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Reproductive success in the Mexican rewardless *Oncidium cosymbephorum* (Orchidaceae) facilitated by the oil-rewarding *Malpighia glabra* (Malpighiaceae)

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Abstract The pollination of one plant species can be facilitated by the presence of one or more neighboring plant species and evidence has been found in some rewardless species of orchid that benefit from the presence of rewarding plant species in the neighborhood. There are two pollination mechanisms by which a non-rewarding orchid attracts pollinators and increases its reproductive success: (1) A magnetic species effect that occurs even though the flowers do not resemble those of the other species, and (2) floral mimicry where the mimic's flower resembles that of the model plant species. *Oncidium cosymbephorum* is a Mexican rewardless epiphytic orchid whose flowers look like those of the rewarding shrub *Malpighia glabra* (Malpighiaceae). The resemblance of *O. cosymbephorum* to the oil-offering flowers of *M. glabra* attracts the same pollinators, and the fitness of the orchid is higher when *M. glabra* is present than when it is absent. We evaluated the facilitation by *M. glabra* of the orchid's pollination for natural and artificial clumps of *O. cosymbephorum* close to and far from *M. glabra* over 4 years. Two experiments were performed at five different study sites to evaluate the effect of the presence and absence of *M. glabra* on the reproductive success of *O. cosymbephorum*. In experiment 1, we recorded fruit set production in natural and artificial monospecific clumps of the orchid, and in natural and artificial heterospecific clumps of *O. cosymbephorum* and *M. glabra*. In experiment 2, we recorded the fruit set of *O. cosymbephorum* at different sites where individuals grow in monospecific clumps, both before and after cultivated individuals of oil-producing *M. glabra* had been planted in their vicinity. Both experiments showed that the reproductive success of *O. cosymbephorum* was greater in the presence of *M. glabra* than it was in its absence. This study provides experimental evidence for the magnetic species effect. Floral similarity between *O. cosymbephorum* and *M. glabra*, should be experimentally tested to determine whether it is adaptive.

Keywords Floral mimicry · Fruit set · Magnetic species effect · Plant–animal interaction · Plant–plant interaction · Pollination · Pollinators

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Introduction

Most flowering plants offer different rewards to attract pollinators (Rathke 1988; Waser et al. 1996); however, a small number of Angiosperms are rewardless (Ackerman 1986; Renner 2006). These plant species have developed alternative strategies to ensure constant visits by pollinators and enhance their reproductive success. One of these is to take advantage of neighboring plant species that offer rewards (Laverty 1992; Johnson et al. 2003a; Renner 2006; Juillet et al. 2007), and another is deceptive pollination (Ackerman 1986; Johnson and Nilsson 1999; Jersáková et al. 2006; Renner 2006).

Pollination success in non-rewarding plants that flower in association with reward-producing plants will be enhanced (facilitation) or diminished (competition) depending on pollinator behavior (Laverty 1992; Lammi and Kuitunen 1995; Johnson et al. 2003a; Internicola et al. 2006, 2007). Pollination by facilitation is an amazing phenomenon that has been gaining the attention of ecologists who want to understand how the pollination mechanisms between reward and rewardless species work (Johnson et al. 2003a; Jersáková et al. 2006; Juillet et al. 2007). Several studies have recorded that animal-pollinated plants, especially those pollinated by insects, may have higher visitation rates when co-occurring in communities with species that attract pollinators (Thomson 1978; Feinsinger 1987; Feldman et al. 2004; Moeller 2004). This has been recorded as beneficial to non-rewarding species growing in the same plant community and close to individual species that offer a reward (Laverty 1992; Johnson et al. 2003a, Juillet et al. 2007). Few studies have demonstrated the intra- inter- or multi-species interactions of facilitation for pollinator attraction and flower pollination (Feldman et al. 2004; Moeller 2004; Hegland and Totland 2005). On the other hand, in a plant community it is unusual to find several places where both rewarding and non-rewarding species occur along with places where the rewardless species grows in monospecific clumps (Johnson 2000; Internicola et al. 2006, 2007). Understanding the relative importance of floral traits (morphology, color, display, and density) between rewarding and rewardless species in a system of pollination facilitation is crucial to further our understanding of reproductive ecology (Johnson et al. 2003a).

The Orchidaceae is one of the largest families of Angiosperms and its species exhibit some of these mechanisms of pollination by facilitation (Ackerman 1986; Jersáková et al. 2006). One third of the orchid species have rewardless flowers (van der Pijl and Dodson 1966; Ackerman 1986), so they obtain pollinator services by mimicking a rewarding model plant (flowers appear similar) (Johnson 1994, 2000), or by taking advantage of their proximity to a rewarding plant (flower similarity not necessary) (Johnson et al. 2003a; Juillet et al. 2007). Rewardless orchid species are a unique study model because pollinium (structure containing pollen grains) is not eaten by the pollinator, and it is deposited in different body places of the pollinators than pollen of the facilitating plant species (Neiland and Wilcock 1998; Johnson and Nilsson 1999).

Facilitation between rewarding and rewardless plant species that share pollinators will have one of two principal mechanisms: the magnetic species effect (Thomson 1978; Laverty 1992) or Batesian floral mimicry (Dafni and Ivri 1981a; Johnson 1994, 2000). In the magnetic species effect hypothesis, a rewarding species increases the pollination success of rewardless plants by increasing the local abundance of pollinators (Thomson 1978; Laverty 1992). Non-rewarding plant species profit from their proximity to plants that receive more pollinator visits (Laverty 1992; Johnson et al. 2003a). The dependence of a rewardless orchid on a rewarding plant species for pollination has been shown in a few convincing cases (Alexandersson and Ågren 1996; Johnson et al. 2003a; Juillet et al. 2007). However, other studies have shown that the presence of rewarding species did not improve the fitness of the rewardless orchids (Lammi and Kuitunen 1995; Alexandersson and Ågren 1996; Internicola et al. 2006). The evidence for the magnetic species effect as a positive pollination mechanism in non-rewarding orchids is both inconclusive and contradictory. For example, Lammi and Kuitunen (1995) reported increased fruit set in the terrestrial orchid *Dactylorhiza incarnata* in the absence of nectar-producing *Viola* flowers, whereas Alexandersson and Ågren (1996), Internicola et al. (2006), Johnson et al. (2003a), and Juillet et al. (2007) found that the presence of nectar-producing neighboring plants improves the pollination success and fruit set in the orchids *Calypso bulbosa*, *Dactylorhiza sambucina*, *Traunsteinera globosa*, and

Anacamptis morio (respectively). Furthermore, the understanding of the magnetic species effect and the ecological and evolutionary forces that maintain this reproductive system remain unclear.

Batesian floral mimicry is another pollination facilitation mechanism in non-rewarding orchid species. This system is operating if the reproductive fitness of the mimic is higher when it occurs sympatrically with the rewarding model species, than in the absence of the model, and when the effect is constant over time and space (Roy and Widmer 1999; Johnson 2000). In Batesian floral mimicry, additional evidence must be provided to conclude that an orchid is exploiting an adaptive resemblance to a particular plant species (Roy and Widmer 1999). Such evidence might include matching spectral reflectance and behavioral experiments to establish that pollinators are unable to distinguish between the mimic and the model plants (Dafni and Ivri 1981a; Johnson 1994, 2000; Jersáková et al. 2006). A few studies support the theory that the presence of a model is necessary for reproduction by the mimic (Dafni and Ivri 1981a; Johnson 1994, 2000; Gigord et al. 2002), but there is no experimental evidence. On the other hand, Bierzychudek (1981) reported that monospecific clumps of the rewardless *Epidendrum radicans* and heterospecific clumps of this orchid with *Lantana camara* and *Asclepias curassavica* had similar fruit production, suggesting that the fitness of the mimic is similar in the presence or the absence of the model.

As far as we know, few natural and artificial manipulated experiments have demonstrated that the reproductive success of a rewardless orchid species is greater in the presence of rewarding species than in that of monospecific rewardless natural and artificial populations (Gigord et al. 2002; Johnson et al. 2003a; Anderson and Johnson 2006; Internicola et al. 2007). Furthermore, very little is known about the constancy of this pattern over time and space in the monospecific rewardless and heterospecific populations (Roy and Widmer 1999; Johnson et al. 2003a).

In this study, we evaluate the reproductive success of the rewardless *O. cosymbephorum* (Orchidaceae) in the presence of the rewarding *M. glabra* (Malpighiaceae). The orchid's flowers resemble those of *M. glabra* and both are pollinated by the female *Centris* bees (Carmona-Díaz 2001). We experimentally test whether the presence of *M. glabra* increases the reproductive success of *O. cosymbephorum* and if that relationship is constant throughout time and across their distributions.

Methods

Study sites

This study was carried out between July 2000 and December 2003 at five sites in Veracruz, Mexico where *O. cosymbephorum* grows naturally isolated or in mixed clumps with *M. glabra* (hereafter referred to as monospecific and heterospecific groups): Agaltepec Island (monospecific and heterospecific groups), Pipiapan, Mimiahua, and Amamaloya (monospecific groups) in the Los Tuxtlas Biosphere Reserve, and at the La Mancha Coastal Research Centre of the Instituto de Ecología, A. C. (monospecific and heterospecific groups) (Fig. 1).

Agaltepec (18°24′ N, 95°05′ W; area 8.3 ha; altitude 430 m a.s.l.), Amamaloya (19°26′ N, 95°31′ W; area 30 ha; altitude 250 m a.s.l.), and La Mancha (19°36′ N, 96°22′ W; area 30 ha; altitude 30 m a.s.l.) have subdeciduous tropical forest as dominant plant community (Castillo-Campos and Medina 2005; Serio-Silva et al. 2002; Castillo-Campos and Laborde 2004). Their climate is highly seasonal, with a rainy season (July–October) and dry season (March–May). The mean annual temperature and precipitation are 26°C and 1,980–2,000 mm, respectively. Pipiapan (18°25′ N, 95°18′ W; area 200 ha; altitude 500 m a.s.l.) and Mimiahua (18°24′ N, 95°10′ W; area 500 ha; altitude 400 m a.s.l.) have tropical rain forest as dominant plant community (Castillo-Campos and Laborde 2004; Cristobal-Azkarate et al. 2005). The rainy season is from June to November, and the dry season from March to May. The mean annual temperature and precipitation are 25–26°C and 2,000–2,100 mm, respectively.

Rewarding plant

Malpighia glabra L. (Malpighiaceae) is a deciduous shrub 1–5 m in height with a wide Neotropical distribution from Florida (United States of America) to northern Brazil (Anderson 1979). In Mexico, this species occurs on both the Atlantic and Pacific coasts. The flowering season in the coastal populations occurs from July to October and in the highlands, from September to December. Shrubs can produce 500 inflorescences (Carmona-Díaz 2001), and each inflorescence produces 1–4 magenta flowers (Fig. 2) that reward its pollinators—solitary female bees *Centris ruthannae*—with oil and pollen (Buchmann 1987; Vogel 1990). In the tropical rain forest and deciduous forest, *M. glabra* occurs in clusters of 5–15 individuals per 25 m^2 (Carmona-Díaz 2001).

Rewardless plant

Oncidium cosymbephorum Morren (Orchidaceae) is an endemic epiphytic orchid found in the states of Tamaulipas, Veracruz and Tabasco in Mexico (Jiménez 1993; Carmona-Díaz 2001). Inflorescences bear resupinate non-rewarding flowers (1–25) that are magenta in color (Fig. 2) (Jiménez 1993; Carmona-Díaz 2001; Chase et al. 2005). Flowers are not selfing, so pollinator visits are required for them to set fruit

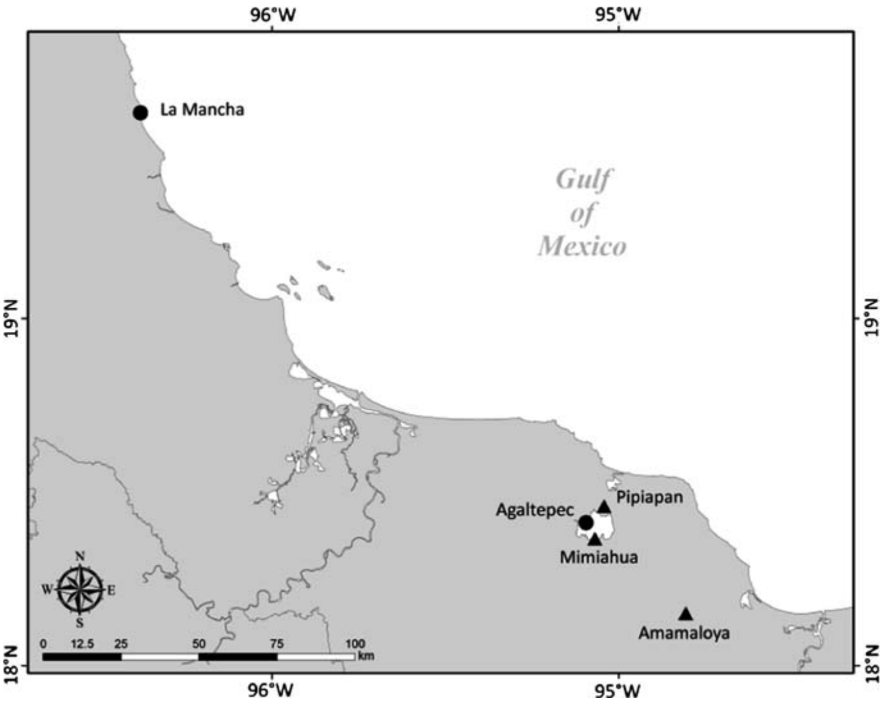

Fig. 1 Study sites with monospecific clumps of *Oncidium cosymbephorum* (Orchidaceae) (▲) and heterospecific clumps with plants of *O. cosymbephorum* and *Malpighia glabra* (Malpighiaceae) (●) at Los Tuxtlas Biosphere Reserve, and at La Mancha on the coast of the Gulf of Mexico

Fig. 2 Flowers of rewarding *Malpighia glabra* (Malpighiaceae) (left) and rewardless *Oncidium cosymbephorum* (Orchidaceae) (right)

(Jiménez 1993; Carmona-Díaz 2001). The flowering season is from July to November depending on the region and environmental conditions. In central Veracruz, *O. cosymbephorum* blooms from July to mid-October and in southern Veracruz the species flowers from September to November. Individual plants typically produce 1–6 fruits, depending on inflorescence size (Carmona-Díaz 2001).

The pollinators

The pollinators of both *M. glabra* and *O. cosymbephorum* are solitary female bees: *Centris ruthannae* Snelling (Anthophoridae) (Buchmann 1987; Carmona-Díaz 2001). *Centris ruthannae* frequently visit *M. glabra* flowers, clinging to the petals and scratching the elaiophores with their fore and hind legs to collect oil. Pollen of *M. glabra* is deposited on the abdomen of the bees ventrally. When visiting *O. cosymbephorum* flowers, they also cling to the petals and exhibit the same behavior as to collect oil in *M. glabra* flowers (Carmona-Díaz 2001). Pollinium of *O. cosymbephorum* is deposited in front of the bee's head. When bee visits a new flower the head touches the estigmata surface depositing the pollinium.

Experimental procedures

Natural and artificial monospecific and heterospecific clumps

In 2001 and 2002 we tested the reproductive success of *O. cosymbephorum* under monospecific and heterospecific growth conditions at Agaltepec Island and La Mancha. All clumps of *O. cosymbephorum* growing naturally with and without *M. glabra* plants in the neighborhood (heterospecific and monospecific groups, respectively) were recorded in both sites. Monospecific plant clumps: We chose three naturally monospecific clumps of *O. cosymbephorum*, and we made three artificial monospecific clumps of *O. cosymbephorum* by cutting the flowers, buds and/or branches of *M. glabra* individuals growing near the orchid individuals. Heterospecific plant clumps: We chose three heterospecific clumps that had intact individuals of both *O. cosymbephorum* and *M. glabra*, and we created three artificial heterospecific plant clumps by transplanting individuals of *O. cosymbephorum* close to naturally monospecific clumps of *M. glabra*. The experimental monospecific and heterospecific patches were separated by at least 100 m, and each was composed of 6–7 orchid plants and 10–14 *M. glabra* shrubs. Each individual orchid was tagged and monitored monthly until fruit production occurred. Fruit set (number of developing fruits per number of flowers produced per plant) was compared among the monospecific and heterospecific clumps as combinations of two fully crossed factors: presence or absence of *M. glabra*, and the type of plant clump (natural or artificially made). Natural and artificial clumps of *O. cosymbephorum* were considered to be monospecific when there were no flowers of *M. glabra* within a distance of 5 m, and heterospecific when both species were closer than 5 m.

Individuals of M. glabra close to monospecific orchid plants that had been isolated

A second experiment was carried out to test the effects of rewarding *M. glabra*'s presence on the reproductive success of isolated monospecific *O. cosymbephorum* plants. We chose naturally monospecific orchid clumps, three clumps each at Pipiapan and Amamaloya, and two each at Mimiahua and Agaltepec Island. The fruit set of clumps containing six to ten individual orchid plants was recorded in 2000 and 2001. In 2002, a total of 120 shrubs of *M. glabra* were taken from Agaltepec Island and potted individually. When the shrubs bloomed, ten plants were put near to each of the previously monitored *O. cosymbephorum* clumps. A set of monospecific orchid patches monitored in 2000 and 2001 was used as a control at each site. Fruit set for each *O. cosymbephorum* individual with or without *M. glabra* plants nearby was recorded. In 2003 all the orchid clumps were transformed into monospecific groups again (all containers with *M. glabra* plants were excluded), and the orchid fruit set was recorded. The number of orchid plants was different between years because not all the individuals flowered in each year of the study.

Data analysis

The fruit set produced by natural and artificial clumps of *O. cosymbephorum* was analyzed using a factorial ANOVA. Factors were site, year, condition (presence or absence of *M. glabra*), and type of plant clump (natural or artificial). The response variable was fruit set (Zar 1986). We included the type of plant clump as a factor because artificial clumps might have an independent effect on fruit set. The effect of the nearby rewarding *M. glabra* plants on the reproductive success of *O. cosymbephorum* plants that had been isolated was tested as follows. In order to determine if the orchid flower display (flower number) was similar throughout the study, we performed a Kruskal-Wallis test with the factors, site and year. The 2002 fruit set was compared between sites using an ANOVA. Fruit set data were arcsine transformed before analyses, and all analyses were done with STATISTICA software V.7. Post-hoc analyses were developed in order to identify the significant differences.

Results

Natural and artificial monospecific and heterospecific plant clumps

At both the sites studied (Agaltepec Island and La Mancha) and for both years (2001 and 2002) *O. cosymbephorum* individuals in the presence of *M. glabra* shrubs had a larger fruit set than plants separated from the rewarding plants in both natural and artificial groups (Table 1). There were significant differences between sites, years, condition (presence or absence of *M. glabra*), and for the site × condition, and year × condition interactions. The interaction between the four factors analyzed was not significant (Table 2) (one way ANOVA, Tukey test at $P < 0.05$ level).

Table 2 Comparison of the fruit set produced by monospecific and heterospecific clumps (natural and artificial) of *Oncidium cosymbephorum* (Orchidaceae) using a factorial ANOVA, with site (La Mancha and Agaltepec Island), year (2000 and 2001), condition (monospecific or heterospecific clump), and type (natural or experimental) as factors, and fruit set as the response variable

Variable and source of variation	Df	*F*-value	*P*-level
Site	1	9.9	0.002
Year	1	32.2	0.0001
Condition	1	442.5	0.0001
Type	1	1.1	0.296
Site × year	1	0.1	0.745
Site × condition	1	8.2	0.005
Year × condition	1	37	0.0001
Site × type	1	0.1	0.755
Year × type	1	0.7	0.407
Condition × type	1	1.2	0.266
Site × year × condition	1	0.0	0.985
Site × year × type	1	2.5	0.116
Site × condition × type	1	0.3	0.563
Year × condition × type	1	1.1	0.303
Site × year × condition × type	1	3.3	0.07

Table 1 Mean (±S.E.) number of flowers and fruits produced by *Oncidium cosymbephorum* (Orchidaceae) individuals in monospecific (M) and heterospecific (H) clumps (natural = N and artificial = A) at Agaltepec and La Mancha recorded for 2 years

	2001			2002		
	Number of flowers	Number of fruits	Fruit set (%)	Number of flowers	Number of fruits	Fruit set (%)
Agaltepec						
M-N	17.5 ± 2.12 (387)	0.18 ± 0.08 (4)	0.68 ± 0.38	15.6 ± 1.92 (344)	0.18 ± 0.08 (4)	0.30 ± 0.32
M-A	18.8 ± 9.4 (452)	0.16 ± 0.3 (4)	0.68 ± 0.41	13.7 ± 1.9 (330)	0.12 ± 0.3 (3)	0.50 ± 0.32
H-N	10.20 ± 0.97 (195)	3.50 ± 0.36 (67)	20.95 ± 1.75	13.1 ± 1.97 (276)	2.0 ± 0.34 (44)	11.33 ± 2.20
H-A	15.40 ± 1.67 (324)	4.20 ± 0.46 (90)	18.18 ± 1.99	10.9 ± 1.42 (230)	2.4 ± 0.43 (51)	11.86 ± 1.8
La Mancha						
M-N	10.9 ± 1.08 (208)	0.10 ± 0.07 (2)	0.36 ± 0.25	10 ± 0.93 (190)	0.15 ± 0.08 (4)	0.81 ± 0.46
M-A	14.4 ± 1.78 (332)	0.17 ± 0.08 (4)	0.38 ± 0.19	15.3 ± 1.55 (353)	0.21 ± 0.09 (3)	0.81 ± 0.35
H-N	12.2 ± 1.10 (233)	2.89 ± 0.51 (55)	13.66 ± 1.52	13.4 ± 1.44 (255)	2.31 ± 0.42 (44)	8.56 ± 1.4
H-A	15.9 ± 1.37 (350)	4.09 ± 0.51 (90)	14.74 ± 1.55	17.3 ± 1.66 (364)	2.4 ± 0.36 (51)	7.9 ± 0.95

Monospecific and heterospecific clumps were 6–7 orchids and 14 individuals of *Malpighia glabra* (Malphigiaceae), respectively. The total number of flowers and fruits is given in parentheses

Individuals of *M. glabra* close to monospecific orchid plants isolated

In 2000 and 2001, isolated individuals of *O. cosymbephorum* did not produce any fruit at the Mimiahua, Amamaloya, or Agaltepec Island sites. At Pipiapan *O. cosymbephorum* plants produced only two fruits in 2000 and none in 2001 (Table 3). In 2002, *O. cosymbephorum* individuals in the proximity of cultivated *M. glabra* individuals had a larger fruit set than orchids separated from the rewarding species at all the sites studied (Table 3). In 2003, when all plants of *M. glabra* were excluded, *O. cosymbephorum* individuals did not produce any fruit set again. Sites differed significantly in fruit set ($F_{3,88} = 4.01$, $P < 0.01$; Tukey test $P < 0.05$) and flower production ($H = 58.48$ $P < 0.001$), but there were no differences in flower production between years ($H = 7.38$, $P < 0.11$).

Discussion

Ours findings are consistent with the magnet species effect hypothesis (Thomson 1978), *O. cosymbephorum* benefits from the presence of the oil-producing plant. The reproductive success in *O. cosymbephorum* was significantly enhanced by the presence of individuals of *M. glabra* even though the orchid offers no flower reward to female *Centris* bees. Therefore, the presence of *M. glabra* to the orchid appears to be crucial to attract pollinators. Pollination facilitation has been documented for other non-rewarding orchid species (Alexandersson and Ågren 1996; Johnson et al. 2003a; Juillet et al. 2007).

Facilitation of *O. cosymbephorum* by *M. glabra*, as an ecological force, occurred along the geographic range of their distribution as evidenced by the results from La Mancha and Agaltepec Island that have different biophysical characteristics and are 188 km apart. Facilitation also occurred throughout the 2-year period of both study sites. Similar results were observed at Pipiapan, Amamaloya, and Mimiahua sites where *M. glabra*'s presence facilitated the orchid pollination. These findings were consistent throughout the 4 years of systematic monitoring.

Natural habitat conditions and heterospecific or monospecific clumps affect fruit set in non-rewarding orchids (Sabat and Ackerman 1996; Neiland and Wilcock 1998; Johnson and Nilsson 1999). Several studies indicate that the frequency of rewarding and non-rewarding plants (e.g. Internicola et al. 2006), pollinator density (Johnson et al. 2003a, b), floral display (Juillet et al. 2007), and spatial distribution (Johnson et al. 2003a) directly affect the fruit production of a rewardless species. Thus, the greater number of fruits on Agaltepec Island relative to La Mancha likely results from these factors. On Agaltepec Island (8.3 ha), *M. glabra* forms larger clumps and is more abundant (1,400 individuals) than at La Mancha (30 ha) (341 individuals), so Agaltepec Island provides both more abundant and denser rewards to pollinators. A small habitat facilitates foraging on rewarding species by pollinators and, therefore, pollen or pollinarium flow (Johnson 1994; Roy and Widmer 1999). Under these circumstances,

Table 3 Fruit production of *O. cosymbephorum* recorded at four sites over 4 years

Site	2000		2001		2002				2003	
	N-M		N-M		H-A		N-M		N-M	
	N (fl/fr)	Fs (%)	N (fl/fr)	Fs (%)	N fl/fr	Fs (%)	N (fl/fr)	Fs (%)	N (fl/fr)	Fs (%)
Agaltepec	18 (297/2)	0.67	18 (273/0)	0	20 (381/50)	13.12	20 (365/0)	0	28 (561/0)	0
Amamaloya	32 (292/0)	0	32 (384/0)	0	20 (362/41)	11.32	20 (355/0)	0	40 (350/0)	0
Mimiahua	17 (333/0)	0	17 (353/0)	0	20 (371/68)	18.32	20 (350/0)	0	27 (267/0)	0
Pipiapan	25 (197/0)	0	25 (205/0)	0	20 (193/25)	12.95	20 (201/0)	0	35 (387/0)	0

Individuals of *Oncidium cosymbephorum* (Orchidaceae) occurring naturally in monospecific clumps (N-M) in 2000 and 2001. In 2002, the clumps were made heterospecific by planting *Malpighia glabra* (Malphigiaceae) shrubs close to the orchids (H-A). Some of the clumps of orchids were kept monospecific (N-M). In 2003, all orchids were monospecific (M-N) again. n = Individual number; fl = flower number; fr = fruit number; Fs = fruit set female *Centris* bees can visit more flowers of *M. glabra* and *O. cosymbephorum* per unit of time.

The hypothesis of Batesian floral mimicry offers an alternative explanation to the magnet species effect for our results (Dafni and Ivri 1981a; Johnson 1994, 2000). In a Batesian floral mimicry system, the fitness of the mimic should be higher in the presence of the model than in its absence (see Johnson 1994, 2000; Roy and Widmer 1999). Our data allow us to conclude that *O. cosymbephorum* depend upon *M. glabra*, but they do not allow to insure that one of the plant species is the mimic and the other is the model. The presence of *M. glabra* is a determinant of fruit production by the orchid on both spatial and temporal scales. We found that natural monospecific clumps of *O. cosymbephorum* that had not produced any fruit for two consecutive years, suddenly produced fruits when cultivated flowering individuals of *M. glabra* were in their vicinity. This suggests that some kind of particular interaction occurs between *O. cosymbephorum* and *M. glabra*. *Oncidium cosymbephorum* is sympatric with *M. glabra*, it has lower plant frequency, its flowering time overlaps that of *M. glabra*, it shares pollinators with *M. glabra*, and its flowers resemble those of *M. glabra* in both color and morphology (Carmona-Díaz 2001). When *Centris* bees visited *M. glabra* flowers, they included the flowers of *O. cosymbephorum* on their foraging route. Our results of the increase in fruit set, indirectly suggest that bees do mistake the flowers of *O. cosymbephorum* for those of *M. glabra*. Not all bee-visited flowers are expected to be successfully pollinated because fertilization only takes place if the pollen is cross-compatible (Carmona-Díaz 2001).

A few cases of floral mimicry have provided evidence that some rewardless orchids produce more fruits when grown adjacent to their model plant (Dafni and Ivri 1981a, b; Johnson 1994, 2000). It has been argued that in some Batesian floral mimicry systems, the resemblance between model and mimic is so strong that pollinators fail to distinguish between them (Johnson 1994, 2000). However, these studies did not explore spatial and temporal variation or constancy. Our results provide experimental evidence for pollination facilitation and suggest that the study system is a possible case of Batesian floral mimicry.

Future field studies and specific experiments are necessary to address whether the facilitation of pollination that we have documented here is an adaptive similarity of the rewardless plant species, or simply a general phenomenon that can occur even when the flowers of the orchid do not resemble those of the nearby rewarding species.

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References

Ackerman JD (1986) Mechanisms and evolution of food deceptive pollination systems in orchids. Lindleyana 1:108–113

Alexandersson R, Ǻgren J (1996) Population size, pollinator visitation and fruit production in the deceptive orchid *Calypso bulbosa*. Oecologia 107:533–540. doi:10.1007/BF00333945

Anderson W (1979) Floral conservatism in Neotropical Malpighiaceae. Biotropica 11:219–223. doi:10.2307/2388042

Anderson B, Johnson SD (2006) The effects of floral mimics and models on each others' fitness. Proc R Soc Lond B Biol Sci 273:969–974. doi:10.1098/rspb.2005.3401

Bierzychudek P (1981) *Asclepias*, *Lantana* and *Epidendrum*: a floral mimicry complex? Biotropica 13:54–58. doi:10.2307/2388070

Buchmann SL (1987) The ecology of oil flowers and their bees. Annu Rev Ecol Syst 18:343–369. doi:10.1146/annurev.es.18.110187.002015

Carmona-Díaz G (2001) Floral mimicry between *Oncidium cosymbephorum* Morren (Orchidaceae) and *Malpighia glabra* L. (Malpighiaceae). Master of Science Thesis. Universidad Veracruzana, Xalapa, Veracruz, Mexico

Castillo-Campos G, Laborde J (2004) La vegetación. In: Guevara S, Laborde J, Sánchez G (eds) Los Tuxtlas: El Paisaje de la Sierra. Instituto de Ecología A.C.. Unión Europea, Xalapa, Ver, pp 231–265

Castillo-Campos G, Medina ME (2005) Árboles y arbustos de la Reserva Natural de La Mancha, Veracruz, México. Instituto de Ecología A.C., Xalapa, Ver, p 143

Chase MW, Hanson L, Albert VA, Whitten WM, Williams NH (2005) Life history evolution and genome size in Subtribe Oncidiinae (Orchidaceae). Ann Bot (Lond) 95:191–199. doi:10.1093/aob/mci012

Cristobal-Azkarate J, Vea J, Ascencio N, Rodríguez-Luna E (2005) Biogeographical and floristic predictors of the presence and abundance of mantled howlers (*Alouatta palliata mexicana*) in rainforest fragments at Los Tuxtlas, Mexico. Am J Primatol 67:209–222. doi:10.1002/ajp.20178

Dafni A, Ivri Y (1981a) Floral mimicry between *Orchis israelitica* Baumann and Dafni (Orchidaceae) and *Bellevalia flexuosa* Boiss (Liliaceae). Oecologia 49:229–232. doi:10.1007/BF00349193

Dafni A, Ivri Y (1981b) The flower biology of *Cephalanthera longifolia* (Orchidaceae) pollen imitation and facultative floral mimicry. Plant Syst Evol 137:229–240. doi:10.1007/BF00982788

Feinsinger P (1987) Effect of plant species on each other's pollination: is community structure influenced? Trends Ecol Evol 2:123–126. doi:10.1016/0169-5347(87)90052-8

Feldman TS, Morris WF, Wilson WG (2004) When can two plant species facilitate each other's pollination? Oikos 105:197–207. doi:10.1111/j.0030-1299.2004.12845.x

Gigord LDB, Macnair M, Stritesky M, Smithson A (2002) The potential for floral mimicry in rewardless orchids: an experimental study. Proc R Soc Lond B Biol Sci 269:1389–1395. doi:10.1098/rspb.2002.2018

Hegland SJ, Totland O (2005) Relationships between species' floral traits and pollinator visitation in a temperate grassland. Oecologia 145:586–594. doi:10.1007/s00442-005-0165-6

Internicola A, Juillet N, Smithson A, Gigord LDB (2006) Experimental investigation of the effect of spatial aggregation on reproductive success in a rewardless orchid. Oecologia 150:435–441. doi:10.1007/s00442-006-0530-0

Internicola A, Page PA, Bernasconi G, Gigord LDB (2007) Competition for pollinator visitation between deceptive and rewarding artificial inflorescences: an experimental test of the effects of floral colour similarity and spatial mingling. Funct Ecol 21(5):864–872. doi:10.1111/j.1365-2435.2007.01303.x

Jersáková J, Johnson SD, Kindlmann P (2006) Mechanisms and evolution of deceptive pollination in orchids. Biol Rev Camb Philos Soc 81:219–235. doi:10.1017/S1464793105006986

Jiménez R (1993) Los géneros *Lophiaris* y *Oncidium* en México. Primer Simposio Internacional de Orquideología, Xalapa, Veracruz, México

Johnson SD (1994) Evidence for Batesian mimicry in a butterfly-pollinated orchid. Biol J Linn Soc Lond 53:91–104

Johnson SD (2000) Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behavior. Biol J Linn Soc Lond 71:119–132

Johnson SD, Nilsson LA (1999) Pollen carryover, geitonogamy, and the evolution of deceptive pollination system in orchids. Ecology 80:2607–2619

Johnson SD, Peter CI, Nilsson LA, Ågren J (2003a) Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. Ecology 84:2919–2927. doi:10.1890/02-0471

Johnson SD, Alexandersson R, Linder HP (2003b) Experimental and phylogenetic evidence for floral mimicry in a guild of fly-pollinated plants. Biol J Linn Soc Lond 80:289–304. doi:10.1046/j.1095-8312.2003.00236.x

Juillet N, Gonzalez MA, Page PA, Gigord LDB (2007) Pollination of the European food-deceptive *Traunsteinera globosa* (Orchidaceae): the importance of nectar-producing neighbouring plants. Plant Syst Evol 265:123–129. doi:10.1007/s00606-006-0507-9

Lammi A, Kuitunen M (1995) Deceptive pollination of *Dactylorhiza incarnata*: an experimental test of the magnet species hypothesis. Oecologia 101:500–5003. doi:10.1007/BF00329430

Laverty TM (1992) Plant interaction for pollinator visits: a test of the magnet species effect. Oecologia 89:502–508

Moeller DA (2004) Facilitative interactions among plants via shared pollinators. Ecology 85:3289–3301. doi:10.1890/03-0810

Neiland MR, Wilcock C (1998) Fruit set, nectar reward, and rarity in the Orchidaceae. Am J Bot 85:1657–1671. doi:10.2307/2446499

Rathke BJ (1988) Interactions for pollination among co-flowering shrubs. Ecology 69:446–457. doi:10.2307/1940443

Renner SS (2006) Rewardless flowers in the Angiosperms and the role of insect cognition in their evolution. In: Waser NM, Olerton J (eds) Plant pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago, pp 123–144

Roy BA, Widmer A (1999) Floral mimicry: a fascinating yet poorly understood phenomenon. Trends Plant Sci 8:325–330. doi:10.1016/S1360-1385(99)01445-4

Sabat AM, Ackerman JD (1996) Fruit set in a deceptive orchid: the effect of flowering phenology, display size, and local abundance. Am J Bot 83:1181–1186. doi:10.2307/2446202

Serio-Silva JC, Rico-Gray V, Hernández-Salazar LT, Espinosa-Gómez R (2002) The role of *Ficus* (Moraceae) in the diet and nutrition of a troop of Mexican howler monkeys *Alouatta palliata mexicana*, released on an island in Southern Veracruz, Mexico. J Trop Ecol 18:913–928. doi:10.1017/S0266467402002596

Thomson JD (1978) Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. Am Midl Nat 100:431–440. doi:10.2307/2424843

Van der Pijl L, Dodson CH (1966) Orchid flowers, their pollination and evolution. University of Miami Press, Coral Gables

Vogel S (1990) History of the Malpighiaceae in the light of pollination ecology. Mem N Y Bot Gard 55:130–142

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043–1060. doi:10.2307/2265575

Zar JH (1986) Biostatistical analysis. Prentice-Hall, New Jersey