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1 Increase in the thermal preference of plant communities related to climate change

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ABSTRACT

Latitudinal and altitudinal range shifts in response to climate change have been reported for numerous animal species, especially those with high dispersal capacities. In plants, the impact of climate change on species distribution or community composition has been documented mainly over long periods (decades) and in specific habitats, often forests. Here, we studied the change in thermal preferences of temperate flora in different habitats in France over a short period (2009-2017), using data from a standardized participatory monitoring scheme. We report a fast increase in the thermal preference of plant communities, both at national and regional scale, which we relate to climate change. This change in thermal preference mainly resulted from increased abundance of annual, warm-adapted species. Our results suggest that plant communities could have been modified rapidly under climate change. Whether such changes are sufficient to cope with the current climate warming remains to be ascertained.

KEYWORDS

Plants, monitoring, thermal preference, climate change, life span, citizen science.

INTRODUCTION

Climate change is considered a significant global threat to biodiversity [1–3], with impacts on biodiversity from individuals to ecosystems. In ecological communities, climate change drives compositional changes, in particular via latitudinal and altitudinal shifts, especially in species with high dispersal capacities, including birds, insects or marine invertebrates [3–5]. In less mobile species, such as plants, elevation has shifted upward during the 20th century in highland French temperate forests [6], although not as fast as temperatures. In contrast, lowland forests plant communities have not shifted northward, highlighting a higher inertia of the latter [7]. Whether and how plant communities are able to track climate changes in all habitat types is still unclear.

Most studies demonstrating an effect of climate change on plant communities used heterogeneous data collected over decades and focused on a particular habitat, owing to the scarcity of available data. To improve our understanding of how climate change and other drivers could influence biodiversity, real-time monitoring data on the basis of highly standardized schemes are required across large spatio-temporal scales [8]. Citizen science, defined as the involvement of volunteers in research [9], represents a powerful tool that can contribute to investigating the impacts of climate change on biodiversity [4,10]. Such monitoring makes it possible to report subtle changes in biological studies of climate change, including analyses of phenology, from populations to communities.

In this study, we examine nine years of change in plant community composition in a variety of habitats across France, using data collected through a participatory monitoring scheme, to assess whether such data can be used to detect short-term effects of climate warming. We address the following questions: (1) has the average thermal preference of plants changed over the past nine years? (2) Can this change be related to climatic variables? (3) What are the species most responsible for this change?

MATERIALS AND METHODS

Monitoring data

We used data from Vigie-flore, a French citizen science program monitoring wild flora and having involved a total of 321 skilled amateur botanists. The data were collected yearly between 2009 and 2017 in 586 1kmx1km squares sampled from a systematic grid (one square every 10 km), which ensures representative sampling of habitats types. Each square contains eight systematically distributed 10m² plots (Figure S1), each divided into ten 1m²-quadrats. In each plot, the presence of all vascular plants was recorded in each quadrat, as well as habitat type following the CORINE biotope nomenclature [11], a European hierarchical classification of vegetation types. For each plot, the number of quadrats in which a species was observed provides a proxy for species abundance. On average there were 2.9 years of observation per plot, and 5.3 plots sampled per 1 km² square (hence a total of 3,118 plots).

Species characteristics

We collected information for two species-specific attributes most likely to be related to climate change: (1) the Ellenberg temperature indicator value (hereafter ETIV), characterizing the optimum temperature class for growth and survival of a species (nine classes), and (2) life span (Electronic Supplementary Material I and Table S1). ETIV and life span were available for 1,709 and 1,780 of the 2,428 species sampled, respectively, representing 83.6% and 89.3% of total observations. We calculated the community-weighted Mean Temperature Preference (hereafter MTP), i.e. the abundance-weighted sum of ETIV of all species [12]. We also calculated the same index with presence/absence data instead of abundance, to test whether temporal trends could be detected with lower resolution data [13]. Finally, we calculated the MTP within two extreme life span classes: annuals vs. perennials. The survey sites are not distributed homogeneously in space and time, which may cause spurious temporal trends in

MTP due to a spatial displacement of sampled sites. To control for this, we performed the same analysis at a regional level, in Île-de-France region, the region with the highest density of sites (188 squares sampled throughout the nine years, Figure S1).

Climate data

We used a random forest analysis to extract the most important climatic variable explaining MTP, which was mean annual temperature (Electronic Supplementary Material II and Table S2).

Statistical analyses

We performed Bayesian hierarchical models to estimate the temporal trend in MTP (1) at a national scale and within Île-de-France, (2) using either abundance data or presence/absence data and (3) of annuals vs. perennials species (Electronic Supplementary Material III). We then examined the relationship between the 2009-2017 change in MTP in a plot and the temporal change in mean annual temperature, using Spearman's correlation coefficients. To identify which species drove the community-level trends, we used Bayesian models to estimate the temporal trend in abundance for the 550 most common species (75 annuals and 349 perennials) that were observed at least four out of nine years and in at least ten squares (Electronic Supplementary Material III). We tested whether species trends were related to life-span (annual and perennial plants), to ETIV, or to the interaction of both variables by a linear regression in which each species was weighted by the inverse of the standard error associated with the estimated temporal trend. All analyses were performed using R version 3.2.4 [14] (Electronic Supplementary Material IV).

RESULTS

At the community level, MTP increased through time at the national scale, both with abundance and presence/absence data (Figure 1a,c). This increase was also observed within Île-de-France (Figure 1c and S2). At the national scale, the temporal trend was significantly larger in northern vs. southern France (not shown). The increase in MTP of plant communities occurred simultaneously with an increase in mean annual temperature (Electronic Supplementary Material II, Table S3, Figure S3), such that there was a significant positive but weak correlation between MTP change and the mean annual temperature change over time (Figure 1d): plots in which the temperature has increased tended to be also plots for which MTP has increased. Moreover, we found a significant increase in MTP of annual, but not of perennial species, at national and regional scales (Figure 1b,c).

Changes at the community level were explained by differences in temporal trends among species. We found a significant positive relationship between species temporal trends and life span (Estimate=0.194, $n=424$, $df=1.402$, $F=3.978$, $P=0.047$, Figure 2a,b). The interaction between ETIV and life span was close to significance (Estimate=-0.028, $n=424$, $df=1.402$, $F=3.013$, $P=0.083$), but no relation was found between temporal trends and ETIV.

DISCUSSION

Our work complements longer-term, single habitat studies by documenting a small but steady increase in MTP over all habitat types at national and regional scales, detectable over nine years only, most likely driven by temperature change. This increase is measurable even with presence/absence data, suggesting a true reshuffling of plant communities, as opposed to mere abundance fluctuations of common species. In contrast to Bertrand and collaborators [7], who observed no response of lowland forest plant communities to climate change on a longer period, we show with a dataset encompassing mostly low-altitude sites that lowland plant

communities can be modified by climate change, despite their limited dispersal capabilities. The difference may arise because our dataset contained a high proportion of open habitats, in which plant communities may experience higher turnover than in forests. MTP changes appear to be driven chiefly by changes in occurrence or abundance of annuals, with rapid life cycles, as revealed by the examination of the temporal trends of the 550 most common species (79 % of observations). The general pattern of a decline of cold-adapted species and a relative stability, or increase, of warm-adapted species is consistent with longer-term studies documenting responses to climate change via species latitudinal and altitudinal range shifts, or local changes in abundance (including local decline and extinction of cold-adapted species), particularly in European and North American temperate forests [6,7,15–17].

The detection of this subtle but rapid change in plant communities was made possible by citizen science monitoring and a large sampling effort in space and time. Such data can be of great value [18] but still come with several downsides deserving further attention. For example, possible biases could be related to uneven sampling effort, identification errors or uncomplete trait data. Spatial heterogeneity in the sampling effort was addressed by examining trends within a small region. Identification errors, as well as missing trait data are unlikely to be systematically biased in favor of high thermal preference, such that these problems should not influence our results. Finally, the observed trend in MTP could be caused partly by temporal changes in species phenology. Because the Vigie-flore protocol recommends a single annual spring survey, there may be a phenology-influenced bias in species detection and identifiability against undeveloped or non-flowered species. Climate change has led to phenological shifts in flowering plants [19], which could increase the detectability of warm-adapted species as the climate warms.

Whether such rapid community changes are sufficient to cope with the current climate

warming remain to be ascertained. Future research efforts could also be focused on analyzing trends in MTP across habitats or protection regimes and on identifying possible consequences of changes for plant-pollinator interactions.

COMPETING INTERESTS

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

VD, NM and EP conceived the ideas and designed methodology; GM, VD and EP analysed the data; GM and EP led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

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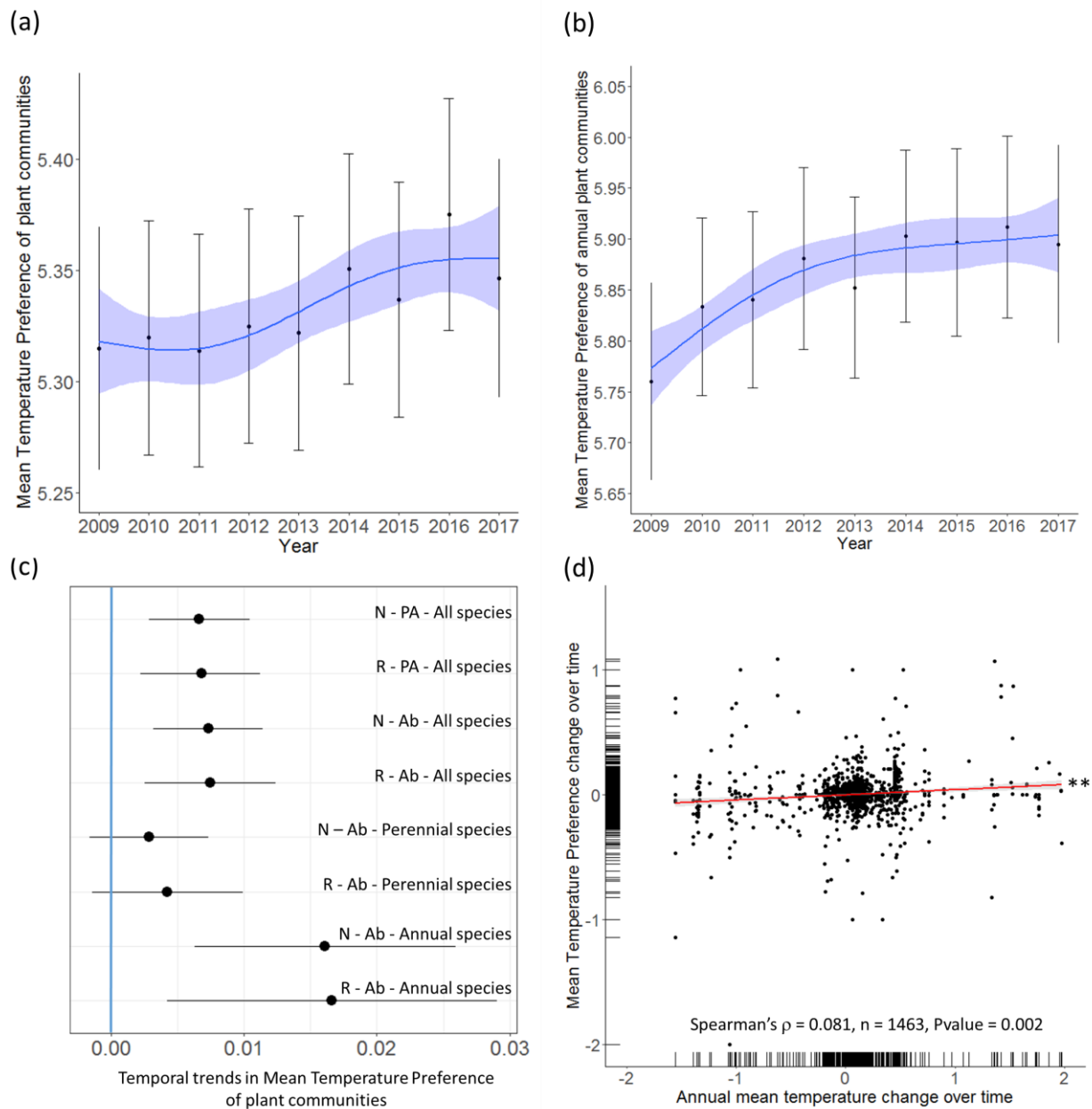
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- 225
- 226



228

229 Figure 1. National temporal trend in MTP of plant communities from 2009 to 2017 calculated
230 with abundance data, (a) for all species or (b) annual species only. The blue line is a
231 generalized additive model estimate of the temporal trend, with its associated standard error
232 (blue band). The black dots and error bars correspond to the inter-annual variations of the
233 variable, with its associated standard error. (c) Temporal trends in MTP from 2009 to 2017
234 estimated using Bayesian models. N/R: National/Regional scale, Ab/PA:
235 Abundance/Presence-Absence data. Dots indicate the mean of the posterior distribution, and

236 bars correspond to the 95 % credible interval for the temporal trends. (d) Correlation between
237 the plant MTP change and the annual mean temperature change over time. Each point
238 represents one plot.

239

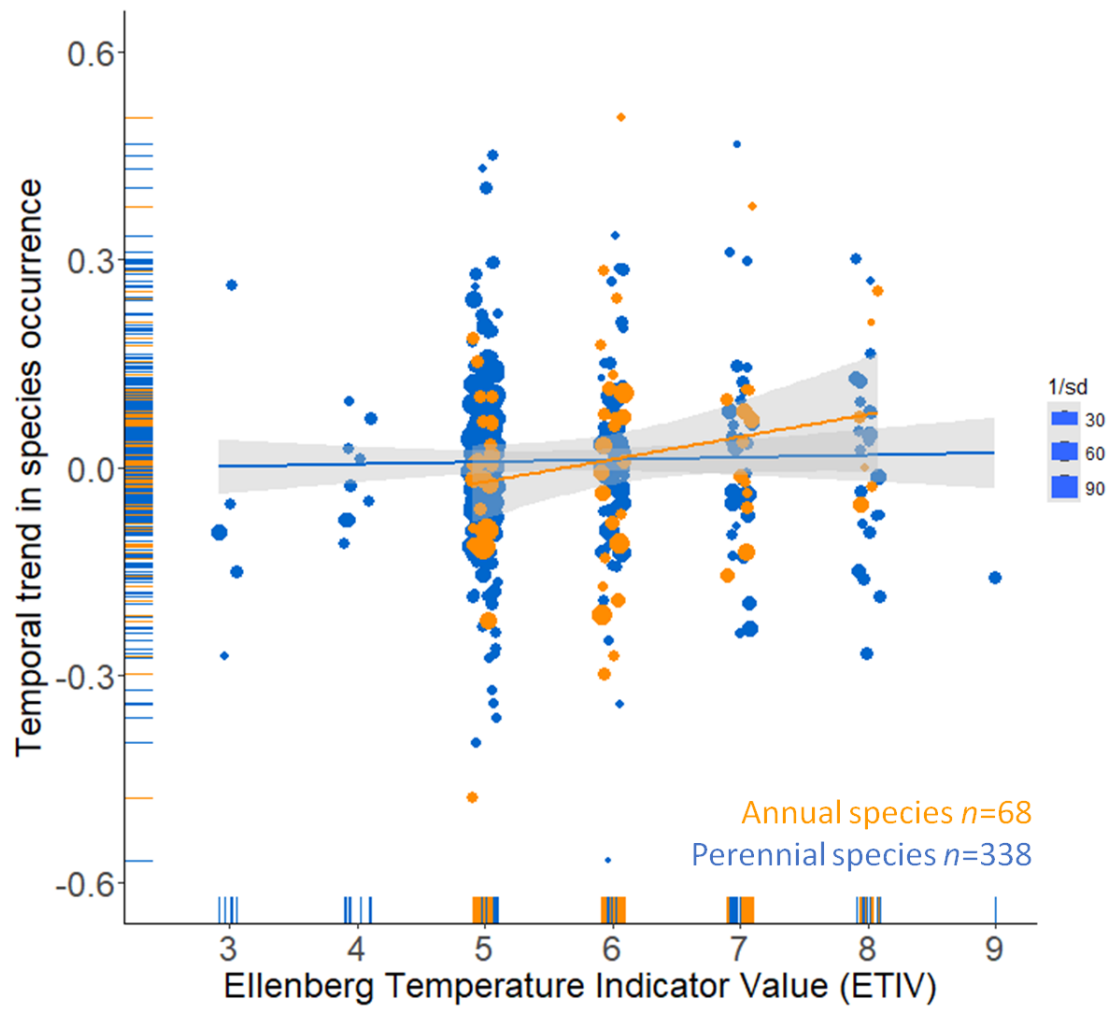


Figure 2. Relationship between the temporal trends of the most common species and their ETIV for annuals and perennials. Each dot represents the temporal trend for a species, with a size proportional to the inverse of the standard error. The lines correspond to the regressions, with their associated standard error (grey band).

I. Species attributes

We collected information for two species-specific attributes: (1) the Ellenberg temperature indicator values (hereafter ETIV), characterizing the optimum temperature class for growth and survival of a species (nine classes), from the database Baseflor [1], and (2) life span, described using seven broad classes obtained by combining classes from the Biolflor [2] and LEDA [3] databases (Table S1).

Table S1. Procedure used to combine life span information from Biolflor and LEDA traitbases.

| Life span (Biolflor database) | Life span (LEDA database) | Single or combined life span categories | Occurrence |
|--|--|---|------------|
| a (annual) | Annuals | annual | 17 |
| a (annual) - b (biennial) | Annuals | annual/biennial | 1 |
| b (biennial) | Annuals | annual/biennial | 1 |
| p (pluriennial-pollakanthic) | Annuals | annual/pluriennial | 1 |
| a (annual) | annuals + perennials | annual/pluriennial | 1 |
| p (pluriennial-pollakanthic) | annuals + perennials | annual/pluriennial | 1 |
| p (pluriennial-pollakanthic) | annuals + perennials + poly-annuals < 5 years (short-lived perennials) | annual/pluriennial | 2 |
| a (annual) - b (biennial) - p (pluriennial-pollakanthic) | annuals + perennials + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| a (annual) - p (pluriennial-pollakanthic) | annuals + perennials + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 2 |
| p (pluriennial-pollakanthic) | annuals + perennials + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 5 |
| p (pluriennial-pollakanthic) | annuals + perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | annuals + perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | annual/biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | annuals + perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/biennial/pluriennial | 2 |
| a (annual) | annuals + perennials + summer annuals | annual/pluriennial | 2 |
| a (annual) | annuals + perennials + summer annuals + strict monocarpic bi-annuals and poly- | annual/biennial/pluriennial | 1 |

| | | | |
|--|--|-----------------------------|----|
| | annuals | | |
| a (annual) - b (biennial) | annuals + perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 3 |
| a (annual) - p (pluriennial-pollakanthic) | annuals + perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) | annuals + perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) - h (pluriennial-hapaxanthic) | annuals + perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) | annuals + perennials + summer annuals + winter annuals | annual/pluriennial | 2 |
| a (annual) | annuals + perennials + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 3 |
| a (annual) - b (biennial) | annuals + perennials + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| a (annual) | annuals + perennials + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) - p (pluriennial-pollakanthic) | annuals + perennials + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) - b (biennial) - h (pluriennial-hapaxanthic) | annuals + perennials + winter annuals | annual/biennial/pluriennial | 1 |
| a (annual) | annuals + perennials + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | annuals + poly-annuals > 50 years (long-lived perennials) | annual/pluriennial | 1 |
| a (annual) | annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 16 |
| a (annual) - b (biennial) | annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 4 |
| a (annual) - b (biennial) - p (pluriennial-pollakanthic) | annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) | annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 3 |
| b (biennial) - h (pluriennial-hapaxanthic) | annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| a (annual) | annuals + summer annuals | annual | 34 |
| a (annual) | annuals + summer annuals + poly-annuals > 50 years (long-lived perennials) | annual/pluriennial | 1 |
| a (annual) | annuals + summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 10 |
| a (annual) - b (biennial) | annuals + summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 2 |
| a (annual) | annuals + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) | annuals + summer annuals + winter annuals | annual | 5 |

| | | | |
|---|--|-----------------------------|-----|
| a (annual) | annuals + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 18 |
| a (annual) - b (biennial) | annuals + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| a (annual) | annuals + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) | annuals + winter annuals | annual | 2 |
| a (annual) | annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 11 |
| a (annual) - b (biennial) | annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 2 |
| a (annual) | perennials | annual/pluriennial | 2 |
| a (annual) - p (pluriennial-pollakanthic) | perennials | annual/pluriennial | 2 |
| b (biennial) - p (pluriennial-pollakanthic) | perennials | biennial/pluriennial | 1 |
| h (pluriennial-hapaxanthic) | perennials | pluriennial | 1 |
| p (pluriennial-pollakanthic) | perennials | pluriennial | 396 |
| p (pluriennial-pollakanthic) | perennials + poly-annuals < 5 years (short-lived perennials) | pluriennial | 28 |
| p (pluriennial-pollakanthic) | perennials + poly-annuals < 5 years (short-lived perennials) + poly-annuals > 50 years (long-lived perennials) | pluriennial | 1 |
| p (pluriennial-pollakanthic) | perennials + poly-annuals < 5 years (short-lived perennials) + poly-annuals > 50 years (long-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | pluriennial | 3 |
| p (pluriennial-pollakanthic) | perennials + poly-annuals < 5 years (short-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | pluriennial | 26 |
| p (pluriennial-pollakanthic) | perennials + poly-annuals > 50 years (long-lived perennials) | pluriennial | 11 |
| p (pluriennial-pollakanthic) | perennials + poly-annuals > 50 years (long-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | pluriennial | 2 |
| a (annual) | perennials + poly-annuals 5-50 years (medium-lived perennials) | annual/pluriennial | 1 |
| a (annual) - p (pluriennial-pollakanthic) | perennials + poly-annuals 5-50 years (medium-lived perennials) | annual/pluriennial | 2 |
| p (pluriennial-pollakanthic) | perennials + poly-annuals 5-50 years (medium-lived perennials) | pluriennial | 84 |
| a (annual) | perennials + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) - h (pluriennial-hapaxanthic) | perennials + strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 3 |
| b (biennial) - h (pluriennial-hapaxanthic) - p (pluriennial-pollakanthic) | perennials + strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 1 |
| b (biennial) - p (pluriennial-pollakanthic) | perennials + strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 3 |
| p (pluriennial-pollakanthic) | perennials + strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 4 |

| | | | |
|--|--|-----------------------------|---|
| b (biennial) | perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | biennial/pluriennial | 2 |
| b (biennial) - p (pluriennial-pollakanthic) | perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | biennial/pluriennial | 1 |
| a (annual) - b (biennial) - h (pluriennial-hapaxanthic) - p (pluriennial-pollakanthic) | perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | annual/biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | biennial/pluriennial | 1 |
| b (biennial) - p (pluriennial-pollakanthic) | perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials) | biennial/pluriennial | 2 |
| p (pluriennial-pollakanthic) | perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials) | biennial/pluriennial | 3 |
| a (annual) - p (pluriennial-pollakanthic) | perennials + summer annuals | annual/pluriennial | 3 |
| b (biennial) - h (pluriennial-hapaxanthic) - p (pluriennial-pollakanthic) | perennials + summer annuals | annual/biennial/pluriennial | 1 |
| h (pluriennial-hapaxanthic) - p (pluriennial-pollakanthic) | perennials + summer annuals | annual/pluriennial | 3 |
| a (annual) - b (biennial) - p (pluriennial-pollakanthic) | perennials + summer annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) - p (pluriennial-pollakanthic) | perennials + summer annuals + poly-annuals < 5 years (short-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | annual/pluriennial | 1 |
| p (pluriennial-pollakanthic) | perennials + summer annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/pluriennial | 2 |
| a (annual) - b (biennial) | perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| h (pluriennial-hapaxanthic) - p (pluriennial-pollakanthic) | perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) | perennials + summer annuals + winter annuals | annual/pluriennial | 1 |
| b (biennial) - p (pluriennial-pollakanthic) | perennials + summer annuals + winter annuals | annual/biennial/pluriennial | 1 |
| b (biennial) - h (pluriennial-hapaxanthic) | perennials + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | perennials + winter annuals | annual/pluriennial | 1 |
| p (pluriennial- | perennials + winter annuals + poly-annuals | annual/pluriennial | 1 |

| | | | |
|--|---|-----------------------------|----|
| pollakanthic) | > 50 years (long-lived perennials) | | |
| a (annual) - b (biennial) | perennials + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) | perennials + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) - h (pluriennial-hapaxanthic) | perennials + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| a (annual) - b (biennial) | poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| b (biennial) | poly-annuals < 5 years (short-lived perennials) | biennial/pluriennial | 1 |
| b (biennial) - p (pluriennial-pollakanthic) | poly-annuals < 5 years (short-lived perennials) | biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | poly-annuals < 5 years (short-lived perennials) | pluriennial | 8 |
| p (pluriennial-pollakanthic) | poly-annuals < 5 years (short-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | pluriennial | 5 |
| p (pluriennial-pollakanthic) | poly-annuals > 50 years (long-lived perennials) | pluriennial | 3 |
| p (pluriennial-pollakanthic) | poly-annuals > 50 years (long-lived perennials) + poly-annuals 5-50 years (medium-lived perennials) | pluriennial | 2 |
| a (annual) - p (pluriennial-pollakanthic) | poly-annuals 5-50 years (medium-lived perennials) | annual/pluriennial | 1 |
| b (biennial) - p (pluriennial-pollakanthic) | poly-annuals 5-50 years (medium-lived perennials) | biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | poly-annuals 5-50 years (medium-lived perennials) | pluriennial | 32 |
| a (annual) | strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 2 |
| a (annual) - b (biennial) | strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) | strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 14 |
| b (biennial) - h (pluriennial-hapaxanthic) | strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 5 |
| b (biennial) - p (pluriennial-pollakanthic) | strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 1 |
| a (annual) - b (biennial) - h (pluriennial-hapaxanthic) | strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| b (biennial) - h (pluriennial-hapaxanthic) | strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | biennial/pluriennial | 1 |
| p (pluriennial-pollakanthic) | strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | biennial/pluriennial | 1 |
| a (annual) | summer annuals | annual | 65 |
| a (annual) - b (biennial) - p (pluriennial-pollakanthic) | summer annuals | annual/biennial/pluriennial | 1 |
| a (annual) - p (pluriennial-pollakanthic) | summer annuals | annual/pluriennial | 1 |
| p (pluriennial-pollakanthic) | summer annuals | annual/pluriennial | 1 |
| a (annual) | summer annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/pluriennial | 1 |

| | | | |
|---|---|-----------------------------|----|
| a (annual) - p (pluriennial-pollakanthic) | summer annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/pluriennial | 1 |
| a (annual) | summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 9 |
| a (annual) - b (biennial) | summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| a (annual) - b (biennial) - h (pluriennial-hapaxanthic) | summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) | summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) - p (pluriennial-pollakanthic) | summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 2 |
| a (annual) - p (pluriennial-pollakanthic) | summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) | summer annuals + winter annuals | annual | 19 |
| a (annual) - b (biennial) | summer annuals + winter annuals | annual/biennial | 1 |
| a (annual) - p (pluriennial-pollakanthic) | summer annuals + winter annuals + poly-annuals < 5 years (short-lived perennials) | annual/pluriennial | 1 |
| a (annual) | summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 4 |
| a (annual) - b (biennial) | summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| a (annual) - b (biennial) | summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | annual/biennial/pluriennial | 1 |
| a (annual) | winter annuals | annual | 6 |
| a (annual) - b (biennial) | winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial | 1 |
| a (annual) - p (pluriennial-pollakanthic) | winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| b (biennial) | winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| NA | annuals | annual | 5 |
| NA | annuals + summer annuals | annual | 3 |
| NA | perennials | pluriennial | 57 |
| NA | perennials + strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 1 |
| NA | perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials) | annual/biennial/pluriennial | 1 |
| NA | poly-annuals 5-50 years (medium-lived perennials) | pluriennial | 3 |
| NA | strict monocarpic bi-annuals and poly-annuals | biennial/pluriennial | 1 |
| NA | strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials) | biennial/pluriennial | 1 |
| NA | summer annuals | annual | 26 |
| NA | summer annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 6 |
| NA | summer annuals + winter annuals | annual | 1 |
| NA | summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals | annual/biennial/pluriennial | 1 |
| NA | winter annuals | annual | 1 |
| a (annual) | NA | annual | 72 |
| a (annual) - b (biennial) | NA | annual/biennial | 7 |

| | | | |
|---|----|-----------------------------|-----|
| a (annual) - b (biennial) - h (pluriennial-hapaxanthic) | NA | annual/biennial/pluriennial | 1 |
| a (annual) - p (pluriennial-pollakanthic) | NA | annual/pluriennial | 4 |
| b (biennial) | NA | biennial | 10 |
| b (biennial) - h (pluriennial-hapaxanthic) | NA | biennial/pluriennial | 2 |
| b (biennial) - p (pluriennial-pollakanthic) | NA | biennial/pluriennial | 3 |
| h (pluriennial-hapaxanthic) - p (pluriennial-pollakanthic) | NA | pluriennial | 1 |
| p (pluriennial-pollakanthic) | NA | pluriennial | 284 |
| p (pluriennial-pollakanthic) - p (pluriennial-pollakanthic) | NA | pluriennial | 1 |
| NA | NA | NA | 917 |

II. Climate data and Random Forest analysis

For each plot, we collected daily mean temperature, daily minimum temperature, daily maximum temperature and daily precipitation sum between 2009 and 2017 from the ENSEMBLES dataset [26], using data from the nearest E-OBS station in France on a 0.25 degree grid. Climate data were extracted using the R package climateExtract [27], and devtools [28]. We then calculated 10 climatic variables per plot, two using annual data (mean annual temperature and annual temperature anomaly) and eight using information from January to May (growing period of many plants): mean temperature, temperature anomaly, mean maximum temperature, number of heatwave days ($T^{\circ}\text{C} > 27^{\circ}\text{C}$), freezing days ($T^{\circ}\text{C} < 0^{\circ}\text{C}$), rainy days, drought days, and pluviometry. The temperature anomaly is the sum of the differences between the observed daily temperature and the mean temperature over a period on a site.

We then performed a Random Forest regression analysis to identify the climatic variable(s) explaining the greatest variability in MTP of plant communities. The Random Forest analysis

275 is a nonparametric technique derived from classification and regression trees. This method,
276 which has been applied in various ecological studies [4,5], shows high accuracy and the
277 ability to model complex interactions between variables. To perform the model, we defined
278 two essential parameters: *mtry*, i.e. the number of variables to try at each split, and *ntree*, i.e.
279 the number of trees to run. To maximize the accuracy of the Random Forest analysis, i.e.
280 minimize the measure of the prediction error (Out Of Bag (OOB) error), *mtry* and *ntree* can
281 be varied. We determined the parameter *mtry* thanks to the internal RF function TuneRF [R
282 package randomForest, 6]; this function computes the optimal number of variables starting
283 from the default (total number of variables/3 for regression) and tests half and twice this
284 threshold for the value with the minimum OOB error rate. It is already known that a *mtry* of 1
285 can produce good accuracy [6,7], but it is recommended to include at least two variables to
286 avoid using also the weaker regressors as splitters [8]. Here, even if the best accuracy was
287 obtained for a *mtry* of 1, we performed the Random Forest regression analysis with a *mtry* of
288 2 following Grömping [8]. The *ntree* parameter was set to 1000 to obtain stable results.

289 Variable importance of the 10 climatic variables (i.e. the mean annual temperature, the annual
290 temperature anomaly, and eight variables estimated from January to May: mean temperature,
291 temperature anomaly, mean maximum temperature, number of heatwave days, freezing days,
292 rainy days, drought days, and pluviometry) was estimated as the total decrease in node
293 impurities, measured by residual sum of squares from splitting on the variable, averaged over
294 all trees.

295 Finally, as a result of the Random Forest regression analysis, we selected the annual mean
296 temperature, the most relevant climatic variable by ranking the variables according to their
297 importance measure (Table S2).

298 We performed a linear regression of the annual mean temperature against years to describe the
299 temporal trend of climate change on the sampled plots of the study. We included geographical

coordinates in the model to account for residual spatial autocorrelation. We recovered one slope per square, since climate data were only available at that scale; all plots within a scale were thus attributed the same temporal trend in climate data, describing the temporal trend of annual mean temperature.

Table S2. Importance measures of the 10 climatic variables resulting from a Random Forest regression analysis and explaining the share of variability of the MTP of plant communities.

| Climatic variables | Importance |
|--|-------------------|
| Annual mean temperature | 725 |
| Number of freezing day from January to May | 365 |
| Mean temperature from January to May | 342 |
| Mean maximum temperature from January to May | 243 |
| Number of drought day from January to May | 204 |
| Pluviometry from January to May | 160 |
| Annual temperature anomaly | 135 |
| Temperature anomaly from January to May | 133 |
| Number of rainy day from January to May | 99 |
| Number of heatwave day from January to May | 55 |

III. Estimation of temporal trends in mean temperature preference and species occurrence

We performed Bayesian hierarchical models to estimate the temporal trend in MTP of plant communities (1) at a national scale and within Île-de-France, (2) using either abundance data or presence/absence data and (3) of annuals vs. perennials species. The underlying model describes the MTP value as a function of year for all plant communities. We assumed that MTP of plant communities was normally distributed, with a mean that depended linearly on year, geographical coordinates and survey square, and constant variance. The linear model was the following:

$$MTP_{ijk} = m + a*year_i + b*lat_{ijk} + c*long_{ijk} + d*lat_{ijk}^2 + e*long_{ijk}^2 + Square_j + \sigma_{ijk}^2$$

where MTP_{ijk} is the mean temperature preference of the plant community in plot k of square j and year i , m is the intercept, lat and $long$ are the latitude and longitude of the plot, $Square$ is the random effect of square with variance σ_s^2 and σ_{ijk}^2 is the residual variance.

We also performed Bayesian hierarchical models to generate estimates of the temporal trend in common species abundance, as estimated at the 10m² plot level by the number of 1m² quadrats in which these species were observed. We selected the 550 most common species that were observed at least four out of nine years and in at least ten squares. We modeled species abundance assuming a binomial distribution with $n = 10$ trials and a logit-transformed probability p depending linearly on year, survey plot, square and geographical coordinates as follows:

$$\text{logit}(p_{ijk}) = m + a*year_i + b*lat_{ijk} + c*long_{ijk} + d*lat_{ijk}^2 + e*long_{ijk}^2 + Square_j + Plot_k$$

where p_{ijk} is the probability to observe the species in each 1m² square of plot k of square j and year i , m is the intercept, lat and $long$ are the latitude and longitude of the plot, $Square$ is the random effect of square with variance σ_s^2 , $Plot$ is the random effect of plot with variance σ_p^2 .

For all Bayesian hierarchical models, we chose only non-informative priors, sampled from Gaussian distributions with a mean of 0 and a variance of 10^{10} for most parameters, and gamma distributions with shape parameter $k = 0.001$ and rate $\beta = 0.001$ for precision (inverse of variance) parameters. Parameters were estimated using WinBUGS [9]. Four chains were run using priors to draw 100,000 samples, discarding the first 50,000 iterations. Samples were thinned by 1 in 10 to reduce autocorrelation and obtain mean trends from the remaining posterior distributions. Convergence was checked using the Rhat statistics (all Rhat < 1.2) and WinBUGS traceplots (superposition of the 4 chains). Posterior mean community and species trends were interpreted as different from zero when 95 % of the highest posterior density interval did not include zero.

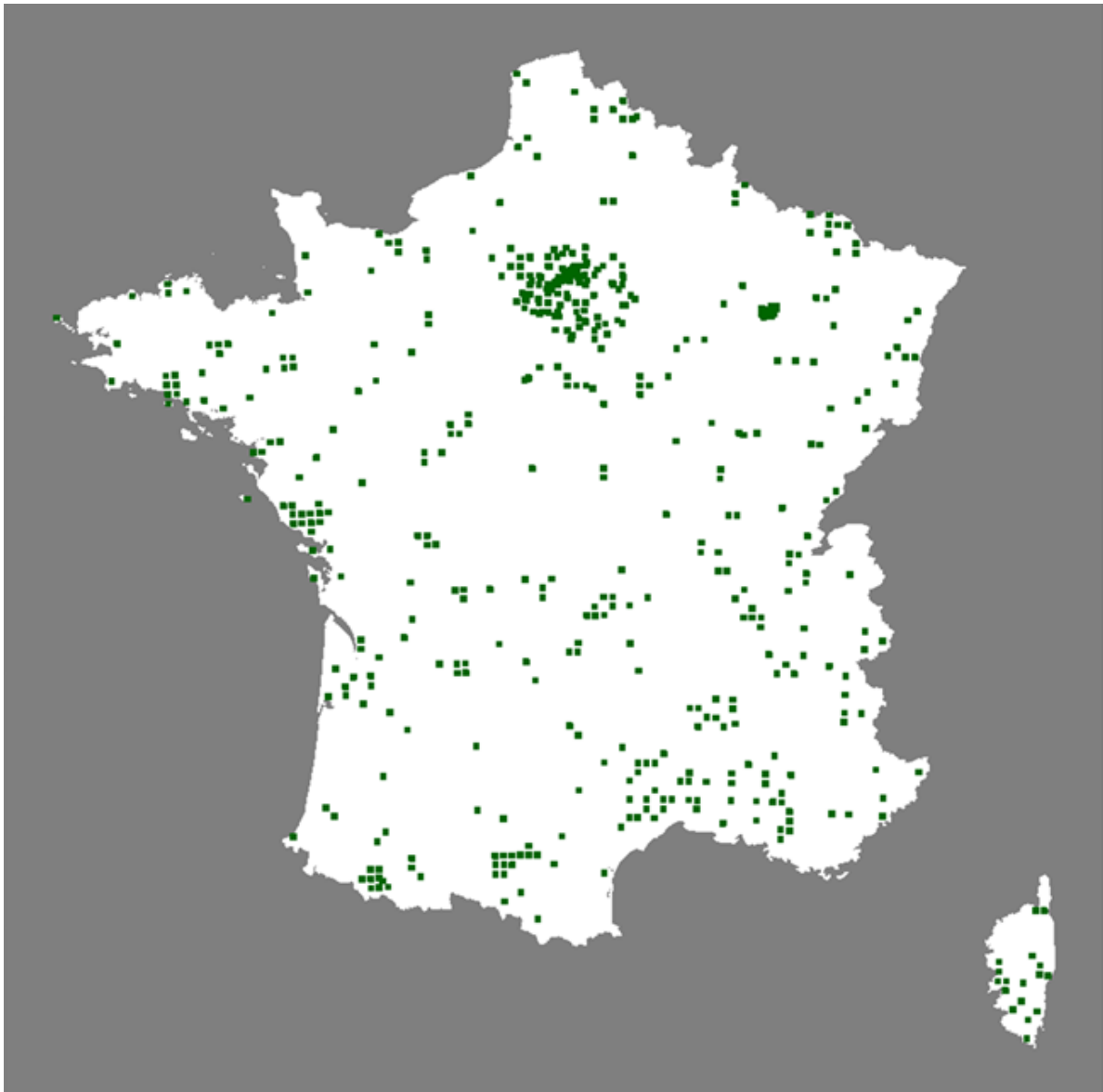
IV. R packages used

All analyses were performed using R version 3.2.4 [10] and R packages *Taxonstand* version 2.1 [11], R packages *TR8* [12], R packages *climateExtract* version 0.2.0 [13], R packages *randomForest* [6], R packages *caret* version 6.0-78 [14], R packages *plotmo* version 3.3.4 [15], R packages *R2jags* version 0.5-7 [16], R packages *mcmcplots* version 0.4.2 [17], R packages *car* [18], R packages *lme4* [19], R packages *nlme* version 3.1-131 [20], R packages *dplyr* version 0.7.3 [21], R packages *reshape2* [22], R packages *devtools* version 1.13.4 [23], R packages *effects* version 2.1.0 [24], R packages *ggplot2* version 2.1.0 [25], R packages *ggthemes* version 3.4.0 [26], R packages *gridExtra* version 2.3 [27]. Plant functional traits were collected using the R package *TR8* [12].

Table S3. Type II Anova results for the linear mixed models testing for a temporal change in the mean annual temperature over time.

| Fixed effects | <i>n</i> | Estimate | Standard error | Chisq | <i>P</i> value |
|---------------------|----------|----------|----------------|---------|----------------|
| Year | 7854 | 0.1094 | 0.0032 | 1203.82 | <0.001 |
| Longitude | 7854 | 3.9921 | 0.7605 | 27.56 | <0.001 |
| Latitude | 7854 | -7.5612 | 1.9008 | 15.82 | <0.001 |
| Longitude*Longitude | 7854 | -0.0318 | 0.0096 | 10.89 | <0.01 |
| Latitude*Latitude | 7854 | 0.0819 | 0.0204 | 16.15 | <0.001 |
| Longitude*Latitude | 7854 | -0.0872 | 0.0158 | 30.30 | <0.001 |

Figure S1. Spatial distribution of the Vigie-flore survey squares.



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362

363 Figure S2. Regional temporal trend in MTP of plant communities from 2009 to 2017
364 calculated with abundance data in Île-de-France. The blue line is a generalized additive model
365 estimate of the temporal trend, with its associated standard error (blue band). The black dots
366 and error bars correspond to the inter-annual variations of the variable, with its associated
367 standard error.

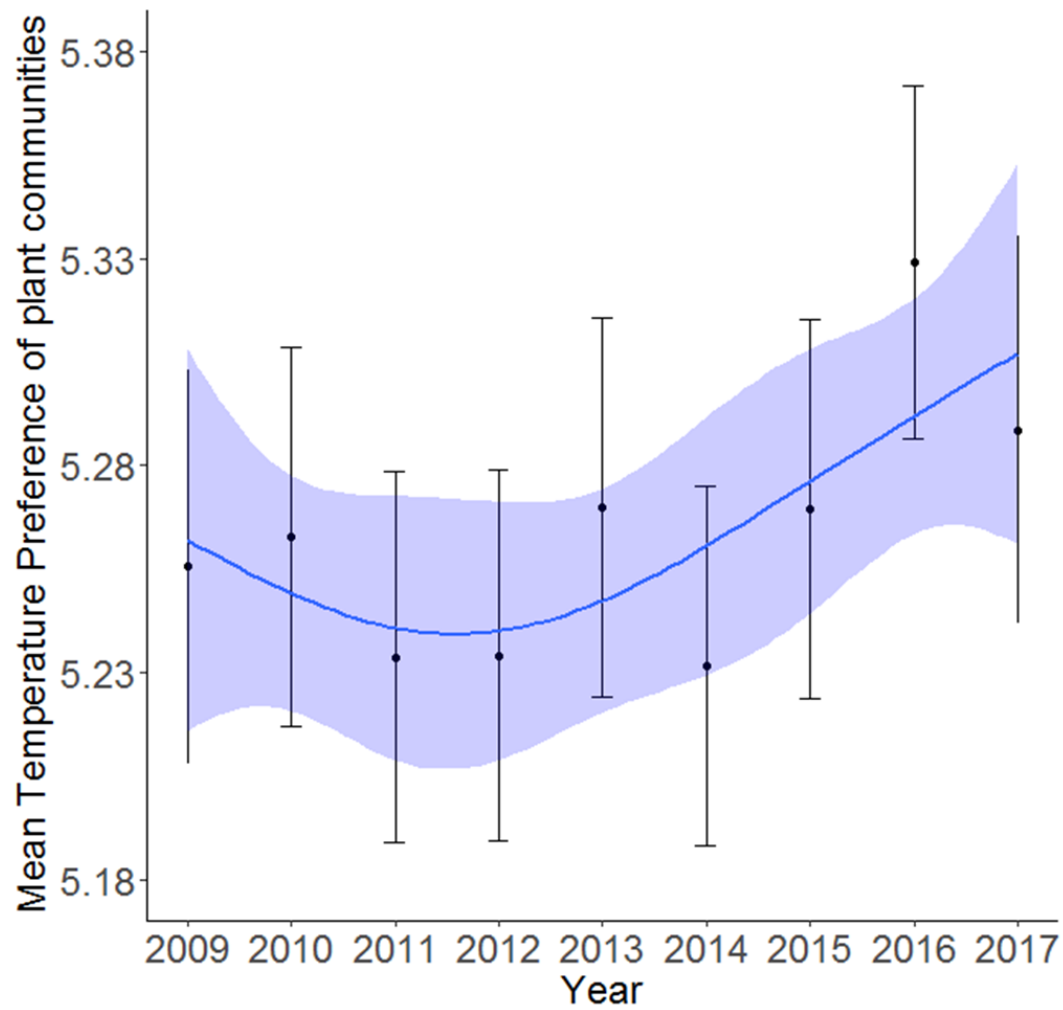
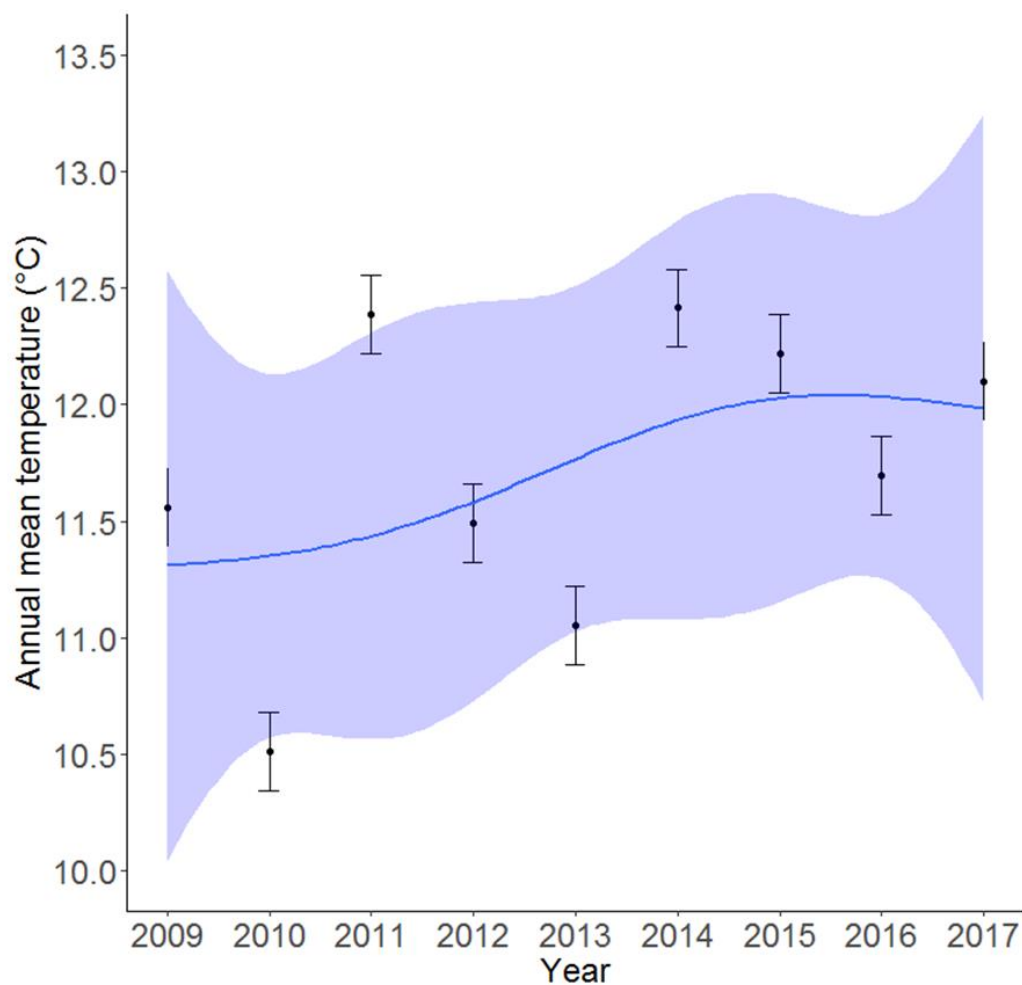


Figure S3. Temporal trend of annual mean temperature estimated from 2009 to 2017 on sampled sites in France. The blue line is a generalized additive model estimate of the temporal trend, with its associated standard error (blue band). The black dots and error bars correspond to the inter-annual variations of the variable, with its associated standard error.



List S1. The 321 Vigie-flore volunteers involved in the wild flora monitoring:

Abadie Jean-Claude, Abadie Juliet, Abraham Christelle, Aguetant Laurent, Allemand Denis, Anglaret Cédric, Arnould Loic, Arondel Bruno, Association Asterella, Association Les Amis Du Jardin Botanique Littoral Paul Jovet, Association Les Marais Du Verdier, Association Tela Botanica, Aupoix Alain, AUTRET Françoise, Avenas Élise, Avril Damien, Balard Yvette, Balloux Gabriel, Baradat Mathilde, Barbet-Massin Morgane, Barreda Flavie, Bastin André, Batsere Françoise, Baudet Nicolas, Baurens-Franc Christophe, Bebin Clément, Bégin Sophie, Benezet Ruddy, Béraud Jean-Marc, Berger Romain, Biancardini Famille, Bircker Loic, Bodiguel Brigitte, Boisbineuf Christelle, Boissier Marc, Bonnafoux Florence, Bonnafoux Vincent, Bonneau Pierre, Bonneil Philippe, Bos Nathalie, Bosquet Christian, Bouard Hervé,

386 Boudies Catherine, Bouffard Frédéric, Bouligand Sandrine, Boutegege Serge, Bouveris
387 Nicole, Bouvier Chantal, Brajon Émilie, Brasseur Jean-Emmanuel, Breuil Anne, Briand
388 Françoise, Brin Antoine, Buckvald Nathalie, Bultel Yvan, Burchianti Mireille, Busch
389 Geneviève, Callewaert Pierre, Calme Catherine, Calmet Claire, Camenen-Houdayer Danièle
390 Canel Celie, Canevet Marie-Françoise, Caron Matthieu, Casenave Isabelle, Catieau Alexis,
391 Causeur Nicole, Cellier Pierre, Chabanois Gérard, Chamaux Jérôme, Chammard Émilie,
392 Chappert-Bessiere Joceline, Chapuis Gabriel, Chardinal Sophie, Chatelain Marion, Cherrier
393 Camille, Chevalier Adeline, Chevalier Richard, Chiffolleau Bertrand, Cholet Jérémie, Clochard
394 Alain, Cocquempot Marine, Coiffard Clément, Collectivité Territoriale (Reserve Naturelle)
395 Poupart, Conservatoire Botanique National Du Bassin Parisien Cbnbp, Coupiac Louis, Couric
396 Pauline, Crouzet Pierre, Cuille Rosalie, Danet Pierre, De Chastenet Cedissia, De Kerimel
397 Aymeric, De La Brosse Caroline, Delafoy Arielle, Delisle Pascal, Delphin Chantal,
398 Deschatres Aurelien, Desvois Régine, Devers Florence, Dezerald Hervé, Domenech Boris,
399 Douard Anne, Douarre Marie, Druez Flora, Dubosc Sarah, Duffaut Philippe, Dumas
400 Françoise, Dumez Nicolas, Durand Alexandre, Duron Quiterie, Duytschaever Francis, Engel
401 Geneviève, Eriksson Marion, Esnault Sarah, Etcheverry Georgette, Farcat Charlotte, Fatz
402 Pierre-Marie, Féral Camille, Fernandes Val, Filleur Lucas, Fournel Isabelle, Fourvel Jean-
403 Marc, Fried Guillaume, Galerme Jean Baptiste, Galerme Jean Pierre, Garnier Boudier Joanne,
404 Gatto Claire, Gaudry Jérôme, Gauthier Jacques, Gelin Muriel, Gelmetti Anne Marie, Geneix
405 Gilles, Georganidis Michèle, Germaine Clémence, Ghesquiere Jean-Christophe, Ghestem
406 Murielle, Goguet Liselotte, Gombault Clémentine, Gorremans Jean-Luc, Gotteland Pierre,
407 Gourdel Laurence, Gourlin Benjamin, Grange Milena, Grignon Céline, Guais Daniel,
408 Guichard Bernard, Guiller Clémence, Guittet Jean, Haeffner Hugues, Haenggi Philippe,
409 Hance Emmanuel, Happe David, Heuze Sylvère, Hillion Jeanne, Hubert Eric, Hugot Nicolas,
410 Huve Rosalia, Indorf Marc-Frederic, Jacot Pierre-Alain, Jagoda Daniel, Jardin Botanique

411 Besançon, Jargeat Patricia, Javaux Benjamin, Jaymond Delphine, Joset Henri, Jourdan
412 Christine, Joyaux Sandrine, Jullin Franck, Kania Daniel, Laffargue Lucie, Lafon Céline,
413 Lagier Anne-Marie, Lallemand Johann, Lambert Cécile, Lamouroux Paule, Lanciaux
414 Maxime, Lantuejoul Eric, Larbouillat Annick, Lavialle Jeanne, Le Fur Patrick, Le Garrec
415 Sandra, Leblanc Marie, Leclerc Catherine, Leduc Vinciane, Lefebvre Manon, Lekieffre Alix,
416 Lemoine Yves, Lemouzy Claire, Leneveu Justine, Lenne Patricia, Lepage Elen, Lequeuvre
417 Charly, Lerat Christine, Lerat Elodie, Lesné Sébastien, Leveslin Gérard, Leviol Isabelle,
418 Levy-Leonesio Patricia, Locqueville Jonathan, Lodziak Michel, Lonchamp Jean-Pierre,
419 Longeot Yves, Luciani Bernadette, Luigi Catherine, Mace Bruno, Machon Nathalie, Magrou
420 Nathalie, Maguet Nicolle, Marchal Pierre-Luc, Marsteau Christine, Martin Gabrielle, Martin
421 Hilaire, Martin Nicolas, Martinelli Marion, Masonnave François, Massouh Jacques, Master
422 Promo, Mathieu Daniel, Mathieu Joël, Maurel Noëlie, Meyer Claire-Lise, Michel Prisca,
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