

Research



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Community ecology

Short-term climate-induced change in French plant communities

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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 broaden the results of such long-term, focused studies by examining climate-driven changes in plant community composition over a large area (France) encompassing multiple habitat types and over a short period (2009–2017). To this end, we measured mean community thermal preference, calculated as the community-weighted mean of the Ellenberg temperature indicator value, using data from a standardized participatory monitoring scheme. We report a rapid increase in the mean thermal preference of plant communities at national and regional scales, which we relate to climate change. This reshuffling of plant community composition corresponds to a relative increase in the abundance of warm- versus cold-adapted species. However, support for this trend was weaker when considering only the common species, including common annuals. Our results thus suggest for the first time that the response of plant communities to climate change involves subtle changes affecting all species rare and common, which can nonetheless be detected over short time periods. Whether such changes are sufficient to cope with the current climate warming remains to be ascertained.

1. Introduction

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

Owing to the scarcity of available data, most studies demonstrating an effect of climate change on plant communities used heterogeneous data collected over decades and focused on a particular habitat. To understand better how climate change and other drivers influence biodiversity, real-time monitoring data

using standardized schemes are required across large spatio-temporal scales [9]. Citizen science, the involvement of volunteers in research [10], represents a powerful tool that can contribute to investigating the impacts of climate change on biodiversity [4,11]. Such monitoring makes it possible to report subtle responses to climate change.

In this study, we examine nine years of change in plant community composition 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 beyond alpine or forest areas. The systematic sampling of monitoring sites particularly encompasses numerous lowland open habitats, which have received limited attention in studies of the response of plant communities to climate change. We address the following questions: (1) has the mean plant community thermal preference changed over the past nine years? (2) Can this change be related to climatic variables? (3) Are the temporal changes in mean community thermal preference and in abundances of individual species related to species lifespan?

2. Material and methods

(a) Monitoring data

We used data from Vigie-flore, a French citizen science programme monitoring wild flora. The data were collected yearly by 321 skilled amateur botanists between 2009 and 2017 in 586 1×1 km squares sampled from a systematic grid (one square every 10 km), which ensures representative sampling of habitats. Each square contains eight systematically distributed 10 m^2 plots (electronic supplementary material, figure S1) divided into 10 1 m^2 quadrats. In each quadrat, the presence of all vascular plants was recorded, as well as habitat type following the CORINE biotope nomenclature, a European hierarchical classification of vegetation types [12]. Most squares were in open habitats (27% artificial land cover, 29% farmland, 16% meadows versus 22% in forests, electronic supplementary material, I). For each plot, the number of quadrats in which a species was observed provides a proxy for species abundance. Individual plots were recorded at different intensities over time, depending on the behaviour of recorders, such that on average there were 2.9 years of observation per plot, and 5.3 plots sampled per 1 km^2 square, for a total of 3118 plots.

(b) Species characteristics

We collected information for two species-specific attributes most likely to be involved in plant species response 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) lifespan (electronic supplementary material, II and table S1). ETIV and lifespan were available for 1709 and 1780 out of the 2428 species sampled, representing 85.6% and 89.3% of total observations, respectively. We calculated the community-weighted mean thermal preference (hereafter MTP), i.e. the abundance-weighted sum of ETIV of all species [13]. We also calculated MTP with the presence/absence data instead of abundance, to test whether temporal trends could be detected with lower resolution data [14]. Finally, we calculated MTP within two extreme lifespan classes: annuals versus 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, the region with the highest site density

(188 squares sampled throughout the nine years; electronic supplementary material, figure S1).

(c) Climate data

For each plot, we collected daily precipitation sum, mean, minimum and maximum temperature between 2009 and 2017, from which we calculated 10 climatic variables per plot. Two variables used annual data: mean annual temperature and annual temperature anomaly; while the remaining eight used information from January to May (the growing period of most plant species): 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. We used a random forest analysis to extract the most important climatic variable explaining MTP, which was mean annual temperature (electronic supplementary material, III and table S2).

(d) Statistical analyses

We first checked for a potential bias attributable to uneven sampling effort by verifying that there was no temporal trend in the average latitude of sampled sites. We then used 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) in communities where only annuals versus only perennials species were retained (electronic supplementary material, IV). Note that this approach captures changes in the relative abundance of species with fixed thermal preference rather than changes in species-specific adaptation to new climatic conditions. We then examined the relationship between (1) the temporal change in MTP in a plot between 2009 and 2017, and (2) the temporal change in mean annual temperature over the same period, using Spearman's correlation coefficient.

To further investigate the role of species lifespan in 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) observed at least four out of nine years and in at least 10 squares (electronic supplementary material, IV). We tested whether species trends were related to lifespan (annuals versus perennials), 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 [15] (electronic supplementary material, V).

3. Results

At the community level, MTP increased through time at the national scale, both with abundance and presence/absence data (figure 1*a,c*), particularly in northern France (electronic supplementary material, IV). This increase was also observed within Île-de-France (figure 1*c* and electronic supplementary material, figure S2). The increase in MTP of plant communities occurred simultaneously with an increase in mean annual temperature (electronic supplementary material, III, table S3 and figure S3), such that there was a significant positive but weak correlation between MTP change and the mean annual temperature change over time (figure 1*d*): plots in which the temperature had increased tended to be also plots for which MTP had increased. Moreover, we found a significant increase in MTP of annual, but not of perennial species, at national and regional scales (figure 1*b,c*).

Changes at the community level were weakly explained by differences in temporal trends for common species

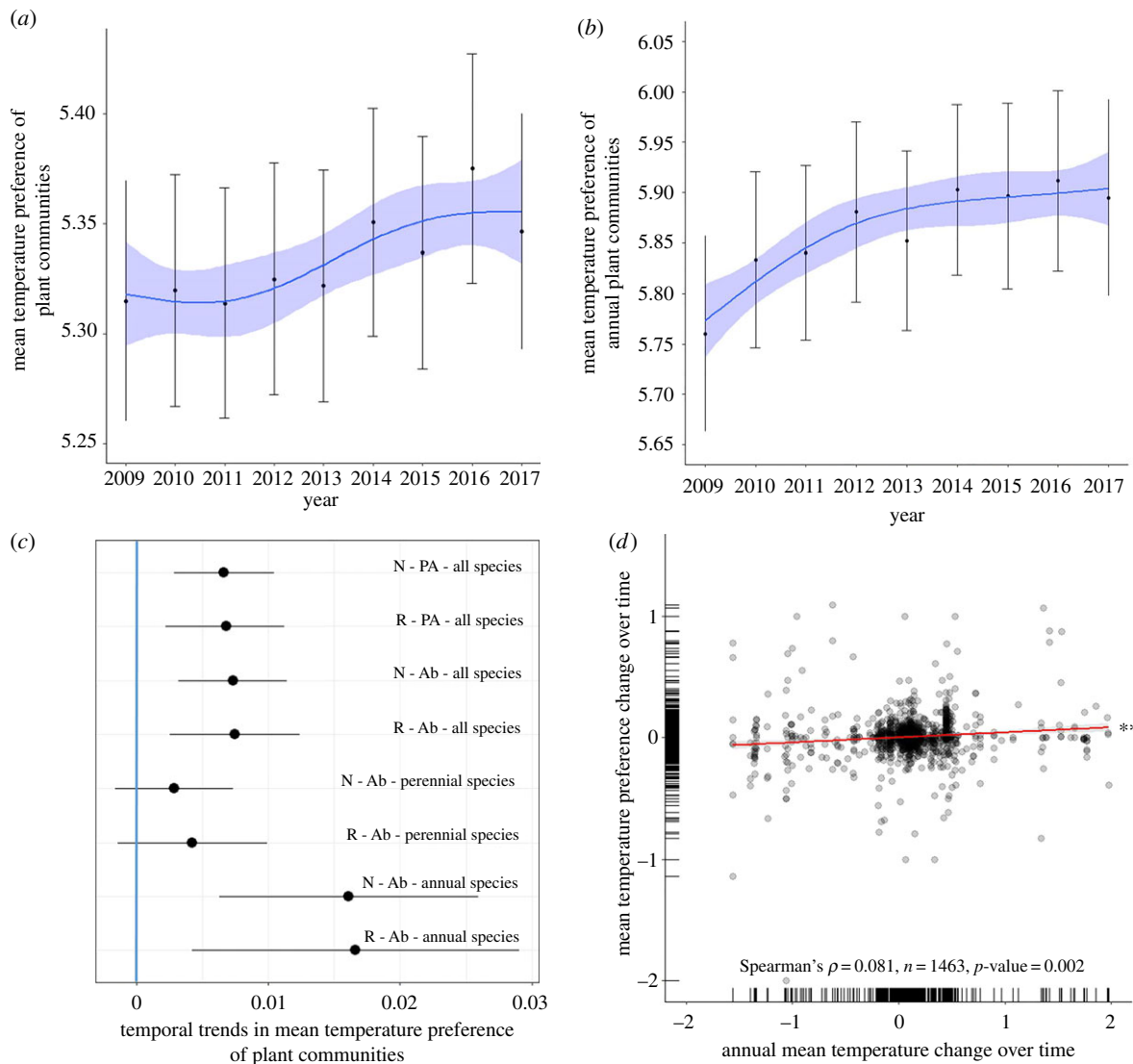


Figure 1. National temporal trend in MTP of plant communities from 2009 to 2017 calculated with abundance data, (a) for all species or (b) annual species only. The blue line is a generalized additive model estimate of the temporal trend, with its associated standard error (blue band). The black dots and error bars correspond to the inter-annual variations of the variable, with its associated standard error. (c) Temporal trends in MTP from 2009 to 2017 estimated using Bayesian models. N/R: national/regional scale, Ab/PA: abundance/presence–absence data. Dots indicate the mean of the posterior distribution, and bars correspond to the 95% credible interval for the temporal trends. (d) Correlation between the plant MTP change and the annual mean temperature change over time. Each point represents one plot.

considered independently. We found a significant relationship between species temporal trends and lifespan (estimate = 0.194, $n = 424$, d.f. = 1.402, $F = 3.978$, $p = 0.047$; figure 2). The interaction between ETIV and lifespan was marginally significant (estimate = -0.028 , $n = 424$, d.f. = 1.402, $F = 3.013$, $p = 0.083$), but no relation was found between temporal trends and ETIV.

4. Discussion

Our work complements longer-term, single habitat studies by documenting a small but steady increase in MTP of plant communities over all habitat types at national and regional scales, detectable over nine years only, and 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 *et al.* [7], who observed no response of lowland forest plant communities to climate change over 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 [8]. MTP changes resulted from local increases in the relative abundance of warm- versus cold-adapted species, which, over nine years, are detectable in annuals but not perennials. Yet, examination of the temporal trends of the 424 most common annual or perennial species did not reveal this pattern. Non-congruence of the community versus species-level analysis, the latter covering only 55% of the observations, suggests that all species, including rarer species, are affected and calls for a more thorough analysis of species traits likely to drive the observed changes.

The general trend of increased relative abundance of warm- versus cold-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

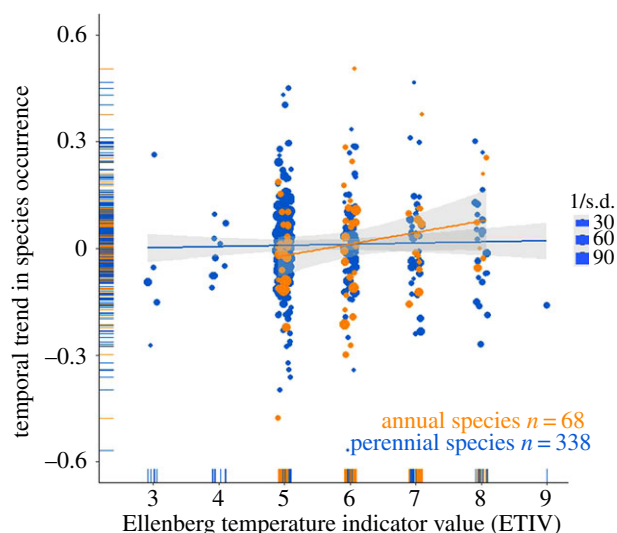


Figure 2. Relationship between the temporal trends of the most common species and their ETIV for annuals (orange) and perennials (blue). Each dot represents the temporal trend of a species, sized proportionally to the inverse of the standard error. Lines correspond to the regressions (with slopes not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

extinction of cold-adapted species) [6–8,16,17]. Yet, the causal role of climate change in the observed increase in the MTP of plant communities still has to be confirmed, for example, by checking that this increase is sustained in the near future, or by examining possible confounding drivers, such as eutrophication or urbanization. Urbanization is unlikely to be responsible for increased MTP, because only a quarter of plots are located in urban areas. Although the Ellenberg nitrogen indicator value is weakly but positively correlated with ETIV, the mean community nitrogen preference or the abundance of nitrophilous species did not increase over the same period (electronic supplementary material, VI and figure S4). Therefore, eutrophication should have a limited role in the observed increase in MTP.

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 come with several caveats deserving further attention. For example, possible biases could be related to uneven sampling effort, identification errors or incomplete trait data. The effect of spatial heterogeneity in the sampling effort was tested by examining trends within a small region. Identification errors and missing trait data are unlikely to be systematically biased in favour of high or low species 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 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 a sufficient response to current climate warming, or instead reflect mostly a maladaptive loss of cold-adapted species, remains to be ascertained. Future research efforts could also focus on analysing trends in MTP across habitats or protection regimes and on identifying possible consequences of changes for biotic homogenization or plant–pollinator interactions.

Data accessibility. Datasets and code are available at <https://sandbox.zenodo.org/record/245806#.W7OIVqKaHvY>.

Competing interests. We declare we have no competing interests.

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