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ORIGINAL ARTICLE

Long-term comparison of the orchid bee community in the tropical dry forest of Costa Rica

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Abstract

Global bee decline and its impact on pollination in agricultural and natural ecosystems have attracted public attention. However, more data are needed to show their generality and intensity in different ecosystems, especially in the tropics. For centuries, the tropical dry forest (TDF) of Costa Rica underwent intense deforestation, but in the last four decades, a large part of this forest has entered a recovery process. Using data of orchid bees generated by Janzen et al. (*Ecology*, 63, 66) in TDF in the Santa Rosa sector of the Guanacaste Conservation Area (ACG), we posed a general question: What changes have occurred in diversity, composition, and seasonality of the euglossine bee community in the TDF during the last 40 years and how are these changes related to the current recovery of this forest. We sampled euglossine bees during 2018–2019 using methods similar to those applied previously. To characterize the response of euglossine bees to habitat loss, we extended the sampling to pastures adjacent to the protected area. With the loss ($n = 4$) and gain ($n = 3$) of bee species, we did not find significant changes in overall species richness between now and 40 years ago. However, the composition of the euglossine community in the protected area in 1977 was more similar to that found in current pastures than to the current community in forests, where the presence of forest-dependent species has been favored. It is possible that TDF regeneration in Santa Rosa has led to changes in the composition of the community of these bees.

Abstract in Spanish is available with online material.

KEYWORDS
bee decline, biodiversity, climate change, euglossine, habitat loss, land-use change, pollinators, species richness

1 | INTRODUCTION

Alarming news about global bee decline has recently attracted the attention of governments, the private sector, and the general public (Goulson et al., 2015; LeBuhn & Vargas, 2021; NRC, 2007; Potts et al., 2010; Wagner, 2020; Wilson et al., 2017). This concern is based on the role of bees as important pollinators of crops and therefore the large economic and ecological impacts that the loss of these organisms would have (Gallai et al., 2009; Klein et al., 2007; Kremen et al., 2002; Michener, 2007; Ricketts et al., 2008). Although several studies have shown a reduction in bee populations, the evidence comes principally from studies on honey bees (*Apis mellifera*) (Ellis et al., 2010; Kulhanek et al., 2017; Potts et al., 2010) and bumblebees (*Bombus* spp.) (Cameron et al., 2011; Colla & Packer, 2008; Grixti et al., 2009; Jacobson et al., 2018; Kosior et al., 2007). Some studies in Europe and the United States have included other bee species, but they have not shown a clear pattern, since populations of some species have decreased, while others have remained stable or even increased (Bartomeus et al., 2013; Biesmeijer et al., 2006; Herrera, 2019; Hofmann et al., 2018; Kammerer et al., 2021; Mathiasson, & Rehan, 2019; Ollerton et al., 2014; Van Dooren, 2019; Winfree et al., 2009). The tropics have been poorly studied, despite their high bee diversity. The few long-term (multiyear) studies performed in this region have shown an apparent decrease, not only in species richness but also in abundance (Frankie et al., 2009; Martins et al., 2013; Vega-Hidalgo et al., 2020), although some studies have not shown a clear decline (Nemésio et al., 2015; Roubik, 2001; Roubik & Ackerman, 1987).

Bee decline has multiple drivers, such as pesticides, pathogens, and global warming, but habitat loss has been identified as the main cause (Goulson et al., 2015; Kremen et al., 2002; Sánchez-Bayo & Wyckhuys, 2019; Williams et al., 2010; Winfree et al., 2009). Among tropical ecosystems, tropical dry forest (TDF) is one of the most endangered vegetation types on the planet (Gerhardt & Hytteborn, 1992; Janzen, 1988; Miles et al., 2006). For centuries, the TDF of Costa Rica underwent intense deforestation (Janzen, 2000), but in the last four decades, a large part of this forest has entered a recovery process (Alberta-CCT, 2002; Arroyo-Mora et al., 2005; Calvo-Alvarado et al., 2009; CIEDES-CCT-CI, 1998; Tapia, 2016; Figure S1). During the period of greatest deforestation, Janzen et al. (1982) monitored seasonal changes in male euglossine bee diversity between 1977 and 1979 in Santa Rosa National Park, now known as the Santa Rosa sector of the Guanacaste Conservation Area (ACG, in Spanish). A comparison of current euglossine bee diversity with that observed in the past may help us to understand the effects of habitat change on the bee community.

Euglossine bees (Apidae: Apinae), also known as orchid bees, are restricted to the Neotropics (Nemésio, 2009). These bees are characterized by their wide flight range. Therefore, they have been considered important pollinators of plants with scarce and widely dispersed individuals (Dressler, 1982; Janzen, 1971; Pokorny et al., 2015). Euglossine bees obtain several resources from plants, including pollen, nectar, resins, and fragrances (in the specific case of males) (Ramírez et al., 2002). Most euglossine species are associated with humid forests (Brosi, 2009; Dressler, 1982; Nemésio & Silveira, 2006; Silveira et al., 2015), which contrasts with other groups of bees where the greatest diversity is found at xeric sites (Brito, 2017; Michener, 2007). A negative effect of forest loss on taxonomic diversity and phenological patterns has been found (Cândido et al., 2018; Powell & Powell, 1987; Roubik & Ackerman, 1987). However, some euglossine bees can also use early successional and other open habitats, such as pastures (Brosi, 2009; Moreira et al., 2017; Tonhasca et al., 2002). Predictions regarding euglossine bee responses to environmental changes must consider possible differences in life-history traits among species (Cane, 2001; Moreira et al., 2017).

The recent gain in forest cover in the ACG interacts with other factors that can trigger a decline in bees, such as climate change, making this an interesting place to follow the dynamics of the local euglossine bee community. To understand the effect of potential habitat gain on euglossine populations, we addressed the following questions: (a) What changes have occurred in the diversity, composition, and seasonality of the euglossine bee community in the TDF of Santa Rosa during the last 40 years? (b) How are these changes related to the current recovery of the dry forest? To answer these questions, we replicated, as much as possible, the sampling carried out by Janzen et al. (1982) in Santa Rosa. Although Janzen et al. (1982) did not sample pastures, the area was dominated by them; we therefore included disturbed areas outside the protected area of Santa Rosa to address the following questions: (c) Are differences in orchid bee diversity, composition, and seasonality between sites related to forest cover (forest vs. pastures)? (d) Is the bee community of sites within current pastures similar to the community observed in 1977? As habitat loss is one of the main drivers of bee decline and orchid bees are more associated with forested habitats, we expect that by increasing forest cover in the region, there will be an increase in euglossine bee diversity. We expected to observe differences in the diversity, seasonality, and composition of the euglossine community in current forests compared with that observed 40 years ago due to changes in vegetation over the years. In addition, since Santa Rosa was a region dominated by pastures in the past, we expected a greater similarity between the euglossine community in 1977 and that observed in current pastures.

2 | METHODS

2.1 | Study site

We carried out this study during 2018 and 2019 in the Santa Rosa sector of the Guanacaste Conservation Area and adjacent areas in the northwest part of the province of Guanacaste, Costa Rica (10°45′-11°00′N, 85°30′-85°45′W; Figure S2). The Santa Rosa sector is located on a plateau at 300 m a.s.l. This sector is dominated by tropical dry forest (TDF), has an average annual temperature range of 26.6–27.5°C, and receives an average annual rainfall of 1390–1800 mm, with a high degree of annual variation (Gillespie et al., 2000; Janzen, 2000; Magnani, 2018). TDF is characterized by marked seasonality, with six dry months from late December to mid-June, a period when most woody plants lose their leaves (Gillespie et al., 2000; Janzen, 1993). In mature TDF, it is common to find trees such as madroño (*Calycophyllum candidissimum*), madero negro (*Gliricidia sepium*), ojoche (*Brosimum alicastrum*), guácimo macho (*Luehea speciosa*), chicle (*Manilkara chicle*), chaperno (*Lonchocarpus minimiflorus*), and manteco (*Trichilia martiana*) (Powers et al., 2009).

2.2 | Sampling sites

We selected three sites located at 300 m a.s.l. on the Santa Rosa Plateau sampled by Janzen et al. (1982), which were forest fragments surrounded by pastures in 1977–1979 and that today are embedded in a continuous forest matrix. The original forest fragments were composed of a deciduous regenerating secondary forest (first site) a semievergreen forest (second site), and the third was an oak forest (Janzen et al., 1982). At present, these sites preserve their original vegetation types but have continuous forest cover composed of a mosaic of old and secondary growth (Figure S2). To determine the effect of forest cover on the euglossine bee community and the species better adapted to altered habitats, three sampling sites outside the protected area were included in this study. These sites were dominated by a mosaic of cattle pastures and small forest fragments near the protected area. The first site was located 5.5 km from the limits of the Santa Rosa sector, near the Inter-American Highway intersection with Quebrada Grande. The second site was in the Las Melinas neighborhood in Cuajiniquil 2.8 km from Santa Rosa, and the third site was located in Hacienda Rosa María 1.5 km south of the Casona de Santa Rosa, approximately 500 m away from the protected area (Figure S2). These sites were at approximately the same altitude as the forest sites. Bee collections were obtained using the same methods and during the same time intervals in all locations. The sites located outside the protected habitats will be called “pasture-dominated sites.”

2.3 | Bee sampling

We used the male population as a representative of the general population of euglossine bees. Males are easy to sample because they collect fragrances, which can be used to attract them to specific sites (Roubik & Hanson, 2004). Sampling was performed during the years 2018–2019 (four sampling periods per year, see below). We sampled during the same months as in the previous study (Janzen et al., 1982): in the middle of the dry season (March) and beginning, middle, and end of the rainy season (June, August, and December, respectively). We maintained the same sampling effort used by Janzen et al. (1982), one day at each sampling site (three in forests and three in pastures). In their study, the three chosen sites were sampled on a single day simultaneously. We sampled each site separately because instead of collecting all bees attracted to the fragrances, as was performed in the previous study, we did not collect the bees that we could identify to the species level in the field. We sampled from 0700 h to 1100 h using the same five chemical attractants: cineol, eugenol, methyl cinnamate (solid dissolved in 95% ethanol), benzyl acetate, and methyl salicylate, purchased from Sigma-Aldrich, with 99% purity (the purity was not specified in the previous study). In Janzen et al. (1982), heavy blotter paper was used to expose the attractants, while we used 5-cm-diameter balls of surgical cotton (100% pure) on which to place 3 ml of each attractant (cotton was used to facilitate capture). Due to the volatilization of the attractants, at 0900 h, we again moistened the cotton with 3 ml of attractant. Janzen et al. (1982) did not specify the amount of attractant used, but we assume it was at the saturation point. These baits were placed 1.5 m above the ground hanging from branches of trees or shrubs as in the previous study and uniformly monitored approximately every 10 min. In the case of pastures, we used living fences from which to hang the cotton balls.

Unlike the previous study, we identified most species in the field with a 40×, 25 mm hand lens and then released them. To avoid recounting the same individual, we marked bees on the wing with a permanent fine-tip marker using different colors for each sampling site. In this way, we were able to detect recaptured bees during the same sampling period. Due to the difficulty of accurately assessing some characteristics, such as the mid-tibial tufts, individuals of some species (e.g., *Euglossa variabilis*, *Euglossa townsendi*, and *Euglossa heterosticta*) were vouchered for laboratory identification. For bee identification, we used the keys in "Orchid bees of Tropical America" (Roubik & Hanson, 2004). The 4 genera are abbreviated as follows: *Euglossa* = Eg., *Eulaema* = El., *Exaerete* = Ex. and *Eufriesea* = Ef. The most important taxonomic change is that the species previously reported as *Euglossa viridissima* is currently recognized as *Euglossa dilemma* in Costa Rica (Eltz et al., 2011). We deposited the collected bees in the Zoology Museum of the University of Costa Rica (Museo de Zoología, MZUCR).

2.4 | Statistical analysis

We tabulated the abundance of each species by season for each sampling site and year. To prepare statistical tests and comparative graphs, we used the R program (R Core Team, 2019) and specific packages that are mentioned in each analysis. During 2018, we sampled for two consecutive days at each site during each sampling period to consider the daily variation in the same season. We did not observe significant changes in species richness and abundance between days (Table S1); therefore, statistical analysis used only data from the first sampling day at each site. To compare the alpha diversity of the current euglossine bee community (2018–2019) at forest and grassland sites with the diversity observed 40 years ago, we calculated rarefaction curves with the first two orders of Hill numbers (q) (Hill, 1973). Janzen et al. (1982) did not provide per-site data but only data summed per month. We also pooled the data from each site and therefore had one dataset per month, four per year, for each habitat type (forest or pastures). In Hill numbers, the first order ($q = 0$) indicates species richness, in which the abundance of individuals does not matter; the second order ($q = 1$) is the effective number of typical species, with each species having a weight proportional to its abundance (Chao et al., 2014). For this analysis, we used the *iNEXT* package to plot rarefaction/extrapolation curves for each order of Hill numbers using the bootstrap method. With this curve, we obtained a rarefied number of species (small samples) based on the reference sample and species number observed. The extrapolated number of species (large samples) is determined at the same time for increased sample size to determine the number of species present in the assemblage but not detected in the sampling (Chao et al., 2014; Hsieh et al., 2016). To study the effects of the year (1977, 2018, and 2019), habitat (forest or pastures), and month (March, June, August, and December) on the species composition of euglossine bee communities, we carried out a multivariate analysis of variance with permutations (ADONIS) using the Bray–Curtis distance *vegan* package (Oksanen et al., 2019). We also pooled the data of sites, as we did in the previous analysis; therefore, we had four datasets for each year for each habitat (one for each month). Prior to the analysis, the data were standardized to observe the proportional contribution of each species to the composition of the community. For this, we used the *acomp* function from the *compositions* package (van den Boogaart et al., 2021). In the ADONIS analysis, the significance of the effects was tested using an approximate *F*-test, obtained by dividing the mean square distances between and within groups defined by the model effects. We used a nonmetric multidimensional scaling analysis (NMDS) using the isoMDS function from the *MASS* package (Venables & Ripley, 2002) to graph the results. To determine whether there were species associated with a specific habitat type (forests and pastures), we used an indicator species analysis (ISA) from the *indicspecies* package (De Caceres & Legendre, 2009). Data from 2018 and 2019 forests and pastures were used in this analysis. Finally, to test the effects of habitat and season on the abundance of the more common euglossine bee species, we used a generalized linear model with a Poisson distribution, where habitat (forest or pastures) and month (March, June, August, and December) were the main effects. This analysis was repeated for each species with more than 50 individuals in current forests and pastures; we judged that species with smaller sample sizes did not provide sufficient information to test seasonality or habitat effects.

3 | RESULTS

We observed a slight decrease in euglossine species richness, 15 species in 2018, and 14 in 2019, compared with 18 species in 1977 reported by Janzen et al. (1982) (Table S2). In 2018, we found a greater abundance with 1,019 individuals, followed in 2019 by 907, whereas in 1977, Janzen et al. (1982) collected 720 individuals at the same sampling sites. On the other hand, compared with forest sites, we found fewer individuals and fewer euglossine species in pasture-dominated sites. In 2018, we observed 502 bees belonging to 10 species at these sites, while in 2019, we observed 291 individuals distributed in nine species.

In the rarefaction curves, we observed a slight overlap in confidence intervals of the pooled species richness between forest fragments in 1977 and those in 2018 and 2019, indicating that it was not significantly different. However, we observed a trend toward reduced species number and less uniformity in the euglossine bee community for recent years. Also, the pooled euglossine species richness in forests (three sites) was higher than the same figure in pastures (three sites) in 2018 and 2019, which did not show differences between them (Figure 1a). When we gave each species a proportional weight relative to its abundance (*q*1), we did not observe significant differences in the effective number of species between forests from 1977, 2018, and 2019. However, it was greater than that in pastures for both years (Figure 1b). For all years (1977, 2018, and 2019), there was a slight decrease in richness and abundance

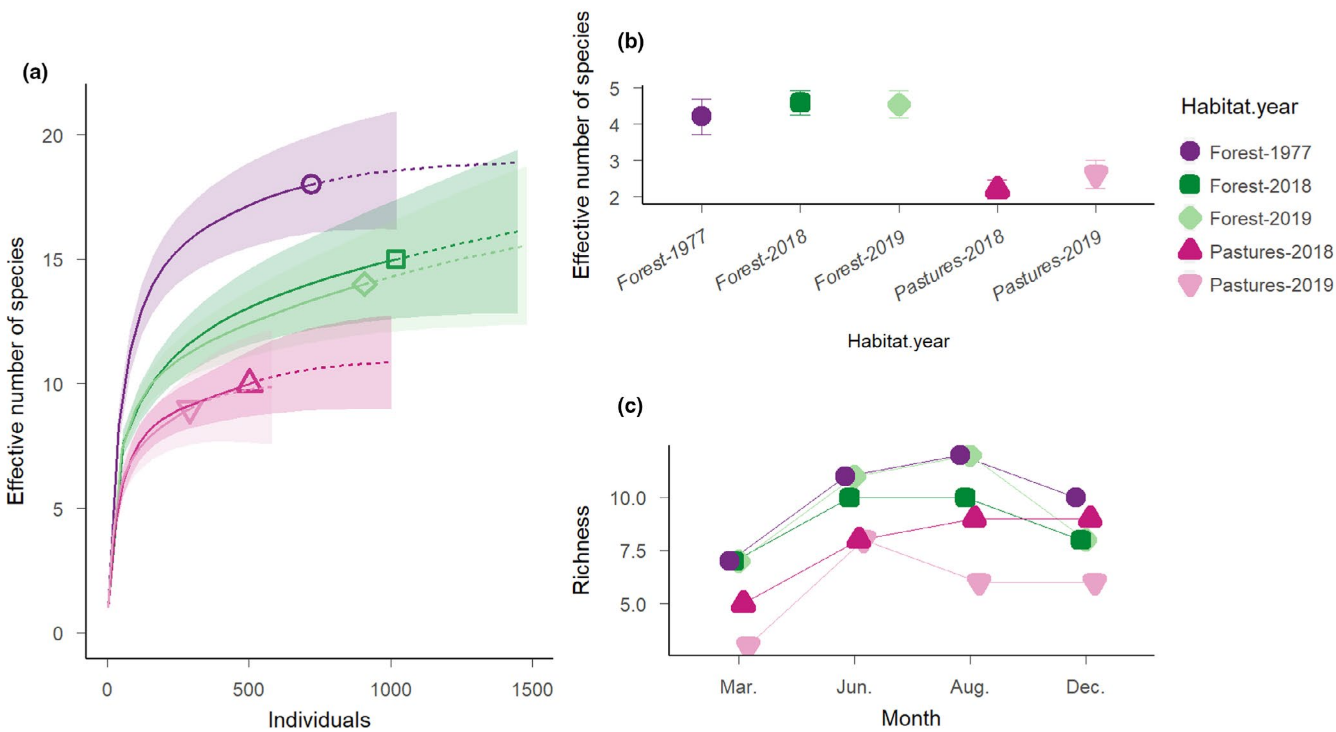

FIGURE 1 Diversity of euglossine bee species in tropical dry forest of Guanacaste Conservation Area, Costa Rica in 1977, 2018, and 2019, as well as that of adjacent pastures in 2018 and 2019. (a) Effective number of all species ($q = 0$) as a function of the number of individuals sampled. The shaded area represents the calculated confidence intervals, the solid lines indicate the observed data, and dotted lines indicate the extrapolation of species richness for 1500 individuals. (b) Effective number of typical species ($q = 1$) and (c) observed species richness by month for each year (1977, 2018, and 2019) and habitat (forest and pastures)

of individuals in the middle of the dry season (March) and a slight increase in general richness and abundance in the early and middle rainy seasons (June and August) (Figure 1c, Table S3).

Four species reported in forest fragments in 1977 did not appear in those same forest sites in 2018 and 2019: *Eg. azureoviridis*, *Eg. bursigera*, *Eg. hansoni*, and *Eg. hemichlora*. However, in 2018 and 2019, we found three species not reported in 1977: an individual of *Eg. allosticta* in both years, one of *Eg. ignita* in 2018, and one of *Eg. sapphirina* in 2019 (Figure 2). In terms of relative abundance, of the nine common species in 1977 (>10 individuals), seven species remained similar or even increased their relative abundance (*Eg. dilemma*, *Eg. variabilis*, *Ex. smaragdina*, *Eg. tridentata*, *Eg. imperialis*, and *Eg. townsendi*), one species became rare (*Eg. mexicana*), and two were not found (*Eg. hemichlora* and *Eg. bursigera*). Of the nine rare species in 1977 (<10 individuals), four remained relatively rare (*Ex. frontalis*, *Eg. igniventris*, *Eg. heterosticta*, and *Ef. schmitiana*), two became a little more common (*El. cingulata* and *El. meriana*), one became rarer (*El. nigrita*), and two were not found (*Eg. azureoviridis* and *Eg. hansoni*) (Figure 2).

In both the present and previous study, *Eg. dilemma* was the most abundant species. The next most abundant species in 1977 was *Eg. hemichlora* (not found in the present study) and *Eg. variabilis*, which together with *Eg. dilemma* represented 80% of all individuals collected at that time (Figure 2). For 2018 and 2019, *Eg. dilemma*, *Eg. imperialis*, and *Eg. tridentata* were the most abundant species, contributing 82% to the total species in 2018 and 84% in 2019. At pasture-dominated sites, we again found that *Eg. dilemma* was the most abundant species followed by *Eg. tridentata* and *Eg. variabilis* in 2018, the order of these last two being reversed in 2019, which together represented almost 90% of all individuals for both years (Figure 2).

The ADONIS analysis showed that habitat type and year affected euglossine community composition ($F = 6$, $R^2 = .57$, $df = 4$, $p = .001$). The forest euglossine community in 1977 was more similar to the pasture communities in 2018 and 2019 (Figure 3). These results were caused lower frequencies in 1977 forests and current pastures of species that were especially abundant in 2018–2019 forests (*Eg. imperialis*, *Ex. smaragdina*, and *El. meriana*) (Figure 2). These results were consistent with indicator species analysis, where *Eg. imperialis* ($A = 0.97$, $B = 1$, IndVal $= 0.98$, $p = .001$), *Ex. smaragdina* ($A = 0.94$, $B = 0.75$, IndVal $= 0.84$, $p = .003$) and *El. meriana* ($A = 0.91$, $B = 0.58$, IndVal $= 0.73$, $p = .029$) could be used as indicator species of forest habitats in 2018 and 2019. For example, when we broke down the components of the *Eg. imperialis* indicator value, we could see that if we found *Eg. imperialis* at a site, the probability that it was a forest was 97% (*A*), while if we were at a site previously classified as a forest, the probability of finding *Eg. imperialis* was 100% (*B*). The rest of the species did not seem to be specifically associated with any type of vegetation cover in 2018 and 2019.

Regarding the seasonality of the euglossine bee community, we observed that community composition did not change with month ($F = 1.94$, $R^2 = .14$, $df = 3$, $p = .078$; Figure 3). *Eg. dilemma* was the most abundant species in all seasons and years, but the rest of the species did not show a clear pattern in the years studied. However, the most abundant species in forests in 2018 and 2019 showed a different pattern of seasonality: The peak abundance for *Ex. smaragdina* was March, while *Eg. dilemma*, *Eg. tridentata*, and *Eg. variabilis* were more abundant in August; and *El. meriana* showed greater abundance in June and *Eg. imperialis* abundance increased in December (Figure 4, Table 1). The seasonality patterns of these species were much less pronounced in pasture-dominated sites (Figure 4).

4 | DISCUSSION

We found that between 1977 and the 2018–2019 period, the number of orchid bee species decreased slightly (three fewer species in 2018 and four in 2019), which represents a 15% reduction in the number of species observed 40 years ago. However, new rare species were detected in 2018–2019. Although we observed a tendency for reduced evenness and species richness, rarefaction analysis of species diversity showed that the difference between sampling periods was not significant. These results were not expected based on the increase in forest cover in the region since 1977. Two long-term studies carried out in large protected areas where the forest

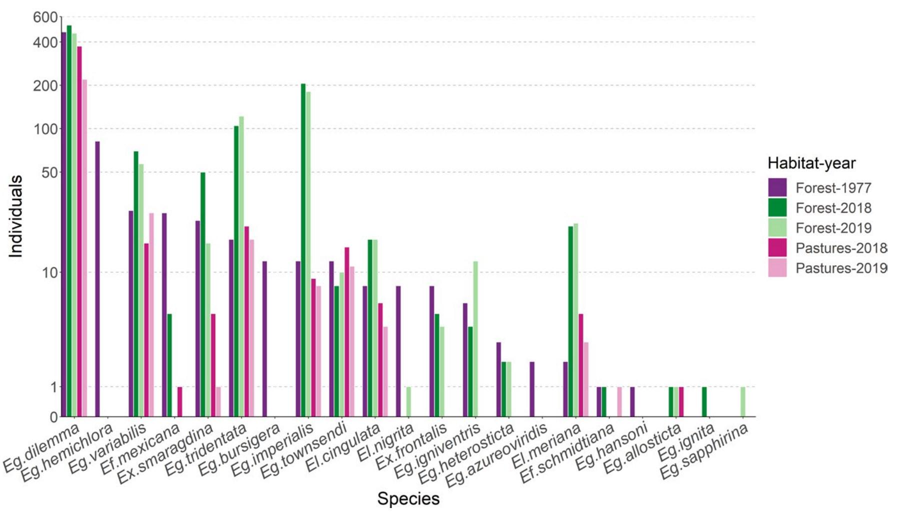

FIGURE 2 Individuals of each euglossine bee species found in the forests in 1977 and forests and pastures in 2018 and 2019 in the tropical dry forest of Costa Rica in the ACG protected area. Species ordered from largest to smallest number of individuals for 2018 and 2019. Note that the *y*-axis shows the original abundances but on a pseudologarithmic scale

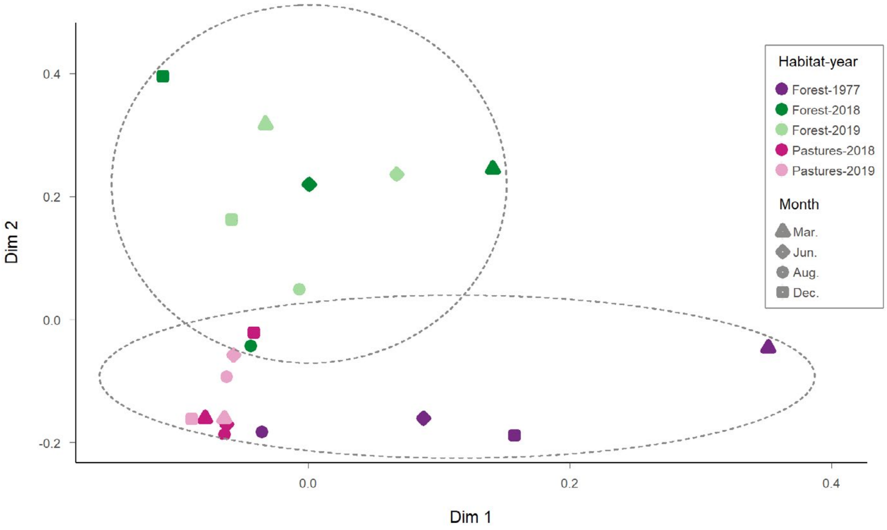

FIGURE 3 Nonmetric multidimensional scaling (nMDS) using Bray–Curtis distance for the euglossine bee community composition in 1977, 2018, and 2019 in the tropical dry forest in the Guanacaste Conservation Area, Costa Rica ($k = 3$, stress = 4.45). Point colors represent the combinations of habitat and year, and point shapes represent the month of the year

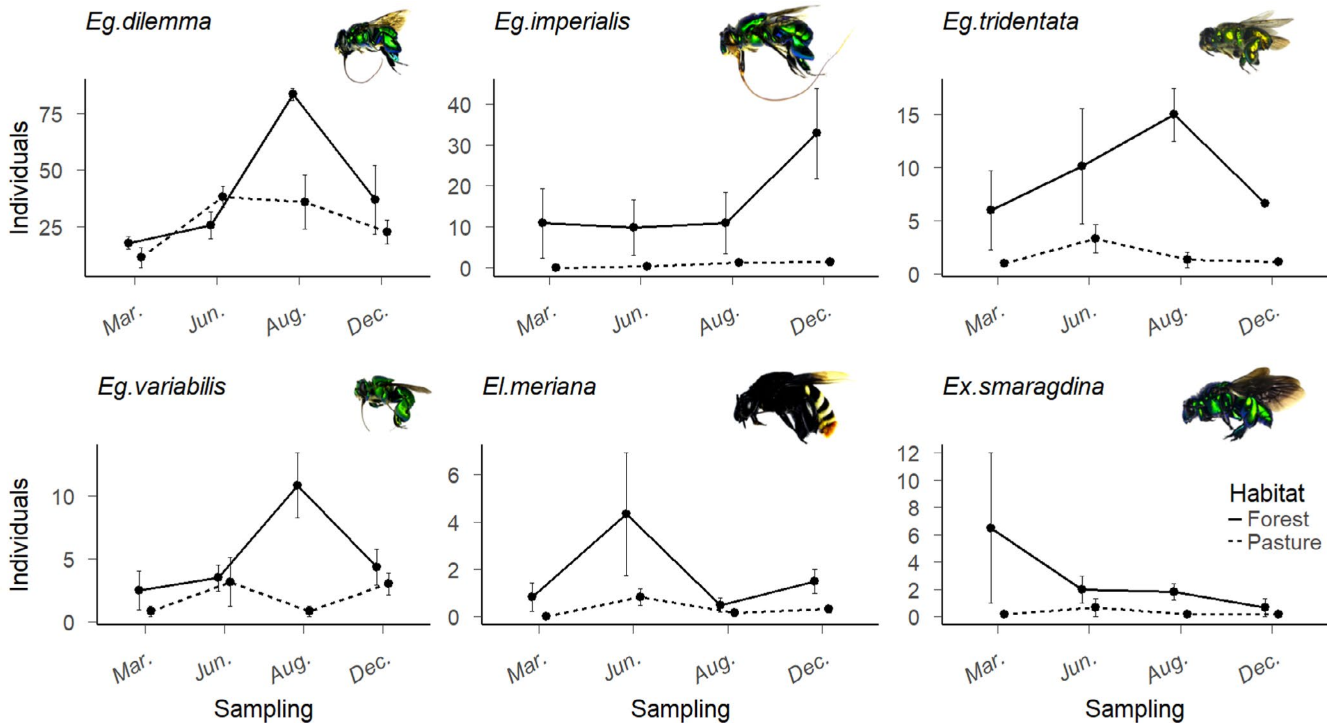

FIGURE 4 Average seasonal abundance (±SE) for the six more abundant euglossine bee species in forests (solid line) and pastures (dotted line) during 2018 and 2019 in the tropical dry forest in the Guanacaste Conservation Area, Costa Rica

remained stable also revealed that orchid bee populations showed long-term stability compared with other groups of insects (Roubik, 2001; Roubik & Ackerman, 1987). In contrast, Vega-Hidalgo et al. (2020) demonstrated that even in areas without evident human pressures, this group of bees showed a strong population decline. Nemésio et al. (2015) also carried out a long-term study in forest fragments of Belo Horizonte, southeastern Brazil. In a span of 7 years, they showed that the euglossine bee community remained stable due to the conservation of these fragments. It should be noted that the euglossine community of the Santa Rosa forest did not suffer a strong loss of euglossine bee diversity, as was observed in the present pasture-dominated areas. Small fragments today are part of a continuous forest matrix and could prevent the extensive loss of bee diversity and mitigate negative factors such as climate change, invasive bee species, and pesticide use (Chapagain, 2011; Moritz et al., 2005; Paini, 2004; Roubik et al., 1986).

Although there was only a small change in species richness, our results show changes in the composition of the euglossine community in the TDF of Santa Rosa. Four species from 1977 did not appear in the recent census, but we found three species not reported in 1977. For instance, *Eg. hemichlora* was the second most abundant species in 1977, but it was absent in the current study. This species is distributed from México to Colombia (Ramírez et al., 2002; Roubik & Hanson, 2004). Although *Eg. hemichlora* appears in

TABLE 1 Coefficients of the effects of habitat and sampling month on the number of bees captured with chemical attractants for six dominant species of euglossine bees from the tropical dry forest of Costa Rica in 2018 and 2019. The coefficient, intercept, *Z* value, and significance of the coefficient (*Z*-test) are shown. The intercept represents the basal level in March in the forest habitat

		Month			Habitat
Species	Intercept	June	August	December	Pastures
Eg. dilemma					
Estimated	2.89	0.35	1.53	0.71	−0.43
Z	21.24	2.00	10.21	4.28	−2.00
p	**<.001**	**.046**	**<.001**	**<.001**	**.046**
Eg. imperialis					
Estimated	2.38	−0.09	0.09	1.13	−3.48
Z	13.58	−0.38	0.36	5.63	−8.40
p	**<.001**	.706	.718	**<.001**	**<.001**
Eg. tridentata					
Estimated	1.77	0.67	0.83	0.09	−1.67
Z	8.01	2.49	3.16	0.30	−7.04
p	**<.001**	**.013**	**.001**	.763	**<.001**
Eg. variabilis					
Estimated	0.97	0.65	1.16	0.74	−0.95
Z	3.16	1.74	3.35	2.01	−4.06
p	**.001**	.082	**.001**	**.044**	**<.001**
El. meriana					
Estimated	−0.50	2.08	−0.69	0.69	−2.35
Z	−0.70	2.77	−0.57	0.80	−3.18
p	.48	**.005**	.571	.423	**.001**
Ex. smaragdina					
Estimated	1.84	−0.92	−1.20	−2.30	−2.83
Z	8.10	−2.19	−2.59	−3.10	−3.89
p	**<.001**	**.028**	**.010**	**.002**	**<.001**

Bold indicates statistically significant *p*-value ($p<.05$).

some species inventories, and aspects of its mating behavior and nest architecture have been described (Ackerman, 1989; Eltz et al., 2003; Murgas et al., 2018; Parra & Nates-Parra, 2009; Zimmermann et al., 2009), we did not find any information to help explain why we did not observe this species. Although we are confident that we did not overlook *Eg. hemichlora*, further sampling is needed to confirm this puzzling absence. Some studies have argued that species at the edge of their climatic distribution are more prone to decline (Arbetman et al., 2017; Williams, 2005). This could apply to the absence of the other three species in the current study (*Eg. bursigera*, *Eg. hansoni* and *Eg. azureoviridis*), for which Costa Rica is the northern limit of their distribution (Ramírez et al., 2002; Roubik & Hanson, 2004).

As we hypothesized, the euglossine community in current pastures is more similar to the community found in 1977 forest fragments, which today are embedded in a continuous forest matrix. Both the 1977 forest fragments and current pastures had similar abundances of species, such as *Eg. variabilis*, *Eg. townsendi*, and *Eg. dilemma*. In the case of *Eg. townsendi*, Cândido et al. (2018) observed that it can be found even in small forest patches. It has also been observed that *Eg. dilemma* prefers hot, dry environments, and survives at highly degraded sites (Eltz et al., 2011; Zimmermann et al., 2011).

On the other hand, we found that *Eg. imperialis*, *El. meriana*, and *Ex. smaragdina* were closely associated with current forest fragments. In reference to *Eg. imperialis*, this has been previously proposed as a bioindicator of forests (Mateus et al., 2015; Rosa et al., 2015). For *Ex. smaragdina*, we did not find information on its response to habitat loss. However, this species is a kleptoparasite mainly of *El. nigrita* (Gárofalo & Rozen, 2001; Silva, 2009). *El. nigrita* has been associated with open sites such as savannas (Silveira et al., 2015; Tonhasca et al., 2002), but in our study, it was represented by only a single individual. In the absence of *El. nigrita*, *Ex. smaragdina* could use *El. meriana* as an alternative host (Nemésio & Silveira, 2006; Silva, 2009), a common species in our study. Also, *El. meriana* is the main host for *Ex. frontalis*, the latter having remained the same compared with 40 years ago.

With fewer floral resources, higher temperature, and lower humidity in open places such as pastures, these habitats are avoided by many forest bee species (Cândido et al., 2018; Morato, 1994; Tonhasca et al., 2002). It has been proposed that larger bee species with high flight capacity should be less affected by fragmentation and habitat loss (Greenleaf et al., 2007). In the present study, the three most abundant euglossine species in pastures were small, while the three forest indicator species were the largest species found. Similar results were observed previously in other studies, where the smallest bees were found in disturbed areas dominated by crops, while the largest bees were not found outside the forest (Milet-Pinheiro & Schlindwein, 2005; Rosa et al., 2015). We found that large euglossine species avoided fragrance baits located near a forest border (Rosa María Ranch, the nearest pasture sampling site to the Santa Rosa sector, see Figure 2), which suggests that some euglossine bee species avoid open areas. Alternatively, territory fidelity by male euglossine bees might explain species composition changes over short distances in response to vegetation changes (Armbruster, 1993; Coswosk et al., 2018; Pokorny et al., 2015).

We observed a seasonal change in the abundance of some euglossine bee species in the TDF, as also noted 40 years ago (Janzen et al., 1982). In 2018 and 2019, most species increased their abundance during the middle of the rainy season (August), while in 1977, the peak occurred at the end of the rainy season (December). Other studies have observed similar patterns, where the greatest diversity of euglossine bees occurs in the rainy season, a pattern associated with the variation in the amount and type of floral resources throughout the year (Andrade-Silva et al., 2012; Dressler, 1982; Frankie et al., 1983; Ramírez et al., 2015). Janzen et al. (1982) proposed that the seasonal fluctuation in euglossine diversity is due to the movement of bees from lowland dry forests to humid highland forests, pursuing resources available in wet habitats. Others have proposed that abundance changes are instead due to bees' synchronous emergence and not to mass migration (Ackerman, 1983; Roubik & Ackerman, 1987). Seasonal fluctuations of euglossine bee populations can also be affected by climate change, since the latter can affect the availability of plant resources, as well as bee phenology, for example, the length of larval development, voltinism, and diapause (Forrest et al., 2015).

We observed a loss of three or four euglossine bee species in the TDF of Santa Rosa compared with 40 years ago, which could be considered a reduction. However, it is also necessary to highlight the limitations of this comparison. First, in terms of methodology, the two studies used very similar methods, but they were not exactly the same. In Janzen et al. (1982), all individuals were collected and vouchered. Here, nearly all the bees were captured and then released. We selected this method because using baits removes an unnecessary number of orchid bees. We also note that because we had a low number of replicates, we are unable to draw strong conclusions regarding orchid bee population trends in Santa Rosa.

There were changes in bee community structure, such as species replacement (including one of the most abundant species in 1977), with the relative increases in forest-dependent species. These changes in community structure and the similarity between the forest bee community in 1977 and the pasture samples in 2018–2019 agree with our initial hypothesis regarding the possible effect of forest recovery on the bee community. The expansion of secondary forests in Santa Rosa since 1977 has favored forest-associated euglossine species, but has also offset the effects of other factors of decline by keeping species richness more or less stable. Although none of the euglossine species reported here is endemic to TDF, the euglossine bee community structure and composition are unique. Euglossine bees play an important role in TDF, especially by pollinating many plant species with large-bee flower pollination syndrome (Frankie et al., 1983). Today, only 1.7% of the original TDF of Central America is under protection and the habitat is greatly threatened by climate change (Calvo-Alvarado et al., 2009; Griscom & Ashton, 2011; Janzen & Hallwachs, 2019). Monitoring changes in the bee community and other indicator taxa is therefore valuable to document the effects of conservation efforts.

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CONFLICTS OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.qfttdz0jk (Bravo et al., 2021).

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