plant biology

Plant Biology ISSN 1435-8603

SHORT RESEARCH PAPER

Assessing the geographic dichotomy hypothesis with cacti in South America

A. A. Arzabe[1,2], L. F. Aguirre[1], M. P. Baldelomar[3] & M. A. Molina-Montenegro[3,4]

1 Centro de Biodiversidad y Genética, Universidad Mayor de San Simón, Cochabamba, Bolivia
2 Laboratorio de Conservación Biológica, Facultad de Ciencias, Universidad de Chile, Ñuñoa, Santiago, Chile
3 Centro de Ecología Molecular y Funcional, Instituto de Ciencias Biológicas, Universidad de Talca, Talca, Chile
4 Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile

Keywords
Cactaceae; geographic dichotomy hypothesis; pollination syndrome; South America.

Correspondence
Marco A. Molina-Montenegro, Centro de Ecología Molecular y Funcional, Instituto de Ciencias Biológicas, Universidad de Talca, Campus Lircay, Talca, Chile. E-mail: marco.molina@utalca.cl

Editor
Z.-X. Ren

Received: 13 June 2017; Accepted: 15 November 2017

doi:10.1111/plb.12669

ABSTRACT

- The Cactaceae is one of the most conspicuous and ecologically important plant families in the world. Its species may have specialist or generalist pollination systems that show geographic patterns, which are synthesised in the Geographic Dichotomy Hypothesis.
- Here, we assess this hypothesis in five countries in both tropical and extratropical regions, evaluating the pollinator visitation rate and pollinator identity and abundance. We calculate the Shannon diversity index (H′) and evenness (J) and evaluate differences between latitude parameters with a Student *t*-test.
- Overall, we found more specialised pollination systems in all tropical sites; the richness, diversity and evenness of pollinators was reduced in comparison to extratropical regions, where the pollination system was generalised.
- Our results support the geographic dichotomy hypothesis in the cacti of South America, suggesting that environmental factors underlying the latitudinal patterns can help to explain differences in the pollination syndrome between tropical and extratropical regions.

INTRODUCTION

The Cactaceae is one of the most conspicuous and ecologically important plant families in the world, found mainly in arid and semi-arid ecosystems (Rojas-Sandoval & Melendez-Ackerman 2009). Cactus morphology varies widely in different ecosystems (Nobel 2002; Zenteno-Ruíz *et al.* 2009). Their flowers are sessile and solitary, usually campanulate, with radial (actinomorphic) or bilateral (zygomorphic) symmetry. They may have specialist or generalist pollination, and in some cases the morphology of the flowers regulates the type of pollinator, thus being classified as bee, hummingbird, bat or moth flowers (Soriano *et al.* 2000; Nobel 2002; Schlumpberger & Renner 2012).

Pollinators are very important in the reproduction of Cactaceae, because in spite of having asexual reproduction (vegetative apomixis and agamospermy), sexual reproduction is more widespread (Nobel 2002; Ramawat & Gopal 2010). Self-pollination or autogamy is an economic form of reproduction, functioning as a genetic barrier, preventing or reducing hybridisation, while cross-pollination or allogamy favours the wide diversity observed in cacti (Nobel 2002). Some studies have proposed a hypothesis on the distribution and bat-pollination syndromes of cacti. This hypothesis, known as the 'Geographic Dichotomy', affirms that cacti have a generalised pollination system in extratropical areas where pollinators are more variable and resources more limiting, while in tropical areas, where resources are more reliable and pollinator communities more stable, cacti tend to have specialised pollination systems (see Valiente-Banuet *et al.* 1996).

Most studies that assessed this hypothesis have been done in the Northern Hemisphere, the few in the Southern Hemisphere were done with one single cactus species and were focused on identifying whether the reproductive characteristics and the pollinators of the cactus fulfil this hypothesis (Nassar *et al.* 1997; Valiente-Banuet *et al.* 1997, 2004; Larrea-Alcázar & López 2011; Ortega-Baes *et al.* 2011). Hence, as far as we know, our study may be the first to address empirically the geographic dichotomy hypothesis with cacti from South America.

To assess the geographic dichotomy hypothesis we evaluated pollination activity in cacti from ten sites (five from tropical areas and five from extratropical areas). Specifically, we predict that independent of their floral characteristics (floral morphology), if these species depend primarily on cross-pollination, cacti from tropical latitudes should show more specialised pollination, while those from extratropical latitudes should show more generalised pollination.

MATERIAL AND METHODS

This study was conducted in ten sites located in five countries in both tropical and extratropical regions, ranging from 00°49′S to 33°09′S (Fig. 1). In each site only one cactus species was studied in order to avoid sympatric interactions.

To assess the pollinator visitation rate we monitored 30 individuals of the chosen species at each site (one flower

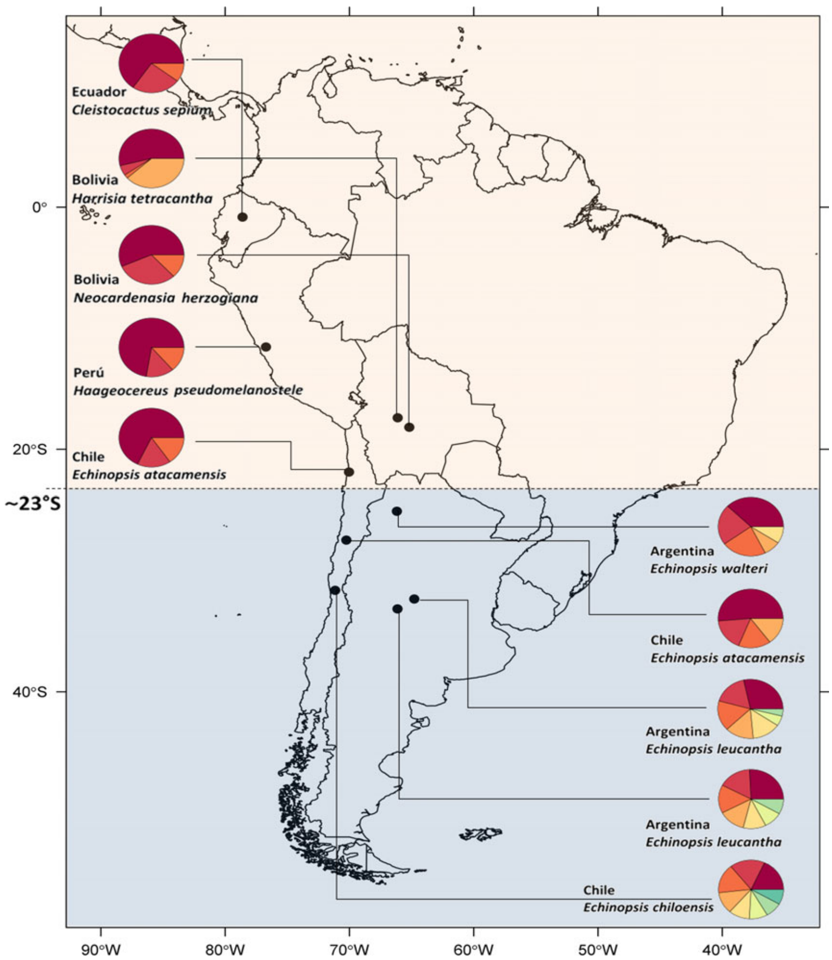

Fig. 1. Map highlighting the study sites in tropical latitudes (pale pink) and extra-tropical latitudes (pale blue) as well as the species of cacti used in each site. Circle division (size and color) is proportional to the frequency of each pollinator recorded in the site. The dotted line located at 23°S indicates the division between tropical and extratropical latitudes.

per individual). For each flower we recorded the visits in eight sessions of 15 min for 6 days between 06:00 and 20:00 h for tropical sites, and eight sessions of 15 min for 5 days between 08:00 and 20:00 h for extratropical sites. The height of the target flower of each individual was similar to minimise preference effects of the pollinators, and the floral density was similar between individuals to avoid differential attraction of pollinators. The agents that visited the flowers were photographed and recorded, considering that they should land on the flower to be counted as visitors. If the same agent returned to the flower it was only counted as one visit. All the observers wore similar clothing and were rotated to reduce systematic errors. In addition, we conducted a supplemental hand-pollination experiment in each species of cactus in the tropical and extratropical sites, showing that seed output is pollen-limited in all species of cacti (Table 1). Finally, we checked in the field that each species is self-incompatible, as previously suggested in other studies (Schlumpberger & Badano 2005; Walter 2010; Ossa & Medel 2011; Gorostiague & Ortega-Baes 2017).

All visits were recorded and their relative abundance estimated for each cactus species. Species identity and abundance were used to calculate the Shannon diversity index (H′) and evenness (J). Evenness was calculated as H′/ln S, where S is the species richness expressed as the number of species (Magurran 2010). Variation in species richness S, Shannon index H′ and evenness J were used to assess the relationship between latitude and specialised *versus* generalised pollination. Pearson correlation was used to assess these latitudinal relationships.

RESULTS

The number of different species visiting flowers of cacti in extratropical sites was 1.9-fold higher than in tropical sites (mean = 3.2 and 6.2 for tropical and extratropical sites, respectively; Fig. 1). In addition, the pollinator visitation rate was 1.4-fold higher in extratropical sites than in tropical sites (mean = 8.1 and 11.4 for tropical and extratropical sites, respectively; Fig. 1). Although richness and abundance of pollinators was higher in extratropical sites, the frequency of visitation was more homogeneous among the different pollinator species compared to tropical sites, where only a few pollinator species were very frequent (Fig. 1).

The richness and diversity of pollinators was significantly related ($r^2 = 0.74$, $P = 0.022$ and $r^2 = 0.68$, $P = 0.014$) to latitude (Fig. 2). Similarly, evenness of pollinators increased significantly with latitude ($r^2 = 0.54$, $P = 0.041$), indicating that evenness was higher in sites of extratropical latitudes than in sites from tropical latitudes (Fig. 2).

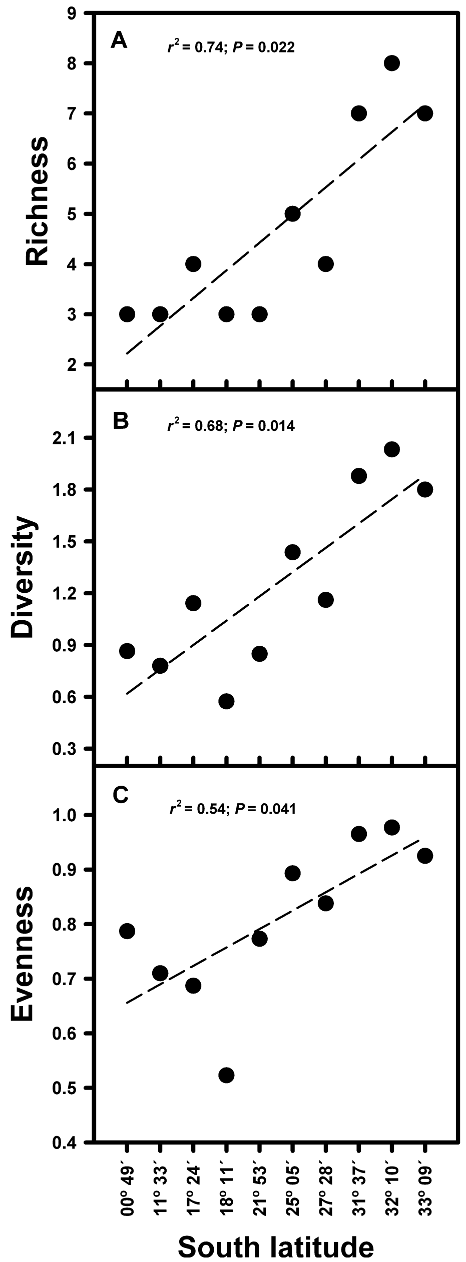

Fig. 2. Richness (A), diversity (B) and evenness (C) of pollinator visitation recorded along a latitudinal gradient. Mean of visitations in sessions of 15-min are shown.

DISCUSSION

We found a more specialised pollination system in tropical sites, where the richness, diversity and evenness of pollinators were reduced compared to the extratropical regions where the pollination system was more generalised, as suggested in the geographic dichotomy hypothesis. Nevertheless, these results do not agree with other studies done in the Northern Hemisphere, Southern Hemisphere and in islands, where the biotic specialisation of mutualistic networks was significantly lower in tropical than temperate latitudes (Schleuning *et al.* 2012), probably because the climate conditions and resource availability of these places were very different from places where the hypothesis was previously demonstrated (Nassar *et al.* 1997; Larrea-Alcázar & López 2011).

Table 1. Cactus species used in this study and main pollinators that could be identified. In addition, percentage increase in seed output when each cactus species was manually provided with cross pollen. The increase in seed output is obtained by comparing it with the percentage seed output when the cactus species were naturally pollinated in each population. To assess this pollen limitation we compared a single flower in ten different individuals (five per each treatment) in each cactus species from each population.

Species	Population	Vectors of pollination	Increase in seed output (%)
Cleistocactus sepium	00°49′	Bats and Hummingbirds	63
Harrisia tetracantha	11°33′	Hymenoptera (Apidae and Vespidae)	39
Neocardenasia herzogiana	17°24′	Hymenoptera and Coleoptera	45
Haageocereus pseudomelanostele	18°11′	Bats and Hummingbirds	43
Echinopsis atacamensis	21°53′	Bees, Wasps, Hummingbirds and Hawkmoths	57
Echinopsis walteri	25°05′	Hymenoptera Bees and Vespidae)	69
Echinopsis atacamensis	27°28′	Bees, Wasps, Hummingbirds and Hawkmoths	76
Echinopsis leucantha	31°37′	Moths, Bees and Birds	112
Echinopsis leucantha	32°10′	Moths, Bees and Birds	97
Echinopsis chiloensis	33°09′	Hawkmoths, Bees and Dipterans	86

Since the geographic dichotomy hypothesis was formulated in the mid-1990s (Valiente-Banuet *et al.* 1996; Nassar *et al.* 1997) it has been assessed in different cactus species with the bat pollinator syndrome, particularly in the tropics of the Northern Hemisphere (Valiente-Banuet *et al.* 1997; Ibarra-Cerdeña *et al.* 2005). It has been evaluated in extratropical areas (Molina-Freaner *et al.* 2004; Valiente-Banuet *et al.* 2004), but all the studies were centred mainly in tropical and extratropical areas of Mexico. However, different results were obtained when this hypothesis was evaluated on islands or in the Southern Hemisphere. In Puerto Rico (Rivera-Marchand & Ackerman 2006) and Bolivia (Larrea-Alcázar & López 2011) the hypothesis was only partially corroborated, because even though these studies reported a high number of pollinators, they found an affinity to a single pollinator (bees and hummingbirds, respectively). In Ecuador, Muchhala *et al.* (2009) found a generalised pollination system instead of a specialised one.

The geographic transition from specialised to generalised pollination systems is clearly shown in this study by the asymmetry in evenness of pollinator visitation rate. Nonetheless, it is necessary to understand the effectiveness of each pollinator in order to be able to infer change among generalisation *versus* specialisation with higher accuracy along latitude. Although little insight has been gained about the mechanism underlying the transition of the pollination systems, floral traits (timing, colour, reward), climate (temperature, seasonality of precipitation) and year-to-year variation in the assembly of pollinators and resources have been suggested to be involved in this transition (Ruiz *et al.* 1997; Ortega-Baes *et al.* 2011; Schleuning *et al.* 2012). Although species richness and diversity of pollinators would be indicative of a generalised pollination syndrome, complementary information is needed to effectively test the hypothesis. In addition, more studies should be done to address and unravel factors behind this pattern, considering both the variation in abiotic and biotic factors between tropical and extratropical latitudes, but the present study has identified promising research avenues to accomplish this goal.

ACKNOWLEDGEMENTS

The authors thank the Country Club Cochabamba and the Autonomous Municipal Government of Aiquile for allowing the field experiments, also the Postgraduate Department of the Agronomy Faculty and the Major University of San Simón. We appreciate the comments from Daniel Larrea Alcázar and Jafet Nassar on an early version of the manuscript. MAM-M thanks the research programme 'Adaptation of Agriculture to Climate Change' PIEI A2C2, Universidad de Talca.

REFERENCES

Gorostiague P., Ortega-Baes P. (2017) Pollination biology of *Echinopsis leucantha* (Cactaceae): passerine birds and exotic bees as effective pollinators. *Botany-Botanique*, **95**, 53–59.

Ibarra-Cerdeña C.N., Iniguez-Davalos L.I., Sanchez-Cordero V. (2005) Pollination ecology of *Stenocereus queretaroensis* (Cactaceae), a chiropterophilous columnar cactus, in a tropical dry forest of Mexico. *American Journal of Botany*, **92**, 503–509.

Larrea-Alcázar D.M., López R.P. (2011) Pollination biology of *Oreocereus celsianus* (Cactaceae), a columnar cactus inhabiting the high subtropical Andes. *Plant Systematics and Evolution*, **295**, 129–137.

Magurran A.E. (2010) *Desert Plants*. Springer, Berlin, Germany.

Molina-Freaner F., Rojas-Martínez A., Fleming T.H., Valiente-Banuet A. (2004) Pollination biology of the columnar cactus *Pachycereus pecten-aboriginum* in north-western México. *Journal of Arid Environments*, **56**, 117–127.

Muchhala N., Caiza A., Vizuete J.C., Thomson J.D. (2009) A generalized pollination system in the tropics: bats, birds and *Aphelandra acanthus*. *Annals of Botany*, **103**, 1481–1487.

Nassar J., Ramirez N., Linares O. (1997) Comparative pollination biology of Venezuelan columnar cacti and the role of nectar-feeding bats in their sexual reproduction. *American Journal of Botany*, **84**, 918–927.

Nobel P.S. (2002) *Cacti: Biology and Uses*. University of California Press, Los Angeles, CA, USA.

Ortega-Baes P., Saravia M., Suhring S., Godinez-Alvarez H., Zamar M. (2011) Reproductive biology of *Echinopsis terscheckii* (Cactaceae): the role of nocturnal and diurnal pollinators. *Plant Biology*, **13**, 33–40.

Ossa C.G., Medel R. (2011) Notes on the floral biology and pollination syndrome of *Echinopsis chiloensis* (Cactaceae) in a population of semiarid Chile. *Gayana Botánica*, **68**, 213–219.

Ramawat K., Gopal K. (Eds) (2010) *Desert Plants*. Springer, Berlin, Germany.

Rivera-Marchand B., Ackerman J.D. (2006) Bat pollination breakdown in the Caribbean columnar cactus *Pilosocereus royenii*. *Biotropica*, **38**, 635–642.

Rojas-Sandoval J., Melendez-Ackerman E. (2009) Pollination biology of *Harrisia portoricensis* (Cactaceae), an endangered Caribbean species. *American Journal of Botany*, **96**, 2270–2278.

Ruiz A., Santos M., Soriano P.J., Cavelier J., Cadena A. (1997) Relaciones mutualísticas entre el murciélago *Glossophaga longirostris* y las cactacéas columnares en la zona árida de la Tatacoa, Colombia. *Biotropica*, **29**, 469–479.

Schleuning M., Fründ J., Klein A.-M., Abrahamczyk S., Alarcón R., Albrecht M., Andersson G.K., Bazarian S., Böhning-Gaese K., Bommarco R., Dalsgaard B., Dehling D.M., Gotlieb A., Hagen M., Hickler T., Holzschuh A., Kaiser-Bunbury C.N., Kreft H., Morris R.J., Sandel B., Sutherland W.J., Svenning J.C., Tscharntke T., Watts S., Weiner C.N., Werner M., Williams N.M., Winqvist C., Dormann C.F., Blüthgen N. (2012) Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology*, **22**, 1–7.

Schlumpberger B.O., Badano E. (2005) Diversity of floral visitors to *Echinopsis atacamensis* subsp. Pasacana (cactaceae). *Haseltonia*, **11**, 18–26.

Schlumpberger B.O., Renner S.S. (2012) Molecular phylogenetics of *Echinopsis* (Cactaceae): polyphyly at all levels and convergent evolution of pollination modes and growth forms. *American Journal of Botany*, **99**, 1335–1349.

Soriano P.J., Ruiz A., Nassar J.M. (2000) Notas sobre la distribución e importancia ecológica de los murciélagos *Leptonycteris curasoae* y *Glossophaga longirostris* en zonas áridas Andinas. *Ecotropicos*, **13**, 91–95.

Valiente-Banuet A., Arizmendi M.D.C., 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.

Valiente-Banuet A., Rojas-Martinez A., Arizmendi M.D.C., Davila P. (1997) Pollination Biology of Two Columnar Cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, Central Mexico. *American Journal of Botany*, **84**, 452–455.

Valiente-Banuet A., Molina-Freaner F., Torres A., Del Coro Arizmendi M., Casas A. (2004) Geographic differentiation in the pollination system of the columnar cactus *Pachycereus pecten-aboriginum*. *American Journal of Botany*, **91**, 850–855.

Walter H.E. (2010) Floral biology of *Echinopsis chiloensis* ssp. *chiloensis* (Cactaceae): evidence for a mixed pollination syndrome. *Flora*, **205**, 757–763.

Zenteno-Ruíz F., López R.P., Larrea-Alcázar M.D. (2009) Patterns of spatial distribution of *Parodia maassii* (Heese) A. Berger (Cactaceae) in a semi-desert of the subtropical Andes, the prepuna. *Ecología en Bolivia*, **44**, 99–108.