Pollinator specificity and seasonal patterns in the euglossine bee-orchid mutualism at La Gamba Biological Station

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The plant family Orchidaceae exhibits some of the most spectacular and intricate adaptations for insect pollination. Across the Neotropical region male euglossine bees provide pollination services to approx. 700 orchid species that have evolved scent production in exchange for sexual reproduction. Male orchid bees collect scents from flowers and other sources to concoct perfume mixtures that they use as pheromone analogs during courtship display. Although the pollination biology of some of these associations has been studied in detail for some orchid taxa, community-wide analyses of this mutualism are lacking. Here I present an analysis of the plant-pollinator affiliation patterns and phenology among scent-producing orchids and male euglossine bees based on 960 bee-orchid interactions obtained over the course of five years of sampling at La Gamba Biological Station (south-western Costa Rica). I identify a highly nested plant-pollinator network that is composed of 24 bee species and 17 orchid genera. Some orchid genera exhibit pronounced flowering seasonality, with most of the diversity of interactions taking place during the dry season (March-April) and few orchid taxa blooming throughout the year. The architecture of the plant-pollinator network also revealed a substantial degree of pollinator sharing among orchid genera, suggesting that distantly related lineages independently converged on the use of similar pollinator bee assemblages.

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Die Pflanzenfamilie Orchidaceae weist einige der spektakulärsten und komplexesten Anpassungen zur Insektenbestäubung im Pflanzenreich auf. In der gesamten Neotropis liefern männliche Prachtbienen Bestäubungsdienste für ca. 700 Orchideenarten, die im Gegenzug für die sexuelle Reproduktion Düfte entwickeln und bereitstellen. Männliche Prachtbienen sammeln Düfte von Blüten und anderen Quellen, um daraus Duftmischungen zu bilden, die während der Partnerwerbung als Pheromonanaloge eingesetzt werden. Obwohl die Bestäubungsbiologie für einzelne dieser Orchideentaxa und Assoziationen bereits eingehend untersucht wurde, fehlt es nach wie vor an einer umfassenden Analyse dieser Mutualismen. Hier präsentiere ich eine Analyse der Pflanzen–Bestäuber Zugehörigkeitsmuster und der Phänologie bei Duft-produzierenden Orchideen und männlichen Prachtbienen, basierend auf 960 Bienen–Orchideen Interaktionen, die im Laufe von fünf Jahren Datenerhebung an der Tropenstation La Gamba (im südwestlichen Costa Rica) beobachtet wurden. Es zeigt sich ein stark geschachteltes Pflanzen–Bestäuber Netzwerk bestehend aus 24 Bienenarten und 17 Orchideengattungen. Manche Orchideengattungen zeigen eine deutliche Blütesaisonalität, wobei der Großteil der Interaktionen während der Trockenzeit (März bis April) stattfindet und nur wenige Orchideentaxa während des ganzen Jahres blühen. Die Struktur des Pflanzen–Bestäuber Netzwerkes zeigte auch einen erheblichen Anteil an Bestäubern, der von mehreren Orchideengattungen geteilt wird. Dies legt die Vermutung nahe, dass weit-entfernte Orchideenlinien unabhängig auf die Interaktion mit ähnlichen Bestäuberbienen konvergierten.

Keywords: Euglossa, Gongora, orchid pollination, pollinaria, pollination networks.

Introduction

Plant-pollinator associations have profoundly influenced the evolution of both flowering plants and insect pollinators (Willmer 2011). Some plant-pollinator associations are highly specialized, with many intricate and fascinating examples occurring in the tropical regions of the world. Specialized plant-pollinator interactions provide excellent opportunities for studying the evolution of floral adaptation, pollinator-mediated selection, and the origin of new species via floral isolation (Kay & Sargent 2009, Schiestl & Schlüter 2009). However, many of these associations remain poorly investigated and even basic information about their natural history, phenology and association patterns remains scarce.

Euglossine bees are one of the most important insect pollinators in tropical America (Roubik 1989, Ramírez et al. 2002). Male and female euglossine bees (>230 spp.) collectively pollinate thousands of flowering plant species while foraging for nectar, pollen, and resins (Ramirez-Arriaga & Martinez-Hernandez 1998, Ramírez et al. 2002, Ospina-Torres et al. 2015, da Silva et al. 2016). Additionally, male euglossine bees exhibit unique adaptations for the acquisition and storage of perfume compounds from flowers and other sources, including hundreds of orchid species (Dressler 1982, Williams & Whitten 1983, Ramírez et al. 2002). Male euglossine bees collect perfume mixtures throughout their life and continually expose them during elaborate courtship displays (Pokorny et al. 2017, Eltz et al. 2019). Because euglossine bees often fly long distances while foraging for perfume compounds, they provide crucial pollination services to numerous orchid species with fragmented and/or low-density populations (Janzen 1971, Pokorny et al. 2014).

Approximately 700 species of orchids, equivalent to 10 % of the Neotropical Orchidaceae, have evolved a suite of traits that enable pollination by male euglossine bees (Ramírez et al. 2002). Euglossine-pollinated orchids emit concentrated floral scents as rewards and exhibit a variety of mechanisms that ensure the release and proper attachment of pollinaria onto the body of the male bees. It was previously believed that euglossine-pollinated orchids depended exclusively on male bees for cross-fertilization and that male bees depended exclusively on orchid flowers for perfume acquisition (and therefore access to mates). However, it is now clear that, while orchids depend exclusively on male euglossine bees for pollen transfer (and therefore sexual reproduction), male euglossine bees can acquire perfume compounds similar to those produced by orchids from other hosts, including fungi, leaves, and rotting vegetation (Ackerman 1983, Whitten et al. 1993, Pemberton & Wheeler 2006, Ramírez et al. 2011). Using comparative methods, I showed that the association between euglossine bees and their orchid hosts is highly asymmetric (Ramírez et al. 2011). Under this scenario, the opportunities for reciprocal selection (coevolution) were significantly reduced during the diversification of these two lineages (Ramírez et al. 2011).

Most euglossine-pollinated orchids belong to closely related lineages within the orchid tribe Cymbidieae, with the majority of species concentrated in the subtribes Stanhopeinae, Catasetinae and Zygopetalinae. Each of these three orchid lineages is monophyletic (Chase et al. 2015) but they are interspersed among lineages that are not pollinated by euglossine bees and instead exhibit food deceptive pollination syndromes (Whitten et al. 2007, Ramírez et al. 2011, Whitten et al. 2014). Therefore, the euglossine pollination syndrome appears to have evolved multiple times independently. Moreover, although the phylogenetic relationships within Zygopetalinae are not fully resolved (Whitten et

al. 2014), it is likely that male euglossine pollination evolved more than once within this group. As a result, the total number of independent origins of euglossine pollination may be as high as 4 or 5 events.

Some euglossine-orchid associations have been studied in great detail (Dodson & Frymire 1961, Dodson 1962, Dressler 1968, Hills et al. 1972, Zimmerman et al. 1989, Milet-Pinheiro et al. 2015, Hetherington-Rauth & Ramírez 2015, Pansarin et al. 2018). However, most of the interactions are known from a few focal orchid taxa or a narrow seasonal time window. With the exception of the study conducted by Ackerman in Central Panama (Ackerman 1983), community-wide and year-round surveys of bee-orchid associations are lacking. Thus, the affiliation networks, the diversity patterns, and the phenological cycles of euglossine-orchid mutualisms remain largely understudied.

Here I report the results of a survey of euglossine-orchid associations conducted by my students, colleagues and myself over a five-year period at La Gamba Biological Station in south-western Costa Rica. Because all orchids produce pollen masses (pollinaria) that are attached to the pollinator's body while visiting flowers, it is possible to track plant-pollinator associations by capturing pollinaria-laden bees using synthetic chemical baits. In most cases orchid pollinaria can be readily identified to genus based on morphological traits. The analysis I present here is based on 960 pollinaria-laden bees collected along the trail system around La Gamba Biological Station. Here I analyze the diversity, phenology, and association patterns of euglossine-pollinated orchids and their euglossine bee pollinators.

Materials and Methods

Pollinaria-laden bees were lured and collected using six different chemical baits that attract a wide variety of euglossine bee species: methyl salicylate, eugenol, 1,8-cineol, 1,4-dimethoxybenzene, vanillin and methyl cinnamate. All compounds were obtained from Sigma-Aldrich. The latter three compounds were purchased as solid crystals and dissolved in 200-proof ethanol. Each compound was applied separately to a blotter paper pad (5 × 5 cm) attached to a tree trunk 1.5 m above ground, separated from other baits by at least 5 meters. Bees were captured with hand nets as they approached the chemical baits. Pollinaria were carefully removed with forceps and deposited and preserved in 1.5 mL vials containing silica gel. Bees were pinned, identified and stored in the bee collection at UC Davis. Baits were typically presented between 8:00AM and noon and replenished as needed. Baits were presented along the trail system around La Gamba Biological Station at the same locations.

The sampling area was composed of secondary tropical forest, surrounded by patches of primary forest. The area receives an average annual rainfall of approximately 6,000 mm. The sampling was conducted between 2013 and 2018, with most of the collecting effort taking place during the dry season (March-April), but additional collections were made once a week throughout the year between 2015 and 2016. Pollinaria were identified to genus and bees were identified to species using a reference collection. I analyzed data using basic R packages. Bipartite networks were visualized and analyzed using the R package *bipartite v*2.07.

Rainfall patterns were calculated as averages for the past 20 years, and were measured with an automated meteorological station located at La Gamba Biological Station.

Results and Discussion

In previous surveys conducted by Dr. Tamara Pokorny, Dr. Thomas Eltz and myself, we found that the euglossine bee community occurring around La Gamba Biological Station is composed of 35 species belonging to four genera (*Euglossa*, *Eufriesea*, *Eulaema* and *Exaerete*, see Fig. 1 for four exemplary bee-orchid interactions). In this study, I found a total of 24 species of euglossine bees carrying orchid pollinaria, including three of the four genera present in the area (*Euglossa*, *Eulaema* and *Exaerete*, Fig. 2). I found pollinaria from a total of 17 orchid genera (Fig. 2), most of which belong to the three major orchid lineages that are known to exhibit scent-production and pollination by male euglossine bees (*i.e.* orchid subtribes Stanhopeinae, Catasetinae and Zygopetalinae, Fig. 2). Additionally, I found pollinaria belonging to other orchid lineages, including the genus *Lycaste* (subtribe Maxillariinae), the genus *Macroclinium* (subtribe Oncidiinae) and the genus *Notylia* (subtribe Oncidiinae). The first genus has not been reported for the area but the latter two are known to occur and are common around La Gamba Biological Station (Gegenbauer et al. 2013). These three genera have been previously described to exhibit male euglossine

Fig. 1: Scent producing orchids and their euglossine bee pollinators: an orchid *Gongora sp.* with bee *Euglossa tridentata* (top left; photo by T. Eltz), orchid *Mormodes sp.* with bee *Euglossa tridentata* (top right; photo by T. Eltz), orchid *Catasetum maculatum* with bee *Eulaema cingulata* (bottom left; photo by S.R. Ramírez), orchid *Notylia barkeri* with its bee pollinator *Euglossa championi* carrying pollinaria on clypeus (bottom right; photo by S.R. Ramírez). – Abb. 1: Duft-produzierende Orchideen und ihre jeweiligen Prachtbienen-Bestäuber: Orchidee *Gongora sp.* mit Biene *Euglossa tridentata* (oben links; Foto: T. Eltz), Orchidee *Mormodes sp.* mit Biene *Euglossa tridentata* (oben rechts; Foto: T. Eltz), Orchidee *Catasetum maculatum* mit Biene *Eulaema cingulata* (unten links; Foto: S.R. Ramírez), Orchidee *Notylia barkeri* und Biene *Euglossa championi* mit Pollinaria am Clypeus (unten rechts; Foto: S.R. Ramírez).

pollination syndrome (Ramírez et al. 2002). In addition, I found pollinaria from other orchid groups that lack floral scent production and male euglossine pollination syndrome, including *Sobralia* and *Vanilla,* both of which have been proposed to rely on food deception for pollinator attraction (Neubig et al. 2015).

The resulting bee-orchid pollination network was highly nested (Fig. 2; nestedness index=11.74). This network architecture is typical of plant-pollinator mutualistic interactions (Jordano & Bascompte 2013), and conforms well to what has been described for the

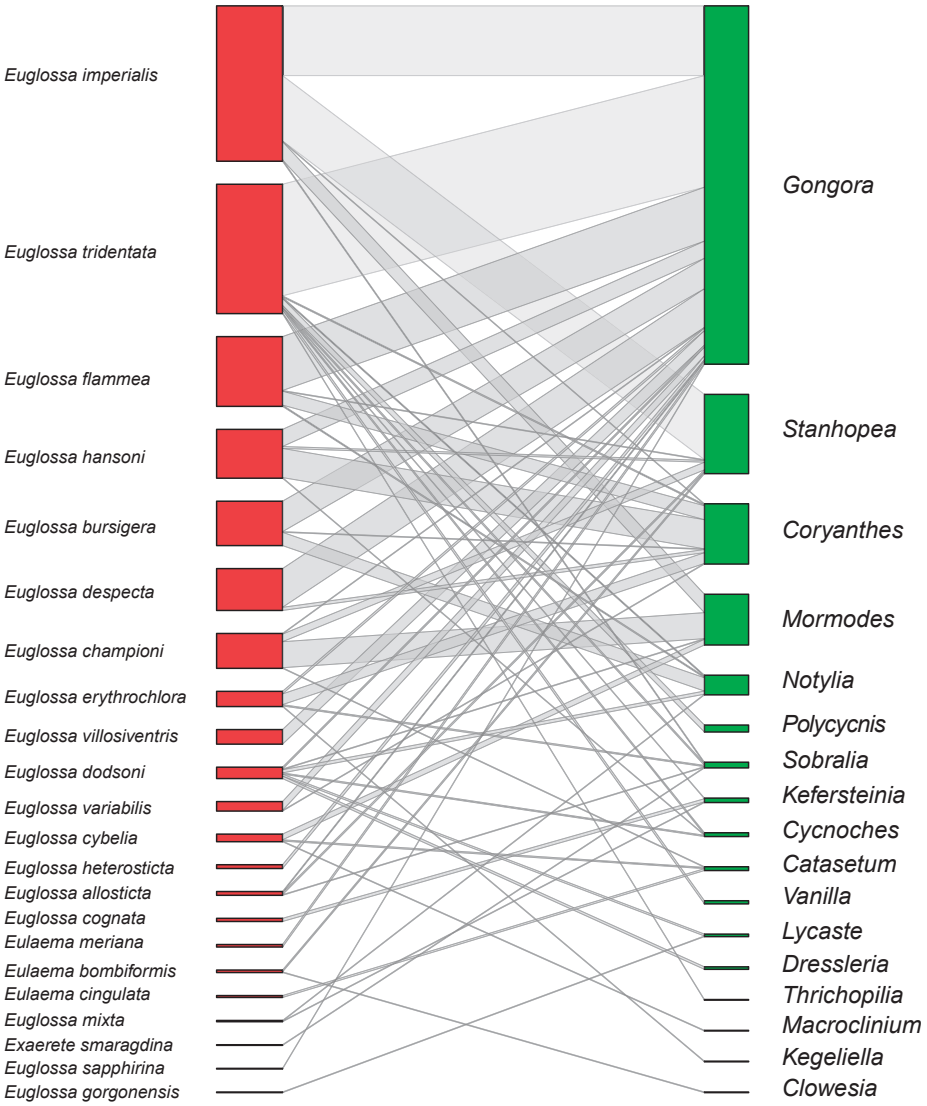

Fig. 2: Orchid-euglossine bee interaction network inferred from pollinaria records of all orchid genera and bee species. – Abb. 2: Orchideen-Prachtbienen Interaktionsnetzwerk, abgeleitet aus Pollinaria-Nachweisen aller Orchideengattungen und Bienenarten.

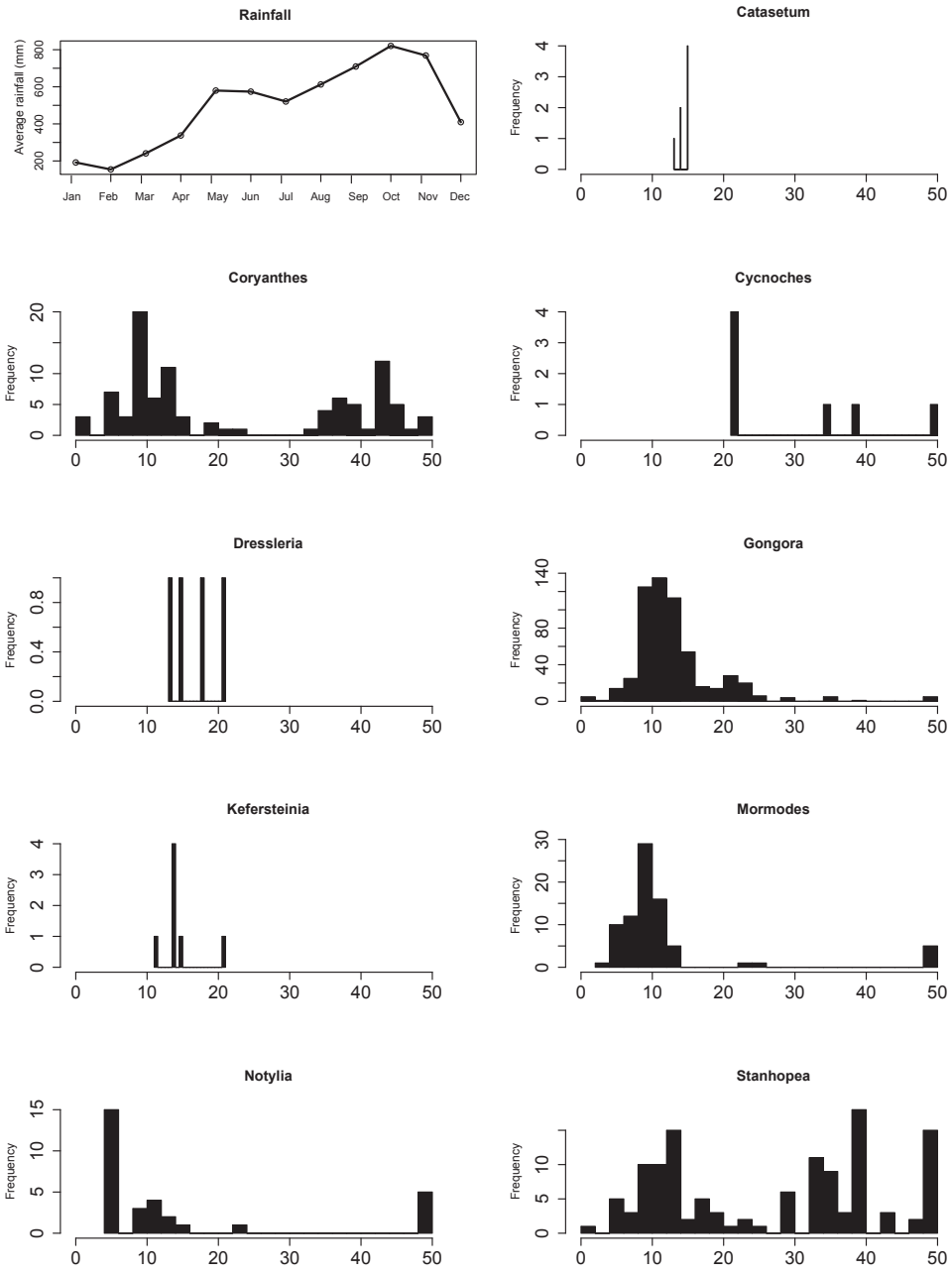

Fig. 3: Average monthly rainfall (1997–2017) and blooming phenology of the most common orchid genera based on weekly census data. – Abb. 3: Durchschnittlicher Monatsniederschlag (1997–2017) und Blütephänologie der häufigsten Orchideengattungen, basierend auf wöchentlichen Erhebungen.

architecture of other euglossine bee-orchid networks (Ramírez et al. 2011). The numerically most abundant bee species in the network were *Euglossa imperialis* (245), *E. tridentata* (204), *E. flammea* (110) and *E. hansoni* (77) (Fig. 2). Moreover, the bee species with the highest degree indices (*i.e.* the number of connections to different orchid nodes) were *E. dodsoni* (9 orchid genera), *E. imperialis* (6 orchid genera), *E. hansoni* (4 orchid genera) *E. flammea* (4 orchid genera), *E. erythrochlora* (4 orchid genera) and *E. championi* (4 orchid genera). Conversely, the numerically most abundant pollinaria were those of the orchid genera *Gongora* (571), *Stanhopea* (125), *Coryanthes* (95), *Mormodes* (80) and *Notylia* (31). The orchid genera with the highest degree indices in the network were *Gongora* (15 bee species), *Coryanthes* (8 bee species), *Stanhopea* (6 bee species), *Sobralia* (5 bee species) and

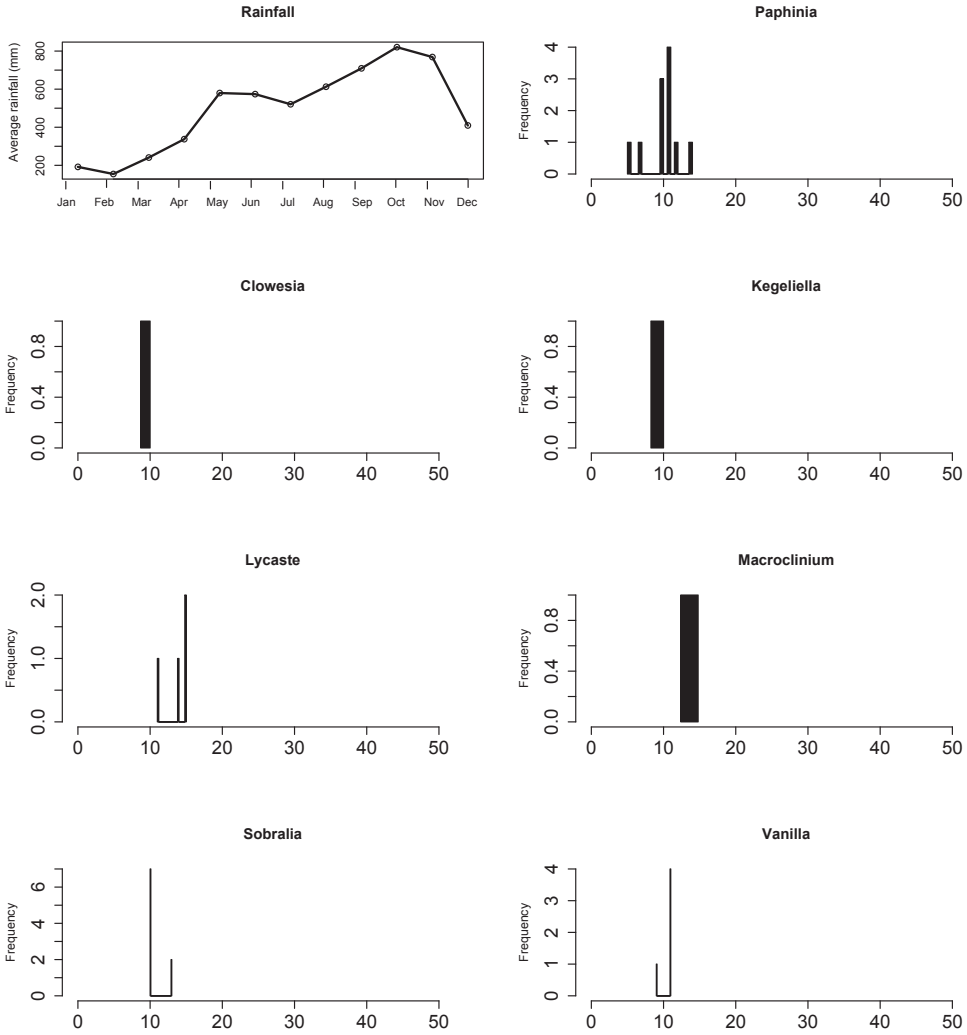

Fig. 4: Average monthly rainfall (1997–2017) and blooming phenology of rare orchid genera based on weekly census data. – Abb. 4: Durchschnittlicher Monatsniederschlag (1997–2017) und Blütephänologie seltener Orchideengattungen, basierend auf wöchentlichen Erhebungen.

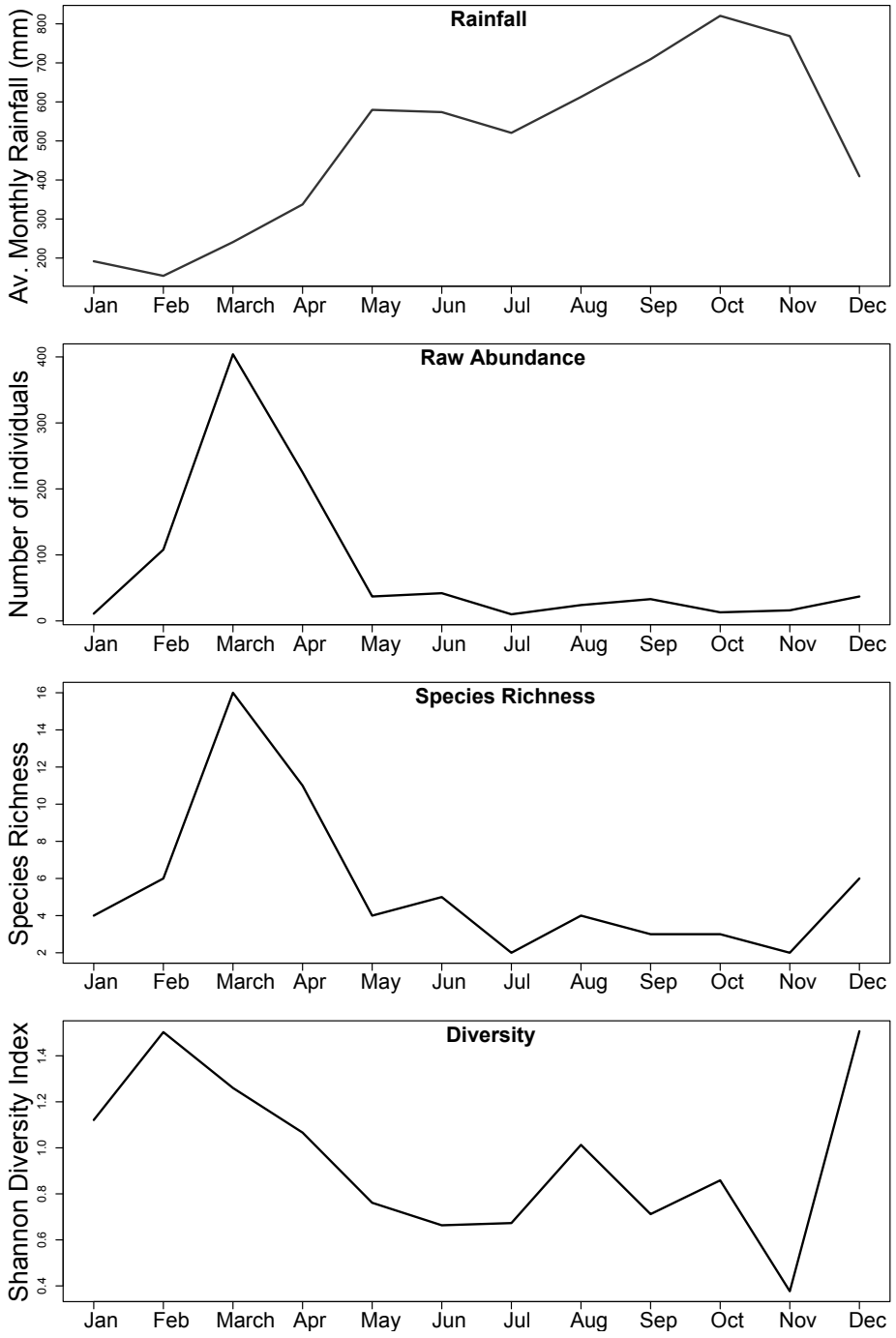

Fig. 5: Average monthly rainfall (1997–2017) and phenology in raw abundance, species richness, and diversity. – Abb. 5: Durchschnittlicher Monatsniederschlag (1997–2017) und Phänologie der Abundanz, Artenvielfalt und des Diversitätsindex.

Notylia (5 bee species). The pollination network also revealed a substantial amount of pollinator sharing among orchid genera. Since these orchid lineages represent independent origins of the euglossine pollination syndrome, the observed pollinator sharing likely corresponds to convergent evolution of traits that facilitate pollinator attraction. Future studies on the chemical composition of the floral scent of these orchid taxa should reveal whether the same or different scent molecules mediate the attraction of similar bee assemblages.

The analysis of the phenology of bee-orchid associations revealed that the majority of interactions occur during the dry season in the early months of the year (March-April, Figs. 3, 4). Specifically, I found that abundance, species richness and diversity of orchid taxa peaked during the dry season (Fig. 5). In fact, species richness and diversity were negatively correlated with monthly rainfall (Pearson's correlation $p<0.05$ for both richness and Shannon diversity). This pattern is similar to the phenology patterns described previously in Central Panama (Ackerman 1983), where flowering phenology also peaks during the dry season. Although most species of *Euglossa* and *Eulaema* are active year-round, it has been proposed that orchid flowering times have evolved to peak during the dry season to coincide with the highest levels of bee activity (Ackerman 1983). It appears that the seasonality patterns that I observed here are more pronounced than in Central Panama, possibly due to a more severe rainfall differential.

Interestingly, the genera *Stanhopea* and *Coryanthes* exhibit a bimodal blooming pattern (Fig. 3). Moreover, careful inspection of the pollinator associations of *Coryanthes* revealed that the pollinaria collected during the dry season were recovered from several bee species including *E. bursigera*, *E. despecta*, *E. erythrochlora*, *E. flammea*, *E. hansoni*, *E. tridentata* and *E. variabilis*, whereas the pollinaria recovered during the wet season were found only on *E. hansoni* bees. This observation may indicate the presence of two (or more) species with distinct blooming periods in the genus *Coryanthes*. However detailed pollinator observations and genetic work are required to confirm this assertion. This pattern was detected despite the greater sampling effort during the dry season, therefore indicating that sampling bias is unlikely to result in equivocal patterns of phenology. These patterns of flowering asynchrony with respect to the period of highest bee activity (dry season) are similar to the pattern described for two species of *Catasetum* in Panama (Zimmerman et al. 1989). Multiple factors may conspire to shape the timing of flowering phenology, including plant growth, leaf production, herbivore pressure, seed predation, and flower predation. The balance of these forces may ultimately shift flowering phenology towards time periods of lower (suboptimal) bee activity.

The phenology analysis also revealed that the majority of orchid genera present in the bee-orchid network bloom during a relatively narrow seasonal period, with most orchid genera being observed in the dry season (Figs. 3, 4). The genus *Gongora* was by far the most abundant pollinarium type in this study and also showed a pronounced blooming peak during the dry season (March-May, Fig. 3). Although at first glance this pattern may suggest the presence of a single species of *Gongora* in the area, ongoing work by colleagues and myself has indicted the presence of several cryptic species that can only be differentiated via floral scent chemistry, each of which attracts a unique set of bee pollinators (Hetherington-Rauth & Ramírez 2016). However, morphological examination of the pollinaria collected in this survey did not reveal any diagnostic traits that allow the separation of cryptic species. Other genera with narrow blooming times may also contain several cryptic species, and additional work is needed.

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