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Thematic Review

The contribution of the BIOTA/FAPESP Program to the knowledge on pollination and plant reproduction

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Abstract: Interactions between plant and pollinators are associated with the origin and maintenance of species diversity, as well as ecosystem functioning. The potential of pollination as an ecosystem service is evidenced by its association with food production. Understanding pollination at the landscape scale is essential for characterizing the pollination service for several crops that depend on pollinators for fruit and seed set that make up the human diet. Our aim was to carry out a literature review of studies and projects funded by BIOTA/FAPESP to illustrate the main research approaches developed in the field of Pollination Biology, especially related to plant-pollinator interactions. Plant-pollinator interactions in the Atlantic forest were leveraged as a result of this long-term research program, during which several papers were published in international journals. Pollination by bees (melittophily) was the most representative pollination system studied. In addition to melittophily, other interactions were studied such as pollination by hawkmoths (sphingophily), by hummingbirds (ornithophily) and by bats (chiropterophily). The specific mutualistic relationships between fig trees and fig wasps were also subject of studies within the Program. At the beginning of the BIOTA/FAPESP Program, there were many gaps in basic information about pollination and breeding systems of Brazilian native plant species. Thus, the Program was fundamental to fuel research on the natural history of plants and pollinators from the Atlantic forest. Overall, the Program funded studies that investigated themes such as functional pollination ecology, pollinator effectiveness, plant population genetics, structure and dynamics of plant-pollinator interaction networks, as well as geographic distribution and macroevolution of pollination systems, as well as genetic and molecular studies of native plant populations focusing on pollen flow and genetic structure of populations. Additionally, studies on pollination in the context of landscape ecology had the aim of assessing the effects of forest fragmentation on the functioning of plant populations and their interactions with pollinators and the relationships between landscape structure and ecological processes, biodiversity, and ecosystem service. Therefore, the Program had a prominent role in producing basic data with great implications for understanding the ecology and promoting the conservation of plant-pollinator interactions.
Keywords: *Abiotic and biotic pollination; pollen transport; reproduction; species diversity; functional ecology; ecosystem services.*

Contribuição do Programa BIOTA/FAPESP para o conhecimento sobre polinização e reprodução em plantas

Resumo: A interação planta-polinizador está associada à origem e manutenção da diversidade de espécies de plantas e ao funcionamento dos ecossistemas. O potencial da polinização como serviço ecossistêmico é destacado quando associado à produção de alimentos. Compreender esta interação na escala da paisagem é

essencial para caracterizar o serviço de polinização para muitos cultivos que dependem dos polinizadores para a formação de frutos e sementes que integram a dieta humana. O objetivo deste trabalho foi realizar uma revisão bibliográfica de estudos e projetos financiados pelo BIOTA/FAPESP para ilustrar as principais abordagens de pesquisa desenvolvidas no campo da Biologia da Polinização, especialmente relacionadas à interação planta-polinizador. As interações planta-polinizador na Mata Atlântica foram alavancadas como resultado desse programa de pesquisa de longo prazo, durante o qual vários artigos foram publicados em revistas internacionais. A polinização por abelhas (melitofilia) foi o sistema de polinização mais representativo estudado. Além da melitofilia, outras interações foram estudadas, como a polinização por mariposas (esfingofilia), por beija-flores (ornitofilia) e por morcegos (quiropterofilia). As relações mutualísticas específicas entre figueiras e vespas do figo também foram objeto de estudos no âmbito do Programa. No início do Programa BIOTA/FAPESP, havia muitas lacunas sobre informações básicas sobre polinização e sistemas de reprodução de espécies vegetais nativas brasileiras. Assim, o Programa foi fundamental para desenvolver pesquisas sobre a história natural de plantas e polinizadores da Mata Atlântica. No geral, o Programa financiou estudos que investigaram temas como ecologia funcional da polinização, eficácia de polinizadores, genética de populações de plantas, estrutura e dinâmica de redes de interação planta-polinizador, bem como distribuição geográfica e macroevolução dos sistemas de polinização, além de estudos genéticos e moleculares de populações de plantas nativas com foco no fluxo de pólen. Adicionalmente, estudos sobre polinização no contexto da ecologia da paisagem tiveram como objetivo avaliar os efeitos da fragmentação florestal no funcionamento das populações de plantas e suas interações com os polinizadores e as relações entre a estrutura da paisagem e os processos ecológicos, biodiversidade e serviços ecossistêmicos. Portanto, o Programa teve um papel de destaque na produção de dados básicos com grandes implicações para o entendimento da ecologia e promoção da conservação das interações planta-polinizador.

Palavras-chave: *Interações bióticas e abióticas; transporte de pólen; reprodução; diversidade de espécies; ecologia funcional; serviços ecossistêmicos.*

Introduction

Pollination is a fascinating and unintentional process that is related to plant sexual reproduction and it involves pollen transport either by abiotic (wind and water) or biotic vectors (invertebrate and vertebrate animals), in which the expected result is fruit and seed set (Willmer 2011, Ollerton et al. 2011, IPBES 2016). Pollinators often collect pollen and nectar for protein and energetic nutritional requirements, respectively (Willmer 2011). Interactions between plants and pollinators are associated with the origin and maintenance of species diversity, as well as ecosystem functioning (Andresen et al. 2018).

Pollinators are mostly insects, such as bees, flies, butterflies, moths, wasps, beetles and thrips, but there are also vertebrate pollinators, such as birds, bats, non-flying mammals and lizards (Rech et al. 2014, BPBES/REBIPP 2019). In Brazil, bees are the most abundant group of pollinators, being essential in agriculture, as they pollinated 78.9% of the main agricultural crops (BPBES/REBIPP 2019).

This ecological interaction provides many benefits to humans, and it is classified as a regulatory, provisional and cultural ecosystem service (IPBES 2016, Costanza et al. 2017, BPBES/REBIPP 2019). The pollination process is responsible for genetic variability of native plant populations that support biodiversity and ecosystem functions (regulating service); reliable and diversified supply of fruits, seeds, and honey (provisioning service) and the promotion of cultural values related to traditional knowledge (cultural service) (IPBES 2016, Costanza et al. 2017, BPBES/REBIPP 2019). The potential of pollination as an ecosystem service is evidenced by its association with food production. The first global economic valuation of the ecosystem service of pollination was of US $ 70 billion/year (Costanza et al. 1997). More recently, this ecosystem service was valued at € 153 billion (Gallai et al. 2009). This number was updated in IPBES's Pollinators, Pollination and Food Production Assessment Report, estimated between US $ 235 billion and US $ 577 billion (IPBES 2016). In Brazil, it is estimated that pollination related to agricultural production has an annual value of US $ 12 billion (Giannini et al. 2015, BPBES/REBIPP 2019).

During the first two decades of the BIOTA/FAPESP Program, several projects were developed with the aim of understanding the diversity of interactions between plants and pollinators. Studies that describe the natural history of the plant-pollinator interaction revealed important details for the maintenance and conservation of the species that participate in the pollination process. Studies of population and community ecology are important to understand the spatio-temporal distribution of pollination interactions, comprising the behavior of these interactions in different landscapes related to diverse scenarios. Understanding pollination at the landscape scale is essential for characterizing the pollination service for several crops that depend on pollinators for fruit and seed set that integrate the human diet.

In this study, our aim was to carry out a literature review of studies and projects funded by BIOTA/FAPESP to illustrate the main research approaches developed in the field of Pollination Biology, specially related to plant-pollinator interactions. We conducted a systematic review of the literature in the databases Web of Science and Dimensions, starting in 1999, using the following search terms "Pollination" AND "BIOTA/FAPESP". In addition, we consulted the virtual library of FAPESP with the search terms "Pollination" OR "Pollinators" (in English and Portuguese) considering the filter "Programs focused on specific themes – Research in Biodiversity", in order to identify the projects supported by the BIOTA Program and related to plant-pollinator interaction. The search resulted in eight

projects (Supplementary Material 1). Publications related to these projects were also included. After removing duplicate studies, the review resulted in 63 studies, including scientific articles (57), book chapters (1) and thesis (5) (Supplementary Material 2). We also evaluated the objectives and impacts of projects funded by the BIOTA/FAPESP Program (Supplementary Material 3). In addition to the scientific impacts, these projects indirectly helped build initiatives for the restoration and conservation of the Atlantic Forest.

Below, we present an overview of the major approaches developed within the BIOTA Program, from the first studies on the natural history of plants and pollinators, then ecological-evolutionary studies, to studies in the context of landscape ecology and ecosystem services. We were able to identify the contribution of the BIOTA/FAPESP Program to the consolidation of the Pollination Biology research in Brazil, mainly in the state of São Paulo, and the potential for developing innovative research on this topic in the future.

Studies on the Natural History of Plants and Pollinators

Studies on the natural history of angiosperms have always been important for Brazilian Pollination Biology and gained prominence in recent decades with the support of the BIOTA/FAPESP Program. The ecology of plant-pollinator interactions in the Atlantic forest was leveraged as a result of this long term research program, especially the ones concerning two of the world's richest plant families: Orchidaceae and Fabaceae. During the Program, several papers were published in international journals (e.g. Pansarin et al. 2008a,b, 2018, Sazima et al. 2009, Brito et al. 2010, Agostini et al. 2011, Amorin et al. 2013, Moré et al. 2012, Nunes et al. 2013, 2015, 2017, Avila et al. 2015, Saab et al. 2021).

Pollination by bees (melittophily) (Figure 1A) was the most representative pollination system studied in this period, as expected from the global pattern of dominance of bees as pollinators (Ollerton 2017). Such studies used different approaches, but most of them had a greater focus on plants. In those studies, researchers explored questions related to floral traits, such as differences in stamen sizes and their relationship to pollination (Valadão-Mendes et al. 2022, Saab et al. 2021) and the functional convergence between flowers of different families (Sazima et al. 2009). The floral resources offered by plants were studied in detail, analyzing the floral anatomical structure, nectar production dynamics, and chemical composition of the different resources (Pansarin et al. 2008a, Agostini et al. 2011, Souza et al. 2017, Guimarães et al. 2018). Also, differences in the reproductive system of each species under different environmental conditions were the topic of several studies (Pansarin et al. 2008b, Brito et al. 2010, Brito & Sazima 2012). Other studies have focused mainly on bee pollinators, offering lists and reviews of the main pollinating agents in the studied areas (Gaglianone et al. 2011, Imperatriz-Fonseca et al. 2011, Cordeiro et al. 2013), and showed that the specificity of the relationships between plants and bee pollinators may not be confirmed when the studies are carried out in detail (Nunes et al. 2017, Pansarin et al. 2018).

In addition to melittophily, other interactions were studied within the BIOTA/FAPESP Program, such as pollination by hawkmoths (sphingophily) (Figure 1B), by hummingbirds (ornithophily) (Figure 1C) and bats (chiropterophily) (Figure 1D). Using palynological

Figure 1. Some pollination systems studied by BIOTA/FAPESP Program. 1A: *Cirrhaea* sp. pollinated by *Euglossa cordata* (Photo by Ludmila M. Pansarin); 1B: *Inga sessilis* pollinated by the hawkmoths *Erinnyis ello* (Photo by Felipe Wanderley Amorim); 1C: *Stifftia fruticosa* pollinated by the male hummingbird *Thalurania glaucopis* (Photo by Ivan Sazima & Marlies Sazima); and 1D: *Mucuna urens* pollinated by the bat *Glossophaga soricina* (Photo by Ivan Sazima & Marlies Sazima).

techniques, Avila et al. (2010) showed the diversity of pollen types found in Sphingidae, while Moré et al. (2012) demonstrated that phenotypic selection is dependent on the match between the long tongue of hawkmoths and flower nectar spur in a highly specialized long-spurred orchid. In the Atlantic forest hummingbirds are the main group of birds that act as pollinators of flowers, and our understanding of this interaction was expanded by the study by Lunau et al. (2011) that unprecedentedly showed that the avoidance of achromatic colors by bees provides a private niche for these birds. Other studies also allowed us to better comprehend the diversity and the morphological, anatomical, and functional aspects of ornithophilous flowers (Rocca & Sazima 2008, Stahl et al. 2012, Nunes et al. 2013, 2015).

The fascinating specific mutualistic relationships between fig trees and fig wasps was also subject of studies within the Program, such as the results published by Farache et al. (2009) and Cruaud et al. (2010, 2011). These studies addressed the strict cospeciation and historical biogeography between them. On the other hand, generalist plants were also represented within the context of natural history, like two representatives of Fabaceae *Inga sessilis* (Figure 1B) and *Inga subnuda*, pollinated by four different groups of animals: hummingbirds, bees, hawkmoths and bats (Amorim et al. 2013, Ávila et al. 2015).

Studies on Ecology and Evolution of Plant-Pollinator Interactions

At the beginning of the BIOTA/FAPESP Program, there were many gaps in basic information about pollination and breeding systems of Brazilian native plant species, as well as on behavior of native pollinators. The Program was fundamental to fuel research on the natural history of plants and pollinators from the Atlantic forest. As the knowledge on pollination, breeding systems and pollinator behavior assembled, the research questions moved to ecological and evolutionary aspects of plant-pollinator interactions and plant reproduction, without neglecting the task of documenting basic natural history data. Overall, BIOTA/FAPESP funded studies that investigated themes such as functional pollination ecology, pollinator effectiveness, plant population genetics, structure and dynamics of plant-pollinator interaction networks, as well as geographic distribution and macroevolution of pollination systems (Supplementary Material 2). Below, we provide an overview of these studies and some of their findings.

Research on the functional pollination ecology encompassed from specialized pollination systems (e.g. long-tubed hawkmoths and long-spurred orchids, Moré et al. 2012) to generalized ones (e.g. generalist brush flowers, Ávila Jr. et al. 2015), although we noted a preference for specialized systems among the studies (bat, hummingbird or large bee pollination systems, Supplementary Material 2). In this context, it was shown that nectar traits may change along the flower lifespan, matching the preferences (Agostini et al. 2011, Amorim et al. 2013) and availability of pollinators (Stahl et al. 2012, Souza et al. 2017). There was also a focus on flower colour, with studies demonstrating how colour variation within flowers (Saab et al. 2021), within plants (Brito et al. 2015), within populations (Bergamo et al. 2016) and between plant species (Lunau et al. 2011) are related to the visual abilities of bees and/or hummingbirds. Finally, studies have demonstrated the role of floral scent in attracting Euglossini bees (Nunes et al. 2017) and in maintaining high pollinator visitation in rewardless flowers (Guimarães et al. 2018). Overall, these studies focused on particular traits of plants and pollinators, advancing our knowledge of physiological, morphological, and behavioral adaptations that mediate plant-pollinator interactions.

Some studies helped reveal the consequences of distinct floral visitors and their behavior on the outcomes of plant-pollinator interactions. In this regard, BIOTA/FAPESP has funded research on the specialized fig pollination system, investigating the negative and positive effects of figs and fig-wasps on each other (e.g. Elias et al. 2008). Such accumulated knowledge contributed to a review of the evolutionary impacts of this interaction on figs and fig-wasps (Cruaud et al. 2011). At the level of single plant species, it was shown how bee body size determines which floral visitors are mutualists and which are antagonists in *Jacaranda caroba* (Quinalha et al. 2017). Similarly, a study revealed that nectar rewards in *Sophora tomentosa* and *Crotalaria vitellina* are available only for long-tongued bee pollinators but not for small antagonists (Brito et al. 2010). Moreover, bill length determined which hummingbird species were more effective in depositing pollen on the stigmas of the bromeliad *Vriesea rodigasiana* (Rocca et al. 2006). In sum, BIOTA/FAPESP contributed not only to the understanding of the evolution of specialized fig pollination systems but also to how pollinator traits influence their performance as mutualists or antagonists in plant species with distinct flower morphologies.

BIOTA/FAPESP also funded genetic and molecular studies of native plant populations focusing on how the pollen flow via pollinators influenced populations' genetic structure. Using microsatellite markers, one study revealed high outcrossing rates and infrequent selfing in progenies of *Qualea grandiflora*, implying that pollinators were effective in promoting cross-pollination (Antiqueira & Kageyama 2015). A limited pollen flow was found among *Copaifera langsdorfii* populations, which suggests that long-distance pollination is rare in the studied area (Antiqueira et al. 2014). The opposite pattern was reported for *Centrolobium tomentosum*, in which most of the gene flow between populations was through pollen instead of seeds (Sujii et al. 2021). The role of pollinators was also evident in a comparative study involving *Tibouchina pulchra*, in which low-altitude populations showed high pollinator visitation and outcrossing rates, while high-altitude populations showed low pollinator visitation and more selfing (Brito et al. 2016). These studies highlight the potential of combining genetic and ecological approaches to reveal complex evolutionary processes.

There was a great effort in documenting interactions for entire plant-pollinator assemblages. This effort resulted in several studies investigating the structure and dynamics of plant-pollinator networks. For instance, flower morphology (Valadão-Mendes et al. 2022) and bee body size (Raiol et al. 2021) determined bee-plant interactions and influenced the structure of bee-plant networks. We highlight the BIOTA Gradiente Funcional project, which funded studies of plant-pollinator interactions along altitudinal gradients, including plant-bee (Pinheiro et al. 2018), plant-hummingbird (Vizentin-Bugoni et al. 2014) and plant-hawkmoth networks (Sazatornil et al. 2016). These studies stressed the importance of plant and pollinator traits in shaping network structure. All this knowledge also contributed to broader investigations at regional and global scales, showing how plant-bee networks change along environmental gradients (Giannini et al. 2015) and how niche processes influence plant-hummingbird network dynamics (Simmons et al. 2019). In this sense, BIOTA/FAPESP

greatly contributed to our understanding of plant-pollinator patterns and processes at the community level.

Finally, there were also great advances in registering plant and pollinator occurrences, greatly advancing our understanding of broad geographic and macroevolutionary patterns of pollinators and pollination systems. Such efforts were mainly focused on bees, which generated occurrence databases of oil-collecting bees (Gaglianone et al. 2011), Euglossine bees (Cordeiro et al. 2013) as well as bee-pollinated plants in general (Imperatriz-Fonseca et al. 2011) for the state of São Paulo. Advancing the knowledge of bees and their associated plants also promoted ecological niche modeling studies, which are important to predict how pollination systems may face anthropogenic threats such as climate change (Giannini et al. 2010). In this context, by combining ecological niche modeling and analysis of pollen loads, it was shown which plant species are important to protect two Euglossine bee species across their distribution (Miranda et al. 2021). As data on pollination systems also accumulated, it was possible to conduct studies investigating macroevolutionary patterns of the pollination of tropical plant groups (e.g. Stanhopeinae orchids, Pansarin et al. 2018). Therefore BIOTA/FAPESP had a prominent role in producing basic data with great implications for understanding the ecology and promoting the conservation of plant-pollinator interactions.

Pollination as an Ecosystem Service and the Landscape Effect: Applied Approach and Future Perspective

Based on projects funded by BIOTA/FAPESP, studies on pollination in the context of landscape ecology began in 2006 with the aim of assessing the effects of forest fragmentation on the functioning of plant populations and their interactions with pollinators (Supplementary Material 1 – Projects supported by BIOTA/FAPESP Program – project 2004/10299-4, coordinator Rodrigo Augusto Santinelo Pereira) and the relationships between landscape structure and ecological processes, biodiversity and ecosystem services (Supplementary Material 1 – Projects supported by BIOTA/FAPESP Program – project 2013/23457-6, coordinator Jean Paul Walter Metzger).

In this sense, pollination is considered an ecosystem service when it contributes to food production. For instance, for the production of Arabica coffee, biotic pollination promotes an 18% increase in fruit set assessed in a global review (Moreaux et al. 2022). Additionally, forest cover near plantations contribute to increased coffee yields and insect diversity in Brazil (Saturni et al. 2016, Medeiros et al. 2019, González-Chaves et al. 2022), but forest proximity is also important (González-Chaves et al. 2020).

Moreover, studies with a focus on the sustainable use and conservation of pollinators (Supplementary Material 1 – Projects supported by BIOTA/FAPESP Program – project 2004/15801-0, coordinator Vera Lucia Imperatriz Fonseca and project 2017/21097-3, coordinator Osmar Malaspina) have demonstrated that stingless bees have the potential to increase production of several crops, such as eggplants (Nunes-Silva et al. 2013). Thus, as several crops are dependent on biotic pollination for food production, this reflects the demand for this service. On the other hand, the supply of pollination depends on the amount of habitat and vegetation cover in forest remnants, so the provision of this service can be compromised by changes in land use and land cover over time. Based on modeling of predicted land use and land cover changes associated with agriculture expansion (between the years 2012 and 2030) in São Paulo state, the demand for pollination will increase by 40% by 2030, while pollinator supply will decrease by 3% (Barbosa et al. 2020).

The knowledge about the geographic distribution of Meliponini bees and their interactions with plants allowed the development of initiatives related to the creation and availability of this information in databases (Cartolano Júnior 2009), (Supplementary Material 1 – Projects supported by BIOTA/FAPESP Program – project 2004/15801-0, coordinator Vera Lúcia Imperatriz-Fonseca). Available information on a wide range of pollinator species and their interactions with plants can be used in studies of functional ecology and ecosystem restoration. Montoya-Pfeiffer et al. (2020) demonstrated that the abundance and diversity of bee communities and the frequency and diversity of the interacting plant species in restoration plantings were lower than those in primary forest fragments but higher than those in anthropogenic wetlands and sugarcane fields, suggesting that restoration plantings better enhance bee community recovery and functionality than other disturbed habitats. The authors also concluded that restoration efforts should include the provisioning of nesting resources and management and conservation of primary forest remnant fragments that represent source habitats for them.

From now on, the assembled information about plant-pollinator interactions can be used to guide decision-making, for example in restoration programs regarding the choice of priority of plant species for bee visitation, which highlight that these plant species are clustered in a small number of phylogenetically-diverse plant families (Campbell et al. 2019). Finally, the support of the BIOTA/FAPESP Program to projects on cross-cutting themes with pollination and developed under the demand of environmental and agricultural agencies has enabled the state of São Paulo to play a leading role in developing applied research for decision-making (Projects supported by BIOTA/FAPESP Program – project 2016/17680-2 , coordinator Gerd Sparovek).

Supplementary Material

The following online material is available for this article:

Supplementary Material 1 – Projects supported by BIOTA/FAPESP Program.

Supplementary Material 2 – Publications resulted from a systematic review of the literature in the databases Web of Science and Dimensions, starting in 1999, using the following search terms “Pollination” AND “BIOTA/FAPESP”. In addition, we consulted the virtual library of FAPESP with the search terms “Pollination” OR “Pollinators” (in English and Portuguese) considering the filter “Programs focused on specific themes – Research in Biodiversity”, in order to identify the projects supported by the BIOTA Program and related to plant-pollinator interaction.

Supplementary Material 3 – Projects supported by BIOTA/FAPESP Program; main goals and impact indexes. Abbreviations: BP.TT = Scholarship in Brazil: Technical Training Program; BP.IC = Scholarship in Brazil: Scientific Initiation; BP.MS = Scholarship in Brazil: Master; BP.DR = Scholarship in Brazil: PhD; BP.DD = Scholarship in Brazil: PhD (Direct); BE.PQ = Scholarships abroad: Research. Information from the FAPESP Virtual Library (https://bv.fapesp.br/pt/) and from the BIOTA/FAPESP Program website (https://www.biota.org.br/).

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Conflicts of Interest

The authors declare that they have no conflict of interest to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that require approval by an Institutional Committee.

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