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## Floral neighbourhood effects on pollination success in red clover are scale-dependent

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### Summary

1. Plant-pollinator interactions are highly important because of its direct link to plant fitness and because such interactions involve species at different trophic levels. Our understanding of competitive and facilitative interactions among plants for pollination is of large importance to govern conservation of species and management of crop production. Still we know little about the scale dependency of plant-plant interactions for pollinator visitation which is central to both basic and applied ecology.

2. Here, I tested whether plant-plant interactions for bumblebee visitation and subsequent reproduction were scale-dependent by studying the ecologically and economically important red clover (*Trifolium pratense*) and its floral neighbourhood. I expected that high floral densities at small scale could trigger facilitative interactions due to concentration effects of pollinators. This was expected to change into competitive interactions when floral densities became higher at coarser scales because of dilution effects. I also expected that increased bumblebee visitation would increase fruit production in red clover.

3. The interaction for pollination success in red clover appeared to be scale-dependent in the landscape under study. At plot scale, the bumblebee visitation rate to red clover inflorescences increased with both intra- and interspecific floral density, indicating facilitative interaction for pollinator visitation among red clover flowers and its nearest floral neighbourhood. Increased visitation of bumblebees led to subsequent increased fruit set, but there was a saturating effect as fruit set did not increase when visitation rates exceeded a certain level. As the floral neighbourhood became denser at a coarser scale, the interactions for pollinator visitation changed towards competition.

4. This study shows that key ecological processes such as plant-pollinator interactions may indeed be scale-dependent and that the relative importance of competition and facilitation among plants for attracting pollinators may change with scale. The density of the floral neighbourhood of a focal species (e.g. key-, rare-, crop species) may thus be of large importance for its pollination and fruit production. My findings suggest that increasing floral densities at fine scales may have facilitative effects on pollinator visitation to red clover, whereas pollinators may be drawn away when floral resources become denser at coarser scale.

**Key-words:** bumblebees, crop, fruit set, landscape, magnet species, pollen limitation, pollination, reproduction, *Trifolium pratense*, visitation rate

### Introduction

Currently, there is large emphasis on the pollination of crop species and the importance of wild pollinators for such pollination service (Garibaldi *et al.* 2013). It has become clear that the surrounding landscape is of huge importance to the diversity and abundance of pollinators

which is positively affecting the pollination and production of crop species (Kennedy *et al.* 2013). Ever since Darwin proposed 'the struggle for existence' as one of the leading principles of natural selection and evolution (Darwin 1859), many ecologists have mainly emphasized the role of competition in ecological interactions (Callaway & Walker 1997; Bruno, Stachowicz & Bertness 2003). Interactions for pollination are of special interest in ecology because it has such direct link to plant fitness through reproduction

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and because interactions involve species both within and among trophic levels (Feinsinger 1987; Palmer, Stanton & Young 2003). Understanding both competitive and facilitative interactions for pollinator visitation is of large importance to govern conservation of species and management of entomophilous crop production (e.g. Ghazoul 2006), but the current studies seldom discuss their finding within the context of plant–plant interactions.

In pollination studies, both facilitation and competition appear to occur relatively frequent (Waser 1983; Bell, Karzon & Mitchell 2005; Ghazoul 2006). Several mechanisms that could explain the direction of interactions for pollination has been suggested. Pollinators generally act as optimal foragers and prefer to visit patches with high floral densities showing a type of concentration effect (Thomson 1981; Hambäck & Englund 2005; Hegland & Boeke 2006), but may visit proportionally fewer flowers when patch size increases because of dilution effects (Goulson 2000a; see also Veddeler, Klein & Tschardt 2006; Dauber *et al.* 2010; Nielsen *et al.* 2012). Such optimal foraging behaviour is likely to have consequences to the plant–plant interactions for pollinator visitation and likely to be a function of the density of floral resources (Kunin 1993; Hegland, Grytnes & Totland 2009). It has been suggested that at relatively low-to-intermediate floral densities facilitation among plants may be most common, whereas competition prevails when floral densities become relatively high (Rathcke 1983; Feinsinger 1987) which may derive from the mentioned concentration and dilution effects.

Flowers that are located in patches with high floral densities, or together with pollinator-attractive plant species, may experience increased visitation when pollinator behavioural responses to floral densities are larger than expected from a linear relationship between floral density and pollinator visitation. A few studies have evaluated the relative importance of competition and facilitation for pollinator visitation within the same study community and found that facilitation slightly prevails above competition (Moragues & Traveset 2005; Hegland, Grytnes & Totland 2009; Hegland & Totland 2012). Whether such increased visitation results in subsequent facilitated reproduction depends on plant characteristics such as degree of out-cross-dependent seed set (Fishman & Wyatt 1999; Hegland & Totland 2012) and pollen limitation (Hegland & Totland 2008, 2012).

Coflowering neighbours at coarser scales have the potential to compete and draw pollinators away from focal plants as shown, for example, in some alien–native plant interactions (Chittka & Schürkens 2001; Bjerknes *et al.* 2007). The interaction among flowering individuals, both at intra and interspecific level, may depend on the density of the floral neighbourhood and as floral densities may vary within habitats or landscapes such interactions may be scale-dependent. A few studies have evaluated the effect of intraspecific floral densities on patch visitation of trophic mobile resource agents such as pollinators at various scales (Veddeler, Klein & Tschardt 2006; Dauber *et al.*

2010; Nielsen *et al.* 2012). The scale dependency of pollinator assemblages and crop production has received considerable more attention. It has, for example, been showed that increased distance to forest or semi-natural patches decrease the pollinator activity and the subsequent production of crops (Klein *et al.* 2007; Ricketts *et al.* 2008), showing that pollination interactions are highly context-dependent (Diekötter *et al.* 2007). A recent study showed that *Trifolium pratense* in urban environment competed for visitation of bees with coflowering neighbours, but that the competitive interaction was context-dependent and modified by the amount of green area available (Hennig & Ghazoul 2011) which may indicate interspecific dilution or concentration effects.

Here, I test whether plant–plant interactions for bumblebee visitation and subsequent reproduction may be scale-dependent, that is, whether the balance between competition and facilitation changes with the scale whereon floral resources are quantified. I tested this by studying the bumblebee visitation to an ecological and economical important and highly pollinator-dependent plant species, red clover (*T. pratense*) in relation to its floral neighbourhood. Specifically, the hypotheses was explored as to whether H1) increased floral densities at small scale trigger facilitative interactions, whereas increased floral densities at coarser scales result in competitive interactions for bumblebees; and H2) increased bumblebee visitation increase fruit production of red clover.

## Methods

### STUDY AREA AND SITES

The study was conducted in the landscape around the village Kaupanger (61.18°N, 7.25°E), located by a bay of the Sognefjord in western Norway in 2006. The landscape contains of a diverse collection of habitats, but is dominated by meadows surrounded by pine forest in a hilly landscape. The climate of the study landscape is temperate and relatively warm for this latitude, and the closest climate station (Lærdal; ca. 15 km away) had a mean July temperature of 17.7 °C in 2006 (www.eklima.no). 12 study sites were established in semi-natural grasslands, mainly edge vegetation of meadows, where there was no disturbance of mowing, grazing or trampling of people or cattle during the study period. All sites faced southwards and were in open treeless habitats with little shading and are on 5–130 m altitude. The maximum distance between sites was 4 km and the closest were ca. 100 m apart. The differences between sites should likely not be due to differences in the composition of the bumblebee community as most species can cover such distances.

### STUDY SPECIES

*Trifolium pratense* (red clover) was the focal species in this study. It is known as a widespread species occurring throughout the world, also as an important crop species, that is attractive to pollinators (Pywell *et al.* 2005). Around 50–200 nectar-rich flowers are situated in each inflorescence which is mainly visited by long-tongued insects (Free 1993). Red clover is reckoned as self-sterile, and outcross pollination is required for successful seed set (Proctor, Yeo & Lack 1996). Each fruit, that is, pod, can produce one seed,

and seed set under natural conditions varies from 34 to 66.5%, or from 37 to 107 seeds per head (see Free 1993 for references). Earlier studies in the region (e.g. Hegland *et al.* 2010) showed that there is a wide array of different pollinators visiting the flowers of *T. pratense*, but that long-tongued bumblebees such as *Bombus pratorum* and *B. hortorum* are dominating.

## POLLINATOR OBSERVATIONS

Within each site, we established one circular observation plot of 2.5 m radius (19.6 m<sup>2</sup>). The plot was deliberately selected to contain at least 30 flowers of red clover and minimum one other species of Fabaceae at the beginning of the study, the 30th of June. Within these plots, we observed visitation of bumblebees, *Bombus* spp., to flowers of red clover and co-occurring flowering species. Pollinator observations were performed in 30-min period at 5 days at each site between the 30th of June and the 19th of July. No observations were made during periods of rainfall or directly thereafter. Two observers simultaneously observed the plot and recorded the number of visits of bumblebees to inflorescences of all plant species. The pollinator visitation rate was defined as the number of bumblebee visits to inflorescences of red clover divided by the number of inflorescences. The species name of each bumblebee entering the plot was recorded, except for non-social cuckoo bumblebees that were grouped. All people involved in pollinator sampling were trained (>2 field seasons) in observing pollinator visitation and determining bumblebee species at sight.

After each observation period, we also surveyed the bumblebee fauna on the site scale, to enable analyses of the importance of bumblebee density at a scale larger than the plot size (see data analysis for details). Two 50 m transects were placed in south–north and east–west direction, respectively, each through the centre of the observation plot. We counted the number of each bumblebee species observed by walking these transects in slow pace (time use was recorded and included in the analysis).

## FLORAL DENSITY AND DIVERSITY

We counted the number of inflorescences of all flowering plant species in the focal 2.5-m-radius plot. To account for the spatial dependency in plant–plant interactions for bumblebee visitation, we also surveyed the floral abundance on two larger scales. First, we placed four 25-m lines from the centre of the observation plot in each main compass direction and marked the 10 and 25 m distance. Between the plot edge and the 10 m distance, we counted the number of flowers and inflorescences of plant species in three randomly placed 1 × 1 m plots in each of the four sections made by the lines, a total of 12 plots on this ‘intermediate’ scale. We repeated the procedure between the 10 and 25 m border by counting inflorescences in five plots in each subsection, totally 20 plots on this ‘site’ scale. The measurements of flower abundance on the 10- and 25-m-radius scales were performed thrice, in the beginning, the middle and the end of the study period. The scales were chosen to cover the variation in sizes of habitats inhabited by red clover in the studied landscape. Also, the main pollinators, bumblebees, are likely able to choose among patches of various foraging quality at these scales (e.g. Goulson 2000a).

Intraspecific floral densities were defined as the mean number of red clover inflorescences at each spatial scale. The combined intra- and interspecific floral density was defined as the mean number of purple inflorescences, including red clover, because interactions for pollinators appear to be strongest among flowers of similar colours (Hegland, Grytnes & Totland 2009; Hegland & Totland 2012). I also performed separate exploratory analyses on floral densities of Fabaceae, all flowering species (both with and without red clover floral densities included) and the most common

co-occurring plant species (*Trifolium repens*, *Vicia cracca*, *Lotus corniculatus*), sharing bumblebee pollinators with red clover in the study landscape.

## REPRODUCTIVE SUCCESS

Ten infructescences were collected in paper bags from each site within the focal plots on September 3, ca. 7 weeks after pollinator observations had ended, to address the variation in reproductive success in red clover across sites. The fruits were dried in air temperature for ca. 1 year before fruits with seeds were counted and all seeds weighed. Reproductive success was measured as the mean of number of fruits multiplied with the total seed weight per infructescence per site and is called female fitness.

To control for mother plant or site resource effects, I measured the height of the plants from which infructescences were collected. Although red clover is known to be almost exclusively dependent on pollinators to set seed, we evaluated whether this was also true for our study population. Five inflorescences were bagged at four different sites before flowers had opened. Infructescences were collected from bagged plants on September 3. The count showed that there was a small fraction of seeds produced in some of the individuals, but the mean fruit set across the 20 bagged infructescences was only 3%.

## DATA ANALYSIS

To investigate how bumblebees responded to plot scale variables, I first ran exploratory correlation analysis among bumblebee variables (no. visits to plot, no. individuals visiting plot and bumblebee richness) and floral density variables (red clover, purple-coloured species, total flower density) using Pearson correlation. Following this exploratory analyses, the H1 hypothesis was specifically tested, that is, whether the directions of plant–plant interactions for bumblebee visitation was scale-dependent, by constructing multiple regression models to analyse the relative importance of the three study scales. The mean visitation rate to red clover inflorescences per focal plot (mean visits/inflorescence/30 min; measured across five sampling periods) was used as response variable, and the mean floral densities for each scale (mean no. inflorescences/plot; measured three times during study period) was used as predictor. Means were used as data were not collected with the same temporal resolution. All variables were log-transformed to meet assumptions of homogeneity of variance and normality of residuals in regression analysis. Analyses were executed separately for intraspecific and purple floral densities because these variables were not independent (see also Table 1). I started with full models and selected the best model by removing the predictor variables (floral density at the three different spatial scales) with lowest *P*-value until all variables retained in the model had *P* < 0.1. As predictor variables may be correlated (Table 1), potential multicollinearity was addressed by inspecting the variance inflation factor (VIF). The multiple regressions were performed in SPSS Statistics 20 (IBM 2011).

To test whether there was a relationship between bumblebee visitation rate and female fitness (H2-hypothesis), I first tested whether female fitness was correlated with resource availability represented by densities of bumblebees in transect walks (i.e. the sexual resource) and individual plant height (as proxy for environmental resource availability). Secondly, I tested the specific expectation that reproduction could be affected by the interactions for bumblebee visitation by relating mean bumblebee visitation rates with mean fruit set per site. The test was accomplished by comparing linear and quadratic regressions for log-transformed variables based on AIC-values using the curve estimation procedure in SPSS.

**Table 1.** Pearson correlation coefficients for floral densities across scales

Variables	Red clover (2.5 m radius)	Red clover (10 m radius)	Red clover (25 m radius)	Purple flower density (5 m radius)	Purple flower density (10 m radius)	Purple flower density (25 m radius)
Red clover (2.5 m radius)	1					
Red clover (10 m radius)	0.63**	1				
Red clover (25 m radius)	−0.25	−0.26	1			
Purple flower density (2.5 m radius)	0.98	0.64**	−0.22	1		
Purple flower density (10 m radius)	0.13	0.60*	−0.04	0.21	1	
Purple flower density (25 m radius)	−0.32	−0.07	0.36	−0.32	0.60*	1

\* $P < 0.05$ .\*\* $P < 0.01$ .**Table 2.** Multiple regression analysis showing the effect of floral densities at different spatial scales and at the bumblebee visitation rates to red clover

Model type	Variables in selected model	Predictor			Model	
		$\beta$	$P$	VIF	d.f.	$R^2$
Intraspecific floral density	Red clover (plot scale)	0.91	0.008	1.54	2.9	0.57*
	Red clover (intermediate scale)	−0.70	0.029	1.54		
Interspecific floral density	Purple flower density (plot scale)	1.04	0.003	1.57	3.8	0.71*
	Purple flower density (intermediate scale)	−0.79	0.140	1.73		
	Purple flower density (site scale)	0.43	0.095	1.40		

\* $P < 0.05$ .

## Results

### CHARACTERISTICS OF BUMBLEBEE AND FLORAL COMMUNITY IN KAUPANGER

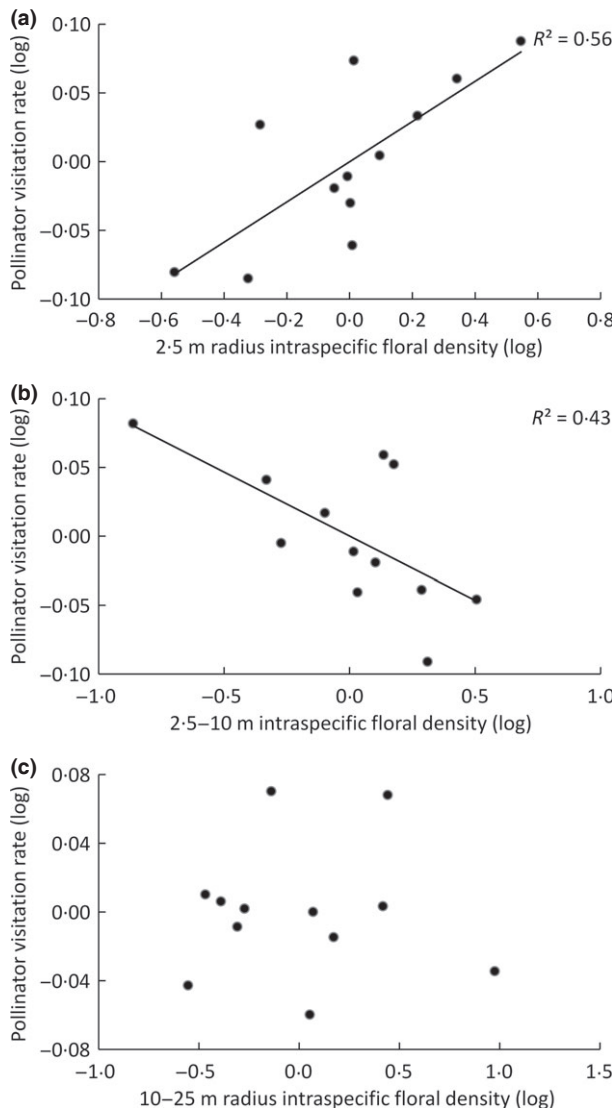
Most characteristics of bumblebee abundance and floral community composition varied across sites. We recorded in total 1045 bumblebees individuals entering plots, and the species were in order of abundance: *Bombus lucorum* (45%), *B. pascuorum* (37%), *B. hortorum* (7%), *B. lapidarius* (3%), *B. pratorum* (3%), *B. hypnorum* (2%) and cuckoo bumblebees (4%). The mean number of bumblebee individuals entering the plots during 30-min observation period was 17.4 (range 1–79), making at average 133.4 (range 4–600) visits per individual wherefrom averagely 67.8 (range 0–541) was to red clover inflorescences. The mean red clover floral density in 2.5-m-radius plots was 113.6 (range 5–659), whereas the density of purple inflorescences was 134.4 (range 5–683). The total number of bumblebee visits to focal plots correlated with floral characteristics such as the floral density of red clover ( $r = 0.81$ ,  $N = 12$ ,  $P = 0.001$ ) and purple-coloured species ( $r = 0.82$ ,  $N = 12$ ,  $P = 0.001$ ), as well as total floral densities ( $r = 0.78$ ,  $N = 12$ ,  $P = 0.003$ ) of the whole plot. Bumblebee visitation to focal plot appeared not affected by the flowering plant species richness ( $r = 0.11$ ,  $N = 12$ ,

$P = 0.73$ ) in the plot. As the number of bumblebee individuals visiting plots were closely correlated with the number of visits ( $r = 0.85$ ,  $N = 12$ ,  $P < 0.001$ ), the patterns of correlation with floral community characteristics were identical to bumblebee abundance for this variable. Bumblebee richness was not correlated with the floral characteristics (densities and diversity) at plot scale (all  $P$ -values  $> 0.14$ ).

### ARE INTERACTIONS FOR BUMBLEBEE VISITATION TO RED CLOVER SCALE-DEPENDENT (H1)?

Bumblebee visitation rate to red clover was positively affected by floral density of red clover at a 2.5-m-radius scale (plot scale: Table 2; Fig. 1a), negatively affected by floral density of red clover at 10 m-radius scale (intermediate scale: Table 2; Fig. 1b) and not affected at 25-m-radius scale (site scale; excluded from final model). There was a positive relationship between purple floral density and bumblebee visitation rate at the 2.5-m-radius scale (plot scale: Table 2; Fig. 2a), a negative relationship at the 10-m-radius scale (intermediate scale: Table 2; Fig. 2b) and a marginal positive relationship at the 25-m-radius scale (site scale: Table 2; Fig. 2c). Using the other interspecific variables, densities of Fabaceae inflorescences, *Trifolium repens*, *Vicia cracca*, *Lotus corniculatus* individually or



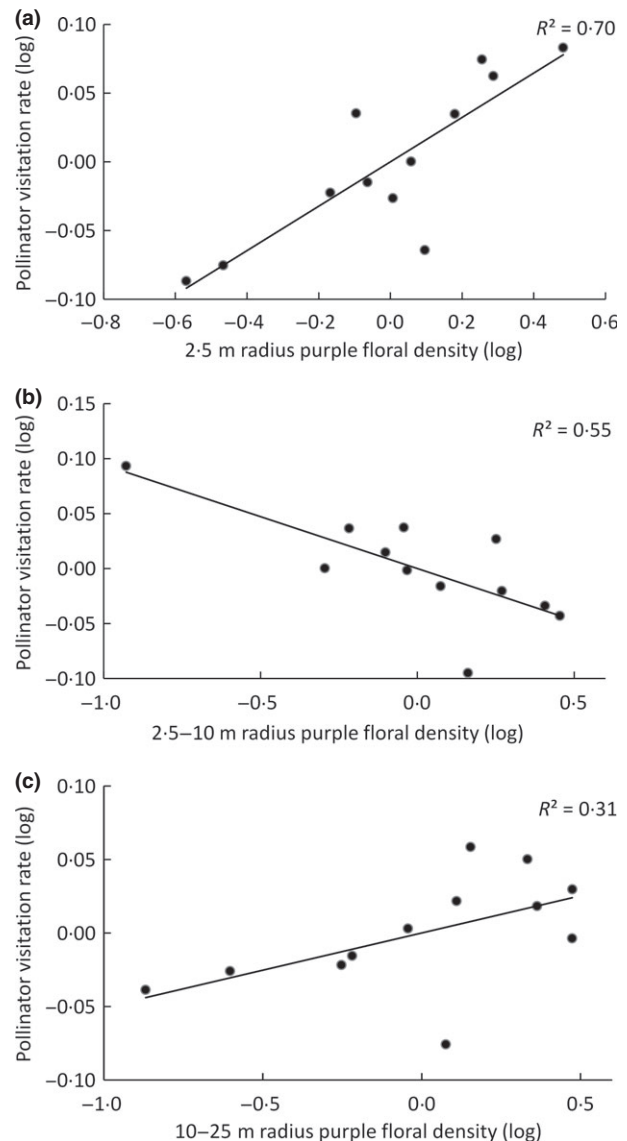


**Fig. 1.** Partial regression plots based on the residuals from the multiple regression model for relationships between the intraspecific floral density at (a) 2.5-m-radius (plot) scale; (b) 2.5- to 10-m-radius (intermediate) scale; and (c) 10- to 25-m-radius (site) scale and the pollinator visitation rates of red clover in the Kaupanger landscape, western Norway.

combined did not result in any significant regression models.

#### DOES THE VARIATION IN BUMBLEBEE VISITATION CORRESPOND TO VARIATION IN REPRODUCTION (H2)?

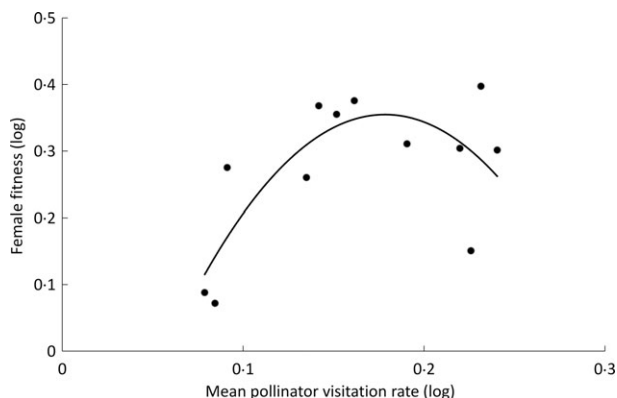
Mean viable fruit per infructescence was 25.6 (range 0 to 84), the proportion of viable fruits was 35% (0–92.5%), and the average seed weight per infructescence was 0.034 g (range 0.0005–0.127 g). The variation in resource availability among study sites appeared not to affect the female fitness (no. seeds  $\times$  total seed weight per infructescence) in red clover as neither plant height ( $r = 0.14$ ,  $N = 12$ ,  $P = 0.67$ ) nor the site density of bumblebees as measured



**Fig. 2.** Partial regression plots based on residuals from the multiple regression model for relationships between the combined intraspecific and interspecific floral density as described by purple flowers at (a) 2.5-m-radius (plot) scale, (b) 2.5- to 10-m-radius (intermediate) scale and (c) 10- to 25-m-radius (site) scale, and pollinator visitation rates of red clover in the Kaupanger landscape, western Norway.

through transect walks ( $r = -0.21$ ,  $N = 12$ ,  $P = 0.50$ ) correlated with female fitness.

Testing H2 specifically, I found that the variation in bumblebee visitation rates could explain female fitness in red clover, but not in a linear way as the best model contained visitation rate as a second-order term (Fig. 3,  $R^2 = 0.52$ , d.f. = 2 and 9,  $P = 0.035$ ,  $\beta_1 = 4.4$ ;  $\beta_2 = -3.9$ ). Visual inspection of the plot suggests that the reproductive success is limited only in sites with the low visitation frequency and that above a certain threshold, there appears to be no effect of visitation frequency on female fitness.



**Fig. 3.** The quadratic relationship between mean pollinator visitation rate to red clover and female fitness (no. seeds  $\times$  total seed weight per infructescence) in the Kaupanger landscape, western Norway.

## Discussion

The interaction for pollinator visitation in red clover appeared to be scale-dependent in the landscape under study. The results confirmed our H1-hypothesis and the expectations of visitation effects based on theory of optimal foraging pollinator behaviour in relation to floral resources (e.g. Thomson 1981; Goulson 2000a). I found that at plot scale, the pollinator visitation rate to red clover inflorescences increased with the intraspecific floral density and this strongly indicates facilitative interactions for pollinator visitation among red clover and its nearest floral neighbourhood. This positive interaction for pollinators may translate into increased reproductive success as there is an increased female fitness at sites going from low-to-intermediate pollinator visitation rates. Competitive interactions also play a significant role in this study system as pollinator visitation to red clover inflorescences decreases when floral density increases at the intermediate spatial scale. Facilitation changed to competition for bumblebee visitations when the floral neighbourhood became denser at coarser scales.

This study presents evidence that can hint further towards the mechanism behind the direction of plant–plant interactions for pollination. Floral nectar and pollen are the key resources for pollinators such as bumblebees and they therefore tend to optimize their foraging to areas with high densities of resource-rich flowers. This may have led to positive spillover effects for intra- and interspecific flowers in the immediate neighbourhood, that is, through concentration effects (e.g. Thomson 1981; Veddeler, Klein & Tschardtke 2006). However, when the density of interacting floral resources become relatively higher at coarser scales, the same optimized behaviour of pollinators lead to a decreased visitation in the focal flowers due to dilution effects (e.g. Veddeler, Klein & Tschardtke 2006). The larger effect (i.e. higher  $\beta$ -values) of the interspecific models relative to intraspecific models, and the non-significance of the other floral combinations, strengthens the idea that

pollinator behaviour is the key mechanism to explain such pollination interactions. Several studies have shown that pollinators such as bumblebees cannot easily discriminate among flowers that resemble each other in colour and/or morphology (Lavery 1994; Chittka, Gumbert & Kunze 1997; Goulson 2000b) and that this lack of colour discrimination may have effects on bumblebee selection of patches and subsequently plant–plant interactions for pollination and consequently reproduction (Hegland, Grytnes & Totland 2009; Hegland & Totland 2012).

The current results are also of high importance to species conservation and crop production. One of the main effects of landscape disturbance and fragmentation on pollinator assemblages is the reduction in flowering density (Hadley & Betts 2012). Our results suggest that high floral densities within a relative small patch may have facilitative effects for the species present. Facilitation may extend the persistence of rare plants in degraded landscapes by acting against Allee effects and provide increased opportunities for population recovery (Ghazoul 2006; Dauber *et al.* 2010). The change in direction of interactions across multiple spatial scales may help us to optimize pollination of crop plants. First, the magnitude of fruit set in red clover populations corresponded to the variation in bumblebee visitation rates among sites highlighting the importance of pollinators to fruit yield of crop species known from other studies (Klein, Steffan-Dewenter & Tschardtke 2003; Ricketts *et al.* 2004; Winfree *et al.* 2007). This positive relationship is, however, not linear and only partly verified our H2-hypothesis. It appeared that individual inflorescences may become saturated and receive sufficient visitation for effective fruit set above a certain visitation level. The saturating female fitness at sites with high levels of visitation may come from increased biparental inbreeding and reduced quality of pollen known to affect seed set (Ramsey & Vaughton 2000; Finer & Morgan 2003). Secondly, it shows that plant–plant interactions for pollinator service may be of high importance to understand patterns of pollinator visitation to crop species. Most crop–pollinator studies focus mainly on the importance of distance to, or proportion of, natural and semi-natural habitats in strongly fragmented landscapes as driver for the pollination of the investigated crop species (Klein *et al.* 2007). In fact, these studies seldom mention that the floral neighbourhood at various scales, and competitive and facilitative interactions among co-occurring flowers are crucial factors in understanding why the crop production often is found to be landscape or context-dependent. Veddeler, Klein & Tschardtke (2006), however, found that floral density of coffee from branch via shrub and field scales affected bee visitation such that higher floral densities at branch and shrub scale resulted in higher visitation (i.e. concentration effects), whereas visitation decreased with increasing floral densities at field scale (i.e. dilution effects). On the other hand, studies of context-dependent reproduction in native species are often specifically focused on the importance of floral neighbourhood for pollination and plant–plant interactions (Campbell 1985; Campbell & Mot-

ten 1985; Feinsinger & Tiebout 1991; Caruso 1999; Ghazoul 2006; Hegland & Totland 2012), but are often performed on smaller scales which do not give the coarser scale information that the crop studies do (but see Dauber *et al.* 2010; Nielsen *et al.* 2012 for some intraspecific examples).

This study adds insight into the scale dependency of facilitation and competition for pollinator visitation among plants. The positive effect of floral density at plot scale to bumblebee visitation of red clover, combined with negative effect of increased floral density at intermediate scale and marginal positive effect on site scale, highlights that the scale dependency reported for pollinator behaviour (Steffan-Dewenter, Munzenberg & Tschardt 2001; Steffan-Dewenter *et al.* 2002; Veddeler, Klein & Tschardt 2006) may also be directly linked to the finer scale floral neighbourhood and its subsequent effects on plant female fitness.

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