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## Relationships between species' floral traits and pollinator visitation in a temperate grassland

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**Abstract** Knowledge about plant–plant interactions for pollinator service at the plant community level is still scarce, although such interactions may be important to seed production and hence the population dynamics of individual plant species and the species compositions of communities. An important step towards a better understanding of pollination interactions at the community level is to assess if the variation in floral traits among plant species explain the variation in flower visitation frequency among those species. We investigated the relative importance of various floral traits for the visitation frequency of all insects, and bumblebees and flies separately, to plant species by measuring the visitation frequency to all insect-pollinated species in a community during an entire flowering season. Visitation frequency was identified to be strongly positive related to the visual display area and the date of peak flowering of plant species. Categorical variables, such as flower form and symmetry, were important to the visitation frequency of flies only. We constructed floral similarity measures based on the species' floral traits and found that the floral similarity for all species' traits combined and the continuous traits separately were positively related to individual visitation frequency. On the other hand, plant species with similar categorical floral traits did not have similar visitation frequencies. In conclusion, our results show that continuous traits, such as flower size and/or density, are more important for the variation in visitation frequency among plant species than thought earlier. Furthermore, differences in visitation frequency among pollinator groups give a poor support to the expectations derived from the classical pollination syndromes.

**Keywords** Visual display · Floral density · Facilitation · Competition · Plant–plant interactions · Plant community · Pollination syndromes

### Introduction

The interactions among plant species and pollinators at the plant community level are complex and still poorly understood, although an increasing number of pollination studies are concentrating on interactions at the community level (e.g. Olesen and Jordano 2002). The community approach is necessary to draw general conclusions about pollination interactions (Jordano 1987; Memmott 1999; Waser et al. 1996) and studies of plant–plant interactions, for pollination are an important part of the community approach. The two most common plant–plant interactions are pollinator attraction and heterospecific pollination (e.g. Campbell and Motten 1985; Waser and Fugate 1986; Feinsinger 1987; Caruso 1999). While heterospecific pollination is a purely competitive interaction, pollinator attraction can also be facilitative. As a consequence, attractive and generalist plant species that have many interactions with animals in visitation webs have the largest potential to affect other plant species through both types of plant–plant interactions.

Other studies describing plant–pollinator interactions at the community level (e.g. Herrera 1988; Petanidou and Vokou 1993; Bosch et al. 1997; Memmott 1999; Dicks et al. 2002; Dupont et al. 2003) have not focused on why plant species differ in their attractiveness to potential pollinators, although there is a large variation in floral traits among species within a community. Simultaneously, there are large variations in the attractiveness, in terms of flower visitation frequency, among plant species of the same community; some are highly attractive while others seem never to receive visits (e.g. Schemske et al. 1978; Pleasants 1980; Herrera 1988; Inouye and Pyke 1988; McCall and Primack 1992; Tot-

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land 1993; Elberling and Olesen 1999; Memmott 1999). Surprisingly, very few have studied if this large variation in interspecific pollinator attractiveness is related to the variation in floral traits among species (but see McCall and Primack 1992). Several relevant ecological questions can be addressed by investigating this issue. First, can commonly observed patterns within species, such as increased pollinator attraction to larger flowers (Conner and Rush 1996; Goulson et al. 1998; Ohashi and Yahara 1998; Pickering 2001) also be established in among-species relationships? Second, do species with a similar combination of floral traits have similar attractiveness on pollinators, and can such information help us predict how species interact (i.e. facilitate or compete) for pollinator visitation, for example if any species within a plant community act as 'magnets' (e.g. Lavery 1992; Memmott 1999)? Third, can classical pollination syndromes (e.g. Fægri and van der Pijl 1979), that mainly focus on categorical floral traits, explain why pollinator groups (e.g. bumblebees and flies) tend towards preferring some plant species above others, or are continuous floral traits, such as flower size and floral density, more important in explaining the variation in visitation frequencies of such pollinator groups? We address these questions by examining how species' floral traits (number of visual displays, visual display area, number of flowers per visual display, length of flowering period, date of peak flowering, flower colour, flower shape, flower symmetry, and abundance of insect-pollinated plant species within a community) relate to visitation frequency of plant species within a community.

## Materials and methods

### Study community

Our study site is a species-rich grassland/meadow of the intermediate dry, medium base-rich lowland grassland-type (Fremstad 1997), situated on the border between the boreo-nemoral and south-boreal zone in the inner region of the Sognefjord, west Norway. The grassland is located in a steep slope about 10–20 m above sea level and 50 m away from the shore. The climate is relatively warm and dry; the closest climate station (Lærdal) had a mean July temperature of 17.3°C and temperatures ranging from 7.7°C to 30.5°C during the study season (DNMI 2003).

We delimited an area of approximately 50×50 m by an electric fence during the field season to avoid disturbance by sheep and red deer that have grazed in the area since the fields were abandoned in the early 1960s. The surrounding area is dominated by deciduous forest and contains several patches of similar floral composition as the study site. A total of 38 insect-pollinated flowering species, with different floral traits, occurred inside the study site. Twenty-seven of these species flowered simultaneously at peak flowering in mid-July (see Table 1 for the plant species included in

the analysis). The nomenclature follows Lid and Lid (1994).

Bumblebees (*Bombus* spp.) and flies (Diptera) dominated the visitor pool and accounted for 61% and 26 % of the total 3,634 recorded visits, respectively. The other pollinator groups recorded were different bees (Apidae, except bumblebees, 5%), beetles (Coleoptera, 5%), butterflies (Lepidoptera, 2%) and ants (Formicidae, 1%).

### Data collection

We sampled data between 28 May 2003 and 18 August 2003, with the highest sampling intensity in July. This period covered the entire flowering season of most plant species in the community, and thus the main period for pollination. To determine the attractiveness of each plant species in the community to potential pollinators, we conducted a visitation survey inside 20 permanent plots of 1.5×1.5 m, randomly positioned at the start of the fieldwork and used throughout the entire season. Within the plots, we monitored the visitation frequency by counting the number of visits, including identification of the main visitor group (Diptera, *Bombus* spp., non-*Bombus* Apidae, Lepidoptera, Coleoptera, Formicidae), to visual displays for every insect-pollinated plant species during 10-min observation periods. Most periods were obtained between 10 a.m. and 4 p.m. In total we conducted 201 (i.e. 2,010 min) observation periods during the flowering season. We reduced the amount of non-pollinating insects in our data set by only counting the visits, where the visitor actually landed on the visual display and stayed for more than 1 s. To measure floral density, we counted the number of visual displays of each plant species inside the plot after every period. Depending on the species, a visual display consisted of a single flower, a flowering head/inflorescence or a group of flowers occurring together in a recognisable visual unit (see Table 1). We measured the area of visual displays, as a measure of flower size, of 10–20 randomly selected plants of each species and calculated the mean visual display area of each species according to the shape of the flowers. The area of visual displays with a circular outline (e.g. *Leucanthemum vulgare*) was calculated using the formula:  $\pi r^2$ , and for other flat visual displays (e.g. *Achillea millefolium*) we used the formula: length×width. When visual displays also had a depth dimension (e.g. *Trifolium pratense*), the formula:  $2\pi r^2 d + \pi r^2$  were used (see Table 1 for formulas used for each species). On the same random collection of plants, we also counted the number of flowers per visual display and calculated the mean per species. We determined the length of the flowering period and the date of peak flowering for each species by counting the number of open visual displays inside all the 20 plots, every 3–6 days during the season. For those species that we could not determine the actual start or end of flowering because it extended the study period (e.g. *Potentilla*

**Table 1** Basic characteristics of plant species, in the study community Rudsviki by the Sognefjord in west Norway, that were included in our analyses

Species	Abbreviations	Flower formula	Visual display	Flower shape	Flower symmetry	Main visitor	All insects	Bumblebees	Flies	Flower colour	Community abundance
<i>Achillea millefolium</i>	Achimill	lxw	H	O	A	Coleoptera	0.38	0.15		White	R
<i>Alchemilla</i> ssp.	Alchessp	lxw	G	O	A	Fornicidae	0.25		0.04	Yellow	R
<i>Campanula rotundifolia</i>	Camprotu	$2\pi r^2 d + \pi r^2$	S	O	A	Bombus	2.35	1.65	0.69	Blue-violet	A
<i>Carum carvi</i>	Carucarv	lxw	H	O	A	Diptera	0.94	0.05	0.68	White	I
<i>Centaurea jacea</i>	Centjace	$\pi r^2$	H	T	A	Bombus	3.26	2.93	0.12	Pink-red	I
<i>Clinopodium vulgare</i>	Clinpodi	$\pi r^2$	G	T	Z	Bombus	2.62	2.38	0.20	Pink-red	I
<i>Euphrasia stricta</i>	Euphstri	$2\pi r^2 d + \pi r^2$	G	O	Z	Bombus	2.38	1.91	0.46	White	A
<i>Filipendula ulmaria</i>	Filiulma	lxw	G	O	A	Bombus	11.38	8.38	1.23	White	R
<i>Fragaria vesca</i>	Fragvesc	$\pi r^2$	S	O	A	Diptera	0.43		0.31	White	R
<i>Galium album</i>	Galiabu	lxw	G	O	A	Diptera	1.21		0.72	White	I
<i>Galium boreale</i>	Gali bore	lxw	G	O	A	Coleoptera	0.38	0.02	0.18	White	I
<i>Galium uliginosum</i>	Galiulg	$\pi r^2$	G	O	A	Diptera	0.88	0.02	0.63	White	A
<i>Galium verum</i>	Gali veru	lxw	G	O	A	Diptera	1.33		0.84	Yellow	R
<i>Hypericum maculatum</i>	Hypemacu	$\pi r^2$	S	O	A	Bombus	3.13	2.68	0.44	Yellow	A
<i>Knautia arvensis</i>	Knauarve	$\pi r^2$	H	T	Z	Bombus	2.00	1.18	0.12	Pink-red	R
<i>Leucanthemum vulgare</i>	Leucvulg	$\pi r^2$	H	T	Z	Coleoptera	0.34		0.13	Yellow	I
<i>Linum catharticum</i>	Linucart	$\pi r^2$	G	O	A	Diptera	0.20		0.20	White	I
<i>Lotus corniculatus</i>	Lotucorn	$2\pi r^2 d + \pi r^2$	G	T	Z	Bombus	0.28	0.14	0.09	Yellow	A
<i>Myosotis arvensis</i>	Myosarve	$\pi r^2$	G	O	A	Diptera	0.14		0.14	Blue-violet	R
<i>Plantago lanceolata</i>	Planlanc	lxw	H	O	A	Diptera	0.43	0.02	0.33	White	A
<i>Polygala vulgaris</i>	Polyvulg	$2\pi r^2 d + \pi r^2$	H	O	Z	Bombus	0.73	0.53	0.11	Blue-violet	A
<i>Potentilla erecta</i>	Poteerec	$\pi r^2$	S	O	A	Diptera	3.66	0.41	2.15	Yellow	I
<i>Prunella vulgaris</i>	Prunvulg	$2\pi r^2 d + \pi r^2$	H	T	Z	Bombus	3.64	3.35	0.35	Blue-violet	A
<i>Ranunculus acris</i>	Ranuacri	$\pi r^2$	S	O	A	Diptera	0.46		0.35	Yellow	I
<i>Trifolium pratense</i>	Trifprat	$2\pi r^2 d + \pi r^2$	H	T	Z	Bombus	4.20	3.77	0.12	Pink-red	A
<i>T. repens</i>	Trifrepe	$2\pi r^2 d + \pi r^2$	H	T	Z	Bombus	1.16	1.02	0.05	White	I
<i>Veronica officinalis</i>	Vetrooffi	$2\pi r^2 d + \pi r^2$	B	O	Z	No visits	0			Blue-violet	R

Abbreviations of species names refer to Fig. 2; Flower formulas for calculations of area of visual displays:  $\pi r^2$  ( $r$  = radius) for flowers with circular outline,  $lxw$  (length  $\times$  width) for other square-shaped visual displays, and for visual displays with depth dimension we used the formula  $2\pi r^2 d + \pi r^2$  ( $d$  = depth); Visual display are *S* single flower, *H* flower head/inflorescence and *G* group or branch of flowers. Flower shapes are *O* open and *T* tubular. Flower symmetries are *A* actinomorphic and *Z* zygomorphic. Main visitor show the insect group that visited a species most frequently. All insects, bumblebees and flies are the mean visitation frequencies of the pollinator groups (included in the analyses) to each plant species; open spaces indicate that species were not visited by the pollinator group. Flower colours as perceived by human eyes. Community abundance is *R* rare, *I* intermediate and *A* abundant

*erecta*), we extrapolated their flowering period curves by a maximum of 15 days in any direction to obtain a date of flowering start and/or stop. Unfortunately, we were unable to obtain comparable data on nectar and pollen amounts of each species as a consequence of the large amount of species and their temporal variation in floral reward production (see also Lack 1982).

## Data analysis

To examine the relationship between single floral trait variables and visitation frequency of species, we performed simple linear regressions for continuous variables and one-way analysis of variance (ANOVA) for categorical variables (Table 2). We used stepwise analysis of co-variance (ANCOVA) to determine the relative importance of floral traits (both continuous and categorical) in explaining variation in pollinator visitation frequency among species on the community level. In the stepwise ANCOVA, we used a backward selection of variables because some of the categorical variables had more than two levels (Zar 1999). We checked all the data and the residuals from the ANCOVA with normal probability plots and tested the standardised residuals with a Kolmogorov-Smirnov test for normality, using the Lilliefors option in SYSTAT (Wilkinson 2003). Variables with a non-normal distribution were log-transformed, until normality of residuals was ensured. All models presented passed these assumption tests. We also inspected the residuals to detect outliers (leverage > 0.2), but since none of the potential outliers affected the direction or statistical significance of the results in our analyses we chose not to remove them.

We tested the homogeneity of slopes-assumption of ANCOVA according to the methods described by Glantz and Slinker (2001). No interactions between categorical and continuous variables occurred, showing that none of the continuous variables had heterogeneous slopes with the response variable.

The visitation frequency of each species (response variable) was defined as the mean number of visits per period, and thus a measure of the species' attractiveness to potential pollinators. Our predictors included the continuous variables: (1) number of visual displays (mean per species calculated from the mean per plot), (2) number of flowers per visual display (mean per species), (3) visual display area (mean per species), (4) length of flowering period (number of days per species), (5) date of peak flowering (per species), and the categorical variables: (6) flower shape (open or tubular flowers), (7) flower symmetry (actinomorphic or zygomorphic flowers), (8) flower colour (white, yellow, blue-violet or pink-red flowers; as seen by human eyes), (9) abundance in the community (rare: flowering in 1–6 plots; intermediate: flowering in 7–13 plots; and abundant: flowering in 14–20 of the 20 plots at the peak flowering of each species). Hereafter we commonly term these predictors as floral traits.

Those plant species that were observed in less than 11 periods throughout the study period were not included in the final analysis, yielding a sample size of 27 plant species that were visited by all the insects (all insects). Analyses using visitation frequency of bumblebees (*Bombus* spp.; 18 plant species) and flies (Diptera; 25 plant species) were performed separately. Other groups of pollinating insects (e.g. beetles and butterflies) did not perform enough visits to a sufficient amount of plant species to be included as separate visitor groups in the statistical analysis. However, their visits are included in the visitation frequency of all the insects group.

We used the principal component analysis (PCA) to ordinate the plant species according to their floral similarity. Species with similar scores along the first axis have a similar set of traits (i.e. higher floral similarity), whereas species that are far from each other along the first axis have dissimilar floral traits. The PCAs were run using all floral traits combined and the continuous and categorical predictors separately. We assessed if the degree of floral similarity among species was related to the

**Table 2** Mean visitation frequency per period of insect-pollinated plant species from the temperate grassland in Rudsviki by the Sognefjord, west Norway, grouped by categorical variables, for plant species visited by the total visitor pool (all insects), bumblebees (*Bombus* spp.) and flies (Diptera)

Visitor group	Statistics	Flower shape		Flower symmetry		Flower colour				Community abundance		
		Open	Tubular	Actino- morphic	Zygo- morphic	White	Yellow	Blue- violet	Red- pink	Rare	Intermediate	Abundant
All insects (27)	Mean	1.62	2.19	1.73	1.89	1.80	1.35	1.38	3.02	1.99	1.43	2.01
	<i>N</i>	(19)	(8)	(18)	(9)	(11)	(7)	(5)	(4)	(8)	(10)	(9)
	SE	±0.60	±0.53	±0.63	±0.49	±0.98	±0.55	±0.71	±0.47	±1.36	±0.41	±0.49
Bumblebees (18)	Mean	1.44	2.11	1.63	1.78	1.45	1.08	1.84	2.56	3.24	1.13	1.56
	<i>N</i>	(11)	(7)	(10)	(8)	(8)	(3)	(3)	(4)	(3)	(6)	(9)
	SE	±0.51	±0.75	±0.83	±0.46	±1.02	±0.81	±0.82	±0.54	±2.59	±0.51	±0.49
Flies (25)	Mean	0.56*	0.12*	0.54*	0.16*	0.48	0.58	0.27	0.14	0.45	0.48	0.33
	<i>N</i>	(17)	(8)	(17)	(8)	(10)	(7)	(4)	(10)	(6)	(10)	(9)
	SE	±0.13	±0.02	±0.13	±0.05	±0.11	±0.28	±0.14	±0.02	±0.20	±0.20	±0.08

The numbers of plant species visited by the different visitors groups and the number of plant species in each floral trait category is given in parentheses. Deviations from means are given as standard errors (SE). Means that were significantly different ( $P \leq 0.05$ ) within categories in a one-way ANOVA are marked with \*



visitation frequency by performing a simple linear regression between the scores of the first axis and the visitation frequency of all the insects. All statistical analysis was done with the statistical program SYSTAT 10.0 (Wilkinson 2003).

## Results

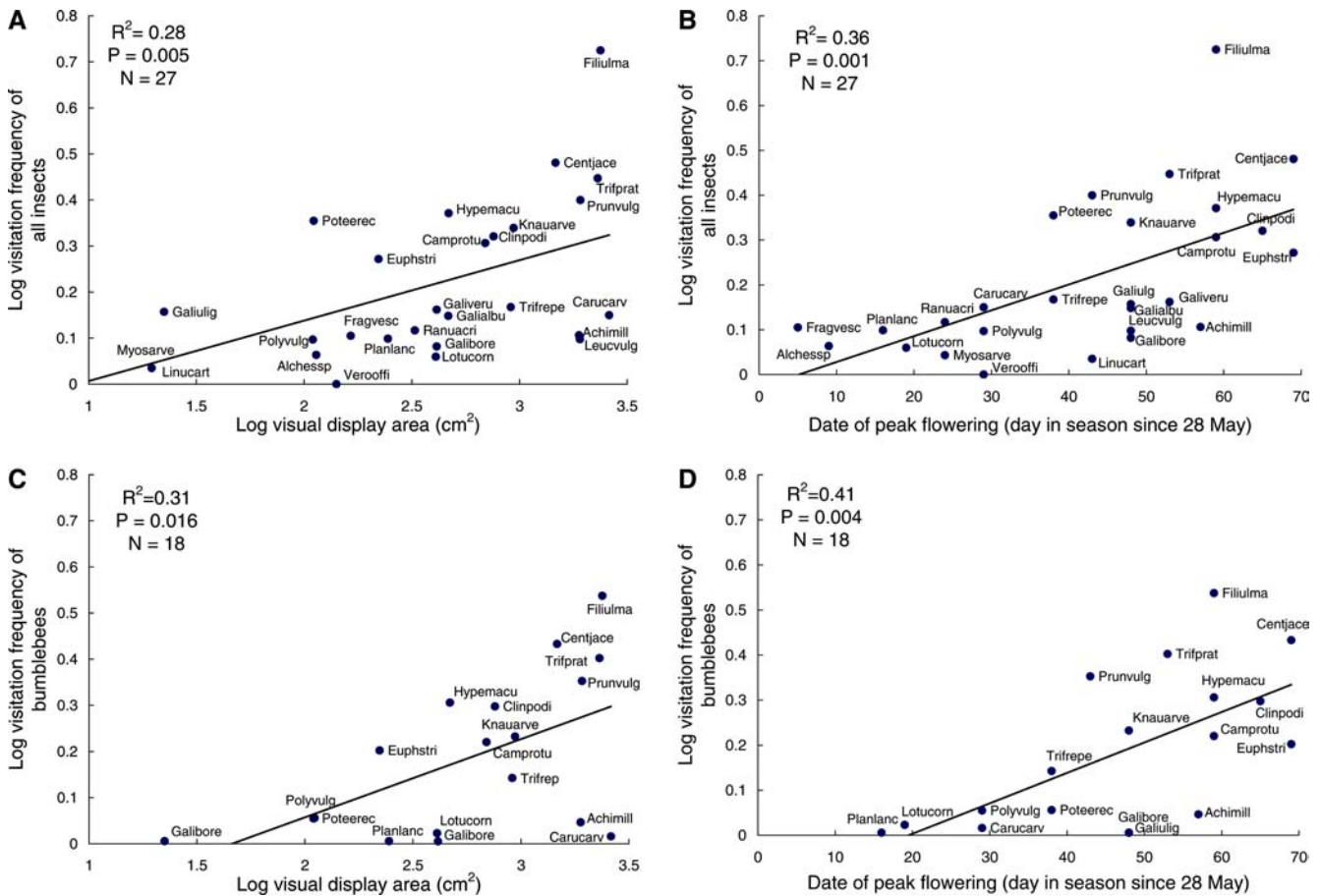
### Single predictor models

Visitation frequency of all insects combined increased with visual display area ( $N=27$ ,  $P=0.005$ ; Fig. 1a) and date of peak flowering ( $N=27$ ,  $P=0.001$ ; Fig. 1b), but was not significantly affected by the number of visual displays per plot; number of flowers per visual display and length of flowering period ( $N=27$ , all  $P>0.35$ ). None of the categorical variable explained differences in all insects visitation frequencies ( $P>0.57$ ; Table 1).

Bumblebee visitation frequency also increased with visual display area ( $N=18$ ,  $P=0.016$ ; Fig. 1c) and date of peak flowering ( $N=18$ ,  $P=0.004$ ; Fig. 1d), but was

not significantly affected by the number of visual displays per plot; number of flowers per visual displays and length of flowering period ( $N=18$ ,  $P>0.29$ ). None of the categorical variable explained differences in bumblebee visitation frequencies ( $P>0.37$ ; Table 1).

Visitation frequency of flies showed no significant linear relationships with any of the continuous predictors: visual display area, date of peak flowering, number of flowers per visual displays and length of flowering period ( $N=25$ ,  $P>0.15$  for all variables), but were marginally positive related to the number of visual displays per plot ( $N=25$ ,  $P=0.09$ ). On the other hand, flies visited plant species with open flowers more frequently than species with tubular flowers ( $F_{1,23}=6.82$ ,  $P=0.016$ ,) and species with actinomorphic flowers more frequently than species with zygomorphic flowers ( $F_{1,23}=4.72$ ,  $P=0.04$ ). None of the other categorical variables explained differences in the visitation frequency of flies (flower colour:  $F_{3, 21}=0.75$ ,  $P=0.53$ ; abundance:  $F_{2, 22}=0.06$ ,  $P=0.95$ ) among plant species for any of the visitor groups when analysed separately.



**Fig. 1 a–d** Simple linear regressions on the relationship between mean visitation frequency of all insects and **a** visual display area and **b** date of peak flowering; and between mean visitation frequency of bumblebees and **c** visual display area and **d** date of peak flowering among insect-pollinated plant species in the temperate grassland Rudsviki by the Sognefjord in west Norway.

Only the significant relationships are presented. See text for  $P$  values of non-significant relationships. Each point represents a plant species and is based on mean values from all observations on that plant species. The multiple coefficients of determination ( $R^2$ ), probability values ( $P$ ) and numbers of observations ( $N$ ) are given for each relationship. The full species names are given in Table 1

## Multiple predictor models

All stepwise ANCOVA models explained a substantial amount of the interspecific variation in visitation frequency for each visitor group ( $R^2 \geq 0.45$ ; Table 3). Both visitation frequency of all insects and bumblebees increased with visual display area and date of peak flowering, while there were no differences in visitation frequency for categorical variables (Table 3). The final model for flies included six significant or close to significant predictors (Table 3). Visitation frequency of flies increased with the length of flowering period, visual display area and date of peak flowering, while it decreased with the number of flowers per visual display. Visitation frequency of flies also differed significantly between flower symmetries and among flower colours.

The PCA on all floral traits of species resulted in a first axis, explaining 27.4% of the total variation in floral traits among species. Species scores along the first PCA-axis showed a significant relationship ( $N=27$ ,  $P=0.006$ ) with the visitation frequency of all insects, indicating that plant species with similar combinations of floral traits had more equal visitation frequency than species with dissimilar multivariate expression of floral traits (Fig. 2). A PCA with only continuous floral traits yielded a first axis explaining 35.6% of the total variation in floral traits. There was a significant relationship between species scores along the first axis and visitation frequency of species ( $P=0.003$ ,  $R^2=0.30$ ). A PCA on the categorical predictors explained 52% of the total variation in the components, but the species scores along the first axis showed no significant relationship with the visitation frequency ( $P=0.14$ ,  $R^2=0.09$ ).

## Discussion

To our knowledge, no other studies have examined the relative importance of floral traits of species for attraction of potential pollinators at the interspecific level within a community, even if such data often are available. In our study, the area of visual display appears to have a particularly important, and positive, effect on a species ability to attract potential pollinators. Since there is a positive correlation between the visual display area of a species and its floral density in patches (i.e. the product of a species' mean visual display area and mean number of visual displays within the plots;  $r=0.801$ ,  $P<0.001$ ), we cannot determine the relative importance of display area and floral density in patches for the interspecific variation in visitation frequency. Both species with large displays, like *Filipendula ulmaria* and *Centaurea jacea*, or species that often occur with high floral density in patches, like *T. pratense* and *Prunella vulgaris*, are among the most attractive to visiting insects. Interestingly, our results at the interspecific level are in accordance with patterns found on the intraspecific level, demonstrating that individuals with many flowers or that occur in dense conspecific patches often receive most visits (e.g. Goulson et al. 1998; Ohashi and Yahara 1998; Totland and Matthews 1998; Pickering 2001). Potential pollinators may prefer plant species with larger displays and/or those growing in dense patches to minimise costs of searching for rewards. Visual cues in themselves, such as the area of the floral display, can also influence the decisions of which flowers or inflorescences within a plant population an individual insect chooses to visit (Medel et al. 2003). Moreover, within a species there is often a correlation between the area of

**Table 3** Stepwise analysis of co-variance on the relationship between plant traits (predictors) and visitation frequency (response) to insect-pollinated plant species in the temperate grassland Rudsviki by the Sognefjord in west Norway

Visitor group	Predictor variable	df	$\beta$	SE	$F_{Anova}$	$P_{Anova}$	$R^2$
All insects (27)	Date of peak flowering	1	0.468	0.002	8.170	0.009	0.459
	Log visual display area	1	0.338	0.043	4.264	0.050	
	Error	24					
Bumblebees (18)	Date of peak flowering	1	0.515	0.002	7.894	0.013	0.581
	Log visual display area	1	0.413	0.055	5.235	0.037	
	Error	15					
Flies (25)	Flowering period	1	0.625	0.001	18.117	0.001	0.724
	Flower symmetry	1			17.280	0.001	
	Log no. of flowers in visual display	1	-0.496	0.012	6.915	0.018	
	Log visual display area	1	0.466	0.016	6.114	0.025	
	Date of peak flowering	1	0.368	0.000	5.469	0.033	
	Flower colour	3			2.665	0.083	
	Error	16					

Models are based on a backward selection of variables,  $\alpha$  to enter and remove=0.05, and tolerance=0.2. The numbers of plant species included in the analysis of each visitor group are given in parentheses. Degrees of freedom (df) are presented for each predictor and for the error of the model. Standardised coefficient ( $\beta$ ) and standard error (SE) are given for continuous variables;  $F$ -ratios

and  $P$  values are specified for each variable, and the multiple coefficient of determination ( $R^2$ ) for each model. Only predictors included in the final model are presented, but all floral trait variables specified in the methods were included in the analysis. The order of presentation reflects the variables order of importance (see  $\beta$  and  $F$  values)

the visual display and the amount of nectar (Stanton and Preston 1988; Cresswell and Galen 1991; Duffield et al. 1993; Inoue et al. 1995) or pollen (Stanton and Preston 1988) produced. If correlations between flower size and reward quantity are also established in interspecific relationships, that may explain why visual display area is important in explaining the variation in pollinator attraction among plant species. Bumblebees, that dominated the visitor pool in our study, may learn quickly and adapt to flower species with the highest reward (Goulson 2003 and references therein). Therefore a correlation between floral display area and floral rewards may increase the visitation to plant species with such visual cues and indicate that visual cues can be important for insects' choice of flowering species in a species-rich plant community.

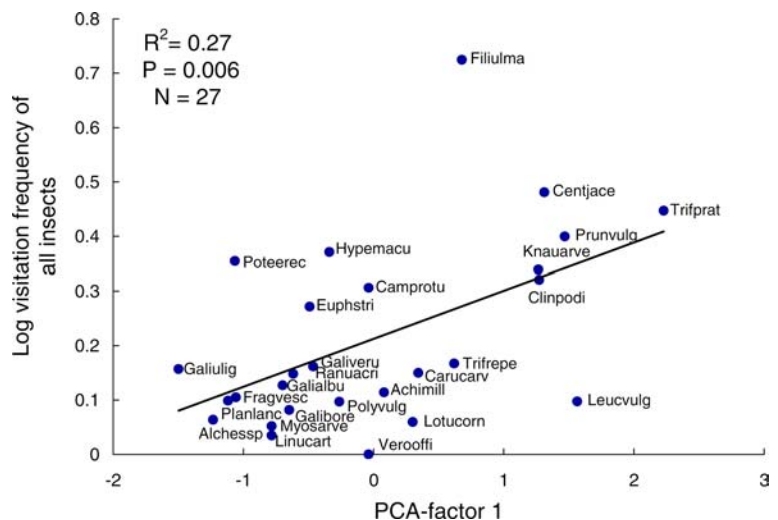
Pollinator species do not necessarily base their choice of flowering species on single floral traits. Indeed, our correlation between floral trait similarity among plant species and visitation frequency showed that plant species with similar combinations of traits have comparable attractiveness to potential pollinators. This indicates that several floral traits affect the flower choice of insects. Given that there was no significant relationship between PCA-axis 1 based on categorical variables and visitation frequency (only a trend;  $P=0.14$ ), whereas a similar regression based on continuous floral traits was highly significant ( $P=0.003$ ), our results also suggest that the role of continuous floral traits in explaining variation in among-species attraction of potential pollinators is larger than thought earlier (see for example Fægri and van der Pijl 1979).

Late-flowering species had higher visitation frequencies than early-flowering species, a result consistent with earlier studies in similar habitats (e.g. Thomson 1982; McCall and Primack 1992). An interpretation of this pattern has at least two components. First, the number of potential pollinator species and their abundance will normally increase throughout the season in northern lowland ecosystems, and hence many plant species that

flower relatively late have the highest visitation. In our study area, especially bumblebees increase in abundance during the flowering season (Hegland and Totland, unpublished). Second, the number of insect-pollinated species in bloom increased during the flowering season at our study site (Hegland and Totland, unpublished). As a consequence, there is no competition for pollinator attraction among plant species, thus there is higher visitation frequency to species flowering simultaneously late in the season. Feinsinger (1987) argued that facilitation for pollinator visitation among plants by co-flowering could be at least as important as competition resulting in divergent flowering. However, only a handful of studies have reported indications for facilitative interactions to attract pollinators among co-flowering plant species (Thomson 1978; 1981; Campbell and Motten 1985; Laverty 1992).

The term "magnet"-species has been used for highly attractive plant species that facilitate visitation frequency of less attractive plant species (Laverty 1992). Based on the ANCOVA models for all insects' and bumblebees' visitation frequency, such a potential "magnet"-species in our study community has large visual displays, alternatively high floral density in patch, and late flowering, for example *Filipendula ulmaria*, *C. jacea* and *T. pratense* (see Fig. 2). Identifying potential "magnet"-species among the fly-pollinated species is more complicated since there are many more traits included in the ANCOVA-model, but *P. erecta* is one of the species that closely fit the predictions made by that model, such as long flowering period and actinomorphic flowers (see Table 3 for the other significant traits). In an analysis of a grassland community, Memmott (1999) found that on plant species, *Daucus carota* attracted many more visitors (42% of total) and visitor species (61% of total) than the other species in the community. As suggested by Memmott (1999), an interesting experiment would be to manipulate the densities of such attractive species to investigate the effects on several, not just one, other species. Such an experiment could reveal

**Fig. 2** Simple regression on the relationship between mean visitation frequency of all insects and species scores of floral traits along the first PCA-axis for each insect-pollinated plant species in the temperate grassland Rudsviki by the Sognefjord in west Norway. The PCA is based on all floral traits measured (see [Materials and methods](#)). The multiple coefficients of determination ( $R^2$ ), probability values ( $P$ ) and numbers of observations ( $N$ ) are given. The full species names are given in Table 1





which facilitation or competition is the most important interaction for pollinator attraction of plant species that co-flower at the plant community level. Amongst others, such an experiment may have implications for predictions of community-level effects of extinction or introduction of highly attractive plant species.

Bumblebees are regarded to be of large importance for pollination of both wild and cultivated crops in temperate ecosystems, and they are often more efficient than, for example, honeybees (Goulson 2003). We do not know of any study that has compared the relative importance of different pollinator groups for different plant species' reproduction on the community level. However, results from studies of single species may suggest that bumblebees are the most important pollinator for many plant species (e.g. Meynie and Bernard 1997, Aizen 2001, Kandori 2002). Moreover, our results show that bumblebees perform a large fraction of visits to those species that are visited by more pollinator groups (see Table 1). Furthermore, the results for all insects resemble those for bumblebees, indicating that species traits important to bumblebees contribute substantially to determining the visitation frequency of all insects.

The plant traits related to bumblebee- and fly-visitation frequencies in our community have a poor fit to patterns predicted by classical pollination syndromes. Only flies had a visitation frequency that significantly depended on categorical floral traits, preferring species with actinomorphic and open flowers, a pattern consistent with the fly-pollination syndrome (Fægri and van der Pijl 1979, see also Pellmyr 2002 and references therein). The most frequently visited plant species by flies; *P. erecta*, *F. ulmaria* and *Galium verum*, all have actinomorphic and open flowers. Bumblebee visitation frequencies, on the other hand, did not differ between levels of categorical floral traits. Consequently, our results suggest that the classical pollination syndromes do not necessarily reflect the visitation pattern of a whole group of pollinators. For example, among bumblebee species there is considerable variation in important morphological traits, such as tongue length, that determine if individuals of a species choose to visit a plant (Goulson 2003). The species most frequently visited by bumblebees in our study community *F. ulmaria*, *T. pratense*, and *P. vulgaris*, are species that have differences in categorical floral traits, for example flower colour. McCall and Primack (1992) found that bees in a woodland-meadow community preferred plant species with purple flowers, while flies preferred species with open flowers, thus partly confirming visitation patterns predicted by pollination syndromes. However, in tundra and fynbo, other floral traits appeared to be important determinants of floral preference by bees and flies (McCall and Primack 1992). Our results suggest that classical pollination syndromes represent a too simple picture of the interactions that occur between pollinators and plant species at the community level. An alternative to a taxonomical division of pollinators is a separation

of pollinators into functional groups (e.g. Fenster et al. 2004), implying that for example short- and long-tongued bumblebees are partitioned into separate groups. Furthermore, even if categorical traits (here: flower symmetry and shape) may be important for visitation frequency, our results indicate that their importance has been exaggerated relative to continuous traits (here: display area and/or floral density) in understanding the variation in visitation frequency among plant species within a community.

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