Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops

ROMINA RADER*, JAMES REILLY*†, IGNASI BARTOMEUS*‡ and RACHAEL WINFREE*†

*Department of Entomology, Rutgers, The State University of New Jersey, 93 Lipman Drive, New Brunswick, NJ 08901, USA, †Department of Ecology, Evolution and Natural Resources, Rutgers, The State University of New Jersey, 93 Lipman Drive, New Brunswick, NJ 08901, USA

Abstract

If climate change affects pollinator-dependent crop production, this will have important implications for global food security because insect pollinators contribute to production for 75% of the leading global food crops. We investigate whether climate warming could result in indirect impacts upon crop pollination services via an overlooked mechanism, namely temperature-induced shifts in the diurnal activity patterns of pollinators. Using a large data set on bee pollination of watermelon crops, we predict how pollination services might change under various climate change scenarios. Our results show that under the most extreme IPCC scenario (A1F1), pollination services by managed honey bees are expected to decline by 14.5%, whereas pollination services provided by most native, wild taxa are predicted to increase, resulting in an estimated aggregate change in pollination services of +4.5% by 2099. We demonstrate the importance of native biodiversity in buffering the impacts of climate change, because crop pollination services would decline more steeply without the native, wild pollinators. More generally, our study provides an important example of how biodiversity can stabilize ecosystem services against environmental change.

Introduction

The ability of agricultural production to keep up with the growing human population (Gregory & George, 2011; Tilman *et al.*, 2011) may be further taxed by climate change because rising temperatures are predicted to reduce yields for several important food crops (Lobell *et al.*, 2011). In addition to these direct effects acting through plant physiology (Porter & Semenov, 2005), climate change may have indirect effects on crop production mediated by insect pollinators, which contribute to production for 75% of the leading global food crops (Klein *et al.*, 2007).

Climate change might affect crop pollination through its effects on managed and/or wild pollinators. The honey bee, *Apis mellifera*, is by far the most versatile and ubiquitous managed pollinator, increasing yield in 96% of animal-pollinated crops (Klein *et al.*, 2007). However, domestic honey bee stocks in the USA and central Europe (van Engelsdorp *et al.*, 2008; Potts *et al.*,

2010b), and also feral honey bee colonies (Kraus & Page, 1995), are declining in many regions due to the ectoparasitic mite *Varroa destructor* (Mesostigmata: Varroidae) and other pests and diseases. This dependence of agricultural crops on pollination by a single species is thus an increasingly risky strategy (Winfree, 2008; Potts *et al.*, 2010a). Wild pollinator species can perform equal to or better than the honey bee as pollinators for some crops (Jarlan *et al.*, 1997; Winfree *et al.*, 2007; Jauker & Wolters, 2008; Rader *et al.*, 2009), and furthermore contribute to crop production even when honey bees are present (Garibaldi *et al.*, 2013).

It is biologically reasonable to expect that climate warming will have strong effects on insects including pollinators. Climate change impacts on insects are frequently calculated at broad temporal (e.g. date of first seasonal emergence, Sparks & Yates, 1997) or spatial scales (e.g. geographical shifts in range, Parmesan, 2006). Such studies typically find that insects are already responding strongly to the changing climate (Deutsch *et al.*, 2008; Morris *et al.*, 2008). Smaller scale changes are also likely, however, because most insects are primarily ectotherms (Willmer & Unwin, 1981), and even small changes in temperature can alter their activity and foraging behaviour (Heard & Hendrikz, 1993; Stone, 1994). Although temperature can be positively related to pollinator activity at flowers (Herrera, 1997;

‡ Present address: Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, SE-75007, Sweden

Correspondence: Romina Rader, Department of Physical Geography and Quaternary Geology, Stockholm University, Stockholm, SE 10691, Sweden, tel. +46 707558530, fax +46 8164671, e-mail: RominaRader@gmail.com

Willmer & Stone, 2004), important pollinators such as bees reach high temperature thresholds after which they provide few pollination services, because they spend less time foraging and more time cooling (Heinrich, 1979, 1980, 1993; Cooper *et al.*, 1985). Different species are likely to respond to temperature in different ways, due to variation in thermoregulatory ability, reflectance and body size (Heinrich, 1974; Willmer & Unwin, 1981; Bishop & Armbruster, 1999).

If pollinator species respond differentially to climate warming, then crop plants that are pollinated by a diversity of species may be buffered against the effects of climate change. Broadly, this idea is known as response diversity, and could occur with respect to many types of environmental changes and for different ecosystem services (Walker *et al.*, 1999; Elmqvist *et al.*, 2003). In the case of pollination, environmental factors including temperature, precipitation and wind speed affect pollinator foraging and thus could lead to response diversity (Bluthgen & Klein, 2011). For example, in North American almond orchards, honeybees were sensitive to high winds and foraged less, whereas wild pollinators were less sensitive and provided pollination services even under high wind conditions (Brittain *et al.*, 2013).

In this study, we use a long-term data set to develop daily temperature-dependent activity surfaces for eight bee taxa that pollinate watermelon (*Citrullus lanatus*). We investigate the importance of fine-scale interactions between pollinator-dependent crop plants and their pollinators in response to rising temperatures using IPCC projections (IPCC, 2007). We determine whether daily activity patterns differ by bee species, and use this information to predict the likely impacts of rising temperatures upon pollinator activity patterns and thus crop pollination function. We also explore the potential for wild pollinators to stabilize any changes in function associated with climate change.

Materials and methods

Crop species

We used watermelon *C. lanatus* as a model crop because (i) it has unisexual flowers and thus is completely dependent on insect pollination to set fruit (Delaplane & Mayer, 2005); (ii) its flowers attract a diverse pollinator assemblage (Winfree *et al.*, 2007); and (iii) watermelon flowers are open for only 1 day such that lifetime pollination to individual flowers can be measured in a single day's field work.

Pollinator activity at crop flowers

To measure pollinator visitation rate to flowers, we established one 50-m transect of crop row within each of 18 watermelon farms. Data were collected during the peak bloom of watermelon at each farm, from 29 June to 20 August in 2005, 2007, 2008 and 2010. All farms were situated within a 90 by 60 km region of central New Jersey and eastern Pennsylvania, USA. Data were collected at each of the 18 farms on two separate days in 2005, on 1 day at each farm in 2007 and 2008, and on 3 days at each farm in 2010. Pollinator visitation rate to flowers was calculated by conducting 45-s surveys of groups of flowers at 40 equally spaced points along each transect. At each point, we observed visits to as many flowers as we could view simultaneously. We surveyed each transect three times per day between 8:00 hours and 13:00 hours, which is the period during which watermelon flowers are open. For purposes of relating our measures of bee activity to hourly temperature records, we recorded our flower visitation rate data in units of bee visits per flower per time. Data were not collected when it was rainy, or when wind speed was >4.6 m s^{-1} (90% of records were collected at wind speeds below 2.4 m s^{-1}). After collecting the flower visitation rate data, we collected bees from watermelon flowers with hand nets for 30 min and used these specimens for species identification, as further detailed below.

Pollinator species identification

In the field, we recorded all pollinator visits to flowers and visually identified each individual pollinator 'on the wing' to one of twelve species groups. In this study, we analyse data for eight dominant species groups, which in combination account for 98% of all pollinator visits and an estimated 95% of all pollination function, across our entire data set. Three of our analysed groups contain a single species that is readily identifiable on the wing: *A. mellifera*, *Melissodes bimaculata* and *Peponapis pruinosa*. The remaining five groups each contained 3–14 species, based on species-level identifications of specimens netted from the same sites on the same days (Tables S1 and S2). Four groups were dominated by one or two species: the group *Bombus impatiens* was dominated by *B. impatiens* which accounted for 98% of records; the group *Ceratina* was dominated by *Ceratina calcarata/dupla* (females of these two species are not separable even under a dissecting microscope) which accounted for 82% of records; the group 'green bees' was dominated by *Augochlora pura* which accounted for 89% of records; and the group 'tiny dark bees' was dominated by *Lasioglossum imitatum* which accounted for 65% of records. The last group, 'small dark bees', was the most speciose and comprised 14 species including *L. versatum* (40% of records) and *L. pilosum* (14%). Hereafter, we refer to both individual species and groups as 'taxa'. See Data S1 for further details on the species composition of the observation groups and for tests of the assumptions made by grouping species (Tables S1–S3).

Pollen deposition

To measure the number of watermelon pollen grains deposited on stigmas during a single pollinator visit, we bagged unopened, virgin female watermelon flowers with pollinator-exclusion mesh and later offered these flowers individually to bees foraging on watermelon flowers. After the bee visited the

flower, the flower was protected from further pollinator visits, placed in a floral tube and allowed to sit at room temperature for ca. 24 h to allow the pollen to adhere to the stigma. Stigmas were then removed, softened in 10% KOH, stained with 1% fuchsin and prepared as microscopic slides so that the number of watermelon pollen grains on the stigma could be counted with a compound microscope. Control flowers were left bagged until the end of the field day, and contained few pollen grains (mean = 1, mode = 0, N = 95 stigmas).

Temperature records

For each hour and day that bee visitation rate was recorded at each farm, we assigned a temperature based on temperature records accessed from local weather stations. We obtained records from weather stations that were positioned close to each farm (median = 6 km, range 1–14 km). We used the same weather stations for each year of data collection to reduce variability among weather temperature records per farm and across time. Temperature data were also collected during our data collection at each farm, and these temperatures were correlated with weather station records and explained a large proportion of the variation (R^2 = 0.59). The transect-level records, however, diverged from the weather station records at high temperatures (above 30 °C), likely because our field thermometers overestimated high temperatures due to the instruments not being insulated. Thus, because precision at high temperatures is important for our analyses and weather station measurements are less likely to be influenced by measurement error, we used weather station data instead of field measurements to reduce the potential for measurement and instrument bias.

Generating the pollinator response surfaces

Both temperature and time of day are important determinants of pollinator activity but they are not independent. Therefore, we included both time of day and temperature to calculate pollinator response surfaces. Each response surface consists of a two dimensional grid with time of day on the x axis, temperature on the y axis and the flower visitation rate for the bee taxa being analysed as the z axis (outcome variable). For each pollinator taxon, the flower visitation rate was calculated as the total number of visits from that taxon/total flowers observed during one transect observation period (visits per flower per hour). Hourly visitation rates were pooled by taxon across farms and years to estimate a taxon-specific mean and variance for each cell in the temperature-time grid. We scaled 1 h of time to 2 °C of temperature as this combination roughly matched the variation in time and temperature within our system. For example, on a typical day, temperature increases by roughly 10 °C over 5 h from 8:00 hours to 13:00 hours. As a form of sensitivity analysis, we generated surfaces for three different distance metrics: 2 °C = 1 h, 3 °C = 1 h, and 1 °C = 1 h. The resulting surfaces were very similar, especially in the densely sampled central region (Data S1).

To generate a mean and a variance for the flower visitation rate within each cell of the temperature-time grid, we used the

k-nearest neighbour algorithm (Bremner et al., 2005). Preliminary analyses indicated that k = 30 points provided a good balance between sample size and spatial resolution (Data S1). We then used a 2-D local polynomial smoothing function (loess function in the 'stats' package, R Development Core Team, 2012) to simplify the response surfaces, thereby making the simulation less sensitive to, for example, the particular times of day that were sampled within each hour.

Current and future temperature predictions

To compare pollinator activity and pollination function between current and future temperature scenarios, we used the Intergovernmental Panel on Climate Change (IPCC) scenarios specific to the USA east coast region (NECIA, 2007) for both the present (i.e. 2005–2010) and future (i.e. 2050–2055 and 2094–2099) time periods. In accordance with recommendations from the IPCC data provider (Hayhoe et al., 2008), we used the IPCC-based temperature predictions in all of our simulations for the current period (i.e. 2005–2010) instead of estimating our own from temperature data measured at our field sites. This method controls for the prediction process itself because it compares the future climate predictions to the current predictions based on the same model. We investigated two scenarios proposed by the IPCC in its fourth and latest assessment report (IPCC, 2007). The A1F1 (hereafter referred to as A1) is the most extreme climate change scenario and predicts a global mean warming from 2.4 to 6.4 °C by 2099, whereas the B1 scenario is the least extreme and predicts a mean warming from 1.1 to 2.9 °C.

The IPCC predictions provide an estimated daily maximum and minimum temperature for the month of July (which encompassed 83% of our data records and which we thus used as the basis of our simulation). To incorporate daily and yearly variations in temperature, we simulated changes in temperature (i) among the hours within a given day; (ii) among the days within the month; and (iii) among years over the 5-year time period. We estimated these in a several-step process that incorporated multiple sources of uncertainty. First, for each simulated day we used the July minimum and maximum temperatures to calculate daily temperature profiles using a truncated sine curve (Parton & Logan, 1981), which provides the best fit to the way in which temperature changes across the course of a day at our study sites (Data S1; Fig. S1). Second, to incorporate the empirical day-to-day variability in minimum and maximum temperatures, we used a day-to-day variance estimated from our data for each day in July from two representative weather stations (KLOM and KLU) for 2 years of our study (2007 and 2010). Finally, to account for variation in temperature among years, we calculated the yearly variance in the mean temperatures for each of the 5 years from the IPCC-based temperature predictions. We did this both at the time over which our bee data were collected (i.e. 2005–2010), and at two future time periods (i.e. 2050–2055 and 2094–2099). In this way, we draw a minimum and maximum temperature for each simulated day while accounting for within – day, within – month and among year variability.

Our modelling approach investigates climate change solely via increases in temperature. Even though changes in rainfall during the bloom period could affect pollination in principle, changes in summer rainfall patterns are expected to be modest relative to increases in temperature in our study region (NECIA, 2007).

Estimating pollination function per flower visit

For each bee taxon, we estimated single-visit pollen deposition as a function of time of day. We include time of day in our estimates of pollen deposition as the quantity of watermelon pollen available declines with time of day, due to removal by bees (Stanghellini *et al.*, 2002). We estimated a value for both the mean and the variance for a given time of day from a distribution based on the mean and SE predicted for that time of day by a linear regression analysis. This technique incorporates our uncertainty about the actual value of pollen deposition at that time of day, given the variability in the data (Data S1; Fig. S2).

Estimating pollination services

To estimate the pollination function contributed by each pollinator taxon under both the present and future conditions, we developed a Monte Carlo model that combines our various

forms of data. We started with a simpler model that had been developed to estimate present-day pollination function for a subset of the data analysed here (Winfree *et al.*, 2007). In this study, we modify this basic model to incorporate input parameters related to the temperature-dependent activity surface for each pollinator species group, combined with current and future temperature predictions.

The model input is a three-stage process that incorporates future temperature predictions, the number of visits by each taxon and the amount of pollen deposited per visit (Data S1). Each iteration of the simulation represents the lifetime of one female watermelon flower (because flowers are open for only 1 day, this is one flower-day), and estimates the pollination services delivered to that flower as the number of watermelon pollen grains deposited on the stigma. Pollen deposition by each bee taxon is simulated separately (because taxa have different parameter values) and then summed to estimate the total pollination per flower.

Each iteration of the simulation proceeds as follows. First, for each simulated flower-day we draw an hourly temperature profile (see above). Second, the model simulates the flower visitation rate for each bee taxon. Here, we overlay the temperature profile on the response surfaces (mean and variance; see above) to obtain expected means and variances for the number of visits that flowers receive as a function of time of day and temperature (Fig. 1; Fig. S3). This mean and variance is used to draw a simulated number of visits by a particular
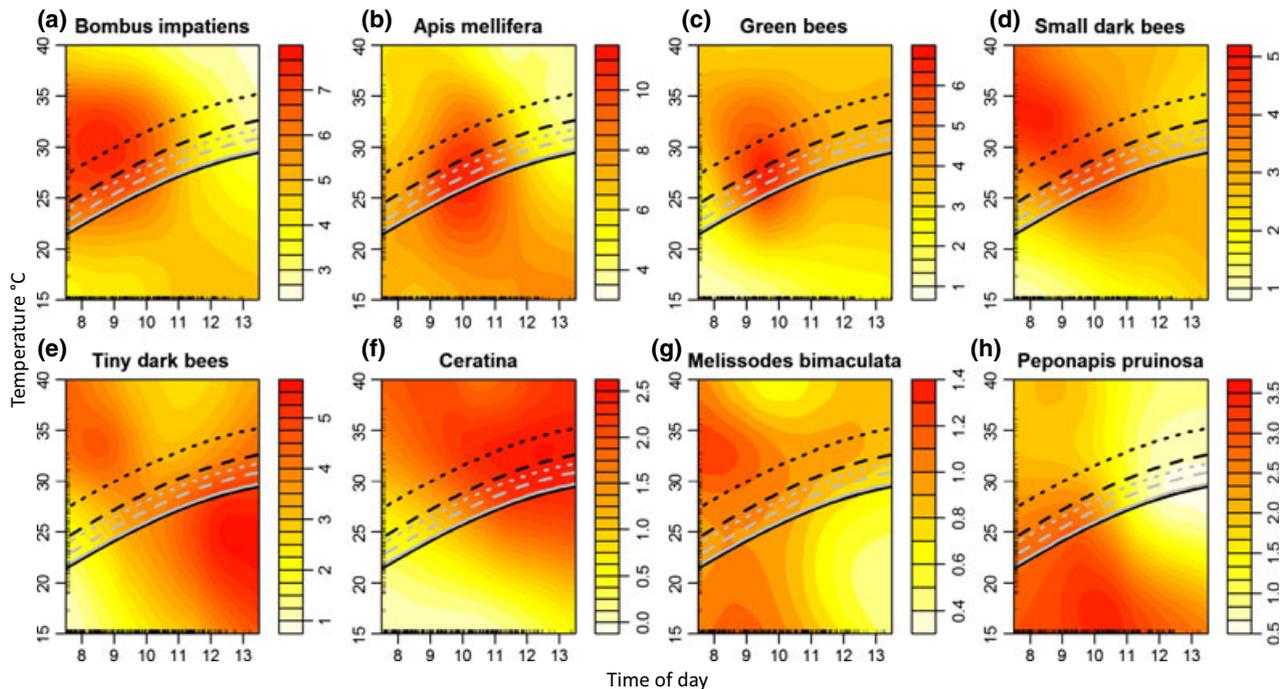

Fig. 1 Response surfaces of all pollinator species groups in relation to temperature and time of day. Activity is measured as visits per flower per hour, with regions of higher activity plotted as red and lower activity as yellow. The markings on the *x* and *y* axes (the 'rug') indicate sampling effort; areas with low sampling effort are an extrapolation from the data. Black lines represent mean predicted temperature for A1 climate change scenario; grey lines represent mean predicted temperature for B1 climate change scenario. Solid lines are mean predicted temperatures for time period 2005–2010; dashed lines are for time period 2050–2055 and dotted lines are for time period 2094–2099. Note changes in scale of legend among taxa.

taxon in a given hour from a negative binomial distribution. Third, hourly measures are then converted into estimates of the total pollination services delivered to a given flower over its 1 day lifetime, by summing the pollen delivered by each bee taxon over the 6 h flowers are open, from 7.30 to 13.30 (Data S1).

We ran 5000 iterations (i.e. 5000 flowers) of the simulation to obtain the mean number of pollen grains deposited by each bee taxon, and by all bees in combination for current and projected future temperatures (for either 2049–2055 or 2094–2099). We calculated SE by using all the error propagated through the model for each form of input data, then taking the SE over the number of either present or future days over which mean pollination per day was being estimated (Data S1).

Because within-species variation in bee abundance across sites could potentially bias our estimates of bee activity as a function of temperature, we took various steps to ensure that our estimates of visitation were based on taxa known to be present, and hence potentially active, at each specified temperature and time interval (Data S1). Finally, as a way of contextualizing the predicted changes in pollination services that we report for climate warming, we calculated present-day spatial variation in pollination services for comparative purposes (Data S1).

Results

At the 18 farms we surveyed over 4 years, we found 31 species of insect pollinators visiting watermelon flowers, observed 16 708 pollinator visits to 47 216 flowers and obtained 417 records of pollen deposition in single visits to previously unvisited flowers.

Our response surfaces, which represent pollinator activity patterns, showed that taxa exhibit diverse responses to both temperature and time of day (Fig. 1). For example, under current conditions, *A. mellifera* is most active at temperatures between 24 and 30 °C and from 9:00 to 11:00 hours. In contrast, *M. bimaculata* is most active above 30 °C and before 9:00 hours (Fig. 1). Pollination efficiency, as measured by pollen deposition in single visits to experimental flowers, also differed among bee taxa (Fig. 2, Kruskal–Wallis $\chi^2 = 80.6$, df = 7, $P < 0.0001$; Data S1; Table S4).

When pollen deposition was combined with visitation rate in accordance with temperature in the simulation model, the resulting prediction was that some taxa increase in their contribution to future pollination function under climate change whereas others decrease (Fig. 3). For example, total pollen deposition by *Ceratina* is predicted to increase by 86.4% under the most extreme A1 climate change scenario for 2094–2099. In contrast, total pollen deposition by the honey bee, *A. mellifera*, is predicted to decline by 14.5% under the same extreme A1 scenario (Fig. 3).

Even though the predicted changes for particular individual taxa were large in some cases, the aggregate
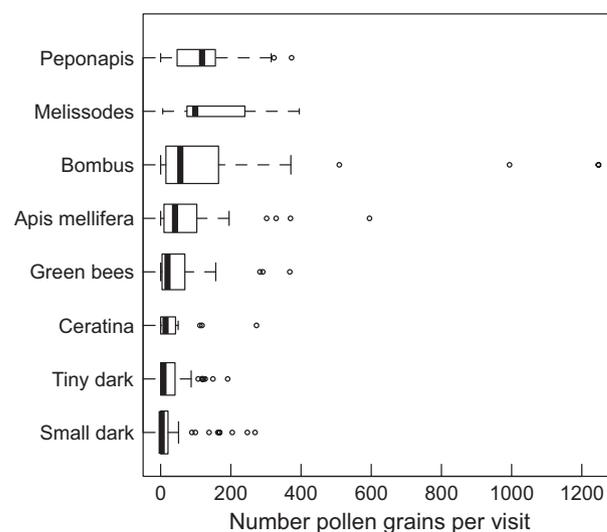

Fig. 2 Pollen deposited in a single visit by each species group. Box indicates quartiles with median marked as a horizontal line; points are outliers and whiskers (error bars) above and below the box indicate the 90th and 10th percentiles.
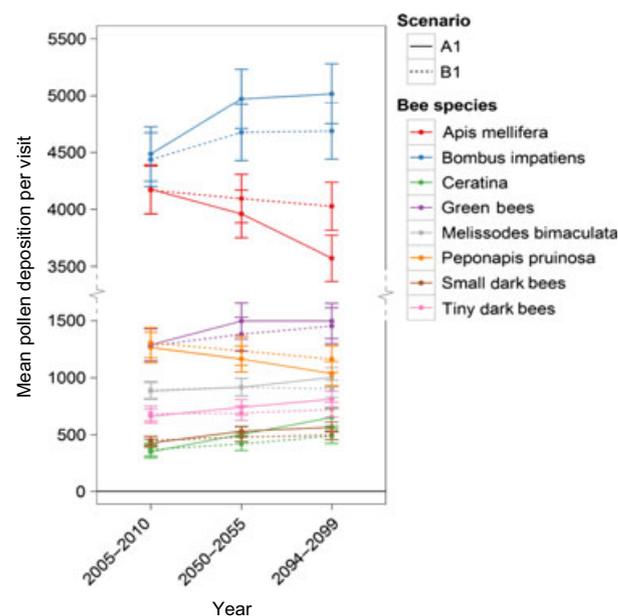

Fig. 3 Mean day-long pollen deposition per flower ±SE as estimated by the simulation for each taxon.

change in pollination services to watermelon flowers was only +4.6% (2094–2099, A1 scenario). This is because declines in pollen deposition by some taxa were offset by increases in other taxa. Pollination services provided by the managed honey bee are predicted to decline under climate warming, whereas six of the seven wild bee taxa are predicted to increase their pollination services.
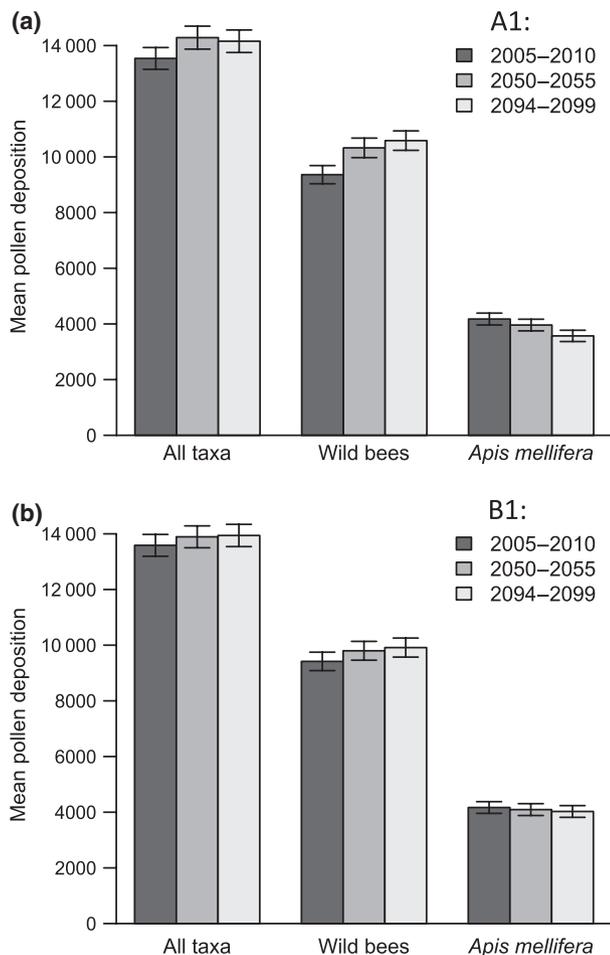
Fig. 4 Mean day-long pollen deposition per flower ±SE as estimated by the simulation for all taxa, wild bees and *Apis mellifera*.

Altogether, in the absence of taxa that increase under future climate change, pollination services would be expected to decline by 15.3% (Fig. 4). When for comparative purposes we calculated present-day variation in pollination services across space, we found that the mean percentage difference between farms was 47% (Data S1).

Discussion

It is critical to understand how global food needs will be met in the coming decades, given the predictions for human population growth, intensifying land use, and climate change (Foley *et al.*, 2011; Tilman *et al.*, 2011). To date, estimates of how climate change might affect crop production have focused on the direct effects of climate warming on crop plants (e.g. Long *et al.*, 2006; Tubiello *et al.*, 2007; Georgescu *et al.*, 2011). Potential indirect effects on insect pollination of crops have been little studied, although most crop plants benefit from animal

pollination (Klein *et al.*, 2007). Here, we show that climate warming will alter pollinator activity patterns, and hence pollination, of a model pollinator-dependent crop plant. However, despite large percentage changes in the pollination provided by particular taxa, the aggregate pollination services are predicted to change little (ca. 5%). This is because differential responses to climate warming by diverse taxa pollinating watermelon may buffer pollination services against climate change.

Our results are consistent with the biological insurance hypothesis, which proposes that the maintenance of ecosystem functions and services will be enhanced by having a diverse assemblage of species providing the service (Lawton & Brown, 1993). Specifically, our results suggest that a mechanism known as response diversity may stabilize pollination services against climate change. Response diversity occurs when multiple species providing the same ecosystem service respond differentially to environmental change, thus buffering the aggregate service (Winfree & Kremen, 2009; Laliberté *et al.*, 2010; Karp *et al.*, 2011). Specifically, we found that pollination services from the sole managed agricultural pollinator in this system, the honey bee, are predicted to decline under warming, but these decreases are offset by increases in the pollination provided by wild taxa (Fig. 3). The buffering effects of wild pollinators are particularly strong because in our study system, aggregate pollination services provided by wild taxa exceed the services provided by honey bees (Fig. 4).

The honey bee is the main pollinator of agricultural crops in many parts of the world, thus changes in the pollination services it provides will have large ramifications for crop production (Free, 1993; Klein *et al.*, 2007). *A. mellifera* populations have already been negatively affected by a number of pests and diseases worldwide (Oldroyd, 2007; van Engelsdorp *et al.*, 2008). Our results predict that climate warming will further reduce the pollination services provided by honey bees to midsummer crops in our climatic zone, because we found that honey bees were most active on flowers at the relatively cool temperatures of 24–30 °C. Our models predict that future warmer temperatures will be beyond the optimal activity range for honey bees (Fig. 1), causing a 14.5% reduction in the pollination services they provide. The reduced flower visitation by honey bees that we observed above 35 °C is unlikely to be directly due to thermoregulatory ability because *A. mellifera* can tolerate temperatures above 40 °C (Cooper *et al.*, 1985). Rather, the decrease is likely to be indirect due to the behavioural changes associated with high temperatures, including reduced foraging duration and flight distances as bees spend more time collecting water for hive thermoregulation (Cooper *et al.*, 1985).

As our model focuses on the plant–insect interaction as opposed to the response by either partner (i.e. potential changes in the watermelon plant's flowering phenology independent of its pollinators, or the activities of the insect pollinators not connected with watermelon flowers), there are several potential effects that are not included in our estimates of pollen deposition. First, just as the seasonal phenologies of plants and pollinators have already shifted with climate warming (Bartomeus *et al.*, 2011), plant and pollinator diurnal phenologies may also adapt to enable activity at an earlier, cooler time of day. In plants, this response has recently been demonstrated in rice whereby early flower opening in response to warmer air temperatures helped to avoid sterility caused by heat stress at anthesis (Kobayasi *et al.*, 2010). Although we do not include plant or pollinator diurnal adaptation in our model, our results are conservative with respect to this possibility. If watermelon plants shift their diurnal phenology to earlier in the day, in parallel to the changes we predict for pollinators, then changes in future aggregate pollination function are likely to be even smaller than the modest changes predicted here, which are themselves smaller than the present-day variation in pollination services among sites (Data S1).

Second, our approach does not fully incorporate long-term adaptations that may occur once farmers adjust their expectations of future climate. These changes could include increasing the number of honeybee hives supplied to insect-pollinated crops, expansion of crop area into cooler regions, planting of new crop varieties (Liu *et al.*, 2010) or altering of planting dates (Lauer *et al.*, 1999). Variation in the seasonal availability of crop flowers could, in turn, result in different pollinator species being present, as could geographical range shifts of pollinators in response to climate change (Parmesan *et al.*, 1999; Memmott *et al.*, 2007; Deutsch *et al.*, 2008; Bartomeus *et al.*, 2013). Either scenario could secondarily affect the diurnal timing of pollinator activity, but such changes are beyond our ability to predict at present.

Our investigation of behaviourally mediated changes in pollination services predicts that climate warming will affect pollinator species' activity patterns differentially, causing some to increase and others to decrease in their provision of pollination services. Due to the differential responses among taxa and the diversity of taxa that pollinate watermelon, aggregate pollination services delivered to crop flowers are predicted to increase slightly, even under the most extreme climate change scenario. Because in the absence of wild taxa, pollination services would be predicted to decline, our results demonstrate the importance of native biodiversity in buffering the impacts of environmental change.

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Supporting Information

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

Data S1. Supplementary details concerning methodology.
Figure S1. Plot of temperature and time of day for the 91 sampling days.
Figure S2. Regression lines demonstrating the decline in pollen deposition with time.
Figure S3. Time-temperature response surfaces of variance among the eight species.
Table S1. Species composition of the five taxonomic groups.
Table S2. Error rate assigning pinned specimens to species groups.
Table S3. Differences in pollen deposition within species groups.
Table S4. Differences in pollen deposition among species groups.