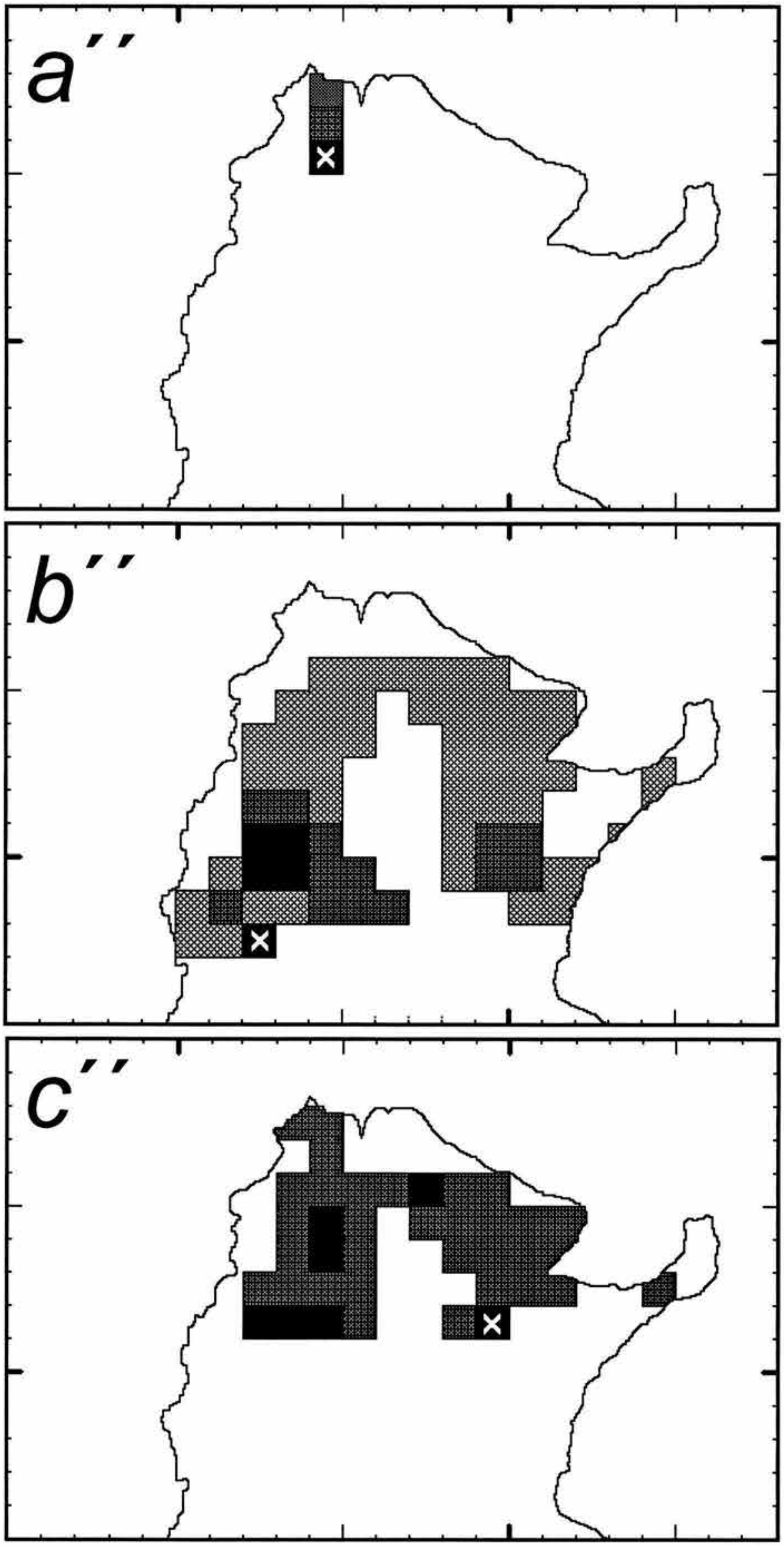

Figure 7. Floristic similarity in globose cacti centred in three selected quadrats, representing different Provinces: (*a´´*) Prepuna, (*b´´*) Monte and (*c´´*) Chaco.

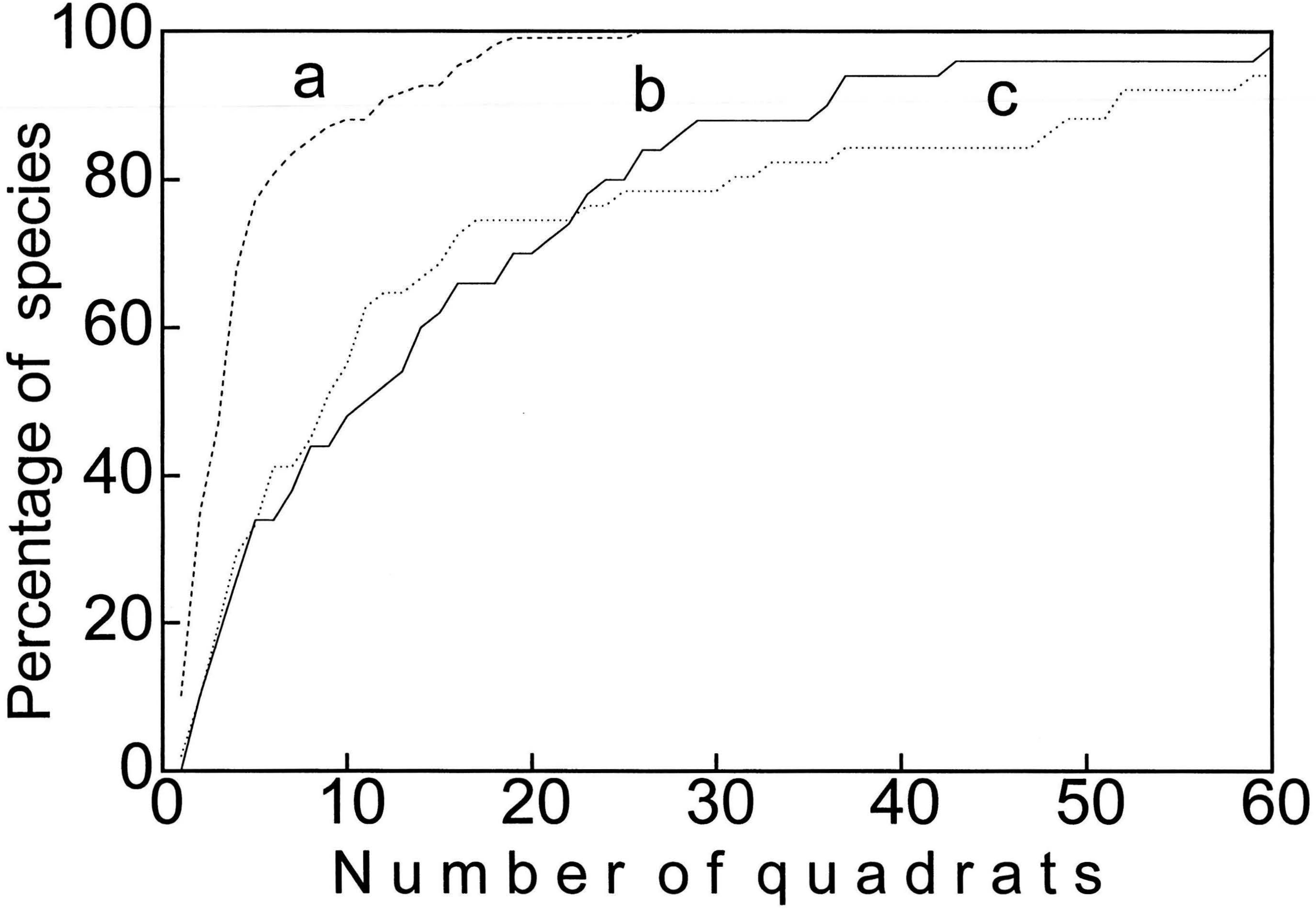

Figure 8. Geographic range of the different growth forms: (*a*) columnar; (*b*) opuntioid and (*c*) globose.

III. DIFFERENTIATION DIVERSITY PATTERNS OF ARGENTINE CACTI AND THEIR RELATIONSHIP TO ENVIRONMENTAL FACTORS.

Title: Differentiation diversity of Argentine cacti and its relationship to environmental factors.

Authors: Mourelle, Cristina and 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 (or species turnover) patterns of the three main cactus growth forms (columnar, opuntioid and globose) in 318 (1°x1°) squares covering Argentina. We analysed the degree of association between species turnover of each growth form with the spatial variation of a set of fifteen environmental variables.

Species turnover was estimated in two manners: (a) by calculating species turnover along latitudinal and longitudinal gradients, and (b) 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 chiefly associated with variations 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 variations 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 and 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 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 heterogenous areas, where large-scale transitions between biomes occur, have exceptionally high species turnover, and are important target areas for the conservation of biodiversity.

Keywords: differentiation diversity, dispersal capacity, environmental variables, growth forms, species turnover.

Introduction

The concept of biological diversity has been subdivided into two main components: (a) local richness or inventory diversity, and (b) differentiation diversity, also known as replacement or turnover between species assemblages. Both components apply on a wide range of scales. The first concept has been commonly labelled in the literature as α-diversity, when applied within a community or a homogenous habitat, but has also been defined as γ-diversity when applied at a landscape level, and as ε-diversity at a regional level (Whittaker 1977). The second component has received from different authors a large array of names, like (a) internal β-diversity or pattern diversity, (b) β-diversity, between-habitat diversity or between-site diversity, and (c) 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 in a local or regional scale, have long been major topics in the ecological and biogeographical literature, focusing on its 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, or 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, (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 aggregated within this category the short-stemmed barrel cacti. Globose cacti, the smallest growth form, are more or less spherical in shape. Opuntioid species are non-ribbed cacti 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 around 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 and 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 at 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, etc.), or a measure of their temporal variability (e.g. the standard deviation of mean monthly temperature, the standard deviation of total monthly precipitation, etc.). None of the studies mentioned above related species turnover with 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 which occur 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: (a) columnar cacti, including the shorter-stemmed barrel cacti, (b) globose cacti, and (c) opuntioid, with 50, 109 and 50 species respectively (a complete species list is given in Mourelle & Ezcurra 1996). All the analyses were done for each growth form separately. We excluded from our analysis the five pereskioid species and the fourteen 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 some ten species) were also excluded. The map of Argentina was divided into a grid of 318 cells of 1° × 1°. For each species we digitised into a data base the grid squares 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 some 9,000 km^2 in the southernmost latitudes with registered cactus species (an analysis of the potential sources of error introduced by units with variable area is presented in Mourelle & Ezcurra 1996).

Species richness and species turnover

In this study, species richness was defined as the local number of cactus species contained in a square of 1° × 1°. Differentiation diversity (species turnover) was calculated in two different manners: (a) by estimating turnover along geographical gradients following latitudinal or longitudinal transects one degree wide, and (b) 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 $\beta_w = k / \ln 2$, 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 $\log_2$ or "octaves" scale; 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 and Smith 1981). Similarities (S) were calculated using Sorensen's Coefficient of Community (Whittaker 1960, Whittaker 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 and Shmida 1984, Shmida and 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 takes only into consideration changes between adjacent squares, Wilson and Shmida's approach emphasises local species turnover and hence reflects more the effects of short-distance environmental heterogeneity, while Whittaker's measure emphasises species turnover along extensive distances and reflects more the effects of distributional amplitude of the species in the group.

For both methods, we estimated turnover rates along fifteen longitudinal transects (or less in some growth forms) and fifteen 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 Sorensen'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 Sorensen'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 that are present in the neighbouring square and absent in the central square, *l* is the number of species that 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 Wilson and Shmida's index 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 $0<n\leq8$ 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 into 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 by means of time-series analysis of long-term linear trends the relationship between species turnover in longitudinal transects and their latitudinal position; 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

Sixteen environmental variables were digitised for the whole country on a 1° × 1° scale. We used two geographic variables (latitude and longitude); eleven climatic variables (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 defficiency 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; the difference between the last two measures, and annual primary productivity calculated from Lieth's (1975) index of evapotranspiration), and three topographic variables aimed at estimating small-scale environmental heterogeneity as discussed in Palmer and Dixon (1990; we measured altitudinal range calculated as the difference between the maximum and the minimum altitude within a square; topographic variability calculated as the standard deviation of the altitude of nine points selected systematically within each square, and mean altitude calculated as the average of the nine within-square points; see also Mourelle & Ezcurra 1996).

To estimate the spatial heterogeneity of the climatic and topographic variables we calculated (a) the mean and the variance of each variable between the squares of the latitudinal and longitudinal transects described in the previous section, and (b) 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). Regressions were done 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 collection intensity

The number of species detected in a given area is a diminishing returns function of the number of herbarium specimens that have been collected (Soberón & Llorente 1993). Based on the properties of accumulation functions (Mourelle & Ezcurra 1996), we incorporated to our regression models the logarithm of the number of voucher specimens registered per square (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.

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 with the mean collection effort, or with its within-transect variation.

Longitudinal transects

In contrast with 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 on average 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 complex measure of environmental heterogeneity. As with the longitudinal transects, species turnover in latitudinal transects was not significantly related, for any growth form, with the mean collection effort, or 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 twelve 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, 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, like 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 occurred in plains with high topographic and climatic homogeneity, like 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) were 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) was also 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).

Discussion

Species turnover along transects

Differences in turnover rates between longitudinal and latitudinal transects were related with different variables, for the same group. Species turnover in latitudinal transects was mostly related with the mean values of some environmental variables within the transect, while in longitudinal transects it was always related to the between-squares variation of some 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 formed by 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 to increase 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 in several groups like birds (MacArthur 1965,1967), insects and the plants they feed on (Janzen & Schoener 1968), bryophytes (Wolf 1993) and mammals (Willig & Sandlin 1991), among others. The prediction, however, did not clearly hold for our cacti.

Species turnover in individual squares

No association was found between species richness and species turnover. In all growth forms, the squares with high species turnover tended to fall in areas where transitions between different biogeographic provinces occur, 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 NW, in the transition between the Pampas grasslands and the surrounding, more arid ecosystems. The opuntioid species 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 that 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 NW squares, a region occupied by a succession of 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 NW, 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 NW, 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-NW 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 causality should be concluded 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 hard 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 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 with this, in our data set species turnover 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 NW, 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 here presented have important implications for conservation biology. As a general rule, environmentally heterogeneous regions, together with regions where large-scale transitions between biomes occur, have 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.

Acknowledgements

The authors thank the enthusiastic support received from Roberto Kiesling and Omar Ferrari during C. Mourelle's travels in Argentina. This paper is part of the first author's doctoral research at UNAM, supported by a scholarship from the Noyes-Smith Sciences Foundation. The research received finantial support from the National Council of Science and Technology (CONACyT).

References

Barthlott, W. & Hunt, D. R. 1993. Cactaceae. In: Kubitzki, K. (ed.) *The families and genera of vascular plants,* pp. 161-197. Springer-Verlag, Berlin, Heidelberg.

Begon, M., Harper, J. L. & Townsend, C. R. 1990. *Ecology: individuals, populations and communities*. 2nd ed. Blackwell Scientific Publications, Boston.

Brown, J. H. 1981. Two decades of Homage to Santa Rosalia: Toward a general theory of diversity. *Am. Zool.* 21:877-888.

Brown, J. H. 1988. Species diversity. In: Myers, A. A. & Giller, P. S. (eds.) *Analytical Biogeography: An integrated approach to the study of animal and plant distribution,* pp. 57-89. Chapman and Hall, London.

Cody, M. L. 1975. Toward a theory of continental species diversities: Bird distributions over mediterranean habitat gradients. In: Cody, M. L. & Diamond, J. M. (eds.)

Ecology and evolution of communities, pp. 214-257. Harvard University Press, Cambridge, Mass.

Cody, M. L. 1986. Diversity, rarity, and conservation in mediterranean-climate regions. In: Soulé, M. E. (ed.) *Conservation biology: The science of scarcity and diversity*, pp. 123-152. Sinauer Associates, Sunderland, Mass.

Cody, M. L. 1993. Bird diversity components within and between habitats in Australia in Species diversity In: Ricklefs, R. E. & Schluter, D. (eds.) *Species diversity in ecological communities: Historical and geographical perspectives*, pp.147-158. The University of Chicago Press. Chicago and London.

Colwell, R. K. & Coddington, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc., London* 345:101-118

Cornell, H. V. & Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *J. Anim. Ecol.* 61:1-12.

Cowling, R. M., Gibbs Russell, G. E., Hoffman, M. T. & Hilton-Taylor, C. 1989. Patterns of plant species diversity in southern Africa. In: Huntley, B. J. (ed.) *Biotic diversity in southern Africa*, pp. 19-49. Oxford University Press, Cape Town.

Draper, N. R. & Smith, H. 1981. *Applied Regression Analysis*, 2nd ed. Wiley & Sons, New York, NY.

Figueira, J. E. C., Vasconcellos-Neto, J., Garcia, M. A. & Souza, A. L. T. D. 1994. Saurochory in *Melocactus violaceus* . *Biotropica* 26:295-301.

Gibson, A. C. & Nobel, P. S. 1986. *The Cactus Primer*. Harvard University Press, Cambridge, Massachusetts.

Harrison, S., Ross, S. J. & Lawton, J. H. 1992. β–diversity on geographic gradients in Britain. *J. of Anim. Ecol.* 61:151-158.

Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81-101.

Janzen, D. H. & Schoener, T. W. 1968. Difference in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49:96-110.

Janzen, D. H. 1986. Chihuahuan desert nopaleras: Defaunated big mammal vegetation. *Ann. Rev. Ecol. Syst.* 17:595-636

Kadmon, R. & Pulliam, H. R. 1993. Island Biogeography: Effect of geographical isolation on species composition. *Ecology* 74:977-981.

Lieth, H. 1975. Modeling the primary productivity of the world. In: Lieth, H. & Whittaker, R. H. (eds.) *Primary Productivity of the Biosphere*, pp.237-263. Springer Verlag, Berlin & New York.

McCullagh, P. & Nelder, J. A. 1989. *Generalized Linear Models*, 2nd. ed. Chapman and Hall, London.

MacArthur, R. H. 1965. Patterns of species diversity. *Biol. Rev.* 40:510-533.

MacArthur, R. H. 1969. Patterns of communities in the tropics. *Biol. J. Linn. Soc.* 1:19-30.

Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, N.J.

Meave, J. A. 1991. Maintenance of tropical rain forest plant diversity in riparian forests of tropical savannas. Ph.D. Thesis. York University. Toronto. Ontario. Canada.

Mourelle, C. & Ezcurra, E. 1996. Species richness of Argentine cacti: A test of some biogeographic hypotheses. *J. Veg. Sci.* 7(5):667-680.

Nobel, P. S. 1981. Influence of freezing temperatures on a cactus, *Coryphanta vivipara. Oecologia* 48:194-198.

Nobel, P. S. 1982. Low temperature tolerance and cold hardening of cacti. *Ecology* 63:1650-1656.

Palmer, M. W. and P. M. Dixon. 1990. Small-scale environmental heterogeneity and the analysis of species distributions along gradients. *J. Veg. Sci.* 1:57-65.

Payne, C. D. 1986. The Glim System Release 3.77 Manual. Numerical Algorithms Group, Oxford.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: A review of concepts. *American Naturalist* 100:33-45.

Pielou, E. C. 1975. Ecological Diversity. John Wiley & Sons, N.Y.

Pielou, E. C. 1979. Biogeography, Wiley & Sons, NY.

Retuerto, R. & Carballeira, A. 1990. Phytoecological importance, mutual redundancy and phytological treshold values of certain climatic factors. *Vegetatio* 90:47-62

Rhode, K. 1992. Latitudinal gradients in species diversity: The search for a primary cause. *Oikos* 65:514-527.

Ricklefs, R. E. and Schluter, D. 1993. Species diversity: Regional and historical influences. In: Ricklefs, R. E. & Schluter, D. (eds.) *Species diversity in ecological communities: Historical and geographical perspectives*, pp.350-363. The University of Chicago Press. Chicago and London.

Rosenzweig, M. L. & Abramsky, Z. 1993. How are diversity and productivity related? In: Ricklefs, R. E. & Schluter, D. (eds.) *Species diversity in ecological communities: Historical and geographical perspectives*, pp.52-65. The University of Chicago Press. Chicago and London.

Routledge, R. D. 1977. On Whittaker´s component of diversity. *Ecology* 58:1120-1127.

Sánchez, O. & López, G. 1988. A theoretical analysis of some indices of similarity as applied to biogeography. *Folia Entomológica Mexicana* 75:119-145.

Scheiner, S. M. & Rey-Benayas, J. M. 1994. Global patterns of plant diversity. *Evolutionary Ecology* 8:1-18.

Schluter, D. & Ricklefs, R. E. 1993. Species diversity, an introduction to the problem. In: Ricklefs, R. & Schluter, D.(eds.) *Species diversity in ecological communities: Historical and geographical perspectives,* pp 1-10. The University of Chicago Press. Chicago and London.

Schmida, A. & Wilson, M. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.

Soberón, J. & Llorente, J. 1993. The use of species accumulation functions for the prediction of species richness. *Conserv. Biol.* 7:480-488.

Steenbergh, W. F. & Lowe, C. H. 1977. Ecology of the saguaro.II: Reproduction, germination, establishment, growth, and survival of the young plant. National Park Service Scientific Monograph Series, no. 8, U.S. GPO, Washington, D.C.

Tueller, P. T., Tausch, R. J. & Bostick, V. 1991. Species and plant community distribution in a Mojave-Great Basin desert transition. *Vegetatio* 92:133-150.

Valido, A. & Nogales, M. 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary islands. *Oikos* 70:403-411.

Valiente-Banuet, A., Arizmendi, M., Rojas-Martínez, A. & Domínguez-Canseco, L. 1996. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. *Journal of Tropical Ecology* 12:103-119.

Vargas-Mendoza, M. C. & Gonzalez-Espinosa, M. 1992. Habitat heterogeneity and seed dispersal of *Opuntia streptacantha* (Cactaceae) in nopaleras of central Mexico. *Southwestern Naturalist* 37:379-385

Westoby, M. 1985. Two main relationships among the components of species richness. *Proc. Ecol. Soc. Aust.* 14:103-107

Whittaker, R. M. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279-338.

Whittaker, R. M. 1972. Evolution and measurement of species diversity. *Taxon* 21:213-251.

Whittaker, R. M. 1977. Evolution of species diversity in land communities. *Evol. Biol.* 10:1-67.

Wilson, M. & Mohler, C. L. 1983. Measuring compositional change along gradients. *Vegetatio* 54:129-141.

Wilson, M. & Schmida, A. 1984. Measuring β diversity with presence-absence data. *Journal of Ecology* 72:1055-1064.

Willig, M. R. & Sandlin , E. A. 1991. Gradients of species density and species turnover in New World bats: A comparison of quadrats and band methodologies. In: Mares,

M. A. & Shmidly, D. J. *Latin American Mammalogy: History, Biodiversity and Conservation.* University of Oklahoma Press.

Wolf, J. H. D. 1993. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Ann. Missouri Bot. Gard.* 80:928-960

Yee, T. W. & Mitchell, N. D. 1991. Generalized additive models in plant ecology. *J. Veg. Sci.* 2:587-602.

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

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 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	.33	+	0.04
	β_t	Variance of mean annual temperature	.18	+	0.15
Opuntioid	β_w	Variance of mean altitude	.18	+	0.15
	β_t	Variance of mean altitude	.49	+	0.008
Globose	β_w	Variance of mean annual water deficiency	.59	+	0.004
	β_t	Variance of mean altitude	.67	+	0.003

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 in longitudinal transects		Longitudinal trend in 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

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 of mean annual temperature	0.63	+	<0.001
	Variation of collection effort	0.08	+	0.01
Opuntioid	Mean annual temperature	0.47	-	<0.001
	Variation of mean annual precipitation	0.16	+	0.004
	Variation of collection effort	0.03	+	0.04
Globose	Mean percentage of summer rainfall	0.65	+	<0.001
	Variation of collection effort	0.05	+	0.05

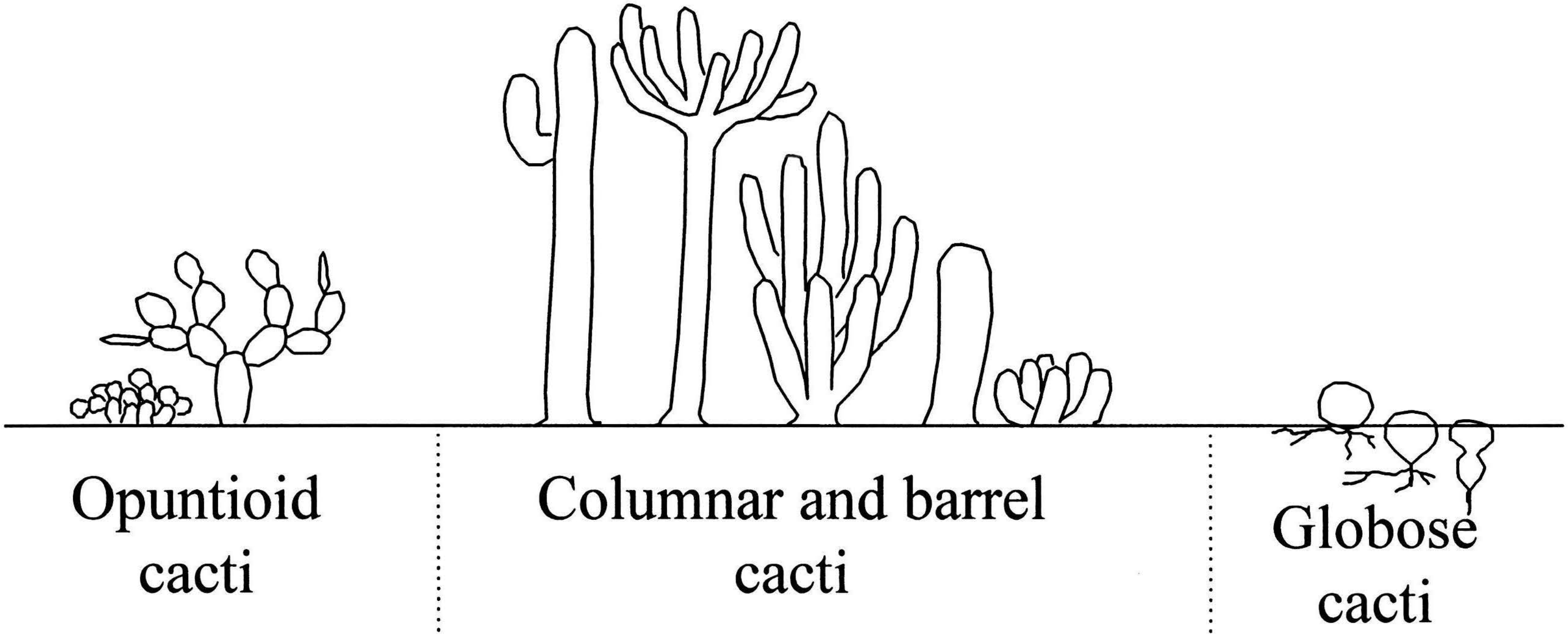

Figure 1. Schematic representation of the three cactus growth forms studied. The columnar group also includes **barrel cacti**, which are short-stemmed but not globose. Columnar and globose growth forms belong to the subfamily Cactoideae; most of the columnar genera belong to the tribes Trichocereeae and Cereeae while the globose genera belong mostly to the tribe Notocacteae. All opuntioid species belong to the subfamily Opuntioideae (Mourelle & Ezcurra 1996).

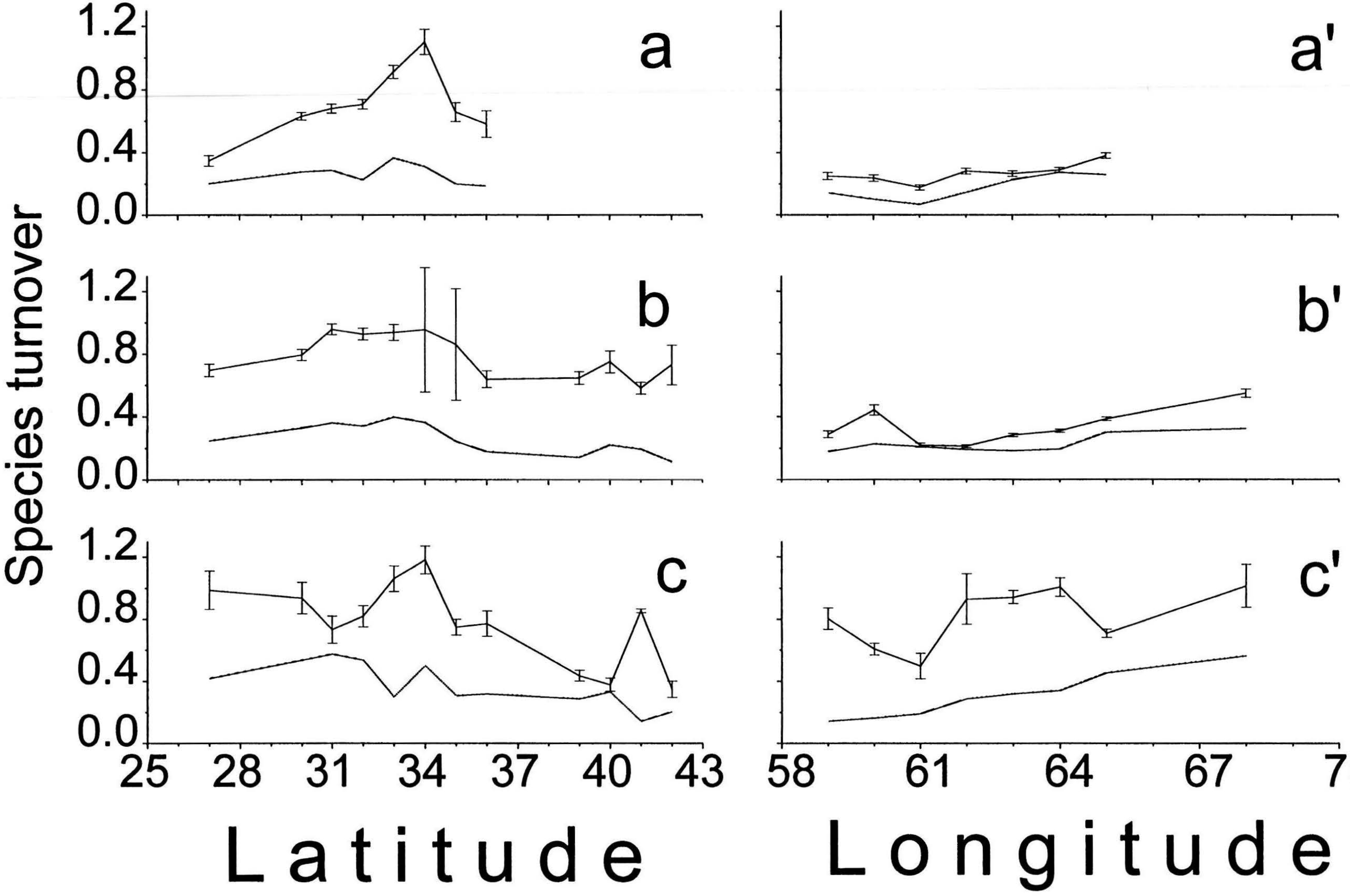

Figure 2. Turnover rates in longitudinal transects plotted against latitude (*a, b, c*) and turnover rates in latitudinal transects plotted against longitude (*a´, b´, c´*) for columnar species (*a, a´*); opuntioid species (*b, b´*) and globose species (*c, c´*). In all cases, β_w is plotted in a continuous line and β_t in broken line (see Table 3).

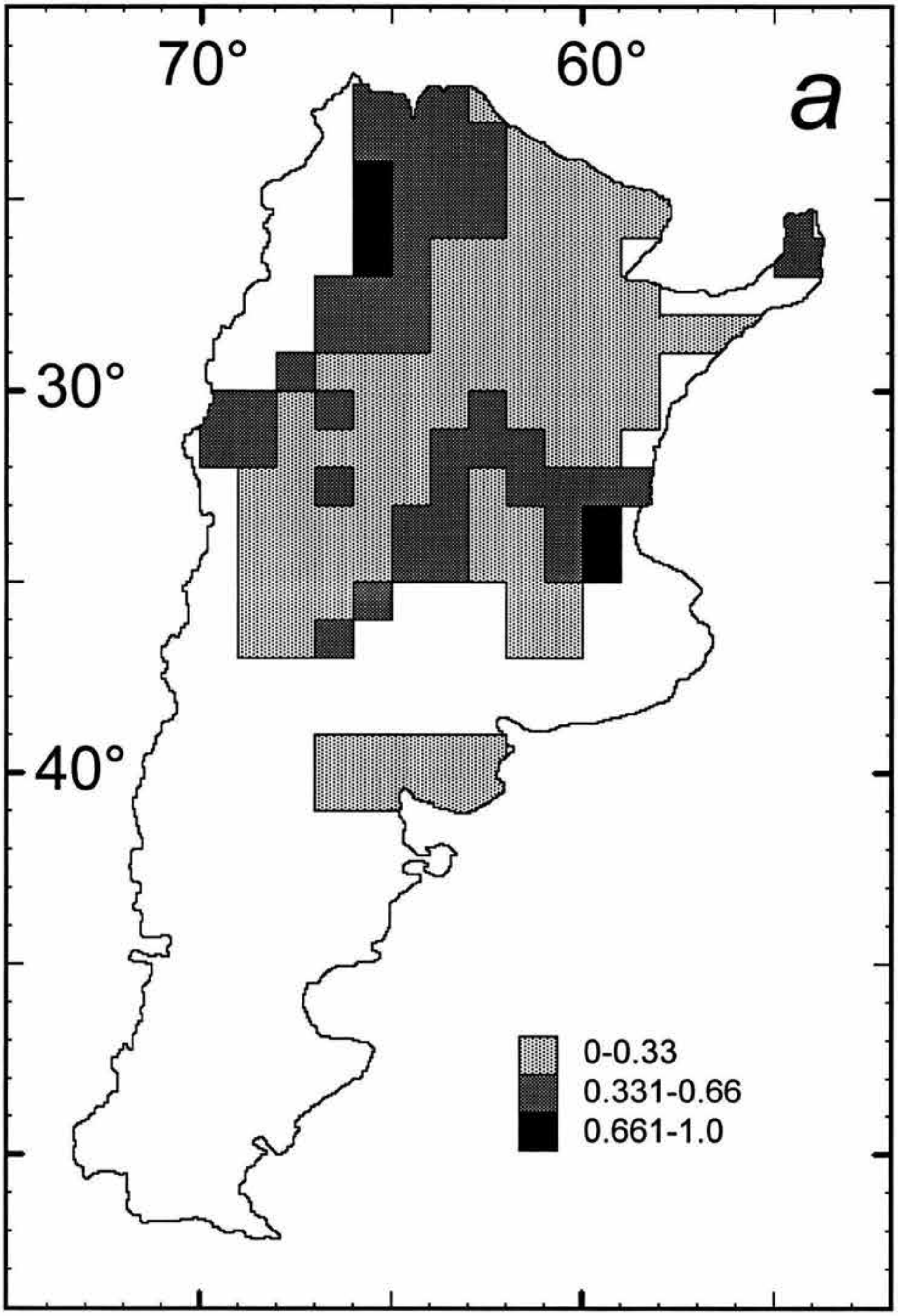

Figure 3. Map of Argentina showing areas of low, intermediate and high beta diversity in individual quadrats for columnar species

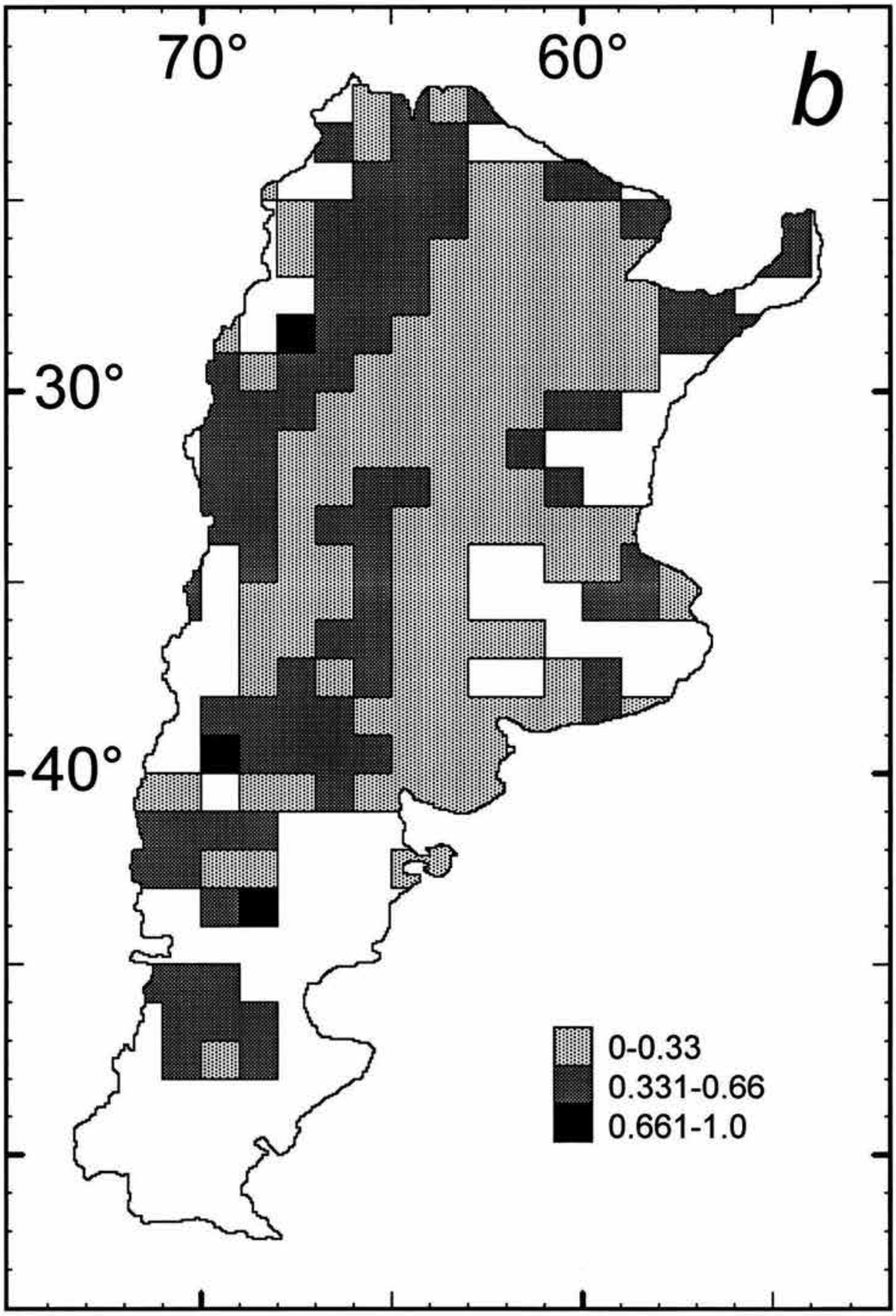

Figure 3. Map of Argentina showing areas of low, intermediate and high beta diversity in individual quadrats for opuntioid cacti.

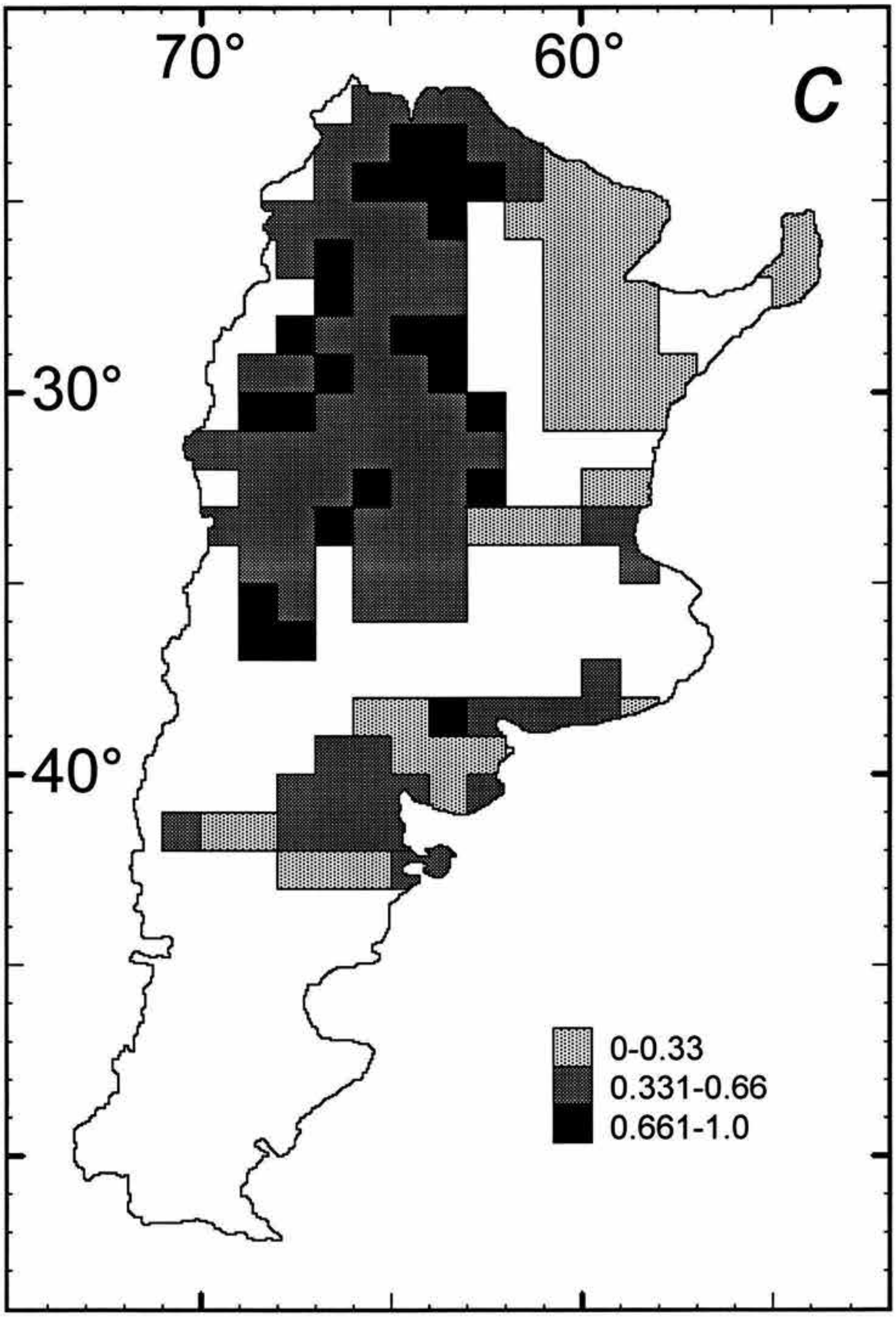

Figure 3. Map of Argentina showing areas of low, intermediate an high beta diversity in individual quadrats for globose cacti.

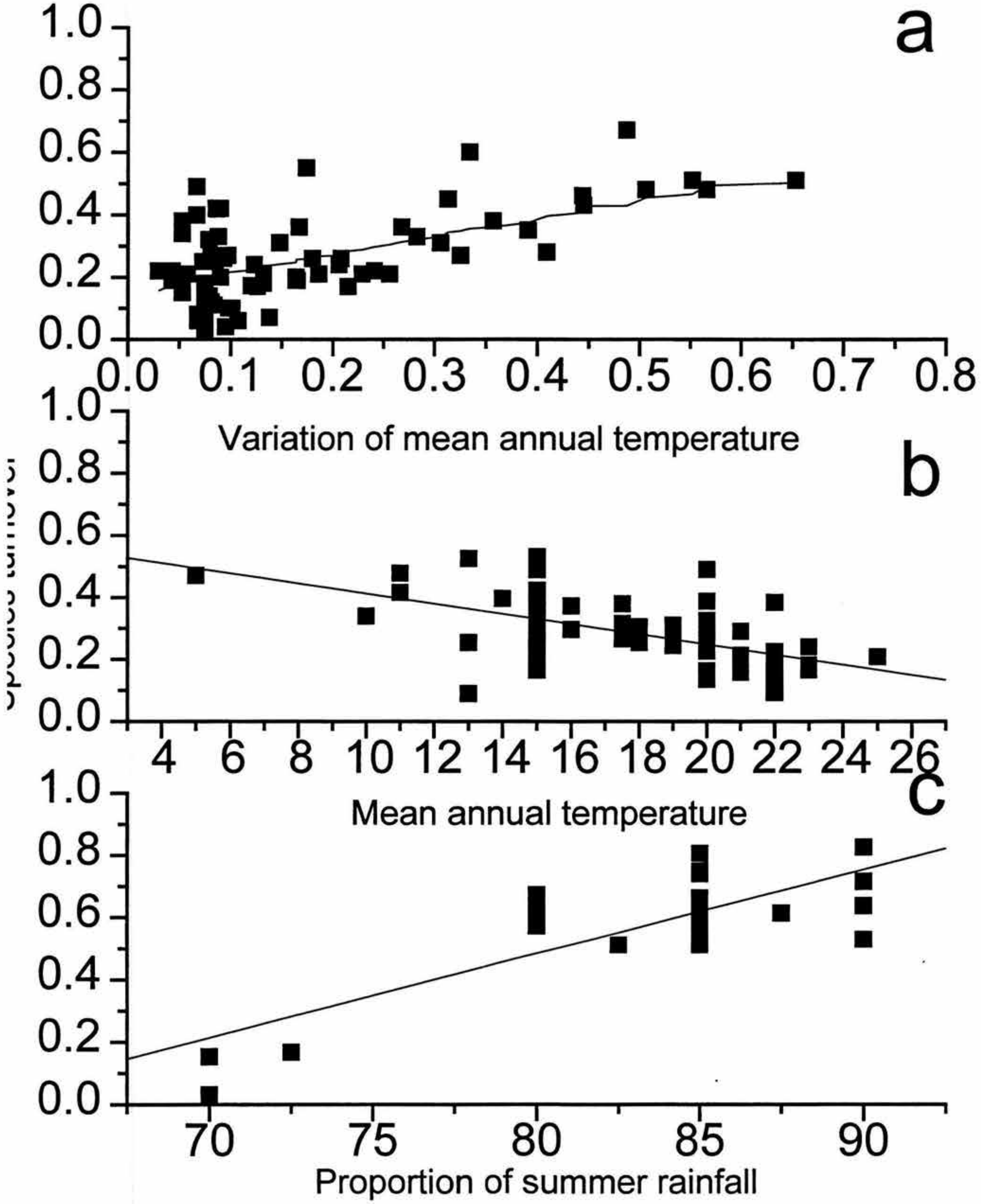

Figure 4. Regressions between quadrat β-diversity and their best predictor for (*a*) columnar, (*b*) opuntioid and (*c*) globose species (see also Table 4)

IV. RAPOPORT´S RULE: A COMPARATIVE ANALYSIS BETWEEN SOUTH AND NORTH AMERICAN COLUMNAR CACTI.

Rapoport´s rule: a comparative analysis between south and north american columnar cacti.

The geographic range of species belonging to many taxonomic groups tends to decrease towards the tropics. This latitudinal pattern has been well documented over the past thirty years, and several explanations have been put forth, including environmental history (Rapoport 1975, 1982), competition (Rapoport 1975, 1982; Rosenzweig 1975; Anderson and Koopman 1981), local climate and species environmental tolerances (Stevens 1989), the “mass effect” (the establishment of species in sites where they cannot self-maintain, Stevens 1989, 1992), the species dispersion capabilities and their ecophysiological properties (Stevens 1989; France 1992), and, lastly, sampling bias (Colwell et al. 1994). The empirical biogeographic rule that states that an equatorward increase in species richness is often paralleled by a decrease in the mean latitudinal range of species was named "Rapoport´s rule" by Stevens (1989), after the Argentine biogeographer Eduardo Rapoport, who first made reference to this phenomenon (see Rapoport 1975, 1982).

The idea that geographical ranges increase from the tropics towards the poles, has received close attention over the last six years (Stevens 1989; Pagel et al. 1991; France 1992; Rhode 1992; Rhode et al. 1993; Colwell et al. 1994; Ruggiero 1994; Smith et al. 1994). Although Rapoport's rule has been tested on several groups in different regions, most of these studies have focused mainly on North America and on animals (almost exclusively on mammals). A comparative study addressing the relationship between mean latitude and latitudinal range for one group of species in more than one continent (e.g., South and North America) has not been done.

The purpose of this note is to examine the occurrence of Rapoport's rule for species of columnar cacti along tropical-subtropical gradients in both South and North America. We chose this group of plants because they have been well collected in both continents as a result of their conspicuousness in the field. Our objective was to investigate if the rule did indeed apply in the same manner in two different continents, or if, alternatively, biogeographic differences between continents could introduce differences in the way the rule is expressed.

METHODS

Two data bases, one for the 60 species of columnar cacti that occur in Mexico and the other for the 50 columnar species that occur in Argentina, were used (for the list of species, see the Appendix). The first data base contained 2200 records (i.e., geo-referenced localities) of Mexican species, some of which may range into border countries (USA and Guatemala). The second data base included 1050 geo-referenced records of Argentine species, also ranging in some cases into border countries (Bolivia, Brazil, Chile, Peru, Paraguay, and Uruguay). All records came from herbarium labels or published references, and they were digitized into 1°×1° maps of North and South America.

The latitudinal range of each species was calculated as the difference between the highest latitudinal boundary of the quadrat farthest from the Equator, minus the lowest latitudinal boundary of the quadrat nearest to the Equator. In a similar manner, we calculated for each species its longitudinal range by substracting the lowest longitudinal boundary of the quadrat nearest to the Greenwich Meridian from the highest longitudinal boundary of the quadrat farthest from the Meridian. We also calculated the area occupied by each species, as the sum of the areas of each quadrat where the species was found to occur. Finally, the mean latitude of each species was calculated as the average of the latitudes of the central point of all the quadrats where the species was recorded. Thus, for both Mexican and Argentine columnar cacti, the original data base was summarized into a new data base where each species was represented by (a) its mean latitude, (b) its latitudinal range, (c) its longitudinal range, and (d) its area of distribution.

This data base was not apt for regression analysis, as the dispersion of the points, taking mean latitude as the independent variable and any of the other three variables as the dependent one, failed to conform to the standard criteria of homoscedasticity (homogeneity of variances) that are required for valid regression tests (Fig. 1). To obtain a set of points that conformed to the required statistical criteria, we first sorted all the species by their mean latitude, both for Mexico and Argentina. We then merged the species in groups of five, starting from the five most tropical species. For each group, we calculated the mean latitude of the group as the average of the five mean latitudes. Similarly, we calculated the mean latitudinal range, the mean longitudinal range, and the mean distribution area of each group. Finally, we included in the new data base the standard deviation of these values. Thus, the Mexican data base was reduced from 60 species to twelve mean data points, and the Argentine data base was reduced from 50 species to ten data points. The data points obtained with this method are truly independent, and avoid the statistical problem of non-independence criticized by Rhode (1993) on Steven's original method.

With these mean values we did a series of regression analyses taking always the mean latitude of each group of five species as the independent variable, and the mean latitudinal and longitudinal ranges, the mean distribution area, and the standard deviations of these values, as the dependent variables. We also included as independent variables the mean continental width, and the habitat heterogeneity that corresponded to each mean latitude. The mean continental width was calculated by measuring, for each species, the nearest distances from the species center of distribution to the Atlantic and to the Pacific Oceans, adding these two distances and then averaging the resulting value for each group of five species. We used a map of scale 1:400.000 for North America and of scale 1:800.000 for South America. Habitat heterogeneity was estimated in two different ways: (a) by counting the total number of phytogeographic units or provinces (to which we shall refer also as habitats) intersected by a linear transect at each mean latitude (if the same unit was found several times along a transect, it was counted each time it was found), and (b) by counting the total number of distinct vegetational units (i.e., without repetitions). For South America we used Cabrera's (1980) map of biogeographic provinces, and for Mexico we used Rzedowski's (1990) phytogeographic map, supplemented by Aldrich (1963) for the USA and by Loftas (1972) for Central America.

Finally, we digitized the number of columnar cactus species in each quadrat of the 1°×1° grid. In order to test whether a latitudinal trend in species richness existed in both North and South America, these species-richness values were regressed against quadrat latitude. For this purpose, log-linear models were used as species richness values are frequency counts (Crawley 1993; see also Mourelle and Ezcurra in press).

RESULTS

In Mexico, the mean latitudinal range was significantly correlated with mean latitude (r = 0.91, P = 0.00004; fig 1A) and with mean continental width (r = 0.57, P = 0.05). Additionally, both the mean distribution area of the species and the mean longitudinal range were also significantly correlated with latitude and continental width (r = 0.89, P = 0.0001, and r = 0.87, P = 0.0002 for distribution area against latitude and continental width, respectively; and r = 0.60, P = 0.04, and r = 0.63, P = 0.03 for longitudinal range against the same variables).

In contrast, the Argentine species did not show a significant linear association between mean latitudinal range and mean latitude (r = 0.38, P = 0.28; fig. 1B) or between latitudinal range and any other predictor. In a similar manner, the mean distributional areas and the mean longitudinal ranges were uncorrelated with the possible predictors.

In both hemispheres, however, the variation of the latitudinal ranges tended to decreased significantly towards the Equator (r = 0.80, P = 0.003 for Mexico, r = 0.68, P = 0.03 for Argentina; fig. 2). In Mexico, an outlying point of low variation in latitudinal ranges was found at mean latitude 28°24´. This point corresponds to five wide-ranging species (*Pachycereus schottii*, *Bergerocactus emoryi*, *Carnegia gigantea*, *Stenocereus gummosus*, *Stenocereus thurberii*) of the northern Sonoran Desert in Mexico and Arizona, a region where there are no microendemisms. Solely because of this point, the number of habitats was also a significant predictor of variation in latitudinal range in the Mexican columnar cacti. If the point is removed, however, latitude becomes the best predictor of the variation in latitudinal range. That is, at higher latitudes, species with wide ranges tend to coexist in both continents with species with restricted ranges or microendemisms. In Mexico, a similar trend was found for the standard deviation of the distributional areas, which were significantly correlated with latitude ($r = 0.62$, $P = 0.03$). In Argentina, the variation of the distributional areas was uncorrelated with latitude.

Finally, in both continents a significant inverse relationship was found between species-richness and latitude ($r^2 = 0.20$, $P < 0.0001$ for Mexico, and $r^2 = 0.54$, $P < 0.0001$ for Argentina). In both continents species richness decreased with increasing latitude (fig. 3).

DISCUSSION

In Mexico, the mean latitudinal ranges of the species were positively correlated with mean latitude, confirming Rapoport's rule. This, however, did not occur in Argentina. Additionally, both in Mexico and in Argentina the variation in the latitudinal ranges increased significantly with latitude, a fact that suggests that wide-ranging species should be more common at temperate latitudes. From this point of view, the data set of Argentine columnar cacti partially supports Rapoport´s rule, in the sense that it shows that the widest ranging species should be found at higher latitudes.

Some clues explaining this contrasting behaviour can be found in Rapoport (1975). He argues that North America is wider at temperate latitudes, and tends to become narrower towards the tropics. South America, in contrast, follows an opposite trend: continental width increases towards the Equator (fig. 4). Rapoport suggested that an alternative explanation of the decreasing ranges towards the tropics could lie in the shape of the continent, as a factor restricting habitat width (Maurer 1994). In Mexico, continental width and latitude increase together. This means that, if there is a trend for species ranges to increase towards the temperate regions, this trend will be enhanced even further by the combined effect of continental width. In South America, in contrast, the possible effect of greater ranges towards the temperate latitudes will tend to be cancelled by the counter effect of a decreasing continental width.

In conclusion, the evidence from columnar cacti suggest that, although Rapoport's rule seems to be an important determinant of species ranges, other effects that frequently co-vary with latitude, such as habitat width, may be playing an extremely important role. It is interesting, in this sense, to note that many of the confirming evidences for Rapoport's rule have originated from distribution data of North American species (Stevens 1989; Pagel 1991; France 1992; Rohde 1993). When data from South America or Australia have been analyzed (Smith et al. 1994; Ruggiero 1995), the rule is not always satisfied, and other factors such as continental width and habitat heterogeneity may to play a role as important as the predicted effect of latitude on species ranges.

According to Stevens, Rapoport´s rule and the latitudinal gradient in species richness are both the outcome of the same process: temperate individuals have evolved broader tolerances to climatic factors than tropical individuals, and the broad tolerance has in turn led to wider latitudinal extent in the geographical range of high-latitude species than in the range of lower-latitude species. It is interesting to note that, while Rapoport's rule holded for the Mexican species but did not clearly apply to the Argentine data set, species richness increased significantly towards the tropics in both regions. This contradicts Steven's idea that decreasing species ranges could be a principal factor explaining the temperate-tropical gradient in species diversity. In our data set from Argentina, the species-richness gradient occurs even if Rapoport's rule does not hold (Mourelle and Ezcurra in press).

APPENDIX

COLUMNAR SPECIES LIST

ARGENTINE 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 hankeanus Web.
Cereus stenogonus K. Sch.
Cleistocactus baumannii (Lem.) Lemaire
Cleistocactus ferrarii R. Kiesling
Cleistocactus jujuyensis (Backbg.) Backbg.
Cleistocactus smaragdiflorus (Web.) Britton et Rose
Denmoza rhodacantha (SD) Britton et Rose
Echinopsis leucantha (Gill.) Walp.
Echinopsis rodotricha R. Mey
Harrisia bonplandii (Parmentier) Britton et Rose
Harrisia martinii (Labouret) Britton et Rose
Harrisia pomanensis (Weber) Britton et Rose
Harrisia tortuosa (Forbes) Britton et Rose
Lobivia chrysochete Werdermann
Lobivia ferox 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 cabrerae R. Kiesling
Trichocereus candicans (Gillies) Britton et Rose

Trichocereus fabrisii R. Kiesling
Trichocereus huascha (Web.) Britton et Rose
Trichocereus lamprochlorus (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

MEXICAN COLUMNAR CACTI

Backebergia militaris (Audot) Bravo ex Sánchez-Mejorada
Bergerocactus emoryi (Engelm.) Britt. et R.
Carnegia gigantea (Engelm.) Britt. et R.
Cepahalocereus senilis (Haworth) Pfeiffer
Cephalocereus apicicephalium Dawson
Cephalocereus columna-trajani (Karw.) Schumann
Cephalocereus totolapensis (Bravo et MacDougall) Buxbaum
Escontria chiotilla (Weber) Rose
Mitrocereus fulviceps (Weber) Backeberg ex Bravo
Myrtillocactus cochal (Orcutt) Britt. et R.
Myrtillocactus geometrizans (Martius) Console
Myrtillocactus schenkii (Purpus) Britt. et R.
Neobuxbaumia euphorbioides (Haworth) Buxbaum
Neobuxbaumia macrocephala (Weber) Dawson
Neobuxbaumia mezcalaensis (Bravo) Backeberg
Neobuxbaumia multiareolata (Dawson) Bravo
Neobuxbaumia polylopha (De Candolle) Backeberg
Neobuxbaumia sanchez-mejoradae Lau
Neobuxbaumia scoparia (Poselger)Backeberg
Neobuxbaumia squamulosa Sheinvar et Sánchez-Mejorada
Neobuxbaumia tetetzo (Coulter) Backeberg
Pachycereus gatesii (M.E.Jones) D. Hunt

Pachycereus gaumeri Britt. et R.
Pachycereus grandis Rose
Pachycereus hollianus (Weber) Buxbaum
Pachycereus marginatus (DC:) Britt. et R.
Pachycereus pecten-aboriginum (Engelmann) Britt. et R.
Pachycereus pringlei (S. Watson) Britt. et R.
Pachycereus schottii (Engelm.) Hunt
Pilosocereus alensis (Web.) Byles et Rowley
Pilosocereus chrysacanthus (Web.) Byles et Rowley
Pilosocereus collinsii (Britton et Rose) Orcutt
Pilosocereus cometes (Scheidweiler) Britton et Rose
Pilosocereus purpusii (Britt. et R.) Byles et Rowley
Pilosocereus quadricentralis (Dawson) Backeberg
Polaskia chende (Gossel.) Gibson et Horak
Polaskia chichipe Backeberg
Stenocereus alamosensis (J. Coulter) Gibson et Horak
Stenocereus beneckei (Enrenberg) Buxbaum
Stenocereus chacalapensis (Bravo) Bravo
Stenocereus chrysocarpus Sánchez-Mejorada
Stenocereus dumortieri (Scheidlweiler) Buxbaum
Stenocereus eichlamii (Britton et Rose) Buxbaum
Stenocereus eruca (Brandegee) Gibson et Horak
Stenocereus fricii Sánchez-Mejorada
Stenocereus griseus (Haworth) Buxbaum
Stenocereus gummosus (Brangdegee) Gibson et Horak
Stenocereus kerberi (Schumann) Gibson
Stenocereus laevigatus (Salm-Dyck) Buxbaum
Stenocereus martinezii (González Ortega) Bravo
Stenocereus montanus (Britton et Rose)
Stenocereus pruinosus (Otto) F. Buxbaum
Stenocereus queretaroensis (Weber) Buxbaum
Stenocereus quevedonis (González Ortega) Bravo
Stenocereus standleyi (González Ortega) Buxbaum
Stenocereus stellatus (Pfeiffer) Riccobono
Stenocereus thurberii (Engelmann) Buxbaum
Stenocereus treleasei (Vaupel) Backeberg
Stenocereus weberi (Coulter) Backeberg

LITERATURE CITED

Aldrich, J. W. 1963. Geographic orientation of American Tetraonidae. Journal of Wildlife Management 27:528-545.

Anderson, S. and K. F. Koopman. 1981. Does interspecific competition limit the sizes of ranges of species? Novitates American Museum 2716:1-10.

Cabrera, A. L. and A. Willink.1980. Biogeografía de América Latina. Serie de Biología. Monografía no.13. Organization of American States, Washington D.C.

Colwell, R. K. and G. C. Hurtt. 1994. Non biological gradients in species richness and a spurious Rapoport effect. American Naturalist 144:570-595.

Crawley, M. 1993. GLIM for Ecologists. Blackwell Scientific Publications. Oxford. London.

France, R. 1992. The North American latitudinal gradient in species richness and geographical range of freshwater crayfish and amphipods. American Naturalist 139:342-354.

Loftas, T., ed. 1972. Climate-vegetation maps of Central America. Page 151 in The atlas of the earth. Mitchell Beazley, with George Philip & Son Limited, London.

Maurer, B. A. 1994. Geographical Population Analysis: Tools for the Analysis of Biodiversity. Blackwell Scientific Publications, Oxford.

Mourelle, C. and E. Ezcurra. Species richness patterns of Argentine cacti:A test of some biogeographic hypotheses. Journal of Vegetation Science (in press).

Pagel, M. D., R. M. May and A. R. Collie 1991. Ecological aspects of the geographical distribution and diversity of mammalian species. American Naturalist 137:791-815.

Rapoport, E. H. 1975. Areografía:estrategias geográficas de las especies. Fondo de Cultura Económica, Mexico city.

Rapoport, E. H. 1982. Areography:geographical strategies of species. Trans. B. Drausal. Vol1. Pergamon, New York.

Rhode, K. 1992. Latitudinal gradients in species diversity:the search for the primary cause. Oikos 65:514-527.

Rhode, K., M. Heap and D. Heap .1993. Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. American Naturalist 142:1-16.

Rosenzweig, M. L. 1975. On continental steady states of species diversity. Pages 121-140 in M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Belknap Press, Cambridge, Mass.

Ruggiero, A. 1994. Latitudinal correlates of the sizes oif mammalian geographical ranges in South America. Journal of Biogeography 21:545-559.

Rzedowski, J. 1990. Vegetación potencial. Biogeografía (IV.8.2). Atlas Nacional de México. Instituto de Geografía. UNAM, Mexico city.

Smith, F. D. M., R. M. May and P. H. Harvey .1994. Geographical ranges of Australian mammals. Journal of Animal Ecology 63:441-450.

Stevens, G. C. 1989. The latitudinal gradient in geographical range:how so many species coexist in the tropics. American Naturalist 133:240-256.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport´s latitudinal rule to altitude. American Naturalist 140:893-911

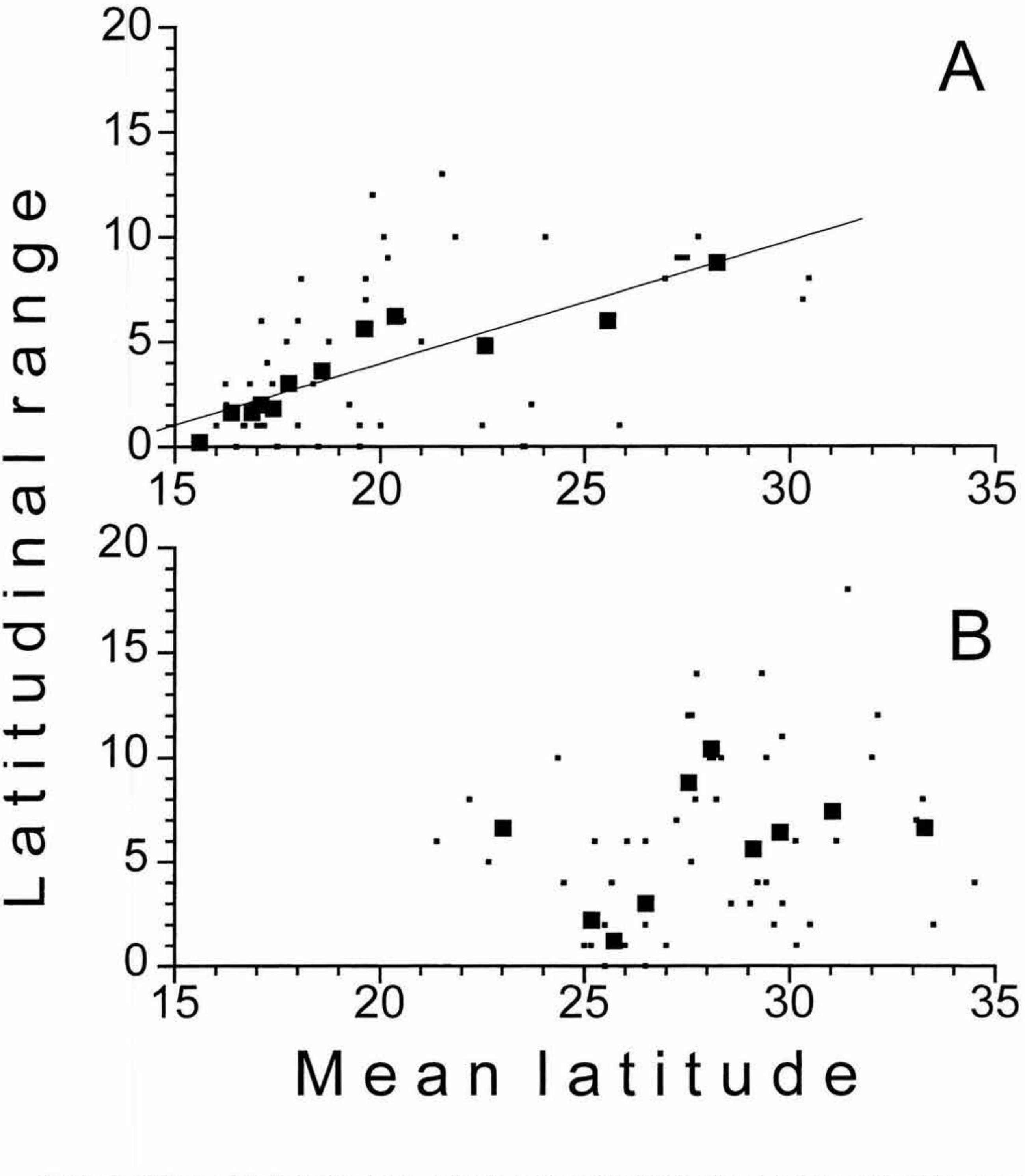

Figure 1. Relationship between mean latitude and mean latitudinal range for groups of five species in (A) Mexico and in (B) Argentina. The significant regression line is indicated for Mexico. The smaller data points show the dispersion of the original (ungrouped) data.

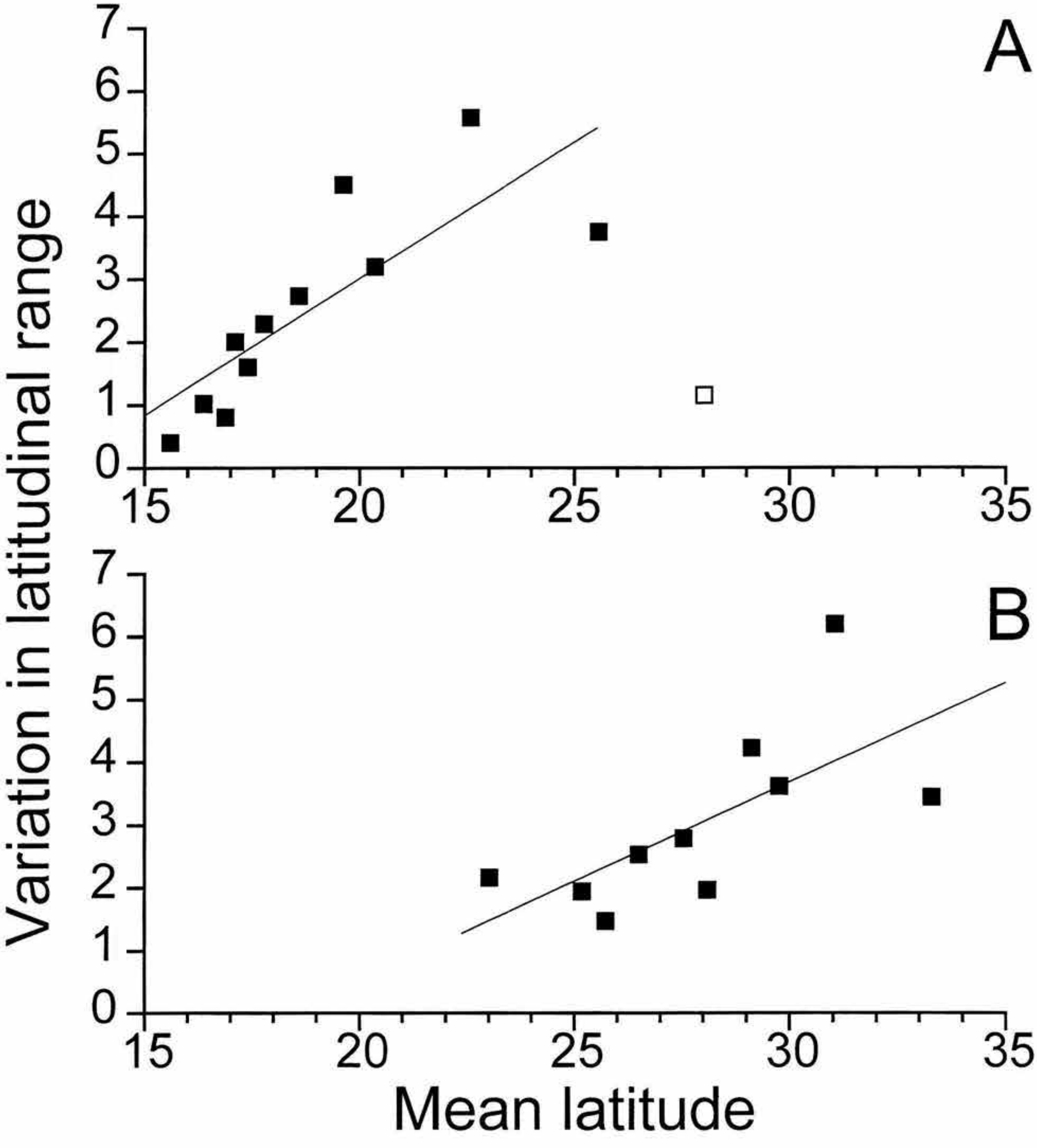

Figure 2. relationship between mean latitude and the standard deviation of the mean latitudinal range for groups of five species in (A) Mexico and in (B) Argentina. The significant regression lines are indicated for both countries, the outlying nothernmost data point in Mexico (shown as an open square) was not included in the regression.

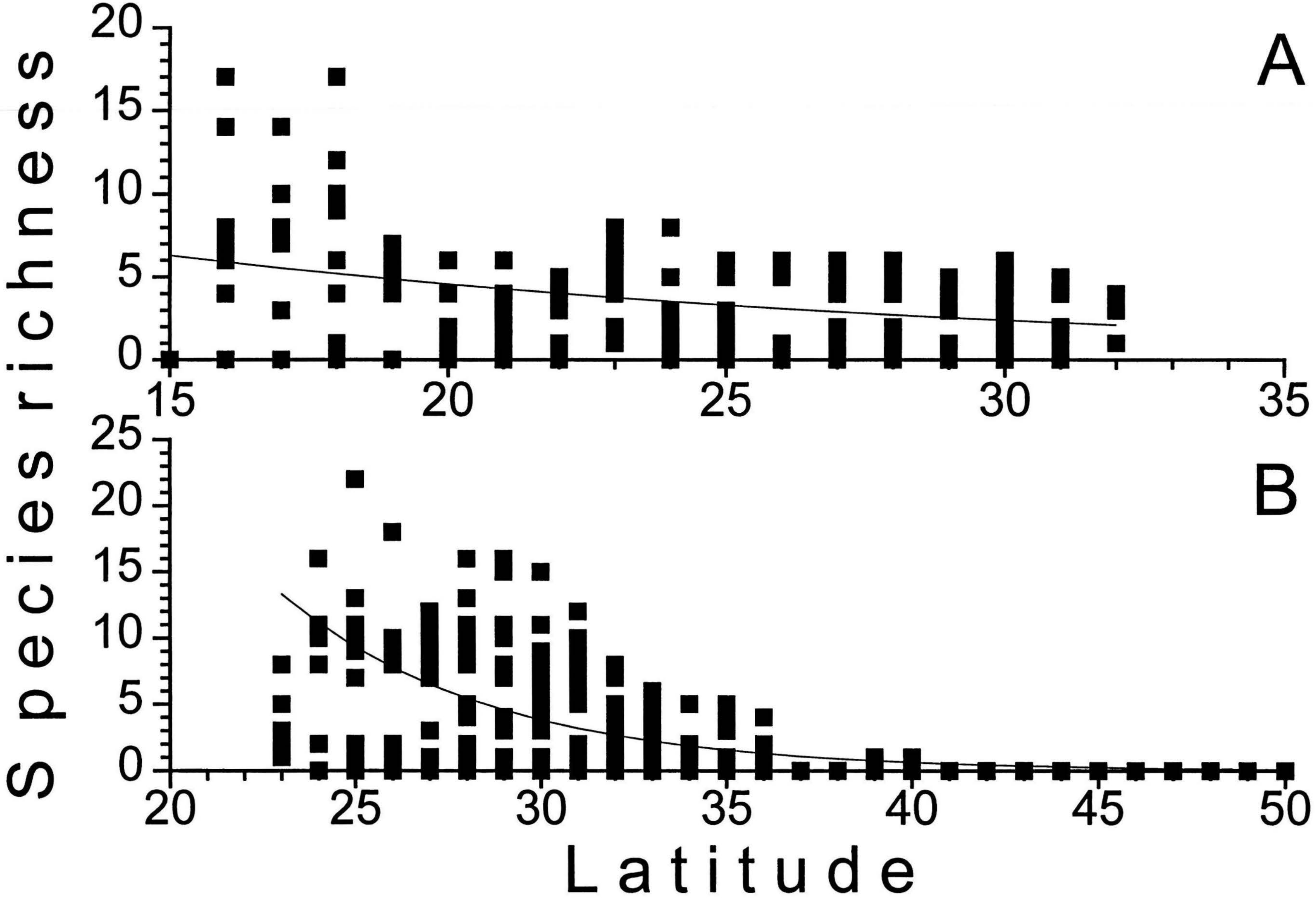

Figure 3. Relationship between latitude and species-richness for 1°x1° quadrats in (A) Mexico and (B) Argentina. The log-linear regression curves are shown for both countries.

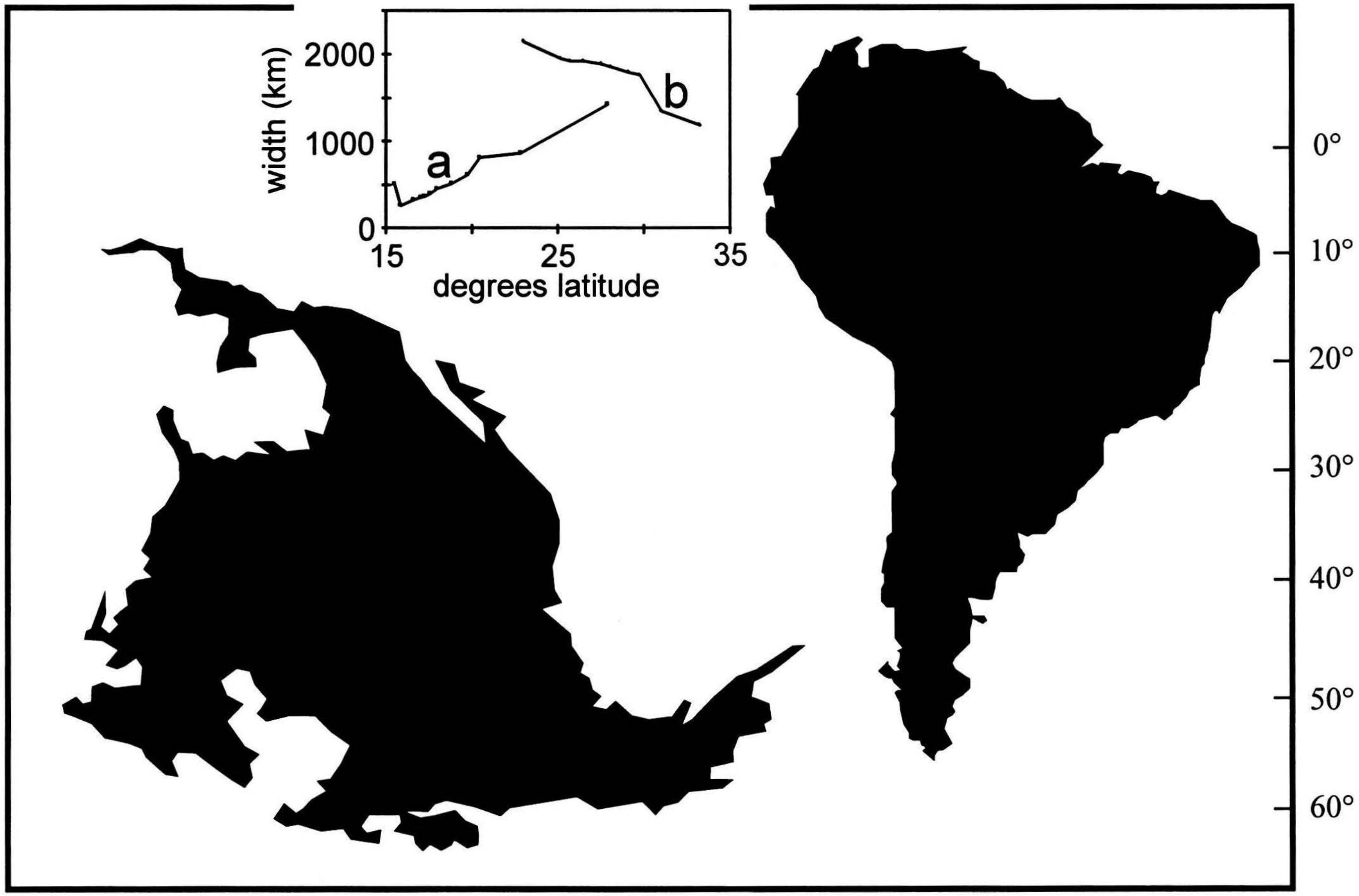

Figure 4. Maps of North and South America, plotted on the same latitudinal scale. The upper plot shows the relationship between continental width and latitude for (*A*) Mexico and (*B*) Argentina.

V. CONCLUSIONES

CONCLUSIONES

Los tres artículos que conforman esta tesis presentan un análisis sobre las tendencias biogeográficas de la familia Cactaceae, distinguiendo los dos elementos fundamentales de la diversidad biológica a gran escala: la diversidad α, considerada aquí como la riqueza de especies, la diversidad β o el recambio de especies y el efecto conjunto de ambos. En esta tesis no se hace referencia ni a la abundancia relativa de las especies ni a su variación genética. El análisis se basa en las especies de las tres formas de crecimiento más frecuentes dentro de la familia: la columnar, la opuntioide y la globosa.

En la introducción se señaló la importancia de la heterogeneidad ambiental o de la variación espacial en los distintos descriptores del clima y de la topografía como un factor evolutivo determinante de la riqueza y del recambio de especies. Este factor (la heterogeneidad ambiental) se puso a prueba en las distintas etapas de nuestro trabajo.

En el primer artículo se relaciona la riqueza de especies de las tres formas de crecimiento de las cactáceas en Argentina con algunas hipótesis biogeográficas. Los factores ambientales relacionados con las hipótesis de la benignidad (o “favorabilidad”) del ambiente y de la variación climática explicaron una amplia proporción de la varianza total en la riqueza de especies de las tres formas de crecimiento. Las variables relacionadas con la heterogeneidad del hábitat o con los niveles de energía interceptada fueron en general pobres predictores de la riqueza específica, con la excepción del caso de las globosas, para las cuales la heterogeneidad del hábitat fue un predictor significativo. De las tres formas de crecimiento, las opuntioides forman el grupo que llega más al sur del continente, confirmando su amplia tolerancia a climas extremos y, en particular, a las bajas temperaturas. Esta tolerancia puede deberse a su crecimiento modular y a la plasticidad morfológica de sus cladodios terminales (Gibson y Nobel 1986, Nobel 1985). La mayor riqueza de este grupo se encuentra principalmente en regiones cálidas, con las lluvias concentradas en los meses de verano.

Contrariamente a las opuntioides, las columnares parecen estar fuertemente restringidas por las bajas temperaturas, confirmando las tendencias observadas a nivel mundial en plantas suculentas por Burgess y Shmida (1988), quienes sostienen que no se observan cactáceas en áreas con heladas frecuentes. La riqueza de las columnares decrece abruptamente por debajo de los 34°S y por arriba de los 3000 m de altitud. En síntesis, estas especies parecen ajustarse a la hipótesis de la benignidad climática. Las globosas, además de asociarse significativamente con las lluvias de verano, se encuentran principalmente en áreas de sustrato rocoso. Al estar significativamente asociadas a lugares marcadamente estacionales con lluvias de verano, las opuntioides y las globosas responden a la hipótesis de la variación climática. Es importante notar que los valores promedios de las variables climáticas no fueron en ningún caso predictores significativos de la riqueza. Contrariamente a las observaciones de Currie (1991, Currie y Paquin 1987) y de acuerdo con Whittaker (1965) y con Richerson y Lum (1980), la productividad y la evapotranspiración potenciales fueron pobres predictores. Además de las variables climáticas, se detectó una cierta heterogeneidad en el esfuerzo de colecta, la cual podría modificar parcialmente nuestros resultados. Por ejemplo, en dos de las zonas más ricas y mejor colectadas en cactáceas, la Prepuna y el Monte, la riqueza de estas zonas se podría atribuir parcialmente a los efectos de la colecta. Sin embargo, su alta diversidad parece deberse estadísticamente a un efecto aún mayor que la intensidad de colecta. Es posible que estas zonas hayan funcionado como refugios para las especies de cactáceas durante el Pleistoceno y que este hecho se vea reflejado en su diversidad actual.

En el segundo artículo de este trabajo, se busca entender qué tipo de heterogeneidad ambiental está afectando el reemplazo de las especies en sus diferentes formas de crecimiento entre sitios o cuadros y a lo largo de gradientes ambientales. Las diferentes tasas de recambio de las especies en los transectos latitudinales y longitudinales se relacionan con diferentes variables del ambiente para una misma forma de crecimiento. La diversidad β en los transectos latitudinales se asoció significativamente con la media de los valores de las variables ambientales en el transecto. La diversidad β en los transectos longitudinales se relacionó principalmente con la variación de las variables dentro del transecto. La posible causa de este patrón puede encontrarse en la distribución de las variables ambientales en Argentina. Dado que en el norte de Argentina la altitud aumenta y las precipitaciones disminuyen marcamente hacia el oeste, los transectos longitudinales atraviesan un número mayor de ecosistemas y de zonas climáticas que los transectos latitudinales, que corren de norte a sur y cruzan biomas más homogéneos en cuanto a tipo de vegetación y precipitación. De esta manera, los mejores predictores del recambio de especies en sentido longitudinal son variables que miden la intensidad del cambio ambiental. Por el contrario, los mejores predictores del recambio de especies en transectos latitudinales, son variables que miden la posición relativa del transecto N-S dentro del gradiente E-O.

Es interesante observar que para la forma columnar, la variación en la temperatura es el mejor predictor en el recambio entre sitios y en el recambio a lo largo de los transectos. Dado que la temperatura fue el factor limitante en el número de especies de las columnares, parece lógico asociar el recambio de especies con la variación espacial en la temperatura. La temperatura media anual, el mejor predictor de las opuntioides, coincidentemente es baja en las áreas de mayor recambio de especies en esta forma de crecimiento. El mejor predictor del recambio entre cuadros para las globosas es la proporción de lluvias en verano: se puede observar que las áreas de alto reemplazo de especies se ubican en zonas de lluvias netamente de verano. Además, es notable para las tres formas de crecimiento que las áreas con altas tasas de recambio coinciden con algunas fronteras entre biomas, donde los cambios ambientales y biológicos son muy pronunciados. Si bien los modelos de regresión identificaron variables que se asocian a cambios ambientales, es importante subrayar que no existe forsozamente una causalidad.

Comparadas con las opuntioides y las columnares, las globosas - que tienen una baja capacidad de dispersión (Barthlott y Hunt 1993) - presentaron una mayor proporción de cuadros con diversidad β alta. En general, la diversidad beta fue menor en las opuntioides y en las columnares, dos formas de crecimiento que tienen en general una mayor capacidad de dispersión (Barthlott y Hunt 1993). Podríamos concluir que la heterogeneidad ambiental y las limitaciones en la dispersión juegan un papel importante en la diversidad β de estas formas de crecimiento (Harrison et al. 1992).

Los gradientes en la riqueza y en el recambio de especies observados nos llevaron a la tercer etapa de estudio, en la que estudiamos de manera comparativa los gradientes en el intervalo latitudinal de las especies de cactáceas columnares de sud y Norteamérica. En México, los intervalos latitudinales medios de la especies se correlacionaron positivamente con la latitud media, confirmando la Regla Rapoport. Es decir, en México el intervalo de distribución latitudinal de las especies columnares disminuye hacia el trópico. Sin embargo, esta regla no se cumple estrictamente para las cactáceas de Argentina. Una posible interpretación de este resultado puede encontrarse en la forma del continente. En México, el área del continente y la latitud aumentan de manera paralela. En Argentina, por lo contrario, el efecto de los amplios intervalos hacia las zonas templadas puede verse anulado porque el continente se hace más angosto hacia altas latitudes. Sin duda, otras posibles explicaciones pueden buscarse en los tamaños de los hábitats, su heterogeneidad y la variación climática, pero nuestro estudio muestra claramente que la regla biogeográfica que predice que las especies tropicales son más estenoicas en su distribución, no se cumple necesariamente en todos los continentes por igual. Adicionalmente, dado que tanto en Argentina como en México el número de especies de cactáceas columnares aumenta hacia el trópico, no parece correcto atribuir la causa de la mayor riqueza de los trópicos a la menor amplitud geográfica de las especies tropicales.

A manera de síntesis, los resultados de esta tesis nos permiten inferir las siguientes conclusiones:

1.- Aunque el clima no cause especiación, circunscribe o delimita cambios en la riqueza de especies y de formas de crecimiento a lo largo de dos vectores de potencial variación: el tiempo y el espacio.

2.- Los modelos estadísticos que describen las relaciones clima-riqueza de especies proveen una herramienta única para modelar la riqueza de especies, acorde a el clima actual, y podría potencialmente servir para predecir lugares altamente vulnerables a la extinción de especies frente a esceneraios de cambio climático (por ejemplo, el calentamiento global).

3.- La densidad en la colecta puede sesgar de manera significativa los resultados de los modelos de regresión en los estudios a gran escala geográfica. En este trabajo, aunque el esfuerzo de colecta explicó una proporción importante de la variación residual en la riqueza de especies, se relacionó débilmente con el recambio en el número de especies. Se puede concluir que los valores estimados de la diversidad de diferenciación o diversidad β son menos sensibles estadísticamente a los sesgos en la colecta que los de la riqueza de especies o diversidad α.

4.- Los mejores predictores del recambio de especies no siempre coinciden con los de la riqueza de especies. Si una determinada variable es el mejor predictor para la diversidad α, es lógico pensar que la variación en ésta lo será para el recambio de especies. Sin embargo, sólo en el caso de las columnares, la temperatura y la variación de la temperatura fueron los mejores predictores de la diversidad α y β, respectivamente, confirmando las fuertes restricciones térmicas de esta forma de crecimiento. La riqueza de las globosas y las opuntioides está significativamente determinada por la estacionalidad de las lluvias, mientras que el recambio de especies en estas formas de crecimiento depende esencialmente de la precipitación en el primer caso y de la temperatura o de variables asociadas a variaciones a la temperatura en el segundo caso.

5.- En las globosas, la forma de crecimiento que presenta la mayor especificidad de hábitat y la menor capacidad de dispersión, se observó en general una tasa de recambio mayor que en las columnares y en las opuntioides. Podríamos concluir que tanto la heterogeneidad en el hábitat como las limitaciones en la dispersión juegan un rol determinante en el recambio espacial de las especies.

6.- Las regiones ambientalmente heterogéneas y las que presentan importantes transiciones entre biomas muestran una riqueza de especies excepcional y pueden estar sujetas a programas específicos de manejo y de conservación que tengan en cuenta esa elevada diversidad.

7.- Aunque la regla Rapoport se cumple para las cactáceas de México pero no para las de Argentina, la mayor riqueza de especies en los trópicos, observado en los dos hemisferios, no puede explicarse según las predicciones de Stevens (1989), las que describen que la disminución de los ámbitos de distribución de las especies hacia los trópicos es un factor determinante de la riqueza de especies. Sin duda, otros factores que varían con la latitud como el tamaño del hábitat y su heterogeneidad pueden estar jugando un papel de la misma importancia.

REFERENCIAS

Barthlott, W. y Hunt, D. R. 1993. Cactaceae. In: Kubitzi, K. (ed.) *The families and genera of vascular plants*, pp. 161-197. Springer-Verlag, Berlin, Heidelberg.

Burgess, L. T. y Shmida, A. 1988. Succulent growth forms in arid environments. In: Whitehead, G. G., Hutchinson, C. F., Timmermann, B. D. y Varady, R. G. (eds.) *Arid Lands Today and Tomorrow.* Proceedings of an International Research and Development Conference at Tucson, Az., pp. 383-395. Westview Press, Boulder, Colorado y Belhaven Press, London.

Currie, D. J. y Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* **329**:326-327.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist* **137**:27-49.

Gibson, A. y Nobel, P.S. 1986. *The Cactus Primer*. Harvard University Press, Cambridge, MA.

Harrison, S., Ross, S. J., y Lawton, J.H. 1992. Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology* **61**:151-158.

Nobel, P. S. 1985. Form and orientation in relation to PAR interception by cacti and agaves. In: Givnish, T. J. (ed.) *On the Economy of plant form and function*, pp. 83-103. Cambridge University Press, Cambridge.

Richerson, P. J. y Lum, K-W. 1980. Patterns of plant species diversity in California: relation to weather and topography. *American Naturalist* **116**:504-536.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* **133**:240-256

Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* **147**:250-260

APENDICE

(Documentos probatorios del status de los artículos presentados)

Journal of Vegetation Science 7: 667-680, 1996
© IAVS; Opulus Press Uppsala. Printed in Sweden

Species richness of Argentine cacti: A test of biogeographic hypotheses

Mourelle, Cristina & Ezcurra, Exequiel

Centro de Ecología, UNAM, Apartado Postal 70-275, 04510 - Mexico, D.F., Mexico;
Fax +52 5 6228995; E-mail eezcurra@miranda.ecologia.unam.mx

Abstract. Patterns of species richness are described for 50 columnar, 109 globose and 50 opuntioid cacti species in 318 grid cells (1° × 1°) 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, opuntioid species, globose species and all forms combined. Opuntioid 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 opuntioid 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) opuntioid cacti, (d) epiphytic cacti and (e) pereskioid 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 *Trichocereeae* and *Cereeae*, while the genera of the globose species belong mostly to the Tribe *Notocacteae* (Gibson & Nobel 1986). Opuntioid 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 opuntioid 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 *Hylocereeae* of the subfamily *Cactoideae*. The pereskioid 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

Journal of Vegetation Science
International Association for Vegetation Science
Editor: Prof. Eddy van der Maarel

Date: 1997-03-04

To: Dr. Cristina Mourelle
México DF

Ref: Review result

Dear Cristina,

This letter is concerned with:

○ Review of manuscript no.
● Review of the revised manuscript no. **VS 1471**

The following decision has been taken with regard to the manuscript:

● It has been accepted for publication: **1997-02-20**
○ It may be accepted after ○ minor ○ moderate ○ major revision
○ It needs a major revision; a revised version will be reviewed again
○ It needs to be reduced to pp of print, figures and tables included
○ It has not been accepted for publication, but a new manuscript may be submitted
○ It has not been accepted for publication

The following information is added

○ Manuscript pages with referee comments are included
○ Please correct the following points regarding JVS style:
○ Title and headings not in capitals ○ Keywords alphabetical ○ Add Nomenclature source
○ No underlining ○ Citation as in Instructions ○ Journal abbreviations as in BIOSIS data base
○ Final revisions of papers will normally be checked by the Editorial Office regarding coherence, carefulness of citation, missing statistics, quality and necessity of figures, etc.

Additional editorial comments:

Congratulations with one more nice paper. I was uncertain about the acceptance date. Mike Palmer had written "acceptable" but you seem to wait for a final letter, which is this one, as you understand. The final revision arrived 1997-02-19 and I put the formal acceptance date on the paper when I put it on the pile "papers to process" in my JVS office at home. But there is a long queue, so it was not before today the letter was written.

At a first inspection I have few remarks. There are some minor deviations from the JVS instructions, but not serious enough to send the diskette back. The paper is a little long. In case we need a reduction, I suggest to omit Fig. 4 and replace it by a regression equation in the text. Anyway, these equations would be good to add; why not add them in Table 4? That is all for the moment. Proofs may not arrive before May; there is a chance for inclusion in issue 8-3, June.

With best wishes, also for Exequiel,

Yours sincerely,

Eddy
Eddy van der Maarel

<u>Please note</u> that a page charge of 300 SEK (ca. 45 US$) per printed page is levied. Authors and coauthors who are dues-exempt members of IAVS are exempt from this charge. All other authors and coauthors of published papers should subscribe to the journal in at least two consecutive years, or be connected to a department with a library subscription to JVS in order to enjoy exemption. Please contact Eddy van der Maarel for further details.

Department of Ecological Botany, Uppsala University, Villavägen 14, S-752 36 Uppsala, Sweden

Vol. 150, No. 1 The American Naturalist July 1997

NOTES AND COMMENTS

RAPOPORT'S RULE: A COMPARATIVE ANALYSIS BETWEEN SOUTH AND NORTH AMERICAN COLUMNAR CACTI

CRISTINA MOURELLE* AND EXEQUIEL EZCURRA†

Centro de Ecología, ~~UNAM~~, Apartado Postal 70-275, 04510-Mexico, D.F., Mexico

iversidad
acional
utónoma
e México

Submitted July 23, 1996; Revised October 15, 1996; Accepted October 29, 1996

The geographical range of species belonging to a number of taxonomic groups tends to decrease toward the Tropics (Stevens 1989). This latitudinal pattern has been well documented over the past 30 yr, and several explanations have been put forth, including environmental history (Rapoport 1975, 1982), competition (Rapoport 1975, 1982; Rosenzweig 1975; Anderson and Koopman 1981), local climate and species environmental tolerances (Stevens 1989), the mass effect (the establishment of species in sites where they cannot self-maintain; Stevens 1989, 1992), the species dispersion capabilities and their ecophysiological properties (Stevens 1989; France 1992), and sampling bias (Colwell and Hurtt 1994). The empirical biogeographical rule that states that the latitudinal extent of the geographical range of organisms is positively correlated with the latitude at which these organisms are found was named Rapoport's rule by Stevens (1989), after the Argentine biogeographer Eduardo Rapoport, who first made reference to the correlation between range and latitude (see Rapoport 1975, 1982).

The idea that geographical ranges increase from the Tropics toward the poles has received close attention over the last several years (Stevens 1989; Pagel et al. 1991; France 1992; Rohde 1992; Rohde et al. 1993; Colwell and Hurtt 1994; Roy et al. 1994; Ruggiero 1994; Smith et al. 1994; Rohde 1996; Rohde and Heap 1996). Although Rapoport's rule has been tested on several groups in different regions, most of these studies have focused on animals (Rohde 1996; Rohde and Heap 1996), and few of them have been done for South America (Ruggiero 1994). A comparative study addressing the relationship between mean

---

* E-mail: cmourell@miranda.ecologia.unam.mx.

† E-mail: eezcurra@servidor.unam.mx.

Am. Nat. 1997. Vol. 150, pp. ~~000–000~~.

131–142.