

REVIEW ARTICLE

Ecology and evolution of negative and positive interactions in Cactaceae: lessons and pending tasks

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Background: The Cactaceae is a diverse and conspicuous Neotropical family that has evolved a wide variety of adaptations during co-evolution with their interacting species. Recent research has indicated complex ecological and evolutionary interactions involving cacti and other organisms.

Aims: We reviewed four studies involving cacti that have important implications for our understanding of the evolution of life traits and maintenance of cactus diversity. Also, these studies illustrate how the modern theoretical background of the ecology and evolution of species interactions is influencing the research in Cactaceae.

Methods: The studies showed here are (1) the evolutionary ecology of a mistletoe-cactus parasitism in central Chile, (2) the effect of an exotic grass on the demography of a threatened cactus in Puerto Rico, (3) the herpetochory in a tropical genus of cacti in Venezuela, and (4) the role of abiotic and biotic factors on the floral morphology in globose cacti species in northern Chile.

Results: The parasitic interaction between the mistletoe and a columnar cactus highlights the importance of spine length as a defensive co-evolving trait. Reproductive success in the endemic cactus in Puerto Rico was depressed by the presence of the exotic grass. Lizards actively fed on fruits of a tropical group of cacti, increasing the germination percentages of seeds. Climatic gradients might induce morphological change in the flowers of Mediterranean cactus species.

Conclusions: Interactions involving cacti reflect a complex scenario of ecological and evolutionary processes which may account for several patterns of the diversity of Cactaceae. In this sense, to enhance the on-going research, we emphasise the necessity of the development of a cactus interaction database; the assessment of detrimental effects of invasive species on cactus diversity; and the quantification of multi-species interactions.

Keywords: American continent; Caribbean; climatic drivers; grass invasion; parasitism; pollination; seed dispersal; succulent

Introduction

The Cactaceae, with more than 1600 recognised species, is one of the most conspicuous and diverse Angiosperm families in the Neotropics (Anderson 2001). Although mostly restricted to arid and semi-arid ecosystems, the family is almost continuously distributed in North and South America and the Caribbean, from southern Canada to Patagonia, across a wide range of vegetation types (e.g. tropical and temperate forests, Andean high-altitude vegetation and deserts). The role of cacti in the maintenance of ecosystem functioning, and the long history of their use by humans in their cultural practices, has resulted in the recognition of the importance of these plants for ecosystem services, especially in arid climates (Nobel 2002; Ashworth et al. 2009).

As a result of the inherent complexity of the evolutionary trajectory of the family in different habitats and communities, cacti have developed a broad spectrum of positive and negative ecological interactions with diverse groups of organisms. The framework provided by ecological interactions, antagonistic or mutualistic, enables the study of the extent to which the current diversity of life has

resulted from reciprocal adaptive adjustments (e.g. morphological traits) in multi-species and complex ecological scenarios (Levey et al. 2002; Thompson 2005; Morand and Krasnov 2010). With regard to cacti, a number of recent studies have provided new perspectives on the role of mutualistic and antagonistic interactions in demographic and evolutionary phenomena (e.g. Holland and DeAngelis 2001; Nobel 2002; Fleming and Valiente-Banuet 2002; Wolf and Martínez del Río 2003; Ritz et al. 2007; Fleming et al. 2009; Schlumpberger et al. 2009; Castillo-Landero and Valiente-Banuet 2010; Medel et al. 2010).

Positive interactions involving cacti have received far more attention than negative ones. Probably most, if not all, cactus species are involved in pollination or seed dispersal mediated by animals (Valiente-Banuet et al. 1997a, 1997b; Fleming et al. 2001; Fleming and Valiente-Banuet 2002), sometimes evolving extreme obligate mutualisms, such as in the case of the senita cactus *Lophocereus schottii* Engelm. Britton & Rose, exclusively pollinated by the senita moth *Upiga virescens* Hulst in the Sonoran desert (Holland and Fleming 1999). Cacti also offer other less-explored benefits to other plants by acting as nurse species (Valiente-Banuet

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1991; Godínez-Álvarez and Valiente-Banuet 1998), providing refuges against herbivores (Rebollo et al. 2002), and being substrate and structural support for epiphytes and hemi-epiphytes (Pinto et al. 2006; Medel 2001), and nesting sites for birds (Hernández et al. 2003).

In angiosperms, many traits present in the flowers and fruits are closely related to the type of animals that pollinate and disperse them (Bronstein et al. 2006; Bronstein 2009; Mitchell et al. 2009). Most cacti have xenogamous flowers (but see Sahley 1996; Nassar et al. 1997; Rojas-Sandoval and Meléndez-Ackerman 2009), which suggests a long history of flower–pollinator interaction and adaptive evolution in relation to specific pollinators (Fenster et al. 2004). Several examples of cactus–animal pollination systems, mainly from North America (Tehuacán-Cuicatlán Valley and Sonoran Desert), show how flower morphology and mating systems respond to a myriad of interactions with birds, mammals, and insects that feed on floral resources (Valiente-Banuet et al. 1997a, 1997b; Fleming et al. 2001, 2009; Grant and Grant 2006). Given the wide geographic range of some xenogamous cactus species, it can be expected that populations may show a diverse set of adaptations to a variety of pollinator assemblages (Schlumpberger et al. 2009), with differences in floral traits linked to animal attraction (“the most effective pollinator principle”, Stebbins 1970) or to intra-floral pollen transport (Kalisz and Vogler 2003). This strong link between pollinator assemblages and floral morphology has been observed in the two columnar cactus species *Echinopsis ancistrophora* Speg. and *E. chiloensis* ssp. *chiloensis* (Colla) H.Friedrich and G.D.Rowley (tribe Trichocereae) in Argentina and Chile, respectively (Schlumpberger et al. 2009; Walter 2010). This specialisation in particular pollinator taxa provides an appropriate scenario on which to test the role of natural selection and other evolutionary forces in shaping the origin and canalisation of specific flower traits.

We show four examples of cactus interactions that have important implications for our understanding of the evolution of life traits and maintenance of cactus biodiversity. We considered these examples of interactions involving cacti as negative or positive, although we acknowledge that they are the extremes of an essentially continuous categorisation. Negative interactions between cacti and other organisms are illustrated by (1) the evolutionary ecology of a host–parasite system in columnar cacti from Chile (Figure 1a), and (2) the population dynamics of an endemic cactus threatened by a strongly invasive competitor grass in Puerto Rico (Figure 1b). Positive interactions are illustrated by studies on (3) the seed dispersal ecology of *Melocactus* species by lizards in Venezuela and Brazil (Figure 1c), and by (4) the evolution of floral morphology in the endemic *Eriosyce* subgen. *Neoporteria* (Britton & Rose) Helmut Walter in Chile, in relation to biotic and abiotic drivers (Figure 1d). Finally, we discuss future research directions in order to address poorly explored aspects of interactions within the Cactaceae, and claim that this diverse group of plants can help to clarify some general aspects of the theoretical background of the ecology and evolution of species interactions.

Negative interactions

Evolutionary ecology of a cactus–mistletoe interaction in Chile

Parasitism is an exceptional interaction in cacti, albeit probably more widespread than currently known, since several cases of cryptic parasitism with fungi as parasites have been reported (Suryanarayanan et al. 2005; Ayala-Escobar et al. 2006; Pereira et al. 2007). One of the few examples of parasitism includes two columnar cactus species of central Chile that are endoparasitised by a member of the family Loranthaceae, *Tristerix aphyllus* Tiegh. ex Barlow & Wiens (Kuijt 1988), which presents specific adaptations to overcome the tangle of spines of the cactus (Medel 2000; González et al. 2007). The antagonistic interaction between parasites and cactus is not restricted to a pair-wise species system. For instance, unlike many parasites that use the pollinators of their hosts as vehicles for spore transmission, mistletoes have a mutualistic relationship with their vectors (i.e. birds that participate in the seed dispersal process), hence providing a clear example of a tripartite interaction system. The reliance of mistletoes on bird mutualisms for seed transmission makes the epidemiology of the mistletoe–cactus interaction distinctive. The effect of parasite infection and prevalence of disease transmission via a mutualistic vector is largely unknown (but see Martínez del Río et al. 1996; Medel et al. 2004).

The host–parasite interaction composed of *T. aphyllus*, a mistletoe endemic to the arid and semi-arid regions of Chile, and several cactus species of the genera *Echinopsis* Zucc. (tribe Trichocereae) and *Eulychnia* Phil. (tribe Notocactaceae) represents a suitable system in which to explore the historical and ecological determinants of host–parasite associations in plants (Figure 1a). Unlike all the other species of Loranthaceae, *T. aphyllus* has leaves reduced to minute scales (Kuijt 1969, 1988), which has been hypothesised to represent a derived adaptation that helps to prevent water loss and desiccation in the cactus–mistletoe system (Mauseth 1991). In Chile, the current distribution of the host–parasite interaction extends from 27° S to 35° S.

Tristerix aphyllus is distributed by the Chilean mockingbird *Mimus thenca* Mol. (Mimidae), the only bird that disseminates the mistletoe seeds. The bird swallows whole ripe fruits and the mucilaginous seeds pass through the digestive system of the bird intact (Martínez del Río et al. 1995). Seed deposition on cacti is often aggregated and occurs especially on short-spined and previously parasitised individuals (Medel et al. 2004). Once deposited by the bird, the seeds often adhere to the spines of cacti and send out an elongated reddish morphological structure that protrudes from the seed endosperm (radicle, hereafter) that grows for up to 8 weeks or until making contact with the epidermis of the cactus to form a morphological zone of contact from which several filaments penetrate into tissues of the cactus through stomatal openings (see details in Mauseth et al. 1984, 1985). Once inside the cactus, the plant grows for 18 months before emerging from inside the cactus as a red inflorescence to repeat the cycle (Botto-Mahan

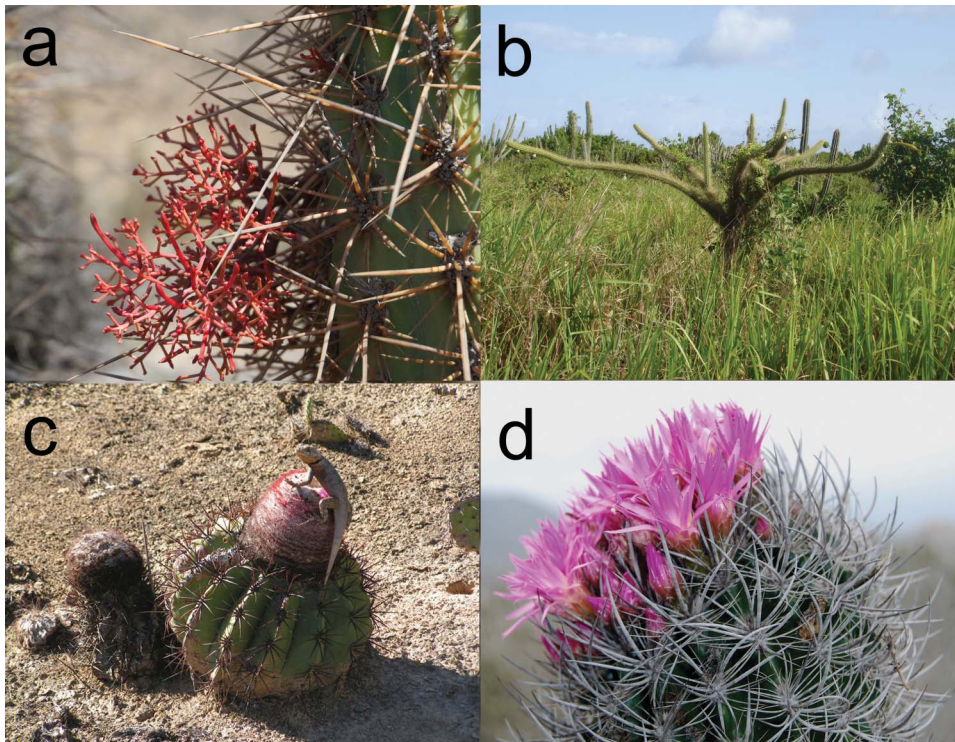


Figure 1. Cases of studies involving positive and negative interactions in Cactaceae; (a) *Tristerix aphyllus* parasitising *Echinopsis chiloensis* in Central Chile; (b) *Harrisia portoricensis* growing within a patch of the invasive grass *Megathyrsus maximus* in Puerto Rico; (c) the disperser lizard *Tropidurus hispidus* above *Melocactus curvispinus* cephalium in Venezuela and, (d) flower of *Eriosyce clavata* spp. *nigrihorrida* with specialised flower morphology in Central Chile. Images by (a) R. Medel, (b) J. Rojas-Sandoval, (c) V. Sanz and (d) P.C. Guerrero.

et al. 2000) (Figure 1a). The spines of Chilean columnar cacti have a dual functional value in relation to parasitism by *T. aphyllus*. Firstly, they represent a first barrier against infection by discouraging birds from perching on top of the cactus columns (Medel 2001). Investigations on the role of cactus spines as a defensive trait against infection by *T. aphyllus* in a local system of two cactus species, *Echinopsis chiloensis* (Colla) H.Friedrich & G.D.Rowley and *Eulychnia acida* Phil., indicated that bird visits to cacti and mistletoe seed deposition tended to be low on long-spined individuals. Spines of unvisited specimens of the two species were 1.29 and 2.32 cm longer on average than spines of individuals that received bird visits (Medel 2000). Similarly, spines of *E. chiloensis* and *E. acida* without seed deposition were longer than spines of individuals with deposited seeds (Medel 2000). Secondly, long spines prevent cacti from becoming infected when the first barrier is passed. By increasing the distance between the trapped sticky seeds and the cuticle of the cactus, they provide a physical barrier that often prevents infection, except by mistletoe seeds with the ability to produce extremely long radicles during the infection process. As infection by *T. aphyllus* decreases fruit and seed production and often suppresses reproduction in the host entirely (Silva and Martínez del Río 1996; Medel 2000), short-spined individuals are strongly selected against, and long spines can be expected to evolve as a result of parasite-mediated selection. This expectation has been corroborated in a 10-year

study of phenotypic selection on spine characters. Parasite-mediated selection, albeit variable across years, was found to promote long spines in *E. chiloensis* and *E. acida* (Medel et al. 2010).

Tristerix aphyllus does not parasitise all *Echinopsis* and *Eulychnia* species; several occur outside the geographical range of *T. aphyllus*. This suggests that those cactus species have not had a history of association with the mistletoe. Interestingly, the correlation between spine length and parasite prevalence fits well with the observation that the distribution range of short-spined cacti (*Echinopsis deserticola* (Werderm.) H.Friedrich & G.D.Rowley, *E. spinibarbis* (Otto) A.E.Hoffm., *Eulychnia iquiquensis* Britton & Rose, and *E. saint-pieana* F.Ritter) does not overlap with that of *T. aphyllus* at present (Medel et al. 2010). The observation that *Echinopsis litoralis* (Joh.) H.Friedrich & G.D.Rowley and *Eulychnia castanea* Phil. present short spines in spite of experiencing some level of infection suggests that these species might have only recently been integrated into the co-evolving system, or possess alternative defensive mechanisms.

Evidence indicates that (1) host species with high levels of infection at present tend to have long spines; (2) host species living outside the distributional range of the mistletoe at present have shorter spines than their relatives, probably because, unlike parasitised species, they have never been involved in an 'arms-race' co-evolution; and (3) the pattern is consistent in Chilean cactus species

belonging to different genera. Overall, these lines of evidence suggest that co-evolution is a phenomenon in action in the mistletoe–cactus system. Identification of the traits relevant to the interaction has enabled exploration of a range of questions that include local, phylogenetic, and geographical perspectives. Taken together, all the pieces of evidence indicate a phenomenon far more complex than previously thought. Intermittent local selection combined with a high host species turnover across localities suggests a very dynamic co-evolutionary process that is reflected in the variable levels of host–parasite trait matching and mismatching at the regional scale. In spite of this local and regional complexity, the long-term phylogenetic signal indicates a strong association between cactus defensive characters and parasitism, suggesting that the mistletoe is responsible for the extremely long spines presented by some Chilean columnar cacti. Regardless of the inherent community complexity in each locality, the signal left by the co-evolutionary process suggests that antagonistic interaction is an ongoing process across the cactus–mistletoe system. Current work on the phylogeographic structure of the interaction will help us to understand the genetic and historical determinants of the co-evolving cactus–mistletoe system across landscapes.

Responses of the native cactus *Harrisia portoricensis* Britton. (tribe *Trichocereae*) to the presence of the exotic grass *Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs (*Poaceae*)

The impacts of invasive species are among the primary threats to the conservation and management of biodiversity around the world (D'Antonio et al. 2000; Levine et al. 2003; Asner et al. 2004; Gardener et al. 2011). Biodiversity changes mediated by the interaction of exotic/invasive species with native species have been documented (Callaway and Aschehoug 2000), but how cactus regeneration and diversity are affected is only starting to be understood. Knowledge of the effects of invasive species on communities of arid and semi-arid areas is important since such areas represent >35% of the world's terrestrial surface and contain high species diversity and endemism (Cowling et al. 1996; Myers et al. 2000).

Within plant communities, endemic and rare species, due to their small population sizes, restricted geographic ranges, and, in many cases, poor competitiveness are particularly vulnerable to the impact of invasions by exotic species (Walck et al. 1999; Thomson 2005). In the Americas, exotic grasses are common invaders of tropical dry forests, where cacti are frequently dominant components of the native flora (Williams and Baruch 2000). Studies on grass invasions have demonstrated that exotic grasses can alter ecosystem functions (D'Antonio and Vitousek 1992; Levine et al. 2003) by changing community composition, fire regimes, hydrology, and nutrient cycles (D'Antonio et al. 2000; Fairfax and Fensham 2000; Ehrenfeld 2003; Mack and D'Antonio 2003; Brooks et al. 2004; Corbin and D'Antonio 2004; Ravi et al. 2009).

Considering that tropical dry forests represent one of the most endangered biomes in the world, the spread of exotic grasses into these habitats may result in the displacement and extinction of many species whose distributions are restricted to this habitat. Although cactus species are often dominant elements in dry, arid, and semi-arid forest communities, very few studies have addressed the effects of grasses on demographic parameters of cacti (Burger and Louda 1994; Morales-Romero and Molina-Freaner 2008).

Harrisia portoricensis is a slender columnar cactus formerly endemic to four Caribbean islands. At present, this species is locally extinct on the island of Puerto Rico and is geographically restricted to the small islands of Mona, Monito and Desecheo (USFWS 1990). *Harrisia portoricensis* is a night-flowering cactus listed as a threatened species under US Federal Regulations (USFWS 1990). The largest remnant population of *H. portoricensis* can be found on Mona Island; areas on the island where this cactus species is most abundant have been invaded by *Megathyrsus maximus* (Figure 1b), a perennial grass species introduced from Africa in the twentieth century, for use as livestock feed (Cintrón and Rogers 1991). Currently the grass species occurs ubiquitously and is spreading across the island (Rojas-Sandoval 2010).

Since 2007, various observations and field experiments have been conducted with *H. portoricensis* and *M. maximus*, on Mona Island to evaluate the effects of this exotic grass species on the demography (reproduction, recruitment, survival) and growth of the endangered cactus species (J. Rojas-Sandoval and E. Meléndez-Ackerman, pers. comm.). Results of these experiments have demonstrated that the presence of *M. maximus* negatively affected *H. portoricensis* throughout its life cycle; the survival, growth, and reproduction of *H. portoricensis* plants were depressed in the presence of *M. maximus*, compared with plants growing without the exotic grass (Rojas-Sandoval 2010). For *H. portoricensis*, the early stages appear to be more vulnerable to the presence of the exotic grass than adult stages. For instance, seed germination and seedling recruitment of *H. portoricensis* occurs only in areas without *M. maximus*, and the survivorship of juvenile and adult plants in areas without the grass is significantly higher (>70% for juveniles and >90% for adults) than in areas where the grass is present (30% for juveniles and 68% for adults).

Reproductive output (bud and flower production) and plant reproductive success (fruit production) of *H. portoricensis* are depressed by the presence of *M. maximus*. *Harrisia portoricensis* growing in areas without the grass produces more than twice as many buds, flowers, and fruits than plants growing in areas with the grass. Studies have also shown that the growth of *H. portoricensis* plants is better in areas without the grass than in areas with the exotic grass. Overall, results of these experiments suggest that modifications of the natural environment by the presence of *M. maximus* have added an additional level of vulnerability threatening the persistence of *H. portoricensis* on Mona Island. Given the large number of threatened

and endangered cactus species (Walter and Gillett 1998; Ortega-Baes and Godínez-Alvarez 2006), studies such as this one highlight the need for more investigation on the impact of invasive species on the demographic parameters of native cacti and the mechanisms by which native species interact with exotic species.

Positive interactions

Herpetochory in the genus Melocactus (tribe Cereeae)

Seed dispersal in cacti has been by far less studied than pollination. However, contributions to this topic underline the importance of biotic dispersal in the regeneration process of these plants through facilitation of germination and seed deposition under nurse plants (Bregman 1988; Valiente-Banuet 1991; Côrtes-Figueira et al. 1994; Godínez-Álvarez and Valiente-Banuet 1998; Godínez-Álvarez et al. 2003; Naranjo et al. 2003; Munguía-Rosas et al. 2009). The lower emphasis on seed dispersal is unfortunate, since this process may be a key factor in setting biogeographic patterns in some species. The case of the cactus *Rhipsalis baccifera* (J.S.Muell.) Stearn (tribe Rhipsalideae) is singular, because it is the only cactus species whose natural distribution extends to southern Africa, Madagascar and Sri Lanka, presumably caused by long-distance dispersion by birds (Barthlott and Taylor 1995). Birds and mammals are important seed dispersal agents in ecosystems worldwide. The role of other animals as seed vectors of vascular plants is less documented (Valido and Olesen 2007), but the available evidence indicates that in certain types of environments they can play a primary, or sometimes exclusive function as seed dispersers. Herpetochory is still considered an infrequent seed dispersal system in cacti and other angiosperms (Valiente-Banuet and Godínez-Álvarez 2002; Olesen and Valido 2003; Valido and Olesen 2007), mostly because it has not been examined in detail among the various tribes within Cactaceae that produce fruits which could be attractive to reptiles as food or water sources.

Frugivory by lizards has been reported in at least 18 plant families, 85 genera and 280 species, with predominance in insular ecosystems (Valido and Olesen 2007). Olesen and Valido (2003) explained the adoption of frugivory in island lizards as an evolutionary response to arthropod scarcity, high population densities of lizards, and reduced exposure to predation; these authors extended the arthropod-scarcity hypothesis to other habitats characterised by permanent or temporal scarcity of animal prey, such as arid regions, for example the arid and semi-arid areas in the Americas and the Caribbean, where the cactus family is a dominant plant group. The fleshy berries of these plants represent an important food and water source for many animals in arid zone ecosystems (Mellink and Riojas-López 2002). Cacti that produce fruits during most of the year (e.g. *Stenocereus griseus* (Haw.) Buxb., *Melocactus curvispinus* Pfeiff.; Nassar et al. 1997; Nassar and Ramírez 2004) provide a particularly reliable resource during periods when other plants do not produce flowers

and fruits. Based on these features, it should be expected that cacti be an important component of the diet of many desert reptiles. To date, more than 24 such species have been identified (A. Valido, pers. comm.). This includes several species of *Opuntia*, several genera of columnar cacti and members of the genus *Melocactus*. According to Taylor (1991), the monographer of *Melocactus* "... lizards may be the commonest of local dispersal agents" (Figure 1c).

The genus *Melocactus* is composed of 37 species of globose cacti, distributed between Mexico and Peru, in Brazil, and also present on several islands in the Caribbean (Taylor 1991). Its most prominent morphological feature is a cephalium of bristles and dense trichomes on the stem apex at reproductive maturity. Flowers and fruits are produced in this cephalium, and while immature they remain concealed inside it, only emerging when flowers mature and fruits are ripe. Frugivory and seed dispersal by lizards has been studied in three of the species: *Melocactus violaceus* Pfeiff. (Côrtes-Figueira et al. 1994), a species from coastal and montane areas in north-eastern and south-eastern Brazil; *M. schatzlii* H.Till & R.Gruber, a species from the Venezuelan and Colombian intra-Andean xeric areas (Casado 2009). The study on *M. curvispinus* included weekly monitoring of flower and fruit availability and fruit removal during a 1-year period, observations of fruit consumption by lizards and birds (two sites \times twice per month \times two 6-h periods of observations per site) during 6 months, analysis of 140 samples faeces of lizards, and germination experiments to determine germination rates in seeds after washing with water, seeds with fruit pulp and seeds obtained from lizard faeces.

The three species produce similar claviform berries, from pink to intense red, 1.5–2.5 cm long. Most of their content (>85%) is water, a valuable resource especially during the long dry season in the desert. Fruits become available during the morning, and sometimes fruit emergence extends into the afternoon. In two of the species (*M. schatzlii* and *M. curvispinus*) fruits are produced during most of the year. This could promote a close dependence by the lizards on melocacti fruit as their main source of water, a hypothesis yet to be tested.

In all three species, the main fruit consumers were lizards (*M. violaceus*: 100% *Tropidurus torquatus* Wied; *M. schatzlii*: 72.5% *Ameiva provitae* García-Pérez, 17.5% *Cnemidophorus lemniscatus* L.; *M. curvispinus*: 57.1% *Ameiva bifrontata* Cope, 28.6% *Cnemidophorus senectus* Ugueto, Harvey & Rivas, 14.3% *Tropidurus hispidus* Spix). In *M. schatzlii* 10% of fruit consumption was attributed to birds, but most of it by a granivorous species (7.5% *Tiaris bicolor* L.). Even though no birds were observed feeding on fruits of *M. curvispinus*, stomach contents analysed in specimens of *Mimus gilvus* Vieillot and *Cardinalis phoeniceus* Bonaparte captured in the study area indicated that these species might feed on melocacti fruits. Most faecal samples of the above reptiles retrieved in the field contained intact seeds of melocacti (9–34 seeds/sample), thus supporting their role as seed dispersal agents of these plants. The effect of seed ingestion by lizards on the percentage and rate

Table 1. Percentage of seed germination and day of germination initiation in seeds of melocacti ingested by lizards in comparison with seeds obtained directly from fruit pulp and washed with water. Data obtained from Côrtes-Figueira et al. (1994), Casado (2009) and V. Sanz, J.M. Nassar and E. Silave (unpublished data).

Treatment	<i>M. violaceus</i>	<i>M. schatzlii</i>	<i>M. curvispinus</i>
Seeds with pulp	0	First day: 7 th day; 90% after 33 days	First day: 9 th day; 95% after 39 days
Washed seeds	0	First day: 3 rd day; 92% after 26 days	First day: 4 th day; 100% after 10 days
Seeds ingested	First day: 6 th day; 36% after 36 days	First day: 3 rd day; 81% after 48 days	First day: 4 th day; 96% after 10 days

of germination was positive (Table 1). In *M. schatzlii* and *M. curvispinus*, germination was initiated several days earlier (3–4 days) in ingested seeds than in seeds with fruit pulp (7–9 days), but the total percentage of seeds germinated from lizards' faeces (81–96%) did not exceed that observed in seeds with fruit pulp (90–95%). *Melocactus violaceus* presented a special case of germination facilitation by lizards, since only seeds that passed through the guts of *Tropidurus torquatus* germinated.

Overall, these findings indicate that lizards do feed on fruits of melocacti, a resource that serves as their main supply of water during most of the year in some cases. These animals are the main fruit consumers of the studied species of *Melocactus* and they are bona fide seed dispersal agents because they ingest the seeds and move them around, and seeds remain viable once they are deposited in the faeces; in some cases such seeds germinate sooner than those not ingested. Altogether, the available evidence suggests that the conditions exist for the evolution of a facultative interaction between melocacti and lizards in the arid and semi-arid regions of the Neotropics.

Our knowledge of seed dispersal within melocacti is still restricted to three species; the general similarities among fruits of all species in the genus suggest that the whole group evolved this dispersal strategy. This can be interpreted as an example of what could be occurring in other groups of cacti, for which basic information on their dispersal ecology is still lacking. Exploring species with fruits similar to those of melocacti may be useful. One example is the fruits of *Mammillaria*; similar in colour to melocacti fruits, although smaller and rounder, they are equally accessible to lizards (A. Valiente-Banuet, pers. comm.). Once the representation of herpetochory within the cactus family has been resolved, the ecological and evolutionary implications of this dispersal system can be addressed (Cadotte 2006; Dwyer and Morris 2006; Jordano et al. 2007).

The role of hummingbirds and climatic factors in the variation of floral morphology of Eriosyce subgen.

Neoporteria (Britton & Rose) Katt. (tribe *Notocactaceae*)

It has been suggested that the pollinator assemblages (Sprengel 1996; Fenster et al. 2004) and climate factors may induce changes in reproductive structures, influencing

floral shape and morphology (Schemske and Bierzychudek 2001, 2007). The influence of climatic variables on floral morphology has received less attention, although climatic variability and abiotic gradients may induce morphological variation in life history traits, vegetative structures and the reproductive investment of plants, with consequences on the evolutionary dynamics of plants, as has been demonstrated for colour polymorphism observed in *Linanthus parryae* Greene (Schemske and Bierzychudek 2001, 2007). Climate may affect the size and shape of flowers, hence confounding the real effect of pollinators on the evolution of flower morphology, particularly when species are distributed along a steep abiotic gradient of precipitation, or temperature. Studies that simultaneously explore the contribution of abiotic and biotic components on floral evolution are still limited, although the development of this line of research should contribute an additional perspective on evolutionary and ecological trends in pollination syndromes.

Gradients of precipitation in northern and central Chile range from an almost complete absence of rainfall to >1000 mm annual precipitation (Guerrero et al. 2011b). To evaluate the relative role of hummingbirds and climatic factors in the variation of floral morphology, we examined the morphology of flowers in nine cold season-blooming taxa of *Eriosyce* subgen. *Neoporteria* (*Neoporteria*, hereafter) in relation to biotic and abiotic factors. We considered only plants with autumn and winter blooming, because in cold seasons insects are less active, and therefore plants should receive proportionally more pollination from hummingbirds, and this should have a measurable effect on the evolution of flower morphology. It has been suggested that hummingbirds are the main promoters of specific floral morphologies (trochilophilous syndrome, Schmidt-Leubuh et al. 2007), such as fused red corollas and abundant nectar with low sugar concentration. Along with quantifying the presence of four hummingbird species (*Oreotrochilus leucopleurus* Gould, *Patagona gigas* Vieillot, *Rhodopis vesper* Lesson and *Sephanoides sephanioides* Lesson), climatic variables including temperature and precipitation were studied. *Neoporteria* taxa are endemic to northern and central Chile between 25° S and 36° S, inhabiting areas with elevated oceanic influence in the southern Atacama Desert and in the Mediterranean zone of Chile. Flowers of these plants are fuchsia coloured, visited by hummingbirds,

and fit well to the ornithophilous syndrome (Ritter 1980; Walter 2008). Seed dispersal is limited and depends on fruit removal by animals (Kattermann 1994).

We used an index, based on 14 traits that reflected the overall floral morphology of *Neoporteria* (for details see Guerrero et al. 2011a). The index ranged between 0 ('specialist', trochilophilous flowers) and 1 ('generalist', wide and less tubular flowers). Occurrence probabilities were obtained using information on sampling localities from a literature search, and from museum collections (Field Museum, Chicago; Smithsonian Museum of Natural History, Washington; Vertebrate Museum of Berkeley, Berkeley). Since we focused on plants with autumn and winter blooming, we generated distribution maps of hummingbirds using maximum entropy modelling (Phillips et al. 2006; Elith et al. 2011), based on samples collected or observed in autumn or winter. We regressed the floral morphological index (response variable) against the modelled occurrence probabilities of hummingbird species and a different climatic data set than that used for modelling the occurrence probabilities.

Our results indicated that autumn–winter-blooming *Neoporteria* present a variable specialisation index (range: 0.03–1.00) (Figure 2); the species with most generalist floral morphology were *E. sociabilis* (F.Ritter) Katt. and *E. taltalensis* (Hutchison) Katt.; *E. clavata* (Söhrens ex K.Schum.) Helmut Walter and *E. clavata* subsp. *nigrihorrida* (Backeb. ex A.W.Hill) Helmut Walter showed the most specialised flower morphology (Figure 1d). All four hummingbird species had high probabilities of occurrence ($\geq 75\%$) along the coast of central Chile during the winter season. The multivariate model that best described the variation of the specialisation index included summer temperature and *S. sephanoides* occurrence probabilities. These results indicate that although the presence of *S. sephanoides* might be crucial in canalising the floral morphology to a trochilophilous syndrome, a fraction of the floral variation in *Neoporteria* may be attributable to summer temperatures. The direct relationship between summer temperature and flower specialisation is less clear. There are no studies linking climatic variables with floral morphology in a mechanistic mode, excepting works that describe the impact of climate on the structure of pollinator assemblages (e.g. Herrera 1995; Arroyo et al. 2006; Hegland et al. 2009). Our research suggests that climatic gradients might induce morphological change, although more experiments are needed for further generalisation. As we have shown, summer temperatures may be a relevant factor in determining flower shape in *Neoporteria*, since global climate change affects precipitation and temperature regimes in Chile (Falvey and Garreaud 2009; Vicuña et al. 2010), and thus may impact cacti–hummingbird interactions. This is an unresolved topic that may be addressed with a greater availability of geographically explicit high-resolution abiotic information and long-term ecological research sites that contribute to inferring past tendencies and projecting putative consequences of global warming on plant–animal interactions. We will continue assessing

the way that biotic and abiotic factors impact on floral morphology, and elucidate the possible effects of climate change and biodiversity loss on the cactus–pollinator interaction.

Outlook

A structured and effective international collaboration among research groups that leads to a research agenda that targets a number of promising lines in future research is proposed.

1. *Develop a Cactus Interactions Database.* Techniques, such as ecological niche modelling (Graham and Fine 2008; Guerrero et al. 2011a), phylogenetic perspectives on communities (Fine and Kembel 2010), and network representation (Verdú and Valiente-Banuet 2008) offer new insights into ecological and evolutionary questions; however, this requires a systematised management of information, from local to regional scales. Internet-based technologies have been widely used for species list inventories that can be applied to generate inventories of mutualistic and antagonistic interactions involving cacti. The development of this database should proceed hand in hand with new developments in phylogenetic systematics, a critical shortcoming in our current knowledge of cactus evolution, and also using the available tools to analyse ecological interaction networks.
2. *Invasion biology.* Biological invasions may affect native cacti in their natural habitats, impacting negatively the long-term persistence of cactus communities (Burger and Louda 1994; Morales-Romero and Molina-Freaner 2008; Rojas-Sandoval 2010). Also, invasion by naturalised cacti has important consequences for the composition of communities in several European countries (Vilà et al. 2003; Essl and Kobler 2009) and in Australia (Foxcroft et al. 2011). Invasion biology studies focused on cacti provide new insights regarding the mode of spread and establishment of plants, and identification of traits relevant to naturalisation in the invaded regions. For example, comparisons of the architecture of interactions between native and invaded communities may provide important information on the mechanisms of local adaptation in long-lived species. These could indicate answers that can be applied to natural habitats and support conservation strategies.
3. *Multi-species interactions.* Pollination, seed dispersal and nurse plant associations are fundamental ecological interactions that can be critical for the maintenance of some species of cacti. In specialist species, seed set relies on the pollination services by a particular group of vertebrate or insect species. Pollinator loss could threaten the long-term maintenance of the populations of the species

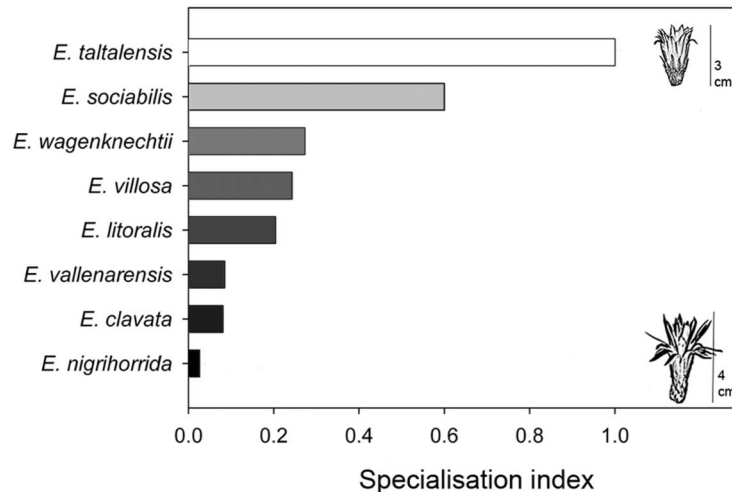


Figure 2. Specialisation index of the overall floral morphology based on 14 traits of the *Eriosyce* taxa with autumn and winter blooming. Darker greys indicate more specialised flowers. Note that the names of *E. clavata* subsp. *nigrihorrida* (Backeb. ex A.W.Hill) Helmut Walter, *Eriosyce subgibbosa* (Haw.) Katt. var. *litoralis* (F.Ritter) Katt., *E. subgibbosa* subsp. *vallenarensis* (F.Ritter) Katt., *E. subgibbosa* subsp. *wagenknechtii* (F.Ritter) Katt., were truncated in the figure. Illustrations represent the flower of *E. taltalensis* (top) and *E. clavata* subsp. *nigrihorrida* (bottom).

that had co-evolved with the pollinators. The same applies to seed dispersers. Ecosystem degradation could decrease the population densities of nurse plants that help establish some species of cacti during their initial life stages (Castillo-Landero and Valiente-Banuet 2010; Castillo et al. 2010). It is important to conduct studies to identify these key interactions and to evaluate their status.

Tackling the three issues listed above will lead to an improvement of our knowledge of the ecology and evolutionary biology of cactus interactions. Such information can provide of the required level of knowledge to aid decision-making regarding conservation management, such as sustainable use, ecological restoration, and environmental education to help the preservation of cactus diversity.

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The Latin American and Caribbean Society of Cactaceae and other Succulents (SLCCS) organised a symposium at the Latin American Congress of Botany in La Serena, Chile held in October 2010. This meeting brought together researchers from many of the regions that are currently investigating diverse questions in the area of positive–negative interaction spectra using cacti as the main focal species. The broad aim of this symposium was to share perspectives and experiences in the issues of ecology and evolution of species interactions involving cacti. The organisation of this symposium was supported by ICM Proyecto 02–005, PFB – 23 – 2008 and Grant ACT 34/2006. CONICYT scholarships funded the work of PG (D-21070301, AT-24090076) and GC (BTT-23100127). Thanks to Laszlo Nagy and anonymous reviewers for helpful comments on this manuscript.

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