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Lise Maciejewski, Emilien Kuhn, Anne Gégout-Petit, Jean-Claude Gégout. Natura 2000 forest habitats: climatic debt in lowlands and thermophilization in highlands. *Biodiversity and Conservation*, 2020, 29 (13), pp.3689-3701. 10.1007/s10531-020-02044-z . hal-03045938

HAL Id: hal-03045938

<https://hal.science/hal-03045938>

Submitted on 21 Apr 2023

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TITLE: Natura 2000 forest habitats: climatic debt in lowlands and thermophilization in highlands

Running head: habitat shift

NAMES OF THE AUTHORS: Lise Maciejewski^{a,b}, Emilien Kuhn^a, Anne Gégout-Petit^c and Jean-Claude Gégout^a

Affiliations of the authors:

^a Université de Lorraine, AgroParisTech, INRAE, UMR Silva, 14 rue Girardet F-54000 Nancy, France.

^b OFB, MNHN, CNRS, UMS 2006 PatriNat, CP 41, 36 rue Geoffroy-Saint-Hilaire F-75005 Paris, France.

^c Université de Lorraine, CNRS, Inria, IECL, B.P. 70239, F-54506 Vandoeuvre-lès-Nancy Cedex, France

Email Adresses

Lise Maciejewski lise.maciejewski@agroparistech.fr

Emilien Kuhn kuhn.emilien@brasserietumulte.fr

Anne Gégout-Petit anne.gegout-petit@univ-lorraine.fr

Jean-Claude Gégout jean-claude.gegout@agroparistech.fr

ORCID:

Lise Maciejewski 0000-0002-9142-0507

Emilien Kuhn 0000-0001-8371-1630

Jean-Claude Gégout 0000-0002-5760-9920

Corresponding author: Lise Maciejewski, lise.maciejewski@agroparistech.fr

KEYWORDS: climate change; forest ecosystem; global warming; habitat of Community interest; Habitats Directive; public policies.

ACKNOWLEDGMENTS

We thank the providers of the NFI, Sophy and EcoPlant databases, as well as the people who collected floristic data. We also thank I. Seynave, V. Perez and D. Dallery who managed databases, C. Piedallu who provided climatic data, and J. Touroult for proofreading.

The acquisition and the organization of historical floristic data were funded by the French Agency for Environment and Energy Management (ADEME), the National Forest Office (ONF) and the French National Research Agency (ANR) as part of the 'Investissement d'Avenir' program (ANR-11-LABX-0002-01, Lab of Excellence ARBRE). A part of this study was also funded through a grant to EK from the ADEME and the Regional Council of Lorraine.

DECLARATIONS

Funding

The acquisition and the organization of historical floristic data were funded by the French Agency for Environment and Energy Management (ADEME), the National Forest Office (ONF) and the French National Research Agency (ANR) as part of the 'Investissement d'Avenir' program (ANR-11-LABX-0002-01, Lab of Excellence ARBRE). A part of this study was also funded through a grant to EK from the ADEME and the Regional Council of Lorraine.

Conflicts of interest/Competing interests

No conflict of interest or competing interests.

Availability of data, material and code

Habitat data, automatic classification program and code used in this study are available from the corresponding author on reasonable request.

Ethics approval

Not applicable

Consent to participate

Not applicable

Consent for publication

Not applicable

ABSTRACT

Natura 2000 is a European network of sites dedicated to the conservation of vulnerable habitats. The definitions of Natura 2000 habitats are mainly based on plant communities. We investigated if the increase of the dominance of warm-adapted species observed in plant communities, described as thermophilization, had already led to measurable changes in Natura 2000 forest habitats.

We created 5,701 pairs of neighboring forest plots by gathering plots surveyed before 1987 and after 1997 to reflect historical and recent climatic conditions. A Natura 2000 habitat type was assigned to each vegetation plot using an automatic classification program. We calculated a temperature index that synthesized the temperature range of each habitat, and compared the habitat temperature indexes of the recent and historical plots of each pair.

We highlighted a significant overall shift of $4.8\% \pm 1.78$ (CI 95%) of the pairs toward warmer habitats over the studied period. While the shift was not significant in lowlands, $11.1\% \pm 3.0$ (CI 95%) of the pairs evolved toward warmer habitats in highlands.

The excess of pairs with a warmer habitat in the recent period was interpreted as thermophilization of Natura 2000 forest habitats. Therefore, global warming has been strong enough to induce actual changes at the coarse-grained habitat resolution specifically targeted by public policies. The absence of significant results in lowlands suggests the existence of unrealized potential habitat changes, which can be considered as a climatic debt. These results call for differential prioritization levels and implementations of public policies for nature conservation in lowlands and highlands.

INTRODUCTION

Nature conservation was initially developed for species preservation (Kiss 2005). Faced with the homogenization of ecosystems and landscapes due to human omnipresence, conservationists aimed for a more integrated vision of nature. Plant ecologists have developed and used the concept of habitat for a century, close to the notion of ecosystem but initially based on plant community (Yapp 1922). In Europe, legal frameworks and most of the efforts dedicated to biodiversity conservation are committed to habitat management and restoration. The European Directive 92/43/EEC (EC Council 2006) on the conservation of natural habitats and of wild fauna and flora (the Habitats Directive) sets the framework for the European Union's policies on nature conservation. The given definition of the term habitat is a *“terrestrial or aquatic area distinguished by geographic, abiotic and biotic features, whether entirely natural or semi-natural”* (art.1). The targeted habitats designated to be of Community interest (also named ‘Natura 2000 habitat’, ‘habitat type’ or ‘habitat’ hereafter) are rare, or in danger of

disappearance, or display outstanding examples of typical characteristics of one of the biogeographical regions in Europe. Natura 2000 habitat types are classified and described in the EUR 28 Interpretation Manual (European Commission DG Environment 2013). Phytosociology principles have been used to describe plant communities at the European level for one century, this is why phytosociology was chosen as a basis to define the terrestrial Natura 2000 habitats (Guarino et al. 2018). The basic unit of the phytosociological classification is the association, defined by its characteristic combination of plant species (Braun and Furrer 1913).

Researchers, policymakers, and conservationists now widely agree that the Earth's climate is changing, with major impacts on biodiversity (Hannah et al. 2002; Araujo et al. 2011). Previous studies have shown that climate warming has led to an increase of the dominance of warm-adapted species in plant communities described as thermophilization (De Frenne et al. 2014), observed mainly in highlands (Bertrand et al. 2011; Gottfried et al. 2012). This thermophilization trend lags behind climate warming, particularly in lowlands (Bertrand et al. 2011, 2016; Savage and Vellend 2015; Alexander et al. 2018). Despite their potential usefulness for policymakers and Natura 2000 managers, published results dealing with the impact of climate warming on plant species and communities are often not expressed in the categories used by stakeholders, and translating them remains difficult (Jeanmougin et al. 2016).

A recent survey of the LIFE program Natur'adapt conducted among 497 nature conservation professionals in France and Europe showed that even if climate change is a priority issue for nine out of ten stakeholders, two thirds of nature professionals do not take climate change into account in their management practices (de Sadeleer and Coudurier 2019). This situation can be explained by the lack of biologically relevant metrics of climate risk for local-scale climate vulnerability assessments and adaptation planning, but also the lack of results or a lack of translations of the results on ecosystem types specifically targeted by public policies and at a resolution used in local management by practitioners (Ordonez and Williams 2013; de Sadeleer and Coudurier 2019).

In a protected area, the habitat typology accounted for by the Natura 2000 habitat classification system (European Commission DG Environment 2013) provides the means to identify, map, manage ecosystems (De Cáceres et al. 2015), and then restore them. Only few studies have investigated the future impacts of climate change on the Natura 2000 network, and they predict habitat range shifts (Araujo et al. 2011; Bittner et al. 2011; Barredo et al. 2016). But the current impacts of recent climate warming on Natura 2000 habitats have not been studied yet. Therefore, we investigated if the changes recently observed on plant communities linked with climate warming were sufficient to be already visible at a coarse-grained scale such as Natura 2000 habitats. Considering the previous studies (Bertrand et al. 2011, 2016; Gottfried et al.

2012; Savage and Vellend 2015; Alexander et al. 2018), we also studied whether differences could be found between lowlands and highlands. Detecting early changes in Natura 2000 habitat with climate warming and differences between biomes is of crucial importance for political choices and the subsequent management practices.

METHODS

We studied Natura 2000 habitats in temperate and mountainous French forests excluding riparian and bog forests, and we investigated if the habitats under recent climatic conditions were characteristic of warmer temperature than the habitats under historical climatic conditions. We first characterized the temperature range of each habitat by creating a temperature index per habitat type that synthesized the range of temperature extracted for each plot where the habitat was found and considered as historically typical by experts. This temperature index enabled us to study the thermal responses of habitats. To this end, we used large databases of floristic plots to generate pairs of historical and recent neighboring plots. In order to disentangle temporal effects from potential spatial effects, we also paired two historical plots to highlight a potential effect of differences in plot location. Although pairing plots requires controlling the distance between the paired plots and their altitude, the huge advantage compared with permanent plot devices is that massive databases can be used and show slight trends over large areas. This was not feasible with the limited number of permanent plots available.

Floristic data

We extracted vegetation plots from three databases: Sophy, EcoPlant, and the national forest inventory (NFI) of France. A plot included a complete floristic inventory with the species cover and plot location variables. Sophy is a phytosociological database that gathers a compilation of complete floristic inventories carried out at the plot level from 1914 to 2000 (Brise et al. 1995). EcoPlant is a phyto-ecological database with phytosociological inventories from 1922 to 2011 mainly focused on forest ecosystems (Gégout et al. 2005). In these two data sources, the plot size is the 400 m² standard size of a phytosociological inventory in a forested area (Braun-Blanquet et al. 1932). The database provided by the NFI of France (Hervé 2016) included floristic inventories of 700-m² plots inventoried between 1991 and 2014 and uniformly distributed across the forests of mainland France. We only kept plots with vegetation surveys conducted between April and October and whose coordinates were available with less than 1 km accuracy. A total of 116,760 floristic plots, including vascular plants and terricolous bryophytes, were extracted from these three databases (Kuhn and Gégout 2019).

Assignment of a Natura 2000 habitat type to each vegetation plot

An automatic classification program based on a program developed in 2012 by Gégout and Coudun to classify floristic inventories of the French temperate and mountainous forests was used to assign a phytosociological association to the vegetation. This automatic classification program used the complete floristic composition of the plot for assignment, and its results were similar to those of expert judgments (Gégout and Coudun 2012). The list of phytosociological associations that defined each habitat available in Gégout et al. (2009) was used to assign a habitat type to each plot whenever relevant.

Production of a temperature index per Natura 2000 habitat type

We defined a temperature index from plots whose habitat was assigned and considered as typical in terms of vegetation composition by experts, i.e. where most of the expected species were encountered (Guinochet 1973). We created a temperature index (TI) per habitat type that synthesized the range of temperature extracted for each plot considered as historically typical. We used 3,379 plots to compute a TI for 15 frequent forest habitats in France. We calculated a TI for each habitat as the average value of the mean annual temperatures of the 1960-1990 period for each plot. Annual temperatures were extracted at a 30-second resolution for each plot with the Worldclim climate database version 1.4 (Hijmans et al. 2005). We avoided a possible disequilibrium between communities and climate linked to recent climate change by using plots and temperatures surveyed over the 1960-1990 period, before the warming period in France. We used at least 7 typical plots per habitat type to calculate a significant TI. The 15 studied Natura 2000 habitats were based on 80 phytosociological associations and covered the diversity of broadleaf and coniferous non hydromorphic Natura 2000 forest habitats of lowlands and mountainous areas of temperate France.

Pairing plots

Definition of the historical and recent periods

In France, recent climate warming is characterized by a relative stability of mean annual temperatures until the 1980s, a strong increase in temperature from the end of the 1980s until the end of the 1990s, followed by a period of relative stability (Kuhn and Gégout 2019). A close look at annual average temperatures allowed us to define the period before 1987 as historical, and the period after 1997 as a warmer recent period. There was no significant temperature trend in the last three decades of the historical period or during the recent period (linear regressions $p = 0.60$ and 0.75 , respectively). The mean temperature warming between the historical period and the recent period as measured by the French meteorological network is 1.13°C (Kuhn and Gégout 2019), and this increase was not significantly different in lowlands as compared to highlands before 2008 (Bertrand et al. 2011).

The historical-recent dataset (HIS-REC dataset)

We created pairs of neighboring plots comprising one historical plot and one recent plot each (Fig. 1). We assumed that pairing historical and recent non-permanent plots spatially was an extreme case of resurveying historical plots with a large uncertainty on plot location. To limit uncertainty, we created pairs by iteratively selecting the geographically closest historical and recent plots among all pairing possibilities. The maximum allowed difference in elevation within each pair of plots was 200 m, and the maximum distance allowed between two plots within a pair was 5 km (Kuhn and Gégout 2019). We selected pairs of plots including Natura 2000 habitat types present in the temperate and mountainous areas of France (pairs of the Mediterranean area excluded). Thus, we created a historical-recent dataset (HIS-REC dataset) of 5,701 pairs of historical and recent plots (Tab. 1 and supporting information Table S1 for the list of the studied habitats). The average distance between plots within pairs was 1,477 m (SE 16). The altitudinal difference between the recent and historical plots was negative or positive; the average difference was 2.0 m (SE 0.9). By calculating the average value among pairs without taking the + or – symbol into account, this difference was 44.9 m (SE 0.7) in absolute value. Once plots were paired, the average years of the historical and recent plots were 1974 and 2006, respectively. Data were also stratified according to the mean altitude of the pairs (from 2 to 2,389 m a.s.l.). Lowlands were defined as the areas below 500 m a.s.l., while highlands were defined as the areas at an altitude of 500 m a.s.l. or above.

The historical-historical dataset (HIS-HIS dataset)

To highlight a potential effect of differences in plot location, we used the previously described procedure to create 4,585 pairs of two historical plots (Tab. 1). The average distance between two plots was 586 m (SE 14). The average altitudinal difference between two plots was 0 m (SE 0.1) and 22.5 m (SE 0.6) in absolute value. The average difference between the two plot years was 2 years.

Light-controlled subset of the historical-recent dataset

Forest practices evolved over the last century (Pignard 2000), with a potential impact on the forest cover. The forest cover influences incident light, which affects floristic composition and could impact habitat assignment. Therefore, we created subsets of the historical-recent dataset to control the potential forest canopy cover differences between the two periods. Light indexes for each species listed in the French forest flora (Rameau et al. 1989, 1993) were extracted and recoded from qualitative assessment to a quantitative index ranging from 1 (shade tolerant) to 7 (heliophilous), following Ellenberg & Leuschner (2010). Species absent from the French forest flora were considered as heliophilous species of open environments and were assigned an index of 8. Then, we calculated a bio-indicated light value for each vegetation plot as the

average value of the light index of each species recorded in the floristic inventory. Next, we calculated the difference in bio-indicated light within the pairs of historical and recent plots. The gradient of differences in bio-indicated light was divided into ten classes (five classes of negative differences and five of positive differences). An equal number of pairs was randomly selected in each positive class and its negative equivalent. It resulted in a zero-centered distribution of differences in bio-indicated light. This subsampling procedure resulted in the selection of 3,905 pairs of plots named “light-controlled subset of the historical-recent dataset” (Tab. 1). The average distance between two plots was 1,476 m (SE 20). The average altitudinal difference between two plots was -3.0 m (SE 1.1) and 45.3 m (SE 0.8) in absolute value. The average years of the historical and recent plots were 1974 and 2006, respectively.

Comparison of the habitat temperature indexes between periods

We calculated the differences between the temperature indexes of the habitats assigned to the recent and historical plots ($\Delta T_{\text{pair}} = T_{\text{recent}} - T_{\text{hist}}$) for each pair of plots. The objective was to determine whether the habitat in the recent climatic conditions was characteristic of warmer, colder or equal temperature conditions than the habitat in the historical climatic conditions. If the habitat assigned to the two plots was identical, the difference between the temperature indexes was null ($\Delta T_{\text{pair}} = 0$). If the difference between the temperature indexes of the pair was negative ($\Delta T_{\text{pair}} < 0$), we hypothesized that the evolution of plant communities led to a habitat characteristic of colder conditions, the pair had “cooled down”. If the difference between the temperature indexes of the pair was positive ($\Delta T_{\text{pair}} > 0$), we hypothesized that the evolution of plant communities led to a habitat characteristic of warmer temperatures, the pair had “warmed up”. Then we calculated the percentage of pairs with null, positive and negative ΔT_{pair} for each dataset, and compared them. The proportion of pairs displaying the same habitat in the two plots was not excluded from the analyses.

From a theoretical viewpoint, in permanent plots undergoing no change in environmental conditions or in forestry practices, the habitats assigned to the two plots for each pair should be identical, with null values for ΔT_{pair} . But pairing plots can lead to habitat differences partly due to differences in plot location. Thus, part of the ΔT_{pair} could theoretically be null but also partly positive or negative. But with no environmental changes or in forestry practices, equal numbers of positive and negative ΔT_{pair} were expected. We checked this assumption by investigating if there was an identical percentage of pairs that had warmed up and cooled down using the HIS-HIS dataset. We tested the hypothesis of an impact of recent warming on habitat by searching for a significant excess of “warmed up” pairs versus “cooled down” pairs using the HIS-REC dataset. We tested for a potential effect of canopy changes between periods using the light-controlled subset of the HIS-REC dataset.

We applied a McNemar's test (χ^2 -test for paired data, $df=1$) to test the significant excess of the percentages of “warmed up” versus “cooled down” pairs (hereafter named “changing pairs”). The principle was to compare the observed percentage of “warmed up” and “cooled down” pairs to the theoretical percentage: an equal number of pairs warmed up and cooled down. Therefore theoretical frequencies assigned the changing pairs an equal probability of 0.5 to each modality. Then, we subtracted the percentage of “cooled down” pairs from the percentage of “warmed up” pairs: $[(\% \text{ of pairs } \Delta T_{\text{pair}} > 0) - (\% \text{ of pairs } \Delta T_{\text{pair}} < 0)]$. This result was considered as the excess of pairs of plots with a warmer habitat temperature index in the recent period. Using a χ^2 -test, we calculated the associated 95% confidence interval considering that the plots had been paired. We used the same methodology for the light-controlled subset of the HIS-REC dataset. For the HIS-HIS dataset, the same analyses were run by calculating the temperature index differences between the two historical plots of each pair: $\Delta T_{\text{pair}} = T_{\text{hist}_i} - T_{\text{hist}_j}$. The positions of the two plots i and j of the pair in the equation were selected randomly. Then, using a χ^2 -test, we checked for significant differences between the excess of pairs of plots with a warmer habitat temperature index in the recent period according to the dataset.

Finally, we also calculated the average value of all temperature indexes of the habitats present in the recent period, and the average value of all TIs of the habitats present in the historical period, and calculated the difference: $\Delta \text{Mean}(T)_{\text{dataset}} = \text{Mean}(T_{\text{recent}}) - \text{Mean}(T_{\text{hist}})$. Then, we performed a paired-sample Student's t -test to check for significant differences between the temperature indexes of the recent and historical periods. We used the same methodology for the light-controlled subset of the HIS-REC dataset and for the HIS-HIS dataset.

RESULTS

For a slight majority of the pairs of the HIS-REC dataset, the historical and recent plots displayed the same habitats (53.0% of the pairs). Pairs displaying the same habitats within the two plots were more frequent in lowlands (55.4%) than in highlands (48.7%) (Tab. 1).

In the HIS-REC dataset, the percentage of “warmed up” pairs (25.9%) was higher than the percentage of “cooled down” pairs (21.1%) (Tab. 1): the pairs of “warmed up” plots ($\Delta T_{\text{pair}} > 0$) were in a significant excess of $4.8\% \pm 1.78$ (CI 95%) (Fig. 2). When we controlled the canopy cover conditions, the light-controlled subset also evidenced a significant excess of $3.6\% \pm 2.15$ (CI 95%) (Fig. 2). These two excesses were not significantly different between them (Fig. 2). In contrast, the HIS-HIS dataset showed no significant excess of pairs of plots with a positive ΔT_{pair} (Fig. 2).

The percentage of “warmed up” pairs in lowlands was not significantly different than the percentage of “cooled down” pairs in the HIS-REC dataset, in the light-controlled HIS-REC

dataset, and in the HIS-HIS dataset (Tab. 1, Fig. 2). In contrast, in highlands we observed significant excesses of the pairs of plots with a warmer habitat in the recent period: $11.1\% \pm 3.0$ (CI 95%) in the HIS-REC dataset (Fig. 2), and $13.4\% \pm 3.7$ (CI 95%) in the light-controlled HIS-REC dataset (Fig. 2). The HIS-HIS dataset showed no significant excess of pairs of plots with a positive ΔT_{pair} (Fig. 2).

Lastly, we observed the same pattern for the mean TI values of the habitats according to the periods: for the HIS-REC dataset and the light-controlled HIS-REC dataset, we observed a slight but significant increase in the average TI between the historical and recent periods in the total dataset. The difference was higher in highlands but not significant in lowlands (Tab. 2). We observed no significant difference between the mean TIs of the HIS-HIS dataset (Tab. 2).

DISCUSSION

This study highlights a significant shift toward warmer Natura 2000 forest habitats of temperate and mountainous forests in France between historical and recent periods over a large diversity of frequent forest habitats.

As permanent plots were not available in sufficient numbers, we paired historical and recent neighboring plots, following previous studies (Hijmans 2011; Kuhn and Gégout 2019). We used huge databases to investigate slight trends over a large area. Using the HIS-HIS datasets built with pairs of two historical plots, we checked for the absence of biases due to differences in plot location. Thus, the changes highlighted by the comparison between historical and recent plots were interpreted as a temporal trend. Changes in forestry practices and climatic changes over the last century could both have affected this temporal trend. The evolution of forestry practices (Pignard 2000) brought about changes in the canopy cover that influenced plant communities (Danneyrolles et al. 2019). We controlled the canopy cover conditions with the light-controlled subset of the HIS-REC dataset, ran the tests again and obtained similar results. Thus, we ensured that the evolution of the canopy cover had not influenced the results. Besides, a change in the rainfall regime could have influenced the changes in plant communities (Harrison et al. 2015). But the decade-scale variation in rainfall remained the same before and after 1987 (Lenoir et al. 2008), so that it cannot have directly influenced the changes we observed. Therefore, recent climate warming and perhaps other indirect climatic factors linked with temperature such as seasonality were the likely drivers of the observed increase in the dominance of habitats characteristic of warmer conditions. In agreement with the existing definition of plant communities of De Frenne et al. (2014), the excess of pairs with a warmer habitat temperature index in the recent period was interpreted as thermophilization of Natura 2000 forest habitats induced by recent climate warming.

These results are congruent with previous studies regarding the changes induced by recent climate warming on plant communities in various temperate and mountainous ecosystems (De Frenne et al. 2013; Savage and Vellend 2015). This study complements previous community level results at the habitat level. It is the first evidence that global warming is strong enough to induce changes at the coarse-grained resolution of Natura 2000 habitat types specifically targeted by public policies and used in local management. This coarse-grained resolution is the likely reason why the average and highland increases of the habitat TI were of a lesser extent than the thermophilization highlighted at the community level which can exceed 0.5°C in mountains (Bertrand et al. 2011).

We studied lowlands and highlands separately, and found a substantial shift toward warmer Natura 2000 forest habitats in highlands. In contrast, we observed no significant change in lowlands. However, the measured temperature increase exceeded one degree in lowlands and highlands across the French territory in the recent decades (Bertrand et al. 2011; Kuhn and Gégout 2019). Consequently, we can guess that unrealized potential habitat changes are under way in lowlands, and they can be considered as a climatic debt (Bertrand et al. 2011).

Public policies for habitat conservation are currently implemented in the same way across the whole French territory. But this study shows that climate warming has differential impacts on habitats in lowlands and highlands. These differences call for differential prioritization levels and implementations of conservation strategies in lowlands and highlands. In lowlands where a climatic debt is being developed, several studies suggest that the current inertia of plants and plant communities is due to a high level of anthropogenic habitat fragmentation (Bertrand et al. 2011; Wessely et al. 2017). Therefore, we advise to allow species and habitats to track their climatic envelope over time by facilitating dispersal to newly suitable areas. To do so, many studies call for improving the connectivity of Natura 2000 networks, even if the advice is mostly generic and devoid of practical instruments and criteria (van Teeffelen et al. 2015). The priority for mountain areas is to check that the existing network of sites represents the current diversity of natural habitats, but also to keep on updating this network to ensure that the future natural habitat diversity will also be accurately represented. Moreover, implementing management measures aimed at maintaining dynamics rather than a given structure and composition in each site can bring flexibility to managers (van Teeffelen et al. 2015). In that sense, setting conservation targets at regional scales rather than local scales can allow them to welcome the emergence of new habitats or the loss of previously existing ones.

Although conservation organizations and government agencies are developing “adaptation strategies” to facilitate the adjustment of human society and ecological systems to altered climate regimes (Mawdsley et al. 2009), the impact of climate change is still poorly and hardly

taken into account by local managers in their daily planning (de Sadeleer and Coudurier 2019). For example, forest managers still have reservations about the current usefulness of available scientific knowledge for their own areas and circumstances (de Koning et al. 2014). This study could help to take a step toward better including the climate change effects into local management because it is based on Natura 2000 habitats directly used by decision-makers and local managers and highlights regionalized impacts.

SUPPLEMENTARY MATERIAL

Table S1. List of the studied Natura 2000 habitat types (* indicates priority habitat types), and number of plots in the HIS-REC dataset assigned to each of the Natura 2000 habitats.

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FIGURE CAPTIONS

Fig. 1: Location of the pairs composed of one historical and one recent forest floristic plot (HIS-REC dataset). Dots correspond to the centroid of each pair (n=5,701).

Fig. 2: Differences between the percentages of pairs of plots with a positive ΔTl_{pair} ($\Delta Tl_{pair} > 0$) and a negative ΔTl_{pair} ($\Delta Tl_{pair} < 0$) for each total dataset on the left (a.), and then stratified according to the mean altitude of the pairs, with lowlands in the center (b.) and highlands on the right (c.). The 95% confidence intervals were calculated considering that the plots had been paired. The lowercase letters (a, b, c) at the bottom of the figure indicate significantly different values, i.e., two values displaying the same letter are not significantly different.

For the HIS-HIS dataset, all the tests were performed considering one of the two plots randomly chosen as the recent one ($\Delta Tl_{pair} = Tl_{recent} - Tl_{hist}$ for the HIS-REC dataset and its light-controlled subsets; $\Delta Tl_{pair} = Tl_{hist_i} - Tl_{hist_j}$ for the HIS-HIS dataset).

FIGURES WITH CAPTIONS

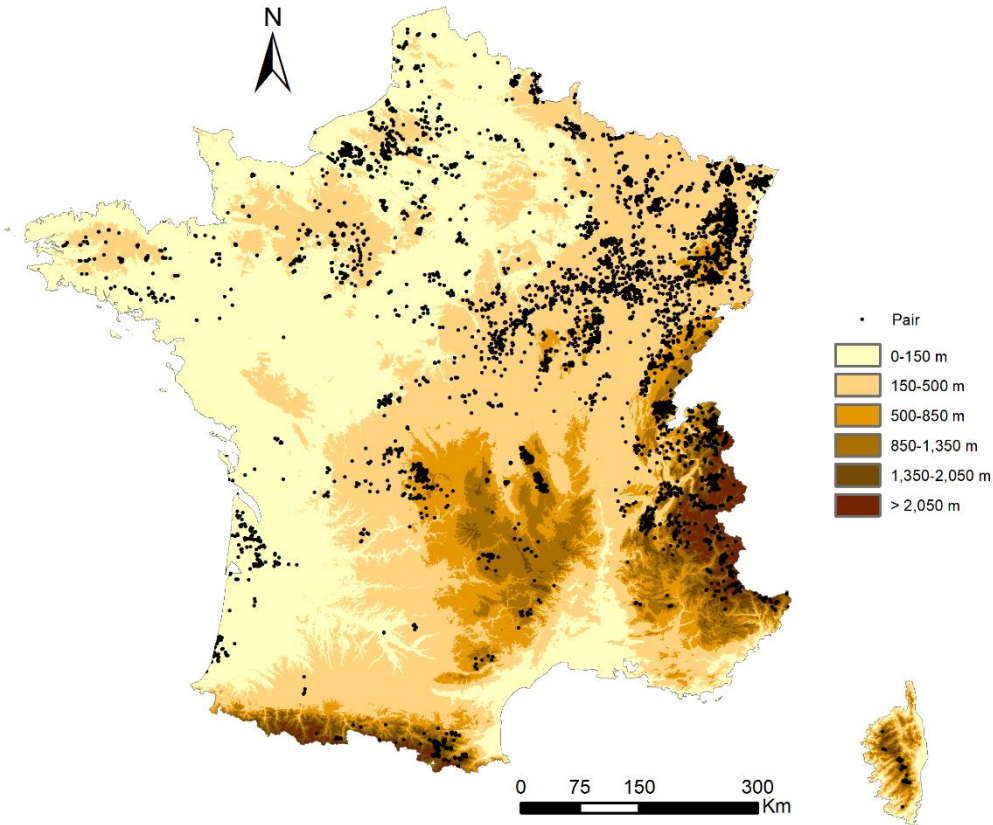


Fig. 1: Location of the pairs composed of one historical and one recent forest floristic plot (HIS-REC dataset). Dots correspond to the centroid of each pair (N=5,701).

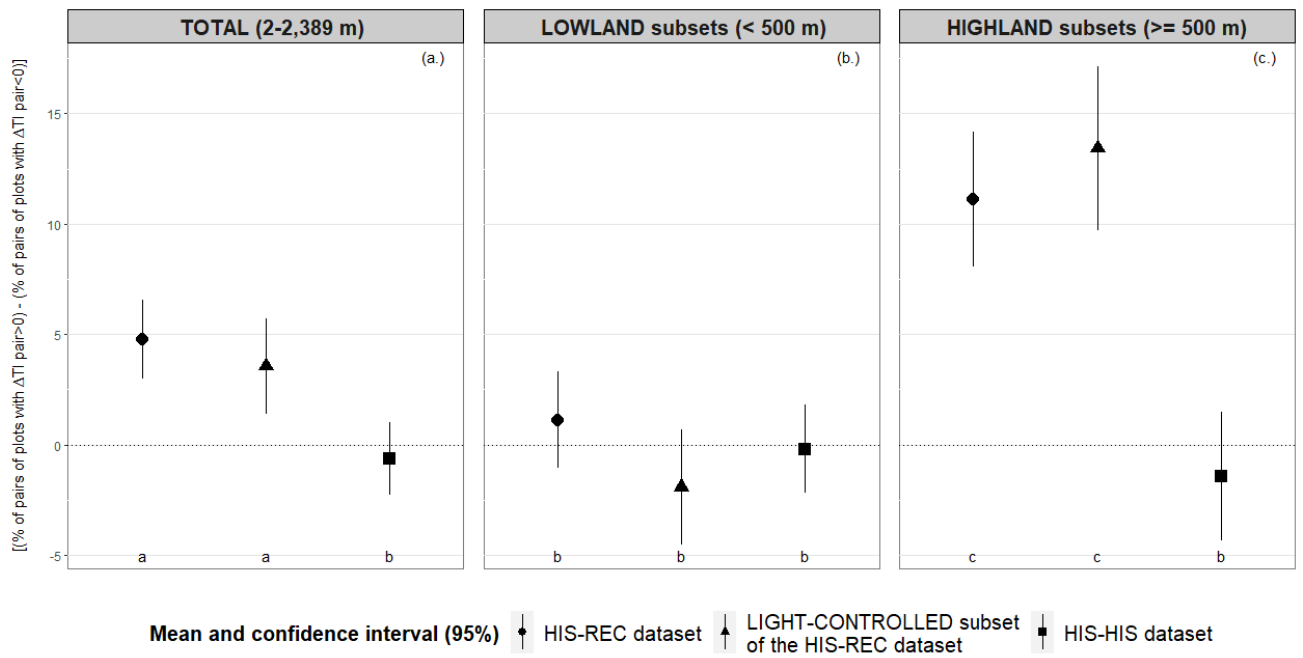


Fig. 2: Differences between the percentages of pairs of plots with a positive $\Delta T_{i_{pair}} > 0$ and a negative $\Delta T_{i_{pair}} < 0$ for each total dataset on the left (a.), and then stratified according to the mean altitude of the pairs, with lowlands in the center (b.) and highlands on the right (c.). The 95% confidence intervals were calculated considering that the plots had been paired. The lowercase letters (a, b, c) at the bottom of the figure indicate significantly different values, i.e., two values displaying the same letter are not significantly different.

For the HIS-HIS dataset, all the tests were performed considering one of the two plots randomly chosen as the recent one ($\Delta T_{i_{pair}} = T_{i_{recent}} - T_{i_{hist}}$ for the HIS-REC dataset and its light-controlled subsets; $\Delta T_{i_{pair}} = T_{i_{hist_i}} - T_{i_{hist_j}}$ for the HIS-HIS dataset).

TABLES

Table 1: Numbers of pairs of plots with a negative, null or positive temperature index difference (ΔT_{pair}) within the pair in each dataset and subset and according to the mean altitude of the pairs (total dataset, lowland and highland subsets).

Datasets and subsets	Pairs of plots	$\Delta T_{\text{pair}} < 0^{\text{a}}$	$\Delta T_{\text{pair}} = 0^{\text{b}}$	$\Delta T_{\text{pair}} > 0^{\text{c}}$
	N	n (% of N)	n (% of N)	n (% of N)
Historical-Recent dataset (HIS-REC dataset)				
Total (2-2,389 m)	5,701	1,204 (21.1)	3,021 (53.0)	1,476 (25.9)
Lowland subset (< 500 m)	3,624	787 (21.7)	2,009 (55.4)	828 (22.8)
Highland subset (\geq 500 m)	2,077	417 (20.1)	1,012 (48.7)	648 (31.2)
Light-controlled subsets of the HIS-REC dataset				
Total (2-2,389 m)	3,905	847 (21.7)	2,072 (53.1)	986 (25.2)
Lowland subset (< 500 m)	2,512	580 (23.1)	1,400 (55.7)	532 (21.2)
Highland subset (\geq 500 m)	1,393	267 (19.2)	672 (48.2)	454 (32.6)
Historical-Historical dataset (HIS-HIS dataset)^d				
Total (2-2,389 m)	4,585	759 (16.6)	3,096 (67.5)	730 (15.9)
Lowland subset (< 500 m)	2,965	459 (15.5)	2,053 (69.2)	453 (15.3)
Highland subset (\geq 500 m)	1,620	300 (18.5)	1,043 (64.4)	277 (17.1)

^a $\Delta T_{\text{pair}} < 0$: pairs of plots with a negative difference between the recent and historical temperature indexes associated to the habitats of each plot, i.e. pairs that have “cooled down.”

^b $\Delta T_{\text{pair}} = 0$: pairs of plots with a null difference between the temperature indexes associated to the habitats of each plot.

^c $\Delta T_{\text{pair}} > 0$: pairs of plots with a positive difference between the temperature indexes associated to the habitats of each plot, i.e. pairs that have “warmed up”.

^d For the HIS-HIS dataset, all the calculations were performed considering one of the two plots randomly chosen as the recent one ($\Delta T_{\text{pair}} = T_{\text{recent}} - T_{\text{hist}}$ for the HIS-REC dataset and its light-controlled subsets; $\Delta T_{\text{pair}} = T_{\text{hist}_i} - T_{\text{hist}_j}$ for the HIS-HIS dataset).

Table 2: Paired-samples Student's *t*-test comparing the mean values of all temperature indexes of the recent period with those of the historical period according to the mean altitude of the pairs (total datasets, lowland and highland subsets).

Datasets and subsets	T-test		
	<i>p</i> -val ^a	Estimates ^b	CI 95% ^c
Historical-Recent dataset (HIS-REC dataset)			
Total (2-2,389 m)	***	0.06	0.03
Lowland subset (< 500 m)	ns	0.00	0.02
Highland subset (>= 500 m)	***	0.17	0.06
Light-controlled subsets of the HIS-REC dataset			
Total (2-2,389 m)	***	0.05	0.03
Lowland subset (< 500 m)	ns	-0.03	0.03
Highland subset (>= 500 m)	***	0.20	0.08
Historical-Historical dataset (HIS-HIS dataset)^d			
Total (2-2,389 m)	ns	0.00	0.03
Lowland subset (< 500 m)	ns	0.01	0.02
Highland subset (>= 500 m)	ns	-0.03	0.06

^a *p*-val = *p*-value (***: significant at 0.01%; ns: non-significant).

^b Estimates = values of the differences between the mean value of all temperature indexes of the recent and historical periods.

^c CI 95% = the associated 95% confidence interval of the mean.

^d For the HIS-HIS dataset, all the tests were performed considering one of the two plots randomly chosen as the recent one ($\Delta T_{\text{pair}} = T_{\text{recent}} - T_{\text{hist}}$ for the HIS-REC datasets and its light-controlled subsets. $\Delta T_{\text{pair}} = T_{\text{hist}_i} - T_{\text{hist}_j}$ for the HIS-HIS datasets).