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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 2). 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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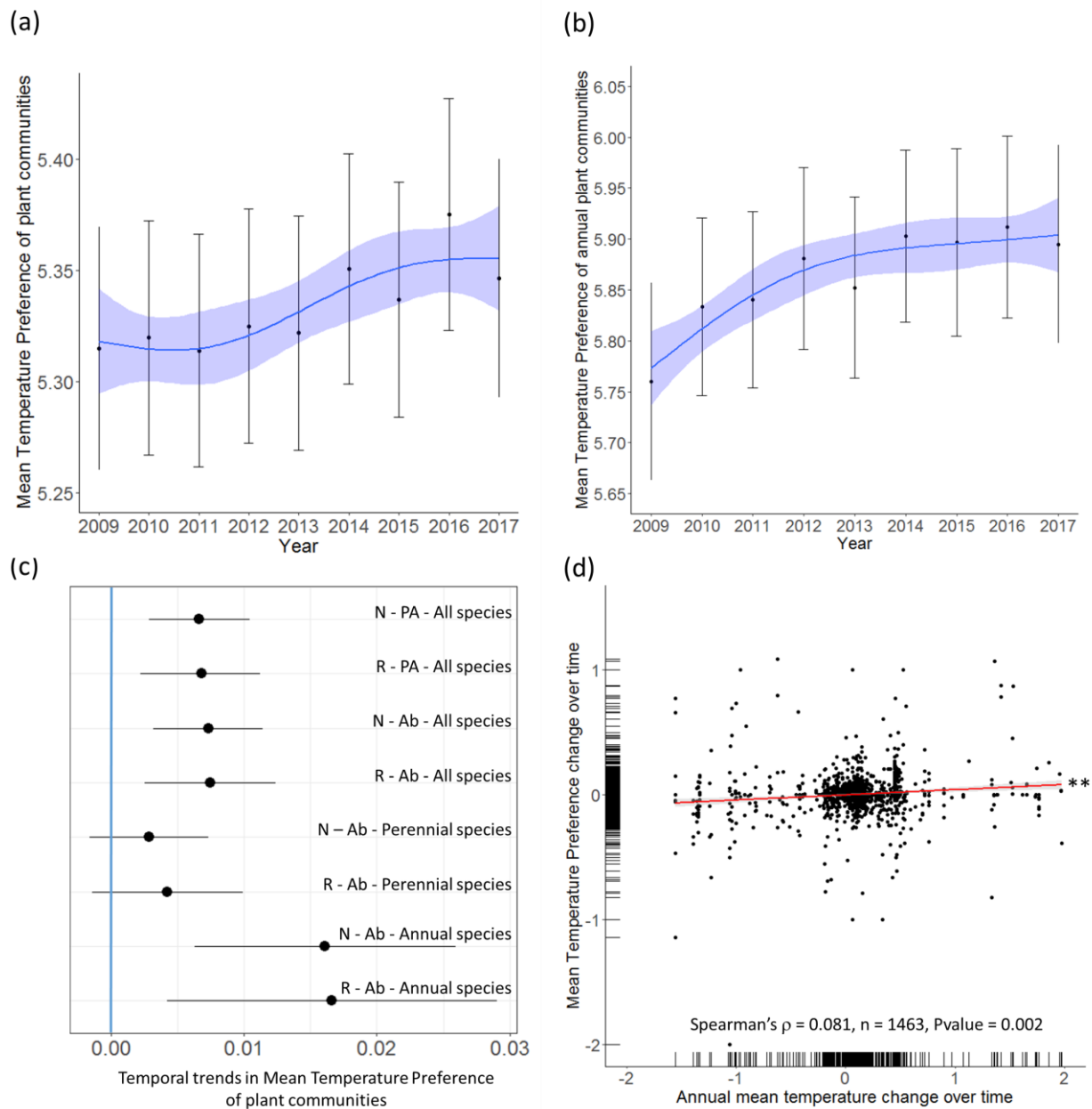
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229 Figure 1. National temporal trend in MTP of plant communities from 2009 to 2017 calculated
230 with abundance data, (a) for all species or (b) annual species only. The blue line is a
231 generalized additive model estimate of the temporal trend, 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.

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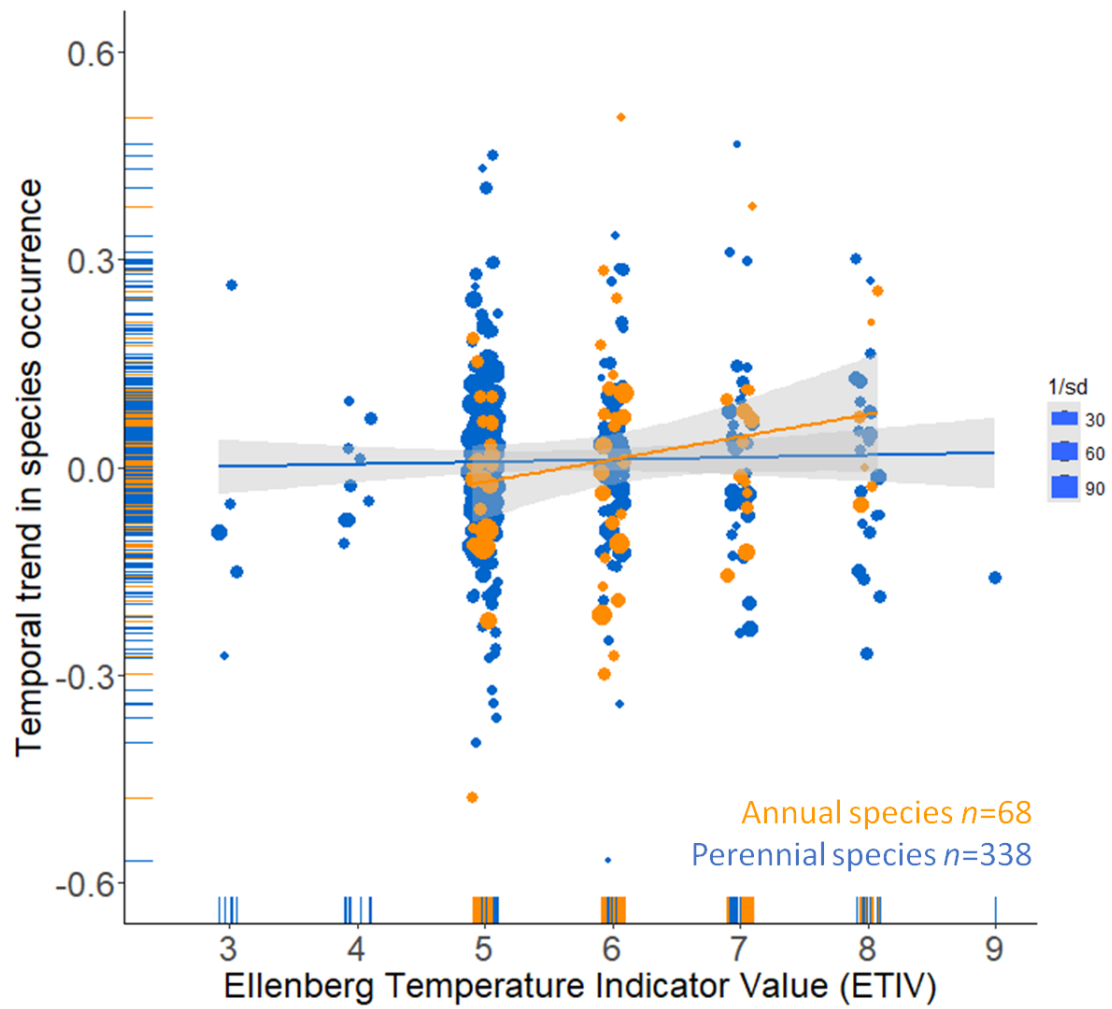


Figure 2. Relationship between the temporal trends of the most common species and their ETIV for annuals and perennials. Each dot represents the temporal trend for a species, with a size proportional to the inverse of the standard error. The lines correspond to the regressions, with their associated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

ELECTRONIC SUPPLEMENTARY MATERIAL

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 [4], 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 [5], and devtools [6]. 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

is a nonparametric technique derived from classification and regression trees. This method, which has been applied in various ecological studies [7,8], shows high accuracy and the ability to model complex interactions between variables. To perform the model, we defined two essential parameters: *mtry*, i.e. the number of variables to try at each split, and *ntree*, i.e. the number of trees to run. To maximize the accuracy of the Random Forest analysis, i.e. minimize the measure of the prediction error (Out Of Bag (OOB) error), *mtry* and *ntree* can be varied. We determined the parameter *mtry* thanks to the internal RF function TuneRF [R package randomForest, 9]; this function computes the optimal number of variables starting from the default (total number of variables/3 for regression) and tests half and twice this threshold for the value with the minimum OOB error rate. It is already known that a *mtry* of 1 can produce good accuracy [9,10], but it is recommended to include at least two variables to avoid using also the weaker regressors as splitters [11]. Here, even if the best accuracy was obtained for a *mtry* of 1, we performed the Random Forest regression analysis with a *mtry* of 2 following Grömping [11]. The *ntree* parameter was set to 1000 to obtain stable results.

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

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

We performed a linear regression of the annual mean temperature against years to describe the 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:

73 $MTP_{ijk} = m + a*year_i + b*lat_{ijk} + c*long_{ijk} + d*lat_{ijk}^2 + e*long_{ijk}^2 + Square_j + \sigma_{ijk}^2$
 74 where MTP_{ijk} is the mean temperature preference of the plant community in plot k of square j
 75 and year i , m is the intercept, lat and $long$ are the latitude and longitude of the plot, $Square$ is
 76 the random effect of square with variance σ_s^2 and σ_{ijk}^2 is the residual variance.
 77 We also performed Bayesian hierarchical models to generate estimates of the temporal trend
 78 in common species abundance, as estimated at the 10m² plot level by the number of 1m²
 79 quadrats in which these species were observed. We selected the 550 most common species
 80 that were observed at least four out of nine years and in at least ten squares. We modeled
 81 species abundance assuming a binomial distribution with $n = 10$ trials and a logit-transformed
 82 probability p depending linearly on year, survey plot, square and geographical coordinates as
 83 follows:
 84 $logit(p_{ijk}) = m + a*year_i + b*lat_{ijk} + c*long_{ijk} + d*lat_{ijk}^2 + e*long_{ijk}^2 + Square_j + Plot_k$
 85 where p_{ijk} is the probability to observe the species in each 1m² square of plot k of square j and
 86 year i , m is the intercept, lat and $long$ are the latitude and longitude of the plot, $Square$ is the
 87 random effect of square with variance σ_s^2 , $Plot$ is the random effect of plot with variance σ_p^2 .
 88 For all Bayesian hierarchical models, we chose only non-informative priors, sampled from
 89 Gaussian distributions with a mean of 0 and a variance of 10^{10} for most parameters, and
 90 gamma distributions with shape parameter $k = 0.001$ and rate $\beta = 0.001$ for precision (inverse
 91 of variance) parameters. Parameters were estimated using WinBUGS [12]. Four chains were
 92 run using priors to draw 100,000 samples, discarding the first 50,000 iterations. Samples were
 93 thinned by 1 in 10 to reduce autocorrelation and obtain mean trends from the remaining
 94 posterior distributions. Convergence was checked using the Rhat statistics (all Rhat < 1.2) and
 95 WinBUGS traceplots (superposition of the 4 chains). Posterior mean community and species
 96 trends were interpreted as different from zero when 95 % of the highest posterior density
 97 interval did not include zero.

99 IV. R packages used

100

101 All analyses were performed using R version 3.2.4 [13] and R packages *Taxonstand* version
 102 2.1 [14], R packages *TR8* [15], R packages *climateExtract* version 0.2.0 [5], R packages
 103 *randomForest* [9], R packages *caret* version 6.0-78 [16], R packages *plotmo* version 3.3.4
 104 [17], R packages *R2jags* version 0.5-7 [18], R packages *mcmcplots* version 0.4.2 [19], R
 105 packages *car* [20], R packages *lme4* [21], R packages *nlme* version 3.1-131 [22], R packages
 106 *dplyr* version 0.7.3 [23], R packages *reshape2* [24], R packages *devtools* version 1.13.4 [6], R
 107 packages *effects* version 2.1.0 [25], R packages *ggplot2* version 2.1.0 [26], R packages
 108 *ggthemes* version 3.4.0 [27], R packages *gridExtra* version 2.3 [28]. Plant functional traits
 109 were collected using the R package *TR8* [15].

110

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162

163

164 Table S3. Type II Anova results for the linear mixed models testing
165 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

166

167

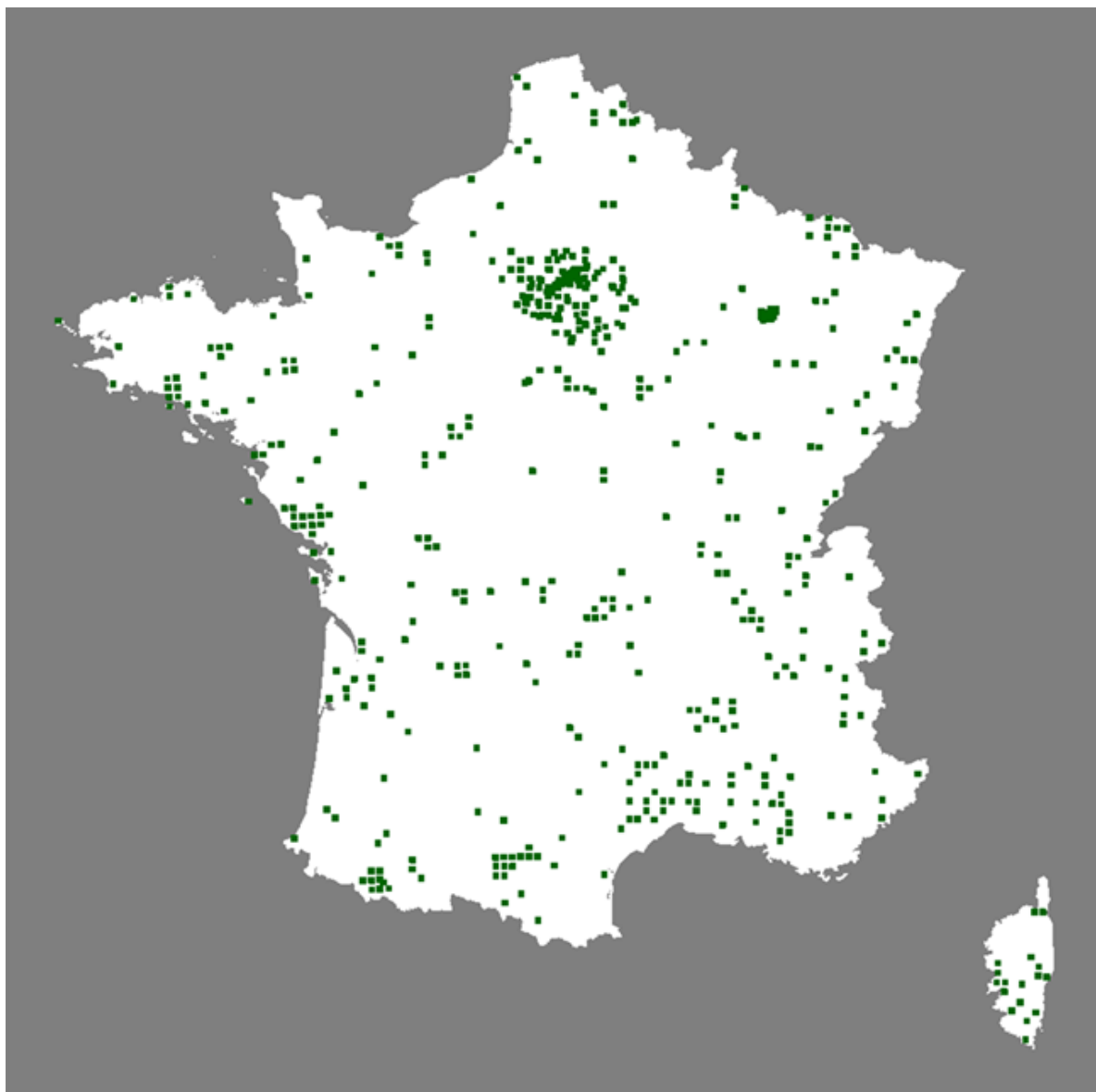
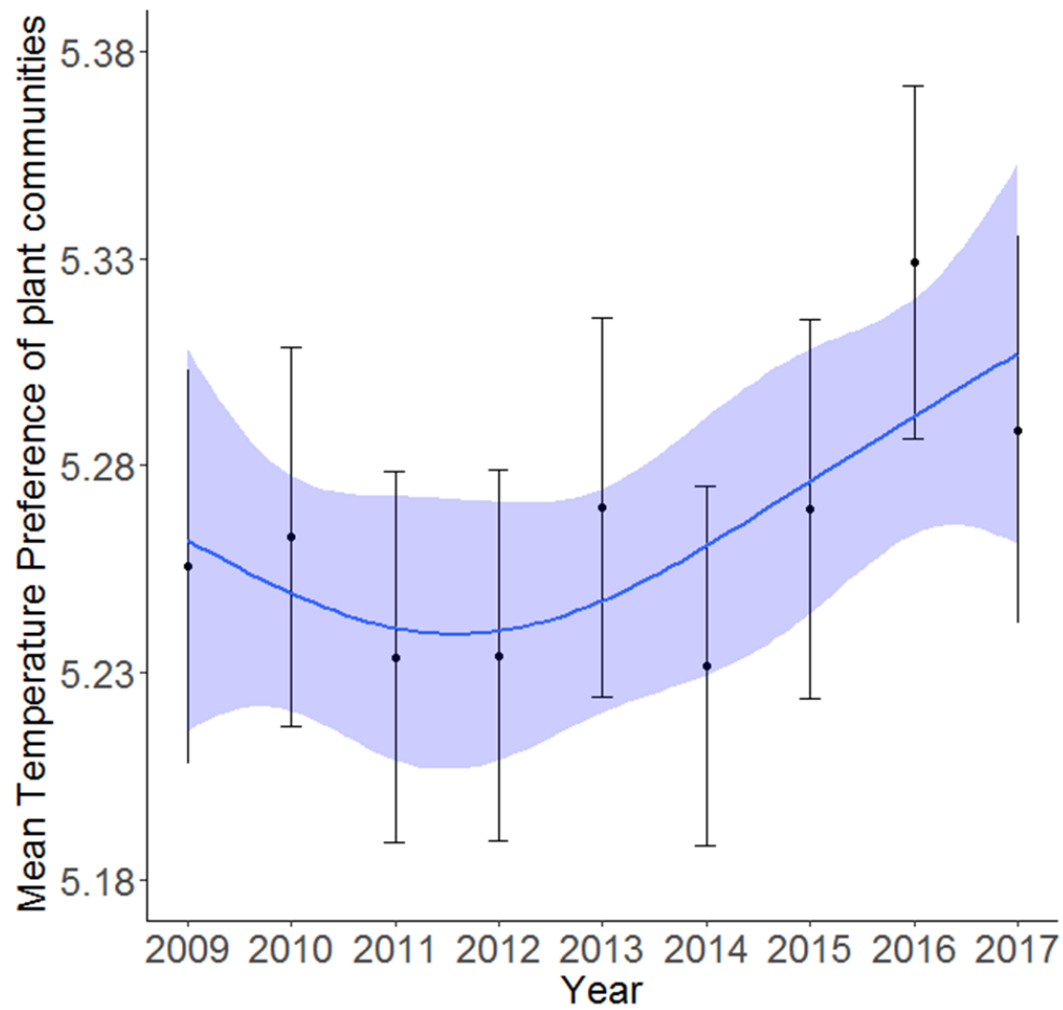


Figure S1. Spatial distribution of the Vigie-flore survey squares.



171

172 Figure S2. Regional temporal trend in MTP of plant communities from 2009 to 2017

173 calculated with abundance data in Île-de-France. The blue line is a generalized additive model

174 estimate of the temporal trend, with its associated standard error (blue band). The black dots

175 and error bars correspond to the inter-annual variations of the variable, with its associated

176 standard error.

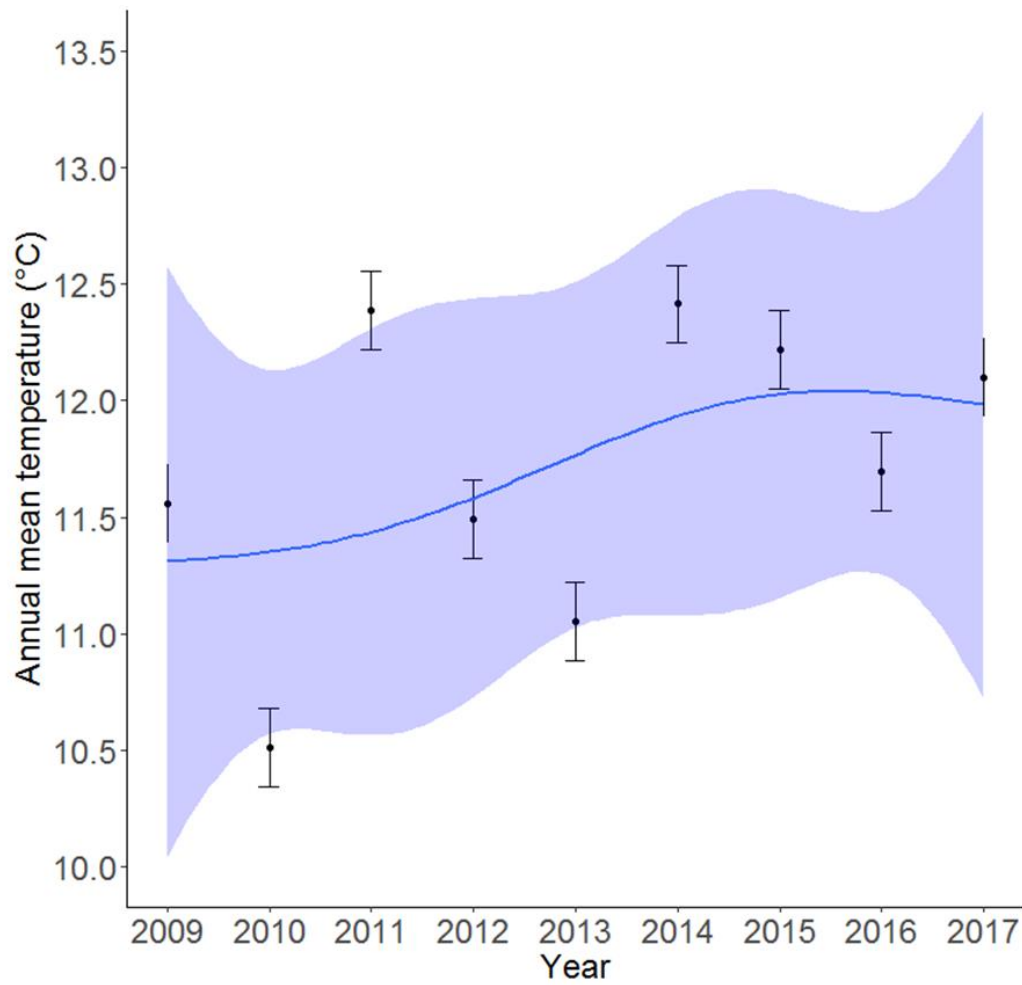


Figure S3. Temporal trend of annual mean temperature estimated from 2009 to 2017 on sampled sites in France. The blue line is a generalized additive model estimate of the temporal trend, with its associated standard error (blue band). The black dots and error bars correspond to the inter-annual variations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

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

184 Abadie Jean-Claude, Abadie Juliet, Abraham Christelle, Aguetant Laurent, Allemand Denis,

185 Anglaret Cédric, Arnould Loic, Arondel Bruno, Association Asterella, Association Les Amis

186 Du Jardin Botanique Littoral Paul Jovet, Association Les Marais Du Verdier, Association Tela

187 Botanica, Aupoix Alain, AUTRET Françoise, Avenas Élise, Avril Damien, Balard Yvette,

188 Balloux Gabriel, Baradat Mathilde, Barbet-Massin Morgane, Barreda Flavie, Bastin André,

189 Batsere Françoise, Baudet Nicolas, Baurens-Franc Christophe, Bebin Clément, Bégin Sophie,

190 Benezet Ruddy, Béraud Jean-Marc, Berger Romain, Biancardini Famille, Bircker Loic,

191 Bodiguel Brigitte, Boisbineuf Christelle, Boissier Marc, Bonnafoux Florence, Bonnafoux

192 Vincent, Bonneau Pierre, Bonneil Philippe, Bos Nathalie, Bosquet Christian, Bouard Hervé,

193 Boudies Catherine, Bouffard Frédéric, Bouligand Sandrine, Boutegege Serge, Bouveris

194 Nicole, Bouvier Chantal, Brajon Émilie, Brasseur Jean-Emmanuel, Breuil Anne, Briand

195 Françoise, Brin Antoine, Buckvald Nathalie, Bultel Yvan, Burchianti Mireille, Busch

196 Geneviève, Callewaert Pierre, Calme Catherine, Calmet Claire, Camenen-Houdayer Danièle

197 Canel Celie, Canevet Marie-Françoise, Caron Matthieu, Casenave Isabelle, Catieau Alexis,

198 Causeur Nicole, Cellier Pierre, Chabanois Gérard, Chamaux Jérôme, Chammard Émilie,

199 Chappert-Bessiere Joceline, Chapuis Gabriel, Chardinal Sophie, Chatelain Marion, Cherrier

200 Camille, Chevalier Adeline, Chevalier Richard, Chiffolleau Bertrand, Cholet Jérémie, Clochard

201 Alain, Cocquempot Marine, Coiffard Clément, Collectivité Territoriale (Reserve Naturelle)

202 Poupert, Conservatoire Botanique National Du Bassin Parisien Cbnbp, Coupiac Louis, Couric

203 Pauline, Crouzet Pierre, Cuille Rosalie, Danet Pierre, De Chastenet Cedissia, De Kerimel

204 Aymeric, De La Brosse Caroline, Delafoy Arielle, Delisle Pascal, Delphin Chantal,

205 Deschatres Aurelien, Desvois Régine, Devers Florence, Dezerald Hervé, Domenech Boris,

206 Douard Anne, Douarre Marie, Druez Flora, Dubosc Sarah, Duffaut Philippe, Dumas

207 Françoise, Dumez Nicolas, Durand Alexandre, Duron Quiterie, Duytschaever Francis, Engel

208 Geneviève, Eriksson Marion, Esnault Sarah, Etcheverry Georgette, Farcat Charlotte, Fatz
209 Pierre-Marie, Féral Camille, Fernandes Val, Filleur Lucas, Fournel Isabelle, Fourvel Jean-
210 Marc, Fried Guillaume, Galerme Jean Baptiste, Galerme Jean Pierre, Garnier Boudier Joanne,
211 Gatto Claire, Gaudry Jérôme, Gauthier Jacques, Gelin Muriel, Gelmetti Anne Marie, Geneix
212 Gilles, Georganidis Michèle, Germaine Clémence, Ghesquiere Jean-Christophe, Ghestem
213 Murielle, Goguet Liselotte, Gombault Clémentine, Gorremans Jean-Luc, Gotteland Pierre,
214 Gourdel Laurence, Gourlin Benjamin, Grange Milena, Grignon Céline, Guais Daniel,
215 Guichard Bernard, Guiller Clémence, Guittet Jean, Haeffner Hugues, Haenggi Philippe,
216 Hance Emmanuel, Happe David, Heuze Sylvère, Hillion Jeanne, Hubert Eric, Hugot Nicolas,
217 Huve Rosalia, Indorf Marc-Frederic, Jacot Pierre-Alain, Jagoda Daniel, Jardin Botanique
218 Besançon, Jargeat Patricia, Javaux Benjamin, Jaymond Delphine, Joset Henri, Jourdan
219 Christine, Joyaux Sandrine, Jullin Franck, Kania Daniel, Laffargue Lucie, Lafon Céline,
220 Lagier Anne-Marie, Lallemand Johann, Lambert Cécile, Lamouroux Paule, Lanciaux
221 Maxime, Lantuejoul Eric, Larbouillat Annick, Lavialle Jeanne, Le Fur Patrick, Le Garrec
222 Sandra, Leblanc Marie, Leclerc Catherine, Leduc Vinciane, Lefebvre Manon, Lekieffre Alix,
223 Lemoine Yves, Lemouzy Claire, Leneveu Justine, Lenne Patricia, Lepage Elen, Lequeuvre
224 Charly, Lerat Christine, Lerat Elodie, Lesné Sébastien, Leveslin Gérard, Leviol Isabelle,
225 Levy-Leonesio Patricia, Locqueville Jonathan, Lodziak Michel, Lonchamp Jean-Pierre,
226 Longeot Yves, Luciani Bernadette, Luigi Catherine, Mace Bruno, Machon Nathalie, Magrou
227 Nathalie, Maguet Nicolle, Marchal Pierre-Luc, Marsteau Christine, Martin Gabrielle, Martin
228 Hilaire, Martin Nicolas, Martinelli Marion, Masonnave François, Massouh Jacques, Master
229 Promo, Mathieu Daniel, Mathieu Joël, Maurel Noëlie, Meyer Claire-Lise, Michel Prisca,
230 Mistarz Margaux, Mollereau Aurore, Monferrand Christophe, Monthus Alain, Montpiéd
231 Pierre, Moragues Angels, Morelon Stéphanie, Morin Delphine, Morlon Claire, Motard Éric,
232 Muratet Audrey, Mutuel Arnaud, Naudin Marie-Noëlle, Nesty Matthieu, Nettleship-Begin

233 Pierre, Neveu Dany, Nicolas Dole, Nonglaton Gilles, Noraz Éloise, Onf Bergerie, Ostermann
234 Lukas, Oszczak Joëlle, Oudot Le Secq Marie-Pierre, Parachout Marie, Pascal Marie-Élise,
235 Pelatan François, Pellecuer Hélène, Perret Jeannette, Peyrard Morgan, Picard Francis, Pichard
236 Adeline, Pirot Manuel, Plessier Claudine, Politi Bertoncini Alzira, Ponchant Monique, Pons
237 Virginie, Porcher Pascale, Quénaon Christine, Ravot Charlotte, Raynaud Xavier, Réal Juliette,
238 Régentête Christine, Rémaud Dominique, Rémaud Marie Bernadette, Renault Gérard,
239 Réserve Naturelle Nationale Saint-Mesmin, Ressayre Patrick, Revault Pascal, Riberol Lionel,
240 Rist Delphine, Rivière Yann, Robert Jean-Louis, Rodrigues Mélanie, Ropars Lise, Rossier
241 Dominique, Rouger Caroline, Roussel Dany, Rouveyrol Paul, Sahl Amandine, Sanson Karine,
242 Sapaly Élise, Sartre Isabelle, Scheidegger Anne, Serret Patrick, Signoret Sandrine, Silberfeld
243 Thomas, Sonneville Hélène, Soulas Patrick, Spicher Fabien, Stratmains Emmanuel, Tasso
244 Dominique, Tauran Julien, Texier-Pauton Élodie, Thébault Ludovic, Thiebaut David, Thys
245 Évelyne, Tinchant Anne, Tinguy Hugues, Torre Fabrice, Tositti Arnaud, Toty Anne, Truong
246 Minh-Xuan, Turcati Laure, Tzvetan Gwladys Mai, Valette Nicolas, Van Panhuys-Sigler
247 Michèle, Vérite Vincent, Viallon Camille, Vidal Rodolphe, Videlot Vincent, Vilard Vanessa,
248 Villeneuve Aurélie, Virton-Lavorel Anthony, Wahl Marie-Salomé, Waligorski Stanislas,
249 Wernert Dominique, Wolff Anne, Ybres Nicolas.