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How does plant richness affect pollinator richness and temporal stability of flower visits?

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Pollinators play a key role in the reproduction of most plant species, and pollinator and plant diversity are often related. We studied an experimental gradient of plant species richness for a better understanding of plant–pollinator community interactions and their temporal variability, because in non-experimental field surveys plant richness is often confounded with gradients in management, soil fertility, and community composition. We observed pollinator species richness and frequency of visits six times in 73 plots over two years, and used advanced statistical analysis to account for the high number of zeroes that often occur in count data of rare species. The frequency of pollinator visits increased linearly with both the blossom cover and the number of flowering plant species, which was closely related to the total number of plant species, whereas the number of pollinator species followed a saturation curve. The presence of particularly attractive plant species was only important for the frequency of flower visits, but not to the richness of pollinators. Plant species richness, blossom cover, and the presence of attractive plant species enhanced the temporal stability in the frequency of pollinator visits. In conclusion, grasslands with high plant diversity enhance and stabilize frequent and diverse flower visitations, which should sustain effective pollination and plant reproduction.

Pollinators provide a major ecosystem service through their key role in the reproduction of most plant species (Burd 1994, Fontaine et al. 2006, Klein et al. 2007). Because a loss in plant–pollinator interactions can lead to parallel declines of plant species and their associated pollinators (Biesmeijer et al. 2006), understanding plant–pollinator community interactions is critical for the conservation of biodiversity.

Enhanced plant species richness has been hypothesized to promote richness of pollinators because of plant species-specific pollinator preferences and a better pollen and nectar resource availability over space and time (Linsley 1958, Eickwort and Ginsberg 1980, Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003, Hegland and Totland 2005, Fontaine et al. 2006, Ghazoul 2006, Blüthgen et al. 2007, Holzschuh et al. 2007, Kwaiser and Hendrix 2008). Increases in plant diversity have been shown to reduce the variability of pollinator population densities over time (Ghazoul 2006), indicating a higher stability of the pollinator community, thereby reducing extinction risk. Enhanced pollinator richness should also increase functional redundancy, so that potential extinctions may be compensated by remaining species (Yachi and Loreau 1999, Zamora 2000). In addition to species richness, floral abundance is another important variable structuring pollinator communities (Potts et al. 2003, 2006). Greater floral abundance means higher resource availability for pollinators, which may also contribute to temporal variability (we will refer in the following to dynamic stability as defined by McCann 2000).

In published studies on the impact of plant species richness on pollinator communities, differences in plant species richness were mostly the result of differences in intensity of land use, making it difficult to attribute changes in plant–pollinator interactions directly to differences in plant diversity. Intensive land management often reduces plant species richness via changes in plant community composition, while fertilization and irrigation may increase flower size, leading to a higher nectar and pollen availability (Lau and Stephenson 1994, Spaethe et al. 2001, Thompson 2001, Cartar 2004), which affects pollinators (Cartar 2004). Hence, disentangling the effects of plant species richness, plant community composition, and other habitat variables on the structure of pollinator communities is still a major research objective.

We studied the relationship between plant and pollinator richness, as well as the frequency and stability of pollinator visits, using a large-scale experimental manipulation of plant species richness. Plant species composition was randomized in sown experimental plots to avoid confounding effects of community structure (e.g. species identity). This small-scale mosaic in plant species richness allowed pollinator species to select preferred plots within their foraging ranges (Steffan-Dewenter et al. 2002, Westphal et al. 2003, Greenleaf et al. 2007). The pollinator communities included two social pollinator groups, honey bees and bumble bees, which are polyphagous and have large foraging ranges (Eickwort and Ginsberg 1980, Westphal et al. 2006, Greenleaf et al. 2007). We also observed solitary bees (non-eusocial bees), many of which are specialized with respect to flower use (Eickwort and Ginsberg 1980), and hover flies, some of which are specialized and others generalized (Haslett 1989).

The general aim of our study was to analyze the influence of number of flowering plant species, which was closely related to overall plant species richness, and of blossom cover, on pollinator species richness and frequency of pollinator visits. In particular, we explored:

1. how the number of flowering plant species, blossom cover, and plant species identity are related to pollinator species richness and the frequency of pollinator visits;
2. the importance of the number of flowering plant species and blossom cover for different pollinator guilds such as bumble bees, honey bees, solitary bees, and hover flies;
3. the relationship between the number of flowering plant species and the dynamic stability of pollinator flower visits.

Material and methods

Study area and experimental design

The Jena experiment is located to the north of Jena, Germany, on the floodplain of the river Saale (50°55′N, 11°35′E; 130 m a.s.l.) and was established in 2002. The site (ten hectares) was an arable field for the 40 years before the experiment started and thus was strongly fertilized to increase crop productivity, but no fertilizer was added during the experimental period. Plots were mowed every June and September, a management regime also used in meadows designed for intensive hay production. To maintain the sown species richness level we weeded all plots every April and July.

The main experiment comprises 82 plots, each of 400 m^2 area, with six levels of plant species richness (1, 2, 4, 8, 16 and 60 species). Species used in monocultures and mixtures were selected randomly from a species pool of 60 common grassland species (species list in Roscher et al. 2004 and Supplementary material Appendix 1 and 2). Monocultures, two-species mixtures, four-species mixtures and eight-species mixtures are represented with 16 replicates each, 16-species mixtures with 14 replicates and the 60-species mixtures with four replicates. The 20×20 m plots were grouped into four blocks (randomized complete block design) along abiotic gradients (mainly soil sand content, Roscher et al. 2004) reflecting distance to the river Saale, and diversity treatments were assigned equally within blocks. For our study we chose all plots ecept for nine that contained only grasses, i.e. 73 plots.

Pollinator observations

For observations of pollinators we used a quadrat of 80×80 cm within each 20×20 m plot. In 2005 we observed on 24–25 May and 15–16 June, before the first mowing in late June, and again on 18–19 August, after mowing. In 2006 we observed on 6–9 June and 17–18 June, before the first mowing, and again on 1–5 August. This resulted in 438 observations (73 plots $\times$ 2 years $\times$ 3 periods per year). Observations were only conducted on sunny days (at least 18°C, to have similar insect activity) with no or little wind ($< 2\ \mathrm{m\ s^{-1}}$) between 09:00 and 17:00 h. Observations within a block were carried out within two days, so weather conditions would be similar within blocks. The sequence of plot observations was not correlated with plant richness level within plots.

We observed pollinating insects for 36 min in each plot (2 years $\times$ 3 periods per year $\times$ 6 min). We identified pollinators directly to genus or morphospecies and species level in the field. We tallied 'species numbers' and 'frequencies of pollinator visits' and also the plant species visited by each pollinator individual. We define the frequency of pollinator visits as the number of flower visits per plot during the observation period. Pollinators were grouped into honey bees, solitary bees, bumble bees and hover flies. We define solitary bees as all non eu-social bees. After each observation period we collected all unknown species for further identification in the laboratory, and were thus able to identify all Hymenoptera and hover flies to species level. We morphotyped and pooled the remaining pollinators of the insect orders Lepidoptera, Coleoptera, and Diptera (except the hover flies) into one group ('remaining pollinators') for analyses.

After each observation period we tallied the 'number of flowering plant species' within the 80×80 cm observation area and estimated the 'blossom cover' (%) of each flowering plant species as a percentage of the total area.

Statistical analyses

We analyzed whether pollinator species richness data were close to species saturation using EstimateS software ver. 8 (Colwell 2006). All plots of one plant species richness level were summarized and the abundance-based coverage estimator was calculated with 500 randomizations to calculate percentage species saturation.

Our observation data included an excess of zeroes (no pollinators observed), which is usual for pollinator observation data with short-sampling intervals. Therefore standard parametric statistical models were not appropriate. We instead applied a so-called zero-inflated Poisson model (Lambert 1992, Cunningham and Lindenmayer 2005) to describe pollinator species richness and the frequency of pollinator visits. In this approach the distribution of the response variable is modelled as a mixture of a Bernoulli distribution, which accounts for the proportion of extra zeroes, and a negative binomial distribution whose expectation is modelled as a function of covariates.

Preliminary studies in 2004 showed a high attractiveness of the three legume species *Onobrychis viciifolia*, *Medicago varia* and *Lotus corniculatus* and the herbaceous species *Knautia arvensis*, *Leucanthemum vulgare* and *Crepis biennis.* We summarized these six species in a variable 'presence of attractive plants'.

We fitted a series of hierarchical models including the block, the number of plant or flowering plant species per plot, the blossom cover (%), and the presence of attractive plants as independent variables. Response variables were pollinator species richness and the frequency of all pollinator visits, as well as species richness and frequency of visits of bumble bees, solitary bees, honey bees and hover flies. As further dependent variables we chose the number of pollinator species and the frequency of pollinator visits per resource unit, which was an area of flowers covering 1 m^2, calculated from the estimates of blossom cover we had for our observation plots (80×80 cm).

Starting from the constant null model we added covariables sequentially. The statistical significance of model improvement was assessed using likelihood ratio tests. Variables without significant influence were omitted in subsequent models. Because we were particularly interested in the shape of positive relationships. For the effects of number of flowering species and blossom cover, we contrasted a linear model with a saturation model based on the Michaelis–Menten function $f(x) = b1 \times x/(b2 + x)$. These competing models could not be included in the sequence of hierarchical models and were therefore directly compared based on values of Akaike's information criterion (AIC), with smaller AIC values providing a more adequate description of the observed data. The model comparison was performed using the packages 'gnlm' and 'rmutil' of the statistical software R (R Development Core Team, <http://www.R-project.org.>).

For further analyses we used software Statistica ver. 6. Correlations between explanatory variables were analyzed using Spearman's rank correlations. The coefficient of variance (CV) in the frequency of pollinator visits was calculated as standard deviation/mean × 100. We analyzed this inverse measure of temporal stability (between six sampling days within two consecutive seasons) in linear regressions with the number of flowering plants, the number of pollinator species, the blossom cover and the presence of attractive plant species as explanatory variables. In the text, we give arithmetic means ± 1 SD.

Results

Vegetation

The number of sown plant species was positively related to the final number of flowering plant species (Table 1; $n = 73$, Spearman's $R = 0.55$, $p < 0.001$), and to percent blossom cover ($n = 73$, Spearman's $R = 0.45$, $p = 0.001$), which was higher in plots with attractive plant species ($n = 73$, Spearman's $R = 0.36$, $p = 0.002$).

Since the number of sown plant species was closely correlated to the final richness of flowering species, which is a major resource for pollinators, we used only the final richness in the following analyses. All analyses were also done with the number of sown plant species, resulting in the same patterns (data not shown).

Pollinator community

Altogether we counted 5722 flower visits during our 438 observation periods. Honey bees *Apis mellifera* were most abundant with 2824 visits (49.4%), followed by bumble bees (genus *Bombus*) with 1673 visits (29.2%), solitary bees with 233 visits (4.1%), and hover flies with 93 visits (1.6%). Altogether we observed 29 wild bee species from seven genera (Supplementary material Appendix 1). The most common genera in both years were bumble bees, followed by solitary bees in the genera *Lasioglossum* and *Andrena.* Additionally, we identified ten hover fly species from seven genera (Supplementary material Appendix 2). We did all analyzes with original species data, as the mean species saturation per plant-richness level was high (84.62 ± 10.7%).

Thirty-two of the 60 plant species of the experimental species pool (including sixteen grass species, which are not insect-pollinated), were visited by pollinators. *Onobrychis viciifolia* was the plant species with the highest pollinator-visitation rate (3430 visits), followed by *Knautia arvensis* (742 visits), and *Medicago varia* (552 visits). Twenty-two species had visitation rates below one percent of all visits, and the visitation rates of the remaining seven plant species ranged from one to six percent. Eleven plots were not visited by pollinators at all during our observations (Supplementary material Appendix 1, 2).

Effects of the plant community on pollinator species richness

The number of pollinator species was strongly positively affected by the number of flowering plant species and blossom cover (Table 2, Fig. 1a–b), but both relationships were nonlinear and saturating. The overall number of pollinator species increased rapidly from one to nine flowering plant species and from one to 15% blossom cover and reached a saturation point above these values. The numbers of bumble bee and solitary bee species increased linearly with the number of plant species but were saturated at approximately 17% blossom cover (Table 2). The number of hover fly species also increased with blossom cover up to a saturation point at around 15% blossom

Table 1. Overview of the different variables representing the vegetation across the plant species gradient of the Jena experiment. All values are means across 2005 and 2006 (±SD).

Sown plant species richness	Mean number of flowering plant species	Mean blossom cover (%)
Monocultures	1.0 ± 0.0	3.0 ± 3.4
2 species	1.6 ± 0.8	5.7 ± 4.9
4 species	2.1 ± 0.8	7.2 ± 8.7
8 species	3.8 ± 1.5	9.3 ± 9.1
16 species	6.8 ± 2.0	10.9 ± 7.3
60 species	12.5 ± 1.7	15.1 ± 4.6

Table 2. Model selection for pollinator species richness and the frequency of pollinator visits. Variables were added sequentially, and likelihood ratio test were used to assess statistical significance of each response variable compared to the model in the previous column or the one that contained the last significant variable. Explanatory variables were (1 identity of the experimental block, (2) number of flowering plant species per plot, (3) percent blossom cover of the observed plot, and (4) presence of attractive plant species. The table shows AIC values for models including different predictor variables. In case of a significant relationship to the response variable the shape of this relationship was analysed by a direct comparison of the AIC values of a linear and a saturating model based on the Michaelis–Menten model function. Bold font indicates significances. Minus signs indicate negative correlations, pluses positive ones. The second row shows the degrees of freedom (DF) for the null model and for each of the explanatory variables. * =p <0.05; ** =p <0.01; *** =p <0.001.

Explanatory variable response variable\	Null model	+block	+number of flowering plant species	+blossom cover/ plot (%)	+presence of attractive plant species
DF	70	3	Linear 1 Saturated 2	Linear 1 Saturated 2	1
No. of all pollinator species	393	397	379*** (+) **376*** (+)**	348*** (+) **317*** (+)**	318
No. of bumble bee species	212	218	**208** (+)** 212	194*** (+) **191*** (+)**	192
No. of solitary bee species	187	190	**181** (+)** 184* (+)	179* (+) **172*** (+)**	174
No. of hover fly species	126	131	126 128	125 **122* (+)**	124
Frequency of all pollinator visits	745	746	**734*** (+)** 745	**697*** (+)** 712*** (+)	**693* (+)**
Frequency of honey bee visits	549	551	**547* (+)** 548	**529*** (+)** 547	530
Frequency of bumble bee visits	468	468	**465* (+)** 468	**460** (+)** 469	460
Frequency of solitary bee visits	307	311	307 306	307 **304* (+)**	303
Frequency of hover fly visits	200	201	201 202	**192*** (+)** 197* (+)	192
No. of pollinator species m^{-2} flowers	849	851	**841** (−)**	**795*** (−)**	**788** (−)**
Frequency of pollinator visits m^{-2} flowers	1129	1135	1131	1128	1131

cover, but was not related to the number of flowering plant species. The number of pollinator species per resource unit (1 m^2 of flowers) declined with increasing number of flowering plant species (Table 2, Fig. 2) and with increasing availability of floral resources (blossom cover/plot, Table 2). Overall pollinator species richness and the number of pollinator species in the main pollinator groups were not related to the presence of attractive plant species. We did not find a block effect in any models using species richness of pollinators as the response variable (Table 2).

Effects of the plant community on the frequency of pollinator visits

The overall frequency of pollinator visits was positively and linearly correlated with the number of flowering plant species (Table 2, Fig. 1c). Plots with one flowering plant species experienced around twenty flower visits per plot, while we found as many as 200 flower visits in the plots containing twelve flowering plant species. Such a strong positive relationship was also found between blossom cover and the overall frequency of pollinator visits (Table 2, Fig. 1d). The presence of attractive plant species also exhibited a positive effect on the overall frequency of pollinator visits (Table 2). The number of flowering plant species and percent blossom cover also had strong positive effects, when only the frequencies of honey bees and bumble bees were considered (Table 2), whereas the visitation rate of solitary bees and hover flies was only influenced by increasing blossom cover. All variables that responded significantly to the frequency variables were linearly related and did not show any signs of saturation (Table 2).

We detected no correlations between the overall frequency of pollinator visits per resource unit and the explanatory variables of number of flowering plant species, percent blossom cover, or the presence of attractive plant species (Table 2). Block effect was not significant in any of the models analyzing the frequency of pollinator visits (Table 2).

Effects of plant species richness on the temporal variability of pollinator visits

Temporal variability in the frequency of pollinator visits across all six observational periods per plot declined with increasing number of flowering plant species (Fig. 3a; $F_{1,60} = 12.27$, $p < 0.001$), pollinator species richness (Fig. 3b; $F_{1,60} = 11.97$, $p < 0.001$), blossom cover ($F_{1,60} = 17.44$, $p < 0.001$), as well as in those plots where attractive plant species were present ($F_{1,60} = 7.39$, $p = 0.008$). Patterns were similar in each year for the number of flowering plant species (2005: $F_{1,58} = 15.41$, $p < 0.001$; 2006: $F_{1,46} = 4.89$, $p = 0.032$), for pollinator species richness (2005: $F_{1,58} = 32.78$, $p < 0.001$; 2006: $F_{1,46} = 46.89$, $p < 0.001$), for blossom cover (2005: $F_{1,58} = 12.10$, $p < 0.001$; 2006: $F_{1,46} = 11.61$, $p = 0.001$), and for the presence of attractive plant species (2005: $F_{1,58} = 4.16$, $p = 0.046$; 2006: $F_{1,46} = 5.87$, $p = 0.019$).

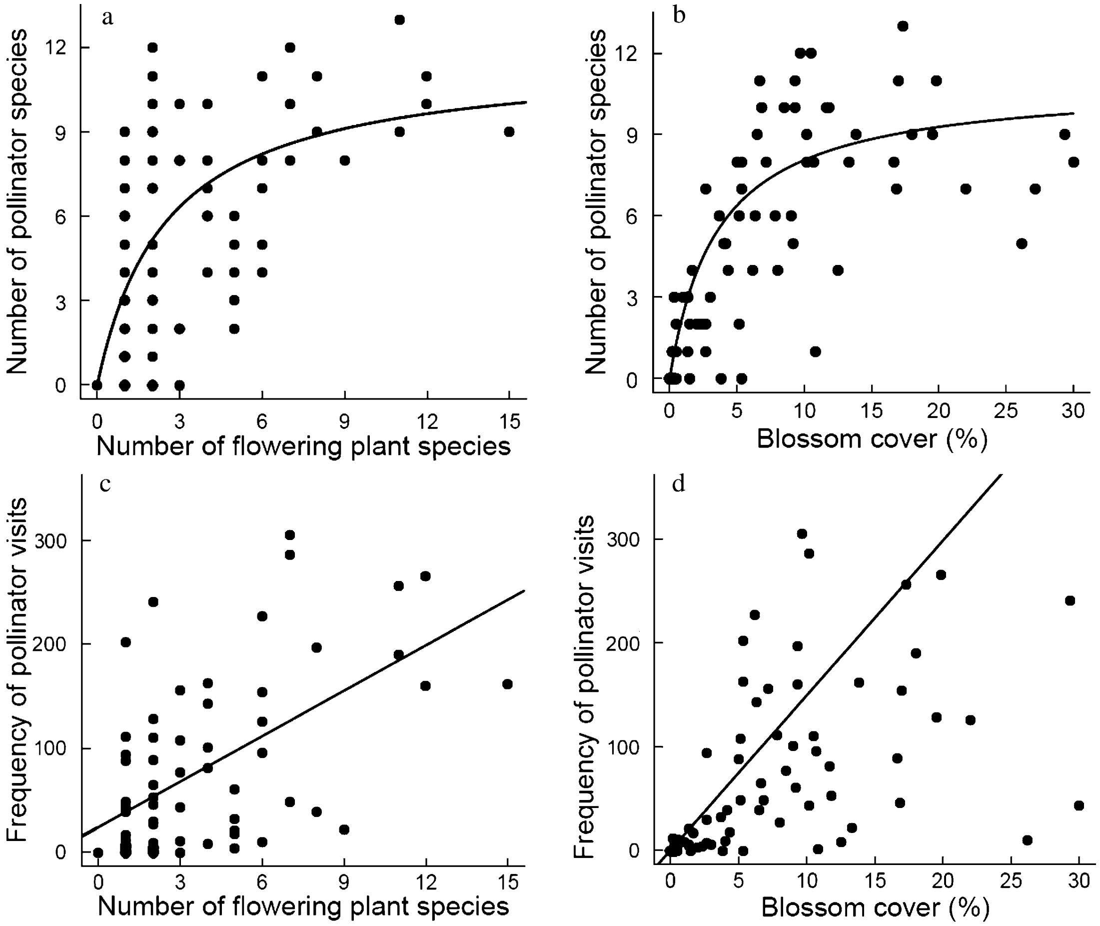

Figure 1. Effects of the number of flowering plant species and blossom cover (%) on the number of pollinator species (a and b) and the frequency of pollinator visits in 36 min of observation in 2005 and 2006 (c and d). Solid lines show predictions based on the saturated (a and b) and the linear (c and d) zero-inflated negative binomial model, respectively. For statistics see Table 2.

Discussion

The results of this experimental study show the great importance of the number of flowering plant species for high numbers of pollinator species and the frequency and stability of visits. Almost all of these positive relationships were found across different pollinator guilds (exceptions: species richness of hover flies and frequency of solitary bee visits), indicating the strength of the overall patterns.

The positive impact of the number of flowering plant species on pollinator species richness and overall frequency of visits may be explained by increasing floral resource heterogeneity (nectar and pollen), which increases attractiveness for many pollinator species seeking single and multiple resources (Tscharntke et al. 1998, Potts et al. 2003, Ghazoul 2006). In earlier studies of successional fallows (Steffan-Dewenter and Tscharntke 2001) and wheat fields (Holzschuh et al. 2007), bee species richness increased with plant species richness, whereas bee abundance could be best explained by blossom cover. These findings and ours in this study contrast with the results of Hegland and Boeke (2006) who found no effects of plant species richness on pollinator species richness. Such contrasting results may have been caused by confounding factors, which are usually associated with field studies. For example, plant richness is often related to changes in plant community structure, soil fertility, and disturbance caused by land-use management. Hence, an experimental design such as the Jena experiment, with plant species richness being experimentally manipulated, is needed to draw reliable conclusions on the importance of plant species richness per se.

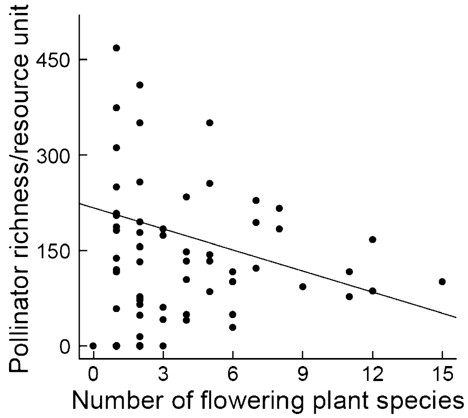

Figure 2. Effects of the number of flowering plant species on the number of pollinator species/ resource unit (m^2 flowers). The solid line shows predictions based on the linear zero-inflated negative binomial model. For statistics see Table 2.

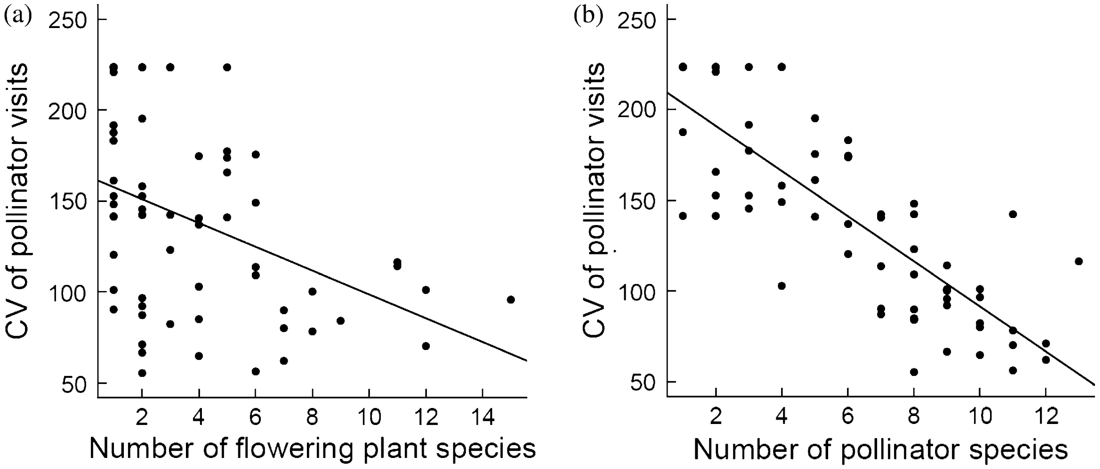

Figure 3. Effects of (a) the number of flowering plant species and (b) the number of pollinator species on the coefficient of variation (CV between six sampling days within two consecutive seasons) in the frequency of pollinator visits. Solid lines show least square linear regression fits. For statistics see Results.

When we used the number of sown plant species instead of the number of flowering plant species as an explanatory variable the results were similar (data not shown) which leds support to the quality and consistency of our data.

In addition to the richness of flowering plant species, the availability of food resources (blossom cover) was expected to show a strong impact on the pollinators, as found by Hegland and Boeke (2006). Our results support this expectation, but interestingly, the effects on pollinator species richness were best explained with Michaelis–Menten models indicating saturation, whereas the effects on the frequency of pollinator visits were best explained with linear models.

By analogy to the resource concentration hypothesis for herbivores (Root 1973), pollinator species richness and the frequency of pollinator visits should increase with increasing blossom cover. An alternative hypothesis is that abundant food resources lead to a dilution in pollinator density, which would predict a humped-shaped response of pollinators to blossom cover (as shown by Veddeler et al. 2006 for coffee farms). Our findings support a resource concentration hypothesis for the frequency of pollinator visits, but not pollinator richness, which exhibited a saturation effect with no changes in pollinator richness from 15% to 30% blossom cover. This plot-level effect contrasts with the finding that per resource unit, pollinator richness decreased with the number of flowering plant species, supporting the hypothesized dilution effect. Totland and Matthews (1998) suggested that the pool of available pollinators may be often limiting, based on their findings of a negative relationship between flower density and the visitation rates of pollinators.

The presence of attractive plant species significantly increased the frequency of pollinator visits, but not the number of pollinator species per plot. Hence, the consistent effects of the number of flowering plant species and blossom cover on species richness and frequency of visits across all pollinator groups may indicate the higher value of these vegetation characteristics compared to the availability of particularly attractive plant species.

With respect to the temporal stability of pollinator visits, our results pertain to the long-standing diversity–stability debate (Pimm 1991, Naeem and Li 1997, McCann 2000, Loreau et al. 2003, Tilman et al. 2006). This debate began with Elton (1958) and MacArthur (1955), who assumed that diverse communities are more stable. The positive relationship between species richness and stability in our system may have been caused by the fact that plant species richness increases the probability of having more pollinator species that are less sensitive to changing floral resources (Naeem and Li 1997, Naeem 1998). In addition, higher plant and thereby higher pollinator diversity may enhance functional redundancy of pollinator species, thereby stabilizing the frequency of flower visits (Zamora 2000). Both ideas reflect the insurance hypothesis of biodiversity proposed by Yachi and Loreau (1999) in that more species in a functional group provide insurance in ever-changing environments. Ghazoul (2006) argued that the positive impact of plant species richness on the dynamic stability of pollinators can have different causes. Complementary attraction is one mechanism leading to maximal attraction of pollinators by a combined floral display, thereby dampening variability in pollinator dynamics (Rathcke 1988, Moeller 2004). This small-scale mechanism differs from the broad-scale mechanism proposed by Moeller (2004) in which diverse floral communities diversify and stabilize pollinator communities by providing a more temporally continuous supply of floral resources. Both hypotheses provide a mechanistic understanding of higher stability in pollinator visitation and increased species richness of pollinators with increasing number of flowering plant species.

In summary, the number of flowering plant species and blossom cover enhanced pollinator species richness as well as the frequency and stability of pollinator visits. Frequency of pollinator visits increased linearly with both the blossom cover and the number of flowering plant species, which was closely related to the total number of plant species, whereas the number of pollinator species followed a saturation curve. The presence of particularly attractive plant species was only important for the frequency, but not the richness of pollinators. Plant species richness, blossom cover, and the presence of attractive plant species enhanced the temporal stability in frequency of pollinator visits. Both species-rich and strongly-flowering plant communities therefore appear to be critical in grasslands to ensure high diversity, and stability of pollinator frequency, which in turn are critical for the reproductive success and sustained stability of the plant communities themselves.

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Supplementary material (available online as Appendix O16819 at <www.oikos.ekol.lu.se/appendix>), Appendix 1 and 2.

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