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 1980s. 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 depended on their level of pollinator dependence: pollinator-independent plants generally showed weaker phenological shifts than pollinator-dependent plants. When examining the temporal co-occurrence of plant-pollinator pairs from 1980 onwards, the temporal trends in their synchrony also differed among pollinator groups, and tended to become more synchronized, mainly because the phenology of plants responded more strongly to climate change and plants caught up with the pollinators. However, if the observed trends continue, many interactions may become more asynchronous again in the future. Our study suggests 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

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, Gordo & Sanz [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 of

large spatial and temporal scales [21]. These data are increasingly 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 collection dates of herbarium specimens of a plant species in a year can be used as a proxy for 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 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 shifts of 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 [25–28]. For the plants, we restricted ourselves to species covered by the BioFlor database of plant traits [29], 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 [30]. We used the R package *rgbif* [31] 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* [32] to check the names against the GBIF backbone taxonomy and determine the actual accepted name.

Prior to the data analyses, we subjected the data to several steps of quality control. First, we removed all records from before 1980 as these turned out to be too inconsistent, with few records per year and large gaps with years without records. We also removed the records from 2021 as the year had not been complete at the time of our analysis. Second, we removed all records from the days of year (DOY) 1, 95, 121, 163, 164, 166 and 181, and in particular DOY 365 and 366 from the natural history museum of Luxemburg, because the high numbers of records on these days indicated that either records without collecting date had been assigned these by default, or the dates were used by BioBlitz events where very 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 some records for which no elevation or temperature data could be obtained (see below).

To ensure reasonable coverage of the studied time interval, we then restricted the records to species which had at least 10 occurrence records in every decade covered (2020 included in the last decade).

After these data curation steps, we maintained just above 12 million occurrence records that covered altogether 1,764 species, with 11.4 million records of 1.438 plant species, around 590.000 records of 207 species of butterflies and moths, some 76.000 records of 20 bee species and 30.000 records of 22 fly species, and almost 25.000 records of 77 species of beetles (**Table 1**). 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 S 1**). While plants had relatively even record numbers across years, the 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 recording of species occurrences by citizen naturalists, and which made up most of the insect occurrence data for Germany in GBIF.

Temperature and elevation 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 temperature data from the Climate Research Unit (CRU, https://crudata.uea.ac.uk) at the University of East Anglia, specifically the Time-Series dataset version 4.05 [33], which contains gridded temperature data from 1901-2020 at a resolution of 0.5° longitude by 0.5° latitude. From this dataset we extracted the monthly mean temperatures and averaged them to obtain the annual mean temperatures at the sites of occurrence records. To be able to control for elevation at the locations of occurrence records, we used elevation data at a 90 m resolution from the NASA Shuttle Radar

Topography Mission (SRTM), obtained from the SRTM 90m DEM Digital Elevation Database [34] and accessed through the *raster* package [35] in R.

To classify plants by their level of pollinator dependence we used plant trait data from BioFlor [29]. 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.

Data analysis

All data wrangling and analysis was done in R [36]. Before analysing species reactions, we wanted to check for consistent patterns of climate change in Germany. For this, we fitted a linear model to the unique annual mean temperature values at the sites of the records (i.e., the 0.5° * 0.5° grid cells) in our data over time.

To understand phenology changes in plants and insects, we first estimated the phenological shifts in each group as the slopes of linear regressions linking activity, i.e., the DOY of a record to its year of observation. We estimated group-specific phenological shifts in two linear mixed-effect models: one that estimated shifts over time and one that related phenology variation to temperature. Both models included the DOY of a record as the response variable, and the latitude, longitude, and elevation of a record as fixed effects. The temporal-change model additionally included the year of a record as a fixed effect and as a random effect across species; the temperature-change model instead included the annual mean temperature at the site of a record as a fixed effect and as random effect across species. We used the *lme4* package [37] in R to fit these models and assessed model fits by visually inspecting the relationships between residuals and fitted values, and between residuals and covariates (**Supplementary material 1 and 2**). Although there were some systematic patterns in the residuals (for example residuals of low fitted values tended to be higher than residuals of high fitted values), the random effects from the models agreed well enough with more complex generalized additive models, so we considered our linear model reasonably robust. After estimating average group-level phenological shifts, we compared these between the different insect orders and plants through ANOVAs, using Tukey post-hoc tests for pairwise tests of differences. We assessed the normal distribution of the slopes through boxplots and checked potential outliers for their plausibility by examining the data from which these slopes were estimated. The same procedure was used in all subsequent ANOVAs. To test for an association between temporal shifts and temperature change, we calculated Pearson correlations between the slopes of time- and temperature-relationships within each group.

Next, we tested whether phenology trends differed between plant groups with different levels of pollinator dependence. We performed an ANOVA testing for differences in the average shifts of plants of different levels of pollinator dependence, and then determined

pairwise differences between groups with a Tukey post-hoc test. Again, we did this both for temporal and temperature-related shifts.

Finally, we analysed the synchrony of plants and pollinators using the data on individual plant-pollinator interactions. For each plant-insect pollinator pair we calculated the differences of the slopes and intercepts estimated for plants and pollinators to obtain a linear equation describing the change in their asynchrony. To test for differences in the average shift between groups of interactions, we ran ANOVAs on both the temporal and temperature-related asynchrony shift data and used Tukey post-hoc tests to examine pairwise differences between the groups. As analyses of the directions and magnitudes of asynchrony shifts do not provide any information about the actual state of asynchrony in an interaction, we further calculated the estimated values of the regressions of asynchrony for each unique year or temperature point in our dataset. We used these data to then calculate and visualize the percentages of interactions per group and year/temperature point in which insects were active earlier than plants.

Results

We observed a strong overall trend of climate warming. Across all records, the annual mean temperature increased by 0.49 °C per decade ($F_{1, 8477}$ = 2038, R^2_{adj} = 0.19, P < 0.001 for the linear model), with a total increase of around 2 °C across the entire study period 1980-2020 (**Figure S 2**).

Temporal trends in plant and insect phenology

The phenology of plants advanced on average more strongly than that of any of the insect pollinators (**Table 1, Figure 1A, C, Figure S 3A**). Among the insect groups, the flies showed the strongest average temporal shifts, while changes were weaker in butterflies/moths and

bees, and beetles even slightly delayed their activity by almost one day per decade. ANOVA indicated significant differences among the five studied taxonomic groups ($F_{4, 1759} = 33.44$, $P < 0.001$), with plants showing significantly stronger temporal shifts than butterflies/moths, bees, and beetles, respectively (Tukey post-hoc test significant at $\alpha = 0.05$), and both flies and butterflies/moths advancing more strongly than beetles.

Temperature sensitivity of plant and insect phenology

In all studied taxonomic groups except for the beetles, the climate sensitivities of phenology mirrored their temporal trends (**Table 1, Figure 1B, C, Figure S 3B**), again with plants showing the strongest negative association between temperature and activity, followed by the flies, then butterflies/moths and bees. Surprisingly, despite their lack of temporal shifts, the beetles also showed a similar temperature as the butterflies/moths and bees. ANOVA confirmed that there were significant differences among the studied taxonomic groups ($F_{4, 1759} = 22.19$, $P < 0.001$), although not as clear as in the shifts over time. Here, the only clear differences were between plants and bees, and between plans and butterflies/moths (Tukey post-hoc test, significant at $\alpha = 0.05$).

Pollinator dependence

The phenology of plants, and its temporal trends, differed only moderately among plants of different levels of pollinator dependence (**Table 2**, **Figure S 4**). In all three groups, 85-90% of the plants advanced their flowering over time, but ANOVA indicated differences among the groups ($F_{2, 1039} = 7.20$, $P < 0.001$), with slightly weaker temporal shifts in the insect-independent plants, and significant pairwise differences for the comparison between insect-independent and intermediate plants as well as between insect-independent and -dependent plants (Tukey post-hoc tests, significant at $\alpha = 0.05$). The results were similar for the

temperature sensitivities, with generally high fractions (81-92%) of plants showing negative temperature-phenology relationships in all three groups, but groups also differing from each other ($F_{2, 1039} = 10.24$, $P < 0.001$). This was mainly driven by weaker average temperature sensitivities of the pollinator-independent plants, which differed significantly from the insect-dependent and intermediate plants, respectively (Tukey post-hoc tests, significant at $\alpha = 0.05$).

Synchrony of plant-pollinator interactions

When examining the synchrony of individual plant-pollinator interactions, we found that the three pollinator groups differed in the magnitude and direction of synchrony changes (**Figure 2A, B**), but that except in hoverflies interactions with plants did not become more asynchronous but rather more synchronized during the last decades (**Figure 2C**). The magnitudes of temporal changes were generally greatest for plant-bee interactions, and plant-butterfly interactions were shifting less than plant-hoverfly interactions (ANVOA: $F_{2, 3985} = 326.8$, $P < 0.001$; significant post-hoc tests for pairwise comparisons between all groups; **Table 3**; **Figure 2C**). Moreover, in all three pollinator groups, the insects tended to be the earlier partners in interactions, at least historically. However, in all three groups there was also a trend towards a decreased fraction of earlier insects, with plants catching up over time in plant-butterfly interactions, or even ‘overtaking’ the insects in plant-hoverfly interactions (**Figure 2 B, C**). The results are similar when we examined plant-pollinator synchrony in relation to temperature changes. Here, too, the average changes in synchrony were strongest in the plant-bee interactions (**Table 3;** ANOVA: $F_{2, 3985} = 87.32$, $P < 0.001$ for differences between the three groups), and the phenological advances of insects generally decreased with increasing temperatures, or even turned around at high temperatures in the case of plant-hoverfly interactions (**Figure S 5**).

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 taxonomic 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 most strongly, but also substantial variation among the different insect groups. These changes took place across a period in which the mean annual temperature showed a marked increase in Germany. As peak flowering historically occurred after peak insect activity, these trends led to an increase in plant-pollinator synchrony during the last decades but could potentially lead to future desynchronization if climate change continues.

Plants and insects also differed in their overall temperature sensitivity. While plants shifted on average by ca. five days per degree of warming, even the most sensitive insect groups, the flies, shifted much less with ca. one day per degree of warming. The largest difference between plants and an insect group, the beetles, was almost three and a half days per degree of warming.

Even though groups did not always exhibit temperature sensitivities that reflected their phenology shifts over time, there were clear correlations of individual species shifts over time with their temperature sensitivities. Therefore, it seems likely that the two are causally related, i.e., that anthropogenic climate warming is responsible for the observed phenology shifts.

Lastly, we found an interesting, albeit unexpected, difference between pollinator-dependent and pollinator-independent plants, with pollinator-independent plants showing

much weaker phenology shifts than both intermediately and entirely pollinator-dependent plants.

Caveats

When interpreting the results of our study, it is important to consider some caveats of the collections data and occurrence records we used, as the majority of them did not originate from scientific recording schemes. For instance, the spatial distribution of collections data is usually quite heterogeneous, and so was our data (**Figure S 1**). We attempted to correct for spatial heterogeneity in our models by including geographical information. Also, it is likely that not all of the recorded plants were in bloom at the time of recording, or that not all insects recorded were imagines.

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 advancing faster than insects. The phenology advances of plants in our data are generally stronger than reports from previous publications. Fitter & Fitter [14] performed a long-term observation study of changes in first flowering dates of hundreds of plant species in England, comparing flowering during 1991-2000 with 1954-1990, and found an average advancement of -4.5 days. This is much less than the -7.2 days per decade we found over the period from 1980 to 2020. A more recent long-term analysis by CaraDonna et al. [38] of phenology changes in subalpine meadow plants in the Rocky Mountains found an even stronger average advancement of first flowering of -6.4 days per decade on the level of the entire community during the study period from 1974 to 2012. Since CaraDonna et al. [38] also analysed 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. Both less than the advancement we found.

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 [39]. 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 [40], and by -7.7 days per decade in California [41]. The magnitude of the shifts observed in England is similar to what we estimated for butterflies/moths in Germany (on average -4.0 days per decade). Bartomeus et al. [42] found that bee phenology in New York advanced by -1.9 days per decade during 1965-2011, which is also less than the -2.6 days per decade we found in our data, which might be explained by the additional nine years of data we analysed. Data on the phenology shifts of hoverflies are scarce [43], but Olsen et al. [44] found an advancement of -6.2 days of the 10th percentile of collection day (their measure of first flight) during 2000 to 2018, which would be stronger than the -5.0 we found. Together with previous results, our data indicate that phenological changes of insects are accelerating during the last decades, but that spring phenology probably shifts more strongly than peak phenology.

Temperature sensitivities of plant and insects

Although the temperature sensitivities of groups did not entirely mirror their shifts over time, we found strong correlations between temporal shifts and temperature sensitivities at the species level. This strongly suggests a link between phenology shifts and climate change, supporting previous studies such as CaraDonna et al. [38] and Song et al. [45]. We found that temperature sensitivities, i.e., associations between temperature and phenology, strongly

differed among taxonomic groups. Plants were generally more sensitive to temperature than insect pollinators. Previous studies on insect phenology in the temperate zone (reviewed in [39]) have shown that increased spring temperatures are often associated with earlier insect emergence, but that this pattern cannot be generalized as easily as for plants, as the temperature–phenology relationships of insects are more complex. While many insects are able to plastically respond to warmer temperatures by speeding up their rates of development (and thus potentially emerge earlier), others have been found to not respond, or even to delay their phenology. This might be due to the dependence of insect development on other cues such as rainfall [46], 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; [39]), or because species overwinter in diapause states in which they are not temperature-sensitive [47]. Fründ et al. [47] 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 some species with negative temperature sensitivity in our data which delayed their phenology. This also connects well to some of the findings reviewed by Forrest [48], 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 [49]. Furthermore, warming can change the number of generations per year (voltinism; [39]). 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 [50] 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 [51].

Pollinator-dependence of plants

We found that pollinator dependence influenced the plants' reaction to climate. However, counterintuitively, pollinator-dependent plants shifted more strongly than pollinator-independent plants. Our finding seems to confirm Fitter & Fitter [14] who also 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. Pollinator-dependent plants advancing faster than pollinator-independent plants would also be in accordance with our observation that pollinators historically are the earlier partner in interactions. Following this idea, and of course ignoring the many other factors influencing plant phenological changes, one could conclude that the strong shifts plants exhibited over time and the large temperature sensitivities they show, allow plants to catch up with their pollinators.

Changes in plant-pollinator synchrony

When we analysed the synchrony of plant-pollinator interactions, we found clear trends in shifting synchrony, but they 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. 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 impacts of phenological mismatches [6] 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 [52].

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Authors contributions

JF and FMW conceived the study; JF and FMW collected analysed the data, JF analysed it, 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.

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Table 1 Sizes of the studied taxonomic groups their numbers of records, their ranges of records per species, the extents of their average temporal shifts (± 1 S.E.) of phenology, average temperature sensitivities (± 1 S.E.), and the respective fractions of species that advance over time, or with increasing temperatures.

Group	**# Species**	**# Records**	**# Records / Species**			**Temporal shifts**		**Temperature sensitivity**	
			Min	**Median**	**Max**	**Days / decade**	**% Advancing**	**Days / 1 °C**	**% Advancing**
Beetles	77	24,758	55	196.0	1,879	0.93 ± 0.94	44%	-1.68 ± 0.52	73%
Flies	22	30,927	166	674.5	9,194	-5.03 ± 0.88	91%	-3.88 ± 0.71	91%
Bees	20	76,438	91	599.0	15,059	-2.61 ± 2.04	65%	-2.01 ± 1.3	60%
Butterflies/ Moths	207	589,970	69	803.0	33,228	-4.02 ± 0.32	86%	-1.94 ± 0.25	74%
Plants	1,438	11,357,981	62	2,280.0	121,612	-7.24 ± 0.19	86%	-5.15 ± 0.15	84%

Table 2 Average temporal shifts and temperature sensitivities (each ± 1 S.E.) of plants with different levels of pollinator dependence, and the respective fractions of species that advance over time, or with increasing temperatures.

Insect Dependence	**# Species**	**Temporal shifts**		**Temperature sensitivity**	
		Days / decade	**% Advancing**	**Days / 1 °C**	**% Advancing**
Pollinator-dependent	148	-8.56 ± 0.61	90%	-5.76 ± 0.45	91%
Intermediate	665	-7.59 ± 0.27	87%	-5.62 ± 0.23	85%
Pollinator-independent	229	-5.95 ± 0.43	85%	-3.7 ± 0.35	81%

Table 3 Changes in asynchrony of plant-pollinator interactions, separately by pollinator groups. Temporal changes (± 1 S.E.) are in days / decade, and temperature sensitivities (± 1 S.E.) are expressed as days / °C.

Interaction group	# Pairwise interactions	# Plant species	# Pollinator species	Temporal shifts [days / decade]	Temperature sensitivities [days / 1 °C]
Bee - Plant	924	230	12	-11.38 ± 0.41	-5.64 ± 0.26
Butterfly - Plant	1,782	227	39	-2.1 ± 0.2	-2.59 ± 0.17
Hoverfly - Plant	1,282	194	17	-3.47 ± 0.21	-1.84 ± 0.17

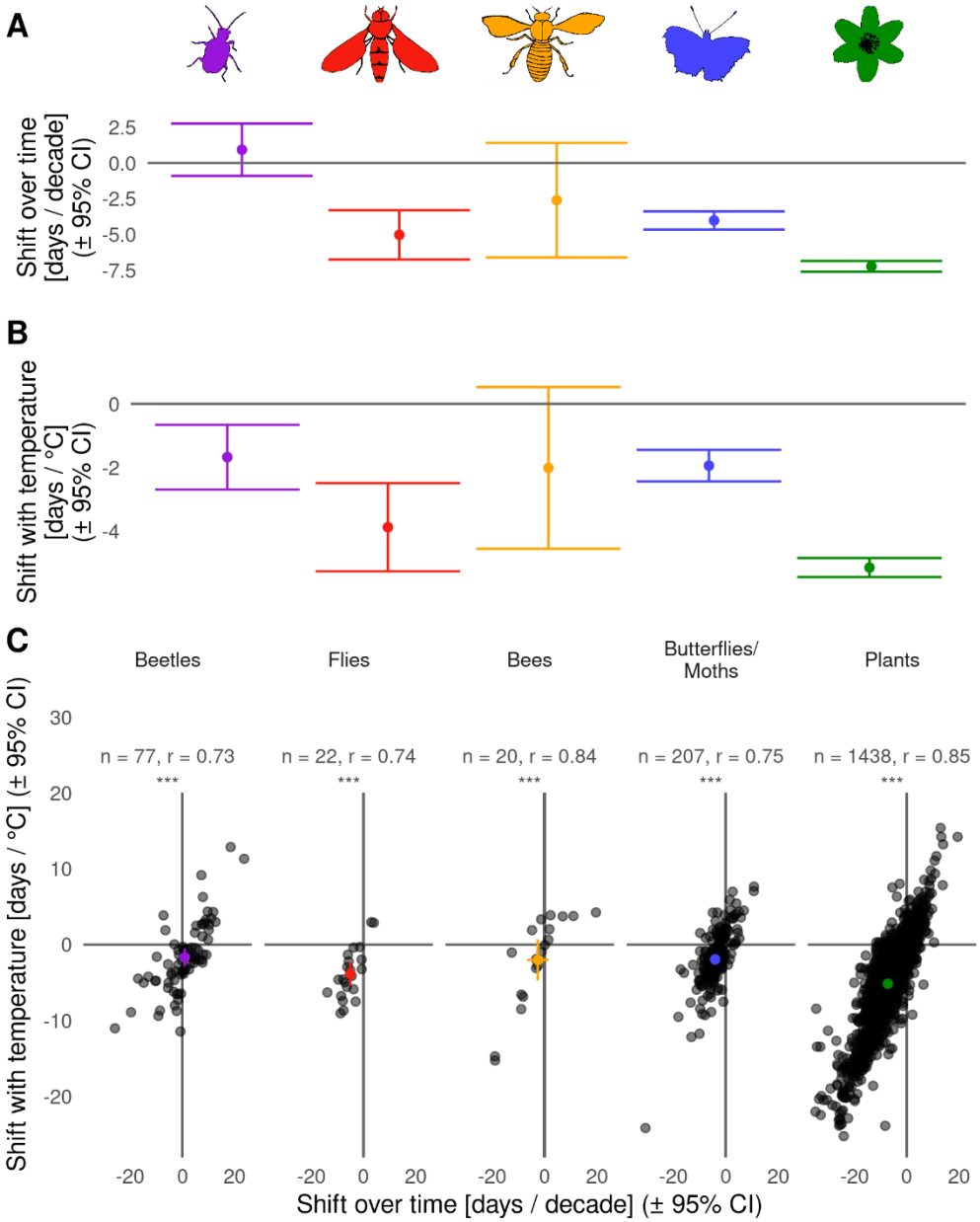
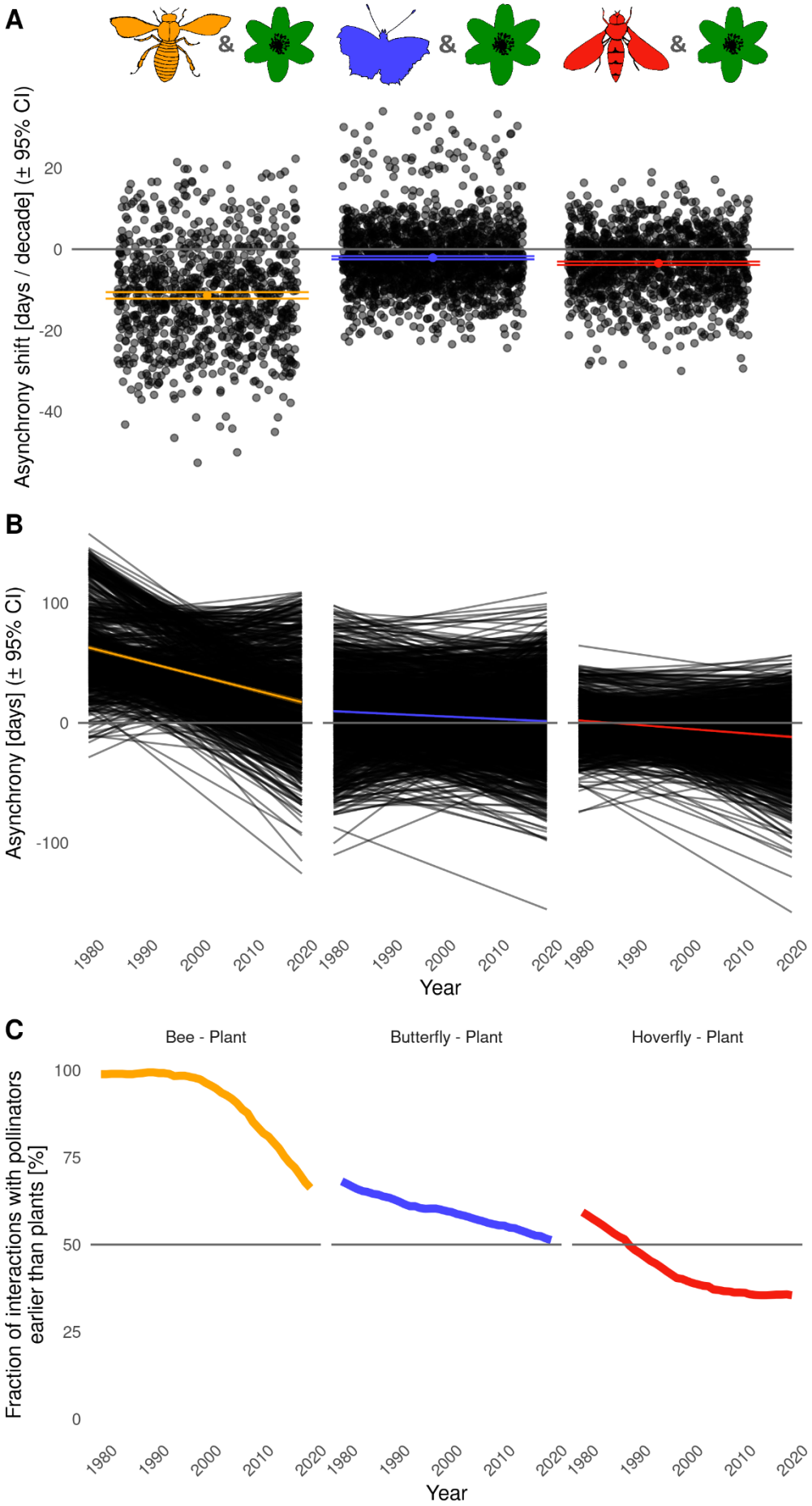


Figure 1. Temporal trends (A) and temperature sensitivities (B) and their correlation (C) of the phenology (peak flowering/activity) of plants and pollinator groups, with the coloured dots indicating the averages for each group. Black dots indicate individual species slopes confidence intervals. Given above the dots are group size (*n*), Pearson correlation coefficient (*r*), and the significance level of the correlation (***: $P < 0.001$).


A
&
&
&
Asynchrony shift [days / decade] (± 95% CI)
20
0
-20
-40
B
Asynchrony [days] (± 95% CI)
100
0
-100
1980
1990
2000
2010
2020
Year
C
Bee - Plant
Butterfly - Plant
Hoverfly - Plant
Fraction of interactions with pollinators earlier than plants [%]
100
75
50
25
0
1980
1990
2000
2010
2020
Year

612

Figure 2. Asynchrony of individual plant-pollinator interactions, and their temporal trends, separated by pollinator groups. (A) Average decadal asynchrony changes of individual interactions (grey dots), and the means for each group (coloured dots and 95% CI whiskers). (B) Group average changes of asynchrony (black dots: individual interactions yearly asynchrony, grey contours: indication of point density, coloured lines: linear regression for each group). (C) Fraction of interactions with earlier insect activity per group.