

Biodiversity buffers pollination from changes in environmental conditions

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Abstract

A hypothesized underlying principle of the diversity-functioning relationship is that functional groups respond differently to environmental change. Over 3 years, we investigated how pollinator diversity contributes to the magnitude of pollination service through spatial complementarity and differential response to high winds in California almond orchards. We found honey bees preferentially visited the top sections of the tree. Where wild pollinators were present, they showed spatial complementarity to honey bees and visited the bottom tree sections more frequently. As wind speed increased, honey bees' spatial preference shifted toward the bottom tree sections. In high winds ($>2.5 \text{ m s}^{-1}$), orchards with low pollinator diversity (honey bees only) received almost no flower visits. In orchards with high pollinator diversity, visitation decreased to a lesser extent as wild bee visitation was unaffected by high winds. Our results demonstrate how spatial complementarity in diverse communities can help buffer pollination services to environmental changes like wind speed.

Keywords: climate change, Ecosystem services, Global change, Insurance, Orchard crop, Pollinators, Spatial complementarity, Wild bees, Wind speed

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Introduction

Understanding the relationship between species diversity and ecosystem functioning is a key issue given the global decline in biodiversity (Chapin *et al.*, 1997; Butchart *et al.*, 2010; Hooper *et al.*, 2012). Ecosystem functions such as nutrient cycling, soil formation, and pollination are crucial to environmental stability so an understanding of how and why these functions are related to species diversity will help to predict the broader consequences of species losses (Hunt & Wall, 2002; Solan *et al.*, 2004; Cardinale *et al.*, 2012). Complementarity is niche differentiation by species/taxa which increases the efficiency of resource use. Large overlap between niches can indicate functional redundancy in a system, that is different species/taxa are doing similar things. The functional redundancy and complementarity of species has been widely discussed, as it has implications for ecosystem functioning and prioritizing species conservation (Walker, 1992; Blüthgen & Klein, 2011). There are several examples from studies of plants that show complementarity can contribute to a positive relationship between diversity and functioning (Cardinale *et al.*,

2007; Allan *et al.*, 2011; Isbell *et al.*, 2011). However, little is known about the role of complementarity in ecosystem functions mediated by organisms such as pollinators.

Ecosystem functions can translate into short- or long-term ecological or economic benefits to humans and in such cases are referred to as ecosystem services. Pollination is an ecosystem service crucial for wild plant reproduction (Ollerton *et al.*, 2011), food production (Klein *et al.*, 2007), and human nutrition (Eilers *et al.*, 2011), with bees being the main service provider (Klein *et al.*, 2007). Complementarity is thought to play an important role in pollination service. With greater pollinator diversity and therefore, potentially greater complementarity, an increase in pollination service and therefore, fruit set may result. Pollination success in coffee (*Coffea arabica* L. and *C. canephora*, Pierre ex A. Froehner) was found to be positively correlated with pollinator functional group richness (Klein *et al.*, 2008). In addition, pollinator functional diversity explained more of the variance in the seed set of pumpkin (*Cucurbita moschata*, Duch. ex Poir.) than species richness (Hoehn *et al.*, 2008). However, as yet there are only a few studies on complementarity in pollination function and, to our knowledge, no data on how spatial complementarity of pollinator communities interacts with environmental change.

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Diversity in an ecosystem may appear redundant under a particular set of environmental conditions or at a given time. However, different species may not respond equally or in the same way to environmental changes. The diversity of what appear to be functionally similar species under one set of environmental conditions may buffer ecosystem function against fluctuations in these conditions, a condition known as response diversity (Chapin *et al.*, 1997; Yachi & Loreau, 1999). It has been observed that some non-*Apis* bees such as bumble bees (*Bombus* spp.) and *Osmia cornuta* (Latreille) are more able to forage under inclement weather conditions than honey bees (Corbet *et al.*, 1993; Willmer *et al.*, 1994; Vicens & Bosch, 2000; Tuell & Isaacs, 2010). For example, in apple orchards *O. cornuta* and muscoid flies (Family Muscidae) were observed foraging under light rain when honey bees were not active and *O. cornuta* was the only pollinator species observed foraging in the orchards under high wind speeds (Vicens & Bosch, 2000). Such complementarity could be an extremely important mechanism for ensuring stable crop production.

Agriculture has become increasingly pollinator dependent (Aizen *et al.*, 2009) and recent findings of declines in both wild and managed bees have raised concerns about the potential impact on pollination services (Allen-Wardell *et al.*, 1998; Aizen & Harder, 2009; Gallai *et al.*, 2009; Potts *et al.*, 2010a,b; Cameron *et al.*, 2011). For a large number of crop species, pollination is provided by honey bees (*Apis mellifera* L.), but there are many examples of crop species for which non-*Apis* pollinator species are more effective for fruit set on a per visit basis (e.g. almond (Bosch & Blas, 1994), coffee (Klein *et al.*, 2003), and blueberry (Javorek *et al.*, 2002; Klein *et al.*, 2007)). Almond is a mass flowering crop, which requires biotic pollination and flowers early in the year when high wind speeds, low temperatures, and precipitation are common. In 23 almond orchards, the percentage fruit set was positively associated with the richness of flower visitors in the orchard and the species richness of wild bees (Klein *et al.*, 2012). In this study, we investigated complementarity in almond, as a potential mechanism for this positive diversity-function relationship. Using the same 23 almond orchards, we investigated whether wild flower visitors showed spatial complementarity with honey bees and how spatial complementarity altered under changing environmental conditions (Fig. 1). Our aims were to explore (i) if different flower visitor taxa share or partition spatial niches at the tree scale; (ii) if flower visitor taxa show differential abilities to forage at high wind speeds and (iii) if the change in environmental conditions causes those taxa that forage at high wind speeds to change their spatial

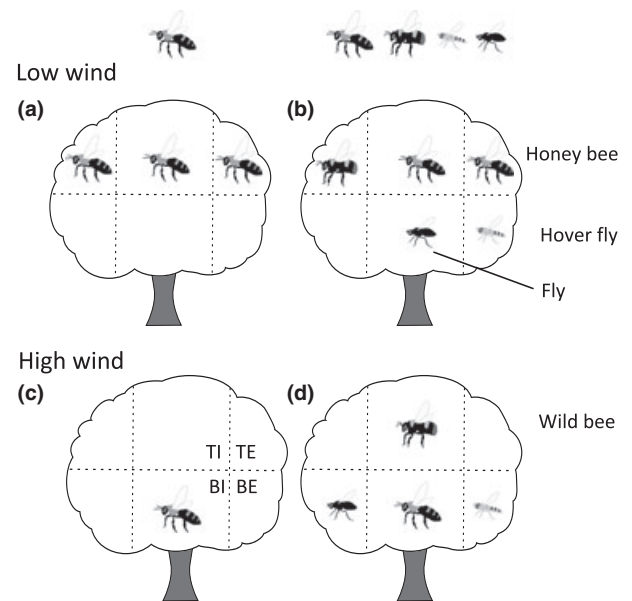


Fig. 1 A depiction of flower visitation in different sections of almond trees [top interior (TI), top exterior (TE), bottom interior (BI), and bottom exterior (BE)], in orchards with low and high pollinator diversity, under changing environmental conditions, in this case wind speed. Low diversity orchards contain only or mostly honey bees (a), but in high diversity orchards, almond flowers receive visits from a range of pollinator taxa including wild bees (b). Pollinator taxa may show spatial complementarity in their foraging preferences (b), improving pollination service to the tree. At high wind speeds, spatial preferences of pollinator taxa may be altered and flower visits by some taxa may decrease disproportionately (c). In high diversity systems, this decrease may be partly buffered by wild pollinators (d).

niche. Information from our study is important for predicting the consequences of functional pollinator diversity loss in a changing world.

Materials and methods

The study was conducted in Colusa and Yolo Counties, in the Sacramento Valley in Northern California (38°42' to 38°57' N and 121°57' to 122°14' W) from 2008 to 2010. Data to investigate the foraging location of pollinators within the tree were collected in February and March 2008 in 23 almond orchards. All orchards were stocked with honey bee hives during the almond bloom (average of two hives per acre). In each orchard, visitors to almond flowers were observed and recorded during 20 s observation periods. Observations were conducted on five trees at the edge (outer row) of the orchards and five trees 100 m inside the orchard (or 50 m inside in four smaller orchards, mean tree height 6 m). Each tree was visually split into four sections: top interior, top exterior, bottom interior, and bottom exterior (Fig. 1). At each tree on a given day, each of the four sections was observed twice. Each tree section was observed successively in a random order and the number of flowers under observation was noted.

Observations were carried out under sunny to lightly overcast skies when temperatures were above 13 °C (Delaplane & Mayer, 2000) and wind speed was low, which is defined here as equal to or less than 2.5 m s⁻¹, standard for pollinator observations (Winfree *et al.*, 2007). These observations were carried out in each orchard on three separate days. During a 20-s observation period, a group of flowers (mean = 19) was observed and the number of visits made to the flowers under observation was recorded. Each flower-visiting individual was assigned to one of the following categories: honey bee, wild (non-*Apis*) bee, hover fly (family: Syrphidae), and all-others (predominantly Diptera). The wild bees were also identified to species/morphospecies (for a full list see Table S1 in Klein *et al.*, 2012). The number of flowers observed was recorded and the wind speed was measured using a Kestrel wind meter. Wind speed measurements were taken at the beginning and end of a set of observations of five trees, in an orchard in a day. The average of the start and end wind speeds was used in statistical analyses.

High wind speed observations were undertaken in 2008, 2009, and 2010 as described above, in a subset of four of the orchards (see Table S1 in Supporting Information for details) when the wind speed was greater than 2.5 m s⁻¹. The high wind observations were not conducted on days with low temperatures (threshold for observations 13 °C, min. 15 °C, mean 18 °C) or high cloud cover. The orchards were categorized as either 'low pollinator diversity' or 'high pollinator diversity'. These classifications were based on standard flower visitor observations (as described above) and were related to the orchards' amount of surrounding natural habitat (>30% wild bees present, <5% wild bees absent, Klein *et al.*, 2012). In the low pollinator diversity category, no wild bees were observed visiting almond flowers under high or low (≤ 2.5 m s⁻¹) wind speeds whereas, in the high diversity category wild bees were observed on all observation days. Observations at high wind speeds were only conducted at the orchard edge, to maximize the contrast between the low and the high diversity situations as wild insect diversity decays from the orchard edge to the interior (Klein *et al.*, 2012).

Statistical analyses

Spatial partitioning. The observations in the 23 orchards in 2008 under low wind speeds were used to investigate the foraging location of flower visitors within the trees, as all orchards had been sampled equally. The flower visitor community was divided into four functional taxa (see above). The frequencies of visits by each of the taxa were analyzed in separate models. Due to a large number of zeros, data were summed for each observation day across trees at the edge and trees in the interior of each orchard. The explanatory variables were the location within the tree (top interior, top exterior, bottom interior, bottom exterior) and the wind speed (m s⁻¹). The number of flowers observed was included as an offset (log transformed) as it was a covariate known to affect the flower visit counts. The random variables were the location (edge or interior), nested within the observation day, nested within the orchard. For the wild bees, hover flies, and all-others the error distribution was

Poisson. For honey bees, the error distribution was lognormal Poisson with a subject level random variable to account for overdispersion (Maindonald & Braun, 2010). For all models, stepwise deletion was carried out (where $P > 0.05$). After the removal of an explanatory variable, the models with and without the variable were compared by analysis of variance (ANOVA, maximum likelihood fitting) to test the loss of explanatory power from the removal of the variable (P values cited in the text are from these ANOVA model comparisons). When there was no significant difference ($P > 0.005$) between the models, the explanatory variable was removed.

High vs. low wind speeds. Data were collected under high wind speeds (>2.5 m s⁻¹) in four orchards (two high diversity orchards with wild bees and two low diversity orchards without wild bees) in 2008, 2009, and 2010 (see Table S1). These data were analyzed with the data collected at the orchard edge in the same four orchards under low wind speeds in 2008. To isolate the impact of wind speed from other environmental variables such as temperature, we conducted observations on days with high wind speeds and sunny conditions. High wind data were collected over 3 years as windy days were often also cooler and rainy; with windy, sunny days being rarer. In 2008, observations of flower visits were carried out over three separate days, per orchard and wind category. The data were summed across all five trees at the orchard edge observed in a day, in an orchard. The frequency of flower visits was the response variable in a mixed model with a lognormal Poisson error distribution. The orchard's pollinator diversity category, wind speed, and their interaction were included as explanatory variables. The wind speed was calculated as the average of the start and end wind speed of the observation period. Year was also included as an explanatory variable and the number of flowers observed as an offset (log transformed). Observation day nested within the orchard were included as random variables.

Only the observations in the two high pollinator diversity orchards were selected to analyze the effect of wind speed on the frequency of flower visits by each taxa. The high wind observations in 2008, 2009, and 2010 and the low wind observations from the same orchards in 2008, at the orchard edge only were analyzed. The data were summed across the five trees observed on each day, in each orchard. The number of flower visits recorded by each taxa was the response variable. The explanatory variables were the wind speed, the year and an offset of the number of flowers observed (log transformed). Observation day nested within the orchard and a subject level random variable were included. A Poisson error distribution was selected. A modified version of this model was used to analyze the data from the four orchards with observations at both high and low wind speeds, to explore a possible interaction between the frequencies of flower visits in different sections of the tree, under different wind conditions. The model was the same as previously described with the orchard's pollinator diversity category, the wind level, the location within the tree, and their interactions included as explanatory variables.

To explore any differences in the spatial patterns of the four taxa under low and high wind speeds, only the data from the

two high diversity orchards were selected. The same model as above was used with the wind level, the location within the tree and their interaction as the explanatory variables. The model was run with the frequency of flower visits by each taxa as the explanatory variable. For all models, stepwise deletion (where $P > 0.05$) was carried out and an ANOVA comparison made between the model with and without the variable as previously described. The aforementioned analyses of flower visitation in high and low wind speeds were repeated only using the data from 2008. All analyses were carried out in R version 2.14.1 (R core development team, 2011, library lme4).

Results

Spatial partitioning

The frequency of flower visits to the four tree sections differed for all visitor taxa ($P < 0.05$) except wild bees (Table 1). Honey bees more frequently visited flowers in the top parts of the tree (Fig. 2a), while hover flies and all-others were more frequently in the lower parts of the tree (Fig. 2b, Table 1). Wild bees were relatively evenly distributed throughout the tree ($P = 0.091$; Table 1, Fig. 2b), with a tendency to visit the lower sections more frequently than the upper sections. At low wind speeds (up to 2.5 m s^{-1}), honey bees were the only taxa whose location in the tree altered with wind speed (Table 1). As wind speed increased (continuously up to 2.5 m s^{-1}), the proportion of honey bees in the top sections of the tree decreased and the proportion in the lower sections of the tree increased (Fig. 3).

High vs. low wind speeds

There was a significant interaction ($\chi^2 = 13.60$, $df = 1$, $P < 0.001$) between the wind speed and the orchard's pollinator diversity category on the frequency of visits to almond flowers. At high wind speeds, the fre-

quency of flower visits in the low pollinator diversity orchards decreased dramatically to almost zero (Fig. 4a). In the high pollinator diversity orchards, the drop in the frequency of flower visits under high wind speeds was much less severe (Fig. 4b). The frequency of visits did not differ between years ($\chi^2 = 0.44$, $df = 2$, $P = 0.805$).

In the high diversity orchards, the frequency of visits by wild bees ($\chi^2 = 0.17$, $df = 1$, $P = 0.678$) and all-others ($\chi^2 = 1.73$, $df = 1$, $P = 0.189$) was not affected by high wind speeds. The frequency of visits by honey bees ($\chi^2 = 23.19$, $df = 1$, $P < 0.001$) and hover flies ($\chi^2 = 7.36$, $df = 1$, $P = 0.007$) decreased under high wind speeds (Fig. 4b). The frequency of flower visits did not differ between years in any of the taxa ($P > 0.05$).

The frequency of flower visits also showed an interaction between the location within the tree, wind speed, and the orchard's pollinator diversity category ($\chi^2 = 12.41$, $df = 3$, $P = 0.006$). In low diversity orchards, under high wind speeds the frequency of flower visits dropped to zero in all sections of the tree except for the bottom interior (Fig. 4c). Under high wind speeds, in the low diversity orchards the preference of honey bees for the top sections of the tree switched to the bottom interior. In the high pollinator diversity orchards, there was a smaller decrease in the frequency of flower visits, spread evenly throughout the tree (Fig. 4d). In the high diversity orchards, only wild bees ($\chi^2 = 8.51$, $df = 3$, $P = 0.037$) changed their spatial preference under high wind speeds (other taxa $P > 0.05$). Wild bee visits decreased in the bottom sections of the tree and increased in the top interior section under high wind speeds (Fig. 4d). In the subset of high diversity orchards in which high wind speed data were collected, the spatial preferences of honey bees appeared less pronounced. The frequency of visits by all visitors and each of the taxa did not differ between years ($P > 0.05$).

Table 1 The spatial location of flower visitor taxa in almond trees (BE, bottom exterior; BI, bottom interior; TE, top exterior; TI, top interior) in 23 orchards under low wind speeds (2008 data). The frequency of flower visits in the four tree sections was tested using mixed models, with location within the tree, wind speed (m s^{-1}) and their interaction as explanatory variables (see methods)

	Honey bees		Wild bees		Hover flies		All-others
Location within tree	219.9***		6.5		26.1***		17.3***
BE:BI	10.3**	BE			3.0		0.0
TI:BI	82.3***	TI			18.0***	BI	12.1***
TE:BI	82.5***	TE			18.6***	BI	5.3*
TI:BE	52.2***	TI			6.8***	BE	11.4***
TE:BE	49.1***	TE			6.8**	BE	4.7*
TE:TI	1.1				0.0		1.9
Wind speed	2.4		0.8		0.9		0.4
Location × wind	9.4*		5.1		6.1		2.7

The table gives χ^2 values (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) from the log likelihood comparison of models before and after the removal of a variable. The table also indicates which sections received significantly higher visitation in any given contrast.

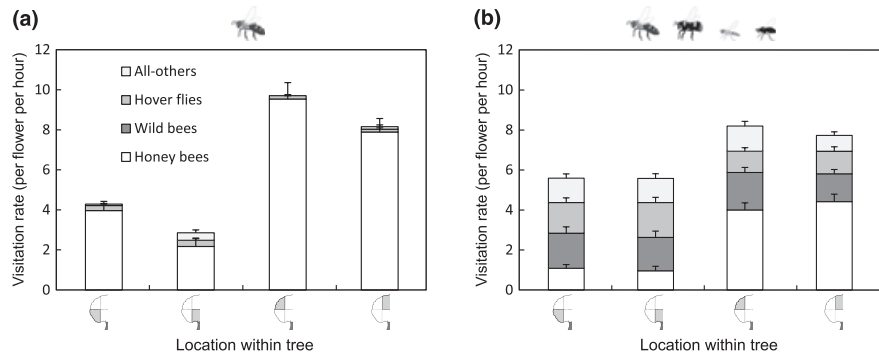


Fig. 2 The spatial preferences of different flower-visiting taxa within almond trees. Observations were collected in 23 orchards of varying pollinator diversity under low wind speeds. Here, data from the two extremes of pollinator diversity are presented. Nine of the 23 orchards were categorized as low pollinator diversity (a) (no wild bees observed), and another nine of the orchards as high pollinator diversity (b) (wild bees observed on all observation days).

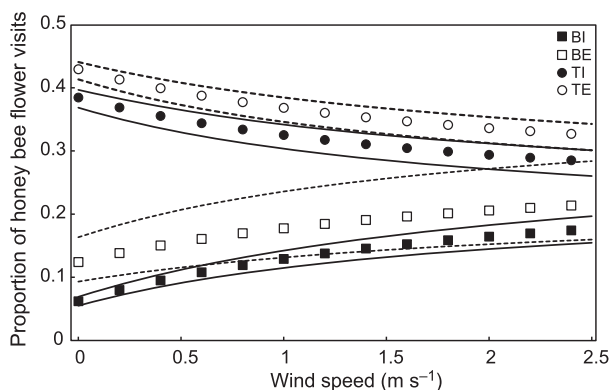


Fig. 3 In low wind speeds ($\leq 2.5 \text{ m s}^{-1}$), we analyzed the frequency of flower visits by honey bees in different sections of almond trees in 23 orchards. There was a significant interaction between the location within the tree [top interior (TI), top exterior (TE), bottom interior (BI), and bottom exterior (BE)] and wind speed. The graph shows the proportion of honey bees in the different tree sections predicted by the model (95% confidence intervals are shown, see methods for details).

The analyses using only the data from 2008 produced similar results to those from all 3 years (see Data S1 in Supporting Information for details).

Discussion

Here we show how pollinators differ in their responses to environmental change, in this case wind speed. For the first time, we demonstrate an interaction between pollinators' spatial foraging preferences and environmental change. At present, most response diversity-functioning examples come from biomass and microcosms (Elmqvist *et al.*, 2003; Valone & Barber, 2008; but see Winfree & Kremen, 2009). Our results show that wild pollinators help to sustain pollination

services under extreme weather conditions when the service by honey bees declines. We also show that functional pollinator taxa use different spatial niches depending on wind speeds. These results demonstrate complementarity among pollinators in foraging behavior and differential responses to altered environmental conditions, providing mechanistic support for a positive relationship between diversity and the magnitude of pollination services.

Diversity buffered almond trees from a reduction in flower visitation under altered environmental conditions. Individual almond orchards can be in bloom for up to 2 weeks. From 1983 to 2011, in February and March when the almonds are in flower, the number of days when the average wind speed exceeded 2.5 m s^{-1} was 13 and 15, respectively (data from California irrigation management information system, Davis station near study orchards). There is therefore a high chance of high wind speeds during almond bloom. The differential abilities of wild bee species to fly and forage under high wind speeds differentiates their environmental niche from honey bees (Boylemakowski & Philogone, 1985; Willmer *et al.*, 1994; Vicens & Bosch, 2000) and our results show that their spatial niches can change under changing environmental conditions. Honey bees were the most sensitive visitor taxa to wind speed. The wild bee *Andrena cerasifolii* (Cockerell) was particularly abundant at high wind speeds (37% of all visits under high wind speeds in the high diversity orchards, 7% under low wind speeds in the same orchards). The physiological and/or behavioral mechanism by which bees such as *A. cerasifolii* and *O. cornuta* (Vicens & Bosch, 2000) can forage at higher wind speeds than honey bees are not well established and merit further investigation.

A diverse community of flower visitors supplies a greater magnitude of pollination service in almond

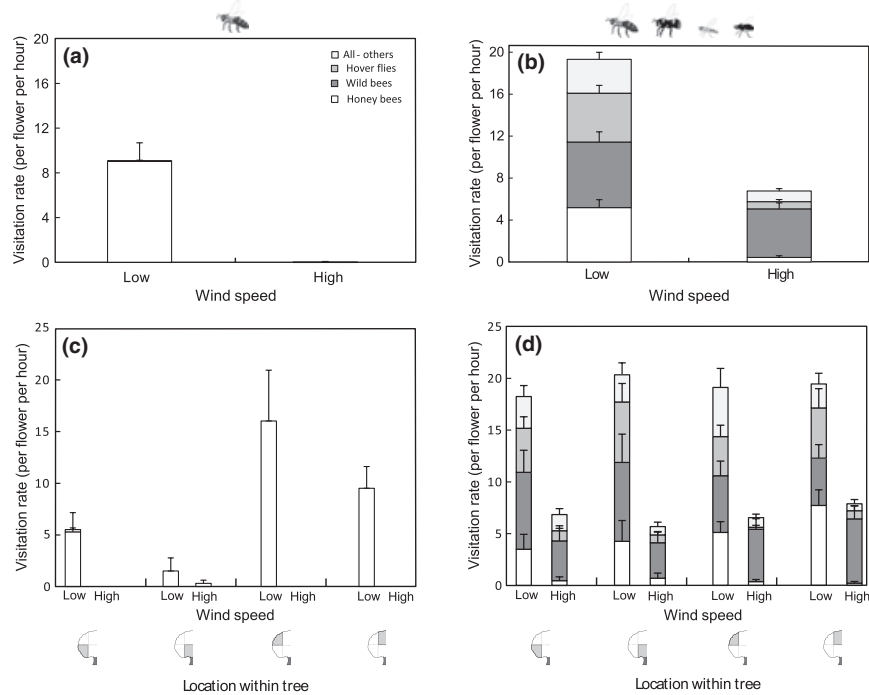


Fig. 4 Observations of flower visitation in low and high wind speeds were made in two low pollinator diversity orchards ($n = 44$ 20 s obs.) and two high diversity orchards ($n = 44$ 20 s obs.). In high wind speeds, flower visitation was more strongly affected in low pollinator diversity orchards (a) than in high diversity orchards (b). The spatial preferences of honey bees (c) and wild bees (d) changed in high wind speeds.

orchards by visiting a greater proportion of the spatial niches in the tree. Greater pollinator diversity has been associated with increased fruit set in almond (Klein *et al.*, 2012). In Klein *et al.* (2012), the fruit set in the different tree sections was not specifically compared. However, the present study shows that pollinator diversity can improve the spatial distribution of pollination service through complementary foraging locations within trees, providing evidence of a mechanism through which diversity can increase fruit set. Honey bees showed a preference for foraging in the top parts of the tree. Hover flies and other flies can be reasonably effective pollinators of almond flowers (A-M. Klein, C. Brittain & C. Kremen, unpublished data) and they foraged more in the lower parts of the tree, filling the vacant niches. The foraging location of the wild pollinators may have been related to competition with the honey bees, different microclimatic preferences, and/or minimizing energy costs (Willmer & Corbet, 1981). When fewer honey bees were present on sunny days with high wind speeds, the spatial preference of wild bees switched to the top interior of the tree, which under low wind speeds was heavily visited by honey bees. We did not observe many direct interactions between honey bees and wild pollinators suggesting that resource, as opposed to interference competition

was more likely. Spatial complementarity can occur at different scales and has also been demonstrated within flowers in strawberries (Chagnon *et al.*, 1993). At high wind speeds, honey bees preferred to forage in the bottom interior section of the trees. This section may be more sheltered from the wind, reducing the energy costs for flying between flowers and the oscillation of the flowers they are trying to land on (Pinzauti, 1986). There can be differences between the shape of almond trees of different varieties, ages, and management. These differences may affect how exposed or attractive the different sections of the tree are to the different pollinator taxa.

This study selected orchards with extremely diverse pollinator communities for comparison. For the many almond orchards isolated from natural habitat, management such as restoring flowering secondary habitat strips may be necessary to support wild pollinators (Klein *et al.*, 2012). In addition, managed *Osmia* species can provide an opportunity for isolated orchards to diversify their pollination service. *O. cornuta* has been found to forage at lower temperatures and higher wind speeds than honey bees in apple orchards (Vicens & Bosch, 2000).

With increasing demand for biotic pollination in crop production (Aizen & Harder, 2009), the importance of

wild insects and their functional diversity in sustaining pollination services and food production may become increasingly important over time and with environmental change. The presence of wild bees can help protect pollination services in the face of climate change by increasing the range of responses of pollinators to climatic fluctuations. In almond, under high wind speeds a dramatic drop in visitation by honey bees was buffered by wild bees (where present). By only considering wind speed here, we may be underestimating the potential response diversity of pollinators (Boyle & Philogène, 1983; Boylemakowski & Philogène, 1985; Winfree & Kremen, 2009). Following heavy rainfall, we noted that honey bees resumed foraging more quickly than wild bees (personal observations in almond). Other factors such as temperature and the timing of the onset of flowering may elicit different responses. At present, there is limited knowledge of the diversity of response traits of wild bee and other pollinator species; however, this study demonstrates the importance of diversity for sustaining pollination services under just one of many potential changes in environmental conditions. Therefore, instead of relying on a single species, the conservation of pollinator biodiversity in general is recommended to help ensure the sustainability of pollination services in the future (Chapin *et al.*, 2000; Chapin *et al.*, 2010).

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Supporting Information

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

Table S1. The length of flower visitor observations and average wind speeds in almond orchards over 3 years when observations were conducted at high wind speeds ($>2.5 \text{ m s}^{-1}$).

Data S1. The analysis of flower visitation in high and low wind speeds for data collected in 2008 only.