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Phenological shifts alter the seasonal structure of pollinator assemblages in Europe

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Pollinators play an important role in terrestrial ecosystems by providing key ecosystem functions and services to wild plants and crops, respectively. The sustainable provision of such ecosystem functions and services requires diverse pollinator communities over the seasons. Despite evidence that climate warming shifts pollinator phenology, a general assessment of these shifts and their consequences on pollinator assemblages is still lacking. By analysing phenological shifts of over 2,000 species, we show that, on average, the mean flight date of European pollinators shifted to be 6 d earlier over the last 60 yr, while their flight period length decreased by 2 d. Our analysis further reveals that these shifts have probably altered the seasonal distribution of pollination function and services by decreasing the overlap among pollinators' phenologies within European assemblages, except in the most northeastern part of Europe. Such changes are expected to decrease the functional redundancy and complementarity of pollinator assemblages and, therefore, might alter the performance of pollination function and services and their robustness to ongoing pollinator extinctions.

Numerous studies on plants, birds, amphibians and insects reveal that on average various phenological events—such as flowering or initiation of flight season—now take place earlier in the season than in the past decades because of climate warming[1]. Despite this general trend, a substantial inter-specific variation is observed in these responses, spatially[2] (for example, across latitudes) and temporally[2,3] (for example, spring versus summer species). This heterogeneity in species responses together with the fact that most studies focus on taxonomic rather than functional groups[1] challenges our ability to assess the consequences of phenological shifts for the functioning of communities and ecosystems across large spatial scales.

By modifying the set of species co-occurring in time, heterogeneity in phenological responses can induce mismatch among interacting species[4], thereby affecting community structure and related functions. One key issue to our understanding of the impact of climate warming on ecological functions is thus to assess how phenological shifts combine themselves among the species assemblage involved in a given function. This requires us to quantify the phenological responses of a large proportion of the species, not only in terms of mean flight date (MFD) shifts but also of changes in phenology length, a currently overlooked aspect of species responses[5]. The few studies that started to tackle this issue revealed important changes in patterns of species temporal overlap in several local communities of plants and amphibians, as a result of non-uniform phenological shifts[4,6,7]. However, these studies remain restricted to a small set of functional or taxonomical groups and to a small set of local communities.

Pollination is a key ecosystem function[8,9] mainly performed by four insect orders in Europe: Hymenoptera, Diptera, Lepidoptera and Coleoptera[10]. These flower visitors present a continuum of pollination efficiency, but the diversity within pollinator assemblage has been proved to increase pollination performance[11]. Current theoretical knowledge indicates that the level of heterogeneity in phenological responses to climate warming among pollinators can strongly affect pollination networks[12]. However, the quantification of the phenological responses of pollinators to climate warming is still limited, with studies focused on butterflies[13,14] and, to a lesser extent, on bees[3] and hoverflies[15]. A better understanding of the consequences of climate change on pollination thus requires a much more complete assessment of changes in pollinator phenology, including more species and changes in both timing and duration of the seasonal activities.

We took advantage of recent developments of large biodiversity databases and museum collections and we compiled a database of over 19 million records of flower visitor occurrences (Supplementary Table 1), spanning the period 1960–2016. This database includes 2,023 European species from the 4 main insect orders of pollinators: Hymenoptera, Diptera, Lepidoptera and Coleoptera (Extended Data Fig. 1). Numerous species exhibit distinct modes in their phenology, either because they are multivoltine (that is, multiple generations per year) or because the phenology differs between sexes or social casts. Since different modes from a species can shift in a different direction, we studied each mode separately, leading to 2,248 phenology modes (see Methods). For each phenology mode, we estimated changes in MFD and flight period length (FPL) over the years by modelling the mean and variance of collection dates (see Methods). Similarly to previous studies working with historical records[3], due to the lack of long-term standardized monitoring for many flower visitor taxa and at large spatial scales, our analysis relies on opportunistic data. However, such datasets have been shown to give estimates of phenological shifts quantitatively consistent with those based on standardized monitoring data[15,16].

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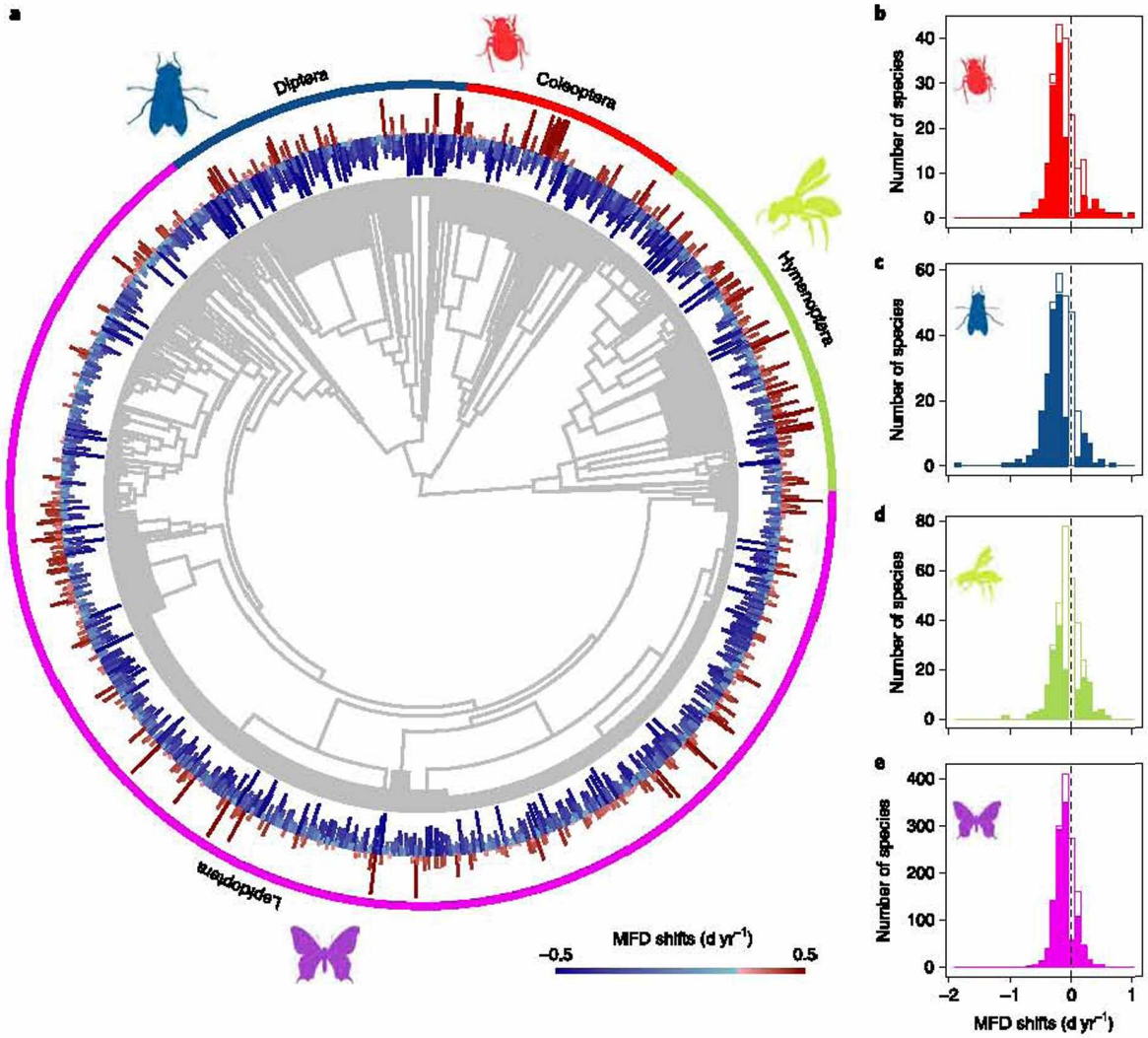

Fig. 1 | MFD shifts of European flower visitors between 1960 and 2016. a, Phylogeny of the studied species and MFD shifts (n = 2,248). The bars around the phylogeny tips are proportional to the MFD shifts and coloured in blue and red for phenological advancement and delay, respectively. Values below −0.5 and above 0.5 d yr^{-1} are truncated to preserve readability. **b–d**, Histograms show MFD shifts for all studied species of Coleoptera (**b**, red, n = 194), Diptera (**c**, blue, n = 305), Hymenoptera (**d**, light green, n = 322) and Lepidoptera (**e**, magenta, n = 1,427). Filled bars represent the number of species with values significantly distinct from zero; open bars correspond to the number of species with a value non-significantly distinct from zero (dashed line). The MFD shifts shown here are predicted for the averaged latitude, longitude and altitude of each species' records.

Results

We find that the MFD changes on average at a rate of −0.104 ± 0.004 d yr^{-1} (mean ± s.e.m.) implying that European pollinators are flying on average 5.8 d earlier in 2016 than in 1960, a value consistent with previous estimations on bees[3] and butterflies[13]. Climate warming appears as a likely cause as MFD shift mainly occurred after 1980, following the temperature increase (Supplementary Method 1 and Extended Data Fig. 2). Considering FPL, we find that on average the standard deviation of collecting dates decreases slightly with time, at a rate of −0.016 ± 0.003 d yr^{-1} (mean ± s.e.m.), which corresponds to a decrease of 1.8 d of the FPL over the last 56 yr. This reduced FPL might be due to a reduced genetic variability on phenology caused by a directional selection on phenology advancement. Indeed, we know that a directional selection on a phenotypic trait can reduce the variance of this trait[17], and the significant positive Pearson correlation between the changes over time of MFD and FPL (r = 0.09, $t_{df=2,246}$ = 3.89, $P = 1 \times 10^{-4}$) can suggest such a mechanism. However, whether these changes are adaptive or not, and the mechanisms underlying these responses (adaptation versus phenotypic plasticity), remain unknown.

Despite these overall trends, we observe a substantial heterogeneity among species in the response of MFD and FPL (Fig. 1 and Extended Data Fig. 3). Of the phenologies studied, 13% exhibit a significantly delayed MFD whereas 30% do not exhibit any significant shift (Supplementary Table 2). Such heterogeneity is even more striking for FPL changes, where 27% of the phenologies studied are significantly lengthened and 43% are unchanged (Supplementary Table 2). If an increase of winter temperature is known to advance species phenology by reducing the development time[18], some species also react in an opposite way[18,19], which might explain observed variations in MFD shifts. Turning to the heterogeneity in FPL responses, a temperature increase can either reduce or increase FPL (for example, by reducing insect lifespan[20] or by increasing the number of generations within years[14]).

We further show that this heterogeneity in phenological responses is related to the evolutionary history of species as shown by the strong phylogenetic signal in MFD shifts (Pagel's λ = 0.75, $P < 0.001$) and in FPL changes (Pagel's λ = 0.82, $P < 0.001$). This phylogenetic signal is related to strong differences among orders in these phenological shifts, Diptera and Coleoptera advancing their

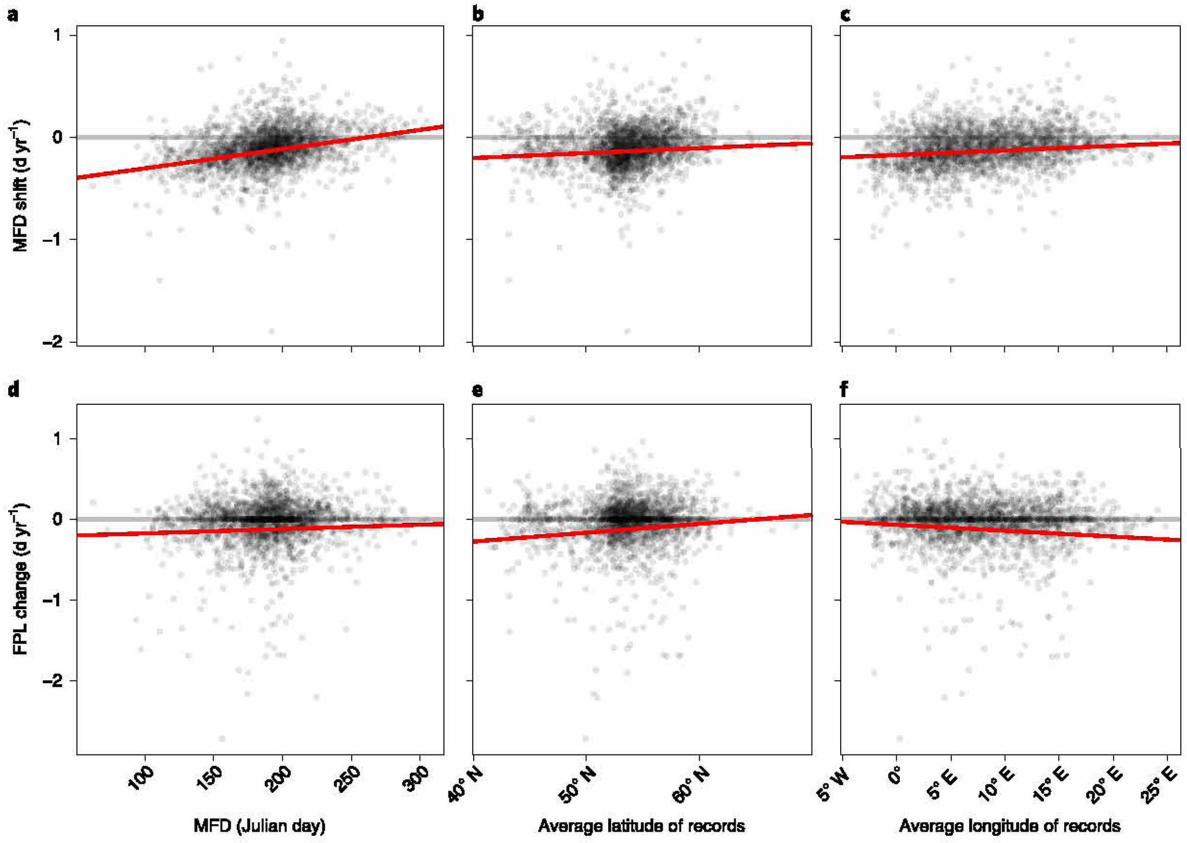

Fig. 2 | Spatial and seasonal heterogeneity in phenological shifts among species. a–f, MFD shifts (**a–c**) and changes in FPL (**d–f**) against species MFD (**a**,**d**) and averaged latitude (**b**,**e**) and longitude (**c**,**f**) of species records. Horizontal grey lines show the 0 value; red lines are phylogenetic generalized least-squares predictions. Estimates and standard errors are shown in Supplementary Table 4.

MFD more than Lepidoptera and Hymenoptera while Coleoptera decrease their FPL more than the other orders (Supplementary Table 3). However, the phylogenetic signal remains significant within orders for MFD shifts (Supplementary Table 3). This phylogenetic signal indicates that species traits underlying phenological responses are conserved across the phylogeny.

MFD and FPL responses also demonstrate spatial and seasonal heterogeneity among species. Species with southern and western distribution areas show a stronger MFD advancement than species with northern and eastern distribution areas (Fig. 2b,c and Supplementary Table 4), matching previous results on European plants[2]. We also find that species with northern and western distribution areas experience a smaller decrease in FPL than species with southern and eastern distribution areas (Fig. 2e,f and Supplementary Table 4). In addition, we find a seasonal pattern where spring species experience a significantly greater advancement than summer/autumn species (Fig. 2a), consistently with previous results on American bees[3] and European plants[2]. Regarding FPL, we find that earlier species shorten their flight period more than later species (Fig. 2a–d and Supplementary Table 4). Such differences could be explained by the fact that summer/autumn and northern species might rely more on photoperiod, a determining factor of insect phenology[21], than spring and southern species. Such patterns have been shown for plants[22,23], but studies on this point for insects are missing.

We further show that the MFD shifts vary within species in a way that echoes the patterns found at the inter-specific level. Indeed, we detect a significant positive interaction between the latitude and year effects for 29% of species, indicating that southern populations experience a stronger shift of their MFD towards earlier dates than northern populations (Supplementary Table 2). By contrast, no longitudinal pattern was found. The seasonal pattern of stronger advancement earlier in the season is also found at the intra-specific level. Among the 190 species with multimodal phenology and sufficient data to study them, 59% have their first mode advancing significantly faster than their second mode while the opposite pattern occurs only in 10.5% of the species (Extended Data Fig. 4).

To assess the consequences of these phenological shifts for the seasonal structure of pollinator assemblages across space, we analysed changes in the phenological overlap of species co-occurring within locations of 5°×5° grid cells in Europe, between 1980 and 2016. We used the linear models for MFD and FPL to predict the phenologies of each species for each grid cell predicted for both years (Fig. 3a). Considering that all phenologies are unimodal, we modelled them by Gaussian density distribution, to calculate the pairwise phenological overlap among all pairs of pollinators present in a grid cell (see Methods). We averaged these measures among pollinators belonging either to the same or to different insect orders (see Methods).

First, we show that species co-occurrence in time increases towards the beginning of the season and then abruptly decreases in the second half of the season (Extended Data Fig. 5), consistently with the average advancement of pollinator MFD. This indicates that the advance of MFDs has probably shifted the pollination function and services to earlier in the season. Second, assuming no changes in abundance/distribution of species, we show that both within- and among-orders average overlaps in phenology have decreased within the last 36 yr in most parts of Europe, except in the extreme northern

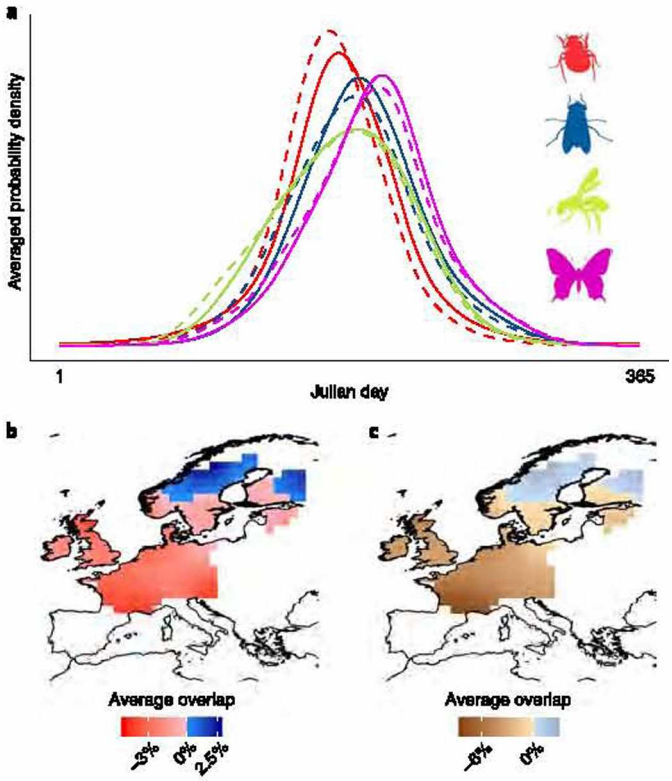

Fig. 3 | Changes in within- and among-orders average overlaps in phenology between 1980 and 2016 across Europe. a, Average phenology over all species in 1980 (solid lines) and in 2016 (dashed lines) for one grid cell (centroid = 55,0) by orders: Coleoptera (red), Diptera (blue), Hymenoptera (light green) and Lepidoptera (magenta). The average phenology is calculated by averaging all probability density functions (Gaussians representing phenologies) over all species of each order, assuming identical species abundances. **b**,**c**, Observed changes in the average overlap among phenologies between 1980 and 2016, within orders (**b**) and among orders (**c**). Uncoloured cells are under-prospected. The number of species by order across Europe is shown in Extended Data Fig. 6.

part (Fig. 3b,c). The observed increase of the overlap among phenologies in northern Europe is probably due to the fact that there, in contrast to other regions, the average MFD shift is almost null whereas the FPL slightly increases (Fig. 2). Sufficient data on long-term dynamics of plant–pollinator networks are currently missing to fully assess the consequences of such changes in the seasonal structure of pollinator assemblages on pollination function. However, the within-order and among-order overlaps should be related to temporal redundancy and complementarity within pollinator assemblages, respectively. Indeed, the pervasive phylogenetic signal within pollination networks indicates that related pollinators tend to visit the same plants[24,25]. This implies that species with overlapping phenologies and belonging to the same insect order should visit the same set of co-flowering plant species and thus belong to the same pollinator functional group. By contrast, species with overlapping phenologies but from different insect orders are expected to provide a complementary pollination function, by visiting different sets of co-flowering plant species.

Therefore, the observed decrease in the overlap within insect orders, by lowering the temporal redundancy among pollinators, might decrease the robustness of plant–pollinator interaction networks to pollinator extinction[26]. A decrease in the overlap may also have beneficial effects for pollinators by decreasing competition for nectar and pollen resources, but such competition release might in turn restrict pollinator visits to the most profitable plant species following optimal foraging theory predictions[27]. Turning to the observed decrease in phenology overlap among pollinator orders, it suggests a decrease in temporal complementarity within pollinator assemblages, thereby weakening the pollination function delivered to plant communities[28]. This result echoes theoretical findings on pollination networks showing that the more phenologies are scattered over the season, the more community diversity decreases[29].

Discussion

Our results show that flower visitor responses to climate warming depend on their evolutionary history, geographical location and seasonal earliness. This high variation in species phenological responses is expected to drive heterogeneity in the consequences of climate warming on pollination function across Europe and across the season. For most parts of Europe, the observed modifications of the seasonal structure of pollinator assemblages are expected to have negative consequences on pollination, while in northeastern Europe they might have positive effects on pollination as they result in an increased phenology overlap, both within and among pollinator orders (Fig. 3). Moreover, in most parts of Europe, observed changes are expected to have a positive effect on pollination performance and robustness early in the season but a negative effect from the middle to the end of the pollination season (Extended Data Fig. 5). Thus, our results highlight the importance to assess responses at large spatial and temporal scales and to include many species, to capture the high spatial and seasonal heterogeneity in the consequences of climate change on pollinator assemblages and related function.

Climate warming is recognized as a major threat to biodiversity. Our results suggest that climate warming, by reducing pollinator co-occurrence in time within seasons, has had a negative effect on the delivery of pollination function as well as on its resistance to further perturbations, in most parts of Europe. Such findings raise the question of potential interactive effects between climate warming and other pressures related to global change such as agricultural intensification[30,31], which could amplify expected negative effects on pollination. In addition to its effect on species phenology, climate warming is expected to affect the spatial distribution[32] and the abundance[31] of flower visitors, and so are other drivers of global change. How such effects combine with those observed in this study remain unknown. This stresses the need to explore multiple responses of species to multiple drivers of global change to assess potential synergistic effects among species responses to global change drivers over large scales.

Methods

Constructing the database on flower visitor phenologies. *Assembling data on flower visitor occurrences in time and space.* European flower visitors mainly belong to four insect orders—Coleoptera, Diptera, Hymenoptera and Lepidoptera[10]. We first looked for occurrence data (that is, sighting at a given date and location) of species that belong to these insect orders and that are defined as floricolous in scientific or grey literature. We restricted our search to European species listed in Fauna Europaea[33]. The data are from 15 distinctive sources, summarized in Supplementary Table 1, with a high proportion from the Global Biodiversity Information Facility (GBIF). After the removal of duplicates (same species, date and locality), the database initially included about 30 million occurrences between 34° and 72° of latitude north and between −15° and 32° of longitude.

Modelling multimodal phenologies and removing larval records. Numerous species exhibit distinct modes in their phenology, either because they are multivoltine (that is, multiple generations per year) or because the phenology differs between sexes or social casts. Since different modes in the same species are temporally distant, they might not respond to the same environmental cues. As a consequence, each mode might potentially shift in a different direction and should thus be studied separately. Furthermore, larvae might be easier to spot than adults for Lepidoptera and some Coleoptera. Thus, a substantial proportion of records may actually be larvae, which are not floricolous and should be removed from the analysis. To split the occurrences of multimodal imago phenology into distinct modes as well as to identify larval occurrences, we developed the following method.

The first step of the method was to detect multimodality. Since phenologies vary spatially, multimodality can be the product of sampling in different localities.

To take this spatial variation into account, for each species separately, we fitted the following linear mixed-effects model accounting for spatial variables on the Julian day of the records:

$$Y_{ik} = \mu + \rho_1 \times \text{latitude}_k + \tau \times \text{longitude}_k + \theta \times \text{altitude}_k + \varphi_i + E_{ik} \quad (1)$$

where Y_{ik} is the Julian day of the observation k of the year i, μ is the grand mean (intercept), ρ_1 and τ_1 are latitude and longitude effects, respectively, and θ is an altitude effect. φ_i is a random year effect (factor) and E_{ik} is the error term (independent and identically distributed, following $N(0,\sigma^2)$). The residuals of this model thus represent the collection dates once spatial and altitudinal variations have been removed. To detect multimodality in the distribution of these residuals, we smoothed the distribution with the R function density, using the value 1.3 for the adjust parameter and counted the number of local maxima (nbmax) that reaches 7% of the highest mode. We used this cutoff to remove small peaks on the edges of the phenology and we defined the value of the threshold after a visual inspection of phenologies. Several modes were initially detected for 494 species. For each of these species, we checked in scientific and grey literature whether a multimodal phenology was expected. In 208 cases, there was no strong biological support of existing multimodal phenology and we thus considered these species had one single mode. After this step, 288 remaining species showed a multimodal phenology (nbmax > 1). We applied the second step only for these species.

The second step of the method was to attribute each record to a specific mode. To do so, we used clustering Gaussian mixture models implemented in the mclust R package[34], considering a number of Gaussians from one to nbmax. This clustering model allows us to initialize the attribution of each record to a given mode. Using the classification given by these clustering models, we run linear mixed-effects models, similar to the one described in equation (1) but with the addition of a mode effect (β_j):

$$Y_{ijk} = \mu + \rho_1 \times \text{latitude}_k + \tau \times \text{longitude}_k + \theta \times \text{altitude}_k + \beta_j + \varphi_i + E_{ijk} \quad (2)$$

We kept the number of modes that minimize the Bayesian information criterion of this linear mixed-effects model. We then manually changed the mode of poorly predicted points. If the change improved the likelihood of this mixed-effects model, we retained it and continued this process iteratively. We stopped the process when changing the mode of poorly predicted points did not further improve the likelihood of the model. The R script of the full method is available at https://github.com/f-duchenne/Flower-visitors-phenology. Although the mode effect (β_j) is independent from the spatial variables and altitude in equation (2), our method still allows us to take into account spatial and altitudinal variation in the number of modes (Extended Data Fig. 7). We confronted the relevance of detected modes regarding what we know on the biology of species. We found that our method distributes records among modes in a highly consistent way. Some examples can be seen in Extended Data Fig. 7. We identified 19 species for which we had a mode corresponding to larval phenology, and we removed the corresponding records. Overall, this analysis led to 2,473 unimodal phenologies from 2,179 species.

Database after selection process. Following the separation of distinct phenological modes for each species and the removal of larval records, we selected phenologies (or phenological modes) with at least 400 records during the period 1960–2016 and with at least 40 records from the period 1960–1980, to be able to study phenological shifts between early and more recent periods. We removed species ($n = 30$) with phenology peaking during winter by excluding species with a MFD before 60 or after 306 Julian days. Studying the phenology of such species raises methodological questions that we will not address here. We also removed records with imprecise localization (above 1 km²) except those for small countries (Luxembourg, Belgium, Switzerland, the Netherlands, Denmark, Lichtenstein, Monaco, Andorra and Kosovo). Thus, our dataset includes some records with imprecise localization (above 1 km²), but they represent less than 0.1% of the final dataset. This selection process led to 19,845,792 occurrence records with 2,248 phenologies for 2,023 species (Supplementary Table 1). The repartition of records among insect orders and throughout the study period is presented in Extended Data Fig. 1. Supplementary Table 1 indicates the amount of data coming from the various data sources.

Analyses of species phenological shifts over time. *Estimating species phenological shifts.* To estimate changes in both the MFD and the FPL, we modelled jointly the mean and the variance of collection dates using the dispmod R package[35], which performs two nested linear models, one for the mean and one for the variance. Due to computational limits, it was not possible to use one model including the whole dataset, modelling both MFD shifts and FPL changes, and modelling spatial effects properly for each species. Thus, we studied each species and phenology mode separately. For each phenology mode, the model for the mean collection date was:

$$\begin{aligned} Y_k = {} & \mu + (\pi + \alpha \times \text{latitude}_k + \delta \times \text{longitude}_k) \times \text{year}_k + \\ & (\rho_1 + \gamma_1 \times \text{longitude}_k) \times \text{latitude}_k + (\rho_2 + \gamma_2 \times \text{longitude}_k^2) \times \text{latitude}_k^2 \\ & + (\rho_3 + \gamma_3 \times \text{longitude}_k^3) \times \text{latitude}_k^3 + \tau_1 \times \text{longitude}_k + \tau_2 \times \text{longitude}_k^2 + \tau_3 \times \\ & \text{longitude}_k^3 + \theta \times \text{altitude}_k + E_k \end{aligned} \quad (3)$$

Y_k is the Julian day of the observation k, μ is the grand mean (intercept), and π is the time effect on the mean collection date as well as on its variation across latitude (α) and longitude (δ). ρ_1, ρ_2 and ρ_3 and τ_1, τ_2 and τ_3 are linear, quadratic and cubic effects for latitude and longitude, respectively, γ_1, γ_2 and γ_3 are spatial interaction terms, θ is an altitude effect and E_k is the error term (independent and identically distributed, following $N(0,\sigma^2)$).

The joint model for variance of collection date was:

$$\log(\sigma^2) = \mu_v + \rho_v \times \text{latitude}_k + \tau_v \times \text{longitude}_k + \theta_v \times \text{altitude}_k + \pi_v \times \text{year}_k \quad (4)$$

where σ^2 is the variance of the collection date, μ_v is a constant term, ρ_v, τ_v, θ_v and π_v are latitude, longitude, altitude and year effects, respectively. We performed model simplification based on the Akaike information criterion, first on the model for the mean collection date, removing only the polynomial effects of latitude and longitude (γ_1, γ_2, γ_3, ρ_2, ρ_3, τ_2 and τ_3) and interactions between the spatial variables and the time effect (α and δ), and second on the model for the variance in the collection date.

The MFD shifts presented in the paper are $\pi + \alpha \times \overline{\text{latitude}} + \delta \times \overline{\text{longitude}}$ from equation (3), where $\overline{\text{latitude}}$ and $\overline{\text{longitude}}$ are the averaged latitude and longitude of the species records, respectively. The FPL changes are the π_v from equation (4) for each species.

Phylogenetic analysis. To get a phylogeny of all the studied species, we combined several published phylogenies. We used the phylogeny from Rainford et al.[36] as the backbone to which we added some available and recent phylogenies to get a phylogeny at the genus level for Papilionoideae[37], Vespidae[38] and Apoidea[39]. For all other families, genera (as defined by the GBIF taxonomy) were inserted on a polytomy positioned midway between the family origin and the tip. Then species from each genus were placed on a polytomy positioned midway between the genus origin and the tip. This method does not allow a good estimation of the recent evolutionary history but because there is no phylogeny of insects at the species or genus level, it is the only way to include all species responses and account for intra-family heterogeneity. Moreover, because these polytomies were not too old relative to the entire phylogeny, it should not strongly affect our results. As they are not present in our phylogeny, three families of Diptera (Heleomyzidae, Limoniidae and Pediciidae) and two Lepidoptera species (*Sphrageidus similis*, Lymantriidae, and *Agria desoptilete*, Lycaenidae) were excluded from the phylogenetic analysis.

We estimated the phylogenetic signal in phenological shifts using Pagel's λ (ref. [40]) implemented in the phylosignal R package[41], because it is much more robust to polytomies than Blomberg's K (ref. [42]).

Links between phenological traits and phenological shifts. To test whether the seasonal precocity and the spatial distribution of species were linked to phenological shifts, we used the following phylogenetic generalized least-squares model implemented in the caper R package[43] controlling for Pagel's λ of the residuals at the maximum likelihood:

$$\text{PS}_z = \mu + (\alpha) \times \text{MFD}_z + (\beta) \times \text{latitude}_z + (\delta) \times \text{longitude}_z + E_z \quad (5)$$

where PS_z is the phenological shift (that is, MFD shift or FPL change) of the species z, μ is the grand mean (intercept), α is the effect of the MFD calculated with recent records (from 2000), β is the effect of the average latitude of records, ρ is the effect of the average longitude of records and E_k is an error term following $N(0,\sigma^2)$.

Analyses of the seasonal structure of pollinator assemblages. *Predicting species phenology in different locations and years.* To assess the effect of phenological shifts at the scale of the full pollinator assemblages, we calculated changes in the overlap among phenologies. As phenological shifts depend on location, we discretized the studied area in cells of 5° × 5°. This size was chosen to smooth the differences in sampling effort among localities. To ensure a representative pollinator assemblage, we included only grid cells with at least 3 insect orders with 20 species with at least 30 records each. The remaining cells were considered as under-prospected. Thus, species are considered present in a grid cell if it has at least 30 records between 1960 and 2016. By doing so, we assume that the compositions of species assemblages are the same in 1980 and in 2016, which allows us to study only the effect of phenological shifts on seasonal structure. We considered that all species have the same abundance, and a circular Gaussian phenology. We used wrapped circular normal distributions instead of a classical Gaussian distribution to take phenologies that span winter into account. We estimated the mean and the standard deviation of these Gaussians for the years 1980 and 2016 and for each grid cell, using the predictions of the linear models used to estimate phenological shifts, described in equations (3) and (4).

Calculation of phenological overlaps within assemblages. For each sufficiently prospected grid cell, we calculated the pairwise overlap among the pollinator phenologies present in the given grid cell. We considered that all species have the same abundance, and a circular Gaussian phenology. The overlap between two phenologies is the integral of the minimum of both Gaussians. We calculated two overlap measures for each grid cell: the first one focusing on the overlap within insect orders and the other one among insect orders. To give equal weight to each

insect order, and thus avoid over-representation of Lepidoptera, we first calculated the mean overlap by insect order, or by pair of insect orders, respectively, for the overlap within and among orders. Second, we averaged these mean values per grid cell. Finally, to have more robust values, we repeated this overlap calculation after shifting segmentation of the latitude and the longitude by 1.25°, 2.5° and 3.75°. Then we averaged values obtained by 1.25°×1.25° grid cells for both measures, overlap within and among orders.

To study the seasonal dynamic of overlap changes, we calculated a proxy of the phenological overlaps day by day in 1980 and in 2016 for each grid cell (Extended Data Fig. 5). We did not use exactly the same calculation of overlap as previously for computational reasons. To simplify the calculation method, we aggregated predicted phenologies at the order level to get a density distribution by order, henceforth called order phenologies, as presented in Fig. 3a. Then we calculated the pairwise overlap among the order phenologies day by day for both years, 1980 and 2016, and for each grid cell. We also evaluated the day-by-day density value for each order phenology for both years, 1980 and 2016, and for each grid cell. This density value is a proxy of the phenological overlap within order, because we assume that every species has the same constant abundance. Then we calculated the daily changes of both these indices between 1980 and 2016 (Extended Data Fig. 5). We did so for only one grid pattern (that is, without sliding windows).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The final dataset analysed in this paper is available at https://zenodo.org/record/3480120.

Code availability

The codes used to extract data from the GBIF, to separate modes of multimodal phenologies and to estimate phenological shifts are available at https://github.com/f-duchenne/Flower-visitors-phenology.

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Author contributions

F.D., C.F. and E.T. conceived the project. F.D. assembled the dataset and performed the statistical analysis. F.D., C.F., E.T., D.M. and M.E. interpreted the results. M.D., M.Persson, J.S.P., M.Pollet and P.V. provided data and biological expertise on the studied species. F.D. wrote the paper with contributions from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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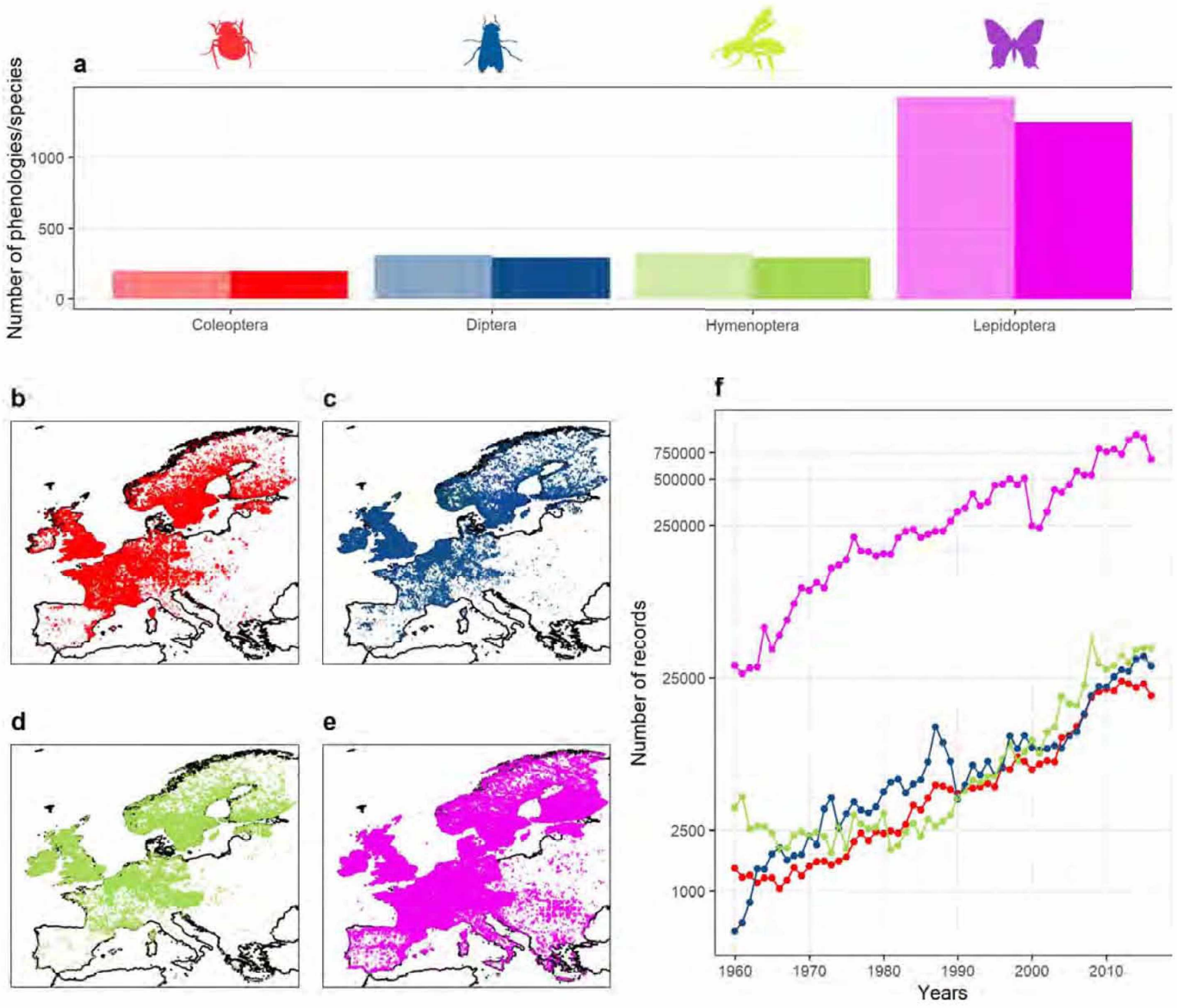
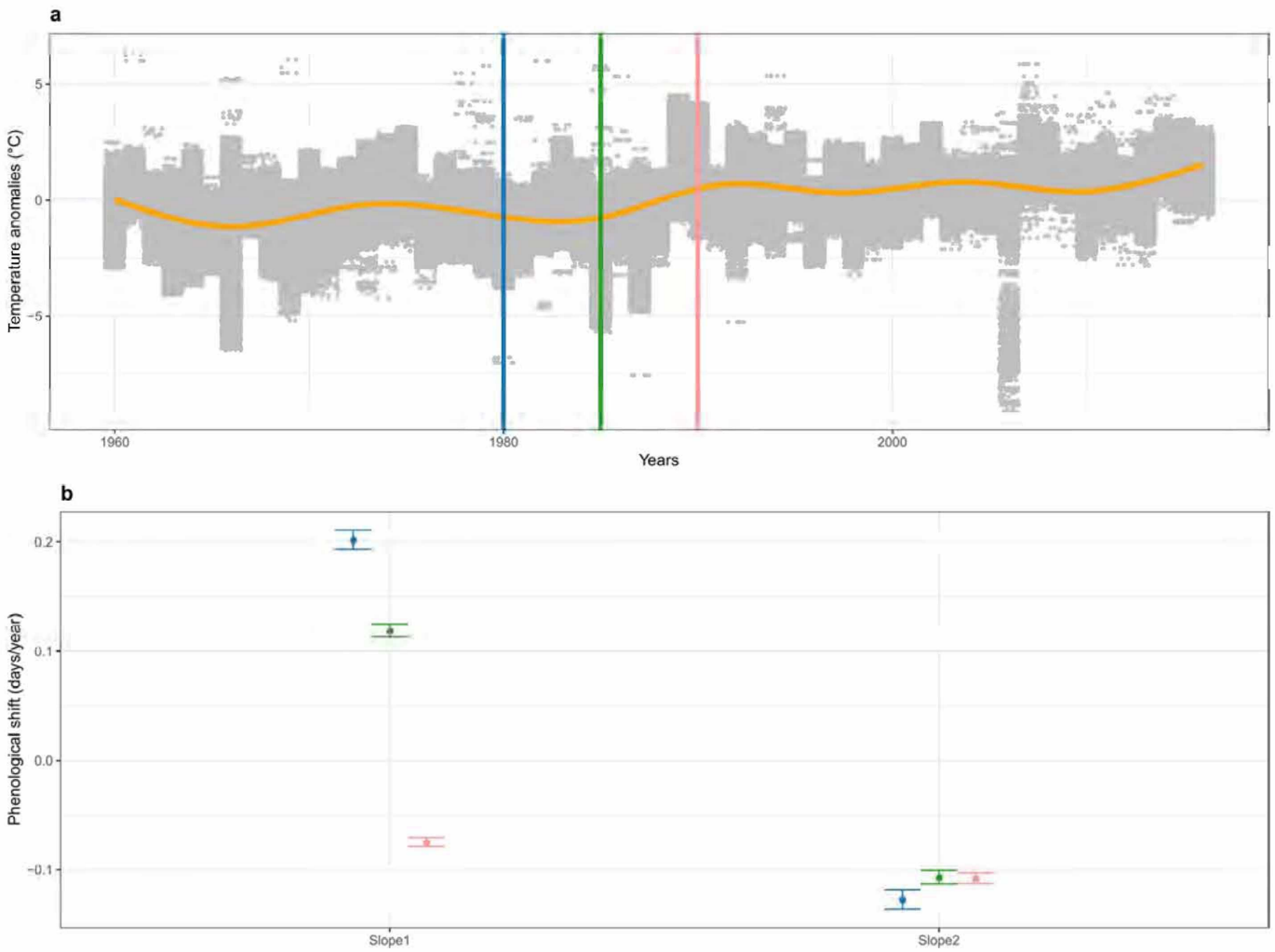
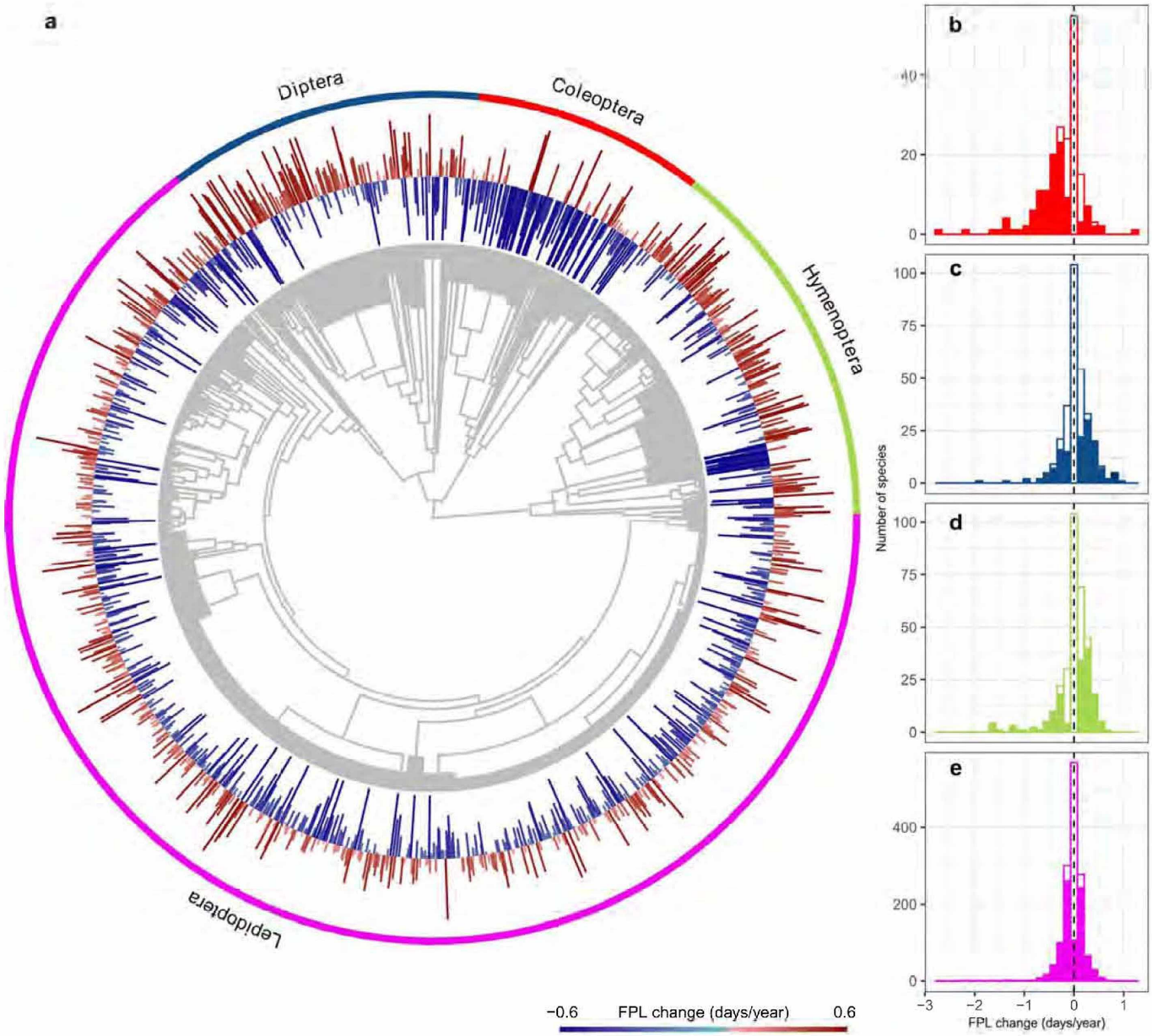


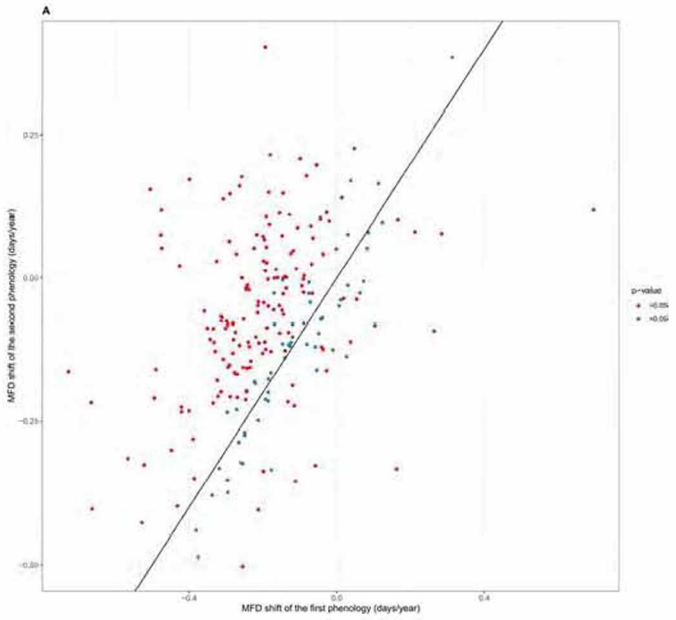
Extended Data Fig. 1 | Spatial and temporal distribution of records by order. a, Number of phenologies (light colors, left) and species (dark colors, right) for each insect order. **b-e**, Spatial and **f**, temporal distribution of records for Coleoptera (**b**, red), Diptera (**c**, blue), Hymenoptera (**d**, light green) and Lepidoptera (**e**, magenta). Y-axis of (**f**) is on a $\log_{10}$ scale.



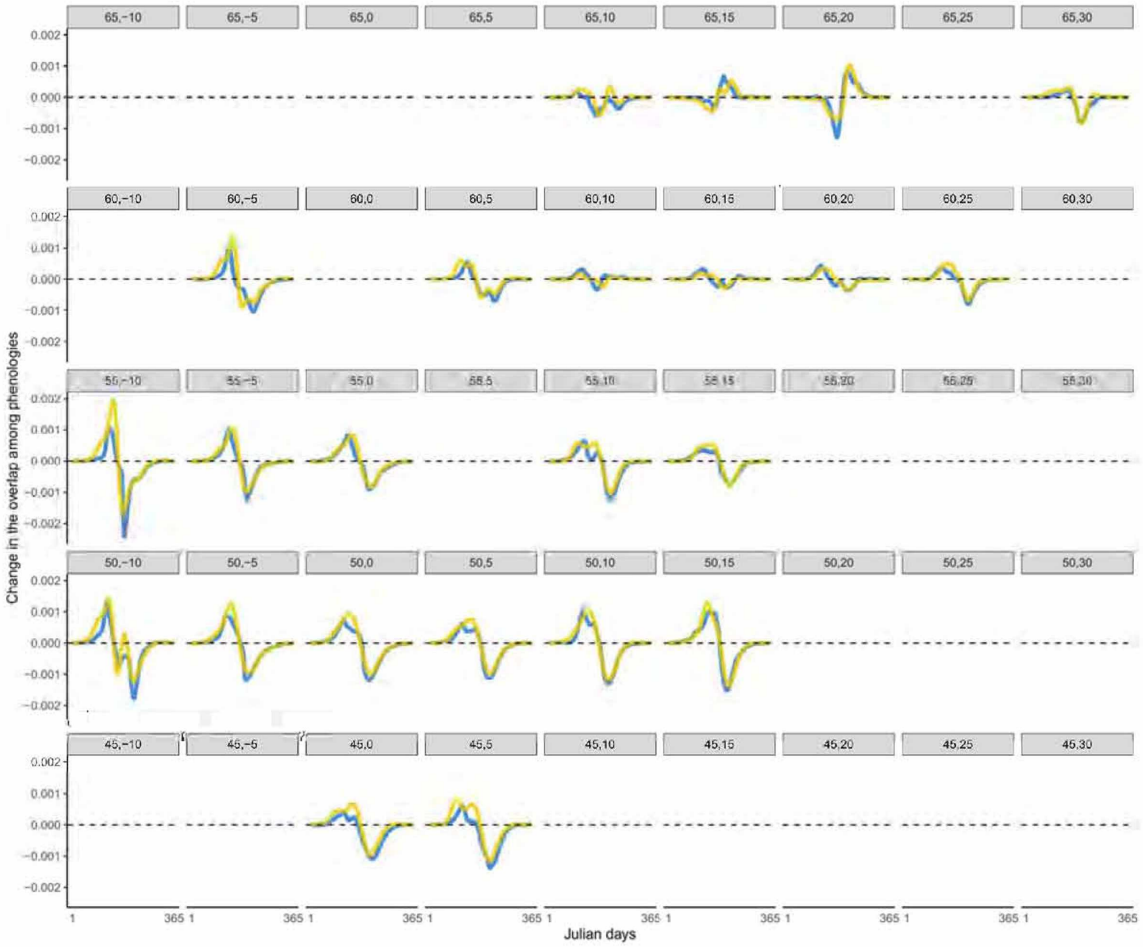
Extended Data Fig. 2 | Average MFD shifts before and after the temperature increase. a, Temperatures anomalies on the first 150 days of each year against years. The orange curve represents the result of a LOESS fit. Vertical lines show the position of the 3 breakpoints chosen to define periods used in (**b**). **b**, Mean flight date shifts for the whole pollinator assemblage by period, before the breakpoints (Slope1) and after the breakpoints (Slope 2).



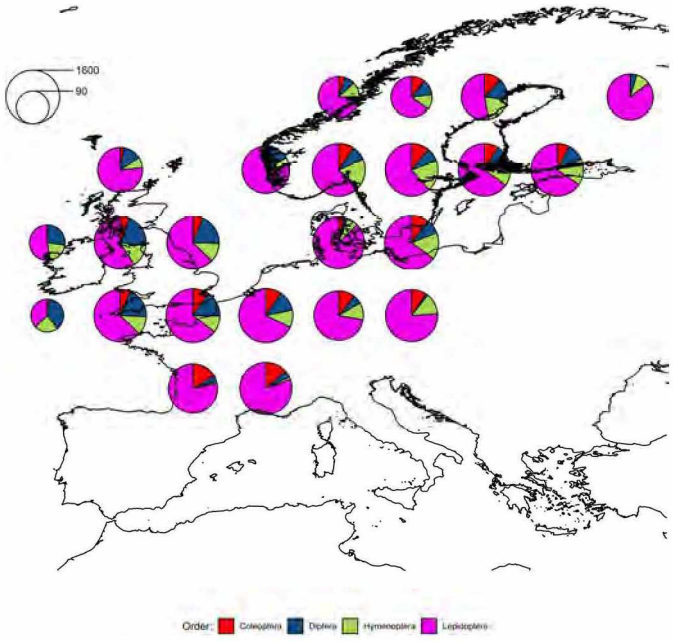
Extended Data Fig. 3 | Flight period length (FPL) changes of European flower visitors between 1960 and 2016. a, Phylogeny of studied species showing FPL shifts. The bars around the phylogeny tips are proportional to the FPL shifts and colored in blue and red for shortening and lengthening, respectively. Values are truncated to −0.6 and to 0.6 days/year to preserve readability. Histograms show FPL shifts for all studied species of **b**, Coleoptera (red), **c**, Diptera (blue), **d**, Hymenoptera (light green) and **e**, Lepidoptera (magenta). Full bars represent species with values significantly distinct from zero whereas open bars are species with a value non-significantly distinct from zero. FPL shifts shown here are predicted for the averaged latitude and longitude of each species' records.



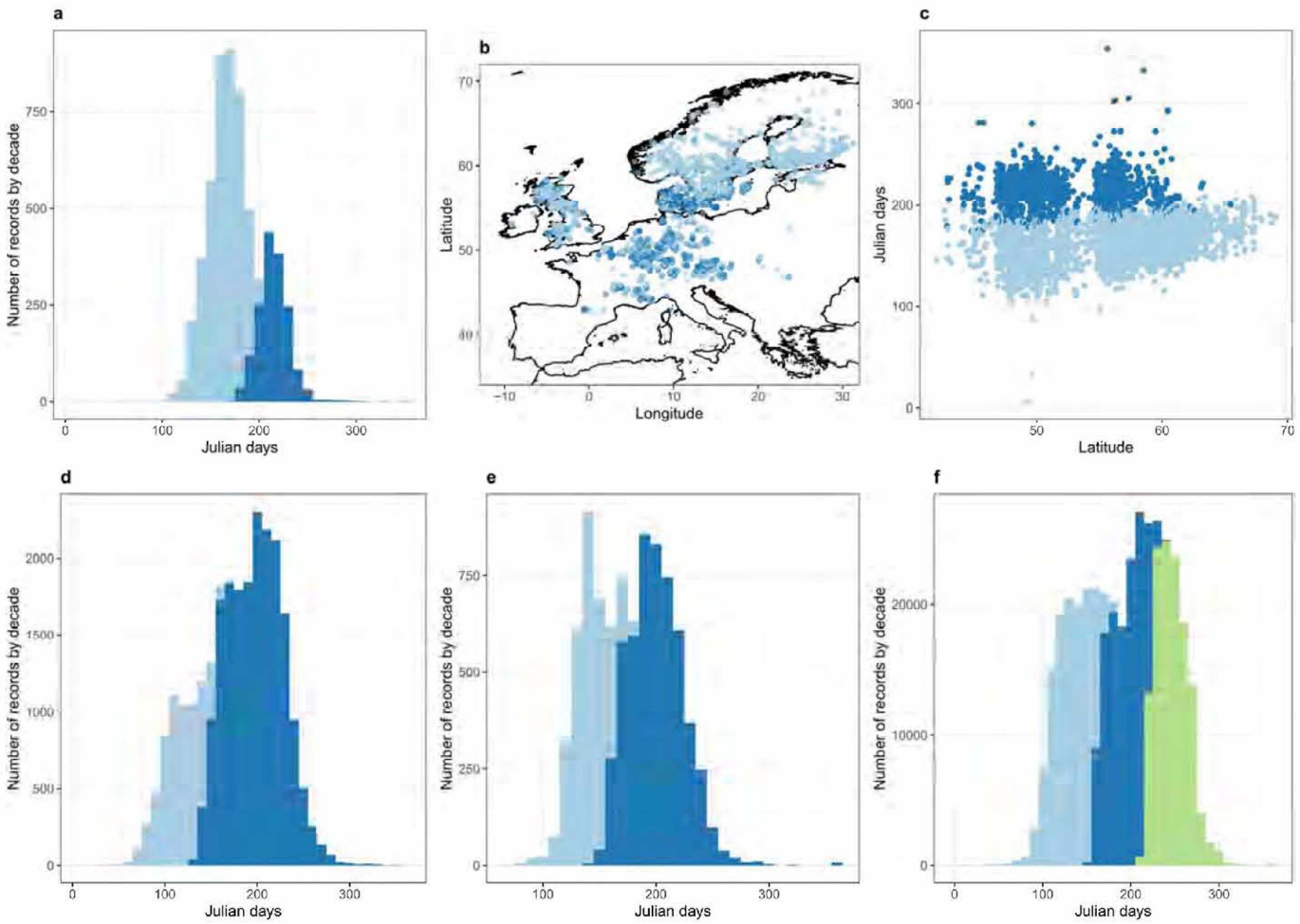
Extended Data Fig. 4 | MFD shifts of the second mode against MFD shifts of the first mode for multimodal phenologies. Mean flight date (MFD) shifts of the second mode against MFD shifts of the first mode for all 190 species presenting a multimodal phenologies with enough data in 2 modes to study both (cf. Methods). Color indicates p-value (red: <0.05 and blue >0.05) of the Z test comparing both shifts. The black line is the first bisector. Red points above the first bisector show species with a first mode advancing significantly more than the second one, while red points under the first bisector show the opposite pattern and blue points do not show any significant differences between two mode shifts.



Extended Data Fig. 5 | Seasonal changes in the overlap among phenologies between 1980 and 2016. Changes in the overlap among orders (blue) and within orders (yellow) between 1980 and 2016 along the season, considering only grid cells with enough data (see Supplementary Fig. 6). Cells are sorted by latitude then longitude (Lat,Long).



Extended Data Fig. 6 | Spatial distribution of phenologies in grid cells. Number of phenologies by order in 5° × 5° grid cells, considering only grid cells with enough data, that is with at least 3 insect orders including at least 20 species with at least 30 records each.



Extended Data Fig. 7 | Examples of multimodal phenologies split into distinct modes. The example of *Epirrhoe tristate* (Lepidoptera) shows how our method distributes records in function of **a**, Julian days, **b**, space and especially **c**, latitude. Other examples for *Bombus lapidarius* (**d**, Hymenoptera), *Melitaea phoebe* (**e**, Lepidoptera) and *Pararge aegeria* (**f**, Lepidoptera). For the *Bombus*, we can see that our method is able to separate emerging queens (light blue) and workers/males (dark blue) phenology, whereas we also detect 3 modes for *Pararge aegeria* and 2 for *Melitaea phoebe* in agreement with what we know about the voltinism of these species.

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Study description	We estimated changes in mean flight date and flight period length over the years by modeling the mean and variance of collection dates. To do this, we used the dispmod R package which allows to fit Gaussian dispersion regression models. Such model implies two nested linear models, one for the mean and one for the variance. In order to take into account non-linear spatial variation in phenology we included spatial variables (latitude and longitude in interaction and with polynomials terms) and altitude. To take into account spatial variation in changes of mean flight date over years we included an interaction between spatial variables and years.
Research sample	We used occurrence data (i.e. sighting at a given date and location) from large open biodiversity databases (GBIF and Waarnemingen), but also records from Natural History Museum and private collections (cf. Table S1).
Sampling strategy	We used the GBIF database and the French Natural History museum collections because they contain many historical records, allowing reconstructing historical phenologies. Other databases provided recent records.
Data collection	F. Duchenne aggregated all databases, removing duplicated records from the same species, same julian day and year and same grid cell (0.01°x0.01° in WGS84).
Timing and spatial scale	We looked for data from 1960 to 2016. This time window includes a period before the strong recent climate warming in Europe and allows evaluating phenological shifts on a standardized period for all species included. For the spatial scale, we focused on Europe, because it is a region with many historical records on insects and because European Fauna is more or less homogeneous.
Data exclusions	We did not exclude data without reporting it in methods. We exluded species with less than 400 records during the period 1960-2016 and with less than 40 records from the period 1960-1980, to be able to study phenological shifts between early and more recent periods. For multimodal phenologies, we removed modes corresponding to larval phenology (cf. methods).
Reproducibility	Our analysis does not include randomization or Bayesian statistics, so statistics can be reproduced identically using the available scripts on the cited Github.
Randomization	We do not use randomizations.
Blinding	Blinding was not used in our study because we used already collected records, without any discrimination among them, and all data exclusions was done in a protocoled way described in methods.

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