

# The pollination ecology of *Phemeranthus punae* (Montiaceae) in southern Bolivia

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**Summary:** *Phemeranthus punae* (R.E.Fr.) Eggli & Nyffeler (Montiaceae) is a perennial geophytic herb from the pre-Puna vegetation in the Andes of south-west Bolivia and north-west Argentina. Flowering plants have been observed for several seasons. Flowers are almost exclusively visited by at least three species of ants (Formicidae: likely *Forelius pruinosus* Roger, *Linepithema* sp. and *Camponotus bruchi* Forel). The ants move freely and rapidly on the plants and switch to neighbouring plants within less than five seconds. Pollen grains adhere to legs and bodies of the ants, which visit the flowers to feed on the nectar. The low stature of *P. punae*, its horizontally spreading to ascending inflorescences and the small flowers conform to the ant pollination syndrome characteristics formulated by Hickman (1974). It is concluded that the observed ants are the pollinators of the species in the study area.

**Zusammenfassung:** *Phemeranthus punae* (R. E. Fr.) Eggli & Nyffeler (Montiaceae) ist eine mehrjährige, geophytische, krautige Pflanze aus der Pre-Puna-Vegetation der Anden im Südwesten Boliviens und im Nordwesten Argentinien. Blühende Pflanzen wurden während mehrerer Jahre beobachtet. Die Blüten werden fast ausschließlich durch mindestens drei Ameisenarten besucht (Formicidae: wahrscheinlich *Forelius pruinosus*, *Linepithema* sp. und *Camponotus bruchi*). Die Ameisen bewegen sich frei und rasch auf den Pflanzen und wechseln innerhalb von weniger als fünf Sekunden zu benachbarten Exemplaren. Pollenkörner kleben an den Beinen und Körpern der Ameisen, die die Blüten besuchen, um

den Nektar aufzunehmen. Der niedrige Wuchs von *P. punae*, die horizontal ausgebreiteten bis aufsteigenden Blütenstände und die kleinen Blüten entsprechen dem von Hickman (1974) beschriebenen Ameisen-Bestäubungssyndrom. Die beobachteten Ameisen werden als die Bestäuber der Art im Untersuchungsgebiet betrachtet.

**Resumen:** *Phemeranthus punae* (R.E.Fr.) Eggli & Nyffeler (Montiaceae) es una hierba geofítica perenne de la vegetación de la Prepuna Andina en el suroeste de Bolivia y noroeste de la Argentina. Se observaron plantas durante varias épocas de floración consecutivas. Las flores son visitadas casi exclusivamente por al menos tres especies de hormigas (Formicidae: probablemente *Forelius pruinosus*, *Linepithema* sp. y *Camponotus bruchi*). Las hormigas se mueven libremente y rápidamente sobre las plantas y se trasladan entre plantas vecinas en menos de cinco segundos. Los granos de polen se pegan a patas y cuerpo de las hormigas mientras que visitan las flores para alimentarse del néctar. El tamaño bajo de *P. punae* y las inflorescencias con flores chicas creciendo en inflorescencias horizontales o levemente ascendentes corresponden a las características del síndrome de polinización de hormigas establecido por Hickman (1974). Se concluye que las hormigas observadas son los polinizadores de la especie en la área estudiada.

## Introduction

A significant driver of evolution is gene flow between individuals of a species (or of several intercompatible species). Gene flow occurs mainly at two levels for plants which, in their overwhelming majority, are sessile organisms:

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pollen transfer and seed dispersal, plus to a minor degree through distribution of vegetative propagules. Wind (anemophily, anemochory), water (hydrophily, hydrochory) or animals (zoo-phily, zoochory) are the main vectors that assure gene transfer over space, from centimetres to hundreds if not thousands of kilometres.

Given the importance of pollen transfer, it is not surprising that pollination features have been intensely studied for more than a century (Faegri & Van der Pijl, 1971; Faegri & Van der Pijl, 1979; Willmer, 2011). Many different mechanisms have evolved to secure successful transfer of pollen to conspecific stigmas – of another individual (genet) or of the same flower or a flower on the same individual (ramet) in the case of non-spontaneously self-pollinating self-compatible species. Generally, ‘the process of pollination is messy and wasteful’ (Parker, 2014), and only a tiny fraction of all pollen grains reach conspecific stigmas.

The importance of animal vectors for pollen and thus gene transfer is of such magnitude that recurrent occurrences of similar ‘key and lock’-like systems between flowers and co-evolved animals (or between animals and co-evolved flowers) have come to be recognized as distinct pollination syndromes (see Willmer (2011) and literature there cited). Separate syndromes with characteristic combinations of floral traits (colour, size and shape, scent, nectar composition and volume, time of anthesis and nectar production) have been described for pollination by bees (melittophily), flies (myophily), butterflies (psychophily), moths (phalaenophily and sphingophily), beetles (cantharophily), wasps (sphecophily), birds (ornithophily), and bats (chiropterophily), while pollination by snails or non-flying mammals is often seen as oddities, and ants are merely treated in the context of generalist pollination systems (Willmer, 2011).

Ants are generally regarded as being among the dominant organisms of the world (Hölldobler & Wilson (1990) cited from Gómez & Zamora (1992)). Ant/plant interactions are varied and common: Mutualistic relations between ants that protect plants from herbivory by insect larvae, in return for rewards provided by extrafloral nectaries, are probably the best known such interactions (e.g. McIntosh (2002), McIntosh (2005) and Ness (2006) for an example involving the stem succulent *Ferocactus* (Cactaceae), but note that such relationships are not always mutualistic, cf. Alma et al. (2015) for *Opuntia sulphurea*), apart from the intricate ant-/ant-garden plants relationships. Ants can, however, themselves

be herbivorous and even florivorous (Ashman & King, 2005), and leaf-cutter ants place a severe burden on the plants which they attack (for florivory in cacti see e.g. Eggli & Giorgetta (2015) for *Cereus aethiops* Haworth, and Eggli & Giorgetta (2017) for *Parodia microsperma* (F.A.C.Weber) Spegazzini and *Acanthocalycium thionanthum* (Spegazzini) Backeberg). Ants as flower visitors are generally regarded as casual commensalists or nectar thieves (ants are termed the ‘prototype of nectar thieves’ by Faegri & van der Pijl (1971, cited from Hickman (1974), or are regarded as parasites of plant/pollinator systems (e.g. Norment (1988) for the Gentianaceae *Frasera speciosa* Douglas ex Grisebach, or Wyatt (1980) for the Apocynaceae *Asclepias curassavica* Linné; see Wyatt (1980), Ashman & King (2005), Vega et al. (2009a), Vega & Herrera (2012), Vega & Herrera (2013) and Le Van et al. (2014) for discussions of other antagonistic influences of ants on pollination systems). Their potential role as pollinators is usually interpreted as being minimal (Beattie, 1985; Rostás & Tautz, 2010; Willmer, 2011). Several reasons are invoked why ants are negligible as pollinators: 1–smooth body surfaces are not amenable to pollen transport; 2–body surface chemistry resulting from exudates of metapleural glands which due their antibiotic effects affect the viability of pollen grains (e.g. Beattie et al.; 1984; Beattie, 1985; Wagner, 2000); 3–travel distances by ants (generally 1–2m) in general are small and especially between-plant movements – essential for the pollination of obligately outcrossing plants – and are regarded as insufficient.

On the other hand, the sheer number of ants present on plants in many communities automatically causes high numbers of possible pollen transfer events whenever plants are flowering, and even though the service quality of the individual flower visit by ants may indeed be low, the number of such visits likely compensates the low chance of successful pollen transfer (see Gómez & Zamorra (1992: 410) and Herrera (1987) on aspects of quantity vs. quality). Also, ants are so diverse that observations made in one plant / ant community cannot be safely extrapolated to other communities, especially across boundaries of major ecosystems. Ant morphologies vary widely between the generally naked smooth surfaces of many ants from temperate climates to densely hairy ants that are more prevalent in subarid and arid climates. These differences likely affect pollen dispersal likelihood and frequencies. The most frequently invoked reason why ant pollination is unimportant is the presumed negative influence of ant body surface chemistry

on pollen viability ('antibiotic hypothesis' of Gómez et al., 1996): Many ants secrete antibiotic (antibacterial, antifungal) compounds via metapleural glands that have been found to negatively impact pollen viability (Beattie, 1985). However, Beattie's experiments were done using four species of plants not pollinated by ants, and pollen was exposed to ant secretions for thirty minutes (Beattie, 1985) (compare with visit durations of six to sixty seconds in the present study), and the same criticism holds true for the study by Wagner (2000) who experimented with pollen of a presumably bee-pollinated *Acacia* species. Gómez et al. (1996) found that three of the seven ant species encountered in their study of seven plant species in Spain had no metapleural glands, and that the presence of metapleural secretions does not determine the ants' effectiveness as pollinators. According to Rostás & Tautz (2010), it is unknown whether metapleural secretions of pollinating ants deviate from those of non-pollinating ants and are less toxic to pollen, or whether the pollen of ant-pollinated plants could be more resistant. Gómez et al. (1996: 242) justifiably argue that 'ants visiting flowers should be judged potential pollinators until proven otherwise'.

Because of the assumed insignificance of ant pollination (Rostás & Tautz 2010 list only about thirty reports), no syndrome has been generally accepted so far for pollination by ants. The respective term 'myrmecophily' is preferably used to describe the mutualistic interrelationship between ants and ant-garden plants in the humid tropics (i.e. ant-mediated seed-dispersal of epiphyte species, and growth of these plants on ant nests). Since ants are almost ubiquitous in almost all places of the planet inhabited by plants, and since they are commonly observed on plants, their assumed non-involvement with pollination is surprising. Since pollination ecology is a well-researched field, it appears that ant pollination indeed is of rare occurrence. Overview evaluations of pollination syndromes such as those by Ollerton et al. (2009) or Rosas-Guerrero et al. (2014) do not include an 'ant syndrome' at all, or do not even mention ants as pollinators.

The relatively few studies that suggest ants as pollinators are summarized, amongst others, by Beattie (1985), Gómez & Zamora (1992), Gómez et al. (1996) or Ashman & King (2005). The first more or less uncontested report is that by Hagerup (1943) for *Seseli libanotis* W.D.J.Koch (Apiaceae) in Denmark. Already Hagerup (1932) suggested (although he did not actually report observations of ants as pollinators) that ant pollination is

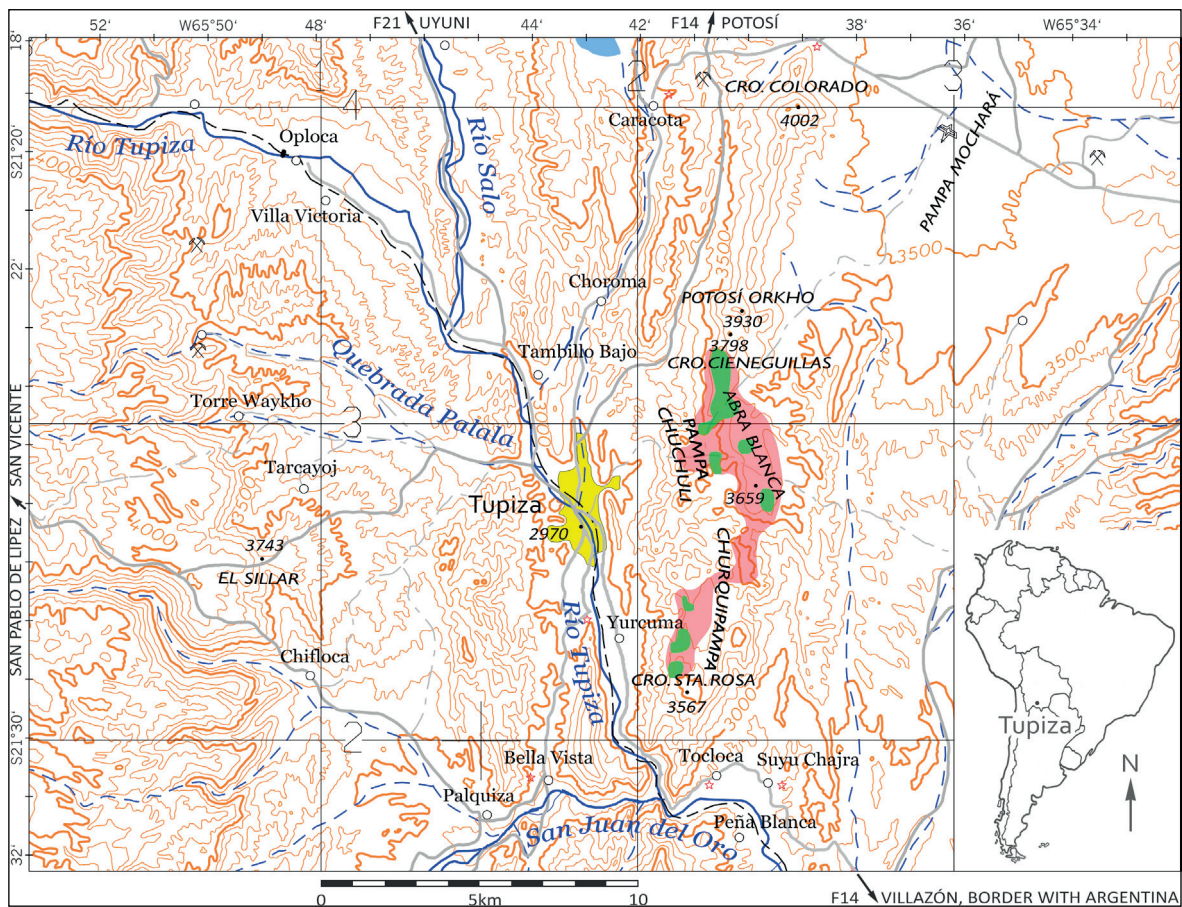
particularly likely for plants from desert climates, a claim that he firmly reiterated in 1943 by saying that ants represent the most important pollinators in the 1932-study area (Timbuktu, Mali, sub-Saharan Africa).

Hickmann (1974), in his study of *Polygonum cascadenae* W.H.Baker (Polygonaceae) from hot dry slopes in Oregon, USA, first suggested traits indicative of successful ant-flower interactions. Accordingly, the syndrome components are 1–plants inhabit dry habitats with high frequency and activity of ants; 2–nectar is readily accessible to short-tongued small insects; 3–plants are of low stature and/or prostrate, with flowers near the ground; 4–plants occur in dense stands and neighbouring individuals often have interdigitating branches; 5–plants of a population flower more or less synchronously with few flowers open at a time per plant to maximize inter-plant foraging; 6–flowers are more or less sessile; 7–pollen number per flower is low to avoid frequent self-grooming of the ants; 8–seed number per flower is low so that few pollen grains are needed for complete seed set; 9–flowers are small with minimal visual attraction; and 10–nectar quantity is small but large enough to support ants with their low energy need. Amongst the six undisputed cases of ant pollination at that time, four agreed 90–100% with these syndrome characteristics, while the other two were interpreted as having a mixed pollination system where ants are one of several pollinators.

Already Beattie (1985) pointed out that Hickman's original suggestions need reinterpretation since plants from many other habitats also show pollination by ants, e.g. the orchid *Epipactis palustris* (Linné) Crantz from swampy meadows (Brantjes, 1981), several species from high alpine habitats (Petersen, 1977), the dioecious *Borderea chouardii* Gaussen & Heslot (Dioscoreaceae) from sheer cliff faces (García et al., 2012), the Mediterranean root holoparasite *Cytinus hypocistis* (Linné) Linné (Cytinaceae) (Vega et al., 2009b), or the Bromeliad *Vriesea neoglutinosa* Mez from the Brazilian Atlantic Rainforest (Magalhães et al., 2018). Beattie (1985) also raises the question whether Hickman's proposed ant syndrome could be the result of a general adaptation to small insects, whether flying or walking, and that mixed generalized pollination systems could be in effect.

As far as succulents are concerned, two species have been reported as being ant-pollinated: Wyatt (1981) found that the self-incompatible, diminutive annual herb *Diamorpha smallii* Britton (Crassulaceae, treated as *Sedum smallii* (Britton) Ahles by 't Hart & Bleij 2003) is frequented by





**Figure 1.** The study region in SW Bolivia (Dept. Potosí, Prov. Sud Chichas, region east of the city of Tupiza). The general area is indicated in red, and the observations for this study were made in the green-coloured areas. Map by Mario Giorgetta.

small native bees and flies, but that ants are the most abundant floral visitors, and that they act as effective pollinators – large numbers of sticky pollen grains adhere to hairs and indentations primarily of the ant's thorax. Ants appear, accordingly, to be the primary pollinators of the species. According to Wyatt (1981), *Diamorpha* shares several key characters with other ant-pollinated taxa, such as occurring in hot dry habitats, high local plant densities, small-sized plants with overlapping inflorescences of more or less uniform height, low pollen and seed number per flower, and low nectar volume per flower. Wyatt & Stoneburner (1981) report the pollinating ants to be two species of *Formica*. Ants probe the nectaries of the flower before moving to the next flower, and they move between overlapping inflorescences, but movements between different rock outcrops inhabited by *Diamorpha* are restricted. Interestingly, the sympatrically

occurring and often synchronously flowering and overall similar winter-annual *Sedum pusillum* Michaux is only rarely visited by ants, and is mainly visited by two species of flies (Wyatt, 1983) as well as small bees and two species of butterflies (Clausen, 1975). For the perennial diminutive herb *Sedum anglicum* Hudson, Gómez et al. (1996) found that the population investigated in south-east Spain is almost exclusively visited by the ant *Proformica longiseta* (70–100% of all flower visitors), and that the role of ants as pollinators in other species depends on their relative abundance compared to other pollinators.

Here, we add a further species of succulent plant that is pollinated by ants.

## Material and methods

**Study site:** The general study region is situated in south-west Bolivia, Department of Potosí, Province Sud Chichas, on a mountain ridge east





**Figure 2.** Part of the study region at the high plain of Abra Blanca, looking to the North, 3,645m a.s.l. (8. March 2018). The shrubs are *Baccharis boliviensis*, the columnar cacti in the background are *Oreocereus celsianus*. The yellow flowers in the foreground are *Hypochaeris sessiliflora*.



**Figure 3.** Dense flowering population of *Phemeranthus punae* in an open carpet on shallow rocky ground at Cerro Cieneguillas, 3,616m a.s.l., 14 March 2016. The larger yellow flowers are *Portulaca perennis*, the pink flowers are *Ipomoea plummerae*, and the small white flowers are *Oziroë acaulis*.



**Figure 4.** Flowering specimen of *Phemeranthus punae*, showing the characteristic succulent terete leaves and the spreading inflorescences, at Cerro Cieneguillas, 3,647m a.s.l., 28 March 2016.

of the town of Tupiza, running north to south (Figure 1). The study areas are formed by quite flat high plateaus at an altitude between 3,300 and 3,700m a.s.l. with prevalent short vegetation on sedimentary soils mixed with scattered pebbles, stones and small boulders of sandstone and limestone, with very little organic matter derived from the scattered vegetation. The open vegetation is of the ‘puna norteña’-type of Ibisch & Mérida (2003) with yearly average temperatures of c. 9°C and temperature ranges of -5 to 25°C, and annual precipitation amounts of some 360mm (Ibisch & Mérida, 2003). The climate is

characterized by humid summers and dry winters with marked variability of precipitation from year to year. The vegetation is characterized by scattered shrubs and an open cover of low-growing herbaceous perennials (Figures 2 and 3). The vegetation consists of scattered shrubs and herbs, as well as several species of cacti, and a few succulents from the families Portulacaceae and Anacampserotaceae.

**Study species:** *Phemeranthus punae* (R.E.Fr.) Eggli & Nyffeler is a low-growing, herbaceous, perennial, drought-deciduous geophyte (Figures 3, 4 and 5), common and widely distributed in





**Figure 5.** Complete plants of the study species *Phemeranthus punae* dug out to show the irregularly shaped caudex with one to several vegetation points, leaves in tight rosettes, and the spreading inflorescences, at Churquipampa, 3,321m a.s.l., 2 March 2012.



**Figure 6.** The typical laterally spreading inflorescence of *Phemeranthus punae*, often resting on the ground, at Pampa Chuchuli, 3477m a.s.l., 11 March 2017.



**Figure 7.** Young inflorescences of *Phemeranthus punae* are sometimes completely erect at Churquipampa, 3,337m a.s.l., 7 March 2016. The violet flower buds on the right are of *Ipomoea plummerae*.

the general area at altitudes around 3,500m a.s.l. It survives the dry season by means of a tuberous underground caudex, which can be branched and then supports two or three leaf rosettes. The narrowly elongate terete leaves appear quickly after the first rains of the season, and are soon

followed by the branched inflorescences (Figures 6 and 7) with numerous, smallish (c. 8mm diameter), yellow, diurnal flowers. Flowering usually starts towards the end of the rainy period in late summer (early March). Plants of this species have been found to be self-compatible and autonomously self-pollinating in cultivation, where spontaneous seed set occurs regularly (pers. obs. C. Hunkeler at the Sukkulentensammlung, Zürich). The classification of the study species has been under revision in recent years. Traditionally, the species was classified as *Talinum* (e.g. Eggli, 2002) in the family Portulacaceae *sensu lato*. Molecular analyses have shown that the species of *Phemeranthus* form a clade completely separate from *Talinum*, and on the basis of these results, Nyffeler & Eggli (2010) have accepted *Phemeranthus* as a separate genus in the resurrected family Montiaceae.

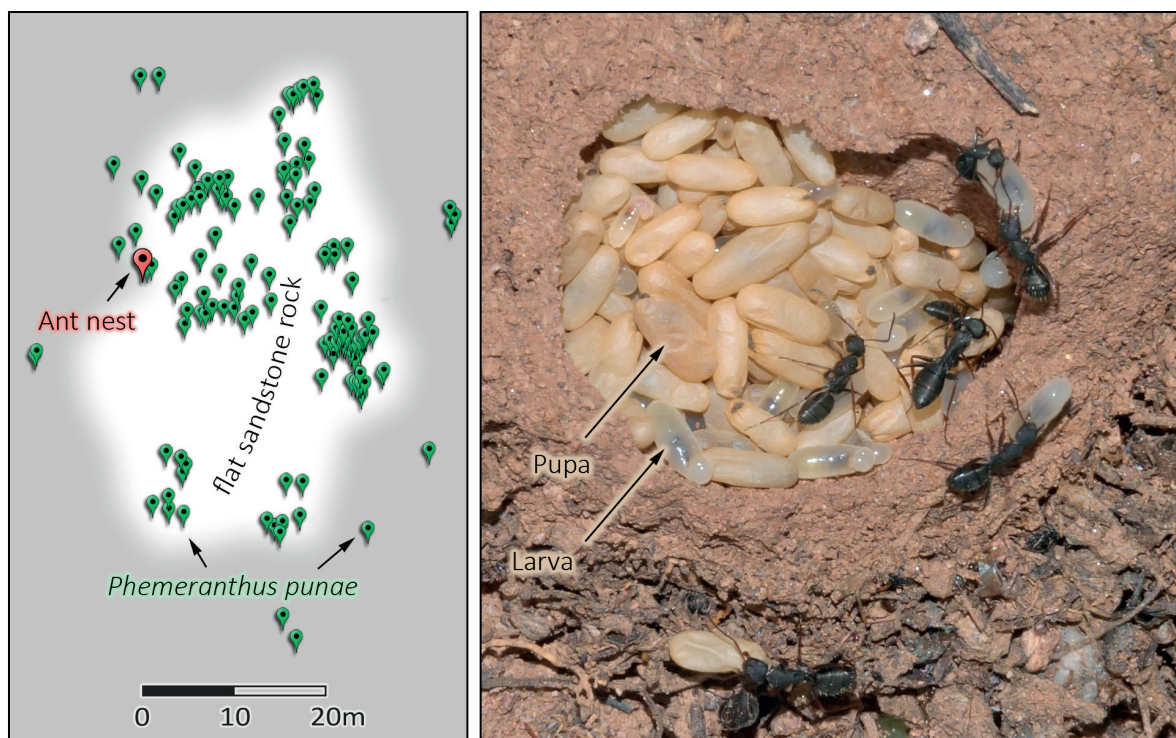
The geographical range of *P. punae* is simply given as Argentina by Eggli (2002). It is specifically known from the provinces of Salta and Jujuy in northern Argentina (from altitudes between 3,240 and 3,700m a.s.l., pers. obs. UE), as well as from the department of Potosí in adjacent southern Bolivia (pers. obs. MG, Mendoza & Wood, 2013). In the region of the study site, its presence was noted at six places at altitudes between 3,306 and 3,674m a.s.l.

**Methods:** More than 300 detailed observations were made during a total of ninety-three days in the summer months of February and March in the years 2015, 2016, 2017, 2018 and 2019 during extended visits to the general area of the study site. No quantitative experiments could be conducted, but ant-plant interactions were documented with 311 photographs.

## Results

At the study site, *P. punae* forms populations consisting of numerous individuals (Figure 8), in scattered groups of few specimens or as isolated individuals over an area of approximately 8km<sup>2</sup>, typically on shallow ground on low sandstone slabs (Churquipampa) or in temporarily wet depressions with limestone rubble (Cerro Cieneguillas, Abra Blanca). The distance between individuals is usually in the range of 30–100cm, but can be less so that the laterally spreading inflorescences overlap. Distances between groups of individuals can be as much as 200m. Plants usually grow in the open and were in full growth during the study visits, each with a well-developed cluster of turgid succulent leaves. Most plants produce several inflorescences, which are usually horizontally spreading, frequently contacting the ground, to





**Figure 8.** Map of a local population on the Churquipampa at 3,332m a.s.l., next to a nest of the ant *Camponotus bruchi*, discovered when lifting a small rock piece. The population of *Phemeranthus punae* consists of 143 GPS-marked plants and is concentrated on a flat sandstone rock.



**Figure 9.** *Forelius pruinosus* probing a flower of *Phemeranthus punae* for nectar (left), and carrying the coloured seed of the cactus *Tunilla soehrensii* cf. (right), both at Churquipampa, 3,334–3,358m a.s.l., 28 March 2018.

somewhat ascending sideways (Figures 4 and 5), but can occasionally also be oriented more or less vertically (Figure 7). The plants of a colony flower synchronously (Figure 3) over a period of about two weeks when conditions are optimal. The flowering period between different colonies in the study region can differ as much as two weeks (cf. dates in figure 15). As far as observed, the flowers

open only once on a single day and only in sunny weather. On completely sunny days, flowers are open from 12:00 to 13:30 hours, but after cloudy mornings, they open and close later, e.g. 13:30–15:00 hours. They close when clouds appear, and do not re-open when sunny conditions return. Nectar is visible as glossy liquid on the flower bottom around the ovary.





**Figure 10.** *Linepithema* sp. probing a flower of *Phemeranthus punae* for nectar, at Churquipampa, 3,331m a.s.l., 27 March 2018.



**Figure 11.** *Camponotus bruchi* approaching an inflorescence of *Phemeranthus punae*, at Churquipampa, 3,334m a.s.l., 27 March 2018.

Three species of ants (Formicidae) were commonly and regularly observed as flower visitors. The three species are of roughly similar size and behave in the same manner. By far the most common ant visitor is a reddish-brown ant, most probably *Forelius pruinosus* (Dolichoderinae; Figure 9)<sup>1</sup>, followed in frequency by *Linepithema* sp. (Dolichoderinae; Figure 10). The third species is *Camponotus bruchi* cf. (Formicinae; Figure 11), which is easily distinguished by the black colour and somewhat larger bodies<sup>2</sup>. Individuals of all these ants move freely on the plants. They

usually first patrol the leaves and then ascend the inflorescence axis. The ants move rapidly among the interdigitating inflorescences of neighbouring plants when they are in close contact. They 'dive' into open flowers with their heads, presumably to suck nectar, which is easily accessible to their short mouth parts. While doing so, they often contort their bodies and cling to the stamens with their legs. Neighbouring individuals of *Phemeranthus* are rapidly reached within less than five seconds. *Forelius pruinosus* is overall the most common floral visitor, but relative frequencies can vary



**Figure 12.** Digital enlargements of photographs showing ants visiting flowers of *Phemeranthus punae* at Churquipampa, 3,331–3,339m a.s.l.; note the scattered pollen grains on the ant's bodies. (left) *Forelius pruinosus*, 7 March 2016, (right) *Linepithema* sp., 27 March 2016.

locally on a small scale and especially when the vegetation composition changes. When leaving a flower, pollen grains are visible adhering to the legs and bodies of the ants (Figure 12). It appears that pollen is slightly sticky, as it was observed to adhere even to the naked legs of the ants.

Visitation frequencies were documented with repeat photographs (Figure 13). A freshly opened flower was visited by three different individuals of *Forelius pruinosus* within ten minutes. The individuals moved around on the flower for six to fifty seconds.

In addition to ants, individuals of an unidentified solitary species of sand wasp of the genus *Ammophila* (Sphecidae: Ammophilinae) were occasionally observed to probe flowers accessible from the ground for nectar (Figure 14). Neither local native solitary bees nor non-native honeybees were observed as visitors.

Supplemental observations were made at nearby locations to establish whether the observations at the main Churquipampa population can be generalized for the study region. All the visitors found at the main site occur throughout the study region, as documented for *Forelius pruinosus* from five additional locations (Figure 15).

## Discussion

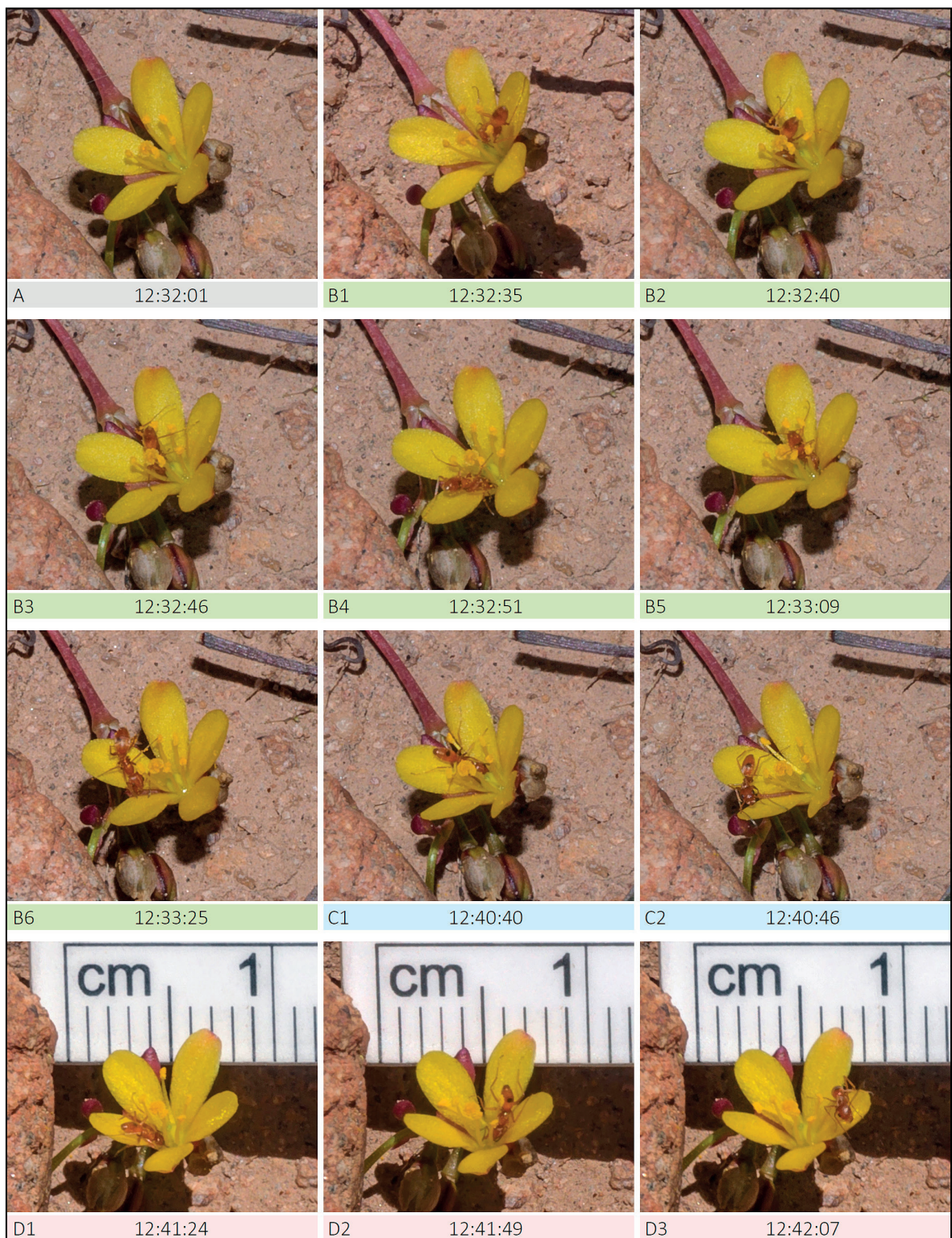
*Phemeranthus punae* shares the traits of *Diamorpha smallii* that were enumerated as characteristic for ant pollination by Wyatt (1981:

1214), using the 'ant syndrome' characters first formulated by Hickman (1974) – plants are low-growing in often dense populations, have spreading inflorescences that interdigitate when plants are growing close enough to each other, show synchronous flowering, and have small open flowers and readily accessible nectar. The observations here communicated leave no doubt that the three observed species of local ants are regular and frequent flower visitors that transport pollen between flowers and plants.

*Phemeranthus punae*, like most of the other ant-pollinated flowers studied, has small flowers. With c. 8mm diameter, they are slightly larger than the range of 4–7.5mm reported for the seven species studied by Gómez et al. (1996). Four of the species from that study had white flowers (as do *Sedum anglicum* and *Diamorpha smallii*), and one each had yellow, pink or purple flowers. The coloured flowers of *P. punae* thus differ from the majority of the ant-pollinated plants studied so far, but are by no means unique. The coloured flowers could be indicative that a mixed pollination system was in effect in the evolutionary past, or speculatively the colour is a remnant from the evolutionary past of the species when pollination by non-ant insects might probably have relied on attractively coloured flowers.

Ant travel distances of as much as ten metres were observed by Wyatt (1981) for the ants visiting *Sedum* (*Diamorpha*) *smallii*, but 1–2m were more common, and foraging behaviour was





**Figure 13.** Ten minutes in the life of a freshly opened flower of *Phemeranthus punae* at Churquipampa, 3,339m.a.s.l., 7 March 2016, visited by three different individuals (B1–B6, C1–C2, D1–D3) of the ant *Forelius pruinosus*, on a sunny day with several quick moving clouds intermittently covering the sun (photographs A and B2 to C2 taken with flash, the others with natural light).





**Figure 14.** A sand wasp *Ammophila* sp. probing a flower of *Phemeranthus punae* for nectar at Cerro Cieneguillas, 3,534m a.s.l., 8 March 2018.

found to be dependent on plant density. Gómez et al. (1996) found that of the five unambiguously ant-pollinated taxa of their study, only *Sedum anglicum* is likely exclusively pollinated by ants, while the other plant taxa are also visited by other insects. In the case of the studied populations of *P. punae*, flying insects were rare throughout all the study years, with the exception of occasional individuals of a local solitary sand wasp. Since the observations span five consecutive seasons, it appears safe to conclude that flying insects do not contribute significantly to pollination success, and that ants constitute the main, if not unique pollen vectors of the species.

*Metapleural gland secretions considerations:* Whether the ants observed to visit the flowers of *P. punae* possess metapleural glands or not is unknown but likely unimportant, since the statements on the possible damaging activity of metapleural secretions on pollen rest on weak foundations (see introduction).

*Limitations of the study:* *P. punae* is widespread, and our study was conducted with seven plant colonies in a single region within an area of c. 8km<sup>2</sup>. For the Churquipampa colony, the entire flowering period of the colony of 10–14 days was studied in all study years. It is therefore unlikely, that year-to-year variations in the pollinator fauna

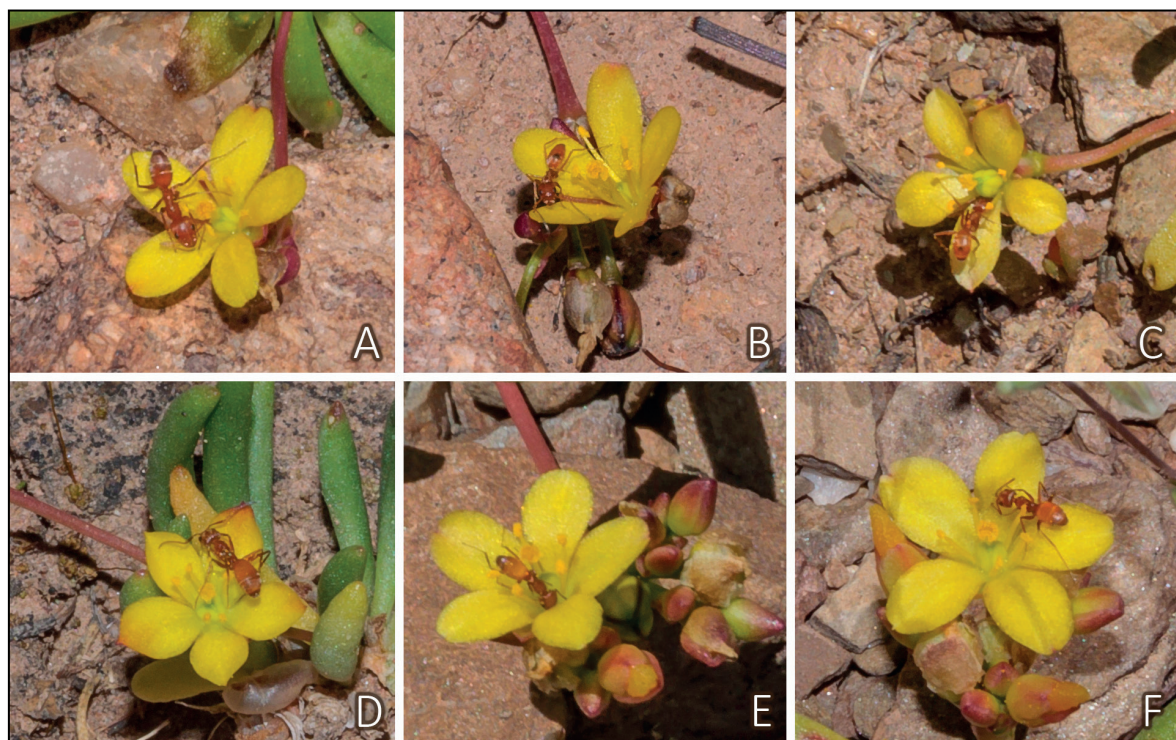
were overlooked, but we do not know whether other pollinators possibly play an important role in other populations from throughout the range of the species. Herrera (1988) and Schürch et al. (2000) have shown that the pollinator assemblage can be extremely variable both in time (throughout a season, and from year to year) and space (between populations, and within populations). While our observations show only ants as pollinators, other vectors could be present in other regions.

## Conclusions

On the basis of field observations, we show that the likely pollinators of *Phemeranthus punae* are three species of small ants, *Forelius pruinosus*, *Camponotus bruchi* cf. and *Linepithema* sp. *P. punae* completely conforms to the ant pollination syndrome elements as formulated by Hickman (1974). After *Sedum* (*Diamorpha*) *smallii* and *Sedum anglicum* (both Crassulaceae), *P. punae* (Montiaceae) is the third known case of likely ant pollination amongst succulent plants.

## Acknowledgments

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**Figure 15.** Individual flowers of *Phemeranthus punae* from six different observation places, each showing a visiting *Forelius pruinus*.

- A – Churquipampa, -21.47613°, -065.68866°, 3,334m a.s.l., 28 February 2018  
 B – Churquipampa, -21.47635°, -065.68861°, 3,339m a.s.l., 7 March 2016  
 C – Cerro Cieneguillas, -21.41544°, -065.68265°, 3,534m a.s.l., 10 March 2018  
 D – Pampa Chuchuli, -21.42482°, -065.67882°, 3,487m a.s.l., 19 March 2016  
 E – Cerro Cieneguillas, -21.41523°, -065.68287°, 3,522m a.s.l., 11 March 2018  
 F – Cerro Cieneguillas, -21.41525°, -065.68284°, 3,528m a.s.l., 11 March 2018

## Notes

1. The genus *Forelius* is present throughout the Americas and is most diverse in north-west Argentina. *Forelius pruinus* is common in the hot arid regions of the southern USA and adjacent Mexico, but is also recorded from Colombia (<https://www.antweb.org>, accessed January 2020). Our identification is tentative and is based on data from the cited website.
2. Unidentified species of these ant genera *Camponotus*, *Forelius* and *Linepithema* have also been reported to be associated with the cactus *Opuntia sulphurea* in Argentina and Bolivia, where they exploit extrafloral nectaries (Alma et al., 2015).

## References

- ALMA, A.M., POL, R.G., PACHECO, L.F. & VÁSQUEZ, D.P. 2015. No defensive role of ants throughout a broad latitudinal and elevational range of a cactus. *Biotropica* **47**: 347–354.
- ASHMAN, T.-L. & KING, E.A. 2005. Are flower-visiting ants mutualists or antagonists? A study in a gynodioecious wild strawberry. *American Journal of Botany* **92**: 891–895.
- BEATTIE, A.J. 1985. Ant pollination. In: A.J. Beattie (ed.) *The evolutionary ecology of ant-plant mutualisms*: 96–109. Cambridge, Cambridge University Press.
- BEATTIE, A.J., TURNBULL, C.L., KNOX, R.B. & WILLIAMS, E.G. 1984. Ant inhibition of pollen function: A possible reason why ant pollination is rare. *American Journal of Botany* **71**: 421–426.
- BRANTJES, N.B.M. 1981. Ant, bee and fly pollination in *Epipactis palustris* (L.) Crantz (Orchidaceae). *Acta Botanica Neerlandica* **30**: 59–68.
- CLAUSEN, R.T. 1975. *Sedum of North America north of the Mexican Plateau*. New York, Cornell University Press.
- EGGLI, U. 2002. *Talinum*. In: U. Eggli (ed.): *Illustrated handbook of succulent plants, Dicotyledoneae*: 425–433. Berlin, Heidelberg and New York, Springer-Verlag.
- EGGLI, U. & GIORGETTA, M. 2015. Flowering phenology and observations on the pollination



- biology of South American cacti. 2. *Cereus aethiops*. *Haseltonia* **21**: 19–40.
- EGGLI, U. & GIORGETTA, M. 2017. 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. *Haseltonia* **23**: 97–109.
- FAEGRI, K. & VAN DER PIJL, L. 1971. *Principles of pollination ecology*. Second edition. Oxford, Pergamon Press.
- FAEGRI, K. & VAN DER PIJL, L. 1979. *Principles of pollination ecology*. Third edition. Oxford, Pergamon Press. [The ‘completely revised’ edition of 2013 marketed in the Internet is merely a digitalization of the third edition from 1979.]
- GARCÍA, M.B., ESPADALER, X. & OLESEN, J.M. 2012. Extreme reproduction and survival of the true cliffhanger: The endangered plant *Borderea chouardii* (Dioscoreaceae). *PLoS One* **7**(9): e44657.
- GÓMEZ, J.M. & ZAMORA, R. 1992. Pollination by ants: Consequences of the quantitative effects on a mutualistic system. *Oecologia* **91**: 410–418.
- GÓMEZ, J.M., ZAMORA, R., HÓDAR, J.A. & GARCÍA, D. 1996. Experimental study of pollination by ants in Mediterranean high mountain and arid habitats. *Oecologia* **105**: 236–242.
- HAGERUP, O. 1932. On pollination in the extremely hot air at Timbuctu. *Dansk Botanisk Arkiv* **8**: 1–18.
- HAGERUP, O. 1943. Myre bestovning. *Svensk Botanisk Tidskrift* **46**: 116–123.
- HART, H. T. & BLEIJ, B. 2003. *Sedum*. In: U. Eggl (ed.): *Illustrated Handbook of Succulent Plants. Crassulaceae*: 235–332. Berlin, Heidelberg and New York, Springer-Verlag.
- HERRERA, C.M. 1987. Components of pollinator ‘quality’: Comparative analysis of a diverse insect assemblage. *Oikos* **50**: 79–90.
- HERRERA, C. M. 1988. Variation in mutualisms: The spatio-temporal mosaic of a pollinator assemblage. *Biological Journal of the Linnean Society* **35**: 95–125.
- HICKMAN, J.C. 1974. Pollination by ants: A low-energy system. *Science* **184**: 1290–1292.
- HÖLLDOBLER, B. & WILSON, E.O. 1990. *The ants*. Cambridge, Harvard University Press.
- IBISCH, P.L. & MÉRIDA, G. (eds.) 2003. *Biodiversidad: La riqueza de Bolivia. Estado de conocimiento y conservación*. Santa Cruz de la Sierra, Ministerio de Desarrollo Sostenible / Editorial FAN.
- LE VAN, K.E., HUNG, K.-L., MCCANN, K.R., LUDKA, J.T., & HOLWAY, D.A. 2014. Floral visitation by the Argentine ant reduces pollinator visitation and seed set in the coast barrel cactus, *Ferocactus viridescens*. *Oecologia* **174**: 163–171.
- MAGALHAES, A.F.P., MARUYAMA, P.K., TAVARES, L.A. F. & MARTINS, R.L. 2018. The relative importance of hummingbirds as pollinators in two bromeliads with contrasting floral specializations and breeding systems. *Botanical Journal of the Linnean Society* **188**: 316–326.
- MCINTOSH, M.E. 2002. Plant size, breeding system, and limits to reproductive success in two sister species of *Ferocactus* (Cactaceae). *Plant Ecology* **162**: 273–288.
- MCINTOSH, M.E. 2005. Pollination of two species of *Ferocactus*: Interactions between cactus-specialist bees and their host plants. *Functional Ecology* **19**: 727–734.
- MENDOZA, J.M. & WOOD, J.R.I. 2013. Taxonomic revision of *Talinum* (Talinaceae) in Bolivia with a note on the occurrence of *Phemeranthus* (Montiaceae). *Kew Bulletin* **68**: 233–247.
- NESS, J.H. 2006. A mutualism’s indirect costs: The most aggressive plant bodyguards also deter pollinators. *Oikos* **113**(3): 506–514.
- NORMENT, C.J. 1988. The effect of nectar-thieving ants on the reproductive success of *Frasera speciosa* (Gentianaceae). *American Midland Naturalist* **120**: 331–336.
- NYFFELER, R. & EGGLI, U. 2010. Disintegrating Portulacaceae: A new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data. *Taxon* **59**: 227–240.
- OLLERTON, J., ALARCON, R., WASER, N.M., PRICE, M.V., WATTS, S., CRANMER, L., HINGSTON, A., PETER, C.I. & ROTENBERRY, J. 2009. A global test of the pollination syndrome hypothesis. *Annals of Botany* **103**: 1471–1480.
- PARKER, A. J. 2014. *The ecological context of pollination: Variation in an apparent mutualism*. Ph.D. thesis. Toronto, University of Toronto, Department of Ecology and Evolutionary Biology.
- PETERSEN, B. 1977. Pollination by ants in the alpine tundra of Colorado. *Transactions of the Illinois State Academy of Sciences* **70**: 349–355.
- ROSAS-GUERRERO, V., AGUILAR, R., MARTÉN-RODRÍGUEZ, S., ASHWORTH, L., LOPEZARAIZA-MIKEL, M., BASTIDA, J.M. & QUESADA, M. 2014. A quantitative review of pollination syndromes: Do floral traits predict effective pollinators? *Ecology Letters* **17**: 388–400.
- ROSTÁS, M. & TAUTZ, J. 2010. Ants as pollinators of plants and the role of floral scents. In: Z. Dubinsky & J. Seckbach (eds.): *All flesh is grass. Cellular origin, life in extreme habitats and astrobiology* **16**: 151–161. Berlin, Springer.



- SCHÜRCH, S., PFUNDER, M. & ROY, B. A. 2000. Effects of ants on the reproductive success of *Euphorbia cyparissias* and associated pathogenic rust fungi. *Oikos* **88**: 6–12.
- VEGA, C. DE & HERRERA, C.M. 2012. Relationships among nectar-dwelling yeasts, flowers and ants: Patterns and incidence on nectar traits. *Oikos* **121**: 1878–1888.
- VEGA, C. DE & HERRERA, C.M. 2013. Microorganisms transported by ants induce changes in floral nectar composition of an ant-pollinated plant. *American Journal of Botany* **100**: 792–800.
- VEGA, C. DE [ET AL. 2009a], HERRERA, C.M. & JOHNSON, S.D. 2009. Yeasts in floral nectar of some South African plants: Quantification and associations with pollinator type and sugar concentration. *South African Journal of Botany* **75**: 798–806.
- VEGA, C. DE [ET AL. 2009b], ARISTA, M., ORTIS, P.L., HERRERA, C.M. & TALAVERA, S. 2009. The ant-pollination system of *Cytinus hypocistis* (Cytinaceae), a mediterranean root holoparasite. *Annals of Botany* **103**: 1065–1075.
- WAGNER, D. 2000. Pollen viability reduction as a potential cost of ant association for *Acacia constricta* (Fabaceae). *American Journal of Botany* **87**: 711–715.
- WILLMER, P. 2011. *Pollination and floral ecology*. Princeton, Princeton University Press.
- Wyatt, R. 1980. The impact of nectar-robbing ants on the pollination system of *Asclepias curassavica*. *Bulletin of the Torrey Botanical Club* **107**: 24–28.
- WYATT, R. 1981. Ant-pollination of the granite outcrop endemic *Diamorpha smallii* (Crassulaceae). *American Journal of Botany* **68**: 1212–1217.
- WYATT, R. 1983. Reproductive biology of the granite outcrop endemic *Sedum pusillum* (Crassulaceae). *Systematic Botany* **8**: 24–28.
- WYATT, R. & STONEBURNER, A. 1981. Patterns of ant-mediated pollen dispersal in *Diamorpha smallii* (Crassulaceae). *Systematic Botany* **6**: 1–7.