

# Pollinator conservation at the local scale: flower density, diversity and community structure increase flower visiting insect activity to mixed floral stands

Sven M. Vrdoljak<sup>1</sup> · Michael J. Samways<sup>1</sup> · John P. Simaika<sup>2</sup> 

Received: 11 March 2016 / Accepted: 18 August 2016  
© Springer International Publishing Switzerland 2016

**Abstract** Insect pollinators play a keystone role in terrestrial ecosystems. The parallel declines in plant and pollinator communities emphasizes that plant-pollinator interactions at the community level are highly relevant for biodiversity conservation. Here we examine relationships between plants and flower-visiting insects (anthophiles) at the scale of local floral patches. We conducted a visitation survey during the spring flowering season, a peak time for pollinator activity in the threatened Cape Floristic Region, South Africa. We tested floral density, diversity and composition as predictors of anthophile diversity (measured at the family/family group level) and visitation rates in multispecies stands of flowers. Although different anthophile groups responded differently, generally anthophile visitation rates and diversity were positively affected by floral density, diversity and community structure. Anthophiles were more abundant and diverse in areas with a high density and diversity of flowers. Plant community structure affected both the likelihood of occurrence and activity of anthophiles in the plots. The two mass flowering species examined here, *Relbania fruticosa* and *Salvia chamaeleagnea*, were strong determinants of anthophile activity,

greatly increasing visitation rates, even though there was, on average, lower floral density and diversity. Our results show that anthophile activity is affected by highly localised, small-scale factors, namely the density and diversity of flowers and community structure. Important among these factors are patches of high quality habitat, high in floral abundance and diversity, both of which should be included in landscape-level plans for pollinator conservation, providing stepping stones for these insects in transformed landscapes.

**Keywords** Localized conservation · Small-scale conservation · Flowering plant · Flower · Pollinator · Mass flowering · Scarabs · Syrphids · Tabanids

## Introduction

Insect pollinators play a keystone role in most terrestrial ecosystems. A decline in pollinator populations has serious consequences for the long-term sustainability of natural and managed ecosystems (Potts et al. 2010). At the same time, habitat loss and fragmentation decreases the local abundance and diversity of plants (Winfree et al. 2009). The nature of plant-pollinator interactions means that a decline in one group of these mutualistic partners can result in parallel declines in the other (Aizen et al. 2012), leading to possible cascading community-level declines and extinctions (Thomann et al. 2013). Consequently, an understanding of the interactions between plants and pollinators is highly relevant for biodiversity conservation, particularly when considering the value of remnant habitats for biodiversity conservation.

Plant-pollinator interaction webs in ecosystems will contain a mix of specialised and generalised interactions

**Electronic supplementary material** The online version of this article (doi:10.1007/s10841-016-9904-8) contains supplementary material, which is available to authorized users.

✉ John P. Simaika  
simaikaj@sun.ac.za

<sup>1</sup> Department of Conservation Ecology and Entomology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

<sup>2</sup> Department of Soil Science, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

(Astegiano et al. 2015), although most seem to be more dominated by generalised interactions (Maldonado et al. 2013). Large floral displays may act as long-distance cues for anthophiles-flower-visiting insects (Hempel De Ibarra et al. 2015) affecting foraging behaviour in many ways. Size and density of floral patches can affect both the number of anthophiles attracted to a patch, and the way in which they forage in that patch (Dauber et al. 2010). Plants with larger floral displays may improve foraging efficiency, making them more attractive to foraging anthophiles (Hanoteaux et al. 2013). If anthophiles choose among available floral patches they may select those with a higher density of flowers (Westphal et al. 2003). High floral density of particular species may also increase the effective constancy of anthophiles, increasing the number of visits to those species (Dauber et al. 2010).

Plant species with large floral displays may also affect visitation to their neighbours (Carvalho et al. 2014). Although co-flowering plants can be thought of as competing for pollinators, it is also possible that they facilitate visitation and pollination to neighbours (Brunet et al. 2015). Indeed, visitations to single plant species are affected by the surrounding community (Johnson et al. 2003). Thus, the quality and quantity of pollination services may be improved by proximity to floral resources or through facilitation by ‘magnet species’ (Seifan et al. 2014). The downside of these interactions is increased competition for pollination services in large patches of flowers (Johnson et al. 2012). Furthermore, common plant species are also likely to affect the attractiveness of a patch to anthophiles, positively affecting both richness and abundance of insect visitors (Hegland and Boeke 2006; Ebeling et al. 2008). In addition to species richness, the community structure of floral patches has an effect on species presence and abundance. Understanding these interactions at the patch scale can have important implications for conservation planning, particularly in fragmented or disturbed habitats. The Cape Floristic Region (CFR) is such a fragmented area where lowland habitats exist only as small scattered fragments, embedded within a transformed matrix (Kehinde and Samways 2012).

Here we determine whether relationships between plants and anthophiles observed at the landscape level persist at the local patch scale. We test how well anthophile presence and activity are predicted by floral diversity, floral density and floral composition in observation plots, and how the effects of these predictors differ between different anthophile groups. We do this by testing three hypotheses. First, we hypothesize that there is a positive relationship between anthophile activity and floral density and diversity in mixed floral patches. Secondly, the composition of mixed floral patches affects anthophile activity. Thirdly, the abundant, mass-flowering species affect anthophile visitation to nearby plant species.

## Study area and methods

### Study area

We conducted visitation surveys in a highly threatened lowland renosterveld community in the CFR during the spring flowering season, a peak time for pollinator activity. The study area was in the Elandsberg Private Nature Reserve (33.27°S, 19.03°E) and on the surrounding Bartholomeus Klip farm, near Hermon, Western Cape Province, South Africa, in the lowlands (<300 m asl). This 4000 ha reserve encompasses the largest remaining contiguous patch of West Coast Renosterveld, and some marginal abandoned farmland. We chose this area, as we needed a control with near natural and natural vegetation. Renosterveld is an evergreen, fire prone, shrubland, dominated by the cupressoid leaved Asteraceae, in particular renosterbos (*Elytropappus rhinocerotis*), with an understory of grasses (Poaceae) and a rich diversity of spring flowering geophytic plants (Mucina and Rutherford 2006). Renosterveld has been highly transformed, with <10% remaining in isolated fragments (Kemper et al. 1999). The two main vegetation types in the Elandsberg Reserve are Swartland alluvium fynbos and Swartland shale renosterveld, both critically endangered (Mucina and Rutherford 2006). The surrounding farmland includes wheat fields and areas under grazing by livestock. The area receives a mean annual rainfall of about 500 mm.

### Data collection

We conducted a visitation survey within 20 plots in the Elandsberg reserve and surrounding area. The study was highly intensive, involving a team of four co-ordinated observers, who conducted visitation surveys in marked, 2 × 2 m plots. Each set consisted of five plots, with each plot at least 10 m apart. These were located randomly within four sets chosen to represent the reserve area and its surrounding remnants of natural vegetation. Distances between sets varied between 1000 and 3000 m. Two sets fell within the main reserve area, and two outside the reserve, in patches of natural vegetation surrounded by wheat fields.

Over 4 days from 9 to 12 October 2007, the four observers collected 46 h and 40 min of simultaneous observation data from four sets of observation plots. This sampling regime ensured comparison between the sample plots without confounding effects of variable weather or phenological changes in floral abundance and composition. The sampling time fell within the spring flowering period in the area, which is associated with high floral abundance and pollinator activity. All days were sunny, with temperatures 15–31 °C at the nearest weather station, Diemerskraal (33.35°S, 18.55°E) between 09:00 and 17:00 h. Weather

data were provided by the AgroMet-ISCW, Agricultural Research Council.

Visitations were surveyed within the plots by counting visits by insects to visual displays of insect-pollinated plant species during 10 min observation periods. Insects were visually identified to family/family groupings (see electronic supplementary material for description of anthophiles collected). This was done as a compromise between precise identification and being able to rapidly identify and record insects on the wing. Visits were only recorded when the visitor landed on, or made contact with, the visual display for more than 1 s. Over the 4-day sampling period, plots were observed four times daily, twice in the morning (09:00–10:30; 11:00–12:30 h) and twice in the afternoon (13:30–14:30; 15:00–16:30 h), run concurrently in each of the four sites.

Flowering plants in the plots were identified and counted, and the number of visual displays per plant species in the entire plot was recorded. Depending on the plant species, a visual display could be a single flower, an inflorescence, or a group of flowers that formed a recognisable visual unit. Counts were repeated each day, and this information was used to calculate the floral density and diversity of plots. Analyses of flowering plant species were limited to species that received more than one visit during the study period.

### Variable calculations

To relate absolute importance (species richness) and relative importance (heterogeneity) of floral density, diversity and composition to anthophile activity, standardised variables were calculated. The number of flowers per plot could not be used, as such a measure is dependent upon flower size, as well as what the observer defines as a single floral unit, both of which differ between species. To obtain a standardised measure of floral density, we instead calculated the total area of floral display in each plot.

Mean floral area was determined per plant species by measuring 10–20 randomly selected plants per species, and calculating the inflorescence size (as an area) according to the shape of the flowers. Visual displays with a circular outline were calculated using the formula:  $\pi r^2$ . For other flat visual displays the formula: length  $\times$  width was used. Displays without a depth component were categorized as ‘open floral density’. When visual displays also had a depth dimension the formula  $2\pi r^2 d + \pi r^2$  was used. Displays with a depth dimension were called ‘tubular floral density’. All 20 plots had open flowers, while 16 plots had tubular flowers. The daily floral counts per plot and mean floral areas per species were used to calculate total floral areas per plot as a measure of total floral density as different visitor groups may respond differently to such flowers.

For diversity variables, the species richness of insect pollinated plants in bloom in each plot, called ‘total floral diversity’, was used, as well as separate variables for plants with tubular (tubular floral diversity) and open flowers (open floral diversity). To obtain a measure of the floral composition of each plot, we used Principal Components Ordination (PCO) based on a Euclidean distance matrix of the log-transformed floral area per plant species in each plot. First axis PCO scores were used to measure the compositional similarity between plots (called here ‘floral composition’). The analyses were done in Permanova+ for Primer V6 (Anderson et al. 2008).

Two locally abundant plant species, *Relbania fruticosa* and *Salvia chamaeleagnea*, which had high floral density and high visitation frequency in plots in which they occurred, were chosen as ‘mass-flowering’ (MF) plant species. There were 12 plots with mass flowering species, and eight plots with non-mass flowering species. Samples were coded as ‘+MF’ (mass flowering) or ‘–MF’ (non-mass flowering) depending on the presence or absence of MF species and for each sample, the area and number of visits were calculated separately for non-MF and MF plants. Fifteen plant species occurred in both +MF and –MF plots. These species were used to test the effect of the potential magnet species on neighbouring plants. To account for the effect of floral display area on visitation, a visitation index (VI) was calculated for each species. For a species in a particular sample  $VI = \text{number of visits/floral area to give the visits/cm}^2/10 \text{ min observation period}$ .

### Data analyses

As data were nested and multiple observations made on the same day, data were summarized based on day and plot. Anthophile groups that were observed in <30 observation periods were excluded from the analyses. Thus a robust dataset of 1771 visits represented in 280 observation periods remained for analysis, represented by Diptera, Coleoptera and Hymenoptera, and the separately analysed visitor groups as represented by the scarab beetles, buprestid beetles, other beetles, calyptrate flies, tabanid flies, and syrphid flies. To check for spatial autocorrelation, a matrix of distance between plots and matrices of differences (Bray-Curtis) between plots for the measured variables were constructed. The associations between plot distance and variable difference for all variables was tested with a Mantel test using the PopTools add-in for Microsoft Excel. No significant associations were found for any of the variables tested (all  $r < 0.14$ ,  $p > 0.06$ ), showing that the study design successfully minimised the probability of spatial autocorrelation.

To investigate the relationships between floral variables and the number of anthophile groups visiting the plots, we

used Spearman rank correlation in Statistica 8. Distance-based linear models (DistLM) were calculated to investigate the effects of floral density, diversity and composition on flower-visiting insect activity (number of visits to each plot) in Primer V6. DistLM is a routine for modelling the relationship between multivariate data as represented by a resemblance matrix, and one or more predictor variables. A step-wise selection procedure was used and Akaike's Information Criterion (AIC, Akaike 1973) was applied as the selection criterion for assessing the quality of the step-wise model. Before analysis, a Pearson correlation of variables between sets was done, and highly correlated variables ( $<-0.9$  and  $>0.9$ ) removed. This resulted in the variable 'total floral density' being removed from further analysis.

The RELATE function in Primer V6 was used to test the relationship between insect visitation and flowering plant composition. RELATE allows a user to compare two sets of multivariate data based on a matching set of samples, by calculating a rank correlation coefficient between all the elements of their similarity matrices (Clarke and Warwick 2001).

A biplot based on Detrended Correspondence Analysis (DCA) was used to visualize the floral composition of each plot. To understand the relationship between floral composition on anthophile visitation, we used Canonical Correspondence Analysis (CCA). The DCA and CCA were performed in CANOCO 4.53.

To test the potential magnet effects of MF species, we compared total VI per plot and VI per each of the fifteen co-occurring plant species as well as total visits, area of MF and area of non-MF species per plot using non-parametric Mann–Whitney  $U$  tests, as sample sizes, and sample variance of +MF versus –MF plots were not equal for most

species. The Mann–Whitney  $U$  tests were performed using Statistica 8.

## Results

### Activity of different flower visitor groups

The visitor pool was dominated by Coleoptera and Diptera, which accounted for 46 % and 36 % respectively of all visits. The top three visitor groups were scarabs (29 %), calyptrate flies (19 %) and other flower-visiting beetles (19 %). All other groups accounted for no  $>10\%$  each of the total visitations.

The strengths and directions of significant Spearman-rank correlations of insect visitor activity with flower variables varied between insect groups (Table 1). The activity of the overall insect assemblage increased with total floral density and in particular tubular density, but decreased with floral composition. Coleoptera had a negative relationship with tubular diversity, open flower density and floral composition. The scarab beetles had negative relationships with open flower diversity and density, tubular diversity, and floral composition. Buprestid beetles had negative relationships with tubular flower diversity and floral composition. No significant relationships were found for other beetles. In contrast to the beetle groups, the Diptera and calyptrate flies had positive, strongly significant relationships with all flower diversity, flower density and floral composition variables. Syrphid activity was positively related to total flower diversity and open flower diversity. Hymenoptera activity responded negatively to floral composition but positively to tubular flower density. Visitor diversity (here at the family/family group level) was positively correlated with total

**Table 1** Spearman rank correlations between anthophiles and floral diversity, density and composition

	Total floral diversity	Open diversity	Tubular diversity	Total floral density	Open density	Tubular density	Floral composition
Insects	0.02	0.02	0.01	<b>0.19**</b>	0.02	<b>0.31**</b>	<b>–0.18**</b>
Diptera	<b>0.30**</b>	<b>0.19**</b>	<b>0.30**</b>	<b>0.25**</b>	<b>0.20**</b>	<b>0.35**</b>	<b>0.29**</b>
Coleoptera	–0.18	–0.07	<b>–0.247**</b>	0.01	<b>–0.132*</b>	0.08	<b>–0.38**</b>
Hymenoptera	–0.01	–0.02	0.02	0.08	–0.01	<b>0.13*</b>	<b>–0.12*</b>
Buprestids	0.03	0.10	<b>–0.143*</b>	0.05	–0.06	0.06	<b>–0.26**</b>
Calyptrate flies	<b>0.34**</b>	<b>0.18**</b>	<b>0.408**</b>	<b>0.22**</b>	<b>0.269**</b>	<b>0.29**</b>	<b>0.26**</b>
Other beetles	–0.00	0.01	–0.02	0.06	0.04	0.06	–0.08
Scarabs	–0.24	<b>–0.18**</b>	<b>–0.18**</b>	0.02	<b>–0.19**</b>	0.12	<b>–0.41**</b>
Syrphids	<b>0.12*</b>	<b>0.17**</b>	–0.06	0.06	0.05	0.02	0.04
Tabanids	0.03	0.02	0.04	0.11	–0.01	<b>0.20**</b>	0.05
Visitor diversity	<b>0.13*</b>	<b>0.14*</b>	0.03	<b>0.21**</b>	0.07	<b>0.28**</b>	<b>–0.13*</b>

Significant correlations are in bold

\* $P < 0.05$ ; \*\* $P < 0.01$

and open floral diversity, total and tubular floral density, but negatively correlated with floral composition.

The most commonly included variables in the models resulting from the stepwise regressions using DISTLM, were tubular flower diversity, floral composition and tubular flower density, while the least common were total diversity, open diversity, and open area (Table 2). The best models for other beetles, all insects, Coleoptera and Diptera (Table 3) had low explanatory power (range of 12–19%). By contrast, the variables used in the best models for Scarabidae, Tabanidae and Syrphidae explained 59, 45 and 30% of the total model variation respectively. The worst performing models were those of the Hymenoptera, buprestids and calyptrate flies (range 4–6% of explained variation out of total model).

**Table 3** Best model results for each model group from the DISTLM analysis and percent explained variation out of fitted and total models

Visitor groups	AIC	R <sup>2</sup>	RSS	No. vars
All insects	1645.9	0.16	619,710	4
Coleoptera	1120.8	0.14	326,940	3
Diptera	893.06	0.12	273,060	2
Hymenoptera	412.03	0.06	152,130	1
Buprestids	231.32	0.06	11,753	1
Calyptrate flies	452.13	0.04	29,512	1
Other beetles	470.16	0.19	27,435	3
Scarabidae	441.1	0.59	20,115	3
Syrphidae	174.88	0.30	9151.4	3
Tabanidae	197.78	0.45	8513.2	4

**Table 2** Stepwise regression with AIC selection procedure results of DISTLM analyses between flower-visiting insect groups and the predictor variables floral density, diversity and composition in a lowland renosterveld community

Visitor group	Variable	AIC	SS (trace)	Pseudo-F	p	Prop.	Cumul.	Res.df
All insects	Tub. divers	1656.70	64,080.00	19.23	0.001	0.09	0.09	202
	Composition	1646.90	37,912.00	12.00	0.001	0.05	0.14	201
	Tot. divers	1646.30	8114.10	2.59	0.018	0.01	0.15	200
	Tub. density	1645.90	7393.80	2.37	0.031	0.01	0.16	199
Coleoptera	Composition	1123.30	38,145.00	15.83	0.001	0.10	0.10	142
	Open. divers	1122.00	7687.90	3.24	0.047	0.02	0.12	141
	Tub. density	1120.80	7473.80	3.20	0.053	0.02	0.14	140
Diptera	Tub. divers	893.78	31,091.00	12.45	0.001	0.10	0.00	112
	Composition	893.06	6585.40	2.68	0.039	0.02	0.12	111
Hymenoptera	Tub. divers	412.03	10,532.00	3.39	0.028	0.06	0.06	49
Buprestids	Tub. divers	231.32	778.88	2.52	0.105	0.06	0.06	38
Calyptrate flies	Open. density	452.13	1297.10	3.21	0.064	0.04	0.04	73
Other beetles	Open. density	476.47	2663.90	6.56	0.007	0.08	0.08	77
	Composition	472.74	2188.00	5.72	0.012	0.06	0.14	76
	Tub. divers	470.16	1636.80	4.47	0.03	0.05	0.19	75
Scarabidae	Composition	444.13	27,140.00	93.70	0.001	0.55	0.55	76
	Open. divers	441.35	1309.50	4.74	0.018	0.03	0.58	75
	Tub. density	441.10	588.31	2.16	0.114	0.01	0.59	74
Syrphidae	Tub. density	178.56	1102.70	2.50	0.15	0.08	0.08	27
	Tub. divers	175.39	1950.60	5.08	0.023	0.15	0.23	26
	Tot. divers	174.88	827.48	2.26	0.168	0.06	0.30	25
Tabanidae	Tub. density	207.94	1791.50	4.19	0.046	0.12	0.12	32
	Composition	203.52	2356.60	6.44	0.018	0.15	0.27	31
	Tub. divers	197.87	2284.40	7.57	0.009	0.15	0.42	30
	Tot. divers	197.78	538.03	1.83	0.167	0.03	0.45	29

The p value is based on 9999 permutations

AIC Akaike's information criterion, Prop percent variation explained by variable in model, Cumul. cumulative percent variation explained by model, Res.df residual degrees of freedom, Composition floral composition, Tub. divers tubular flower diversity, Tot. divers total flower diversity, Open. density open flower density; Tub. density tubular flower density



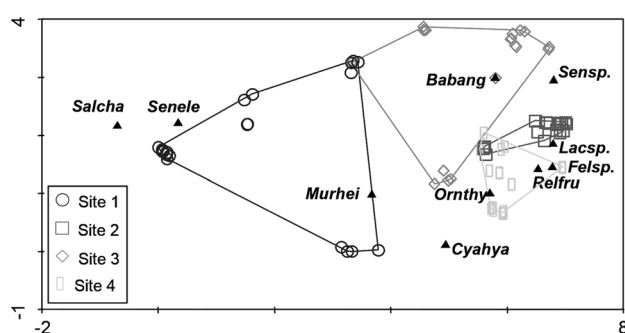
## Relationship of floral composition to anthophile activity

There was a strongly significant relationship between floral composition and anthophile activity ( $Rho=0.92$ ,  $p<0.001$ ). The DCA showed that plots within the same sites tended to be more similar in terms of their floral composition and plots grouped by site had a small degree of overlap (Fig. 1, sum of all eigenvalues=5.915; cumulative percentage variance of first four axes=30.5). In terms of visitation rates (sum of all eigenvalues=1.177; cumulative percentage variance of first four axes=41.1), a similar, but more distinct pattern of separation of the sites can be seen in the CCA biplots of visitation data (Fig. 2) constrained by the floral composition of the plots.

## Effects of mass-flowering plant species

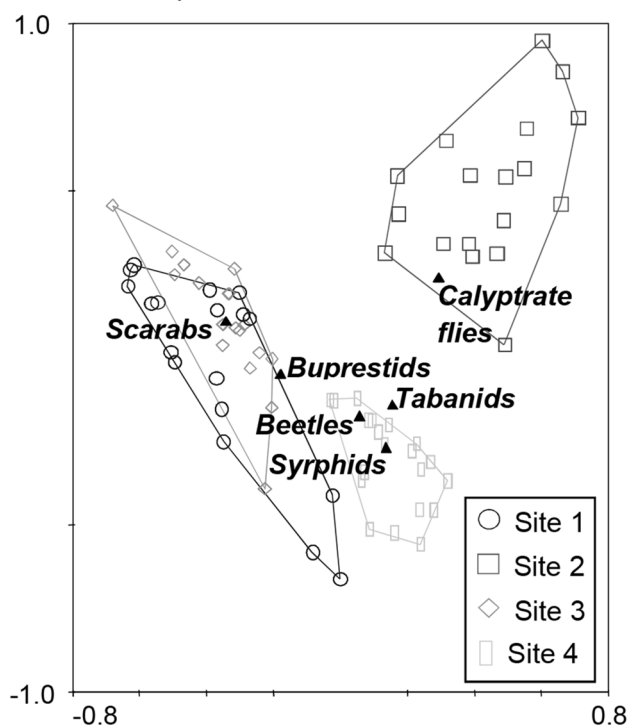
Plots containing *S. chamaeleagnea* or *R. fruticosa* (+MF plots) had a lower floral display area than -MF plots where these species were absent (Fig. 3a, Mann–Whitney  $U=672$ ;  $p<0.001$ ). Floral diversity was also lower in plots with *S. chamaeleagnea* and *R. fruticosa*, but not significantly so. Despite the lower floral density, total visitation per plot was significantly higher in +MF plots (Mann–Whitney  $U=468$ ;  $p<0.001$ ) compared to -MF plots (Fig. 4a). However, most of visits in +MF plots were made to whichever of these two mass-flowering, magnet species were present, with far less made to -MF plants (Fig. 4b). The area of other -MF species in the plots was not significantly ( $U=863$ ;  $p=0.276$ ) different between plots that contained MF plants and those that did not.

Pooled visits to all non-MF species per plot was higher in -MF plots ( $U=797$ ;  $p=0.037$ ). However, no significant



**Fig. 1** DCA biplot of floral composition of 2×2 m plots used in visitation surveys in a lowland Renosterveld community (eigenvalues: axis 1=0.908; axis 2=0.437. Sum of all eigenvalues=5.915; cumulative percentage variance of first four axes 30.5). The top ten out of 36 plant species in terms of weight in the DCA model are indicated by solid triangles (Babang, *Babiana angustifolia*; Cyahya, *Cyanella hyacinthoides*; Felsp, *Felicia* sp.; Lacsp, *Lachenalia* sp.; Murhei, *Murhertia heisteria*; Ornthy, *Ornithogalum thyrsoides*; Salcha, *Salvia chamaeleagnea*; Senele, *Senecio elegans*; Sensp, *Senecio* sp.; Relfru, *Relhania fruticosa*)

## Anthophile visitation



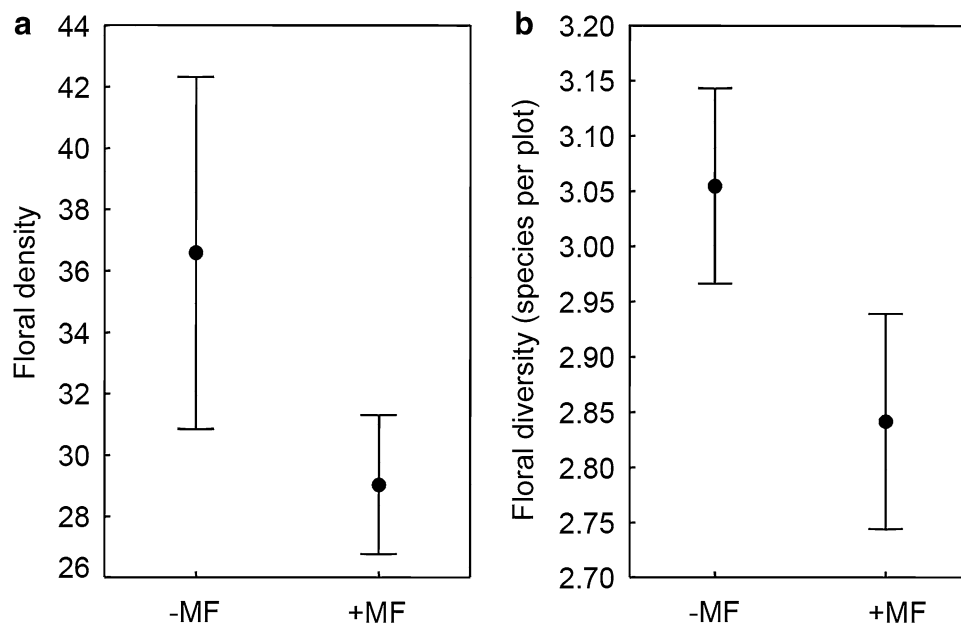
**Fig. 2** CCA biplots of flower-visiting insect visitation (sum of all canonical eigenvalues=1.177; cumulative % variance of first four canonical axes=41.1; Monte Carlo permutation test (all axes):  $F=3.766$ ;  $p=0.002$ ) in plots in four sites in a lowland Renosterveld community. Anthophile groups are indicated by solid triangles. Sites 2 and 3 are situated within the Elandsberg Nature Reserve while sites 1 and 4 are remnants of natural vegetation in agricultural land outside the reserve

effects of presence of *S. chamaeleagnea* or *R. fruticosa* (All  $p>0.07$ ) were detected when the 15 species that co-occurred with MF species were tested individually, but the small, uneven sample sizes greatly lowered the statistical power of these tests (Table 4).

## Discussion

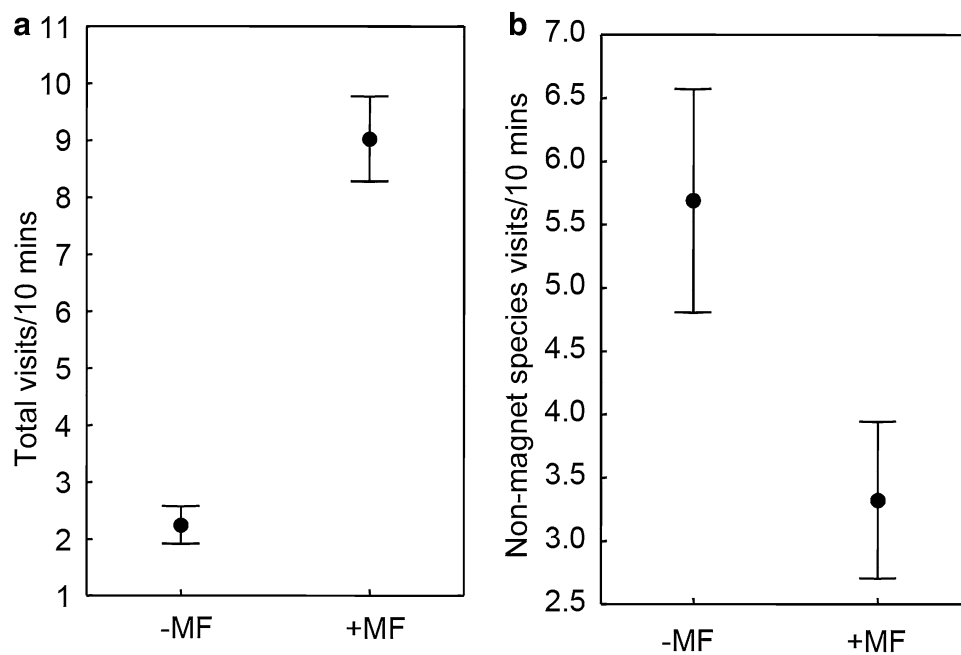
### Attractiveness of floral patches

Beetles, particularly the monkey beetles (Scarabidae) are one of the most important pollinator guilds in the Fynbos biome of South Africa (Mayer et al. 2006). The Fynbos biome, along with the Succulent Karoo biome contain the majority of the world's monkey beetles. Indeed, a third of all herbaceous species native to the Sand Plain Fynbos of South Africa are scarab-pollinated (Picker and Midgley 1996). Similarly, among the Diptera, short-proboscid flies such as Muscidae are prevalent as well as long-proboscid flies such as the Tabanidae, the latter which are important



**Fig. 3** **a** Floral density (total area of floral display) and, **b** diversity (number of flowering species) in plots with (+MF) or without (–MF) the abundant, mass flowering plant species *Relhania fruticosa* and

*Salvia chamaeleagnea* in a lowland Renosterveld community. N = 280 (110 non-magnet plots; 170 magnet plots). Mean values for each group shown ( $\pm$ SE)



**Fig. 4** Visitation frequency in plots with (magnet) or without (non-magnet) the abundant plant species *Relhania fruticosa* and *Salvia chamaeleagnea* in a lowland Renosterveld community. Mean number

of visits per 10 min visitation period ( $\pm$ SE) are shown for, **a** all plant species in the plot and, **b** all other species except *R. fruticosa* and *S. chamaeleagnea*. N = 280 (110 –MF plots; 170 +MF plots)

pollinators of tubular-shaped flowers. Johnson (2004) suggests that the pollinator system observed in southern Africa developed this way because the region's bee fauna, in contrast to that of temperate regions, is by comparison to the southern African flora not particularly rich.

Anthophiles were more likely to occur and be active in areas of high floral density, although the effect of floral density varied between anthophile groups. This relationship may simply be a function of them optimising foraging by selecting areas with a high floral density (Hegland and

**Table 4** Differences in visitation frequency and areas of floral display in plots with (+MF plots) and without (–MF plots) the abundant, mass-flowering species *Relbania fruticosa* and *Salvia chamaeleagnea*

Variable	<i>U</i>	<i>Z</i>	+MF plots		–MF plots	
			N	Mean (±SE)	N	Mean (±SE)
Total visits	4675	–7.064**	170	9.02 (±0.75)	110	2.25 (±0.33)
Non-MF visits	7985	2.062*	170	3.32 (±0.62)	110	5.69 (±0.88)
Total floral density	6716	–3.979**	170	29.03 (±2.27)	110	36.58 (±5.73)
Non-MF floral density	8629	–1.089	170	19.32 (±2.28)	110	36.58 (±5.73)
Floral diversity	8585	1.155	170	2.84 (±0.08)	110	3.05 (±0.08)
VI by plant species						
All non-MF species	7970	0.0371*	170	1.77 (±0.49)	110	2.66 (±0.43)
<i>Albica flaccida</i>	45.5	0.458	7	0.00	15	0.10 (±0.08)
<i>Aspalathus</i> sp	110	0.000	17	0.02 (±0.05)	13	0.03 (±0.08)
<i>Babiana angustifolia</i>	1865.5	–0.996	80	0.62 (±0.23)	52	0.95 (±0.26)
<i>Berkheya armata</i>	123	–1.502	27	1.87 (±0.74)	13	4.99 (±2.01)
<i>Cotula turbinata</i>	209	–0.579	11	0.00	43	2.94 (±1.37)
<i>Cyanella hyacinthoides</i>	397.5	–0.689	60	0.58 (±0.37)	15	0.00
<i>D. pluvialis</i>	75	0.363	15	0.00	11	3.34 (±3.34)
<i>Felicia</i> sp	405	–0.489	100	0.24 (±0.09)	9	0.00
<i>Heliophila</i> sp	175.5	–0.215	9	0.00	41	0.19 (±0.13)
<i>Moraea lewisae</i>	134	0.017	10	2.70 (±1.8)	27	1.68 (±0.62)
<i>Murhertia heisteria</i>	264	–0.291	13	>0.01 (±0.00)	43	0.01 (±0.01)
<i>Osteospermum tomentosum</i>	256	–0.287	30	2.62 (±0.91)	18	2.71 (±1.31)
<i>Senecio elegans</i>	186	–0.927	30	1.63 (±0.62)	15	0.59 (±0.25)
<i>Senecio</i> sp	331.5	–0.098	52	0.20 (±0.20)	13	0.00

For a species in a particular sample VI=number of visits/floral area to give the visits/cm<sup>2</sup>/10 min observation period. Mann–Whitney *U* tests used for differences between magnet and non-magnet plots. Significant effects are marked (\**p* < 0.05; \*\**p* < 0.01)

Boeke 2006) so as to maximise rewards (Hempel De Ibarra et al. 2015). Intraspecific studies have shown that individual plants that have more inflorescences, or those occurring in dense conspecific patches tend to receive more visits from pollinators (Lázaro et al. 2009). Commonly occurring flowers may also receive more visits through frequency dependent effects (Dupont et al. 2003). Similar patterns have been observed in mixed stands of flowers (Hegland and Totland 2012). These relationships may be variable (Grindeland et al. 2005), suggesting that other factors may also affect the attractiveness of floral patches to anthophiles.

Assuming that anthophile activity (number of visits per plot) is correlated with anthophile density in the lowland renosterveld community studied here, anthophiles are more abundant and diverse in areas with a high density and diversity of flowers. However, the effects of these two variables are difficult to separate as they are strongly correlated with areas of high floral density also having more diverse floral resources.

Effects of plant community structure (i.e. differences in the relative abundances of different species in mixed floral stands) consistently affected both the likelihood of occurrence and activity of anthophiles in the plots. Although

spatially distant plots were likely to have similar density and diversity of flowers (as shown by lack of spatial autocorrelation of these variables), they could be separated on the basis of their floral composition, which in turn affected the composition of the anthophile community observed in these plots. Syrphid flies for example, are a group which visits many different flowers, yet have been shown to exhibit constancy (Goulson and Wright 1998), as well as having innate preference for certain colours (Lunau 2014). If anthophiles were displaying constancy to certain floral forms or colours, their distribution among floral patches would have been affected by diversity and floral composition, as well as by floral density. Because floral constancy can increase foraging efficiency, many insects focus their attention on one or a few species during a foraging bout (Gegeer and Laverty 2001). Anthophile preference for certain flowers could explain the similar grouping of sites by plant community structure and anthophile visitation. This behaviour does not preclude foragers switching among species at low floral densities (Vázquez et al. 2012) which would result in a less distinct ordination of sites by anthophile presence in the plots rather than plant community structure, as was the case here.



## Effects of mass-flowering species

The two mass flowering species examined here, *R. fruticosa* and *S. chamaeleagnea*, were strong determinants of anthophile activity, greatly increasing visitation rates, even though there was, on average, lower floral density and diversity. High visitation rates by scarabs (monkey beetles) to *S. chamaeleagnea* explains the negative relationship between scarabs and floral diversity, as *S. chamaeleagnea* was highly favoured by scarabs despite relatively lower floral diversity. We observed in this study that beetles are often attracted to large or dense floral displays, approaching and landing on them from above, preferring to remain on the display and moving between inflorescences by walking rather than flying. This behaviour would result in higher abundances of beetles on large floral displays than those of other anthophiles, which may only visit briefly.

Although plots where the two MF species occurred had much higher levels of anthophile activity than those without, additional visits were made primarily to whichever MF species was present. Neighbouring plants appeared not to benefit from any kind of magnet species effect, and may have been outcompeted for floral visitors and subsequently lower visitation rates per unit area of non MF-species in these plots. Rathcke (1983) proposed that visitation rates increase with increasing floral resources until anthophiles reach a saturation point, after which visitation decreases. Goulson (2000) proposes that this is due to increased competition between individual plants for anthophiles. So although mass flowering species can enhance pollinator densities, these effects may not necessarily directly benefit neighbouring plant species through facilitative effects (Elliott and Irwin 2009) such as those demonstrated in other studies of magnet species effects (Johnson et al. 2003; Ghazoul 2006).

## Implications for conservation

Our study shows the effects of short-term, small scale-factors on anthophile activity at the community level. Although these effects differed between various anthophile groups, resource availability plays an important role. As with Hegland and Boeke (2006), there seems to be a general ‘hotspot’ response (Thomson 1982) by pollinators to patches of favoured resources. This suggests that provided they are species rich and abundantly flowering (Ebeling et al. 2008), maintaining patches of natural or even semi-natural vegetation within the largely transformed lowlands of the Cape Floristic Region is beneficial for maintaining populations of flower-visiting insects.

Creating conservation headlands, such as wildflower rich field margins increases local pollinator densities in Europe (Pywell et al. 2006) and may be an effective means of enhancing habitat for anthophiles at the local

scale, although natural remnants are likely to be of greater value than restored habitat (Kohler et al. 2007). Patches of high quality habitat may provide useful stepping stones for arthropods in transformed landscapes but the scale at which such benefits occur is important. Kohler et al. (2007) found the beneficial effects of high quality habitats within farmland were spatially restricted, extending <150 m into the surrounding matrix. This may reflect the fine scale at which insects respond to environmental and habitat variables.

Landscape management approaches to biodiversity conservation operate broadly, at the level of entire communities. However, the conservation of more specialised plants and insects may require more directed efforts (and more directed investigation) given the variable response of different groups of anthophiles, particularly specialist species that may be more susceptible to fragmentation and area effects (Pauw 2007; Dauber et al. 2010). The importance of providing high-quality habitats for pollinators within transformed landscapes is often emphasised, yet it is not always easy to define a ‘high quality habitat’.

Habitat quality of restored field margins and remnant habitats in agricultural lands is affected by local scale factors such as the density, diversity and community structure of floral resources within patches (Mandelik et al. 2012). Landscape level effects such as the context of these patches within the surrounding matrix and the type of land use on adjacent lands, will also affect the abundance and diversity of both plants and anthophiles in remnant habitats (Pywell et al. 2006; Boutin et al. 2008). Our study shows that anthophile activity is affected by several highly localised, small-scale factors, namely the density and diversity of flowers and composition of floral resources (community structure), which should be considered in management plans at the landscape scale. The results emphasise the importance of maintaining not only a high abundance, but also a high diversity of floral resources in habitat remnants for the conservation of anthophiles.

**Acknowledgments** SMV was supported by the German Federal Ministry of Education and Research, through the BIOTA Africa project, and by the National Research Foundation of South Africa (NRF) and Stellenbosch University. MJS acknowledges financial support from the NRF and Mondi. JPS was supported by an NRF Incentive Fund for Rated Researchers. We thank Elandsberg Nature Reserve. G. Pedersen, R. Gaigher, P. Grant, D. Snyman and M. Brand assisted with data collection in the field.

## References

- Aizen MA, Sabatino M, Tylianakis JM (2012) Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science* 335(80):1486–1489. doi:10.1126/science.1215320

- Akaike H (1973) Information theory and an extension of the maximum likelihood principle. *Int Symp Inf theory*. doi:[10.1007/978-1-4612-1694-0](https://doi.org/10.1007/978-1-4612-1694-0)
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Astegiano J, Massol F, Vidal MM et al (2015) The robustness of plant-pollinator assemblages: linking plant interaction patterns and sensitivity to pollinator loss. *PLoS One* 10:e0117243. doi:[10.1371/journal.pone.0117243](https://doi.org/10.1371/journal.pone.0117243)
- Boutin C, Baril A, Martin PA (2008) Plant diversity in crop fields and woody hedgerows of organic and conventional farms in contrasting landscapes. *Agric Ecosyst Environ* 123:185–193. doi:[10.1016/j.agee.2007.05.010](https://doi.org/10.1016/j.agee.2007.05.010)
- Brunet J, Thairu MW, Henss JM et al (2015) The effects of flower, floral display, and reward sizes on bumblebee foraging behavior when pollen is the reward and plants are dichogamous. *Int J Plant Sci* 176:811–819. doi:[10.1086/683339](https://doi.org/10.1086/683339)
- Carvalho LG, Biesmeijer JC, Benadi G et al (2014) The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecol Lett* 17:1389–1399. doi:[10.1111/ele.12342](https://doi.org/10.1111/ele.12342)
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth
- Dauber J, Biesmeijer JC, Gabriel D et al (2010) Effects of patch size and density on flower visitation and seed set of wild plants: a pan-European approach. *J Ecol* 98:188–196. doi:[10.1111/j.1365-2745.2009.01590.x](https://doi.org/10.1111/j.1365-2745.2009.01590.x)
- Dupont YL, Hansen DM, Olesen JM (2003) Structure of a plant-flower-visitor network in the high-altitude sub-alpine desert of tenerife, Canary islands. *Ecography (Cop)* 26:301–310. doi:[10.1034/j.1600-0587.2003.03443.x](https://doi.org/10.1034/j.1600-0587.2003.03443.x)
- Ebeling A, Klein AM, Schumacher J et al (2008) How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117:1808–1815. doi:[10.1111/j.1600-0706.2008.16819.x](https://doi.org/10.1111/j.1600-0706.2008.16819.x)
- Elliott SE, Irwin RE (2009) Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in *Delphinium barbeyi* (Ranunculaceae). *Am J Bot* 96:912–919. doi:[10.3733/ajb.0800260](https://doi.org/10.3733/ajb.0800260)
- Gegeer RJ, Lavery (2001) The effect of variation among floral traits on the flower constancy of pollinators. In: Chittka L, Thomson JD (eds) *Cognitive ecology of pollination*. Cambridge University Press, Cambridge, pp 1–20
- Ghazoul J (2006) Floral diversity and the facilitation of pollination. *J Ecol* 94:295–304. doi:[10.1111/j.1365-2745.2006.01098.x](https://doi.org/10.1111/j.1365-2745.2006.01098.x)
- Goulson D (2000) Why do pollinators visit proportionally fewer flowers in large patches? *Oikos* 91:485–492. doi:[10.1034/j.1600-0706.2000.910309.x](https://doi.org/10.1034/j.1600-0706.2000.910309.x)
- Goulson D, Wright N (1998) Flower constancy in the hoverflies *Epsyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). *Behav Ecol* 9:213–219. doi:[10.1093/beheco/9.3.213](https://doi.org/10.1093/beheco/9.3.213)
- Hanoteaux S, Tielbörger K, Seifan M (2013) Effects of spatial patterns on the pollination success of a less attractive species. *Oikos* 122:867–880. doi:[10.1111/j.1600-0706.2012.20801.x](https://doi.org/10.1111/j.1600-0706.2012.20801.x)
- Hegland SJ, Boeke L (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecol Entomol* 31:532–538. doi:[10.1111/j.1365-2311.2006.00812.x](https://doi.org/10.1111/j.1365-2311.2006.00812.x)
- Hegland SJ, Totland Ø (2012) Interactions for pollinator visitation and their consequences for reproduction in a plant community. *Acta Oecologica* 43:95–103. doi:[10.1016/j.actao.2012.06.002](https://doi.org/10.1016/j.actao.2012.06.002)
- Hempel De Ibarra N, Langridge K V, Vorobyev M (2015) More than colour attraction: behavioural functions of flower patterns. *Curr Opin Insect Sci* 12:64–70. doi:[10.1016/j.cois.2015.09.005](https://doi.org/10.1016/j.cois.2015.09.005)
- Johnson SD (2004) An overview of plant–pollinator relationships in southern Africa. *Int J Trop Insect Sci* 24:45–54. doi:[10.1079/IJT20043](https://doi.org/10.1079/IJT20043)
- Johnson SD, Peter CI, Nilsson LA, Ågren J (2003) Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84:2919–2927
- Johnson SD, Hollens H, Kuhlmann M (2012) Competition versus facilitation: conspecific effects on pollinator visitation and seed set in the iris *Lapeirousia oreogena*. *Oikos* 121:545–550. doi:[10.1111/j.1600-0706.2011.19516.x](https://doi.org/10.1111/j.1600-0706.2011.19516.x)
- Kehinde T, Samways MJ (2012) Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agric Ecosyst Environ* 146:162–167. doi:[10.1016/j.agee.2011.10.020](https://doi.org/10.1016/j.agee.2011.10.020)
- Kemper J, Cowling RM, Richardson DM (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biol Conserv* 90:103–111. doi:[10.1016/S0006-3207\(99\)00021-X](https://doi.org/10.1016/S0006-3207(99)00021-X)
- Kohler F, Verhulst J, Van Klink R, Kleijn D (2007) At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *J Appl Ecol* 45:753–762. doi:[10.1111/j.1365-2664.2007.01394.x](https://doi.org/10.1111/j.1365-2664.2007.01394.x)
- Lázaro A, Lundgren R, Totland Ø (2009) Co-flowering neighbors influence the diversity and identity of pollinator groups visiting plant species. *Oikos* 118:691–702. doi:[10.1111/j.1600-0706.2008.17168.x](https://doi.org/10.1111/j.1600-0706.2008.17168.x)
- Lunau K (2014) Visual ecology of flies with particular reference to colour vision and colour preferences. *J Comp Physiol Neuroethol Sens Neural Behav Physiol* 200:497–512. doi:[10.1007/s00359-014-0895-1](https://doi.org/10.1007/s00359-014-0895-1)
- Maldonado MB, Lomáscolo SB, Vázquez DP (2013) The Importance of Pollinator generalization and abundance for the reproductive success of a generalist plant. *PLoS One* 8:1–6. doi:[10.1371/journal.pone.0075482](https://doi.org/10.1371/journal.pone.0075482)
- Mandelik Y, Winfree R, Neeson T, Kremen C (2012) Complementary habitat use by wild bees in agro-natural landscapes. *Ecol Appl* 22:1535–1546. doi:[10.1890/11-1299.1](https://doi.org/10.1890/11-1299.1)
- Mayer C, Soka G, Picker M (2006) The importance of monkey beetle (Scarabaeidae: Hopliini) pollination for Aizoaceae and Asteraceae in grazed and ungrazed areas at Paulshoek, Succulent Karoo, South Africa. *J Insect Conserv* 10:323–333. doi:[10.1007/s10841-006-9006-0](https://doi.org/10.1007/s10841-006-9006-0)
- Mucina L, Rutherford M (2006) The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria, pp 749–790
- Pauw A (2007) Collapse of a pollination web in small conservation areas. *Ecology* 88:1759–1769
- Picker MD, Midgley JJ (1996) Pollination by monkey beetles (Coleoptera: Scarabaeidae: Hopliini): flower and colour preferences. *African Entomol* 4:7–14.
- Potts SG, Biesmeijer JC, Kremen C et al (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* 25:345–353. doi:[10.1016/j.tree.2010.01.007](https://doi.org/10.1016/j.tree.2010.01.007)
- Pywell RF, Warman E, Hulmes L et al (2006) Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biol Conserv* 129:192–206. doi:[10.1016/j.biocon.2005.10.034](https://doi.org/10.1016/j.biocon.2005.10.034)
- Rathke B (1983) Competition and facilitation among plants for pollination. In: Real L (ed) *Pollination biology*. Academic Press, Orlando, pp 305–329
- Seifan M, Hoch E-M, Hanoteaux S, Tielbörger K (2014) The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. *J Ecol* 102:953–962. doi:[10.1111/1365-2745.12256](https://doi.org/10.1111/1365-2745.12256)
- Thomann M, Imbert E, Devaux C, Cheptou PO (2013) Flowering plants under global pollinator decline. *Trends Plant Sci* 18:353–359. doi:[10.1016/j.tplants.2013.04.002](https://doi.org/10.1016/j.tplants.2013.04.002)

- Thomson JD (1982) Patterns of visitation by animal pollinators. *Oikos* 39:241–250. doi:[10.2307/3544491](https://doi.org/10.2307/3544491)
- Vázquez DP, Lomáscolo SB, Maldonado MB et al (2012) The strength of plant–pollinator interactions. *Ecology* 93:719–725. doi:[10.1890/11-1356.1](https://doi.org/10.1890/11-1356.1)
- Westphal C, Steffan-Dewenter I, Tschardt T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol Lett* 6:961–965. doi:[10.1046/j.1461-0248.2003.00523.x](https://doi.org/10.1046/j.1461-0248.2003.00523.x)
- Winfree R, Aguilar R, Vázquez DP et al (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90:2068–2076. doi:[10.1890/08-1245.1](https://doi.org/10.1890/08-1245.1)