#### FORESTGEO ARTHROPOD INITIATIVE ANNUAL REPORT 2021

#### Program coordinator: Yves Basset, Smithsonian Tropical Research Institute (STRI), bassety@si.edu

#### I. BACKGROUND AND PARTICIPATING FORESTGEO SITES

The 'ForestGEO Arthropod Initiative' aims at monitoring key arthropod assemblages over long-term and studying insect-plant interactions over the network of the Forest Global Earth Observatories (ForestGEO, <u>https://forestgeo.si.edu/research-programs/arthropod-initiative</u>). The Initiative integrates with ongoing monitoring of plant dynamics within the ForestGEO network, causes minimum possible impact to the plots and focus on a priority set of assemblages chosen for their ecological relevance, taxonomic tractability and ease of sampling. At each participating ForestGEO site, the first years of the program are usually devoted to a 'baseline' survey. The baseline survey is followed by longer-term programs of field work and analysis, organized into two main sub-programs: monitoring, and key interaction studies. The monitoring sub-program is directed to detecting long-term changes, as reflected in priority assemblages, driven by climatic cycles, climatic change and landscape scale habitat alteration. Monitoring protocols are derived from those used during the baseline survey. The food web approach of interaction studies targets interactions between plants and specific insect assemblages, with different protocols than those used for monitoring.

So far, the Arthropod Initiative involves seven ForestGEO sites: Yasuni in Ecuador, Barro Colorado Island (BCI) in Panama, Khao Chong (KHC) in Thailand, Tai Po Kau (Hong Kong), Dinghushan and Xishuangbanna (XTBG) in China and Wanang (WAN) in Papua New Guinea. At BCI, four full-time research assistants were in charge of arthropod monitoring protocols in 2020: Filonila Perez, Ricardo Bobadilla, Yacksecari Lopez and Alejandro Ramirez. The program coordinator, YB, doubled as BCI site supervisor. Greg Lamarre (University of South Bohemia) is research associate at STRI and collaborate on most projects based in Panama. The collections and staff of the ForestGEO Arthropod Initiative in Panama are based at the Tupper complex.

Most of the insect monitoring at KHC in 2021 was under the responsibility of Montarika Panmeng (Tim), Manat Reungaew (Jeen), Phiengruthai Suwanbandit (Kae), who replaced Kanyakarn Sripila (Tong), Sontaya Promchaisri (Mos), Sutipun Putnaul (bell) and Tassanai Kaewyod (Est). Many thanks Kae for your dedicated and efficient work during these past years. Supervision at KHC was assured by Sarayudh Bunyavejchewin, Nantachai Pongpattananurak, (Kasetsart University, Bangkok), Watana Sakchoowong (Thai National Parks Wildlife and Plant Conservation Dept) and YB. At WAN, Francesca Dem (Binatang Research Centre), Vojtech Novotny (Czech Academy of Sciences and University of South Bohemia) and YB supervised assistants Roll Liplip, Ruma Umari, Fidelis Kimberg and Ananias Kamam, who were in charge of ForestGEO protocols.

In 2021, the covid pandemic affected again insect monitoring at these sites. On BCI, monitoring was performed with the usual schedule but was delayed as STRI did not operate most of the year at full capacity. However, the integrity and continuity of the BCI data were preserved. At KHC, the pandemic also disrupted normal operations, but data were also preserved, while operations were mostly normal at WAN.

# **II. TAXONOMIC STUDIES AND DNA BARCODING**

David Donoso (Escuela Politécnica Nacional, Ecuador) continued working on BCI ants, which amount to nearly 400 species. Alejandro Ramirez is improving the taxonomy of the reduviids of BCI as part of his MSc at the University of Panama. Apart from this, most of the taxonomic efforts in 2021 focused on cleaning data obtained from the sequencing of 950 specimens at the University of Guelph, mostly Lepidoptera, focal and non-focal groups. These data will consolidate the 14,000 insect sequences available in projects ABCI, AKHC and AWAN on the Barcode of Life (BOLD) platform. We also now have gigabites of data related to several DNA metabarcoding projects on the mBrave platform. Currently, this includes data collected with Berlese and light traps, but a new project funded by SENACYT in Panama will allow us to amplify these data with additional protocols in years 2022-2023. DNA metabarcoding should help us one day to efficiently monitor most of arthropod species on BCI and at other sites.

#### III. MONITORING: BARRO COLORADO ISLAND, KHAO CHONG AND WANANG

Year 2021 represented the thirteen year of insect monitoring at BCI. So far, the BCI database contains data on 659,537 arthropods, including 2,413 focal species (1,765 of which with pictures, 73%) and 73,540 pinned specimens in our collections (275 drawers). Each year we collect at BCI 330 insect samples (80 light trap samples, 50 Winkler samples, 120 butterfly transects, 40 termite transects and 40 bee bait samples) and in 2021 this represented 31,607 arthropods. Francisco Serrano (University of Panama) is progressing with his MSc thesis on the passalid beetles of BCI. The project on insect thermal tolerance under the responsibility of Greg Lamarre had to be remodeled in 2021 because of the covid-19 pandemic. Benita Laird-Hopkins (university of South Bohemia) reported her attention to temperate butterflies, as travel to Panama was difficult

during most of 2021. Esme Ashe-Jepson from Cambridge University in UK started collecting data on Panamanian butterflies with interns Ana Cecilia Zamora and Amanda Savage, and work is progressing well. Ernesto Bonadies (PhD student) and Daniel Soutos-Villaros (both University of South Bohemia) are studying the genome of common insect pollinators on BCI and preliminary results are encouraging. In 2021, analyses of monitoring and functional data from BCI focused mostly on orchid bees, arctiine moths and rhinoceros beetles.

2021 represented our eleventh year of monitoring at KHC. We collected 370 insect samples (80 light trap samples, 50 Winkler samples, 120 butterfly transects, 40 termite transects and 80 McPhail samples). So far, our database includes 243,863 specimens (36,945 pinned specimens in collections) and 2,510 focal species. We still need to improve on processing quickly insect samples and including representative insect pictures in our database. At WAN, 2021 represented the ninth year of insect monitoring. The ForestGEO insect database contains data on 87,000 specimens, but apart from butterflies and fruitflies, few of these specimens are yet identified.

Simon Segar (Harper Adams University, U.K.), Greg Lamarre and YB were invited to coin an international pre-COP26 virtual event on the theme of insect decline. Dave Roubik (STRI) and YB joined efforts to analyze 40 and 10 years of monitoring orchid bees at Pipeline Road and BCI, respectively. The conclusions reached by the two datasets are similar and emphasize the stability of these local populations. We reproduce the integrality of the article in Appendix I.

# **IV. INTERACTION STUDIES**

We are still in the process of analyzing data resulting from the study of seed predators and herbivore damage on seedlings at the three sites of BCI, KHC and WAN. These studies were funded by the Grant Agency of the Czech Republic and result from a collaboration with Sofia Gripenberg (University of Reading), Owen Lewis (University of Oxford), Richard Ctvrtecka; Philip Butterill, Leonardo Ré Jorge (University of South Bohemia) and Simon Segar (Harper Adams University). The first phase of these projects (seed predators) has been completed with one publication in *Oikos* in 2021 and other papers published previously. The second phase monitored the survivorship of seedlings in control plots and in plots treated with insecticide, to evaluate the action of insect herbivores on seedlings. Richard Ctvrtecka is helping YB to database all the results and our seedling damage database includes now + 4 mio records. We expect to start analyzing these impressive data soon.

The project "Integrating genomic and trophic information into long-term monitoring of tropical insects: pollinators on Barro Colorado Island, Panama" has been delayed by the covid pandemic (Ernesto Bonadies, Daniel Souto-Villaros, Greg Lamarre and YB). Preliminary data are very encouraging, and we hope to secure all relevant data in 2022.

# V. FORESTGEO ARTHROPOD DATABASE

The web version of the ForestGEO Arthropod database, which essentially mirrors snapshots of data for the sites of BCI, KHC and WAN, is now on-line at <a href="https://fgeoarthropods.si.edu/">https://fgeoarthropods.si.edu/</a>. The database and related web pages will allow to foster scientific collaboration via a better visibility of the ForestGEO Arthropod Initiative. It is maintained by Phil Butterill (University of South Bohemia). Next year we plan to include in the database the insect seed predator data, which represent over 80,000 insect records with hostplant information. We now have a new web site presenting the research activities of YB and collaborators at <a href="https://striresearch.si.edu/yves-basset-lab/">https://striresearch.si.edu/yves-basset-lab/</a>

# **VI. SCIENTIFIC OUTPUT**

In 2021, the ForestGEO Arthropod Initiative trained, at the sites of BCI, KHC and WAN, 14 assistants (4: BCI, 6: KHC, 4: WAN); 2 interns (BCI); two MsSc student (BCI) and one PhD students (BCI). Collectively, we wrote 5 publications in 2021, and many manuscripts are in preparation (see below). We hope that the "new normal" of 2022 will allow us to pursue our monitoring and research programs without much difficulty, as well as starting new collaborations leading to an increasing number of exciting publications.

#### Publications related to the ForestGEO Arthropod Initiative in 2021:

Roubik, D.W., Basset, Y., Lopez, Y., Bobadilla, R., Perez, F. & Ramírez Silva, J.A. 2021. Long-term (1979-2019) dynamics of protected orchid bees in Panama. *Conservation Science and Practice*, in press.

- Leponce, M., Corbara, B., Delabie, J.H.C, Orivel, J., Aberlenc, H.-P.,Bail, J., Barrios, H., Campos, R.I., Cardoso do Nascimento, I., Compin, A., Didham, R.K., Floren, A., Medianero, E., Ribeiro, S.P., Roisin, Y., Schmidl, J., Tishechkin, A.K., Winchester, N.N., Basset, Y. & Dejean, A. (2021) Spatial and functional structure of an entire ant assemblage in a lowland Panamanian rainforest. *Basic and Applied Ecology*, 56, 32-44.
- Basset, Y., Jorge, L.R., Butterill, P.T., Lamarre, G.P.A., Dahl, C., Ctvrtecka, R., Gripenberg, S., Lewis, O.T., Barrios, H., Brown, J.W., Bunyavejchewin, S., Butcher, B.A., Cognato; A.I., Davies, S.J., Kaman, O., Klimes, P., Knížek, M., Miller, S.E., Morse, G.E., Novotny, V., Pongpattananurak, N., Pramual, P., Quicke, D.L.J., Sakchoowong, W., Umari, R.,

Vesterinen, E.J., Weiblen, G., Wright, S.J. & Segar, S.T. 2021. Host specificity and interaction networks of insects feeding on seeds and fruits in tropical rainforests. *Oikos*, **130**, 1462-1476.

- Davies, S.J, Abiem, I., Salim, K.A., Aguilar, S., Allen, D., Alonso, A., Anderson-Teixeira, K., Andrade, A., Arellano, G., Ashton, P.S., Baker, P.J., Baker, M.E., Baltzer, J.L., Basset, Y.,..., Zuleta, D. 2021. ForestGEO: understanding forest diversity and dynamics through a global observatory. *Biological Conservation*, 253, 108907.
- Finnie, S., Sam, K., Leponce, M., Basset, Y., Drew, D., Schutze, M.K., Dahl, C., Damag, M., Dilu, M., Gewa, B., Kaupa, B., Keltim, M., Koane, B., Kua, J., Lilip, R., Mogia, M., Philip, F., Ray, B., Sam, L., Tulai, S., Uma, C., Umari, R., Valeba, J., Yalang, J. & Novotny, V. 2021. Assemblages of fruit flies (Diptera: Tephritidae) along an elevational gradient in the rainforests of Papua New Guinea. *Insect Conservation and Diversity*, 14, 348-355.

#### Other publications of the program coordinator in 2021:

Novotny, V., Miller, S.E., Hrcek, J., Baje, L., Basset, Y., Lewis, O.T., Stewart, A.J.A. & Weiblen, G.D. 2021. Correction. *The American Naturalist*, **198**, 438-439.

#### Selected manuscripts in preparation related to the ForestGEO Arthropod Initiative:

Comparison of traditional and DNA metabarcoding samples for monitoring tropical soil arthropods (Formicidae, Collembola and Isoptera). Submitted to *Scientific Reports*.

Functional groups of rhinoceros beetles (Coleoptera, Dynastinae) in Panama.

More winners than losers over 12 years of monitoring tiger moths (Erebidae: Arctiinae) on Barro Colorado Island, Panama. Submitted to *Biology Letters*.

Functional classification of Neotropical tiger moths (Erebidae-Arctiinae) provides insight on patterns of expected vulnerability to climate change.

Long-term population trends of adult Lepidoptera in a tropical forest: Barro Colorado Island, Panama.

Long-term monitoring of social insects in tropical rainforests.

Calibrating biodiversity for long-term monitoring: detecting changes in assemblage composition from temporarily and spatially variable insect data.

Invasive ants in the Yasuni National Park. Where do they come from?

Ant male flights in a Neotropical seasonal forest are shaped by low relative humidity and not by rainfall or moonlight.

How do tropical and temperate butterflies deal with changing temperatures?

The merit of using metabarcoding for monitoring tropical insect communities: a comprehensive test in one of the best studied tropical forest.

**Plate I.** Representative activities/items for the ForestGEO Arthropod Initiative in 2021. (1) Amanda Savage and Ana Cecilia Zamora collecting live butterflies for experiments related to thermal tolerance. (2) Insect soup from a light trap sample before and after homogenization for processing with DNA metabarcoding. (3) Preliminary analysis of taxonomic diversity (no. of barcode index number) in light trap metabarcoding samples between wet and dry seasons. Taxa more abundant in the wet season are colored blue while those in the dry season are colored light brown. (4) One of the few epigeous and non-arboreal termite nests in Panama: *Amitermes foreli* (Basset, Donoso, Bobadilla near Meteti in Darien). (5) Soldier of *A. foreli* (picture R. Scheffrahn). (6) Tanglegram comparing functional groups vs. phylogenetic tree for species of Panamanian Dynastinae. Species names are colorized according to functional groups. (7) Preliminary interaction network for the target pollinator species and plant species at BCI (GACR pollinator project). (8) Advert for the COP26 pre-meeting about insect decline, session organized by Segar, Lamarre and Basset. (9) Setting light traps at Khao Chong. (10) Long-term trends in orchid bee abundance and biomass at Pipeline Road, Panama, 1979–2018 (Roubik *et al.*, 2021). (11) Opening screen of the ForestGEO Arthropod Initiative database. (12) Example of distribution over time of one arctiine species (Lamarre *et al.*, submitted).



APPENDIX I. FULL TEXT OF ROUBIK ET AL. 2021 (see next page).

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#### CONTRIBUTED PAPER

Conservation Science and Practice

WILEY

# Long-term (1979-2019) dynamics of protected orchid bees in Panama

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# Abstract

Plants and pollinators are linked but their dynamics are scarcely known. Chemical monitoring of male "orchid bees" at two sites revealed 75% of species were stable or increasing. Forest bees of 33 species, with live sighting at Pipeline Road (PR), and trapping on Barro Colorado Island (BCI), included 132,000 individuals. No species or community changes occurred in strong El Niño-Southern Oscillation (ENSO) climate events, which lasted 145 total months during more than 70 bee generations. Parasite and host bees fluctuated in unison. A few very common species, adapted to relatively disturbed habitat, diminished over time at PR, while sightings and traps revealed stable abundance ranks in Euglossa 40 years on BCI. Bee abundance and biomass were stable but 50% of species had few records. Orchid bees appear more stable in older forest, they were evidently insulated from ENSO disturbance, and probably benefit from the increasing abundance of flowering lianas and vines.

#### KEYWORDS

Barro Colorado Island, El Niño, ENSO, euglossines, live sighting, monitoring, pollinatorplant systems, species abundance, trapping

#### INTRODUCTION 1

Our understanding of long-term population dynamics relies on data from designated census points over several decades (Didham et al., 2020; Terborgh, 1989). In large nature preserves, a consensus from such data corroborates reasons for conserving forest and wildland residents, including mutualists like pollinators (Nichols & Williams, 2006; Tepedino & Portman, 2021). We asked whether a protected mature forest environment maintains its pollinators. Despite a plethora of discussion,

there is almost no information on native bees in this setting (Dicks et al., 2021; Herrera, 2019; Murray, Kuhlmann, & Potts, 2009; Winfree, Griswold, & Kremen, 2007). The consequences of greater or lesser seed production on plant fitness (e.g., Xiao et al., 2017) is also a significant but neglected correlate of pollinator service in a natural habitat (Thomson, 2019) and remains unaddressed here. Using rigorous and continuous data collection, still rare in this line of research (Bonebrake, Christensen, Boggs, & Ehrlich, 2010) and unavailable for this length of time in other studies on

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pollinators or tropical bees that we are aware of, we focus on pollinator availability and fluctuation as we assess the impact of major cyclic climate events on populations.

Although many species are perennial in tropical forests, large seasonal and yearly changes in insect species abundance occur, and they appear similar to temperate zone patterns (Ackerman, 1983; Wolda, 1978). Available long-term studies on bees or pollinators (Cane, 2021; Soroye, Newbold, & Kerr, 2020; Van Klink et al., 2021) seldom include or analyze global climatic disturbances that influence temperature and drought, or heavy rains-notably the "El Niño-Southern Oscillation" (ENSO). Simulation study often neglects to examine dynamics in either pollinators or plants (Imbach et al., 2017). That general approach, due to a lack of long-term data, must replicate contemporary samples in space (Faleiro, Nemésio, & Loyola, 2018; Nemésio & Silveira, 2006), rather than over time. For the latter, a few investigators observe that natural population trajectories can reverse or change significantly over multiple decades, but remain unexplained (Condit, Pérez, Lao, Aguilar, & Hubbell, 2017; Freed & Cann, 2010; Macgregor, Williams, Bell, & Thomas, 2020; Thomson, 2019). Because pollinator declines are appreciated almost exclusively using historic records (e.g., collection or field sighting) in anthropogenic or disturbed settings (Burkle, Marlin, & Knight, 2013; Cane, 2021; Gegear, Heath, & Ryder, 2021; Zattara & Aizen, 2021), we see the necessity of questioning the conservation and management outlook for large reserves. We tested the impact of nine strong to very strong ENSO climatic events during 1979-2019 using forest bees in Panama. The resident "orchid bee" species, very long-tongued mainly solitary bees with no food stores or management of any kind, were studied throughout this period. The males come quickly to chemical scent baits and do not dwell in established nests but instead shelter in the wild (Roubik & Hanson, 2004). We also compared two census methods simultaneously, and related our data to a pioneer study, in the same location, of 1979. If our data confirm pollinator or bee decline indicated in other studies, then a radical departure in the expectation for forest preserves, their management, and the activity of pollinators is underscored. Instead, we found interesting changes in species abundances, much stability, and some increases, which we examine here.

# 2 | METHODS

# 2.1 | Study sites and field methods

We investigated a lowland tropical pollinator community during four decades in protected forests, one a  $16 \text{ km}^2$ island and one close by on the mainland. Our field methods, established in 1980 (Roubik & Ackerman, 1987) have been widely employed for bee studies in tropical America (Ackerman, 1983; Roubik, 2004). Our study area's core forest is approximately  $15 \times 50$  km (GoogleEarth, 2020 image), of which 280 km<sup>2</sup> is protected in Barro Colorado Nature Monument and nearby Soberanía National Park (Supporting Information; Methods).

The studies were along Pipeline Road (PR) and on trails of Barro Colorado Island (BCI). The study area, classified as moist seasonally dry forest with 2,600 mm annual rainfall, 9° N latitude, 80° W longitude, has been protected since 1914, when the Panama Canal was first operating. It contains secondary and old forest types. Our bee monitoring methods were developed in a year-long study of wild euglossine "orchid bees" on BCI during 1979-1980 (Ackerman, 1983), using 16 chemical attractants and nondestructive live sighting. We used the three most effective baits at PR and continued in monthly censuses 1979-2018. Using the permanent forest study plot (Condit et al., 2017) near the hilltop center of BCI, our additional monitoring 2009-2019 used 10 McPhail traps (BioBest Group NV: Belgium), placed 1.3 m aboveground, at 300 m intervals along five trails. Traps were employed for 1 week, baited with 7 ml reagent grade 1-8 cineole (Merck: Germany) mixed in 100 ml of vehicle radiator coolant, then bees were taken to the laboratory for identification (taxonomic guides in Supporting Information). Like the live-sighting method, the positions of attractant baits were fixed during our study. Bees were generally monitored monthly or quarterly.

# 2.2 | Community statistics

Our analyses of abundance among all but the rarely sampled bee species, and trends in long-term data that combined all species, used nonparametric statistics, leastsquares regression, Pearson correlations and multivariate methods developed from vegetation analysis. Rank clock plots of dominant species, species richness, species turnover, mean rank shifts and rate of community change were also evaluated (Supporting Information; Methods).

# 2.3 | ENSO climate anomaly impact

Detailed ENSO weather data (Oceanic Niño Index [ONI], www.cpc.ncpe.noaa.gov) allowed analysis of 9 total El Niño or La Niña "strong to very strong" intervals, which spanned 22 years and included 145 months, 58 of which we had data from at PR (Table 2, Table S1). Relatively warm or cool years in the tropical Pacific can result in substantially greater or less than normal precipitation and **TABLE 1** Total counts of male bees using 16 chemical baits on BCI (1979–1980), at Pipeline Road, Soberania National Park (PR, 1979–2018) using three maximally effective baits (live counts), and at BCI (2009–2019) using the most attractive chemical, in 10 replicate traps; Eg. = Euglossa, Ef. = Eufriesea, El. = Eulaema, Ex. = Exaerete; abundances deemed common, uncommon or rare (with no species analyses here) follow natural breaks in abundance, i.e. for BCI at *dressleri* and *nigrita*, then at *pulchra* and *villosiventris*, at PR, *championi* and *flammea*.

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26 Eg. cyanaspis 59 Eg. hemichlora
25 Eg. igniventris 54 Eg. cybelia
24 El. bombiformis 40 Ex. smaragdina
20 Eg. cybelia 29 Ef. anisochlora
20 Ex. smaragdina 25 Ef. concava
17 Eg. purpurea 24 Eg. villosiventris
14 Eg. hemichlora 9 Eg. flammea
8 Eg. villosiventris 8 Eg. purpurea
4 Ef. anisochlora 4 Eg. ignita
4 Eg. flammea 4 Eg. asarophora
4 Ef. duckei 2 El. speciosa
3 Eg. gorgonensis 2 Ef. lucifera

# 4 of 10 WILEY-Conservation Science and Practice

#### **TABLE 1** (Continued)

Count	BCI 2009–2019 Genus, species	Count	BCI 1979–1980 Genus, species	Count	PR 1979–2018 Genus, species
		3	El. polychroma	1	Ef. dressleri
		2	Eg. townsendi	1	Ef. duckei
		1	Eg. ignita		

Abbreviations: BCI, Barro Colorado Island; PR, Pipeline Road.



**FIGURE 1** Long-term trends in orchid bee (a) abundance and (b) biomass (dry weight) at Pipeline Road, Soberania National Park site, 1979–2018 (all species and four genera). (c) Bees attracted to baiting pad. (d) Baited McPhail trap with bees

temperature in Panama and much of the globe (La Niña, El Niño, respectively; Wright & Calderon, 2006). The tallies for bees in a census month were assigned to a 3-month running mean ONI climate datum for a particular month, classified as neutral, La Niña, or El Niño intervals.

# 3 | RESULTS

Data from our medium- to long-term sampling of the 4 native orchid bee genera (*Euglossa*, *Eulaema*, *Eufriesea*, and the parasitic bee *Exaerete*) comprise 257 time-series points, each with 8–28 bee species included (means = 22

and 13, respectively, PR and BCI). There were 596 months in the combined studies; therefore, slightly less than half the total months spanning our studies had data. An average sample on PR was 342 individuals (range 53–923), and the mean of total bees trapped at BCI, using 10 traps, was 1,093 (range 114–2,750). We identified all, including 44 species and 132,000 individuals (Table 1). The same species of bees at PR were previously censused for a year using 16 attractants on BCI and as expected, annual bee abundance peaks were followed by pronounced lows in late wet season. Our trap methodology was ineffective; however, censusing the larger-bodied bees, *Exaerete, Eufriesea*, and *Eulaema*, because it

was designed to prevent too many bees from entering (see Section 4).

Total abundance and biomass were stable, both at PR and BCI (Figures 1 and 2), with about 75% of all species stable or increasing (Figures S1-S3). The 19 BCI Euglossa registered the same relative abundance rankings in 1979–1980 and 2009–2019 (Wilcoxon z = -1.489, p = .136; Table 1). The most common *Eulaema* species and Eg. imperialis (the largest Euglossa) were among the top-10 bees in abundance both on BCI (1979-1980, top 3, 4, and 5 species) and at PR (top 1, 5, and 6 species). Seasonality in species abundance varied little (Figure S4). Even though no difference was found in the two-ranked species abundance lists that we compared, separated by 30-40 years in 19 Euglossa at BCI, this was not the case for the PR-more recent BCI comparison (z = -2.296, p = .021) or for the orchid bees of PR (1979–2018) and BCI (1979–1980), z = -4.443, p < .0001. In the long term, PR displayed the positive directional change of an unstable community ( $R^2 = .009, F_{1.701} = 6.45, p = .011$ ), but did not in the shorter-term at BCI ( $R^2 = .014$ ,  $F_{1,43} = 0.60, p = .44$ , Figure S5). The directional change may be interpreted as the decline in Eg. imperialis, the most common species-the "Imperial bee", which totaled 26-48% of all bees in all three censuses (Table 1, Figure 2). Although it declined at PR, its abun-dance was stable during the last half of the series (F tests,

p < .001, p = .294). Two of the most abundant *Eulaema* on BCI (Ackerman, 1983) and PR also declined significantly at PR (Figure S2) and further account for the community trend. Other, larger *Eulaema* increased. Rank clock plots suggested that in the long-term (PR) *Eg. imperialis* was declining but in recent years populations experienced a slight increase (Figure S4). Regression analysis also showed that the Imperial bee either declined or increased, comparing two halves of the study at PR, while seven other *Euglossa* steadily increased and five declined (Figures 2, S1, and S3). *Euglossa dissimula* appeared to be stable despite much variation, whereas *Eg. despecta* increased slightly after 1979 (Figure S1).

Community dynamics during the study period (Figure S5) indicate there were small differences in species richness over time, slightly decreasing, although 2018 richness was higher than in 1979. There was a large peak of species turnover in 1998. Exclusion of Imperial bee data in our analyses, or dividing the almost 40-year duration of study into two parts, changed the long-term dynamics of all *Euglossa* from stable to increasing at PR, but had no effect on stability of the total euglossine community there; neither were affected on BCI (Figure 2). These parallel study periods at our two sites were closely similar for *Euglossa* spp. Remarkably, in total over 98% of individual bees consisted of only half the total species monitored in either study, one with all encountered



**FIGURE 2** Time-series abundance data at two Panama forests of *Euglossa* species and total bees with and without the dominant species *Euglossa imperialis* included. (a–c) Pipeline Road, 1979–2018; (d–f) Pipeline Road, 2009–2018, for comparison with (g–i) Barro Colorado Island, 2009–2019

TABLE 2	ENSO impact (3-month running averages given by the ONI), bee abundance, and trend tests for orchid bees (Euglossa,
Eulaema, Exa	uerete, Eufriesea) monitored on BCI (Nature Monument) and Pipeline Road (Parque Nacional Soberanía) Panama, during
1979–2019	

Population status/locality	Species abundances			
	Increase	Decrease	Stable	
BCI	2	2	15	
PR	7	8	15	
Fisher exact test, $p = .14$				
	Increase	Decrease	Stable	
Common	11	4	12	
Uncommon	1	7	18	
Fisher exact test, $p = .005$				
ONI				
	Abundance during climatic events at PR			
	El Niño	La Niña	Neutral	
>Median	20	10	63	
≤Median	15	13	67	
Fisher exact test, $p = .57$				

Abbreviations: BCI, Barro Colorado Island; ENSO, El Niño-Southern Oscillation; ONI, Oceanic Niño Index; PR, Pipeline Road.

orchid bees, and one counting only one of four genera. Many species were always in low abundance. Further, the more common species tended to increase while less common species decreased (Fisher test, p = .005, Table 2), with notable exceptions.

The larger bees, Eulaema and Eufriesea, and Exaerete, their parasite, had sufficient live sighting data for an analysis for PR. Of 11 species, 3 increased, 2 declined, and 6 were stable. We found a significant positive relationship between Exaerete and certain Eulaema and Eufriesea, the potential hosts of similar size (r = .143 - .266, p = .0 - .05; Table S3). The larger *Eulaema* (bombiformis, meriana) increased, along with their probable brood parasite Exaerete frontalis, as the smaller El. nigrita and El. cingulata declined. At PR, there was a considerably greater proportion of *El. bombiformis*, the largest orchid bee, compared to the original live sighting at BCI (Table 1). One relatively abundant Eufriesea, Ef. corusca, did not appear in either of our studies because it comes to vanillin attractant, which we did not employ.

The linear regression results for *Euglossa*, with 22 species monitored on PR and 19 at BCI, showed 7 increasing, 6 declining and 9 stable in the former, and 2 declining and 17 stable (2 increased slightly) in the latter (*F* tests, p > .05; Figures S1 and S3). One, *Eg. dressleri*, declined in both studies, while *Eg. hansoni* (p = .06) and *Eg. variabilis* (p = .09) increased on BCI. The BCI data (2009–2019) lacked *Eg. crassipunctata*, a common species at PR and on BCI (Table 1; Ackerman, 1983; Roubik &

Ackerman, 1987). Overall, 26 and 11% of *Euglossa* species declined at PR or BCI, respectively. Eight rare species, including *Euglossa*, among the 42 species followed on PR, did not appear in the latter half of the 40-year PR study (also see Roubik, 2001).

Within 145 ENSO "climatic event" months (a strong or very strong La Niña or El Niño, 9 total events), our 58 census results were no different from those of 130 neutral climate periods at PR (p = .57, Table 2). None of the 33 "core" species at PR displayed a correlation between abundance and climate anomalies (Table S1). At both study sites, years categorized according to ONI events had no bearing on faunal composition of bee communities (adonis tests, PR:  $F_{2,35} = 0.023$ , p = .967; BCI:  $F_{2,7} = 0.407$ , p = .812; Figure S6).

# 4 | DISCUSSION

As found in other studies using permanent plots for a similar length of time (trees on BCI, Condit et al., 2017; nesting bees and wildflowers in the north temperate zone, Cane, 2021) nature is often not in equilibrium. Our findings contradict those of Faleiro et al. (2018). Their data were based on sampling in many sites for abundance differences among 37 orchid bee species in Brazilian Amazonia, some associated with disturbed habitats (see also below). Predictions were presented from a climate modeling approach that uses contemporary species presence/absence data. General decline, with some

exceptions, was envisioned, accompanying climate change. We assume that the climate changes during our Panama studies encompass most of those seen over the time of orchid bee residence—including the largest changes during the Neogene—but we may be mistaken.

Did our census data contradict presence/absence predictions for particular reasons? We remain largely ignorant of the evolutionary history of the bees we studied and the communities in which they perform. Cases of fossil studies cover far greater timescales (Botta, Dahl-Jensen, Rahbek, Svensson, & Nogués-Bravo, 2019; Clark & McLachlan, 2003), but our study systems do not allow such an extensive view. Although a strong El Niño dry season was positively correlated with orchid bee abundance at PR during the first 240 months of our study (Roubik, 2001), we found no apparent longer-term responses in the bee community or among individual species to the ONI events as a whole. Our census data included almost half the months in a total of 50 years of study. The ENSO events arose during 145 of those 596 months at the PR site, and the corresponding 58 monthly bee census results did not predictably vary to any extent that we could detect. In addition, the observation that seeds are more abundant on BCI in El Niño years (Wright & Calderon, 2006), thus more abundant flowers may then influence bee abundance, lacks confirmation here. We are only beginning to discover which resources are of major importance to most bees. We suggest that neither presence/absence data nor species dynamics in long-term studies are conclusive for judging species or community resilience in natural habitats and native communities. Both evolutionary and adaptive potentials remain to be deciphered. Nonetheless, a significant advantage for core species within protected reserves, on a scale comparable to foraging ranges of the species in question, further examined below, seems to be the inescapable conclusion of the present work.

Bee populations were mostly on the rise or stable, 74% at PR (39 years), 79% on BCI (11 years). A plausible explanation is the preservation and increase of major orchid bee resources. The increasing abundance of vine and liana flowers in the Neotropics (Schnitzer, Bongers, Burnham, & Putz, 2014) a prominent orchid bee resource (Dressler, 1982; Ramirez, Dressler, & Ospina, 2002; Roubik & Moreno, 2021), should support orchid bee population increases and stability. The primary floral resources required by orchid bees-sheltered nectar in long, tubular flowers, or sheltered pollen in poricidal anthers-and floral resin, may well be relatively less affected by rain or drought. Their phenology, however, is not a variable that we can analyze here. Euglossines differ from other common tropical bees, which hoard food in their nests and often use easily foraged, open flowers that have maximum abundance during dry season and early wet season (Roubik, 1989).

Remarkably, because they constituted less than 2% of the total individuals censused, 50% of orchid bee species were scarcely detected annually at our sites. We suggest that many studies that fail to encounter certain species have a significant challenge in verifying that their sampling is adequate or sufficient. We were nonetheless able to accumulate data to make inferences about the population dynamics of scarce bees (Table 2) and found that less abundant bees were more likely to decline. Yet some of the most abundant species also decreased over time. Our two study sites were dissimilar in having a proportionately greater old forest area in BCI compared to the PR area, which, considering the several to many kilometer flight capability of orchid bees (Pokorny, Loose, Dyker, Quezada-Euán, & Eltz, 2015; Wikelski et al., 2010), may be an underlying cause of differences, although bees on the island certainly access the mainland. A migratory lifestyle for euglossine males, but not their females-whose sheltered nests in the wild are difficult to encounter and very little studied-is conceivable. Male dispersal covers 50 km for a medium-sized Euglossa in the Yucatan, Mexico lowland (Pokorny et al., 2015). Male euglossines, which have no nest, can potentially find sheltered or favorable habitats within Central Panama over large distances. There are varied elevations and habitats, but we have no information on whether orchid bees use multiple nests or habitually migrate. The general result for mean ranks analysis on PR indicated some instability at the community level, as certain abundant bees became relatively less common. In contrast, the subset of species studied on BCI, the Euglossa, had rank abundances no different after 40 years, on the forest island.

That a dozen species were dominant, while 42% were uncommon among bees censused at both sites, suggests competing hypotheses. Extreme abundance of Imperial bees does not fit the expected lognormal distribution of species abundance in such diverse natural communities (Chisholm & Pacala, 2010). If bee behavior at the baits influenced the skewed numbers among species, then the time spent collecting a fragrance bait, or even its detection, may explain differences among species counts. In addition, a given bee species came to either 1, 2, or all 3 baits at PR, so species were sampled unevenly. However, with a fixed protocol, such variables are controlled by sampling rigor. Removal of individuals at baits during intervals of very high abundance does not diminish species counts, and a high (negative) correlation exists between counts and the time of first arrival (Roubik, 2001). Orchid bee abundance in the forest, as suggested by other studies, is indicated by the males at baits (Ackerman, 1983; Janzen, DeVries, Higgins, & Kimsey, 1982), and unless the sex ratio changes,

their numbers should be reliable monitoring indicators. More importantly, because Ackerman's (1983) year-long sampling with 16 chemical attractants was very similar to our BCI data, the results with a single attractant and considering the same Euglossa species suggest live sightings agree with trapping data, and suggest the forest community was quite stable. In contrast, the less skewed dominance of the Imperial bee during BCI's initial survey (Table 1) and the design of traps so that not all large bees were collected, but smaller bees enter, demands further qualification and limits generalization based on the genus Euglossa alone. We purposely limited trapping of the three abundant largebodied genera, which live long and pollinate many flowers (Dressler, 1982). The Euglossa as a whole were increasing moderately after data of the single dominant species, Imperial bees, were excluded for PR. And on the contrary, on BCI no trend was found in either case (Figure 2). Absence of a trend does not signify stability in itself, but the absence of a trend on BCI compared to PR in the abundance of the same Euglossa species, with similar annual variation, strongly suggests the island experienced less change than the mainland.

Conservation efforts seek an expected result, but in studies such as ours, questions still remain about the staof succession in the habitat (Clark & tus McLachlan, 2003; Clements, 1936), the methods used to follow its residents (Bonebrake et al., 2010; White, 2019), and here, the multifaceted natural histories of bees and plants (Dressler, 1982; Ramirez et al., 2002). Tree mortality and growth in the 50-ha BCI plot has stabilized after drought in the 1980s, and the forest is changing (Condit et al., 2017). We also see orchid bees in a particular biological paradigm and time frame. The conservation of orchid bees, because they are not managed nor producers of commercial products, yet obviously visit and interact with many flowering plants, requires reasonably intact, mature natural habitat. In this status, during a 40-year interval, we found no decline or susceptibility to cyclic climatic changes, although suggested in much shorter studies (Ramirez, Hernández, Link, & López-Uribe, 2015; Vega-Hidalgo et al., 2020). The magnitude of seasonal fluctuations in abundance was large, but we observed little directional change over time.

# 5 | CONCLUSION

Eight rare species in the first 20 years of study on PR did not appear later, and *Eg. dressleri* was declining at both our study areas, which might mean they ordinarily centered in higher elevations or different rainfall regimes (Roubik & Ackerman, 1987). Nevertheless, none of the core species in our study declined or increased during periods of a given ENSO climate event, usually a year or longer. Those drought or high rainfall periods (Table S1) greatly exceeded an average orchid bee generation time of 2 months (Dressler, 1982) and allow our study to assess changes in survival or reproduction during over 70 bee generations that were monitored during such conditions. As to whether "wild" bees are increasing, declining or maintaining their populations, and whether "climate change" is driving those populations in any particular direction seems now, on the available evidence, largely unknown for non-Anthropocene habitat. Our study suggests great overall stability during decades. Some tropical forests still maintain their organismal inventories, and may be more amenable to partial restoration or rescues than commonly believed. Modeling research efforts, although they may show what certain conditions portend, are not based on the needed deep history, but rather upon what can be garnered from contemporary environments and very few detailed studies. Studies like ours, which include highly adapted species assemblages, may still be improved upon. We need innovative ways to compare stable core species assemblages, their remnants, or ancient assemblages, with those that we see today.

We also hypothesize that community succession is occurring, whereby some abundant species decline and others take their places, exemplified with *Euglossa* and particularly the Imperial bee, *Eg. imperialis*. Some *Eulaema* and Imperial bees depend on abandoned nest cavities (e.g., from *Atta* ants) that are more common in disturbed sites, and those species range from Brazil to Mexico (Faleiro et al., 2018; Roubik & Hanson, 2004; Silva, Macêdo, Ascher, & DeMarco Jr., 2015). They remove competitive pressure as they decline in older forest and provide opportunities for other species. Although orchid bee communities in the large forest we studied were not declining, we still lack basic information to propose specific reasons for their dynamics.

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# **CONFLICT OF INTEREST**

The authors declare no conflicts of interest.

# **AUTHOR CONTRIBUTIONS**

**David W. Roubik** and **Yves Basset**: Designed research, collected and analyzed data, and wrote the manuscript. **Yacksecari Lopez**, **Ricardo Bobadilla**, **Filonila Perez**,

Conservation Science and Practice

and **José Alejandro Ramírez Silva** made field collections and laboratory identifications.

# DATA AVAILABILITY STATEMENT

Our data archives are deposited in Smithsonian FigShare, https://doi.org/10.25573/data.16598810.v1.

#### ETHICS STATEMENT

Recognition of live orchid bee males was done in the field by DWR and sampling was carried out using traps on BCI by coauthors.

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