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RESEARCH PAPER

Pollinator community responses to the spatial population structure of wild plants: A pan-European approach

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Abstract

Land-use changes can alter the spatial population structure of plant species, which may in turn affect the attractiveness of flower aggregations to different groups of pollinators at different spatial scales. To assess how pollinators respond to spatial heterogeneity of plant distributions and whether honeybees affect visitation by other pollinators we used an extensive data set comprising ten plant species and their flower visitors from five European countries. In particular we tested the hypothesis that the composition of the flower visitor community in terms of visitation frequencies by different pollinator groups were affected by the spatial plant population structure, viz. area and density measures, at a within-population ('patch') and among-population ('population') scale. We found that patch area and population density were the spatial variables that best explained the variation in visitation frequencies within the pollinator community. Honeybees had higher visitation frequencies in larger patches, while bumblebees and hoverflies had higher visitation frequencies in sparser populations. Solitary bees had higher visitation frequencies in sparser populations and smaller patches. We also tested the hypothesis that honeybees affect the composition of the pollinator community by altering the visitation frequencies of other groups of pollinators. There was a positive relationship between visitation frequencies of honeybees and bumblebees, while the relationship with hoverflies and solitary bees varied (positive, negative and no relationship) depending on the plant species under study. The overall conclusion is

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that the spatial structure of plant populations affects different groups of pollinators in contrasting ways at both the local ('patch') and the larger ('population') scales and, that honeybees affect the flower visitation by other pollinator groups in various ways, depending on the plant species under study. These contrasting responses emphasize the need to investigate the entire pollinator community when the effects of landscape change on plant–pollinator interactions are studied.

Zusammenfassung

Änderungen der Landnutzung können die räumliche Populationsstruktur von Pflanzenarten verändern, wodurch wiederum die Attraktivität von Blütenaggregationen für verschiedene Bestäubergruppen auf unterschiedlichen Skalen beeinflusst werden kann. Um zu erkunden, wie Bestäuber auf die räumliche Heterogenität in der Verteilung von Pflanzen reagieren und ob Honigbienen den Blütenbesuch durch andere Bestäuber beeinflussen, nutzten wir einen umfangreichen Datensatz, der 10 Pflanzenarten und deren Blütenbesucher in 5 europäischen Ländern umfasste. Im Einzelnen testeten wir die Hypothese, dass die Zusammensetzung der Blütenbesuchergemeinschaft (ausgedrückt als die Besuchshäufigkeit der einzelnen Gruppen) durch die räumliche Struktur der Pflanzenpopulation (gemessen als Fläche und Dichte) auf der lokalen Skala innerhalb der Population ("patch") und auf der übergeordneten Skala ("population") beeinflusst wird. Wir fanden, dass die patch-Größe und die Populationsdichte die räumlichen Variablen waren, die am besten die Variation der Besuchshäufigkeiten innerhalb der Bestäubergemeinschaft erklärten. Honigbienen zeigten höhere Besuchshäufigkeiten in größeren Pflanzenbeständen (patch), während Hummeln und Schwebfliegen höhere Besuchszahlen in weniger dichten Populationen aufwiesen. Die Besuchshäufigkeit der solitären Bienen war in weniger dichten Populationen und kleineren Beständen höher. Wir testeten auch die Hypothese, dass Honigbienen die Zusammensetzung der Bestäubergemeinschaft beeinflussen, indem sie die Besuchshäufigkeiten der anderen Bestäubergruppen verändern. Wir fanden eine positive Beziehung zwischen den Besuchshäufigkeiten von Honigbienen und Hummeln, aber die Beziehung zu Schwebfliegen und solitären Bienen variierte mit der betrachteten Pflanzenart (positiv, negativ, keine Beziehung). Insgesamt sind unsere Schlussfolgerungen, dass die räumliche Struktur von Pflanzenpopulationen sowohl auf der lokalen (patch) als auch der übergeordneten Skala (Population) unterschiedliche Bestäubergruppen unterschiedlich beeinflusst und dass Honigbienen den Besuch durch andere Bestäubergruppen -abhängig von der betrachteten Pflanzenart- beeinflussen. Diese kontrastierenden Reaktionen unterstreichen die Notwendigkeit, vollständige Bestäubergemeinschaften zu untersuchen, wenn die Auswirkungen von Landschaftsveränderungen auf Pflanze-Bestäuber-Interaktionen erforscht werden.

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Introduction

Human-induced landscape fragmentation is considered to be one of the greatest threats to global biodiversity (Forman 1995; but see Winfree, Aguilar, Vazquez, LeBuhn, & Aizen 2009). Large-scale land-use changes can reduce the total amount of habitable land for many species and fragment population distributions that were formerly continuous. This may, in turn, negatively affect the viability of species, either directly by changing their abundance, distribution and genetic diversity (Hartl & Clark 2007) and/or indirectly by affecting the structure and dynamics of species interactions (Rathcke & Jules 1993; Dauber et al. 2010). The population dynamics and ultimate survival of many plant and animal species depend on mutualistic relationships such as pollination and seed dispersal interactions. Therefore, the maintenance of ecological interactions is of utmost importance for the conservation of biodiversity and associated ecosystem functioning and services (Kearns, Inouye, & Waser 1998).

Fragmentation and habitat loss may affect population sizes and distributions of both partners of a mutualistic relationship and thereby alter their interaction patterns in complex ways (Kearns et al. 1998; Mustajarvi, Siikamaki, Rytönen, &

Lammi 2001; Dauber et al. 2010). Several studies have shown that pollinators respond to the spatial structure of plant populations by selectively visiting areas rich in floral resources (i.e. larger and denser patches and populations: Jennersten & Nilsson 1993; Kunin 1997; Steffan-Dewenter, Münzenberg, Bürger, Thies, & Tschardtke 2002). Indeed, theory predicts that pollinators should have higher visitation frequencies in larger and denser aggregations of flowers as these facilitate more efficient foraging (e.g. Heinrich 1979). On the other hand, the rate of locating larger and denser patches has been shown to increase slower than the number of flowers within the patch, and as a consequence, the visitation frequency on a per flower basis almost always decreases in larger and denser floral aggregations (Hambäck & Englund 2005).

Spatial heterogeneity in plant populations has been shown to affect pollinator attraction at different spatial scales. For example, studies on *Viscaria vulgaris* have shown that visitation frequencies of bumblebees were higher in larger flower patches (Nielsen & Ims 2000) and larger plant populations (Mustajarvi et al. 2001), whereas their visitation frequencies at a regional scale, is affected positively by plant density (Jennersten & Nilsson 1993). In other words, flower visitation is affected by the distribution of a plant in flower at

several different spatial scales (Dauber et al. 2010). At the same time, the results from the above studies reveal that they were not consistent in their definitions of spatial aggregations of flowers (patches, populations, regions). This inconsistency highlights the need for coherent definitions and standardized sampling protocols if studies of plant–pollinator relationships are to be synthesized and results directly compared.

In Europe, most pollinator species are insects, and bees and hoverflies are the most important taxa (Schweiger et al. 2007). Despite being important pollinators of certain plant species, several insect pollinator taxa were not emphasized in this study due to the low number of visits they conducted to the focal plant species (e.g. Lepidoptera, Coleoptera and several families of Diptera).

Social bees optimize their foraging by selectively utilizing hot spots of floral resources at distances up to several kilometres from nest sites (Waddington & Holden 1979; Steffan-Dewenter & Kuhn 2003). By recruiting co-workers honeybees can group-forage and are therefore more efficient on a per capita basis by exploiting the most rewarding patches and populations. Bumblebees have also been shown to forage most efficiently in floral hot spots (Heinrich 1979). The bumblebee's ability to locate these hot spots might be affected by their particular search behaviour, the physical outline of the flower aggregations and/or the nature of the surrounding vegetation. All else being equal, we expect more flower visits from honeybees and bumblebees in larger and denser plant populations, and in larger and denser patches within the populations. On the other hand, solitary bees, being smaller with shorter optimal foraging distances may be constrained to single habitat fragments or plant populations (Gathmann & Tscharntke 2002). As a result, solitary bees may be more sensitive to the spatial distribution of floral resource aggregations at the 'patch' scale, providing higher visitation frequencies in larger and denser patches. However, all bees also depend on the availability of additional resources, such as nesting sites and nest building materials and in many cases also a diversity of floral resources. In the case of solitary bees we believe these additional resources to be particularly important for their local floral visitation frequencies as they have to occur within their spatially more limited range (Gathmann & Tscharntke 2002).

Many hoverfly species are drifters, not central place foragers. The foraging behaviour of these insects should therefore resemble a more random search, as opposed to bees that could recruit fellow workers (honeybees) or at least get familiar with their local habitat and revisit hot spots of resources. However, our limited knowledge on the exact search behaviour of hover flies made predictions hard to make.

Visitation by a given pollinator taxon may not only be driven by plant population structure, but may also be influenced by the activity and visitation rates of other pollinator groups. Pollinators have been shown to compete for resources, with competitively superior species excluding other species or groups of species from highly rewarding

floral resources (Morse 1981; Goulson 2003a). For example, several studies have investigated interactions between domesticated honeybees and other taxa, e.g. bumblebees (Willmer, Bataw, & Hughes 1994; Thomson 2004, 2006; Walther-Hellwig et al. 2006; Goulson and Sparrow 2009), stingless bees (Roubik 1980; Roubik, Moreno, Vergara, & Wittmann 1986) and solitary bees (Evertz 1995; Kato, Shibata, Yasui, & Nagamasu 1999). Despite the honeybees' competitive superiority, reduced wild bee diversity or local extinctions of native bee species as a result of introduced honeybees have rarely been reported (Paton 1993; Moritz, Härtel, & Neumann 2005; but see Paine 2004).

To assess how pollinators respond to spatial heterogeneity of plant distributions and whether honeybees affected the rest of the pollinator community, we used a large data set comprising ten plant species throughout Europe, sampled using a standardized protocol. The protocol focused on gathering data on flower visitation in relation to variation in plant population structure at two spatial scales. Our goal was to focus on how the spatial structure of the plant species at different spatial scales affected flower visitation by different pollinator groups and whether there were general patterns across plant species, surrounding vegetation types and biogeographic region. We tested the following hypotheses:

1. Plant density and the area of plant occurrence at a patch and population scale, affects visitation frequencies by different pollinator groups.
2. Honeybees affect the composition of the pollinator community by altering the visitation frequencies of other groups of pollinators.

Methods

Plant species and study sites

Ten entomophilous plant species from five different families were selected in six areas representing four biogeographic regions throughout Europe (Table 1). The species were chosen because they are relatively common in the respective study regions, where they display a fragmented distribution. We selected between six and eight populations per species, defined either as naturally discrete aggregations of plant individuals or, in fragmented habitats, as all plant individuals of the focal species occurring in a habitat fragment. For each population we measured the area of the population (which in many cases was equal to the area of the habitat fragment) and the number of plants in order to describe the size of the population in terms of (i) the population area and (ii) its average density, although population area and density measures at this spatial resolution were in many instances only approximate. For each species we selected populations with contrasting spatial characteristics, designated as 'large' vs. 'small' and 'dense' vs. 'sparse' populations, respectively. To account for the among-species

Table 1. List of the ten focal plant species studied in different biogeographic regions in Europe with details on their ranges in size and density of patches and populations. Average values and standard deviations of population area (m²) and population density (plants [inflorescences per m²] and population density (flowers per m²) and maximum and minimum values of patch area (m²) and patch density (plants [inflorescences per m²] and population density (flowers per m²) are given.

Location	Plant species	Observation period	Population area (m ²)		Population density (flowers per m ²)		Patch area (m ²)		Patch density (flowers per m ²)	
			Large	Small	Dense	Sparse	Max	Min	Max	Min
Leeds (UK)	<i>Primula farinosa</i> L.	26. May–20. Jun	11,929 ± 4337	339 ± 131	31.9 ± 4.6	10.3 ± 4.8	2500	0.4	35.5	0.5
Leeds (UK)	<i>Origanum vulgare</i> L.	10. Jul–4. Aug	17,500 ± 2673	2116 ± 1805	88.6 ± 10.7	14.2 ± 11.1	396	0.6	118.6	2.8
Reading (UK)	<i>Clinopodium vulgare</i> L.	10. Aug–30. Aug	444,495 ± 39,350	64,646 ± 112,602	0.5 ± 0.6	0.03 ± 0.02	445	12	50.5	2.3
Göttingen (Ger)	<i>Primula veris</i> L.	14. Apr–3. May	21,959 ± 11,168	2438 ± 1840	3.6 ± 2.1	0.4 ± 0.3	172	0.2	108.7	6.5
Göttingen (Ger)	<i>Hippocrepis comosa</i> L.	5. May–18. Jun	38,776 ± 0	7877 ± 5477	0.2 ± 0.2	0.04 ± 0.03	16	0.2	625	162.5
Bologna (Italy)	<i>Ononis masquillierii</i> Bertol.	5. Jun–29. Jun	4125 ± 668	450 ± 341	3.2 ± 2.4	0.8 ± 0.2	260	0.3	116.7	1.2
Tartu (Estonia)	<i>Verbascum nigrum</i> L.	4. Jul–16. Jul	86,786 ± 14,005	24,950 ± 8758	0.01 ± 0.003	0.003 ± 0.001	125	3	6.9	0.2
Lesvos (Greece)	<i>Thymus capitatus</i> L.	13. Jun–20. Jul	2366 ± 897	542 ± 287	2.4 ± 0.2	1.5 ± 0.5	2630	3.8	4.6	0.4
Lesvos (Greece)	<i>Echium plantagineum</i> L.	18. Apr–13. May	12,645 ± 6537	2765 ± 559	9.2 ± 3.1	0.7 ± 0.4	216	5.2	72.3	4.3
Lesvos (Greece)	<i>Ballota acetabulosa</i> L.	3. Jun–5. Jul	13,591 ± 1370	4362 ± 1510	0.1 ± 0.1	0.03 ± 0.01	645	16	1.3	0.1

variation in population area and density, these attributes were chosen as locally defined relative terms. For example, large populations of a locally rare species (e.g. *Thymus capitatus* [2366 ± 897 m², mean ± SE]) might be smaller than a small populations of one of the commoner species in the study (e.g. *Clinopodium vulgare* [64,646 ± 112,602 m², mean ± SE]) (Table 1). Population areas and densities varied substantially throughout the season. It was therefore impossible to obtain reliable size and density estimates to be included in our analyses as continuous variables. The populations were therefore assigned two binomial variables: size (small, large) and density (dense, sparse). Populations were selected to be distant to each other in order to represent independent flower visiting communities (Steffan-Dewenter et al. 2002; Greenleaf, Williams, Winfree, & Kremen 2007; Dauber et al. 2010).

Within each population we selected four patches defined as continuous aggregations of individuals of the focal plant species. Patches within a population were located at least 2 m from each other. We measured the area (m²) and plant density (number of flowering plants or inflorescences per m²) of each patch. Given the variation in species growth forms, inflorescences were used as the recording unit for *T. capitatus* and *Hippocrepis comosa*. For all species we selected contrasting patches within each population that were ‘small’ and ‘large’, as well as ‘dense’ and ‘sparse’. Exact measurements of the area and the plant counts at the patch level allowed us to use both patch area and patch density as continuous variables in our analyses. Patch areas ranged from 0.16 to 2630 m² (116.3 ± 16.5 m², mean ± SE) and patch densities from 0.1 to 625 plants (or inflorescences) per m² (54 ± 7.2, mean ± SE). The absolute values of patch area and density varied largely among plant species (Dauber et al. 2010; Table 1). We standardized patch area and density within each plant species giving the variables a mean of zero and standard deviation of one (z-transformation) to ensure that the patterns found were due to variations in patch area and density per se. For various practical reasons (such as insufficient numbers of suitable plant populations or local soil erosion), data were not gathered from all patches and populations in all species; in total we included in the analyses 273 patches from 75 populations (3.64 ± 0.08, mean ± SE, patches per population).

Flower visitation frequency

To obtain data on flower visitation, each patch was observed between three and six times (rounds) during the peak flowering period of the focal plant species. Flower visitor observations were carried out within an ‘observation unit’ selected in each patch. Observation units were based on the number of flowers that were feasible to observe for the respective plant species and were selected on each round of observation. The number of flowers within observation units ranged from 14 (*Primula veris*) to 306 (*Verbascum nigrum*). Observation units were surveyed for 15 min per

round during the peak of pollinator activity between 06.00 and 18.15 h, depending on geographic region. To account for diurnal patterns in pollinator activity we ensured that all observation units were observed both before and after noon. Observation days were chosen to be representative of the prevailing weather conditions suitable for pollinator activity in the respective regions, and extreme or atypical conditions (very windy and cold; rain or overcast) were avoided. Observers stayed as distant as possible from the observation unit, remained still for a few minutes before starting the observations, and made minimal movements during the observation period. We recorded the number of insects entering the observation unit and visiting at least one flower, as well as the number of flowers visited by each insect. All flower visits were recorded and treated as separate events and we refer to all visitors as pollinators hereafter (although this may not be the case in all instances). Temperature during the time of observation was also recorded.

To estimate the composition of the pollinator community, visitors were identified on the wing and assigned to coarse taxonomic categories: honeybees, bumblebees, solitary bees and hoverflies (Syrphidae), all the above are hereafter referred to as pollinator groups. See Fig. 1 for the proportion of flower visits conducted by insects from the focal and non-focal groups.

Statistical analysis

We used values averaged over all observations conducted within each patch as response and predictor variables in our statistical models. Average values were used because the number of 15-min pollinator observations varied among the patches (3–6 observations) due to different flowering duration of the focal species and local climatic conditions, and because repeated measurements of the same patches were not independent. For visitation frequency for each pollinator group we therefore used average number of visits per flower during 15 min of observation in each patch.

To assess how the pollinator community, partitioned into different pollinator groups, was affected by the spatial heterogeneity of the plant species (area and density on patch and population scale), we first used a multivariate approach. Based on the visitation frequencies recorded by the groups of pollinators in each patch, we conducted a Principal Component Analysis (PCA) using the software Canoco for Windows 4.5 (Leps & Smilauer 2003). As a second step we used the score of each patch along the PCA axes 1 and 2 as response variables in separate linear mixed model analyses. We used patch area, patch density, population area, population density and temperature as fixed factors in the models. To account for the hierarchical structure of our data we included plant species and population identity nested within plant species as random factors. We used the Akaike Information Criterion (AIC) in a stepwise forward selection

procedure to identify the best model describing the variation in the response variables (i.e. the flower patches location along the PCA axes). We started with a model including none of the spatial variables ('Null' in Table 2) and added single variables in new models until further variables did not improve (lower) the AIC value. We also report the full model, including all spatial variables and temperature, for comparison. In all further analyses we used the observed visitation frequencies for the different pollinator groups as variables.

To understand the relationship between the spatial variables, temperature and visitation frequency of honeybees and the visitation frequencies of the other pollinator groups we used hierarchical modelling with Bayesian inference. Due to the relatively low number of study units (plant patches) for each plant species, we first assessed whether our model parameters should be included in the model at all and whether they were global or plant specific (see Appendix A for the model simplification procedure). This model simplification procedure was done using the bumblebee visitation data, but the results were applied also to the other pollinator groups. We used model selection to assess the effect of honeybee visitations on the visitation of the other pollinator groups. This was done for each of the pollinator groups separately (see Appendix A for the Bayesian comparison of models). Finally we ran the best model for each pollinator group and estimated posterior distributions for the relevant regressors by use of Markov Chain Monte Carlo (MCMC) iterations. We based our parameter estimates and credibility intervals on 2 chains of 100,000 MCMC permutations, with the first 10,000 permutations in each chain discarded as burn-in. To avoid autocorrelation among the permutations only every 100th iteration was used, resulting in a total of 1000 iterations in each analysis. We used parallel tempering (2 chains) in order to deal with possible multi-modality in the posterior distributions.

Results

Visitation frequencies varied among the plant species, from *Ononis masquillierii* receiving on average 0.35 visits per flower per hour, to *Origanum vulgare* receiving on average 4.24. The composition of the pollinator community was highly variable among the plant species studied (Fig. 1).

Spatial variables

Principal Component Analysis (PCA) indicated that 75.6% of the variation in visitation frequencies by the four pollinator groups within the 273 patches was explained by the first two ordination axes with eigenvalues of 0.452 and 0.304, respectively. The linear mixed effect model that best explained the distribution of the patches along PCA axis 1 contained patch area as the only explanatory variable (Table 2) with higher

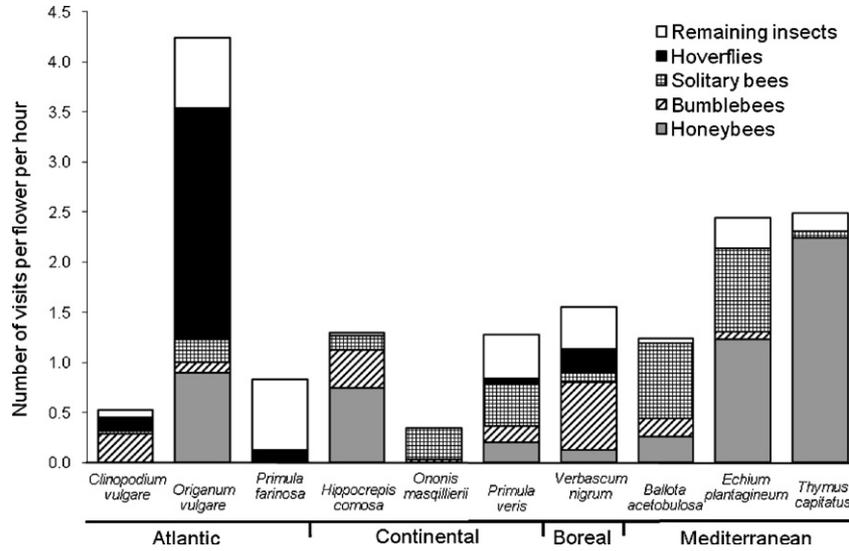


Fig. 1. The distribution of visitation frequencies of the different pollinator groups to the 10 plant species studied. Visitation frequencies are the number of visits paid by each pollinator group per flower and hour of observation. The ‘remaining insects’ group contained a diverse array of taxa, including Muscidae, Empididae, Bombyliidae, Lepidoptera, Coleoptera and Hemiptera. The composition of taxa making up this group varied for the different plant species. This group was therefore not included in the statistical analyses. The plant species are ordered by the biogeographic region in which they were studied (see also Table 1).

values along PCA axis 1 associated with larger patches. The linear mixed effect model that best explained the distribution of the patches along PCA axis 2 contained population density as the only explanatory variable (Table 2) with higher values along PCA axis 2 associated with sparser populations. This indicates that patch area and population density were the most important explanatory spatial variables for the pollinator communities under study and they were therefore used in the following analyses. The higher R^2 -value for the models including plant species as a random factor suggests

that there are some plant-specific variation in the relationships between the pollinator community and the spatial variables.

Visitation frequencies

Based on our model simplification procedure we decided to include the spatial variables (patch area and population density) and temperature in the models and keep their regressors global (Appendix A Table S1).

Table 2. Description of the mixed effect models explaining the positioning of the flower patches along ordination axes 1 and 2 resulting from Principal Component Analysis (PCA) of the visitation frequencies conducted by the four pollinator groups. Null models contain only the random factor (plant species), global models contain the random factor and all fixed factors (spatial variables and temperature) and best models contain the random factor and the fixed factors giving the lowest AIC value. R^2 values are given for the models with and without the random factor to illustrate the importance of this factor for the model fit. No interaction terms improved the models, so none of these are included in the global models.

All patches	PCA1			PCA2		
	Null	Global	Best	Null	Global	Best
Model						
AIC	514.7	513.9	509.6	405.1	413.5	400.5
R^2 fixed effects		0.08	0.01		0.06	0.03
R^2 fixed and random effects	0.86	0.86	0.86	0.92	0.92	0.92
Estimates						
Intercept	-0.020	-1.452	-0.192	0.062	0.363	0.224
Patch area		0.058	0.075		-0.036	
Patch density		0.047			-0.003	
Population area		0.633			-0.363	
Population density		0.148			-0.435	-0.350

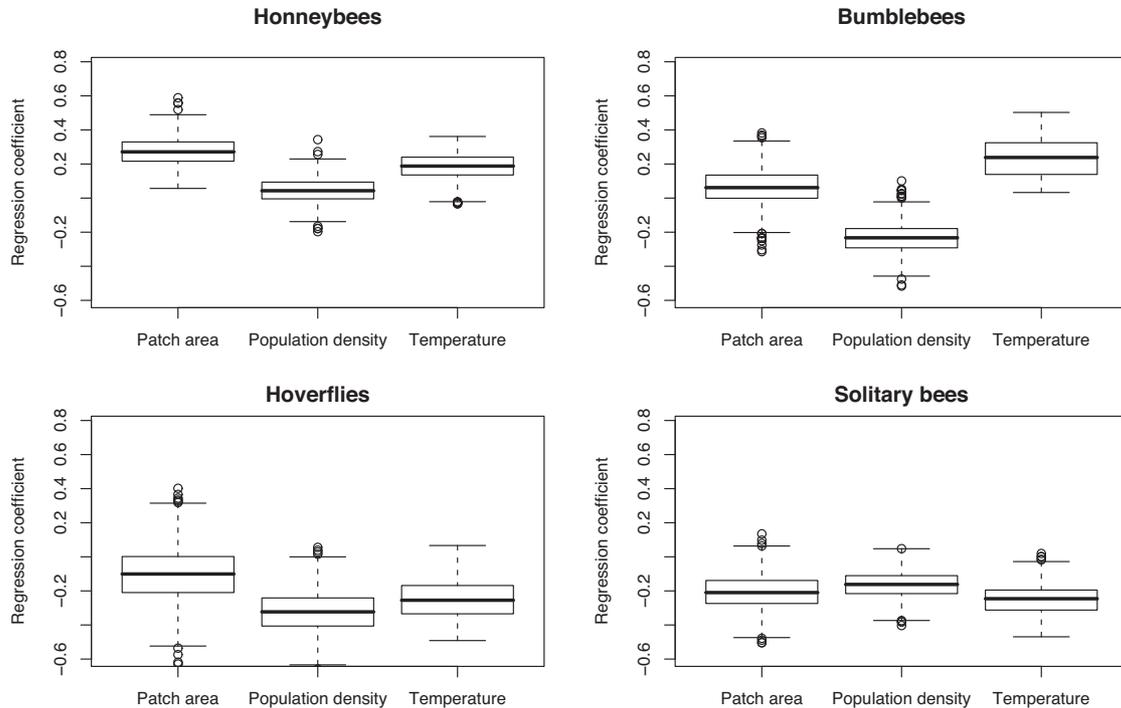


Fig. 2. Box-plots of the regression coefficients for the spatial covariates and temperature, in units of standard deviations. These units were used to better illustrate the effect of each covariate on the response (visitation frequency of the different pollinator groups) when viewed over the natural spread of each covariate. The thick horizontal line represents the median and the box representing the 25% and 75% quartiles (IQR). The whiskers are drawn at the lowest data point falling above $1.5 \times \text{IQR}$ and at the largest data point falling within $1.5 \times \text{IQR}$. Data points falling outside the whiskers are shown as circles. For population density on honeybees, patch area on hoverflies and of both spatial variables on bumblebees, a large proportion of the distribution of regression coefficients that falls on the opposite side of zero as compared to the mean value. Since there is a log-link in our response-covariate model, a parameter value of $+1$ means that the visitation frequency will increase by a factor of $\exp(1) = e$ if the covariate increases one standard deviation in value. Similarly a parameter value -1 will decrease the same visitation frequency by a factor of $\exp(-1) = 0.37$ if the covariate increases one standard deviation in value. Note the variation in regression coefficients among the different pollinator groups, not only in value but also in direction.

Honeybees had higher visitation frequencies in larger patches and dense populations, though the support for the effect of population density was weak. There was also a positive effect of temperature on honeybee visitation frequencies (Fig. 2). Bumblebees had higher visitation frequencies in sparse populations and larger patches, though the support for effects of patch size area was weak. Also for bumblebee visitation frequencies there was a positive effect of temperature (Fig. 2). Solitary bees showed higher visitation frequencies in sparse populations, smaller patches and at lower temperatures, though the support for the effect of the spatial variables was weak (Fig. 2). Hoverflies had higher visitation frequencies in sparse populations and small patches, though the support for effects of patch area was weak. There was a negative effect of temperature on the visitation frequency of hoverflies (Fig. 2).

Effect of honeybees on the rest of the pollinator community

Three of the 10 study species (*H. comosa*, *T. capitatus* and *Echium plantagineum*) were predominantly visited by honeybees. For these three species, 58 out of 91 patches

were dominated by honeybee visits (>50% of the visits to the focal plant species were conducted by honeybees). Considering all study species, honeybees dominated the visitor community in 18 of the 75 populations and 69 out of the 273 patches included in this study. Indeed, we found that visitation frequencies of honeybees had an effect on the visitation frequencies of all the other pollinator groups. Our model selection procedure revealed that the effect of honeybee visitation frequency was plant species-specific for solitary bees and hoverflies, while for bumblebees the effect was global (similar in all plant species) (Fig. 3 and Appendix A Fig. S7). We found strong support for an effect of honeybees on solitary bees and hoverflies while for bumblebees the support was weak but sufficient to include it in the model (Appendix A Fig. S7). For bumblebees the effect of visitation frequency of honeybees was negative (-1.36 [$-2.41, -0.26$], median [95% credibility interval]). For the eight plant species visited by solitary bees and honeybees the effect of honeybee visitation frequency was negative in 5 (2) and positive in 3 (1) (number of plant species with strongly supported effect in parentheses). For the five plant species visited by hoverflies the effect of honeybee visitation frequency was negative in 4 (1) and positive in 1 (1) species.

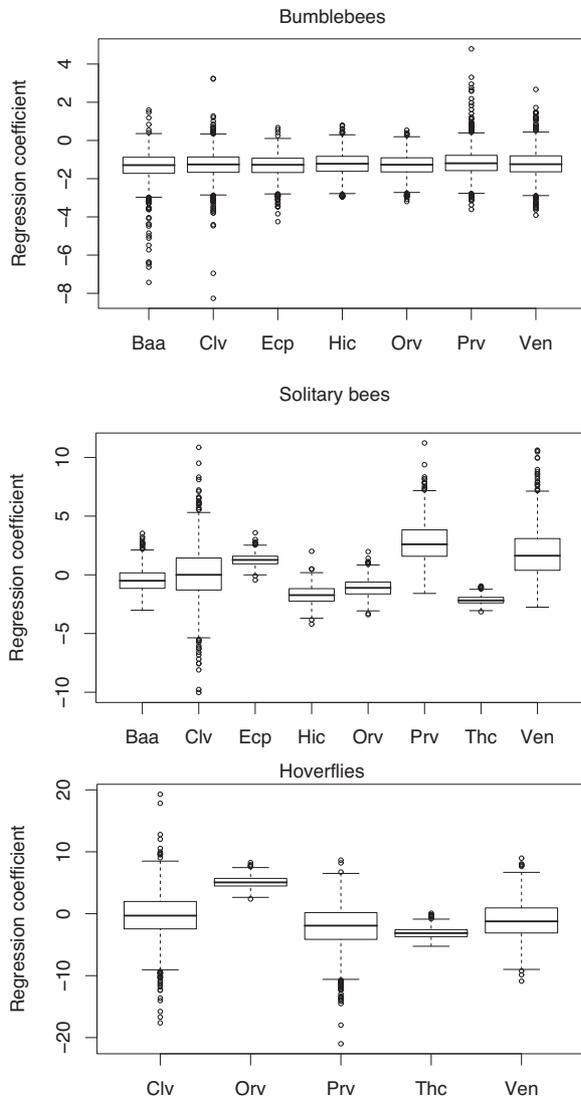


Fig. 3. Box-plots of the regression coefficients for the effect of honeybee visitation frequency on the visitation frequency of the other pollinator groups. The thick horizontal line represents the median and the box representing the 25% and 75% quartiles (IQR). The whiskers are drawn at the lowest data point falling above $1.5 \times \text{IQR}$ and at the largest data point falling within $1.5 \times \text{IQR}$. Data points falling outside the whiskers are shown as circles. Our model selection procedure revealed that for solitary bees and hoverflies the effect of honeybees was plant species-specific, while the effect on bumblebees was global (similar in all plant species). The plant species specific regression coefficients are reported also for bumblebees to illustrate the similarity of the effect being the rationale for using a global regression coefficient. Note that honeybees did not occur in sympatry with the other pollinator groups in all plant species. Plant species abbreviations are: Orv = *Origanum vulgare*, Clv = *Clinopodium vulgare*, Prv = *Primula veris*, Hic = *Hippocrepis comosa*, Ven = *Verbascum nigrum*, Thc = *Thymus capitatus*, Ecp = *Echium plantagineum*, Baa = *Ballota acetabulosa*.

Discussion

Spatial plant population structure affects pollinator community composition

We have shown that five taxonomic groups of pollinators respond to the spatial structure of plant populations in contrasting ways. The responses, seen as variations in flower visitation frequencies, varied not only in strength, but also in direction, among the pollinator groups (Fig. 2). Despite the differences in plant traits and among-species variation within the pollinator groups we identified some general trends in the relationship between the pollinator community composition and the spatial structure of the plant populations under study.

Visitation frequencies by honeybees were higher in the larger patches and denser populations. This was expected because, first, beekeepers selectively place their hives in the proximity of abundant floral resources (dense plant populations). Increased visitation frequency by honeybees can therefore result from their fidelity to plant species offering large amounts of floral rewards combined with the placing of the hives close to dense aggregations of beekeepers' 'focal plants'. *T. capitatus* is a typical example, a plant much sought after by Greek beekeepers. Second, regardless of where the hives are placed, honeybees optimize their foraging by exploiting floral hot spots (Waddington & Holden 1979), i.e. denser populations and larger patches, by recruiting nest-mates.

Visitation frequency by hoverflies was lower in large patches and decreased in denser populations. Sutherland, Sullivan, and Poppy (2001) found that hoverfly densities were positively related to the number of flowers within the patch (patch density), though not providing any estimate of flower visitation frequencies. This may suggest that even if the number of hoverfly individuals increases with the number of flowers available, the increase is not sufficient to keep up the flower visitation rate on a per flower basis (Hambäck & Englund 2005).

Solitary bee visitation was negatively affected by population density and patch area, though the support for the spatial variables was weak. Many solitary bees are less mobile than social bees and are in practice confined to a single habitat fragment (population) and make optimal foraging decisions on a more local (patch) scale (Gathmann & Tschardt 2002). In this case, however, our results did not follow our expectations, as the visitation frequencies by solitary bees were higher in smaller patches and sparse populations. The negative relationship with temperature can be explained by the solitary bees' high abundance and diversity in the warmer Mediterranean biogeographic region (Petanidou & Ellis 1993). Here they might suffer from high temperatures due to their lower thermoregulating abilities resulting in decreased activity and consequently lower visitation frequencies in the warmer patches.

Contrary to our expectations, bumblebee visitation was negatively related to population density. The negative relationship might have been the result of an abundance of resources for bumblebees in the denser populations which resulted in reduced visitation frequencies on a per flower basis. Floral resources utilized by bumblebees and honeybees show considerable overlap (Forup & Memmott 2005) and the apparent negative relationship between visitation frequencies of honeybees and bumblebees might suggest that the bumblebees are competitively excluded from the larger patches and denser populations, as has been shown in other studies (Walther-Hellwig et al. 2006; Goulson & Sparrow 2009). The positive relationship between visitation frequencies of bumblebees and temperature can be explained by the bumblebees' relatively higher abundance in colder climates at higher latitudes (Goulson 2003b; see also Fig. 1) where they, despite being active also at relatively low temperatures, increase their activity with increasing temperatures.

Honeybees affect pollinator community composition

The effect of honeybees on the visitation frequencies of the remaining pollinator community varied among the pollinator groups and the plant species studied (Fig. 3). The effect of honeybees on hoverflies was negative in *T. capitatus* but positive in *O. vulgare*. For the remaining three plant species where the two occurred in sympatry there seems to be no effect of honeybees. Also for solitary bees the effect of honeybees was variable among the plant species studied. Only for two plant species (*H. comosa* and *T. capitatus*) the effect of honeybee visitation frequency was negative while for *E. plantagineum* the effect of honeybees was positive.

The effect of honeybees on bumblebees was negative and the effect was global over all plant species studied. This suggests that there is competition for floral resources between honeybees and bumblebees, resulting in lower visitation frequencies of bumblebees where honeybees are abundant.

When looking at plant species visited by several pollinator groups our results reveal in even more detail the complexity of this system. For instance for *O. vulgare* honeybees have a negative relationship with bumblebees, a positive relationship with hoverflies and no relationship with solitary bee visitation frequencies. In *E. plantagineum* the relationship with honeybees was negative for bumblebees and positive for solitary bees. However, for *T. capitatus*, the plant species with the highest visitation frequency of honeybees, the relationship with honeybees was negative for both solitary bees and hoverflies. Since beekeepers actively search for this plant species and place their hives in areas where it is abundant this suggests that beekeepers decisions might have negative effects on the wild pollinator community.

Synthesis and wider implications

Although the literature on the ecological effects of landscape fragmentation on plant–pollinator relationships is large and growing, general patterns are hard to identify. The lack of consistency in findings may be related to species-specific traits such as individual pollinator mobility (Debinski & Holt 2000), plant and pollinator population size together with the species' competitive ability (Henle, Davies, Kleyer, Margules, & Settele 2004), differences in sampling methods and protocols used, as well as the employed spatial and temporal scale (Debinski & Holt 2000; Lindenmayer, Margules, Saunders, & Wissel 2004).

Although the absolute values of patch and population area and density included in our study were highly variable, reflecting the natural variation in patch and population sizes associated with each plant species, the values of the spatial variables are relative within each plant species and are directly comparable among them. Therefore, by including ten different plant species, we show that the relationship between visitation frequencies of important pollinator groups and the area and density of plant patches and populations did not seem to depend on the absolute area range of the studied patches and populations, despite the high plant specific differences in visitation frequencies.

Our results support the findings of several other studies showing relationships between the size and density of local plant aggregations and visitation frequencies of important pollinators (e.g. Jennersten & Nilsson 1993; Nielsen & Ims 2000). In particular, our results show that the spatial distribution of plants (i.e. patch area and population density) affect the composition of the pollinator community which may ultimately affect the viability of pollinator populations.

Human-induced disruption of plant populations may enforce particularly strong effects on the pollinator community as pollinators may not be adapted to a fragmented plant distribution (Oostermeijer et al. 2000). Smaller and sparser plant aggregations may not suffice in sustaining viable populations of important groups of pollinators, consequently reducing pollination services to the plants (Jennersten & Nilsson 1993; Kunin 1997; Oostermeijer et al. 2000; Mustajarvi et al. 2001). Recent intensification of human land use has been identified as one major cause of landscape fragmentation and negative effects experienced in both plant and pollinator populations have been highlighted (Rathcke & Jules 1993; Lienert 2004; but see Winfree et al. 2009) and may have led to the parallel declines of pollinators and pollinator-dependent wild plants reported at larger scales (Biesmeijer et al. 2006). As we have shown in this study, the composition of the pollinator community is sensitive to the spatial structure of plant populations at different spatial scales. Therefore, in addition to any direct effects for the plants growing in small or sparse patches and populations, there may be indirect consequences due to pollinator community responses to the spatial structure of plant species. For the pollinator

community investigated in this study, we found (1) highly variable responses to the spatial distribution of floral resources among the groups of pollinators, which we attribute to differences in resource requirements, species mobility (including beekeepers' decisions), behaviour and competition among the different pollinator groups; and (2) that honeybees affected the visitation by other pollinator groups. We therefore stress that the entire pollinator community should be studied if one aims at investigating the effects of habitat fragmentation on plant–pollinator interactions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2012.08.008>.

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