Research

Co-flowering neighbors influence the diversity and identity of pollinator groups visiting plant species

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The generalization–specialization continuum exhibited in pollination interactions currently receives much attention. It is well-known that the pollinator assemblage of particular species varies temporally and spatially, and therefore the ecological generalization on pollinators may be a contextual attribute. However, the factors causing such variation and its ecological and evolutionary consequences are still poorly understood. This variation can be caused by spatial or temporal variation in the pollinator community, but also by variation in the plant community. Here, we examined how the floral neighbourhood influenced the generalization on pollinators and the composition of pollinators of six plant species differing in generalization levels and main pollinators. The diversity, identity and density of floral species affected both the level of generalization on pollinators and the composition of visitors of particular plant species. Although the relationships to floral neighbourhood varied considerably among species, generalization level and visitation by uncommon pollinators generally increased with floral diversity and richness. The generalization level of the neighbourhood was negatively related to the generalization level of the focal species in two species. The number of flowers of the pollinator-sharing species and the number of flowers of the focal species had different effects on the composition of visits in different species; attributable to differences in facilitation/competition for pollinator attraction. We propose that an important ecological implication of our results is that variation in species interactions caused by the pollination context may result in increased community stability. The main evolutionary implication of our results is that selection on flower and pollinator traits may depend, to an unknown extent, on the composition of the co-flowering plant community.

It is now well understood that plant–pollinator interactions in any given community can be described as a network, in which many plant species are visited by more than one pollinator taxa, and many pollinator taxa visit more than one plant species, whereas obligate one-to-one links of plants and pollinators are rare (Waser et al. 1996, Memmott 1999, Olesen and Jordano 2002). Recent studies have shown high levels of ecological generalization (Jordano 1987, Herrera 1988, Waser et al. 1996) and asymmetrical relationships, i.e. specialized species frequently depend on a core of generalist species as partners (Bascompte et al. 2003, Memmott et al. 2004, Vázquez and Aizén 2004, Petanidou et al. 2008), in plant–animal interactions at the community-level. The interest in understanding the origin, evolution and maintenance of these generalization–specialization patterns has increased over the last years (Johnson and Steiner 2000, Fenster et al. 2004, Waser and Ollerton 2006) because they are not predicted by the classical view of pollination syndromes, which suggests the convergence in floral morphology of unrelated plant species to specialize on the same type of pollinators (Vogel 1954, Faegri and van der Pijl 1966) and because they may have important implications for community resilience to perturbations

(Olesen and Jordano 2002, Bascompte et al. 2003, Memmott et al. 2004) and for the evolution of floral traits (Waser et al. 1996, Aigner 2001, Fenster et al. 2004).

Although it is well-known that the pollinator assemblage of particular species varies temporally and spatially (Herrera 1988, Horvitz and Schemske 1990, Kwak et al. 1991, Gómez and Zamora 1999, Fenster and Dudash 2001, Price et al. 2005), the factors causing such variation, and its ecological and evolutionary consequences, are still poorly understood. Variation in the pollinator assemblage of particular species can be caused by spatial (Gómez and Zamora 1999, Herrera 2005) or temporal (Horvitz and Schemske 1990, Price et al. 2005) variation in the population densities of individual pollinator species, but it may also be caused by variation in the plant community. Co-flowering plant species may compete with or facilitate each other in terms of pollinator services (Thomson 1982, Rathcke 1983, Waser 1983, Callaway 1995) and therefore they can affect each other's pollinator visits. Many empirical studies have examined how pollinator-sharing influences patterns of pollinator foraging (Stout et al. 1998, Johnson et al. 2003), and how this affects visitation rates (Feinsinger et al. 1991, Brown et al. 2002, Moeller 2004), interspecific

pollen transfer (Waser 1983, Caruso 1999, Bell et al. 2005), and plant reproductive success (Feinsinger et al. 1991, Brown et al. 2002, Ghazoul 2006). In addition, the floral neighborhood might also influence the diversity and composition of visits that particular plant species receives, because the attractiveness of a plant species for a particular pollinator might not only depend on the characteristics of the individual plant species itself (Grindeland et al. 2005, Kudo and Harder 2005) and its abundance (Kunin 1997, Bosch and Waser 2001, Grindeland et al. 2005), but also on the attractiveness of co-flowering plants, and their abundance (Thomson 1982, Stout et al. 1998, Hegland and Totland 2005, Toräng et al. 2006, Hersch and Roy 2007).

The ecological generalization level (generalization level, hereafter) of a particular plant species can be expected to increase with the diversity and number of flowers in the neighbourhood because the diversity of insects visiting a patch might increase with the number and diversity of flowers (Hegland and Boeke 2006). In addition, the generalization level of a particular plant species is also expected to increase with the plant species' own abundance (Stang et al. 2006), because a plant that offers a greater reward will be visited by more individual pollinators, and consequently, it is more likely that receives visits by a higher number of species. However, the net effect of the neighbourhood on a particular plant species may ultimately depend on the plant species' degree of ecological specialization, i.e. the tendency of plants to use a relative small proportion of the available flower-visitor fauna as pollinators (Armbruster 2006), and on the taxonomic identity of its main pollinators. Thus, competition among pollinator-sharing plant species for the attraction of their main pollinator might result in fewer partner species in the most evolutionarily specialized plant species (because they are more attractive for their main pollinator) and in more partners in the others. For example, plants possessing floral traits preferred by bees may be more likely to be visited exclusively by bees when growing next to plants that have unspecialized flower morphology. Facilitation may result in decreased generalization, when it occurs among pollinator-sharing species that jointly attract their main pollinators (Moeller 2004); whereas it may result in increasing generalization when it occur among co-flowering species that do not share their main pollinators (Ghazoul 2006). Particular responses of plant species may also depend on aspects of the particular foraging behavior of their main pollinators, such as the degree of preference, fixed specialization and floral constancy (Waser 1986, Chittka et al. 1999, Chittka and Raine 2006). Thus, it can be expected that plant species strongly specialized on pollinators showing fixed specialization or high flower-constancy behavior, such as bees, are less affected by the floral neighbourhood in terms of composition of their pollinators, than plant species specialized in less specialized or less flower-constant pollinators.

Our objective was to investigate the role of co-flowering species on the level of generalization on pollinators and the faunal composition of the pollinators of six plant species differing in generalization levels and main flower visitors. By using data on the pollinator groups visiting these species, we related the local variation in generalization levels and composition of pollinator visits to local variation in the floral neighbourhood. Our specific questions were: 1) does a diverse or dense neighbourhood increase the generalization on pollinators of particular plant species by increasing the visits of uncommon pollinators (i.e. those that are infrequent visitors of the species)? 2) Does the generalization of a particular plant species increase with its abundance? 3) Does the generalization of specialized plant species decrease when they occur in a non-specialized neighbourhood? 4) Is the response to the floral neighbourhood greater for the main pollinators (i.e. those that conduct most of the visits) of generalist plant species than for those of specialists?, and 5) Do plants specialized on bees have a lower response to the neighbourhood context than plants specialized on other insects?

Material and methods

Study areas

We conducted our study in two different plant communities in the southern part of Norway. One community is located at 300 m altitude at Ryghsetra (59°44′03″N, 10°02′48″E), Buskerud county, ca 2.5 km southeast of Mjøndalen, and within a species-rich semi-natural meadow. The blooming season in the meadow starts in early-mid May and terminates in mid-late August, and during this period ca 55 species bloom. The flower visitor assemblage of this community in the study year consisted of 72.7% bumblebees, 11% muscoid flies, 5.5% solitary bees, 4.7% hover flies, 2.4% ants, 1.6% butterflies, 0.9% honeybees, 0.5% beetles, 0.5% beeflies and 0.04% wasps.

The other community is located on a southwest exposed slope at ca 1500 m altitude on Sandalsnuten, Finse, in the northern part of Hardangervidda (∼60°N, 7°E), in the alpine region of southwest Norway. The blooming season in this community starts in late June and terminates in late August, and during this period ca 25 species bloom. The flower visitor assemblage of this community in the study year consisted of 85.8% muscoid flies, 7.9% butterflies, 3.6% bumblebees and 2.5% hover flies.

Study species

In order to study the effects of the floral neighbourhood on pollinator visits, we selected four species (*Potentilla erecta, Galium mollugo, Leucanthemum vulgare* and *Centaurea jacea*) from Ryghsetra, and two (*Astragalus alpinus* and *Leontodon autumnalis*) from Finse. All these perennial herbs were pollinated by more than one pollinator group, i.e. the main pollinator group did not represent more than 90% of the visits. In addition, they were very abundant in their communities (Table 1) and occurred in diverse floral contexts. Relevant characteristics of these species are listed in Table 1.

Sampling: flower visitation and flower density

In 2006, we sampled flower visitation and flower density within 30 permanent plots of 2 × 2 m in each community. At Ryghsetra, where the meadow was large and relatively

Table 1. Characteristics of the study plant species. Ab. (%): abundance, i.e. percentage of plots the species was present in; Start Flow.: the day that the species started flowering in the study communities in 2006 (day/month); Len. fl.: Length of the flowering period (days); No. sp. fl. sim.: maximum number of species flowering simultaneously with the study species in the community; N: number of observation periods recorded; No. obs. plot: average number of observations on the same plot; Days bet. obs.: average number of days between observations in the same plots. Pollinator visits: number of visits conducted by different pollinator groups to each plant species during the study period (main pollinator group in bold); PG$_{TOT}$: pollination generalization level calculated using Simpson's diversity index and all recorded observations (see text for details).

Species	Family	Ab. (%)	Start flow.	Len. flow.	No. sp. fl. sim.	n	No. obs. plot	Days bet.obs.	Pollinator visits										PG$_{TOT}$
									Muscoid flies	Hover flies	Bumblebees	Solitary bees	Honey bees	Ants	Butterflies	Beetles	Wasps	
Potentilla erecta	Rosaceae	80	08/06	42	11	63	2.0	12.3	44	12	0	**90**	1	23	0	2	0	2.76
Galium mollugo	Rubiaceae	96.7	24/06	26	14	48	1.8	11.4	**54**	13	0	2	0	4	0	2	0	1.81
Leucanthemum vulgare	Asteraceae	86.7	17/06	33	12	34	1.4	11.1	**58**	23	0	3	0	0	0	10	1	2.25
Centaurea jacea	Asteraceae	60	05/07	14	10	30	2.0	4.9	47	67	**1607**	37	4	0	22	0	0	1.23
Astragalus alpinus	Fabaceae	76.7	03/07	27	10	43	2.3	6.5	25	0	**55**	0	0	0	48	0	0	2.92
Leontodon autumnalis	Asteraceae	56.7	21/07	16	10	33	2.2	4.1	**114**	9	0	0	0	0	7	0	0	1.29

homogeneous, we placed the plots in a systematic way, along two lines and separated by ca 3 m. At Finse, on the other hand, where vegetation was not homogenous across the whole area, we placed the plots haphazardly within suitable sub-areas in the community, with a minimum separation between plots of ca 3 m. Twenty additional non-permanent plots were located at Ryghsetra during June (the community flowering peak). The location of these additional plots was haphazardly changed after every observation period. This was necessary in order to sample sufficient variation in the floral neighbourhood. The inner 1×1 m square of each 2×2 m plot was marked and flower visitation was observed within it. We estimated flower/inflorescence density inside both the 2×2 m plots and the 1×1 m inner squares within the plots. This plot size (2×2 m) might allow the study of the effects of floral neighbourhood on pollinator visitation (Ghazoul 2006, Hegland and Boeke 2006).

We observed pollinator visitation from 13 May to 19 July at Ryghsetra and from 3 July to 5 August at Finse. These periods covered the whole flowering period for most of the plant species in both communities during the study years. The observations were conducted every day that weather conditions allowed pollinator activity (27 and 23 days at Ryghsetra and Finse, respectively), between 09:00 and 18:00 h, during 20-min periods. The order of observation of plots was random, but we did not observe the same plot more than once during a day. During each observation period we noted the number and identity of flower visitors to flowers or inflorescences (depending on the species) of any species occurring in the inner 1×1 m plot (not only to the six study species). A visit was defined to have occurred when there was contact between the visitor's body and the reproductive organs (stigma or anther) of the flower. We categorized each visitor into 10 pollinator groups. These pollinator groups were clusters of pollinator species that behave in a similar way in the flowers and might therefore exert similar selective pressures (Fenster et al. 2004). The groups were: bumblebees *Bombus* spp., solitary bees (mainly Andrenidae, Anthophoridae, Halictidae and Colletidae; all of them of similar small size) honeybees *Apis mellifera*, ants (Formicidae), wasps (Icneumonidae, *Vespula* spp., etc), hover flies (Syrphidae), muscoid flies (mainly Muscidae, Anthomyiidae), beetles (Coleoptera), butterflies (Lepidoptera) and beeflies *Bombylius minor*. In total, we recorded 2656 pollinator visits in the whole plant community during 118 observation periods at Ryghsetra (4.4 observation periods day^{-1} in average), and 2125 pollinator visits in the whole plant community during 134 observation periods at Finse (5.8 observation periods day^{-1} in average). However, the number of observation periods per study species varied from 30 to 63, since the study plant species did not occur in all the plots and did not flowered during the whole season. Table 1 shows the number of visits and observation periods recorded per each studied species.

We obtained the visitation rate per flower (or inflorescence) by each visitor group to each study plant species in each 20-min observation period, by dividing the number of flower visits by a given visitor group to one plant species by the number of open flowers or inflorescences of this plant species in the 1×1 m inner square. To characterize the

floral neighbourhood, we counted the number of open flowers (or inflorescences) of every species occurring in the plots after each observation period in the 2 × 2 m plots (see below for variables used in the analyses).

We used the individual observation periods (i.e. 20 min of observation to a given plot) as sample units, although this potentially could cause pseudo-replication if observations within the same plot are not independent. This was because, due to our sampling procedure, we did not have replicated measurements of all the plots for each species and we could therefore not include plot as a factor in the analyses. Nevertheless, we believe that the risk of pseudo-replication is small because we never observed the same plot twice in the same day and because the average number of observations on the same plot during the whole season was around 2 for all the study plant species (Table 1). Moreover, the observations on the same species in same plots were highly separated in time (ranging from 4–12 days, Table 1). Thus, the floral neighbourhood (i.e. the number and identity of open flowers) changed considerably between observations in the same plot. In addition, there were no significant differences in generalization levels among plots that were observed more than once for any of the species (*Potentilla erecta*: p = 0.697, *Galium mollugo*: p = 0.068; *Leucanthemum vulgare*: p = 0.456; *Centaurea jacea*: p = 0.791; *Astragalus alpinus*: p = 0.575; *Leontodon autumnalis*: p = 0.455), suggesting that other site-specific characteristics, such as pollinator nests, shade, wind exposure or proximity to forest did not significantly influence the visitation patterns at the scale of the small meadow used here. Another potential caveat with our approach could be that the pollinator diversity is not constant during the whole flowering period of the study species. To examine this potential caveat we calculated an index of pollinator diversity for each of the sampling days in each community (using Simpson's diversity index and the total number of pollinator visits recorded in the whole community), and included this variable ('pollinator diversity in the community') in the analyses. In this way we can account for the effect of variation in insect assemblage diversity over time on the generalization level of the plant species, and differentiate this effect from the effect of variation in floral neighbourhood.

Index of pollination generalization

For each of the study species we calculated indices of pollination generalization (PG hereafter) in order to estimate the level of generalization on pollinators of plant species. For that, we followed Sahli and Conner (2006) and used Simpson's (1949) diversity index: $1/D = 1/\Sigma_{i=1}^{S} p_i^2$, where p_i is the proportional visitation for the pollinator group i, and S is the pollinator richness, i.e. the number of pollinator groups visiting a plant species. A value of 1 means all the visits that the plant species received were performed by a single pollinator group. This index includes both richness and evenness and gives higher weight to common taxa (Gurevitch et al. 2006), which prevents us from over-emphasizing incidental visits.

First, we calculated PG for each species using all the visits that the plant species received during the flowering period (PG_{TOT}). PG_{TOT} was considered as a measure of the overall generalization level of the species (see calculated values in Table 1). We then used it to characterize the floral neighbourhood. Second, we calculated PG for each observation period (PG_{OBS}) for each species, in order to evaluate how the floral neighbourhood can affect the PG of a particular species.

Floral neighbourhood

In order to describe the floral neighbourhood of each study plant species in each observation period, we considered the following variables:

1. Total number of flowers, excluding the number of flowers of the focal species.
2. Number of flowers of the focal species.
3. Number of flowers of the pollinator-sharing species, excluding the number of flowers of the focal species. In order to detect those plant species that shared their main pollinators in the community, we grouped the plant species according to the relative abundance (the proportion of the total) of the different insect groups as their pollinators. For that, we performed cluster analyses using the PRIMER package (Clarke and Gorley 2001). Cluster analyses are based in a similarity coefficient (S) which measures how similar any pair of samples are in terms of the biological communities they contain (in this case, how similar any pair of plant species are in terms of their pollinator assemblage). Such similarity coefficient ranges from 100% (if two plant species are totally similar) to 0% (if two plant species are totally dissimilar). The dissimilarity coefficient is: δ = 100 − S, and shows the degree to which two plant species are unlike each other. We used the Bray–Curtis coefficient, since it is the most commonly used in ecological work (Clarke and Gorley 2001). Once the cluster analyses were performed, we conducted similarity percentage analyses (Simper; Clarke and Gorley 2001) to estimate the average similarities within the obtained groups (using similarities between all pairs of plant species within a group), and the average dissimilarities among the groups (computing dissimilarities between all pairs of plant species belonging to different groups). We excluded from this calculation those species that received fewer than 10 visits during the study period. Figure 1 shows the groups of pollinator-sharing species considered in this study, the average similarities within the groups and the average dissimilarities among the groups.
4. Plant richness, i.e. number of different plant species occurring in bloom during the observation period.
5. Plant diversity, estimated using Simpson's (1949) diversity index where p_i is, in this case, the proportional abundance for the plant species i (i.e. the percentage of open flowers/inflorescences of this species with respect to the total), and S is plant species richness.
6. Generalization level of the neighbourhood. This variable consists of an average (weighted by the
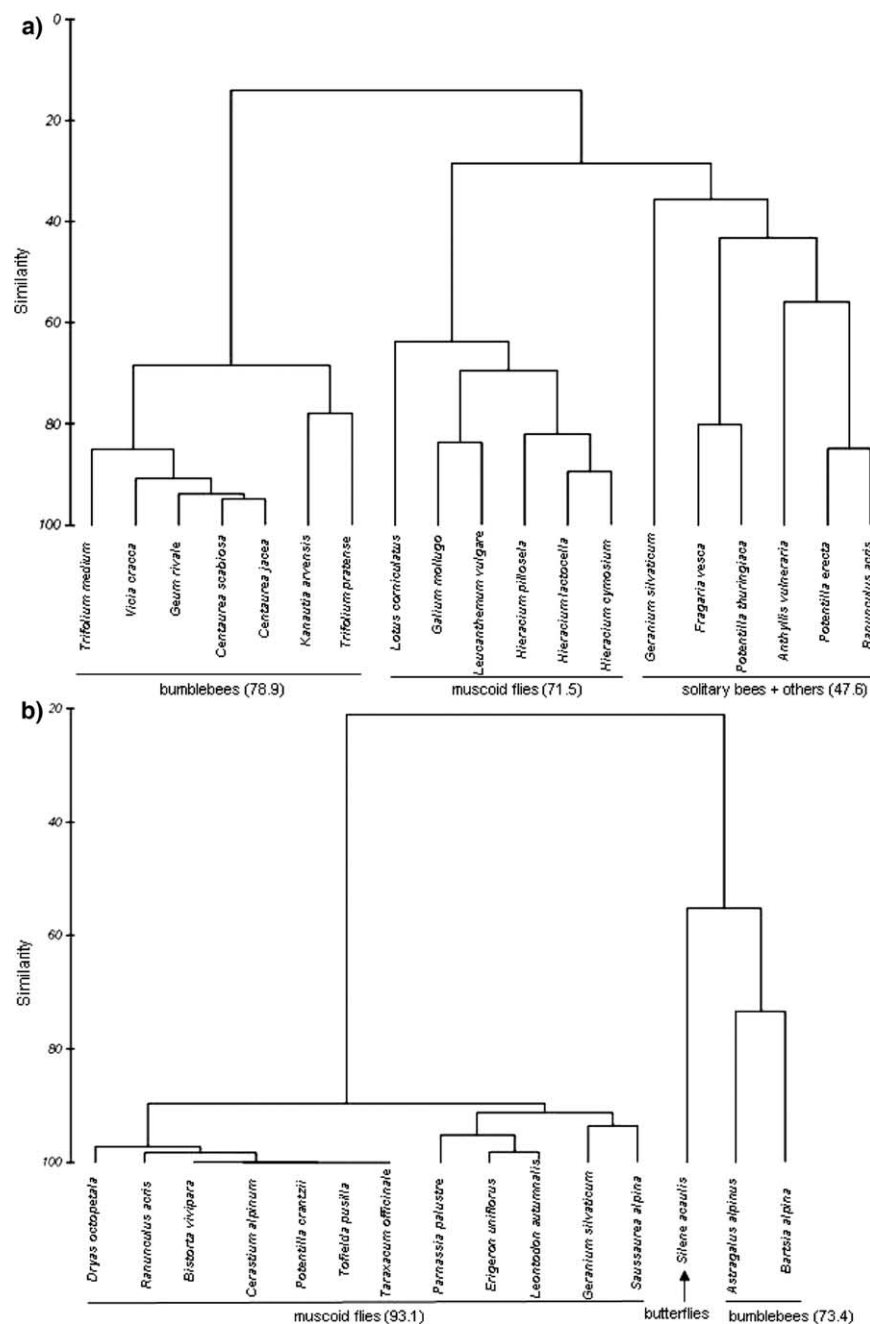
Figure 1. Clusters showing the pollinator-sharing species in the study communities: (A) Ryghsetra (average dissimilarity percentages between groups: bumblebees-mucoid flies: 87.1; bumbebees-bees: 84.8; bees-muscoid flies: 71.6), and (B) Finse (average dissimilarity percentages between groups: bumblebees-muscoid flies: 83.7; bumblebees-butterflies: 44.8; butterflies-muscoid flies: 69.2). Average similarity percentages within groups are shown into brackets next to the main pollinator of each group. Similarity and dissimilarity percentages are based on Bray–Curtis similarity matrix (Simper; Clarke and Gorley 2001).

abundance) of the PG_{TOT} of all the species flowering during the observation period (excluding the focal species). We excluded from this calculation those species that received fewer than 10 visits during the whole study period to avoid an overestimation of specialization levels.

We considered separately the total number of flowers and the number of flowers of pollinator-sharing species because we expected the second variable to be more predictive than the first one, at least for the most specialist plant species studied. On the other hand, we expected plant diversity to be more predictive than plant richness, since the effects of rare species on other species' visits might be low.

Statistical analyses

In order to determine if the floral neighbourhood affected PG_{OBS}, we performed separate multiple regression analyses

(using Systat 10) for each of the six focal species. In these analyses, the six variables listed in the section 'Floral neighbourhood', the total number of visits to flowers/inflorescences, the visitation rate to the focal species during each observation period, the pollinator diversity in the community each observation day, date (from the first to the last day of observation) and time of the day (four categories: two-hour intervals) were included as independent predictor variables, and PG_{OBS} was included as the dependent variable. The tolerance values of variables were used to reveal the amount of co-linearity among the independent variables. We used backward stepwise regressions where the variables were removed from the model when the p-values were higher than 0.15. Variables were log-transformed to achieve normality.

We also conducted separate canonical correspondence analyses (CCAs; Canoco ver.4.5) for each of the six species, in order to determine if the floral neighbourhood affected the composition of their pollinators. The sampling unit was the observation period. The dependent variables were the numbers of visits from each particular group of pollinator to a particular plant species during an observation period. We used the number of visits of each group instead of the percentage of visits in order to include all the observation periods recorded, and not only those that received pollinator visits. A pollinator group was included in the analyses only when it performed at least one visit to the particular plant species during the entire study period. We downweighted the rare species in order to control for differences in abundance of pollinator taxa. In these analyses, we introduced the same predictor variables as used in the multiple regression analyses, except the visitation, total number of visits, date and time of the day. However, total number of visits, date and time of the day were included as covariates in the analyses, since they might also affect the composition of the visits. Whenever necessary, we log-transformed the data to improve the model fit. We used Monte Carlo permutation (1000 permutations) tests to assess statistical significance of the association between composition of the pollinator visits and the floral neighbourhood. First, we obtained the significance of the whole ordination; and second, a forward stepwise method was used to determine which variables related to the floral neighbourhood significantly explained variation in pollinator composition (Ter Brak and Smilauer 2002).

Results

Effects of floral neighbourhood on the generalization level

The results from the stepwise multiple regressions on each species are summarized in Table 2. For half of the study species (*Potentilla erecta* and *Galium mollugo* at Ryghsetra and *Leontodon autumnalis* at Finse; Table 2a, 2b, 2f) the results showed significant relationships between PG_{OBS} and several variables characterizing the floral neighbourhood. However, the variables related to PG_{OBS} differed among species. The plant richness/plant diversity, the generalization level of the neighbourhood, and the total number of flowers, were the neighbourhood variables that most strongly influenced the PG_{OBS} of these species. PG_{OBS}

increased with plant richness in two species (*Potentilla* and *Galium*) and plant diversity in one species (*Leontodon*). PG_{OBS} decreased with the generalization level of the neighbourhood in two species (*Galium* and *Leontodon*), and decreased with the total number of flowers in one species (*Potentilla*). Other factors that were positively and significantly related to PG_{OBS} of these species were the total number of visits (*Potentilla* and *Galium*), visitation rate (*Leontodon*), the pollinator diversity in the community (*Potentilla*), date (*Galium*) and time of the day (*Leontodon*).

On the other hand, *Leucanthemum vulgare* and *Centaurea jacea* at Ryghsetra, and *Astragalus alpinus* at Finse, did not show significant relationships between PG_{OBS} and variables characterizing the floral neighbourhood (Table 2c–e). For *Leucanthemum,* we only found a marginally significant relationship between PG_{OBS} and the total number of pollinator visits, for *Centaurea* only pollinator diversity in the community was significant, whereas for *Astragalus* only the species' own visitation rate significantly explained variation in PG_{OBS}.

Effects of floral neighbourhood on the composition of visits

For five of the six study species we found significant relationships between several variables describing the floral neighbourhood and the faunal composition of pollinators. Moreover, the variation in the floral neighbourhood explained a high percentage of the variance in the faunal composition of pollinators to these five plant species (between 27.1 and 75.9%). Again, the variables related to the composition of the visitor assemblage differed among the plant species (see Table 3 for the results of the CCAs on each plant species).

Potentilla
The floral neighbourhood affected the composition of pollinators visiting *Potentilla* (Table 3a). Both the number of flowers of pollinator-sharing species and plant diversity entered as significant variables, while plant richness was marginally significant (Table 3a). All the other variables characterizing the floral neighbourhood were not significant. The number of honeybee, solitary bee and beetle visits to *Potentilla* increased with the number of flowers of pollinator-sharing species. The number of visits of muscoid flies, hover flies and ants increased with the diversity of plant species and the total number of species (Fig. 2a).

Galium
The floral neighbourhood affected the composition of pollinators of *Galium* (Table 3b). Plant richness, the generalization level of the neighbourhood, and the number of flowers of pollinator-sharing species had significant effects, and plant diversity had a marginally significant effect, on the composition of visits to *Galium*. None of the other variables were significant (Table 3b). The number of solitary bee and hover fly visits to *Galium* increased with the number of species and the generalization level of the neighbourhood, and it also increased as the number of flowers of pollinator-sharing species decreased (Fig. 2b).

Table 2. Results of the stepwise multiple regression analyses relating variables describing the floral neighbourhood (see text for details), total number of visits, visitation rate, pollinator diversity in the community, date and time of the day to the index of pollination generalization (PG$_{OBS}$) for the different study plant species. Standarized coeficient (ß) and standard error (SE) are given; t-ratios and p-values are specified for each variable, and the squared multiple coefficient of determination (R^2), sample size (n) and F-ratios and p-values for the whole models. Only variables with p <0.15 were included in the final models, but all the variables specified in the methods were included in the analyses. The order of presentation reflects the order of importance of variables (see ß values). Differences in n between Table 1 and 2 are due to the absence of pollinators during some observation periods.

Species	Variable	ß	SE	t	p
a) *Potentilla erecta*	Total number of flowers	−0.664	0.001	−2.897	**0.008**
	Plant richness	0.484	0.053	2.285	**0.031**
	Pollinator diversity in the community	0.458	0.124	2.142	**0.043**
	Total number of visits	0.435	0.023	2.394	**0.025**
	Whole model: $R^2 = 0.316$, n = 29, $F_{4, 24} = 2.77$, p = 0.049				
b) *Galium mollugo*	Date	0.794	0.003	4.558	**0.001**
	Total number of visits	0.518	0.013	3.820	**0.003**
	Generalization level of the neighbourhood	−0.487	0.125	−3.396	**0.007**
	Plant richness	0.478	0.020	2.648	**0.024**
	Flowers of the pollinator-sharing species	0.282	0.002	1.688	0.122
	Whole model: $R^2 = 0.827$, n = 16, $F_{5, 10} = 9.57$, p = 0.001				
c) *Leucanthemum vulgare*	Total number of visits	0.393	0.027	1.958	0.064
	Whole model: $R^2 = 0.154$, n = 23, $F_{1, 21} = 3.83$, p = 0.064				
d) *Centaurea jacea*	Pollinator diversity in the community	0.528	0.147	3.286	**0.003**
	Whole model: $R^2 = 0.278$, n = 30, $F_{1,28} = 10.8$, p = 0.003				
e) *Astragalus alpinus*	Visit rate	0.441	0.138	2.455	**0.026**
	Total number of visits	0.345	0.011	1.898	0.076
	Flowers of the pollinator-sharing species	0.326	0.002	2.034	0.059
	Generalization level of the neighbourhood	0.319	0.647	1.964	0.067
	Whole model: $R^2 = 0.658$, n = 21, $F_{4, 16} = 7.69$, p = 0.001				
f) *Leontodon autumnalis*	Generalization level of the neighbourhood	−0.721	0.274	−3.929	**0.001**
	Plant diversity	0.581	0.056	3.115	**0.005**
	Time of the day	0.497	0.051	3.232	**0.004**
	Visit rate	0.461	0.039	2.881	0.008
	Whole model: $R^2 = 0.506$, n = 28, $F_{3, 24} = 5.89$, p = 0.002				

Leucanthemum
None of the variables related to the floral neighbourhood significantly explained variation in the composition of visits to *Leucanthemum* (Table 3c; Fig. 2c).

Centaurea
The floral neighbourhood affected the identity of visitors to *Centaurea* (Table 3d). The number of flowers of *Centaurea* entered as a significant variable and plant diversity as marginally significant, while all the other variables were not significant (Table 3d). The number of hover fly visits to *Centaurea* increased with its own flower density, and the number of honeybee visits increased with plant species diversity (Fig. 2d).

Astragalus
The composition of pollinators to *Astragalus* varied with the floral neighbourhood (Table 3e). Flower density of *Astragalus* and plant diversity entered as significant variables, while all the other variables were not significant (Table 3e). The number of bumblebee visits to this species increased with its own number of flowers, and the number of muscoid visits increased with plant diversity (Fig. 2e)

Leontodon
The floral neighbourhood also affected the composition of pollinators to *Leontodon* (Table 3f). Plant diversity and number of flowers of pollinator-sharing species entered as significant variables, and the generalization level of the neighbourhood as marginally significant. None of the other variables were significant (Table 3f). The number of hover fly visits to *Leontondon* increased with plant diversity and the number of butterfly visits increased with the number of flowers of pollinator-sharing species (Fig. 2f).

Discussion

The variation in density, identity and diversity of the co-flowering neighbourhood can affect both the diversity and the composition of pollinators of particular plant species. Five of the six study plant species (*Potentilla*, *Galium*, *Centaurea*, *Astragalus* and *Leontodon*) showed variation in the pollinator visits received in relation to variables describing the floral neighbourhood. The floral neighbourhood influenced both the generalization levels and the composition of the visits of three of these five species (*Potentilla*, *Galium* and *Leontodon*), whereas for the two bumblebee-pollinated species (*Centaurea* and *Astragalus*) only the composition of their visitor assemblage was directly affected by the floral neighbourhood.

The responses of the five species that were affected by the co-flowering neighbourhood were, however, species-specific, as expected based on their differences in generalization levels and main pollinators (Table 1); and as expected based on the differences in pollinator assemblage between the two study areas, since Finse is a typical alpine community

Table 3. Results of canonical correspondence analyses (CCAs) relating different variables describing the floral neighbourhood (see text for details) to the composition of pollinators for the different study plant species. Percentage of the variance explained by the two first ordination axes (%V), F and p-values for the canonical ordination and explanatory variables (those variables that entered in the ordination with p-values ≤0.07) are given. The sum of all eigenvalues is after accounting for the covariables.

Plant species	% V	F	p	Explanatory variables
a) *Potentilla erecta*	38.9	2.34	0.003	Flowers of the pollinator-sharing species (p =0.019) Plant diversity (p =0.005) Plant richness (p =0.070)
				Sum of all canonical eigenvalues /sum of all eigenvalues: 0.5/1.115
b) *Galium mollugo*	75.8	5.35	0.008	Plant richness (p =0.005) Generalization level of the neighbourhood (p =0.011) Flowers of the pollinator-sharing species (p =0.028)
				Sum of all canonical eigenvalues /sum of all eigenvalues: 0.798/0.922
c) *Leucanthemum vulgare*	25.9	0.66	0.78	
				Sum of all canonical eigenvalues /sum of all eigenvalues: 0.251/0.939
d) *Centaurea jacea*	27.1	1.70	0.038	Flowers of the focal species (p =0.004) Plant diversity (p =0.05)
				Sum of all canonical eigenvalues /sum of all eigenvalues: 0.221/0.717
e) *Astragalus alpinus*	58.8	3.33	0.005	Flowers of the focal species (p =0.025) Plant diversity (p =0.03)
				Sum of all canonical eigenvalues /sum of all eigenvalues: 0.485/0.825
f) *Leontodon autumnalis*	39.0	2.35	0.037	Plant diversity (p =0.022) Flowers of the pollinator-sharing species (p =0.025) Generalization level of the neighbourhood (p =0.067)
				Sum of all canonical eigenvalues /sum of all eigenvalues: 0.324/0.830

(Olesen and Jordano 2002, Devoto et al. 2005), with lower diversity of insects and higher frequency of fly visits than Ryghsetra (Study areas). Even so, some relationships were similar for some species. First, the results of the CCAs showed that plant richness and/or plant diversity increased the visits of uncommon pollinator groups (Table 1) to all these five study species (Fig. 2). Several studies have shown positive relationships between the richness of floral resources and pollinator diversity both at landscape level (Steffan-Dewenter and Tscharntke 1999, Potts et al. 2003, Ricketts et al. 2008) and at smaller scale (Hegland and Boeke 2006), probably because diverse and rich communities and neighbourhoods may attract a much diverse pollinator fauna. This increase in the visits of uncommon pollinators, related to an increase in plant diversity or richness, translated into an increase in generalization levels in three of these species (*Potentilla*, *Galium* and *Leontodon*; Table 2). However, it did not translate into a change in generalization levels in *Centaurea* and *Astragalus*, the two bumblebee-pollinated species. Bumblebees often show flower-constancy and limit their visits to one or a few species during foraging bouts, because including more species in their diet may incur costs in terms of accuracy (Chittka et al. 1996, 1999, Gegear and Laverty 1998). While other pollinators may shift between species, bumblebees may be faithful to these two plant species even in a diverse neighbourhood, thereby depleting reward amounts and discouraging other pollinators. Thus, although there is also an increase in the visits of uncommon pollinators to *Centaurea* and *Astragalus* with an increase in plant diversity, bumblebees still conduct the largest amount of the visits to them. Consequently, their generalization level (calculated using relative frequencies) is less affected by this factor. In a similar way, a greater faith of solitary bees than flies to *Potentilla* could be the reason for which *Potentilla* becomes less generalized when it occurs with a great number of other flowers.

The generalization level of neighbors was negatively related to the generalization levels of two study species (*Galium* and *Leontodon*). This could result from the competitive abilities of the neighboring species for attracting the pollinators. Increasing the generalization level of the neighbourhood represents an increase in the number or abundance of generalist neighbors (since we used PG_{TOT} and not PG_{OBS} for the estimation of the generalization level of the neighbourhood). Specialist plant species might be less affected when they compete for their main pollinators against more generalist species. Both *Leontodon* and *Galium* are much visited by muscoid flies (87.8% and 72% of the visits respectively; Table 1) and therefore, their generalization level decreases in the competition for flies within a generalist neighbourhood.

We did not find a relationship between generalization levels and number of flowers of the focal species (Stang et al. 2006). However, the number of flowers of *Centaurea* and *Astragalus* had a significant effect on their own composition of visitors. In *Centaurea*, the number of visits of hover flies (uncommon pollinator; Table 1) increased with its number of flowers; whereas in *Astralagus*, the number of bumblebee visits (its main pollinators; Table 1) increase with its own density. It is commonly observed that dense patches of a flowering species are more attractive for pollinators than scarce ones (Kunin 1997, Bosch and Waser 2001) and that pollinators foraging within a patch focus on the most prevalent plant species, as expected by optimal foraging theory (Stephens and Krebs 1986, Hersch and Roy 2007). The fact that it was the number of visits of an uncommon pollinator which increased with flower density in *Centaurea*, whereas it was the number of visits of the main pollinators that increased with flower density in *Astralagus* may be due
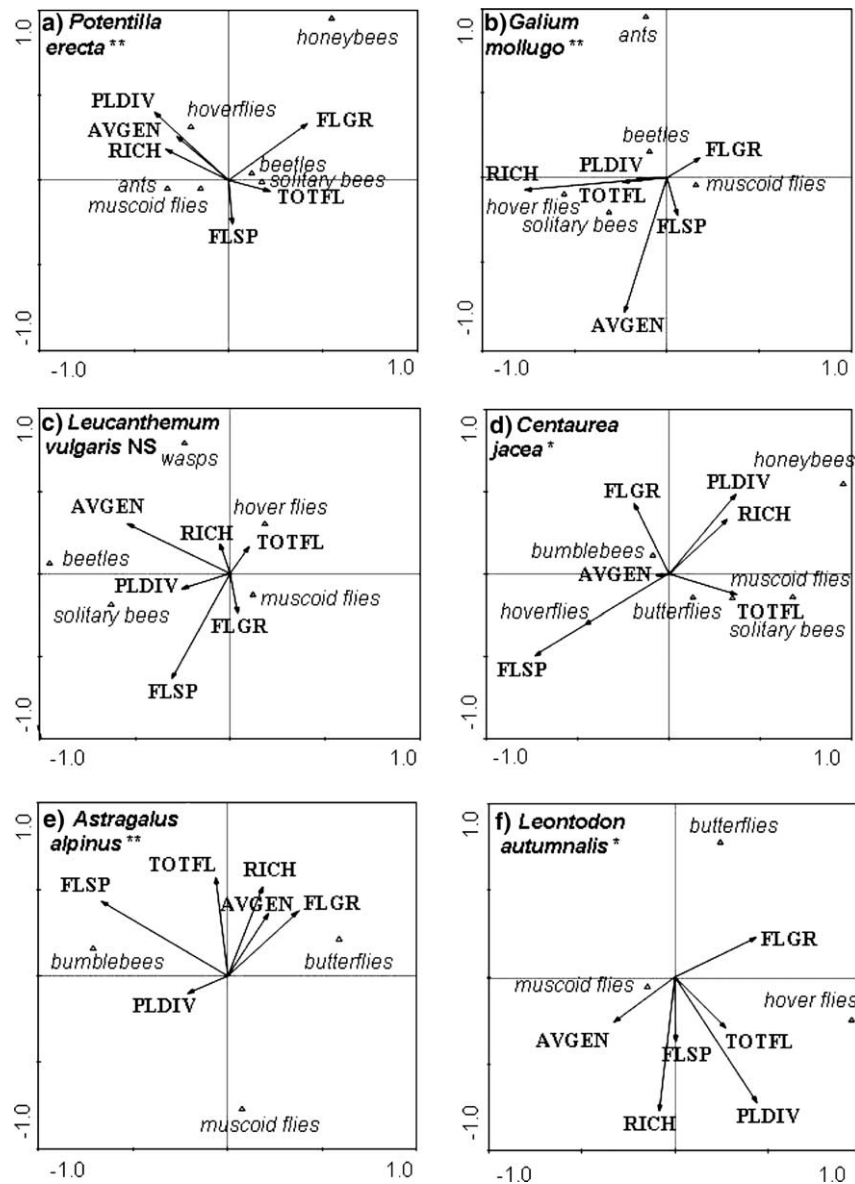
Figure 2. Biplots corresponding to canonical correspondence analyses (CCAs) conducted for each species and utilized to study the relationships between the number of visits of each pollinator group (triangles, italic lowercase) and variables describing to the floral neighbourhood (arrows, uppercase). TOTFL: total number of flowers; FLSP: number of flowers of the focal species; FLGR: number of flowers of pollinator-sharing species; RICH: plant richness; PLDIV: Plant diversity; and AVGEN: generalization level of the neighbourhood. Date, time of the day and total number of pollinator visits to the focal species during an observation period, were introduced as covariates in the models (see text for details). Arrows indicate the direction and strength of the relationship between each environmental variable and each axis. Relationship with an axis increases with the length of the arrow and decreases with the angle respect to that axis. Significance of the whole model: **: $p < 0.01$; *: $p < 0.05$; NS: not significant.

to differences in the pollinator assemblage between their communities. At Ryghsetra, during the blooming period of *Centaurea*, the most abundant pollinator in the community was the bumblebees, which preferred *Centaurea* over the other flowering species. Availability of resources for pollinators is not only the number of flowers but the number of flowers relative to the number of pollinators that forage on them. Therefore, given the very high number of bumblebees foraging for *Centaurea* flowers, the availability of flowers for bumblebees is likely low. Bumblebees (as other pollinators) may reduce patch-selectivity when

resources are scarce. On the contrary, hover flies at Ryghsetra, which visited many species and had a low abundance, might have chosen the plants that offered higher rewards and/or those that reduced floral handling or search times, in order to maximize their energy gain per unit time invested in foraging (Stephens and Krebs 1986, Hersch and Roy 2007). Thus, hover flies may have focused on the patches with higher density of *Centaurea*, when they foraged for this plant species. At Finse, on the other hand, the number of bumblebees was very low (Study areas). It is likely that the excess of resources for the few bumblebees in

this community make them to focus on the patches with higher density of *Astragalus* flowers, since they are supposed to forage economically (Stephens and Krebs 1986).

The number of pollinator-sharing species did not affect the generalization levels either, but it did affect the composition of visits to *Potentilla*, *Galium* and *Leontodon*. An increase in this variable resulted in an increase in the main pollinators of *Galium* and *Potentilla*, suggesting facilitation between pollinator-sharing species due to joint attraction. Comparable results have been reported for *Clarkia xantia* ssp. *xantiana*: populations occurring with pollinator-sharing congeners were visited twice as often by specialist bees than populations occurring alone (Moeller 2004). However, an increase in the number of pollinator-sharing species was related to an increase in uncommon pollinators in *Leontodon* (butterflies, hover flies; Table 1). We attribute that to the competitive environment of this species since *Leontodon* (Finse) co-flowered with several species that were even more specialized in flies than itself (Fig. 1). Thus, it is possible that for *Leontodon*, a pollinator-sharing neighbourhood was mainly composed of a diverse array of stronger competitors for flies.

The results of this study may have important ecological implications in relation to stability and persistence of plant communities. As some theoretical models have predicted (Kunin and Iwasa 1996, Rodríguez-Gironés and Santamaria 2004), and our results support, the reproductive interactions at any given time and place will depend on the availability of resources and the relative profitability of different interactions (Emlen 1966, MacArthur and Pianka 1966). The identity and frequency of pollination interactions will change when one or more of the components in the pollination context change. Thus, if species of plants or pollinators disappear from or are introduced into a community, the whole rules of interactions assembly might change. This could result in pollinators visiting plant species that they would not visit under other conditions, or result in pollinators avoiding flowers that they otherwise would visit. In order to predict if loss of individual species can cause cascading loss of other species, and to devise optimal conservation strategies to minimize such additional losses, we need a better understanding of how plant-animal interaction assemblages at the community level function, and especially how interactions change when the context do. Studies relating the variation of pollinators to particular plant species to the temporal or spatial variation in their community-context, as well as experimental manipulations of species involved in the plant–pollinator networks, could be fruitful approaches to obtain such knowledge.

Our results have also an important evolutionary implication: since ecological specialization may be context-dependent, morphological specialization might be a community phenomenon. The role of pollinator-sharing in structuring plant communities has been the focus of many studies (reviewed by Palmer et al. 2003) and competition for pollinators (Rathcke 1983, Waser 1983, Caruso 2002, Bell et al. 2005) and facilitation (Thomson 1982, Rathcke 1983, Johnson et al. 2003) have been recognized as important in floral evolution, however, most of the studies on pollinator-mediated selection on floral traits do not consider the role of interspecific interactions (Andersson and Widén 1993, Alexandersson and Johnson

2002, Schueller 2007, but see Rodríguez-Gironés and Santamaría 2004, 2005). Although our study was at a local scale, we have shown that foraging behavior and pollinator choices change with the floral context. The role that pollinators play as selective agents may be context-dependent on the composition of the pollinator community (Thompson 1999, Fenster and Dudash 2001), but also on the composition of the plant community. This implies that the set of multiple interactions among plants and pollinators in which a particular species is embedded in a particular community must be taken into consideration in studies of floral trait evolution (Memmott 1999, Rodríguez-Gironés and Santamaría 2005).

The design and correlative nature of our study have, however, some logical limitations. First, many pollinators can fly long distances during foraging bouts, and part of the unexplained variation in generalization levels and composition of visits could be due to the fact that some animals are more affected by conditions operating at a lager spatial scale than such used in this study. Studies on effects of the floral neighbourhood on pollinator visitation at different spatial scales could shed light on the scale at which foraging decisions relevant for the generalization of plant species take place. Second, the visitation patterns and frequency of one group of pollinators may be affected, as discussed above, by the presence and abundance of another group (Inouye 1978, Chittka and Waser 1997, Valido et al. 2002). Temporal variations in the composition of pollinator assemblage that are independent of variation in floral composition could also create variations in the competitive relationships among pollinators, and could potentially be hidden under the relationships found. Experimental studies manipulating both insect and plant densities would allow the differentiation between the independent effects of variations in insect and plant assemblages. Lastly, we have used pollinator groups instead of pollinator species (Waser et al. 1996). We used this pollinator characterization to avoid changing the densities and distributions of the animals when they are captured for identification, but also because we believe that such groups are relevant to understand the role that neighbors may have on the ecological and evolutionary generalization of plant species, since the insects within the same group were those observed behaving similarly in the flowers in our communities (Fenster et al. 2004). However, our results could change if pollinator species instead of pollinator groups were used. In such a case, we could expect even greater effects of the neighbourhood on the generalization level and the composition of visits to plant species, because more specific behaviors are likely when species instead of groups are considered.

A merging of the disciplines of foraging theory and pollination ecology is required to understand plant–pollinator interactions at the community level. Although this merging has already begun (Chittka and Thomson 2001; empirical studies: Kunin 1993, Aldridge and Campbell 2007, Hersch and Roy 2007; theoretical models: Kunin and Iwasa 1996, Rodríguez-Gironés and Santamaria 2004), it is still far from complete. Linking pollinator behavior under contrasting contexts to phenotypic selection and pollination success would be desirable in future studies of plant–pollinator interactions. Future studies on ecological

generalization of plant species may also benefit from focusing on how the different components in the plant–pollinator network affect the generalization level of individual species, and to what extent floral or other plant traits are limiting such variation.

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