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Windstorm-induced canopy openings accelerate temperate forest adaptation to global warming

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Abstract

Aim: Climate change is known to be a driver of changes in forest plant communities and to modify disturbance regimes. We investigated whether forest gaps favoured vegetation adaptation to warmer climates by accelerating the shift of plant communities to a warmer-adapted composition independently of canopy closure linked to natural forest dynamics.

Location: Temperate and mountainous forests of France.

Time period: 2002–2018.

Major taxa studied: Vascular plants.

Methods: Using floristic surveys conducted in 2002 and 2018 in 139 permanent plots set up in unmanaged forest gaps created by windstorms in 1999, we assessed the plant communities' changes in context of global warming. We also compared gap communities to closed communities inventoried in undisturbed forest. A community temperature index (CTI) and a community light index (CLI) were computed for each floristic survey with species temperature optima and Ellenberg light indicator values, respectively.

Results: CTI increased significantly in the gaps over the 16 years by 0.11°C/decade on average. During the same period, the CLI decreased, indicating that community thermophilization was not the direct result of an increase in solar radiation linked to gap creation. Models showed that, after canopy recovery, thermophilization was stronger in mountains (+0.54°C) than lowland sites (+0.12°C) compared to undisturbed forests. The difference between former gaps and undisturbed forests resulted from the colonization of warm adapted species and the decline of cold adapted species in gaps.

Main conclusions: For a given canopy closure, our results show that thermophilization of understorey communities is higher in areas with previous disturbances than in undisturbed forests. By increasing the speed of thermophilization, the disturbance regime plays a key role in the adaptation of forest communities to climate warming. The effects of large-scale disturbances on forest plant composition should therefore not be overlooked, especially since disturbance regime tends to intensify with climate change.

KEYWORDS

community temperature index, forest gap, forest succession, global warming, indicator value, natural disturbance, thermophilization, windstorm

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1 | INTRODUCTION

Forest plant communities undergo changes in composition as a result of climate change and, in temperate forests, tend to transition towards a composition adapted to a warmer climate (Bertrand et al., 2011; Gottfried et al., 2012). Plant community compositions are modified in favour of warm climate adapted species at the expense of cold climate adapted species, a process termed 'thermophilization' (De Frenne et al., 2013; Gottfried et al., 2012). At a continental scale, the process is indicated by the migration of herbaceous and tree species to higher altitudes and latitudes (Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008; Savage & Vellend, 2015; Sittaro, Paquette, Messier, & Nock, 2017). Climate change also influences the forest disturbance regime, with an overall increase in the intensity or in the frequency of abiotic or biotic disturbance events such as wildfires, pathogenic invasions or windstorms as has been observed in recent decades (Dale et al., 2001; Overpeck, Rind, & Goldberg, 1990; Schelhaas, Nabuurs, & Schuck, 2003; Seidl, Schelhaas, & Lexer, 2011), leading to an increase in forest damage (Seidl, Schelhaas, Rammer, & Verkerk, 2014). Disturbances are recognized as a key factor in the dynamics of forest vegetation by facilitating the arrival of new species (Pickett & White, 1985). However, to date, the combined effect of rising temperatures and the intensification of disturbances on the composition of plant communities remains unclear. Whether windstorms may actually accelerate long-term adaptation of plant communities to climate change remains a critical unexplored question.

Forest canopies regulate microclimate, influencing most of the ecological processes that govern plant communities (Perry, 1994). Closed forest canopies reduce solar radiation intensity, ground and soil temperatures and thus maintain a cooler microclimate than open canopies (Chen et al., 1999; Norris, Hobson, & Ibisch, 2011; Reifsnyder, Furnival, & Horowitz, 1971). These effects may potentially mitigate the consequences of global temperature increase. Indeed, the thermophilization of understorey plant communities has been shown to be less pronounced when canopies become denser over a resampling interval of 34.5 years (De Frenne et al., 2013). Dense canopy therefore causes an imbalance between the increase in observed temperatures and the adaptation of forest plant communities. This lag in the vegetation response to global warming, referred to as the climatic debt, can also be explained by a second factor: the dispersal capacity of plant species. Only certain species affected by the rise in temperatures have sufficient dispersal capacities to return to their optimal development conditions (Bertrand et al., 2016). Finally, the size of the climatic debt for forest plant communities is also correlated with altitude. Bertrand et al. (2011) reported that thermophilization between 1965 and 2008 was not observed in lowland forests (< 500 m), while it was detected in mountain forests, indicating that climatic debt is higher at low elevation.

By increasing light availability and mean soil temperature (Bauhus, 1996; Gray, Spies, & Easter, 2002; Wright, Coates, & Bartemucci, 1998), canopy openings facilitate the establishment

of new species and promote a strong resetting of the vegetation dynamic cycle (Pickett & White, 1985). Canopy openings could thus be a catalyst of forest adaptation to a new climatic context (Thom, Rammer, & Seidl, 2017). This has already been observed in North America, where disturbances such as stand thinning or wildfires have facilitated an increase in the proportion of southern species and a decline in more northern species in plant communities compared to undisturbed areas (Stevens, Safford, Harrison, & Latimer, 2015). Brice, Cazelles, Legendre, and Fortin (2019) also observed changes in tree species composition over three decades in a temperate-boreal ecotone and showed that canopy disturbances amplified the thermophilization of tree communities. Along the same lines, modelling studies performed in North America and Europe indicate that disturbances may favour faster adaptation of the forest vegetation to a new climatic context at the century scale (Thom et al., 2017; Vanderwel & Purves, 2014). However, previous field reports based on floristic inventories (Brice et al., 2019; Stevens et al., 2015) have focused on the thermophilization process at high elevation at a given date or for a specific taxon. To our knowledge, there are currently no studies that have considered all types of forest vascular plant communities to assess whether thermophilization might occur along a larger elevation gradient in a context of forest disturbance. Moreover, it is still uncertain whether the thermophilization process of forest plant communities already observed in canopy openings is a natural phenomenon related to temporary warmer conditions that will disappear with the closing of the canopy of the newly formed stand or whether it is a permanent phenomenon induced by the resetting of plant communities following canopy opening that is maintained by global climate change. Consequently, the evidence that disturbances could facilitate faster adaptation of forest plant communities to climate change compared to an undisturbed forest remains unclear.

In the present study, we investigated whether canopy opening after a windstorm accelerates the process of thermophilization and reduces the climatic debt of forest vegetation. Our specific objectives were to (a) quantify the magnitude of thermophilization in windstorm-induced canopy openings, (b) test whether this thermophilization was maintained or disappeared with canopy closure, and (c) identify whether thermophilization results from a loss of cold climate adapted species, a gain of warm climate adapted species or from the two processes combined. This study is based on a comparison of forest plant communities assessed in 2002 and 2018 in canopy openings of different sizes created by storms in France in 1999.

2 | MATERIALS AND METHODS

2.1 | Study area

The present study was conducted in temperate forests in France (Figure 1). The forests included in this study are mainly semi-natural hardwood stands dominated by *Quercus petraea* (Matt.) Liebl.,

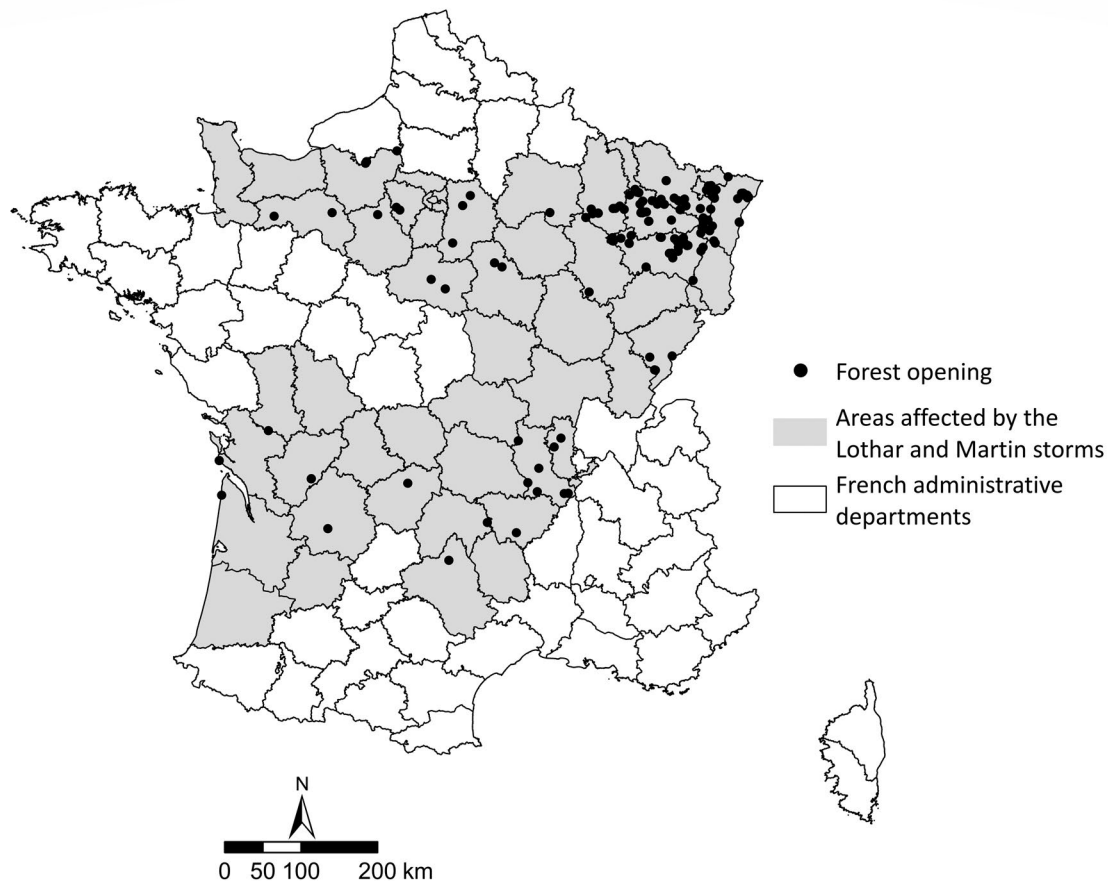


FIGURE 1 Map of the 148 gap plots sampled in the areas affected by the windstorms of 1999 in France

Quercus robur L., *Fagus sylvatica* L. and *Carpinus betulus* L., semi-natural and planted conifer or mixed stands dominated by *Abies alba* Mill., *Picea abies* (L) Karst. and *Fagus sylvatica* L., in lowlands or in mountainous areas. Mean annual temperature is between 5.6°C and 12.9°C and annual precipitation ranges from 651 to 1,606 mm.

In 1999, 968,000 ha of French forests were affected by two windstorms, Lothar and Martin (Inventaire Forestier National, 2003), which destroyed 8% of French forest resources (Pignard, Dupouey, Granier, & Morel, 2009). In 2001, 78 forests that had been impacted by the windstorms were selected for the study. These forests were selected because they allowed us to study a large gap size gradient, ranging from 80 m² to 161 ha in area. This included a total of 142 gaps (Figure 1), in which 1 or 2 plots were established. A total of 148 plots were sampled.

The plots covered a large altitudinal gradient, from 14 to 1,385 m, and were classified into two groups according to their elevation. The 22 plots above 500 m were considered as 'mountain gaps' (MG) and the 126 plots below 500 m as 'lowland gaps' (LG).

In 2002, one or two 10-m-radius circular measurements plots were established in each gap to study the forest vegetation dynamics after disturbance. In 2018, each plot was re-measured, and an additional measurement plot was established in the closest forest that was not impacted by the 1999 windstorms, in order to compare the gaps to undisturbed forests. To choose the control plot allocated

to each gap plot, topography, former stand type and soil conditions were controlled to be as homogeneous as possible to the gap. In addition, control plots were established at least 30 m from the forest edge. Thus, each gap plot had a corresponding control plot in a forest that had not been impacted by the storms.

2.2 | Data collection

Floristic inventories were conducted in the centre of each gap plot in 2002 and 2018, respectively 3 and 19 years after the windstorms. In 2018, inventories were also performed in the adjacent undisturbed plots. All vascular plant species (herbaceous plants, shrubs and trees) were recorded. For this study, we only considered plots with at least five inventoried plant species. This threshold was determined to maximize the quality of predictions without eliminating an excessive number of plots (Pinto et al., 2016). If a gap or a control plot had fewer than five species in a floristic survey, irrespective of the year of sampling, the gap plot and the associated control plot were removed from the analysis. One hundred and thirty-nine pairs of gap and control plots were used in the analysis (22 MG and 117 LG). On average, 23 species were inventoried per year and per plot. Altogether, 477 plant species were recorded and used in subsequent analyses.

2.3 | Spatial climatic normal and climate change

To evaluate the overall temperature increase in France between 2002 and 2018, we used homogenized temporal series data from Météo-France stations. Among the 189 stations available, we selected those located within a 50-km radius around the plots. A total of 70 different Météo-France stations were used to estimate the temperature increase (Supporting Information Figure S1). Monthly minimum and maximum temperatures were used to calculate mean annual temperatures between 1995 and 2018. A linear regression between the mean annual temperature of each station and calendar year indicated an increase of 0.52°C between 2002 and 2018, that is, 0.26°C/decade (Supporting Information Figure S2). Averaging the temperature increase observed at each weather station does not take into account the spatial variability of this increase (Supporting Information Figure S3). However, we aimed to use global information for our study in order to have an indication of the temperature increase actually observed close to the gaps.

The controlled of annual precipitation values, recorded by the same 70 Météo-France stations between 2002 and 2018, was also conducted using a linear regression between 1995 and 2018 (Supporting Information Figure S4). We did not observe any significant trend in the annual precipitation over the studied period.

2.4 | Estimation of community temperature and light indices

Plant species indicator values were used to evaluate the adaptation of plant communities to environmental conditions (temperature and light) in the gaps and in the adjacent undisturbed forests. Temperature indicator values for the plant species studied were calculated using the EcoPlant (Gégout, Coudun, Bailly, & Jabiol, 2005) and Sophy databases (Brisse, de Ruffray, Grandjouan, & Hoff, 1995). A total of 9,654 floristic inventories carried out between 1960 and 1990 and spread all over France were used to calculate the indicator value of the species for the average annual temperature. Gridded climate normals at kilometre resolution (AURELHY model from Météo-France) were used to estimate the instrumental mean annual temperature at each plot for the pre-warming period 1960–1990 (Benichou & Le Breton, 1987). For each of the species, probability of occurrence along the temperature gradient was calculated using Gaussian logistic regression. The temperature response curve for each species was summarized by a synthetic value, the temperature indicator value (TIV), defined as the value of the temperature gradient corresponding to the maximum probability of presence (Gégout, 2006; Gégout, Hervé, Houllier, & Pierrat, 2003; ter Braak & Looman, 1986). Among the 477 plants identified, 251 species had a TIV. On average per survey, 91% of the inventoried species had a TIV. Details of the calculation method are given in Supporting Information M&M.

The community temperature index (CTI) was obtained for each plot and date by averaging the TIV of all species present in the floristic inventory (Ellenberg et al., 1992). CTI was calculated in gap plots

for both 2002 and 2018, and only in 2018 for undisturbed forest plots. For each gap plot, the change in CTI between 2002 and 2018 (ΔT , CTI in 2018 minus CTI in 2002) was computed.

Ellenberg et al. (1992) provided plant species indicator values for several ecological factors in order to use flora to estimate the environmental conditions of a given area. The Ellenberg species-indicator value for light (L) characterizes the light preferences of plant species along a scale of 1 to 9, where 1 represents shade-tolerant species and 9, light-demanding species. Among the 477 plants identified, L was attributed to 302 species. On average per survey, 87% of the inventoried species had an indicator value for light. For each gap and control plot, the community light index (CLI) was estimated by averaging the indicator values for light L of the recorded plant species. Change in CLI between 2002 and 2018 (ΔL , CLI in 2018 minus CLI in 2002) was computed for each gap plot.

2.5 | Index of canopy recovery

Using the community light index in each gap plot (CLI_{gap}) and its adjacent undisturbed forest (CLI_{forest}), we built a canopy recovery index (CRI) to evaluate the degree of canopy closure in gaps between 2002 and 2018:

$$CRI = \frac{CLI_{gap\ 2018} - CLI_{gap\ 2002}}{CLI_{forest\ 2018} - CLI_{gap\ 2002}}$$

Given that each CLI value can vary between 1 and 9, the index is theoretically unbounded. However, because the light level was higher in the gaps in 2002 than in 2008, and higher than the adjacent undisturbed forests in 2018, CRI was usually positive. If no canopy recovery occurred (i.e., CLI in the gaps was identical in 2002 and 2018), $CRI = 0$. On the opposite end of the scale, when gap canopy closure in 2018 became similar to that of the adjacent undisturbed forest, CRI was close to 1 and could even exceed it. Thus, CRI estimated the degree to which CLI in the gaps decreased after the disturbance, between 2002 and 2018, in comparison to the reference undisturbed forests.

2.6 | Classification of cold and warm adapted species

The plant species recorded were classified as cold (SC) or warm (SW) adapted species. This classification was established in order to characterize which type of species induced the observed variations in CTI in the gap plots. Gridded climate normals (kilometre resolution) from Météo-France (Canellas et al., 2014) were used to estimate the mean annual temperature (TM) for the 1961–1990 (TM61–90) and 1981–2010 (TM81–10) periods at each site. Then, species were classified as either SC or SW using the TIV value of each species. Species with a TIV below the TM61–90 value of the plot were considered as SC and those presenting a TIV above the

TM81–10 value of the plot were considered as SW. All species with a TIV between the TM61–90 and TM81–10 values were classified as 'intermediate species'.

2.7 | Statistical analysis

Changes in CTI (ΔT) and in CLI (ΔL) in the gaps between 2002 and 2018 were tested against 0 using a Student's *t* test ($n = 139$).

Thermophilic species are often heliophilic. To test this assumption, the correlation between the 215 recorded species with a TIV and an *L* was studied. A positive correlation would suggest that there was a confounding effect of higher light level in openings thus explaining their progression towards thermophilic plants. We calculated the Pearson correlation coefficient between TIV and *L* of the recorded plants and we tested its departure from 0 with a Student's *t* test ($n = 215$ species).

To assess whether thermophilization of forest plant communities was linked to changes in light level, we studied the relationship between ΔT and ΔL using a linear regression model. As light level is dependent on the surface area of the opening, we integrated this variable into the model to test whether ΔT depends on the surface area of the openings. In the same way, we integrated the altitudinal class in order to test whether ΔT depends on the elevation of the gaps. We tested the effect of the distance to the nearest edge separately from the size of the gap because these variables are positively correlated (Pearson's correlation coefficient $r = .63$ in our sample). Finally, as several canopy openings were located in the same forest, each forest was considered to be a site, and we integrated site into the model as a random effect with the 'lme4' package (Bates, Maechler, Bolker, & Walker, 2015):

$$\Delta T_i = \beta_0 + \beta_1 \Delta L_i + \varepsilon_i \quad (1)$$

where ΔT_i is the change in CTI of plot *i* ($n = 139$), β_0 the intercept, β_1 the slope for ΔL (change in community light index) and ε_i the random error. We used a type III ANOVA *F*-test, from the package 'car' (Fox & Weisberg, 2019), to evaluate the significance of the β_1 parameter, after examination of the homogeneity of residuals. In an initial phase, gap size (log transformed) or distance to the edge, altitudinal class (lowland or mountain) and a site random effect were introduced in the model. Akaike information criterion (AIC) was not improved with the site random effect, so we removed it from the model. As gap size, distance to the edge and altitudinal class were not significant (p -value $> .05$), they were also discarded from the final model. Then, we tested whether significant thermophilization persisted at a constant light level ($\Delta L = 0$) by testing whether β_0 , the intercept of the model, was significantly different from 0.

To test whether thermophilization may persist after the forest canopy in the gaps had closed, we compared the difference between CTI in the gaps and the CTI of the undisturbed forest to the CRI. The projection of CRI = 1 allowed us to estimate the difference in CTI when the light level was equivalent between disturbed and undisturbed

areas. Again, the altitudinal class, gap size or distance to the edge and site random effect were integrated into the initial model. The following linear regression was carried out on the 2018 data:

$$(CTI_{\text{Gap}} - CTI_{\text{Forest}})_{ij} = \beta_0 + \beta_1 \text{CRI}_{ij} + \text{altitudinal class}_j + \varepsilon_{ij} \quad (2)$$

where $(CTI_{\text{Gap}} - CTI_{\text{Forest}})_{ij}$ is the difference in community temperature index between gap and adjacent undisturbed forest for plot *i* of altitudinal class *j*, β_0 the intercept, β_1 the slope for CRI (degree of canopy closure), altitudinal class_{*j*} the fixed effect of altitudinal class *j* ($j = 1$ or 2 , lowland or mountain) and ε_{ij} the random error. Neither gap size, distance to the edge nor random site effect were significant, and were therefore discarded from the model. The interaction between CRI and the altitude class was also not significant, and thus not included in the model. Based on Model 2, a contrast test (null hypothesis: $\beta_0 + \beta_1 + \text{altitudinal class}_j = 0$) was used to test whether thermophilization was still detected in openings at complete canopy recovery, that is, if $CTI_{\text{Gap}} - CTI_{\text{Forest}}$ was different from 0 when CRI = 1, separately for the two altitudinal classes, lowland and mountain ($j = 1$ or 2).

Finally, to characterize the type of species responsible for the variations in CTI, we compared the proportion of cold (SC) and warm (SW) adapted species between gaps in 2002 and 2018. The proportions of SC and SW between gaps and adjacent undisturbed forests in 2018 (respectively ΔSC and ΔSW) were also studied. After confirming that the distribution of SC and SW for 2002 and 2018 followed a normal distribution, the comparisons of the proportions' distributions were performed using Student's paired *t* tests. In addition, we carried out two linear regression models to study the variation in SC and SW, while taking into account the level of canopy closure. We wanted to test whether ΔSC and ΔSW are maintained at the equivalent canopy closure level (CRI = 1):

$$\Delta SC_i = \beta_0 + \beta_1 \text{CRI}_i + \varepsilon_i \quad (3)$$

$$\Delta SW_i = \beta_0 + \beta_1 \text{CRI}_i + \varepsilon_i \quad (4)$$

with the same definitions as in previous models. Using a contrast test (null hypothesis: $\beta_0 + \beta_1 = 0$), these two regression models allowed us to evaluate whether ΔSC and ΔSW were significantly different from 0 when the canopy was completely recovered, at CRI = 1.

For all statistical tests, the level of significance was fixed at 95%. Analyses were performed in the R programming language, version 3.5.3 (R Core Team, 2019).

3 | RESULTS

3.1 | Correlation between TIV and Ellenberg light indicator values

As expected, at the species level, the Ellenberg light indicator of the recorded plants was significantly and positively correlated to the

TIV, although the correlation was moderate ($r = .21$, p -value = .002, $n = 215$ species). It was thus appropriate to take into account the variation in light indicator values for the analysis of variation in temperature indicator values.

3.2 | Changes in community temperature and light indices between 2002 and 2018

In 2002, the average CTI in the gaps was 9.3°C, with a maximum of 12.3°C and a minimum of 6.3°C (Figure 2a). In 2018, the average CTI was 9.4°C, with a maximum of 12.5°C and a minimum of 6.8°C (Figure 2a). Within 16 years, CTI in forest gaps significantly increased by 0.18°C on average (p -value = .0003). Yet, CLI in the gaps was found to significantly decrease (p -value < $3e-16$) between 2002 and 2018, from 5.3 to 5 (Figure 2b), showing that the light level decreased in the gaps within the 16 years. Despite the decrease in CLI, CTI was found to increase, indicating that the shift in the plant communities towards species with higher temperature preferences was not due to an increase in the presence of light-demanding species.

The analysis of variance showed that gap size, distance to the forest edge and altitude class had no significant effect on the changes in CTI between 2002 and 2018 (ΔT) in the gaps, with p -values of .34 and .21, respectively. Thermophilization of the communities occurred at the same pace in all gaps irrespective of their size. Although not significantly, ΔT was higher in mountain sites than in lowland sites (0.31°C and 0.16°C, respectively).

Comparing the difference in CTI between 2002 and 2018 (ΔT) with the difference in CLI between 2002 and 2018 (ΔL) confirmed that the increase in CTI was not driven by an increase in the CLI. As shown in Figure 3, Model 2 predicts that when ΔL is equal to 0, ΔT is estimated at 0.33°C, significantly differing from 0 (p -value = $1e-7$). In other words, CTI was found to be higher in 2018 than in 2002, before and after controlling for differences in the light level.

3.3 | Effect of the gaps on community thermophilization

To further investigate the impact of canopy opening on the thermophilization process, we compared CTI values in gaps to CTI in adjacent undisturbed forest plots (Figure 2). In 2018, CTI was significantly (p -value = $1e-4$) higher in gaps than in undisturbed forests (9.4°C and 9.2°C, respectively).

Comparing lowland and mountain sites revealed that the effect was more pronounced in mountain sites (Figure 4). The difference in CTI between gaps and undisturbed forests, with CRI equal to 1, was significantly different from 0 in both elevation classes. But the difference was larger (p -value = .003) in mountain sites (0.54°C) than in lowland sites (0.12°C). Gap formation induced a leap forward in the thermophilization of flora with a stronger pattern of thermophilization detected in mountain sites.

3.4 | A decline in cold adapted species

The proportion of warm adapted species (SW) appeared to be slightly higher in 2018 than in 2002 in the gaps (Table 1), and was significantly higher in the gaps compared to undisturbed forests in 2018 (Student's paired t tests; p -value = .05 and p -value = .0002, respectively). The proportion of cold adapted species (SC) was significantly lower in 2018 than in 2002 in the gaps (Student's paired t test; p -value = .003) and it was significantly higher in undisturbed forests when compared to gaps in 2018 (Table 1; Student's paired t test; p -value = $8e-05$). According to the linear regression Model 3, the predicted value of ΔSC when CRI = 1 was negative and significantly different from 0 (contrast test: p -value = .0001) meaning that, at the same level of canopy cover, the predicted proportion of cold adapted species was higher in the undisturbed forests than in the gaps. Similarly, the predicted value of ΔSW when CRI = 1 in the linear regression Model 4 was positive and significantly different from 0 (contrast test: p -value = .0006). The predicted proportion of warm adapted species was higher in the gaps than in the undisturbed forests.

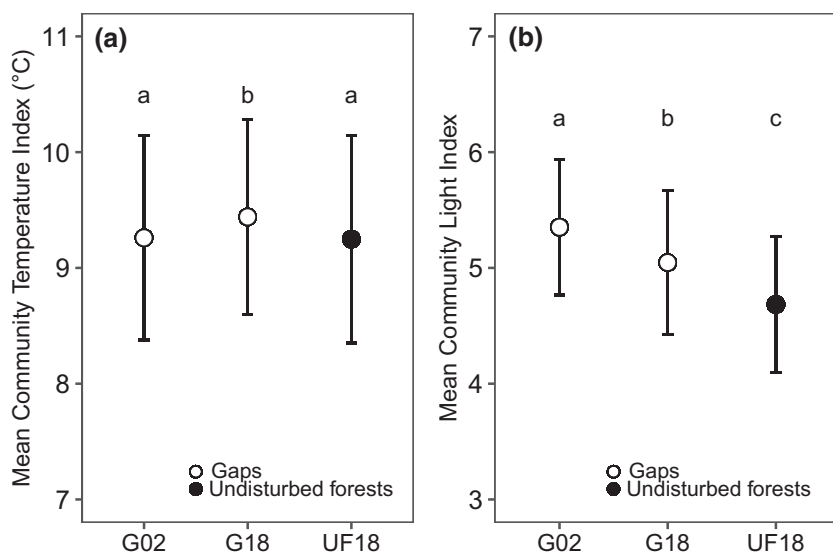


FIGURE 2 (a) Community temperature index and (b) community light index in the gap plots, estimated in 2002 (G02) and 2018 (G18), and in the undisturbed forest plots estimated in 2018 (UF18). Mean values and standard errors. Within each panel, means annotated with the same letter do not significantly differ according to Student's paired sample t tests at $p < .05$

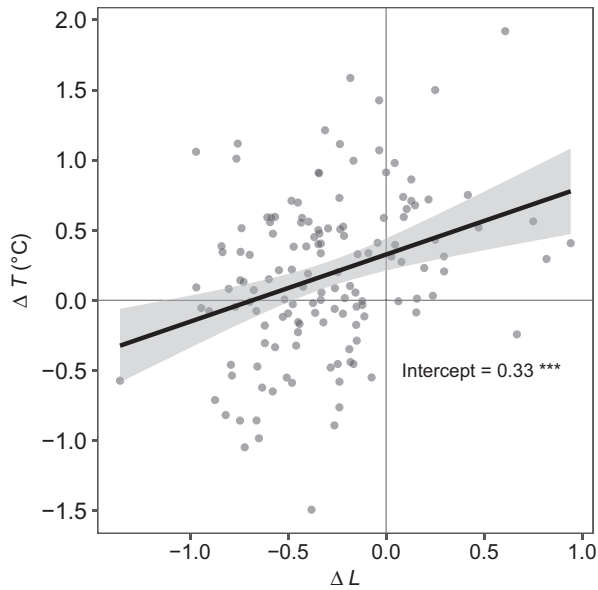


FIGURE 3 Relationship between the community temperature index change between 2002 and 2018 (ΔT) and the community light index change between 2002 and 2018 (ΔL) in the gap plots. Regression line and 95% confidence interval are displayed. The departure from 0 of ΔT when $\Delta L = 0$ (intercept of the regression line) is indicated (** $p < .001$)

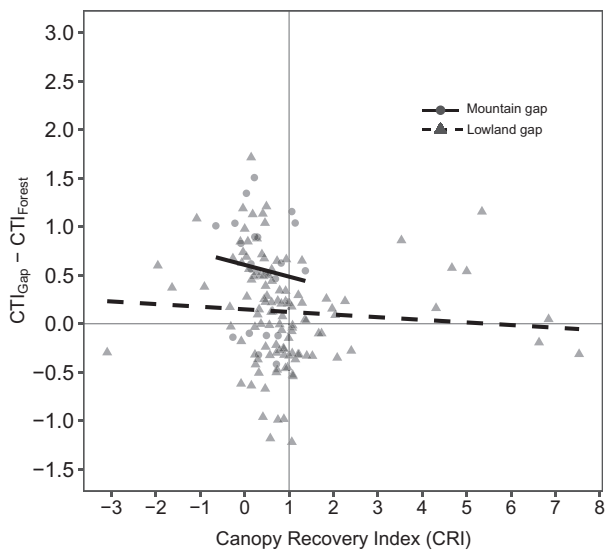


FIGURE 4 Relationships between community temperature index (CTI) difference between the gap plots and the undisturbed forest plots in 2018 ($CTI_{\text{Gap}} - CTI_{\text{Forest}}$), and canopy recovery index (CRI), estimated in gaps of the mountain (circles, plain line) and lowland (triangles, dotted line) sites. The 1 value on the x axis means a complete recovery of cover (i.e., an identical canopy cover for gap plot and undisturbed forest plot associated)

4 | DISCUSSION

The present study highlights the key role of windstorms in the dynamics and adaptation of forest plant communities over a wide

environmental gradient. Both mountain and lowland forest communities that have experienced a canopy-opening period are better adapted to the current climate than those that remained under closed canopy cover. Two decades after a windstorm, our results show that for a given canopy closure, plant communities in historic gaps have reduced their climatic debt more quickly than plant communities in undisturbed forests.

4.1 | Plant community thermophilization: A result of climate change

Studying the evolution of plant forest communities in windstorm induced gaps between 2002 and 2018 revealed a thermophilization process reaching $0.11^{\circ}\text{C}/\text{decade}$, in agreement with the changes in plant composition previously observed in other forests (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Lenoir et al., 2008; Savage & Vellend, 2015). In France, the observed climatic increase in temperature during the same period was about $0.26^{\circ}\text{C}/\text{decade}$ (see Materials and Methods). Thus, there is a difference of $0.15^{\circ}\text{C}/\text{decade}$ between the trends observed in instrumental records and what was bioindicated in the gaps, showing that community adaptation lagged behind the actual increase in temperature. It should be noted that the air temperature recorded by the nearest weather stations but located outside of forests might not be entirely representative of the temperature experienced by the plant species inside the gaps. Indeed, the abrupt opening of the canopy would have caused a local increase in ground temperature (Gray et al., 2002), likely exceeding the temperature increase recorded by weather stations. Thus, considering microclimatic warming, the climatic debt of the vegetation might be even greater.

Previous studies described a lag between the adaptation of vegetation and global warming (Bertrand et al., 2011, 2016; Brice et al., 2019). Recently, Brice et al. (2019), observing tree species in Canada, described a plant community thermophilization of $0.044^{\circ}\text{C}/\text{decade}$ and an increase in background temperature of $0.14^{\circ}\text{C}/\text{decade}$ in forest openings. Several factors might explain the higher thermophilization observed in openings in France, including a higher increase in background temperature compared to Canada (0.26°C and $0.14^{\circ}\text{C}/\text{decade}$, respectively), the higher resistance of tree species to temperature variation (Bertrand et al., 2016) and the fact that woody renewal takes longer than herbaceous plant renewal (Svenning & Sandel, 2013). The rate of species migration stands out as the key factor that explains the relatively strong disequilibrium between vegetation and climate change (Svenning & Sandel, 2013). Species migration can both be influenced by the characteristics of the species, biotic interactions and environmental characteristics. Here we recorded all vascular plant species including herbaceous plants, shrubs, and trees over a wide environmental gradient. We found that despite the greater thermophilization observed in gaps, a significant lag persisted compared to the increase in the observed temperatures. As projections for the coming decades show increasing temperatures, our results suggest that plant communities will not

	Gap 2002 (G02)	Gap 2018 (G18)	Undisturbed forest (UF18)	G18–G02	G18–UF18
Warm adapted species (SW)					
Proportion	.44 (.13)	0.46 (.14)	.42 (.15)	.017*	.037***
Number	10.9	11.1	9.5	0.16	1.5***
Cold adapted species (SC)					
Proportion	.43 (.12)	.40 (.12)	.44 (.14)	–.027***	–.041****
Number	10.3	9.3	9	–1.1***	0.26
Intermediate species (SI)					
Proportion	.13 (.08)	.14 (.1)	.14 (.14)	.01	.0049
Number	3.3	3.4	3.9	0.11	0.51**

Note: Differences between years and between disturbance regimes have been calculated and entered in the table. The average proportion for each species category over all plots is given followed by its standard deviation in parentheses. Significance of differences was tested with a Student's paired t test and represented in bold font (* $p < .1$. ** $p < .05$. *** $p < .01$. **** $p < .0001$. Non-significant otherwise).

adapt as quickly as the increase in temperature and that lags will widen.

4.2 | Disturbances are significant drivers for forest plant communities' adaptation to global warming

In this study, we showed that plant communities that have experienced an opening in the forest canopy due to a wind disturbance are more thermophilic than those that have not experienced an opening. The amplifying effect of disturbances on thermophilization has been reported in previous studies (Brice et al., 2019; Stevens et al., 2015; Thom et al., 2017). By comparing disturbed and undisturbed areas in mountains (> 1,200 m), Stevens et al. (2015) described a correlation between the intensity of the disturbance, like forest thinning or wildfire, and the thermophilization of Californian forest plant communities. Likewise, Brice et al. (2019) reported an effect of disturbances and gap size on the thermophilization process of tree communities in Canada. Thermophilization was higher in disturbed areas (0.044°C/decade) compared to areas without disturbances (0.03°C/decade). In the present study, we measured thermophilization of plant communities including trees and understorey vegetation along a large elevation gradient and a wide range of gap sizes. Thermophilization of 0.11°C/decade was observed despite the progressive closure of the canopy and the subsequent decrease in light demanding species. Taken alone, this canopy closure should have led to a decrease instead of an increase in the CTI, according to the positive correlation between the temperature and light-related traits of the recorded plants. Yet, the abrupt opening of the canopy, by a storm for example, caused a rapid change in the composition of the vegetation, leading to thermophilization. Compared to undisturbed forests, gaps had a 0.19°C higher CTI. At complete canopy closure (when CRI = 1), this difference was predicted to be even higher, 0.54°C and 0.12°C for mountain and lowland gaps, respectively. Due to climate warming, these changes in vegetation composition towards warmer

TABLE 1 Proportion and mean number of warm adapted species, cold adapted species and intermediate species in the gap plots in 2002 and 2018, and in the undisturbed forests in 2018

communities are likely to persist after the complete recovery of the canopy, as was observed in plots that had already reached the closure stage of the adjacent undisturbed forest (Figure 4).

In a previous study, Bertrand et al. (2011) described the modification of forest plant community composition along an elevation gradient in France. They observed an elevation-dependent response: lowland (< 500 m) plant communities lagged behind the increase in temperature whereas mountain plant communities responded faster. In our study, plant community thermophilization occurred in both lowland and mountain forests. But compared to the undisturbed forests, the bioindicated increase in temperature in gaps was much larger in mountain sites compared to lowland sites (0.54°C and 0.12°C, respectively). As highlighted by Jump, Mátyás, and Peñuelas (2009) and Lenoir and Svenning (2015), few studies have reported thermophilization of lowland vegetation, most likely because thermophilization is weaker in lowlands than in mountains (Bertrand et al., 2011). This difference can partly be explained by the shorter distance necessary for a decrease in temperature on mountains as compared to lowlands. It is therefore easier for plants to change their distribution upward on mountains than poleward in lowlands to compensate for the recent climate warming (Colwell, Brehm, Cardelus, Gilman, & Longino, 2008; Jump et al., 2009). Here, we highlighted the major role of disturbances on the dynamic adaptation of plant communities both on mountains and in lowlands. After experiencing a canopy-opening period, forest plant communities do not return to a thermal state similar to that of forests not impacted by storms. It is important to emphasize that the disturbance regimes themselves are also impacted by climate change (Dale et al., 2001; Overpeck et al., 1990; Schelhaas et al., 2003; Seidl et al., 2011), resulting over the last century in an increase in storm-caused forest damage (Seidl et al., 2014). Similar trends over the 21st century might drive plant communities' adaptation to climate change faster than would otherwise be expected. To date, there is little information available on the effect of altitude on disturbance, in particular windstorm

regimes. More information would make it possible to better differentiate hypotheses on the trajectories of thermophilization in lowlands and in mountain forests. In any case, windstorms, and more generally disturbances, stimulate plant community adaptation, a process that could have major importance for the adaptation of lowland plant communities to a warmer climate.

4.3 | The coping mechanism of plant communities through disturbances: The role of the microclimate

Our study reveals the importance of canopy opening history on the adaptation of plant communities. One possible mechanism explaining this faster adaptation might be related to the microclimate generated by the opening of the canopy. Gap creation mostly affects the light regime, air temperature, soil temperature, and moisture (Canham et al., 1990; Gray et al., 2002; Heithecker & Halpern, 2006). Light availability, air and soil temperatures, and water availability tend to increase in gaps, and are generally positively correlated to the gap size (Gray et al., 2002). The buffering effect of the forest canopy on the ground-level microclimate is reduced, thus favouring the development of light-demanding and edge species (Degen, Devillez, & Jacquemart, 2005; Naaf & Wulf, 2007; Schumann, White, & Witham, 2003; Wohlgemuth, Kull, & Wüthrich, 2002). This is in agreement with our 2002 observations in the gaps created by the storms. Plant communities were significantly more light demanding in gaps than in adjacent closed undisturbed forests. The abrupt cover decrease in the tree layer, induced by thinning or climatic disturbances, likely led to changes in the understorey composition, facilitating the appearance of light-demanding and early-successional generalist species (Fischer, Lindner, Abs, & Lasch, 2002; Halpern, 1989; Wagner, Fischer, & Huth, 2011; Whitney & Foster, 1988). De Frenne et al. (2013) have previously described the preponderant role of the forest canopy on the vegetation thermophilization process. When forest canopies became denser, thermophilization was lower while thermophilization was higher when canopies opened. However, their study focused more on the buffering effect of a more or less dense canopy cover on plant community thermophilization rather than on the persistent effects of a sudden opening of the canopy. Compared to their study, the present study highlights the long-term persistence of the communities' thermophilization during the canopy closure. We found that differences in the CTI between the gaps and the undisturbed forests in 2018 was the result of both the colonization of warm adapted species and the local extinction of cold adapted species. This is in agreement with results obtained in mountain areas by Stevens et al. (2015) and Stevens, Miller and Fornwalt (2019) who observed both a decrease in the proportion of cool-mesic species and an increase in warm-xeric species that persisted over time after fires of varying intensity. In our study, a wider altitudinal gradient was used, allowing us to show that the disappearance of the cold adapted species and the increase of warm adapted species occurs in lowlands as well as on mountains. Our study therefore partially contradicts Kuhn and Gégout (2019) who

only showed a significant decrease in cold adapted plants in lowland forests during the 20th century in France. One possible explanation for this difference is that canopy opening resets forest succession and promotes the arrival of new species that are more adapted to warmer climate conditions. However, the loss of cold adapted species was higher than the gain of warm adapted species. This apparent discrepancy can be explained by the fact that the majority of our study sites were located in lowland areas where forests face greater habitat fragmentation with reduced opportunity for short-distance dispersal and the appearance of new warm-adapted species (Jump et al., 2009; Scherrer & Körner, 2011).

To summarize, microclimatic conditions play a major role in the long-term dynamics of plant communities (Zellweger et al., 2020). By creating canopy openings, disturbances cause significant changes to the microclimate. These local microclimatic variations are currently at the origin of the thermophilization observed at the scale of forest plant communities emphasizing the importance of quantifying variation in local-scale environmental conditions to understand the global changes observed in plant communities.

5 | CONCLUSION

This study is the first that investigated the process of thermophilization during canopy closure after wind disturbance. It was performed during the first 20 years following a windstorm, which corresponds to the early stage of forest dynamics. This is probably not long enough to definitively establish that the colonization of warm adapted species and the loss of cold adapted species observed in the gaps are irreversible. However, the increase in the community temperature index caused by the opening of the canopy and the resetting of the forest succession is beyond question, due to the gradual closure of the canopy and the return to forest microclimatic conditions.

Our findings suggest that the synergy between climate warming and the disturbance regime plays a key role in forest vegetation modifications under climate change by increasing the speed of thermophilization. Windstorms disrupt microclimatic conditions by canopy removal and these variations in local climate largely explain the changes in plant communities that can be observed globally. The creation of the openings allows adaptation by leaps of the plant communities, which is maintained over time. Thus, forest plant communities that have experienced a canopy-opening period are more in balance with the current climate. The importance of the effects of large-scale disturbances on the composition of forests should therefore not be overlooked, especially since these unpredictable events tend to intensify with climate change.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Portail Data INRAE at <https://doi.org/10.15454/AZNS3A>.

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BIOSKETCH

The author team has dealt for many years both with global change impacts on forest plant communities and with forest stand dynamics and management. This study takes place in a long-term monitoring programme of forest reconstitution based on more than 100 permanent plots established in large and small gaps created after the windstorms that crossed Europe at the end of the 1990s.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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