

FLOWERING PHENOLOGY AND OBSERVATIONS ON THE POLLINATION BIOLOGY OF SOUTH AMERICAN CACTI. 3. TEMPORALLY ROBUST SEQUENTIAL “BIG BANG” FLOWERING OF TWO UNRELATED SYMPATRIC GLOBULAR CACTI IN NORTHERN ARGENTINA

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Abstract: Sequential flowering of sympatric plant species is a commonly observed phenomenon and is thought to contribute towards maintaining the pollinator community. Sequential flowering is also interpreted as a potential way to reduce competition for pollinators and to reduce interspecific pollen transport.

Within-season sequential flowering is well-known for many species assemblages and usually shows a staggering over weeks and months. Here, we report on the flowering behaviour of two unrelated sympatric cacti (both Cactaceae — Cactoideae) from N Argentina, *Acanthocalycium thionanthum* (Cereeae — Trichocereinae) and *Parodia microsperma* (Notocactaceae). At the start of the flowering season, the two taxa exhibit a temporally stable sequential mass-flowering that is triggered by the first rainfall event after the dry season: On the 6th or 7th day after the rainfall, *Parodia microsperma* starts a 3-day “big-bang” flowering period, and on the 8th or 9th day after the rainfall, *Acanthocalycium thionanthum* also starts a 3-day “big-bang” flowering period, with 1 day of overlap with that of *Parodia*. The sequence and duration, including the 1-day overlap, has been found to be temporally stable in all study years, with c. 90% of all flowers buds of a population opening synchronously in years with average spring rainfall. Later in the season, after the fruits derived from these initial flowerings have ripened, opportunistic flowering (including sporadic local small-scale mass flowerings) is exhibited by both species with no apparent synchronization or sequence. Only once was a second “big bang” flowering observed, likely caused by above-average dry conditions. The species pair is notable for the massive “big-bang” flowering triggered by rainfall with a tightly staggered synchronization, as well as for the change in flowering strategy later in the season.

Keywords: Cactaceae *Acanthocalycium Parodia* Argentina pollination ecology

INTRODUCTION

Only successful reproduction allows the continuation of a population beyond the average lifespan of its individuals. Assuring reproductive success (composed of the components flower production, pollination, fruit / seed ripening, seed dispersal, and seedling establishment) is therefore of prime importance, but must be seen in the context of life history strategies (e.g. r vs K strategies), and resource allocation costs (e.g. as mediated by minimizing competition for pollinator service, or minimizing loss of developing fruits or ripe seeds).

For plants growing in resource-limited environments (especially seasonally recurring water shortage) with large year-to-year differences in availability of resources (both in timing and amount), assuring reproductive success is a particular challenge. As discussed in an earlier contribution (Eggli & Giorgetta 2015a), studies of pollination biology are an important component towards elucidating the ecological network in which a plant taxon is embedded, because successful

pollination is the prerequisite for sexual reproduction.

Species of cacti are often conspicuous and at times dominant elements throughout the vegetation of the arid and semiarid parts of North and South America. The majority of cacti are outcrossing (Anderson 2001: 33, Boyle 2003, Mandujano et al. 2010), i.e. a vector is needed to transport pollen from the stamens of one individual to the stigma of another conspecific individual. Only comparatively few species of the family have been the subject of detailed pollination biology studies (see Schlumpberger 2012 for an overview), and studies of interrelationships between simultaneously or sequentially flowering species are practically non-existent, apart from a study of 5 sympatric species of *Gymnocalycium* in Córdoba (Argentina) (Giorgetti & al. 2015), and the study of the plant-pollinator webs of a complete community in Mendoza (Argentina) (Chacoff & al. 2012).

Flowering periods with a more or less clearly defined duration are well known and easily visible in almost any vegetation from places with seasonal cli-

mates (Vogel 1983, Willmer 2011: 483 and references there cited). A sequence of different species flowering in succession with or without overlap is usually evident. This sequence is as a rule more or less stable from one year to the next, and it is generally associated with the progress of the season, i.e. climate-driven (temperature, day-length, availability of water through thawing of frost, or seasonal precipitation) (Vogel 1983, Elzinga & al. 2007). For cacti, Fleming & al. (1996) found a staggering of flowering periods over several weeks in sympatric columnar species in the Sonoran Desert.

Synchronous flowering, i.e. a more or less complete overlap of the flowering periods of the individuals of a population of a species, is an important prerequisite for successful outcrossing. Depending on the duration of a population's flowering time, cornucopia flowering, steady-state flowering, and big-bang flowering can be distinguished (Willmer 2011: 484). Equally important is the synchronization of the flowering period with the availability of the pollen transfer vector(s). When pollen transfer is animal-mediated, synchronization must involve the individuals of both the plant and the animal populations. In water-limited environments it is assumed that synchronization of both levels can be achieved via the availability of water, i.e. rainfall events trigger the synchronization (Stiles 1977, Opler & al. 1976, Willmer 2011: 488), but other triggers such as changes in temperature or changes in the day-length over the course of the year could also be involved (at least for plants).

Overlap in the flowering period of different plant species that share the same pollinator(s) causes an interaction between the involved plant species, and this is usually regarded as competition (Willmer 2011: 489). Competition can be at the level of attracting pollinator visits (simultaneous flowering can reduce the number of visits to a given species because flowers of other species are also available to the pollinator(s)), or at the level of pollen carrying quantity (simultaneous flowering can "dilute" own pollen and result in heavy loads of foreign pollen that block the stigma to various extents so that germination of conspecific pollen is hindered). Sequential flowering ("phenological separation", Elzinga & al. 2007) is an escape mechanism that reduces competition for visits and reduces pollen movement between species (e.g. Stiles 1977).

Obligatorily outcrossing plant species (such as most cacti) are dependent on the availability of their pollinator(s). If the flowering season of a given plant species is very short, the pollinator is usually dependent on additional plant species that provide food to enable completion of its life cycle beyond the flowering period of that given species. The interaction space between pollinators and the pollinated plants thus rapidly gains additional dependencies with each additional species (both of plants and pollinators) that is involved, and community-level adaptive peaks are assumed to be present (Endress 1994: 213) in this multi-dimensional adaptive space: Sequential flowering of plant species helps to maintain the pollinator community (Stiles 1977, Willmer 2011: 509), i.e. se-

quential flowering has community-wide beneficial effects.

Here, we report on the highly synchronized flowering pattern exhibited by two unrelated sympatric cacti at the start of the rainy summer season in northwestern Argentina, followed by a change of flowering strategy later in the season. It is the first study to address questions of flowering synchrony in an arid environment in highly specialized succulents; previous studies concentrated on shrubs and trees from tropical environments with less seasonality.

MATERIAL AND METHODS

Study organisms: *Parodia microsperma* (F. A. C. Weber) Spegazzini and *Acanthocalycium thionanthum* (Spegazzini) Backeberg are small globose cacti that usually grow as solitary individuals in large scattered populations with hundreds or thousands of individuals. *Parodia* (c. 66 species, widespread in E South America from S Brazil to C Argentina) is classified in the South American tribe Notocactaeae, which embraces 104 species (all globose) in 5 genera (Nyffeler & Eggli 2010). *Acanthocalycium* (5 species, confined to C and N Argentina) is classified in tribe Cereeae, which embraces 439 species (with various growth forms from arborescent to shrubby to solitary and globose) in 34 genera, with few exceptions confined to South America (Nyffeler & Eggli 2010). Within the tribe, *Acanthocalycium* belongs to subtribe Trichocereinae. The classification of the genera assigned to this subtribe is largely unresolved, and some authors (e.g. Hunt & al. 2006) include *Acanthocalycium* in *Echinopsis* s.l. Schlumpberger and Renner (2012) found that *Echinopsis* s.l. is both polyphyletic and paraphyletic relative to other genera of the subtribe, and accept *Acanthocalycium* in expanded form, together with numerous further segregates.

Acanthocalycium thionanthum (Fig. 1a) has a narrow range in N Argentina (NE Catamarca, S Salta, NW Tucumán) and occurs between 1500 and 3000 m (Trevissón & Perrea 2009, Anderson & Eggli 2011). Its flowers are usually sulphur-yellow but can occasionally be pale yellow, and very rarely also white or even pinkish; the colour remains unchanged over the whole anthesis.

Parodia microsperma (Fig. 1b) has a wide range in N and C Argentina (Catamarca, Jujuy, La Rioja, San Juan, Santiago del Estero, Salta, Tucumán) and occurs between 500 and 3000 m (Trevissón & Perea 2009, Anderson & Eggli 2011). It is an exceedingly variable taxon with several dozen synonyms (Anderson & Eggli 2011). Two subspecies (subsp. *microsperma*, ssp. *horrida*) are currently recognized (Hunt & al. 2006, Anderson & Eggli 2011) but show partially overlapping characteristics, and more studies are needed for a full understanding of the variability of the taxon over its whole range. Flower colour can be yellow, orange, or various shades of red. In the study area, all populations except one have yellow flowers, which change to yellow-orange and orange-red and red on the 2nd and 3rd day of anthesis, respectively.



Figure 1. The study organisms, *Acanthocalycium thionanthum* (a) and *Parodia microsperma* (b).



Figure 2. Mixed population of the studied cacti in full bloom at the day of overlap of their “big bang” flowering events.

The geographic areas of the two study taxa overlap considerably in N Argentina (not evident from the distribution maps of Trevisson & Perea 2009). Both taxa grow on stony hillsides and rocky-gravelly alluvial soils, either in the open or in the shade of shrubs. Due to slightly different preferences for soil conditions (see results), mixed populations (Fig. 2) are not common.

The root system of both study species consists of only fibrous roots without water-storage capacity. Most of the roots extend laterally within the superficial 2–6 cm of the topsoil (pers. obs.).

Study site: The study was made near the village of Angastaco (1850 masl), which is situated in the Valles Calchaquíes, Dept. San Carlos, Prov. Salta, NW Argentina. Two sites were studied (Fig. 3): The Cerro Negro site is situated at the foot and lower slopes of Cerro Negro, c. 3 km S of the village of Angastaco, at an altitude of 1980 masl. The Cerro Bayo site is c. 4 km NW of the village of Angastaco, at an altitude of 1925 masl, at the foot of a small hill (simply known as “Morro”) in the foreland of the Cerro Bayo. The sites are separated by c. 3.5 km. Both sites are populated by very numerous individuals of both taxa. The Cerro Negro is predominantly composed of Ordovician metamorphic schists (485–443 My), while the Cerro Bayo consists of pale and rosy intrusive granites (from the same geological period) (pers. comm. Sr. Gustavo, a local geology student, superseding earlier information, e.g. Valencia & Lago 1970).

The climate of the region is characterized by a long dry period from autumn to spring (April to November) that alternates with a wet period in summer (December to March). 80–85% of all rains fall during the

summer months (December to March). No specific climatic data is available for Angastaco (1850 masl), but stations in the general region with published long-term data are those of Cachi (2435 m, 65 km to the N), La Poma (3022 m, 107 km to the N) and San Carlos (1605 m, 35 km to the SE) (additional stations were established in March 2012 in Seclantás and in November 2014 in Cafayate). Mean annual rainfall varies from 95 mm for Molinos (2042 m, 30 km to the NW) to 200 mm for Cafayate (1630 m, 46 km to the SE) (Table 1; Paoli 2003: 10). Average maximum summer temperatures for San Carlos are given as 22.1 °C for January, average minimum winter temperatures as 9.3 °C for June (Table 2, Paoli 2003), and these temperatures are likely also applicable to Angastaco.

Associated cacti in the area are *Cumulopuntia pentlandii* (Salm-Dyck) F. Ritter, *Tephrocactus molinensis* (Spegazzini) Backeberg, *T. weberi* (Spegazzini) Backeberg, *Tunilla soebrensis* (Britton & Rose) D. R. Hunt & Liff agg. (the correct identification of these plants is currently unresolved, and the name is here used in a wide circumscription), *Cereus aethiops* Haworth (see Eggl & Giorgetta 2015b), *Denmoza rhodacantha* (Salm-Dyck) Britton & Rose (see Eggl & Giorgetta 2015a), *Echinopsis atacamensis* (Philippi) H. Friedrich & G. D. Rowley, *Gymnocalycium saglionis* (Cels) Britton & Rose, *G. spegazzinii* Britton & Rose, and *Parodia aureicentra* Backeberg. Other succulents present are *Portulaca pilosa* Linné, *P. cryptopetala* Spegazzini, *P. grandiflora* Hooker, *P. oleracea* Linné, *Talinum polygaloides* Gillies ex Arnott, *Deuterocohnia haumannii* A. Castellanos, and *Jatropha excisa* Grisebach, as well as *Tillandsia capillaris* Ruiz & Pavón, *T. duratii* Visiani and *T. tricholepis* Baker.

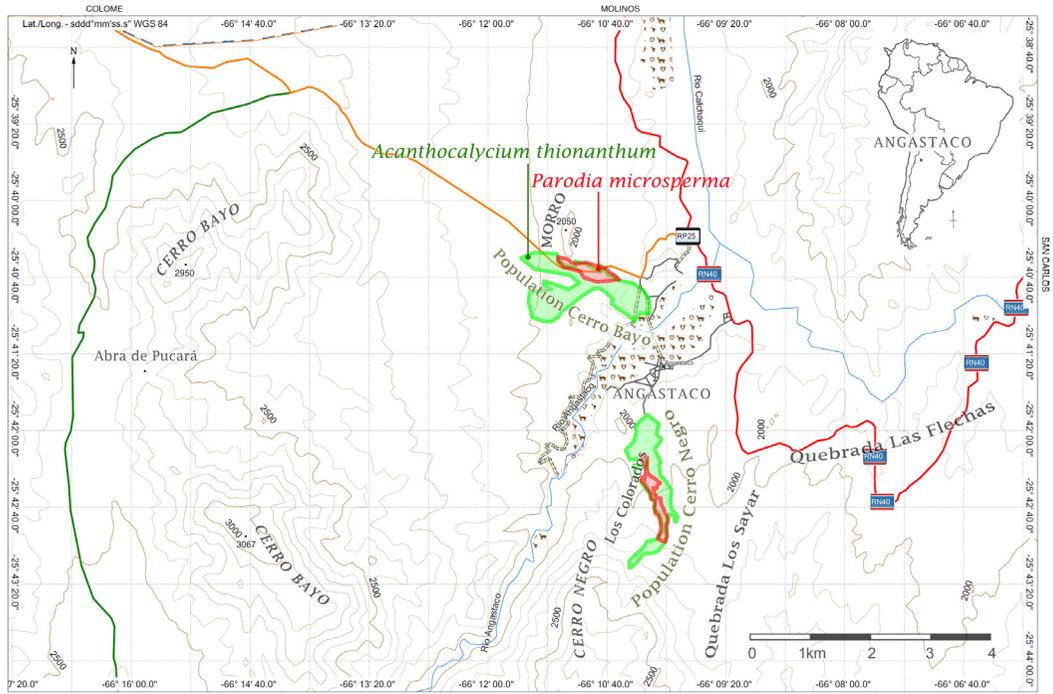


Figure 3. Map of the study region in the Valles Calchaquíes, Salta Province, N Argentina. Populations of *Parodia microsperma* shown in red (0.18 km² at the Cerro Negro site, 0.19 km² at the Cerro Bayo site), populations of *Acanthocalycium thionanthum* shown in green (1.20 km² at the Cerro Negro site, 0.80 km² at the Cerro Bayo Site).

Table 1: Rainfall data (average monthly amounts in mm) from the study region (data from Paoli 2003).

| Place | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Year |
|--------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|
| Cachi 1973–90 | 68 | 36 | 15 | 3 | 0 | 1 | 0 | 1 | 0 | 3 | 5 | 30 | 163 |
| San Carlos 1977–90 | 45 | 15 | 12 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 7 | 29 | 111 |
| La Poma 1974–90 | 59 | 31 | 14 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 3 | 27 | 139 |

Table 2: Temperature data (monthly averages in °C) from the study region (data from Paoli 2003).

| Place | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Year |
|--------------------|------|------|------|------|------|-----|------|------|------|------|------|------|------|
| Cachi 1973–88 | 18.5 | 17.7 | 16.9 | 14.0 | 11.1 | 9.6 | 10.0 | 11.3 | 13.0 | 15.9 | 17.6 | 18.4 | 14.5 |
| San Carlos 1978–88 | 22.1 | 21.4 | 20.5 | 16.5 | 12.7 | 9.3 | 10.7 | 13.0 | 15.0 | 19.2 | 21.0 | 21.9 | 16.9 |
| La Poma | 14.5 | 14.2 | 13.1 | 10.4 | 7.1 | 4.8 | 4.3 | 6.5 | 8.9 | 11.5 | 13.3 | 14.3 | 10.2 |

The studied cacti grow in the open or in the shade of shrubs that are commonly present in the area, such as *Bulnesia schickendanzii* Hieronymus ex Grisebach and *Plectrocarpa rougesii* Descole & al. (both Zygo-phylaceae), and *Cercidium praecox* (Ruiz & Pavón ex Hooker & Arnott) Harms, *Cercidium andicola* Grise-

bach, *Acacia macracantha* Humboldt & Bonpland ex Willdenow, *Prosopis ferox* Grisebach and *Zuccagnia punctata* Cavanilles (all Fabaceae).

Methods: Plants were observed in the field by MG during numerous trips to the region of the Valles Calchaquíes (Salta province) in the past almost 30 years.

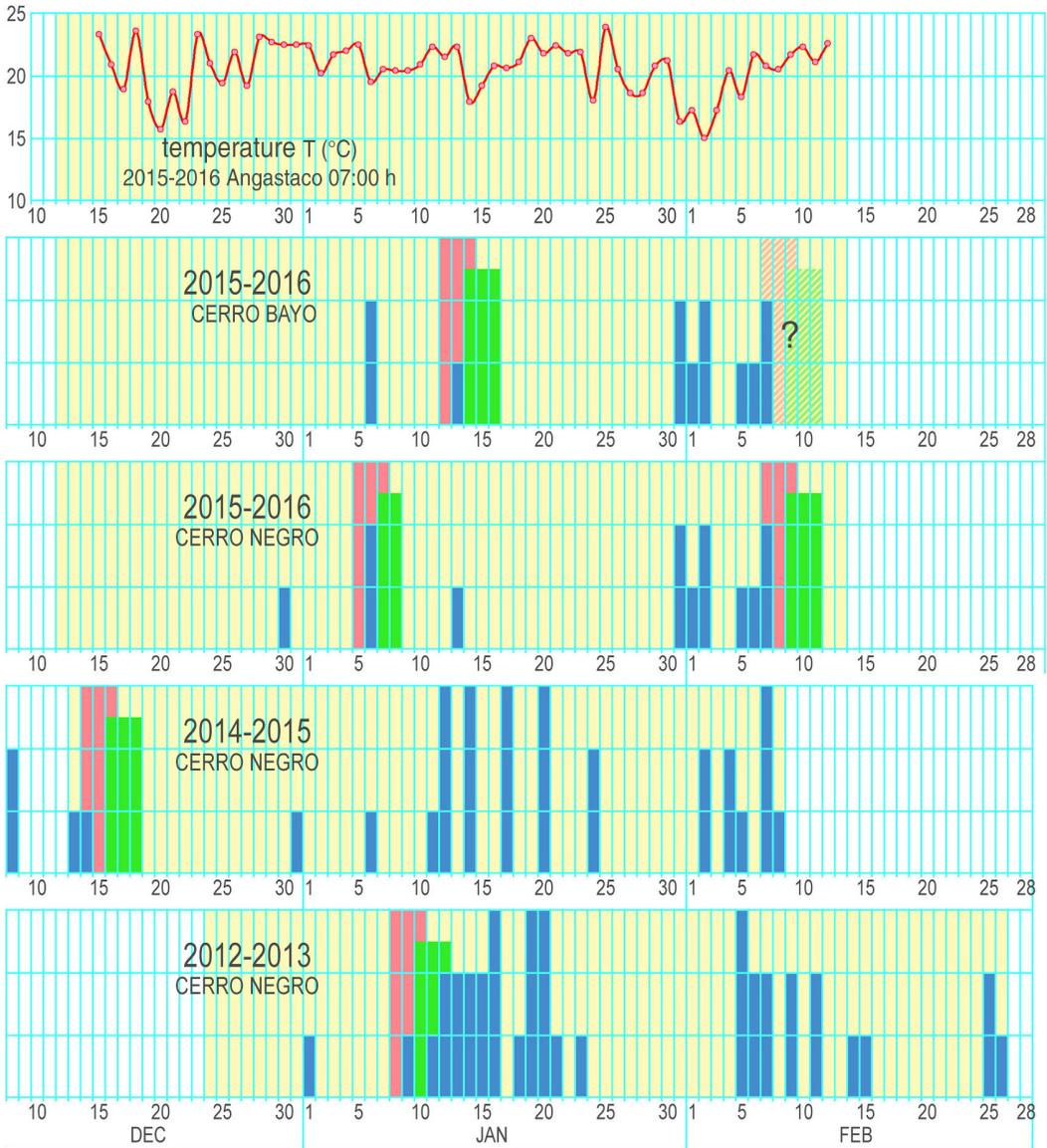


Figure 4: Diagram of rainfall events (dark blue columns, classified as slight, medium, strong, see text), temperatures, and flowering periods (green = *Acanthocalycium*, pink = *Parodia*). The observation periods are shaded in pale yellow. The shaded flowering periods with the question mark in the 2015–2016 Cerro Bayo data indicate the assumed mass flowering of that population (see text for background).

Detailed observations were then conducted by MG between December and February in the summers of 2012/13, 2013/14, 2014/2015 and 2015/16, resulting in a total of 108 days of field observations. The studied plants, their flowering phenology, and flower visitors were documented by a total of 5300 photographs and 17 videos. The flowering phenological data of 2013/14 is incomplete (and therefore not included in Fig. 4) because observations were concentrated on fruit and seed dispersal studies in that summer.

RESULTS

Climate & rainfall: Angastaco has a characteristic microclimate that is drier than that of the immediate surroundings. Based on personal observations, summer rains can be pronounced and locally heavy in the Valles Calchaquíes region, while the immediate surroundings of Angastaco to a distance of c. 20 km remain sunny and dry. Rainfall can be very local even within these immediate surroundings, and vary significantly from heavy rains to no rain at all within a distance of 5 km or less. Since equipment for rain measurements was not available, daily rainfall was classified into three classes — slight, medium or strong

(Fig. 4). “Slight” refers to rains only wetting the soil surface, while “strong” refers to strong to torrential rains of several hours that penetrate deeply into the soil.

The study period 2015/16 was the driest and warmest summer of the past 30 years, and also the preceding 2015 winter was exceptionally dry (pers. comm. of local inhabitants; the 9-month arid phase is also visible in the data from the recently established weather station at Seclantás, 40 km N of the study area and 200 m higher; data not shown). The intensity of the drought is exemplified by the complete absence of the mass flowering (usually around New Year) of the local *Cercidium praecox* populations. Damage of cacti by herbivory was evident throughout the region, and goats and donkeys (rarely also guanacos) consumed flowers and / or roots and plant bodies especially of *Opuntia sulphurea* and *Gymnocalycium saglionis*, but occasionally also of *Acanthocalycium thionanthum*.

Spatial characterization of the populations: An analysis of the distribution of the plants in the study area shows slightly different habitat preferences of the study species: *Acanthocalycium* favours relatively sandy and level sites, whereas *Parodia* prefers rocky sites (such are especially common on the schistose rocks of the Cerro Negro area), but *Acanthocalycium* also occurs on rocky-sandy places, sympatrically with *Parodia* (Figs. 2 & 3). The plants grow in a randomly scattered manner, without any apparent pattern, commonly in open conditions, but not rarely in the shade below shrubs. Population density of *Parodia microsperma* at the study sites is estimated to be c. 1 individual/m², but at some places, as many as 20 individuals/m² can be observed when plants are aggregated in groups. *Acanthocalycium thionanthum* has an estimated density of c. 0.5 individual/m², but can occur in groups of 10–15 individuals.

Growth phenology: At the end of the dry season, plants of both taxa are considerably shrivelled, with tightly interlocking spines from adjacent areoles. Differences between drought-stressed and actively growing plants are, however, minimal, without apparent colour-changes of the epidermis, or clearly demarcated new growth. Flower buds are visible in early December on both study species. The buds are located in the apex of the globose to cylindrical plant bodies and reach a uniform size of 8–9 mm length and 3–4 mm diameter for *Parodia*. The buds of *Acanthocalycium* are located in a circle around the apex of the globose to cylindrical plant bodies, and reach a uniform size of c. 14 mm length and 12 mm diameter. At this size, the buds have a “waiting” phase that can last up to 1 month, until the first rainfall event. After the first rains, the “waiting” buds rapidly resume growth to pre-anthesis size.

Flowering phenology: Rainfall as well as flowering events are visualized in fig. 4 for two sympatric populations of the study species. Each of the species exhibits a “big bang” flowering period of 3 days, with an overlap of 1 day. For both species, about 90% of the flower buds present on flowering-sized individuals of a population open synchronously in hydrologically normal

years; the remaining flowers open in a scattered fashion independent of rainfall events, and as much as 2 weeks before the advent of rains. During the “big bang” flowering, both species open an average of 2–4 flowers per plant, with maximum flower numbers reaching 8 or 9 (–14) for *Parodia*, and occasionally 12 (–14) for *Acanthocalycium*; young adults of both species usually produce a solitary flower only. The life span of individual flowers is a maximum of 3 days, but after successful pollination, flowers close rapidly and do not open again on the next day. The overlap in flowering periods is thus most pronounced when the flowers of *Parodia* are poorly pollinated. Flowers of both species are strictly diurnal and open late in the morning around 10:00 in sunny weather. Flowers of *Acanthocalycium* start to close around 14:00, while those of *Parodia* close 16:00–17:00, or rarely stay open until around 18:00. *Parodia* flowers assume an orange-yellow colour at the 3rd day of anthesis and turn dark red when finally closed; those of *Acanthocalycium* show no colour changes during anthesis. The timing as well as the sequence of anthesis (first *Parodia*, then *Acanthocalycium*) was absolutely stable in all study years. Flowering always starts after a lag phase of 5 days (6 days in the 2012–2013 observation period) after the first rainfall event that terminates the long dry season. Whether this is a “slight” rainfall (periods 2012/13, 2015/16 at Cerro Negro) or a “medium” rainfall (periods 2014/15, 2015/16 at Cerro Bayo) has no influence on the timing of the “big bang” flowering, and whether this first rainfall is early in the season (8 December in the period 2014/15) or late (6 January in the period 2015/16 at Cerro Bayo) also does not have any influence. In addition, “big bang” flowering is not restricted to mixed stands of the study species, but also occurs in pure stands of either of the two cacti (data not shown).

A comparison of the two populations (Cerro Bayo, Cerro Negro, distance c. 3.5 km) studied in the 2015/16 period moreover shows that the relationship between the timing of the first rain and the start of the “big bang” flowering is temporally stable — the first rain at the Cerro Negro site arrived at December 30, 2015 with subsequent flowering starting January 5, 2016, while the first rain at the Cerro Bayo site only occurred on January 6, 2016, with flowering starting January 12, 2016.

The amount of rain needed to induce the “big bang” flowering is unknown, but even relatively small rainfall events are effective: The rainfall event at 01:00 of December 30, 2015 at the Cerro Negro site is classified as “slight”; it consisted of a short and strong rain of c. 20 min. duration. A partial excavation of the root system of the study cacti showed that the soil was wetted to a depth of c. 6 cm (this includes the major part of the rooting horizon of both species), but due to strong evaporation, the top-most 2 cm of the soil were already dry again in the afternoon at 13:30.

Usually, only a single “big bang” flowering event at the start of the rainy season can be observed. The only exception to this pattern is shown by the 2015/16 observations at the Cerro Negro site, where a second “big bang” flowering occurred just a little

bit more than one month after the first such event. This second “big bang” flowering was also related to a rainfall event following a dry period (medium, slight and medium rains over a period of 3 days, fig. 4 top row) and also had a lag phase of 6 days. Whether the near-by Cerro Bayo populations also produced a second “big bang” flowering could not be investigated for lack of time. The reason for the observed second “big bang” flowering is likely the very dry winter of 2015: During the first “big bang” flowering, only c. 70% of the buds present opened. The remaining c. 30% of the buds were underdeveloped (i.e. too small) at that time; they completed development as a result of the first rain and then entered the “waiting” stage, and only opened after the second rain to produce the second flowering event.

Both species produce further flowers later in the season, but only after the fruits resulting from the “big bang” flowering have ripened, i.e. after about 4 weeks. Open flowers are almost never present on fruiting plants, but buds can start to develop while fruits are still ripening. These further flowers are produced in small numbers (compared to the bunch of up to 9 or more flowers in the “big bang” flowerings), and without synchronization between conspecific individuals of the population.

Flower visitors & pollination: Flowers of both study species are visited by several insect species, with considerable variation between the study periods. Observations were made on selected individuals of both species, but no standardized counts were possible due to the area covered by the populations and the scattered arrangement of the plants. Flower visitors observed during the study summers are the following:

Flies:

Bombyliidae: *Hemipenthes* sp. (frequent on both *Acanthocalycium* and *Parodia*), *Anthrax baliopteros* (common on both *Acanthocalycium* and *Parodia*), *Exoprosopa fasciata* (rare on *Acanthocalycium*)

Sarcophagidae: unidentified Sarcophagid (occasionally on *Parodia*)

Syrphidae: Syrphidae sp. (occasionally on both *Acanthocalycium* and *Parodia*)

Bees:

Apidae: *Apis mellifera* (European Honeybee, introduced, visits only *Acanthocalycium* but not *Parodia*) (very common), *Xylocopa* sp. (rare at these low altitudes, rare on *Acanthocalycium*)

Colletidae: *Hylaeus* sp. (common on both *Acanthocalycium* and *Parodia*, a solitary and oligolectic bee associated with many cactus flowers, with very pronounced sexual dimorphism)

Halictidae: *Halictidae* sp. (occasionally on both *Acanthocalycium* and *Parodia*; a small bee, similar to that observed as pollinator of *Denmoza rhodacantha* [Eggl & Giorgetta 2015a], but clearly a different species)

Megachilidae: Unidentified megachilid bee (occasionally on *Acanthocalycium*)

Melittidae: *Dasygoda* sp. (occasionally on both *Acanthocalycium* and *Parodia*)

Butterflies:

Pieridae: *Ascia monuste* and *Phoebis sennae* (both occasionally on *Acanthocalycium*)

Riodinidae: *Aricoris chilensis* (common on *Acanthocalycium*)

Beetles:

Cantharidae: Perhaps *Silis* sp. (commonly and often in large numbers on both *Acanthocalycium* and *Parodia*, and many other cacti)

The species spectrum of the visitors was found to vary considerably from year to year, probably as a result of the differences in arrival and amount of rains (and especially the succession of 2 dry periods 2014/15 and 2015/16), but probably also because of indiscriminate insecticide use on agricultural land. The most important visitors are the introduced honeybee and the unidentified colletid bee (perhaps *Hylaeus* sp.)

Significant antagonistic interactions between pollinator species have also been detected: *Apis mellifera* often has a considerable local dominance and frightens away local solitary bees, and males of Colletidae sp. (perhaps *Hylaeus* sp.) occupy a flower for a considerable time and defend it against any large insect visitors and especially against conspecific males, only allowing conspecific females to visit and feed on the floral rewards. The biology of this interesting species is only sketchily known from anecdotal observations, and its importance as a pollinator (both as to number of successful pollinations as well as to pollen movement frequencies and distances amongst conspecific cactus individuals) remains to be fully ascertained.

In addition, *Anthrax baliopteros* as well as *Hemipenthes* sp. have been found increasingly often in recent years, and the diminishing numbers of visits by local solitary bees could be the direct result, since both parasitize their larvae.

Fruiting phenology: Fruit set of the “big bang” flowering events in 2 of the study periods was 100%, but only c. 40% in 2015/16. Fruits mature within 4 weeks. The fruits of *Acanthocalycium* split open from base to top; the juicy pulp is consumed by ants, and other ants carry away the seeds. The fruits of *Parodia* dehisce at the base; they are completely dry without pulp, and the dry seeds rapidly roll out of the opening, or lie openly in the basal part of the fruit when the flimsy dry top part with the attached dry perianth is removed. No animals were observed to show an interest in the seeds.

In some years (e.g. January 24, 2013), locally devastating florivory was observed for *Acanthocalycium*: Flowers were completely consumed by the leaf-cutter ant *Acromyrmex lobicornis* on the first day of a “big bang” flowering event. These ants are well-known from lowland regions (where they are considered a pest in agriculture), and are widespread (Brenner & Ruggiero 1994), but in the Valles Calchaquíes their occurrence at higher elevations appears to have start-

ed only during the past 30 years. Over the past 5–10 years, these ants have been a common sight throughout the study region, and they were observed to feed extensively on developing, open or spent flowers and even young fruits of various species of cacti. Occasionally, the desert grasshopper *Trimerotropis ochraceipennis* (Acrididae) also feeds on the cactus flowers.

DISCUSSION

Staggered flowering involving species of a monophyletic group is interpreted as a means of minimizing interbreeding by Endress (1994: 213, and references there cited, Borchsenius 2002 for 4 sympatric varieties of the palm *Geonoma*). Secondly, staggered flowering is interpreted as a competition avoidance mechanism, which minimizes pollen flow between plant species and ovule discounting when groups of plant species share a common pollinator guild (Opler & al. 1976: 235, and references there cited, Ashton & al. 1988). Thirdly, staggered flowering within a local or regional community may be interpreted as an “adaptive peak” at the community level (Stiles 1977, Endress 1994: 213) that allows plants to “divide pollinator resources among sympatric ... species” (resource partitioning; Barfod & al. 2011, Giorgis & al. 2015). In the case of a monophyletic group, staggered flowering would be both the cause for and the result of a speciation process and would therefore be tightly coupled with an evolutionary process. In the case of an assumed community-level adaptive high, staggered flowering would be an important component to maintain an equilibrium between the involved species of both plants and pollinators. The case here studied conforms to the competition avoidance interpretation.

Benefits of “big bang” flowering: Flowering strategies operate on the background of resource allocation for pollinator attraction to maximize long-term reproductive success. Opler & al. (1976: 235) argue that mass flowering offers a “strong competition advantage for pollinators over the period of the flowering period” because the brief massive floral display is irresistible and simply swamps other simultaneously flowering species. Indeed there are indications that successful pollinator attraction is not linearly correlated with the intensity of the floral display, but that a certain “threshold density” of flowering individuals is needed (Elzinga & al. 2007: 435). This is confirmed by the experimental study of Augspurger (1981): Individuals of the shrub *Hybanthus parvifolius* (Violaceae) from synchronously flowering populations had greater reproductive success due to greater pollination rates. Mass flowering in this species thus results in higher pollination success, likely because all pollinator attraction is concentrated on the one species because of its massive floral display. It should be noted, however, that flowering patterns differ widely in most vegetations, and mass-flowering species usually co-exist with steady-state flowering species (Augspurger 1983).

Mass flowerings result in greater numbers of potential breeding partners because so many individuals flower in synchrony (Mori & Pipoly 1984), but when

the flowering individuals are closely spaced (as in our study species), mean pollen dispersal distance likely is small. Kitamoto & al. (2006) found some influence of the density of flowering plants on pollen transport distance, but the effects are relatively small, perhaps because their study species *Primula sieboldii* is heterostylous with two floral morphs. In order to maximize gene flow, pollinators should move frequently between flowers of different individuals. Frankie & Haber (1983) have suggested that quality differences between simultaneously open flowers in the form of differences in nectar flow patterns between individual trees would drive the pollinators to move within and between plant individuals, favouring pollen movement. In general, variation in award quantity and quality would favour pollinator movement (Mori & Pipoly 1984). These authors have also suggested that interactions between competing pollinators are important, such as when one pollinator species attacks or frightens another competing pollinator species. Also, “overcrowding” of flowers would probably cause pollinators to move to another flowering plant. Such interactions have been commonly observed in both cacti we studied.

The number of concurrently open flowers, the overlap between the anthesis of different flowers on different plant individuals, and the overall length of the flowering period of the population influence the number of possible mating combinations, and thus likely impacts population genetic structure (Elzinga & al. 2007: 434).

The South African *Lapeirousia oreogena* (Iridaceae) shows that mass flowering can also have a negative impact, at least in a highly specialized pollination system (a single species of long-proboscid fly is the only pollinator), because of intraspecific competition for pollination (Johnson & al. 2012). Obviously, such intraspecific competition is not evident, or without effect, in the cacti studied here, as shown by the almost 100% fruit set, but our study species are both pollinated by several pollinators.

Finally, the timing of the flowering period and flowering density can also be linked to post-pollination / pre-dispersal predation of developing fruits and seeds. Elzinga & al. (2007: 436) report variable relationships between different flowering phenologies and the effect on herbivory phenology. Mass-flowering can minimize herbivory impact by satiating herbivore needs (although support for the predator-satiation scenario comes from a single study only, namely that of Augspurger (1981) (Elzinga & al. 2007: 438)), but in other cases, early or late flowers escaped herbivory more often than mid-season flowers. Anecdotal evidence that this also applies to florivory by the leaf-cutter ant *Acromyrmex lobicornis* was gathered in the 2012/13 summer, where late-coming flowers of *Acanthocalycium* were not attacked, while the mass flowering 6 days earlier was completely consumed. Since *Acromyrmex* only recently colonized the region, its presence is unlikely to exert selective pressures at this time. In addition, the desert grasshopper *Trimerotropis ochraceipennis* is another, though rarely seen, florivore, that would also exert some selective pressures, espe-

cially if it should have historically been more abundant than today.

Triggering “big bang” flowering: Flowering time, and especially the start of anthesis is governed by two components: Initiation of flower buds, and synchronization of anthesis (Vogel 1983, Ashton & al. 1988: 60). In the case of the study species, the timing of the start of bud formation is unknown. After an initial growth phase, flower buds reach a more or less uniform size at the end of November (= the earliest expected end of the dry winter season) and then remain in a “waiting position” until the first rain arrives. The time of bud initiation is thus decoupled from the time of anthesis. This is in line with the results of Opler & al. (1976): They found that bud formation characteristics vary widely in the 12 species they studied from fully developed buds at the start of the dry season in *Croton* to bud formation only “completed after the triggering rain” in the majority of the study species. Augspurger (1983) noted similar differences in the 6 neotropical shrubs studied.

The trigger for flower bud initiation in our cactus pair is likely the duration of the photoperiod, i.e. the transition from short days to long days in the spring, and the study species behave as long-day plants (contrary to the tropical trees and shrubs studied in Costa Rica by Opler & al. 1976, which are interpreted as short-day plants). Cactus species are well-known to have photoperiod-controlled flowering seasons, as witnessed by the short-day behaviour of *Schlumbergera* cultivars (Christmas Cactus) and the long-day behaviour of *Rhipsalidopsis* cultivars (Easter Cactus). Our interpretation of control by photoperiod is backed up by the observation of cultivated material in the northern hemisphere (Sukkulenten-Sammlung Zürich), where buds on both study species start to appear during the month of April. Temperature can, however, not be ruled out as trigger for bud set. The trend lines of daily maximum and minimum temperatures as well as substrate temperatures at 10 cm depth reach their minima around the shortest day (data not shown, from the weather station at Seclantás).

The trigger for anthesis is, according to our phenological data, the first rainfall event after the dry season. Our data leave little doubt that both the synchronization among the conspecific individuals at the level of each species, as well as the sequential flowering periods among the two species with the 1-day overlap are tightly coupled to the first rain of the season. This is especially clearly shown by the two sites studied in the 2015/16 period, which are located at a distance of c. 3.5 km from one another, and which differed in flowering time in complete agreement with the differing times of the local rain events at the two sites (Fig. 4, upper 2 rows). The only difference between the two study species is the fact that *Parodia* has a lag phase of 5 (rarely 6) days between rainfall and the start of anthesis, whereas *Acanthocalycium* has a lag phase of 7 (rarely 8) days. Different lag phases are also reported by Ashton & al. (1988) for sympatric *Shorea* species (Dipterocarpaceae).

It could be speculated that the trigger for the flowering events is not the rainfall event, but a drop in temperature. A comparison of the 2015/16 flowering events with temperature data (Fig. 4) shows no correlation and temperature differences cannot be regarded as triggering flowering events. This is especially visible from the second “big bang” flowering observed 2015/16 at the Cerro Negro site, where the sole and only trigger again must be the rainfall event preceding the flowering with the usual lag phase. It is highly notable that the two unrelated study species share not only the trigger for anthesis, but also behave identically in an extremely dry year where only part (c. 70%) of the buds initially present produced a first mass flowering, followed by a second mass flowering by the remaining buds (c. 30%).

Published studies identify both temperature drops (e.g. “cool nights”) as well as rainfall events as triggers for synchronized flowering (references in Opler & al. 1976: 231, Vogel 1983: 561 and Ashton & al. 1988: 54). In *Shorea beccariana* (Dipterocarpaceae), drought has been found as the trigger for flower bud induction through up-regulation of a drought-associated gene (Kobayashi & al. 2013). For the group of *Shorea* species studied by Ashton & al. (1988), a drop of minimum night time temperatures of only 2°C is assumed to be the trigger that elicits bud formation.

The time of anthesis of pre-formed buds has been linked to changes in temperature, especially to steep temperature drops associated with thunderstorms, in Asian tropical orchids (references in Ashton & al. 1988: 60), and in ex-situ observations of the nocturnally flowering *Epiphyllum oxypetalum* (Cactaceae) (Holtum 1954). Opler & al. (1976) did not differentiate between water availability and temperature changes as triggers of anthesis. The suite of 12 semi-deciduous species shows highly synchronized and often brief flowering periods, and rain in the form of aseasonal, unpredictable and often patchy showers during the normally dry period is regarded as synchronization cue. They estimate that a rainfall of about 25 mm is necessary to trigger flowering and argue that such a rainfall has “little intrinsic physiological importance”. The flowering sequence of their study species is nearly identical irrespective of the date of the triggering rainfall (year-to-year variability of rainfall events are 4–8 weeks), and synchronization between conspecific individuals is greatest in the species that flower most rapidly and which have a particularly short flowering season — the extreme case is *Casearia praecox* (Salicaceae) where the whole population flowers within a single day. The onset of flowering varies 2–16 days after the triggering rainfall, depending on the species. In contrast to the pair of cactus species studied here, there is considerable overlap in the flowering periods of their study species that share the same pollinator guild (Opler & al. 1976: 234, fig. 2), but a fine-scale study of the pollinators involved had not been made. A correlation between the degree of synchronization and the duration of the flowering time has also been found by Augspurger (1983), with increased synchronization correlated with decreasing length of flowering time.

Rainfall has also been identified as trigger in a study of the tropical shrub *Hybanthus parvifolius* (Violaceae; flowers self-compatible but not spontaneously self-pollinating, pollination by the social bee *Melipona*) in Panama (Augsperger 1981): The species has a flowering period of 4 days that is highly synchronized among sympatric individuals. Augsperger could experimentally induce mass flowerings by simulating a rainfall event: A sprinkling of 5 min duration at the trunk base of a *Hybanthus* individual was sufficient to induce flowering 5–6 days after. The neotropical shrubs *Turnera panamensis* (Turneraceae) and *Rinorea sylvatica* (Violaceae) also show rain-triggered flowering in the dry season (Augsperger 1983). Rainfall has also been suggested as the trigger for the partially synchronized flowering in *Miconia minutiflora* (Melastomataceae, pollinated by guild of 14 bee species) (Mori & Pipoly 1984).

“Big Bang” flowering and its relationships with the pollinator fauna: Little research has focused simultaneously on the flowering phenology and the availability of pollinators in resource-limited environments with great year-to-year variability of rainfall. The degree of synchrony needed between flowering plant species and its pollinator(s) depends on various components, but especially the longevity of the pollinator (is it already present when flowering starts?), and its degree of specialization (i.e. the degree of dependence on the one or a few flowering plant species). Minckley & al. (2013: 6) found that the proportion of oligolectic (specialist) bees in the total bee fauna is larger in arid areas because of resource availability fluctuation. They found that in dry years, bee fauna composition changes towards generalist bees, and that bee specialists of non-rain-dependent plants show little year-to-year fluctuations. Our anecdotal observations are similar and in years where scattered light spring-rains punctuated the dry season, especially the bee fauna is much more diverse than in dry years where Bombylids are relatively more abundant.

Insects that service flowers of plants that only flower in response to rainfall must be able to “predict” flowering conditions of their host, i.e. to estimate the availability of flowers on whose rewards they are dependent. Cues that lead to bee emergence from diapause are only poorly known. Rainfall is a likely cue, as postulated by several anecdotal observations (Danforth 1999: 1986). For the oligolectic communal desert bee *Perdita portalis* of N America, Danforth (1999) found that pupation and then emergence is triggered by humidity, with first emergences after only about 5 days after exposure of pre-pupae to humidity, and peak emergence after 8 days. Little is known about the life history of the pollinators we observed on our cactus pair, and more importantly, their food plant spectra are largely unknown. Casual observations show that many of the cactus flower visitors also visit flowers of concurrently flowering leguminous shrubs of the region, especially those of *Cercidium praecox*, and the total amount of rewards produced by cactus flowers is most likely insufficient to maintain the pollinator community. In view of the results by Danforth

(1999), it appears possible that at least part of the pollinators are activated by the same cue (first rainfall that terminates the dry season) and emerge from diapause with a similar lag as the flowers they pollinate. However, not all the pollinator individuals behave the same, and low numbers of all taxa observed were already present before the mass flowering, and were observed to visit the scattered flowers present on *Opuntia sulphurea*. Clearly, much more research into the life history of the observed pollinators of the local cactus community is necessary to answer the open questions about synchronicity and food plant spectra.

Resource-allocation strategies: The flowering strategy of *Parodia* and *Acanthocalycium* differs from the flowering strategies of sympatrically occurring cacti: *Denmoza rhodacantha* (Eggl & Giorgetta 2015a) shows erratic flowering starting towards the end of the dry season, and buds, flowers, and developing and ripe fruits are present simultaneously on the plants throughout the early to mid-summer season. The wide-spread *Opuntia sulphurea* behaves in a similar way (pers. obs.). For *Cereus aethiops* (Eggl & Giorgetta 2015b) bud initiation is dependent on first rains, with a more or less stable development time from bud to anthesis of 37–45 days. *Parodia* and *Acanthocalycium*, on the other hand, start bud growth well in advance of the arrival of summer rains, i.e. the early phases of bud development occur at the expense of stored resources, while the completion of bud growth and the actual flowering is based on the water available from the triggering rainfall event. Cacti are well known for their superficial root systems (Gibson & Nobel 1986: 65, Nobel 1988) that resume activity within hours after a rainfall event (Nobel & Loik 1999, Nobel & Sanderson 1984, North & Nobel 1992) and thus allow rapid rehydration of the plant body (Nobel & Loik 1999, Eggl 2004, Eggl & Giorgetta 2015b). Whereas *Cereus aethiops* prioritizes rehydration of the plant body (Eggl & Giorgetta 2015b) before investing into bud growth (which is continuous from early bud to anthesis, without a waiting phase), *Acanthocalycium* and *Parodia* both prioritize the final stages of bud growth and then floral anthesis before rehydration of the plant body. Different water allocation strategies and concomitant desiccation / rehydration behaviours are thus involved.

Within-season strategy change: Later in a season, both study species show intermittent opportunistic flowering in normally wet years, i.e. after ripening the first fruit crop, individual plants produce small numbers of flowers without any apparent synchronization with conspecific individuals, nor with individuals of the other species. This within-season change in strategy from synchronized “big bang” flowering to scattered flowering (approaching low-level steady-state flowering) in both species is notable, and it can be seen as a way of maximizing reproduction in a fail-safe manner: By the time the first fruit crop has ripened, the plants have restored their water storage to maximum capacity, and have started new growth (i.e. added new areoles as sites of a potential flower). New flowers are then produced as long as sufficient resourc-

es are available; they appear to open in a completely scattered manner when rains are more or less regularly spaced over the summer season, but when rainfall is irregular with long dry intervals, they tend to open in the form of small local mass-flowerings after a rainfall event. These mid- and late-season flowerings assure at least a low level of possible reproduction in cases where the “big bang” flowering has partially or completely failed to produce seeds (unfortunately, our observation periods were not sufficiently long to record fruiting success of these flowers). A similar behaviour has been found in the Mediterranean *Ononis tridentata* (Fabaceae) (Sanchez & al. 2012): This shrub shows a combined spring mass-flowering followed by a steady-state flowering period across the summer and early fall. Fall fruits have seeds with higher weights and higher germination rates. They describe the scenario as a bet-hedging strategy in an unpredictable environment, which is a slightly different concept than our fail-safe interpretation of the behaviour of our study species in view of resource allocation. The change in flowering behaviour involves a change in mating strategy — isolated flowers on scattered individuals have a reduced number of possible mates, and these are scattered over a larger distance, likely resulting in different pollen flow patterns (Elzinga & al. 2007: 434) when compared to the “big bang” flowering.

Benefits of staggered “big bang” flowering: Staggered flowering in a monophyletic group (e.g. subspecies of a species, Borchsenius 2002) can be tightly linked to speciation. Staggered mass-flowering in unrelated plant species belonging to the same “pollination guild” (i.e. with the same or at least a largely overlapping pollinator assemblage) seems counter-intuitive, however, and therefore difficult to explain: While staggered flowering limits interspecific pollen flow when there is strong competition for pollinators (Opler & al. 1976, Willmer 2011: 485), the second-flowering species risks success as the needs of the pollinator could already have been saturated by the flower rewards of the first-flowering species. The evolution of the observed pattern is only possible when the pollinator(s) involved is (are) relatively long-lived (as individuals, or as a population of individuals with overlapping life times) with a combined feeding window that is much longer than the combined mass-flowering events of the plants involved. This seems to be the case in our example, and the staggered flowering will (apart from the partial 1-day overlap period) reliably prevent the loss of pollen to foreign stigmas, and the loss of ovules by the effects of foreign pollen. Since mass-flowerings were also observed in pure stands of both study species, the evolution of the timely sequence of flower opening in mixed populations is even more startling.

Limitations of the study: The observations here reported were all made in the same general region, and thus relate to a single set of more or less interconnected populations. Further populations (pure stands of either species, as well as mixed populations) in other regions should be studied to evaluate whether the pat-

tern observed in the Angastaco region is generally applicable to the study species.

CONCLUSIONS

Our observations present the first well-documented study of a mass-flowering phenomenon in cacti. Available evidence identifies the crucial impact of the first rainfall event that terminates the dry winter season on synchronizing the flowering time of the two unrelated cacti *Parodia microsperma* and *Acanthocalycium thionanthum*. The two cacti differ only in the duration of the lag phase between the time of the rainfall event and the start of the flowering period (5–6 days in *Parodia*, 7–8 days in *Acanthocalycium*). The amount of rainfall (“slight” vs. “medium”) and whether it occurs early or late in the summer season has no influence. The temporal relationship is thus completely stable from year to year. Since flowers of the two species have (with the exception of the honey bee) a shared pollinator assemblage, the staggered flowering is interpreted as a means of minimizing competition for pollinator service. The antagonistic behaviour (attacks of non-conspecifics) of simultaneously present different pollinator species is regarded as a means of increasing pollen dispersal distances and frequencies.

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