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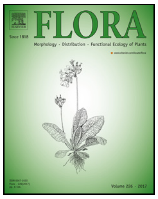

Patterns and mechanisms in plant-pollinator interactions: Stefan Vogel's contribution to contemporary pollination biology☆

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ABSTRACT

The multidisciplinary field of pollination biology was enriched enormously by the contributions of Stefan Vogel (1925–2015). Vogel revived and expanded the pollination syndrome concept and recognized the importance of shifts between pollination modes for angiosperm diversification. He made a number of key discoveries, including perfume and oil reward systems in flowers and pollination of these flowers by highly specialized bees. He also contributed greatly to our understanding of floral mimicry, floral integration, and floral adaptations for bat pollination. Many of his insights were obtained through his field-based research in the tropics and his close ties to faculty and students at various universities in South America. Vogel's work continues to be the inspiration for new scientific endeavours and this special issue of Flora about "Patterns and mechanisms in plant-pollinator interactions" contains a collection of 22 research papers that serve as a tribute to his legacy. The papers cover a wide range of topics and taxa, but can be broadly grouped into the themes of plant-pollinator interactions, functional morphology, floral rewards, floral signals and pollination syndromes, all of which also featured prominently in Vogel's own work.

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1. Introduction

Stefan Vogel, one of the leading pollination biologists of the twentieth century, passed away on November 5, 2015 at his home in Maria Enzersdorf near Vienna, while convalescing from a bout of pneumonia suffered in March of that year. He was 91 years old. During his lifetime Vogel had a very close association with *Flora*, having served on its editorial board for more than 40 years. It is therefore highly appropriate that this special issue of *Flora* celebrates Stefan Vogel's deep and lasting influence on the field of plant pollination biology.

By the middle of last century, when Vogel's interest in pollination biology was born, it was thought that few new contributions could be expected in this field. A post-Darwinian surge in interest had resulted in an impressive body of knowledge, which was synthesized at the beginning of the 20th century in Knuth's *Handbuch der Blütenbiologie* (1898–1905, English version 1906–1909). Against expectations, Vogel's generation sparked a renewal in the field which continues to this day. Though Vogel had a low public profile and held a teleological view of evolution which did not conform to the ideas of the then new modern synthesis, he can be counted among the most influential biologists of this period. Many current research agendas were founded on his seminal work.

Vogel, the youngest of three children born to Wilhelm Vogel and Marianne (nee Hauptmann), was born in April 1925 in the cultural city of Dresden. Surrounded as he was by a family of naturalists and travellers, a fascination with nature, particularly flowers, as well as the desire to visit exotic countries was instilled in him at an early age (Weber and Sonntag, 2006). Growing up near the countryside served to stimulate the development of outstanding powers of observation and a great talent in drawing and painting. His artistic mastery would eventually help him earn a modest living in his youth as a teacher and an artist. However, his true passion was to explore and understand the lives of plants and animals.

Military conscription in 1944 put paid to Vogel's aspirations to study at the University of Dresden. Though destined for the front line in Poland, he was found unfit for combat due to his fragile health, and was sent instead to serve as a draftsman in a munitions factory. After surviving the war, including the incendiary air raid of Dresden, he attended the University of Halle as a freelance student and earned a living as an assistant in the Botanical Museum. Through Professor Hermann Meusel in Halle/Saale he encountered Karl Goebel's plant morphology

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school which was inspired by Goethean natural philosophy. On the recommendation of Professor Meusel, Vogel was eventually admitted to the recently-reopened Johannes Gutenberg University of Mainz where one of Goebel's most prominent pupils, Professor Wilhelm Troll, had been appointed. To move West to Mainz in the French occupation zone, Vogel escaped out from East Germany when a clandestine passing of the checkpoint was still possible. After the East German Republic was created in 1949 and the border to the West German Republic was closed, this would no longer be possible. As a student in Mainz he became acquainted with the morphological-typological view of Troll and the ecological-functional view of Wolfgang von Buddenbrock-Hettersdorff, one of the founders of comparative animal physiology.

Vogel's work is essentially based on detailed observations of natural history phenomena in wild habitats. He studied pollinator behaviour with extreme patience and recorded morphology with remarkable accuracy by examining flowers and insects in the field using a binocular microscope he often carried with him. The scope of his interest was broad, including plant-pollinator interactions, mite-plant interactions (acarodomatia), leaf adaptations and ecology of sublithic algae. When travelling, he always kept thorough records in separate scientific and social notebooks. His exquisitely illustrated field notebooks contain a wealth of unpublished knowledge. His passionate desire to explore exotic places was first satisfied when he and his roommate in Mainz, Klaus Stopp, received funding from the German Research Agency (DFG) to study pollination and dispersal biology in the Cape Flora of South Africa. This enabled them to study this extraordinarily diverse flora over the period of a year, during which much of the time was spent living in a tent in the field. Subsequently he carried out fieldwork mainly in the Neotropics, where he travelled frequently for research purposes and to act as a visiting professor. During his travels he visited Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica and Mexico. Professorships in Universities of Argentina and Brazil helped him to build long-standing collaborations with people he encountered there.

His work had a great impact on the revival of pollination biology, and many of his contributions were adopted by mainstream evolutionary biologists; in particular, his study on the evolutionary diversification associated with different modes of pollination. He also revived the pollination syndrome concept which had been developed by Federico Delpino (van der Pijl, Stebbins, Grant, among others). However, his philosophical approach, inspired by Goethean contemplative natural philosophy, was not completely in conformity with mainstream thinking, which he considered reductionist. Subsequent contributions Vogel also entered the growing pollination biology literature, such as his discovery of "perfume flowers" and "oil flowers". Other outstanding contributions in evolutionary ecology passed largely unnoticed, such as his conceptual framework for floral mimicry, mutualism and parasitism in plant-pollinator interactions, and his pioneer work in the study of floral integration.

2. Vogel's major contributions to pollination biology

2.1. Perception of floral signals by pollinators

Vogel's doctoral thesis concerns flower colour change and nectar guides. His results include the first record of UV-absorbing pigments in flowers (revealed by the reaction of phenol with iron chloride), and predicted their widespread occurrence, which was later confirmed through photographic methods and then later also by reflectance spectrometry.

2.2. Plant diversification in relation to the evolution of pollination syndromes

After studying adaptations for pollination in the Cape flora, where extensive convergence in floral phenotype across plant families and parallel diversification within families and genera was evident, he embraced the ideas of Federico Delpino in applying a "biological concept" to explain angiosperm diversification. This meant that flowers were phenotypically not only suited broadly to pollination by wind, water or insects, but also often further specialized for pollination by different kinds of insects (butterflies, moths, flies, bees, etc.), and by birds. In addition, adaptations of flowers to different animal pollinators could explain diversification within families and genera of plants, and phenotypic similarities across families and genera. In his book "Blütenbiologische Typen als Elemente der Sippengliederung" (Vogel 1954; translated into English in 2012; Vogel, 2012) Vogel discussed the conceptual basis of diversification in families and genera according to pollination modes. He then validated these concepts using data collected from the Cape flora, and assigned pollination syndromes to many other plant species. Vogel wrote this study according to a teleological view, which he later quietly abandoned (Vogel 2007). He resorted to a teleological explanation possibly because a clear concept of evolutionary constraint was lacking at the time. In this regard, Vogel more recently expressed the view that inherent properties of flowers can constrain or favour the adaptation process (Vogel, 2007).

2.3. Functional morphology and floral integration

Vogel was also interested in understanding the function and evolution of floral structures, in other words how morphological and anatomical aspects favour plant-pollinator interactions. For example, he studied mechanisms of pollen adherence (other than the traditional pollenkitt) and the functionality of "kettle-trap" flowers such as *Ceropegia* and *Aristolochia* (e.g., Vogel, 1961).

It is less well-known that early in his career Vogel started to apply the concepts of phenotypic integration and epigenetics to understand flower phenotype evolution. A series of two books on floral organogenesis of Cape orchids are dedicated to explore the principle he called "Koadaptation" meaning, as he explains, phenotypic integration. Vogel understood integration as the reciprocal adjustment (coadaptation) among flower organs that originated separately during development when he stated that "if we wish to view it as a process, it is then possible to treat it as both as an ontogenetic and evolutionary phenomenon". In the same study he suggested applying the epigenetics concept, then already emerging in animal embryology, to explain floral phenotypic integration. That is, that coordination of flower traits is not explained by an intrinsic genetic plan alone and that the interaction among developing organs is influenced by their reciprocal adjustment in the flower.

2.4. Chemical ecology

Vogel discovered that flowers can attract pollinators with rewards other than simply nectar and pollen. His keen powers of observation and deep knowledge of plant and insect biology allowed him single-handedly to discover that male euglossine bees obtained fragrances as a reward that could be collected on the surface of scent glands before they volatilised completely. Vogel realised that the (male) bees were equipped with structures on their front legs for collecting fragrances, and structures on their hindlegs for storing fragrances. He was the first person to describe these structures and to discover how they are utilized during fragrance collection. At the same time he recognized that "fragrance flowers" had evolved independently in four plant families in the Neotropics, particularly the orchids. To study the chemistry of these fragrances he utilized recent advances in thin-layer chromatography which were at that stage being developed in the Ergon Stahl laboratory in Mainz. He had to adapt the protocols to work at low temperatures in order to be able to capture the fragrance components that would otherwise have been lost at ambient temperatures. This approach has since been replaced by gas chromatography and mass spectrometry, but at that time it enabled an initial glimpse into the nature and complexity of floral fragrances.

His monograph on osmophores (Vogel, 1963) is also an inspiring contribution to the chemical ecology of pollination. Here he resorted to methods, innovative in those kinds of studies, to reveal anatomical, cellular and physiological aspects of scent emission, including measurement of thermogenicity and cell electrophysiological features.

Vogel had been long intrigued about "nectaries" in some flowers that, according to his colleague in Mainz, Dimitri Hartl, produced a non-volatile, oily secretion. It was very unlikely that this secretion would be utilized by pollinators in the same way as true nectar. The puzzle was resolved during a visit to Argentina when he was invited as visiting Professor by the University of Buenos Aires and was funded by the Argentinian Research Agency (CONICET) to carry our extensive field work across the country. Key observations allowed him to put together the pieces of the puzzle he had been building/collecting for years. The oily secretion was collected by female solitary bees of the tribes Centridini and Exomalopsini (the paraphyletic Exomalopsini has been split in two tribes, Tapinotaspidini and Tetrapedini, both of which contain oil-collecting species). As he further observed, the oil was utilized by the females as an ingredient of the larval provision and as a lining for the underground brood cells. This discovery opened up a new line of research for him, where he benefited from his versatile genius and ability to gather information from even the least-read corners of the botanical and entomological literature. An impressive body of knowledge including morphological, botanical, entomological, chemical, biogeographic and evolutionary aspects is contained in a series of three books dedicated to the Neotropics, Afrotemperate, Holarctic and Paleotropical biogeographic regions, each of which has its own set of endemic oil-flowers and oil-bees.

2.5. Bat pollination

Before the seminal studies by Vogel, the existence of nectar-feeding bats and of plants that are adapted to utilise these animals as pollinators (chiropterophily), was considered a rarity in neotropical ecosystems. What little was known about bats pollinating flowers was limited to studies carried out in the Old World tropics. Based on observations made during a year in Colombia and another year in the Amazon regions of Bolivia and Brazil, he produced a series of articles that completely changed the scope of this pollination syndrome (Vogel, 1968; Vogel, 1969a,b). Bat pollination was documented by Vogel for the first time in South America and demonstrated for 40 plant species by means of direct observations. Vogel also made a detailed analysis of flower and vegetative traits that could be associated with bat pollination, which led him to suggest that chiropterophily had evolved in a further 15 plant genera, and that bats had been important in the diversification of whole plant families such as the Bromeliaceae, Cactaceae, and Lobeliaceae. He also documented the surprising fact that some nectar-feeding bats, deviating from Old World flying foxes, could drink nectar while hovering, as was already known in hummingbirds. He then deduced that this foraging behaviour was associated with a particular flower architecture which he called "Kurtzglocke" or "Maskenblume" that evolved independently in several bat pollinated linages that had relatively small flowers with disproportionately large nectaries and corollas adjusted to fit just the face or nostrils of bats. Studies later performed in Brazil by Vogel and his close colleagues Marlies and Ivan Sazima, as well as by Isabel Machado, confirmed many of the predicted cases of chiropterophily and greatly expanded our knowledge about this syndrome (Machado et al., 1998; Rocha et al., 2007; Sanmartin-Gajardo and Sazima, 2005; Sazima et al., 1989, 1994, 1999, 2003; Sazima and Sazima 1978, 1980; Vogel et al., 2005). We owe the significant progress in our understanding of nectar-feeding bat biology and on chiropterophily in a geographic context to Vogel.

Vogel greatly influenced the science of pollination biology, and even in his last decade of life contributed highly original perspectives that continue to illuminate future progress in this discipline that he cultivated.

3. Overview of this special issue

The papers in this special issue represent a cross-section of current studies in pollination biology from different parts of the world. These studies address themes that are similar to those in the work of Stefan Vogel and thus serve to continue his legacy. Among these themes are the importance of natural history– field-based discovery and documentation of interactions among species – in pollination studies, the functional fit between flowers and pollinators, a focus on the chemical diversity of floral rewards and on the multimodal signals that flowers use to attract pollinators, and finally pollination syndromes, the patterns of convergent evolution in floral traits that arise among unrelated plants that adapt to functionally similar pollinators.

3.1. Plant-pollinator interactions

A number of the papers in this special issue report the discovery of previously undocumented interactions between plants and pollinators. Etl et al. (2017) report a likely case of collection of perfumes from flowers of *Anthurium acutifolium* by male oil bees using an abdominal hair brush. This is the first known linkage between pollination systems involving perfume and oil-collecting bees. Peter and Venter (2017) confirm a prediction by Vogel of pollination by settling moths in the diminutive African epiphytic orchid *Mystacidium pusillum*. The challenge in predicting pollinators for flowers with an unusual basic architecture ("Bauplan") is addressed by Quintero et al. (2017) in their study of the African parasitic plant *Thonningia sanguinea* (Balanophoraceae). Flowers of this plant are produced at ground level and have been considered likely to be pollinated by carrion flies, but observations in Uganda show that the primary pollinators are actually sunbirds, which is consistent with the large volumes of nectar produced by these flowers. Establishing which pollinators are most effective can be challenging when flowers are visited by many different insects. Quinalha et al. (2017) examined the temporal sequence of interactions between flowers of *Jacaranda caroba* (Bignoniaceae) and various bees. Experimental exclusion of medium and large sized bees, but not small bees, reduced seed set to a level similar to that of flowers from which all visitors were excluded, suggesting that small bees are not effective pollinators. Small bees removed large amounts of pollen from flowers and were thus considered to be cheaters in this system.

Two of the studies in this special issue examine the question of whether there is geographical variation in plant-pollinator interactions within species. Oliveira et al. (2017) examined pollinators of *Unonopsis guatterioides* (Annonaceae) at two widely separated sites in Brazil and found major differences in floral characteristics and pollinator assemblages, with plants at one site having a diverse assemblage of insect visitors while those at the other site seemingly being specialized for pollination by a single perfume-collecting bee species. Ferreiro et al. (2017) studied *Monttea aphylla* (Plantaginaceae), which is unusual in producing both oil and nectar in its flowers. They show that pollinator-mediated selection favours oil production in some populations and nectar production in others. Interestingly, these patterns of selection were not explained by the abundance of the most specialized oil bee visitor (*Centris vardyorum*) which increases with latitude in Argentina, suggesting a more complex geographical mosaic of selection.

Alonso et al. (2017) adopt a community approach in their study of interactions between plants and diurnal pollinators at three sites in Europe and North America. Their study is unusual in using rarefaction curves to attain standardized measures of the diversity of plants used by pollinators (rarefaction is much more commonly used to measure pollinator diversity). A network approach is adopted by Prieto-Benítez et al. (2017) in their review of nursery pollination interactions between *Hadena* moths and plant species in the Caryophyllaceae. They focus on the Mediterranean region, which has received less attention than the north and centre of Europe in previous studies of these interactions.

3.2. Functional morphology

Questions about how much specialization occurs in plant-pollinator interactions and whether traits such as flower depth serve to restrict the assemblage of visitors to those that can access floral rewards have received much attention. Hollens et al. (2017) studied interactions between two oil-producing *Diascia* flowers that vary eight-fold in the length of their floral spurs and four *Rediviva* bees that show two-fold variation in their front legs (used to collect oil from the spurs of *Diascia* flowers). While bees with the longest and shortest legs preferentially visited the long and short spurred *Diascia* species, respectively, the total number of oil bee visitor species was not lower in the longest spurred species, possibly because oil in the proximal sections of the spurs is also available to shorter-legged bees. Burger et al. (2017) consider why two South African *Gomphocarpus* species (Apocynaceae: Asclepiadeae) with apparently morphologically similar flowers show divergence in pollination systems (one species is bee-pollinated, while the other is wasp-pollinated). They find a role for floral scent in selective attraction of wasps to one of the species with freely acccessible nectar, but pollination solely by bees in the other species is more likely explained by a morphological filter that prevents short-tongued insects such as wasps from accessing the nectar. Shuttleworth et al. (2017) found that pollination of the carrion-scented stapeliad *Orbea lutea* subsp. *lutea* was effected exclusively by *Atherigona* flies, even though the flowers of this species also attract many other groups of flies. They found that the *Atherigona* flies were the only visitors whose heads could fit between the inner corona lobes, which is required for the removal and deposition of pollinaria.

3.3. Diversity of floral rewards

Neff and Simpson (2017) provide a timeous and thorough review of the interactions between oil-producing flowers and oil-collecting bees. Originally discovered by Vogel (1969c), this system includes many excellent examples of extreme trait specialization and coevolution, yet many aspects such as the uses of the oils by bees and the geological age of these interactions remain poorly understood. Aside from oil flowers, Vogel also elucidated the interactions between bees and flowers that produce fragrance as a reward for pollinators (Vogel, 1963). Roubik and Knudsen (2017) provide a detailed account of the tibial fragrance bouquets of male *Euglossa mixta* bees, and orchids which they do and do not visit. The found no evidence that bees prefer orchids with fragrances similar to those formed on the hindlegs and support the hypothesis that odour bouquets are used by bees to avoid interspecific reproductive interference.

Trap flowers held a special interest to Stefan Vogel. In this issue, Erbar et al. (2017) examine the structure of nectaries in the pitcher-trap flowers of eight *Aristolochia* species (Aristolochiaceae). They report two type of nectaries – trichomatous and nectarioles, the latter not having been recorded previously in *Aristolochia*. Nectaries in *Aristolochia* are believed to sustain trapped insects and guide them towards the exit, thus promoting pollen export by the flowers. Herrera and Medrano (2017) experimentally test their idea that yeasts in floral nectar of *Helleborus foetidus* (Ranunculaceae) promote pollination success by warming the flowers through metabolic heat production. The effect of warming on pollination success was greatest early in the season, suggesting that it may promote pollinator activity during cold weather.

3.4. Multimodal floral signals

Stefan Vogel pioneered the scientific study of floral scent before the advent of modern capillary GC–MS systems (Vogel, 1963). Raguso and Gottsberger (2017) provide a compact overview of Vogel's contributions to the study of floral scent. Vogel concentrated on histological examination of osmophores (scent-producing regions of flowers) and emphasized metabolic processes, including hypothesised links between floral warming and scent production. Vogel used a staining technique to identify parts of the flower that produce scent, but these regions can now also be identified using highly sensitive scent trapping techniques. Martin et al. (2017) show that short-lived flowers of *Aristolochia gigantea* undergo rapid changes in scent production and that floral scent resembles the vegetative background soon after flowers wilt. Differences in floral scent production among different parts of the flower probably serve to manipulate the behaviour of pollinators. Scent chemistry is key to explaining pollination system specialization in trap flowers. In a study of 14 *Ceropegia* species with trap flowers, Heiduk et al. (2017) find no strong associations between pollination system (all involve various groups of small Diptera) and overall floral scent chemistry. However, a key role for scent in pollinator attraction is implicated by existing experimental studies of *Ceropegia* (Heiduk et al., 2016).

The influence of plant nutrients on scent production has seldom been investigated. Majetic et al. (2017) grew *Petunia* hybrid plants in soils with differing availability of nitrogen, but found little effect on scent production. The main effect of increased nitrogen was to increase the size of the floral display and this probably explained why the pollinators in their experiment preferred plants grown under high soil nitrogen conditions.

Flower colour polymorphisms are found in orchid species with a generalized food deceptive pollination system and it has been hypothesised that these polymorphisms are maintained by negative frequency dependent selection (NFDS) where pollinators switch preference away from the most common colour. To test whether pollinators shift between morph colours when foraging, Groiß et al. (2017) colour-labelled the pollen of purple and yellow morphs of *Dactylorhiza sambucina.* Contrary to the predictions of NFDS, they found that pollinators switched between morphs less often than expected by chance and often showed constancy on the dominant yellow colour in their populations.

3.5. *Pollination syndromes*

In one of his first publications, Vogel (1954) classified plants in the South African flora according to pollination syndromes. Johnson and Wester (2017) re-examine this work in the light of subsequent publications that document the actual pollinators of many of these species. They find that Vogel's assignments of floral syndromes match the recorded pollinators for about 82% of cases, thus confirming the existence of strong correlations between floral phenotype and pollinators. Pollination syndromes are examples of convergent evolution among flowers of unrelated plant species that adapt to functionally similar pollinators. An extraordinary case of such convergence is suggested by Nunes et al. (2017) who demonstrate chemical similarity in the scent of two unrelated orchids pollinated by males of the perfume-collecting bee *Eufriesea violacea.*

4. Conclusions

The contributions to this special issue of Flora are just a small sample of contemporary pollination biology. They are a representation of studies that continue the traditions established by Stefan Vogel and other pioneers in the field. Science is never static and many of the modern methods used in these studies were not available to Stefan Vogel during the time that he was at the peak of his career uncovering new pollination systems in the tropics and elsewhere. However, we think that he would have been pleased to read these papers and we miss the valuable editorial comments that he would have been able to provide on all of the contributions on account of his encyclopaedic knowledge of floral biology and animal pollinators.

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