

Variable pollinator dependence of three *Gastrodia* species (Orchidaceae) in modified Canterbury landscapes

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Abstract: Pollination is an ecosystem service affected by anthropogenic activity, often resulting in reduced fruit set and increased extinction risk. Orchids worldwide have a wide range of pollination systems, but many New Zealand orchids are self-pollinating. We studied the pollination system of three saprophytic native orchids from the genus *Gastrodia* in modified landscapes in Canterbury, New Zealand: *G. cunninghamii*, *G. minor*, and an undescribed taxon *G.* “long column”. The species showed two distinct pollination systems. *Gastrodia cunninghamii* and *G. minor* were autonomous selfing species. In contrast, *G.* “long column” had almost no fruit set when pollinators were excluded, and was visited by the endemic New Zealand bee *Lasioglossum sordidum*, which acted as a pollen vector in order to produce fruit. Visitation rate by *L. sordidum* varied among four sites around Christchurch, and natural fruit set in *G.* “long column” ranged from 76% where *L. sordidum* were abundant to 10% where bees were not observed. Oddly, some of the highest natural fruit-set rates were at a highly modified urban site. Therefore, while some *Gastrodia* species are dependent on native pollinators, they can still persist in highly modified landscapes.

Keywords: bee pollination; fruit set; habitat fragmentation; Halictidae; *Lasioglossum*; pollen limitation

Introduction

There is worldwide concern about the potential effects of anthropogenic change on ecosystem services, including pollination (Daily 1997). Pollination failure can be caused by a variety of factors (Wilcock & Neiland 2002), and can result in reduced fruit set, and increased extinction risk. The Orchidaceae have a wide diversity of pollination systems (van der Cingel 2001) and are more often pollen-limited than other plant families (Larson & Barrett 2000; Newstrom & Robertson 2005). Most orchids are generalists visited by a diversity of pollinators, but there is also a range of unusual specialist pollinator relationships where one or a few insect species visit. Many orchid species reward their pollinators with food (typically nectar), and these can be generalists or specialists (Dixon & Hopper 2009; Micheneau et al. 2009). Other orchids are food deceptive and do not reward their pollinators (Jersákova et al. 2006), and these can also be generalists or specialists (Johnson et al. 2003; Gaskett et al. 2008; Peter & Johnson 2013).

Gastrodia is a genus of mycoheterotrophic orchids that do not contain chlorophyll. Instead, these plants rely on a parasitic fungal association to gain nutrients (Johns & Molloy 1983). One species, *G. elata*, has been successfully cultivated, and this species requires associations with two different fungi (Pridgeon et al. 2005). There are about 20 species of *Gastrodia* distributed throughout eastern Asia and Australasia (Pridgeon et al. 2005). Where pollination has been studied the species fall into two groups. Some species are pollinated by insects, including *G. elata* in Japan pollinated by *Lasioglossum* sp. (family Halictidae) bees (Kato et al. 2006), *G. sesamoides* by a xylocopid bee, and *G. javanica* and *G. similis* by flies (Pedersen et al. 2004; Martos et al. 2013). The reward is

usually pseudopollen, starchy granules produced inside the flower, which the bees collect and store in their pollen baskets (van der Cingel 2001; Pridgeon et al. 2005; Kato et al. 2006), although a recent report suggests *G. similis* may be attracting drosophiloid flies with fermenting-fruit odours (Martos et al. 2013). Another group of species autonomously self-pollinate, as determined by morphology (anthers and stigma in close contact), high fruit set for flowers enclosed in bags, or observing an absence of flower visitors. Definite or probable selfing species include *G. verrucosa*, *G. cunninghamii*, and *G. daminghanensis* (Pedersen et al. 2004; Lehnebach et al. 2005; Hu et al. 2014), and perhaps also *G. orobanchoides* and *G. minor* (van der Cingel 2001). The evidence for *G. exilis* is unclear. Some flowers set fruit when enclosed in pollinator-exclusion bags, but many did not, and natural fruit set was low and variable among plants, so fruit set was speculated to be perhaps reliant on very small insects (Pedersen et al. 2004).

In New Zealand, the flower morphology of many native orchids suggests self-pollination (van der Cingel 2001). In the North Island, the endemic species *G. cunninghamii* was found to be capable of autonomous selfing, and observations recorded no obvious pollinator visits (Lehnebach et al. 2005). Van der Cingel (2001) also states that *G. minor* and an undescribed species with the tag name *G.* “long column” are self-pollinating.

The native insect pollinator species in New Zealand are thought to be relatively generalist in the flowers they visit (Newstrom & Robertson 2005), though recent work still shows definite preferences (Campbell et al. 2010). Some of the most important pollinating insects in New Zealand are the bees (Hymenoptera), many of which are endemic. All of New Zealand’s native bees belong to either the Colletidae or Halictidae (Donovan 2007). *Lasioglossum* (Halictidae) includes four endemic species in New Zealand, of which

L. sordidum is the most widespread and visits the widest range of native and exotic plants. At many sites this species outnumbers other native solitary bees throughout the year, and is a successful competitor of *Apis mellifera* (Donovan 2007). *Lasioglossum* species all nest in the ground and the genus is found in both the North and South Island of New Zealand. These bees are important as pollinators in New Zealand because of both their abundance and their lack of plant specialisation (Donovan 1980).

We studied the pollination systems of three endemic *Gastrodia* species within modified landscapes in the Canterbury Region: *G. cunninghamii*, *G. minor*, and *G. “long column”*. The latter undescribed taxon has quite distinctive flower morphology (Rolfe 2010) and is likely to be described as a separate species (C. Lehnebach, Museum of New Zealand Te Papa Tongarewa, pers. comm.). Specifically, our aims were to determine:

- (1) How many species of *Gastrodia* grow around urban Christchurch?
- (2) Are those *Gastrodia* species capable of autonomous selfing?
- (3) What flower visitors go to *Gastrodia* species?
- (4) How do sites vary in flower visitation rates and natural fruit-set rates?

Methods

Species studied

Gastrodia have perennial underground tubers, which produce non-photosynthetic brown flowering shoots 10–50 cm tall. The species we found were identified using the guide to New Zealand *Gastrodia* (Rolfe 2010), and voucher specimens sent to the Museum of New Zealand Te Papa Tongarewa herbarium (WELT). Both *G. cunninghamii* and *G. “long column”* have inflorescences >30 cm in height with 20–50 flowers per stalk. The species differ in flower structure, with *G. cunninghamii* having a very short column whereas that of *G. “long column”* is the length of the labellum (Fig. 1). Also, *G. “long column”* has a yellow labellum tip which distinguishes it from *G. “long column black”* (Rolfe 2010). *Gastrodia minor*

inflorescences are much smaller, with flower stalks <30 cm in height carrying 2–10 flowers per stalk.

Sites

Six locations around Canterbury were used for this research. Each of the three species was studied at a minimum of two sites (Table 1).

Four sites were in Christchurch City. The Victoria site was a densely settled urban residential area within central Christchurch, within 1.5 km of the Little Hagley and Christchurch Botanic Gardens sites. *Gastrodia “long column”* was found on a residential property under a narrow hedge of *Griselinia littoralis*, *Pittosporum tenuifolium*, and *Coprosma robusta*. The Christchurch Botanic Gardens are a 21-ha area of native and exotic gardens in central Christchurch surrounded by Hagley Park’s 165-ha of lawns and trees. *Gastrodia “long column”* and *G. cunninghamii* were located in garden beds planted predominantly with *Magnolia* and *Rhododendron* cultivars, respectively, each with an overstorey of mature exotic trees (mixed broadleaved–coniferous). The Little Hagley site

Table 1. *Gastrodia* species studied at various sites in and around Christchurch, with number of stems (and bagged stems) observed each year. CBG, Christchurch Botanic Gardens; – , site not used in that year.

Species	Site	Stems (bagged stems)		
		2012	2013	2014
<i>Gastrodia “long column”</i>	Victoria	11 (3)	22 (15)	10 (5)
	CBG	–	8 (5)	13 (6)
	Addington	–	–	14 (5)
	Ohoka	–	–	2 (1)
<i>Gastrodia cunninghamii</i>	Little Hagley	–	–	17 (8)
	CBG	–	–	3 (0)
	Hook.f. Coleridge	–	–	14 (5)
<i>Gastrodia minor</i>	Addington	–	–	19 (7)
	Petrie Ohoka	–	–	11 (6)

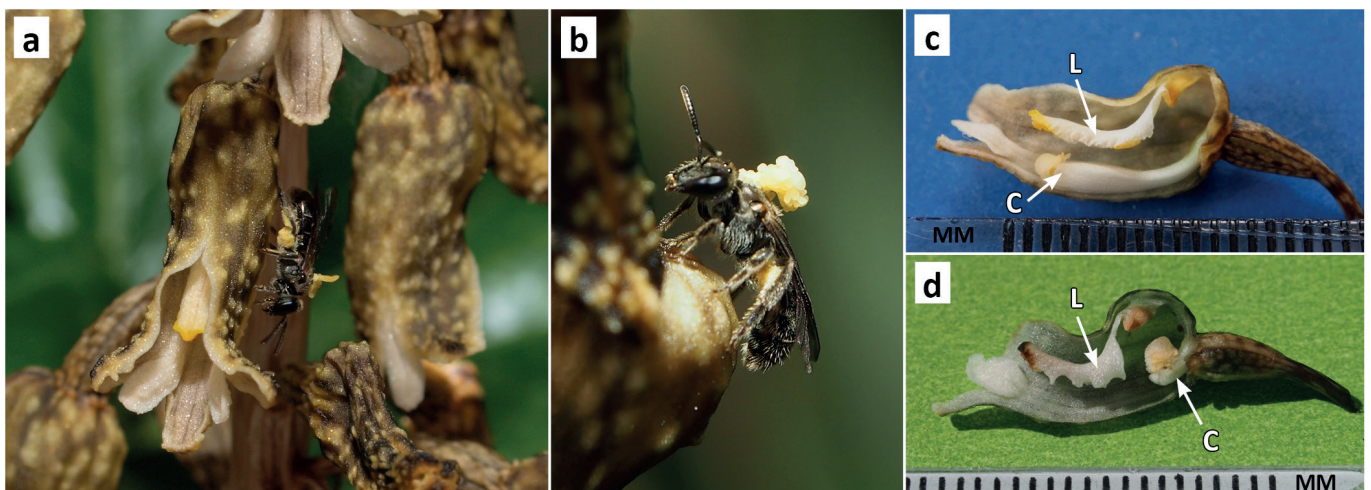


Figure 1. *Gastrodia* spp. flowers. *Lasioglossum sordidum* (with attached pollinia) on *G. “long column”* at Victoria (a) in January 2012 and (b) January 2013. Sectioned flowers of (c) *G. “long column”* from Victoria (January 2013) and (d) *G. cunninghamii* from Little Hagley Park (November 2013), with arrows pointing to the column (C) and labellum (L). Photos by Dave Kelly.

was in the 6.7-ha northern section of Hagley Park (called Little Hagley Park) located between Harper Avenue and the Avon River. This area is largely mature deciduous trees with some native woody regeneration along the riverbank. In Addington the site was a highly modified light industrial area 1.5 km south of the Christchurch Botanic Gardens. It consists of three narrow gardens bordered by concrete paths and buildings. The garden contained silver birch trees (*Betula pendula*) and shrubs.

Two sites were outside Christchurch. The Ohoka site was in rural Canterbury 20 km north of the Christchurch Botanic Gardens, in an area of planted exotic and regenerating native forest. *Gastrodia minor* was located at the border of a conifer woodlot and native plantings; *G. "long column"* was located within the regenerating native forest area among blackberry bushes. Finally, the Coleridge site was in the Harry Hart Arboretum at Lake Coleridge, 80 km west of Christchurch. The Arboretum is a 1.9-ha collection of exotic conifers. *Gastrodia cunninghamii* was located in the understorey beneath a mixed canopy of planted *Pinus* and *Picea* spp.

Flower visitor observations

In 2012, observations were started at the end of the *Gastrodia* flowering season. Visitor observations were conducted during seven 5-min observation periods spread over a week. In 2013, two 20-min observations were taken at each of the two sites. In 2014, visitor observations consisted of multiple 20-min periods at each site. During visitor observations, open unbagged flowers were observed. Insect visitors were categorised into two groups (Adams & Lawson 1993). Visitors that landed on *Gastrodia*, or entered *Gastrodia* flowers without pollinia becoming attached, were noted as suggested pollinators; whereas visitors that were seen bearing pollinia were classed as probable pollinators. Insect species were identified using photographs and where possible insect specimens stored in the University of Canterbury School of Biological Sciences arthropod collection.

Pollinator exclusion

The primary manipulation was to bag flower buds to exclude all insects from before anthesis until fruits ripened or aborted, and record how fruit set compared with unmanipulated (open, unbagged) flowers (Table 1). In 2012 the last-forming flower buds (all at the top of flower stalks) were bagged using white nylon netting to enclose the tops of inflorescences, and fruit set was compared with that in open flowers lower on the same stalks and on other unmanipulated stalks. In 2013, we assessed the effect of flower position (top or bottom of stalk) and bag colour (white or dark brown) on fruit set, but these factors were excluded after initial analyses showed no significant effect ($P = 0.126$ and $P = 0.382$, respectively). In 2014 the entire stalk (or if some flowers were already open on stalks, only the top buds) were bagged using either green or white synthetic netting. Where necessary, the pollination bags were supported by stakes to avoid potential flower damage. The number of flowers and subsequent fruit set for each stalk or portion of stalk were recorded.

Analysis

The statistical programme R, version 3.0.0 (R Development Core Team 2013), was used to analyse fruit set. Replicates were stalks (or portions of a stalk with the same treatment, bagged or not), and the response was binomial (fruit set vs failed) in generalised linear models. When the data were

overdispersed, we used a quasibinomial error distribution and *F*-tests; otherwise a binomial error with chi-square tests were used.

Results

Flower visitors

Across the three years of observation at the Victoria site, *Lasioglossum sordidum* frequently entered flowers of *G. "long column"* and emerged with pollinia attached to their backs; *L. sordidum* were also frequently observed carrying yellowish material (presumably pseudopollen) in the pollen baskets on their legs (Fig. 1). The labellum of *G. "long column"* flowers (Fig. 1c) produces orange-yellow glandular pseudopollen that was not present in *G. cunninghamii*, and *L. sordidum* bees were seen entering *G. "long column"* flowers facing the labellum, consistent with pseudopollen collection and with the pollinia becoming attached to their backs. At this site *L. sordidum* were by far the most frequent insect visitors in all three years. In 2012 we recorded 31 bees in 35 min of observation (0.89 bees/min), in 2013 we saw 35 bees in 40 min (0.88 bees/min), and in 2014 we observed 35 in 60 min (0.58 bees/min). The Christchurch Botanic Gardens had lower visitation rates, with two *L. sordidum* observed in each of 2013 (40-min observation, 0.05 bees/min) and 2014 (60 min, 0.03 bees/min). No *L. sordidum* were observed on *G. "long column"* at either Addington (140 min) or Ohoka (60 min).

Few other species of insect visited *G. "long column"* flowers at any of the sites in the three years of observation. These other visitors were always at low density, most did not enter flowers, and none were seen carrying pollinia. The visitors included *Hylaeus* sp. bees (one individual at Victoria in 2012), *Melangyna novaezealandiae* (Diptera: at Victoria, one individual in 2012 and one in 2014), *Parentia* sp. (Diptera: one at Victoria in 2012), one very small dipteran at Addington (perhaps Stratiomyidae), and one small brown beetle at Ohoka (perhaps a herbivorous bronze beetle, similar to *Eucolaspis brunnea*, Chrysomelidae). There were also unidentified aphids feeding on flower stalks at several sites, and a few unidentified small parasitoid wasps were seen around (but not on) flower stalks at Victoria in 2013 and 2014.

Few or no visitors were seen on the other two *Gastrodia* species. Visitor observations for *G. cunninghamii* yielded three flower visitors at Little Hagley in 2014. In 120 min of observations one individual similar to *Zorion* sp. (Coleoptera: Cerambycidae) and one possible *Hilara* sp. (Diptera: Empididae) were seen entering flowers but not bearing pollinia. Numerous aphids were also seen on the stalks and flowers. No visitors were seen to enter *G. minor* at either site during 100 min of observations at Addington and 60 min of observations at Ohoka.

Fruit set and pollinator exclusion treatment

Pollinator exclusion had no significant effect on fruit set in *G. cunninghamii* or *G. minor* (Table 2). Fruit set for both species was high for both bagged and non-bagged flowers (Fig. 2). There was also no effect of location in either species. In contrast, pollinator exclusion strongly and significantly reduced fruit set in *G. "long column"* (Table 2) with fruit set much lower inside bags (average 3% fruit set across all sites and years) compared with open flowers (average 67%) (Fig. 2). Most bagged stalks set zero fruit, with only five exceptions; these

might represent bagging failure (either small holes allowed insects to enter a bag, already-pollinated flowers inadvertently enclosed in a bag, or insects inadvertently allowed into the bag when it was removed briefly for flower counting).

In *G.* “long column” there was no significant effect of year, and no interaction between bagging and location (Table 2). However, there was a significant main effect of location on fruit set in *G.* “long column” with high open (natural) fruit set occurring at the sites with flowers most frequently visited by

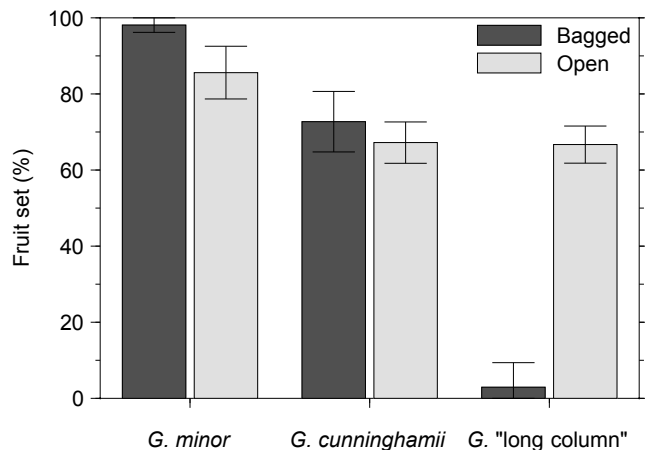


Figure 2. Fruit set response to bagging treatment (pollinator exclusion) for three *Gastrodia* species in and around Christchurch (mean ± SEM).

Table 2. Results of generalised linear models testing the effect of bagging treatment, location and year on the fruit set of *Gastrodia* species. (a) *G.* “long column”, (b) *G. cunninghamii*, (c) *G. minor*. Significant results are in bold. A binomial error and chi-square test was used for *G. minor*, and a quasibinomial error and *F*-test for the other two species.

(a) *G.* “long column”

	d.f.	Deviance	<i>F</i>	<i>P</i> (<i>F</i>)
Bagged	1	1162.8	210.5	<0.001
Location	3	126.1	7.6	<0.001
Year	2	3.8	0.3	0.71
Bagged: Location	3	20.4	1.2	0.30
Residual	95	497.8		

(b) *G. cunninghamii*

	d.f.	Deviance	<i>F</i>	<i>P</i> (<i>F</i>)
Bagged	1	7.5	1.4	0.25
Location	2	20.8	1.9	0.16
Bagged: Location	1	1.2	0.2	0.64
Residual	34	214.6		

(c) *G. minor*

	d.f.	Deviance	<i>P</i> (χ^2)
Bagged	1	3.2	0.07
Location	1	0.6	0.44
Bagged: Location	1	0.6	0.42
Residual	26	21.6	

L. sordidum (Fig. 3). High natural fruit set (75%) was found at the Christchurch Botanic Gardens and Victoria sites where *L. sordidum* were common and very common, respectively, whereas lower fruit set was found at the Addington (32%) and Ohoka sites (10%), both of which had no observed *L. sordidum*.

Discussion

Gastrodia “long column” is apparently dependent on *L. sordidum* for pollination, contrary to van der Cingel (2001) who described it as self-pollinating. In our observations *L. sordidum* was the primary, and possibly the only, pollinator of *G.* “long column”. We saw few other insects entering flowers, and no other insects bearing pollinia. Plants were only observed during the daytime, leaving the possibility of some crepuscular or nocturnal pollination in addition to our evidence for *L. sordidum* pollinating *G.* “long column” by day. The polylectic foraging habits of *L. sordidum* suggest that this bee can forage on any plant whose rewards it can gain access to, it is active for longer periods than the flowering season of many of its host plants, and its small size increases its ability to visit many flowers (Donovan 2007). We assume the reward *G.* “long column” provides to *L. sordidum* is pseudopollen, as some of the bees had full pollen baskets, but have not yet been able to test this assumption from field collections. Lehnebach et al. (2005) suggested aphids might aid *G. cunninghamii* in self-pollination, because aphids were observed inside the flowers (C. Lehnebach, pers. comm.). In our study, aphids were commonly seen feeding on sap on the *Gastrodia* stalks, but none were seen inside flowers or bearing pollinia.

The link between *G.* “long column” fruit-set rates and frequency of *L. sordidum* observed visits suggests that in some areas, *L. sordidum* densities were insufficient to pollinate all flowers. There were two interesting details to this relationship. First, our results imply that even quite low densities of *L. sordidum* are enough for good pollination. For example, Christchurch Botanic Gardens had high fruit set with a low frequency of observed bee visitation and Addington had moderate fruit set even though no *L. sordidum* were sighted in 140 min of observations. We hypothesise that *L. sordidum* are probably required for fruit set in *G.* “long column”, but the bees can be effective pollinators even when visitation rates are below 0.5 visits per hour. However, we cannot exclude the possibility that the Addington plants were pollinated by a different insect

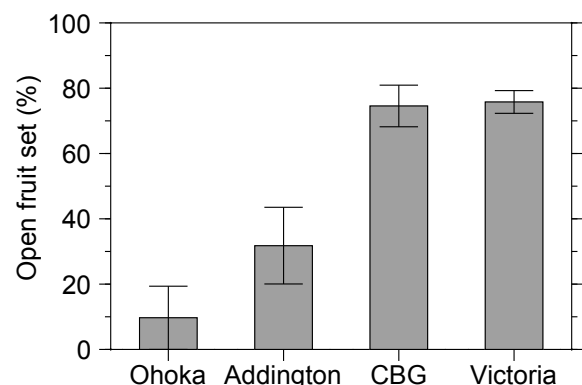


Figure 3. Natural fruit set (% of open flowers that made fruit) in *Gastrodia* “long column” at four sites around Canterbury in 2014 (mean ± SEM). CBG = Christchurch Botanic Gardens.

species since we did not observe *L. sordidum* there. Second, and surprisingly, the *L. sordidum* bees were not most common at the most “natural” or most vegetated sites. Fruit set was better at the three urban sites, including in the light industrial suburb of Addington, than in the countryside at Ohoka. Further work is required to understand the distribution and activities of these bees, and it may be that heavily managed, exotic-plant-dominated agricultural areas are poor *Lasioglossum* habitat. It would be very interesting to compare our visitation and pollination rates to those for *G. “long column”* in native forest areas. Regardless, populations are being sustained in at least some urban environments. Future conservation efforts that focus on *G. “long column”* will need to consider the state of the pollinating insect fauna at target locations.

Fruit-set rates in *G. “long column”* were variable, but at the two best sites, fruit set rates (~75%) were close to those for the *Lasioglossum*-pollinated *G. elata* in Japan (80% and 95% fruit set at two sites in one year) (Kato et al. 2006). We have not seen fruit-set rates for the other insect-pollinated *Gastrodia* species, but fruit set is typically high for autonomously self-pollinating species (as in our study). Thus, our results are similar to overseas studies, which have often found *Gastrodia* species to be either autonomously selfing, or pollinator-dependent and visited by insects. Of course, the problem is to know which applies to a particular species, since those two different scenarios have quite different implications for plant sensitivity to mutualism failure.

Bond (1994) states that when assessing the risk of plant extinctions, the dependence of the plant on mutualistic services must be determined. Information on the pollination requirements and breeding systems can show how many options for successful pollination a plant has under conditions of low pollinator abundance (Bond 1994). While most of New Zealand’s tested native terrestrial orchids are routinely self-pollinating, some insect-reliant species are also present, and many of the endemic terrestrial orchids are considered threatened (Lehnebach et al. 2005).

Our results have conservation implications, because we show that species from the same genus can have different pollination systems. *Gastrodia cunninghamii* and *G. minor* are autonomous-selfing species, reducing their extinction risk from pollination failure. This was previously known for *G. cunninghamii*, but only suspected on the basis of flower morphology for *G. minor*. However, our fieldwork reversed previous assumptions (van der Cingel 2001) that *G. “long column”* was also self-pollinating. In our study *G. “long column”* was apparently dependent on *L. sordidum*, its only observed pollinator, for fruit set. Surprisingly, this relationship is reasonably successful in some urban environments, where the orchids are self-sown and unmanaged populations of *L. sordidum* were able to find the flowering plants. These findings highlight how under-studied native pollination is, and demonstrate the value of pollination research for conservation.

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