Climate warming changes synchrony of plants and pollinators

Running head: Plant pollinator shifts

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Abstract

Climate warming changes the phenology of many species. When interacting organisms respond differently, climate change may disrupt their interactions and affect the stability of ecosystems. Here, we used GBIF occurrence records to examine phenology trends in plants and their associated insect pollinators in Germany since the 1960s. We found strong phenological advances in plants, but differences in the extent of shifts among pollinator groups. The temporal trends in plant and insect phenologies were generally associated with interannual temperature variation, and thus likely driven by climate change. The phenological advancement of plants did not depend on their level of pollinator dependence. When examining the temporal co-occurrence of plant-pollinator pairs from 1980 onwards, the temporal trends in their synchrony again depended on the pollinator group: while the synchrony of plant-butterfly interactions remained unchanged, interactions with bees and hoverflies tended to become more synchronized, mainly because the phenology of plants responded more strongly to climate change and plants caught up with these pollinators. If the observed trends continue, these interactions are expected to become more asynchronous again in the future. Our study demonstrates that climate change affects the phenologies of interacting groups of organisms, and that it also influences their synchrony.

Keywords: asynchrony, GBIF, mismatch, phenology, pollination mode, Germany

Introduction

Phenological events are periodically occurring events in the life cycle of organisms. The timing of these events often depends on environmental factors such as temperature or photoperiod, and it is well known that climate change affects some of these and thus changes the phenologies of many organisms [1]. With such phenology shifts, there is increasing risk of phenological mismatches between interacting organisms, potentially exceeding the natural resilience of ecosystems [2]. Climate change-induced phenological shifts have been documented extensively for individual species [3], but we still know much less about how these shifts affect ecological interactions. Kharouba et al. [4] recently reviewed 54 published interaction studies across ecosystems and interaction types and found no clear general trend, with about half of the studied interactions becoming more asynchronous but the other half becoming even more synchronized through climate change.

Plant-pollinator systems are among the biotic interactions expected to suffer most from a mismatch of phenological events [5]. Several previous studies have observed mismatches [6,7], but in others pollinators and plants seemed to be able to keep up with each other [8]. An interesting question in this context is also which of the two partners is advancing faster if there is an increasing mismatch. So far, the evidence here is also mixed. For instance [9] found pollinators to advance faster than trees, and Parmesan [3] that butterflies advanced faster than herbaceous plants, but in a study by Kudo & Ida [10] it was the plants – spring ephemerals – that advanced faster than their bee pollinators.

Mismatches of plant-pollinator interactions can have negative consequences for both partners. For the pollinators, this can include lower survival rates, a decreased overall fitness and higher parasite loads [11]. Moreover, mismatches might also impact pollinator demography, the body sizes [6] and frequencies of sexes, and thus population viability [11]. On the plant side, desynchronized pollinator interactions are mainly expected to impact plant fitness and thus long-term population growth and survival. For instance, Kudo & Ida [10] found that seed counts were reduced in early-flowering spring ephemerals after desynchronization with their bee pollinators. However, in another study fly-pollinated plants did not show similar responses [12].

Plants differ in their level of dependence on plant pollinators, and an intriguing question therefore is to what extent phenology responses to climate change are linked to the pollinator dependence of plants. Bond [13] theorized that wind-pollinated plants might experience little negative consequences of climate change as they do not depend on interactions with animals. Conversely, insect-pollinated plants may be subject to strong selection toward phenologies that are in synchrony with their pollinators. This hypothesis was later corroborated in an empirical study by Fitter & Fitter [14]. A more recent study on orchids [15] found that pollination mode influenced the degree of plant advances in flowering phenology, indicating that self-pollinating and thus pollinator-independent plants were not constrained by pollinator phenology. The main idea of these previous studies is that all else being equal, pollinator-independent plants should exhibit stronger phenological shifts in response to the same climate changes.

Testing hypotheses about plant-pollinator responses to climate change is not trivial. Since changes in phenology take place on the scale of decades [16], we need long-term data. A possible source of long-term data on plant phenology are herbarium specimens [17,18], which can indicate the day of year that a specific species was flowering in a given location and year. Herbarium data provide unique historical depth, but they need to be treated with caution because of the sampling biases associated with them [19,20]. In recent years the digitization of herbaria as well as other collections and observation data, including on other taxa such as pollinating insects, e.g. from long-term monitoring networks, is creating an increasing number of public data bases that contain vast amounts of natural history data that cover large spatial and temporal scales [21]. These data bases are increasingly being used for analyses of broad ecological trends and global changes [20,22]. One of the largest and most important hubs of large-scale and long-term ecological data sets is the Global Biodiversity Facility (GBIF), an intergovernmental initiative and public data base that provides access to biodiversity data compiled from various individual sources like academic institutions, government agencies or independent collections (GBIF, 2019).

Another matter is finding a measure for changes in phenology. Primack et al. [23] demonstrated that the average collection date of the herbarium specimens of a plant species in a year can be used as a proxy for peak flowering time in that year. The same approach of using occurrence records in natural history collections or other data bases can in principle be used to estimate the activity times of other groups of organisms such as insects (4 and references therein). For instance, analyses of natural history collections in the UK have demonstrated phenology changes in bees [7] and butterflies [24]. Thus, the peak occurrences of plants and insects in GBIF may be used to estimate activity shifts of different groups, as well as their synchrony. When we use the term ‘activity’ in this paper, we refer to the period in an organism’s life when it can interact with its ecological partner. For plants this is the period of flowering, for insect pollinators the period of flight.

We used data from GBIF to study phenological mismatches between plants and pollinators in Germany, at the level of taxonomic groups as well as individual interactions. We asked the following questions: (i) Are there long-term trends in the phenology of plants and pollinators? (ii) If yes, are phenology trends related to climate change? (iii) How are phenological changes of plants related to their pollinator dependencies? (iv) How does climate change affect the synchrony of plant-pollinator interactions?

Methods

Phenology data

We worked with occurrence records of plants and insects available from the GBIF database [25–36]. For the plants, we restricted ourselves to species covered by the BioFlor database of plant traits [37], because we needed to be able to classify plants by their level of pollinator dependence (see below). For the insects we restricted ourselves to beetles (Coleoptera), flies (Diptera), bees (Hymenoptera) as well as butterflies and moths (Lepidoptera), as these groups contain most insect pollinators [38]. We used the R package *rgbif* [39] to download all available records of the above taxa from GBIF. Our basic criteria for including records were that they originated from Germany, and that they referred to either a living specimen (e.g., a captured insect), a human observation, just an observation (i.e., when the exact type of observation was not clear), or a preserved specimen (e.g., an herbarium record). If names of plant species were not accepted names, we used the R package *taxsize* [40] to check the names against the GBIF backbone taxonomy and determine the actual accepted.

Prior to the data analyses, we subjected the data to several steps of quality control (**Figure S1**). First, we removed all records from before 1960 as these turned out to be too inconsistent, with few records per year and large gaps between years with records. We also removed the records from 2020 as the year had not been complete at the time of our analysis. Second, we removed all records from the first and last days of years because the high number of records on those days indicated that records without a recorded collecting date had been given these as default dates. Next, we removed all records from “GEO Tag der Artenvielfalt”, a German bioblitz event where large numbers of records are taken on a specific day of the year. Including these data would have strongly biased the intra-annual distributions of our records. Finally, we removed the records from several collections which appeared to have misclassified these as being of German origin, probably through a combination of coordinate rounding and determining countries of origin automatically from these coordinates. We identified these sets of records by visually inspecting the geographic distributions of the records of each institution; most of these erroneous data sets were from Luxembourg (**Table S1**). There were a few records just outside the boundaries of Germany that we did not remove from our data set because the country information appeared trustworthy and we suspected errors with the recording of the coordinates. Obviously, the latter steps of our quality control were possible only for georeferenced records, which made up 99.97% of the total amount of records. After these data curation steps, we maintained around 11 million plant records and over one million insect records for our data analysis. There were large differences between plants and insects not only in the numbers of records but also in their temporal distribution across the studied period (**Figure S2**). While plants, but also beetles, had relatively even record numbers across decades, the other insect groups, in particular flies and bees, were strongly underrepresented in the earlier decades, and record numbers increased rapidly only in the last 20 years, probably due to the advent of platforms like iNaturalist.org and naturgucker.de, which allow logging of species occurrences by citizen naturalists, and which make up most of our insect data. Beetles were represented, save for one species from the Orsodacnidae, by the Chrysomelidae family.

Climate data, pollinator dependence, and individual interactions

Besides the main phenology data from GBIF, we obtained several other data sets required for our analyses. To test for associations with climate, we used climate data from Deutscher Wetterdienst (DWD, https://www.dwd.de/), specifically the historical (until 2018) and recent (2019) monthly station observations data set [41,42] to calculate the Germany-wide average annual temperatures for 1960-2019. The exact climate data sets used are available at the repository under data availability.

To classify plants by their level of pollinator dependence we used plant trait data from BiolFlor [37]. A species was assigned as pollinator-dependent when it was either known to be self-incompatible and pollinated by an insect, dioecious and pollinated by an insect, or protogynous/protandrous while also being pollinated by an insect. In contrast, species that were pollinated abiotically or through selfing, that exclusively reproduced vegetatively, or were apomicts, were classified as pollinator-independent. If none of the above applied, we assigned an intermediate pollinator dependence. If part of the information above was missing, no pollinator dependence was determined, and the species was excluded from the analyses involving pollinator dependence.

Finally, we obtained data on individual plant-pollinator interactions from a UK database on plant-pollinator interactions hosted by the Centre for Ecology and Hydrology (CEH). This database included all known interactions between plants and flower-visiting bees, butterflies, and hoverflies (but unfortunately neither beetles nor moths) in the UK, a country similar to Germany in terms of climate and species composition. While these interaction data are unlikely to represent all possible species interactions in Germany, we could not find similar data for our study area.

Calculation of plant and insect phenology

For our analyses of plant flowering phenology and pollinator activity times, we averaged all records of a plant or insect species in a year to calculate each year's mean day of the year (DOY) of the occurrence of a species. As discussed above, this occurrence measure was used as an estimate of each year's peak flowering or peak activity time of plants and insects, respectively. Each annual mean DOY was calculated from at least five records of a species per year. To avoid extreme shifts based on too little data, we included only species with records in at least 40% of the years. The median number of records per year for a species in our analyses was 47.

Since our analyses of individual plant-insect interactions (see below) were done at the level of decades, we additionally calculated the decadal means, based on nominal decades (0-to-9), of species DOYs for each of the included species, and only when at least five records existed per decade. These decadal interaction analyses were done only from 1980 onwards, i.e. for four decades, as too few data were available prior to 1980. To be included in our analyses, an interaction's records needed to span the entire period examined.

After clean-up and averaging, a total of 58,895 annual and 1,336 decadal peak DOYs, with the latter based on a median number of 1,686 records, remained in our data set (). The annual activity data included 1,274 plant and 88 insect species. For 948 of the plant species we had information about pollinator dependence: 144 were pollinator-dependent, 204 pollinator-independent, and 600 were classified as intermediate. The 88 insect species consisted of 40 species of beetles, 44 butterflies and moths, three bees and just one fly species. The decadal data included 245 plant and 26 insect pollinator species. All data wrangling and analysis was done in R [44].

Data Analysis

To understand phenology changes in plants versus insects, we first estimated the average phenological shifts in each group. We defined phenological shifts as the slope of the linear regression linking the peak activity (= mean annual) DOY of an individual species to the year of observation. We visually confirmed approximate normal distribution of the individual-species slopes, and that no improbable outliers were present. There were some plants with rather extreme values (**Figure S3**), however these were mostly early-flowering plants which likely experience stronger pressures and therefore stronger phenology shifts [45], and we therefore did not exclude them from our analyses. We compared the mean phenological shifts between plants and insects using an independent-sample Welch's *t*-test, and we further examined the temporal trends between different insect orders and plants in an ANOVA, using a Tukey post-hoc test to determine pairwise differences. We excluded bees and flies from the last step as their numbers were too small to be representative for their respective groups.

Different climatic factors likely affect the timing of early and late activity periods, which might complicate the interpretation of the peak shifts. We therefore also assessed the extent of shifts of first and last day of activity for each species (and consequently the duration of their activity) to understand how asymmetries in the shifts might affect the peak shifts in phenology. For this we estimated the shifts of the decadal average first and last activity day of the year over time in a linear model. We also estimated the shifts of duration of the activity period by first calculating the yearly duration of the activity period as the difference between the last recorded day of activity and the first for each species, taking the decadal average of said duration and then estimating the shift over time in a linear model. We used decadal averages to ensure the differences were due to long-term trends, as the absolute first and last day of activity is just the first and last record of a species in that year and therefore subject to fluctuation.

In addition to the temporal trends in phenology, we also tested for the climate sensitivity of plant and insect phenology. These analyses were analogous to the ones above, except that the explanatory variable was annual mean temperature instead of year of observation, i.e., the data were regression slope parameters of mean annual DOY of a species over the average temperature in that year.

Next, we tested whether phenology trends differed between plant groups with different levels of pollinator dependence. For this, we used the same data as above (slope parameters of individual-species regressions), but we analyzed it with a linear model that included pollinator dependence (dependent, independent, or intermediate) as a fixed factor, and then determined pairwise differences between groups with a Tukey post-hoc test. In addition, we also tested whether mean activity DOY differed significantly between the three pollinator-dependence levels.

Finally, we analyzed asynchrony between plants and pollinators using the data on individual plant-pollinator interactions. For each plant and presumed insect pollinator, we calculated the absolute difference in peak activity times for each decade. A value of zero thus indicated perfect asynchrony, and higher values indicated increasing asynchrony. To test whether asynchrony changed over time we estimated the slopes of the relationship between differences in peak activities and time (decades) for each plant-insect interaction with a linear model. Here, negative slope values indicated a shift towards greater synchrony, and a positive slope a shift towards greater asynchrony. Altogether, there were 1,797 interactions involving 245 plants and 26 insect pollinators, one insect usually associated with multiple plants but seldomly plants with multiple insects. To test for differences in average asynchrony and change of asynchrony between insect groups, we used an ANOVA and assessed pairwise differences with a Tukey post-hoc test.

Results

Temporal trends in plant and insect phenology

The analysis of the peak activity data showed a strong difference in the average temporal shifts of plant and insect phenology (Welch's $t_{100.929} = 6.644$, $P < 0.001$). The phenology of plants generally advanced much more strongly, with an average shift of -4.5 ± 0.2 days per decade (mean ± SE), while across all insects the shift was only -0.4 ± 0.6 days per decade. 84.8% of all plant species but only 56.8% of all insect species advanced their phenology (**Figure 1**). However, these numbers across all insects obscured different trends among the insect orders: when considered separately, butterflies/moths exhibited a strong phenology shift of -3.2 ± 0.8 days per decade (mean ± SE), with 79.5% of the species advancing, whereas the beetles in contrast delayed their peak activity on average by 2.0 ± 0.7 days per decade, with 65.0% of the species following this trend. When plants, butterflies/moths and beetles were analyzed as separate groups, ANOVA indicated significant differences among them ($F_{2,\,1355} = 25.16$, $P < 0.001$), with significant pairwise differences (Tukey post-hoc, $\alpha = 0.05$) between the phenology shifts of beetles and plants, and beetles and butterflies/moths, respectively. (**Figure S4A** and **Figure S5**.)

We found asymmetries between the slopes of first and last day of activity over time (**Figure S6**). In plants, the symmetry was generally skewed towards a stronger shift of the first day of activity (First: -1.2 ± 0.0 mean days/decade ± SE, Last: 0.5 ± 0.0 mean days/decade ± SE) with butterflies/moths behaving similarly (First: -1.4 ± 0.1 mean days/decade ± SE, Last: 0.5 ± 0.2 mean days/decade ± SE), whereas in beetles the last day of activity shifted more strongly (First: 0.1 ± 0.1 mean days/decade ± SE, Last: 0.5 ± 0.1 mean days/decade ± SE). It is also notable that the plants' and butterflies/moths' day of first activity generally advanced while the beetles' day of first activity was rather delayed (**Figure S7**).

Climate sensitivity of plant and insect phenology

The climate sensitivities of the phenologies of plants, butterflies/moths and beetles generally resembled their temporal trends (**Figure 1**), and group differences in climate sensitivities matched those in temporal trends described above. Again, there was a significant difference between plants and all insects (Welch's $t_{96.026} = 8.027$, $P < 0.001$), with plants showing a strong negative association between peak activity and temperature, but a much weaker association for all insects together. On average, plant peak flowering shifted by -7.6 ± 0.2 days per °C (mean ± SE), and 92.5% of the individual species showed earlier flowering with increasing temperature, whereas for insects it was only -1.3 ± 0.8 days per °C, and 63.6% showing a trend towards earlier peak activity (**Figure 1**). When the butterflies/moths were considered separately, however, they showed a fairly strong association with temperature, with an average peak activity shift of -4.4 ± 0.8 days per °C (mean ± SE) and 80% of the individual species advancing, whereas the beetles showed an opposing trend of delayed peak activity, with an average of +1.4 ± 1.1 days per °C temperature change. There were significant differences among the three groups (ANOVA, $F_{2,\,1355} = 45.701$, $P < 0.001$), with significant differences between all pairwise combinations (Tukey post-hoc, $\alpha = 0.05$). (For an overview over all groups, see **Figure S4B** and **Figure S8**.)

Pollinator dependence

The phenology of plants, and its temporal trends, differed very little among plant groups of different levels of pollinator dependence (**Figure S9**). The peak flowering of pollinator-independent plants (average DOY 199.5) advanced on average by -3.9 days per decade, while pollinator-dependent plants (average DOY 196.2) advanced by -5.1 days per decade, and intermediate plants (average DOY 199.5) advanced by -4.5 days per decade. In all three groups, the percentage of plants advancing was 85-86%. None of the differences between groups was statistically significant.

Synchrony of plant-pollinator interactions

When examining the synchrony of individual plant-pollinator interactions, we found that the three pollinator groups differed in their average levels of asynchrony with the plants, but that interactions did not become more asynchronous but rather more synchronized during the last decades (**Figure 2A**). The temporal trends differed strongly among the pollinator groups (ANOVA, $F_{2,\,2522} = 67.750$, $P < 0.001$; Tukey's post-hoc test significant at $\alpha = 0.05$ for all pairwise comparisons: **Figure 2C**): while the synchrony of plant-butterfly interactions remained on average unchanged, plant-pollinator interactions involving bees shifted on average by -2.7 days per decade, with 68% of individual interactions decreasing asynchrony over time. The strongest shifts were in plant-hoverfly interactions which shifted by -6.2 days per decade, with 89% of all interactions showing decreasing asynchrony (**Figure 2A, C**). In all three plant-pollinator groups, asynchrony was mostly due to earlier peak activity of the insects (**Figure 2B**). Interestingly, however, there was a tendency for these patterns to disappear in all three groups over time, presumably because of the stronger phenology shifts of plants (**Figure 1**). Plant-hoverfly interactions (n_{Insect} = 1, n_{Plant} = 132, n_{total} = 132) became on average synchronous in the last decade. For the plant-butterfly interactions (n_{Insect} = 36, n_{Plant} = 231, n_{total} = 1,819) the linear model predicts the point of synchrony to be reached in 2029, and for the plant-bee interactions (n_{Insect} = 4, n_{Plant} = 214, n_{total} = 574) in 2050.

Discussion

In this study, we took advantage of large collections of occurrence records to examine phenological trends of flowering plants and insect pollinators in Germany. We asked whether phenology changes affected the synchrony of plants and insects, and whether observed changes in phenology, and variation therein, were related to the different groups' responses to climate warming. We also examined whether the phenology responses of plants depended on their levels of pollinator dependence. Our results showed that the phenological shifts of plants and insects indeed differed, with plants shifting by several days per decade while insects on average shifting hardly at all. As peak flowering historically occurred after peak insect activity, these trends imply an increase in plant-pollinator synchrony during the last decades, but a potential for future desynchronization if climate change continues.

Plants and insects also differed in their overall temperature sensitivity. While plants shifted on average by over a week per degree of warming, insects shifted by only one day. There were large differences between insect orders in their phenology trends and temperature sensitivities. As groups with greater temperature sensitivity also showed larger phenology shifts over time, it seems likely that the two are causally related, i.e., that anthropogenic climate warming is responsible for the observed phenology shifts. Lastly, there were no differences between pollinator-dependent and -independent plants, suggesting that plants either responded passively to temperature, with advanced flowering in warmer years irrespective of pollinator dependence, or that most plants have sufficient generalist pollinators that can fill in for other, desynchronized pollinator species and thereby reduce selection pressure on plant phenology.

Caveats

When interpreting the results of our study, it is important to consider some caveats of the collections data and occurrence records we used. For instance, the temporal distribution of collections data is usually quite heterogenous, and so was our data (**Figure S2**). Our analysis of the shifts of the first and last days of activity may thus be influenced by varying observation efforts over the years. Particularly, the increasing popularity of nature observation platforms such as www.naturgucker.de, whose records are contained in GBIF, may have resulted in higher probability of detecting early and late occurrences. Besides temporal heterogeneity, occurrence records are usually also not homogenously represented in space. Our study’s measure of phenology, peak occurrence time, does not account for temporal variation of spatial representation of records within Germany, although some areas might be over- or underrepresented in some parts of the studied period. Moreover, our study also does not account for spatiotemporal variation in macro- and microclimate which can influence intraspecific variation in phenology shifts [46] and could therefore potentially induce local mismatches.

When estimating insect peak activity, we did not account for the earlier life stages of insects appearing in the data, despite being not important for pollination. This bias could be most relevant for butterflies and moths, as their larval stages are more conspicuous than fly and beetle larvae. Butterflies/moths are, however, the group with the latest peak activity times for large parts of the studied period, so this bias is either not strong or we are underestimating how late in the year butterflies and moths occur. Similarly, some plants occurrences may have been recorded when plants were not flowering. Flowers are important for plant species identification, and herbarium records are usually made from flowering specimen, but we cannot rule out that some plant occurrence records were based on vegetative plants alone. Finally, in our analyses we focused on peak activity and therefore did not consider the degree of overlap between the flight times of pollinators and the flowering of plants. However, if the durations of activity periods change, then the relative overlap of two interacting groups could change in spite of identical activity peaks, or vice versa. Testing such possibilities with occurrence data, however, requires even higher-resolution data for individual species than in our study.

Phenological shifts over time

The general differences between plants and insects in their advancement of phenology seem to indicate a shift in the synchrony between plants and their pollinators, with plants generally advancing faster than insects. However, the insect groups differed strongly in the extent of their shifts of activity over time, and the overall pattern of a slower phenological shifts was largely driven by the beetles, whereas butterflies/moths kept pace with the phenology changes of plants.

The extent to which plants advanced their phenology in our data is comparable to that found by Fitter & Fitter [14] in their long-term observation study of changes in first flowering dates of hundreds of plant species in England. They compared flowering during 1991-2000 to that between 1954 and 1990 and found an average advancement of 4.5 days. This is surprisingly congruent with our observation of 4.5 days advancement per decade over the whole period from 1960 to 2019. A more recent long-term analysis of phenology changes in subalpine meadow plants in the Rocky Mountains was undertaken by CaraDonna et al. [47] who found an even stronger average advancement of first flowering of 6.4 days per decade. Since CaraDonna et al. [47] also analyzed peak floral abundance, their data should be particularly comparable to our estimation of peak flowering through the DOY of peak occurrence. They found a rate of advancement of 5.3 days per decade in spring peak abundance but only 3.3 days for the summer peak floral abundance. Our results of peak occurrence across the whole year thus fall in between these two estimates.

For insects, previous studies seem to be less consistent, with widespread but not universal advances in springtime phenology (mostly associated with warming) over the last decades [48]. For butterflies, long-term records showed that their times of first flights (correlated with peak appearance) advanced on average by -3.7 days per decade in the 2000s compared to the previous decades in England [49], and by -7.7 days per decade in California [50]. The magnitude of the shifts observed in England is similar to what we estimated for butterflies/moths in Germany (on average -3.2 days per decade).

Temperature sensitivities of plant and insects

We found that associations between temperature and phenology differed among groups but that the magnitude of these associations generally reflected the different groups' phenology shifts observed over time. This strongly suggests a link between the phenology shifts and climate change, corroborating previous studies such as the ones by CaraDonna et al. [47] and Song et al. [46]. We found that plants were generally more sensitive to temperature, i.e., their phenology advanced more strongly, than insect pollinators. Previous studies on insect phenology in the temperate zone (reviewed in [48]) have shown that increased spring temperatures are often associated with earlier insect emergence, but that this pattern cannot be generalized as easily as for the plants, as temperature–phenology relationships of insects are more complex. While many insects plastically respond to warmer temperatures by speeding up their rates of development (and thus potentially emerge earlier), others have been found to respond in counterintuitive ways and delay their phenology. This might be due to dependence on other cues such as rainfall [51], due to cold period requirements of insects during their diapause (climate warming can cause a loss or reduction of this chilling period, and this tends to increase the amount of warming required for subsequent emergence; [48]), or because species overwinter in a diapause state in which they are not temperature sensitive [52]. Fründ et al. [52] also showed that bees overwintering in larval stages responded to higher winter temperatures with delayed emergence, while bees overwintering as adults showed advanced emergence (but had greater weight losses during overwintering). We did see delayed phenology in some of our data, particularly for beetles and bees. This also connects well to some of the findings reviewed by Forrest [45], for instance that during winter above-ground nesting bees experience different temperatures than the plants they feed on during the summer. Such microclimate differences between insects and plants during overwintering may sometimes explain contrasting climate responses. In other cases, delays in the first appearance of adults may result from longer growing seasons. For example, longer growing seasons have reduced selection for rapid development in some high-elevation grasshoppers, in such a way that they reach maturity later — but at a larger size — than in the past [53]. Furthermore, warming can change the number of generations per year (voltinism; [48]). All the above-mentioned mechanisms can cause variation in the phenology shifts of insects with climate warming and may therefore explain why climate change is not always accompanied by phenological advances but might also cause delays – as we observed for the beetles.

Another interesting idea is that the phenological advancement of the plants itself could cause delayed phenology of some pollinators. Wallisdevries & van Swaay [54] found that advanced plant growth led to delayed development of butterflies since the cooling created by shading leaves worsened foraging conditions for the larvae. However, in our study we did not see this effect for butterflies/moths as their phenology shifts closely tracked the shifts of plants, perhaps because of the high levels of specialization of many butterfly larvae [55].

Pollinator-dependence of plants

We did not find any differences in the phenological changes of pollinator-dependent versus pollinator-independent plants. This result is consistent with Rafferty & Ives [56] who found that the phenology shifts of plants were not constrained by their pollinators, because these kept pace with the plants. In contrast, Kudo et al. [57] found a negative effect of flowering advancement in bee-pollinated but not fly-pollinated plants. Fitter & Fitter [14] found significant differences between insect-pollinated plants (-4.8 days shift in day of first flowering) versus wind-pollinated plants (-3.5 days shift) and suggested this was because shifting pollinator activity forced plants to flower earlier. In our study we did not find any such differences, indicating that plant responses to temperature are either entirely passive, or that most plants have generalist pollinators with a long period of activity, so that there is little selection pressure on plant phenology. The data set used in our analysis is larger than those used in the studies cited above, so our results may be regarded as more conclusive and more general, bearing the limitations of the collections data in mind.

Changes in plant-pollinator synchrony

When we analyzed the synchrony of plant-pollinator interactions, we found clear trends in shifting synchrony, but they strongly varied among insect pollinator groups. Since the phenology of plants generally advanced faster than that of the insects during the last decades, but plants had generally been the later partner in most plant-pollinator interactions, these shifts lead to greater synchrony overall. However, if the observed trends continue, then many of the studied interactions will soon reach points of perfect synchrony, and after that the interactions may become more asynchronous again, albeit in the other direction. For plant-hoverfly interactions this point has already been reached. With linear trends and if we assume that observed trends will continue, the points of reversals are expected in approximately 10 years for plant-butterfly interactions and in around 30 years for plant-bee interactions. If interactions will become more asynchronous again in the future, then resilience of pollinator networks, in particular through pollinator generalism, could buffer some of the impact of phenological mismatches [6], and our finding of no differences between pollinator-dependent and pollinator-independent plants support this idea. However, while generalist pollinators make up the larger part of the interactions in most pollination networks, some plant-pollinator interactions are highly specialized, and these might be the ones suffering most from future mismatches [58].

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Authors contributions

JF and FMW conceived the study; JF collected and analyzed the data, and wrote the first draft of the manuscript, with guidance from FMW. JFS and OB provided input to data analysis and manuscript writing. All authors read and approved the final manuscript.

Data availability

The R code used to conduct the analysis is available at https://github.com/jonasfreimuth/Phenological-shifts-germany.

References

[1] Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A. & Schwartz, M. D. 2007 Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* **22**, 357–365.

[2] Memmott, J., Craze, P. G., Waser, N. M. & Price, M. V. 2007 Global warming and the disruption of plant-pollinator interactions. *Ecology letters* **10**, 710–717.

[3] Parmesan, C. 2007 Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biol* **13**, 1860–1872.

[4] Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E. & Wolkovich, E. M. 2018 Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences of the United States of America* **115**, 5211–5216.

[5] Scheffers, B. R., Meester, L. de, Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M. & Dudgeon, D. *et al.* 2016 The broad footprint of climate change from genes to biomes to people. *Science (New York, N.Y.)* **354**.

[6] Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. & Post, E. 2010 The effects of phenological mismatches on demography. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**, 3177–3186.

[7] Robbirt, K. M., Roberts, D. L., Hutchings, M. J. & Davy, A. J. 2014 Potential disruption of pollination in a sexually deceptive orchid by climatic change. *Current biology : CB* **24**, 2845–2849.

[8] Bartomeus, I., Ascher, J. S., Wagner, D. L., Danforth, B. N., Colla, S., Kornbluth, S. & Winfree, R. 2011 Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 20645–20649.

[9] Gordo, O. & Sanz, J. J. 2006 Temporal trends in phenology of the honey bee Apis mellifera (L.) and the small white Pieris rapae (L.) in the Iberian Peninsula (1952-2004). *Ecological Entomology* **31**, 261–268.

[10] Kudo, G. & Ida, T. Y. 2013 Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* **94**, 2311–2320.

[11] Schenk, M., Krauss, J. & Holzschuh, A. 2018 Desynchronizations in bee-plant interactions cause severe fitness losses in solitary bees. *The Journal of animal ecology* **87**, 139–149.

[12] Kudo, G., Nishikawa, Y., Kasagi, T. & Kosuge, S. 2004 Does seed production of spring ephemerals decrease when spring comes early? *Ecological Research* **19**, 255–259.

[13] Bond, W. J. 1995 Effects of Global Change on Plant—Animal Synchrony: Implications for Pollination and Seed Dispersal in Mediterranean Habitats. In *Global Change and Mediterranean-Type Ecosystems* (ed. J. M. Moreno & W. C. Oechel), vol 117, pp. 181–202. New York, NY: Springer New York.

[14] Fitter, A. H. & Fitter, R. S. R. 2002 Rapid changes in flowering time in British plants. *Science (New York, N.Y.)* **296**, 1689–1691.

[15] Molnár, A., Tökölyi, J., Végvári, Z., Sramkó, G., Sulyok, J. & Barta, Z. 2012 Pollination mode predicts phenological response to climate change in terrestrial orchids: a case study from central Europe. *Journal of Ecology* **100**, 1141–1152.

[16] Parmesan, C. 2006 Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669.

[17] Jones, C. A. & Daehler, C. C. 2018 Herbarium specimens can reveal impacts of climate change on plant phenology; a review of methods and applications. *PeerJ* **6**, e4576.

[18] Lang, P. L. M., Willems, F. M., Scheepens, J. F., Burbano, H. A. & Bossdorf, O. 2019 Using herbaria to study global environmental change. *The New phytologist* **221**, 110–122.

[19] Daru, B. H., Park, D. S., Primack, R. B., Willis, C. G., Barrington, D. S., Whitfeld, T. J. S., Seidler, T. G., Sweeney, P. W., Foster, D. R. & Ellison, A. M. *et al.* 2018 Widespread sampling biases in herbaria revealed from large-scale digitization. *The New phytologist* **217**, 939–955.

[20] Maldonado, C., Molina, C. I., Zizka, A., Persson, C., Taylor, C. M., Albán, J., Chilquillo, E., Rønsted, N. & Antonelli, A. 2015 Estimating species diversity and distribution in the era of Big Data: to what extent can we trust public databases? *Global ecology and biogeography : a journal of macroecology* **24**, 973–984.

[21] Newbold, T. 2010 Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Progress in Physical Geography: Earth and Environment* **34**, 3–22.

[22] Chapman, A. D. 2005 *Uses of primary species-occurrence data, version 1.0.* Copenhagen.

[23] Primack, D., Imbres, C., Primack, R. B., Miller-Rushing, A. J. & Del Tredici, P. 2004 Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American journal of botany* **91**, 1260–1264.

[24] Brooks, S. J., Self, A., Toloni, F. & Sparks, T. 2014 Natural history museum collections provide information on phenological change in British butterflies since the late-nineteenth century. *International Journal of Biometeorology* **58**, 1749–1758.

[25] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[26] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[27] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[28] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[29] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[30] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[31] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[32] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[33] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[34] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[35] GBIF: The Global Biodiversity Information Facility. 2019 *GBIF*. www.gbif.org. Accessed 28 March 2019.

[36] GBIF.org. 2020 *Occurrence Download:* The Global Biodiversity Information Facility.

[37] Klotz, S., Kühn, I. & Durka, W. 2002 BIOLFLOR – Eine Datenbank zu Biologisch-Ökologischen Merkmalen der Gefäßpflanzen in Deutschland. In *Schriftenreihe für Vegetationskunde*, vol 38, pp. 1–333.

[38] Kevan, P. G. & Baker, H. G. 1983 Insects as Flower Visitors and Pollinators. *Annu. Rev. Entomol.* **28**, 407–453.

[39] Chamberlain, S. A. & Boettiger, C. 2017 *R Python, and Ruby clients for GBIF species occurrence data*.

[40] Chamberlain, S. A. & Szöcs, E. 2013 taxize: taxonomic search and retrieval in R. *F1000Research* **2**, 191.

[41] DWD Climate Data Center (CDC). 2020 Aktuelle monatliche Stationsbeobachtungen (Temperatur, Druck, Niederschlag, Sonnenscheindauer, etc.) für Deutschland, Qualitätskontrolle noch nicht vollständig durchlaufen. Version recent. Accessed 19 April 2020.

[42] DWD Climate Data Center (CDC). 2020 Historische monatliche Stationsbeobachtungen (Temperatur, Druck, Niederschlag, Sonnenscheindauer, etc.) für Deutschland. Version v007, 2018. Accessed 19 April 2020.

[43] Redhead, J. W., Coombes, C. F., Dean, H. J., Dyer, R., Oliver, T. H., Pocock, M., Rorke, S. L., Vanbergen, A. J., Woodcock, B. A. & Pywell, R. F. 2018 Plant-pollinator interactions database for construction of potential networks: NERC Environmental Information Data Centre.

[44] R Core Team. 2008 R: A language and environment for statistical computing. Vienna, Austria. http://www.r-project.org./.

[45] Forrest, J. R. K. 2015 Plant-pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? *Oikos* **124**, 4–13.

[46] Song, Z., Fu, Y. H., Du, Y., Li, L., Ouyang, X., Ye, W. & Huang, Z. 2020 Flowering phenology of a widespread perennial herb shows contrasting responses to global warming between humid and non□humid regions. *Funct Ecol* **34**, 1870–1881.

[47] CaraDonna, P. J., Iler, A. M. & Inouye, D. W. 2014 Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 4916–4921.

[48] Forrest, J. R. K. 2016 Complex responses of insect phenology to climate change. *Current opinion in insect science* **17**, 49–54.

[49] Roy, D. B. & Sparks, T. H. 2000 Phenology of British butterflies and climate change. *Global Change Biol* **6**, 407–416.

[50] Forister, M. L. & Shapiro, A. M. 2003 Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biol* **9**, 1130–1135.

[51] Bonal, R., Hernández, M., Espelta, J. M., Muñoz, A. & Aparicio, J. M. 2015 Unexpected consequences of a drier world: evidence that delay in late summer rains biases the population sex ratio of an insect. *Royal Society open science* **2**, 150198.

[52] Fründ, J., Zieger, S. L. & Tscharntke, T. 2013 Response diversity of wild bees to overwintering temperatures. *Oecologia* **173**, 1639–1648.

[53] Buckley, L. B., Nufio, C. R., Kirk, E. M. & Kingsolver, J. G. 2015 Elevational differences in developmental plasticity determine phenological responses of grasshoppers to recent climate warming. *Proceedings. Biological sciences* **282**, 20150441.

[54] Wallisdevries, M. F. & van Swaay, C. A. M. 2006 Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biol* **12**, 1620–1626.

[55] Gilbert, L. E. & Singer, M. C. 1975 Butterfly ecology. *Annual Review of Ecology and Systematics* **6**, 365–395.

[56] Rafferty, N. E. & Ives, A. R. 2011 Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecology letters* **14**, 69–74.

[57] Kudo, G., Ida, T. Y. & Tani, T. 2008 Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. *Ecology* **89**, 321–331.

[58] Bascompte, J. & Jordano, P. 2007 Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **38**, 567–593.

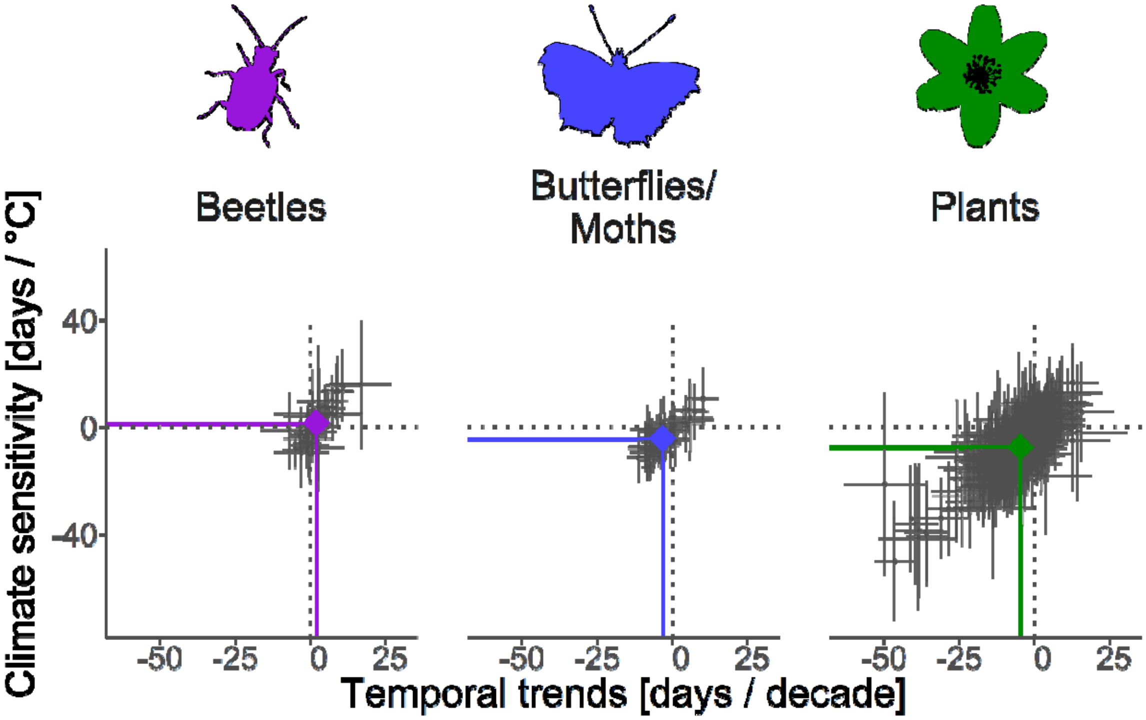


Figure 1. Temporal trends (days per decade) versus climate sensitivities (days per °C temperature change) of the phenology (peak flowering/activity) of plants, beetles, and butterflies/moths, with the colored lines indicating the averages for each group. Grey dots indicate individual species means with the vertical and horizontal bars representing the 95% confidence intervals. For all three groups the relationship between temporal trend and climate sensitivity is highly significant at with $r > 0.8$ and a $P < 0.001$.

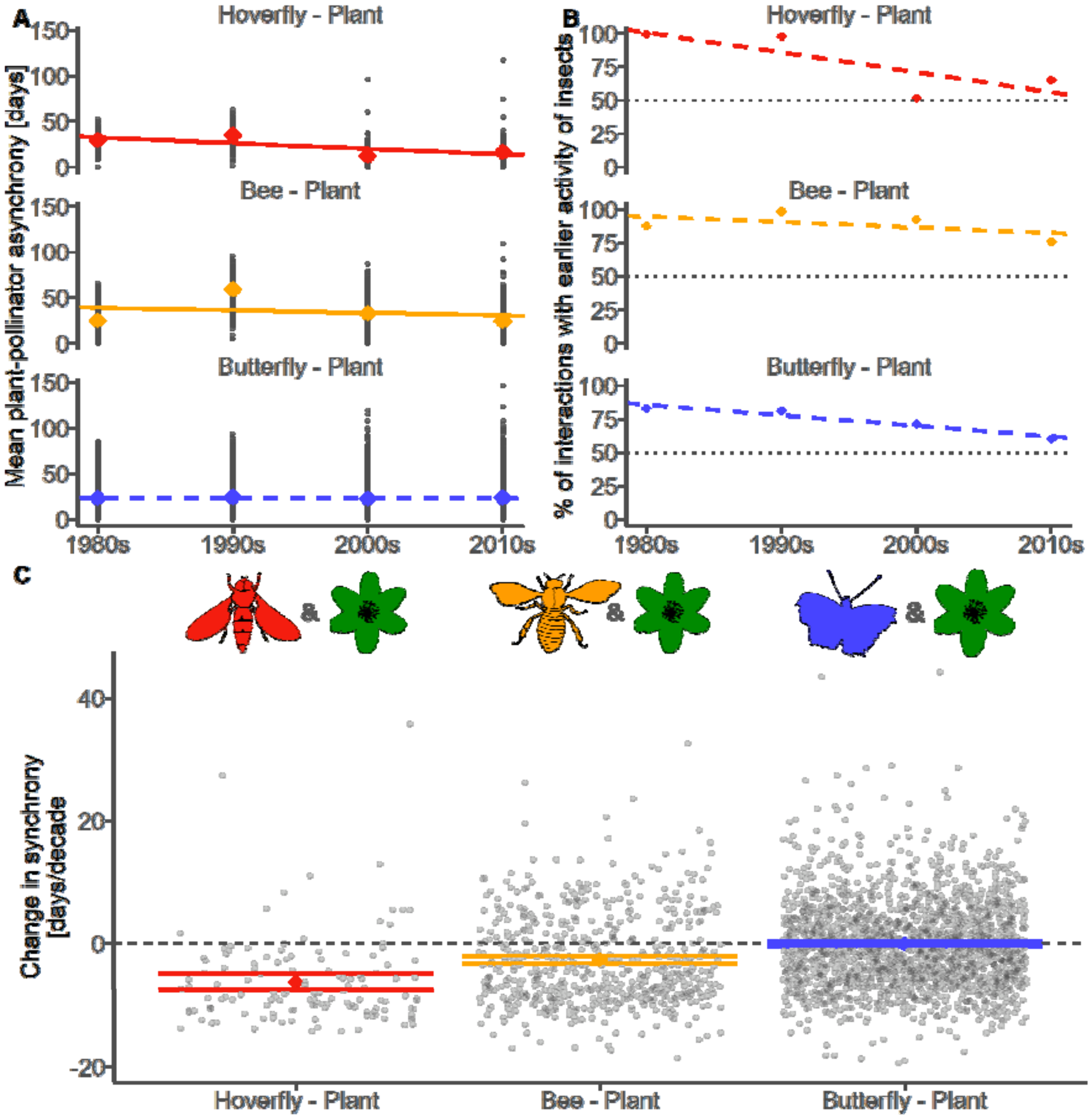
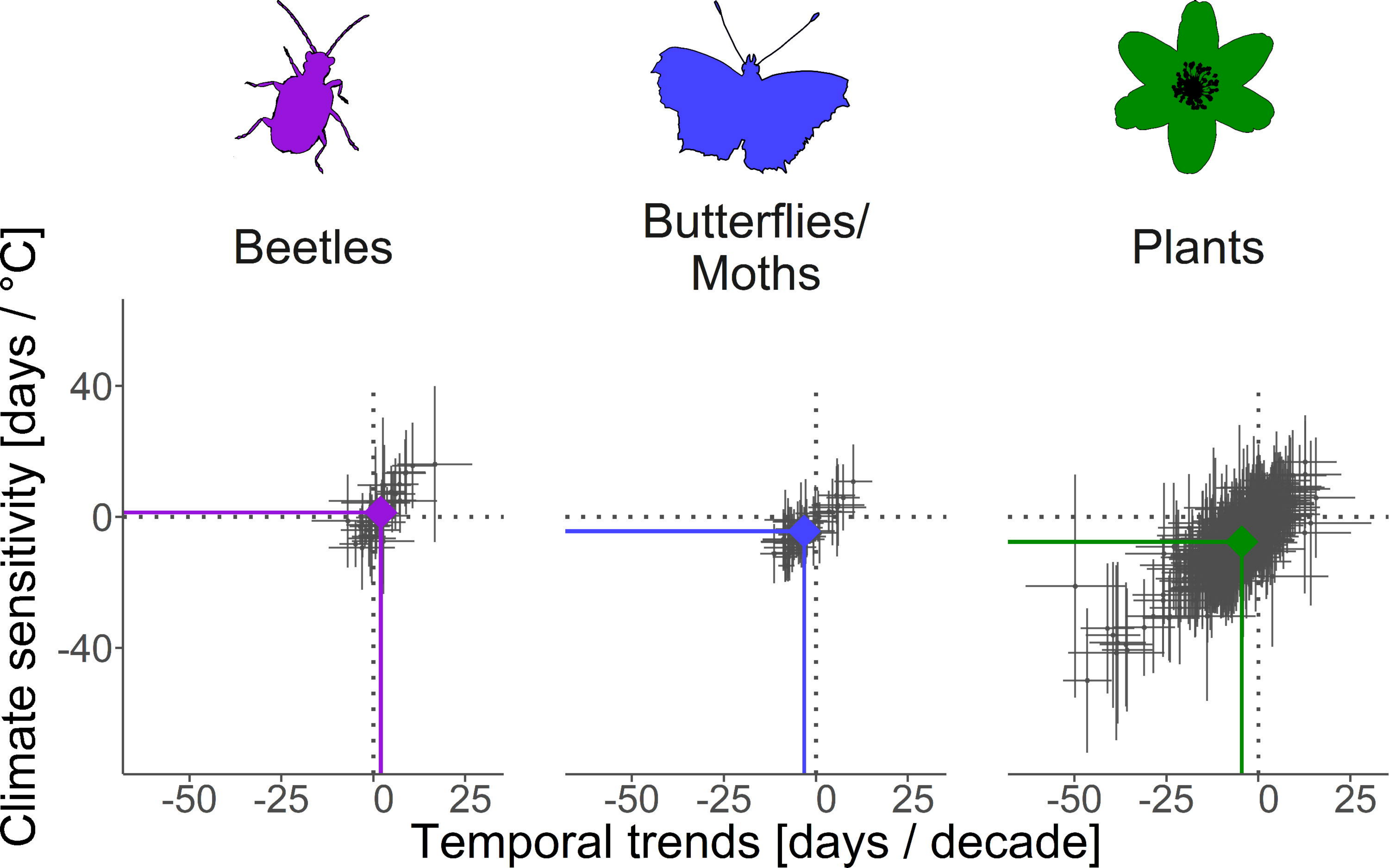
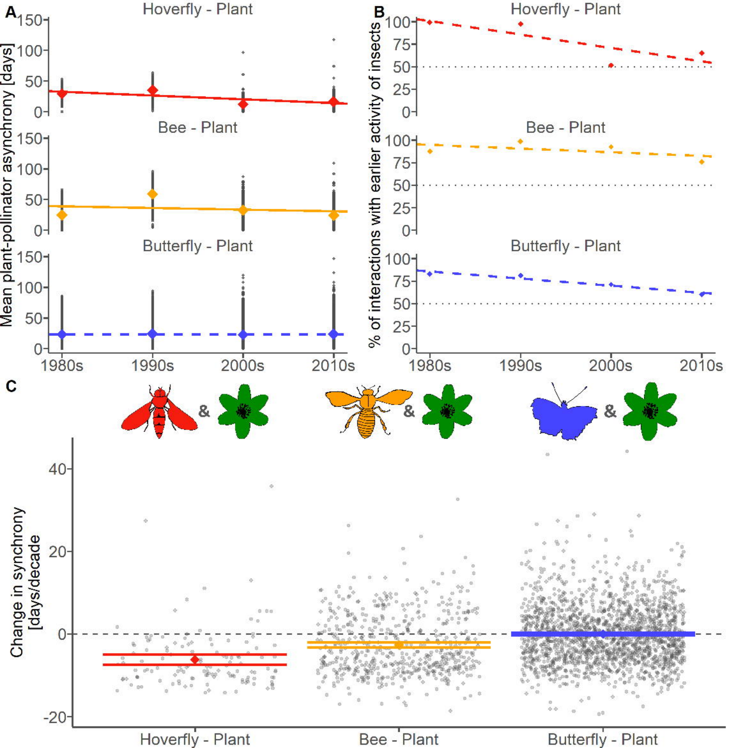


Figure 2. Asynchrony of individual plant-pollinator interactions, and their temporal trends, separated by pollinator groups. (A) Decadal changes of asynchrony (grey dots/lines: individual interactions; colored diamonds/lines: linear regression for each group. (B) Fraction of interactions with earlier insect activity. (C) Average decadal asynchrony changes of individual interactions (grey dots), and the means for each group (colored dots and 95% CI whiskers). Solid lines in (A) and (B) indicate significant linear regressions, dashed lines non-significant ones.



Beetles
Butterflies/ Moths
Plants
Climate sensitivity [days / °C]
40
0
-40
-50
-25
0
25
Temporal trends [days / decade]


A
Hoverfly - Plant
Bee - Plant
Butterfly - Plant
Mean plant-pollinator asynchrony [days]
0
50
100
150
1980s
1990s
2000s
2010s
B
Hoverfly - Plant
Bee - Plant
Butterfly - Plant
% of interactions with earlier activity of insects
0
25
50
75
100
1980s
1990s
2000s
2010s
C
&
&
&
Change in synchrony [days/decade]
-20
0
20
40
Hoverfly - Plant
Bee - Plant
Butterfly - Plant