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1 **Phenological shifts alter the seasonal structure of pollinator assemblages in**
2 **Europe**

3

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17 **Pollinators play an important role in terrestrial ecosystems by providing key ecosystem**
18 **functions and services to wild plants and crops, respectively. The sustainable provision of such**
19 **ecosystem functions and services requires diverse pollinator communities over the season.**
20 **Despite evidence that climate warming shifts pollinator phenology, a general assessment of these**
21 **shifts and their consequences on pollinator assemblages is still lacking. By analyzing**
22 **phenological shifts of over 2000 species, we show that on average the mean flight date of**
23 **European pollinators shifted 6 days earlier over the last 60 years, while their flight period length**
24 **decreased by 2 days. Our analysis further reveals that these shifts have likely altered the**
25 **seasonal distribution of pollination function and services by decreasing overlap among**
26 **pollinators' phenologies within European assemblages, except in the most northeastern part of**
27 **Europe. Such changes are expected to decrease the functional redundancy and complementarity**
28 **of pollinator assemblages and as such, might alter the performance of pollination function and**
29 **services and their robustness to ongoing pollinator extinctions.**

30 Numerous studies on plants, birds, amphibians and insects reveal that on average various
31 phenological events - such as flowering or initiation of flight season – now take place earlier in the
32 season than in the past decades because of climate warming¹. Despite this general trend, a substantial
33 inter-specific variation is observed in these responses, spatially² (e.g. across latitudes), and
34 temporally^{2,3} (e.g. spring *versus* summer species). This heterogeneity in species responses together
35 with the fact that most studies focus on taxonomic rather than functional groups¹ challenges our ability
36 to assess the consequences of phenological shifts for the functioning of communities and ecosystems
37 across large spatial scales.

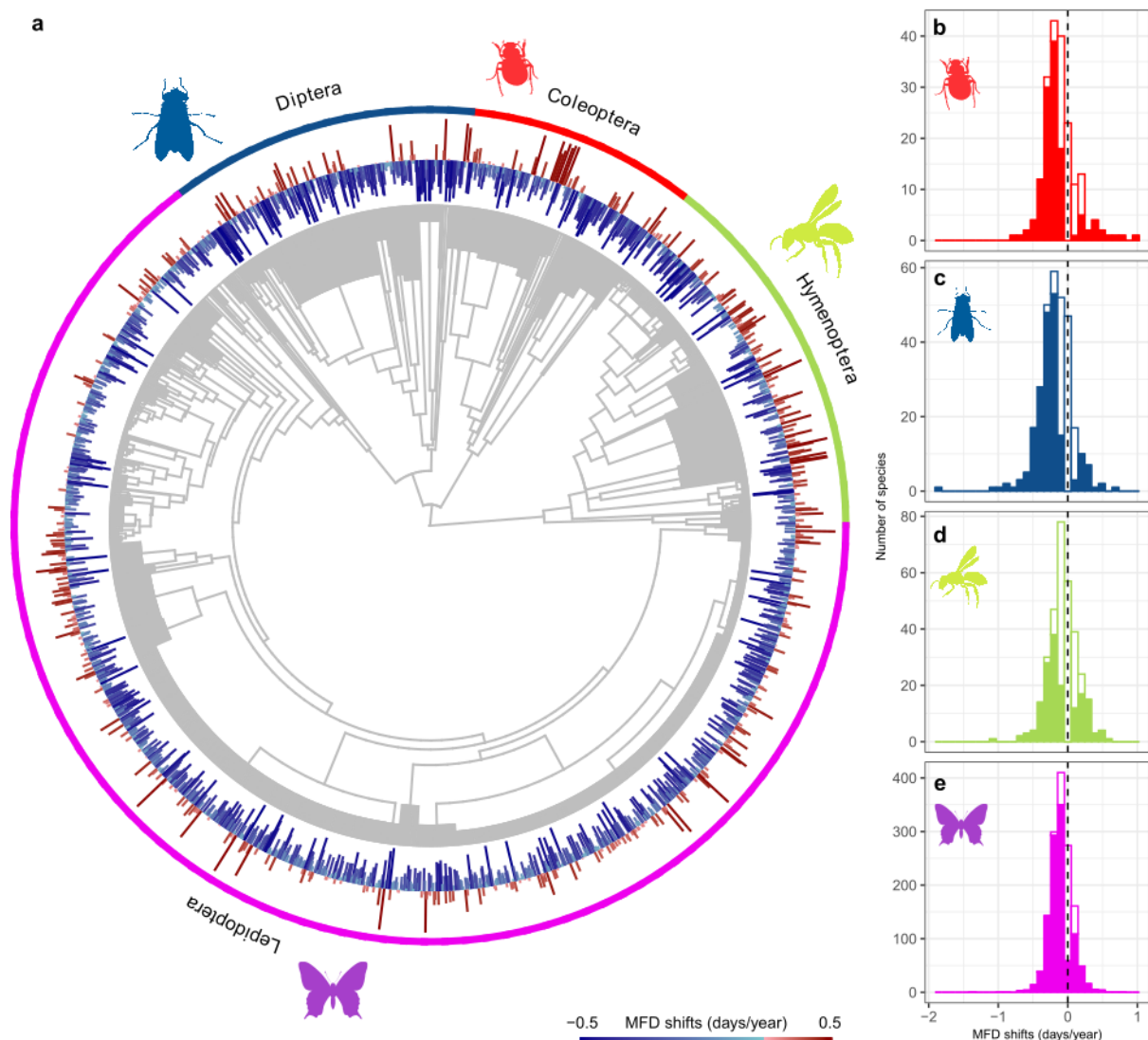
38 By modifying the set of species co-occurring in time, heterogeneity in phenological responses can
39 induce mismatch among interacting species⁴, thereby affecting community structure and related
40 functions. One key issue to our understanding of the impact of climate warming on ecological
41 functions is thus to assess how phenological shifts combine themselves among the species assemblage
42 involved in a given function. This requires to quantify the phenological responses of a large proportion
43 of the species, not only in terms of mean flight date shifts but also of changes in phenology length, a

44 currently overlooked aspect of species responses⁵. The few studies that started to tackle this issue
45 revealed important changes in patterns of species temporal overlap in several local communities of
46 plants and amphibians, as a result of non-uniform phenological shifts^{4,6,7}. However, these studies
47 remain restricted to a small set of functional or taxonomical groups and to a small set of local
48 communities.

49 Pollination is a key ecosystem function^{8,9} mainly performed by four insect orders in Europe:
50 Hymenoptera, Diptera, Lepidoptera and Coleoptera¹⁰. These flower visitors present a continuum of
51 pollination efficiency but the diversity within pollinator assemblage has been proved to increase
52 pollination performance¹¹. Current theoretical knowledge indicates that the level of heterogeneity in
53 phenological responses to climate warming among pollinators can strongly affect pollination
54 networks¹². However, the quantification of the phenological responses of pollinators to climate
55 warming is still limited, with studies focused on butterflies^{13,14} and to a lesser extent, on bees³ and
56 hoverflies¹⁵. A better understanding of the consequences of climate change on pollination thus requires
57 a much more complete assessment of changes in pollinator phenology, including more species and
58 changes in both timing and duration of the seasonal activities.

59 We took advantage of recent developments of large biodiversity databases and museum collections
60 and we compiled a database of over 19 million records of flower visitor occurrences (Supplementary
61 Table 1), spanning the period 1960-2016. This database includes 2023 European species from the 4
62 main insect orders of pollinators: Hymenoptera, Diptera, Lepidoptera and Coleoptera (Extended Data
63 Fig. 1). Numerous species exhibit distinct modes in their phenology, either because they are
64 multivoltine (i.e. multiple generations per year) or because the phenology differs between sexes or
65 social casts. Since different modes from a species can shift in a different direction, we studied each
66 mode separately, leading to 2248 phenology modes (see Methods). For each phenology mode, we
67 estimated changes in mean flight date and flight period length over the years by modeling the mean
68 and variance of collection dates (see Methods). Similarly to previous studies working with historical
69 records³, due to the lack of long-term standardized monitoring for many flower visitor taxa and at
70 large spatial scale, our analysis relies on opportunistic data. However such datasets have been shown

71 to give estimates of phenological shifts quantitatively consistent with those based on standardized
72 monitoring data^{15,16}.



73

74 **Figure 1:** Mean flight date (MFD) shifts of European flower visitors between 1960 and 2016. (a)
75 Phylogeny of studied species and MFD shifts (n=2248). The bars around the phylogeny tips are
76 proportional to the MFD shifts and colored in blue and red for phenological advancement and delay,
77 respectively. Values below -0.5 and above 0.5 days/year are truncated to preserve readability.
78 Histograms show MFD shifts for all studied species of Coleoptera (b, red, n=194), Diptera (c, blue,
79 n=305), Hymenoptera (d, light green, n=322) and Lepidoptera (e, magenta, n=1427). Full bars
80 represent number of species with values significantly distinct from zero whereas open bars correspond
81 to the number of species with a value non-significantly distinct from zero. MFD shifts shown here are
82 predicted for the averaged latitude, longitude and altitude of each species' records.
83

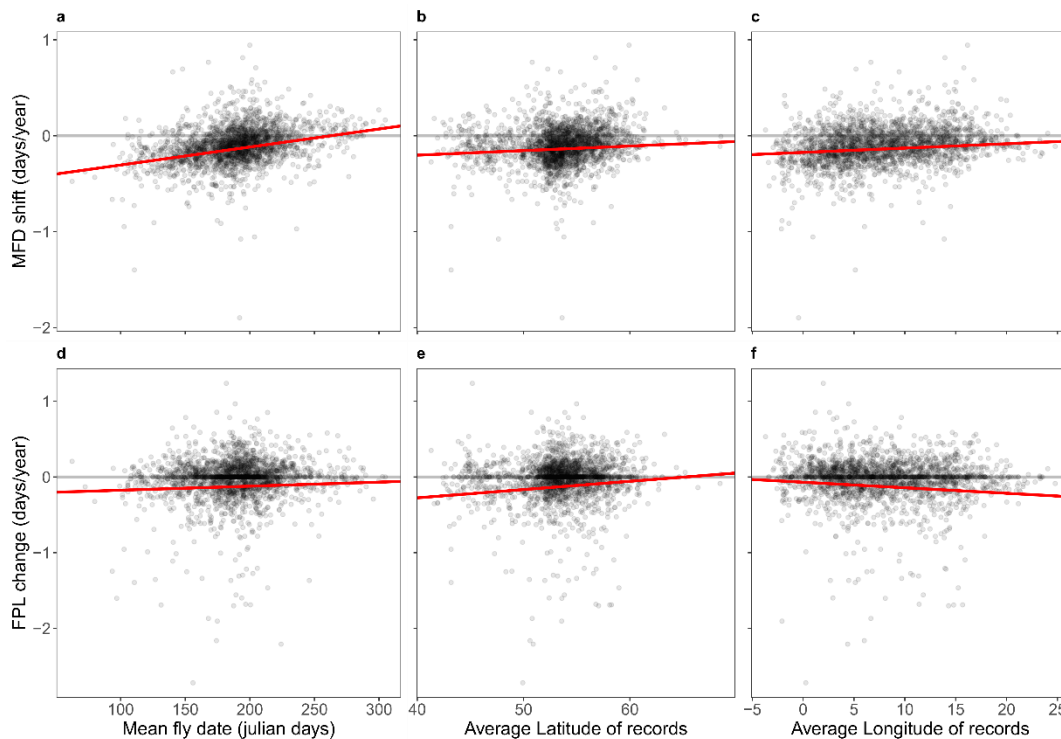
84 **Results**

85 We find that the mean flight date changes on average at a rate of -0.104 ± 0.004 days/year (mean \pm
86 SE) implying that European pollinators are flying on average 5.8 days earlier in 2016 than in 1960, a
87 value consistent with previous estimations on bees³ and butterflies¹³. Climate warming appears as a
88 likely cause as mean flight date shift mainly occurred after 1980, following the temperature increase
89 (Supplementary Method 1, Extended Data Fig. 2). Considering flight period length, we find that on
90 average the standard deviation of collecting dates decreases slightly with time, at a rate of -
91 0.016 ± 0.003 days/year (mean \pm SE), which corresponds to a decrease of 1.8 days of the flight period
92 length over the last 56 years. This reduced flight period length might be due to a reduced genetic
93 variability on phenology caused by a directional selection on phenology advancement. Indeed, we
94 know that a directional selection on a phenotypic trait can reduce the variance of this trait¹⁷, and the
95 significant positive Pearson correlation between the changes over time of mean flight date and flight
96 period length ($r = 0.09$, $t_{df=2246}=3.89$, p-value = $1e-4$) can suggest such a mechanism. However,
97 whether these changes are adaptive or not, and the mechanisms underlying these responses (adaptation
98 vs phenotypic plasticity), remain unknown.

99 Despite these overall trends, we observe a substantial heterogeneity among species in the response
100 of mean flight date and flight period length (Fig. 1, Extended Data Fig. 3). 13% of the phenologies
101 studied exhibit a significantly delayed mean flight date whereas 30% do not exhibit any significant
102 shift (Supplementary Table 2). Such heterogeneity is even more striking for flight period length
103 changes, where 27% of the phenologies studied are significantly lengthened and 43% are unchanged
104 (Supplementary Table 2). If an increase of winter temperature is known to advance species phenology
105 by reducing the development time¹⁸, some species also react in an opposite way^{18,19}, which might
106 explain observed variations in mean flight date shifts. Turning to the heterogeneity in flight period
107 length responses, a temperature increase can either reduce or increase flight period length, for example
108 by reducing insect lifespan²⁰ or by increasing the number of generations within years¹⁴.

109 We further show that this heterogeneity in phenological responses is related to the evolutionary
110 history of species as shown by the strong phylogenetic signal in mean flight date shifts (Pagel's $\lambda =$

111 0.75, p-value < 0.001) and in flight period length changes (Pagel's $\lambda = 0.82$, p-value < 0.001). This
112 phylogenetic signal is related to strong differences among orders in these phenological shifts, Diptera



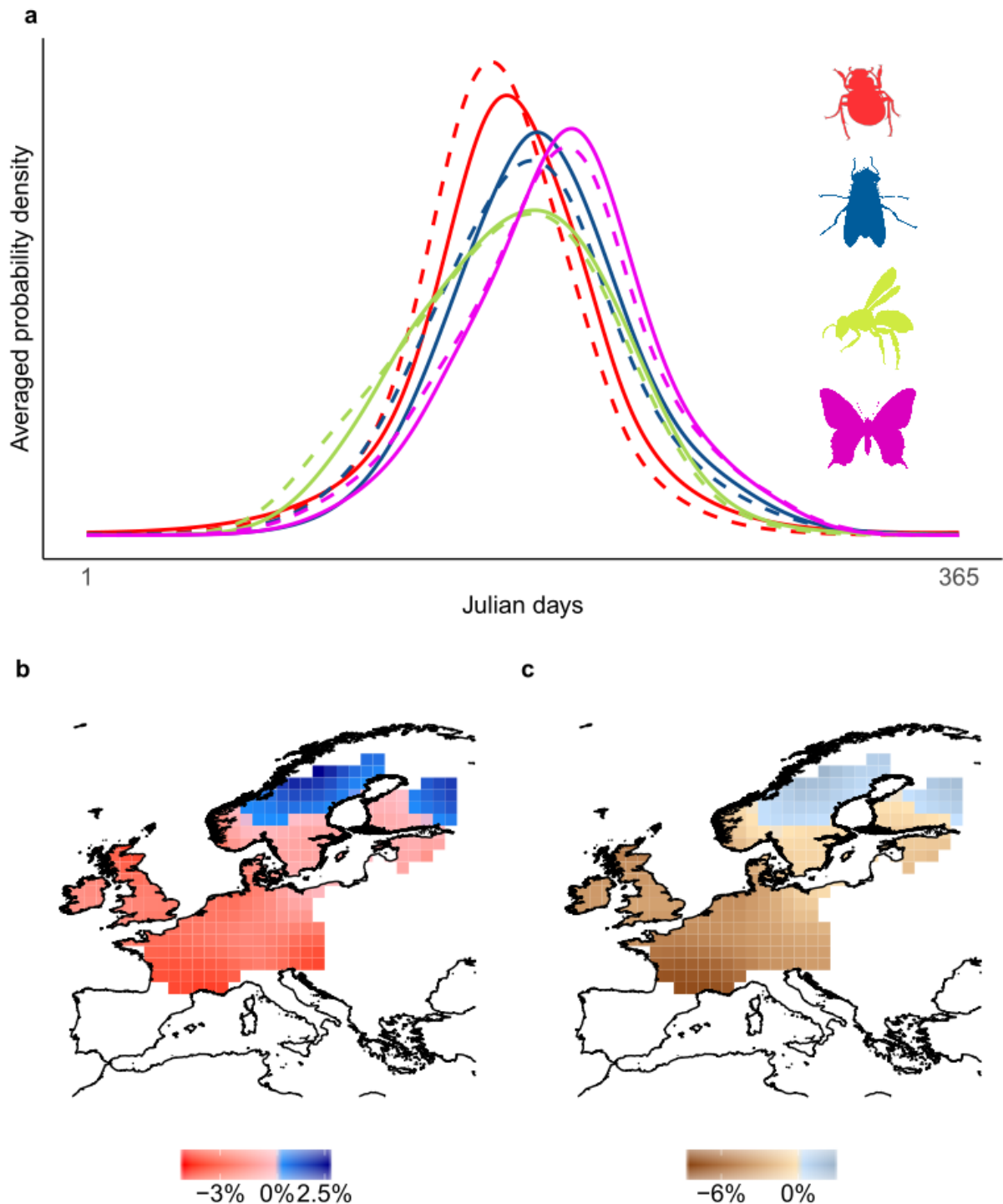
113 and Coleoptera advancing their mean flight date more than Lepidoptera and Hymenoptera while
114 Coleoptera decrease their flight period length more than other orders (Supplementary Table 3).
115 However the phylogenetic signal remains significant within orders for mean flight date shifts
116 (Supplementary Table 3). Such phylogenetic signal indicates that species traits underlying
117 phenological responses are conserved across the phylogeny.

118
119 **Figure 2:** Spatial and seasonal heterogeneity in phenological shifts among species. Mean flight date
120 (MFD) shifts (top panels) and changes in flight period length (FPL, bottom panels) against species
121 MFD (a, d) and averaged latitude (b, e) and longitude (c, f) of species records. The horizontal grey
122 lines show the 0 value whereas red lines are PGLS predictions. Estimates and standard errors are
123 shown in Supplementary Table 4.
124

125 Mean flight date and flight period length responses also demonstrate spatial and seasonal
126 heterogeneity among species. Species with southern and western distribution areas show a stronger
127 mean flight date advancement than species with northern and eastern distribution areas (Fig. 2b-c,
128 Supplementary Table 4), matching previous results on European plants². We also find that species
129 with northern and western distribution areas experience a smaller decrease in flight period length than

130 species with southern and eastern distribution areas (Fig. 2e-f, Supplementary Table 4). In addition we
131 find a seasonal pattern where spring species experience a significantly greater advancement than
132 summer/autumn species (Fig. 2a), consistently with previous results on American bees³ and European
133 plants². Regarding flight period length, we find that earlier species shorten their flight period more
134 than later species (Fig. 2a-2d, Supplementary Table 4). Such differences could be explained by the fact
135 that summer/autumn and northern species might rely more on photoperiod, a determining factor of
136 insect phenology²¹, than spring and southern species. Such patterns have been shown for plants^{22,23},
137 but studies on this point for insects are missing.

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



147 **Figure 3:** Changes in within- and among-orders average overlaps in phenology between 1980 and
 148 2016 across Europe. (a) Average phenology over all species in 1980 (solid lines) and in 2016 (dashed
 149 lines) for one grid cell (centroid = 55,0) by orders: Coleoptera (red), Diptera (blue), Hymenoptera
 150 (light green) and Lepidoptera (magenta). The average phenology is calculated by averaging all
 151 probability density functions (Gaussians representing phenologies) over all species of each orders,
 152 assuming identical species abundances. Observed changes in the average overlap among phenologies
 153 between 1980 and 2016, within orders (b) and among orders (c). Uncolored cells are under-
 154 prospected. Number of species by order across Europe is shown in Extended Data Fig. 6.
 155

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

164 First, we show that species co-occurrence in time increases towards the beginning the season and
165 then abruptly decreases in the second half of the season (Extended Data Fig. 5), consistently with the
166 average advancement of pollinator mean flight date. This indicates that the advance of mean flight
167 dates have likely shifted the pollination function and services earlier in the season. Secondly, assuming
168 no changes in abundance/distribution of species, we show that both within- and among-orders average
169 overlaps in phenology have decreased within the last 36 years in most parts of Europe, except in the
170 extreme northern part (Fig. 3b-c. The observed increase of the overlap among phenologies in the
171 northern Europe is likely due to the fact that there, in contrast to other regions, the average mean flight
172 date shift is almost null whereas the flight period length slightly increases (Fig. 2). Sufficient data on
173 long-term dynamics of plant-pollinator networks is currently missing to fully assess the consequences
174 of such changes in the seasonal structure of pollinator assemblages on pollination function. However,
175 the within order and among order overlaps should be related to temporal redundancy and
176 complementarity within pollinator assemblages, respectively. Indeed, the pervasive phylogenetic
177 signal within pollination networks indicates that related pollinators tend to visit the same plants^{24,25}.
178 This implies that species with overlapping phenologies and belonging to the same insect order should
179 visit the same set of co-flowering plant species and as such, belong to the same pollinator functional
180 group. On the contrary, species with overlapping phenologies but from different insect orders are
181 expected to provide complementary pollination function, by visiting different sets of co-flowering
182 plant species.

183 As such, the observed decrease in the overlap within insect orders, by lowering the temporal
184 redundancy among pollinators, might decrease the robustness of plant-pollinator interaction networks
185 to pollinator extinction²⁶. A decrease in the overlap may also have beneficial effects for pollinators by
186 decreasing competition for nectar and pollen resources, but such competition release might in turn
187 restrict pollinator visits to the most profitable plant species following optimal foraging theory
188 predictions²⁷. Turning to the observed decrease in phenology overlap among pollinator orders, it
189 suggests a decrease in temporal complementarity within pollinator assemblages, thereby weakening
190 the pollination function delivered to plant communities²⁸. This result echoes theoretical findings on
191 pollination networks showing that the more phenologies are scattered over the season, the more
192 community diversity decreases²⁹.

193 **Discussion**

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

207 Climate warming is recognized as a major threat to biodiversity. Our results suggest that climate
208 warming, by reducing pollinator co-occurrence in time within seasons has had negative effect on the
209 delivery of pollination function as well as on its resistance to further perturbations, in most part of

210 Europe. Such findings raise the question of potential interactive effects between climate warming and
211 other pressures related to global change such as agricultural intensification^{30,31}, which could amplify
212 expected negative effects on pollination. In addition to its effect on species phenology, climate
213 warming is expected to affect the spatial distribution³² and the abundance³¹ of flower visitors, and so
214 are other drivers of global change. How such effects combine with those observed in this study remain
215 currently unknown. This stresses the need to explore multiple responses of species to multiple drivers
216 of global change in order to assess potential synergistic effects among species responses to global
217 change drivers over large scale.

218 **Material and Methods**

219 **Constructing the database on flower visitor phenologies**

220 *Assembling data on flower visitor occurrences in time and space*

221 European flower visitors mainly belong to four insect orders – Coleoptera, Diptera, Hymenoptera
222 and Lepidoptera¹⁰. We first looked for occurrence data (i.e. sighting at a given date and location) of
223 species that belong to these insect orders and that are defined as floricolous in scientific or grey
224 literature. We restricted our search to European species listed in Fauna Europaea³³. Data are from 15
225 distinctive sources, summarized in the Supplementary Table 1, with a high proportion from the Global
226 Biodiversity Information Facility (GBIF). After the removal of duplicates (same species, date and
227 locality), the database initially included about 30 million of occurrences between 34° and 72° of
228 latitude North and between -15° and 32° of longitude.

229 *Modelling multimodal phenologies and removing larval records*

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

239 The first step of the method was to detect multimodality. Since phenologies vary spatially,
240 multimodality can be the product of sampling in different localities. In order to take this spatial
241 variation into account, for each species separately, we fitted the following linear mixed-effects model
242 accounting for spatial variables on the Julian day of records.

243
$$Y_{ik} = \mu + \rho_1 \times latitude_k + \tau \times longitude_k + \theta \times altitude_k + \varphi_i + E_{ik} \quad (1)$$

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

257 The second step of the method was to attribute each record to a specific mode. To do so we used
258 clustering Gaussian mixture-models implemented in the *mclust* R package³⁴, considering a number of
259 gaussians in 1 to *nbmax*. This clustering model allow us to initialize the attribution of each record to a
260 given mode. Using the classification given by these clustering models, we run linear mixed-effects
261 models, similar to the one described in equation (1) but with the addition of a mode effect (β_j):

$$262 \quad Y_{ijk} = \mu + \rho_1 \times latitude_k + \tau \times longitude_k + \theta \times altitude_k + \beta_j + \varphi_i + E_{ijk} \quad (2)$$

263 We kept the number of modes that minimize the Bayesian Information Criterion (BIC) of this linear
264 mixed-effects model. We then manually changed the mode of poorly predicted points. If the change
265 improved the likelihood of this mixed-effects model we retained it and continued this process
266 iteratively. We stopped the process when changing the mode of poorly predicted points did not further
267 improve the likelihood of the model. The R script of the full method is available here:
268 <https://github.com/f-duchenne/Flower-visitors-phenology>. Although the mode effect (β_j) is
269 independent from spatial variables and altitude in equation (2), our method still allows to take into
270 account spatial and altitudinal variation in the number of modes (Extended Data Fig. 7). We

271 confronted the relevance of detected modes regarding what we know on the biology of species. We
272 found that our method distribute records among modes in a highly consistent way. Some examples can
273 be seen in Extended Data Fig. 7. We identified 19 species for which we had a mode corresponding to
274 larval phenology, and we removed the corresponding records. Overall, this analysis lead to 2473
275 unimodal phenologies from 2179 species.

276 *Database after selection process*

277 Following the separation of distinct phenological modes for each species and the removal of larval
278 records, we selected phenologies (or phenological modes) with at least 400 records during the period
279 1960-2016 and with at least 40 records from the period 1960-1980, to be able to study phenological
280 shifts between early and more recent period. We removed species (n=30) with phenology peaking
281 during winter by excluding species with a mean flight date before 60 or after 306 Julian days.
282 Studying the phenology of such species raises methodological questions that we will not address here.
283 We also removed records with imprecise localization (above 1km²) except for small countries
284 (Luxembourg, Belgium, Switzerland, Netherlands, Denmark, Lichtenstein, Monaco, Andorra and
285 Kosovo). Thus, our dataset includes some records with imprecise localization (above 1km²) but they
286 represent less than 0.1% of the final dataset. This selection process lead to 19 845 792 occurrence
287 records with 2248 phenologies for 2023 species (Supplementary Table 1). The repartition of records
288 among insect orders and throughout the study period is presented in Extended Data Fig. 1.
289 Supplementary Table 1 indicates the amount of data coming from the various data sources.

290 **Analyses of species phenological shifts over time**

291 *Estimating species phenological shifts*

292 To estimate changes in both the mean flight date (MFD) and the flight period length (FPL), we
293 modeled jointly the mean and the variance of collection dates using the *dispmo* R package³⁵ which
294 performs two nested linear models, one for the mean and one for the variance. Due to computational
295 limits it was not possible to use one model including the whole dataset, modelling both, MFD shifts
296 and FPL changes, and modelling spatial effects properly for each species. Thus, we studied each

297 species and phenology mode separately. For each phenology modes, the model for the mean collection
298 date was:

$$\begin{aligned} 299 \quad Y_k = & \mu + (\pi + \alpha \times \textit{latitude}_k + \delta \times \textit{longitude}_k) \times \textit{year}_k + (\rho_1 + \gamma_1 \times \textit{longitude}_k) \times \textit{latitude}_k + \\ 300 \quad & (\rho_2 + \gamma_2 \times \textit{longitude}_k^2) \times \textit{latitude}_k^2 + (\rho_3 + \gamma_3 \times \textit{longitude}_k^3) \times \textit{latitude}_k^3 + \tau_1 \times \\ 301 \quad & \textit{longitude}_k + \tau_2 \times \textit{longitude}_k^2 + \tau_3 \times \textit{longitude}_k^3 + \theta \times \textit{altitude}_k + E_k \quad (3) \end{aligned}$$

302 Y_k is the Julian day of the observation k , μ is the grand mean (intercept), π is the time effect on the
303 mean collection date as well as on its variation across latitude (α) and longitude (δ). ρ_1, ρ_2, ρ_3 and
304 τ_1, τ_2, τ_3 are linear, quadratic and cubic effects for latitude and longitude, respectively, $\gamma_1, \gamma_2, \gamma_3$ are
305 spatial interactions terms, θ is an altitude effect and E_k is the error terms (independent and identically
306 distributed, following $N(0, \sigma^2)$).

307 The joint model for variance of collection date was:

$$308 \quad \log(\sigma^2) = \mu_v + \rho_v \times \textit{latitude}_k + \tau_v \times \textit{longitude}_k + \theta_v \times \textit{altitude}_k + \pi_v \times \textit{year}_k \quad (4)$$

309 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,
310 longitude, altitude and year effects respectively. We performed model simplification based on the
311 Akaike Information Criterion (AIC), first on the model for the mean collection date, removing only
312 polynomials effect of latitude and longitude ($\gamma_1, \gamma_2, \gamma_3, \rho_2, \rho_3, \tau_2, \tau_3$) and interactions between spatial
313 variables and time effect (α and δ), and second on the model for the variance in collection date.

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

317 *Phylogenetic analysis*

318 In order to get a phylogeny of all the studied species we combined several published phylogenies.
319 We used the phylogeny from Rainford et al.³⁶ as the backbone to which we added some available and
320 recent phylogenies to get a phylogeny at the genus level for Papilionoidea³⁷, Vespidae³⁸ and
321 Apoidea³⁹. For all other families, genus (as defined by the GBIF taxonomy) were inserted on a

322 polytomy positioned midway between the family origin and the tip. Then species from each genus
323 were placed on a polytomy positioned midway between the genus origin and the tip. Such method
324 does not allow a good estimation of the recent evolutionary history but because there is no phylogeny
325 of insects at the species or genus level, it is the only way to include all species responses and take in
326 account for intra-family heterogeneity. Moreover, because these polytomies were not too old relative
327 to the entire phylogeny, it should not affect strongly our results. Because they are not present in our
328 phylogeny three families of Diptera (Heleomyzidae, Limoniidae and Pediciidae) and two Lepidoptera
329 species (*Sphrageidus similis*, Lymantriidae, and *Agria desoptilete*, Lycaenidae) were excluded from
330 phylogenetic analysis.

331 We estimated phylogenetic signal in phenological shifts using Pagel's λ ⁴⁰ implemented in the
332 *phylosignal* R package⁴¹, because it is much more robust to polytomies than Blomberg's K ⁴².

333 *Links between phenological traits and phenological shifts*

334 To test if the seasonal precocity and the spatial distribution of species were linked to phenological
335 shifts, we used the following phylogenetic generalized least squares model (PGLS) implemented in the
336 *caper* R package⁴³ controlling for the Pagel's lambda of the residuals at the maximum likelihood:

$$337 \quad PS_z = \mu + (\alpha) \times MFD_z + (\beta) \times latitude_z + (\delta) \times longitude_z + E_z \quad (5)$$

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

342 **Analyses of the seasonal structure of pollinator assemblages**

343 *Predicting species phenology in different locations and years*

344 To assess the effect of phenological shifts at the scale of the full pollinator assemblages, we
345 calculated changes in the overlap among phenologies. Because phenological shifts depend on location,
346 we discretized the studied area in cells of $5^\circ \times 5^\circ$. This size was chosen in order to smooth the
347 differences in sampling effort among localities. To ensure a representative pollinator assemblage, we

348 only included grid cells with at least 3 insect orders with 20 species with at least 30 records each. The
349 remaining cells were considered as under-prospected. Thus species are considered present in a grid-
350 cell if it has at least 30 records between 1960 and 2016. By doing so, we assume that the composition
351 of species assemblages are the same in 1980 and in 2016, which allows to study only the effect of
352 phenological shifts on seasonal structure. We considered that all species have the same abundance, and
353 a circular Gaussian phenology. We used wrapped circular normal distributions instead of a classical
354 Gaussian distribution in order to take phenologies that span winter into account. We estimated the
355 mean and the standard deviation of these Gaussians for the years 1980 and 2016 and for each grid cell,
356 using the predictions of the linear models used to estimate phenological shifts, described in equations
357 (3) and (4).

358 *Calculation of phenological overlaps within assemblages*

359 For each sufficiently prospected grid cell we calculated pairwise overlap among pollinator
360 phenologies present in the given grid cell. We considered that all species have the same abundance,
361 and a circular Gaussian phenology. The overlap between two phenologies is the integral of the
362 minimum of both gaussians. We calculated two overlap measures for each grid cell: the first one
363 focusing on the overlap within insect orders and the other one among insect orders. To give equal
364 weight to each insect order, and thus avoid over-representation of Lepidoptera, we first calculated the
365 mean overlap by insect order, or by pair of insect orders, respectively for the overlap within and
366 among orders. Second, we averaged these mean values per grid cell. Finally, in order to have more
367 robust values, we repeated this overlap calculation after shifting segmentation of the latitude and the
368 longitude by 1.25° , 2.5° and by 3.75° . Then we averaged values obtained by $1.25^\circ \times 1.25^\circ$ grid cells for
369 both measures, overlap within and among orders.

370 In order to study the seasonal dynamic of overlap changes, we calculated a proxy of the
371 phenological overlaps day by day in 1980 and in 2016 for each grid cell (Extended Data Fig. 5). We
372 do not use exactly the same calculation of overlap as previously for computational reasons. To
373 simplify the calculation method, we aggregated predicted phenologies at the order level to get a
374 density distribution by order, henceforth called order phenologies, as presented in Fig. 3a. Then we

375 calculated the pairwise overlap among order phenologies day by day for both years, 1980 and 2016,
376 and for each grid cell. We also evaluated the day-by-day density value for each order phenologies for
377 both years, 1980 and 2016, and for each grid cell. This density value is a proxy of the phenological
378 overlap within order, because we assume that every species has the same constant abundance. Then we
379 calculate the daily changes of these both indexes between 1980 and 2016 (Extended Data Fig. 5). We
380 did so for one grid pattern only (i.e. without sliding windows).

381 **Authors contribution**

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

386 **Data availability**

387 The final dataset analyzed in this paper is available here: <https://zenodo.org/record/3480120>.

388 **Code availability**

389 Codes used to extract data from the GBIF, to separate modes of multimodal phenologies and to
390 estimate phenological shifts are available here: <https://github.com/f-duchenne/Flower-visitors-phenology>.
391

392 **Competing interests**

393 The authors declare no competing interests.

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