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Euglossini orchid bees in Panama: a state of the art review

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Daniela Rincón¹ , Julián Monge-Nájera^{2*} , Dumas Gálvez^{3,4,5} , David W. Roubik⁵ , Willinton Barranco^{1,4} , Jormerys Chancay⁷ , Yostin Añino^{3,6,7,8} 

¹Universidad del Magdalena, Santa Marta, Colombia. ²Universidad Estatal a Distancia, Laboratorio de Ecología Urbana, San José, 2050 Costa Rica.

³Coiba Scientific Station, City of Knowledge, Calle Gustavo Lara, Bld. 145B, Clayton, 0843-01853, Panamá. ⁴Universidad de Panamá, Programa Centroamericano de Maestría en Entomología, Ciudad de Panamá, Panamá. ⁵Smithsonian Tropical Research Institute, Balboa, Ancón, Panamá. ⁶Programa de Doctorado en Ciencias Naturales para el Desarrollo (DOCINADE), UNED, Instituto Tecnológico y Universidad Nacional de Costa Rica, San José, Costa Rica. ⁷Universidad de Panamá, Museo de Invertebrados G.B. Fairchild, Ciudad de Panamá, Panamá. ⁸Universidad de Panamá, Programa de Maestría en Estadística Aplicada, Ciudad de Panamá, Panamá. E-mail: julianmonge@gmail.com*

Abstract

Euglossini, or orchid bees, are Neotropical bees known for their fragrance harvesting behavior. This review, done by experts and conducted under Preferred Reporting Items for Systematic Reviews and Meta Analyses guidelines, summarizes four decades (1966-2022) of literature on their biology in Panama, including taxonomy, ecology, behavior, and conservation. Research has mostly explored floral preferences, learning behaviors, and the impact of resource availability on foraging. Orchid flowering phenology matches peaks of male bee abundance. Over 50 new species have been described, with variations in species composition across habitats and seasons. There is a higher genetic polymorphism in colonial genera, and a debate on diploid males and social evolution. Studies have focused on colonial social structure, parasites, fragrance harvesting, geographic variation, and nesting behavior. Phylogenetic analyses have shed light on social behavior evolution, and comparative phylogeography has indicated recent speciation. Physiology has linked body mass and flight performance. There are conflicting reports on higher biodiversity in the understory versus the canopy. Population changes are influenced by environmental and anthropogenic factors. Molecular phylogenetics has dated bee diversification to 27-42 million years ago. Flight muscle membrane composition has been linked to metabolic rate evolution, and historical nest remnants have aided floristic diversity reconstruction. Long-term monitoring indicates a stable or increasing species diversity, despite climate change. Research in Panama has provided a vast field of knowledge on these bees, deepening our understanding and justifying their protection in the Neotropical region. Urgent research is needed on Euglossini bee genetics, fragrance roles, orchid pollination, metabolic rates, climate impacts, plant-pollinator dynamics, evolutionary history, and effective conservation strategies.

Additional keywords: Euglossini, Neotropical bees, fragrance harvesting, taxonomy, ecology, behavior, diversity, genetics, physiology, Panama.

Resumen

Las Euglossini, o abejas de las orquídeas, son abejas neotropicales conocidas por su comportamiento de recolección de fragancias. Esta revisión, realizada por expertos y conducida según las directrices de los Preferred Reporting Items for Systematic Reviews and Meta Analyses, resume cuatro décadas (1966-2022) de literatura sobre su biología en Panamá, incluyendo taxonomía, ecología, comportamiento y conservación. Se han estudiado preferencias florales, comportamientos de aprendizaje e impacto de la disponibilidad de recursos, con variaciones en la composición de especies a través de hábitats y estaciones, y se han descrito más de 50 especies nuevas. La fenología floral de las orquídeas coincide con los picos de abundancia de abejas macho. Hay mayor polimorfismo genético en géneros coloniales y se debate sobre los machos diploides y la evolución social. Los estudios se han centrado en la estructura social colonial, parásitos, recolección de fragancias, variación geográfica y comportamiento de anidación. Los análisis filogenéticos han arrojado luz sobre la evolución del comportamiento social, y la filogeografía comparativa ha indicado una especiación reciente. La fisiología ha vinculado la masa corporal y el rendimiento de vuelo. Hay informes contradictorios sobre una mayor biodiversidad en el sotobosque o en el dosel. Los cambios poblacionales están influidos por factores ambientales y antropogénicos. La filogenética molecular ha datado la diversificación de las abejas en 27-42 millones de años. La composición de la membrana del músculo de vuelo se relaciona con la evolución de la tasa metabólica, y los restos históricos de nidos han ayudado a reconstruir la paleodiversidad florística. El monitoreo a largo plazo indica una diversidad de especies estable o en aumento, a pesar del cambio climático. La investigación en Panamá ha proporcionado un vasto campo de conocimiento sobre estas abejas, profundizando nuestra comprensión y justificando su protección en la región neotropical. Urge investigación sobre genética de las abejas, fragancias, polinización, tasas metabólicas, efectos climáticos, dinámica planta-polinizador, historia evolutiva y estrategias de conservación.

Palabras clave: Euglossini, abejas neotropicales, recolección de fragancias, taxonomía, ecología, comportamiento, diversidad, genética, fisiología, Panamá

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Introduction

Euglossini are an exclusively Neotropical tribe of intriguing bees, known as ‘orchid bees’ for the male behavior of fragrance harvesting from orchids and other sources. Euglossines have interactions with a plethora of tropical flowers, for example, the Snow White Stanhopea (*Stanhopea candida*); the Monkey Goblet (*Catasetum macrocarpum*). Warczewitzii’s Clowesia (*Clowesia warczewitzii*), the Sack-shaped Catasetum (*Catasetum saccatum*) and the Five-Lined Gongora (*Gongora quinquenervis*) (Roubik and Hanson 2004, Roubik and Moreno 2021).

Orchid bees, known for their wide-ranging flower attraction and male response to chemical lures, have been extensively studied in Panama, including pioneering studies on taxonomy (Dressler, 1978a), ecology (Ackerman, 1983a, 1983b, 1983c), behavior (Zimmerman and Madriñán, 1988), diversity (Roubik 1989, Vega-Hidalgo et al. 2020), genetics (Roubik et al. 1996) and physiology (Darveau et al. 2005a, 2005b). Such literature provides valuable information but, until now, has defied a critical summary. Here we present a PRISMA (Preferred Reporting Items for Systematic Reviews and Meta Analyses), method state of the art for the scientific literature on Euglossini in Panama. The objective of this systematic review is to comprehensively analyze the existing literature on tropical Euglossini bees in Panama, including all aspects of their biology, like their taxonomy, ecology, behavior and conservation status.

Materials and Methods

A systematic search was carried out following the guidelines set forth by the PRISMA method which standardizes the collection of studies information (Moher et al. 2009). Our search was based on a clear question: what does the existing literature on tropical bees, basically tells us about all aspects of their biology, including their taxonomy, ecology, behavior and conservation status?

For the compilation of the studies, we created an academic profile on Google Scholar to save all the results of a search that used the keywords ‘Euglossini’, ‘Euglossinae’, ‘abejas de las orquídeas’, ‘orchid bees’, ‘abelhas das orquídeas’, ‘Euglossa’, ‘Exaerete’, ‘Eufriesea’, ‘Eulaema’ and ‘Aglae’.

We carried out web scraping to the profile (Añino et al. 2021) by means of the software ‘Publish or Perish’, which creates a database in csv format for use in Excel. We used our expert criteria to manually curate the database by debugging duplicates, and removing articles not related to Euglossini. Eleven publications by Robert L. Dressler were not available on the web and were added to the database, for a total of 73 articles. We added twelve articles from David W. Roubik that were also missing and did a generalized search in Dimensions to exclude the possibility that some articles were missing from the Google Scholar search. All the articles found in Dimensions were already included in the Google Scholar profile. Finally, the 73 articles were classified by decade for their temporal sequential reading and subsequent thematic summary, and we included articles published until May 2022.

State of the Art: Euglossini in Panama

As a biodiversity hotspot, Panama is rich in the complex biological phenomena associated with the evolution of Euglossine orchid bees and, in 1966, Dodson was the first author to publish on the ethology of Euglossini, when the topic was mostly unknown, highlighting their importance in the pollination of many species of orchids; together with the description of their nests, nest-building behavior, mating behavior and pollination specificity of certain species (Dodson 1966).

In 1969, orchidologist Robert Dressler and collaborators (Rickefs et al. 1969), pioneered the study of Euglossini diversity in Panama, providing morphological descriptions, data on relative abundance patterns in four locations, and suggesting that there are differences in the proportions of long-tongued and/or large-bodied species across locations. In the 1970s, Williams and Dressler (1976) highlighted the importance of the aromas emitted by plants in pollination by male euglossines, as in the case of the genus *Spathiphyllum*, which produces floral odors similar to those of some orchids.

Dressler contributed significantly to the taxonomy of this group; he described the morphological characters of *Euglossa* that allowed to regroup these species into four subgenera. Subsequently, he described seven new species and one new subspecies from Mexico and Central America (Dressler 1978b). He also explained the

Müllerian mimetic complex of *Eulaema bombiformis*, *E. meriana* and *E. seabrai* in the Amazon basin, where they are extremely similar, while in the east coast of Brazil the mimetism does not occur and the three species are easily distinguished. In other places such as the coast of Venezuela and northern Central America, these species form a distinct mimetic complex, which the author suggests that it evolved in isolation (Dressler 1979).

1980-1989: Taxonomic and Natural History Studies of Euglossini

Fifteen studies were published during this decade, with the review by Dressler (1982a) as the most cited work, in which he describes generalities about orchid bees: distribution and classification, the structure of their nests, sociality, nest parasites, seasonal variation in population abundances, reproductive behavior, courtship and mating. He also describes the characteristic structure of males and describes the resources that they collect from the plants, such as nectar, pollen, resins, and the role these compounds play in their biology.

Dressler (1982b, 1982c) described eleven new *Euglossa* species and provided a key for the identification of males of the *Euglossa analis*, *E. cybelia* and *E. piliventris* species groups, and added six new geographic records of the *Euglossa cordata* group, and six of the *E. purpurea* group, compared with their closest ally species. Together with Lynn Kimsey, he provided a detailed list of species in the tribe, including synonymy, complete type data and complete references (Kimsey and Dressler 1986).

Ackerman (1983) also made important contributions on their diversity and ecology, comparing the composition of species between lowland and highland sites of the tropical humid forest of Barro Colorado Island, defining the ranges of dominance, the phenological profiles of the species and seasonal changes on richness and abundance. Years later, Ackerman (1989) examining variation in fragrance availability and preferences, reported interspecific and intraspecific variations in fragrance choice among an assemblage of Euglossini in Barro Colorado Island and Campana National Park. Ackerman made valuable behavioral observations, like the pollination mechanism of the plant *Cochleanthes lipscombiae*, in which euglossines extend their long tongues inside the flower in search of nectar, which, once loaded

with pollinaria, deposits them on the stigma and obtains a new charge of pollinaria by dislodging the anther (Ackerman 1983b). He also performed an experiment on nectar-seeking behavior in Barro Colorado Island, using two species that feed on *Calathea latifolia*, discovering that euglossine bees learn the specific locations of the inflorescences in which they forage, with fidelity to the site; however, when changes in resource availability occur, these bees adjust their feeding habits (Ackerman et al. 1982).

Subsequently, Ackerman (1983c) examined the seasonal and geographic relationships and the possible interdependence in the orchid-euglossine relationship. Orchids require euglossines for pollination and their flowering matches the maximum activity of their pollinators; however, these bees do not show host specificity, indicating that the orchid-male euglossine interaction does not seem to represent a mutually obligatory relationship. On the other hand, Ackerman and Montalvo (1985) explore the largely unknown topic of longevity, through cage breeding experiments with and without fragrances. They found that fragrance compounds increased longevity, perhaps as nutritional requirements and as pheromone precursors, and these bees are long-lived with an increase in longevity related to increases in body size.

Zimmerman and Madriñan (1988) corroborated the long lifespan of euglossines found by Ackerman and Montalvo (1985) but adding that they may show an age-dependent decrease in the reproductive activity of males. The search for chemical products was not restricted to the youngest bees, all bees leave their territories periodically throughout their lives to search for these compounds. In 1989, Zimmerman, et al., confirmed that most orchids that are pollinated by euglossine males fit the predictions of the *Pollinator Tracking Hypothesis*, because the flowering times match the peak abundance of the males that pollinate them. A later study confirmed this by monitoring the growth patterns and flower production of the orchid *Aspasia principissa*, determining the relative importance of the pollinator and the limitation of resources in fruit production (Zimmerman and Aide 1989).

The contributions of David Roubik and Ackerman during this decade consist of an extensive 7-year study

on Barro Colorado Island and the cloud forest at 900m near the Pacific Ocean (Cerro Campana Protected Area), where the abundance patterns of these bees were monitored. By studying 51 local orchid species, they found that bee populations were stable, that larger populations were more stable, and that the most abundant bees visited more orchid species (Roubik et al. 1982, Roubik and Ackerman 1987).

1990-1999: A new discipline for the study of Euglossini in Panama

During this decade, genetic studies of this group were introduced and work by authors such as David Roubik and Thomas Eltz meant the first advances to understand genetics, evolution, fragrances, behavior, and eusociality. Orchid bees had not been studied for population genetic traits, and, interestingly, none of the approximately 200 species have social behavior (Roubik and Hanson, 2004), a characteristic that sets them apart from other corbiculate bees, some of which form colonies with caste differentiation. Roubik et al. (1996) found almost no polymorphism in *Eufriesea* and *Exaerete*, while *Euglossa* and *Eulaema*, the colonial genera, are highly polymorphic and have high proportions of diploid males. However, one year later, Eltz et al. (1997) reported haploid karyotypes in males and no cases of diploidy in *Euglossa hyacinthina* and *E. cyanaspis*. Advances in genetics allowed elucidated phylogenetic relationships, starting by the fact that the Euglossini tribe belongs to the Apinae subfamily, and is related to the tribes Meliponini, Apini and Bombini (Koulianos et al. 1999). The issue of eusociality and diploidy in Euglossini remains controversial.

On the other hand, Roubik studied the behavior of these bees in mixed colonies, analyzing the limits of sociality in a mixed colony of *Eulaema polychroma* and *E. cingulata*, from which the kleptoparasite mutilids and *Exaerete* emerged and did not interact aggressively. This nest, and one reported in a previous study, both in natural forest, had around 75% parasitism, a high rate that may promote sociality in euglossine as a strategy to cope with parasites. However, the lack of relatedness in the mixed *Eulaema* colony suggests that non-kin tolerance could decrease kin selection and the evolution of eusociality (Roubik 1990). Still, it is now known that increased diversity within colony members can provide large benefits in

bees and other social insects; for instance, by increasing colony performance and disease resistance, among others (Tarpay 2003, Olroyd and Fewell 2008, Soper et al. 2021). Therefore, euglossine bees may provide unique systems to explore evolutionary trends of sociality (e.g. Saleh and Ramírez 2019).

Kato et al. (1992) also studied foraging and food preferences by males in four *Euglossa* species in captivity, with a strong preference for solutions with 51% and 34% of sucrose as compared to solutions with 17% or only water. The preference for high proportions of sugar was corroborated by Roubik et al. (1995), by analyzing the concentration of sugar in the nectar consumed by Euglossini species (35-65%); which is relevant for pollination services, since heterogeneity and optimal nectar sweetness are likely key mechanisms causing collector fidelity (Roubik et al. 1995).

Eltz and Roubik made important contributions through analysis of two *Euglossa* species, discovering the ability of males to store highly variable amounts of a complex and specific mixture of scents in their hind tibiae (Eltz et al. 1999). They proposed that these compounds may serve as markers of “good genes” for potential mates, and males can even steal the fragrances from corpses: *Eulaema meriana* males extracted and stored chemicals from a recently killed male (Eltz et al. 1999). Roubik did experiments with three dead males of this species and observed that they attracted another male, but no females, which led him to consider that the chemical harvesting behavior is an indicator of age, feeding capacity and suitability as a mate (Roubik 1998).

Roubik et al. (1993) also explored preferences for understory or canopy strata in a study of 20 species from 10 genera, that included non-euglossine bees, and found that large euglossines tend to forage high, which is related to their better ability to lose heat during flight. Some medium-sized diurnal forest bees avoid the exposed upper canopy, while some nocturnal bees can forage there.

2000-2009: Genetics and behavior

This decade is characterized by a considerable increase in the number of studies developed on orchid bees, including the relationship of male diploidy with the evolution of eusociality. In a first study, Roubik et al.

(1996) found that, in nine species, only four had diploid males (in total, 55 were diploid and 144 were not diploid). Diploid males had previously been found in other groups of bees with populations experiencing a loss of allelic variation and hence inbreeding (Roubik et al. 1996). However, Takahashi et al. (2001) found in Brazil that euglossines have low numbers of diploid males. Roubik (2001a) attributed this difference to geographic variation, suggesting that migration plays a role and that low eusociality is a protection mechanism against polymorphic females cooperating with abundant diploid males (Roubik 2001b).

To examine non-social behavior in Euglossini, Soucy and Giray (2003) investigated natural nests of *Euglossa hyacinthina*, a species that can nest in solitary or in groups (i.e. communal nesting but without social organization). In this case, the production of offspring is lower in group nests, but solitary females must leave their nests to forage, favoring the attacks of some natural enemies. This agrees with what was observed by Riveros et al. (2009) in *Euglossa dodsoni*, whose form of behavior in the colony is similar to *E. hyacinthina*, although the latter has larger and more resistant nests.

Zayed et al. (2004) proposed the use of the frequency of diploid males as a criterion to assess the sustainability of bee populations, because several studies report high abundances in the populations, but without the high levels of sterile diploid males. One example is *Euglossa imperialis*, with a high production of diploid males, yet the most abundant bee in the forests of Panama; however, genetically, its long-term persistence is limited. Kawakita et al. (2008) built a robust phylogeny of the four tribes to understand the evolution of eusociality, corroborating that Bombini and Meliponini are putative monophyletic groups, and restricting Meliponini and Apini.

The first studies of comparative phylogeography involving Panamanian species, were based on mtDNA of 14 species from the Andes and the Amazon basin. The mtDNA divergences within species were consistently low in 12 monophyletic species, and reference to closely related outgroups suggested recent speciation for most species (Dick et al. 2004). The first studies on physiology, beginning with Darveau et al. (2005a), found that body mass strongly affected the specific metabolic rates of the hovering flight mass, and that the flutter rate variation is

explained by the variation in wing loading. Furthermore, the effect of body size on flight energy is influenced by the relationship between wing shape and kinematics, which directly influence their scale of metabolic rate.

Borrell (2004) demonstrated that the four major genera (*Eufriesea*, *Euglossa*, *Enlaema* and *Exaeretè*) are suction feeders, which led to a lower optimal sugar concentration that is required by these bees. This was experimentally corroborated with work on *Euglossa imperialis* that showed in fact that orchid bees maximize their rate of energy intake by feeding on nectars with sugar concentrations between 30 and 40%. Suárez et al. (2005a, 2005b) used orchid bees as an alternative system to other bees to investigate the metabolic fuel used by bees for flight and corroborated that flight depends on the oxidation of carbohydrates. These authors evaluated the relative importance of variation in enzyme concentration and metabolic regulation, a topic that remains little studied, *in vitro* flight measurements of 14 species and revealed that the flapping frequencies, and metabolic rates decrease in heavier bees.

Another common topic was the collection and storage of floral fragrances. In experiments on the detection of fragrance components, Schiestl and Roubik (2003) concluded that the detection mechanism is based on peripheral and central nervous processes. They have an innate preference for certain odors, showing memory when collecting odors, and accuracy in the amount they collect as a result of negative feedback (Eltz et al. 2005). Moreover, there is a species-specific attraction within species where each one recognizes the fragrance complex to which it belongs (Zimmermann et al. 2006). The hypothesis that fragrance storage is an indicator of genetic quality in males and have evolved through sexual selection was tested experimentally by Eltz et al. (2003) but did not find evidence that the amount of fragrances stored by the male correlated with number of matings achieved. In fact, display activity was the only factor correlating with mating frequency. Interestingly, they discovered that males display a leg-crossing movement possibly related to odor release. Therefore, at the time, the relevance of fragrance collection by males to improve mating success had not experimental support.

Finally, large-scale diversity monitoring was carried out to study the spatial distribution of arthropods, including

euglossines (Basset et al. 2007). In Panama, Roubik (2001b) showed an oscillation in species abundance and diversity from 1979 to 2000 as a result of climatic events such as El Niño. Ramírez et al. (2002) provided a review on taxonomy, distribution, and behavior, among others during this decade; but this review is now outdated by two decades.

2010-2019: A diverse and productive decade

As in the previous decade, there was a large volume of articles on subjects such as diversity and vertical stratification. In the Darién National Park, a five-year study found that the bees decreased in richness and abundance over time, probably from environmental factors that included a reduction of resources (Santos et al. 2018). Overall, clear trends in stratum distribution were difficult to establish, studies varied in their outcomes: 22 species of *Enfriesea*, *Euglossa* and *Eulaema* were identified in the humid tropical forest of Monte Fresco, with the highest values of richness and abundance in the canopy (Santos et al. 2011). In the submontane broadleaf forest of Guna de Madugandí, higher values were observed in the understory (14 species; Santos et al. 2012). In the Darién National Park, the understory had the greatest diversity and abundance (Santos 2014).

Guardia and Santos (2014) described diversity and vertical stratification in the cloud forests of the Omar Torrijos National Park, sampling for 6 months in the rainy and dry seasons and finding 31 species of 3 of the 4 genera reported for Panama. From 2006 to 2015, eighteen species from four genera were reported from the Azuero Peninsula, with population decreases caused by agriculture and livestock production (Santos and Añino 2016). Other localities such as the Ustupu (Kuna) community produced similar results to the other studies (Osorio and Santos 2018).

Koo and Santos (2015) found 4 genera of Euglossini at Chagres National Park, where *Euglossa* was the most diverse and abundant; they were present in Cerro Azul and Cerro Jefe, but the highest number of species and individuals occurred in Cerro Jefe. They suggested that high richness and abundance in these cloud forests could reflect lower human activity; however, Elizondo (2015) stated that Cerro Azul was affected by fragmentation from poultry production, plantations, and urbanization;

and Cerro Jefe from telecommunication antennas, tourism, and urban development. However, other studies in the Neotropics found that abundance and diversity are not affected by habitat fragmentation and disturbance, in part thanks to their large foraging ranges, with, for example, *Excaerete frontalis* males traveling up to 5 km (Wikelski et al. 2010).

In this decade, progress was also made in understanding the specificity in plant-pollinator relationships, as a factor that in the long term favors the stability of the pollinator populations, and flowering abundance and duration. Ackerman and Roubik (2012) did a continuous 7-year census, with flowering and pollination phenology data from 37 plant species: pollinator specificity was not related to any of these variables.

Roubik and Knudsen (2017) studied courtship odors of *Euglossa mixta* in the island of Coiba and mainland Panama; fragrances seem analogous between orchids and bees: through female choice, they can reduce interspecific interference or competition, promote crossbreeding and favor adornments. Shorter reports indicate that *Euglossa hemichlora* and *Euglossa imperialis* are the hosts of *Pappognatha panamensis* (Parasitoid wasps) (Cambra et al. 2015) and that *Apiomerus hirtipes* (Hemiptera) prey on some *Euglossa* species (Santos et al. 2016).

Another topic studied in depth in this period was the evolutionary history of these bees. Authors such as Ramírez et al. (2010) did molecular phylogenetics of the entire Euglossini tribe, with five genera, eight subgenera and 126 of the approximately 200 known species. Extant bees shared a more recent common ancestor at 27–42 Mya. The first episodes of diversification shared a history on both sides of Mesoamerica, where the orchid bees dispersed in the Caribbean, and through the isthmus of Panama, matching the hypothesis that recent geological events contributed to the diversification of the rich Neotropical biota. Tongue length and body size changed in coincidence with the origin of *Euglossa* and *Enfriesea*. Later, studies of a taxonomic and physiological nature, such as those by Francoy et al. (2012), provided an efficient morphometric mechanism for the identification of *Euglossa* species.

Rodríguez et al. (2015) found that the composition of the flight muscle membrane plays an important role in the diversity of flight metabolic rate, with an effect of

body mass and phylogeny in a lesser degree. These bees illustrate the correlated evolution between membrane composition and metabolic rate, supporting the proposed functional link in the Membrane Pacemaker Hypothesis. Finally, this decade ends with the work of Galgani-Barraza et al. (2019), who based on pollen from the remains of large nesting aggregations, made in 1871-1876 by *Eufriesea surinamensis* and found in a restoration of the Basilica Cathedral, reconstructed the floristic diversity of Panama City during the 19th century, with stored pollen from 48 plant species (43 genera, 23 families).

2020-2022: Studies continue

In this early part of the decade, work on diversity, richness and abundance extends to more localities. For example, in Darién National Park, Vega-Hidalgo et al. (2020) found that variation between understory and canopy was higher in the dry season and found no difference in richness and abundance between strata. This contrasts with Reyes et al. (2020), who found richness and abundance to be slightly higher in the understory in Coclé. Añino et al. (2022) recently carried out a meta-analysis, including all the studies comparing strata in the neotropics, finding that abundance tends to be higher in the understory; however, diversity is similar in both strata. Roubik et al. (2021) found that 75% of the species were stable, or increasing, despite climatic events in Pipeline Road (Soberania National Park) and Barro Colorado Island. Abundance and biomass remained stable for 50% of the species, but half of the species were rare.

This comprehensive review of Panamanian Euglossini answers our original question about what the existing literature tells us about all aspects of their biology, including their taxonomy, ecology, behavior and conservation status. We found that, from their unique fragrance harvesting to their role as pollinators, they have an intricate web of interactions, remarkable adaptations and a complex evolutionary history. Research in Panama has been varied and can be useful to understanding and protecting these bees in the rest of the Neotropical region. Other countries with orchid bees and significant research are Brazil, Colombia, Costa Rica, and Mexico (Roubik and Hanson, 2004), but considering the country sizes, the contributions of Panama and Costa Rica seem remarkable.

Concrete fields in particular need of new research

This comprehensive review indicates that efforts can now be focussed on male diploidy and haploidy; fragrance chemical composition, impacts of habitat change; Long-term monitoring; and phylogenetics of species outside Panama.

Conflict of Interest

The authors thank the Panamanian government for financial support and declare that there are no conflicts of interest. Añino and Rincón proposed the study and acted as team leaders. All authors participated in the study according to their fields, and all authors read and accepted the final version of the article.

Author contribution statement

Conceptualization: YA, DR, WB. Data curation: DR, JC, YA. Formal analysis: YA, DR, JM, DG. Investigation: All authors. Methodology: YA, DR, JC. Writing - original draft: DR, DG, JM, DWR, YA. Writing - review and editing: All authors.

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Literature Cited

- ACKERMAN JD. 1983. Specificity and mutual dependency of the orchid—euglossine bee interaction. *Biological Journal of the Linnean Society*, 20:301-314.
- ACKERMAN JD. 1989. Geographic and seasonal variation in fragrance choices and preferences of male euglossine bees. *Biotropica*, 21:340-347.
- ACKERMAN JD, MESLER MR, LU KL, MONTALVO AM. 1982. Food-foraging behavior of male Euglossini (Hymenoptera, Apidae), vagabonds or trapliners? *Biotropica*, 14, 241-248.
- ACKERMAN J.D., MONTALVO A.M. 1985. Longevity of euglossine bees. *Biotropica*, 17: 79-81.
- AÑINO Y, ROMERO-ROMERO, E. & GÁLVEZ, D. 2022. Vertical stratification in orchid bees (Apidae: Euglossini)? a meta-analysis. *Apidologie*, 53(26): 1-13. <http://doi.org/10.1007/s13592-022-00939-0>
- AÑINO YJ, MONGE-NÁJERA J, MURILLO-GONZÁLEZ D, MICHÁN-AGUIRRE L. 2021. Cómo aplicar la ciencia métrica a la investigación ecológica. *Ecosistemas*, 30: 2256.

- BASSET Y, CORBARA B, BARRIOS H, CUÉNOUD P, LEPONCE M, ABERLENC HP, WINCHESTER NN. 2007. IBISCA-Panama, a large-scale study of arthropod beta-diversity and vertical stratification in a lowland rainforest, rationale, study sites, and field protocols. *Bulletin of the Royal Belgian Institute of Natural Sciences. Entomology*, 77:39-69.
- BORRELL BJ. 2004. Suction feeding in orchid bees (Apidae, Euglossini). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271: S164-S166.
- CAMBRA RA, ROUBIK DW, QUINTERO ARIAS D. 2015. Hospederos de *Pappognatha panamensis* Quintero Cambra, 2005 (Hymenoptera, Mutillidae) y su primer registro de distribución para Costa Rica. *Boletín del Museo de Entomología de la Universidad del Valle*, 16: 5-7.
- DARVEAU CA, HOCHACHKA PW, WELCH JR KC, ROUBIK DW, SUÁREZ RK. 2005a. Allometric scaling of flight energetics in Panamanian orchid bees, a comparative phylogenetic approach. *Journal of Experimental Biology*, 208: 3581-3591.
- DARVEAU CA, HOCHACHKA PW, ROUBIK DW, SUÁREZ R.K. 2005b. Allometric scaling of flight energetics in orchid bees, evolution of flux capacities and flux rates. *Journal of Experimental Biology*, 208: 3593-3602.
- DICK CW, ROUBIK DW, GRUBER KF, BIRMINGHAM E. 2004. Long-distance gene flow and cross-Andean dispersal of lowland rainforest bees (Apidae, Euglossini) revealed by comparative mitochondrial DNA phylogeography. *Molecular Ecology*, 13: 3775-3785.
- DODSON CH. 1966. Ethology of some bees of the tribe Euglossini (Hymenoptera, Apidae). *Journal of the Kansas Entomological Society*, 39: 607-629.
- DRESSLER RL. 1978a. An infrageneric classification of *Euglossa*, with notes on some features of special taxonomic importance (Hymenoptera, Apidae). *Revista de Biología Tropical*, 26: 187-198.
- DRESSLER RL. 1978b. New species of *Euglossa* from Mexico and Central America. *Revista de Biología Tropical*, 26: 167-185.
- DRESSLER RL. 1979. *Eulaema bombiformis*, *E. meriana*, and Mullerian Mimicry in Related Species (Hymenoptera, Apoidea). *Biotropica*, 11: 144-151.
- DRESSLER RL. 1982a. Biology of the orchid bees (Euglossini). *Annual Review of Ecology and Systematics*, 13: 373-394.
- DRESSLER RL. 1982b. New species of *Euglossa* II. (Hymenoptera, Apidae). *Revista de Biología Tropical*, 30: 121-129.
- DRESSLER RL. 1982c. New species of *Euglossa*. III. The *bursigera* species group (Hymenoptera, Apidae). *Revista de Biología Tropical*, 30: 131-140.
- ELIZONDO L. 2015. Abejas de las orquídeas como indicadores ecológicos en el Parque Nacional Chagres. Comentarios a Koo Santos, 2015. *Revista Científica CENTROS*, 5: 43-45.
- ELTZ T, ROUBIK DW, LUNAU K. 2005. Experience-dependent choices ensure species-specific fragrance accumulation in male orchid bees. *Behavioral Ecology and Sociobiology*, 59: 149-156.
- ELTZ T, SCHMID M, ROUBIK DW. 1997. Haploid karyotypes of two species of orchid bees (Hymenoptera, Apidae, Euglossini). *Journal of the Kansas Entomological Society*, 70(20): 142-144.
- ELTZ T, WHITTEN WM, ROUBIK DW, LINSEMAIR KE. 1999. Fragrance collection, storage, and accumulation by individual male orchid bees. *Journal of Chemical Ecology*, 25: 157-176.
- ELTZ T, ROUBIK DW, WHITTEN MW. 2003. Fragrances, male display, and mating behavior of *Euglossa hemichlora*, a flight cage experiment. *Physiological Entomology*, 28: 251-260.
- FRANCOY TM, DE FARIA FRANCO F, ROUBIK DW. 2012. Integrated landmark and outline-based morphometric methods efficiently distinguish species of *Euglossa* (Hymenoptera, Apidae, Euglossini). *Apidologie*, 43: 609-617.
- GALGANI-BARRAZA P, MORENO JE, LOBO S, TRIBALDOS W, ROUBIK DW, WCISLO WT. 2019. Flower use by late nineteenth-century orchid bees (*Eufriesea surinamensis*, Hymenoptera, Apidae) nesting in the Catedral Basílica Santa María la Antigua de Panamá. *Journal of Hymenoptera Research*, 65: 74-81.
- GUARDIA R, SANTOS A. 2014. Diversidad y estratificación vertical de abejas de las orquídeas (Hymenoptera, Euglossinae) del Parque Nacional Omar Torrijos Herrera, Coclé, Panamá. *Centros*, 3(2): 1-16.
- KATO M, ROUBIK DW, INOUE I. 1992. Foraging behavior and concentration preferences of male Euglossine bees (Hymenoptera, Apidae). *Tropics*, 1: 259-264.
- KAWAKITA A, ASCHER JS, SOTA T, KATO M, ROUBIK DW. 2008. Phylogenetic analysis of the corbiculate bee tribes based on 12 nuclear protein-coding genes (Hymenoptera, Apoidea, Apidae). *Apidologie*, 39(1): 163-175.
- KIMSEY LS, DRESSLER RL. 1986. Synonymic species list of Euglossini. *Pan-Pacific Entomologist*, 62(3): 229-236.
- KOO S, SANTOS A. 2015. Diversidad y abundancia de las abejas de las orquídeas en los bosques nubosos del parque nacional Chagres, Panamá, República de Panamá. *Centros*, 4: 168-187.
- KOULIANOS S, SCHMID-HEMPEL R, ROUBIK DW, SCHMID-HEMPEL P. 1999. Phylogenetic relationships within the corbiculate Apinae (Hymenoptera) and the evolution of eusociality. *Journal of Evolutionary Biology*, 12: 380-384.
- MOHER D, LIBERATI A, TETZLAFF J, ALTMAN D. 2009. Preferred Reporting Items for Systematic Reviews and Meta-Analyses, The PRISMA Statement. *Annals of Internal Medicine*, 151(4): 264.

- OLDROYD B, FEWELL J. 2008. Large fitness benefits from polyandry in the honey bee, *Apis mellifera*. *Trends in Ecology & Evolution*, 23(2): 59-60.
- OSORIO-ARENAS M, SANTOS A. 2018. Estudio sobre el conocimiento de la diversidad de abejas de la orquídea (Apidae, Euglossini) en la comunidad de Ustupu, Comarca Kuna Yala, Panamá. *Scientia*, 28(1): 61-71.
- RAMÍREZ S, DRESSLER RL, OSPINA M. 2002. Abejas euglosinas (Hymenoptera, Apidae) de la Región Neotropical, Listado de especies con notas sobre su biología. *Biota Colombiana*, 3(1): 7-118.
- RAMIREZ S, ROUBIK DW, SKOV C, PIERCE NE. 2010. Phylogeny, diversification patterns, and historical biogeography of euglossine orchid bees (Hymenoptera, Apidae). *Biological Journal of the Linnean Society*, 100(3): 552-572.
- REYES LEDEZMA KY, SANTOS-MURGAS A, GONZÁLEZ P, GÓMEZ IY, BARRIOS-VARGAS A. 2020. Diversidad alpha y beta de abejas Euglossini (Hymenoptera, Apidae) en el dosel y sotobosque del cerro Turega, provincia de Coclé, Panamá. *Tecnociencia*, 22: 205-225.
- RICKLEFS RE, ADAMS RM, DRESSLER RL. 1969. Species diversity of *Euglossa* in Panama. *Ecology*, 50(4): 713-716.
- RIVEROS AJ, HERNÁNDEZ EJ, WCISLO WT. 2009. Nesting Biology of *Euglossa dodsoni* Moure (Hymenoptera, Euglossinae) in Panama. *Journal of the Kansas Entomological Society*, 82(2): 210-214.
- RODRÍGUEZ E, WEBER JM, PAGÉ B, ROUBIK DW, SUÁREZ RK, DARVEAU CA. 2015. Setting the pace of life, membrane composition of flight muscle varies with metabolic rate of hovering orchid bees. *Proceedings of the Royal Society B*, 282(1802): 2014-2232.
- ROUBIK DW. 1989. Ecology and natural history of tropical bees. New York: Cambridge University Press. 514 p.
- ROUBIK DW. 1990. A mixed colony of *Eulaema* (Hymenoptera, Apidae), natural enemies, and limits to sociality. *Journal of the Kansas Entomological Society*, 63(1): 150-157.
- ROUBIK DW. 1993. Tropical pollinators in the canopy and understory, field data and theory for stratum "preferences". *Journal of Insect Behavior*, 6: 659-673.
- ROUBIK DW. 1998. Grave-robbing by male *Eulaema* (Hymenoptera, Apidae), implications for euglossine biology. *Journal of the Kansas Entomological Society*, 71(2): 188-191.
- ROUBIK DW. 2001a. Searching for genetic pattern in orchid bees, a reply to Takahashi et al. *Evolution*, 55(9): 1900-1901.
- ROUBIK D.W. 2001b. Ups and downs in pollinator populations, when is there a decline? *Conservation Ecology*, 5(1): 2.
- ROUBIK DW, ACKERMAN J.D. 1987. Long-term ecology of euglossine orchid-bees (Apidae, Euglossini) in Panama. *Oecologia*, 73(3): 321-333.
- ROUBIK DW, ACKERMAN JD, COPENHAVER C, SMITH BH. 1982. Stratum, tree, and flower selection by tropical bees, implications for the reproductive biology of outcrossing *Cochlospermum vitifolium* in Panama. *Ecology*, 63(3): 712-720.
- ROUBIK DW, BASSET Y, LOPEZ Y, BOBADILLA R, PEREZ F, RAMÍREZ JA. 2021. Long-term (1979–2019) dynamics of protected orchid bees in Panama. *Conservation Science and Practice*, 3(12): e543.
- ROUBIK DW, HANSON PE. 2004. Abejas de orquídeas de la América tropical, Biología y guía de campo. Heredia, Costa Rica: Editorial INBio. 370 p.
- ROUBIK DW, KNUDSEN JT. 2017. An embellishment that became a mutualism, Inquiries on male bee tibial bouquets and fragrance-producing orchids in Panama and oceanic islands (Apidae, Apinae, Euglossini, Orchidaceae, Epidendroideae). *Flora*, 232: 117–127.
- ROUBIK DW, MORENO JE. 2021. Pollen used by euglossines, Fighare, Panama City, Smithsonian Tropical Research Institute. [Online]. [Downloaded 31 August 2024]. Available: https://smithsonian.figshare.com/articles/figure/Euglossini_Pollen/14823660/1
- ROUBIK DW, WEIGHT LA, BONILLA MA. 1996. Population genetics, diploid males, and limits to social evolution of euglossine bees. *Evolution*, 50(2): 931–935.
- ROUBIK DW, YANEGA D, BUCHMANN SL, INOUE DW. 1995. On optimal nectar foraging by some tropical bees (Hymenoptera, Apidae). *Apidologie*, 26(3): 197–211.
- SALEH NW, RAMÍREZ SR. 2019. Sociality emerges from solitary behaviors and reproductive plasticity in the orchid bee *Euglossa dilemma*. *Proceedings of the Royal Society B*, 286: 20190588.
- SANTOS A. 2014. Monitoreo de abejas de las orquídeas (Hymenoptera, Apidae) en el parque Nacional Darién, República de Panamá. *Centros*, 3(2): 121–142.
- SANTOS MURGAS A, ABREGO J, LÓPEZ CHOG, MONTEZA C, OSORIO M, GUARDIA R, ÁLVAREZ E, QUIROZ K, AÑINO Y, CARRANZA BR, VILLARREAL C. 2018. Abejas de las orquídeas (Hymenoptera, Apidae, Euglossini) del Parque Nacional Darién, Panamá. *Tecnociencia*, 20(2): 59–69.
- SANTOS MURGAS A, ABREGO J, AÑINO Y, LÓPEZ O. 2016. Notas sobre depredación de *Apiomeris hirtipes* Hemiptera, Reduviidae sobre abejas de la orquídea Apidae, Euglossinae. *Revista Científica Centros*, 5(2): 46–52.
- SANTOS MURGAS A, CHONG OGL, ARGUELLO RIS. 2011. Estratificación vertical de las abejas de las orquídeas Euglossinae en un bosque tropical húmedo, monte fresco, Cerro Azul, Panamá. *Tecnociencia*, 13(2): 99–108.
- SANTOS MURGAS A, MUÑOZ R, MEDIANERO E, OSORIO-ARENAS MA, CARRANZA R. 2012. Abejas de las orquídeas Hymenoptera, Apidae, Euglossini en la

- Comarca Guna de Madungandí, Provincia de Panamá, Panamá. *Scientia*, 22(2): 77–91.
- SANTOS MURGAS A, AÑINO RAMOS YJ. 2016. Contribución al conocimiento de la diversidad de abejas de las orquídeas Apidae, Euglossini de la Península de Azuero, Panamá. *Tecnociencia*, 18(2): 45–58.
- SCHIELTL FP, ROUBIK DW. 2003. Odor compound detection in male euglossine bees. *Journal of Chemical Ecology*, 29(1): 253–257.
- SOPER DM, EKROTH AKE, MARTINS MJF. 2021. Direct evidence for increased disease resistance in polyandrous broods exists only in eusocial Hymenoptera. *BMC Ecology and Evolution*, 21(189): 1–10.
- SOUCY SL, GIRAY T, ROUBIK DW. 2003. Solitary and group nesting in the orchid bee *Euglossa hyacinthina* (Hymenoptera, Apidae). *Insectes Sociaux*, 50(3): 248–255.
- SUÁREZ RK, DARVEAU CA, WELCH JR KC, O'BRIEN DM, ROUBIK DW, HOCHACHKA PW. 2005a. Energy metabolism in orchid bee flight muscles, carbohydrate fuels all. *Journal of Experimental Biology*, 208(18): 3573–3579.
- SUÁREZ RK, DARVEAU CA, HOCHACHKA, PW. 2005b. Roles of hierarchical and metabolic regulation in the allometric scaling of metabolism in Panamanian orchid bees. *Journal of Experimental Biology*, 208(18): 3603–3607.
- TAKAHASHI NC, PERUQUETTI RC, DEL LAMA MA, DE OLIVEIRA CAMPOS LA. 2001. A reanalysis of diploid male frequencies in euglossine bees (Hymenoptera, Apidae). *Evolution*, 55: 1697–1699.
- TARPY DR. 2003. Genetic diversity within honeybee colonies prevents severe infections and promotes colony growth. *Proceedings of the Royal Society B*, 270(1510): 99–103.
- VEGA-HIDALGO Á, AÑINO Y, KRICHILSKY E, SMITH AR, SANTOS-MURGAS A., GÁLVEZ D. 2020. Decline of native bees (Apidae: Euglossa) in a tropical forest of Panama. *Apidologie*, 51(6): 1038–1050.
- WIKELSKI M, MOXLEY J, EATON-MORDAS A, LOPEZ-URIBE M.M., HOLLAND R, MOSKOWITZ, D., KAYS, R. 2010. Large-range movements of neotropical orchid bees observed via radio telemetry. *PLoS One*, 5(5): e10738.
- WILLIAMS NH, DRESSLER RL. 1976. Euglossine pollination of *Spathiphyllum* (Araceae). *Selbyana*, 1(4): 349–356.
- ZAYED A, ROUBIK DW, PACKER L. 2004. Use of diploid male frequency data as an indicator of pollinator decline. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 271(suppl_3): S9–S12.
- ZIMMERMAN JK, AIDE TM. 1989. Patterns of fruit production in a neotropical orchid, pollinator vs. resource limitation. *American Journal of Botany*, 76(1):67–73.
- ZIMMERMAN JK, MADRIÑÁN S. 1988. Age structure of male *Euglossa imperialis* (Hymenoptera, Apidae, Euglossini) at nectar and chemical sources in Panama. *Journal of Tropical Ecology*, 4(3): 303–306.
- ZIMMERMANN Y, ROUBIK DW, ELTZ T. 2006. Species-specific attraction to pheromonal analogues in orchid bees. *Behavioral Ecology and Sociobiology*, 60(6): 833–843.