

Orchid bees (Hymenoptera: Apidae: Euglossini) of Cusuco National Park, State of Cortés, Honduras

Kenneth W. McCravy^{1,2,*}, Joseph Van Dyke^{2,3}, Thomas J. Creedy^{2,4,5,6},
and David W. Roubik⁷

Abstract

Orchid bees (Hymenoptera: Apidae: Euglossini) are abundant and important pollinators of Neotropical forests, but orchid bee diversity is still poorly known in much of Mesoamerica, particularly in cloud forests. This paper presents results of a 2012 to 2013 survey of orchid bee diversity in Cusuco National Park, a cloud forest environment in northwest Honduras. Orchid bees were collected using insect nets at bait stations with chemical attractants. Bait stations were located at 68 sample sites throughout the park. We collected 4,293 orchid bees representing 24 species and 4 genera. One species, *Euglossa imperialis* Cockerell, accounted for 67.6% of the total individuals collected. A substantial easterly range extension was established for *Eufriesea pallida* (Kimsey). Our study provides the first intensive inventory of cloud forest orchid bee diversity in the region. Furthermore, it provides baseline data for future studies of orchid bees in a key biodiversity area that is threatened by human population growth and associated land use changes.

Key Words: Mesoamerican euglossines; Neotropical cloud forest; pollinator biodiversity; habitat fragmentation

Resumen

Abejas de las orquídeas (Hymenoptera: Apidae: Euglossini) son polinizadores abundantes e importantes de los bosques neotropicales, pero la diversidad de las abejas de orquídeas es aún poco conocida en gran parte de Mesoamérica, sobre todo en los bosques nublados. Este artículo presenta los resultados de un sondeo del 2012-2013 de la diversidad de las abejas de orquídeas en el Parque Nacional Cusuco, un ambiente de bosque nublado en el noroeste de Honduras. Las abejas de orquídeas fueron recolectadas a través de redes para insectos en estaciones de cebo con atrayentes químicos. Las estaciones de cebo se encuentran en 68 puntos de muestreo por todo el parque. Hemos recolectado 4.293 abejas de las orquídeas que representan 24 especies y 4 géneros. Una especie, *Euglossa imperialis* Cockerell, representó el 67,6% del total de individuos recolectados. Una extensión significativa de rango hacia el este fue establecida para *Eufriesea pallida* (Kimsey). Nuestro estudio provee el primer inventario intensivo de la diversidad de las abejas de orquídeas en los bosques nublados en la región. Además, se provee datos de referencia para futuros estudios de abejas de las orquídeas en un área clave de biodiversidad que se ve amenazada por el crecimiento de la población humana y los cambios asociados al uso del suelo.

Palabras Clave: euglossines mesoamericanas; bosque nublado neotropical; biodiversidad de los polinizadores; fragmentación del habitat

Orchid bees (Hymenoptera: Apidae: Euglossini) are ubiquitous and important pollinators that can comprise up to 25% of Neotropical forest bee communities (Roubik & Hanson 2004). There are over 200 known species of orchid bees, and the tribe ranges from Mexico to Argentina (Roubik & Hanson 2004; Nemésio & Silveira 2007) as well as southern North America (Minckley & Reyes 1996; Skov & Wiley 2005; Pemberton & Wheeler 2006; Eltz et al. 2011). However, knowledge of orchid bee diversity varies greatly with location. In Mesoamerica, for instance, Ramírez et al. (2002), in their catalog of Neotropical orchid bee species, list about 69 species records for Panama, but only about 10 for Honduras. A more recently published catalog of bee species and their geographic ranges published by Moure et al. (2012) lists about 66 orchid bee species records for Panama, but only about 20 for Honduras. This latter number is undoubtedly a function of the dearth of orchid bee studies in Honduras. Ascher & Pickering's (2015) Discover Life database has 29 spe-

cies listed for Honduras, although this may be less accurate due to the broad and under-verified source data used by this resource.

Much of their ecological importance stems from the behavior of male orchid bees, which are among the few pollinators that visit flowers to collect aromatic compounds or associated chemicals (Roubik & Hanson 2004). These fragrances appear to be associated with species recognition, competition, and mate choice (Zimmermann et al. 2009). Orchid bees are best known for their associations with orchids, and are important pollinators of roughly 650 species in this plant family. However, they are associated with many other plant species as well, spanning about 30 families (Dressler 1982; Ackerman 1983; Roubik & Hanson 2004; Ackerman & Roubik 2012). Gilbert (1980) cited orchid bees as particularly important Neotropical "link organisms," stating that "a single euglossine species may link plant species from all stages and strata of a forest into a system of indirect mutualism."

¹Department of Biological Sciences, Western Illinois University, 1 University Circle, Macomb, Illinois 61455, USA; E-mail: KW-McCravy@wiu.edu (K. W. M.)

²Operation Wallacea, Hope House, Old Bolingbroke, Spilsby, Lincolnshire, PE23 4EX, UK; E-mail: JW-VanDyke2@wiu.edu (J. V. D.), thomas@tjcreedy.co.uk (T. J. C.)

³Department of Biology, West Virginia University, Morgantown, West Virginia 26505, USA

⁴Hope Entomological Collections, Oxford University Museum of Natural History, Parks Road, Oxford, OX1 3PW, UK

⁵Department of Life Sciences, Imperial College London, Exhibition Road, London, SW7 2AZ, UK

⁶Natural History Museum, Cromwell Road, London, SW7 5BD, UK

⁷Smithsonian Tropical Research Institute, Ancon, Balboa, Republic of Panama; E-mail: roubikd@si.edu (D. W. R.)

*Corresponding author; E-mail: KW-McCravy@wiu.edu (K. W. M.)

Mesoamerica is one of the world's biodiversity hotspots (Mittermeier et al. 1999). Cusuco National Park, containing primarily high elevation cloud forest in northwest Honduras, is a site of critical conservation concern based on its vertebrate fauna (Le Saout et al. 2013), but little is known of the invertebrate diversity within the park. Cusuco National Park has been designated a Key Biodiversity Area, but is threatened by human population growth and associated land cover changes driven by practices such as conversion of forests to coffee plantations (Green et al. 2012). To expand our knowledge of the orchid bee fauna of Honduras, and to provide baseline data on orchid bee diversity in a location of concern that is undergoing rapidly changing land use patterns, we conducted a survey of the orchid bees of Cusuco National Park.

Materials and Methods

STUDY LOCATION

The study was done from mid-Jun to early Aug in 2012 and 2013 at Cusuco National Park, about 30 km west of San Pedro Sula in the State of Cortés, in northwest Honduras (Fig. 1a). Cusuco National Park is an area of about 23,400 ha and ranges in elevation from just above sea level to 2,425 m. Habitat types include disturbed and undisturbed mature broadleaf forest, secondary broadleaf forest, disturbed pine–broadleaf forest, mature pine forest, open disturbed grassland, open disturbed logged areas, and open coffee plantations. Monthly mean rainfall for all sample sites ranged from 60.8 mm in Mar to 252.4 mm in Jun, with mean total annual rainfall of 1,786.0 mm. Mean total annual rainfall by habitat type ranged from 1,743.0 mm for disturbed broadleaf forest (Mar minimum = 60.9 mm, Jun maximum = 245.8 mm) to 1,835.5 mm for secondary broadleaf forest (Mar minimum = 61.8 mm, Jun maximum = 258.3 mm). Mean precipitation for each sample site was extracted from downsampled WorldClim data (www.worldclim.org) interpolated from weather station data in San Pedro Sula.

SAMPLING OF ORCHID BEES

Orchid bees were collected with insect nets at bait stations, which consisted of a cotton ball with a chemical attractant suspended about 1.7 m above the ground by a string. Five bait stations, about 5 m apart, were established during each collection period. Five chemical attractants were used (benzyl acetate, cineole, eugenol, methyl salicylate, and vanillin), with each cotton ball receiving 30 drops of one of these initially; re-application with 20 additional drops was done every 30 min. Occasionally, fewer bait stations or attractants were used for specific smaller-scale studies. The collection period was 9:00 a.m. to 11:00 a.m. Collections were done at 68 established sample sites, each within 2 km of 1 of the 7 research camps located throughout the park (Fig. 1b): Base Camp (15.4964°N, 88.2119°W), 14 sites; Buenos Aires (15.4997°N, 88.1794°W), 14 sites; Cantiles (15.5133°N, 88.2417°W), 4 sites; Cortecito (15.5233°N, 88.2886°W), 8 sites; El Danto (15.5283°N, 88.2775°W), 10 sites; Guanales (15.4886°N, 88.2342°W), 6 sites; and Santo Tomas (15.5611°N, 88.2975°W), 12 sites. Most sites were sampled twice. Identifications of specimens collected in 2012 were done by D. W. Roubik; specimens collected in 2013 were identified using reference specimens and Roubik & Hanson (2004). Voucher specimens were deposited in the Western Illinois University Entomology Collection and Oxford University Museum of Natural History (OUMNH).

DATA ANALYSES

The Chao excel sheet calculator (Ecological Archives E090-073-S1, Chao et al. 2009) was used to calculate the Chao1 asymptotic species richness estimate. The Morisita–Horn index of similarity, calculated using EstimateS (Colwell 2013), was used to compare species composition between years.

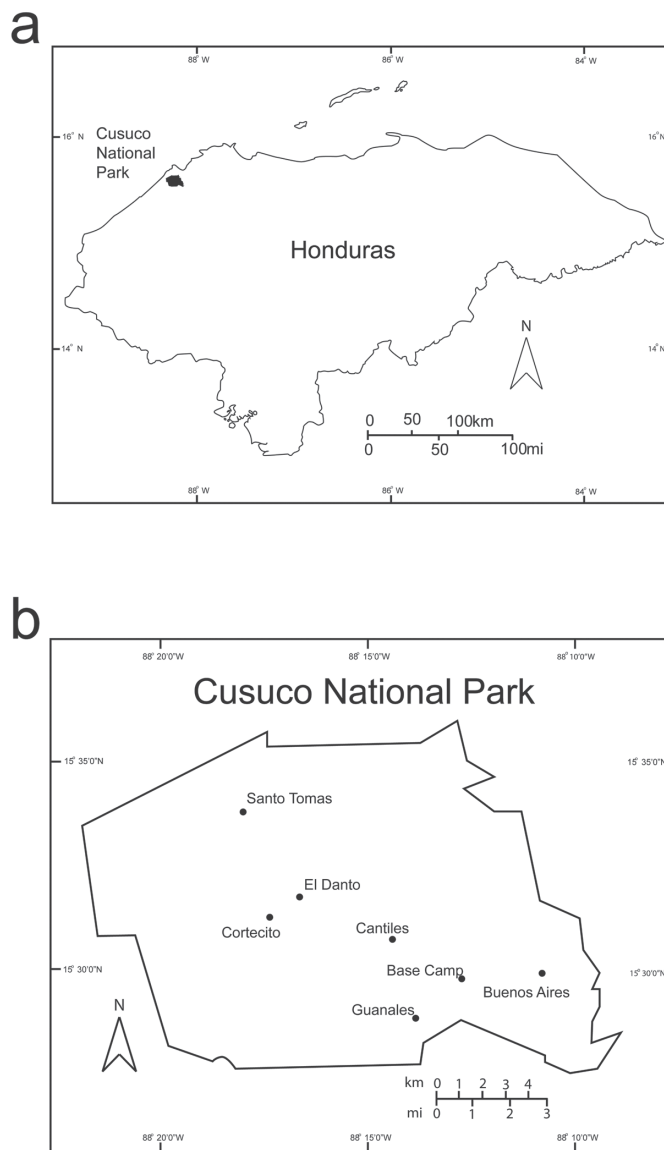


Fig. 1. (a) Location of Cusuco National Park and (b) locations of research camps within the park.

Results

We collected 4,293 orchid bees representing 24 species during this study (Table 1). These results, combined with records in other lists and databases (Table 2), total 40 species of orchid bees recorded for Honduras. *Euglossa imperialis* Cockerell was the most abundant species collected in our study, comprising 67.6% of the total collection. The Chao1 estimate produced an estimated asymptotic richness of 24.67. The Morisita–Horn index of similarity in species composition between years was 0.987.

We collected 12 species that were not previously recorded for Honduras in Moure et al. (2012) (Table 1); one of these, *Euglossa dilemma* Bembé & Eltz, was a more recently recognized species. *Eulaema marcii* Nemésio is included by Moure et al. (2012) and Ramírez et al. (2002) in *Eulaema cingulata* F. However, *E. cingulata* is now considered South American, with *E. marcii* occurring in Central America and Mexico (D. W. Roubik, personal observation). Two of the species (*Eulaema meriana* [Olivier] and *Euglossa townsendii* Cockerell) not recorded as occur-

Table 1. Numbers, relative abundances, and locations of orchid bee species collected at Cusuco National Park, Honduras, during Jun to Aug 2012 and 2013.

Species	2012	2013	Total	% of total	Camps ^b
<i>Eufriesea mexicana</i> (Mocsáry, 1897)	12	68	80	1.86	BA, BC, GU
<i>Eufriesea pallida</i> (Kimsey, 1977) ^a	1	0	1	0.02	BC
<i>Eufriesea rugosa</i> (Friese, 1899) ^a	0	14	14	0.33	BA, BC
<i>Eufriesea schmidtiana</i> (Friese, 1925) ^a	1	1	2	0.05	BC, ST
<i>Eufriesea surinamensis</i> (Linnaeus, 1758)	2	0	2	0.05	BA
<i>Euglossa allosticta</i> Moure, 1969	1	4	5	0.12	BA, BC, GU
<i>Euglossa cybelia</i> Moure, 1968 ^a	13	20	33	0.77	All
<i>Euglossa dilemma</i> Bembé & Eltz, 2011 ^a	198	118	316	7.36	All
<i>Euglossa hansonii</i> Moure, 1965 ^a	0	3	3	0.07	BA
<i>Euglossa heterosticta</i> Moure, 1968	26	26	52	1.21	BA, BC, CO, DA, GU
<i>Euglossa ignita</i> Smith, 1874 ^a	1	1	2	0.05	BC, DA
<i>Euglossa imperialis</i> Cockerell, 1922 ^a	1,041	1,861	2,902	67.60	All
<i>Euglossa mixta</i> Friese, 1899	21	16	37	0.86	BA, BC, GU, ST
<i>Euglossa obrima</i> Hinojosa-Díaz, Melo & Engel, 2011	3	2	5	0.12	BA, BC, CA, ST
<i>Euglossa obtusa</i> Dressler, 1978	60	102	162	3.77	All
<i>Euglossa purpurea</i> Friese, 1899	4	3	7	0.16	BA, GU
<i>Euglossa townsendi</i> Cockerell, 1904 ^a	1	0	1	0.02	BA
<i>Euglossa tridentata</i> Moure, 1970 ^a	12	22	34	0.79	BA, BC, DA, GU, ST
<i>Euglossa variabilis</i> Friese, 1899	38	8	46	1.07	BA, GU, ST
<i>Eulaema luteola</i> Moure, 1967	33	102	135	3.10	All
<i>Eulaema marcii</i> Nemésio, 2009	83	313	396	9.22	BA, BC, CA, DA, GU, ST
<i>Eulaema meriana</i> (Olivier, 1789) ^a	9	38	47	1.10	BA, BC, CA, DA, GU
<i>Eulaema polychroma</i> (Mocsáry, 1899)	3	1	4	0.09	BA, BC, DA
<i>Exaerete smaragdina</i> (Guérin-Méneville, 1844) ^a	4	3	7	0.16	BA, ST
Total	1,567	2,726	4,293	100.00	
Species Richness	22	21	24		

^aNot listed as occurring in Honduras in Moure et al. (2012).

^bBA = Buenos Aires, BC = Base Camp, CA = Cantiles, CO = Cortecito, DA = El Danto, GU = Guanales, ST = Santo Tomas.

Table 2. Additional species of orchid bees recorded for Honduras that were not collected in our study, with literature sources.

Species ^{a,b}	Source ^c
<i>Eufriesea coerulescens</i> (Lepelletier, 1841)	A, B, C
<i>Eufriesea mussitans</i> (Fabricius, 1787)	B, C
<i>Eufriesea ornata</i> (Mocsáry, 1896)	C
<i>Euglossa asarophora</i> Moure and Sakagami, 1969	C
<i>Euglossa bursigera</i> Moure, 1970	C
<i>Euglossa cognata</i> Moure, 1970	A, B
<i>Euglossa cordata</i> (Linnaeus, 1758)	B
<i>Euglossa deceptrix</i> Moure, 1968	B
<i>Euglossa despecta</i> Moure, 1968	C
<i>Euglossa dodsoni</i> Moure, 1965	C
<i>Euglossa gorgonensis</i> Cheesman, 1929	B
<i>Euglossa hemichlora</i> Cockerell, 1917	B
<i>Euglossa sapphirina</i> Moure, 1968	C
<i>Euglossa viridissima</i> Friese, 1899	A, C
<i>Eulaema bombiformis</i> (Packard, 1869)	A, B, C
<i>Exaerete frontalis</i> (Guérin-Méneville, 1844)	C

^a*Eulaema seabrai* Moure, 1960 is listed as likely but not yet reported for Honduras by Ramirez et al. (2002). However, this species is now considered South American, with *Eulaema luteola* Moure, 1967 (formerly *Eulaema seabrai luteola*) occurring in Central America and Mexico (D. W. Roubik, personal observation).

^b*Eulaema cingulata* (F., 1804) is listed as occurring in Honduras by Ramirez et al. (2002) and Moure et al. (2012), but nomenclature is problematic for this species. These two works include *Eulaema marcii* Nemésio, 2009 within *E. cingulata*, whereas Ascher & Pickering (2015) treat the 2 species separately, with *E. marcii* occurring in Honduras and *E. cingulata* not reported for Honduras. *Eulaema cingulata* is now considered South American, with *E. marcii* occurring in Central America and Mexico (D. W. Roubik, personal observation).

^cA = Ramirez et al. (2002), B = Moure et al. (2012), C = Ascher & Pickering (2015).

ring in Honduras by Moure et al. (2012) are listed as occurring in Honduras by Ramirez et al. (2002). Based on distributions given in Moure et al. (2012), 3 of the species collected in our study represent range extensions. Two of these are northwestern extensions: *Euglossa cybelia* Moure, approximately 700 km from Puntarenas, Costa Rica, and *Euglossa hansonii* Moure, approximately 1,100 km from Colón, Panama. The third, *Eufriesea pallida* Kimsey, represents a nearly 400 km easterly range extension from Chiapas, Mexico. Of the 10 species not recorded as occurring in Honduras in Moure et al. (2012) or Ramirez et al. (2002), all but one (*E. pallida*) have specimens recorded from Honduras in Ascher & Pickering’s (2015) Discover Life checklist, although many of the specimen records are incomplete. It should also be noted that the range of *E. townsendi* is uncertain and under study, but it has been verified in Panama (D. W. Roubik, personal observation).

Discussion

There appears to be little published information on orchid bee species richness at higher elevation cloud forest locations. In Mesoamerica, Roubik & Ackerman (1987) identified 50 orchid bee species at a 900 m elevation cloud forest location at Cerro Campana, Panama, over the course of a 7 yr study. Ackerman & Roubik (2012) reviewed 30 yr of euglossine pollination data at this and 2 other sites, and the aforementioned Cerro Campana site had 11 species of *Eufriesea*, far more than lower elevation sites. Janzen et al. (1982) collected 27, 18, and 13 species of orchid bees at 3 locations in Costa Rica in 1977 to 1979, with sample sites ranging from near sea level to about 300 m elevation. Our species richness of 24

appears to be relatively low compared with other studies, where Chao1 estimates at 6 sites in Panama and the Amazon region range from 37 to 52 total species, and 27 to 44 species were actually sampled (Roubik 2004). The current species listed for Nicaragua include 32 euglossines (Hinojosa-Diaz & Engel 2012). Comparisons among studies are difficult because of sample size differences, bait presentation differences, and study lengths, along with variation in surrounding habitat quality, from which bees arrive during longer placement in the field.

Our species richness was near the Chao1 estimate of total species richness present of 24.67. Even so, our inventory is likely incomplete. Use of different attractants could result in new species collections, because many orchid bee species are attracted to specific chemical attractants (Roubik & Hanson 2004). In addition, it is possible that we failed to collect rare highland Mesoamerican species, or species such as *Euglossa cyanura* Cockerell, a Panamanian and possibly Costa Rican species that does not visit any known chemical baits (1 undescribed species occurs in Costa Rica; D. W. Roubik, personal observation). Also, because our study was limited to a 2 mo period each year, it is possible that some seasonal orchid bee species were not collected, although in general orchid bee populations tend to be fairly stable over the course of a year (Roubik & Ackermann 1987). Members of the genus *Eufriesea* are known to be highly seasonal, and for this reason are poorly represented in many collections (Roubik & Hanson 2004).

The total *Eufriesea* species in our Honduras study was less than half the species recorded in the highland site of Cerro Campana, in Panama, and parallels the roughly 50% total species richness of the Honduran compared to the Panamanian site. Our sampling was done during the rainy season, which is the period when most species of *Eufriesea* are active (Janzen et al. 1982). In Janzen et al.'s (1982) Costa Rica study, which included mid-wet season sampling, Jun to Aug sampling yielded 70.4% (19 of 27 species), 83.3% (15 of 18 species), and 46.2% (6 of 13 species) of the total species collected for each of the 3 locations. This suggests that wet season sampling, or any one season where there are at least 2 (wet and dry) seasons per year, may miss some of the total species present. However, their mid-wet season sample sizes for the 3 locations (360, 391, and 265) were much smaller than ours, and this difference could affect comparisons because species richness is associated with sample size. The Morisita–Horn index of similarity of 0.987 in our study indicates a high degree of similarity in species composition between years, and suggests that species composition may not vary significantly from year to year, although more data are needed to verify this result.

Orchid bees are ecologically important components of Neotropical ecosystems (Roubik & Hanson 2004). At least one governmental agency, the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA), recognizes orchid bees as key organisms for environmental assessments (Nemésio & Vasconcelos 2014). Our study is the first intensive inventory of orchid bee species in western Honduran cloud forest. Further studies of the diversity, ecology, and conservation status of orchid bees are needed in this understudied and threatened location. Our findings expand knowledge of orchid bee diversity in this region, and provide baseline data for future monitoring of this group in relation to potential impacts of deforestation and climate change.

Acknowledgments

We thank Brandon Taylor, Fabian Wagner, Harriet Downey, Katie Williams, and numerous Operation Wallacea volunteers, staff, and local guides for invaluable assistance with orchid bee collecting. We also thank Sarah Wilcer (Western Illinois University) for help with orchid bee pinning and labeling, and Shane Mason (Western Illinois University) for making and contributing the maps for Fig. 1. We thank Opera-

tion Wallacea for invaluable financial and logistical support, and the Western Illinois University Office of Sponsored Projects and Research Foundation for generous funding for this study.

References Cited

- Ackerman JD. 1983. Diversity and seasonality of male euglossine bees (Hymenoptera: Apoidea) in Central Panama. *Ecology* 64: 274–283.
- Ackerman JD, Roubik DW. 2012. Can extinction risk help explain plant–pollinator specificity among euglossine bee pollinated plants? *Oikos* 121: 1821–1827.
- Ascher JS, Pickering J. 2015. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila), http://www.discoverlife.org/mp/20q?guide=Apoidea_species (last accessed 13 Aug 2016).
- Chao A, Colwell RK, Lin C-W, Gotelli NJ. 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology* 90: 1125–1133.
- Colwell RK. 2013. EstimateS: statistical estimation of species richness and shared species from samples, Version 9 [Online], <http://purl.oclc.org/estimates> (last accessed 13 Aug 2016).
- Dressler RL. 1982. Biology of the orchid bees (Euglossini). *Annual Review of Ecology and Systematics* 13: 373–394.
- Eltz T, Fritzsche F, Petch JR, Zimmermann Y, Ramírez SR, Quezada-Euan JG, Bembe B. 2011. Characterization of the orchid bee *Euglossa viridissima* (Apoidea: Euglossini) and a novel cryptic sibling species by morphological, chemical, and genetic characters. *Zoological Journal of the Linnean Society* 163: 1064–1076.
- Gilbert LE. 1980. Food web organization and the conservation of Neotropical diversity, pp. 11–33 *In* Soule M, Wilcox B [eds.], *Conservation Biology*. Sinauer Associates, Sunderland, Massachusetts.
- Green S, Slater K, Burdekin O, Long P. 2012. Cusuco National Park, Honduras: 2012 Status Report. Operation Wallacea, Lincolnshire, United Kingdom.
- Hinojosa-Diaz IA, Engel MS. 2012. A checklist of the orchid bees of Nicaragua (Hymenoptera: Apoidea: Euglossini). *Journal of the Kansas Entomological Society* 85: 135–144.
- Janzen DH, De Vries PJ, Higgins ML, Kimsey LS. 1982. Seasonal and site variation in Costa Rican euglossine bees at chemical baits in lowland deciduous and evergreen forests. *Ecology* 63: 66–74.
- Le Saout S, Hoffmann M, Shi Y, Hughes A, Bernard C, Brooks TM, Bertzky B, Butchart SHM, Stuart SN, Badman T, Rodrigues ASL. 2013. Protected areas and effective biodiversity conservation. *Science* 342: 803–805.
- Minkley RL, Reyes SG. 1996. Capture of the orchid bee, *Eulaema polychroma* (Friese) (Apoidea: Euglossini) in Arizona, with notes on northern distributions of other Mesoamerican bees. *Journal of the Kansas Entomological Society* 69: 102–104.
- Mittermeier RA, Myers N, Mittermeier CG [eds.]. 1999. Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. CEMEX/Conservation International, Mexico City, Mexico.
- Moure JS, Melo GAR, Faria Jr LRR. 2012. Euglossini Latreille, 1802, *In* Moure JS, Urban D, Melo GAR [orgs], *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region [Online Version]*, <http://www.moure.cria.org.br/catalogue> (last accessed 13 Aug 2016).
- Nemésio A, Silveira FA. 2007. Diversity and distribution of orchid bees (Hymenoptera: Apoidea) with a revised checklist of species. *Neotropical Entomology* 36: 874–888.
- Nemésio A, Vasconcelos HL. 2014. Effectiveness of two sampling protocols to survey orchid bees (Hymenoptera: Apoidea) in the Neotropics. *Journal of Insect Conservation* 18: 197–202.
- Pemberton RW, Wheeler GS. 2006. Orchid bees don't need orchids: evidence from the naturalization of an orchid bee in Florida. *Ecology* 87: 1995–2001.
- Ramírez S, Dressler RL, Ospina M. 2002. Abejas euglossinas (Hymenoptera: Apoidea) de la Región Neotropical: listado de especies con notas sobre su biología. *Biota Colombiana* 3: 7–118.
- Roubik DW. 2004. Long-term studies of solitary bees: what the orchid bees are telling us, pp. 97–104 *In* Freitas BM, Pereira JOP [eds.], *Solitary Bees: Conservation, Rearing and Management for Pollination*. Imprensa Universitaria, Fortaleza, Brazil.
- Roubik DW, Ackermann JD. 1987. Long-term ecology of euglossine bees (Apoidea: Euglossini) in Panama. *Oecologia* 73: 321–333.
- Roubik DW, Hanson PE. 2004. *Orchid Bees of Tropical America: Biology and Field Guide*. INBio, Santo Domingo de Heredia, Costa Rica.
- Skov C, Wiley J. 2005. Establishment of the Neotropical orchid bee *Euglossa viridissima* (Hymenoptera: Apoidea) in Florida. *Florida Entomologist* 88: 225–227.
- Zimmermann Y, Ramírez SR, Eltz T. 2009. Chemical niche differentiation among sympatric species of orchid bees. *Ecology* 90: 2994–3008.