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Applications of pollination biology in studies of evolution, ecology and agriculture: Perspectives and trends from South Africa

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ABSTRACT

Pollination is an essential process for the reproduction of most plants and usually involves animals as agents of pollen dispersal. Pollination biology in the broad sense is therefore relevant to many different scientific fields. Here we examine how pollination biology in South Africa has contributed to our understanding of evolutionary biology, fundamental and applied ecology and agriculture. Due to its high levels of biodiversity and relatively intact ecosystems, South Africa has unique geographical advantages for research involving pollination systems. Some of the highlights of evolutionary work include studies of the functions of floral structure, signals and rewards, including various kind of floral deception, elucidation of convergent floral evolution in plants specialized for pollination by particular animal groups, and advances in our understanding of coevolution and pollinator-driven plant speciation. In terms of ecology, there has been impactful research on the ecological dependence of plants on pollinators for seed production and the influences of population and community contexts on pollination processes, as well as applied applications in terms of risks of mutualism failure and the use of plant reproductive traits for predicting the spread of invasive species. In agriculture, there have been ground-breaking studies of the biology of honeybees and estimates of the value of natural habitats for pollinator services. Studies of pollination biology have proven highly valuable in advancing understanding in a wide range of fields in biology globally, and work in South Africa has contributed significantly, particularly over the past five decades.

1. Introduction

Pollination biology has a rich scientific tradition that goes back to the first elucidations of the function of flowers by Sprengel and the work of Darwin who viewed flowers as outstanding examples of adaptation through natural selection (Baker, 1979). Pollination biology entered a phase of experimental approaches inspired by the physical sciences in the early twentieth century and then from the late 1940s it started to play a key role in the development of biosystematics due to the recognized importance of pollinator mediated gene flow for population genetics, particularly outcrossing rates and divergence of populations (Grant, 1949; Baker, 1979). From the 1990s to the present, pollination biology has become highly multidisciplinary through incorporation of a wide range of tools drawn from molecular biology, biochemistry, chemistry, neurobiology, and physics (Willmer, 2011).

Despite the existence of numerous textbooks and edited volumes that deal specifically with the topic of pollination biology, our perspective is that it is best viewed as a research specialization that has applications in many broader fields, including botany, entomology, systematics, evolutionary biology, ecology, agriculture, and conservation biology. The continuing relevance of pollination biology is due to the reliance of most higher plants on animal-mediated pollination for seed production (Rodger et al., 2021) and from the dietary specialization on flowers in thousands of animal species, mostly insects, but also birds and mammals (Ollerton, 2017). This interdependency of literally hundreds of thousands of plant and animal species forms a key part of the ecology of natural ecosystems.

The focus of this article is on the various applications of pollination biology, using examples from research conducted in South Africa. The review was occasioned by the 50-year anniversary of the meetings of the South African Association of Botanists (SAAB). But even without this anniversary, there are other logical reasons for a focus on South Africa. Perspectives on pollination from the southern hemisphere are important because the study of pollination was historically centred in the temperate northern hemisphere, which is

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characterized by low levels of biodiversity due to glacial extirpations and very high levels of anthropogenic habitat transformation. Research from the biodiverse regions of the southern hemisphere, such as South Africa, are particularly important for a balanced global perspective (Johnson and Steiner, 2000).

The initial SAAB meeting in 1975 coincided with the peak of the biosystematics era. This era spanned a period from the late 1930s to about 1990 and was characterized by enormous progress in evolutionary biology due to enrichment of systematics with ideas from genetics and ecology. Biologists such as Verne Grant and Ledyard Stebbins, who were plant systematists with an appreciation for understanding floral diversity, were driving progress in evolutionary biology and pollination biology was flourishing (Baker, 1979). But South Africa was still in the grips of the apartheid system and was intellectually isolated. With very few exceptions, South African evolutionary biologists and ecologists did not make globally significant contributions during the early biosystematics era and this also applied to pollination biology. A key inflection point was the discovery of rodent pollination in South African proteas (Wiens and Rourke, 1978). These findings published in *Nature* reignited interest in pollination of South African plants and stimulated a wave of further research on the pollination of proteas, culminating in a series of important reviews and edited volumes published in the 1980s (Collins and Rebelo, 1987; Rebelo, 1987). Also in the 1980s, a seemingly obscure paper on pollination of *Diascia* flowers by oil-collecting bees (Vogel, 1984) triggered an intensive program, still ongoing, of research into the pollination biology of oil-producing flowers in the Scrophulariaceae and Orchidaceae (Manning and Brothers, 1986; Steiner and Whitehead, 1990; Waterman et al., 2011). The late 1980s saw the first synthesis of pollination biology in South Africa (Rebelo, 1987). Interest in the topic then snowballed and by the early 1990s, when South Africa was preparing for the first democratic elections and was opening up to the world, there was a proliferation of studies of pollination systems in a wide range of South African plant families.

There are now >1500 papers on various aspects of pollination biology conducted in South Africa (see Section 5 for the search terms we used to locate these papers) and it was obviously impossible for us to cover all those publications in one review. We therefore focused mostly on impactful papers, which we define as those that have been cited frequently (one measure of their influence) or that represent historical inflection points in research. These historical inflection points are often represented by natural history discoveries that trigger subsequent research programs and we provide several examples of such developments. In some cases we have also identified recent papers that are likely to become influential over time.

We have organized the review according to the major scientific fields to which pollination biology has contributed. We outline the scope of each field and then highlight particular studies and explain their broader relevance for the field. At the end of the review we highlight some overall research trends from a bibliometric analysis and then discuss the outlook for future applications of pollination biology in each field.

2. Evolutionary biology

Evolutionary biology is the study of the evolutionary processes that give rise to biodiversity. It includes studies of natural selection, speciation and the classification of organisms. There is now widespread recognition that speciation is often characterized by shifts between ecological niches (Schluter, 2000). Consequently, contemporary evolutionary biology includes a focus on the environmental drivers of trait evolution as well as the use of molecular tools to determine relationships among organisms.

2.1. Evolutionary ecology

The oldest applications of pollination biology from the times of Sprengel and Darwin involved the study of trait function and this work, which flourishes up to the present day, can be considered to fall under the field of evolutionary ecology (or the closely allied field of functional ecology). Unlike classical population and community ecology, which are focused on studies of abundance and distribution and are covered later in this review, evolutionary ecology is mainly focused on investigations of the functional basis of trait variation in nature (Fox et al., 2001).

2.1.1. Trait function

In South Africa, the first studies of the pollination function of floral traits were conducted in the mid-nineteenth century by naturalists, such as Mary Barber and Roland Trimen, who corresponded extensively with Darwin (Johnson, 2009; Adit and Johnson, 2024). In the late nineteenth century, the most notable studies of pollination were conducted by George Scott-Elliot (1891) and Rudolf Marloth who incorporated his observations into his Magnum Opus *The Flora of South Africa* (Marloth, 1913–1915). Amongst his many discoveries, Marloth was the first biologist to recognize the association of the Mountain Pride butterfly with a guild of plants with narrow-tubed red flowers (Fig 1). Investigations of floral trait function continue to be critically important because floral diversification is a major feature of the angiosperm radiation (Harder and Johnson, 2009).

With rare exceptions, studies of the function of floral traits cannot be conducted solely in the laboratory or greenhouse. A critical requirement is the documentation of pollinators in natural environments and the difficulty of this step is often under-appreciated by non-specialists. In some cases it can take years, even decades, to accumulate sufficient observations to be able to link a floral trait with a particular animal agent of pollination. While trait functions can be inferred from ecological associations and patterns of convergent evolution, they are most reliably determined through the use of experimentation involving trait manipulation or the use of artificial flowers.

Notable experimental examples of studies of trait function in South African plants include manipulation of floral visual signals using paint or sunscreen (Peter and Johnson, 2008; Hansen et al., 2012), manipulation of flower angles (Campbell et al., 2016), removal of staminal hairs or callus-like structures that mimic pollen (Duffy and Johnson, 2015; Newman et al., 2022), using artificial flowers to assess colour preferences of monkey beetles (Picker and Midgley, 1996) and long-proboscid flies (Jersáková et al., 2012), and rearranging flowers on inflorescences to test functions of protandry (Jersáková and Johnson, 2007),

In the case of chemical signals emitted by flowers, the process of identifying trait functions is more complex and usually involves identification of volatiles using gas chromatography coupled with mass spectrometry (GCMS), test of electrophysiological responses of antennae to volatiles in the case of insects, and then field or laboratory tests of their behavioural effectiveness. Notable studies include trapping of beetle pollinators using different volatile lures (Steenhuisen et al., 2013; Suinyuy et al., 2015), responses of oil bees to floral volatiles (Waterman, et al., 2011; Schäffler et al., 2015), and tests of the responses of rodents and elephant shrews to floral volatiles (Johnson et al., 2011; Wester et al., 2019; Johnson and Govender, 2022)

There has long been a recognition that the behaviour, sensory abilities and digestive physiology of pollinators hold the key to understanding the functional significance of many floral traits. For this reason, zoologists have always played a very active role in the study of plant-pollinator interactions. In South Africa, the animal physiologist Sue Nicolson played a crucial role in studies of the digestive physiology of key animal pollinators, including bees, beetles, birds and rodents (Nicolson and Fleming, 2003; Wright et al., 2018).

Fig. 1. The pollination mutualism between the mountain pride butterfly *Aeropetes tulbaghia* and the montane succulent *Crassula coccinea* L. showing (left) an original painting from Marloth's Flora of South Africa (Marloth, 1913-1915) and (right) a contemporary photograph of the same interaction. This butterfly is now known to be a keystone pollinator of a large guild of South African plants with red flowers (Johnson and Bond, 1994; Johnson, 2010). Photo by Anton Pauw.

She became a leading global authority on floral nectar and animal nectarivory (Nicolson et al., 2007), and also carried out significant work on the nutritional value of pollen to animals (Nicolson and Human, 2013). Among her key findings were recognition of the degree of convergence in digestive physiology between hummingbirds and specialized passerine nectarivores (Nicolson and Fleming, 2014) and its implications for the evolution of nectar sugar composition in bird-plants (Johnson and Nicolson, 2008)

2.1.2. *Convergent evolution and pollinator niches*

Flowers of distantly related plants that share particular pollinator groups tend to show patterns of convergent evolution in floral traits (e.g., Goldblatt and Manning, 1999; Pauw, 2006; Shuttleworth and Johnson, 2012; Johnson and Raguso, 2016; Kemp et al., 2019). These patterns, known as pollination syndromes, have been controversial as some biologists have questioned whether there is sufficient statistical support for these patterns and whether pollination systems are usually specialized enough to lead to the evolution of discernible pollination syndromes in the majority of angiosperms (Waser et al., 1996). While the flora of the temperate northern hemisphere may lack extensive specialization in pollination systems, this is not the case in South Africa where specialized pollination systems are an important aspect of the flora (Johnson and Steiner, 2000, 2003)

In 1950 Stefan Vogel, a young German botanist who would later become a leading global figure in the field of floral biology, spent a year studying pollination and floral syndromes in the flora of South Africa and subsequently published an important monograph on his findings (Vogel, 1954), recently translated into English (Vogel, 2012). An analysis has shown that a very high proportion of the species that Vogel assigned to specific syndromes and that have been studied in the field are indeed pollinated by the animals that were predicted from these floral syndromes (Johnson and Wester, 2017)

One of Vogel's key findings was the repeated observation of similar floral syndromes being present among multiple plant families (convergence), and different syndromes being present within families (divergence). This observation resonates with many unrelated examples of niche exploitation, with perhaps the best-known example being bill shape in birds that relates to various feeding niches (Schluter, 2000). The basis for niche specialization is trade-offs in trait deployment that prevent most organisms from being efficient supergeneralists. It has been argued that floral pollination syndromes are simply another example of the same phenomenon and that the key to understanding these syndromes is to investigate pollinator niches and trade-offs in deployment of floral traits (Johnson, 2010; Phillips et al., 2020). In some cases, pollinator niche specialization is extreme and involves exploitation of a very particular pollinator body part, such as its tongue (Pauw, 1998) or its wings for pollen transfer (Johnson et al., 2023), or even the mating drive of just one sex of a pollinator species (Cohen et al., 2021).

2.1.3. *Mimicry*

Mimicry represents a special category of resemblance among organisms. In most cases mimics evolve to resemble model organisms without influencing the evolution of the model organisms. This one-sided pattern has been termed advergent evolution. Mimics derive their fitness from being cognitively misclassified by animals. Floral mimics resemble either the food sources, mating partners, or oviposition sites of their animal pollinators (Johnson and Schiestl, 2016).

South African biologists have contributed many examples to the literature on floral mimicry. In the case of Batesian food source

mimicry, these include studies that show that mimicry can lead to population divergence of floral traits in mimetic species (Newman et al., 2012) and studies that identify the role of visual traits in these mimicry systems (Peter and Johnson, 2008; Jersáková, et al., 2012). Notable studies of sexual mimicry, include the discovery of sexual deception of fly pollinators in the daisy *Gorteria diffusa* Thunb. (Johnson and Midgley, 1997) which triggered an extensive multinational program of research devoted to understanding the function and developmental basis of floral traits in this species (Ellis and Johnson, 2009; Thomas et al., 2009, 2010; Kellenberger et al., 2023), and also the discovery and chemical elucidation of sexual deception of longhorn beetles in a *Disa* orchid species (Cohen, et al., 2021). In the case of oviposition site mimicry, local biologists have published notable papers on importance of oligosulfides for attraction of carrion flies in *Eucomis* (Hyacinthaceae) (Shuttleworth and Johnson, 2010) and *Satyrium* (Orchidaceae) (van der Niet et al., 2011) and also identified visual signals and volatile compounds responsible for faecal mimicry in *Wurmbea* (Colchicaceae) (Johnson et al., 2020)

2.1.4. Phenotypic selection

Floral traits evolve when they are variable, heritable and influence plant fitness. By correlating variation in floral traits with seed production or pollen export, it is possible to infer whether they are potentially under selection. This is ideally done using natural variation in populations, but paradoxically traits that are under strong selection often show little variation. For this reason, studies of phenotypic selection on floral traits often focus on hybrid zones or on variation that is re-introduced through introgressive hybridization or by physical manipulation of floral traits. In South Africa, studies of phenotypic selection have focused on the evolution of the long nectar tubes that are characteristic of flowers in the region that are pollinated by hawkmoths (Alexandersson and Johnson, 2002) and long-proboscid flies (Pauw et al., 2009; Newman et al., 2015; Anderson et al., 2016).

2.1.5. Coevolution

The concept of coevolution was proposed by Darwin who imagined a scenario whereby selection favours longer-tubed flowers when this results in pollinators making better contact with the anthers and stigma, and for selection to consequently favour longer mouthparts of pollinators to access the nectar in these longer-tubed flowers. The reciprocal evolutionary effect of traits of mutualistic partners is expected to result in strong matching of traits at the population level. The idea has received important support from studies of long-proboscid fly pollination systems in South Africa, where the evidence shows both the expected population-level trait co-variation and matching, as well as the fitness advantages for plants and pollinators that were suggested by Darwin (Anderson and Johnson, 2008; 2009; Pauw, et al., 2009).

Some of the strongest patterns of coevolution emerge from mutualistic interactions between plants and insects that use flowers as brood sites. There is a long history of studies of these mutualisms in figs and cycads in South Africa (Nefdt and Compton, 1996; Donaldson, 1997) and some of the most notable recent advances have involved the partial elucidation of the volatile chemistry that mediates these mutualisms (Cornille et al., 2012; Suinyuy, et al., 2015).

2.2. Taxonomy and systematics

The focus of the field of systematics is centred around taxonomy - the discovery and description of biodiversity and the synthesis of this information into a predictive classification system which is aimed to reflect evolutionary/phylogenetic history. More expansive recent definitions of the field of systematics explicitly include a focus on the evolutionary processes that generate biodiversity (Daly et al., 2012). For our purposes this would include divergence in the pollinator niche and the critical role that pollinators play as agents of gene flow.

The population-level process of adaptation to different pollinators can ultimately result in plant speciation (Van der Niet and Johnson, 2012; Johnson, 2025), and if this process occurs repeatedly, may result in lineage diversification that gives rise to adaptive radiation (Schluter, 2000; Johnson, 2006). As such, pollinators as drivers of speciation and diversification are clearly relevant for a modern systematics agenda. However, even though pollination systems are not traits per se, the effect of pollinators on trait evolution combined with the fact that traits are relevant for building classification systems, also implies that it is relevant to consider pollination systems in a more traditional, trait-focused perspective on systematics. In the sections below we highlight the connection between pollination systems and systematics, by first considering how pollination biology has influenced biological classification and macroevolutionary research, with a focus on the key role of phylogenetic inference, then by considering how macroevolutionary patterns have been used to elucidate drivers of speciation, and finally by reviewing the evidence for a role of pollinators in population divergence and how this has influenced species delimitation.

2.2.1. Lineage diversification

The field of systematics has a long tradition in South Africa, owing partly to the recognition of the unique nature of the Cape flora, based on high species richness combined with high levels of endemism (Linder, 2003). However, plant reproductive biology and pollination biology in particular was not considered in systematics research until the second part of the 20th century with the work of biologists such as Jens Clausen, Verne Grant, Ledyard Stebbins and Peter Raven (Baker, 1979). Over the past 35 years in South Africa, the pollination systems in many florally diverse lineages, such as Iridaceae, Orchidaceae, and Ericaceae, have been studied in detail and have both informed classification systems and been accepted as important factors in diversification (Johnson et al., 1998; Goldblatt and Manning, 2006; Pirie et al., 2011; Waterman, et al., 2011).

The early treatment of pollination systems in classification systems needs to be considered from the interplay between researchers' consideration of traits for building classifications and the effect of pollinators on trait evolution. Adaptation to particular functional pollinator groups among distantly related plant species may lead to floral trait similarity due to convergent evolution (Faegri and van der Pijl, 1979). When such traits, that are under pollinator selection, are used for taxonomic classification, it may lead to a situation whereby distantly related species are classified as members of the same taxon, i.e. – when viewed from a phylogenetic perspective – the recognition of polyphyletic groups. This is considered undesirable in systematics, and figuring out whether diagnostic traits were the result of convergent evolution or not was one of the biggest challenges for systematists working during the era when classifications were mainly built on morphological trait variation. A case in point was the initial recognition of small genera in the Iridaceae that contained bird-pollinated species that shared a suite of floral traits that are characteristic of bird pollination. However, closer examination of non-floral traits showed that species in these genera were best assigned to several larger genera that included a wide diversity of pollination systems (Goldblatt, 1990). This is consistent with the general consensus that many large genera that arise through pollinator-driven adaptive radiations from a common ancestor will include species representing a diversity of pollination systems (Grant and Grant, 1965). A parallel pattern of investigation occurred in the large genus *Erica*, where a previous sectional classification was based on variation in corolla shape that is correlated with four distinct pollination syndromes - wind, insect, long-proboscid fly, and bird (Rebelo et al., 1985). Recent phylogenetic analysis has shown that these sections are largely artificial, and that monophyletic clades often contain species with highly diverse corolla shapes and different pollination syndromes (Pirie, et al., 2011; Van der Niet et al., 2014; Pirie et al., 2024) (Fig 2).

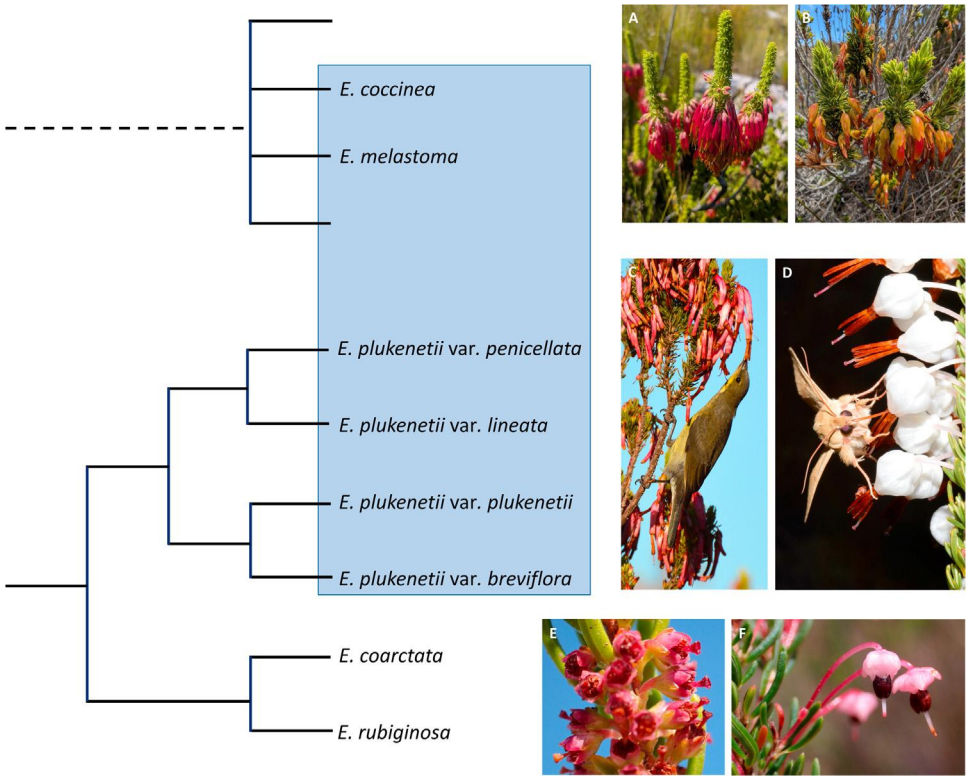

Fig. 2. Pollination biology can influence systematics and shed light on evolutionary processes that is useful for classification. In *Erica*, the section Gigandra comprised several species, contained within the blue rectangle, that were all characterized by long floral tubes. Recent phylogenetic analyses have shown that the species of Gigandra are not monophyletic (Pirie et al. 2024). Long floral tubes are an adaptation to accommodate the long bills of nectar drinking sunbird pollinators and this trait has evolved convergently many times and therefore does not constitute a synapomorphy. The species *E. coccinea* (A) and *E. melastoma* (B) are part of a different clade (together with a large number of taxa that are indicated by the branches without taxon labels) than the other species of section Gigandra, which are more closely related to *E. coarctata* (E) and *E. rubiginosa* (F), two species with minute flowers that are likely adapted for wind- and insect pollination. The floral diversity within *E. plukenetii* has also been a source of taxonomic debate, and currently two varieties with highly diverse floral morphology adapted for sunbird- (var. *plukenetii*, (C)) and moth-pollination (var. *breviflora*, (D)) respectively, are ecotypes of the same monophyletic species.

Multiple transitions in pollination systems within lineages has now been demonstrated repeatedly in macroevolutionary studies that combine phylogenetic inference with data on pollination systems (Waterman et al., 2009; Valente et al., 2012; Van der Niet and Johnson, 2012). Even early studies in which phylogenies were reconstructed based on morphological characters showed evidence for repeated independent evolution of pollination systems (Johnson, et al., 1998), despite some concerns that application of the parsimony principle may lead to incorrect grouping of species with similar pollination systems (Armbruster, 1992). Another increasingly common application of phylogenies is to use them to statistically strengthen the case for trait-environment associations being a result of adaptation. An example is an analysis of the genus *Leucadendron* (Proteaceae) that identified associations between floral traits and wind- versus insect pollination systems (Welsford et al., 2016)

2.2.2. *Patterns of speciation*

There has long been interest in the environmental drivers of speciation in the Cape Floristic Region. Initial hypotheses on drivers of diversification focused on the geographical mosaic of factors determining the plant growth environment, including soil types and climatic gradients (Goldblatt, 1997). Johnson (1996) noted that some Cape lineages show greater diversification in floral traits than they do in vegetative traits, suggesting that pollinators may play an important role in diversification. In an attempt to formalize the study of radiation of an entire modern flora, Linder (2003) published an influential study in which he recognized monophyletic “Cape clades”, species-rich lineages that had undergone their initial and most of their subsequent radiation in the Cape Floristic Region, and also proposed various candidate drivers of diversification. A large number of phylogenetic studies, resulting from the revolution in molecular systematics, have been used to identify sister species and compare these for various ecological factors, including pollination systems. Several studies using comparisons of sister species of Orchidaceae and Iridaceae genera confirmed that these often differ in pollination systems (Manning and Linder, 1992; Goldblatt and Manning, 1996). In a large meta-analysis across multiple genera, van der Niet & Johnson (2009) demonstrated the general importance of ecology for speciation in Cape lineages. Despite some studies emphasizing a role for soil shifts in speciation of Cape plants (Schnitzler et al., 2011), other studies have found that soil shifts were less frequent than pollinator shifts, as exemplified in a detailed analysis of *Lapeirousia* (Forest et al., 2014).

There is a long-standing controversy about the role of reinforcement in speciation. Some authors have proposed a speciation model in which initial divergence occurs through adaptation to different, but adjacent soil types, followed by reinforcement of speciation through selection for reproductive isolation mediated by adaptation to different pollinators (Goldblatt and Manning, 1996). Some support for this model was found in an analysis which showed that joint shifts in soil type and pollination system were particularly prevalent in sister species with overlapping ranges (Van der Niet et al., 2006). However, in an analysis of flowering time shifts in wind-pollinated Restionaceae, Linder (2020) failed to find an association between flowering time shifts and sympatry. Given these uncertainties about reinforcement, a model in which reproductive isolation evolves as a by-product of adaptation to different pollinators or abiotic conditions, therefore remains the most plausible. In a recent study, Newman and Johnson (2025) identified both pollinator behavior and ecogeographic isolation as factors leading to reproductive isolation among partially sympatric interfertile orchid species. Ecogeographic

isolation among plant populations is common in the South African flora, rendering the need for isolating mechanisms that operate in sympatry obsolete in most cases. A particularly common mode of plant speciation in southern Africa appears to be ecogeographical isolation of lineages combined with pollinator shifts that drive trait divergence in these lineages.

2.2.3. Intraspecific variation and ecotypes

Since speciation is initiated when populations diverge, a focus on population-level divergence of ecotypes, rather than 'mature' (sister) species, may provide the best clues of the drivers of speciation (Johnson, 2025). The role of pollinators has, as such, been investigated through a process of reciprocal illumination between species-level taxonomy combined with natural history and experimental botany. Taxonomically complex groups often provide the impetus for investigating ecological associations with phenotypic variation. The first example of this was the recognition that in the two subspecies of *Satyrium hallackii* Bolus, the short-spurred taxon is pollinated by relatively short-tongued carpenter bees, whereas the long-spurred taxon is chiefly pollinated by hawkmoths (Johnson, 1997). Many subsequent cases, often inspired by the recognition of intraspecific taxa based on floral variation below the species level, have confirmed the existence of pollination ecotypes (eg. Pauw, et al., 2009; Peter and Johnson, 2014; Van der Niet, et al., 2014)

In some cases the recognition of population-level variation precedes systematic decisions, especially when this variation is relatively subtle and not recognized by systematists. Intensive study of the orchid *Satyrium longicauda* Lindl. in terms of morphology, genetics, floral scent chemistry and pollinations systems, revealed the existence of multiple coexisting forms, some of which are being described as distinct species. Most forms are moth-pollinated, but one form was found to be pollinated by oil-bees and still retains vestigial traits associated with moth pollination (Castaneda-Zarate et al., 2021). This study is at the interface between micro- and macroevolution and illustrates the role of pollinators as drivers of speciation and lineage diversification.

3. Ecology

Ecology is the study of the abundance and distributions of organisms and how these are influenced by interactions with other organisms and abiotic environments. Ecology is traditionally (and somewhat artificially) subdivided into population and community level approaches. Much of the contemporary work on ecology is applied and this includes invasion and restoration ecology.

3.1. Population ecology

The abundance of both plants and their pollinators has important consequences for their viability. Plants in small populations can fail to attract pollinators or may experience a lack of mating partners. Reduced fecundity and viability in small populations is known as the Allee effect and is an example of underpopulation. Several studies in South Africa have shown low rates of pollination in small populations that are consistent with Allee effects (Ward and Johnson, 2005; Geerts and Pauw, 2012), but this is not always the case (Johnson et al., 2009). In populations of *Brunsvigia orientalis* Ait. ex Eckl. and *B. radulosa* Herb. smaller populations receive fewer pollinator visits, set fewer seeds, and have a lower proportion of juveniles, suggesting population declines (Ward and Johnson, 2005; Geerts and Pauw, 2011a).

At the other end of the plant abundance spectrum, plants in very large populations can experience competition for pollinators. This has been shown in *Lapeirousia oreogena* Schltr. ex Goldblatt where mass-flowering can lead to saturation of available pollinators and reduced seed production. Rathcke (1983) suggested that there will be a level of abundance (e.g., population size and density) at which pollination is maximized. The reality is more complex because of inter-specific interactions among plant species that share pollinators (see 3.2).

The relative abundance of pollinators will obviously affect levels of plant pollination and this has implications for population viability. Population growth rates below zero will ultimately lead to population extirpation, while positive growth rates allow population persistence. For changes in the abundance of a particular pollinator to matter for plant population persistence, these changes in abundance must translate into changes in seed set and ultimately the rate of establishment of new plants. A decline in the abundance of a particular pollinator may not cause a decline in pollination rate, if the lost function is replaced by a different pollinator. In turn, a decline in the rate of pollinator-mediated pollination may not cause a decline in seed set if plants are capable of autonomous self-fertilization. And in turn again, a decline in seed production may not cause a reduction in plant population growth rate if the plant species can reproduce vegetatively or is long-lived. A close link between pollinator abundance and plant population growth rate may therefore be expected in plant species that require specialist pollinators, need cross-pollination for seed production, and need high rates of seed production to compensate for high rates of adult mortality (Bond, 1994).

In the city of Cape Town, the loss of the oil-collecting bee *Rediviva peringueyi* (Friese) due to fragmentation of renosterveld habitat has caused a contemporaneous shift in the species composition of the guild of oil-secreting orchids. The guild has become impoverished by the local extirpation of species that were unable to reproduce vegetatively, consistent with their greater dependence on seeds and pollination for population persistence (Pauw and Hawkins, 2011). Across the SW Cape, the species composition of the oil-secreting guild varies predictably in relation to oil-bee abundance: highly clonal species occur widely, including in habitats where the bees are naturally rare, whereas non-clonal species are limited to areas of high bee abundance (Pauw and Bond, 2011). Consistent with these findings, Duffy and Johnson (2017b) found that the distributions of several South African plant species with specialized pollination systems was best explained by a combination of pollinator abundance and abiotic factors, rather than by abiotic factors alone.

3.2. Community ecology

Pauw (2013) argued that the effect of plant abundance on rates of pollination can impact on coexistence of species in communities. Less frequent species may be favoured ecologically if they receive proportionally more visits per individual than do abundant species. This may occur if more common species saturate their specialized pollinators and some of their flowers remain unvisited (cf. Johnson et al., 2012). If intraspecific competition for pollinators is greater than interspecific competition then this may facilitate coexistence and greater species diversity through pollination niches (Pauw, 2013).

To test for the existence of pollination niches, Benadi and Pauw (2018) recorded pollination rate in a community of 33 fynbos plant species. Visitation rate indeed declined sharply with increasing abundance as expected from intraspecific competition, but visitation rate was also somewhat depressed in very rare species such that the resulting relationship between visitation rate and relative abundance was hump-shaped, as predicted by Rathke (1983) (Fig. 3). These findings imply that the rarest plant species could become extinct from the community due to an Allee effect, whereas, above an abundance threshold, intraspecific competition for pollination could limit the reproductive output of common species, thus promoting the maintenance of plant diversity in one of the most diverse regions of the world (Benadi and Pauw, 2018).

Facilitative interactions among species in communities will also lead to greater community level diversity and this has been well-

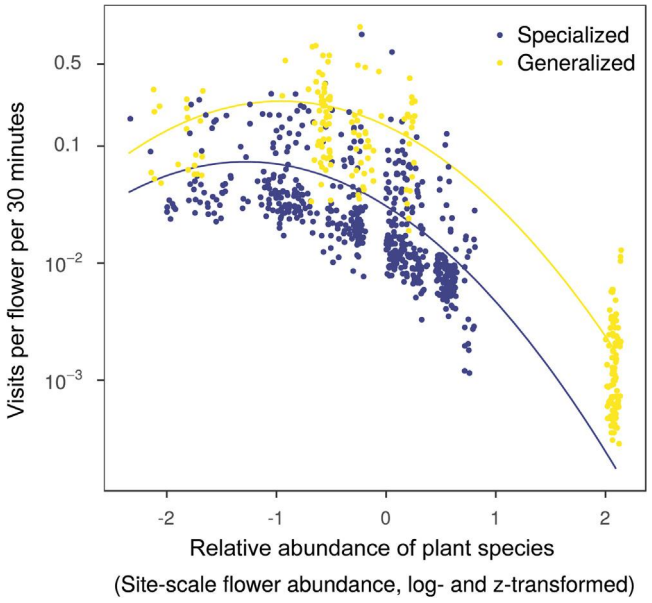

Fig. 3. An example of effects of relative abundance of plants in a community and level of specialization in pollination system on the rate of pollinator visitation. Competition among plants for pollinator services at higher levels of abundance may constrain population growth rates and allow for higher species richness in plant communities by preventing competitive exclusion. Modified from Benadi and Pauw (2018).

documented in some non-rewarding plant species that rely on rewarding species to subsidize their pollinators. For example, pollination success of the deceptive orchids *Disa pulchra* Sond. and *Eulophia zeyheriana* Sond. is positively influenced by the local abundance of nectar-producing plant species (Peter and Johnson, 2008; Duffy and Johnson, 2017a). It is likely that facilitative interactions also occur among guilds of rewarding plant species that share pollinators, but this has seldom been investigated (Pauw and Johnson, 2018; Kemp, et al., 2019).

The description of community level networks of interactions among plants and their animal visitors has been extremely popular worldwide over the last 25 years, but this approach has not been widely adopted in South Africa, apart from a few exceptions (Ollerton et al., 2003; Pauw and Stanway, 2015; Stanley et al., 2020). The reasons for this reluctance to embrace network methodology is unclear and most likely relates to scepticism about whether most of the flower visitors that feature in these networks are really pollinators and also whether these networks have any deeper ecological significance beside being a description of patterns in nature. Another possible reason is that in diverse communities of plants with highly specialized pollination systems and low rates of visitation, it is simply not feasible to accumulate sufficient observations through observing "focal" species in order to accurately represent a pollination network. For example, the rate of bird visitation to the orchid *Satyrium rhodanthum* Schltr. was estimated as one visit every 13 days (van der Niet et al., 2022). The most detailed network study was conducted by Pauw and Stanway (2015) in the Cape region and they reported high levels of pollinator specialization on plants and also identified some key methodological concerns about network metrics that are commonly used to measure levels of specialization.

3.3. Applied ecology

3.3.1. Habitat loss and fragmentation

South Africa combines a growing human population and rapid development with very high levels of biological diversity. Natural areas are left as islands in a rising sea of urbanization and agriculture. This raises the question what effect habitat fragmentation has on pollinators and their dependent plants. South Africa has uniquely specialized pollination systems (Johnson and Steiner, 2003; Pauw and Stanway, 2015), making them particularly vulnerable to disruption. Indeed, several studies have documented declines in specialized pollination in small habitat fragments, especially when these are in an urban matrix (Johnson et al., 2004). For example, the very long-billed Malachite sunbirds (*Nectarinia famosa* L.) do not penetrate far into urban areas (Pauw and Louw, 2012), leaving a guild of long-tubed bird-pollinated plants with low levels of seed production (Geerts and Pauw, 2009a; Geerts, 2016). The oil-collecting bee, *Rediviva peringueyi*, is equally sensitive to urbanization. Pollination by this species has declined from historically high levels to zero in small urban conservation areas as Cape Town has expanded (Pauw, 2007; Pauw and Hawkins, 2011).

The effect of habitat fragmentation is less pronounced when generalized pollination systems are considered and when the matrix is agricultural rather than urban. Results of studies on the effects of habitat fragmentation on pollination in renosterveld shrublands embedded in a matrix of wheat and canola have yielded mixed results (Donaldson et al., 2002; Hauber et al., 2022). In some cases, traits of pollinators can predict their responses to urbanization. Among nectar-feeding birds, a greater reliance on nectar and a habit of nesting near ground level predicted sensitivity to urbanization in Cape Town (Coetzee et al., 2018).

3.3.2. Invasion biology

Alien plants can potentially affect the pollination of native species via shared pollinators. Invasion of fynbos by Australian *Acacia* species has been shown to substantially decrease visitation rates to adjacent populations of *Roepera fulva* (L.) Beier & Thulin and *Carpobrotus edulis* (L.) N.E.Br., while increasing the community-wide visitation rate by small beetles which were abundant on *Acacia* flowers (Gibson et al., 2013; Brett et al., 2024). In contrast, the bird-pollinated alien Proteacae *Banksia speciosa* R.Br. had no effect on the pollination of a native, bird-pollinated Proteaceae species (Adedoja et al., 2021). Evidently, the alien-native interaction can range from competitive, through commensalistic, to facilitative. Interestingly, the strength of the interaction can potentially be predicted by the degree of similarity in floral traits, which in turn predicts the overlap in pollinator fauna (Gibson et al., 2012). Often, alien invasion coincides with other anthropogenic impacts on pollination. In a grassland study, butterflies were important pollinators in the large, uninvaded grassland area, but were almost entirely absent from fragments surrounded by pines and invaded by alien *Rubus* brambles (Hansen et al., 2018).

Pollination systems affect plants' invasion potential. Many invasive species are facultative selfers and are not dependent on pollinators (Rambuda and Johnson, 2004; Van Kleunen et al., 2008). For alien plants that rely on sexual reproduction and outcrossing, the availability of suitable pollinators in the novel range is often a key factor determining their ability to produce viable seeds. However, the extent to which pollinator limitation of seed production slows the process of invasion is still being debated (Geerts and Adedoja, 2021; Geerts and Le Roux, 2025). Alien plant species that rely on specialist pollinators are expected to be less likely to recruit pollinators in new environments than are alien species with more generalized pollination systems (Adedoja, et al., 2021). However, several alien plant species with specialized pollination systems, such as the bird-pollinated *Nicotiana glauca* Graham, the hawkmoth pollinated *Lilium formosanum* A. Wallace and the buzz-pollinated *Senna didymobotrya* (Fresen.) H.S. Irwin & Barneby, have been shown to recruit new pollinators in their invasive range (Van Kleunen and Johnson, 2005; Geerts and Pauw, 2009b; Rodger et al., 2010; Johnson and Raguso, 2016). In these cases, the presence of ecologically analogous pollinators, or even the same pollinator species, likely facilitated invasion. Alien plant species with more generalized floral morphologies are

often pollinated by honeybees in South Africa facilitating invasion (eg. Coombs and Peter, 2010; Geerts and Le Roux, 2025).

In contrast to countries such as Argentina, Australia and New Zealand, there have not been major concerns in South Africa about the impacts of alien pollinators, possibly because honeybees, which have caused the most impact worldwide, are native to this region. Even though there are a small number of alien flower-visiting insect species, their effects are largely unknown (Le Roux et al., 2020). Some documented examples include alien wasps pollinating *Ficus* (Ware and Compton, 1992), and an alien butterfly (*Pieris brassicae* L.) pollinating the invasive *Lythrum salicaria* L. (Geerts and Adedoja, 2021)

3.3.3. Restoration ecology

Pollination restoration usually starts with restoring the plant community (Menz et al., 2011). A strong, positive association between nectar-feeding birds and nectar availability suggests that this strategy should be successful in restoring bird pollination (Schmid et al., 2016; Geerts et al., 2020; Neu et al., 2023). Indeed, nectar-feeding bird pollinators return when nectar-rich plants in restored riparian areas mature (Mangachena and Geerts, 2019). Similarly, the planting of nectar gardens on school grounds (Mnisi et al., 2021), and the inclusion of indigenous bird-pollinated plants in suburban gardens (Coetzee, et al., 2018) has increased the abundance of nectar-feeding birds in Cape Town and may help to reconnect small natural fragments to larger conservation areas.

4. Agriculture and agroecosystems

The ability of pollinators to increase crop yield is well known, and therefore the small number of studies on crop pollination in South Africa is surprising (Melin et al., 2014b). While honeybees are critical for pollination of deciduous fruit trees in the Western Cape (Melin, et al., 2014b), they make up as little as 9 % of pollinators of mango (Carvalheiro et al., 2010). Several studies have found that nearby natural areas have a positive effect on crop pollination, likely because they act as a source of wild pollinators (Carvalheiro, et al., 2010; Carvalheiro et al., 2011)

South Africa is home to two native subspecies of honeybees, *Apis mellifera capensis* Escholtz, which is restricted to the Western and Eastern Cape Provinces, and *A. m. scutellata* Lepeletier, which occurs in the remainder of the country (Hepburn and Crewe, 1991). Globally, South Africa has the highest genetic diversity and a high densities of honeybee colonies, many of which are unmanaged (Jaffe et al., 2010). Unmanaged honeybees visit about 40 % of the plant species in some grassland communities, and are important pollinators of only about 30 % of these species (Stanley, et al., 2020). Managed honeybees in South Africa have not experienced the same dramatic declines recorded in Europe (Osterman et al., 2021). Colony losses, specifically for beekeepers using *A. m. scutellata*, have mostly been attributed to the *A. m. capensis* worker social parasite, a problem unique to South Africa (Neumann and Moritz, 2002).

Within their native range, beekeeping often increases honeybee density far above natural levels (Melin et al., 2014a). A small number of studies have considered the effects of beekeeping on other pollinators and on native plant species in South Africa (Hargreaves et al., 2010; Geerts and Pauw, 2011b; Diller et al., 2022; Morton, 2023). In the case of impact on birds, direct interference rather than competition for shared resources seems most likely (Geerts and Pauw, 2011b). Addition of hives led to decreased fecundity of a bird-pollinated *Aloe* sp. and this was ascribed to pollen theft by honeybees (Hargreaves, et al., 2010). In another study, honeybees were found to transfer mainly incompatible self pollen among flowers of an *Aloe* species, and consequently did not contribute to seed production (Diller, et al., 2022).

5. Publication trends

To assess long-term trends in pollination studies in South Africa, we used the search term "pollinat*" in Clarivate™ (Web of Science) to find full articles (conference abstracts were excluded) that include the words "pollination", "pollinators", or "pollinated" in the title and then filtered this list to include only the South African region. We then analysed trends over time for these papers in comparison with those of several other countries, including the United States (representing a developed First world economy), Brazil (representing another biodiverse southern hemisphere country) and China (representing an economically powerful country with an ambitious science agenda).

The analysis showed that South Africa produced up to 6 % of world output in the field of pollination biology in 2009 (Fig 4A), but there has been no growth in total output since 2010 and this translates to a declining share of global publications (Fig 4B). The current output is about 2.5 % of global publications which is similar to countries such as Sweden, Switzerland, Spain, the United Kingdom and Australia.

The USA still leads in terms of the number of publications on the topic of pollination, but its share of global output has declined steadily from around 50 % to around 25 % currently (Fig 4B) and even the number of publications from the USA is showing signs of a recent decrease (Fig 4A). Brazil and China had similar output to South Africa until about 2010 and then diverged on a path of much greater growth (Fig 4A). This is likely due to much greater investments by Brazil and China into higher education and their much larger numbers of academics and postgraduate students. But the number of publications from Brazil has seemingly now also recently reached a plateau. Only China has shown a consistent increase in the number of publications and will soon surpass the USA in terms of the proportion of papers globally, but of course these analyses do not take the quality or impact of papers into account and thus do not represent the full picture of global trends.

We also examined the journal categories in which pollination-related papers from South Africa have been published. In decreasing order, these categories are plant sciences (40.3 %), ecology (28.3 %), evolutionary biology (14.8 %), entomology (8.2 %), biodiversity conservation (5.9 %), zoology (5.8 %), genetics and heredity (5.5 %), biology (5.4 %), multidisciplinary sciences (5.4 %), environmental sciences (4.2 %), biochemistry and molecular biology (3.9 %), forestry (2.9 %), agronomy (2.6 %) and horticulture (1.6 %). It should be kept in mind that many papers that are ecological or evolutionary in focus would have been published in journals in the plant sciences category, so this breakdown provides only a rough indication of the spectrum of topics, but nevertheless confirms the multidisciplinary nature of pollination-related research.

6. Outlook

Over the past 50 years, a significant number of studies of pollination biology in South African ecosystems, by researchers based at South African institutions, have advanced understanding of evolutionary and ecological processes and contributed to theory building. South Africa's relatively strong historical performance in pollination-related research reflects its natural geographical advantage in terms of opportunities for ecological and evolutionary research and capacity building of local research infrastructure. However, there is a trend of stagnation in output compared to some other countries in the past 10 years (Fig 4) and this begs the question of what causes this and whether this can be turned around. One possibility is that pollination biology has reached a saturation point because of the limited number of academic positions and scholarships in a country with few universities. This is unlikely to change soon as the South African economy has been largely stagnant since 2010. Given these realities, increased

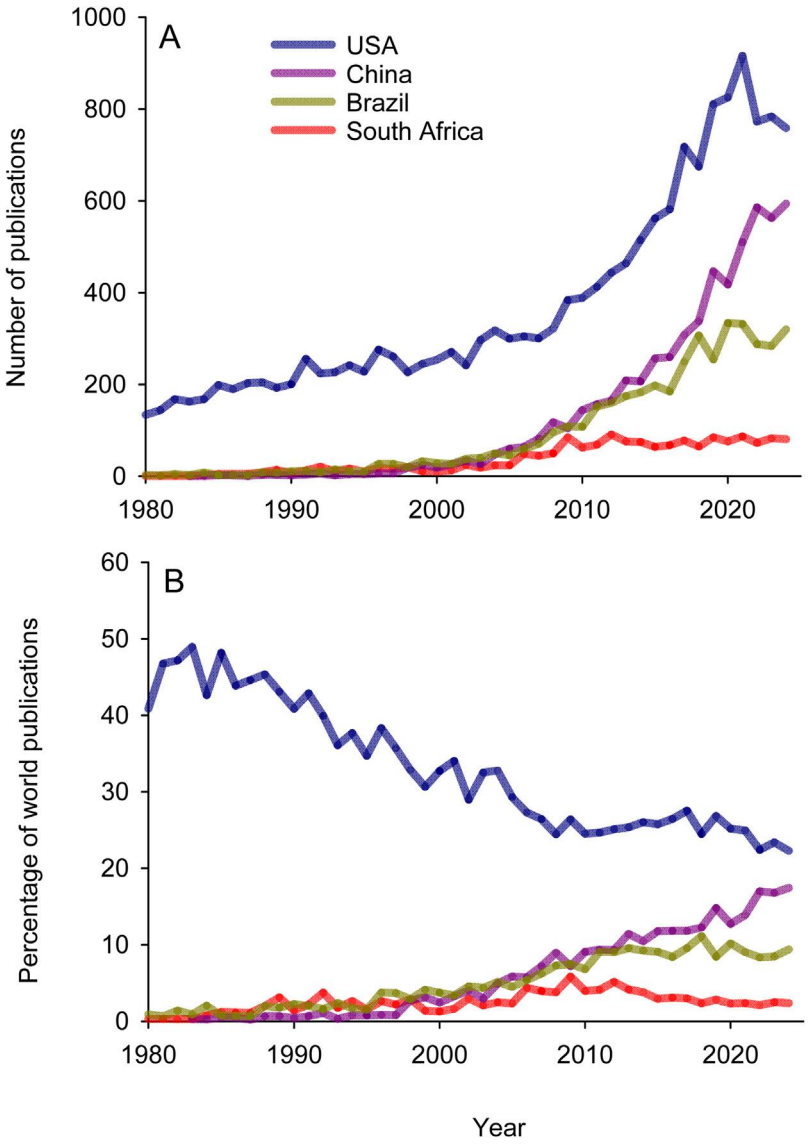

Fig. 4. Trends in the publication of papers involving pollination research, illustrating the remarkable growth in output by China and Brazil and the apparent plateau and even slight decline in publications from the USA and South Africa. A. Number of publications. B. Percentage of global publications.

international collaboration would be the best way to make sure that research momentum can be sustained.

One of the most interesting insights that we gained when writing this review is about the role of natural history discoveries in precipitating further multidisciplinary research. Some of the many examples we mentioned include the discoveries of pollination by small ground-dwelling mammals in *Protea* (Wiens and Rourke, 1978) and oil bee pollination of *Diascia* (Vogel, 1984) and of mimicry of resting flies in the South African daisy *Gorteria diffusa* (Johnson and Midgley, 1997), all of which were followed by dozens of papers that addressed increasingly detailed questions about these systems. The message is that basic discovery-based science needs to be supported in order to lay the groundwork for addressing some of the major questions in evolutionary biology and fundamental ecology. The scope for discovery-based science in biodiverse regions of the world remains enormous, even as many biologists in the First World have moved to desktop meta-analysis of existing data. New tools, such as motion activated cameras, are making a major contribution to these natural history discoveries (Cozien et al., 2019).

In terms of building on natural history discoveries, South Africa is clearly lagging behind the adoption of modern phylogenomic tools, even though the few available studies show that these methods have the potential to change the perspective on the evolution of biodiversity, both in terms of the estimation of the extent of phylogenetic diversity, and the processes underpinning its evolution (Musker et al., 2024).

The main growth in pollination biology worldwide over the past two decades has been in its application to applied problems in agriculture, but South Africa has lagged behind in this trend. Perhaps the most important aspect of this research in agriculture is the continual increase in demand for managed honeybee pollination services. This, coupled with declining natural habitat, is resulting in a high number of managed honeybees in natural areas outside of the pollinating season in spring. Even though honeybees are native to the region, high numbers of these generalist foragers might disrupt pollination and subsequently influence plant reproduction, but this is largely unknown and impacts assessed from short-term studies have been varied (Morton 2023; Hargreaves, et al., 2010; Diller, et al., 2022). Therefore, long-term studies assessing managed honeybee impacts in natural areas in South Africa are long overdue.

The suboptimal pollination of crops such as blueberries and green house tomatoes by honeybees has resulted in pressure to introduce

bumblebees (*Bombus*) for agriculture (Martin et al., 2022). *Bombus* is not native to Africa south of the Sahara. They are super-generalists and may outcompete functionally similar native pollinators such as carpenter bees (*Xylocopa* spp.). Alternative pollination solutions for these crops warrant more attention in order to reduce the pressure to import potentially harmful alien pollinators.

Another key issue in pollination conservation is whether the full complement of pollinators can be restored during vegetation rehabilitation following activities such as mining, agriculture or alien invasive plant removal (Menz, et al., 2011). This remains largely unexplored in the South African context, despite some large-scale and expensive restoration projects.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Steven D. Johnson: Writing – original draft, Visualization, Formal analysis, Conceptualization. **Sjirk Geerts:** Writing – review & editing. **Anton Pauw:** Writing – review & editing, Visualization. **Timotheüs van der Niet:** Writing – review & editing, Visualization.

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