



Research article

Potential supply of floral resources to managed honey bees in natural mistbelt forests

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ARTICLE INFO

Article history:

Received 23 March 2016

Received in revised form

11 December 2016

Accepted 12 December 2016

Keywords:

Forage value

Honey bee plant richness

Nectar

Plant diversity

Pollen

South Africa

ABSTRACT

Honey bees play a vital role in the pollination of flowers in many agricultural systems, while providing honey through well managed beekeeping activities. Managed honey bees rely on the provision of pollen and nectar for their survival and productivity. Using data from field plot inventories in natural mistbelt forests, we (1) assessed the diversity and relative importance of honey bee plants, (2) explored the temporal availability of honey bee forage (nectar and pollen resources), and (3) elucidated how plant diversity (bee plant richness and overall plant richness) influenced the amount of forage available (production). A forage value index was defined on the basis of species-specific nectar and pollen values, and expected flowering period.

Up to 50% of the overall woody plant richness were found to be honey bee plant species, with varying flowering period. As expected, bee plant richness increased with overall plant richness. Interestingly, bee plants' flowering period was spread widely over a year, although the highest potential of forage supply was observed during the last quarter. We also found that only few honey bee plant species contributed 90 percent of the available forage. Surprisingly, overall plant richness did not significantly influence the bee forage value. Rather, bee plant species richness showed significant and greater effect. The results of this study suggest that mistbelt forests can contribute to increase the spatial and temporal availability of diverse floral resources for managed honey bees. Conservation efforts must be specifically oriented towards honey bee plant species in mistbelt forests to preserve and enhance their potential to help maintain honey bee colonies. The implications for forest management, beekeeping activities and pollination-based agriculture were discussed.

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1. Introduction

Insect pollinators provide a vital service of pollination to flowering plants by foraging and transferring the pollen from one flower to another. Of all insects, bees are crucial pollinators, as they are fully dependent on floral resources (nectar and pollen) for forage provision (Buchmann and Nabhan, 1996; Shepherd et al., 2003). Bees feed on the floral resources of a wide variety of flowering plants, from natural and semi-natural habitats to surrounding agricultural landscapes (Ricketts et al., 2008), and contribute to the

pollination of more than 66% of the world's crop species (Kremen et al., 2004).

With the increasing worldwide decline in insect pollinators (and thus reduction of pollination services) as a result of landscape fragmentation and modern agricultural practices (Potts et al., 2010; Whitehorn et al., 2012), honey bees (*Apis* spp.) have increasingly been managed for apiculture and provision of pollination services (de Lange et al., 2013). For instance, honey bee colonies can be managed and maintained by beekeepers in natural and semi-natural habitats that provide floral resources, and moved afterwards to other places (e.g. agricultural farms) when they are needed for pollination (Allsopp and Cherry, 2004; de Lange et al., 2013; Johannsmeier, 2005; Melin et al., 2014). Allsopp and Cherry (2004), and Johannsmeier (2005) documented the potential forage supply by many eucalypt species to honey bees in Western

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Cape province of South Africa, with some being excellent sources of high quality pollen. These authors argued that beekeepers rely on the flowering season of eucalypt plantations to maintain honey bee colonies, which will provide pollination service for deciduous fruits (e.g. apples, pears, plums and berries) in the following season. In addition, after the fruit pollination season, the majority of honey bee colonies used in the Western Cape for pollination services are maintained within eucalypt plantations (Allsopp and Cherry, 2004). However, because these plantations are fast growing monocultures with short rotation periods, and do not harbour high floral diversity, they provide forage resources of limited value (Allsopp and Cherry, 2004; de Lange et al., 2013). Conversely, protected natural forests usually support high floral diversity, and are primary sources of diversified floral resources for honey bees and other wild pollinators. Beekeepers report that the natural Fynbos in the Western Cape is a main forage source for honey bees from April to July (de Lange et al., 2013).

Limpopo (South Africa's northernmost province) is one of the most productive provinces, in terms of commercial timber (pine and eucalypt plantations) and agriculture (especially fruits and tea). The natural vegetation in Limpopo province is dominated by large and fragmented patches of mistbelt forests surrounded by plantations and agricultural areas (Mensah et al., 2016). Despite the high floral diversity in these mistbelt forests, there is little investigation and argument regarding their potential to provide floral and nesting resources for honey bees. As a corollary, very little is known about the suitability of mistbelt forests for beekeeping activities, as main or alternative sources of honey bee forage, in a typical forage-calendar year, similar to the Fynbos in the Western Cape province (de Lange et al., 2013; Melin et al., 2014).

The abundance and diversity of floral resources reflect a continuous supply of forage from different species and therefore, encourage honey bees to remain on site (Torné-Noguera et al., 2014). Yet, the availability of floral resources to honey bees in natural forests varies according to several factors such as distance from colonies (Jha and Kremen, 2013; Williams and Winfree, 2013), species-specific flowering phenology, tree size (Pardee and Philpott, 2014; Scaven and Rafferty, 2013), and spatial distribution of honey bee plants, which in turn determine the spatial and temporal distribution of flower and nesting resources (Torné-Noguera et al., 2014).

The abundance of floral resources at plant level is governed by whether (and how intensively) a honey bee plant flowers, i.e. the flowering area (Scaven and Rafferty, 2013), which however can be a poor predictor of visitation (Hülsmann et al., 2015). On trees, flowers and leaves both originate from buds, which are carried by twigs. Thus, the flowering area of a honey bee flowering plant will likely correlate with the amount of foliage, which in turn correlates with tree size and age (Otárola et al., 2013). Therefore, at plant community and forest stand scales, stand structural characteristics of bee plant species (stem density and stem basal area) will likely determine the potential amount of floral resources that attract honey bees from a distance (Hülsmann et al., 2015; Jha and Kremen, 2013; Pardee and Philpott, 2014).

At the plant community and forest stand scales, the diversity of floral resources would be governed by bee plant diversity because new bee plant species in flowers, added to the community, would likely contribute new species-specific phenological characteristics such flower production, pollen and nectar production. As pointed out by Blüthgen and Klein (2011), different plant species that flower together would contribute more to the production of floral resources than any of them alone, suggesting functional complementarity effects at the plant community level. Also, due to species-specific phenological/structural characteristics (longer flowering period, better quality of pollen and nectar, greater stand density

and basal area), some bee plant species would likely contribute more to the overall forage production than other species.

In this paper, we aimed to quantify the availability of forage to honey bees in mistbelt forests, and how bee forage provision varied with honey bee plant diversity and overall plant diversity. We carried out field plot inventories in natural evergreen mistbelt forests in South Africa to (1) examine the diversity and relative importance of honey bee plants, (2) explore the temporal availability of honey bee forage (nectar and pollen resources), and (3) elucidate how plant diversity (bee plant richness and the overall plant richness) influences the bee forage production. For the first objective, we assessed the diversity of honey bee plants, and determined the most important honey bee forage plant species; we also asked whether plot level variation in all plant species richness was positively associated with variation in bee plant species richness. This association may not be straightforward, as rich plots (in terms of species) can contain very few bee plant species. Also, at the plot level, bee plant species represent a proportion of all plant species, with the strength of the association varying based on the relative abundance of honey bee plants across the study plots. In other words, no association would be expected if the distribution of honey bee plant richness across the studied plots showed early asymptotic trend. Second, we defined a forage value index (FVI, based on the species-specific nectar and pollen value, and the expected flowering period), and explored the temporal availability of the nectar and pollen forage value. Finally, we used the defined FVI as proxy for forage production, and modelled its relationships with plant diversity (plant richness and bee plant richness). We assumed that both overall plant richness and bee plant richness would positively influence the forage value.

2. Material and methods

2.1. Study area

The study was carried out in the Limpopo province located in the northern part of South Africa. The province is characterized by a succession of landscapes with highly varied topography, from zones of flat lowland plains to zones of high mountains, through mosaics of foothills and low mountains. The areas of low mountains and foothills are used for commercial and small scale subsistence farming, and commercial timber managed by forest companies. Many fragmented patches of natural forests and degraded woodlots non-suitable for forest plantations are also found in this area (Geldenhuys, 2002). Some crops fields (especially fruits) are established in the surrounding environment of natural and planted forests (eucalypt), and benefit from pollination services provided by wild pollinators and managed honey bees (Carvalho et al., 2010; Melin et al., 2014). The specific area selected for this study is the Woodbush-De Hoek natural forest (23°50'S, 30°03'E), considered as part of the Limpopo mistbelt forests (Mucina and Rutherford, 2006). The Woodbush-De Hoek forest covers a total area of about 6, 626 ha, and is one of the largest forest blocks of the Northern Mistbelt Forest group (Cooper, 1985; Geldenhuys, 2002). The woody flora is predominated by canopy species such as *Podocarpus latifolius*, *Combretum kraussii*, *Syzygium gerrardii* and understorey species such as *Peddiea africana*, *Oricia bachmannii*, *Kraussia floribunda* (Mucina and Rutherford, 2006).

2.2. Sampling for floristic data

The data used in this study was collected from a sample plot survey, based on a stratified random sampling design set in a 708 ha (hectare) forest block in the Woodbush De Hoek forest. The stratification of the research area was based on three classes of slope

(flat: 1.5%–15.3%, gentle: 15.3%–29.19% and steep: 29.19%–43.1%); four classes of aspect (North, South, West and East); and three classes of elevation (low: 1174–1332 m a.s.l., medium: 1332–1490 m and high: 1490–1648 m). The reason for stratifying the study area was to account for environmental heterogeneity during data collection. Thirty 0.05 ha circular plots were randomly established within the stratified compartments and used as sample plots for tree species above 10 cm diameter. Inside each 0.05 ha circular plot, a smaller circular plot of 0.025 ha was also set for recording trees with 5–10 cm diameter. Tree species names, density and diameter at breast height (dbh) were collected. This floristic data was completed with information on honey bee forage resources for each plant species. We used the work on ‘Beeplants of South Africa’ (Johannsmeier, 2005, 2016) to gather the information on nectar/pollen values and flowering time of each plant species. The information is only applicable to the honey bee, as other pollinators have other specific preferences. Plant species names and synonyms were referenced using <http://www.tropicos.org/> and <http://www.ipni.org/>. The nectar and pollen values of honey bee plants were ranked from 0 (no nectar/pollen is available to, or collected by honey bees) to 4 (very good and major source), with 1, 2 and 3 denoting poor, minor to medium, and medium to good source of nectar/pollen, respectively (Johannsmeier, 2005). The nectar values assigned to a bee plant refer to the amount of nectar that is available to honeybees in a flower of that plant (Johannsmeier, 2005). The forager method (which consists of assessing the relative abundance of pollen foragers), pollen analysis of honey and evaluation of trapped pollen were used by Johannsmeier (2005) to rate the bee plants. The flowering time (number of months) refers to the period within which the forage plants are expected to flower.

2.3. Data analysis

The main objectives of this study were to: (1) assess the diversity and relative importance of honey bee plants, (2) explore the temporal availability of honey bee forage (nectar and pollen resources) in the mistbelt forests, and (3) determine how plant diversity (bee plant richness and the overall plant richness) influences the bee forage production.

2.3.1. Assessing diversity and relative importance of honey bee plants in mistbelt forests

Species richness (total number of bee plant species recorded) and Shannon-Wiener (H) diversity index were used to assess honey bee plant diversity (see SI 1). Sample plots based species-accumulation curve was additionally established using “Bio-diversityR” package (Kindt and Coe, 2005) in R 3.2.3 statistical software (R Core Team, 2015). We next determined whether the variation in overall species richness influenced the variation in bee plant species richness using generalized linear model (GLM). Bee plant richness was modelled as count data, using GLM with a Poisson link function. Over-dispersion in bee plant richness was tested using the “qcc.overdispersion.test” function of library “qcc” (Scrucca, 2004) of the R statistical software.

To identify the most important honey bee plant species, we first defined a Forage Value Index for each plant species in each sample plot, based on the flowering time, nectar and pollen values, as follows:

$$FVI_{ij} = RD_{ij} \times (N_i + P_i) \times \frac{FT_i}{12} \quad (1)$$

where FVI_{ij} is the Forage Value Index of the i th honey bee plant species in the j th sample plot. N_i , P_i and FT_i are respectively the

nectar value, pollen value and the flowering time (number of months) of the i th honey bee plant species. The value 12 in the above formula refers to the number of months in a year. RD_{ij} denotes the relative density of the i th honey bee plant species in the j th sample plot, and is calculated as follows (Curtis, 1982):

$$RD_{ij} = \frac{G_{ij}}{\sqrt{Dg_{ij}}} \quad (2)$$

where G_{ij} and Dg_{ij} are the basal area of the stem and quadratic mean diameter of the i th honey bee plant species in the j th sample plot, respectively. The basal area (expressed in m^2) was computed as the sum of the cross-sectional area at 1.3 m above the ground level of all bee plants recorded inside a plot. The reason of using the relative density (as defined by Curtis (1982)) in the FVI index, is that it provides a simple and convenient scale of density that accounts for tree size, which scales with crown size and therefore with flowering area and amount of flowers (Otárola et al., 2013). We next assessed the relative FVI (RFVI, %) of each honey bee plant species, by dividing the plot-based average FVI of each bee plant species by the total (all bee plant species) plot-based average FVI. RFVI is indicative of the relative contribution of each honey bee plant species to the total forage value. RFVI was thus calculated using the following formula:

$$RFVI = \frac{\frac{1}{z} \times \sum_{j=1}^z FVI_{ij}}{\sum_{i=1}^s \left(\frac{1}{z} \times \sum_{j=1}^z FVI_{ij} \right)} \times 100 \quad (3)$$

where z is the total number sample plots, s is the total number of honey bee plant species and FVI_{ij} is the Forage value index of the i th honey bee plant species in the j th sample plot.

2.3.2. Exploring the availability of forage resources (nectar and pollen) in mistbelt forests

To explore the availability of forage resources for honey bees, we first examined the distributions of bee plant species nectar/pollen values and flowering time (number of months). We next explored the temporal repartition of honey bee flowering plants from January to December. We also defined a monthly forage value for the nectar and the pollen separately, by summing up the respective nectar and pollen values of all bee plant species flowering in each month. We additionally considered the total forage value (i.e. nectar plus pollen). The monthly forage values were plotted to determine the period of greater potential of availability of forage resources.

2.3.3. Modelling forage value and plant diversity (overall plant richness and bee plant richness)

Here, we used species richness at plot level to account for the variation of plant diversity (all plant species, including honey bee plants). For honey bee plant diversity, we considered the plot level bee plant richness. As for forage value, we calculated the plot level FVI (FVI_j) for all honey bee plant species by summing up the FVI_{ij} values as follows:

$$FVI_j = \sum_{i=1}^s FVI_{ij} \quad (4)$$

where s is the total number of honey bee plant species and FVI_{ij} is the Forage value index of the i th honey bee plant species in the j th sample plot. FVI was modelled as function of overall plant richness and honey bee plant richness by fitting separate GLMs with Gaussian error structure, FVI being normally distributed (Shapiro-

wilk statistic = 0.936; $P > 0.05$). The GLMs were fitted to assess (1) the individual effect of overall plant species richness on FVI, and (2) the individual effect of bee plant richness on FVI. The GLMs were performed using the “glm” function in the R statistical software. The overall significance of the models was tested by comparing the obtained deviance with the asymptotic chi-square.

3. Results

3.1. Diversity of woody bee plants and important bee forage plant species

Out of 50 woody plant species identified during the inventory, 24 species (48%) were honey bee plant species and belonged to 23 genera and 19 families (SI 2). The *Rutaceae* and *Stilbaceae* families were ranked first and had the highest number of bee plants species ($n = 3$, 12.5% each), followed by the *Rubiaceae* family ($n = 2$, 8.3%). The remaining families were weakly represented, with only one species each. Of the 24 bee plant species, 15 species were enumerated between 5 and 10 cm dbh while 22 species were recorded for stem of >10 cm dbh. The Shannon diversity index was estimated at 2.17 for the >5 cm dbh data, and did not vary much between 5 and 10 cm ($H = 2.07$) and >10 cm dbh classes ($H = 2.08$). The species-accumulation curve based on the number of plots showed an asymptotic trend towards a unique value (25 species; Fig. 1A), suggesting that the sampling was adequate and the actual value of bee plant richness was not far from being completely recorded within the study region. The results from the Poisson GLM showed that bee plant species richness increased with increasing overall plant species richness ($\beta = 0.08$; $P = 0.002$). The plot of bee plant richness against overall plant richness (Fig. 1B) also showed steep linear trend suggesting that diversity was a significant predictor of bee plant richness.

3.2. Temporal availability of forage resources (nectar and pollen)

The patterns of availability of bee forage resources (nectar and pollen; Fig. 2) showed a tendency to a bell shape with more than 20 honey bee plant species being medium sources of nectar and pollen. Meanwhile, very few species (less than 5) were revealed to be excellent sources of nectar and pollen (Fig. 2).

Examination of the distribution of the flowering period of bee forage plants revealed great variation (Fig. 3). The flowering periods of five and six months were the most represented (13 species). In addition, the flowering periods overlapped for most species. However, the period from September to February was found to be

the one at which several honey bee plants (from 10 to 18 species) produce flowers (Fig. 3).

October to November was the period of greatest production of pollen whereas November to December was the period of the greatest production of nectar (Fig. 4). Altogether, October to December was the period of year the forage value (and thus the forage provision) was at its maximum whereas April to July is the period of minimal forage provision (Fig. 4).

The important bee plant species based on the RFVI are shown in Table 1. Examination of the RFVI to reveal the important bee plant species showed that *Syzygium gerrardii* was the most important honey bee plant in terms of forage provision. It was followed by *Combretum kraussii*, *Ochna arborea*, *Nuxia floribunda* and *Nuxia congesta*. Out of the 24 identified honey bee plant species, the ten most important contributed 90.59% of the total forage supply, mostly covered the period from September to December.

3.3. Individual effect of overall plant richness and honey bee plant richness on FVI

Results of GLMs testing the individual effects of overall plant richness and bee plant richness on FVI are shown in Table 2. FVI was influenced by bee plant richness ($\beta = 0.004$; $P < 0.001$), but not by total plant richness ($P = 0.275$). The bee plant richness alone explained up to 40.3% of the variation of the FVI.

4. Discussion

Many previous studies have elucidated the positive relationship between area of natural forests (within a certain foraging distance) and abundance of flower visiting insects (especially wild and managed bees), pollination success, seed set and fruit production in agricultural systems (Bennett and Isaacs, 2014; Carvalheiro et al., 2011, 2010; Ricketts et al., 2004; Taki et al., 2011). The present study provides evidence for the potential of forests to supply forage to insect pollinators, by exploring the availability of honey bee plant species and forage resources (nectar and pollen) for managed honey bees in natural mistbelt forests. We found that (1) 48% of the woody plants were honey bee plant species; (2) bee plant richness increased with overall plant richness; (3) bee plants' flowering period was spread over the year season; (4) the highest potential of forage supply was observed during the last quarter; (5) few bee plant species greatly contributed the bee forage provision; and (6) bee plant richness, not the overall plant richness, influenced the bee forage value.

Twenty four plant species (accounting for 48% of woody plant

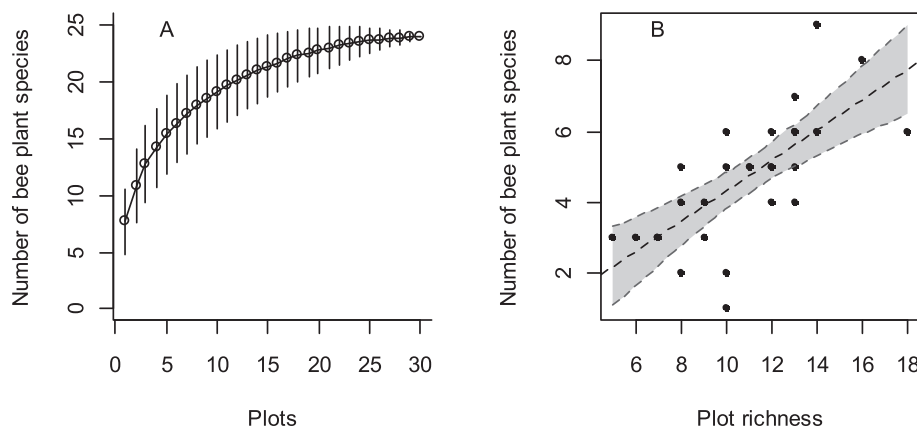


Fig. 1. Species-accumulation curve for bee plant species (A), and scatterplot of the relationship between bee plant richness and all plant richness (B).

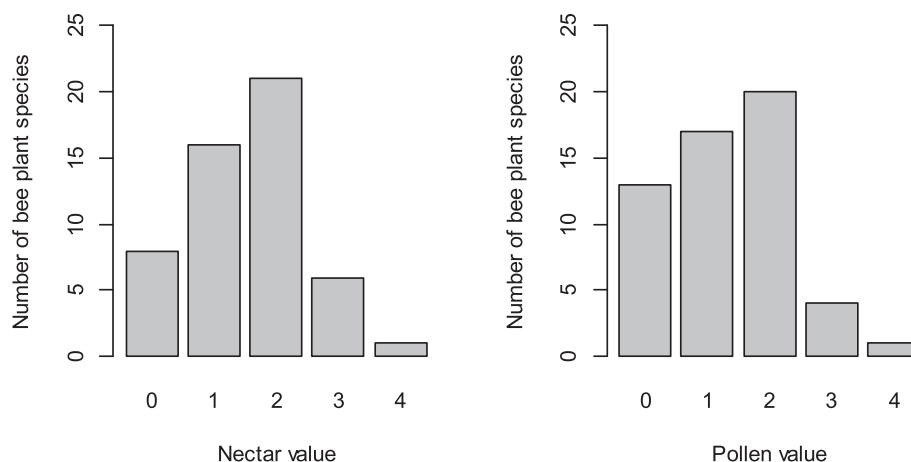


Fig. 2. Distribution of bee plant nectar and pollen values.

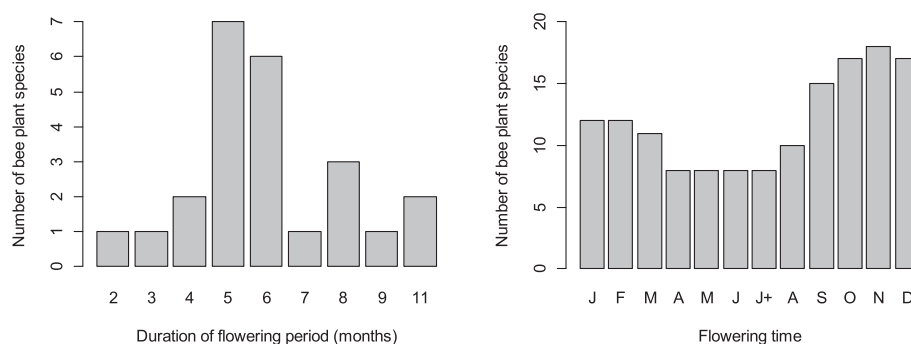


Fig. 3. Distribution of flowering period (number of months) and time (month of the year) of bee plant species.

richness) with highly diversified genera and families, were identified as sources of nectar and pollen for honey bees. The diversity of bee plants suggests diversity of flowers and differences in plant nectar and pollen quality (Blüthgen and Klein, 2011; Di Pasquale et al., 2013; Hülsmann et al., 2015), which are prerequisites to attract and maintain honey bee colonies. As pointed out by Blüthgen and Klein (2011), pollen and nectar from different bee plant species may be more nutritious than pollen or nectar from a single plant species. Therefore, the diversity of bee plants in the mistbelt forests would promote balanced nutrition for honey bees through mixed diet (pollen and nectar from different species), and enhance complementary nutrition (Blüthgen and Klein, 2011). Although this study was limited to woody and shrub plants only, which constitutes a major gap as small shrubs and forbs also provide pollen and nectar resources (Johannsmeier, 2005), the findings concur with the fact that mistbelt forests are important to conserve bee plant species. These natural forests contain a highly diverse range of tree and shrubs species, and their conservation will promote the availability of honey bee plant species for use in beekeeping activities.

Some bee forage plant species flower simultaneously, providing advantage for differential visitation and resource specialisation with wild bees and other insect pollinators (Taki et al., 2011). Different pollinator species can pollinate different plant species, due to complementary specialisation of plant-pollinator interactions (Blüthgen and Klein, 2011). By examining all woody bee plant species, we found highly varying flowering periods, as expected in environments with high plant diversity (Garbuzov and Ratnieks, 2014). The variation in bee plants' flowering period in addition to the diversity of bee plants could be beneficial to honey

bee colonies and beekeepers. Variation in phenology of bee plant species increases the temporal availability of bee forage, thus could help to sustain these colonies, either spatially or temporally (Blüthgen and Klein, 2011). As managed honey bees can contribute to honey production and crop pollination (Allsopp et al., 2008), the actual pattern of temporal availability of forage indicates that opportunities exist to develop beekeeping activities for honey production, and to maintain the honey bee colonies for pollination services in surrounding environments (Melin et al., 2014). The finding that flowering occurred throughout the year suggests that beekeepers can manage the honey bee colonies for a long period. In addition, due to their longer flowering period, some bee plant species can be more attractive than others (Garbuzov and Ratnieks, 2014). Therefore, these results support the fact that mistbelt forests can be included in the forage calendar of the apiculture industry in the Limpopo province.

Crops production in many agricultural fields of the study region are based on use of honey bee hives to supplement pollination services (Carvalho et al., 2010; Melin et al., 2014). The number of bee plants flowering, the nectar and pollen values, as well as the forage value peaked from September to December, a period which complements well – in terms of forage availability – the March–April and July–September flowering seasons for sunflower (*Helianthus annuus* L.) and mango, Kent cultivar (*Mangifera indica* L.), respectively (Carvalho et al., 2011, 2010). We therefore suggest that honey bee hives be moved close to these mistbelt forests from September to December, to help maintain their colonies, after being placed near sunflower fields during March–April, and mango fields from July to September. However, as flowering period is sensitive to rainfall and soil moisture conditions, and climate/micro-climate

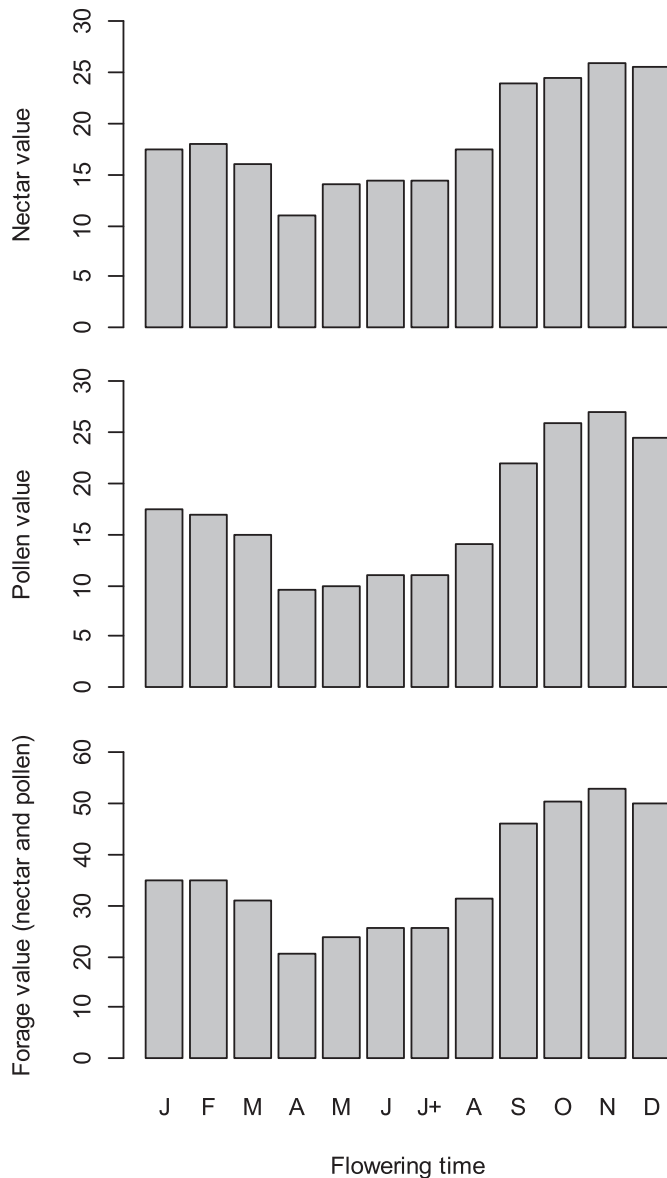


Fig. 4. Temporal repartition of the forage value (nectar and pollen values).

conditions are continually changing, long term research should be undertaken to determine whether the flowering period of these honey bee plants shifts over time.

The assessment of the forage value was based on the assumption that availability of floral resources would increase with increasing bee plant structures (stem density and stem basal area). The use of honey bee plant structures as weighing variables at plot level, can simply be explained by the importance of tree size for the amount of flower resources available (Otárola et al., 2013). In a recent study, Otárola et al. (2013) showed that the total flower coverage and the flowering time increased with increasing tree size. Similarly, Hülsmann et al. (2015) related the blooming product (a measure of the flowering area) to the abundance of flowering plants and the amount of floral resources. However, because this study was not based on observation of honey bees, it is important to make cautious interpretations; indeed very abundant flowering plant taxa (family or species) can attract foraging bee species much less than does a rare particular taxa. For instance, richness in pollen protein of particular plant families can have a marked influence on

Table 1

Important honey bee plant species with respective RFVI (relative forage value index); the 10 most important species are highlighted in bold.

Family	Species	RFVI (%)
Myrtaceae	<i>Syzygium gerrardii</i>	34.81
Combretaceae	<i>Combretum kraussii</i>	10.76
Ochnaceae	<i>Ochna arborea</i>	7.90
Stilbaceae	<i>Nuxia floribunda</i>	7.42
Stilbaceae	<i>Nuxia congesta</i>	6.53
Rosaceae	<i>Prunus africana</i>	6.05
Curtisiaceae	<i>Curtisia dentata</i>	5.22
Asteraceae	<i>Brachylaena transvaalensis</i>	4.25
Euphorbiaceae	<i>Croton sylvaticus</i>	3.87
Rubiaceae	<i>Kraussia floribunda</i>	3.79
Achariaceae	<i>Kiggelaria africana</i>	3.57
Rutaceae	<i>Calodendrum capense</i>	0.89
Salicaceae	<i>Trimeria grandifolia</i>	0.85
Malvaceae	<i>Dombeya burgessiae</i>	0.83
Rutaceae	<i>Zanthoxylum davyi</i>	0.53
Rubiaceae	<i>Rothmania capensis</i>	0.53
Aquifoliaceae	<i>Ilex mitis</i>	0.47
Stilbaceae	<i>Halleria lucida</i>	0.43
Myrsinaceae	<i>Rapanea melanophloeos</i>	0.39
Fabaceae	<i>Calpurnia aurea</i>	0.27
Oleaceae	<i>Olea capensis</i> ssp <i>macrocarpa</i>	0.24
Rutaceae	<i>Clausena anisata</i>	0.18
Ebenaceae	<i>Diospyros whyteana</i>	0.18
Cannabaceae	<i>Celtis africana</i>	0.03

the observed visitation pattern of bumble bees (Goulson et al., 2005; Hanley et al., 2008), even if these plant families are not very abundant (Hülsmann et al., 2015).

It is generally acknowledged that more diversified forest habitats offer more nesting opportunities (floral and nesting resources) than other natural habitats such as grasslands (Bennett and Isaacs, 2014; Brosi et al., 2007), probably because these forests usually contain hundreds of species (trees and forbs) with different flowering periods and qualities of nectar and pollen. In this study, bee plant species richness rather than overall plant richness showed significant positive effects on FVI. This result supports the idea that higher bee plant diversity can sustain continuous forage supply that is essential for long-lived bee colonies. Specifically, in diversified forest habitats, the more the bee plant species flower, the greater the foraging opportunities. Furthermore, as bees can exhibit a high degree of specialisation (Blüthgen and Klein, 2011), increased forage value (as a result of increased bee plant richness) suggests supplementary opportunities to support additional honey bee hives. In sum, the findings that overall plant richness positively influenced bee plant richness, and that increasing bee plant richness increased FVI, indicate that plant diversity loss would have negative knock-on effects on forage resources (Carvell et al., 2006; Goulson et al., 2005). If the amount of forage provided decreases, fewer honey bees can remain on sites or fewer temporary hives can be supported. These results also suggest that conservation efforts should be specifically oriented towards bee forage species in the mistbelt forests to preserve and enhance their potential to help maintain honey bee colonies.

When analysing the contribution of bee plant species to the forage supply, we found that only few bee plant species contributed to the maximum forage provision. Hülsmann et al. (2015) also reported similar patterns for bumble bees. Thus, not all honey bee plant species in an ecosystem, but rather few are source of majority of nectar and pollen used by honey bees. The finding that few bee plant species greatly contribute to the total forage production is attributable to the fact that these species are abundant or colonise the area more easily. The result also provides insight into the relative importance of few key bee plants vs. a diversified forest plant community to support honey bee populations. While few bee

Table 2
Results of GLMs showing the individual effects of plant diversity (all plant richness and bee plant richness) on forage value index (FVI). Est.: Estimate; SE: Standard Error; Dev.: Deviance; R²: Pseudo R square (%).

Response variable	Predictors	Est.	SE	t	P	Dev.	R ²
FVI	(Intercept)	0.011	0.008	1.37	0.181		
	All plant richness	0.0008	0.0007	1.11	0.275	1.29	04.24
	(Intercept)	0.001	0.005	0.11	0.911		
	Bee plant richness	0.004	0.001	4.35	<0.001	15.49	40.31

plant species are revealed as sources of the majority of the available floral resources, the importance of having diversified plant communities in mistbelt forests is that these forests are more likely to contain the key bee plant species driving the floral resource availability; this possibility suggests that conservation efforts to supplement specific species in or around mistbelt forests could be effective, and almost certainly easier, than increasing overall bee plant richness. In addition, diversified plant communities in mistbelt forests would likely produce diverse pollen/nectar qualities and thus promote a balanced nutrition for honey bees through a mixed diet. Diversified plant communities supplying diverse pollen sources have been shown to impact bee nutrition to optimize pollen protein to lipid ratios (Vaudo et al., 2016).

To summarize, this paper suggests that mistbelt natural forests can support the management of honey bee colonies. From a functional perspective, bee plant richness is important for bee forage (nectar and pollen) availability. Given the bee plant richness in these forests, different flowering bee plant species would produce different flowers, and thus diverse nutritious resources to bee colonies (suggesting resource complementarity). Different flowering bee plant species would also provide these resources at different times of the bees' foraging activities (suggesting phenological complementarity). From a practical perspective, the spatial context (proximity to agricultural fields) of these mistbelt forests facilitates the opportunities for beekeeping activities and honey production, and therefore the possibilities to consider these forests in the apiculture calendar of the area. Honey bee hives can be, for example, placed close to these forests during the peak forage period from September to December. The benefits from the beekeeping activities in these mistbelt forests can serve to offset the costs of promoting their conservation. In addition, most of the deciduous and sub-tropical fruit fields in the surrounding environments of these forests could also benefit from the pollination services. For crop fields which are isolated from natural habitats, field edges could be afforested using the important bee plant species identified in this study. This will help to attract honey bees, and also contribute to sustain pollinator diversity at the proximity of these agricultural fields, thus increasing the benefits of local conservation and pollination services. While we believe that we have highlighted an important aspect of management honey bee colonies, it is useful to mention that our study did not consider any forb species, and this can constitute a major gap. For instance, mistbelt grasslands harbour several forb species, which are also important as sources of bee forage. Therefore, further research studies are necessary to investigate other existing biomes in the area such as grasslands, and functional groups of species to understand their potential contribution to the forage provision.

Acknowledgements

The authors wish to acknowledge the contribution of Martin Johannsmeier who unconditionally provided complementary data on the nectar and pollen values of honey bee plants in South Africa. The authors are also grateful to the anonymous reviewers for their

comments on the first version of this article. SM acknowledges the financial support of the African Forest Forum and the National Research Foundation of the Republic of South Africa through the project "Catchman Letaba" in the RTF funding scheme.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jenvman.2016.12.033>.

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