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Review

Floral biology and pollination in Brazil: history and possibilities

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ABSTRACT

Pollination research in Brazil virtually started with Fritz Muller, whose insights supported Darwin's evolutionary theory. Pollination systems of Brazilian plants were studied mainly by travelling researchers until early last century when native or resident geneticists began to use floral biology information to deal with crop acclimatization and breeding, later applying similar experiments and techniques to investigate native plants. Bee geneticists studied common pollinators of crops, such as coffee and *Citrus*, and even the introduction of feral African honeybees, despite their associated problems, stimulated pollination research. Geneticists attracted Dobzhansky to Brazil, where his research on tree distribution in the Brazilian Amazon represented a turning point for tropical pollination research by prompting the discovery of long-distance pollinating bees, thus bringing pollination back to mainstream evolutionary research. Tropical pollination studies stimulated the emergence of research groups in the Amazon and São Paulo states. In 1998, a seminal conference held in São Paulo called for the need to conserve pollinators and pollination systems. Subsequent research has been integrated under the Brazilian Pollinators Initiative, with research groups established throughout the country. A revived International Pollination Course, a National Pollination Symposium, and cooperative efforts to tackle complex interaction networks may direct future pollination research in Brazil.

Keywords: breeding system, ecological services, floral biology, plant conservation, plant-animal interactions, pollination

Introduction

Pollination is a basic process for the diversification and evolutionary success of the flowering plants. Moreover, studies on pollination biology have provided insights into community organization and are essential for the sustainable use of plants in agriculture and human welfare. This is especially true in a country as Brazil, which is characterized by an enormous plant diversity and has depended on agriculture and natural resources for its development. This special issue of Acta Botanica Brasilica presents a series of papers that focus on the different aspects of plant pollination and reproductive biology, aiming to present a general panorama of these studies in Brazil and providing links with the growing knowledge and interest in this field as a whole. Herein, we outline the history of pollination studies in Brazil and put them into the context of this research field worldwide.

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First, there was a flower

In his seminal review of the history of pollination biology, Herbert Baker separated such studies into an Old testament and a New testament (Baker 1983). He described studies before the XIX century as tentative and often erratic lines of observation in contrast with Darwinian and post-Darwinian studies, which recognized plant pollination and reproductive biology as central for the understanding of evolution and diversification of life on earth (Barônio *et al*. 2016).

Instead of a biblical analogy, we use here a historical one, separating periods which may help to detail the different stages of floral biology studies. A pre-historical age of basic studies in the XVIII was followed by a classical age or an organizing period in the XIX century. Darwin himself was a key figure in organizing this classical period, since some 14 % of all his published papers were on floral biology (Schneckenburger 2009; Rech & Westerkamp 2014). However, he was certainly influenced by at least two other key figures who helped to define floral biology as a study field in itself. Kölreuter (1761) and Sprengel (1793) works based Darwin's own work on plant reproduction, which occupied most of his later life, somewhat helping to consolidate the evolutionary theory and using the evolutionary approach to shed a new light on floral morphology and functioning (Schneckenburger 2009; Rech & Westerkamp 2014). Darwin's fascination for flowers and floral biology, shared by many scholars of the XIX century, led to an enormous interest in this field. By the turn of the century, pollination and floral biology studies were compiled in a monumental study (Knuth 1898-1905), which suggested these studies would become a mainstream research field in the new XX century (Baker 1983). However, this actually marked the end of the classical period.

A kind of middle age followed the XIX century bloom, and was characterized by a segregation between evolution, ecology and genetics during the first half of the XX century, which made floral biology a less interesting endeavor. During this period, floral biology studies were centered on cultivated plants or viewed as a curiosity of travelling botanists, who discovered and/or studied bird and bat pollination systems in detail, among other things (e.g. Porsch 1931; 1932). During the first half of the XX century, due to the two world wars and social unrest, floral biology and pollination studies, to a certain extent, shifted to the New World, and from temperate to tropical areas (Baker 1983; Proctor *et al*. 1996; Vogel 2007). This period, however, was also marked by more applied studies on breeding and plant genetics, besides bee and animal behavior as a whole, which provided a larger toolset to handle studies in natural conditions during the following years (Proctor *et al*. 1996; Vogel 2007).

The post-war Neo-Darwinian synthesis (Mayr & Provine 1980) renewed interest in floral biology. After the relatively stagnant middle age, this renascence, partly enriched by studies in the tropics and on remote islands, helped to put floral biology back into mainstream of evolutionary biology (Baker 1983; Proctor *et al*. 1996; Vogel 2007). This renascence also provided a synthesis in itself, bringing together genetic, physiological, and even molecular biology tools to prompt floral biology studies to another explanatory level (Proctor *et al*. 1996; Endress 1996; Vogel 2007). Nowadays, floral biology and plant reproduction are regarded as vital to understand plant evolution and have provided insights into the evolution and biological diversification as a whole (Friis *et al*. 2011; Sauquet *et al*. 2017; Sokoloff *et al*. 2018). Moreover, in the contemporary age we are facing a pollination crisis, which challenges food safety and human welfare. In this post-modern period, floral biology and pollination studies may help to provide clues on sustainable use of pollination services for agriculture, biodiversity conservation, and human welfare (Garibaldi *et al*. 2011; IPBES 2016; Winfree *et al*. 2018).

Pollination studies in Brazil

A good start

A parallel historical analogy can be attempted for the Brazilian studies in the field of pollination biology. Although there are almost no pre-XIX century studies, Brazil started of well during the classical period, with Fritz Muller's contributions to the mainstream research in Europe, using pollination biology to support Darwin's evolutionary concepts. Born in 1822, the year that Brazil achieved independence, Fritz Muller emigrated to Brazil in 1852, due to his political views. Together with his brother August and both their wives, they resided in Blumenau, at that time a new settlement in the state of Santa Catarina. He kept in contact with friends and family in Europe and maintained a frequent correspondence with Darwin, and with his brother Hermann who was also a biologist. The studies he undertook helped change the way we look at flowers (Rech & Westerkamp 2014).

In addition to discovering a form of mimicry which is now named after him, and publishing his book Für Darwin (Müller 1864), which supported evolutionary theory, Müller made notable discoveries about subjects such as colour change in flowers, division of labor in heteranthery, heterostyly, and dioecy (Baker 1956; Rech & Westerkamp 2014). He also proposed the idea that "ontogeny recapitulates phylogeny" before Haeckel (Hines 2017). Considering the living conditions he encountered during the early period of the Blumenau colony, the over 260 papers published by Fritz Muller are a good indication of the intense nature observations he undertook (Schlenz *et al*. 2012). It is worth mentioning that he hardly ever sent a manuscript for publication, but rather his friends received his letters and re-sent them for publication. Regarding pollination and pollinators, Muller published

around 70 papers encompassing more than 20 plant families (Schlenz *et al*. 2012; Fontes & Hagen 2008; West 2003). Furthermore, his research with plants always focused on natural history case studies, with specific questions and detailed observations (West 2003).

Travelling naturalists and exotic flowers

Beyond Müller, during the rest of classical period and XXst century "middle age", most pollination studies in Brazil were conducted by visiting European and North American researchers and scientific expeditions. Novel "peculiar" pollination systems by birds and bats attracted these researchers' attention, and they described and studied them in much detail (Rech & Westerkamp 2014). Although not locally based, the publications of such visiting naturalists helped foster pollination research in Brazil. Even later in the XX century, tropical diversity continued to attract very good researchers. From the disclosure of bat pollination observed under candlelight and with flash bulbs (Vogel 2007), to the quest for predicted short-style morphs of water hyacinths in the Amazon and Northeast (Barrett 1977), Brazil provided a fertile ground for the development of pollination studies.

Tropical renaissance

The global medieval age for pollination studies was also a period of almost nothing effectively done in Brazil. Studies in Brazil only restarted during the renaissance period, with applied geneticists (native Brazilians or resident researchers) who aimed at solving agricultural problems related to acclimation and breeding, but in doing so, they introduced methods and techniques which helped pollination research. For example, studies on coffee pollination, for example, used bagging and isolation techniques (e.g. Krug 1935; Carvalho & Krug 1949) similar to the ones currently used to characterize mating systems and effective pollination agents (e.g. Maruyama *et al*. 2010). These pollination and breeding experiments and techniques, which allowed the introduction of many crops in Brazil (e.g. Brieger 1945; 2010), were based on studies conducted in North America and Europe which allowed to determine whether cultivated plants were compatible or incompatible, as well as the type of mechanism for the latter (e.g. East & Mangelsdorf 1925; Brieger & Mangelsdorf 1926; East 1932; Gerstel & Mishanec 1950). These experiments also provided the tools to study the reproduction of some Brazilian plants, especially orchids (Brieger 1986).

Geneticists also initiated studies on bee pollination, especially by native Melliponini, which were commonly found in crops such as coffee and *Citrus* (e.g. Nogueira-Neto 1959). Studies on bee genetics and hive management also provided insights on the importance of bee pollination for some Brazilian plants, both crops and native species (Kerr & Laidlaw 1956; Rothenbuhler *et al*. 1968). The introduction and accidental release of Africanized bees by Warwick Kerr (Michener 1975), despite all problems associated, stimulated not only apiculture but also pollination and floral biology research (e.g. Nogueira-Neto 1972, Imperatriz-Fonseca *et al*. 2006). Dr. Kerr himself was important in this process, stimulating research at the different institutions he helped to establish. As we will mention later on, pollination studies in Ribeirão Preto, Manaus, São Luis do Maranhão, and later in Uberlândia were catalyzed by Kerr's enthusiasm for bee studies (e.g. Gottsberger *et al*. 1988) and by the challenges of establishing a sustainable apiculture in tropical America (Roubik 1989). In order to establish such apiculture, he also fostered cross-discipline collaborations involving palynology, taxonomy, ecology and many others.

Brazilian geneticists were also involved in the Neo-Darwinian synthesis revolution, which began in the 1940s (Huxley 1942; Dobzhansky 1959; Mayr & Provine 1980). Many Brazilian geneticists were directly or indirectly linked to Theodosius Dobzhansky, one of the leading figures of the evolutionary discussion arena in the USA at that time. Dobzhansky was attracted to Brazil by a Rockfeller Foundation project and, while in São Paulo, he was mainly involved in teaching and genetic research with natural populations of *Drosophila* flies (Glick 2008). However, surprisingly, his studies on plant distribution in the Amazon represented a turning point for tropical pollination studies. Dobzhansky, along with Clodovaldo Pavan and other researchers mapped tree species in an area of Amazon forest at the Ducke Reserve, near Manaus and showed most species had very sparse representation in the area, with less than one adult individual per hectare (Black *et al*. 1950; Pires *et al*. 1953). The very low population density of many species implied that they were either self-compatible or, if self-incompatible, relied on long distance pollinators. Some authors used these observations to suggest that selfing and genetic drift would lead to local population differentiation and even explain tropical tree diversity (e.g. Fedorov 1966). Genetic drift was a cherished idea for some geneticists because it would allow populations to evade natural selection and competition-prompted evolution and diversification (Mayr 2005; Provine 2004). However, further studies stimulated by that discussion found that most tropical trees were actually self-incompatible (Ashton 1969; Bawa 1974), and led to the discovery of Euglossini (Janzen 1971) and other long distance-flying pollinators (Even not so 'catchy' pollinators as Calliphoridae flies in *Sterculia chicha*, Taroda & Gibbs 1982; and fig-wasps, Nason *et al*. 1996), which serviced large viable populations of outbreeding trees (Bawa 1990; Dick *et al*. 2004). Thus, an unexpected outcome of Dobzhansky's tropical ventures brought pollination back to the mainstream ecology and evolutionary discussion. More than ever, natural selection and possibly competition were the main drivers of evolution and differentiation of tropical trees (West-Eberhard 1983;

Bawa 1992). In an earlier beautiful paper on tropical biology, Dobzansky had already foreseen that biological interactions would play an important role in tropical biota (Dobzhansky 1950), and pollination and breeding studies provided clear examples of coevolved systems and heuristic possibilities (e.g. Sicard & Lenhard 2011). While island habitats select for selfing, as proposed by Baker's law (Baker 1967; Pannell *et al*. 2015), tropical forests were the realm of outcrossing, provided by willing long-distance hopping pollinators and natural selection compliant flowering trees (*e.g.* Chase *et al*. 1996; Gaiotto *et al*. 2003; but see Moeller *et al*. 2017).

Modern age - Schools of pollination studies

Both in Brazil and abroad, the discussion about long distance pollination and tropical plant reproduction called the attention of a new generation of researchers to tropical pollination studies. During the 70s, research groups in Amazon and São Paulo formed both by foreign and Brazilian researchers started to create schools of pollination studies in Brazil. Stimulated by F. Ehrendorfer, Gerhard Gottsberger switched his focus from slime molds to flower-animal interactions and came to Brazil, along with his wife to be Ilse Silberbauer. During their long stay as professors in UNESP-Botucatu, they studied a diversity of Cerrado savannas and Atlantic forest plants (Gottsberger & Silberbauer-Gottsberger 2006). They later moved to São Luis do Maranhão attracted by Warwick Kerr and helped to disseminate pollination studies elsewhere in Brazil. Meanwhile in the Amazon, Ghillean Prance and other botanists studied pollination biology of forest plants, including the emblematic Brazil nut tree (*Bertholletia excelsa* - Lecythidaceae), with its large and complex bee pollinated flowers (Prance 1976), and the even more emblematic *Victoria amazonica*, with its equally large beetle pollinated flowers (Prance & Arias 1975).

While the school of bee pollination research continued to prosper, a floral biology and botanical-driven school started to influence studies in São Paulo. The Plant Biology department was created during the seventies at UNICAMP, in Campinas-SP. The newly established University, under Rector Zeferino Vaz, brought together a diverse group of talented Brazilian and foreign botanists, none of them initially with floral biology as their main research line. They contributed to a floristic project in the Serra do Cipó, which helped focus the research efforts of the newly created department, but also called attention to the diverse and interesting floral biology of the Campo Rupestre plants. Floral biology became an important line of research and teaching at UNICAMP and fostered cooperation with researchers in this line in Brazil and abroad. Starting with fundamental studies on bat and beetle pollination (Sazima & Sazima 1975; Gibbs *et al*. 1977), they created a school of pollination research that quickly became a benchmark in Brazil, with Marlies Sazima as the focal person. Starting from different viewpoints, both bee research and floral biology schools contributed to form different research groups in pollination biology, which are currently established in most Brazilian states and regions (Maués *et al*. 2012).

Taking the initiative

A kind of late synthesis on floral biology and pollination studies started to be developed at the end of last century, bringing together the bee pollination and floral biology schools. In 1998, a seminal conference in São Paulo called attention to the conservation of pollination systems, and a large group of Brazilian and foreign researchers were invited to draw up a conservation initiative for pollinators and pollination (Dias *et al* 1999). As a spin-off of the Rio-92 Meeting, the conference provided a general declaration and proposals of action for an international conservation initiative on pollinators (Kevan & Imperatriz-Fonseca 2002), which helped to focus the effort on pollination studies and conservation both in Brazil and worldwide. Since then, a Brazilian initiative linked to biodiversity conservation and crop pollination studies has slowly integrated pollination study efforts in the country (Imperatriz-Fonseca *et al*. 2006). International pollination courses (Kevan *et al*. 2013), a National Pollination Symposium, and cooperative efforts to tackle interaction networks (see http://www.rebipp.org.br/) have helped to direct future research of this area in Brazil. The initiative also helped to allocate resources to large applied studies (Imperatriz-Fonseca *et al*. 2007) and funded publications over the last two decades (see http://www.mma.gov.br/publicacoes/biodiversidade/category/57-polinizadores).

Current main trends and pollination studies

It is possible to trace at least six different research lines in plant pollination and reproductive biology in Brazil during this XXI century period.

(1) Bee pollination studies have switched from a social bee centered effort to a much more inclusive approach, since solitary bees have been shown to be more important than social bees for many crops and important native plant species (Garófalo *et al*. 2012; Garibaldi *et al*. 2013). For sustainable pollination services, the diversity of native bees appears to be as important as their abundance (e.g. Yamamoto *et al*. 2012) and distribution of natural areas is also vital (DeMarco & Coelho 2004; Saturni *et al*. 2016). These studies always viewed the flora as important for bee maintenance, but the interdependence between the diversity of flowering plants, pollinators, and effective crop pollination service has been highlighted in recent studies.

(2) Floral biology centered studies have also flourished over the last two decades, although case history studies

somehow gave way to comparative, more comprehensive surveys. Natural history case studies still reveals previously unknown complex interactions between flowers and pollinators in the tropics (e.g. Nunes *et al*. 2018), but it is clear that one to one interactions are rare and often anecdotal. Studies moved to the guild level and while syndromes continued to have an heuristic value, field observations showed unforeseen variation in plant pollination systems (Rech *et al*. 2014). Morphological and even phenological adjustments are seldom perfect and studies show dynamic floral polymorphism as the base for the organization of pollination systems (e.g. Moré *et al*. 2012).

(3) Breeding system studies also moved from hand pollination experiments to include molecular markers and other modern approaches (e.g. Gribel 2014; Dias 2017). Accumulated established general trends such as the dependence on active pollination and prevalence of outbreeding for key species and environments (Canuto *et al*. 2014). Nevertheless, apomixis and inbreeding have been shown to be much more common and widespread than previously thought (e.g. Allem 2003; Mendes-Rodrigues *et al*. 2005; Caetano *et al*. 2018). Breeding systems seem to be a population feature, influenced by life forms or habitats, and may help to explain endemism and distribution patterns (e.g. Santos *et al*. 2012). Hence, past and current environmental changes may have an impact on local mating systems and pollen flow (e.g. Carneiro *et al*. 2011).

(4) Community studies have become their own line of work. Research effort on pollination and breeding systems have provided insights into community patterns and organization (Freitas & Sazima 2006). Community studies permitted a comparison of different natural habitats and confirmed general trends, such as the pervasive outbreeding mechanisms among trees in different tropical biomes (Machado *et al*. 2006). The basic studies have also followed changes in breeding and pollination systems after disturbance and habitat fragmentation (e.g. Girão *et al*. 2007; Lopes *et al*. 2009).

(5) The challenge of understanding highly diverse tropical communities has been tackled by interaction network approaches and metrics (Vizentin-Bugoni *et al*. 2018). Studies on plant-pollinator networks have allowed large sets of data to be brought together in comprehensive large scale studies (e.g. Zanata *et al*. 2017). These approaches advanced from simple characterization and metrics (e.g. Bezerra *et al*. 2009) to more sophisticated studies defining compartments, and ecological and evolutionary drivers of community organization (e.g. Maruyama *et al*. 2014). Brazil has great potential to contribute to such community-wide network studies, as most of its biomes are still under-sampled (Vizentin-Bugoni *et al*. 2018), and when studies are conducted, they have contributed with distinct patterns to what was previously assumed (e.g. Souza *et al*. 2018).

(6) Pollination for crop production and pollination management have been highlighted in recent studies using different approaches to understand, evaluate, and model pollination services. Data on Brazilian crop systems, including passion fruit and coffee, contributed to large-scale studies of landscape effect on crop pollination systems (e.g. Ricketts *et al*. 2008; Garibaldi *et al*. 2016; Hipolito *et al*. 2018). These studies showed the impact of habitat fragmentation on pollination systems, which was much stronger for large native bees. Dependence on pollination has increased during the last decades and the value of these services has also increased (Rader *et al*. 2016). Even though general studies have shown that the most consumed crops are somewhat independent from pollination, crops that do depend on pollination are important for cultural and nutritional security (Giannini *et al*. 2015). These general trends provide basic data to model the impact of climate and environmental changes on pollinator's distribution and the sustainable use of pollination systems (Giannini *et al*. 2013).

Frontiers and perspectives

What to do from now on? Despite the economic crisis, which has been shading Brazilian scientific effort as a whole, we are trying to maintain the initiative and synthesis impetus which characterized the last two decades. This *Acta Botanica Brasilica* issue borrows its title from a graduate course on Fundamentals and Frontiers in Pollination Studies (FFEP, in Portuguese), which is now in its fourth annual edition. The Brazilian Pollination Symposium is in its third biannual meeting, to be held in Botucatu in 2018. The International Pollination Course, which had been held annually on 12 occasions, was renewed in 2017 and will be held in Diamantina in 2019. Furthermore, the Brazilian Bee Meeting, a series of meetings on bee biology and pollination, has been also resumed and will be held in Uberlândia in 2018. Supported by Brazilian Environmental Ministry (MMA), a group of Pollination Biology researchers successfully published the book "Biologia da Polinização" (Rech *et al*. 2014). After the publication the group organized itself under the scope of a National Network called REBIPP (Rede Brasileira de Interações Planta-Polinizador). Since its organization, REBIPP has organized the above mentioned international pollination course and is now engaged in the building of a large Nationwide Database of Plant-Pollinator Interaction. The leading group of REBIPP is also deeply engaged in finalizing the National Report on Pollination, Pollinators and Food Production (Relatório Temático sobre Polinização, Polinizadores e Produção de Alimentos no Brasil), which has a similar framework as the IPBES report on the same subject (IPBES 2016). We hope these initiatives will maintain the interest in pollination studies and provide the basic skills and information for young students and the progress of the scientific field as a whole.

And why do we need to continue studying pollination biology? As mentioned in the beginning, we are facing

a possible crisis which may render pollination services unsustainable and even affect the regeneration of natural areas, environmental quality and human welfare. The best practices and a wide knowledge basis of pollination and plant reproduction are needed to avoid and/or adapt to the era of complex environmental changes we will face. This knowledge basis will be important for the International and National initiatives for sustainable use of pollinators and food production (Abrol 2011; IPBES 2016), for the Global strategies for plant and pollinator conservation (e.g. Aizen *et al*. 2018), and to fulfill the Convention of Biological Diversity - CBD targets for the next decades (https://www.cbd.int/sbstta/sbstta-22-sbi-2/sbstta-22-ipi-draft.pdf).

Issue structure

This special issue includes 19 papers on different aspects of pollination biology, from terminology usage to community organization. We hope they constitute a general overview of the effort and diversity within this research field. Some of the papers focus on different aspects of nectar dynamics and availability. Pollen features are also discussed, including water content and size trade-offs in heterandrous species. Pollinator's arrays with different specialization degrees are described, from large Atlantic forest trees to small rupestrian field shrubs. Pollen and nectar availability may help to keep native bees and continuous flowering plants may present restoration potential. Specialization vs. generalization in floral structures, secretion patterns, and breeding systems are also discussed for different groups. The interplay between environmental conditions and floral features may influence reproductive phenology, pollination systems distribution, genetic diversity, and gene flow in natural populations. Last but not the least, the terminology used in the field is revised, seeking to standardize usage.

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