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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 warming<sup>1</sup>. Despite this general trend, a substantial  
33 inter-specific variation is observed in these responses, spatially<sup>2</sup> (e.g. across latitudes), and  
34 temporally<sup>2,3</sup> (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 groups<sup>1</sup> challenges our ability  
36 to assess the consequences of phenological shifts for the functioning of communities and ecosystems  
37 across large spatial scales.

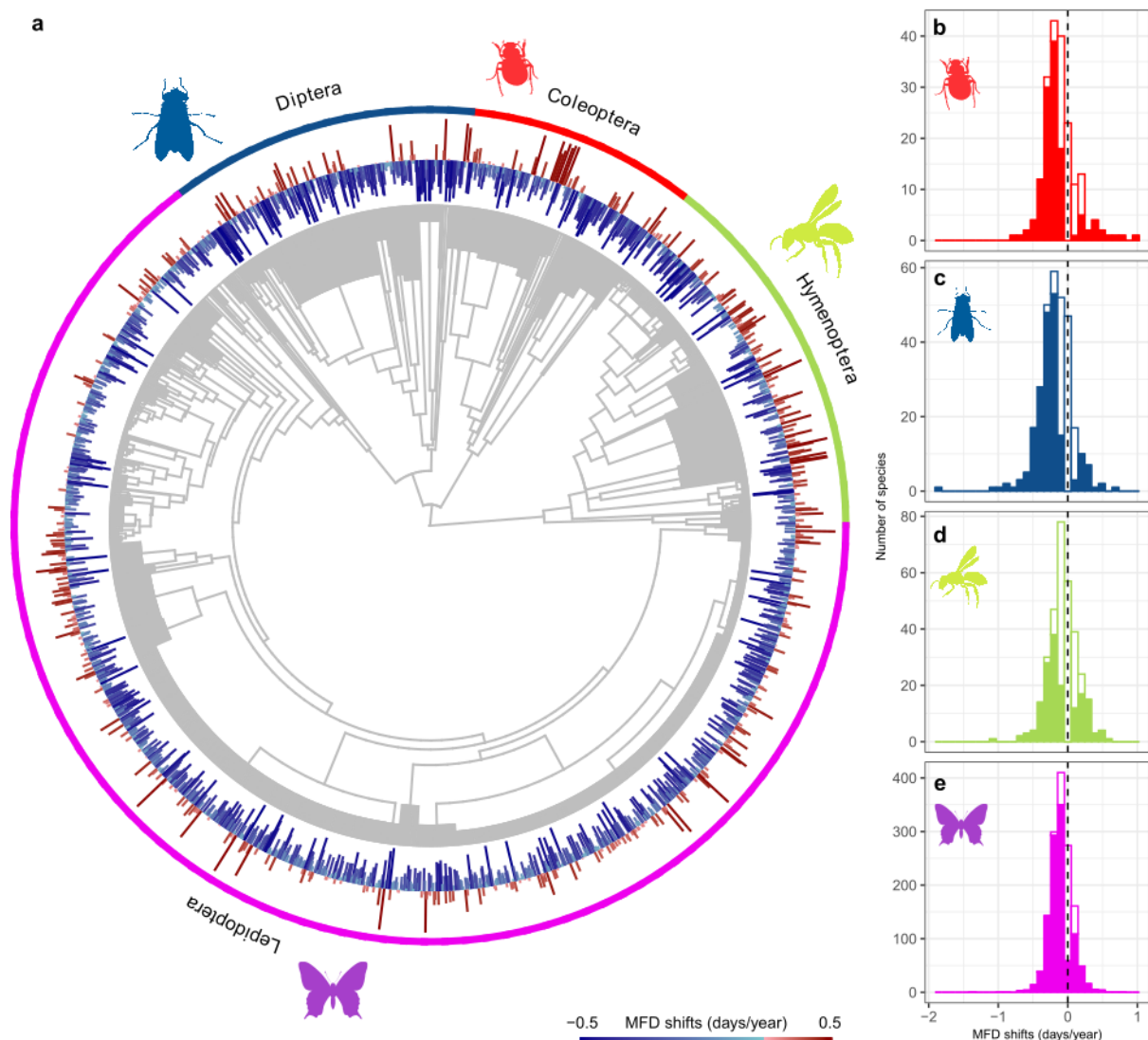
38 By modifying the set of species co-occurring in time, heterogeneity in phenological responses can  
39 induce mismatch among interacting species<sup>4</sup>, thereby affecting community structure and related  
40 functions. One key issue to our understanding of the impact of climate warming on ecological  
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 responses<sup>5</sup>. 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<sup>4,6,7</sup>. 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<sup>8,9</sup> mainly performed by four insect orders in Europe:  
50 Hymenoptera, Diptera, Lepidoptera and Coleoptera<sup>10</sup>. These flower visitors present a continuum of  
51 pollination efficiency but the diversity within pollinator assemblage has been proved to increase  
52 pollination performance<sup>11</sup>. Current theoretical knowledge indicates that the level of heterogeneity in  
53 phenological responses to climate warming among pollinators can strongly affect pollination  
54 networks<sup>12</sup>. However, the quantification of the phenological responses of pollinators to climate  
55 warming is still limited, with studies focused on butterflies<sup>13,14</sup> and to a lesser extent, on bees<sup>3</sup> and  
56 hoverflies<sup>15</sup>. 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 records<sup>3</sup>, 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<sup>15,16</sup>.



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

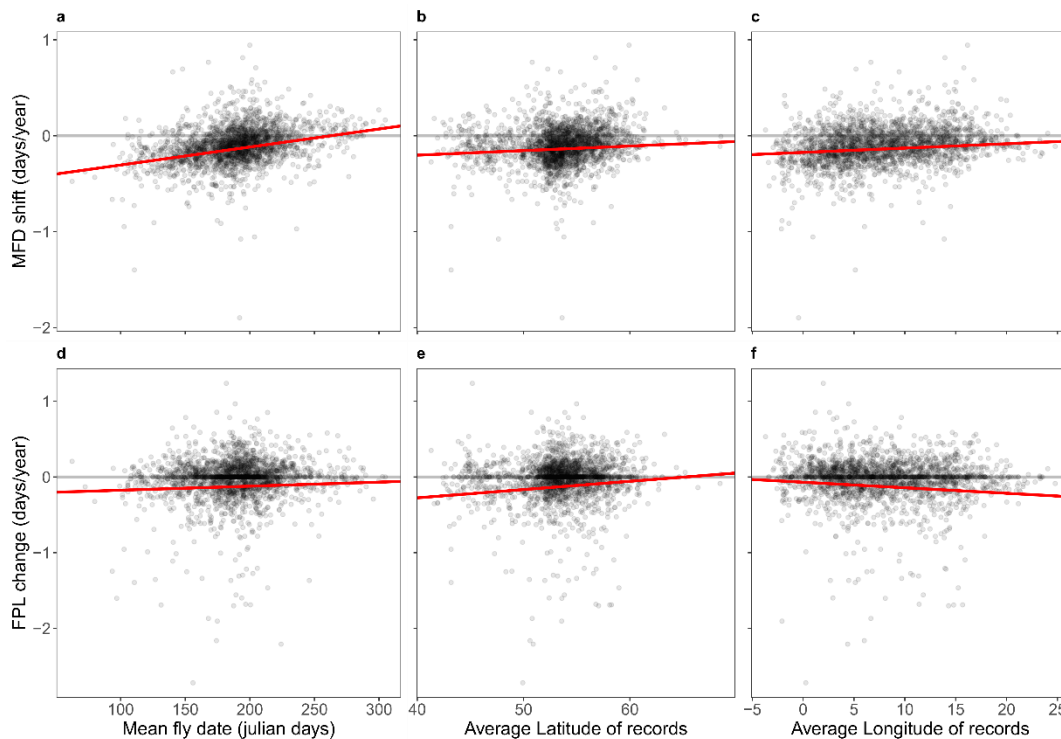
## 84 **Results**

85 We find that the mean flight date changes on average at a rate of  $-0.104 \pm 0.004$  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 bees<sup>3</sup> and butterflies<sup>13</sup>. 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  $0.016 \pm 0.003$  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 trait<sup>17</sup>, 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 time<sup>18</sup>, some species also react in an opposite way<sup>18,19</sup>, 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 lifespan<sup>20</sup> or by increasing the number of generations within years<sup>14</sup>.

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.

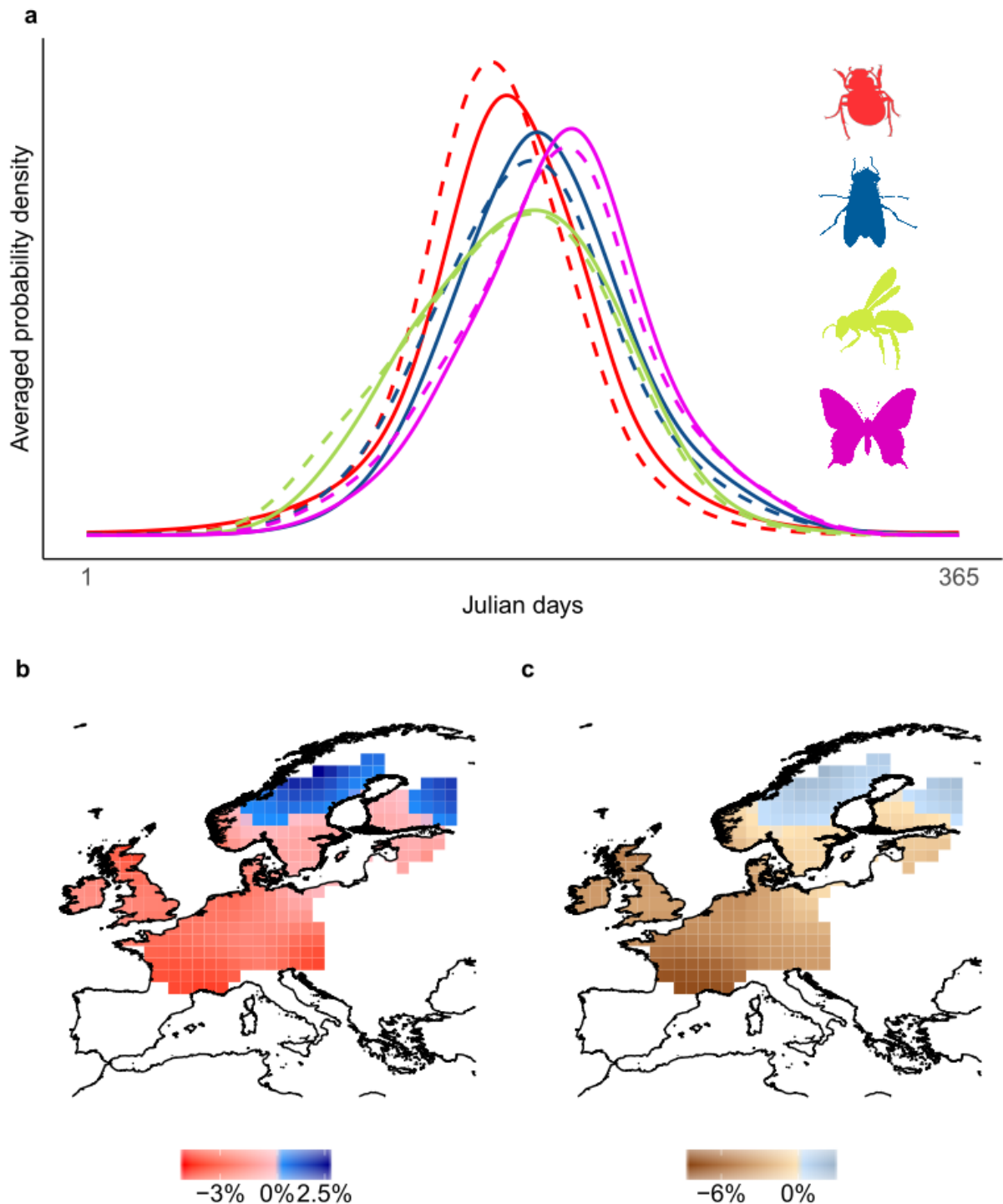
118  
119 **Figure 2:** Spatial and seasonal heterogeneity in phenological shifts among species. Mean flight date  
120 (MFD) shifts (top panels) and changes in flight period length (FPL, bottom panels) against species  
121 MFD (a, d) and averaged latitude (b, e) and longitude (c, f) of species records. 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 plants<sup>2</sup>. 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 bees<sup>3</sup> and European  
133 plants<sup>2</sup>. 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 phenology<sup>21</sup>, than spring and southern species. Such patterns have been shown for plants<sup>22,23</sup>,  
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<sup>24,25</sup>.  
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 extinction<sup>26</sup>. 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 predictions<sup>27</sup>. 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 communities<sup>28</sup>. This result echoes theoretical findings on  
191 pollination networks showing that the more phenologies are scattered over the season, the more  
192 community diversity decreases<sup>29</sup>.

## 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<sup>30,31</sup>, 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 distribution<sup>32</sup> and the abundance<sup>31</sup> 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 Lepidoptera<sup>10</sup>. 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 Europaea<sup>33</sup>. 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  $i$ ,  $\mu$  is the grand mean (intercept),  $\rho_1$   
245 and  $\tau_1$  are latitude and longitude effects respectively, while  $\theta$  is an altitude effect.  $\varphi_i$  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 package<sup>34</sup>, 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 ( $\beta_j$ ):

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

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 ( $\beta_j$ ) 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 1km<sup>2</sup>) 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 1km<sup>2</sup>) 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 *dispmod* R package<sup>35</sup> 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  $k$ ,  $\mu$  is the grand mean (intercept),  $\pi$  is the time effect on the  
303 mean collection date as well as on its variation across latitude ( $\alpha$ ) and longitude ( $\delta$ ).  $\rho_1, \rho_2, \rho_3$  and  
304  $\tau_1, \tau_2, \tau_3$  are linear, quadratic and cubic effects for latitude and longitude, respectively,  $\gamma_1, \gamma_2, \gamma_3$  are  
305 spatial interactions terms,  $\theta$  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  $\sigma^2$  is the variance of the collection date,  $\mu_v$  is a constant term,  $\rho_v, \tau_v, \theta_v$  and  $\pi_v$  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 ( $\alpha$  and  $\delta$ ), 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  $\pi_v$  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.<sup>36</sup> as the backbone to which we added some available and  
320 recent phylogenies to get a phylogeny at the genus level for Papilionoideae<sup>37</sup>, Vespidae<sup>38</sup> and  
321 Apoidea<sup>39</sup>. 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  $\lambda$ <sup>40</sup> implemented in the  
332 *phylosignal* R package<sup>41</sup>, because it is much more robust to polytomies than Blomberg's  $K$ <sup>42</sup>.

### 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 package<sup>43</sup> 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  $z$ ,  $\mu$  is the grand  
339 mean (intercept),  $\alpha$  is the effect of the mean flight date calculated with recent records (from 2000),  $\beta$   
340 is the effect of the average latitude of records,  $\rho$  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-prospectored. 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 prospectored 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  $1.25^\circ$ ,  $2.5^\circ$  and by  $3.75^\circ$ . 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 [phenology](https://github.com/f-duchenne/Flower-visitors-phenology).

### 392 **Competing interests**

393 The authors declare no competing interests.

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