Original article

Pollen diets of two sibling orchid bee species, *Euglossa*, in Yucatán, southern Mexico

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Abstract – We investigated pollen diets of *Euglossa viridissima* Friese and its recently described sibling species, *Euglossa dilemma* Bembé & Eltz, in a degraded dry forest locality near Merida, Yucatán, Mexico. Pollen samples were obtained from nests collected in the rainy season of three consecutive years (2006–2008). *Solanum* sp. (Solanaceae), *Physalis* sp. (Solanaceae), *Ocimum* sp., *Ocimum micranthum* (both Lamiaceae), and *Senna* sp. (Fabaceae) were the dominant taxa, accounting for 88 % of pollen volume across species. Other important pollen taxa were *Croton* spp. (Euphorbiaceae), *Ipomoea* sp. (Convolvulaceae), *Solanum torvum*, *Vigna* sp. (Fabaceae), *Sida* sp. (Malvaceae), and *Randia aculeata* (Rubiaceae). The predominantly buzz-pollinated family Solanaceae alone represented more than 77 % of total pollen volume. Multivariate analysis revealed significant effects of year but not of bee species on nest pollen composition. We conclude that pollen resources overlap substantially among these sibling species, with resource partitioning apparently absent or confined to periods of severe pollen scarcity.

pollen provisions / resource partitioning / floral resource competition / acetolysis / pollen analysis

1. INTRODUCTION

Pollen is the proteinaceous larval food of bees, and competition for pollen resources is believed to be important in structuring bee communities both in temperate and tropical habitats. For instance, in tropical (social) stingless bees, competition for pollen and other floral resources has resulted in a range of different foraging and recruitment strategies and, as a consequence, resource partitioning (Hubbell and Johnson 1978; Eltz et al. 2001a, b). However, there are only few studies that show competitive effects with regard to pollen. For example,

Roubik and Villanueva-Gutierrez (2009) compared the quantitative pollen diets and foraging patterns of European apiary bees and naturalized Africanized honey bees, and two native solitary bees, in Sian Ka'an, a large biosphere reserve in the Yucatán peninsula. It was suggested that the invasive Africanized bees made resident generalist bees (apiary *Apis mellifera* and native solitary bees) expand their diet breadth at the population level, while at the same time increasing their degree of specialization. This latter study is one of the few studies on pollen diets of tropical solitary bees, presumably because nests are exceedingly difficult to find. Orchid bees (Euglossini) are generally no exception in this respect, but some species can be made to nest in artificial cavities like bamboo internodes or small wooden boxes

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placed at appropriate sites (Garofalo et al. 1993; Augusto and Garofalo 2004; Cocom Pech et al. 2008). These species can be studied in detail, including their pollen utilization spectra.

Orchid bees are solitary to primitively social bees of neotropical forests (Dressler 1982; Roubik and Hanson 2004), which are best known for the peculiar volatile collecting behavior of males (Vogel 1966). Male orchid bees visit odoriferous substrates like flowers, leaves of aromatic plants, fungus-infected leaves and logs, rotting fruits etc., and harvest the odors to put together blends of "perfumes" (Whitten et al. 1993; Ramírez et al. 2002; Pemberton and Wheeler 2006; Eltz et al. 2007). These perfumes are later exposed by the males at mating sites, and believed to function as pheromone analogs in courtship (Eltz et al. 2005). The male perfumes are species-specific in chemical composition (Zimmermann et al. 2009a), and perfume analysis has helped in the discovery of cryptic species. Based on chemical and molecular data, it has been established that *Euglossa viridissima*, a common metallic green bee in Mexico and northern Central America, actually consists of two species occurring sympatrically over much of the range (Eltz et al. 2011). The second lineage has recently been described as *Euglossa dilemma* Bembé & Eltz, and the *Euglossa* that has become naturalized in Florida, USA, is *E. dilemma* (Eltz et al. 2011).

Because males of *E. viridissima* and *E. dilemma* differ in the range of volatiles they harvest from their environment, i.e., exhibit "odor resource partitioning", we hypothesized that females may also differ in their floral resources used. Generally, all euglossines are believed to be polylectic, i.e., each species uses pollen from a range of different host plant species (Ramírez Arriaga and Martínez Hernandez 1998; Roubik and Hanson 2004; Silva et al. 2012; Rocha Filho et al. 2012). However, spectra of host plants might not completely overlap in the two species due to ecological character displacement altering habitat use or stratum preferences, spatial foraging patterns or visual preferences. Furthermore, floral resource partitioning could

result as a consequence of differences in olfactory make-up evolved to mediate differential volatile collection in males (see Eltz et al. 2008). To investigate floral resource partitioning, we microscopically analyzed pollen from nests of the two species collected at the same locality and during the same 3 years.

2. MATERIALS AND METHODS

2.1. The Yucatán Peninsula: climate, vegetation, and bees

According to the classification of Köppen (1936), the type of climate that exists in the Yucatán Peninsula is *Aw*, which is defined as hot subhumid, with a mean annual temperature over 22 °C and an annual precipitation between 700 and 1,500 mm, with rainfall during the summer season. According to the precipitation, we can divide the year into two periods, the wet season (June to November) and the dry season (December to May). This classification is very useful in understanding the phenology of flowering plants and foraging choices of bees.

The most common types of vegetation in the Yucatán Peninsula are low deciduous forest, medium-stature semideciduous forest, low-stature semideciduous forest, mangrove, low-stature flooded forest that floods during the wet season, and secondary vegetation in different successional stages (Miranda 1958; Durán and Olmsted 1999). The flora, the vegetation, and the climate are similar throughout the Yucatán Peninsula. In the study area near Merida (see below), there was a secondary vegetation derived from a low deciduous forest.

Ninety native bee species were registered for the Biosphere Reserve of Sian Ka´an, Quintana Roo, but as many as twice this number may occur in the Yucatán Peninsula (Roubik et al. 1990; Roubik et al. 2011; Ayala and Griswold 1988).

2.2. Sampling

Nests of *Euglossa* were obtained by placing wooden boxes (10×3×6 cm) around buildings at the campus of the Universidad Autónoma de Yucatán in Xmatkuil, Mexico (20.52°N, 87.37°W). Boxes

were replaced with new ones on occasion, e.g., when they became moldy, and numbers of boxes varied to some extent over time, but generally there were about 20–40 nest boxes present at any time during the three study years. Nearing the end of the rainy season, between October 10 and November 3 in each of the years 2006, 2007, and 2008, the nests were collected if the boxes were populated with at least five brood cells. These were most likely provisioned during the 4–8 weeks prior to collecting (i.e., in the early to intermediate rainy season, August to October). The time of nest collection corresponded to the peak nesting activity (J. Quezada-Euan, personal observation). The brood cell clusters were kept in a cabinet at 26 °C and 70 % humidity until the offspring emerged. The emergence of males, which can be unambiguously identified to species by mandibular characters, as well as microsatellite genotyping (see Zimmermann et al. 2009b) allowed nest assignment to species. We obtained 27 nests of *E. viridissima* with 4–16 brood cells (mean of 9.6±2.9), and nine nests of *E. dilemma* with 5–14 brood cells (mean of 9.8±3.1). After the bees had hatched, the remains of the brood cell clusters were frozen and later subjected to standard palynological protocols (KOH digestion of entire hatched cell clusters, acetolysis, glycerin jelly mounting). Samples were found to contain large quantities of pollen exines, the outer wall of pollen grains which is normally indigestible for bees and passes their digestive tract largely intact (see also Eltz et al. 2001a, b). In the present case, the pollen on slides may represent a mixture of left-over, uneaten grains plus the remains of consumed pollen from larval meconia (fecal pellets).

2.3. Pollen analysis

After the palynological identification of all the different types of grains present on a slide, pollen grains were counted along transects (600 grains for each sample) in order to determine the relative frequency of the different pollen species in the pollen samples. In this way, each sample composition could be analyzed in terms of (a) pollen type frequency (in percent), (b) relative pollen type volume (in percent), and (c) pollen type occurrence (presence/absence).

A palynological reference collection of the area, with more than 500 pollen species, was used to aid identification of pollen types. It is deposited in the herbarium of El Colegio de la Frontera Sur, Chetumal. Also, the atlas of Palacios-Chávez et al. (1991) on the pollen of the Biosphere Reserve of Sian Ka'an was a very useful reference.

Counts per pollen type were transformed into volumes per pollen type for each sample by using the formulas applied by Villanueva-Gutiérrez and Roubik (2004). For numerical analysis, we standardized volumes by total, yielding percent contributions per type to the total pollen volume of a sample (nest). To quantify similarity/dissimilarity of nest pollen composition, we calculated the Bray–Curtis similarity index and visualized results in two dimensions using nonmetric multidimensional scaling implemented in the software Primer v6 (Clarke and Gorley 2001). To test the effect of the factors "species" and "year" on rank similarities among samples, we calculated a two-way analysis of similarity (ANOSIM) significance test, also using Primer v6. We then averaged percent contributions of pollen types among nests for each species and used these averaged percentages to calculate the Pianka index of niche overlap using the software EcoSim v.7.71 (Gotelli and Entsminger 2001). The index varies between 0 and 1 (complete overlap).

3. RESULTS

We found a total of 45 different types of pollen grains in the samples, each corresponding to a plant taxon (Figure 1) belonging to 17 different plant families. Incidences and volume contributions of the different types varied strongly and were heavily biased in favor of five dominant types. Those were *Solanum* sp., *Physalis* sp. (both Solanaceae), *Ocimum* sp., *Ocimum micranthum* (both Lamiaceae), and *Senna* sp. (Fabaceae). These five types together accounted for 95 % of the grains and 88 % of total pollen volume. All other grains were present only occasionally, and in smaller numbers. Solanaceae alone represented more than 77 % of total pollen volume.

Pollen composition of nest samples varied significantly between the 3 years (ANOSIM $R=$ 0.44; $P<0.001$), but not between species ($R=$ 0.14; $P>0.1$; Figure 2). In 2006, nests of both species were particularly strongly dominated by *Solanum* sp., which accounted for 83.1 % (*E.*
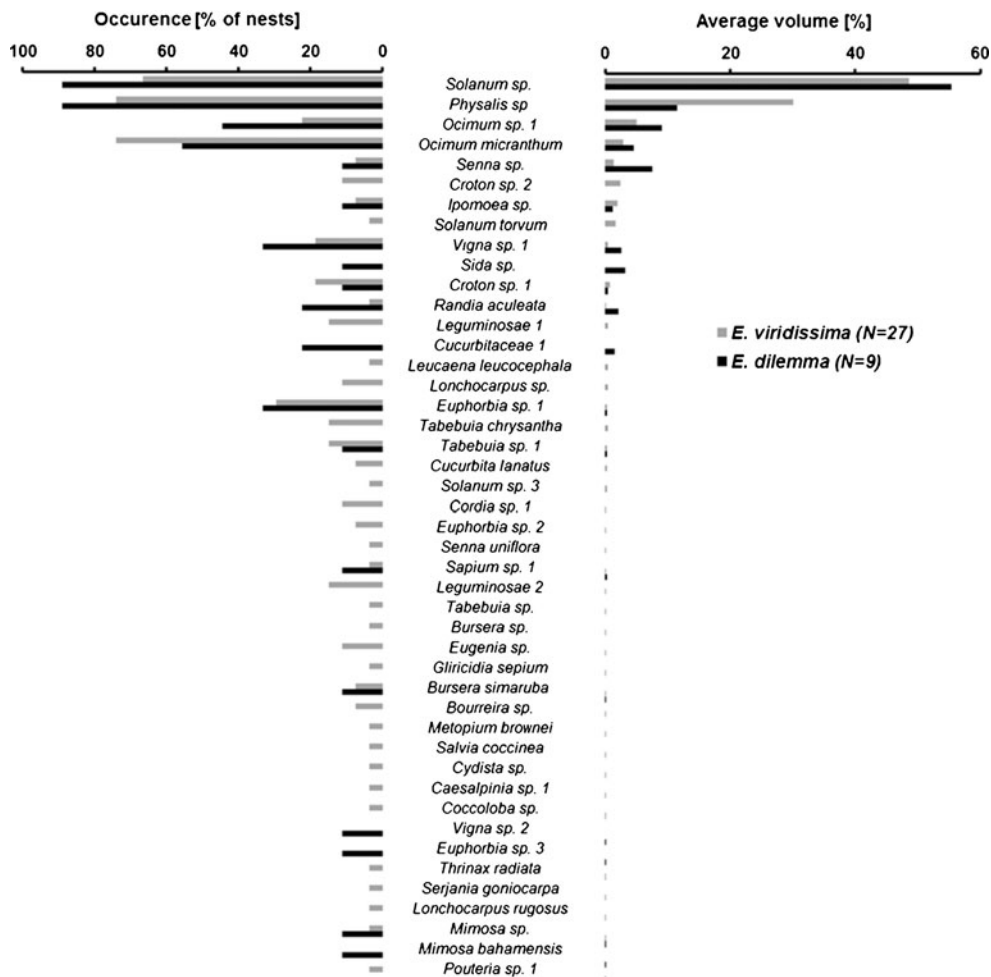
Figure 1. Occurrence and volume contribution of 45 plant taxa to the pollen retrieved from nests of *E. viridissima* (*N*=27) and *E. dilemma* (*N*=9) at Xmatkuil, Yucatán, Mexico.

viridissima, *N*=10) and 89.6 % (*E. dilemma*, *N*=2) of pollen volume in that year. In 2007, the same pollen type represented only 22.3 % (*E. viridissima*, *N*=9) and 51.9 % (*E. dilemma*, *N*=5), in 2008 35.2 % (*E. viridissima*, *N*=8) and 29.8 % (*E. dilemma*, *N*=2). The Pianka index of niche overlap between *E. viridissima* and *E. dilemma* across all nests and years was 0.92, indicating substantial overlap.

Other relatively abundant pollen taxa found in the nest of both *Euglossa* were *Croton* sp2 (Euphorbiaceae), *Ipomoea* sp. (Convolvulaceae), *Solanum torvum* (Solanaceae), *Vigna* sp.

(Fabaceae), *Sida* sp. (Malvaceae), *Croton* sp1 (Euphorbiaceae), *Randia aculeata* (Rubiaceae), a Fabaceae and a Cucurbitaceae (not identified), and *Leucaena leucocephala* (Fabaceae).

According to their occurrence (percentage of nests in which a pollen type was present), the most frequent taxa were *Solanum* sp., *Physalis* sp., *O. micranthum*, *Euphorbia* sp1, *Vigna* sp1, *Croton* sp1, *R. aculeata*, and a Cucurbitaceae (Figure 1). Other pollen types found in relatively many nests were *Croton* sp1, two Fabaceae, *Tabebuia crysantha*, *Tabebuia* sp., *Cordia* sp., *Sapium* sp1, *Eugenia* sp., and *Bursera simaruba*.
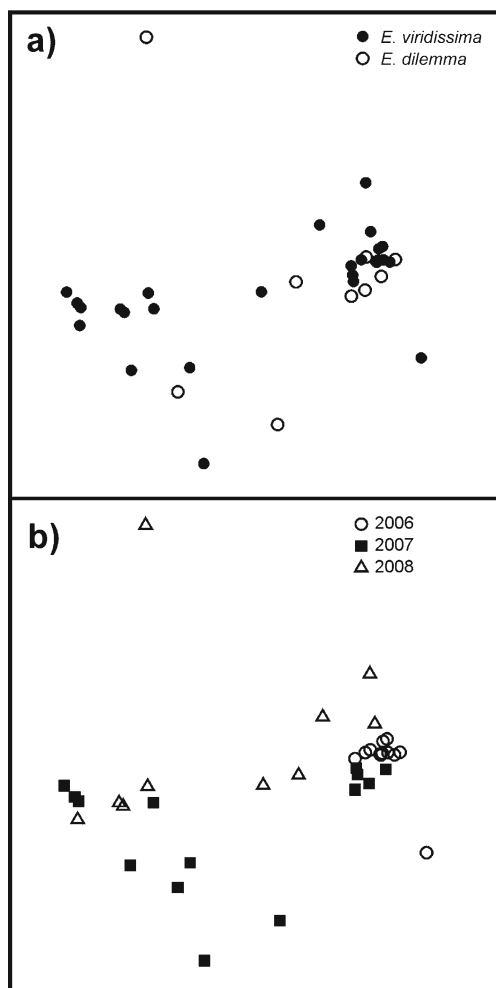
Figure 2. Two-dimensional representation of a non-metric multidimensional scaling analysis (stress= 0.08) with symbols coding for the factor bee species (**a**) or the factor year (**b**). Distance in the two-dimensional plane reflects disparity in pollen type composition. Nests in the tightly packed cluster on the right side of **b** are particularly high in volume of *Solanum* sp. 1. The *E. dilemma* outlier at the top is exceptional in that it contains no Solanaceae pollen.

4. DISCUSSION

Multivariate analysis revealed significant effects of year but not of bee species on nest pollen composition; all major pollen types were shared between species. We conclude that pollen resources overlap substantially among these closely related bees, with pollen resource partitioning either absent, or weak, or confined to periods that were not covered by this study. With regard to the latter, competition for pollen may be more severe in the late rainy season (i.e., in November), when floral resources become rare (see Villanueva-Gutiérrez 2002; Roubik and Villanueva-Gutierrez 2009), but *Euglossa* populations are still high from prior early rainy season growth (indicated by trap nest occupancy; J. Quezada-Euan, personal observation). It is possible that pollen resource use is more different between the two species at this time of the year. Alternatively, (a) pollen might generally not be a limiting resource for *Euglossa* populations in the Yucatecan deciduous forest, or (b) there was insufficient time for interspecific competition to result in competitive character displacement in these closely related species. Molecular clock analyses suggest that *E. dilemma* and *E. viridissima* have diverged only a little more than 100,000 years ago (Eltz et al. 2011). Generally, there is no obvious divergence in morphological structures related to floral resource use, e.g., tongue length or the size and shape of the pollen-carrying corbicula. Mandibular teeth, although they are the distinguishing character between males of the two species, are essentially identical in females. Finally, although the bees are using largely the same resource species, their spatial position in the forest, and the time of their use, are unknown. Such spatiotemporal resource partitioning is known in bees (dos Santos and Absy 2012; Brittain et al. 2012), but the pollen spectra approach would not reveal this.

While not providing evidence for interspecific competitive effects our results provide insights with regard to general euglossine pollen use. Overall, it is clear that *E. dilemma* and *E. viridissima* are broadly polylectic in that they use pollen from a variety of plant species belonging to a range of different plant families (see Cane and Sipes 2006), while at the same time relying heavily on a small number of major sources at a given time. The 45 different pollen types found by the present study suggest

intermediate pollen diversity in *Euglossa* as compared to other solitary bees on the Yucatan peninsula; e.g., 28 pollen types were used by megachilids and 108 by *Centris analis* in the Biosphere Reserve of Sian Ka´an, Quintana Roo (Roubik and Villanueva-Gutierrez 2009). Our results further emphasize the importance of pollen from plant taxa with poricidal anthers for euglossines, i.e., buzz-pollinated plants, especially within Solanaceae and Fabaceae (see Dressler 1982; Silva et al. 2012; Rocha Filho et al. 2012). The genus *Solanum* which typically has poricidal anthers (Buchmann 1983) was the most important plant genus for both species in the late dry/early rainy season. Buzz-pollinated plants, including Fabaceae (mostly *Senna* spp.) and Solanaceae (*Solanum* spp.) have been observed to be visited for pollen by *Euglossa dilemma* in Florida (Pemberton and Wheeler 2006), were the species was recently introduced. Other studies have found buzz-pollinated plants, including Solanaceae, to be abundant in pollen provisions in nests of *Euglossa* spp. in Mexico and Brazil (Ramírez Arriaga and Martínez Hernandez 1998; Cortopassi-Laurino et al. 2009), but the dominance of Solanaceae was not as pronounced as in our study. It is likely that the substantial habitat degradation that is characteristic for the western half of the Yucatán peninsula has affected pollen diets of the study bees, especially with regard to pollen diversity, but perhaps also with regard to the dominant taxa. The abundance of *Physalis* sp. (possibly representing wild tomatillo, *Physalis philadelphica*), but also that of *Solanum* spp., and especially that of the two types of Laminaceae in the diets is probably related to the predominance of more open shrub land in the areas south of Merida. It would be desirable to study pollen diets of both species in a less disturbed setting, e.g., in the forests of Quintana Roo in the eastern and southern parts of the Yucatán peninsula.

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Régimes polliniques de 2 espèces jumelles de l'abeille à orchidée du genre *Euglossa*, dans le Yucatan, au sud du Mexique

Provision de pollen / répartition de la ressource / compétition alimentaire / ressource florale / acétolyse / analyse pollinique

Pollendiäten zweier nahverwandter Prachtbienenarten der Gattung *Euglossa* in Yucatán, südliches Mexiko

Pollenvorräte / Resourcenverteilung / Wettbewerb um pflanzliche Nahrungsquellen / Säureverdauung / Pollenanalyse

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