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RESEARCH PAPER

Temporal and spatial niche complementarity in sunflower pollinator communities and pollination function

Carlos Zaragoza-Trello[a], Montserrat Vilà[a,b], Jeroen Scheper[c,d],
Isabelle Badenhausser[e,f,g], David Kleijn[c], Ignasi Bartomeus[a,*]

[a]*Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio 26, Isla de la Cartuja, 41092 Sevilla, Spain*
[b]*Department of Plant Biology and Ecology, University of Seville, 41012 Sevilla, Spain*
[c]*Plant Ecology and Nature Conservation Group, Wageningen University, 6708 PB Wageningen, The Netherlands*
[d]*Wageningen Environmental Research (Alterra), Animal Ecology Team, 6700 AA Wageningen, The Netherlands*
[e]*INRAE, USC 1339, Centre d'Etudes Biologiques de Chizé, F-79360 Villiers en Bois, France*
[f]*LTSER « Zone Atelier Plaine & Val de Sèvre », CNRS, F-79360 Villiers en Bois, France*
[g]*INRAE, URP3F (Unité de Recherche Pluridisciplinaire Prairies et Plantes Fourragères), F-86600 Lusignan, France*

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Abstract

One of the most invoked mechanisms mediating the positive effect of pollinator diversity on plant reproduction is pollinator's niche complementarity (i.e. partitioning of resource use by different pollinator species). However, the influence of spatial and temporal pollinator's niche complementarity on crop pollination function is rarely tested. We investigated the influence of spatial and temporal niche complementary in explaining sunflower crop production by comparing pollination activity at the edge and centre of crop fields and over the day. We found weaker evidence for spatial niche complementarity than for temporal niche complementarity in pollinator visitation rates. Only the visitation rate of hoverflies slightly differed between the centre and the edge of the fields. Nevertheless, we observed no differences in seed weight between the edge and the centre of the fields, but interestingly, plants allowed to be pollinated only by small-sized pollinators experienced a decline in seed production with distance from the edge. Pollinators did show complementary peak activity periods throughout the day, with *Bombus terrestris* and honeybees preferring to forage early in the day and at cooler temperatures than *B. lapidarius* and solitary bees. Unexpectedly, only morning- and only afternoon-pollinated plants produced similar seed weights, but these were higher than in all-day exposed plants. These findings indicate that sunflower fields shelter a small number of complementary pollinator species groups, which become rapidly redundant as diversity increases. Overall, we show that temporal and spatial niche complementarity effects on yield can unfold in unexpected ways, which are hard to predict without testing for the specific mechanisms.

Keywords: Bees; Seed production; Niche redundancy; Niche partitioning; Sunflower

Introduction

The relevance of biodiversity for ecosystem functioning has been widely explored, with many experimental studies

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*Corresponding author.
E-mail address: nacho.bartomeus@gmail.com (I. Bartomeus).

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showing that an increase in biodiversity promotes ecosystem functioning (Hooper et al., 2005; Cardinale et al., 2012). As a result, there is concern about the accelerated loss of biodiversity for the maintenance of key ecological processes that underlie fundamental ecosystem services (Loreau et al., 2001; Loreau & Hector, 2001). Functional redundancy and complementarity are emergent properties of communities that determine the capacity of ecosystems to cope with environmental changes. One mechanism often invoked to explain the influence of biodiversity on ecosystem service provision is niche partitioning (Naeem et al., 1994; Tilman et al., 1996, 2006). Niche partitioning entails that differences in resource use amongst species (i.e. species complementarity) increasing the efficiency of resource acquisition and hence, enhancing the rate of ecosystem processes (Aarssen, 1997; Huston, 1997; Tilman et al., 1997; Fargione et al., 2007). On the other hand, functional redundancy is defined as the ability to maintain ecosystem function in the event of species loss due to similar performance of species in the community (Walker, 1992; Naeem, 1998). Species complementarity can arise from species differences in resource use over time or over space (Hooper et al., 2005; Cardinale et al., 2006), but the role of niche partitioning in productive systems such as crops has received less attention.

Crop pollination is a key ecosystem service whose delivery is associated with insect biodiversity (Garibaldi et al., 2013). Single species, including the commonly managed honeybee, *Apis mellifera*, are generally not sufficient to provide stable pollination on their own. Indeed, many studies have shown that communities with high richness of wild pollinators increase and stabilise pollination services (Klein et al., 2003; Hoehn et al., 2008; Garibaldi et al., 2013), thereby improving the number and quality of seeds, and ultimately the commercial value of the crops (Winfree et al., 2011; Hoehn et al., 2008; Mallinger & Graton, 2015; Bartomeus et al., 2014). The positive effect of pollinator diversity on pollination function has often been attributed to complementarity amongst pollinator guilds in resource use (Blüthgen & Klein, 2011; Albrecht et al., 2012; Fründ et al., 2013).

Complementarity amongst pollinator species can be manifested at several spatial and temporal scales. At the spatial scale, it can occur within the plant if different pollinators visit flower units located at different plant positions (Brittain et al., 2013; Blüthgen & Klein, 2011; Pisanty et al., 2014) or between the outer and inner parts of the stigma within a flower (Hoehn et al., 2008). Across larger scales, pollinators can also complement each other within Pisanty et al., (2016) and across fields (Winfree et al., 2018). Temporally, the pollinator activity of different species can change throughout the day (Albretch et al., 2012; Fründ et al., 2013; Rader et al., 2013; Pisanty et al., 2016; Venjakov et al., 2016; Miñarro & García, 2018), and also at larger temporal scales, such as seasons or years (Price et al., 2005; Alarcon et al., 2008).

The factors driving niche complementarity amongst pollinators are diverse. For example, pollinators have different thermoregulatory abilities, which determine different activity patterns in response to daily temperature fluctuations (Heinrich, 1974; Bishop & Armbruster, 1999). Similarly, different pollinators might respond differently to light rain or high wind speeds. For instance, in temperate regions, bumblebees (*Bombus spp.)* and *Osmia cornuta* can forage under colder conditions than *A. mellifera* (Willmer et al., 1994; Vicens & Bosch, 2000). However, although the examples of how diversity enhances pollination services via functional complementarity are mounting, there are still few comprehensive evaluations of how temporal and spatial complementarity act simultaneously, and how this complementarity translates to seed crop yield.

Here we use sunflower (*Helianthus annuus* L.), the third most important oil crop worldwide (USDA, 2021), as a model crop system to evaluate the role of spatial and temporal pollinator niche complementarity in explaining crop production. Specifically, we provide simultaneous explorations of the spatial and temporal complementarity in sunflower pollination through flower focal observations and insect sampling at the edge and at the centre of the field and along the day to relate the observed activity patterns to plant seed production. We hypothesise that different pollinator guilds have different activity patterns between positions within the field and throughout the day, and that complementarity in these patterns enhance sunflower seed production.

Materials and methods

Study site, crop and experimental design

The study was conducted in 2015 in the French Long-Term Socio-Ecological Research site (LTSER) “Zone Atelier Plaine et Val-de Sèvre” located in the region Poitou-Charentes, in western France (46.11°N, 0.28°W). The region is characterised by an oceanic climate (mean annual temperature: 12.0 °C, annual precipitation: 820 mm) with hot and dry summers. Poor alkaline soils with low water retention capacity are predominant (Bretagnolle et al., 2018). The study site is an intensively farmed area of 430 km^2 mainly covered with winter cereals (average 2009−2016: 41.5% of the total surface), sunflower (10.4%), oilseed rape (8.3%) and maize (9.6%) (Bretagnolle et al., 2018). Green infrastructures are mainly composed of temporary and permanent grasslands (average 2009−2016: 13.5%) with different forms of management (mowing, set-aside or grazed by cattle), hedgerows along roads and adjacent to field crops, and forest patches (average 2009−2016: 2.9%) dominated by oak (*Quercus sp*.), with an understorey vegetation composed of hornbeam (*Carpinus betulus*), maples (*Acer monspessulanum, Acer campestris*) and beech (*Fagus sylvatica*) (Pettorelli et al., 2006).

Sunflower is an excellent species to study pollinator niche complementarity because of its physiological traits. Apical heliotropism in young sunflowers maintains high and

Table 1. GLMM on differences between centre and edge of the sunflower field on the abundance of the different pollinator guilds. Field plant density is included as a covariable. Wald-statistic values for hoverflies are assigned in the Z-values column.

Guild	*Model distribution*	*Variable*	*Estimate*	*Std. error*	*Z*	*Pr(>|z|)*	*N*
Honeybees	Poisson	Centre (intercept)	4.64	0.80	5.79	<0.00001	48
		Edge	0.02	0.02	0.98	0.33	–
		Density	0.20	0.32	0.60	0.55	–
Bumblebees	Negative binomial	Centre (intercept)	2.27	0.56	4.07	<0.0001	44
		Edge	0.14	0.20	0.67	0.50	–
		Density	0.00	0.23	0.01	0.99	–
Solitary bees	Negative binomial	Centre (intercept)	1.83	0.52	3.55	<0.001	40
		Edge	−0.02	0.16	−0.15	0.88	–
		Density	−0.26	0.21	−1.25	0.21	–
Hoverflies	Gaussian	Centre (intercept)	−0.28	1.15	−0.25	–	16
		Edge	0.88	0.40	2.21	–	–
		Density	0.61	0.44	1.38	–	–

constant heat loads throughout the diurnal cycle (Vandenbrick et al., 2014). Moreover, mature flowers face east permanently to warm up and be more visible and attractive to pollinators (Atamian et al., 2016). Though many sunflower cultivars are partially self- (Robinson, 1980; Mallinger & Prasifka, 2017) and wind-pollinated (Degrandi-Hoffman & Chambers, 2006), it has a significant dependence on insect-mediated pollination with an estimated average contribution of 35% to crop production (Perrot et al., 2019).

The experimental design consisted in the selection of 25 sunflower fields within the study area. Fields were selected such as they were adjacent to a grassland and located in 1-km radius landscapes with a similar and representative landscape composition (i.e. grasslands (mean ± SD: 10.2% ± 3.3) and woodlands (mean ± SD: 3.0% ± 3.5)). That is, we excluded from the selection landscapes with very low or very high cover of grasslands and woodlands (See S1). To avoid spatial autocorrelation, selected fields were at least 1 km apart. Farmer interviews conducted in 2016 provided the name of the sunflower variety sown in each sunflower field. Overall, 15 sunflower varieties were sown (See below for variety seed weight corrections; See Appendix A: Table 1).

Pollinator spatial niche partitioning: sampling within fields

To explore spatial niche partitioning between the edge and centre of the fields we conducted pollinator surveys over a 14-day period (20th-June- 8th August) by walking along two 150 × 1 m standardised transects in all sunflower fields. One transect was located at the field edge next to a grassland, on the 2nd-3rd outer crop rows, while the central transect was located at 25 m from the edge of the field. Transect walks were conducted between 9:00 and 18:00 under dry weather conditions, low wind speeds and temperatures above 15 °C. On days with temperatures exceeding 30 °C, surveys took place between 9:00 – 12:00 and 15:00 – 18:00. Sites were surveyed twice, once in the morning and once in the afternoon on the same day. We recorded all honeybees, bumble bees, solitary bees and hoverflies that visited a sunflower head during 15 min per transect, capturing the pollinators with a butterfly net. Handling time spent on pollinator capture was discounted by stopping the stopwatch during the surveys. In total, the sampling effort was 1500 min. Pollinators that were easily identifiable (e.g. honeybees and some bumblebees) were recorded without capturing. The ones we could not identify in the field were collected in vials with ethyl acetate and were identified in the laboratory (See Appendix A: Table 2).

Pollinator temporal niche partitioning: observations throughout the day

From the original 25 fields, we selected five similar fields that were at the same phenological stage and adjacent to an extensively managed grassland. These grasslands likely constitute the main pollinator habitat in the area and thereby support diverse local pollinator species pools. In each of the five sunflower fields, we conducted intensive pollinator focal observations surveys on two randomly selected sunflower plants located 1 m apart from each other and at least 15 m away from the edge inside of the field. To assess the fine scale temporal variation in visitation rates, each plant was monitored for 15 min every two hours between 9:00 am to 20:00 pm on the same day. During this time, we recorded all floral visitors and classified them into pollinator groups (i.e. *A. mellifera, Bombus terrestris, B. lapidarius* and solitary bees). Hoverfly numbers during focal observations were very low (< 4 specimens observed), and hence they were not included in this analysis. We recorded whether pollinators were gathering nectar or pollen, and documented every encounter (e.g. co-occurring within the same sunflower head) between two pollinator groups. Every two hours, at each time interval we measured air temperature within the field with a

Table 2. GLMM of the effect of temperature and time of the day on the number of visits of different pollinator taxa to sunflowers.

Taxon	Model distribution	Variable	Est.	Std. error	Z	Pr(>|z|)	N
Apis mellifera	(Negative binomial)	(Intercept)	1.71	0.18	9.34	<0.0001	31
		Temperature	−0.50	0.18	−2.83	0.005	–
		Temperature^2	0.10	0.12	0.80	0.43	–
		Time	0.05	0.13	0.40	0.69	–
		Time^2	−0.71	0.22	−3.17	0.002	–
Bombus lapidarius	(Poisson)	(Intercept)	0.85	0.39	2.17	0.03	22
		Temperature	−0.33	0.34	−0.98	0.33	–
		Temperature^2	0.24	0.17	1.39	0.17	–
		Time	0.21	0.19	1.12	0.26	–
		Time^2	−0.67	0.40	−1.65	0.10	–
Bombus terrestris	(Poisson)	(Intercept)	0.41	0.54	0.76	0.45	17
		Temperature	−0.25	0.34	−0.75	0.46	–
		Temperature^2	0.04	0.19	0.21	0.84	–
		Time	0.02	0.26	0.06	0.95	–
		Time^2	−0.09	0.46	−0.20	0.84	–
Solitary bees	(Negative binomial)	(Intercept)	0.73	0.50	1.47	0.14	14
		Temperature	0.13	0.49	0.26	0.79	–
		Temperature^2	−0.03	0.28	−0.10	0.92	–
		Time	1.71	0.18	9.34	<0.0001	–
		Time^2	−0.50	0.18	−2.83	0.01	–

thermometer not exposed to direct sunlight. In total, we surveyed pollinators for 17.5 h (210 min per field).

Pollinator exclusion experiments

To test whether spatial niche partitioning had an effect on pollination function we conducted a flower exclusion experiment across fields. In each of the 25 fields, we selected 10 pairs of sunflower plants evenly spaced every five m along a 50 m transect established five m from the field boundary to 45 m inside the field. At the end of June during the budding stage, we checked that plants within each pair had the same developmental stage and vigour, estimated by stem diameter between the third and fourth internode above the ground (Lerin & Badenhausser, 1995). Before anthesis, we randomly selected one plant within each pair and we covered its head with a fine mesh bag (< 1 × 1 mm), allowing self- and wind-pollination but excluding insect pollination ("no-pollinators" treatment, hereafter). The flower head of the other plant was not bagged and therefore accessible for all flower-visiting insects ("all-pollinators" treatment, hereafter).

Furthermore, to assess differences in pollination function based on insect body size, in each field we selected five additional sunflower plants located five m apart from the edge (i.e. from the third to the seventh selected pairs of open and bagged sunflower plants). These five plants were bagged with a 2 × 7 mm mesh to avoid access of large pollinators i.e. *Bombus, Apis, Eristalis* ("small pollinators" treatment, hereafter).

Finally, to test whether temporal niche partitioning affects pollination function we conducted another exclusion experiment examining morning and afternoon differences in flower-visitation and sunflower seed production. In the five fields where pollinators were surveyed intensively throughout the day (see above), we selected five additional pairs of sunflower plants 10 m apart from the first selected pair of open and bagged sunflower plants and parallel to the field boundary near the adjacent grassland. The flower head of one randomly selected plant within each pair was bagged from 8:00 am to 14:00 pm ("morning treatment", hereafter) while the other flower head was open to pollinators. After 14:00 pm, we switched the bags. The flower head open during the morning was bagged during the afternoon ("afternoon treatment", hereafter). The plant unbagged in the afternoon remained open until the next morning. Each plant had its own bag and we never reused bags for different plants. We repeated the experiment every day from 12 July until the end of flowering.

To control for potential bag effects on seed maturation, we removed all bags soon after flowering (mean bagging duration per field ± SD: 32 days ± 3 days).

Sunflower seed production

We harvested sunflower heads at maturity in September before the field was harvested except for one field which was therefore excluded from the yield analysis. Sunflower heads were then stored in a sheltered, well-ventilated hangar. Then, we threshed each individual sunflower head using a threshing machine (Criquet, Moulis). Full and empty seeds were sorted using a wind blow machine and by conducting a manual check visually and by hand when seeds remained unsorted. Full seeds were dried in a hot chamber for 72 h at 37 °C. Full seeds were counted with an automatic counter (Contador, Pfeuffer) and weighed with an electronic balance (0.01 g accuracy).

To take into account differences in sunflower varieties across fields, we corrected seed production weight to standardise values across varieties (See Appendix A. Table 1). Correcting factors were based on a comparison of yields of bagged and unbagged potted plants of the different available varieties under controlled conditions, in an experiment at Wageningen University Experimental Farm in 2016 (see Appendix A: S1). This experiment allowed us to avoid "variety" as a confounding factor that would prevent us from discerning the contribution of pollinators in the spatial and temporal niche dimensions analysed.

For all sampled fields, to control for differences in plant density around each focus plant, we counted the number of sunflower plants on the same row along 50 cm to the right and 50 cm to the left of the focal plant, and we measured the distance between the two nearest rows. We used these data to estimate plant density at the field scale in order to control for any effect in pollinator abundance or sunflower seed production. Moreover, to account for differences in plant vigour, we measured plant stem diameter and head diameter at harvesting time with a digital calliper (0.01 mm) and a measuring tape, respectively. Plant stem diameter and head diameter were correlated (Spearman correlation $r = 0.47$; $p < 0.001$), so finally we selected stem diameter as a proxy of plant vigour.

Statistical analysis

Spatial niche partitioning

We first explored differences in pollinator composition across fields by calculating pollinator species beta diversity as the "Horn-Morisita" similarity index. This quantitative index ranges from 0 (no similarity) to 1 (complete similarity) and is sensitive to changes in relative abundance rather than to absolute abundance changes. Similarity was analysed with *vegdist* function of "*vegan*" package (2.4−5 v) (Okansen, 2013).

Differences in the spatial niche partitioning within fields were tested with generalised or linear mixed models (GLMM or LMM) in the 25 fields with the location of the transect (centre versus edge) as fixed factor, and the abundances of each pollinator guild pooled over rounds (honey bees, bumble bees, solitary bees, hoverflies) as each of the response variables for a different model. Field site was included as a random factor and field plant density as a covariable. All models were fitted with a Gaussian error except for hoverflies that was fitted using a negative binomial link function.

Temporal niche partitioning

To test for temporal niche partitioning along the course of the day using focal observations we first assumed that the relationship between pollinator visitation rates and daytime are not linear because we expected visits to peak at midday, when temperature values are maximum. Therefore, using the data from the five temporal experimental fields, we used four GLMMs to test the effect of temperature and daytime plus their quadratic terms as fixed factors on the number of visits for the three dominant taxa (*A. mellifera, B. terrestris and B. lapidarius*) and for solitary bees as a group, as response variables. Field site was included as a random factor. Solitary bees were considered as a single group because the individuals were difficult to identify at the species level during focal plant observations. Models were fitted either with a negative binomial or with Poisson distribution depending on taxon. Temperature and time were not correlated (Spearman correlation $r = 0.05$; $p = 0.6$).

To further test for differences across groups of species, we re-analysed the relationship between temperature and activity of the different species with a GLMM with species as a fixed factor and visitation temperature as a response variable. Field site was included as a random factor. We selected temperature as it was an important variable in the initial models and the relationship observed was linear for all species. To see pairwise differences in the range of activity between species, we use post hoc analysis with Tukey contrast within the "*multcomp*" package (v.1.3.5) (Hothorn *et al.*, 2008)

Spatial and temporal differences in sunflower seed production

To analyse the effect of the different flower bagging treatments on seed production we ran linear mixed models (LMM) with treatments as a fixed factor and plant pair nested in the field site as a random factor in order to reflect the paired bagged-control plants. To account for plant vigour differences, the stem diameter measured at harvest was included as a covariable in all models (Lerin & Badenhausser, 1995). In order to control for differences in plant density around each focal plant, plant density was also included as a covariable. For one of the 25 fields we had no yield information because it was collected by the farmers before the experimental plants could be retrieved.

Spatial differences within fields included the exclusion treatment (all, none, small) as a fixed factor, distance from the field edge as a covariable and total seed weight as the response variable with a Gaussian error distribution and the random structure described above. To avoid the confounding factor of "distance from the field edge" we only used the five "all-pollinators" and five "no-pollinators" plants that were in the same rows as the "small-pollinators" treatment in each field. Then, in order to see the effect of distance separately in each treatment we also ran an extra LMM for each experimental treatment (all-, no-, small-) with all plants of each treatment as a fixed factor and seed production weight as the response variable with a Gaussian error distribution.

Temporal differences in seed production for the five fields with the "morning/afternoon" treatment were compared with a GLMM with negative binomial fitting error with the four treatments as fixed factors (all, none, morning and afternoon) and seed weight production as response variable with the same random structure. As above, we only used plants that were in the same row as the morning and afternoon treatments.

Pollinator community structure effect on sunflower seed production

To link the influence of pollinator community structure with their function we used GLMMs to test for the effect of pollinator species richness, abundance and evenness (Pielou Index) on seed production across the 24 fields. In addition to the community descriptors, we added their interaction with the open and bag treatments in order to disentangle the pollinators contribution to seed set, and plant density as a covariate. The plant pair nested in the field site was added as a random factor in order to reflect the paired bagged-control plants. We used VIF (i.e. variance inflation factors) analysis to assess any potential multicollinearity of the explanatory variables in our model.

Prior to all analyses, fixed factor variables were scaled by subtracting the mean and dividing by the standard deviation to improve model convergence. All statistical analyses were performed in R v. 3.3.3 (R Core Team 2013). We used "*dplyr*" package (Wickham et al., 2018; 0.7.7 version) and "*Lubridate*" (Grolemund & Wickham, 2011; 1.7.4 version) package for data treatment. Model fit was evaluated using the '*dHarma*' package (Hartig, 2017; 0.1.5 version) and "*MASS*" package (Venables & Ripley, 2002; 7.3−4.8 version) for negative binomial fit. For paired comparison tests between treatments in seed production we used Tukey post-hoc analysis with "*multcomp"* package (v.1.3.5) (Hothorn *et al*., 2008). For graphic visualization we used "*yarrr*" package (Philips, 2018; 0.1−5 version) and "*ggplot2*" (Wickham, 2016; 2.2.1 version) for data plots; "*visreg*" package (Brehenny & Burchet, 2016; 2.4.1 version) for regression model visualization; and "*fields*" (Nychka et al., 2015; 9.0 version) and "*akima*" (Akima & Gebhardt, 2016; 0.6−2 version) as well as "*Gridextra*"(Auguie, 2017; 2.3 version) packages to construct heatmap plots.

Results

Across the 25 fields surveyed by transect walks, in total we observed 13,099 individual pollinators from 24 species: the honeybee, 5 bumblebees, 13 solitary bees and 5 hoverfly species (See Appendix A: Table 4). The most common species was *A. mellifera* (94%) followed by *B. terrestris* (3%) and *B. lapidarius* (2%). Similarity was overall low (Horn index mean = 0.115; SE = ± 0.01) across fields, indicating high potential for complementarity across fields (see Appendix A: Fig. 2).

Spatial niche partitioning and seed production

The abundance of honeybees, bumblebees and solitary bees was not significantly different between the field edge and the centre. On the contrary, hoverflies were mostly found at the field edge (Table 1, See Appendix A: Fig. 3), but in very low numbers. Sunflower plant density had no significant effect on any pollinator guild (See Table 1, See Appendix A: Fig. 3).

Post-hoc analysis showed differences between all-pollinators and no-pollinator treatments (estimate ± SE; 11.36 ± 1.87; $p < 0.001$), between small- and all-pollinator treatments (−5.06 ± 1.87; $p < 0.05$) and between small- and no-pollinators treatments (6.31 ± 1.88; $p < 0.05$) (Fig. 1). In summary, excluding all pollinators or only big pollinators decreased seed production. However, excluding big pollinators had a smaller effect than excluding them all (Table 3).

Interestingly, the distance from the edge had a steep decrease in seed production in flowers pollinated by small pollinators (−2.31 ± 1.070; $t = -2.29$). This effect was not significant either in flowers exposed to all pollinators (−0.33 ± 0.32; $t = -1.02$) or in bagged flowers with no pollinators (−0.03 ± 0.35; $t = -0.10$; Fig. 2).

Temporal niche partitioning and seed production

In the five fields intensively surveyed throughout the entire day, we observed 360 pollinator visits. Pollen collection was less frequent than nectar foraging except for solitary bees. In total, we registered 147 *A. mellifera*, 65 *B lapidarius*, 32 *B terrestris* and 7 solitary bee individuals foraging for nectar versus 3 *B lapidarius*, 2 *B terrestris* and 29 solitary bees gathering pollen. None of the observed honeybees was carrying pollen. Within the sunflower head, we did not observe interactions amongst pollinators. Indeed, of the 25 encounters between two pollinator species we only observed one aggressive behaviour event between *A. mellifera* individuals and other pollinators visiting the same sunflower head.

Overall, we observed more visits during the morning (9:00 am to 14:00 pm) than during the afternoon (14:00 pm to 20:00 pm): 101 *A. mellifera*, 45 *B lapidarius*, 20 *B terrestris* and 19 solitary bee individuals during the morning versus 66 *A. mellifera*, 27 *B lapidarius*, 15 *B terrestris* and 20 solitary bee individuals in the afternoon (chi-square test: $X^2 = 2.27$; $p < 0.05$).

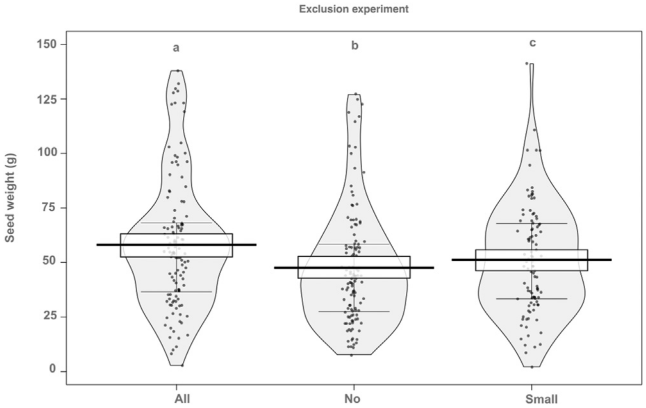

Fig. 1. Raw, Description and Inferential (RDI) plot with sunflower seed weight production differences between All-pollinators (open flowers), No-pollinators (bagged flowers) and Small-pollinators (bagged flowers excluding big pollinators) treatments. Shade represents a smoothed density of the data, points represent raw data, the vertical bar shows quantile lines and horizontal bar central tendencies. Significant differences between groups estimated through posthoc Tukey's contrast are indicated by different letters.

The heat maps illustrating model estimates for each species over the day and across different temperatures showed a potential niche partitioning across taxa (Fig. 3). Solitary bee visits were more frequent at central hours of the day and at high temperatures. However, honeybees were active during a wide range of the day and at lower temperatures than solitary bees. Albeit more variable, a similar range of activity was found in *B. lapidarius*. In contrast, *B. terrestris* tended to be more active at lower temperatures and earlier in the day, but this trend was not significant due to the observed high variability (Table 2). This temporal niche partitioning was mainly driven by the temperatures at which different groups were active. Overall, *B. terrestris* temperature range differed from the rest of the groups. There were significant differences between *A. mellifera* and *B. terrestris* (−2.09 ± 0.79; $p < 0.01$), *B. lapidarius* and *B. terrestris* (−3.04 ± 0.90; $p < 0.05$), and *B. terrestris* and solitary bees (3.57 ± 0.97; $p = 0.001$; Fig. 4).

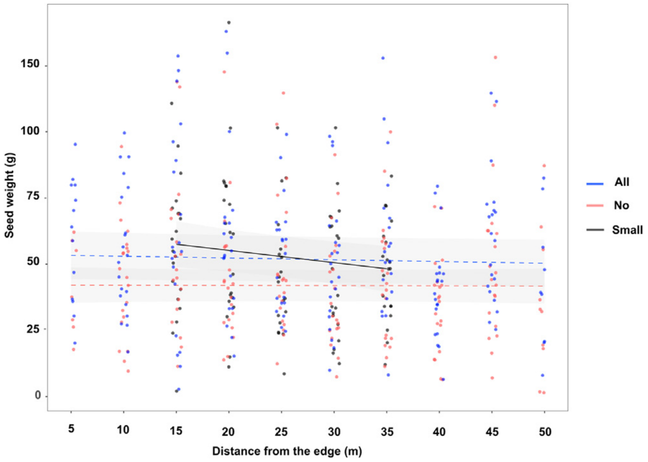

Fig. 2. Relationship between distance to the field edge and sunflower seed weight production in different flower bagging treatments according to GLMM analysis. All-pollinators (open flowers -blue-), No-pollinators (bagged flowers -red-) and Small-pollinators (bagged flowers excluding big pollinators -black-). The dashed lines show non-significant relationships. "Small-pollinators" treatment showed a significant relationship between distance to the field edge and sunflower seed weight production. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

There were significant differences in seed production between temporally restricted, all-day open, and no-pollinators treatments. Surprisingly, there was higher seed production in the morning and afternoon exclusion treatments than in the all-day open treatment (Table 3). *Post-hoc* analysis showed significant differences between all-day open and no-pollinator treatments (11.44 ± 3.08; $p < 0.01$), afternoon and all-day open treatment (14.77 ± 4.73; $p < 0.01$) and all-day open treatment and morning treatments (−28.75 ± 4.72; $p \leq 0.001$) as well as between no-pollinator treatment and afternoon (26.22 ± 4.73; $p < 0.001$) and no-pollinator and morning treatments (−26.90 ± 4.95; $p < 0.001$). Nevertheless, there was no significant difference between afternoon and morning treatments (−2.53; ± 4.09; $p > 0.05$) (Fig. 5). Stem diameter was strongly correlated

Table 3. GLMMs of temporal and spatial pollinator exclusion treatments in sunflower seed weight production.

Model	Variable	Estimate	Std. Error	t	N
Morning/Afternoon	None	−45.86	17.83	−2.57	138
	All	10.40	2.90	3.58	–
	Morning	26.21	4.61	5.68	–
	Afternoon	24.24	4.63	5.24	–
	Density	−7.21	6.17	−1.17	–
	Stem Diameter	5.14	0.41	12.55	–
Small	None	−37.64	15.19	−2.48	298
	All	11.36	1.87	6.06	–
	Small	6.31	1.88	3.36	–
	Plant Distance	−1.08	0.71	−1.52	–
	Density	−3.26	5.06	−0.65	–
	Stem Diameter	4.52	0.28	16.09	–

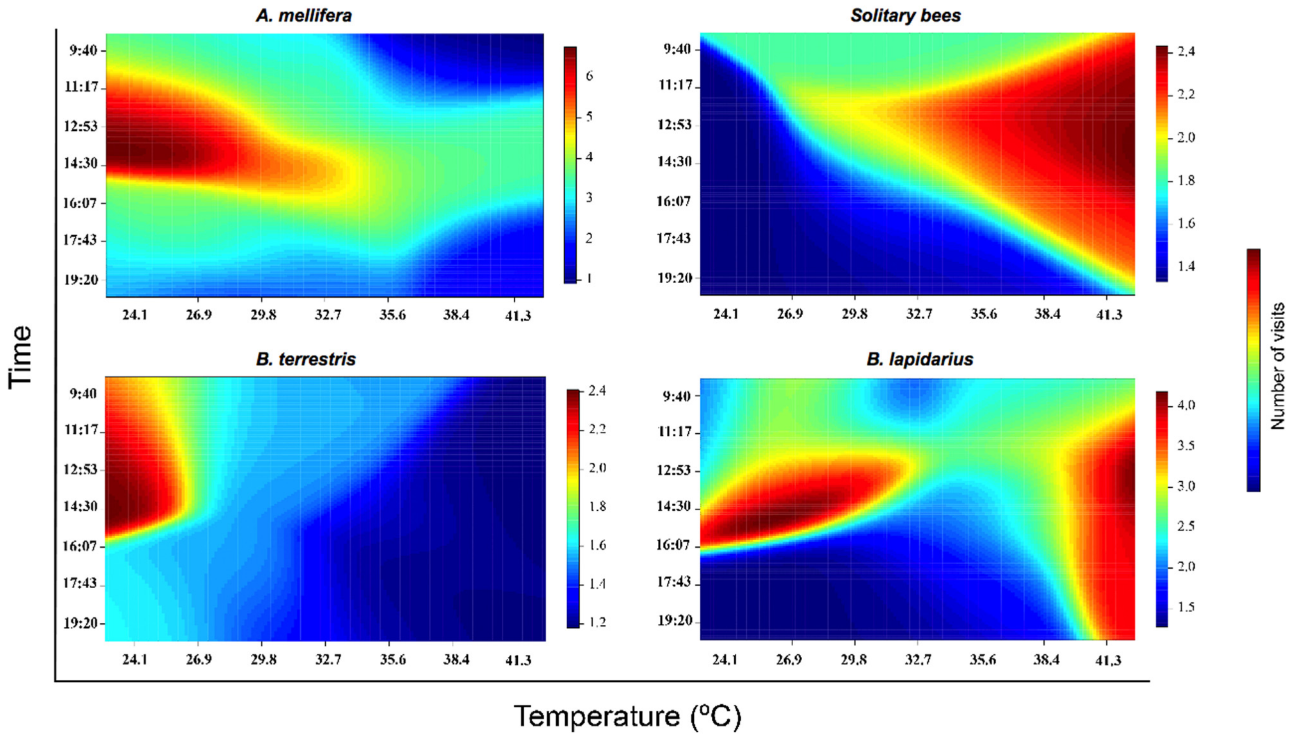

Fig. 3. Heatmap plotting predicted model values of the number of visits on sunflowers for the different pollinator taxa throughout the day (from 9:00 am to 20:00 pm). Temperature ranges from 22.9 °C to 42.5 °C. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

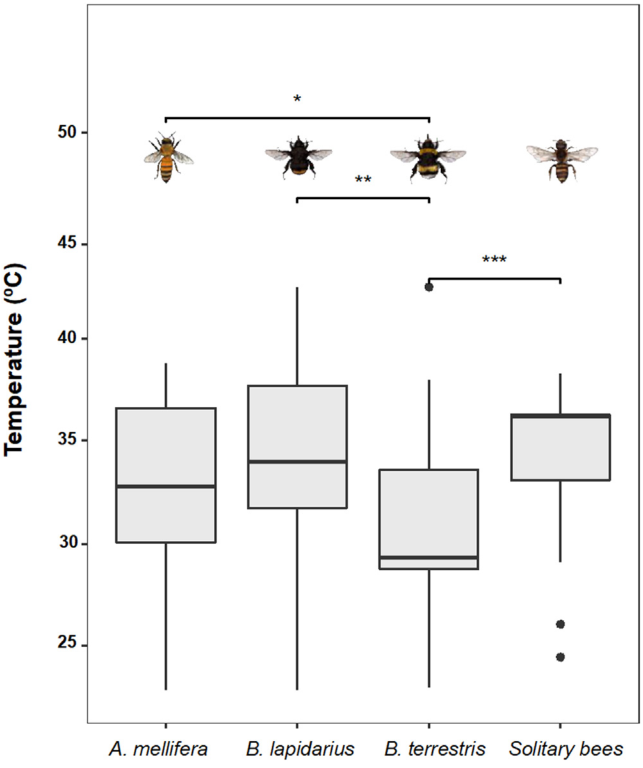

Fig. 4. Box-plot representing the effects of temperature on the activity of different pollinator taxa visiting sunflowers (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$).

with seed production. However, density of plants in the field had no effect (Table 3).

Pollinator community structure association with sunflower seed production

Seed production per plant across the total 24 fields increased on average 20% in open pollinated plants indicating that pollinators increased seed production (Table 4). Overall, seed production was explained mainly by stem diameter. In addition, we found a clear positive effect of species evenness on the seed set, an effect that was lower when pollinators were excluded (‘none’ x evenness= −2.73 ± 1.74; $p = 0.06$). Total richness and abundance had no effect on seed production.

Discussion

Our results indicate niche partitioning in sunflower pollinator communities at temporal and spatial scales. We observed that at the spatial scale there was a decrease in seed production towards the centre of the field only when big pollinators were excluded. This is the first indication that at the field scale, the ubiquitous large pollinators may be redundant, rather than complementary to small pollinators in pollination function. Similarly, at the temporal scale,

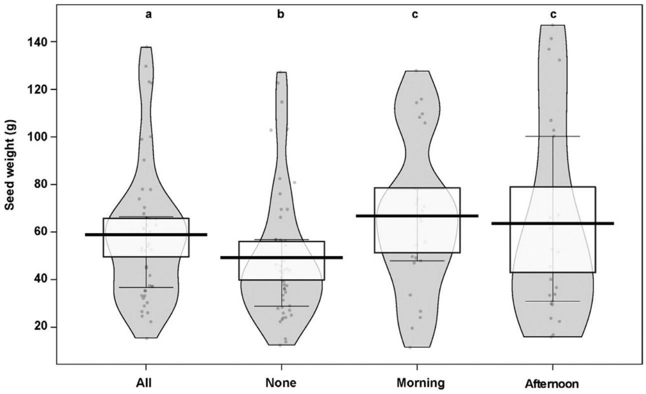

Fig. 5. Raw, Description and Inferential (RDI) plot with sunflower seed weight production differences between all, none, morning and afternoon pollination exclusion treatments. Shades represent a smoothed density of the data, points represent raw data, vertical bar shows quantile lines and horizontal bar central tendencies. Significant differences between groups estimated through the posthoc Tukey's contrast are indicated by different letters.

niche partitioning throughout the day amongst pollinators was not related to complementarity for seed weight production. On the contrary, we found that all-day pollination exposed sunflowers had lower seed weight than sunflowers exposed for half of the day (morning or afternoon). This, again, points to potential pollinator redundancy, in this case with negative effects on yield. Interestingly, pollinator evenness, but not abundance or richness, increased sunflower seed production in sunflowers exposed all day to pollinators.

Spatial niche partitioning and seed production

Spatial niche partitioning amongst pollinators within the field was low. Although not very common in our surveys, there were differences in hoverfly abundance between the edge and the centre of the field. Field margins are well known to act as pollinator refuge and could offer a high availability of food resources for hoverfly adults and larvae as well as shelter from predators or mating sites both during and after the sunflower bloom (Sutherland et al., 2001; Brunbjerg et al., 2018; Cole et al., 2020; Li et al., 2020). Hence hoverflies could spill-over into the field. However, these results have to be considered with caution because hoverflies are highly mobile. Although we did not find an edge effect on solitary bees, pollinator spatial patterns can vary amongst years in sunflower fields, as shown for this same region (Perrot et al., 2019).

The effect of distance to the edge in seed production partially matched the observed visitation patterns. On one hand, when all pollinators were allowed to visit plants there was no decline on seed set with distance. But when big pollinators were excluded, the contribution of small bees and hoverflies was enough to produce high seed production only within the first ten metres from the edge. This result could indicate that, at least for the surveyed year, the benefits of small pollinators occurring near natural areas are redundant compared to the contribution of large pollinators to crop production. These results together reinforce the idea that at the field edges, the conservation contribution of small pollinators is essential for the maintenance of crop yield, but there is a dilution of small pollinators towards the centre of the field (Pufal et al., 2017).

Temporal niche partitioning and seed production

There was a clear temporal niche partitioning throughout the day. The temperature at which bees were most active differed across taxa. However, contrary to our initial hypothesis, these differences did not lead to enhanced seed production. Regarding pollinator foraging activities, even communities, represented more equitably by *A. mellifera, B. terrestris, B. lapidarius* and solitary bees, could maximise temporal niche complementarity between different pollinator taxa. For example, we observed that solitary bees, and to some degree *B. lapidarius,* were more active at high temperatures, potentially complementing pollination by *B. terrestris* and *A. mellifera*, which have higher activity at lower

Table 4. Relationship between seed weight production and the pollinator community structure according to a GLMM with the interaction between experiment treatment and pollinator species richness, abundance and evenness (Pielou Index) as fixed factors. Stem diameter and field plant density were included as covariables. No-pollinators indicate bagged flowers.

Variable	Estimate	Std. Error	t	Pr(>|t|)	n
(Intercept)	56.47	2.81	20.10	0.00	478
Plant density	−3.96	2.87	−1.38	0.18	–
Stem diameter	20.81	0.91	22.93	< 0.001	–
No-pollinators	−11.64	1.19	−9.80	< 0.001	–
Abundance	5.78	3.45	1.68	0.11	–
Richness	−4.39	2.84	−1.54	0.14	–
Evenness	10.12	3.55	2.85	0.01	–
No x Abundance	0.37	1.44	0.26	0.80	–
No x Richness	−1.45	1.20	−1.21	0.23	–
No x Evenness	−2.73	1.44	−1.89	0.06	–

temperatures (Fig. 3). These activity patterns respond to their specific thermoregulatory capability (Bishop & Armbruster, 1999). Nevertheless, these different activity patterns did not translate to differences in seed production during the day. This could be explained by the balance in the relative abundance of the different pollinator taxa in the morning and in the afternoon (see Results section on *Temporal niche partitioning and seed production*), which would lead to achieving similar seed production. Alternatively, given the strong dominance of honeybees during our focal observations, which account for 53% of the visits, these complementary effects on yield may also be diluted in most fields due to the high honeybee densities. Moreover, in our experiment, we did not take into account the pollination efficiency of each species, which could be important in sunflower according to the differences in efficiency observed in *Andrena helianthii* and *Melissodes agilis* (Parker, 1981; Mallinger et al., 2018) compared to the honeybee. Differences in pollinator efficiency is commonly observed in other crop systems (Pisanty et al., 2016; Rader et al., 2013; Garibaldi et al., 2015).

An unexpected finding was a higher seed production in flowers exposed to pollinators during half of the day (morning or afternoon) than in flowers exposed all day. This could indicate that crossing a threshold of pollinator visits, especially from abundant honeybees, could lead to a reduction in fertility due to damage of the stylus or stigma during landing, deposition of low quality pollen or heterospecific pollen deposition (Magrach et al., 2017; Saez et al., 2014; Streher et al., 2020). These results are substantiated by the fact that at the edge rows, with treatments allowing only small pollinators, we observed higher seed weight than in plants exposed to all size pollinators. In any case, the evidence suggests that even in the low-diversity fields, the number of visits and richness levels observed are enough to ensure crop yield, and in most fields we may be observing high densities of managed honeybee visits, with potential negative effects.

Pollinator community structure association with sunflower seed production

We found that pollinator evenness is the main factor associated with an increase in sunflower seed production. This result suggests that an even community, and not necessarily the most abundant, could produce higher seed production in sunflowers. Note that evenness and abundance are weakly correlated in our dataset (R = 0.57), and abundance refers mostly to a single dominant species, the honeybee. Garibaldi et al. (2013) found that an increase in wild insect visitation increases seed production twice as much as a similar increase in honeybee visitation in 41 cropping systems worldwide, thereby showing the efficiency of the pollinating insect assemblage. Interestingly, we observed that some even communities were not particularly rich in species, but the few guilds represented enhanced seed production only when they were balanced in terms of frequency. For instance, at low pollinator abundances e.g. when only small bees or only half of the day are considered, we may be observing higher yields than when all pollinators are considered throughout the day.

On the contrary, other studies have found a positive correlation between *Apis mellifera* abundance and seed production (Greenleaf & Kremen, 2006; Pisanty et al., 2014; Perrot et al., 2019). Some studies associated with interactive encounters between honeybees and other pollinator species which could increase the efficiency of honeybee pollination (Carvalheiro et al., 2011; Greenleaf & Kremen, 2006). Note, that in our study system we observed very few interactions between honeybees and wild bees despite actively looking for them.

In this study, we only focused on two aspects of complementarity, but other sources of complementarity are possible, including pollinator behaviour (Greenleaf & Kremen, 2006; Miñarro & García, 2018), spatial location within plants (Blüthgen & Klein, 2011) or cross-scale complementarity (Winfree et al., 2018). Additionally, exploring a broader time scale encompassing different asynchronous blooming fields would reveal a different complementarity arising from the different phenologies and periods of activity of particular solitary bee species, some of them only active at certain times for a few weeks of the year. Future research should highlight the importance of unravelling the multiscale nature of the complementary mechanisms.

In summary, our findings reveal that temporal and, to a lesser extent, spatial niche complementarity are present in pollinator communities on sunflower fields. However, contrary to our initial hypothesis, we find redundancy in the pollination function for both temporal and spatial scales. Interestingly, we show that at small distances from the edge, small pollinators could fulfil or even improve the pollinator function compared to the all-pollinators' set. This finding highlights the relevance of local wild solitary bees, in spite of being rare in comparison with large-size bees, especially the managed honeybee. In a context of the current pollinator crisis, developing measures of management should favour both, the conservation of local bee communities and support the resilience of seed production without necessarily depending on managed species such as the honeybee (Cole et al., 2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2023.01.001.

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