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Spatial variability in a plant-pollinator community across a continuous habitat: high heterogeneity in the face of apparent uniformity

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Abstract

Large-scale spatial variability in plant-pollinator communities (e.g., along geographic gradients, across different landscapes) is relatively well understood. However, we know much less about how these communities vary at small scales within a uniform landscape. Plants are sessile and highly sensitive to microhabitat conditions, whereas pollinators are highly mobile and, for the most part, display generalist feeding habits. Therefore, we expect plants to show greater spatial variability than pollinators. We analysed the spatial heterogeneity of a community of flowering plants and their pollinators in 40 plots across a 40-Km² area within an uninterrupted Mediterranean scrubland. We recorded 3577 pollinator visits to 49 plant species. The pollinator community (170 species) was strongly dominated by honey bees (71.8% of the visits recorded). Flower and pollinator communities showed similar beta-diversity, indicating that spatial variability was similar in the two groups. We used path analysis to establish the direct and indirect effects of flower community distribution and honey bee visitation rate (a measure of the use of floral resources by this species) on the spatial distribution of the pollinator community. Wild pollinator abundance was positively related to flower abundance. Wild pollinator visitation rate was negatively related to flower abundance, suggesting that floral resources were not limiting. Pollinator and flower richness were positively related. Pollinator species composition was weakly related to flower species composition, reflecting the generalist nature of flower-pollinator interactions and the opportunistic nature of pollinator flower choices. Honey bee visitation rate did not affect the distribution of the wild pollinator community. Overall, we show that, in spite of the apparent physiognomic uniformity, both flowers and pollinators display high levels of heterogeneity, resulting in a mosaic of idiosyncratic local communities. Our results provide a measure of the background of intrinsic heterogeneity within a uniform habitat, with potential consequences on low-scale ecosystem function and microevolutionary patterns.

Keywords: spatial variation, beta-diversity, mosaic community, plant-pollinator interactions, local scale-networks, honey bees

1. Introduction

Understanding how species and communities vary across space and the factors underlying spatial variability is a central topic in community ecology (Ricklefs 1987, Levin 1992). At large spatial scales (global, continental, regional), differences in community composition and structure are clear, mostly driven by climatic and productivity factors (e.g., along latitudinal or altitudinal gradients) and differences in land use resulting in contrasting landscapes (e.g., forests vs. grasslands vs. croplands) (Fernández-Palacios and Nicolás 1995, Lite et al. 2005, Batllori et al. 2009). Each landscape is expected to host a more or less singular community, defined as a group of populations of different species that coexist in space and time (Vellend 2010), whereby all individuals have the same probability to interact (Holyoak et al. 2005). Therefore, within a landscape we would expect few differences in local community composition and structure across space, especially in highly homogeneous landscapes lacking physical or ecological barriers and therefore offering no obvious obstacles to the movement of individuals and species (Post et al. 2007). However, many factors, including microclimatic conditions, biotic interactions such as competition and facilitation, dispersal capacity, historical events, and disturbance regimes have been shown to be important in explaining heterogeneity in community composition at local scales (Fukami et al. 2010). The relative importance of the factors that determine species distribution may differ considerably between sessile (e.g., plants) and mobile organisms. Plants are highly sensitive to microhabitat conditions, so that differences at the scale of a few centimetres in soil depth or sunlight exposure may condition plant establishment and survival (Eriksson and Ehrlén 1992, Jones and del Moral 2005). For this reason, plant species composition is expected to be heterogeneous across space even at very small scales (Whittaker 1960, Field et al. 2009, Grace et al. 2011). By contrast, most animals are highly mobile, which allows them to functionally occupy a larger area at the individual level, and to spread more rapidly at the population level, thus potentially displaying a more homogeneous spatial distribution at small scales (Strong et al. 1984).

Herbivorous animals are spatially linked to the plant species they depend on. Therefore, at the community level, a spatial correspondence between plant and herbivore community composition and richness is expected (Siemann et al. 1998, Blake et al. 2003, Schaffers et al. 2008, Ross et al. 2017). At the population level, if plant resources are limiting, we would expect herbivores to distribute themselves

across space proportionally to resource availability, following an ideal free distribution of herbivory rate and thus minimizing competition for resources, promoting a homogeneous use of resources across space (Fretwell and Lucas 1970). On the other hand, if plant resources are not limiting, we would expect no clear relationship between herbivore abundance and plant abundance, or even a decrease in herbivore frequency per plant resource unit, as increases in plant abundance would not be matched by increases in herbivore abundance (Kennedy and Gray 1993). In any case, the extent to which the local spatial distribution of herbivores follows that of plants is expected to be greater for specialist than for generalist herbivores.

Pollinators are highly mobile herbivores, and therefore an appropriate group of organisms to study local spatial distribution in relation to plant resource distribution. On the one hand, most pollinators are considered to be generalist and opportunistic in their foraging habits (Waser et al. 1996), as exemplified by pollinator species foraging on different plant species in different floral contexts (Tylianakis et al. 2007, Fründ et al. 2010, Janovský et al. 2013). On the other hand, even generalist pollinators such as polylectic bee species (those collecting pollen from various plant families) have been shown to have certain flower preferences, and may locally restrict their visits to one or a few plants (Westrich and Schmidt 1987, Petanidou et al. 2008, Fründ et al. 2010). The fact that some pollinators can be very generalist in their flower choice whereas others show strong flower preferences, makes predictions about the spatial distribution of pollinators complicated.

In this study we analyse the local heterogeneity of a community of pollinators in relation to that of flowering plants in a homogeneous habitat, defined as a habitat dominated by a vegetation type lacking clear abiotic gradients and/or obvious discontinuities. In addition to interactions with plants, the distribution of pollinator communities may also be influenced by interactions among pollinators. Dominant species in general, and managed species (which tend to occur at disproportionately high abundances) in particular, may affect the structure of communities through competitive pressure (Kunte 2008, Cornelissen et al. 2013). In our study area, beekeeping is a common practice (Torné-Noguera et al. 2016). Due to their ability to recruit nest-mate foragers, honey bees (*Apis mellifera*) are able to exploit the

most abundant floral resources very efficiently, showing local flower specialization (Lázaro and Totland 2010), and potentially outcompeting other pollinator species (Torné-Noguera et al. 2016, Henry and Rodet 2018, Valido et al. 2019). Competitive pressure may lead to niche differentiation between honey bees and wild pollinators, whereby honey bees monopolize the most highly-rewarding floral resources forcing wild pollinators to forage on less-preferred plant species (Walther-Hellwig et al. 2006, Geslin et al. 2017). In some cases, honey bee density has been shown to affect wild bee species composition, with special impact on certain, most sensitive, species (Herbertsson et al. 2016, Torné-Noguera et al. 2016).

The aim of this study is to understand the factors determining local variation in a plant-pollinator community across a uniform habitat. We ask the following questions: 1) how does pollinator distribution vary across space? 2) to what extent does pollinator distribution follow plant distribution? 3) are honey bees affecting the spatial distribution of wild pollinators? Because pollinators are highly mobile and, for the most part, can exploit a variety of floral resources, we expect greater heterogeneity in plant than in pollinator community distribution. We also expect pollinator abundance, richness and composition to follow plant community structure. Finally, we expect honey bee visitation rate to have a negative effect on wild pollinator visitation rate and to promote changes in wild pollinator composition across space.

2. Materials and Methods

2.1. Study area

The study was conducted in spring 2015 in the Garraf Natural Park near Barcelona (NE Spain, 41° 17' 34" N, 1° 53' 35.8" E). The Park is located in an area with mild topography (slopes < 20%) composed of small hills and valleys. Soils are poorly developed, derived from karstified limestone bedrocks; IUSS 2015). Originally, the area was occupied by mixed pine (*Pinus halepensis*) and oak (*Quercus* spp.) Mediterranean forests (Folch, 1981; Riera-Esteban-Amat, 1994). However, a long history of recurrent wild fires has promoted a continuous and dense scrubland (< 2 m high) dominated by *Quercus coccifera*, *Pistacia lentiscus*, *Rosmarinus officinalis*, and *Thymus vulgaris* (Riera and Esteban-Amat, 1994, Riera 1998; Lloret et al. 2003). The area can be considered uniform at the landscape scale, lacking clear discontinuities in topography, structural vegetation features or edaphic factors. The climate is

Mediterranean, with a strong sea influence, and a mean annual temperature of 16-17°C. Summers are dry and most precipitation (580-650 mm annually) occurs in spring (March-April) and autumn (September-November) (Ninyerola et al., 2000).

We selected 40 plots of 30 x 40 m across an area of nearly 40 km² (Fig. S1). Mean distance between nearest plots was 760 m (range: 520-1400 m). This distance is assumed to be representative of foraging distances of most pollinator species (Zurbuchen et al. 2010, Dorchin et al. 2013). Plot altitude ranged between 171 and 551 m. Exploratory analyses showed that flower and wild pollinator communities were not affected by altitude.

2.2. Field sampling

Each plot was surveyed on a single day. Although this sampling method does not account for variation in plant-pollinator interactions across time, it is a practical way to survey a high number of plots under comparable phenological conditions (Fründ et al. 2010, Weiner et al. 2011). We surveyed 2-4 plots per day between April 2nd and April 17th. This period corresponds to the flowering peak of the scrubland community (Flo et al. 2018). The field team was composed of 8 people trained to identify the pollinator fauna of the study area. We worked in pairs. Pair composition was changed every day to avoid potential observer bias.

Within each plot, we established four parallel 40 m x 1 m transects separated by 10 m. To characterize flower composition (number of flowers of each plant species), we counted the number of open flowers in the four transects at the beginning of each survey. To sample plant-pollinator interactions we conducted three surveys starting at 11 a.m., 1 p.m. and 3 p.m., respectively. Ambient temperature was registered at the beginning and at the end of each survey. During each survey, two observers walked slowly along the transects and recorded all pollinators observed contacting the reproductive organs of a flower. Some pollinators could be unmistakably identified on site. Others were captured for identification in the laboratory. Most individuals were identified to the species level using identification keys and an extensive reference collection from the study area. A few pollinators could only be identified to the morphospecies level. From these surveys, each plot was characterized based on its pollinator richness (number of species

observed interacting with flowers), pollinator abundance (number of interactions recorded), pollinator composition (abundance of each pollinator species), and pollinator visitation rate (number of interactions recorded / 1000 open flowers). We use visitation rate as a measure of the use of floral resources by pollinators.

2.3. Spatial distribution of the flower and pollinator communities

Spatial variation in species abundance and richness of the flower and pollinator communities and of pollinator visitation rate was quantified using the coefficient of variation among plots. To check whether these variables were spatially autocorrelated we conducted Moran's I tests with the "ape" package (Paradis et al. 2004) in R version 3.4.4 statistical environment (R Core Team 2018). All analyses involving the pollinator community were conducted twice, once including all species and once excluding honey bees (which were, by far, the most frequent flower visitor, see Results).

Weather in general and temperature in particular affects pollinator activity (Vicens and Bosch 2000, Willmer and Stone 2004). In our dataset, maximum ambient temperature (highly correlated to mean temperature; Pearson $r = 0.96$, $p < 0.001$) of the survey day affected positively wild pollinator richness, wild pollinator visitation rate and honey bee visitation rate (general linear models; $n = 40$, $df = 38$, all $p < 0.04$). To extract the effect of temperature, Moran's I tests for these three variables were conducted using the residuals of these linear models. Wild pollinator abundance and honey bee abundance were not affected by temperature (general linear models; $n = 40$, $df = 38$, all $p > 0.1$).

To describe variation in flower and pollinator community composition across sites we calculated beta-diversity between plots with the Bray-Curtis quantitative dissimilarity index (Anderson et al. 2011) using the "betapart" package (Baselga et al. 2018) for R. As pollinator composition could also be affected by temperature, we performed Mantel tests between pollinator composition (including and excluding honey bees) and differences in maximum temperature between plots. None of these tests were significant (all $p > 0.1$). As a result, temperature was not accounted for in pollinator composition autocorrelation analyses. To check for spatial autocorrelation of flower and pollinator community composition, we performed Mantel correlograms with 9999 permutations using the beta-diversity indices and the geographical

distance between plots implemented in the “vegan” package (Oksanen et al. 2018) for R. In these analyses, sample size was 780 possible combinations of pairs of plots.

2.4. Determinants of spatial variation of the pollinator community

Our aim was to understand to what extent the local wild pollinator community was affected by the local flower community and by local honey bee visitation rates. Since honey bee visitation rate may also be affected by the flower community, we used a path analysis approach, which provides the magnitude, significance and causality of relationships among variables. In our case, flower community descriptors (independent or exogenous variables) may have both a direct and an indirect effect (through honey bee visitation rate, intervening or mediating variable) on wild pollinator community descriptors (dependent or endogenous variables). We ran separate models for wild pollinator abundance, richness and visitation rate as dependent variables. The models for wild pollinator abundance and visitation rate included overall flower abundance and maximum ambient temperature (see above) as exogenous variables, and honey bee visitation rate as a mediating variable, which in turn could be directly affected by flower abundance and temperature. The model for wild pollinator richness was similar but also included flower richness as an exogenous variable. We performed these analyses using the “piecewiseSEM” package (Lefcheck 2016) for R. All variables were log-transformed to ensure normality and homoscedasticity of the residuals.

To analyse the effects of flower community composition on wild pollinator composition, we correlated the pairwise (plot x plot) dissimilarity (Bray-Curtis index) matrices of flower and pollinator composition. A strong relationship between the two matrices would indicate a high level of specialization in plant-pollinator interactions, whereas lack of relationship would indicate that pollinators act as generalists and adjust their floral choices to the local flower composition of each plot. As with the other descriptors of the pollinator community, honey bee visitation rate could affect wild pollinator composition. Certain pollinator species could be more affected by honey bee pressure than others (for example, large bees, which require larger amounts of floral resources, would be more likely to be affected by honey bee competition; Nielsen et al. 2012, Torné-Noguera et al. 2016). Likewise, temperature effects on pollinator foraging activity could be greater for some species than for others (Vicens and Bosch 2000, Kühnel and Blüthgen 2015). For these reasons, we generated a pairwise distance matrix of honey bee visitation rate

and one of differences in maximum ambient temperature. Following previous studies facing the challenge of working with a path analysis approach with distance matrices, we used the methodology developed by Leduc and collaborators (Leduc et al. 1992, Paul and Anderson 2013). We thus conducted partial Mantel tests between the sets of matrices involved in each analysis, and used partial Mantel correlation as a measure of the path coefficient and its significance. Because multiple tests are conducted in such analyses, we applied a Bonferroni correction.

3. Results

The flower community was composed of 49 species, and was strongly dominated by *Thymus vulgaris* (61.2% of the flowers recorded) and *Rosmarinus officinalis* (36.4%) (Fig. 1). We recorded 3577 individual pollinators visiting flowers across the 40 plots. The pollinator community comprised 170 species (38.2% dipterans, 23% bees, 17.7% coleopterans, 11.2% wasps, 5.9% lepidopterans and 4% other pollinators), and was clearly dominated by the honey bee (71.8% of the individual pollinators recorded) (Fig. 2). As many as 95 of the pollinator species were found in only one plot.

3.1. Spatial distribution of flower and pollinator communities

Flower abundance was highly variable across space, whereas flower richness showed much lower spatial variability (lower CV, Table 1). Flower composition was also highly variable across space. Beta-diversity of flower composition was 0.52 ± 0.21 (mean \pm SD, Fig. 3). None of these community descriptors showed spatial autocorrelation (Moran's I, all $p > 0.1$, Table 1; Mantel correlogram, $p > 0.05$ for all distance classes, Fig. S2a).

As with flowers, pollinator abundance (both wild pollinators and honey bees) showed greater spatial variation than pollinator richness (Table 1). Visitation rate (of both wild pollinators and honey bees) was also highly variable across space (Table 1). However, none of these variables showed spatial autocorrelation (Moran's I, all $p > 0.1$). Beta-diversity of pollinator composition was 0.56 ± 0.20 (similar to that of flower composition), but increased to 0.86 ± 0.09 when honey bees were excluded (Fig. 3). As mentioned, the honey bee was by far the most abundant pollinator species in the study area. Therefore the

increase in homogeneity when this species was considered is not surprising. Pollinator composition did not show spatial autocorrelation at any distance class except at 900 m (the lowest distance class; including and excluding honey bees: $p = 0.009$ and 0.038 , respectively, Fig. S2b and S2c). Even at that distance class, the correlation coefficients were low (Mantel correlation r , including honey bees = 0.10 , excluding honey bees = 0.07).

3.2. Determinants of spatial variation of the pollinator community

Wild pollinator abundance was moderately related to both temperature and flower abundance (Fig. 4a). Honey bee visitation rate was strongly affected by temperature and less so by flower abundance. Wild pollinator visitation rate also increased with temperature, but displayed a moderate inverse association with flower abundance (Fig. 4b), indicating that, overall, floral resources were not a limiting factor for the wild pollinator community. Wild pollinator richness was positively and moderately related to flower richness, but was not related to flower abundance or temperature (Fig. 4c). Coefficient estimates of the relationships between wild pollinator abundance, wild pollinator visitation rate and honey bee visitation rate with temperature were high (Table S1). Wild pollinator composition was positively related to flower composition (Fig. 4d), but the coefficient estimate was low. Honey bee visitation rate did not explain any wild pollinator variable, thereby indicating lack of competition between honey bees and wild pollinators at the community level (Table S1).

4. Discussion

In this study we measured the variability of flower and pollinator communities across space in a continuous 40-Km² scrubland, thus providing a measure of the background of intrinsic heterogeneity within a uniform habitat. We found that variation of the pollinator community was at least as high as variation of the flower community. At the same time, our results show that the spatial variation of the flower community is a poor predictor of the pollinator community, indicating that other factors besides flower community composition are important to explain pollinator distribution at the local scale. Although honey bees were by far the most abundant flower visitor, we found no indication of negative

effects of honey bees on the wild pollinator community. Overall, these results are congruent with flower resources not being a limiting factor in our study area at the time the surveys were conducted.

Our first question addressed the extent to which pollinator distribution varies across space. We expected pollinator distribution to be more homogeneous than that of flowers for three reasons. First, pollinators are highly mobile organisms and therefore should be able to spread easily across the study area, blurring distribution patterns. Second, the study area was lacking physical barriers or strong environmental gradients limiting individual dispersion. Finally, because our pollinator community is mainly composed of flower-generalist species (Bosch et al. 2009), we did not expect large differences in local pollinator composition. Instead, we found that both flower and pollinator communities displayed similar and highly heterogeneous patterns across space. We found strikingly different pollinator communities in different plots, and these differences did not follow any clear spatial pattern (Fig. 2b). The high variability in pollinator abundance, visitation rate, richness and composition across space together with the general lack of spatial autocorrelation, indicates that each plot hosts a rather unique pollinator community independent from its neighbouring plots. Some studies have found similar levels of variability in pollinator community distribution at spatial scales comparable to that of our study (from hundreds of meters to a few kilometres). However, these studies were conducted either in areas hosting a mosaic of different disturbance regimes and heterogeneous land uses (Potts et al. 2003a), or in separate patches of one type of habitat within a heterogeneous landscape matrix (Dorchin et al. 2017, Carstensen et al. 2014, Simanonok and Burkle 2014). By contrast, our study was conducted in plots within a homogeneous continuous habitat at the landscape level. Phylopatry (or site fidelity), the tendency of individuals to stay at the site they were born rather than spreading to new areas (Dorchin et al. 2013), is a possible mechanism explaining the local idiosyncratic pollinator composition found in our study. The fact that about a quarter of the pollinator species in our study (non-parasitic bees and predatory wasps) are central place foragers, may also contribute to the establishment of local idiosyncratic assemblages. The super-abundant managed honey bee greatly contributed to the homogenization of the pollinator composition across space, as indicated by the increase in beta-diversity when this species was excluded from the analyses. Thus, the turnover of low-abundance wild pollinator species was the main driver of the differences in community composition across the park.

Our second question addressed to what extent pollinator distribution followed the distribution of food resources (flowers). We found a positive relationship between flower abundance and wild pollinator abundance. This relationship appears to be quite common in plant-pollinator communities (Dreisig 1995, Steffan-Dewenter and Tschardt 2001, Westphal et al. 2003, Ebeling et al. 2008). However, increases in flower abundance were not paralleled by proportional increases in pollinator abundance, as reflected by the negative relationship between flower abundance and wild pollinator visitation rate. Therefore, pollinators did not follow an ideal free distribution, indicating that, at the community level, floral resources were not limiting. Other studies have also found deviations from the ideal free distribution. Kennedy and Gray (1993) showed that the distribution of various animal groups, from beetles to ducks, did not follow closely food resource distribution. Resource use rate was lowest in the resource-richest areas and highest in the poorest areas. Similarly, Janovský et al. (2013) found a decrease in flower visitation rate with increased flower abundance and suggested that pollinator saturation may be a commoner phenomenon than previously thought. If flowers were sufficiently abundant, pollinators could locally find the necessary floral resources to satisfy their energy requirements. This situation could lead to a local organization of the relationship between flowers and pollinator abundances, thus ultimately promoting independent communities between localities.

In line with other studies (Steffan-Dewenter and Tschardt 2001, Potts et al. 2003a, 2003b, Fründ et al. 2010, Weiner et al. 2011, Dorchin et al. 2017), we found a clear relationship between flower and pollinator richness. Therefore, even though overall floral resources did not appear to be limiting, the distribution and abundance of certain pollinator species may have been conditioned by the availability of certain, less abundant, flower species. Of 170 pollinator species recorded, 127 (74.7%) visited mostly the two dominant plant species, *R. officinalis* and *T. vulgaris*, and these 127 species accounted for 95.2 % of the visits recorded. The remaining 43 pollinator species were rare and visited mostly rare flower species. Thus, the positive relationship between pollinator and plant richness was mainly driven by interactions among rare species. On the other hand, wild pollinator composition was only moderately related to flower composition. A previous study conducted in the same study area with pan traps (rather than pollinator counts) also found that bee species composition was only weakly affected by flower composition (Torné-Noguera et al. 2014). This result is consistent with the generalist nature of plant-pollinator interactions (Waser et al. 1996) and the opportunistic flower choice displayed by pollinators (Fründ et al. 2010). The

weak relationship between flower and pollinator composition also suggests that pollen/nectar availability is not the only (or the main) factor influencing the spatial distribution of pollinators. Distribution of some pollinator groups that only feed on floral resources during the adult stage (in our study area all pollinator groups except bees) may be more strongly conditioned by the availability of larval food than by flower availability. In bees and predatory wasps, nesting resources may also affect species distribution across space (Potts et al. 2005). However, previous studies conducted in our study area found that nesting resources were not a good predictor of bee community distribution (Torné-Noguera et al. 2014).

Finally, our third question addresses the potential competitive effects of honey bees on wild pollinator communities. As a managed species introduced in large numbers, honey bee abundance is frequently higher than the abundance of all other pollinator species together (Geslin et al. 2017). In our study, honey bees accounted for nearly 72% of the flower visits recorded, one of the highest proportions registered in natural habitats (range: 0-85%, Hung et al. 2018). Consequently, we expected that honey bees would have important effects on the spatial distribution of wild pollinator communities. However, we found no evidence of such effects. For honey bees to exert competitive pressure on other pollinators, floral resources should be limiting, but the negative relationship between flower abundance and wild pollinator visitation rate indicates that this was not the case in our study. Because as much as 99.1 % of honey bee visits were on *R. officinalis* and *T. vulgaris*, it is unlikely that honey bees could have any competitive effects on pollinators visiting other, less abundant, flower species. This result may be related to the time of the year (early spring) in which surveys were conducted, corresponding to the peak of flower production in the park (Flo et al. 2018). At that time, flower visitation rates are low compared to late spring, when floral resources sharply decline and a greater number of pollinator species are active (Bosch et al. 2009, Filella et al. 2013). Therefore, floral resources are more likely to become limiting as the season progresses (Flo et al. 2018). A previous study in the same area encompassing the entire flowering season found evidence of displacement of wild pollinator communities (especially large bees) by honey bees (Torné-Noguera et al. 2016). Differences between habitats and/or seasons in floral resource abundance could explain discrepancies between studies finding negative effects of honey bees on wild pollinators (e.g. Thomson 2004, Walther-Hellwig et al. 2006, Henry and Rodet 2018) and studies not finding these effects (e.g. Steffan-Dewenter and Tschardtke 2000, Roubik and Wolda 2001, Goras et al. 2016).

Some studies have reported high levels of variation in plant-pollinator interactions across years (Petanidou et al. 2008, Dupont et al 2009). We show that these interactions are also highly variable across space, even when comparing plots as close as 500 m within a uniform habitat. Overall, these results underscore a lack of consistency in plant-pollinator interactions. In our study, this lack of consistency is driven by high levels of heterogeneity in both the plants and pollinators, resulting in a mosaic of idiosyncratic local communities in spite of the apparent physiognomic uniformity of the study area. The pollinator community was as variable across space as the flower community. Nonetheless, flower distribution had only a moderate weight explaining the general trends of pollinator distribution across the landscape. The negative relationship between pollinator visitation rate and flower abundance indicates that floral resources are not limiting, and this result has a fundamental effect on the relationship between flowers and pollinators. When resources are not limiting and most pollinators are generalist, pollinators do not need to travel long distances to find food resources because they can find enough resources to satisfy their requirements at short distances, thus promoting local-scale organization of pollinator communities and strong spatial variation. Likewise, sufficient availability of floral resources reduces the potential impact of dominant species on the rest of the community. Ultimately, the spatial variation in flower and pollinator species composition recorded in our study may affect pollination and ecosystem functioning at the local level (Herrera 2000) and may have far-reaching ecological and evolutionary consequences on ecological communities (Gómez et al. 2009). Beyond being structured by climatic gradients and differences in land use, both communities and interactions may show strong imprints of forces acting at a local scale within seemingly uniform tracts of habitat. Dissecting the reasons for, magnitude of and consequences of such small-scale variation is thus an urgent task for community ecologists.

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Figure Legends

Figure 1. Flower community composition across the 40 plots surveyed in the Garraf Natural Park.

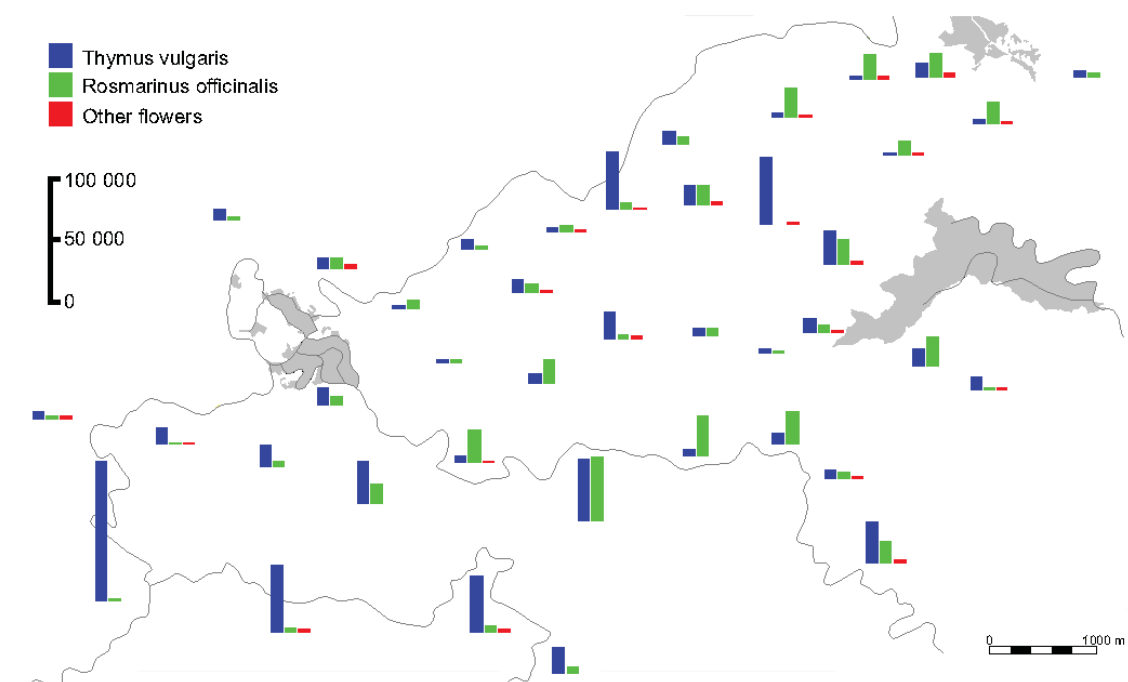


Figure 2. Pollinator community composition across the 40 surveyed plots in the Garraf Natural Park. (a) Honey bee and wild pollinator abundance. (b) Abundance of the 12 most abundant wild pollinator species.

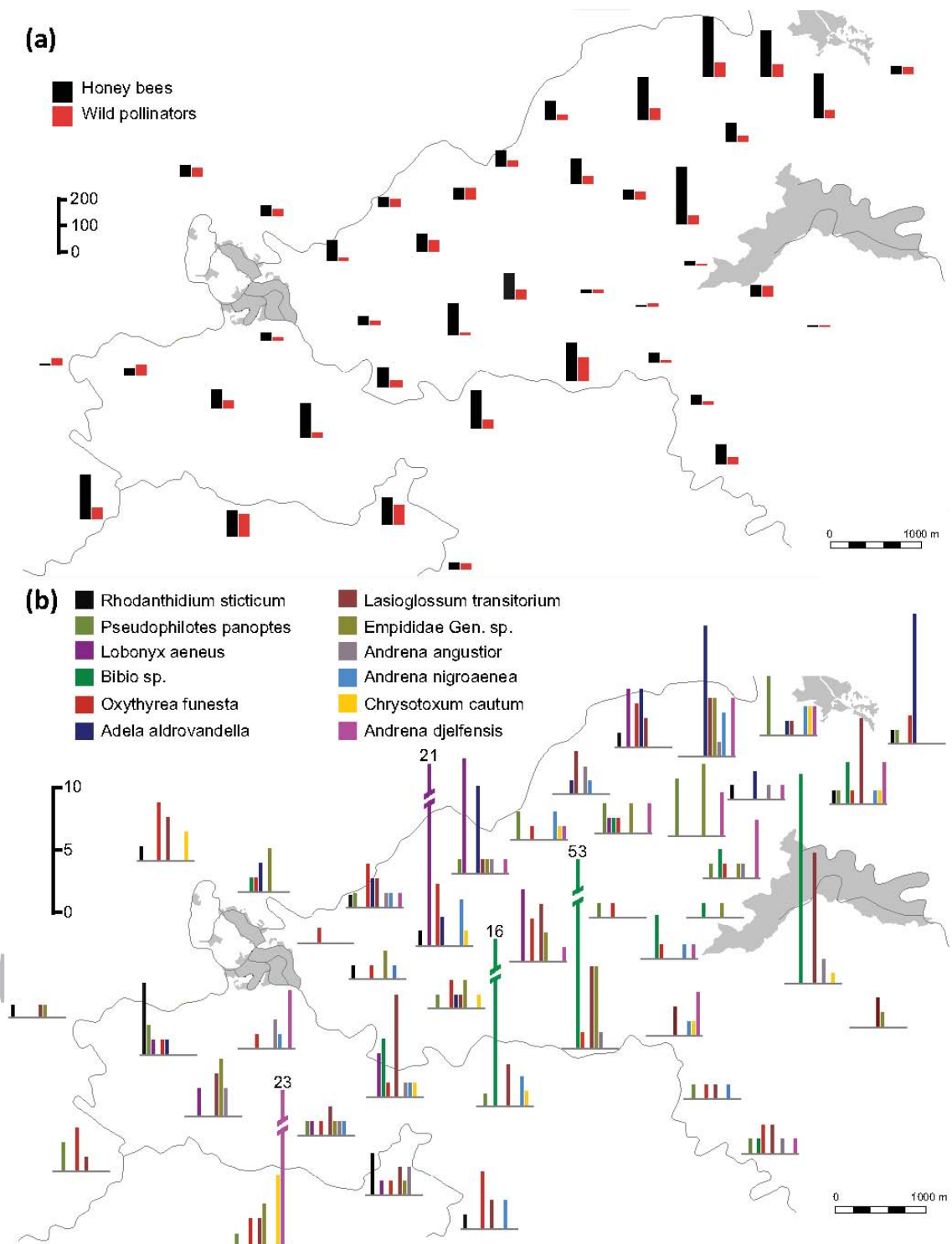


Figure 3. Relationship between geographical distance and differences in species composition, measured as beta-diversity (Bray-Curtis dissimilarity index) in the flower and pollinator (with and without honey bees) communities of the Garraf Natural Park. N= 780 plot pairs.

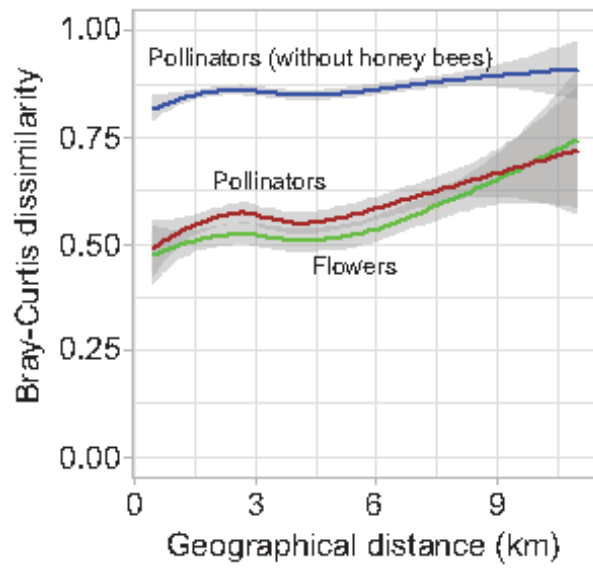


Figure 4. Graphical representation of path analyses measuring the effects of flower community structure and composition, ambient temperature and honey bee flower visitation rate on wild pollinator community structure and composition (response variables in grey boxes). The analysis of wild pollinator composition was performed with distance matrices following the methodology of Leduc et al. (1992). Dotted arrows denote non-significant relationships (after Bonferroni correction in (d)). Solid arrows represent significant positive (black) and negative (red) relationships. Arrow thickness denotes the magnitude of the effect.

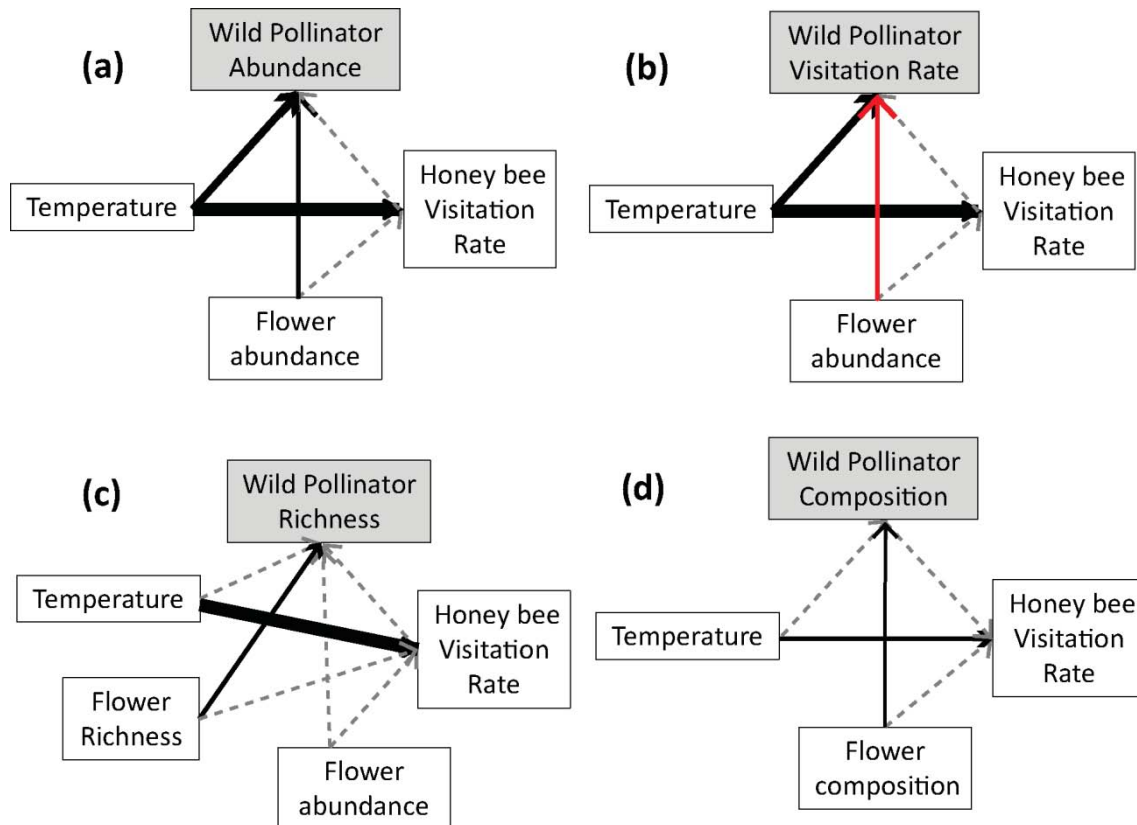


Table Legend**Table 1.** Mean, coefficient of variation, and statistical outputs of Moran's I tests for flower and pollinator community descriptors in the Garraf Natural Park (n= 40 plots).

	Mean	CV (%)	Moran's I	p-value
Flower abundance (Number of flowers)	28277	83	-0.02	0.6
Flower richness (Number of species)	8	35	0.00	0.3
Pollinator abundance (Number of individuals)	89	65	0.01	0.2
Wild pollinators	25	64	-0.02	0.8
Honey bees	64	76	-0.01	0.4
Pollinator richness (Number of species)	14	41	-0.01	0.4
Pollinator visitation rate (Number of pollinators / 1000 flowers)	3.96	58	-0.01	0.7
Wild pollinators	1.29	76	-0.01	0.6
Honey bees	2.68	69	0.01	0.1