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1 Short-term climate-induced change in French plant communities

2

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12

13 **ABSTRACT**

14 Latitudinal and altitudinal range shifts in response to climate change have been reported for  
15 numerous animal species, especially those with high dispersal capacities. In plants, the impact  
16 of climate change on species distribution or community composition has been documented  
17 mainly over long periods (decades) and in specific habitats, often forests. Here, we broaden  
18 the results of such long-term, focused studies by examining climate-driven changes in plant  
19 community composition over a large area (France) encompassing multiple habitat types and  
20 over a short period (2009-2017). To this end, we measured mean community thermal  
21 preference, calculated as the community-weighted mean of the Ellenberg temperature  
22 indicator value, using data from a standardized participatory monitoring scheme. We report a  
23 rapid increase in the mean thermal preference of plant communities at national and regional  
24 scales, which we relate to climate change. This reshuffling of plant community composition  
25 corresponds to a relative increase in the abundance of warm- vs. cold-adapted species.  
26 However, support for this trend was weaker when considering only the common species,  
27 including common annuals. Our results thus suggest for the first time that the response of  
28 plant communities to climate change involves subtle changes affecting all species rare and  
29 common, which can nonetheless be detected over short time periods. Whether such changes  
30 are sufficient to cope with the current climate warming remains to be ascertained.

31

32 **KEYWORDS**

33 Plants, monitoring, mean community thermal preference, climate change, lifespan, citizen  
34 science.

35

## 36 INTRODUCTION

37 Climate change is considered a significant global threat to biodiversity [1–3], with impacts  
38 from individuals to ecosystems. In ecological communities, climate change drives  
39 compositional change, in particular via latitudinal and altitudinal shifts, especially in species  
40 with high dispersal capacities, including birds, insects or marine invertebrates [3–5]. In plants,  
41 which are less mobile, elevation has shifted upward during the 20<sup>th</sup> century, e.g. in highland  
42 French temperate forests [6], although these shifts lag temperature change. In contrast,  
43 lowland forest plant communities have not shifted northward, highlighting their greater inertia  
44 [7] or higher shading mitigating climate warming [8]. Whether and how plant communities  
45 are able to track climate change in all habitats is still unclear.

46 Owing to the scarcity of available data, most studies demonstrating an effect of climate  
47 change on plant communities used heterogeneous data collected over decades and focused on  
48 a particular habitat. To understand better how climate change and other drivers influence  
49 biodiversity, real-time monitoring data using standardized schemes are required across large  
50 spatio-temporal scales [9]. Citizen science, the involvement of volunteers in research [10],  
51 represents a powerful tool that can contribute to investigating the impacts of climate change  
52 on biodiversity [4,11]. Such monitoring makes it possible to report subtle responses to climate  
53 change.

54 In this study, we examine nine years of change in plant community composition across  
55 France, using data collected through a participatory monitoring scheme, to assess whether  
56 such data can be used to detect short-term effects of climate warming beyond alpine or forest  
57 areas. The systematic sampling of monitoring sites particularly encompasses numerous  
58 lowland open habitats, which have received limited attention in studies of the response of  
59 plant communities to climate change. We address the following questions: (1) has the mean  
60 plant community thermal preference changed over the past nine years? (2) Can this change be

61 related to climatic variables? (3) Are the temporal changes in mean community thermal  
62 preference and in abundances of individual species related to species lifespan?

63

## 64 **MATERIALS AND METHODS**

### 65 **Monitoring data**

66 We used data from Vigie-flore, a French citizen science program monitoring wild flora. The  
67 data were collected yearly by 321 skilled amateur botanists between 2009 and 2017 in 586  
68 1kmx1km squares sampled from a systematic grid (one square every 10 km), which ensures  
69 representative sampling of habitats. Each square contains eight systematically distributed 10  
70 m<sup>2</sup> plots (Figure S1) divided into ten 1 m<sup>2</sup>-quadrats. In each quadrat, the presence of all  
71 vascular plants was recorded, as well as habitat type following the CORINE biotope  
72 nomenclature, a European hierarchical classification of vegetation types [12]. Most squares  
73 were in open habitats (27% artificial land cover, 29% farmland, 16% meadows vs. 22% in  
74 forests, Electronic Supplementary Material I). For each plot, the number of quadrats in which  
75 a species was observed provides a proxy for species abundance. Individual plots were  
76 recorded at different intensities over time, depending on the behaviour of recorders, such that  
77 on average there were 2.9 years of observation per plot, and 5.3 plots sampled per 1 km<sup>2</sup>  
78 square, for a total of 3,118 plots.

79

### 80 **Species characteristics**

81 We collected information for two species-specific attributes most likely to be involved in  
82 plant species response to climate change: (1) the Ellenberg temperature indicator value  
83 (hereafter ETIV), characterizing the optimum temperature class for growth and survival of a  
84 species (nine classes), and (2) lifespan (Electronic Supplementary Material II and Table S1).  
85 ETIV and lifespan were available for 1,709 and 1,780 out of the 2,428 species sampled,

86 representing 85.6% and 89.3% of total observations, respectively. We calculated the  
87 community-weighted Mean Thermal Preference (hereafter MTP), i.e. the abundance-weighted  
88 sum of ETIV of all species [13]. We also calculated MTP with presence/absence data instead  
89 of abundance, to test whether temporal trends could be detected with lower resolution data  
90 [14]. Finally, we calculated MTP within two extreme lifespan classes: annuals vs. perennials.  
91 The survey sites are not distributed homogeneously in space and time, which may cause  
92 spurious temporal trends in MTP due to a spatial displacement of sampled sites. To control for  
93 this, we performed the same analysis at a regional level, in Île-de-France, the region with the  
94 highest site density (188 squares sampled throughout the nine years, Figure S1).

95

#### 96 **Climate data**

97 For each plot, we collected daily precipitation sum, mean, minimum and maximum  
98 temperature between 2009 and 2017, from which we calculated 10 climatic variables per plot.  
99 Two variables used annual data: mean annual temperature and annual temperature anomaly;  
100 while the remaining eight used information from January to May (the growing period of most  
101 plant species): mean temperature, temperature anomaly, mean maximum temperature, number  
102 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  
103 pluviometry. We used a random forest analysis to extract the most important climatic variable  
104 explaining MTP, which was mean annual temperature (Electronic Supplementary Material III  
105 and Table S2).

106

#### 107 **Statistical analyses**

108 We first checked for a potential bias attributable to uneven sampling effort by verifying that  
109 there was no temporal trend in the average latitude of sampled sites. We then used Bayesian  
110 hierarchical models to estimate the temporal trend in MTP (1) at a national scale and within

111 Île-de-France, (2) using either abundance data or presence/absence data and (3) in  
112 communities where only annuals vs. only perennials species were retained (Electronic  
113 Supplementary Material IV). Note that this approach captures changes in the relative  
114 abundance of species with fixed thermal preference rather than changes in species-specific  
115 adaptation to new climatic conditions. We then examined the relationship between (1) the  
116 temporal change in MTP in a plot between 2009 and 2017, and (2) the temporal change in  
117 mean annual temperature over the same period, using Spearman's correlation coefficient.  
118 To further investigate the role of species lifespan in the community-level trends, we used  
119 Bayesian models to estimate the temporal trend in abundance for the 550 most common  
120 species (75 annuals and 349 perennials) observed at least four out of nine years and in at least  
121 ten squares (Electronic Supplementary Material IV). We tested whether species trends were  
122 related to lifespan (annuals vs. perennials), to ETIV, or to the interaction of both variables by  
123 a linear regression in which each species was weighted by the inverse of the standard error  
124 associated with the estimated temporal trend. All analyses were performed using R [15]  
125 (Electronic Supplementary Material V).

126

## 127 **RESULTS**

128 At the community level, MTP increased through time at the national scale, both with  
129 abundance and presence/absence data (Figure 1a,c), particularly in northern France  
130 (Electronic Supplementary Material IV). This increase was also observed within Île-de-France  
131 (Figures 1c and S2). The increase in MTP of plant communities occurred simultaneously with  
132 an increase in mean annual temperature (Electronic Supplementary Material III, Table S3,  
133 Figure S3), such that there was a significant positive but weak correlation between MTP  
134 change and the mean annual temperature change over time (Figure 1d): plots in which the  
135 temperature has increased tended to be also plots for which MTP has increased. Moreover, we

136 found a significant increase in MTP of annual, but not of perennial species, at national and  
137 regional scales (Figure 1b,c).

138

139 Changes at the community level were weakly explained by differences in temporal trends for  
140 common species considered independently. We found a significant relationship between  
141 species temporal trends and lifespan (Estimate=0.194,  $n=424$ ,  $df=1.402$ ,  $F=3.978$ ,  $P=0.047$ ,  
142 Figure 2). The interaction between ETIV and lifespan was marginally significant (Estimate=-  
143 0.028,  $n=424$ ,  $df=1.402$ ,  $F=3.013$ ,  $P=0.083$ ), but no relation was found between temporal  
144 trends and ETIV.

145

## 146 **DISCUSSION**

147 Our work complements longer-term, single habitat studies by documenting a small but steady  
148 increase in MTP of plant communities over all habitat types at national and regional scales,  
149 detectable over nine years only, and most likely driven by temperature change. This increase  
150 is measurable even with presence/absence data, suggesting a true reshuffling of plant  
151 communities, as opposed to mere abundance fluctuations of common species. In contrast to  
152 Bertrand and collaborators [7], who observed no response of lowland forest plant  
153 communities to climate change over a longer period, we show with a dataset encompassing  
154 mostly low-altitude sites that lowland plant communities can be modified by climate change,  
155 despite their limited dispersal capabilities. The difference may arise because our dataset  
156 contained a high proportion of open habitats, in which plant communities may experience  
157 higher turnover than in forests [8]. MTP changes resulted from local increases in the relative  
158 abundance of warm- vs. cold-adapted species, which, over nine years, are detectable in  
159 annuals but not perennials. Yet, examination of the temporal trends of the 424 most common  
160 annual or perennial species did not reveal this pattern. Non-congruence of the community vs.

161 species-level analysis, the latter covering only 55 % of the observations, suggests that all  
162 species, including rarer species, are affected and calls for a more thorough analysis of species  
163 traits likely to drive the observed changes.

164

165 The general trend of increased relative abundance of warm- vs. cold-adapted species is  
166 consistent with longer-term studies documenting responses to climate change via species  
167 latitudinal and altitudinal range shifts, or local changes in abundance (including local decline  
168 and extinction of cold-adapted species) [6–8,16,17]. Yet, the causal role of climate change in  
169 the observed increase in the MTP of plant communities still has to be confirmed, for example  
170 by checking that this increase is sustained in the near future, or by examining possible  
171 confounding drivers, such as eutrophication or urbanization. Urbanization is unlikely to be  
172 responsible for increased MTP, because only a quarter of plots are located in urban areas.  
173 Although the Ellenberg nitrogen indicator value is weakly but positively correlated with  
174 ETIV, the mean community nitrogen preference or the abundance of nitrophilous species did  
175 not increase over the same period (Electronic Supplementary Material VI and Figure S4).  
176 Therefore, eutrophication should have a limited role in the observed increase in MTP.

177

178 The detection of this subtle but rapid change in plant communities was made possible by  
179 citizen science monitoring and a large sampling effort in space and time. Such data can be of  
180 great value [18] but come with several caveats deserving further attention. For example,  
181 possible biases could be related to uneven sampling effort, identification errors or incomplete  
182 trait data. The effect of spatial heterogeneity in the sampling effort was tested by examining  
183 trends within a small region. Identification errors and missing trait data are unlikely to be  
184 systematically biased in favour of high or low species thermal preference, such that these  
185 problems should not influence our results. Finally, the observed trend in MTP could be caused

186 partly by temporal changes in species phenology. Because the Vigie-flore protocol  
187 recommends a single annual survey, there may be a phenology-influenced bias in species  
188 detection and identifiability against undeveloped or non-flowered species. Climate change has  
189 led to phenological shifts in flowering plants [19], which could increase the detectability of  
190 warm-adapted species as the climate warms.

191

192 Whether such rapid community changes are sufficient a response to current climate warming,  
193 or instead reflect mostly a maladaptive loss of cold-adapted species, remains to be  
194 ascertained. Future research efforts could also be focused on analysing trends in MTP across  
195 habitats or protection regimes and on identifying possible consequences of changes for biotic  
196 homogenization or plant-pollinator interactions.

197

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202 Karine Princé, Jeanne Vallet, Sandrine Pavoine, Guillaume Fried, François Chiron, Bruno  
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205

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209

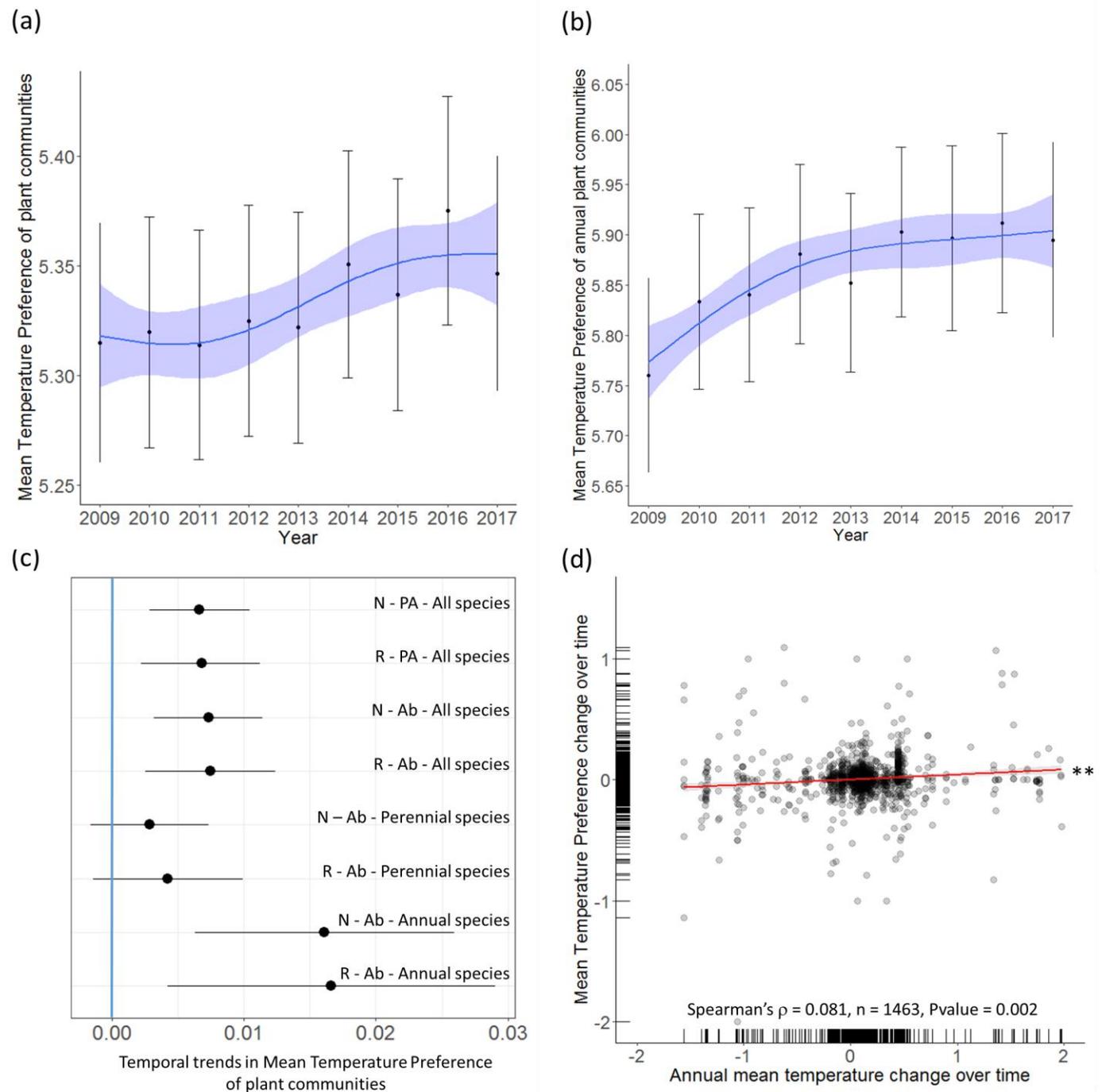
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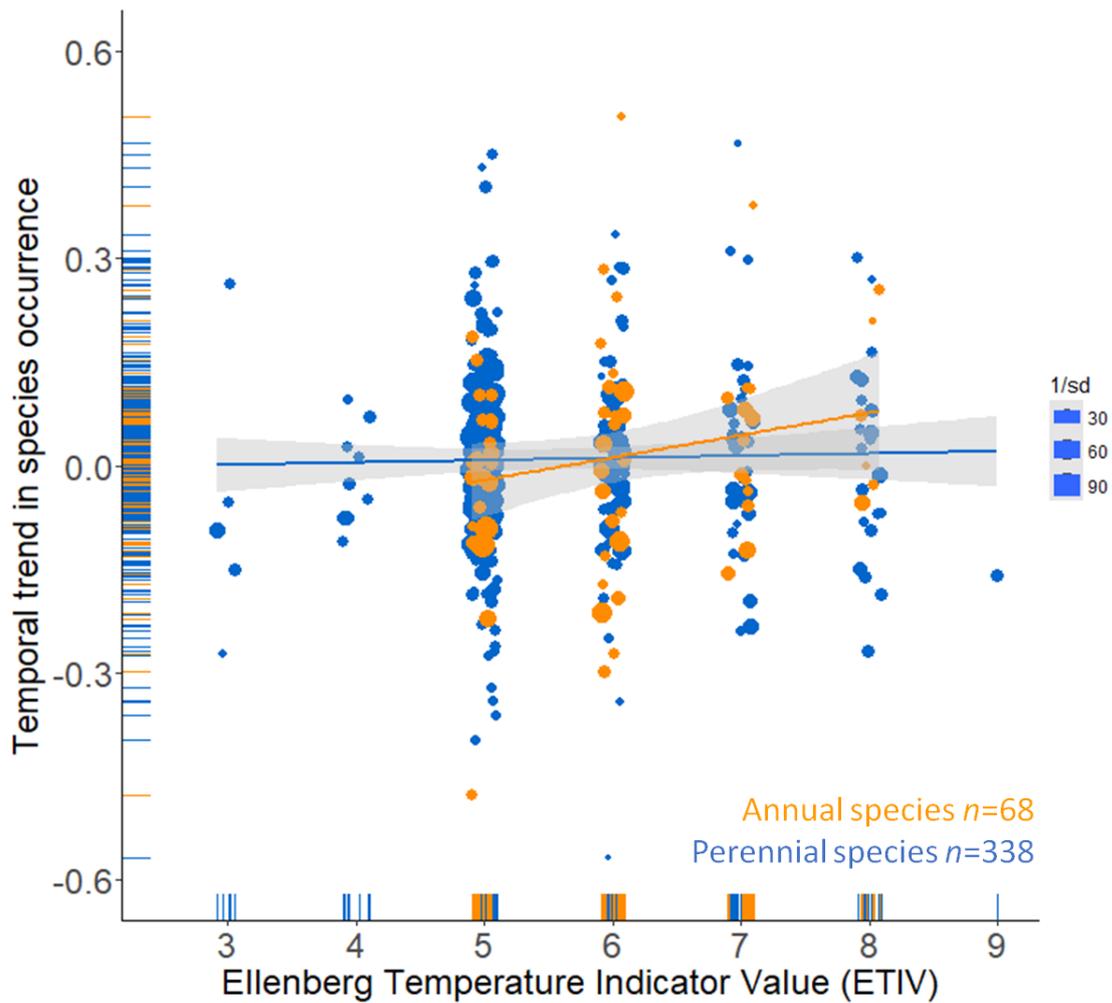
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264



267 Figure 1. National temporal trend in MTP of plant communities from 2009 to 2017 calculated  
 268 with abundance data, (a) for all species or (b) annual species only. The blue line is a  
 269 generalized additive model estimate of the temporal trend, with its associated standard error  
 270 (blue band). The black dots and error bars correspond to the inter-annual variations of the  
 271 variable, with its associated standard error. (c) Temporal trends in MTP from 2009 to 2017

272 estimated using Bayesian models. N/R: National/Regional scale, Ab/PA:  
273 Abundance/Presence-Absence data. Dots indicate the mean of the posterior distribution, and  
274 bars correspond to the 95 % credible interval for the temporal trends. (d) Correlation between  
275 the plant MTP change and the annual mean temperature change over time. Each point  
276 represents one plot.  
277



278

279 Figure 2. Relationship between the temporal trends of the most common species and their  
 280 ETIV for annuals (orange) and perennials (blue). Each dot represents the temporal trend of a  
 281 species, sized proportionally to the inverse of the standard error. Lines correspond to the  
 282 regressions (with slopes not significantly different from zero in both cases), with their  
 283 associated standard error (grey band).

284

285 ELECTRONIC SUPPLEMENTARY MATERIALS

286

287 Short-term climate-induced change in French plant communities

288

289 Gabrielle Martin<sup>1\*</sup>, Vincent Devictor<sup>2</sup>, Eric Motard<sup>3</sup>, Nathalie Machon<sup>1</sup>, Emmanuelle Porcher<sup>1</sup>

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298

## 300 I. Habitat of sampled plots

301 A total of 3,118 plots were sampled in 586 1kmx1km squares between 2009 and 2017 as part  
 302 of the Vigie-flore program. Habitat type following the CORINE biotope nomenclature [1] was  
 303 reported by observers for 2,985 plots (ca. 96% of plots). These plots were distributed among  
 304 the first levels of the CORINE biotope classification as follows: 21 plots in coastal habitats,  
 305 13 plots in wetland, 488 plots in grassland and shrub, 682 plots in woodland, 24 plots in  
 306 marsh and bog, 36 plots in rocky, habitats, 895 plots in agricultural habitats and 826 plots in  
 307 artificial land use.

308

## 309 II. Species attributes

310 We collected information for two species-specific attributes: (1) the Ellenberg temperature  
 311 indicator values (hereafter ETIV), characterizing the optimum temperature class for growth  
 312 and survival of a species (nine classes), from the database Baseflor [2], and (2) lifespan,  
 313 described using seven broad classes obtained by combining classes from the Bioflor [3] and  
 314 LEDA [4] databases (Table S1).

315

316 Table S1. Procedure used to combine lifespan information from Bioflor and LEDA traitbases.

Lifespan (Bioflor database)	Lifespan (LEDA database)	Single or combined lifespan categories	Number of species
a (annual)	Annuals	annual	17
a (annual) - b (biennial)	Annuals	annual/biennial	1
b (biennial)	Annuals	annual/biennial	1
p (perennial-pollakanthic)	Annuals	annual/perennial	1
a (annual)	annuals + perennials	annual/perennial	1
p (perennial-pollakanthic)	annuals + perennials	annual/perennial	1
p (perennial-pollakanthic)	annuals + perennials + poly-annuals < 5 years (short-lived perennials)	annual/perennial	2
a (annual) - b (biennial) - p (perennial-pollakanthic)	annuals + perennials + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
a (annual) - p (perennial-pollakanthic)	annuals + perennials + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	2
p (perennial-pollakanthic)	annuals + perennials + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	5

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

b (biennial) - h (perennial-hapaxanthic)	annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
a (annual)	annuals + summer annuals	annual	34
a (annual)	annuals + summer annuals + poly-annuals > 50 years (long-lived perennials)	annual/perennial	1
a (annual)	annuals + summer annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	10
a (annual) - b (biennial)	annuals + summer annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	2
a (annual)	annuals + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials)	annual/biennial/perennial	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/perennial	18
a (annual) - b (biennial)	annuals + summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	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/perennial	1
a (annual)	annuals + winter annuals	annual	2
a (annual)	annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	11
a (annual) - b (biennial)	annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	2
a (annual)	perennials	annual/perennial	2
a (annual) - p (perennial-pollakanthic)	perennials	annual/perennial	2
b (biennial) - p (perennial-pollakanthic)	perennials	biennial/perennial	1
h (perennial-hapaxanthic)	perennials	perennial	1
p (perennial-pollakanthic)	perennials	perennial	396
p (perennial-pollakanthic)	perennials + poly-annuals < 5 years (short-lived perennials)	perennial	28
p (perennial-pollakanthic)	perennials + poly-annuals < 5 years (short-lived perennials) + poly-annuals > 50 years (long-lived perennials)	perennial	1
p (perennial-pollakanthic)	perennials + poly-annuals < 5 years (short-lived perennials) + poly-annuals > 50 years (long-lived perennials) + poly-annuals 5-50 years (medium-lived perennials)	perennial	3
p (perennial-pollakanthic)	perennials + poly-annuals < 5 years (short-lived perennials) + poly-annuals 5-50 years (medium-lived perennials)	perennial	26
p (perennial-pollakanthic)	perennials + poly-annuals > 50 years (long-lived perennials)	perennial	11
p (perennial-pollakanthic)	perennials + poly-annuals > 50 years (long-lived perennials) + poly-annuals 5-50 years (medium-lived perennials)	perennial	2
a (annual)	perennials + poly-annuals 5-50 years (medium-lived perennials)	annual/perennial	1
a (annual) - p (perennial-pollakanthic)	perennials + poly-annuals 5-50 years (medium-lived perennials)	annual/perennial	2
p (perennial-pollakanthic)	perennials + poly-annuals 5-50 years	perennial	84

	(medium-lived perennials)		
a (annual)	perennials + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
b (biennial) - h (perennial-hapaxanthic)	perennials + strict monocarpic bi-annuals and poly-annuals	biennial/perennial	3
b (biennial) - h (perennial-hapaxanthic) - p (perennial-pollakanthic)	perennials + strict monocarpic bi-annuals and poly-annuals	biennial/perennial	1
b (biennial) - p (perennial-pollakanthic)	perennials + strict monocarpic bi-annuals and poly-annuals	biennial/perennial	3
p (perennial-pollakanthic)	perennials + strict monocarpic bi-annuals and poly-annuals	biennial/perennial	4
b (biennial)	perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials)	biennial/perennial	2
b (biennial) - p (perennial-pollakanthic)	perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials)	biennial/perennial	1
a (annual) - b (biennial) - h (perennial-hapaxanthic) - p (perennial-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/perennial	1
p (perennial-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/perennial	1
b (biennial) - p (perennial-pollakanthic)	perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials)	biennial/perennial	2
p (perennial-pollakanthic)	perennials + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials)	biennial/perennial	3
a (annual) - p (perennial-pollakanthic)	perennials + summer annuals	annual/perennial	3
b (biennial) - h (perennial-hapaxanthic) - p (perennial-pollakanthic)	perennials + summer annuals	annual/biennial/perennial	1
h (perennial-hapaxanthic) - p (perennial-pollakanthic)	perennials + summer annuals	annual/perennial	3
a (annual) - b (biennial) - p (perennial-pollakanthic)	perennials + summer annuals + poly-annuals < 5 years (short-lived perennials)	annual/biennial/perennial	1
a (annual) - p (perennial-pollakanthic)	perennials + summer annuals + poly-annuals < 5 years (short-lived perennials) + poly-annuals 5-50 years (medium-lived perennials)	annual/perennial	1
p (perennial-pollakanthic)	perennials + summer annuals + poly-annuals 5-50 years (medium-lived perennials)	annual/perennial	2
a (annual) - b (biennial)	perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials)	annual/biennial/perennial	1
p (perennial-pollakanthic)	perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials)	annual/biennial/perennial	1
h (perennial-hapaxanthic) - p (perennial-pollakanthic)	perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived	annual/biennial/perennial	1

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

a (annual)	summer annuals	annual	65
a (annual) - b (biennial) - p (perennial-pollakanthic)	summer annuals	annual/biennial/perennial	1
a (annual) - p (perennial-pollakanthic)	summer annuals	annual/perennial	1
p (perennial-pollakanthic)	summer annuals	annual/perennial	1
a (annual)	summer annuals + poly-annuals 5-50 years (medium-lived perennials)	annual/perennial	1
a (annual) - p (perennial-pollakanthic)	summer annuals + poly-annuals 5-50 years (medium-lived perennials)	annual/perennial	1
a (annual)	summer annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	9
a (annual) - b (biennial)	summer annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
a (annual) - b (biennial) - h (perennial-hapaxanthic)	summer annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
b (biennial)	summer annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
b (biennial) - p (perennial-pollakanthic)	summer annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	2
a (annual) - p (perennial-pollakanthic)	summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials)	annual/biennial/perennial	1
a (annual)	summer annuals + winter annuals	annual	19
a (annual) - b (biennial)	summer annuals + winter annuals	annual/biennial	1
a (annual) - p (perennial-pollakanthic)	summer annuals + winter annuals + poly-annuals < 5 years (short-lived perennials)	annual/perennial	1
a (annual)	summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	4
a (annual) - b (biennial)	summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	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/perennial	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 (perennial-pollakanthic)	winter annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
b (biennial)	winter annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
NA	annuals	annual	5
NA	annuals + summer annuals	annual	3
NA	perennials	perennial	57
NA	perennials + strict monocarpic bi-annuals and poly-annuals	biennial/perennial	1
NA	perennials + summer annuals + strict monocarpic bi-annuals and poly-annuals + poly-annuals 5-50 years (medium-lived perennials)	annual/biennial/perennial	1
NA	poly-annuals 5-50 years (medium-lived perennials)	perennial	3
NA	strict monocarpic bi-annuals and poly-annuals	biennial/perennial	1
NA	strict monocarpic bi-annuals and poly-annuals + poly-annuals < 5 years (short-lived perennials)	biennial/perennial	1
NA	summer annuals	annual	26

NA	summer annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	6
NA	summer annuals + winter annuals	annual	1
NA	summer annuals + winter annuals + strict monocarpic bi-annuals and poly-annuals	annual/biennial/perennial	1
NA	winter annuals	annual	1
a (annual)	NA	annual	72
a (annual) - b (biennial)	NA	annual/biennial	7
a (annual) - b (biennial) - h (perennial-hapaxanthic)	NA	annual/biennial/perennial	1
a (annual) - p (perennial-pollakanthic)	NA	annual/perennial	4
b (biennial)	NA	biennial	10
b (biennial) - h (perennial-hapaxanthic)	NA	biennial/perennial	2
b (biennial) - p (perennial-pollakanthic)	NA	biennial/perennial	3
h (perennial-hapaxanthic) - p (perennial-pollakanthic)	NA	perennial	1
p (perennial-pollakanthic)	NA	perennial	284
p (perennial-pollakanthic) - p (perennial-pollakanthic)	NA	perennial	1
NA	NA	NA	917

317

318

### 319 **III. Climate data and Random Forest analysis**

320

321 For each plot, we collected daily mean temperature, daily minimum temperature, daily  
322 maximum temperature and daily precipitation sum between 2009 and 2017 from the  
323 ENSEMBLES dataset [5], using data from the nearest E-OBS station in France on a 0.25  
324 degree grid. Climate data were extracted using the R package climateExtract [6], and devtools  
325 [7]. We then calculated 10 climatic variables per plot, two using annual data (mean annual  
326 temperature and annual temperature anomaly) and eight using information from January to  
327 May (growing period of many plants): mean temperature, temperature anomaly, mean  
328 maximum temperature, number of heatwave days ( $T^{\circ}\text{C} > 27^{\circ}\text{C}$ ), freezing days ( $T^{\circ}\text{C} < 0^{\circ}\text{C}$ ),  
329 rainy days, drought days, and pluviometry. The temperature anomaly is the sum of the  
330 differences between the observed daily temperature and the mean temperature over a period  
331 on a site.

332

333 We then performed a Random Forest regression analysis to identify the climatic variable(s)  
334 explaining the greatest variability in MTP of plant communities. The Random Forest analysis  
335 is a nonparametric technique derived from classification and regression trees. This method,  
336 which has been applied in various ecological studies [8,9], shows high accuracy and the  
337 ability to model complex interactions between variables. To perform the model, we defined  
338 two essential parameters: *mtry*, i.e. the number of variables to try at each split, and *ntree*, i.e.  
339 the number of trees to run. To maximize the accuracy of the Random Forest analysis, i.e.  
340 minimize the measure of the prediction error (Out Of Bag (OOB) error), *mtry* and *ntree* can  
341 be varied. We determined the parameter *mtry* thanks to the internal RF function TuneRF [R  
342 package randomForest, 10]; this function computes the optimal number of variables starting  
343 from the default (total number of variables/3 for regression) and tests half and twice this  
344 threshold for the value with the minimum OOB error rate. It is already known that a *mtry* of 1  
345 can produce good accuracy [10,11], but it is recommended to include at least two variables to  
346 avoid using also the weaker regressors as splitters [12]. Here, even if the best accuracy was  
347 obtained for a *mtry* of 1, we performed the Random Forest regression analysis with a *mtry* of  
348 2 following Grömping [12]. The *ntree* parameter was set to 1000 to obtain stable results.

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

355 Finally, as a result of the Random Forest regression analysis, we selected the annual mean  
356 temperature, the most relevant climatic variable by ranking the variables according to their

357 importance measure (Table S2).

358 We performed a linear regression of the annual mean temperature against years to describe the  
359 temporal trend of climate change on the sampled plots of the study. We included geographical  
360 coordinates in the model to account for residual spatial autocorrelation. We recovered one  
361 slope per square, since climate data were only available at that scale; all plots within a scale  
362 were thus attributed the same temporal trend in climate data, describing the temporal trend of  
363 annual mean temperature.

364

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

<b>Climatic variables</b>	<b>Importance</b>
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

367

368

#### 369 **IV. Estimation of temporal trends in mean temperature preference and species** 370 **occurrence**

371 We performed Bayesian hierarchical models to estimate the temporal trend in MTP of plant  
372 communities (1) at a national scale and within Île-de-France, (2) using either abundance data  
373 or presence/absence data and (3) of annuals vs. perennials species. Note that MTP is  
374 comparable to the Community Temperature Index [13], but is not a direct measure of mean

375 temperature, because ETIV consists in classes of temperature preference. The underlying  
376 model describes the MTP value as a function of year for all plant communities. We assumed  
377 that MTP of plant communities was normally distributed, with a mean that depended linearly  
378 on year, geographical coordinates and survey square, and constant variance. The linear model  
379 was the following:

$$380 \quad MTP_{ijk} = m + a*year_i + b*lat_{ijk} + c*long_{ijk} + d*lat_{ijk}^2 + e*long_{ijk}^2 + Square_j + \sigma^2_{ijk}$$

381 where  $MTP_{ijk}$  is the mean temperature preference of the plant community in plot  $k$  of square  $j$   
382 and year  $i$ ,  $m$  is the intercept,  $lat$  and  $long$  are the latitude and longitude of the plot,  $Square$  is  
383 the random effect of square with variance  $\sigma^2_s$  and  $\sigma^2_{ijk}$  is the residual variance. We chose to  
384 model non-linear spatial patterns in MTP squared latitude and longitude terms over more  
385 complex models, because on visual examination of the relationship between MTP and latitude  
386 or longitude, we expected mostly a linear effect, potentially with a plateau at high or low  
387 latitudes that a second order polynomial model correctly represents.

388 Note that we performed a linear regression to test for an interaction between latitude and  
389 temporal trend of the MTP in order to detect spatial differences at the national scale (not  
390 detailed here). At the national scale, the temporal trend increased significantly with latitude,  
391 i.e. the trend was significantly larger in northern vs. southern France (significant latitude:year  
392 interaction, not shown).

393 We also performed Bayesian hierarchical models to generate estimates of the temporal trend  
394 in common species abundance, as estimated at the 10m<sup>2</sup> plot level by the number of 1m<sup>2</sup>  
395 quadrats in which these species were observed. We selected the 550 most common species  
396 that were observed at least four out of nine years and in at least ten squares. We modelled  
397 species abundance assuming a binomial distribution with  $n = 10$  trials<sup>1</sup> and a logit-  
398 transformed probability  $p$  depending linearly on year, survey plot, square and geographical

---

<sup>1</sup> The 10 quadrats within a plot are always sampled; there are thus no missing data within a plot.

399 coordinates as follows:

$$400 \text{ logit}(p_{ijk}) = m + a \cdot \text{year}_i + b \cdot \text{lat}_{ijk} + c \cdot \text{long}_{ijk} + d \cdot \text{lat}_{ijk}^2 + e \cdot \text{long}_{ijk}^2 + \text{Square}_j + \text{Plot}_k$$

401 where  $p_{ijk}$  is the probability to observe the species in each 1m<sup>2</sup> square of plot  $k$  of square  $j$  and

402 year  $i$ ,  $m$  is the intercept,  $lat$  and  $long$  are the latitude and longitude of the plot,  $Square$  is the

403 random effect of square with variance  $\sigma_s^2$ ,  $Plot$  is the random effect of plot with variance  $\sigma_p^2$ .

404 For all Bayesian hierarchical models, we chose only non-informative priors, sampled from

405 Gaussian distributions with a mean of 0 and a variance of  $10^{10}$  for most parameters, and

406 gamma distributions with shape parameter  $k = 0.001$  and rate  $\beta = 0.001$  for precision (inverse

407 of variance) parameters. Parameters were estimated by fitting the model in a Bayesian mode

408 of inference using JAGS [14], through R [15] using the package R2jags [16]. Four chains

409 were run using priors to draw 100,000 MCMC iterations, discarding the first 50,000

410 iterations. Samples were thinned by 1 in 10 to reduce autocorrelation and obtain mean trends

411 from the remaining posterior distributions. Convergence was checked using the Rubin

412 statistics (Rhat), comparing within-chain variance to between-chain variance [17] (all Rhat <

413 1.2) and visual inspection of the traceplots (superposition of the 4 chains) produced through

414 the R package mcmcplots [18]. Posterior mean community and species trends were

415 interpreted as different from zero when 95 % of the highest posterior density interval did not

416 include zero.

417

## 418 **V. R packages used**

419 All analyses were performed using R version 3.2.4 [15] and R packages *Taxonstand* version

420 2.1 [19], R packages *TR8* [20], R packages *climateExtract* version 0.2.0 [6], R packages

421 *randomForest* [10], R packages *caret* version 6.0-78 [21], R packages *plotmo* version 3.3.4

422 [22], R packages *R2jags* version 0.5-7 [16], R packages *mcmcplots* version 0.4.2 [18], R

423 packages *car* [23], R packages *lme4* [24], R packages *nlme* version 3.1-131 [25], R packages

424 *dplyr* version 0.7.3 [26], R packages *reshape2* [27], R packages *devtools* version 1.13.4 [7], R  
425 packages *effects* version 2.1.0 [28], R packages *ggplot2* version 2.1.0 [29], R packages  
426 *ggthemes* version 3.4.0 [30], R packages *gridExtra* version 2.3 [31]. Plant functional traits  
427 were collected using the R package TR8 [20].

428

## 429 **VI. Relationship between Ellenberg Temperature and Ellenberg Nitrogen Indicators**

### 430 **Values**

431 Across the 1,473 species for which we could obtain Ellenberg indicator values (out of the  
432 2,428 species of the Vigie-flore dataset), we observed that the Ellenberg temperature indicator  
433 value was positively correlated with the Ellenberg nitrogen indicator value (i.e. nitrogen  
434 preference, Pearson's correlation = 0.27), although the correlation was not very strong. There  
435 is thus a possibility that some of the changes in plant community composition we observed  
436 are also driven by ecosystem eutrophication, in addition to climate warming. To rule out this  
437 possibility, we tested whether mean nitrogen preference changed over time in the plant  
438 communities we monitored. To this end, we calculated the Community Weighted-Mean  
439 Ellenberg nitrogen indicator value (hereafter ENIV for the species characteristic, and MNP for  
440 the community-level Mean Nitrogen Preference), in the same way as the Mean Temperature  
441 Preference. We used a Bayesian hierarchical model to estimate the temporal trend in MNP in  
442 plant communities. The linear model was similar to the one we used for Mean Temperature  
443 Preference:

$$444 \text{MNP}_{ijk} = m + a \cdot \text{year}_i + b \cdot \text{lat}_{ijk} + c \cdot \text{long}_{ijk} + d \cdot \text{lat}_{ijk}^2 + e \cdot \text{long}_{ijk}^2 + \text{Square}_j + \sigma_{ijk}^2$$

445 where  $\text{MNP}_{ijk}$  is the mean nitrogen preference of the plant community in plot  $k$  of square  $j$  and  
446 year  $i$ ,  $m$  is the intercept,  $\text{lat}$  and  $\text{long}$  are the latitude and longitude of the plot,  $\text{Square}$  is the  
447 random effect of square with variance  $\sigma_s^2$  and  $\sigma_{ijk}^2$  is the residual variance.

448

449 The temporal trend in MNP was not different from zero (Figure S4,  $-0.0047$ ,  $CI_{95\%}=[-0.013,$   
450  $0.0036]$ ), i.e. the mean Ellenberg value for nitrogen preference of plant communities has not  
451 changed significantly over the past nine years, which suggests that the increase in Mean  
452 Temperature Preference we observed is unlikely to be driven by the (weak) correlation  
453 between the thermal preference and the nitrophily of plant species. In other words, while we  
454 do observe an increase in the relative abundance of thermophilic species (increase in MTP),  
455 the relative abundance of nitrophilous species remains stable.

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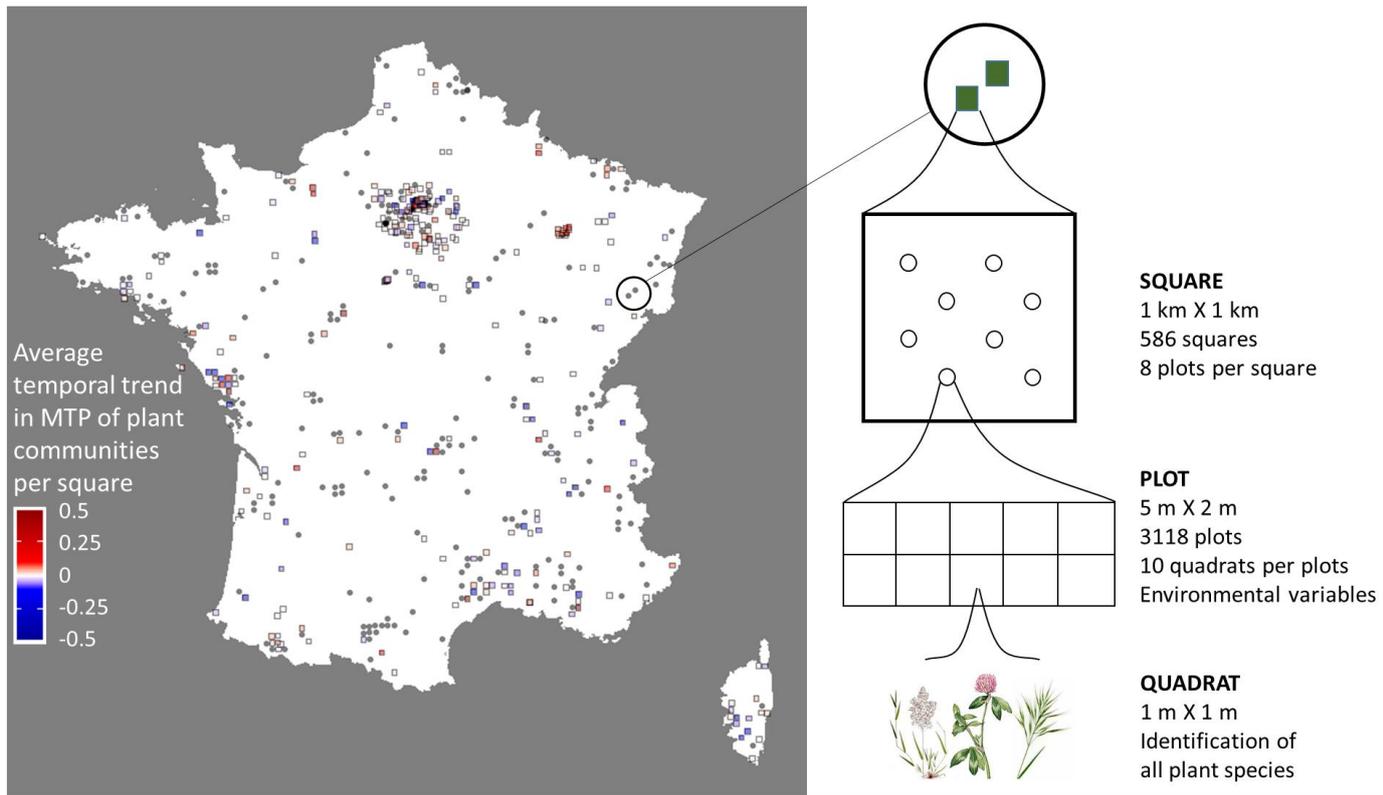
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- 508
- 509

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

<b>Fixed effects</b>	<b><i>n</i></b>	<b>Estimate</b>	<b>Standard error</b>	<b>Chisq</b>	<b><i>P</i> value</b>
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

512

513



514

515 Figure S1. Spatial distribution and hierarchical structure of the Vigie-flore sampling sites.

516 Plant species are sampled in 1 km X 1 km squares. In each square, plant species were

517 recorded in several plots with a standardized protocol. On the map, square colours indicate the

518 average (over all plots) temporal trend in Mean Temperature Preference (MTP) of plant

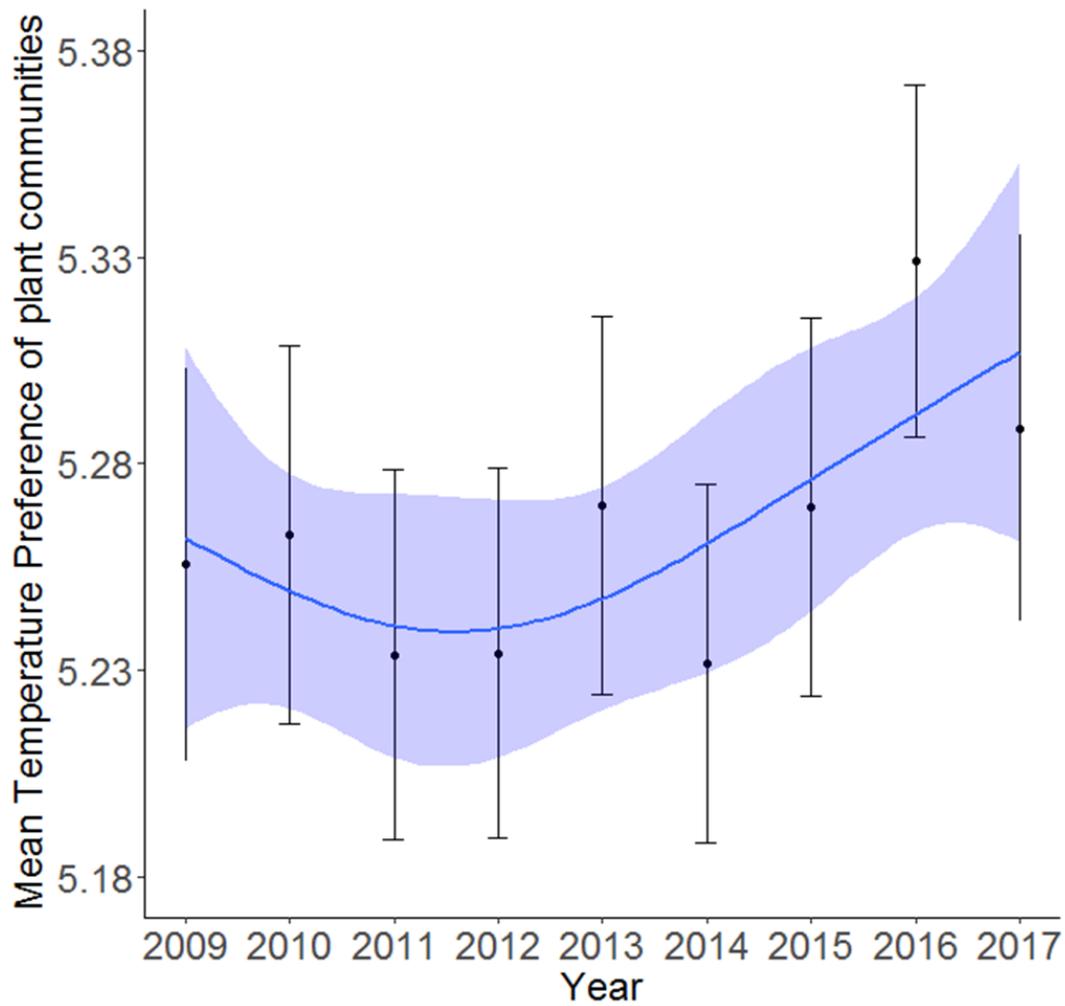
519 communities on the study period. Six squares had average temporal trends in MTP of plant

520 communities greater than 0.5 (0.51, 0.55, 0.62 and 1) or below -0.5 (-0.67 and -0.79), they

521 were capped at 0.5 and -0.5 respectively to improve readability. Plots and squares that were

522 surveyed only once, for which no temporal trend could be calculated, are plotted as circles.

523



524

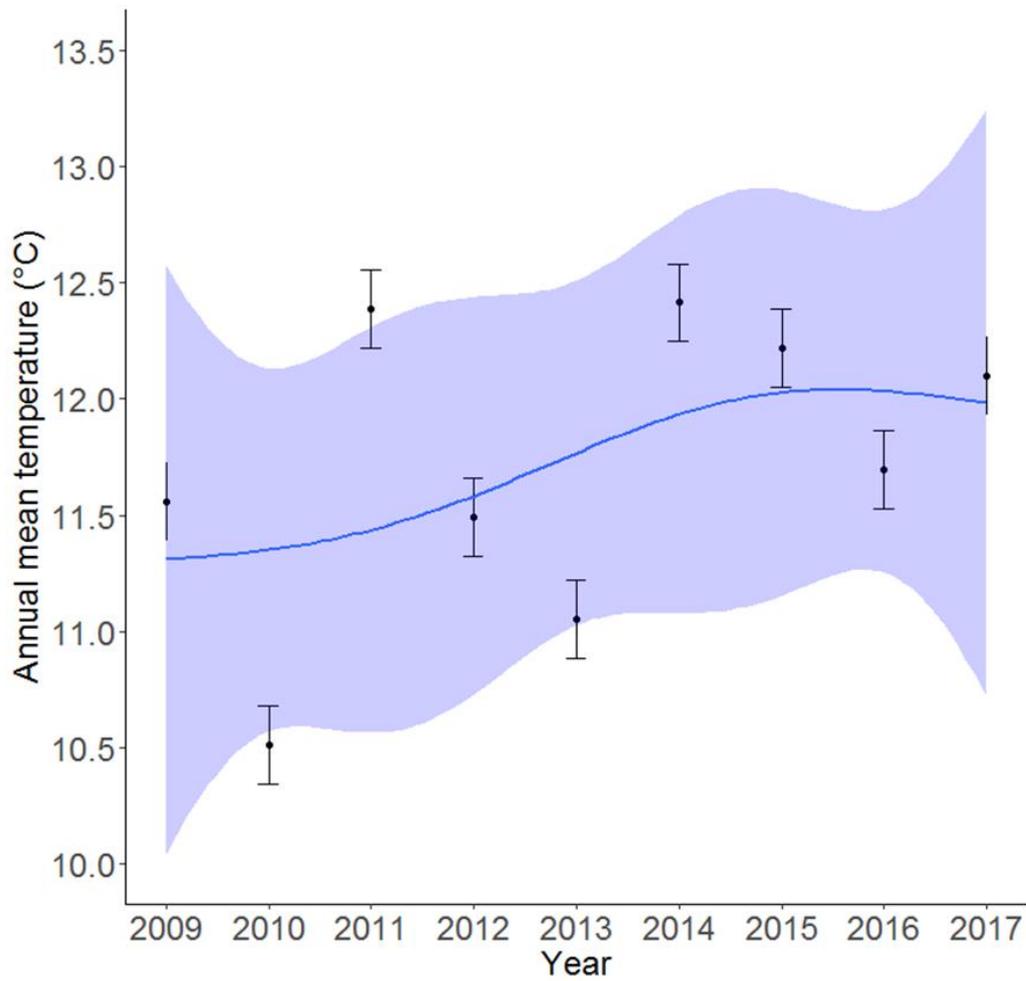
525 Figure S2. Regional temporal trend in MTP of plant communities from 2009 to 2017

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

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

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

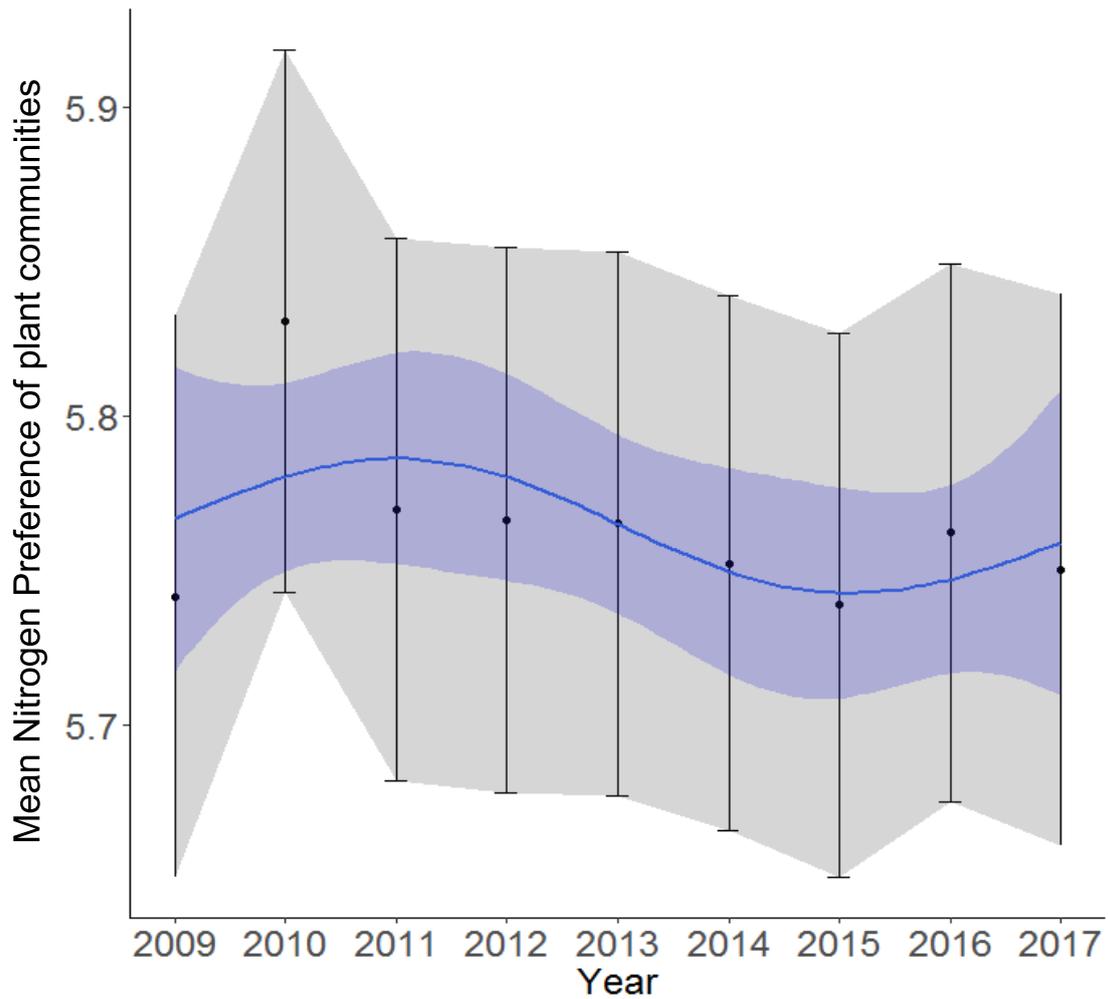
529 standard error.



530

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

535



536

537 Figure S4. National temporal trend in the mean nitrogen preference of plant communities

538 from 2009 to 2017 calculated with abundance data for all species. The blue line is a

539 generalized additive model estimate of the temporal trend, with its associated standard error

540 (blue band). The black dots and error bars correspond to the inter-annual variation of the

541 variable, with its associated standard error.

542

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549 Francine, Baudet Nicolas, Baurens-Franc Christophe, Bebin Clément, Bégin Sophie, Benezet  
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