

LETTER

Biodiversity ensures plant–pollinator phenological synchrony against climate change

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Abstract

Climate change has the potential to alter the phenological synchrony between interacting mutualists, such as plants and their pollinators. However, high levels of biodiversity might buffer the negative effects of species-specific phenological shifts and maintain synchrony at the community level, as predicted by the biodiversity insurance hypothesis. Here, we explore how biodiversity might enhance and stabilise phenological synchrony between a valuable crop, apple and its native pollinators. We combine 46 years of data on apple flowering phenology with historical records of bee pollinators over the same period. When the key apple pollinators are considered altogether, we found extensive synchrony between bee activity and apple peak bloom due to complementarity among bee species' activity periods, and also a stable trend over time due to differential responses to warming climate among bee species. A simulation model confirms that high biodiversity levels can ensure plant–pollinator phenological synchrony and thus pollination function.

Keywords

Bees, crop pollination, ecosystem function, ecosystem services, phenology, pollination, response diversity, stabilising mechanism.

Ecology Letters (2013) **16**: 1331–1338

INTRODUCTION

The idea that biodiversity can buffer ecosystem functioning against the loss of individual species is referred to as the biodiversity insurance hypothesis (Lawton & Brown 1993; Naeem & Li 1997; Loreau *et al.* 2001). This hypothesis predicts that biodiversity can ensure ecosystem functions in two ways: (1) a performance-enhancing effect (i.e. an increase in the mean level of function provided) and (2) a buffering effect (i.e. a reduction in the temporal variance in function). There is an extensive theoretical (Yachi & Loreau 1999) and experimental literature supporting the insurance hypothesis by showing that increased species richness leads to both higher mean ecosystem function and lower variance in function over time (reviewed in Balvanera *et al.* 2006; Cardinale *et al.* 2012). However, far fewer studies have explored this question in non-experimental systems (but see Klein *et al.* 2003; Laliberté *et al.* 2010; Garibaldi *et al.* 2011), and in particular, long-term studies are lacking. The few studies to explicitly explore the effect of scale suggest that it is precisely across large spatiotemporal scales that biodiversity insurance effects might be strongest (Loreau *et al.* 2003; Isbell *et al.* 2009, 2011; Reich *et al.* 2012).

A second knowledge gap in the field of biodiversity–ecosystem functioning research stems from the fact that research on the insurance hypothesis has been dominated by experiments focusing on a single trophic level, most often plants (Balvanera *et al.* 2006). Yet, in reality, interactions among species determine the outcome for many important functions, such as pollination and pest control. In addition, species interactions may be more sensitive to human

disturbances than are the species themselves (Tylianakis *et al.* 2008; Veddeler *et al.* 2010). Interactions require that the species co-occur in space and time; thus, the biodiversity insurance hypothesis might also apply to phenological synchrony among species. Higher richness of potentially interacting species (e.g. either plants or pollinators) could buffer the interaction against fluctuations in the numbers of individual species over time. Perhaps, the main way such buffering could occur is through species' differential responses to environmental change, a mechanism known as response diversity (Ives *et al.* 1999; Walker *et al.* 1999; Elmqvist *et al.* 2003). However, this phenological extension of the biodiversity insurance hypothesis, and the role of response diversity in driving it, has been explored very little (Jiang & Pu 2009).

Here, we investigate phenological synchrony as a novel dimension of the biodiversity–ecosystem functioning relationship, using plants and pollinators responding to climate warming as a model system. Human-mediated climate change has the potential to modify species phenologies in a directional, long-term manner (Parmesan 2006). Average global temperature has already increased by 0.6 °C, resulting in detectable shifts in phenology (Parmesan 2006), notably for species active in early spring (Fitter & Fitter 2002; Bartomeus *et al.* 2011). Different taxa show divergent rates of advance (Root *et al.* 2003), and this makes species interactions particularly vulnerable due to potential phenological mismatch (Visser & Both 2005; Rafferty & Ives 2011). Animal-mediated pollination is a particularly important interaction to understand in the context of climate change, given that animal pollinators are required by most of the world's flowering plant species (Ollerton

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et al. 2011), including most crop plants (Klein *et al.* 2007; Garibaldi *et al.* 2013).

In this study, we use long-term data sets to examine whether pollinator biodiversity could buffer plant–pollinator interactions against climate change, by increasing and stabilising phenological synchrony between apple (*Malus × domestica* Borkh.), a valuable fruit crop and its wild pollinators. We use a 46-year time-series data set on the bloom phenology of commercial apple in New York State, USA, along with an independent data set on the phenology of wild bee species that commonly visit apple flowers, which was collected over the same time period in a broader region centred on the focal apple orchard. First, we used contemporary data to select the key apple visitor species and to test if there is phenological complementarity among them. Second, we compared the empirical rate of phenological advance over time between apple and its diverse set of pollinators, in aggregate, to determine whether phenological mismatch is occurring at the community scale. Third, we asked whether different pollinator species showed different rates of phenological change with respect to apple bloom over time. Such differential responses to climate change could buffer aggregate function in this case, by stabilising phenological synchrony over time. Finally, we conducted a simulation analysis to explore the effect of pollinator species richness on plant–pollinator phenological synchrony. We predicted that increasing biodiversity would: (1) increase the phenological synchrony between apple and its pollinators due to complementarity in phenology across pollinator species, and (2) stabilise changes in synchrony between apple and its pollinators through time, due to the differential rates of phenological change over time across pollinator species. We found that the phenologies of apple and its complete community of 26 key pollinator species have largely shifted at similar rates over 46 years of climate warming, and that asynchrony is likely prevented by the varied rates of phenological change observed among different pollinator species. The capacity of biodiversity to buffer the effects of environmental change for plant–pollinator interactions is supported by the simulation analysis, which shows that high levels of bee diversity increase and stabilise phenological synchrony through time.

METHODS

Data collection and filtering

Study system

Apple is a valuable temperate-zone crop and relies on pollinators for fruit production (Free 1993). Apple blooms in early spring for a restricted period, making it a good indicator of potential phenological mismatches resulting from climate change. Apple has an open, generalised flower morphology, which is accessible to a wide variety of pollinators. To assess which species of pollinators visit apple flowers and, thus, constitute the species of interest for our analysis, we surveyed diversity and abundance of bees visiting apple, in Tompkins, Wayne, and Schuyler counties in upstate New York, USA for three years, in the springs of 2009–2011. A total of 22 orchards (10 in 2009, 6 in 2010, 16 in 2011) were surveyed at least once during the apple bloom on days with temperature > 16 °C, with all data collection completed between 10:00 and 15:30 h. Each orchard contains several varieties, the most common being ‘McIntosh’, ‘Golden Delicious’, ‘Empire’ and ‘Jonagold’. At each site, multiple trials of 15-min timed, aerial netting were conducted

along blossoming tree rows; only bees visiting apple blossoms were collected. All specimens collected were identified to species using taxonomic keys and comparison to expertly identified material, and subsequently deposited in the Cornell University Insect Collection, Ithaca, NY, USA (<http://cuic.entomology.cornell.edu/>). We collected 2730 specimens of 82 bee species visiting apple during 2009–2011 (Table S1). To select the key apple pollinators, we only further analyse the species which in combination accounted for 90% of the total specimens collected (26 species). Removing the tail of rare species reduces the potential insurance that these species can provide, but ensures that all pollinators included are, in fact, important contributors to apple pollination. This is important because rare apple visitors may be very abundant in historical collections having an excessive weight in the phenology analysis. Thus, our analysis assumes that the identity of the most frequent apple visitors did not change dramatically during the past 50 years. This seems a reasonable assumption given that most bee species persisted well in our study area since the 1870s (Bartomeus *et al.* 2013a). As a test on this conservative approach, we provide additional analyses including a wider range of species (38 species in total) found to be important visitors to apple flowers in other historical studies (Phillips 1933), and show that results of this analysis are qualitatively similar to those we report in the main text (See Text S1).

Historical data

Historical records of apple phenology (a mean of mid-season varieties typified by ‘Delicious’ and ‘Empire’ cultivars) were gathered at New York State Agricultural Experiment Station in Geneva, New York (42.868 N, 76.978 W). In each year of the 46-year study period (1965–2011, with data missing only from 2007), an observer recorded the date of mid-bloom, defined as trees having 80–100% of the central blossoms in the flower clusters open. Temperature records for the mean April temperature (average of the maximum plus the minimum daily temperatures divided by two) for each year were obtained from a weather station at the New York State Agricultural Experiment Station, within 1 km of the observed orchards. Data from 1965 to 2001 in this same study were previously reported by Wolfe *et al.* (2005).

Historical data were obtained only for the 26 bee species that collectively accounted for 90% of the visits to apple flowers in our 2009–2011 field study, as described above. Our data were obtained from pinned specimens housed in the Cornell University Insect Collection (70% of the analysed records), and additionally from museum specimen data available through Discoverlife.org, USDA, GBIF and the Illinois Natural History Museum. The Discoverlife.org data set compiles specimens from 13 collections, the majority from the American Museum of Natural History. Overall, ~80% of the analysed records were reported in Bartomeus *et al.* (2013b). Once obtained, all records were filtered and standardised as in Bartomeus *et al.* (2013a). This includes verification by a taxonomic expert, geo-referencing of collection localities and recording collection dates based on information indicated on the specimen label, and double-checking outliers. We then transformed all collection dates to the number of days elapsed since January 1 and refer to this variable as ‘collection day’.

We used only bee specimens collected from 1965 onwards to match the apple phenology records. The geographical extent of the bee specimens used ranges from 41.868° to 43.868° N latitude and –85° to –70° W longitude. The New York State Agricultural

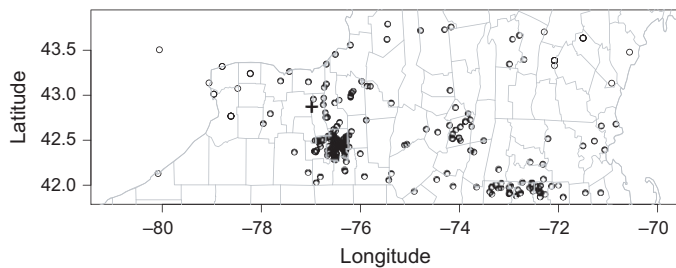


Figure 1 Map of the study area. The cross (+) indicates the location of the New York State Agricultural Experiment Station in Geneva, New York, USA. Each bee collection used is a grey circle, with is maximum density around the city of Ithaca, New York. Grey boundaries are counties within New York State.

Experiment Station in Geneva is located in the central point of the study area (42.868 N, 76.978 W; Fig. 1). These geographical limits (covering only two latitude degrees) were selected to minimise the extent to which underlying geographical variation might complicate an understanding of phenological synchrony, while simultaneously utilising sufficient data points for statistical analysis. Latitude was additionally controlled for in the analysis as described below. To ensure independence of samples, we used only one specimen per species from a given collection event, defined by unique combinations of collector, date and location. Specimens collected on apple were excluded to ensure that our measures of bee phenology and apple bloom phenology were independent (only 95 bee specimens were excluded for this reason; < 0.3% of the records). Honey bees were not included in our analysis because they are a managed species and their phenological patterns, therefore, also reflect management decisions. One exotic species, *Osmia cornifrons*, was also excluded on the grounds that it was introduced to North America in 1970s. Its numbers have increased dramatically, which could lead to sampling artefacts that would mislead our analysis of phenology. For bumble bees (the genus *Bombus*), only gynes were included in the analysis since this caste is predominantly active during apple flowering. In contrast, the worker caste hatches later in the season, thus largely missing apple bloom, and in addition is less sensitive to climate variables in spring (see Bartomeus *et al.* 2011).

Because latitude has a strong effect on bee phenology (Bartomeus *et al.* 2011), we corrected for the effect of latitude prior to conducting the analysis by standardising all bee collection dates to the latitude of the location where the apple bloom data were collected. To do this, we multiplied each collection date by a coefficient resulting from the relationship between latitude and collection date found for a much larger data set of spring bee species throughout the north-eastern USA (5.90 days per latitude degree; Bartomeus *et al.* 2011). Prior to the correction, we checked that year and latitude were not strongly correlated in our data set (year-latitude Pearson correlation = -0.05). Note, that the maximum correction we used was ~ 5 days, and that most records (~ 70%) come from the region near Ithaca, New York (Fig. 1); hence, those records received less than 2 days of correction. Furthermore, our study region is characterised by small elevation shifts, and previous work indicates that within this region longitude has very little effect on bee phenology (Bartomeus *et al.* 2011). All analyses used this latitude-corrected collection day (hereafter referred to simply as collection day). After all of the data filtering steps above, we retained 2230 specimens of 26 species, collected by, at least, 162 collectors in 1044 different collection events.

Statistical analysis

Phenological complementarity among pollinator species in present-day data

We used our present-day (2009–2011) survey data to measure the current extent of phenological complementarity among the bee species that pollinate apple. For this analysis, data from all orchards were pooled to allow us to characterise phenology at the species level. Each year was analysed separately because there were strong phenological differences in weather across years (i.e. early vs. late springs), which could have obscured otherwise consistent patterns among bee species.

Observed rate of phenological change for apple and its pollinators

We used our historical data sets on both apple flowering and bee activity to measure the rate of phenological change over time. First, we measured the rate of phenological advance for apple as the slope of peak bloom against year (in units of days/year). Second, to measure the rate of phenological advance for the pollinator community as a whole, we performed a joint analysis for all specimens of our 26 apple-visiting bee species over time, using R package *nlme* (Pinheiro *et al.* 2013). Overall, advance rate was measured as the slope of bee collection date against year, while bee genus and species nested within genus were also included as random factors. Plant and bee slopes (\pm SE) were compared with *t*-tests. Temperature changes over time were also assessed by regressing mean April temperature against year.

Asynchrony analysis: is response diversity maintaining pollinator synchrony with apple over time?

As our measure of phenological asynchrony, we computed the difference between the date each bee specimen was collected and the date of peak apple bloom in the same year (Fig. 2). Thus, differences with larger absolute values indicate greater *asynchrony* between apple and its pollinators. We restricted the maximum asynchrony that can result in an interaction within realistic thresholds based on apple and bee biology, by excluding in the analysis bees that could not have interacted with apple because their period of activity fell well outside apple's flowering period. We included specimens collected within plus or minus 25 days around the peak bloom date recorded for a given year. This conservative 25-day definition of complete asynchrony accounts for the extended apple bloom period (3–4 weeks in our study area), as well as the fact that bees were likely active before and after the day on which they were collected (species are active a minimum of 4 weeks in our study area; Bartomeus *et al.* 2013a). Specimens excluded from the analysis for being outside of this time window were predominantly mid to late summer specimens of multivoltine species that fly until fall, such as *Augochlora* or *Ceratina*. After filtering our data set to include only specimens collected within \pm 25 days from the peak bloom on each year, we retained 1378 specimens for the analysis (Fig. 3). Sensitivity analysis showed that our results are robust to the choice of threshold (Fig. S1).

We regressed our measure of plant–pollinator asynchrony (i.e. the temporal difference between apple bloom and pollinator activity) against year (Fig. 2c), while including model terms for bee species and the species \times year interaction. A significant interaction would indicate that species show response diversity, or differential changes in their asynchrony with apple bloom over time. Diagnostic plots for all analyses were examined for heteroscedasticity, as well as to ensure the normality of errors.

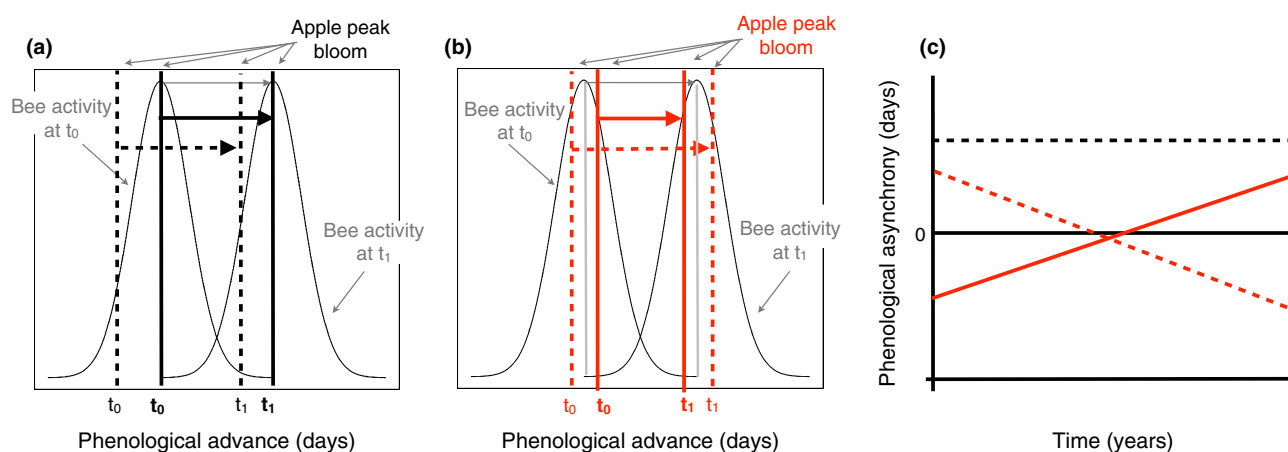


Figure 2 Hypothetical scenarios of phenological advance. Bee activity (fine grey distributions) and apple peak bloom (thick black/red lines) are a schematic representation of our data. (a) A stable scenario where both bees and apple change at the same pace. Change is indicated by the arrow direction between t_0 and t_1 . Both taxa can be synchronised (solid lines) or not synchronised (dotted lines). (b) Unstable scenarios where apple peak bloom advances more slowly (solid lines) or more quickly (dotted lines) than bee activity. (c) The resulting phenological asynchrony over time, which is stable (flat slope) in two scenarios (black lines), but unstable (negative or positive slope) in two others cases (red lines). Note that the asynchrony can either decrease (lines approaching 0) or increase (lines diverging from 0) depending on the relationship between the baseline synchrony observed (y-axis intercept) and the direction of the divergence between bee and apple phenology (slope).

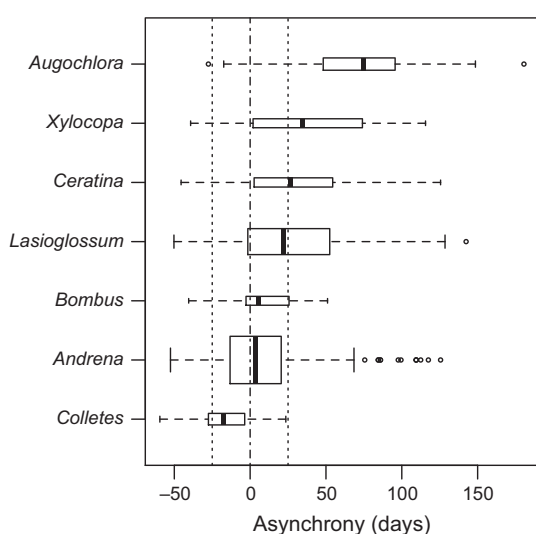


Figure 3 Synchrony between common apple-visiting bee species and apple peak bloom. Data are pooled by genus for concision. Note that some genera such as *Andrena* are centred around the peak bloom date for apple (dash-dot line), while other genera occur before (e.g. *Colletes*) or after (e.g. *Bombus* gynes). Finally, other genera are most active later in the growing season or have several generations active during summer and synchronise with apple bloom only at the beginning of their flight period (e.g. *Lasioglossum*, *Xylocopa*, *Ceratina*, *Augochlora*). Boxplot widths are proportional to the square root of the sample size. The 25 days around the peak bloom date, which encompass all the data used in the main analysis, are indicated with dotted lines. Negative values indicate dates before apple peak bloom, and positive values after.

Simulation analysis: does plant–pollinator phenological synchrony increase with pollinator species richness?

We conducted a simulation analysis to explore the effect of bee species richness on the baseline phenological asynchrony between apple and its pollinators and on the stability of such asynchrony through time (see definition of both measures below). Briefly, the simulation created pollinator communities of different richness levels based on

a random sample of the 26 apple pollinators and, for each richness level, performed a regression analysis of phenological asynchrony of all selected species against year (see Fig. S2 for an schematic view of the simulation).

Baseline phenological asynchrony was defined as the y-intercepts of the regression of plant–pollinator asynchrony against year, which approximates the bee–apple asynchrony at the beginning of the time series (1965). If we observe temporal differences in pollinator activity among bee species (i.e. different pollinator species are complementary in their phenologies), we expect baseline asynchrony (in days) to decrease as pollinator richness increases, because the probability of including complementary species increases. Conversely, if different pollinator species are not complementary in their phenologies then baseline asynchrony should not change with pollinator richness (Fig. S2). While an alternative measure of asynchrony would have been the mean of the entire time series, we used a baseline measure of asynchrony at the y-intercept to obtain measures of mean asynchrony not confounded with the rate of change over time (see below).

The stability of pollinator and apple bloom asynchrony over time was measured as the slope of the above-mentioned regression, i.e. as the rate of change in phenological synchrony over time, with slopes close to zero indicating stability. As pollinator richness increases, we expect the slope of the difference between apple bloom and pollinator activity (i.e. asynchrony) against time to get closer to zero, if pollinator species have differential phenological shifts over time. In this case some pollinator species will be advancing their phenology faster than apple, and others slower than apple, thus cancelling any overall effect (Fig. 2a,c, Fig. S2). Conversely, if the different pollinator species all respond similarly and are consistently shifting their phenologies either faster or slower than apple, then increasing pollinator richness should not have a stabilising effect (Fig. 2b,c).

Our measures of baseline and stability of phenological synchrony as a function of pollinator species richness should be robust estimates for several reasons. First, our measures are an intercept and a slope, respectively, thus they are unbiased and consistent statistical

estimators (Plackett 1950; Lai *et al.* 1978). This means that they should be affected by differences in phenology among species, but less so by the number of individuals in the distribution. To check for possible bias associated with larger uncertainty on the estimates at low richness levels due to smaller sample size, we also present a simulation in which all models are rarefied to the same sample size, which shows qualitatively similar patterns (Fig. S3). Second, we do not interpret the variability across iterations at a given richness level, but rather only the mean value obtained across all iterations at a given richness level. We do this because, as is the case for many biodiversity experiments, the similarity of species composition across the randomly created bee communities within a richness level will be higher at higher richness levels (because fewer options are possible). Therefore, the variability across iterations at a given richness level will be lower at higher richness levels (Fukami *et al.* 2001). Third, because pollinators shifting either earlier or later than apple would be of equal interest, we base all our analyses on the absolute values of each simulated community's response (Fig. S2).

Each iteration of the simulation proceeds as follows. The simulation randomly selects a number of species (from 2 to 24 of the 26 available species). For each of these species pools, it runs the regression between phenological asynchrony and year, using the model described above. It then calculates the two values explained above for each simulated species pool: first, the absolute value of the baseline phenological asynchrony, measured as the predicted value in 1965; second, the stability of phenological synchrony over time (i.e. the rate of change), calculated as the absolute value of the slope. We ran 100 iterations for each species richness level (Fig. S2).

RESULTS

Phenological complementarity among pollinator species in present-day data

Our recent surveys of apple orchards confirm that some bee species are collected early in the apple bloom season, while other species are collected later on. This result is consistent across years (2009: $F_{56,386} = 2.08$, $p < 0.001$; 2010: $F_{40,257} = 1.65$, $p = 0.01$; 2011: $F_{67,832} = 1.86$, $p < 0.001$; Fig. S4). Thus, in the present-day data, bee species show phenological complementarity with regard to their pollinating activity at apple.

Observed rate of phenological change for apple and its pollinators

Both apple and associated bee pollinators are advancing their phenology through time. The phenological advance of apple was previously reported by Wolfe *et al.* (2005) for the period 1965–2001 and is here confirmed with 10 more years of data. The date of apple mid-bloom has advanced by roughly 2 days per decade (year estimate = -0.18 ± 0.07 days per year, $p = 0.01$; Fig. 4a). The key bee pollinators are, in aggregate, advancing their phenology at a similar rate (year estimate = -0.19 ± 0.04 days per year, $p < 0.001$). A simple comparison of the apple and aggregate bee slopes shows that they are not significantly different (*t*-test on the two slopes; $t = 0.13$, p -value = 0.89; Fig. 4a). Note that the bee intercept of this model is greater than that of apple, because this analysis includes species with extended periods of activity (Fig. 3). Lastly, in keeping with the phenological advances shown by apple and its pollinators, the mean

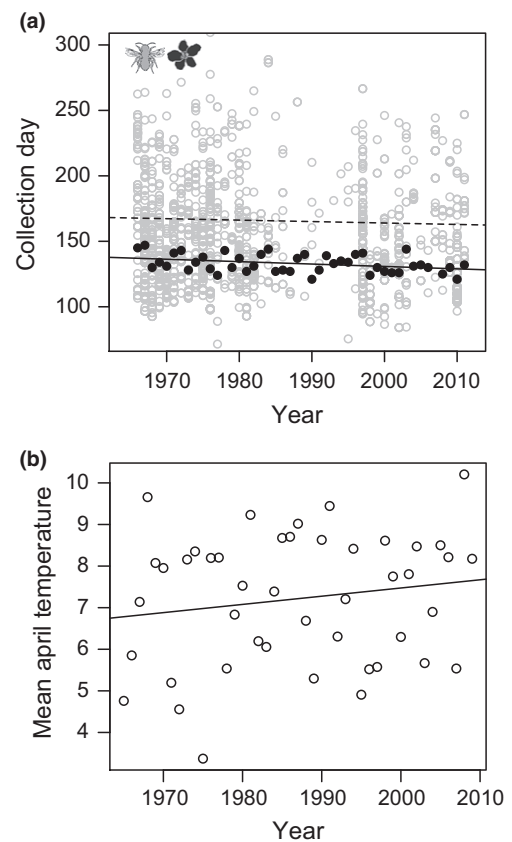


Figure 4 Change in temperature and phenology of apple and its pollinators over a 46-year period. Collection day is expressed in days since 1 January. (a) Apple peak bloom (filled circles and solid regression line) and bee specimens (empty circles and dotted regression line) are shown. Some pollinator species extend into the summer making the bee intercept higher than for apple. (b) Mean daily maximum April temperature is expressed in degrees Celsius.

April temperature has increased in parallel by 0.92 °C in the focal study area. Although this pattern is not significant for our focal data (year estimate = 0.02 ± 0.018 °C per year; p -value = 0.28; Fig. 4b), overall, our larger study region shows a recent significant increase in mean April temperature (Bartomeus *et al.* 2011).

Asynchrony analysis: is response diversity maintaining pollinator synchrony with apple over time?

We further analysed the difference between apple peak bloom and bee collection day for the key apple pollinators, using only specimens that can potentially interact with apple (i.e. collected within 25 days of peak bloom). We find no change in the degree of asynchrony over time (year estimate = -0.005 ± 0.024 days of difference per year, $p = 0.72$), indicating a stable level of phenological synchrony (overall community falls into scenario drawn in Fig. 2a, solid lines). Moreover, the mean phenological synchrony is very high as denoted by the phenological synchrony being centred around zero (Fig. 5; predicted value in 1965 = 0.2). This analysis also revealed a significant interaction term between year and bee species (species \times year interaction term; $F_{25,1316} = 1.76$, $p = 0.01$; Fig. 5), indicating that different bee species showed differential shifts in their phenology with respect to apple over time (i.e. some

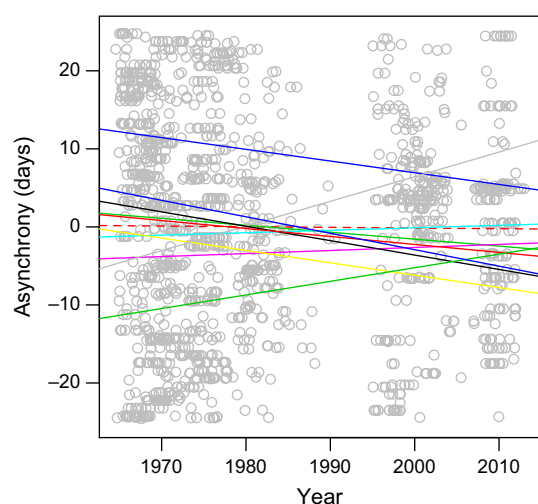


Figure 5 Response diversity among bee species in terms of their phenological shifts over time. Asynchrony (number of days between bee specimen collection date and the peak bloom of apple) as measured over the 46-year period. Dashed red line shows the slope of the full model including all species and is centred around zero. Coloured lines represent the slopes for the each individual bee species with more than 50 records. See Table S2 for individual models.

particular species fall into the scenario drawn in Fig. 2b). See Table S2 for the individual models for each species.

Simulation analysis: does plant–pollinator phenological synchrony increase with pollinator species richness?

The simulation indicates that increasing pollinator species richness increases the baseline phenological synchrony with apple bloom and also stabilises synchrony over time (i.e. makes the slope closer to zero in Fig. 2c). Baseline synchrony increases monotonically from almost 4 days of mean difference between apple and its pollinators at richness levels of two species, to 0.3 days of mean difference at 24 species (Fig. 6a). Similarly, the stability of the phenological synchrony increases with increasing pollinator richness. The rate of phenological dissociation would be 0.11 days per year for a species richness level of 2 (i.e. leading to almost 5 days' mismatch over the 45 years period of the study), but the rate of asynchrony decreases quickly with increasing species richness, such that at the highest richness level it is only 0.02 days per year (Fig. 6b). Overall, as we increase richness, the scenario changes from being qualitatively similar to Fig. 2b to being qualitatively similar to Fig. 2a.

DISCUSSION

The phenologies of a spring blooming plant, apple and its pollinator bee community have advanced at similar rates during the last 46 years. A high diversity of floral visitors appears to be stabilising plant–pollinator phenological synchrony against climate change via the mechanism of response diversity. Different bee species show changes in phenology that are either faster or slower than apple, thus leading to stable phenological synchrony between apple peak bloom and the summed activity of all members of the apple bee community over a 46-year time period. Moreover, we show that at any one time, high bee diversity increases the mean phenological synchrony between pollinators and apple bloom, due to comple-

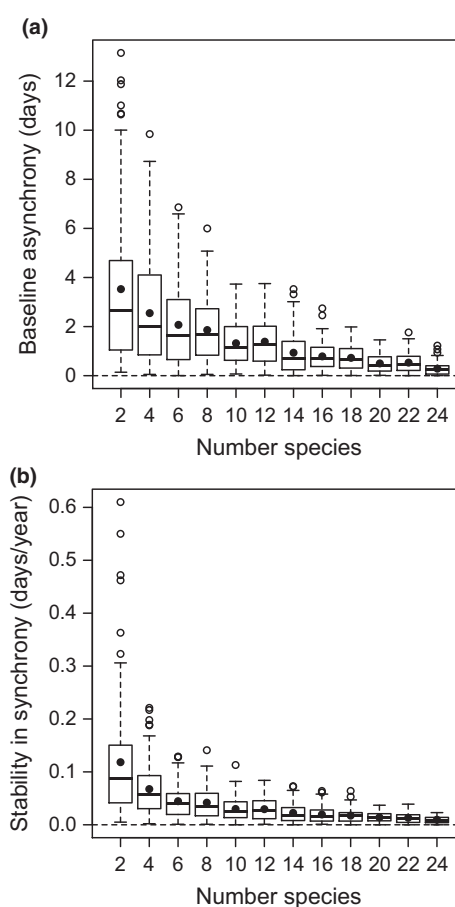


Figure 6 Simulation of biodiversity effects on phenological asynchrony. We randomly selected species to create bee communities of 2–24 species, then calculated the baseline, and stability of, phenological synchrony for each randomly assembled community using linear models as described for the historical data in the main text (see Fig. S2 for a graphical portrayal of this analysis). Results shown here represent 100 iterations for each richness level. Black dots are the mean values reported in the text, and the boxplots reflects the distribution of the 100 iterations. (a) Baseline phenological asynchrony between apple and bees (in days) reported as the absolute value of the predicted difference between apple and bee activity dates in 1965. Larger values indicate greater asynchrony. (b) Stability of phenological synchrony between bees and apple as the absolute value of the slope of the model (in days of difference per year). Greater stability is indicated by slopes closer to zero.

mentarity among bee species in phenological activity (Fig. 2, Fig. S4). Because the frequency of pollinator visits to flowers is a reliable predictor of pollination function, this phenological synchrony is likely to result in more effective apple crop pollination (Vazquez *et al.* 2005; Garibaldi *et al.* 2013).

Previous work has shown that rates of phenological advance related to global warming seem broadly consistent between generalist plants and bees at large spatial scales (Bartomeus *et al.* 2011), and that bees and the plants they pollinate appear to use similar environmental cues to time their spring emergence (Forrest & Thomson 2011). Results from the present study, based on bees associated with a single mass-blooming crop over a 46-year time period show the same pattern: the rate of advance of apple peak bloom in central New York State and the rate of advance of early spring apple pollinators are similar because we found significant phenological shifts in both partners (a mean of 8 days since 1965).

Even though our time series data on apple bloom were limited to a single focal orchard, there is evidence that peak bloom in other apple orchards across a wider geographical region are advancing their phenology at similar rates (Wolfe *et al.* 2005; slope of three orchards = -0.20 days/year, compared with -0.18 days/year in our study), suggesting that our results have generality for the larger region across which our bee data were collected.

In addition to the stabilising effect exerted by the diverse pollinator community, there are several other reasons why we should not expect climate change, at least at its current level, to cause phenological mismatch between plants and pollinators. First, the present-day year-to-year variability in the onset of apple flowering (12 days across a 3-year interval; Fig. S3) exceeds the mean change experienced over the nearly 50-year time series (8 days). Second, we show that even at low diversity levels, we expect only moderate asynchrony (less than 5 days) between bees and apple over the 46-year period. In addition to the insurance provided by biodiversity, evolution may also play an important role in synchronising plant–pollinator interactions (Anderson *et al.* 2012; Gilman *et al.* 2012). For example, bee or plant individuals that become asynchronised might be selected against, in favour of individuals that maintain synchrony. Overall, our results suggest that pollination systems, especially for generalised species such as apple, may be buffered against climate change, but caution is needed when extrapolating these results to more specialised plant–pollinator systems or to predicting future trends under continued climate warming.

The general synchrony observed at the community level in our study system supports the biodiversity insurance hypothesis. In fact, our data support its two main predictions (Yachi & Loreau 1999). First, we demonstrate that high levels of biodiversity increase the mean phenological synchrony between bee pollinators and apple flowering, as some species tend to fly earlier than the apple peak bloom, while others fly later; thus, phenological complementarity among bee species increases the degree of phenological synchrony with apple as species richness increases (Fig. 6 and Fig. S5). Second, high biodiversity levels stabilise the phenological synchrony over time. Species-rich bee communities are more likely to include species with differential responses to climate change, and thus a buffering effect occurs which minimises directional change in phenological synchrony at the community level (Fig. 4). Although we show here that differential phenological responses among bee species play a role in maintaining the community-level synchrony between apple and its pollinators, we do not rule out the possibility that other mechanisms might also play a role. For example, the likelihood of having a bee species in the community that synchronises broadly with apple across all time periods (e.g. *Andrena vicina* Smith) might increase when biodiversity is high. This mechanism, if it occurs, would be consistent with the sampling effect hypothesis found in experiments (Hooper *et al.* 2005). Moreover, although all species included in our analyses are known to be effective apple pollinators, we did not measure actual pollination function in this study and thus leave the possible variation among species in functional efficiency unexplored.

The biological insurance hypothesis has received considerable theoretical and experimental support (Lawton & Brown 1993; Naeem & Li 1997; Leary & Petchey 2009; Hector *et al.* 2010), and some short-term observational studies confirm its effect in real ecosystems (Walker *et al.* 1999; Klein *et al.* 2003; Laliberté *et al.* 2010; Garibaldi *et al.* 2011, 2013). Previous work has found that biodiversity can enhance mean levels of pollination due to

functional complementarity among pollinator species (Albrecht *et al.* 2012; Fründ *et al.* 2013) and also lead to more stable pollination across time or space (Klein *et al.* 2003; Winfree & Kremen 2009), e.g. when pollinators have diverse responses to land use change (Cariveau *et al.* 2013), or to weather conditions (Brittain *et al.* 2013). But long-term temporal effects, such as responses to climate warming, that likely play a critical role in maintaining real-world ecosystem functions have rarely been explored (but see Rader *et al.* 2013 for a modelling approach), despite the fact that biological insurance may be particularly important at large spatial and temporal scales (Loreau *et al.* 2003). Our study adds to several recent lines of evidence indicating that high levels of biodiversity are needed to sustain ecosystem function in real-world ecosystems (Isbell *et al.* 2011; Reich *et al.* 2012).

Historical specimen used for analysis are accessible as a supplementary data set hosted on Dryad doi:10.5061/dryad.9g7d8.

ACKNOWLEDGEMENTS

We thank all those who collected the bees used in our analyses, and the museums for access to their collections and John Ascher for providing taxonomic expertise. We thank S. Droege and collaborators for contributions to the data set, DiscoverLife and GBIF for making the data publicly available and rOpenSci.org for *Rgbif* package. Data capture at Cornell was supported by a National Science Foundation Division of Biological Infrastructure (DBI) grant [Grant 0956388; J.S. Ascher, PI]. Apple bloom data collection and field surveys of bee diversity in central New York apple orchards were supported by Smith Lever and Hatch Funds administered by the Cornell University Agricultural Experiment Station and a USDA-NIFA grant [USDA 2010-03689] to BND. IB was funded by post-doctoral Fellowship EX2009-1017 from the Spanish Education Ministry. We thank three anonymous reviewers for insightful comments that improved the manuscript.

AUTHOR CONTRIBUTIONS

I.B. and R.W. designed research; J.G., M. P., A.N.L. and B.N.D. collected and provided data; I.B. analysed data; I.B. and R.W. lead the manuscript writing, and B.N.D., M. P. and J.G. contributed substantially to revisions.

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Editor, Micky Eubanks

Manuscript received 29 April 2013

First decision made 4 June 2013

Manuscript accepted 29 July 2013