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A survey of pollination in remnant orchid populations in Soconusco, Chiapas, Mexico

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Abstract: Results are presented of a survey of the pollination in remnant populations of 100 species of orchids in the tropical region of Soconusco (below 1,000 m) in Chiapas, Mexico, which has been seriously affected by agriculture, deforestation and severe storms. Pollination was generally highly erratic and zero fruit set was common; a few species appear to be self pollinated. We present a first time report of the bee *Neocorynura* aff. *centroamericana* as the pollinator of *Stelis quadrifida* and flies from the families Cecidomyiidae and Phoridae as pollinators of the miniature orchid *Specklinia marginata.* Pollinators were captured and identified for various common orchid species. Of 1,480 individuals of 11 species of euglossine bees captured using chemical baits, 2.7% carried orchid pollinaria, with peak activity in February in the dry season. Our evidence shows that increasingly rare orchids such as *Brassavola cucullata*, *Kefersteinia lactea*, *Lycaste cruenta*, *Scaphyglottis imbricata* and *Trichopilia tortilis* can be pollinated naturally in *ex situ*, sustainable orchid cultures in rural communities.

Resumen: Se presentan los resultados de un estudio de la polinización en poblaciones remanentes de 100 especies de orquídeas en la región tropical del Soconusco (abajo de 1,000 m) en Chiapas, México, la cual ha sido fuertemente afectada por la agricultura, la deforestación y por tormentas de gran intensidad. En general la polinización fue muy errática y fue común que no hubiera producción de frutos; en unas pocas especies parece haber autopolinización. Presentamos el primer reporte de la abeja *Neocorynura* aff. *centroamericana* como el polinizador de *Stelis quadrifida* y de moscas de las familias Cecidomyiidae y Phoridae como los polinizadores de la orquídea miniatura *Specklinia marginata.* Se capturaron e identificaron los polinizadores de varias especies de orquídeas comunes. De 1,480 individuos de 11 especies de abejas euglosinas capturadas usando cebos químicos, 2.7% llevaban polinarios de orquídeas, con su pico de actividad en febrero, durante la época seca. Presentamos evidencias de que algunas orquídeas cada vez más raras como *Brassavola cucullata*, *Kefersteinia lactea*, *Lycaste cruenta*, *Scaphyglottis imbricata* y *Trichopilia tortilis* pueden polinizarse de manera natural *ex situ*, en cultivos sustentables de orquídeas en comunidades rurales.

Resumo: Os resultados de um inventário da polinização de uma população remanescente de 100 espécies de orquídeas na região tropical de Soconusco (abaixo dos 1,000 m) em Chiapas, México, que foi seriamente afectada pela agricultura, desflorestação e tempestades severas, são apresentados. A polinização era geralmente muito errática e a improdutividade frutícola era comum; umas poucas espécies pareciam ser autopolinadas. Neste trabalho apresenta-se, pela primeira vez, da abelha *Neocorynura* aff. *Centroamericana* como polinizadora da *Stelis quadrifida* e moscas das famílias Cecidomyiidae e Phoridae como polinizadoras da orquídea

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miniatura *Specklinia marginata*. Os polinizadores foram capturados e identificados para várias espécies de orquídeas comuns. Dos 1 480 indivíduos de 11 espécies de abelhas euglossine capturadas usando iscos químicos, 2,7% transportavam pólen de orquídea com um pico de actividade na estação seca em Fevereiro. A nossa evidência mostra, de forma crescente, que orquídeas raras como as *Brassavola cucullata*, *Kefersteinia lacteal*, *Lycaste cruenta*, *Scaphyglottis imbricata* and *Trichopilia tortilis* podem ser cultivadas de forma sustentável com recurso à polinização natural *ex situ* em comunidades rurais.

Key words: Coffee agroecosystem, deforestation, epiphyte, *ex situ* conservation, *Centris*, *Euglossa*, *Eulema*, *Neocorynura*, sustainable orchid cultivation.

Introduction

Pollination and seed set in many orchid species are rare events, particularly in fragmented and disturbed environments and this may undermine the process of sexual reproduction and eventually threaten the survival of these plants. Furthermore, the pollination of most orchid species is generally considered to be a specialized process (Borba & Semir 2001; Dixon *et al*. 2003; Johnson & Steiner 2000; Kearns & Inouye 1997; Tremblay 1992), dependant on one or a very few species of insects (Dressler 1981) which are rarely observed, especially in the case of deceptive orchids (Johnson *et al.* 2003; Widmer *et al*. 2000) and prone to great variation between years (Parra-Tabla & Vargas 2004; Roubik 2001). We cannot put a value to "how low is too low" (Dixon *et al.* 2003) for the pollination rate for the thousands of orchid species currently persisting in precarious environments and science demands repetitions which is difficult, if not impossible to achieve for the many rare, widely dispersed and inaccessible epiphytic orchids.

Pollination rates in the majority of orchids are notoriously low (Peakall & Handel 1993; Widmer *et al.* 2000), evidence of the pollination mechanism is lacking for the majority of species (Pridgeon *et al.* 2005) and there are few studies that have been able to compare pollination and seed set between preserved, natural conditions and disturbed conditions. Johnson & Bond (1992) and Parra Tabla *et al.* (2000), however, indicated that pollinarium removal and seed set in *Disa uniflora* Bergius and *Oncidium* (now *Trichocentrum*) *ascendens*, respectively, were better on preserved sites, although Dressler (1981) mentioned that some orchids may proliferate in disturbed habitats.

The reproductive strategy of tropical epiphytic orchids, which occupy resource-limited niches, may prioritize vegetative reproduction (clonal colonization) (Benzing 2000) and longevity (Nilsson 1992), relegating sexual reproduction to an unpredictable and rare event, which can be heavily rewarded when it occurs by the production of large numbers of seeds (Neiland & Wilcock 1998). Orchids present their pollen in discreet masses called pollinia, which in turn are grouped together to form a single, transportable pollen "package" the pollinarium. This creates an "all or nothing" situation which demands efficient, "loyal" pollinators.

The visits of orchid pollinators may be sporadic and unpredictable, for example, the well studied euglossine bees, in fact, dedicate most of their foraging time to the search for nectar and only occasionally to the harvesting of orchid fragrances (Roubik 1993). Tropical epiphytic orchids are often present as small and widely dispersed populations (Ackerman 1986; Ackerman & Montalvo 1990; Almeida & Figueiredo 2003; Calvo 1993; Dixon *et al*. 2003; Tremblay 1992) and deceptive strategies, especially mimicry of rewarding flower species, may occur when plant population sizes are insufficient to maintain pollinator interest (Sabat & Ackerman 1996).

The region of Soconusco, which includes the Pacific coast and lower reaches of the Sierra Madre mountains of southeastern Chiapas (15°19'N 92°44'W), is a biologically diverse region which is now mostly deforested and dedicated to agriculture, featuring extensive coffee plantations which may act as corridors for pollinating insects

(Townsend & Levey 2005) and effectively replace the tropical humid forest as a refuge for native flora and fauna. Coffee producers, affected by unstable prices and soil erosion, are now diversifying production, including the cultivation of native orchids, motivated both by conservation incentives and economic need.

In the coastal plain and middle altitudes of Soconusco *Prosthechea chacaoensis* is the most flexible and widespread orchid species, found in most habitats. *Erycina crista-galli*, *Notylia barkeri, Campylocentrum micranthum*, *Leochilus scriptus*, *L. oncidioides* and *L. labiatus* are small, twig-epiphytic species which have adapted to life on the abundant coffee trees, whereas other species such as *Trichocentrum ascendans*, *T. oerstedii* and *Guarianthe aurantiaca* are found mainly adhered to the shade trees in coffee plantations (Damon & Colin 2005).

This descriptive study focuses upon pollination as one of the two ecological "bottlenecks" faced by orchids, the other being the relationship with mycorrhizal fungi which are essential for the germination of orchid seeds and the adequate development of the young plants. We assess the pollination of remnant orchid populations in fragments of tropical forest and agroecosystems in Soconusco, at altitudes of between 10-1,000 m, covering 100 out of the approximately 150 orchid species which can be found in the region (Cabrera-Cachón 1999; Damon & Colin 2005). Our results are an important contribution towards the development of strategies for the conservation and sustainable exploitation of native orchid species.

Methods

Flowering periods and fruit set

The observations were made during surveys and collecting trips carried out throughout the lower and middle altitudes of the Soconusco region (10-1,000 m), during the period 1999-2004. The region covers the 16 municipalities of Mapastepec, Acacoyagua, Acapetahua, Esquintla, Villa Comaltitlán, Huixtla, Tuzantán, Huehuetán, Mazatán, Tapachula, Unión Juárez, Cacahoatán, Tuxtla Chico, Metapa, Frontera Hidalgo and Suchiate.

The data consisted of single observations, in which percentage fruit set per inflorescence was calculated. The numbers of inflorescences available for study and the number of flowers per inflorescence were highly variable. Data were not considered comparable and no statistical analysis or calculation of means and standard errors was carried out.

Pollination of 24 species at two sites

Site 1 (The Regional Botanical Garden "El Soconusco", at 80 m in the municipality of Tuzantán in Chiapas) contains a well established, semi-natural collection of low altitude, local species of orchids, and is situated within an area of forest fragments and cocoa and coffee plantations with native trees as shade. Average temperatures and relative humidity during the experimental period, at 11.30 h were 34 °C and 60% and at 17.30 h were 30 °C and 65%. Site 2 (The orchidarium "Santo Domingo, at 900 m in the municipality of Unión Juárez) is located at the edge of an extensive area of coffee plantations with species of *Inga* as shade trees, as well as occasional native forest trees. The orchidarium contains an established, semi-natural collection of middle altitude orchid species from the region. Average temperatures and relative humidity at 11.30 h were 36 °C and 35% and at 17.30 h were 22.5 °C and 85%.

This section of the study involved selecting and marking inflorescences and observing pollinator activity during the entire flowering period of each species. The total number of flowers and total number of seed capsules were counted and % fruit set was calculated. Samples of candidate and confirmed pollinating insects were trapped for identification. Pollinaria carried by captured insects were identified, using the image data base developed by the project "Restauracion y aprovechamiento sustentable de las orquídeas del Soconusco, Chiapas" (CONACyT-SEMARNAT, 2002-C01-0697).

Orchid pollination in rustic, sustainable production units in 4 rural communities

As part of the activities of the project, assessment and training is given for the rustic, sustainable cultivation of native orchids in various coffee-producing communities in the Soconusco region (Damon *et al.* 2005). A total of 32 production units in 4 communities (Table 3) were evaluated during a period of one year, wherein flowering periods and the production of seed capsules were noted, by the authors, on a monthly basis.

Abundance and seasonality of euglossine bees, and pollinaria transportation

The bees were monitored in sites 1 and 2 for approximately 5 hours each day, for two days at each site, every two months (February, April, June, August, October and December) during a period of one year, 2004/5.

Male euglossine bees visit various kinds of flowers, including orchids, to collect drops of a diversity of volatile substances (fragrances) which may be important for the attraction of females (Roubik & Hanson 2004). These bees may be attracted and captured using volatile baits and 18 different substances were selected, of which eucalyptol (1,8-cineole) is considered as the best universal euglossine bee attractant and P-dimethyloxybenzene as a good attractant (Roubik & Hanson 2004) and used both days and the other substances were secondary attractants (Robik & Hanson 2004; unpublished project data) and used on one of the days only. Day 1: ß-ionone, benzyl acetate, D-carvone, methyl cinnamate, methyl benzoate, linalool, ß-pinene, skatole. Eucalyptol, P-dimethyloxybenzene. Day 2: L-carvone, 2-phenyl ethyl acetate, benzyl benzoate, geraniol, vanillin, methyl salicylate, eugenol, T-methyl cinnamate. Eucalyptol, P-dimethyloxybenzene.

Secondary baits were placed at 8 or 9 O'clock in the morning and left for two hours before the primary baits, eucalyptol and P-dimethyloxy-benzene were placed. The volatile substances were transported to the sites in ice-boxes, then applied to cotton dental rolls and hung in the shade from branches or twigs at a height of approximately 1.5 m above the ground. Baits were watched constantly until 13.00 h. All bees that came to the baits were identified using keys supplied by Roubik 2004 (Personal communication) and Roubik & Hanson (2004). To prevent recapture during the same day, captured bees were maintained in plastic jars with sugar water in the shade, until the end of the experimental period, whereupon they were released. Insects that could not be identified, those that carried pollinaria, and a sample of all the species found were killed using an injection of 80% alcohol as suggested by Gómez-Gómez (2004. Personal communication) and stored in labelled jars with calcium chloride for further study.

The pollinaria carried by the bees attracted to the chemical baits were identified, using the image data base, as previously mentioned. The data obtained were then compared with the flowering periods and % fruit set of orchids pollinated by these bees at the same sites.

A revision was made of the bees found in the collection "Abejas de Chiapas" maintained in the Entomology Collection of ECOSUR-Tapachula. Individuals carrying pollinaria were photographed and pollinaria were compared to the image data base.

Results

Flowering periods and fruit set

A number of species of orchids could be found flowering at all times during the year, in the Soconusco region (Table 1, Fig. 1) and the majority of species showed zero fruit set. Various species are autogamous resulting in high pollination rates which may approach 100%, such as *Campylocentrum micranthum*, some populations of *Guarianthe aurantiaca*, *Sacoila lanceolata*, all species of *Isochilus* mentioned in this study, *Deirygyne hemichrea*, *Polystachya foliosa*, some populations of *Stelis quadrifida* and *Oeceoclades maculata*.

Pollination of 24 species at two sites

In Santo Domingo the rainy season continues until mid-November, whereas in Tuzantán it ends at the end of October; in both the sites the dry season ends halfway through June. This study showed that at lower altitudes many orchids have become adapted to the 6 month dry season and many flower during that time. However, at middle altitudes, all the orchid species in this study flowered during the rainy season (Table 2; Fig. 1).

We present a first time report of the bee *Neocorynura* aff. *centroamericana* (Hymenoptera: Halictidae: Augochlorini) as the pollinator of *Stelis quadrifida* (this orchid was previously incorrectly identified as *Anathallis racemiflora*, Solano 2006. Personal communication). Only one individual was observed and captured but this individual spent considerable time passing from one flower to another and manipulated the flowers in a very

Table 1. General observations of flowering periods and percentage fruit set of 100 species of orchids in the region of Soconusco, Chiapas, Mexico, during a 5 year period.

Species	Flowering period	% Fruit set
Arpophyllum medium Reichb.f.	XI	0 (n=3)
Barkeria obovata (C. Presl) Cristenson	I-IV, IX, XII	0-5
Barkeria skinneri (Bateman ex Lindley) A. Rich & Galeotti	VIII-X	0 (n=5)
Brassavola cucullata (L.) R. Br.	IV	Nd
Brassavola nodosa L. (Lindley)	I, III, VI-IX **+**	3-30
Brassia verrucosa Lindl.	V, X	0 (n=10)
Bulbophyllum oerstedii (Reichb.f.) Helmsley	XI	0-2 (n=4)
Campylocentrum micranthrum (Lindley) Rolfe	IV - V, XI	* 50-90
Catasetum integerrimum Hook	III; V - VIII	Male flowers only (n=35)
Caularthron bilamellatum (Reichb.f.) R.E. Schultes	II	* 30-60
Chysis bractescens Lindley	II	Nd
Coelia triptera (Sm.) G. Don ex Steudel	IX	0 (n=1)
Cycnoches ergotonianum Bateman	VIII	Nd
Cycnoches ventricosum Bateman	VI – VIII	Male flowers only (n=12)
Deirygyne hemichrea (Lindley) Schltr.	XII – II	0 (n=5)
Elleanthus cynarocephalus (Reichb.f.) Reichb.f.	VI – IX	0 (n=5)
Encyclia adenocarpa (La Llave & Lex.) Schltr.	I – VI	0-5 (n=6)
Encyclia bractescens (Lindl.) Hoehne	III-IV	0 (n=1)
Encyclia cochleata (L.) Lemée	V – IX **+**	0 (n=5)
Encyclia cordigera (Kunth) Dressler	II – VI	0 – 23
Encyclia livida (Lindley) Dressler	VI-XII	0 (n=2)
Encyclia ochraceae (Lindley) Dressler	VI – XII	0 (n=4)
Encyclia parviflora (Regel) Withner	III	0 – 20
Encyclia selligera (Lindley) Schltr.	II	0 (n=2)
Epidendrum ciliare L.	IV – VII	0
Epidendrum lacertinum Lindley	V	0 (n=5)
Epidendrum melistagum Hágsater	VI – VII	0 – 10 (n=5)
Epidendrum polyanthum Lindley	V – VIII	High, but not counted
Epidendrum aff. *stevensii* o *ramosum*	V, VIII, X	High, but not counted
Epidendrum stamfordianum Bateman	X – III	0-11
Erycina crista-galli (Rchb.f.) N.H.Williams & M.W.Chase	VI – I	0 – 30
Erycina pulsilla (L.) N.H.Williams & M.W.Chase	VI – XII	0 (n=3)
Gongora galeata (Lindley) Reichb.f.	V – VIII	0 – 16 (n=9)
Guarianthe aurantiaca (Bateman ex Lindl.) Dressler & W. E. Higgins	XI – III	* 0-50
Guarianthe skinneri (Bateman) Dressler & W. E. Higgins	I –V	0-30
Habernaria quinqueseta (Michaux.) Sw.	VIII	0 (n=3)
Isochilus amparoanus Schltr.	V	High but not counted
Isochilus carnosiflorus Lindley	Sporadic, III-IX	High but not counted
Isochilus aff. *latibracteatus* A. Rich. & Galeotti	V	High but not counted
Jaquinella cobanensis (Ames & Schltr.) Dressler	III	0 (n=7)
Kefersteinia lactea (Rchb.f.) B.D. Jacks.	VI	Nd
Laelia rubescens Lindl.	X – I	0 – 13 (n=8)
Leochilus oncidioides Knowles & Westc.	XII – I	0 – 15 (n=6)
Leochilus labiatus (Sw.) Kuntze	X – I	0 – 12 (n=16)
Leochilus scriptus (Sw.)Rchb.f.	I-III, VI, X	0 – 6 (n=5)
Lockhartia oerstedii Reichb.f.	II – VII	0
Lycaste cruenta Lindley	V – VII	0 (n=3)
Maxillaria conferta (Griseb.) C. Schweinf. ex León	VIII-X	High, but not counted
Maxillaria crassifolia (Lindley) Reichb.f.	VIII – IX	0 - 100 (n=2)
Maxillaria cucullata Lindl.	III	0 (n=1)
Maxillaria densa Lindl.	XII-I	0
Maxillaria elatior (Reichb.f.) Reichb.f.	X	0
Maxillaria friedrichsthalli Reichb.f.	I – II coast. III – XII mid-altitudes.	0 (n=10) 0 – 0.5 (n=15)

Continued

Table 1. Continued

Species	Flowering period	% Fruit set
Maxillaria hagsateriana Soto Arenas	IX	0 (n=3)
Maxillaria ringens Reichb.f.	VII	0 (n=7)
Maxillaria variabilis Bateman ex. Lindley	IV, X. XI - II	0 – 3
Meiracycllium trinasutum Reichb.f,	III – V	0 – 50
Mormolyca ringens (Lindley) Schltr.	I – VIII	0 – 0.1
Mormodes lineata Bateman ex Lindley	II-III; VII-VIII; XI-XII+	0
Nidemia boothii (Lindley) Schltr.	III – VI	0 – 35
Notylia barkeri Bateman ex Lindley	V-VI; XII – II +	0 – 3
Oeceoclades maculata (Lindl.) Lindl.	VIII	19 (n=1)
Oncidium laeve (Lindley) Beer	IV	0 (n=10)
Oncidium microchilum Bateman ex Lindley	VIII	0 (n=1)
Oncidium ornithorrhynchum Kunth	IX – XI	0 (n=14)
Oncidium sphacelatum Lindl.	IX; XI – III	0 – 7
Ornithocephalus tripterus Schltr	V – IX, XII	0 (n=12)
Osmoglossum pulchellum (Bateman ex Lindley) Schltr.	I – III	0 (n=7)
Platystele ovatilabia (Ames & C. Schweinf.) Garay	IV-VII	Nd
Pelexia sp.	III	0 (n=2)
Pleurothallis matudiana C. Schweinf.	VIII-IX	0 (n=3)
Pleurothallis tubata (Loddd.) Steudel	V	0 (n=1)
Polystachya foliosa Hook (Hook) Reichb.f.	IX – X	27 – 92 (n=5)
Ponera striata Lindley	I	0 – 2
Prosthechea baculus (Rchb.f.) W.E. Higgins	II – IV	0 – 1
Prosthechea chacaoensis (Rchb.f.) W.E. Higgins	II – VII	0 – 30
Prosthechea chondylobulbon (A. Rich & Galeotti) W.E. Higgins	IV	0 (n=1)
Prosthechea cochleata (L.) W.E. Higgins	V – XII	0 (n=7)
Prosthechea radiata (Lindl.) W.E. Higgins	VII	0 (n=2)
Restrepia muscifera (Lindley) Reichb.f. ex Lindley	Nd	0 – 2 (n=3)
Restrepiella ophiocephala (Lindley) garay & Dunsterv.	IX – XI; III	0 – 1
Sacoila lanceolata (Aubl.) Garay	IV	High, but not counted
Sarcoglottis sceptrodes (Reichb.f.)Schltr	II	0 (n=2)
Scaphyglottis imbricata (Lindl.) Dressler	X	0 -3
Scaphyglottis crurigera (Bateman ex Lindley) Ames & Correll	II – VI	0
Scaphyglottis sp.	X –XII	0 (n=1)
Sobralia sp.	XII	0 – 40
Sobralia decora Bateman	II, X – XII	0 – 25
Sobralia macrantha Lindley	V	0
Specklinia endotrachys (Rchb. f.) Pridgeon & M. W. Chase	+	0 (n=7)
Specklinia marginata (Lindl.) Pridgeon & M. W. Chase	II – IV	0-2.5
Specklinia tribuloides (Sw.) Pridgeon & M. W. Chase	IV – V	0 (n=9)
Stanhopea saccata Bateman	VI – VII	0 – 20
Stelis quadrifida. (La Llave & Lex.) Solano & Soto Arenas	V-XII	* 50-90, but in some populations very low
Stelis sp.	VI – X	0 – 2.5
Trichocentrum candidum Lindley	XII	0 (n=9)
Trichocentrum ascendens (Lindl.) M.W.Chase & N.H.Williams	I – VI	0 – 3 (n=11)
Trichocentrum oerstedtii (Rchb.f.) R.Jimenez & Carnevalii	XII –VII	0
Trichopilia tortilis Lindley	III –VI; X	0 – 5 (n=9)
Trichosalpinx blaisdellii (S. Watts) Luer	II, VIII	0 (n=3)
Trigonidium ergotonianum Bateman ex Lindley	IV	0 – 0.2

The range of percentage fruit set presented includes maximum and minimum figures observed, per inflorescence, during 1999-2004.

Where the number of inflorescences sampled is greater than 20, no value for n is given.

+ Flowers may be present all year round in one or more areas at the same time, and some or all years. Aberrant flowering periods may occur when plants are moved between sites or are subject to marked changes in surrounding environmental conditions.

* High percentage fruit set, with no visiting insects, suggests self-pollination; nd - No data.

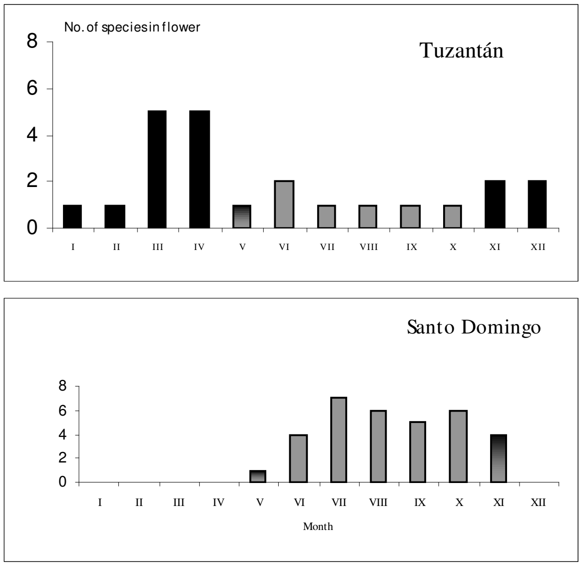

Fig. 1. Flowering period for 24 species of orchids in two sites at different altitudes in the region of Soconusco, Chiapas, Mexico. Black columns signify the dry season, and grey columns the rainy season. Tuzantán 80 m – total of 10 species. Santo Domingo 900 m – total of 14 species.

precise fashion; many of the flowers visited by this bee were later seen to be pollinated and set seed. Flies from the families Cecidomyiidae and Phoridae (plus an unidentified species) were identified for the first time as pollinators of the miniature orchid *Specklinia marginata* (sometimes referred to as *Pleurothallis grobyi* Bateman ex Lindl. in the literature). Male flies of some Cecidomyiidae pollinate terrestrial orchids and also visit flowers of *Ceropegia* that smell faintly of rotten protein (Austin *et al.* 2004). *S. marginata* was also visited by bees of the genus *Plebeia*. Species of the genus *Pleurothallis* in Brazil were reported to be pollinated by flies from the families Phoridae, Chloropidae, Sciaridae and Drosohilidae (Blanco & Barboza 2005; Borba *et al.* 2001; Borba & Semir 2001).

In this section of the study we identified the possible pollinators up to species, genus or family level, for 10 species of orchids, of which three were seen to be carrying pollinaria: *Centris mexicana* carried pollinaria of *Oncidium sphacelatum*; *Euglossa* sp. carried pollinaria of *Sobralia decora*, as well as the flies previously mentioned that carried pollinaria of *S. marginata*.

Potential pollinators observed were: *Eulaema cingulata* for *Cycnoches ventricosum*; *Euglossa viridissima* for *Gongora galeata*, *Mormodes lineata*, *Notylia barkeri* and *Stanhopea saccata*; *Euglossa variabilis* for *S. saccata*; *Trigona fulviventris* for *Nidemia boothii*, most of which are in agreement with the literature. *Restrepia ophiocephala* was visited by flies as expected but none were seen carrying pollinaria and none could be captured.

Small beetles were common visitors to the larger, waxier orchid flowers such as those of *S. saccata*, *C. ventricosum*, *Encyclia cordigera* and *Prosthechea chacaoensis*, but also to the smaller and softer flowers such as *N. boothii* and *Oncidium ornithorrhynchum*. These beetles, although sometimes present in significant numbers, do not appear to interfere with pollinators, but obviously feed upon the tissue of the flowers and may shorten their life. Various species of butterflies and moths were seen visiting the flowers of *Brassavola nodosa*, at all times of day; the pollinator, a sphingid moth was also observed at night but could not be captured.

Orchid pollination in rustic, sustainable production units in 4 rural communities

Although the orchid galleries, being situated fairly near to the farmer's houses, may not be the best place for pollinators, various species were pollinated in one or more communities (Table 3). Numbers of flowers could not be counted, and it was, therefore, not possible to compare this set of data with the data from sections 1 and 2. Flowering dates were only available for some species.

From the data it is interesting to note that *Prosthechea chacaoensis* was the only orchid that was pollinated in 3 of the 4 communities (with the exception of *Guarianthe aurantiaca* which is autogamous); it was not present in the fourth community. We doubt that this species is autogamous, but the pollinator has so far not been observed for this common and weedy species.

Many of the species continued to be pollinated even under these artificial conditions, because the orchid galleries are situated near to forest fragments and the extensive coffee plantations, and even the species that are now scarce in the region: *Brassavola cucullata*, *Brassia verrucosa*, *Lycaste cruenta*, *Prosthechea baculus*, *P. cochleata*,

Table 2. Flowering period and percentage fruit set for 24 species of orchids in two sites in the region of Soconusco, Chiapas, Mexico. *High percentage fruit set, with no visiting insects, suggests self- pollination.

Orchid species	Flowering period [Month(s) I-XII]	Duration of Flowering (Days)	No. Flowers	No. Capsules	% Fruit set
A. Tuzantán (80 m)					
Brassavola nodosa	VI – XII	156	137	4	3
Encyclia cordigera	III – IV	47	93	0	0
Epidendrum stamfordianun	XI – XII	35	817	3	0.5
Mormodes lineata	III	36	16	0	0
Notylia barkeri	III – IV	36	1280	8	0.7
Oncidium sphacelatum	I – II	33	283	1	0.4
Prosthechea chacaoensis	III – V	46	96	0	0
Specklinia marginata	III – IV	30	1470	27	1.9
Stanhopea saccata	VI	4	4	0	0
Sacoila lanceolada	IV	28	4	4	*100
B. Santo Domingo (900 m)					
Barkeria skinneri	IX – X	47	14	0	0
Cycnoches ventricosum	VI – VII	11	14	0	0
Elleanthus cynarocephalus	VIII – IX	18	11	0	0
Erycina crista galli	VII – IX	88	28	0	0
Erycina pusilla	VII – VIII	36	3	0	0
Gongora galeata	VI – VII	17	43	2	4.7
Nidema boothii	V – VI	32	55	14	25.5
Oncidium ornithorrhynchum	X – XI	25	47	0	0
Oncidium sp.	X – XI	46	103	3	0
Ornithocephalus tripterus	VII – VIII	45	103	0	0
Prosthechea cochleata	VI – IX	75	13	0	0
Restrepiella ophiocephala	X – XI	27	69	2	3.0
Sobralia decora	X – XI	6	8	0	0
Stelis sp.	VII – X	72	207	0	0

Scaphyglottis imbricate, Trichopilia tortilis and *Trichocentrum candidum* were pollinated in at least one of the four communities.

Brassavola nodosa is a coastal species and was not pollinated in the galleries which are mostly situated above 600 m. However, this species is well pollinated in the Regional Botanical Garden “El Soconusco”, in Tuzantán, at 80 m, by an unidentified hawkmoth (Sphingidae).

Abundance and seasonality of euglossine bees, and pollinaria transportation

As shown in Fig. 2 A&B, 9 species of Euglossine bees were captured by the volatile baits placed in the study sites at the two altitudes: *Eulema cingulata*, *E. meriana*, *Exaerate frontalis*, *Eufriesia* sp., *Euglossa tridentata*, *E. variabilis*, *E. viridissima*, *E. atrovenata* and *E. mixta*. The unidentified species shown in Fig.2 were later tentatively identified as *E. crininota* and *E. townsendii*, but this requires further clarification.

In Tuzantan, at 80 m, seasonal variation in euglossine abundance was only noted for *E. tridentata*, which peaked during the dry season. At 900 m, in Santo Domingo, four species, *E. viridissima* (which was the most abundant species at this altitude), *E. tridentata*, *E. cingulata* and *E. atroventa*, showed peaks during the rainy season. Zimmerman *et al.* (1992) suggested that many orchid species pollinated by euglossine bees synchronize flowering to coincide with bee availability and in this experiment, when comparing the flowering dates of those orchid species whose pollinaria were found attached to euglossine bees, the majority flower during the rainy season, coinciding with the slight increase in bee abundance at that time; only *N. barkeri* peaks in the dry season but also flowers sparingly at all

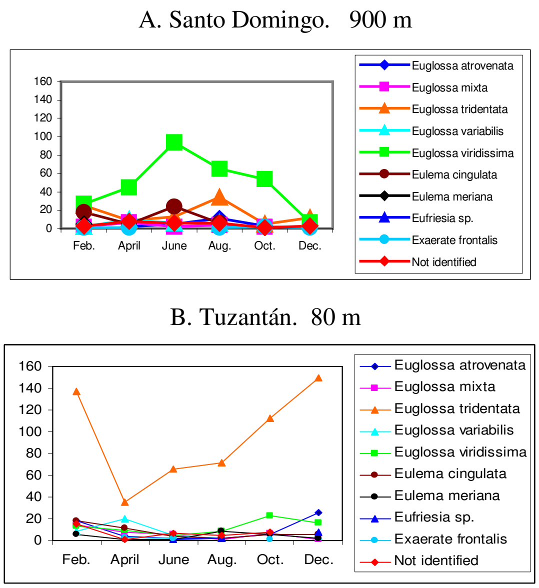

Fig. 2A & B. Numbers of individual euglossine bees captured in two sites in the region of Soconusco, Chiapas, Mexico.

times of the year. A peak in numbers of *E. viridissima* coincided with the flowering period of *Sarcoglottis sceptrodes*, a pollinaria of which was found adhered to this species.

Of the 1,480 individual euglossine bees captured, 41 individuals, equivalent to 2.8% of the total captured, carried orchid pollinaria attached to their bodies: February 5.4% (17 of 313), April 3.6 % (7 of 191), June 0.4% (1 of 250), August 3.3% (8 of 240), October 1.6% (4 of 255), December 1.7% (4 of 235), indicating greater activity in February in the middle of the dry season.

A total of 41 bees were observed carrying pollinaria, some bees were not captured and others carried old, rotten or incomplete pollinia. Twenty-five of the pollinaria were identified to genus or species level (Table 4), and one sample did not coincide with any of the pollinaria in the data base. Comparative details of dates, transporting insect species and the placement of pollinaria on the body of the insects are also shown in Table 4, which includes specimens from the collection "Abejas de Chiapas".

Revision of the collection "Abejas de Chiapas" maintained in the Entomology collection of ECOSUR-Tapachula yielded 15 individual bees carrying pollinaria, of which there were 10 individuals of 7 euglossine genera and 2 species of *Xilocopa* (Table 4). Two individuals of *Bombus willmattae* were found carrying the same unidentifiable pollinaria.

The data show that *E. tridentata* was attracted to cineole, P-dimethoxybenzene, vanillin and eugenol at both sites and *E. viridissima* was attracted to cineole, P-dimethoxybenzene, vanillin, eugenol and T-methyl cinnamate at both sites. The other species show notably different preferences in the two sites. There was no obvious preference shown by euglossine bees carrying orchid pollinaria, but the sample was too small to draw conclusions. Preferences for certain chemical baits did not seem to reflect the aroma of the flowers from which the transported pollinaria came from.

Discussion

At lower altitudes in Soconusco, orchids were seen to flower during the sixth month dry season, whereas at middle altitudes flowering only occurred during the rainy season. The rainy season used to be much more extended, especially at higher altitudes, and it is possible that orchid species are now disappearing from the region, not only due to habitat loss, but also due to an inability to adapt to changes in the climate and seasons. These changes may also affect synchronization between populations of pollinators and plants.

Reproductive success for the majority of the orchid species in Soconusco observed within the time frame of this study was nil, as observed by Tremblay *et al.* (1998) for *Lepanthes caritensis* Tremblay & Ackerman, in Puerto Rico, or very low as for *Schomburgkia tibicinis* Batem. (Rico-Gray & Thein 1987) and *Tolumnia variegata* (Sw.) Braem (Calvo 1993). In the sustainable orchid cultures in rural communities, various species were pollinated, including an isolated plant of *Kefersteinia lactea*, suggesting that some rare orchids may maintain their ability to attract specialist pollinators despite reduced populations and habitat disturbance; the resultant seeds could then be used for mass propagation *in vitro*.

According to Dodson *et al.* (1969), 10% of orchid species are pollinated by bees belonging to the tribe Euglossini (Apidae), and most demonstrate seasonal variation in terms of both abundance and preferences for volatile substances (Ackerman 1989). In the lower and middle altitudes of Soconusco, approximately 25% of the

Table 3. Pollination of orchids in rustic, sustainable production units in 4 rural communities in Soconusco, Chiapas, Mexico. No. plants- No. of plants with capsules-Total no. of capsules: Flowering dates (where known, Arabic numerals).

	Community Municipality Altitude (m) No. production units			
Orchid species	La Patria Tapachula 1060 m 8	Piedra Partida Motozintla 1120 m 9	Santa Rosalía Tapachula 1340 m 9	Santa Rita de las Flores Mapastepec 520 m 6
Brassavola cucullata				23-2-6:
Brassavola nodosa	11		2	
Brassia verrucosa	34-1-1			
Catasetum integerrimum	15-1-1: VI-VII	52	64	
Encyclia cordigera	58-1-1: V-VI	9	25-3-5: V-VI	
Epidendrum stamfordianum	82-2-5: X-XI	7	53	9-1-1:
Guarianthe aurantiaca	286-2-4: I-III	191	252-3-9: II-III	165-2-3:
Guarianthe skinneri	94-7-8: I-III	55	51	
Kefersteinia lactea	1-1-1			
Lycaste cruenta	5	7		7-1-1:
Mormodes lineada	48	3	57	48-1-2:
Oncidium sphacelatum	78-2-3: I-III	42	44	
Prosthechea cochleata	1	18	10-2-6: VI-IX	
Prosthechea baculus	42-1-1:VIII-IX	17	16	
Prosthechea chacaoensis	141-8-24:VI-VII	125-3-7:VI-VIII	179-6-17:VI-VII	
Scaphyglottis imbricata			3-2-6: VI-VII	
Stanhopea saccata	47-2-3: VI-VII	46	28	
Stelis quadrifida	50-2-10: V, VII, X-XII	55	58	
Trichopilia tortilis	56-2-2: III-V	6	15	
Trichocentrum candidum	4-1-1			
Trigonidium ergotonianum	6-1-1		20	

orchid species are pollinated by euglossine bees but out of a possible 26 species in the region with this pollination syndrome, pollinaria were only found from 9 species; the remaining species are now rare in the region and probably remain unpollinated. From Table 4 it is clear that in Soconusco different species of Euglossine bees transport the pollinaria of the same species of orchids at different times of year and placement of the pollinarium may be imprecise, as seen for *M. lineata* and *Encylia* sp. *Euglossa viridissima* was classified by Dodson (1962) as a very generalist pollinator, which he observed pollinating *S. saccata*. In our study, this bee species carried pollinaria of *S. sceptrodes*, *N. barkeri* and *M. lineata* and was also observed visiting *S. saccata* and *G. galeata*. In our study, *Euglossa tridentata* was also shown to be a generalist pollinator, seen transporting pollinaria of *S. sceptrodes*, *C. ergotonianum*, *M. lineata*, *S. saccata* and *N. barkeri*. These orchids are very different and it is possible that generalist pollinators (which may now be replacing rarer, specialist pollinators for some orchid species) may offer an inferior service; the most common visitor is often not the most efficient pollinator (Borba & Semir 2001). The importance of some euglossine bees as orchid pollinators is questionable, as shown by a one-year study of 51 nests of *Euglossa atrovenata*, carried out in Unión Juarez, close to the site in Santo Domingo in this study, at approximately 1,000 masl, where not a single individual was seen to be carrying an orchid pollinaria attached to its body (Arriaga & Hernández 1998). Due to habitat fragmentation and biodiversity reduction, many species of Euglossine bees may have switched their attention to opportunistic and weedy species of plants, and other sources of volatile fragrances such as rotten wood, fungi, or even synthetic chemicals, which may then rest attention from the previously preferred and rarer species from the original vegetation, further accentuating the downward spiral leading to extinction of those species (Kearns & Inouye 1997).

Table 4. Pollinaria transport by bees and flies in two sites in Soconusco Chiapas.

Month	Site	Bee species	Volatile Bait	Position of pollinarium	Orchid species	Comments
JANUARY	S.D.	*Centris mexicana*	-	Frons	*Oncidium sphacelatum*	
MARCH	T.	*E. variabilis*	cineole	Mandible	*Sarcoglottis sceptrodes*	
"	T.	*E. viridissima*	cineole	Mandible	*Sarcoglottis sceptrodes*	Also similar to *D. hemichrea*
"	T.	*E. tridentata*	cineole	Mandible	*Sarcoglottis sceptrodes*	
AUGUST	T	*E. tridentate*	cineole	Mandible	Pollen *S. sceptrodes*. Carried different unidentified stipe.	
"	S.D.	*E. tridentata*	cineole	Tip of abdomen	*Cycnoches ergotonianum*	
"	T.	*E. tridentate*	vanillin	Tip of abdomen	*Cycnoches ergotonianum*	
SEPTEMBER	Ej. Nueva Reforma Acacoyagua	*E. mixta*	-	Between antennae	*Cycnoches ventricosum.*	
FEBRUARY	S.D.	*E. viridissima*	eugenol	Thorax	*Mormodes lineata*	
"	S.D.	*E. viridissima*	cineole	Thorax	*Mormodes lineata*	
"	10 de Abril Acacoyagua	*E. townsendi*		Between antennae	*Mormodes lineata*	
AUGUST	T.	*E. tridentata*	eugenol	Thorax, between wings	*Mormodes lineata*	
"	T.	*E. viridissima*	cineole	Dorsal abdomen	*Mormodes lineata*	
"	T.	*E. atrovenata*	cineole	Dorsal abdomen	*Mormodes lineata*	
NOVEMBER	Ej. Rosario Zacatonales Acacoyagua	*E. tridentate*	-	Dorsal thorax	*Mormodes lineata*	
MAY	Ej. Las Golondrinas, Acacoyagua	*E. tridentate*	-	Towards one side of dorsal thorax	*Stanhopea saccata*	
JULY	Ej. Las Golondrinas, Acacoyagua	*E. atrovenata*	-	Middle of dorsal abdomen	*Stanhopea saccata*	
AUGUST	T.	*Eufriesia* sp.	cineole	Abdomen, between wings	*Stanhopea saccata*	
SEPTEMBER	Ej. Nueva Reforma Acacoyagua	*E. townsendi*	-	Towards one side of dorsal abdomen	*Stanhopea saccata*	
JULY	Ej. Las Golondrinas, Acacoyagua	*Eu. meriana*	-	Towards one side of the abdomen near to the head	*Catasetum integerrimum*	
"	Ej. Las Golondrinas, Acacoyagua	*Eu. cingulata*	-	Towards one side of the abdomen near to the head	*Catasetum integerrimum*	

Continued

Table 4. Continued

Month	Site	Bee species	Volatile Bait	Position of pollinarium	Orchid species	Comments
AUGUST	T.	*Ex. frontalis*	cineole	Between wings	*Catasetum integerrimum*	
"	T.	*Eu. meriana*	cineole	Dorsal abdomen	*Catasetum integerrimum*	
FEBRUARY	T.	*E. variabilis*	cineole	Top mandible	*Notylia barkeri*	
"	T.	*E. viridissima*	p-dimeth.	Lower mandible	*Notylia barkeri*	
"	T.	*E. tridentata*	p-dimeth.	Top mandible	*Notylia barkeri*	
"	T.	*E. tridentate*	cineole	Top mandible	*Notylia barkeri*	
"	T.	*E. tridentata*	vanillin	Top mandible	*Notylia barkeri*	
"	T.	*E. tridentata*	vanillin	Top mandible	*Notylia barkeri*	
FEBRUARY	T.	*E. atrovenata*	cineole		*Encyclia* sp.	By date, most probably *E. adenocarpa*
"	T.	*E. mixta*	p-dimeth.		*Encyclia* sp.	
"	T.	*Eu. Meriana*	benzyl acetate	Thorax	*Encyclia* sp.	
"	T.	*E. atrovenata*	cineole	Between antennae	*Encyclia* sp.	Other possibilities:
"	T.	*E. atrovenata*	cineole	Thorax	*Encyclia* sp.	*E. cordigera*, *P. chacaoensis*
MARCH	Ej. Rosario Zacatonales Acacoyagua	*Xilocopa nautlana*	-		*Encyclia cordigera*	Pollinia also similar to *Prosthechea chondybulbon*
"	Ej. La Palma, Mapastepec	*Xilocopa nautlana*	-		*Encyclia*	
"	Ej. La Palma, Mapastepec	*Xilocopa fimbriata*	-		*Encyclia cordigera* (or *Prosthechea chondybulbon*)	
AUGUST	T.	*E. variabilis*	benzyl benzoate	Frons		Possibilities: *Leochilus, Oncidium, Trichocentrum*
FEBRUARY	T.	Cecidomyiidae and Phoridae flies and one further unidentified species	-	Between antennae	*Specklinia marginata*	

Preference for volatile bait is included for euglossine bees trapped in the two experimental sites.
This table includes specimens of bees carrying pollinaria from the collection "Bees of Chiapas" (ECOSUR-Tapachula; All the sites mentioned fall within Soconusco region).
T. = Tuzantán. 80 m; S.D. = Santo Domingo. 900 m

In general, it appears that pollinator availability is very variable in Soconusco; this question must be addressed for sustainable orchid production and conservation programmes, to include habitat restoration to favour pollinators, including food plants, nesting sites and the reintroduction of the necessary species if required. Some of the pollinators observed in this study coincide with other studies, but reports show clearly that orchids may be successfully pollinated by different pollinators in different areas, although possible with reduced efficiency.

If orchid numbers are severely reduced and there are no suitable insects available, or the attention of available insects is diverted towards new and richer sources of nectar, resins and fragrances, those orchids should then be considered as forming senile, non-viable populations. We do not know enough about orchids (Koopowitz 2001), which are slow growers, require mature trees, stability and may be capricious in their requirements for precise environmental conditions, substrates, mycorrhizal fungi and pollinators. In the light of these results, with minimal pollination opportunities, will the orchids that still offer rewards such as nectar, fragrances, oils or resins evolve to adopt deceit mechanisms, become self-fertile or simply die out? How long will orchids survive in unstable, disturbed habitats with such a low rate of seed set and very few sites to colonize?

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