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Sydney Vennin, Pierre Montpied, Patrick Behr, Anne Thimonier, Jean-Luc Dupouey. Mechanisation of forest operations drives long-term changes in plant communities. *Forest Ecology and Management*, 2025, 585, pp.122562. <10.1016/j.foreco.2025.122562>. <hal-05218819>

**HAL Id: hal-05218819**

**<https://hal.inrae.fr/hal-05218819v1>**

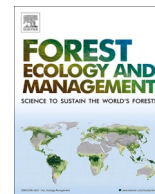
Submitted on 22 Aug 2025

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# Mechanisation of forest operations drives long-term changes in plant communities

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## ARTICLE INFO

### Keywords:

Understory vegetation  
Thermophilisation  
Compaction  
Soil disturbance  
Resurvey  
Forest mechanisation

## ABSTRACT

Using a permanent network of plots, we resurveyed vegetation in a broadleaved forest of northeastern France, tracking the effects of climate change, eutrophication and forest management between 1990 and 2022. To better detect the impact of mechanisation on plant communities, we established subplots based on microtopography (skid trails and wheel tracks) and recorded species separately in these subplots. We then tested changes in species' frequency and used ordination to analyse changes in communities' composition. Shifts were assessed using species' indicator values in plots and subplots, as well as regression analysis of plot shifts on axis 1 of the correspondence analysis as a function of stand characteristics, vehicle disturbances, canopy openings, game pressure, storm impact and ownership. Results showed a progress of non-forest species, hygrophilous species and species preferring wheel tracks and skid trails. Compaction from forestry vehicles was associated with an increase in indicator values for soil moisture and nitrogen. The projection of subplot surveys onto the correspondence analysis confirmed wheel tracks and skid trails as the main driver of observed vegetation shifts. These, as well as canopy openings, were significant in the regression analysis. Although we observed thermophilisation of plant communities (+0.27 °C per bioindication) which lagged behind recorded temperature increase (+1.5 °C), this was only a minor cause of overall vegetation changes. Mechanisation is therefore becoming a driver of vegetation changes at the scale of entire forests. As the use of harvesters in temperate deciduous forests increases, the planning of forestry operations should better account for these impacts on vegetation.

## 1. Introduction

In recent decades, the magnitude of anthropogenic pressures on temperate forest ecosystems has risen, resulting in long term shifts in vegetation composition. Monitoring resulting impacts on biodiversity through field observations is essential. Plot-based vegetation resampling, whereby historical plots are revisited, is an opportunity to do so whilst accounting for the decadal time scale of vegetation changes (Kapfer et al., 2017). Most plant species found in temperate forests have known environmental tolerances. Their presence or absence can therefore help identify drivers of change in ecological communities. Patterns of anthropogenic pressures have shifted over the last decades. Nitrogen deposition has declined, particularly in Europe (Ackerman et al., 2019), with no large-scale response to this decline in understory vegetation (Schmitz et al., 2019). Surges in herbivory populations (Beguín et al., 2016; Carpio et al., 2021) were found to increase species richness to the

detriment of forest specialists (Boulangier et al., 2018). Climate change is responsible for an observed upward shift in plant species optimum elevation in mountainous forests (Lenoir et al., 2020). This results in thermophilisation of vegetation, i.e. the decline in relative abundance of cold-adapted species or increase in that of more warm-adapted species. In lowland forests, vegetation is lagging behind temperature increases (Bertrand et al., 2016), this lag is reduced in cases of canopy disturbances (Stevens et al., 2015) or openings (Dietz et al., 2020). This is likely related to a negative association between canopy density and thermophilisation (de Frenne et al., 2013).

There is another overlooked but significant anthropogenic pressure on forests: mechanisation. Since the mid-twentieth century, the use of vehicles with higher labour productivity to log timber has transformed anthropogenic pressure on forests. Today, logs are for the most part brought to landing sites using forwarders and skidders, and the use of harvesters in broadleaved forests is increasing throughout Europe

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<https://doi.org/10.1016/j.foreco.2025.122562>

Received 9 November 2024; Received in revised form 31 January 2025; Accepted 12 February 2025

Available online 23 March 2025

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(Mederski et al., 2022) and worldwide (Brown et al., 2020). More than 70 % of industrial roundwood harvesting is currently fully mechanised (Lundbäck et al., 2021). Several reviews synthesised consequences for soil, including decreased soil microbial biomass carbon and porosity and increased bulk density (Nazari et al., 2021). These impacts depend on soil properties (Crawford et al., 2021; Nazari et al., 2021), on type and age of trees (Mariotti et al., 2020), on stand condition, yard logistics and forest road network characteristics (Picchio et al., 2020) and on machine weight and passage frequency (Nazari et al., 2021). Soil compaction in turn has negative consequences for ground biota, regeneration and tree productivity (Cambi et al., 2015).

In synchronic studies, ground based mechanised logging is often found to increase understory plant species' diversity, but mainly to the benefit of grasses, ruderals, lianas and invasive species (DeArmond et al., 2021). Godefroid and Koedam (2004) showed a high interspecific variation in the response to measured soil compaction. Compared to undisturbed controls, skid trails and haul roads had higher overall richness and prevalence of wetland and non-native species (Buckley et al., 2003) and favoured light and moisture-demanding species (Brumelis and Carleton, 1989; Mercier et al., 2019), many of which are competitive (Wei et al., 2016). Density of wheel tracks (measured as cumulative rut length using airborne light detection) was also found to be positively correlated to occurrence frequency of wetland species (Mohieddinne et al., 2023).

Few diachronic studies have causally demonstrated a shift of plant communities because of mechanisation-induced trails and tracks. In resurvey studies, silviculture has often been considered through proxies (e.g. changes in canopy cover and composition, Verheyen et al., 2012) or through broad scale transitions between types of management (e.g. from coppice with standards to high forest – van Calster et al., 2007; or from plantation to close-to-nature forestry – Klyngne et al., 2020). A few studies spatially distinguished between areas with different silvicultural treatments to analyse changes in the flora. Godefroid and Koedam (2008) compared the progress of four indicator species for disturbance between stands in a forest. Indicated disturbance was largest in old high forests, in even-aged high forests and in stands with low diversity. Closset-Kopp et al. (2019) compared shifts of plant communities in managed and unmanaged areas and found the highest compositional changes to be in managed stands and on soil types more susceptible to compaction. They concluded on the likely importance of heavy forestry vehicles. However, none of these diachronic studies included a direct assessment of the traces of mechanisation in the field.

Here, we resurveyed a managed forest of northeastern France using a tailored sampling methodology to causally assess the impact of mechanisation. We stratified between trails, wheel tracks and their absence within each plot and conducted relevés in each of these subplots. By then comparing these to the previous relevés, we were able to separate the effect of forestry vehicles. The first systematic sampling of the Amance forest was carried out in 1971, followed by a second campaign in 1990 (Thimonier et al., 1992). Shifts in plant communities between these two dates showed eutrophication of the forest, likely resulting from atmospheric deposition. Carried out in 2022 and 2023, the third campaign aimed to characterise the dynamics of plant communities over the last three decades. Like Thimonier et al. (1992), we assessed the changes in the taxonomic composition of communities and in their mean indicator values.

We hypothesised that intensified movement of forestry vehicles throughout the forest would lead to an increase in species associated with soil compaction and consequent waterlogging. We hypothesised this increase would be most marked in trails and wheel tracks than off them. Regarding climate change, we hypothesised that the increase in atmospheric temperature would lead to the thermophilisation of plant communities. Given that forestry vehicles can remove dominant species and create bare soil surfaces, paving the way for a reshuffling of the plant community, we hypothesised that the greater the soil disturbance linked to forestry vehicles, the higher the thermophilisation of

vegetation. On light, we hypothesised that mechanisation would result in an opening of the canopy and in increased soil disturbance, increasing the prevalence of light demanding species and of soil disturbance species which are often light-demanding as well. We expected these trends to be reflected in changes (or lack thereof) in species frequency and average community indicator values.

## 2. Materials and methods

### 2.1. Study area

Twelve kilometers northeast of the French city of Nancy (6.33°E, 48.76°N), the forest of Amance consists of a wooded area of 1340 ha. It is a lowland forest (altitudes between 210 m and 275 m) with a semi-continental climate (see Appendix Table A.1 for climate normals). Geologically, the forest substratum is composed of limestones, marls and sandstones of the Jurassic covered by silt of varying thickness. Soils are stagnic luvisols (IUSS et al., 2015) with mull and mesotrophic humus forms, and topsoil pH ranges from 4.1 to 7.3 with a mean value of 5.4 (Thimonier et al., 1992). Naturally regenerated broadleaf species dominate, and most notably hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur*). Oaks show recent signs of dieback resulting from processionary caterpillar outbreaks (between 2017 and 2021) and repeated water stress (most recently in 2018 and 2019).

Until the 19th century, coppice with standards were predominant, providing both trees for timber and firewood. The Amance forest was then converted into high forest, with a rotation length of 150–180 years, and the conversion was largely completed in 1982. The Lothar storm of 1999 uprooted parts of the forest. Forest operations have been conducted with skidders and forwarders since the 1970s, with an intensification brought after the Lothar storm in 1999. As of yet, no harvesters are used in the Amance forest. The ownership of the forest is split between national government (29 % of the area), municipal government (12 %), a forestry school (44 %) and private owners (15 %). On average in the region, the live standing volume is 210 m<sup>3</sup>/ha, with a biological production of 4.9 m<sup>3</sup>/ha/year, of which 4.2 m<sup>3</sup>/ha/year is harvested. Selective logging is carried out on average every 8–12 years on each management unit of between 7 and 15 ha, asynchronously and progressively throughout the forest.

### 2.2. Data collection

During the first floristic campaign in the Amance forest, in 1971, a permanent sampling network of 251 circular plots was set up at the nodes of a 200 m\*200 m square grid. In 1990, Thimonier et al. (1992) resampled 221 of these plots (Fig. 1). Plots in early stages of regeneration were discarded. On each 400-m<sup>2</sup> plot, a floristic survey was carried out. Cover abundance of all species was recorded along the Braun-Blanquet scale (Braun-Blanquet, 1932). This was done separately in 3 vegetation layers, according to their height: trees, shrubs and the ground layer (all vascular plants below 2 m height, including woody saplings). If a species was observed only on a given topographic heterogeneity (for example “path”), this was recorded. The total cover percentage of trees, shrubs and ground-layer species were separately recorded.

The third sampling campaign revisited 206 plots in 2022 and 2023 (164 and 42 plots, respectively; referred to as “2022” hereafter), selecting plots which were not in early stages of regeneration. 48 corresponded exactly to the location of the original plot, marked in 1990 by a painting on a tree. GPS coordinates were used to relocate plot centres for the remainder. To account for seasonality as a potential pitfall of resampling studies (Kapfer et al., 2017), plots were revisited within 3 weeks of the 1990 sampling date. Three of the authors of this study conducted the 1990 campaign as well, one of whom sampled 49 % of the 206 plots at both dates. All observations made in 1990, as described

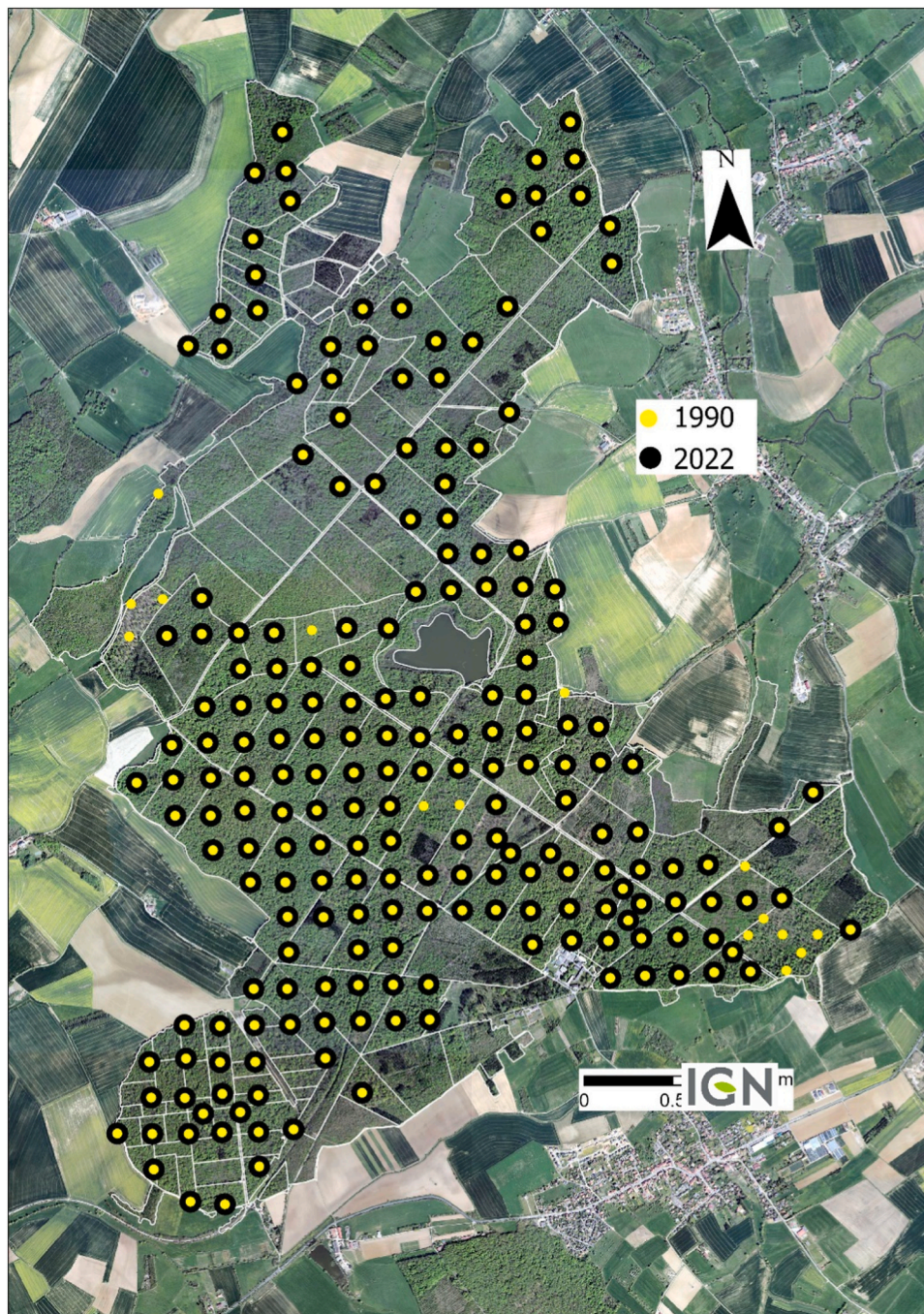


Fig. 1. Airborne image of the Amance forest showing the systematic sampling grid. Plots sampled in both campaigns are represented by 2 concentric circles.

above, were repeated in 2022.

Unlike previous campaigns, the protocol of the third campaign systematised the recording of silvicultural impacts at the species level. In each plot, we distinguished between wheel tracks (W), trails not including wheel tracks (T) and the area outside of any of these disturbances (O). Then, in each of these disturbances, we recorded all the species present. In practice, this meant that some plots contained several subplot surveys, one for each intra-plot disturbance (Fig. 2). We recorded trails on 61 % of the 206 plots visited, covering 12.6 % of the total surface area inventoried, and wheel tracks on 46 % of the plots, covering 1.8 % of the total surface area (Appendix B). Hereafter, we will call *plot survey* the list of species found in the full 400-m<sup>2</sup> and *subplot survey* the list of species found on a specific intra-plot disturbance within a plot. There can therefore be up to three *subplot surveys* making up one *plot*

*survey*. This protocol is based on methods aimed at better characterising vegetation mosaics in relevés (see e.g. synusial phytosociology, Gillet and Gallandat, 1996).

Following a visit of the Amance forest with those who managed it over the last decades, we also recorded indicators of disturbances and history of management at the whole plot level:

- . Structure of the tree stand using national forest inventory categories: young even-aged, even-aged with understory, even-aged without understory and uneven-aged.
- . Diameter class of the largest tree ([8, 17.5[, [17.5, 27.5[, [27.5, 47.5[, [47.5, 67.5[, ≥ 67.5 cm).
- . Proportion of plot area impacted by trails and wheel tracks. In plots with both, the proportion recorded for trails included the one recorded for wheel tracks.

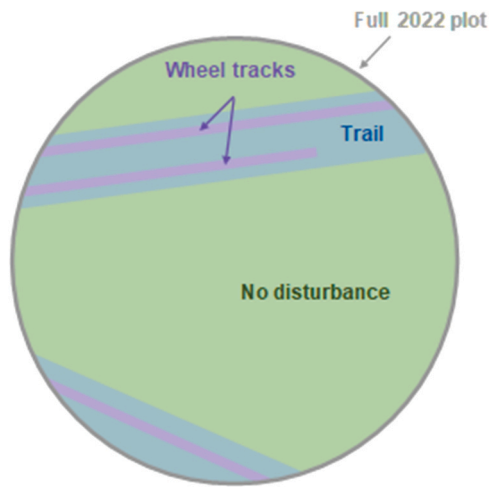


Fig. 2. 2022 plot with surveyed subplots according to disturbance type.

. A combined indicator of Lothar storm impact along a 0–2 scale based on the presence of pits, mounds and standing or fallen large trees, and whether these were present locally or globally on the plot (see Appendix C).

. A combined indicator of game pressure along a 0–10 scale equal to the sum of the following 5 indicators: browsed branches or shoots, deer berths, animal droppings, overturned soil from wild boar foraging and bark with signs of deer rubbing their antlers, each scored as 0 (absent), 1 (occurring locally) or 2 (occurring all over the plot).

### 2.3. Data analysis

Data preparation involved several steps of harmonisation. We removed the tree and shrub layers, keeping only the ground layer (which includes saplings of tree and shrub species). Species which are differentiated today but weren't in previous campaigns were grouped (e.g. *Juncus effusus* and *Juncus conglomeratus*). The number of species found per plot over the two field campaigns was calculated after harmonisation. We identified which species significantly increased or decreased in frequency of occurrence (number of plots a species was found to be present in) between 1990 and 2022. To do so, we conducted an unconditional asymptotic paired McNemar test (threshold p-value = 0.05). This tests the difference between two paired proportions.

Two methods were used to interpret species' change in frequency using their ecology. First, we computed a  $\Phi$  coefficient of association (following the method laid out by Tichý and Chytrý, 2006) between individual species and silvicultural disturbances to soil. We defined two site groups for inventories carried out in 2022: (1) TW, the combination of subplots on skid trail (T) and wheel track (W) (126 subplots) and (2) O, subplots outside of wheel tracks and trails (206 subplots). Because the number of subplots in each of these groups was different, we corrected for the relative size of these two groups following Tichý and Chytrý (2006). We used presence/absence data to calculate group-equalised indices of association between each species and the presence of trails or wheel tracks. Each species was resultingly attributed an index of association to trails or wheel tracks  $\Phi_{TW}$ . Coefficients of association were retained only for species with more than 10 occurrences on all sites (82 species over a total of 182 harmonised species observed in 2022 in the ground-layer stratum).

Second, for illustrative purposes, we used Heinken et al. (2022)'s classification of species into four categories according to their affinity for forest or open habitats (found in closed forest, in forest edges and forest openings, in forests and open vegetation, or mainly in open vegetation). We then identified hygrophilous species as those scoring 7 or higher on a France-specific expert set of indicator values for soil

moisture (see Appendix D).

The second part of the analysis focused on the level of plant communities, namely all of the species present in one plot in the ground layer (which includes woody species of less than 2 m height). We built a presence/absence table of the species in each plot for the two campaigns (campaigns x sites in rows and species in columns), keeping only species which were present in 5 plots or more in one of the campaigns at least, resulting in 113 retained species and 412 retained relevés (2 campaigns x 206 sites). This table was used for a correspondence analysis, which summarises the structure of the rows (sites x campaigns) by columns (species) contingency table, identifying the underlying patterns of association between species, sites and campaigns (Oksanen, 2015). Since we had two surveys per plot (one per campaign), we could account for site effect to look at the temporal variations within sites rather than the spatial variations between sites. To do so, we partialled out the site factor prior to correspondence analysis (Oksanen, 2015). We used correspondence analysis rather than NMDS, because there is no implementation of variable partialling out for the latter. We retained axis 1 only, given it was dominant over the others with a clear drop in the percentage of variance explained in relation to the second axis (8.2 % versus 4.4 %, on a total of 113 variables). According to a permutation test ( $n = 100,000$  random draws without replacement of values within each column -species- of the initial data table), this first axis was highly significant ( $P < 1e-4$ ).

We first tested for the role of soil disturbances in the temporal shift of plant communities, by projecting subplot inventories (made separately in each intra-plot disturbance) as supplementary individuals onto the first factorial axis. We then compared and tested the differences in position of the different types of subplots (T, W or O) along this axis.

We looked at whether wider environmental and management factors contributed to plot-level shifts in plant communities between 1990 and 2022. To do so, we computed the difference between 2022 minus 1990 positions for each plot along the first axis of correspondence analysis. In a first step, we fitted a full multiple linear regression model of this temporal shift as a function of different plot-level explanatory variables:

$$2022_{\text{axis position}} - 1990_{\text{axis position}} = T_{\text{surf}} + W_{\text{surf}} + \text{CanopyOpen} + \text{Ownership} + \text{Storm} + \text{Structure} + \text{DomTree} + \text{GamePressure}$$

with:

$2022_{\text{axis position}}$  (resp.  $1990_{\text{axis position}}$ ): position of the plot in 2022 (resp. 1990) on axis 1 of the correspondence analysis,

$T_{\text{surf}}$  and  $W_{\text{surf}}$ : proportion of a plot surface occupied by trails and wheel tracks, respectively (between 0 and 1),

CanopyOpen: difference 1990 minus 2022 estimated canopy cover above the ground layer (between -1 and 1). Following Fischer (2015), we calculated canopy cover above the ground layer as: tree cover + (1 - tree cover) \* shrub cover (all values as proportions),

Ownership as an integrative descriptor of management, with 4 levels, national, municipal, forestry school and private,

Storm: combined indicator of storm impact (3 levels, see Appendix C),

Structure: structure of the stand (4 levels, see Data collection),

DomTree: diameter class of the largest tree on the plot (see Data collection),

GamePressure: combined indicator of game pressure (continuous scale from 0 to 10, see Data collection).

In a second step, a reduced model was fitted by stepwise selection, using both backward and forward selection of variables and AIC as the optimisation criteria. All variables, both explained and explanatory, were standardised prior to model fitting in order to obtain standardised and therefore comparable regression coefficients. Significance of each variable retained in the final model was tested with a type III ANOVA.

Lastly, we used bioindication to further elucidate overall shifts in plant communities and influence of skid trails and wheel tracks. For each species, optimal annual mean temperature, soil pH, soil nutrition (N),

soil moisture and light requirement were obtained from existing bio-indication datasets (see Appendix D). In addition, we used the previously calculated  $\Phi_{TW}$  as an indicator value of species association with skid trails and wheel tracks. For each of the 6 preceding indicators, we calculated means per plot and per campaign ( $n = 202$  for all indicator values), excluding plots with less than 5 bioindicator species.

Changes in mean indicator values between the two campaigns were visually assessed using boxplots and tested using paired t-tests. We then correlated the difference in mean indicator values per plot (2022 minus 1990) and the difference in plot positions (2022 minus 1990) along the first axis of the correspondence analysis.

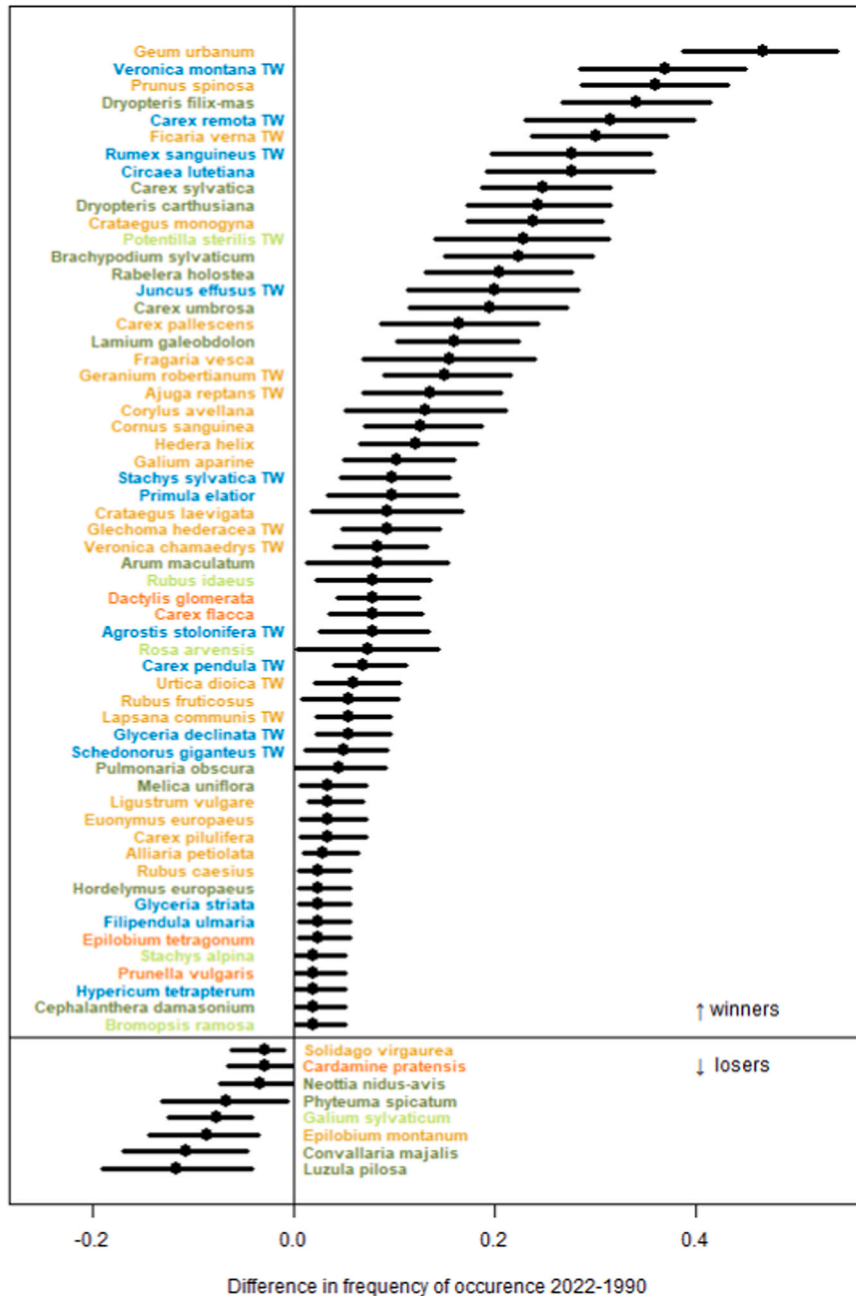
We compared the results obtained using presence-absence of species or cover-abundance data, which were very similar. In line with several

previous studies (see Camiz et al., 2017) we decided to present only the presence-absence analyses, which we consider more reliable. Data analysis was conducted using the spatial analysis software QGIS version 3.22 (QGIS.org, 2022) and the statistical analysis software R version 4.1.2 (RCoreTeam, 2021). In R, we used the *vegan* package for correspondence analysis, *Exact* package for the McNemar test and the *multcomp* package for comparisons of groups in linear models.

### 3. Results

#### 3.1. Shifts in the flora

The total number of species observed was 142 in 1990 and 182 in



**Fig. 3.** Changes in frequency of occurrence of species in the herbaceous layer between 1990 and 2022. Only species with a significant difference of frequency between 1990 and 2022, according to a paired McNemar test, are displayed. Tree species are not shown. Black dots: observed differences in frequency. Black lines: 95 % confidence interval of the difference. Blue: hygrophilous species. Orange: mainly or exclusively non forest species. Yellow: forest and open vegetation species. Light green: forest edge or forest opening species. Dark green: closed forest species. TW: species with positive coefficient of association to trails or wheel tracks.

2022. The mean number of species per plot rose between the two campaigns, from 21.4 to 31.5. This increase was significant ( $P < 1e-4$ ) according to a paired  $t$ -test.

There are 19 species which disappeared in the 2022 campaign, and 59 species which appeared (Appendix E). The McNemar test (Fig. 3) shows there are many more species which significantly increased than species which decreased. Hygrophilous species increased from 15.5 % to 17.9 % ( $P = 0.002$ , according to a Fisher's exact test of comparison of the two proportions) of the total number of species occurrences in 1990 and 2022, respectively. The proportion of occurrences of species positively associated to trails or wheel tracks ( $\Phi_{TW} > 0$ ) rose more, from 14.4 % in 1990 to 19.1 % in 2022 ( $P < 1e-4$ ). The two are linked: nine of the fourteen hygrophilous species which progressed (*Agrostis stolonifera*, *Carex pendula*, *Carex remota*, *Glyceria declinata*, *Juncus effusus*, *Rumex sanguineus*, *Schedonorus giganteus*, *Stachys sylvatica* and *Veronica montana*) also had positive coefficients of association  $\Phi_{TW}$  with skid trails or wheel tracks. Conversely, the hygrophilous species which did not progress did not have a positive  $\Phi_{TW}$ .

However, a set of species also increased in frequency that were negatively associated with trails or tracks ( $\Phi_{TW} < 0$ ), often shrubs or small trees, with a high demand for light (score 7 on the Ellenberg scale, see Appendix E). As a proportion of total occurrences, species with a light score  $\geq 7$  increased from 9.3 % to 14.0 % ( $P < 1e-4$ ).

### 3.2. Shifts in the composition of communities

#### 3.2.1. Correspondence analysis

Correspondence analysis controlling for the site effect shows a clear shift in communities' composition, with two distinct clusters of points corresponding to the two campaigns (Fig. 4A). 61.9 % of the total inertia in the data was accounted for by site effect (spatial differences between plots), whilst the remainder (38.1 %) was accounted for by intra-site effect (temporal differences between 1990 and 2022 for each plot). Among these total intra-site variations, there was a clear gap between the percentage of variance explained by the first axis (8.2 %) and the

second one (4.4 %). Moreover, the shift in community composition between 1990 and 2022 was much higher along the first axis than the second: year effect explained 65 % of the variance in plot position along the first axis, only 4 % for the second axis. As our study focuses on temporal variations, we retained only the first axis in subsequent analyses. The difference in plot position on this axis between 1990 and 2022 was highly significant ( $P < 1e-4$ ) according to a paired  $t$ -test.

Shown in Fig. 4B, the supplementary projected 2022 intra-plot disturbances situate subplots on the factorial axis built from the two campaigns. Remarkably, subplots were arranged in an order of decreasing disturbance level along the 1990–2022 overall vegetation shift, from relevés on wheel tracks, to trails excluding wheel tracks, to relevés outside of any disturbance. The mean positions were highly significantly different between wheel tracks and trails, and between wheel tracks and subplots outside any disturbance ( $P < 1e-4$  for both comparisons), but only weakly between trails and subplots outside disturbances ( $P = 0.09$ ).

#### 3.2.2. Linear model of the shift along the first factorial axis

For the shift in position along the first axis, the explanatory variables selected as statistically significant in the stepwise regression (Table 1) were the surface of wheel tracks in 2022 (the larger the wheel track area in 2022, the larger the shift between 1990 and 2022), the change in field estimated canopy cover (the more the canopy opened up, the larger the shift between 1990 and 2022), and the type of ownership (municipal forest showing more change than national and forestry school properties). The final model was highly significant ( $P < 1e-4$ ,  $n = 197$  due to missing values for 9 plots) but with a low total variance explained (adjusted  $R^2$  of 14 %). Correlation between explanatory variables was weak, at most 0.16 between canopy opening and area of wheel tracks.

#### 3.2.3. Bioindication

Apart from soil pH, all indicator values increased significantly between 1990 and 2022 (Fig. 5, light grey panels). The most significant increases were for mean temperature (+0,27 °C) and  $\Phi_{TW}$ . The average

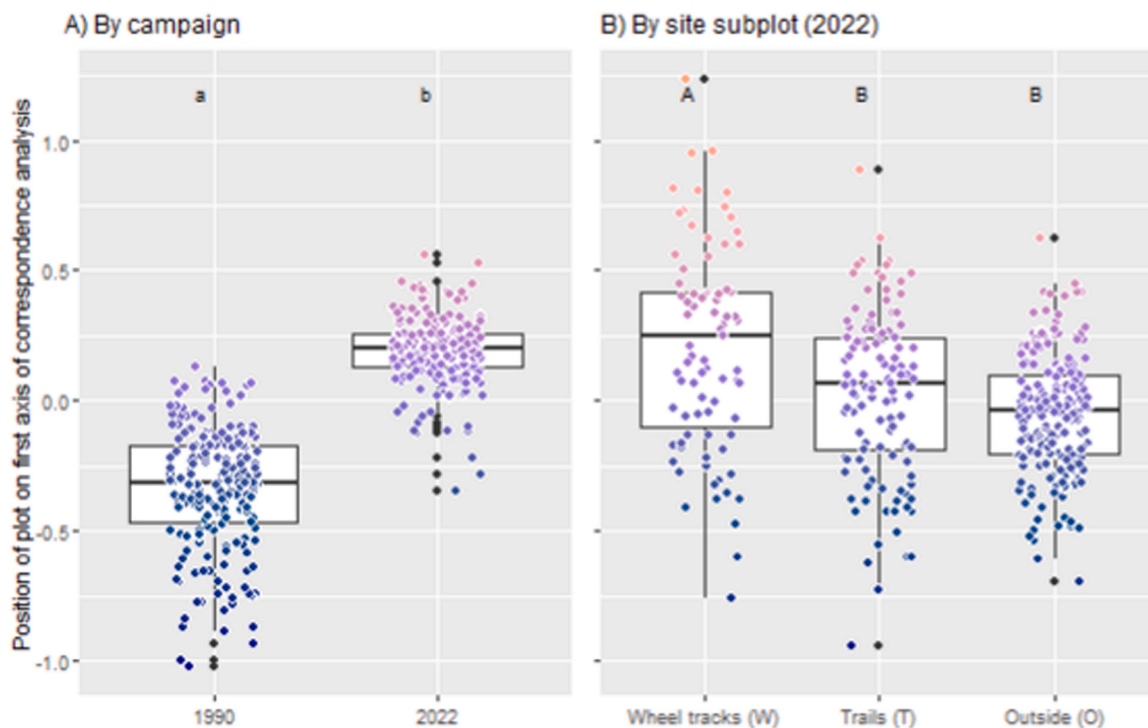


Fig. 4. A) distribution of plot positions on the first axis of correspondence analysis controlling for site effect for the 206 plots sampled in 1990 and 2022; B) distribution of subplot positions projected as supplementary points. Gradient of colours according to position on the first axis. Means annotated with the same letter do not significantly differ at  $p < 0.05$ , according to a paired  $t$ -test in panel A, and to a Tukey's pairwise comparison in panel B.

**Table 1**

Explanatory variables selected in a stepwise regression of the shift along the first factorial axis of the correspondence analysis of vegetation communities and ANOVA results. Levels of the ownership factor sharing the same letter do not significantly differ according to an adjusted multiple comparison test using Tukey contrasts.

Shift in position along the first axis (2022 minus 1990)			
Explanatory variable	Standardised regression coefficient	ANOVA F-value	p-value
Canopy opening (field-estimated difference in canopy cover proportion, 1990 minus 2022)	0.25	13.9	0.0003
Area proportion of wheel tracks in 2022	0.20	9.0	0.003
Ownership forestry school <sup>b</sup>	-0.11	3.0	0.03
municipal <sup>a</sup>	0.12		
national <sup>b</sup>	-0.09		
private (reference level) <sup>ab</sup>	0		

value of plots of the 2022 campaign (Fig. 5, light grey panels) was always the one closest to the median value of the wheel tracks (Fig. 5, dark grey panels). Taking 2022 plots with trails and wheel tracks only, indicator values separated per subplot show that the different types of disturbance harbour species with different environmental preferences (Fig. 5, dark grey panels). For all indicator values except light and mean temperature, the averages per intra-plot disturbance were significantly different and arranged along an increasing gradient from undisturbed subplots to wheel track subplots, with trails (excluding wheel tracks) in between. Correlations between changes in mean indicator values per plot (2022 minus 1990) and changes in plot position on the first factorial axis of the correspondence analysis (Appendix F) show that the latter is highly tied to  $\Phi_{TW}$  indicator of association to silvicultural disturbances to soil ( $r = 0.75$ ), but also to soil moisture ( $r = 0.61$ ) and subsidiarily to light ( $r = 0.45$ ). The correlation of plot shifts with mean temperature indicator is weak ( $r = 0.18$ ).

We compared, on a plot-by-plot basis, mean indicator values in 1990 and mean indicator values in the 2022 subplots outside of disturbances (O). This showed a highly significant difference, i.e. a probable change of vegetation in undisturbed areas for mean temperature ( $P < 1e-4$ ) and light ( $P = 0.002$ ), weakly significant for  $\Phi_{TW}$  index ( $P = 0.04$ ) and nitrogen ( $P = 0.06$ ), with in all cases an increase in bioindicated values for the 2022 subplots outside of disturbances compared to 1990 (see Fig. 5). In contrast, there was no difference for soil moisture nor pH.

#### 4. Discussion

There was an important reshuffling of plant communities in the Amance forest between 1990 and 2022. Species which appeared in the 2022 campaign were for the most part ruderal or non-forest species which thrive in nitrogen-rich habitats or in humid habitats (Appendix E). Species which are not forest specialists were more frequent amongst species which increased than amongst species which decreased (Appendix E). In contrast, the few species which decreased between 1990 and 2022 are more often cited as ancient European woodland species (per Hermy et al., 1999) than species which increased. The two species which decreased the most, *Luzula pilosa* and *Convallaria majalis* are amongst the most distinctive ancient woodland species in Europe.

The increased frequency of occurrence of non-forest, peri-forest and hydrophilic species, and their frequent association to skid trails or wheel tracks testify to the importance of forestry vehicles in the vegetation changes observed in the Amance forest over the last 32 years. The distribution of projected subplots on the correspondence analysis likewise shows that observed shifts in plant communities are tied to the increased frequency of specific species in skid trails and even more markedly in wheel tracks. Similarly, but in the boreal biome, Harvey and Brais

(2002) observed a differential impact on vegetation composition, with shade-tolerant “avoider” species being maintained in less disturbed areas, while skid trails facilitated the establishment of pioneer “invader” species.

There are multiple mechanisms through which forest management and mechanisation can have impacted understory vegetation in the Amance forest: direct destruction of plants, changes in soil hydrology (Cambi et al., 2015) and soil nutrition, changes in canopy cover and light (Baeten et al., 2009), subsequent modifications of microclimate, arrival of agestochoric species (i.e., species dispersed by forestry vehicles) or arrival of invasive species (Naaf and Kolk, 2016).

#### 4.1. Soil hydrology

Hydrophilous species increased in share of the total number of occurrences. Several studies have associated the presence of hydrophilous species to skid trails (Avon et al., 2013; Wei et al., 2016). In line with this, we found the significant overall increase in bioindicated soil moisture to be higher in skid trail subplots and wheel track subplots than off. Temporal changes in bioindicated soil moisture were highly correlated with changes in the  $\Phi_{TW}$  index (Appendix F), indicating that they carry similar information on vegetation change. The high correlation of both with the shift in plot positions between 1990 and 2022 points to the importance of mechanisation-induced disturbances for soil structure and hydrology, and in turn to the importance of changes in soil structure and hydrology for shifts in plant communities.

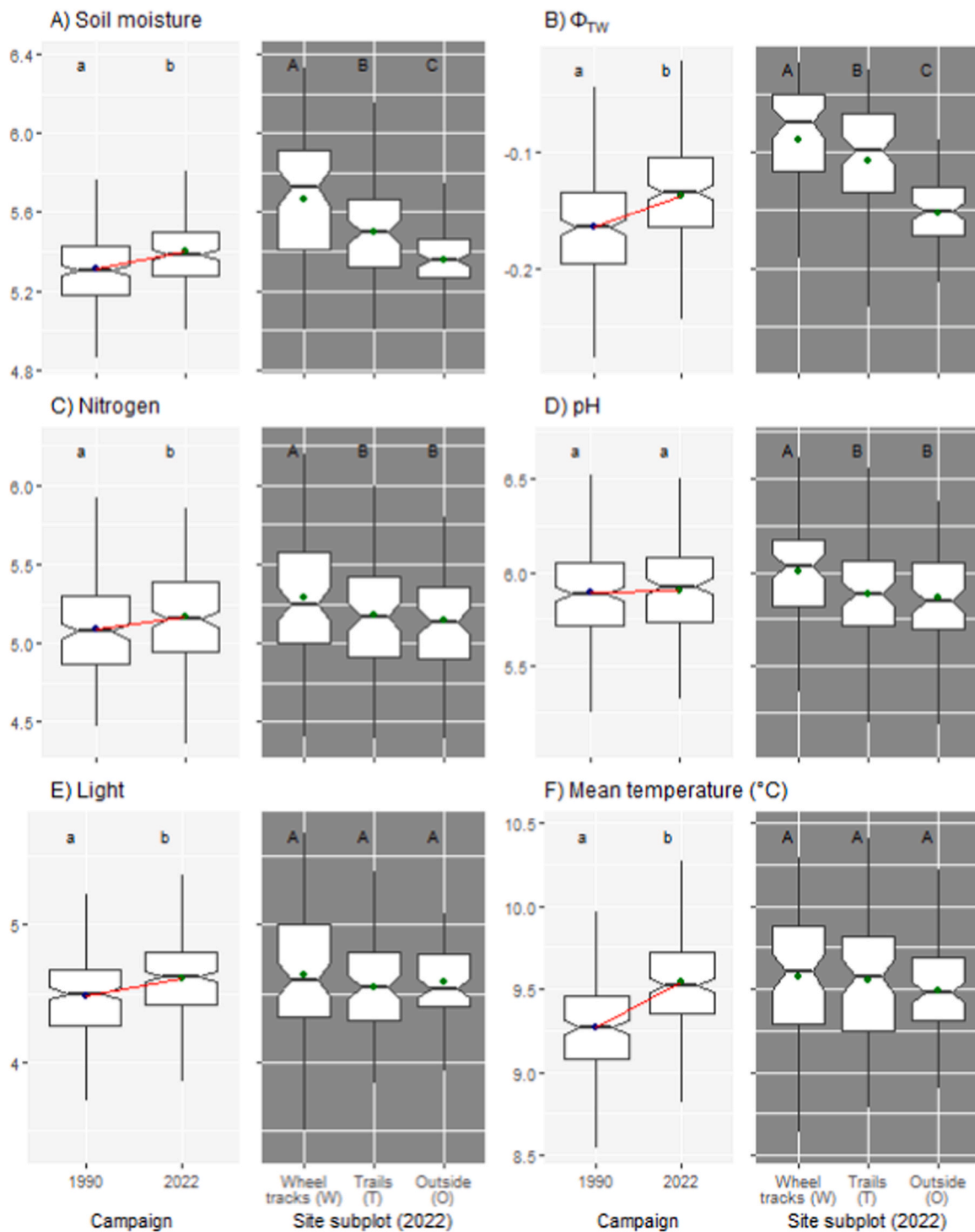
Large machines are known to degrade soil structure and diminish macroporosity, resulting in reduced permeability: Martin (2019) found that the capacity of saturated soil to drain water is three times lower in skid trails compared to zones without machines in the region surrounding the Amance forest; Bonnaud et al. (2019) showed that soil compaction altered perched water table behaviour leading to shifts towards more hydromorphic soils; Buckley et al. (2003) reported increased compaction and moisture on skid trails, associated to more wetland species; and Nazari et al. (2021), in their meta-analysis, reported that logging associated compaction increases bulk density and reduces total porosity.

#### 4.2. Soil nutrition

An increase in the frequency of nitrogen-demanding species had been identified in the first resurvey study of the Amance forest (+0.27 between 1971 and 1990 on the Ellenberg’s N-scale, Thimonier et al., 1992) and has since been observed in multiple other regions (Dirnböck et al., 2014). We showed here that it continued between 1990 and 2022, but to a lesser extent, by 0.08 only.

Atmospheric deposition is one potential explanation for this small persisting eutrophication signal. Yet in their multi-site study of the drivers of the eutrophication signal, Verheyen et al. (2012) found atmospheric deposition to be insignificant. Dirnböck et al. (2014) also compiled long term trends in understory vegetation and found that observed changes in species cover were unrelated to N deposition rates. Moreover, atmospheric deposition has declined since the 90 s (Engardt et al., 2017), including in Lorraine (see time series in Appendix G) where bulk deposition averaged 11.1 kg N.ha<sup>-1</sup>.yr<sup>-1</sup> between 1993 and 2002 but 7.3 kg N.ha<sup>-1</sup>.yr<sup>-1</sup> only between 2011 and 2021. However, including dry deposition, the current level of deposition in Lorraine is probably still close to critical loads of nitrogen for forest vegetation (10–15 kg N.ha<sup>-1</sup>.yr<sup>-1</sup>, Braun et al., 2022).

Disturbance adapted species are generally more nutrient demanding. The eutrophication signal could be related to forestry vehicles’ disturbances. This is suggested by our higher indicator values for nitrogen in wheel tracks and on skid trails than off. Ebrecht and Schmidt (2003), and Avon et al. (2013) also reported higher bioindicated nitrogen in skid trails. This is likely to result from compaction induced modifications to soil hydrology, pH and thus microbial activity. Research on the



**Fig. 5.** In light gray, distribution of mean plot bioindicator values per campaign. The dots represent the mean of each campaign, linked by a red line. Appendix D sets out the meaning of the value range for each indicator.  $\Phi_{TW}$  (panel B) is the index of association to trails and wheel tracks. In dark gray, distribution of 2022 bioindicator values per intra-plot disturbance. Within each panel, means annotated with the same letter do not significantly differ at  $p < 0.05$ . Note that the significance of the difference between O on the one hand and W and T on the other for  $\Phi_{TW}$  was expected and is presented here only as a control, since the indicator was constructed on the basis of this difference.

consequences of compaction on nitrogen availability to plants is not yet conclusive. In a nearby site, on the same type of soil, experimental evidence showed compaction blocked the microbial immobilisation of nitrate, but not its production by decomposers, leading to an increase in nitrate concentration in soil solution (Ranger et al., 2021). Ebrecht and Schmidt (2003) measured an increase in the Ellenberg nitrogen indicator value bioindicated by plants and at the same time a drastic drop in

the net mineralisation of nitrogen measured in soils, showing that increases in the nitrogen indicator value after compaction are not always linked to a real increase in nitrogen availability.

The rise in bioindicated nitrogen seemed to be unrelated to bioindicated acidity. As Diekmann (2003) warns, these two indicator values are inter-correlated and we observed the classic strong correlation between spatial variations in acidity and nitrogen indicator values

( $r = 0.70$  in 2022,  $n = 206$  plots). However, this correlation was weaker when it came to temporal variations in these two indices between 1990 and 2022 ( $r = 0.36$ , Appendix F). The temporal evolutions of pH and nitrogen were indeed different: pH indicator value showed no significant change between 1990 and 2022, while the nitrogen index increased significantly.

Shift of communities along the first axis of the correspondence analysis were strongly correlated to indices of association with skid trails ( $\Phi_{TW}$ ) but only weakly to changes in indicator values for nitrogen. This suggests pressures induced by mechanisation might be overriding increased nitrogen availability as the main driver of vegetation shifts in the last decades.

#### 4.3. Canopy cover and light

Multiple resurvey studies have identified light as a key determinant of changes in understory vegetation (Baeten et al., 2009). Indeed, the significant increase in the indicator value for light and the regression analysis showed that plot-level canopy opening was partly responsible for the 1990–2022 vegetation shift. Openings in the canopy, small gaps created by natural disturbances or larger partial logging, contributed to the progression of species with high light requirements and to tree regeneration. It is not straightforward to separate the effects of openings related to road networks from those due to natural cuts or gaps. Intuitively, trails are associated to canopy openings, and increased photosynthetic active radiation has been reported on haul roads (Buckley et al., 2003). Yet in their study of skid trails, Wei et al. (2015) measured fine scale light heterogeneity and did not find differences between subplots located on or outside the skid trails. Aligning with this, we found that trails and wheel tracks do not have significantly different bioindicated light compared to areas without trails nor wheel tracks in the Amance forest. It may therefore be that the canopy is not more open on trails than elsewhere in the forest. Moreover, a number of trail-avoidant and light demanding tree species also progressed. Counter to our hypothesis, we conclude that canopy openings on or off trails played a role in forest vegetation shifts independently of mechanisation effects.

#### 4.4. Temperature and climate change

Measured temperatures in the Amance forest were stable between 1971 and 1990, but increased by  $1.5\text{ }^{\circ}\text{C}$  for mean temperatures between 1990 and 2022 (see Appendix A). Precipitations stayed stable. Notwithstanding the importance of forest microclimates (de Frenne et al., 2013) and the caution required when downscaling macro- to microclimate, including when looking at bioindication (Marrec et al., 2022), increased temperature should result in the thermophilisation of plant communities. In the Amance forest, bioindicated annual mean temperature significantly increased between 1990 and 2022, albeit five times less rapidly than measured temperatures ( $+0.27\text{ }^{\circ}\text{C}$  in bioindicated temperature in contrast to  $+1.5\text{ }^{\circ}\text{C}$  for measured temperature). Bertrand et al. (2011) observed almost no thermophilisation ( $+0.02\text{ }^{\circ}\text{C}$ ) of vegetation in the French plains between 1965 and 2008. Our results suggest that vegetation resistance to global warming has diminished since then. Large-scale forest disturbances may also significantly reduce temperature buffering in the future (Dietz et al., 2020).

There was no interaction between thermophilisation and mechanization, with similar increases in bioindicated temperature on and off trails or wheel tracks. Despite the fact that light demanding species often exhibit higher bioindicated temperature, we found no correlation between thermophilisation and field-estimated canopy opening and no correlation between thermophilisation and changes in bioindicated light (Appendix F). These findings all suggest that neither logging and associated soil disturbance, nor windthrow and associated canopy openings favoured thermophilisation. This contrasts with De Frenne et al. (2013) who found that the response to climate warming was attenuated in forests whose canopies became denser. It also contrasts with Dietz et al.

(2020) who observed a larger increase in mean temperature indicator value in storm-induced openings. Observed increases in bioindicated temperature irrespective of canopy openings may mean that the resistance thresholds of understory vegetation, hitherto protected by the forest microclimate, are starting to be exceeded. This was also observed by Kermavnar and Kutnar (2024), who detected thermophilisation in Slovenian oak stands over the last three decades.

Although we observed a significant and ongoing thermophilisation, the weak correlation between plot shifts in the correspondence analysis and increases in plot bioindicated temperature show that thermophilisation was not the main driver of observed changes in plant communities in the Amance forest.

## 5. Conclusion

Our results show mechanised forestry operations were the main driver of understory vegetation change in the Amance forest over the last three decades, overriding the previously observed effects of nitrogen deposition between 1971 and 1990.

We found that intensified movement of forestry vehicles throughout the forest resulted in an increase in species associated with soil compaction and consequent waterlogging. This increase is notable in trails and wheel tracks, but also drove shifts in the composition of plant communities at the whole forest level. Albeit not the first driver of shifts in plant communities, global warming also likely resulted in increased bioindicated temperature. Counter to our hypothesis, neither thermophilisation nor bioindicated light were higher in areas directly disturbed by forestry vehicles.

By showing the long-term forest-wide impact of mechanised forest operations on understory vegetation, this study has implications for research and for forest management. The creation and use of skid trails is common in logged forests around the world and affects similar surface percentages as observed in the Amance forest (13 % compared with less than 10 % on average in temperate and tropical forests, DeArmond et al., 2021). Global woody biomass harvest volume has increased by 50 % since the mid-twentieth century and is set to continue rising (Lauri et al., 2019). Mechanisation will therefore increasingly drive changes in plant communities. This needs to be more explicitly accounted for in forest ecology research and when planning forestry operations.

### CRediT authorship contribution statement

**Vennin Sydney:** Writing – review & editing, Writing – original draft, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Dupouey Jean-Luc:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Thimonier Anne:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Behr Patrick:** Validation, Resources, Methodology, Investigation, Data curation, Conceptualization. **Montpied Pierre:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

### Declaration of Competing Interest

The authors declare no competing interests.

### Acknowledgements

We thank Paulina Pinto, Yves Ehrhart, Maxence Arnould, David Gasparatto, Nathalie Leroy, Joseph Levillain, Noémie Pousse and Eleonore Pontoy for their help. We also thank the French “Office national des Forêts” (ONF) and AgroParisTech for access to historical data and to the forest, and the RENECOFOR network for data on nitrogen deposition.

This work was financially supported by the ORION program of the University of Lorraine. The UMR Silva is supported by a grant overseen by the French National Research Agency (ANR) as part of the « Investissements d'Avenir » program (ANR-11-LABX-0002-01, Lab of Excellence ARBRE).

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.122562](https://doi.org/10.1016/j.foreco.2025.122562).

## Data availability

Data will be made available on request.

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