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Watermelon pollinators exhibit complementarity in both visitation rate and single-visit pollination efficiency

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Summary

1. The concept of pollinator niche complementarity maintains that species-rich pollinator communities can provide higher and more stable pollination services than species-poor communities, due to contrasting spatial and/or temporal pollination activity among groups of pollinators. Complementarity has usually been examined in pollinators' patterns of flower visitation or abundance, while largely neglecting the possibility of complementarity in patterns of single-visit contribution to fruit/seed set (pollination efficiency). However, variability in pollination efficiency can greatly affect pollinators' overall pollination services and may therefore contribute an additional, important aspect of complementarity.

2. In this study, we investigated the existence of pollinator complementarity in both visitation rates and pollination efficiencies. The study was conducted in 43 watermelon fields cultivated for seed consumption in a Mediterranean agro-natural landscape in central Israel. We studied spatiotemporal variation in pollinators' visitation activity, measured by repeated observations and netting, and single-visit pollination efficiency, measured by the fruit and seed set rates of hermaphrodite flowers exposed to a single bee visit. Visitation and pollination efficiency were measured throughout the day and season, within and between fields with contrasting availability of nearby wild plants, and among flowers of different sizes.

3. Pollinator species' visitation rates as well as single-visit fruit set efficiencies, but not seed set efficiencies, exhibited significant spatiotemporal variation that contributed to their complementarity. Pollinators' visit frequencies were affected by surrounding land use, location within field, time throughout the season, and time of day. Pollinators' fruit set efficiencies were affected by ovary size and time of day.

4. *Synthesis and applications*. Crop pollinators may exhibit complementarity in both their visitation rates and pollination efficiencies, which can promote the overall level and stability of their pollination services. Complementarity in pollination efficiencies suggests further diversity effects on crop yield, and calls for taking into account the variability in pollination efficiency along spatiotemporal scales rather than considering it a constant, species-specific trait. However, some modes of niche complementarity may not necessarily translate into increased pollination services and crop yield; the relevance and limitations of such mechanisms should be considered in the light of the specific crop and management system studied.

Key-words: biodiversity–ecosystem function, crop pollination, edge effect, field edge, flower size, fruit set, honeybee, Mediterranean agroecosystem, niche complementarity, wild bee

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Introduction

The role of biodiversity in enhancing animal pollination services has received increasing focus in recent years, due to local pollinator declines (Potts *et al.* 2010) coupled with an ever increasing global demand for animal pollination of crops (Aizen *et al.* 2008). Several studies have demonstrated that species-rich pollinator communities can provide higher and more stable pollination services than a single managed pollinator species such as the western honeybee (e.g. Klein, Steffan-Dewenter & Tscharntke 2003; Hoehn *et al.* 2008; Garibaldi *et al.* 2011, 2013). Two main mechanisms have been identified as responsible for this effect: interspecific interactions that alter the behaviour of pollinators (Brittain *et al.* 2013), and spatiotemporal niche complementarity among different groups of pollinators (Blüthgen & Klein 2011). Other mechanisms have also been tested (Winfree & Kremen 2009; Winfree 2013) but empirical studies on this topic are scarce, and our understanding of the mechanisms shaping the diversity–functionality relationships in pollinator communities is limited.

The concept of niche complementarity maintains that pollinators differ in their physiologies and behaviours, and thus forage during different seasons and times of day, on different types of flowers, and in different habitats (Blüthgen & Klein 2011). Therefore, a diverse pollinator community may achieve higher crop yields (Garibaldi *et al.* 2011, 2013), with greater stability and resistance to environmental changes (Winfree & Kremen 2009; Bartomeus *et al.* 2013; Rader *et al.* 2013). Niche complementarity can be manifested in diverse spatial and temporal scales, from variation among years and landscapes (Price *et al.* 2005; Alarcón, Waser & Ollerton 2008) to fluctuations throughout the day (Albrecht *et al.* 2012; Rader *et al.* 2013) or even within a single flower (Chagnon, Gingras & De Oliveira 1993; Hoehn *et al.* 2008).

Complementarity has gained increased research attention in recent years, but major gaps in our understanding still remain. One such gap concerns land-use effects on pollination patterns of different pollinator species. The type of land use surrounding agricultural fields and the distance of the focal crop plant from the field edge affect crop visitation by wild bees. Undisturbed field margins with ample native vegetation may increase pollination services to nearby crops compared to disturbed field margins (Ricketts *et al.* 2008; Garibaldi *et al.* 2014); this effect of increased pollination decays from the field edge towards its centre (Chacoff & Aizen 2006; Gemmill-Herren & Ochieng 2008). However, not all bee groups are equally dependent upon native vegetation along field edges. Some taxa appear to be more adapted to the agricultural environment and have higher abundance in agricultural settings (Klein, Steffan-Dewenter & Tscharntke 2003; Cariveau *et al.* 2013; Kleijn *et al.* 2015). Hence, pollinator activity along field edges and in field interiors may vary among bee groups.

Flower morphology is another important factor that may affect bee complementarity. Since the morphology of a flower affects its advertisement and reward, that is its attractiveness for pollinators (Waser 1983), pollinator groups vary in their preferences for specific parts of flowers and inflorescences, or flowers of different shapes and sizes, and these may in turn create significant differences in fruit or seed set among floral morphologies (Chagnon, Gingras & De Oliveira 1993; Pisanty, Klein & Mandelik 2014). Hence, the effects of both land use and flower morphology may lead to differences among bee groups in their spatial pollination patterns, and possibly to pollination complementarity. However, research into complementary patterns among crop pollinators with respect to land use or floral morphologies is sparse.

Complementarity has usually been demonstrated as contrasting spatial and/or temporal patterns of flower visitation or abundance between pollinator taxa or functional groups (e.g. Winfree & Kremen 2009; Albrecht *et al.* 2012; Brittain, Kremen & Klein 2013; Cariveau *et al.* 2013). However, complementarity can also be manifested in the different behaviours of pollinators within a single floral unit (e.g. pollen deposition vs. redistribution, Hoehn *et al.* 2008), which may further enhance fruit and/or seed set. Furthermore, visitation rates or abundance of different pollinators, taken alone, are an incomplete measure of their pollination services. Pollination efficiency, that is the single-visit contribution to fruit or seed set, also differs substantially among pollinators (Schemske & Horvitz 1984). Different morphologies (e.g. body size, hairiness) and behaviours (e.g. visit duration, pollen vs. nectar collection) of pollinator species can have various outcomes for the visited flower, ranging from nectar/pollen larceny to maximum fruit/seed set (Sahli & Conner 2007). Spatial and temporal variation in single-visit efficiency is common even within a given pollinator species, and thus may potentially exhibit complementary patterns among different species. This variation is related to various floral and environmental variables such as temporal patterns of anthesis, pollen viability and stigma receptivity (Freitas & Paxton 1998; Rader *et al.* 2013), flower location within the plant (Diggle 2003), and overall visitation rates (Hingston & McQuillan 1999). Nevertheless, most studies refer to single-visit pollination efficiency as a species-specific constant trait and fail to measure it along spatiotemporal scales. Very few studies have tested the complementary trends of pollinators along spatial or temporal scales, as manifested in their single-visit efficiencies rather than visitation rates (but see Rafferty & Ives 2012).

In the current study, we investigated the contribution to pollinator complementarity of different levels of spatial, temporal and floral effects on both visitation rates and single-visit pollination efficiencies. Our plant model was seed watermelon *Citrullus lanatus* (Thunb.) Matsum.

& Nakai, a self-compatible crop that is dependent upon insect visitation to set seed and is attractive to various bee species (Free 1993). We studied variation in pollinators' visitation activity and pollination efficiency throughout the day and season, within and between fields with contrasting availability of nearby wild plants, and among flowers of different sizes. Our research questions were as follows: (i) Do bee assemblages visiting watermelon show niche complementarity? (ii) If so, is complementarity expressed by visitation rates, pollination efficiencies, or both? (iii) How does variability in spatial, temporal and floral factors contribute to this complementarity?

Materials and methods

STUDY SYSTEM

The research was carried out during 2009–2012 in the Judean Foothills, a Mediterranean agro-natural ecosystem in central Israel (31·6–31·9°N 34·7–35·0°E, 60–280 m a.s.l.). All data were collected under standardized weather conditions (sunny days, wind velocity <6 m s^{-1}, temperature >18 °C). The Malali cultivar watermelon for seed production is commonly grown in the region under a crop rotation regime, either with drip irrigation or under dryland conditions; hence different fields were tested each year. Fields are sown in March at a density of 3 plants m^{-2}, and reach bloom in mid-May; seeds are harvested in August-September.

On each runner of a Malali plant, flowering progresses from the base to the apex; each day, 0–2 male and/or hermaphrodite flowers open in early morning and wilt in late afternoon. Ovaries which are poorly pollinated, damaged or in excess are aborted, usually within less than a week of anthesis. Fruit development and ripening takes 30–40 days post-anthesis. A single plant typically bears two mature fruits.

The wild bee fauna in the region is diverse, consisting mostly of tiny- to medium-sized, solitary to primitively eusocial bees (Pisanty & Mandelik 2015). Honeybees *Apis mellifera* Linnaeus 1758 are commonly managed for crop pollination and honey production, but feral honeybees are rare due to *Varroa* mites. There is no consensus as to the necessity of placing honeybee hives for watermelon pollination, and practice varies among farmers; the majority of our research fields lacked hives, nevertheless honeybees from nearby hives were usually abundant.

DATA COLLECTION

Data were collected using two complementary approaches. First, to characterize crop-visiting bee assemblages along a land-use gradient, we collected and observed bees in fields spanning a range of land-use intensities ('flower visitor survey'). Next, to evaluate the contribution of different bee guilds to crop pollination and the effect of land-use patterns on this contribution, we observed bees and manipulated plants in fields bordering different types of edges ('pollination study'). Here we focused on land-use effects at short radii, as areas closer to the field are easier to manage (Garibaldi *et al.* 2014) and because in the visitor survey we found highest correlation of land use with crop-visiting bee abundance at short radii (50 m).

Flower visitor survey

A survey of visitors to watermelon flowers was conducted in 32 fields – 19 in 2009 and 13 in 2010, all at a minimum distance of 1 km from each other. In each field, a 25 × 25 m plot was marked at the field edge; in eleven fields that were sufficiently large to test for edge effects, an additional 25 × 25 m plot was marked at the interior of the field, 80–110 m from the edge. Each plot was surveyed on one to two different dates, two times per day, between 7:00–9:00 h and 9:00–11:00 h, with intervals of ≥60 min between successive rounds. Each sampling round included 10 min of slow walking along the rows of the plot and recording the number of observed honeybee (HB), wild bee (WB) and (in the first year of survey) other insect visits to watermelon flowers, followed by an additional 10 min of netting wild bees from watermelon flowers to enable species-level identification. We used both visit observations and nettings to allow accurate assessment of both very common, easily identifiable visitors that preclude netting (i.e. honeybees), together with other, rarer taxa that require skilled identification. We measured the density of watermelon bloom in each plot on each sampling day by counting the flowers in each of 20 1-m diameter circles evenly spaced throughout the plot.

Edge plots varied in their surrounding land use, that is the proportion of agricultural vs. semi-natural habitat (mainly Mediterranean shrubland, but also some patches of planted forests), as calculated from aerial and satellite photos using ArcGIS 9·3 (ESRI, Redlands, California, 2008) at eight different radii (50–2500 m). Plots were surrounded by 0–56% and 10–77% semi-natural habitat at 50 and 2500 m radii, respectively.

Pollination study

A pollination study was conducted in eleven fields, in 2011–2012, during peak watermelon bloom. We selected 16 study plots (ca. 50 × 30 m) along field edges, one to two plots per field, at least 200 m apart. Three distinct types of field edges were classified, representing different land-use intensities: five plots bordered a semi-natural shrubland (batha, hereafter termed 'semi-natural' edge type); three plots bordered intensively managed cotton fields devoid of any wild plants ('no wild vegetation'), and the remaining eight plots bordered disturbed areas that contained some patches of wild plants, and included cotton or ploughed fields, plantations and clearings ('with wild vegetation'). Pairs of plots situated in the same field bordered different edge types. Based on the diversity of bee groups active in each plot, and in order to achieve sufficient representation of all bee groups in the pollination experiments, sampling lasted one to four days per plot. Two types of data were collected:

Visit frequency measurements. Every hour between 0800–1300 h, we randomly selected two patches, each containing hermaphrodite (1–3) and male (1–9) flowers, and recorded the number of bee visits during 3 min of observation per patch. Based on preliminary results, visiting bees were classified into three categories: honeybees (HB), small wild bees (SWB; intertegular distance (ITD) 1·5–2·4 mm) and tiny wild bees (TWB; ITD <1·5 mm). Limited collection of wild bee specimens was conducted between rounds of observation to enable species-level identification of the bee assemblage visiting the crop.

Single-visit pollination experiments. Experiments were conducted in each plot concurrently with visit frequency measurements. One hermaphrodite flower per plant was covered with a muslin bag in the afternoon before anthesis, to prevent insect visits. The following day, flowers were exposed to a single bee visit between 0800 and 1300 h. We recorded the category of the visiting bee, the type of foraging activity (i.e. nectar and/or pollen collection) and the duration of the visit. Only visits in which the bee touched the stigma and/or anthers were considered. To determine whether flower morphology affected the activity of different bee groups, we also measured the ovary width of each test flower (see Adlerz 1966) with a vernier calliper. Immediately after the visit ended the flower was rebagged and marked. Positive and negative control treatments consisted of flowers that were left unbagged/bagged throughout the day of anthesis, respectively. In three plots, we also included a hand pollination treatment, applying pollen to the stigma with a delicate brush. Since developing fruits inhibit additional fruit set in watermelon, all previously set fruits and hermaphrodite flowers present on the tested plant on the day of the experiment were removed, providing the treated flowers with optimal conditions for development (Adlerz 1966). Marked flowers were monitored once a week to check for fruit development or abortion; since aborted fruits bear no mature seeds, differences in fruit set also affect overall seed production and yield. Mature fruits were harvested 30 days post-anthesis, weighed and measured for their diameter and then dissected for seed extraction; the number of fully developed seeds, that is seeds with blackened edges, was recorded.

STATISTICAL ANALYSIS

Statistical analyses were performed using PC-ORD version 5 (MjM Software, Gleneden Beach, OR, USA) (Mantel tests); R software, version 3.1.3 (R Core Team 2015) (generalized linear mixed models); and IBM SPSS Statistics 20, Release 20.0.0 (SPSS Inc., Chicago, IL, USA 2011) (all other analyses).

To test whether our plots were spatially independent, we used Mantel tests (999 iterations) to assess spatial autocorrelation of bee groups' relative visitation rates. We used Sørensen's similarity index to calculate visitation distance matrices. Data showed weakly negative or no autocorrelation among edge plots (visitor survey: $r = -0{\cdot}08$, $P = 0{\cdot}07$; pollination study: $r = 0{\cdot}02$, $P = 0{\cdot}33$), indicating their independence.

We used simple correlation to test the effect of percentage surrounding semi-natural habitat at different radii on bee visitation in edge plots; separate analyses were conducted for shrubland only and for shrubland and planted forests combined. The land-use classification and radius showing highest correlation values were selected for further analysis.

Differences in the response of guilds or taxa to a spatiotemporal predictor, possibly suggesting complementarity, can be indicated by a significant interaction between the 'guild' factor and the predictor. We used this principle to test for complementarity in the effects of spatial, temporal, floral and behavioural variability on bee visitation and single-visit pollination efficiency. Data of bee visitation, netted bee abundance, and fruit set from edge plots were each analysed using generalized linear mixed models (GLMMs), incorporating all levels of spatiotemporal variation as detailed below. Additionally, we analysed differences in bee abundance and visitation between edge and interior plots using a repeated-measures ANOVA (RANOVA), with bee group, location within field, and their interaction as factors. Bees were grouped according to the level of identification possible when working in the field and the limitations of sample size. Hence, although we distinguished between small and tiny wild bees in the pollination study, we grouped them together when modelling fruit set rates against spatiotemporal predictors, after inspecting their similar plotted spatiotemporal trends.

GLMM analyses were designed as follows: In the *visit count* analysis, we modelled the number of bee visits observed per 20 min walk in the field (early and late morning censuses combined), with bee group (HB/WB) as a within-subject factor, and % surrounding semi-natural habitat (at the most explanatory radius), date (number of days since 1st May, regardless of year – reflecting seasonality) and field flower density as covariates. In the *bee capture* analysis, we modelled netted bee presence/absence per 10 min netting round, with bee genus as a within-subject factor (excluding genera with <30 individuals collected), and date, hour and field flower density as covariates. In the *visit frequency* analysis, we modelled bee visitation presence/absence per 3 min patch observation, with bee group (HB/SWB/TWB) and flower gender as within-subject factors, field edge type (semi-natural/with wild vegetation/no wild vegetation) as factor, and date, hour and number of male/hermaphrodite flowers per patch as covariates. In the *fruit set* analysis, we modelled fruit maturation/abortion, with bee group (HB/WB), field edge type, field irrigation (yes/no) and bee pollen collection activity (yes/no) as factors, and date, hour, ovary width and visit duration as covariates. Interaction effects between bee group and other predictors were included in all models; plot was entered as a random variable.

GLMMs were fitted using the LME4 R package, version 1.1-7 (Bates *et al.* 2014) and model selection was done using the MUMIN R package, version 1.13.4 (http://cran.r-project.org/web/packages/MuMIn/index.html). We used a Poisson distribution with a log link function for continuous variables (*visit count* analysis), and a binomial distribution with a logit link function for nominal variables (other analyses). Model performance was evaluated using Akaike's Information Criterion corrected for small sample size (AICc). Models were ranked with ΔAICc, which represent the relative degree of support for each model (Burnham & Anderson 2002). The model with the lowest AICc was regarded as the best-supported model; models with ΔAICc> 2 were not well supported. As auxiliary analyses, we controlled for unbalanced sampling effort among the flower visitor survey plots, by rerunning the GLMM while excluding sites sampled only once; these analyses yielded similar results. In the pollination study, we also tested the effect of ovary width, date and time of day on fruit set rates in control pollination treatments, using binary logistic GLMM.

Results

FLOWER VISITATION

94% of recorded visits to watermelon flowers were by bees; out of these, 85% were by honeybees and 15% by wild bees. 421 wild bee individuals were netted from watermelon flowers, belonging to 51 species of tiny to small body size (ITD range 0·7–2·4 mm) (see species list in Appendix S1, Supporting information). Tiny species consisted mostly of *Lasioglossum*, *Hylaeus*, *Halictus* and

Ceratina spp.; the dominant species were the primitively eusocial *Lasioglossum politum atomarium* (Morawitz, 1876) and the solitary *Hylaeus taeniolatus* Förster, 1871. Small species consisted mostly of *Lasioglossum* and *Halictus* spp.; the dominant species was the primitively eusocial *Lasioglossum malachurum* (Kirby, 1802). Honey and wild bee visitation did not differ between irrigated and dryland fields (rANOVA, $n = 32$, irrigation: $F_{1,30} = 2{\cdot}1$, $P = 0{\cdot}16$; bee group × irrigation: $F_{1,30} = 1{\cdot}4$, $P = 0{\cdot}2$).

The results of the GLMM analyses are summarized in Tables 1, S1 and S2. In the visitor survey, variation in spatial and floral factors showed differing effects on visitation counts of honeybees vs. wild bees, with a single well-supported model (Table 1, *visit count* analysis). The density of watermelon bloom positively affected honeybee, but not wild bee visitation (Fig. 1a). On the other hand, the percentage of surrounding semi-natural habitat positively affected wild bee, but not honeybee visitation at all analysed radii; wild bee visits correlated best with percentage shrubland+forest when measured within a radius of 50 m ($r = 0{\cdot}58$, $P = 0{\cdot}001$, $n = 32$; Fig. 1b). Correspondingly, daily wild bee activity surpassed that of honeybees in only four fields surrounded with ≥30% semi-natural habitat, and only when flower densities were low.

Analysis of netted bee abundance yielded four well-supported models, all of which indicated differing daily patterns of foraging on watermelon among bee genera (Table 1, *bee capture* analysis). Foraging by *Lasioglossum* spp. gradually decreased from early morning to midday, whereas foraging by *Hylaeus* and especially *Ceratina* spp. showed an opposite pattern, increasing from early morning to midday; foraging by *Halictus* spp. increased until 09·30 and then slightly decreased (Fig. 2).

The visit count model and two of the bee capture models also indicated differing patterns of foraging on watermelon throughout the season (Table 1). Foraging by honeybees and *Ceratina* spp. remained mostly constant throughout the season, whereas foraging by *Halictus*, *Lasioglossum* and *Hylaeus* spp. decreased.

Honeybee and wild bee visitation counts did not differ between edge and interior plots (rANOVA, $n = 11$, location: $F_{1,10} = 0{\cdot}1$, $P = 0{\cdot}7$; bee group × location: $F_{1,10} = 0{\cdot}1$, $P = 0{\cdot}7$). However, the wild bee assemblage in interior plots was less diverse than in edge plots and consisted almost entirely of Halictine bees (47 out of 49 netted individuals). It also contained a larger fraction (71% vs. 31%) of small bees (ITD>1·5 mm) (rANOVA, $n = 11$, location: $F_{1,10} = 0{\cdot}3$, $P = 0{\cdot}6$; body size × location: $F_{1,10} = 6{\cdot}3$, $P = 0{\cdot}03$; Fig. 3).

In the pollination study, bee groups' visit frequencies responded differently to field edge type, again with a single well-supported model (Table 1, *visit frequency* analysis). Tiny wild bee visits were more frequent near semi-natural and vegetated edges than near edges with no wild vegetation (mean frequencies ±SE 0·068 ± 0·041, 0·011 ± 0·005 and nil visits·flo^{-1}·min^{-1}, respectively; pairwise contrast test, $P = 0{\cdot}03$), whereas small wild bee and honeybee visits were unaffected by field edge type ($P = 0{\cdot}2$ and 1·0, respectively).

FRUIT AND SEED SET

Out of a total of 405 hermaphrodite flowers which were manipulated, 197 matured and the rest aborted. One plot had exceptionally high fruit maturation (75–80%) regardless of treatment, possibly due to wind-assisted self-pollination; however, its inclusion/exclusion did not affect any of our main findings (see Table S1), and the tables and figures correspond to analyses using all plots. Fruit set differed among treatments and bee groups (Fig. S1). However, the number of fully developed seeds per mature fruit was similar for all treatments (229 ± 11 (mean±SE), $n = 133$; two-way ANOVA with plot as random factor, $F_{4,115} = 1{\cdot}7$, $P = 0{\cdot}17$). Flowers were more likely to set fruit following a honeybee visit than a tiny wild bee visit; the effect of a small wild bee visit on fruit set was less clear due to small sample size ($n = 16$) (Fig. S1).

Analysis of bee groups' single-visit pollination efficiencies yielded six well-supported models (Table 1, fruit set analysis). The size (width) of the flower's ovary had a significant interaction with bee group in affecting fruit set in all six models (Table 1 and Fig. 4a). Fruit set percentage increased with ovary size in flowers visited by a honeybee and in control treatments, but decreased in flowers visited by a wild bee (Fig. 4a and Fig. S2).

Time of day had a significant effect on fruit set percentage, and flowers visited in the afternoon (>12·30 h) hardly set any fruit. In two of the well-supported fruit set models, the effect of time of day on fruit set differed among bee groups (Table 1), with wild bees' efficiencies declining more steeply than honeybees' throughout the day (Fig. 4b). Hence, small wild bees had the highest pollination efficiencies among bee groups during early morning hours (although sample sizes were small), vs. honeybees during late morning hours (Fig. 4b). There was no effect of time of day on fruit set in hand-pollinated flowers ($F_{1,61} = 1{\cdot}1$, $P = 0{\cdot}3$).

Time of day and ovary size also showed contrasting effects on bee behaviour among bee groups. Visit duration showed positive correlation with time of day and ovary size in honeybees (hour: $r = 0{\cdot}41$, $n = 118$, $P < 0{\cdot}001$; ovary size: $r = 0{\cdot}26$, $n = 118$, $P = 0{\cdot}004$), but not in wild bees. Fruit set increased throughout the season for all pollination treatments (Tables 1 and S1), including controls. Flowers situated near different types of field edges did not differ in the propensity to set fruit following a visit by any of the bee guilds tested (Table 1).

Discussion

We found evidence for multiple levels of spatiotemporal niche complementarity between the dominant pollinator species in our study system in both visitation activity (visit

Table 1. Well-supported models (ΔAICc≤2) for the four GLMM analyses used in the study. The number of model parameters (K) is indicated. Variables included in each model are indicated by a cross (+). Interaction effects included in any of the models are boldfaced

Visitor survey – visit count						
AICc	1191·46					
ΔAICc	0					
K	8					
Intercept	+					
Bee group	+					
% semi-natural habitat	+					
Date	+					
Flower density	+					
Bee group × % semi-natural habitat	**+**					
Bee group × date	**+**					
Bee group × flower density	**+**					
Visitor survey – bee capture						
AICc	434·10	434·74	434·94	435·70		
ΔAICc	0	0·64	0·84	1·60		
K	12	13	9	10		
Intercept	+	+	+	+		
Bee genus	+	+	+	+		
Date	+	+	+	+		
Hour	+	+	+	+		
Flower density		+		+		
Bee genus × date	**+**	**+**				
Bee genus × hour	**+**	**+**	**+**	**+**		
Bee genus × flower density						
Pollination study – visit frequency						
AICc	1921·89					
ΔAICc	0					
K	15					
Intercept	+					
Bee group	+					
Field edge type	+					
Flower gender	+					
Date	+					
Hour	+					
No. of flowers in patch	+					
Bee group × field edge type	**+**					
Bee group × date	**+**					
Bee group × hour						
Bee group × flower gender						
Bee group × no. of flowers in patch						
Pollination study – fruit set						
AICc	245·49	245·53	246·74	247·04	247·09	247·42
ΔAICc	0	0·04	1·25	1·56	1·60	1·94
K	7	6	8	5	7	7
Intercept	+	+	+	+	+	+
Bee group	+	+	+	+	+	+
Field edge type						
Pollen collection			+		+	
Irrigation						
Date	+	+	+	+	+	+
Hour	+	+	+		+	+
Ovary width	+	+	+	+	+	+
Visit duration						+
Bee group × field edge type						
Bee group × date						
Bee group × hour	**+**		**+**			
Bee group × ovary width	**+**	**+**	**+**	**+**	**+**	**+**
Bee group × pollen collection						
Bee group × visit duration						

frequencies) and pollination efficiency (single-visit fruit set rates). These complementary patterns may enhance the resilience of the system and lead to increased pollination services and crop yield – although the latter effect has some limitations (see section Niche complementarity and benefits to pollination). Regarding visitation, honeybees

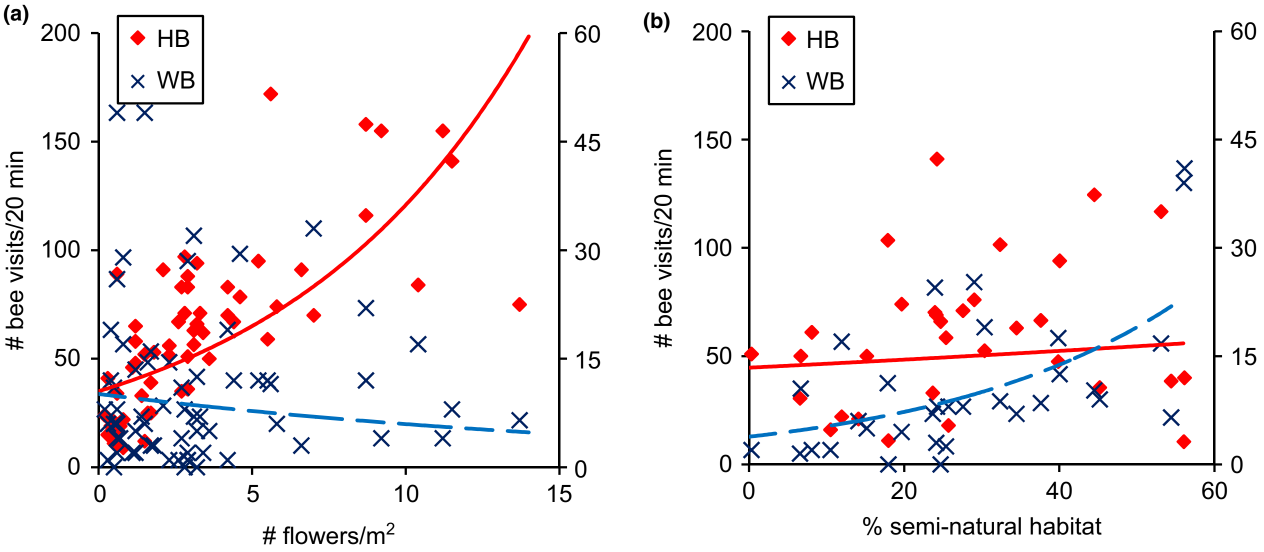

Fig. 1. Variation in daily visitation counts (early morning and late morning censuses combined) in edge plots, as a function of watermelon flower density (a) and % semi-natural habitat at 50 m radius (b). Lines represent the best-supported model (full line = honeybees; broken line = wild bees). HB = honeybees; WB = wild bees.

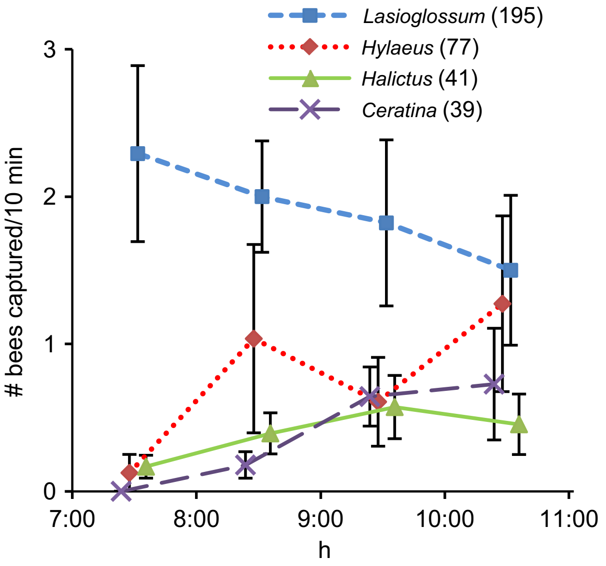

Fig. 2. Daily patterns of abundance (mean±SE, based on netting) of main wild bee visitor genera on watermelon flowers between 07·00–11·00 h, in edge plots. Numbers in parentheses indicate overall individuals caught.

were the main visitors at peak bloom, whereas wild bees were the main visitors during low bloom in fields surrounded with semi-natural habitats; different genera of wild bees were most active during different times of the day; and tiny and small bees were the main wild bee visitors in field edges vs. interiors, respectively. Regarding pollination efficiency, honey and wild bees were oppositely affected by ovary size; and temporal complementarity between honeybees' and small wild bees' efficiencies was suggested by some of the models, although sample size was small for the small wild bee group.

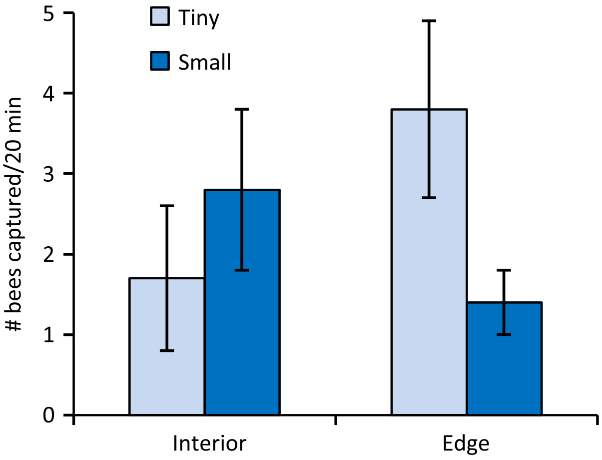

Fig. 3. Daily netted abundance (mean±SE, early and late morning censuses combined) of tiny and small wild bees in the interior vs. edge of watermelon fields.

MECHANISMS LEADING TO COMPLEMENTARY POLLINATION PATTERNS

Visitation patterns

Spatiotemporal differences in visitation patterns among bee groups may be linked to the combined effects of seasonal changes in bee abundance and the availability of watermelon vs. wildflowers, the bees' foraging and nesting preferences, and their flight ranges. Spatially, honeybee visitation to watermelon flowers was dependent mainly on the presence of significant crop bloom, whereas wild bee visitation depended mainly on the availability of suitable semi-natural habitats in close proximity. The distance from components of semi-natural habitat had further

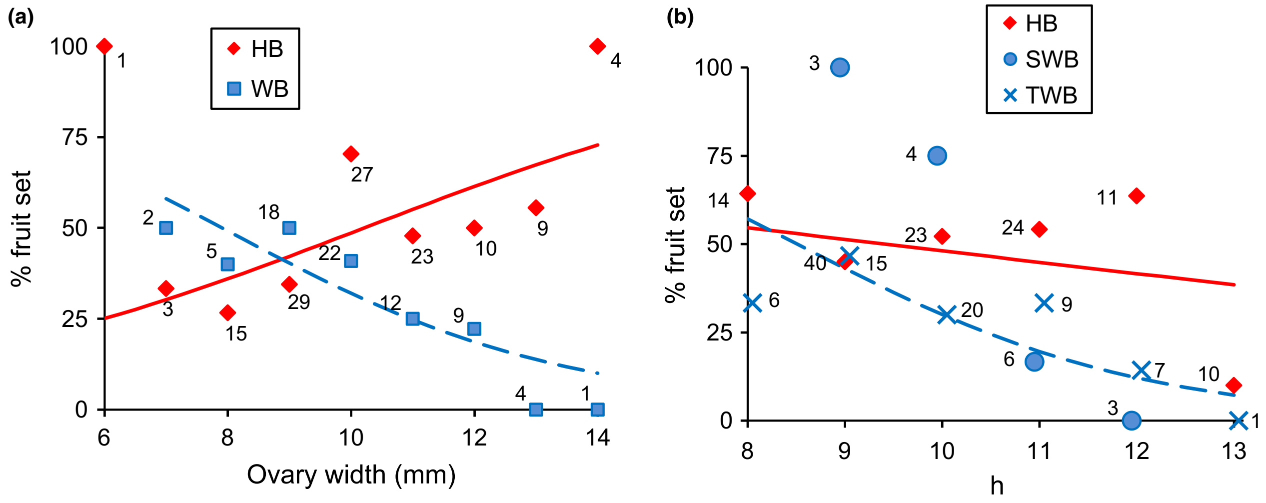

Fig. 4. Variation in single-visit fruit set efficiency as a function of ovary width (a) and hour (b). Lines represent the best-supported model (full line = honeybees; broken line = all wild bees combined), and numbers beside data points indicate sample sizes. HB = honeybees; SWB = small wild bees; TWB = tiny wild bees; WB = all wild bees combined.

variable effects within the wild bee assemblage, with the smallest species (with the shortest flight ranges) being largely confined to field edges containing wild plants, while larger species being more common in field interiors, and unaffected by edge type. Notably, in a related study we found similar contrasts in edge–interior abundance patterns among the main visitors *L. malachurum*, *L. politum* and *H. taeniolatus* using combined net and pan trap sampling (Pisanty & Mandelik 2015). These contrasts likely reflect differences in foraging needs (Potts *et al.* 2003) and/or nesting preferences (Potts *et al.* 2005). Stem nesters such as *Hylaeus* and *Ceratina* spp. were largely confined to field edges, which often contained suitable wild plants with pithy stems, whereas field interiors were dominated by larger-sized Halictini, which prefer horizontal, exposed ground for nesting (Potts *et al.* 2005), typical of many watermelon fields in our system. Furthermore, the increase in average body size in the field interior may be linked to longer flight distances from stable foraging resources (such as wild vegetation surrounding the field) covered by larger species (Greenleaf *et al.* 2007; Pisanty & Mandelik 2015). Although at the time of sampling there was little wild bloom in most field edges and sometimes even in the semi-natural batha, patches of wild plants blooming outside the crop blooming season and year are important as a stable foraging resource for bees (Garibaldi *et al.* 2011, 2014; Mandelik *et al.* 2012).

Differences in temporal activity patterns among bee groups reflect, among other things, the life cycles of the associated taxa (Willmer & Stone 2004). Whereas honeybees are active year round, most wild bee species are active for only limited periods. Even primitively eusocial species such as *L. malachurum* and *L. politum* are often not active continually for more than a few weeks, as there are dormant periods between the flight periods of successive generations (Richards 2000). Similarly, differences in warm-up rates, related to body size, or in pollen vs. nectar foraging, may affect daily foraging patterns (Willmer & Stone 2004).

Fruit set

Pollination efficiencies of honeybees vs. wild bees, as measured by fruit set, responded differently to time of day and ovary size. These differences may be related to the bees' distinct foraging behaviours, pollen vs. nectar preferences, and body sizes. However, some of the wild bee treatments had small sample sizes, and the results should thus be interpreted with caution. Honeybees collected mostly nectar from watermelon flowers, and may have been influenced by increased nectar quantities associated with flowers remaining unvisited for longer times (Stout & Goulson 2002) or those having larger ovaries (Martin 2004). A positive effect of ovary size on fruit set also seems to be the default state for watermelon flowers, as seen in the control treatments (Fig. S2). On the other hand, the smaller number of ovules present in small ovaries (G. Pisanty, O. Afik & Y. Mandelik, unpubl. data) could explain why pollination efficiencies of wild bees decreased in larger ovaries. Ovaries with fewer ovules require fewer pollen grains for fertilization, and thus are more likely to set fruit following deposition of a small amount of pollen. Hence, smaller ovaries are better matched to the limited pollen deposition capabilities of tiny bees such as most of the wild bees in our system.

NICHE COMPLEMENTARITY AND BENEFITS TO POLLINATION

Pollinator niche complementarity, as found in our system, may not necessarily lead to increased pollination services and crop yield (Winfree & Kremen 2009; Winfree 2013). Benefit to pollination from complementary pollinator activity entails that higher outputs are gained when the pollination activity is shared between two (or more) pollinator taxa compared to the same overall level of activity of a single pollinator taxon (Blüthgen & Klein 2011). This necessitates that each of the two taxa surpass the activity of the other one for part of the niche range, rather than one being superior throughout. Graphically, this means that the activity curves of the two taxa need to cross each other (Fig. 5). Hence, strong species dominance can weaken the advantages of niche complementarity (Winfree 2013; Kleijn *et al*. 2015). In our system, the overall stronger performance of honeybees over wild bees in terms of both visitation and pollination efficiency, limits the benefits that may be gained to crop yields from complementary pollinator taxa. However, complementarity may play an increasing role in the event of a decrease in local honeybee densities, for example due to changes in management practices or diseases and pests (Winfree *et al*. 2007), promoting greater evenness in abundance, visitation and overall pollination services delivered among different pollinator species.

Another prerequisite for complementarity to affect overall pollination delivered is independence between different parts of the niche range, so that increased pollinator activity in a certain part of the range cannot compensate for lack of activity elsewhere (Fig. 5a). While this criterion seems to hold along most spatial scales and the broader temporal scales, its existence is less obvious in some circumstances, especially in shorter temporal scales such as the time of day. Since most crop flowers bloom for an entire day or longer (Free 1993), complementary activity of different pollinators throughout the day may be of little relevance, if increased activity at a certain time point can deliver the equivalent overall amount of pollination to the same flower or ovary (Fig. 5b). Under such circumstances, only the areas under the pollinators' activity curves are relevant as a measure of pollination, and the relationship between different taxa's curves and slopes becomes unimportant. Hence, choosing the taxon with the largest area under the curve and increasing its abundance at the expense of other taxa will result in a net increase in pollination (assuming the curves represent equal abundances).

However, the interplay between temporal niche complementarity and pollination services is further complicated by the confounding effects of overriding temporal patterns that limit pollination. A permanent temporal pattern such as the decrease in flower receptivity throughout the day, may render temporal complementarity totally irrelevant (Fig. 5c). On the other hand, a fluctuating temporal pattern, such as an intermittent daily period of wind, rain or pesticide spraying that prevents pollinator activity (see Brittain, Kremen & Klein 2013; Rader *et al.* 2013), constantly modifies the realized niche space available for pollination (Fig. 5d). In such circumstances, different pollinators contribute most to pollination on different days, depending on the shifting daily window of time available for pollination, and complementarity becomes beneficial even for flowers blooming throughout the day.

In the context of our Malali system, the expected contribution of temporal niche complementarity throughout the day to crop yield is limited. This is because all flowers are open from early morning to afternoon, weather conditions during bloom are nearly always optimal for pollinator activity, and pollination conditions (i.e. pollen viability and stigma receptivity) are consistently skewed towards early morning hours. Hence, wild bee genera

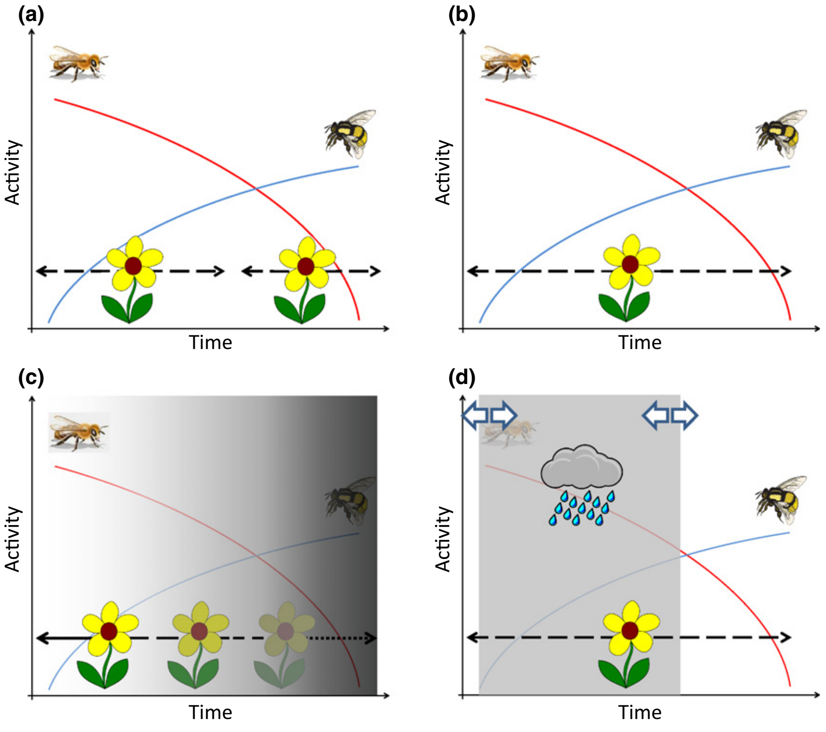

Fig. 5. A schematic representation of temporal niche complementarity between pollinators and the resulting effects on overall pollination delivered. Complementarity increases pollination when different flowers bloom over time (a), or when a fluctuating temporal pattern (rain, shown by grey colour) constantly modifies the realized niche space (d). On the other hand, complementarity may not benefit pollination when the same flower blooms throughout the niche space (b), or when a permanent temporal pattern (a decrease in flower receptivity with time, shown by paler flower colours) interferes with pollination (c).

visiting the flowers earlier during the day (*Lasioglossum* spp.), when pollination efficiencies are highest, and bee guilds having the largest area under the daily pollination efficiency curve (honeybees), are expected to deliver more pollination services than equally abundant assemblages of several complementary taxa. However, complementary patterns similar to those observed in our system may prove highly beneficial for crop production in many other systems of different characteristics.

CONCLUSIONS

Our system has shown multiple spatial and temporal levels of niche complementarity among pollinator groups. Importantly, differing spatiotemporal effects on pollination efficiency were found among groups of pollinators, as measured by single-visit contribution to fruit set. This finding suggests further potential for diversity effects on crop yield, and calls for taking into account the variability in pollination efficiency along spatiotemporal scales. However, the translation of niche complementarity into increased crop yield is not straightforward, and each mode of complementarity should be evaluated carefully in the light of the specific crop, management system and pollination mechanism under study.

We have also shown that differing dependencies of pollinators upon surrounding wild vegetation and semi-natural habitats can lead to spatial complementarity in visitation patterns within and among fields. The presence of wild pollinator groups that are less affected by the proximity of natural habitat components may provide an important buffer for the effects of agricultural intensification (Cariveau *et al.* 2013; Kleijn *et al.* 2015). Flower morphology also interacted differently with distinct pollinator groups, leading to diverse outcomes on pollination efficiency. Further research is required on pollinator complementarity and its connection to specific pollinator life-history traits, in order to improve the overall level and stability of crop pollination services in arable landscapes.

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Data accessibility

Data collected in this study are deposited at the Knowledge Network for Biocomplexity, https://knb.ecoinformatics.org/#view/doi:10.5063/F10K26H8 (Pisanty *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Fruit set percentage following different pollination treatments.

Fig. S2. The effect of ovary size on fruit set percentage in control pollination treatments.

Table S1. Parameter estimates for best-supported GLMMs.

Table S2. Parameter estimates for GLMMs using sites sampled twice.

Appendix S1. List of bee species visiting watermelon.