Pollination ecosystem services in South African agricultural systems

AUTHORS:
Annalie Melin[1,2]
Mathieu Rouget[3]
Jeremy J. Midgley[2]
John S. Donaldson[1,2]

AFFILIATIONS:
[1]South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa
[2]Department of Biological Sciences, University of Cape Town, Cape Town, South Africa
[3]Centre for Invasion Biology, School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa

CORRESPONDENCE TO:
Annalie Melin

EMAIL:
annalie.melin@gmail.com

POSTAL ADDRESS:
South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont 7735, South Africa

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Insect pollinators, both managed and wild, have become a focus of global scientific, political and media attention because of their apparent decline and the perceived impact of this decline on crop production. Crop pollination by insects is an essential ecosystem service that increases the yield and quality of approximately 35% of crops worldwide. Pollinator declines are a consequence of multiple environmental pressures, e.g. habitat transformation and fragmentation, loss of floral resources, pesticides, pests and diseases, and climate change. Similar environmental pressures are faced in South Africa where there is a high demand for pollination services. In this paper, we synthesise data on the importance of different pollinators as a basis for services to South African crops and on the status of managed honeybees. We also focus on insect pollination services for the Western Cape deciduous fruit industry, which is worth ZAR9800 million per year and is heavily reliant on pollination services from managed honeybees. We discuss landscape and regional level floral resources needed to maintain sufficient numbers of managed honeybee colonies. In summary, the available literature shows a lack of data on diversity and abundance of crop pollinators, and a lack of long-term data to assess declines. We highlight key areas that require research in South Africa and emphasise the critical role of floral resource availability at the landscape and regional scale to sustain pollinators. We conclude that understanding the dynamics of how floral resources are used will help inform how landscapes could be better managed in order to provide long-term sustainable pollination services.

Introduction

Insect pollinators, comprising both managed (domesticated, e.g. honeybee *Apis mellifera*) and wild populations (species that exist as non-managed wild populations including wild *Apis* spp.), have become a focus of global scientific, political and media attention because of their apparent decline and the perceived impact of such declines on crop production.[1-8] Crop pollination by insects (predominantly by bee species)[9] is an essential ecosystem service that increases both the yield and quality of an estimated 35% of crop production worldwide.[10] Farmers depend on managed honeybees to pollinate crops in many parts of the world, including areas such as North America where honeybees have been introduced to provide this service.[5,8,11] The decline in honeybees, particularly in North America[2,12] and Europe[4,13], has focused attention on the need for alternative, non-honeybee pollination, particularly the role of wild pollinators and the ecosystem services provided by these pollinators[6] (but see the long-standing debate between Corbet[14,15] and Morse[11] and later between Aebi et al.[16,17] and Ollerton et al.[18] regarding the relative importance and effectiveness of honeybees versus other species). As a result, current pollination ecosystem services research focuses predominantly on conserving wild pollinators and their habitat within and adjacent to the agricultural matrix.[19-21] The original emphasis on managed honeybees for crop pollination was based on their convenience and effectiveness in intensive agricultural systems[5,11], which are typically characterised by relatively large crop areas with little or no natural vegetation within the agricultural matrix as well as a short time period for pollination as a result of the deliberately high level of flowering synchrony within a crop field[7]. Total reliance on wild pollinators would therefore appear to present risks for farmers in these intensive agricultural landscapes and it is still unclear if there are sufficient numbers of suitable wild (non-*Apis*) pollinators to provide effective pollination services.[22] There is a growing body of evidence showing that diverse pollinator assemblages provide better pollination services to crops.[3,23,24]

A recent global study investigated the role and contribution of wild pollinators and managed honeybees as a pollination service to a range of annual and perennial fruit, seed, nut, and stimulant crops across 41 sites worldwide.[25] This study indicated that crop fields with high numbers of both honeybees and wild pollinators resulted in sufficient pollen deposition. In contrast, it was shown that wild insect visitation alone significantly increased fruit set, by twice as much as honeybees did, suggesting wild pollinators provide more effective crop pollination. Moreover, fruit set was shown to increase consistently with visitation from wild pollinators and increased with visitation by a diverse assemblage of pollinators independent of honeybee visitation. The additive interaction between non-*Apis* pollinators and honeybees has been shown to increase fruit set.[26,27] Recommendations for optimal pollination therefore sometimes call for the integration of wild pollinators with managed honeybees.[25,28]

Despite the perceptions of global honeybee decline, long-term global data indicate an increase in managed honeybees,[29-31] except in the USA. However, agricultural demand could outstrip supply of managed honeybees[30] and greater demand for high value fruit and nut crops may further increase demand for pollination services.[32,33] This demand implies that pollination services may experience constraints even without a dramatic decline in honeybees and highlights the need for effective strategies to safeguard reliable pollination services for agriculture. Such strategies could include: improved health of managed honeybees; identifying possible substitutes for managed honeybees[14,34]; increasing and diversifying the suite of wild pollinators where possible (see Corbet[15]); and increasing the effectiveness of wild pollinators[26]. The latter includes conserving suitable food sources and nesting habitat for wild pollinators within the agricultural matrix and raises the question first posed by Ghazoul[35]: 'Is management to secure biodiversity benefits more rewarding for crop production than management less favorable to biodiversity?'

If so, then strategies to improve pollination services need to be aligned with strategies to conserve biodiversity in agricultural landscapes.

Within South Africa, there is a high demand for pollination services for many crops. At the same time, our pollinators are exposed to similar environmental pressures that have resulted in declines elsewhere in the world, e.g. habitat transformation or fragmentation[19,20], loss of diversity and abundance of floral resources[36,37], inappropriate use of pesticides[36,38], spread of pests and diseases[17], and climate change[5]. As a result, it is important to understand the current state of knowledge in South Africa relating to pollination services. In this context, we review the literature of South African pollination services in agricultural systems to highlight issues and identify areas where further research is needed. Firstly, we review the importance of different pollinator species as a basis for services to South African crop production. Secondly, we examine if South Africa is experiencing similar declines in managed honeybees. Thirdly, we focus on the Western Cape deciduous fruit industry, an industry worth ZAR9800 million per year, which is heavily reliant on the provision of pollination services.[89,90] Despite its economic importance, very little has been published on managed pollination services in South Africa. We review the current capacity, economic value and importance of the pollination services. Fourthly, we focus on the landscape and regional level dependence on floral resources to maintain sufficient numbers of managed honeybee colonies and what this may mean for sustainable pollination services.

Importance of pollinator species for South African crop production

One of the assumptions of the global focus on pollination ecosystem services is that a wide variety of species has the potential to contribute to crop pollination and that this diversity of pollinators can be promoted either as an alternative[3,23] or as an adjunct[24,27] to honeybees. The literature indicates that a shortage in the abundance and diversity of wild pollinators could jeopardise crop yields.[40-43] One of the main factors affecting the diversity and abundance of pollinators in the agricultural matrix is available habitat; declines in pollinator diversity in Europe and North America have been correlated with the loss of habitat through agricultural intensification.[3,44,45] In addition, isolation of crop fields from natural and semi-natural habitat has been shown to negatively impact on the stability of wild pollinator richness, visitation rate and fruit set in crops.[21,42,46]

There have been few comprehensive assessments of pollinator assemblages on crops in South Africa and no studies on declines in these assemblages such as that done by Biesmeijer et al.[4] for European systems. Nevertheless, studies on natural systems within South Africa have shown the negative effects of habitat fragmentation on plant–pollinator interactions within the agricultural matrix[47,48] as well as the breakdown of specialist plant–pollinator networks on smaller conservation areas (reserves <385 ha).[49] Furthermore, the impact of overgrazing on pollinators has also been shown to have negative impacts through the loss of host plants and trampling of nesting sites.[50-53] Interestingly, Vrdoljak and Samways[54] found that levels of flower visitor richness within agricultural mosaics can be similar to protected areas, suggesting the potential for natural or semi-natural habitat to facilitate movement of individuals and act as a repository for pollinators. Without long-term monitoring of pollinator populations to assess trends over time, little inference can be made about such changes in wild pollinator populations or their effects on pollination services.

Within South Africa, there have only been nine studies (Table 1), four published in peer-reviewed journals, assessing the importance of different pollinator assemblages as a basis for services to crop production. The contribution of pollinator richness to fruit or seed set has not been thoroughly investigated in South Africa, with a few notable exceptions on sunflower seed[55], mango[56] and rooibos seed[57] crops indicating the importance of pollinator richness. In the case of sunflowers and mangoes, even with a high abundance of honeybees, Carvalheiro et al.[55,56] found diversity of flower visiting insects to be the main contributor to crop productivity. In these two crops, pollinator richness and abundance decreased with distance from natural vegetation, which negatively affected production. In order to reduce these negative effects, Carvalheiro et al.[55,58] found that promotion of 'within-farmland biodiversity' (native flower patches in mango orchards and weeds in sunflower fields) increased pollinator richness which improved crop productivity. Promoting within-farmland biodiversity appears to offer practical cost-effective management options for increasing pollination services. These studies confirm the importance of pollinator richness for some crops and the concomitant need to maintain habitat within the agricultural matrix. Nevertheless, the evidence base linking pollinator richness to crop yield is still relatively weak for most South African systems. In addition, estimating the importance of pollinator richness can be challenging as not all flower visitors actually pollinate plants[57,59] and it is necessary to relate the biology of these species to their behaviour and pollen loads to distinguish flower visitors from pollen vectors[57,59-61]. Additionally, pollen delivery is only one of several factors resulting in successful pollination.[62,63] It is therefore important to determine the key pollen vectors in order for farmers to manage their land more effectively, e.g. providing nesting habitat for these key pollinators.[37,57,64,65]

Despite the findings indicating the importance of wild pollinators, the role and contribution of honeybees (both managed and wild) within South African agriculture should not be overlooked. All but one study (Table 1) on mangoes[55] found honeybees to be the most abundant pollinator (contributing on average 69.2±30.0% of observed insect visitors to flowers) in South African crop fields, including seed, deciduous fruit and tropical fruit crops. A high abundance of honeybees is not uncommon; honeybees are known to be present in many agricultural systems worldwide[25,66] – either because managed hives have been used or because there are wild or feral honeybees[55]. Honeybees in South Africa are indigenous and ubiquitous in natural[67-69] and agricultural systems[55,70] and are an important pollinator to a wide range of indigenous plant species[68,71]. Consequently, assessing the ecological importance of wild honeybees within the agricultural matrix and their contribution to sustainable pollination services is essential. However, doing so is not straight forward, as it would be impossible for researchers to distinguish between wild and managed honeybees as they are the same species.[56,57] In order to determine the relative contribution of wild pollinators, including wild honeybees, researchers would need to (1) account for the presence of managed hives in their experimental design and statistical analysis (see Carvalheiro et al.[55,56]), (2) use isolated fields (greater than 5 km from neighbouring farms), preferably surrounded by natural vegetation, that do not have managed honeybees or (3) close up managed hives once they have been brought into the orchard or crop field.

Honeybees are not efficient pollinators of some crops (as a result of their foraging behaviour and morphology), which is usually compensated for by increasing the number of managed hives.[11,72] Increased frequency of honeybee visitation has been shown to provide sufficient pollen deposition but poor or variable quality pollination.[25] It has been shown that rooibos seed[57], lucerne seed[73,74] and mango[56,58] in South Africa are pollinated effectively by other pollinators. In one study investigating potential pollinators for rooibos seed production, honeybees were abundant but were not considered to be important pollinators.[57] Instead, Gess and Gess[57] found Xylocopinae, Megachilinae and Masaridae were essential pollinators for rooibos seed production. Honeybees are also not considered to be the most efficient pollinators of lucerne[72], even though lucerne seed producers depend on them. Larger bees, such as the carpenter bee (*Xylocopa caffra*), are considered to be more suited to the large flowers of legumes and are more effective as a consequence of their foraging behaviour, during which they trip the flower and affect pollination.[68,73-75] However, in crops where honeybees are abundant, synergistic effects (increasing the movement and rate of visitation of honeybees) of non-*Apis* have been shown to improve pollination efficiency and the potential to increase crop yields.[26,27,55] These findings suggest the possible benefits of integrated management of non-*Apis* and honeybees.[25]

The limited amount of published research (Table 1) on the importance of different pollinator species highlights the need for further research on the diversity and richness of unmanaged pollinators (including

Table 1: A summary of research assessing the importance of different pollinator assemblages as a basis for services to crop production in South Africa

Crop	Citation	Dominant pollinator/flower visitor		Other pollinators/flower visitors recorded		Recorded use of managed hives at time of study	Distance from managed hives included in study	Location in South Africa
		Species	**% Visits**	**Taxa**	**% Visit**			
Apples (*Malus domestica*)	Mouton[76]	*Apis mellifera capensis*	98%	Lepidoptera Hymenoptera Diptera Coleoptera	2%	Yes	2 km	Grabouw, Western Cape
Avocado† (*Persea americana*)	Eardley and Mansell[77]	*Apis mellifera scutellata*	84%	Hymenoptera Coleoptera Lepidoptera Hemiptera Diptera	16%	Yes	No	Tzaneen, Limpopo Province
Litchi† (*Litchi chinensis*)	Eardley and Mansell[78]	*Apis mellifera scutellata* *Plebeina denoiti* *Ctenoceratina* spp. *Braunsapis facialis*	65% 9% 8% 8%	Hymenoptera Chrysididae Coleoptera Diptera Bombyliidae Syrphidae Muscidae	10%	Yes	No	Ofcalaco, Limpopo Province
Mango† (*Mangifera indica)*	Eardley and Mansell[79]	*Apis mellifera scutellata* *Rhyncomya forcipata* *Braunsapis* spp.	32% 16% 13%	Hymenoptera Coleoptera Lepidoptera Diptera	39%	Yes	No	Tzaneen, Limpopo Province
Mango (*Mangifera indica)*	Carvalheiro et al.[56]	*Camponotus* spp. *Monomorium* spp. *Apis mellifera scutellata* *Empididae* spp.	18% 12.60% 9% 9%	Coleoptera Diptera Hymenoptera Lepidoptera	51.40%	Yes	No	Mpumalanga Province
Onion hybrid seed production (*Allium cepa*)	Brand[80]	*Apis mellifera capensis*	91.50%	Coccinellidae Diptera Hemiptera Non-*Apis* bees	8.50%	Yes	No	Southern Karoo and Klein Karoo, Western Cape
Rooibos tea seed (*Aspalathus linearis*)	Gess and Gess[57]	Megachilinae Masarinae Xylocopinae	–	–	–	–	–	Citrusdal to Clanwilliam, Western Cape
Sunflowers (*Helianthus annuus*)	Carvalheiro et al.[55]	*Apis mellifera scutellata*	84%	Coleoptera Diptera Heteroptera Hymenoptera Lepidoptera	16%	Yes	0.67–2 km	Settlers, Limpopo Province
Sunflowers (*Helianthus annuus*)	Shenkute[81]	*Apis mellifera scutellata*	90%	Lepidoptera Coleoptera Diptera Heteroptera Hymenoptera	10%	Yes	1 km	Settlers, Limpopo Province

†We calculated the relative abundance of each species using Eardley and Mansell's[77–79] total counts over 3 years (1994–1996), e.g. Apis mellifera *30%*

indigenous *Apis*). The available literature indicates that honeybees are important, but because the wild component has not been quantified, the most effective pollination services appear to be derived from a combination of honeybees and other pollinators.

Are there declines in managed honeybees in South Africa?

In South Africa, managed honeybees have not experienced the same dramatic declines as recorded for North America and, to a lesser extent, Europe. They appear to have remained healthy despite the appearance of destructive bee pests such as varroa mite[82] and diseases such as American foulbrood.[83,84] It has been reported that South African honeybees exhibit traits of resilience against these pathogens.[84] However, this tolerance of bee pests and diseases in honeybees is not yet fully understood[84] and it would be premature to assume that honeybees in South Africa will not decline as a result of novel pests or diseases. Despite an absence of significant reports of colony losses, data on the number of honeybee colonies in South Africa are irregular and patchy, with the last census conducted in 1975.[85,86] Added to this, the reduced capacity and limited budget available for the Agricultural Research Council to collect data on honeybees means that data on honeybee colonies are unlikely to improve in the short term. Pirk et al.[87] conducted a beekeeper survey assessing the extent and the potential causes of colony losses in South Africa. Their study found colony losses (reported losses over two consecutive years, 2009–2010 and 2010–2011, of 29.6% and 46.2%, respectively) were higher than those considered acceptable in Europe or North America. Colony losses, specifically for beekeepers using *A. m. scutellata,* have, for the most part, been attributed to the *A. m. capensis* worker social parasite, a problem unique to South Africa. Losses of colonies were shown to be significantly increased by migratory beekeeping practices, in particular when beekeepers moved colonies to provide pollination services.

Global analyses of long-term data have shown that the assessment of hive numbers in the context of demand indicates there has been an increase in pollinator-dependent crops[33] rather than a decline in managed honeybees. Allsopp and Cherry[88], and anecdotal reports a decade later, indicate that colony numbers in South Africa are constrained by access to and availability of floral resources and therefore have a limited capacity to cope with any further demand. The lack of suitable sites forces new entrant commercial beekeepers to buy out established businesses for these highly prized sites. Similar assessments, as done by Aizen et al.[29], are needed in South Africa to determine if the current supply of managed hives meets current and predicted increases in demand for pollinator-dependent crops.

Pollination services to the Western Cape deciduous fruit industry

Given the relative importance of pollination to deciduous fruit production in the Western Cape Province, the region provides an important case study for this review. South Africa is a major volume fruit exporter in global terms and the industry is valued at ZAR9800 million per year.[89,90] There is 77 805 ha under deciduous fruit production in South Africa and a little over half this area is concentrated in the Western Cape.[89] Deciduous fruit growers are largely dependent on managed honeybees for pollination (specifically for apples, plums, pears and apricots).[39] Approximately 87% of the honeybee hives in the Western Cape are used for pollination services[82] and large commercial beekeepers transport their hives hundreds of kilometres to provide pollination services to the industry[82,85].

The Western Cape forms part of the Cape Floristic Region (CFR) – an area of distinctive biological diversity and rich in endemic species.[91-93] It is currently estimated that 30% of the CFR has been transformed through agriculture, invasion by alien vegetation and urbanisation.[91,92] The CFR is globally recognised as a significant centre of diversity for bees, one of the most important pollinator groups.[94] Although agriculture in this region abuts natural vegetation, the contribution of other pollinators from natural vegetation appears limited, but has not been sufficiently quantified (Table 1).

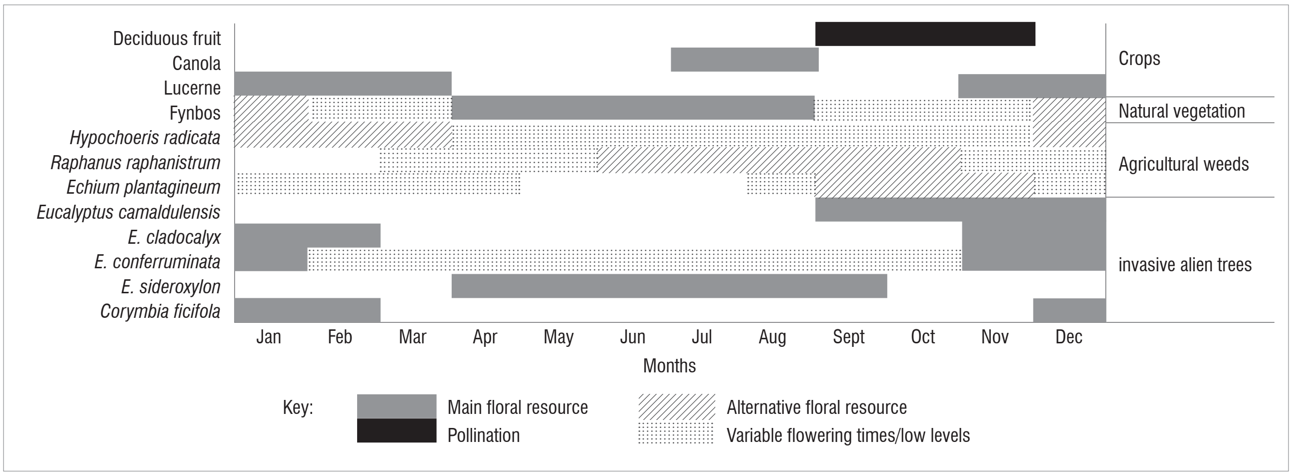
Approximately 30 000 managed hives are required to provide pollination services to the deciduous fruit industry in the Western Cape.[88] On average, each hive can provide 1.7 pollinations (the number of times a hive of suitable strength is used for pollination in crop fields), so that, on average, 51 000 pollinations are supplied each year. Each crop requires different stocking rates of hives to ensure pollination; for example, apples require 2 hives/ha and plums 6 hives/ha.[70,88,95] It has been estimated that deciduous fruit producers in the Western Cape require on average 42 000 pollinations a year.[88] Based on these figures, there is currently approximately a 20% surplus; however, it is unknown if this surplus provides for all possible contingencies, specifically in the light of potential disease outbreaks (e.g. the recent outbreak of the bacterial disease American foulbrood[84] in 2009) or increased demand in pollinator-dependent crops.[29]

Estimates of the economic value of pollination services may be used to prioritise conserving habitat for pollinators in agricultural systems.[96] There is a growing body of scientific literature on methods for valuing ecosystem services, many focusing on the value of managed honeybees as a proxy for wild pollinators, but as yet there is no consensus as to the most appropriate method.[97] Within South Africa, there have been two studies[39,95] valuing pollination services in the Western Cape Province. The direct cost of pollination services to the deciduous fruit industry is estimated as 1% of production costs,[39,89] which is a considerable underestimate of its ecological value. Turpie et al.[95] estimated the value of pollination services from managed honeybees to agricultural crops at ZAR1820 million.[95] Using a different method, Allsopp et al.[39] valued managed pollination services at ZAR46 million and wild insect pollination services at ZAR53 million (based on the 2006 exchange rate used by authors of ZAR6.74388 to USD1).[39] Notwithstanding the need to agree on valuation methods, there may be more important economic questions that have not been addressed. These include the potential increase in crop production costs if there are constraints on managed honeybee numbers (as seen in North America where demand for pollination in almond orchards resulted in significant increases in honeybee rental costs[2]), as well as examining the true cost of pollination services across the supply chain from the provision of forage to crop pollination. Such valuations may better inform land-use planning for the provision of floral resources to ensure sustained managed pollination services.

Landscape and regional level floral resources for managed honeybees

Much like wild bees, honeybees depend on native or alternative floral resources for pollen, nectar and resin when they are not pollinating crops.[3,9,98] Little research has been conducted on the use of floral resources to sustain large numbers of honeybee hives which require a variety of floral resources, depending on the time of year. From September to November, Western Cape beekeepers migrate managed hives from all over the Western Cape to the main fruit-producing areas, e.g. Grabouw, Ceres and Boland. In order to ensure they have strong colonies, beekeepers need to sustain colonies throughout the year. Beekeepers move hives around to take advantage of a range of different floral resources (Figure 1), governed by different flowering times, each fulfilling one or more function(s); for example, honey production, comb build-up, overwintering and swarm trapping (it is common practice in South Africa for beekeepers to trap wild or absconded honeybee populations).[70] Honeybees are successful as managed pollinators because they have a broad diet, forage over long distances and have the ability to locate and utilise discrete patches of resources in the wider landscape.[21] A pressing concern within the South African beekeeping industry is availability and access to suitable floral resources, in particular stands of *Eucalyptus* species for honey production and to maintain hives for pollination services.[88]

The major honeybee plants in the Western Cape, those yielding substantial quantities of pollen and nectar and which are important for colony replenishment, include indigenous vegetation (fynbos), stands of alien



Source: Adapted from Johannsmeier[70,99] and Lange et al.[100]

Figure 1: Seasonal availability of floral resources used by commercial beekeepers to sustain managed hives in the Western Cape Province.

invasive species (*Eucalyptus* spp.) and cultivated crops (canola, citrus and lucerne).[70,88] Interestingly, when looking at this managed system, we see that pollinator floral resources are derived not only from intact natural vegetation but also from human-modified vegetation. These floral resources become available over a temporal and spatial mosaic across the Western Cape. Therefore quantifying the importance of these key floral resources to maintain stable honeybee populations at a landscape or regional level is essential. It is also critically important in light of recent research showing that one of the possible causes of declines in managed hives in North America is a compromised or deficient diet.[36,101] However, it is apparent that in order to understand the complex ecological linkages that exist between the agricultural landscapes and the supporting ecosystem services for managed honeybees, an in-depth analysis is required. Fine-scale data on both the spatial and temporal nature of these resources, their extent, and their seasonal inter-dependence need to be considered when assessing the importance of floral resources.

Not all floral resources are suitable for sustaining hives. Some sites have limited carrying capacities in relation to specific floral resources as a result of nectar flows, pollen availability or seasonality.[102] Furthermore, there are management issues such as access (permission) to certain floral resources (e.g. fynbos in conservation areas[71]), vandalism of hives[70] and high pesticide use[70,88], which result in areas or sites being unsuitable or impossible for keeping honeybees.

In the following sections we discuss the key floral resources used by commercial beekeepers within the Western Cape: crops, alien vegetation, indigenous vegetation and agricultural weeds (Figure 1). Each is discussed in terms of usage, seasonal availability and abundance (area/extent).

Crops (canola, Brassica napus*) – late winter/early spring*

Mass flowering crops, including *Brassica napus* (canola), have been shown to be important for sustaining bumblebee populations in Europe.[65,103] Canola farmers, growing self-compatible varieties, may benefit from insect pollination which has been shown to increase seed set and seed quality.[70,104,105] In the early 1990s, rain-fed canola production was introduced in the winter rainfall region of the Western Cape and grown in rotation with wheat-barley-lucerne.[106] Canola has rapidly become an integral floral resource for beekeepers, particularly for those beekeepers who provide pollination services, as it allows colonies to build-up their strength prior to crop pollination. The high pollen and nectar content of canola stimulates an increase in brood production resulting in an increase foraging for pollen, which is ideal when hives are moved to farms for pollination, as active foragers should equate to better pollination.[67,70,88] Canola is an important attractant for migrating/absconding swarms, enabling beekeepers to trap new swarms (and replenish hive numbers). Currently, 45 000 ha of canola is planted in the Western Cape[107]; and this figure is set to increase.[108,109] However, canola is produced in rotation with other cereal crops on a 1-in-5 or 1-in-10 year cycle,[106] depending on individual farming practices, and not all canola fields are suitable for apiary sites because of heavy pesticide use which increases the risk of colony losses.[88,104] As a result, it is challenging to predict the availability of canola in any particular year or its contribution to apiary sites in maintaining managed honeybees for pollination services.

*Invasive alien trees (*Eucalyptus *spp.) – summer*

Following pollination of deciduous fruit crops, beekeepers move their hives to sites with stands of *Eucalyptus* trees. Beekeepers use eucalypts because they are dependable sources of pollen and nectar, particularly during summer when there is a shortage of alternatives. Eucalypts enable beekeepers to maintain honeybee colonies for pollination for the following season and produce a surplus of honey.[70]

In the Western Cape, commercial beekeepers who provide pollination services depend on three species: *E. cladocalyx, E. camaldulensis* and *E. conferruminata*. Several *Eucalyptus* species have been classified as invasive species under the *Conservation of Agricultural Resources Act (CARA) of 1983*, resulting in programmes aimed at clearing these species.[110] This clearance has raised questions regarding the benefits of these species to beekeepers (and hence agricultural production) relative to the costs associated with invasion; for example, a survey of Western Cape beekeepers found a significant dependency on CARA-listed *Eucalyptus* species.[88] The Department of Environmental Affairs, which coordinates most of the invasive clearing through the Working for Water programme, has been sensitised to these issues and has supported various initiatives to improve the scientific basis for decision-making regarding *Eucalyptus* species, including research on the use of floral resources by honeybees (http://www.sanbi.org/programmes/conservation/pollination-and-honeybees). The evidence gained from these studies is expected to influence the listing of *Eucalyptus* species under the *National Environmental Management Biodiversity Act of 2004*, which will eventually replace the CARA listings. To support the listings, as well as a more evidence-based approach to the management of *Eucalyptus* species, it is essential to have a proper understanding of the dependence of the beekeeping industry on these species. In 2004, it was estimated that the infestation of *Eucalyptus* species for the whole of South Africa (nine provinces) was 62 949 ha, of which 2264 ha was already cleared.[111] These estimates have not been provided on a provincial basis and it is therefore hard to gauge the extent and availability of *Eucalyptus* species to beekeepers in the Western Cape during the summer months. It is also not clear whether beekeepers rely on eucalypt plants that grow in high-risk areas (riparian zones, mountain catchments and high fire-risk zones) or in areas where eucalypts can be retained with a low risk to the environment. However, based on beekeeper observations, Allsopp and Cherry[88] reported that 60% of eucalypts were found to be on land with a low risk of invasion.

Indigenous vegetation (fynbos) – autumn/winter

There are seasonal patterns in the availability of fynbos plants based on rainfall patterns across the region, with approximately 20% in flower at any time.[67,112] Commercial beekeepers use fynbos in autumn for surplus nectar flow, mainly from *Erica,* although they include Aizoaceae, Fabaceae, Proteaceae, Asteraceae and Ericaceae for pollen. [70,99] Exactly which fynbos plants honeybees use is not yet fully understood.[99] Fynbos provides honeybee colonies with sustenance during winter months, which is essential for attaining optimum strength in preparation for the following spring's pollination season.[70,99]

The broad fynbos types favoured by beekeepers include Mountain Fynbos, Western Sandveld and South Coast Fynbos, all of which fall within the CFR. It appears that a relatively high proportion of the CFR is untransformed, with about 20% formally conserved.[91,92] Approximately 50% of Mountain Fynbos, rich and abundant in *Erica* species,[113] falls within the current conservation system.[91,92] How much of this fynbos is suitable, available or utilised by beekeepers is unknown. However, the demand for accessible and suitable fynbos sites, outside of formal reserve areas, by beekeepers currently far exceeds availability.[88] Reserves currently preclude beekeepers bringing in their hives, based on the possible impact that competition from introduced managed hives would have on other pollinators and plant communities.[114] Evidence to date has shown contrasting results – some studies have found negative competitive interactions while others have found no effect between introduced managed honeybees and native bees (see references in Hudewenz and Klein[115]). In the Western Cape, Brand[116] concluded that the short-term introduction of managed hives in a fynbos reserve did not have a significant impact on increasing the overall abundance of honeybees, nor was there a detectable impact on other insect flower visitors. Despite high densities of honeybees from managed hives, Geerts et al.[117] found no significant depletion in nectar on *Protea repens.* However, high densities of honeybees appeared to interfere with sugarbirds foraging on flowers through disturbance competition.[117] Further studies would be needed to assess the impact of introduced honeybees if beekeepers are permitted access to fynbos reserves. However, providing unambiguous evidence of competition, particularly for mobile organisms, is exceptionally difficult.[66,118] Conclusive results would be further hampered by lack of baseline data on natural populations of *Apis mellifera capensis* occurring in fynbos.[114] Despite restrictions, some beekeepers seem to utilise protected areas by placing their hives on private land abutting reserves.[71]

Agricultural weeds – all year round

Annual weeds such as *Echium plantagineum* (echium), *Raphanus raphanistrum* (wild radish), *Plantago lanceolata* (plantain) and *Hypochoeris radicata* (false dandelion), which typically occur in vineyards, farmlands and road verges, provide a minor nectar flow for honeybees (see Johannsmeier[99] for a complete list of weeds).[70,99,119] Availability of weeds is highly variable[70,119] and therefore considered a minor floral resource[70,99]. However, when available, weeds can offer an important source of pollen and nectar for sustaining hives.[119] Pollen from echium and wild radish is reported to be exceptional in terms of crude protein content.[119] Because none of these plants are cultivated or grown in abundance, it would be difficult to estimate their availability as a floral resource.

Summary and future directions

In summary, our review shows the importance of pollinator richness for some crops and the concomitant need to maintain habitat within the agricultural matrix. Nevertheless, the evidence base linking pollinator richness (including indigenous *Apis*) to crop yield is still relatively weak for most South African systems. The available literature indicates that honeybees are important, but as the wild component has not been quantified, the most effective pollination services appear to be derived from a combination of honeybees and other pollinators.

In addition to the need for accurate census data on managed honeybees, assessments to determine if current supply of managed hives meets current and predicted demand for pollinator-dependent crops are needed. Given the relative importance of pollination to deciduous fruit production in the Western Cape and the current demand for managed honeybees, we highlight potential constraints to increase capacity, such as limited access and availability of suitable floral resources. It is therefore necessary to estimate the potential increase in crop production costs if there are constraints on managed honeybee numbers and to examine the true cost of pollination services across the supply chain from the provision of forage to crop pollination. Such economic evaluations may improve land-use planning for the provision of floral resources to ensure sustained managed pollination services. We conclude that understanding the dynamics of how floral resources are used will help inform how landscapes could be better managed in order to provide long-term sustainable pollination services.

Based on the synthesis presented here, we have identified the following research questions that need to be addressed in order to provide a sustainable pollination service to South African agriculture, particularly in the Western Cape:

- What is the contribution of wild pollinators, including wild honeybees, to particular crops?
- Are managed honeybees constrained by available floral resources and, if so, what does this constraint mean for crop production in South Africa?
- Where are the key floral resources in the landscape and can these be mapped and included in regional plans?
- How can landscapes be managed to optimise the use of different elements to sustain pollination services?

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Authors' contributions

A.M. wrote the first draft of the manuscript with contributions from M.R., J.J.M. and J.S.D.

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