Combining multiple investigative approaches to unravel functional responses to global change in the understorey of temperate forests

Global Change Biology

Landuyt, Dries; Perring, Michael P.; Blondeel, Haben; De Lombaerde, Emiel; Depauw, Leen et al

https://doi.org/10.1111/gcb.17086

Received: 8 June 2023 | Revised: 20 November 2023 | Accepted: 20 November 2023
DOI: 10.1111/gcb.17086

RESEARCH ARTICLE

Global Change Biology WILEY

Combining multiple investigative approaches to unravel functional responses to global change in the understorey of temperate forests

Dries Landuyt[1] | Michael P. Perring[2,3] | Haben Blondeel[1] | Emiel De Lombaerde[1] | Leen Depauw[1] | Eline Lorer[1] | Sybryn L. Maes[4] | Lander Baeten[1] | Laurent Bergès[5] | Markus Bernhardt-Römermann[6,7] | Guntis Brūmelis[8] | Jörg Brunet[9] | Markéta Chudomelová[10] | Janusz Czerepko[11] | Guillaume Decocq[12] | Jan den Ouden[13] | Pieter De Frenne[1] | Thomas Dirnböck[14] | Tomasz Durak[15] | Andreas Fichtner[16] | Radosław Gawryś[11] | Werner Härdtle[16] | Radim Hédl[10,17] | Steffi Heinrichs[18] | Thilo Heinken[19] | Bogdan Jaroszewicz[20] | Keith Kirby[21] | Martin Kopecký[22,23] | František Máliš[24] | Martin Macek[22] | Fraser J. G. Mitchell[25] | Tobias Naaf[26] | Petr Petřík[22,27] | Kamila Reczyńska[28] | Wolfgang Schmidt[18] | Tibor Standovár[29] | Krzysztof Swierkosz[30] | Simon M. Smart[31] | Hans Van Calster[32] | Ondřej Vild[22] | Donald M. Waller[33] | Monika Wulf[26] | Kris Verheyen[1]

Correspondence
Dries Landuyt, Forest&Nature Lab, Department of Environment, Ghent University, Melle (Gontrode), Belgium.
Email: dries.landuyt@ugent.be

Funding information
Agentúra na Podporu Výskumu a Vývoja, Grant/Award Number: APVV-19-0319; Akademie Věd České Republiky, Grant/Award Number: RVO 67985939; Directorate-General of the State Forests in Poland, Grant/Award Number: BLP-370; EU Horizon 2020 INFRAIA, Grant/Award Number: 871128; European Research Council, Grant/Award Number: 614839; Fonds Wetenschappelijk Onderzoek, Grant/Award Number: 1200321N, 1221523N, 12ZZV21N and G078921N; Grantová Agentura České Republiky, Grant/Award Number: 21-11487S; BOF; Czech Science Foundation, Grant/Award Number: L200052302

Abstract
Plant communities are being exposed to changing environmental conditions all around the globe, leading to alterations in plant diversity, community composition, and ecosystem functioning. For herbaceous understorey communities in temperate forests, responses to global change are postulated to be complex, due to the presence of a tree layer that modulates understorey responses to external pressures such as climate change and changes in atmospheric nitrogen deposition rates. Multiple investigative approaches have been put forward as tools to detect, quantify and predict understorey responses to these global-change drivers, including, among others, distributed resurvey studies and manipulative experiments. These investigative approaches are generally designed and reported upon in isolation, while integration across investigative approaches is rarely considered. In this study, we integrate three investigative approaches (two complementary resurvey approaches and one experimental approach) to investigate how climate warming and changes in nitrogen deposition affect the functional composition of the understorey and how functional responses in the understorey are modulated by canopy disturbance, that is, changes in overstorey canopy openness over time. Our resurvey data reveal that most changes in understorey functional characteristics represent responses to changes in canopy openness with shifts

For Affiliation refer page on 10

in macroclimate temperature and aerial nitrogen deposition playing secondary roles. Contrary to expectations, we found little evidence that these drivers interact. In addition, experimental findings deviated from the observational findings, suggesting that the forces driving understorey change at the regional scale differ from those driving change at the forest floor (i.e., the experimental treatments). Our study demonstrates that different approaches need to be integrated to acquire a full picture of how understorey communities respond to global change.

KEYWORDS
climate change, forest management, forestREplot, herbaceous layer, mesocosm experiment, nitrogen deposition, plant height, resurvey study, SLA

1 | INTRODUCTION

Climate warming and eutrophying atmospheric deposition are having profound consequences for individual plants, species, communities, and ecosystems around the globe (Malhi et al., 2020; Maskell et al., 2010; Parmesan & Yohe, 2003). As the number of scientific articles in the domain of global change ecology has increased tremendously over the past decade, we have added nuance to our understanding of global change impacts across systems (e.g., Bjorkman et al., 2018; van de Waal & Litchman, 2020). For systems encompassing multiple structural layers such as temperate forest ecosystems, this nuance has led to the recognition of a modulating effect of the overstorey on global change-induced community responses in the understorey, that is, the herbaceous vegetation growing on the forest floor (Landuyt et al., 2020; Segar et al., 2022; Verheyen et al., 2012; Zellweger et al., 2020). These understorey plant communities are pivotal to temperate forest plant biodiversity (Gilliam, 2007; Spicer et al., 2020), and depending on the their functional signature (determined by their cover, leaf traits and height) also affect nutrient and water cycling processes, and tree regeneration rates in these forest systems (De Lombaerde et al., 2021; Landuyt et al., 2019).

Past studies on the understorey's response to global-change drivers such as atmospheric nitrogen (N) deposition and climate warming mainly detected shifts in species composition: excess N deposition was found to increase the dominance of nitrophilous, acid-tolerant or generalist species (Gilliam, 2006; Segar et al., 2022), while climate warming was found to promote warmth-demanding species (De Frenne et al., 2013; Stevens et al., 2015). In contrast, responses of the understorey's functional signature (often expressed in terms of total herbaceous cover and community weighted mean [CWM] functional trait values such as plant height and specific leaf area [SLA]) have been found to be less pronounced or highly context-dependent (Depauw et al., 2020; Perring et al., 2018). A high canopy cover—that might buffer the response of the understorey to these global change drivers—has been put forward as a potential reason for weak or absent understorey responses (Hedwall et al., 2021; Richard et al., 2021; Verheyen et al., 2012; Zellweger et al., 2020). Plant community theory, indeed, states that a limiting resource (such as light) can restrict a community's response to other perturbations in resource availability and growing conditions, as those induced by global-change drivers (von Liebig, 1855). Hence, elevated levels of N availability, as induced by N deposition, might not lead to growth responses and, eventually, shifts in the functional characteristics of the understorey if light availability is still limiting growth (Segar et al., 2022; Strengbom et al., 2004; Verheyen et al., 2012). Following the same reasoning, also functional responses in the understorey to warming can be expected to amplify when canopies open up, which has already been shown in experimental conditions (De Frenne et al., 2015).

Most of the studies reported upon above rely on long-term resurvey datasets that aim to describe plot-level community changes over time by repeating historical plant community surveys up to several decades after initial surveys took place. These resurvey studies can reveal the rather slow responses of the understorey to various global-change drivers. When multiple of those resurvey studies are combined into a larger database, they can span broad environmental gradients in space and time and can reveal understorey responses to a variety of global-change drivers in a representative way (Verheyen et al., 2017). However, within these databases, resurvey studies are generally distributed at random across space, and often lack uniform, plot-level auxiliary data (e.g., soil resources, light availability) to be able to accurately quantify local drivers of change or to be able to control for potentially confounding drivers, leading to low signal-to-noise ratios in general. Moreover, sampling methods and plot selection strategies often depend on the specific objectives of individual resurvey studies. As a result, these so-called *opportunistic resurvey databases* are often plagued by data heterogeneity. To increase the signal-to-noise ratio in understorey research while preserving a regional perspective covering broad environmental gradients, one can carry out new, more targeted, distributed resurvey studies, with an orthogonal (i.e., maximizing independence among the global-change drivers of interest) plot network design and field measurement protocol shaped by a number of clear hypotheses (e.g., Baeten et al., 2013; Depauw et al., 2020; Fischer et al., 2010). Although these *orthogonally distributed resurvey studies* will increase our understanding of understorey responses to global change, they will still fail to distinguish correlation from causation or disentangle the consequences of correlated drivers. For true mechanistic understanding, *manipulative global-change experiments* are needed because they allow canceling out impacts of confounding drivers and enable detailed measurements of several mechanisms of change (Rustad, 2008). The downsides of those experiments are their often short-term nature, artefacts linked to the experimental settings (e.g., artificial belowground processes in pot experiments, unwanted side effects of treatments) and the difficulty to generalize findings towards other species or communities than those included within the experiment. Typically, these different investigative approaches are designed in isolation, making direct comparison among approaches impossible or extremely challenging. As a result, the scientific literature often reflects on those adopted approaches and their findings in isolation and therefore fails to fully exploit the complementarity among approaches (Luo et al., 2011).

In this study, we integrate three complementary investigative approaches, as introduced above, to reveal and understand general patterns of functional understorey responses to N deposition and climate warming, and how changes in light availability induced by moderate canopy disturbances modulate these responses. We focus specifically on functional signature responses, as a proxy for changes in understorey functioning over time. To do so, we compiled data from the forestREplot database, an opportunistic resurvey database focusing on understorey communities in temperate forests, set up an orthogonally distributed resurvey study and designed a large manipulative global-change experiment. We analyzed the different datasets using a uniform statistical approach targeted towards the main hypotheses being tested:

1. Light availability dynamics are the dominant driver of functional changes in the herbaceous understorey of temperate forests.
2. Functional understorey responses to N deposition and climate warming are generally weak, but become more pronounced when canopies open up over time.

We do not expect different approaches to yield identical results, but rather expect that different approaches will supply different pieces of information that will enhance our mechanistic understanding of observed community changes.

2 | METHODS

2.1 | Overview of the data

We report upon data from three studies that were jointly designed, as part of a larger scientific project 'PASTFORWARD', to understand responses of the understorey to key global-change drivers, and especially interactions among those drivers, including climate warming, N deposition and changes in (past) forest management (for an overview of the full study design see http://pastforward.ugent.be). The first dataset we use is based on the forestREplot database, a European-scale compilation of understorey resurvey studies (http://forestreplot.ugent.be), which we refer to as an *opportunistic resurvey database* in this study. The forestREplot database contains understorey community change data collected in a large number of unmanaged or only extensively managed temperate forests across Europe, covering broad environmental gradients in terms of N deposition and climate (Figures 1a and 2a,b). As included forest types are diverse and detailed plot-level data on resource availability (e.g., light and nutrients) is often lacking, the dataset is typified by a large amount of variability. In conjunction, we designed an *orthogonally distributed resurvey study* targeted towards the current study's hypothesis by selecting plots along predefined gradients of the considered global-change drivers (climate and N deposition), while making sure that plots were comparable in terms of site characteristics and forest type (mesophytic deciduous forests and lowland beech forests). For this study, we selected plots in 19 regions, covering the geographical extent of the database (see Figure 2a), that vary in terms of past climatic warming and N deposition rates and combinations thereof (Figure 2b). Within each region, we selected multiple plots with contrasting past management leading to a variety of canopy conditions (mostly in terms of canopy density/openness, see also Figure 2b). To lower amounts of noise and unexplained variability in the data, we complemented vegetation resurveys with detailed plot-level measurements of light and nutrient availability. Finally, we also set up a *manipulative global-change experiment* in a deciduous forest in Belgium where we exposed artificial understorey communities to the considered global-change drivers in a full-factorial design (Figure 1b). To compile these artificial communities, we imported genuine forest soils from several regions spread across the European temperate forest biome, and selected species with contrasting ecological strategies from the database study's species pool.

In the following sections, we outline methodological details of each investigative approach to allow understanding of our synthesis, highlighting key aspects to allow integration across methodologies. Further details on each separate approach can be consulted in earlier publications on these individual studies: see Perring et al. (2018) for the opportunistic resurvey database, Depauw et al. (2020) for the orthogonally distributed resurvey study and Blondeel et al. (2020) for the manipulative global-change experiment. The full dataset can be consulted at figshare (Landuyt et al., 2023).

2.1.1 | Opportunistic resurvey database

The database contained resurvey data from 1700 forest plots (subset of the forestREplot database as analysed in Perring et al. (2018), but retaining only plots with overstorey cover data at both survey dates), scattered across 39 regions spanning the European temperate forest biome (Figure 2a). In each of these plots, understorey and overstorey cover and composition has been recorded at two points in time, with a period of 38 years on average between both survey dates. All plots were situated in ancient forests (continuous forest cover since 1850, as we omitted data from more recent, post-agricultural forests

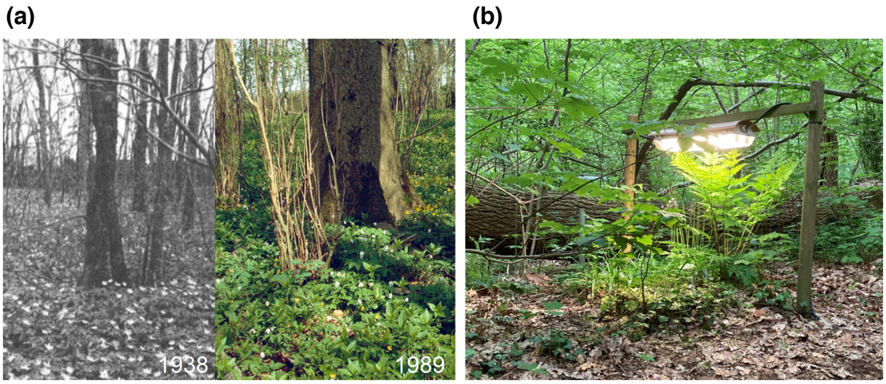

FIGURE 1 Illustration of the applied approaches to investigate understorey responses to global change: understorey resurvey studies (a) and manipulative mesocosm experiments (b). The photos in (a) illustrate a classical resurvey method, where plant species composition is recorded in the same plot at two points in time, here shown as typical views in southern Sweden in 1938 and 1989 (courtesy of Jörg Brunet). Picture (b) shows an experimental understorey plot in the Aelmoeseneie forest, near Ghent, Belgium where light is added to mimic changes in canopy cover (courtesy of Haben Blondeel).

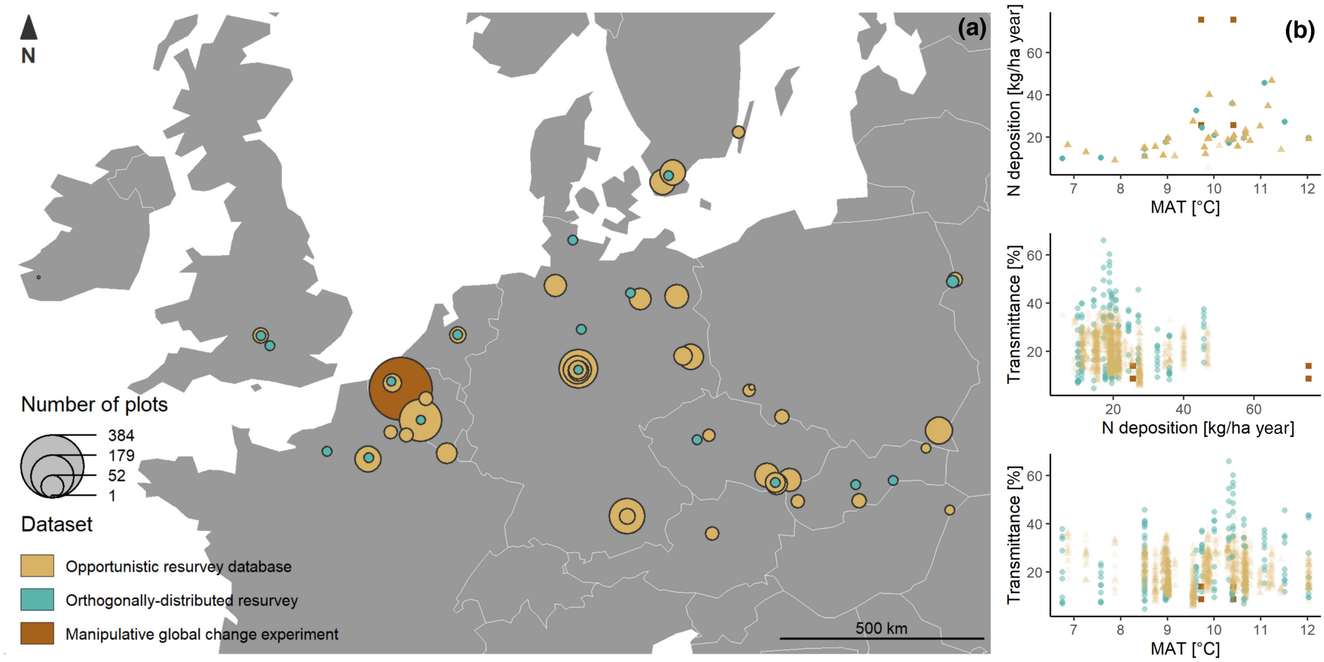

FIGURE 2 Spatial distribution of all studied observational and experimental plots within the West-European temperate forest biome (a) and studied gradients of global-change drivers (b) based on own below-canopy measurements (for the experiment) and on data extracted from CRU TS V4.05 (mean annual temperature data) and EMEP RV4.42 (nitrogen deposition data) for the year 2016 (for the two resurvey approaches). Light availability (transmittance) was estimated based on PAR measurements or estimated based on overstorey canopy cover and/or composition records (see Appendix S3). Nitrogen deposition was extracted from EMEP as the total sum of wet and dry deposition of inorganic nitrogen. Mean annual temperature was calculated for the period 2007–2016. The color legend at the bottom-left also applies for the environmental gradient panels at the right. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

(as described in Perring et al., 2018). As variation in soil properties were not monitored, we relied on (1) community-weighted Ellenberg Indicator Values (EIV, weighted by cover) for soil fertility (EIV-N) and acidity (EIV-R) (based on Ellenberg et al., 2001) and (2) a scoring of the overstorey's litter quality as proxies for forest floor resource availability and growing conditions. These proxies were all based on community composition data at the resurvey. The considered EIVs, on an ordinal scale from 1 to 9, reflect a species' ecological niche in terms of resource availability and/or growing conditions, while litter quality scores reflect tree species-specific litter decomposition rates (based on Baeten et al., 2009; Hermy, 1985; Van Calster et al., 2008; Verheyen et al., 2012).

2.1.2 | Orthogonally distributed resurvey

For the orthogonally distributed resurvey, we selected 192 historical understorey surveys spread across 19 European regions (Figure 2a), along gradients of N deposition and climate (Figure 2b), and conducted a resurvey of those plots in the late Spring of 2015 or 2016 (42 years on average between survey dates). Replicating initial survey methods in each region, as detailed in Depauw et al. (2020), the cover of all understorey species that occurred within these plots was re-estimated. Simultaneously, representative samples of soil were collected for lab analyses, allowing direct characterization of soil acidity (pH) and nutrient content (C:N, Olsen P) (see Maes et al., 2019 for more details), variables that could co-determine community trajectories of change. In addition, data on overstorey composition and canopy openness were recorded by visual cover estimates and densiometer measurements (Lemmon, 1956), respectively. For the initial survey, only composition and cover data were available for the overstorey. Our measurements together with the historical overstorey data allowed a more precise estimation of light availability changes between surveys in comparison with the database study (see Appendix S3). Since historical data on overstorey cover was absent for 20 plots, we here only analyze a subset of 172 plots.

2.1.3 | Manipulative global change experiment

For the experimental study, we planted 384 mesocosm understorey communities in well-drained plastic containers. Per mesocosm, we planted 5 species with contrasting ecological strategies, selected from a common species pool of 15 species (see Appendix S2). Mesocosms were dug into the soil of a deciduous forest in Northern Belgium. Next, mesocosms were exposed to warming (+0.7°C increase of mean annual temperature [MAT], using open top chambers [OTC]), N fertilization (+50 kg N/ha year, through liquid ammonium nitrate (NH_4NO_3) fertilization, minimizing effects on soil pH) and light addition (+24 μmol/m^2 s, mimicking a 5% increase of photosynthetically active radiation (PAR) transmittance, using fluorescent tubes, as shown in Figure 1b). Ambient temperature (MAT of around 10°C at 15 cm above the forest soil), light conditions (around 10% PAR transmitted to the understorey) and N deposition levels (between 20 and 25 kg N/ha year measured in throughfall water) at the experimental site were used as control. These treatments were applied each time to blocks consisting of four mesocosms (referred to as 'plot' in our analyses). As the original study also focused on soil effects (bearing the imprints of past land use) and how they interact with the considered global change treatments, all mesocosms were planted in genuine forest topsoils, collected in ancient (forested since the time of the earliest written records) and recent (afforested after 1960) mature forest plots from eight European regions spread along gradients of N deposition and climate. All collected soil samples were analyzed in the lab to determine their nutrient content (C:N, Olsen P) and acidity (pH). In this synthesis, we aim to control for these soil effects, while testing our main hypothesis which does not focus on those effects specifically. The experiment was set up in 2016 after which the cover of all planted species has been estimated during spring. In May 2021, after 5 years of treatment application, all communities were resurveyed to evaluate community responses.

2.2 | Statistical analysis

2.2.1 | Response variables

As response variables, we considered (i) changes in CWM trait values and (ii) changes in total herbaceous cover, both assessed in terms of log-response ratios (LRR, i.e., the natural logarithm of the ratio between CWM trait values [or cover values] at the resurvey divided by the CWM trait values [or cover values] at the initial survey). We, hence, analyze changes over time and not across space as done in space-for-time analyses. For LRR cover calculations, we added 1% to all cover estimates to avoid division by zero. We focused the analysis on changes in CWM plant height (H) and SLA. These community traits, together with total herbaceous cover, relate to the functional importance of the understorey in temperate forests (Landuyt et al., 2019). CWM trait values were calculated using relative plant cover as weights and using species-specific trait values extracted from a literature trait database according to Perring et al. (2018). To calculate total cover and CWM trait values, we only took into account herb layer species sensu stricto. Hence, we omitted seedlings, climbers and shrubs from all vegetation datasets. In the experiment, however, we included *Hedera helix* as it here behaves as a ground-covering herb.

2.2.2 | Predictor variables

In the analysis, two types of predictor variables were considered, including focal predictor variables that relate to the hypotheses being tested and covariates we aim to control for. Focal predictor variables included (i) absolute changes in light availability (expressed in terms of light transmittance %, ΔLT, derived from overstorey data (tree and shrub cover); see Appendix S3 for details on the calculations for the different datasets), (ii) absolute changes in N deposition rate between survey dates (ΔNdep), and (iii) absolute changes in mean annual temperature (ΔMAT) between survey years (see Appendix S1 for calculation methods and distribution of these predictor variables across the investigative approaches). For the experiment, we included all global-change drivers as binary predictors in accordance with the binary treatments in the experiment. As we do not aim to compare the magnitude of our slope estimates among investigative approaches but only the signs, this methodological choice will not have a bearing on our results.

Covariates included (i) time between the initial survey and the resurvey (years, i.e., fixed for the experiment, and therefore not considered for this approach), and covariates characterizing soil characteristics, including (ii) soil acidity (pH H_2O), (iii) phosphorous availability (Olsen P), and (iv) the carbon-to-nitrogen ratio (C:N). For the database study, we relied on EIV R, EIV N, and an overstorey litter quality score as direct measurements of soil characteristics were not available. These indirect measurements were based on community composition at the resurvey to ensure comparability with the orthogonally distributed resurvey where we account for soil characteristics that were measured at the resurvey only. Finally, we also considered baseline community characteristics (being the CWM SLA, plant height or total herbaceous cover, depending on the modelled response) at the initial survey, as an additional predictor variable to account for the regression to the mean phenomenon when modelling change dynamics (Mazalla & Diekmann, 2022).

2.2.3 | Mixed-effects modelling

We tested our main hypothesis, that is, whether understorey responses to climate warming and N deposition are modulated by changes in canopy openness, using linear mixed-effects models with all covariates and focal predictor variables as fixed main effects. In addition, we included two interaction terms: (i) the interaction between changes in light availability and changes in N deposition rates and (ii) between changes in light availability and changes in MAT (see Table 1 for full R syntax). These interaction terms were included to test whether changes in canopy openness modify understorey responses to changes in MAT and N deposition. Random terms were specified based on dataset structures that differed depending on the investigative approach (see Table 1). Prior to model fitting, all variables were standardized ($M=0$, $SD=1$) and tested for independence based on variance inflation factors. All analyses were performed in R version 4.2.1.(R Core Team, 2022), using packages lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017) and sjPlot (Lüdecke, 2022). In total, nine separate models were fitted, modelling three response variables, each based on three investigative approaches.

3 | RESULTS

3.1 | Observed functional composition changes across investigative approaches

The distribution of the observed community changes was centered around no change across all investigative approaches (Figure 3). Only in the orthogonally distributed resurvey study did CWM plant height increase and herb cover decrease on average between the two survey dates. Across all investigative approaches, the variability in community changes was higher in terms of cover and CWM plant height when compared to community changes in terms of CWM SLA.

3.2 | The main drivers of functional community changes

All fitted mixed-effects models achieved a moderate model fit, denoted by marginal R^2 values between .18 and .45 (Table 2). These

TABLE 1 Overview of the datasets and dataset-specific terms included in the mixed-effects models, using lme4 R-syntax (Bates et al., 2015). Abbreviations refer to soil phosphorous (P), soil carbon (C), soil nitrogen (N), Ellenberg Indicator Values (EIV N and EIV R), litter quality (LQ), light transmittance (LT), nitrogen deposition (Ndep), and mean annual temperature (MAT). Baseline refers to the community weighted mean (CWM) specific leaf area, CWM plant height or herb cover at the initial survey date or at the start of the experiment. 'Δ' refers to absolute changes in the respective drivers between survey dates, '+' signs in between random intercepts indicate crossed random effects.

Dataset	Main effects	Interaction effects	Covariates	Random structure
Manipulative global change experiment	Light + Nitrogen + Warming	+Light:Nitrogen + Light:Warming	+Baseline + pH + Olsen P + C:N	+1|Region +1|Community +1|Plot
Orthogonally distributed resurvey	ΔLT + ΔNdep + ΔMAT	+ΔLT:ΔNdep + ΔLT:ΔMAT	+Baseline + Time interval + pH + Olsen P + C:N	+1|Region
Opportunistic resurvey database	ΔLT + ΔNdep + ΔMAT	+ΔLT:ΔNdep + ΔLT:ΔMAT	+Baseline + Time interval + EIV R + EIV N + LQ	+1|Region

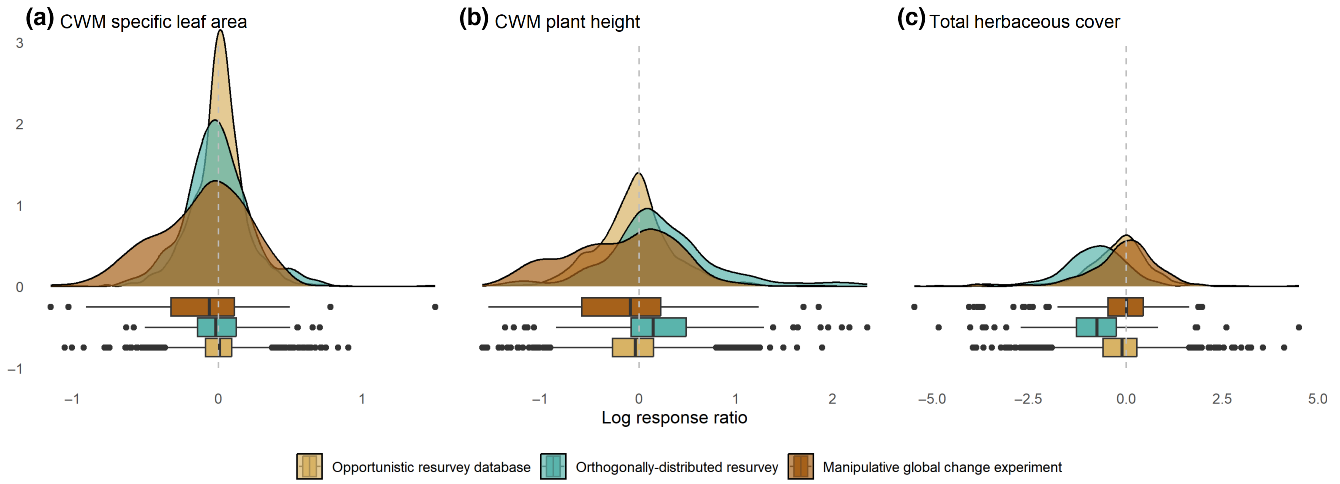

FIGURE 3 Distribution of all response variables: log response ratios of community weighted mean (CWM) specific leaf area (SLA) (a), CWM plant height (b) and total herb cover (c) in the three considered datasets. Log response ratios were calculated as the natural logarithm of the community characteristic (CWM SLA, CWM plant height or total herb cover) at the resurvey divided by the community characteristic at the initial survey (i.e., the vegetation survey directly after planting for the experiment). Positive log response ratios refer to increases of the considered community characteristic, while negative values refer to a decrease over time. Note differences in *x*-axis scales.

TABLE 2 R^2 values for all fitted models. LRR refers to log response ratio, CWM to community weighted mean trait values, SLA to specific leaf area, and R^2_m and R^2_c to marginal and conditional R^2 values respectively, calculated based on Nakagawa and Schielzeth's r^2 calculation for mixed models.

Response	Manipulative global change experiment		Orthogonally distributed resurvey		Opportunistic resurvey database	
	R^2_m	R^2_c	R^2_m	R^2_c	R^2_m	R^2_c
LRR CWM SLA	.39	.55	.43	.63	.45	.54
LRR CWM plant height	.23	.51	.34	.66	.30	.45
LRR total herb cover	.35	.49	.18	.38	.23	.54

high R^2 values were, however, mainly driven by the inclusion of the baseline values (CWM SLA, plant height and cover at the initial survey) as additional predictors in the models (for model outputs without the baseline included, see Appendix S4). Given that marginal R^2 values are comparable among investigative approaches, the analysis also suggests that none of the investigative approaches outcompetes the others in terms of explainable variability in the data. Considering the focal predictor variables, being changes in light availability, changes in N deposition rates and changes in MAT, we found that the different investigative approaches yielded contrasting results (Figure 4).

First of all, we found limited evidence underpinning our main hypothesis, that changes in canopy openness modify how the functional composition of understorey communities responds to N deposition changes and climate warming over time. Only one significant interaction was detected, in experimental settings (Figure 4a). However, we did detect several main effects of the considered global-change drivers (Figure 4b,c,f–i). Based on the database study, an increase of light availability was found to increase herb cover ($p<.01$) and plant height ($p<.05$) (Figure 4f,i). A similar trend, although only significant for herb cover changes ($p<.05$), was observed in the resurvey study (Figure 4h). In contrast, light addition alone did not affect the functional composition of the experimental understorey communities (Figure 4a,d,g). Only in combination with a warming treatment, illumination was found to decrease CWM SLA in the experiment ($p<.05$) (Figure 4a). Effects of climate warming (at the macroscale) were not detected in the orthogonally distributed resurvey (Figure 4b,e,h), while negative effects on herb cover, CWM plant height and CWM SLA were detected in the analysis based on the opportunistic resurvey database (Figure 4c,f,i). In contrast, in the experiment, microclimate warming was found to increase total herb cover ($p<.05$) (Figure 4g). Also the effects of changes in N deposition rates were found to differ among approaches. Increases in N deposition rates were found to decrease total herb cover ($p<.05$, based on the opportunistic resurvey database, Figure 4i) and increase CWM SLA ($p<.05$, based on the orthogonally distributed resurvey, Figure 4b).

The precision of the estimates was found to differ depending on the investigative approach. The precision of the coefficient estimates was found to increase with the number of datapoints, with low precision in the experiment and orthogonally distributed resurvey and higher precision in the database study.

4 | DISCUSSION

By comparing results from three different investigative approaches, we indeed found that changes in light availability are an important

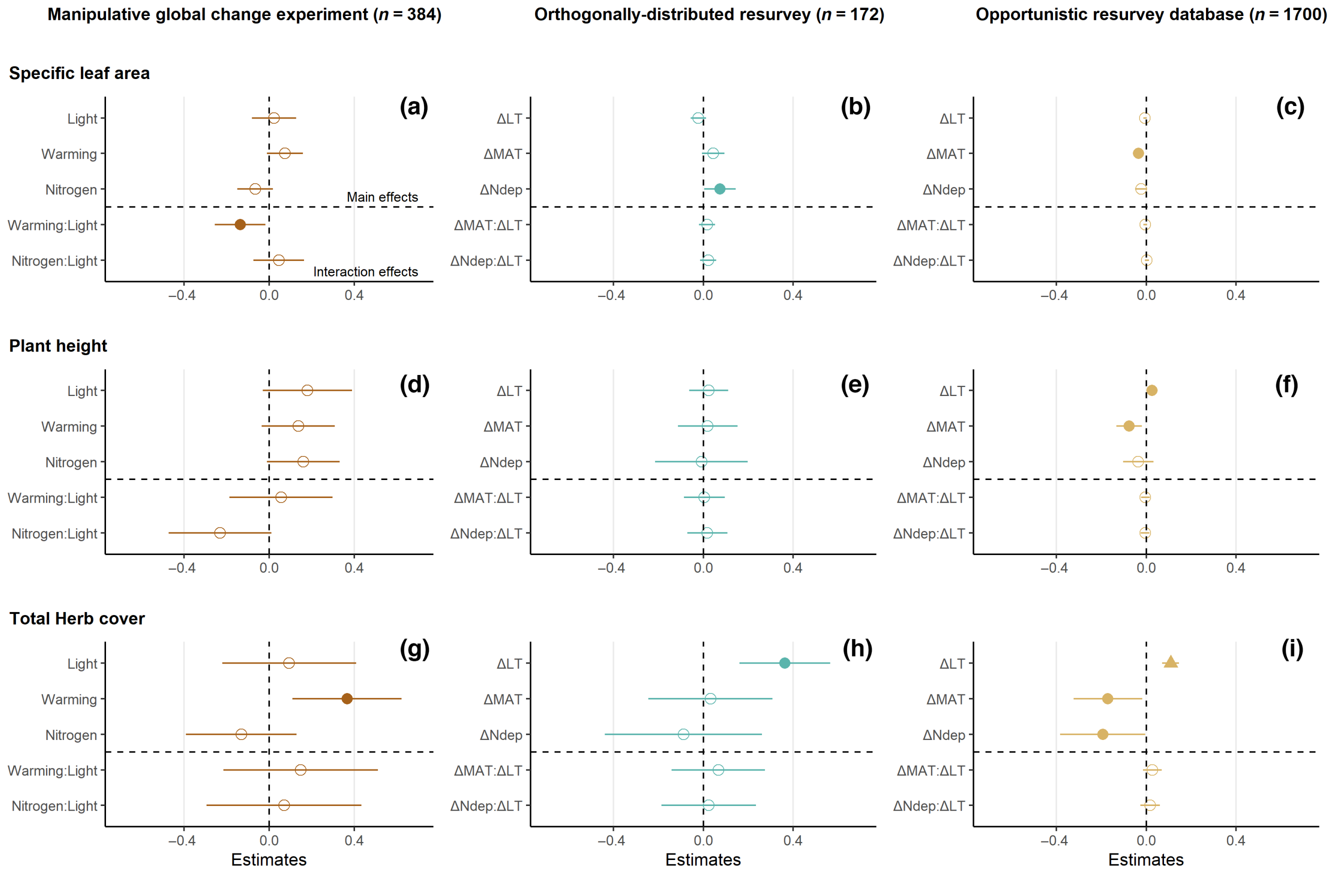

FIGURE 4 Coefficients of the fitted mixed-effects models, separately fitted to standardized data from the manipulative global-change experiment (a, d, g), the orthogonally distributed resurvey (b, e, h) and the opportunistic resurvey database (c, f, i). n denotes the number of experimental units in the experimental study, and the number of vegetation plots for the other two investigative approaches. Open circles denote insignificant slope estimates, while closed circles ($p < .05$), triangles ($p < .01$) and squares ($p < .001$) denote significant slope estimates. Although we included baseline community characteristics (community weighted mean plant height, specific leaf area and herb cover at the initial survey) and a set of covariates as predictors, we excluded the respective slope estimates from the graph. LT, light transmittance; MAT, mean annual temperature; Ndep, nitrogen deposition; Δ, change of these drivers between the initial survey and the resurvey.

driver of functional changes in the understorey, but found limited evidence for our second hypothesis, being that overstorey trees can buffer functional responses in the understorey to global change. While we did detect several main effects of the considered global-change drivers, the number of significant interaction effects between changes in light availability, on the one hand, and changes in N deposition rates and warming on the other hand was limited to one significant interaction between light addition and warming on CWM SLA in experimental settings. Below we discuss all detected main and interaction effects for each global-change driver independently and end the discussion with a reflection on the added value of combining different investigative approaches as done in our study.

4.1 | Canopy effects

The importance of canopy dynamics for steering changes in understorey community composition and structure has already been put forward by multiple studies in the past (Axmanová et al., 2011; Depauw et al., 2020; Landuyt et al., 2020). Most of these studies based their conclusions upon relationships between understorey community composition and overstorey canopy cover or openness. We found similar relationships emerging in the opportunistic resurvey database and orthogonally distributed resurvey study. An increase in light availability over time (as a result of canopy opening due to natural disturbances, tree mortality or management) gave rise to a taller understorey community, with a higher cover. These findings are in line with the literature. Biomass production, which is closely related to plant height and cover (Heinrichs et al., 2010), is promoted when the availability of light (generally the most limiting resource for temperate forest understoreys) increases (Landuyt et al., 2020). Surprisingly, we did not detect a direct response to light addition in the experiment. We can think of two potential explanations for this discrepancy between our observational and experimental findings. First of all, light addition levels in the experiment are subtle compared to light dynamics following canopy changes observed in the field. Being able to detect understorey responses to subtle changes in light availability probably requires more replicates and/or more precise measurements. We expect that more elevated light addition levels will induce more pronounced understorey reponses, also in experimental settings (see e.g., De Pauw et al., 2022). Second, discrepancies between observational and experimental findings can also be explained by the fact that light availability changes in the field are strongly confounded with other changes in resource availability and growing conditions at the forest floor, which was not the case in the experiment. Canopy opening in the field leads to increases in light availability, but also increases in microclimate temperature, vapour pressure deficit, throughfall water, etc. (Von Arx et al., 2013; Zhang, Landuyt, et al., 2022; Zhang, Verheyen, et al., 2022). Our findings across investigative approaches might therefore also suggest that the response of understorey communities to canopy opening cannot be reduced to a simple light response, but should be interpreted as a response to a combination of micro-environmental changes induced by canopy opening.

4.2 | Warming effects and interactions with changes in light availability

The absence of any interaction effects between macroclimate warming and changes in light availability suggests that the effect of macroclimate warming does not increase when the canopy opens up over time. This finding contradicts our expectation but can potentially be explained by water availability dynamics (which we could not quantify) following changes in canopy openness. Microclimate warming following canopy opening might introduce drought stress due to increases in vapor pressure deficit, which may counteract plant growth-enhancing effects of temperature increases. In contrast, the open-top-chambers, that were used to mimic microclimate warming in the experiment, do not induce drought stress (in contrast, a small but significant increase in soil water availability and a decrease in vapor pressure deficit inside OTCs has been reported by De Frenne et al., 2010). As a result, clear warming effects as detected in the experiment (for herbaceous cover, specifically) might not be that clear or even reverse in the field, when water availability effects might be at play as well. Indeed, based on the database study, macroclimate warming was found to have a negative effect on CWM SLA, plant height and total herbaceous cover, which seems to contradict previous findings (Bjorkman et al., 2018; Chelli et al., 2019; Vanneste et al., 2019). A second potential explanation for undetected interaction effects in the two resurvey studies might be the relatively small variability in ΔMAT among sites (especially when compared to the variability in N deposition rate changes and canopy openness changes). This low variability lowers the statistical power to detect responses to warming (which were only detected in the opportunistically distributed resurvey database, characterized by a large sample size) as well as interactions between warming and canopy opening (not detected).

4.3 | Nitrogen deposition effects and interactions with changes in light availability

Interaction effects from a combination of changes in light availability and changes in N deposition rates were again found to be insignificant across methodological approaches. Absence of interaction effects might be related to the fact that changes in N deposition on top of the forest canopy do not necessarily reflect changes in N availability at the forest floor. The relationship between N deposition on top of the canopy and throughfall N differs depending on the degree of canopy opening. While small gaps often increase canopy roughness and, hence, dry deposition of N and throughfall N, large gaps may decrease dry deposition due to a decrease of the canopy's total leaf area and, thus, contact surface (Erisman & Draaijers, 2003). These aspects likely complicate the identification of interactions between N deposition and light availability (driven by canopy openness) in our analysis. However, in the experimental study, where we eliminated potential confounding with changes in the overstorey, we did not detect clear effects of N addition either. For this specific dataset, high levels of background N deposition (>20 kg N ha year, see also Figure 2) may have biased our findings as both treated and control plots probably experienced high levels of N deposition.

Although we did not detect interaction effects, we did detect a few main effects of N deposition changes over time. CWM SLA was found to increase with increasing N deposition (based on the orthogonally distributed resurvey study), while cover was found to decrease (based on the opportunistic resurvey database). Previous studies mainly reported increases of nitrophilous species at the expense of N-efficient species, leading to declines in species richness and biotic homogenization at the stand or landscape scale (Bobbink et al., 2010; Gilliam et al., 2016; Staude et al., 2020). Our detected increase of CWM SLA might be related to that because nitrophilous species are often competitive species, characterized by a higher SLA (Westoby, 1998). In addition, declines in understorey cover, density, or biomass have been reported in experiments in North America (Gilliam et al., 2016) and China (Lai et al., 2018). These negative effects on plant performance (generally following a short period of positive growth responses due to enhanced nutrient availability) have been hypothesized to be related to soil acidification (mainly because high N deposition coincided with high acidifying sulfur deposition in the past) and increased N and base cation leaching following N saturation in temperate forest ecosystems (Bobbink et al., 2010; Gilliam, 2006).

4.4 | Novel insights from integrating methodological approaches

The most striking observation of this synthesis study is that findings differ depending on the investigative approach. Although this might sound discouraging, it actually stresses the need to consider approaches in concert to acquire a full picture of processes underlying plant responses to global change.

First of all, our analysis clearly shows that findings from experimental studies can complement findings based on observational field work. The warming effects detected in the experimental study (on understorey cover and CWM SLA) did not reflect macroclimate warming effects based on observational data. This is likely because changes in microclimate temperature in the field covary, not only with macroclimatic changes, but also (and probably more strongly) with changes in canopy cover (Zellweger et al., 2019). In other words, experiments are helpful to detect drivers that act at the local scale and that directly steer understorey community development, ruling out numerous indirect effects of global-change drivers, as occurring in the field. Field observation, on the other hand, are more robust to report and predict actual changes in the understorey, which is not the case for experiments which are often only maintained for a short period, and where growing conditions and especially the imposed treatments are artificial.

Second, our analysis also shows striking differences between the two observational approaches (opportunistic database and orthogonally distributed resurvey) that actually only differ in terms of data collection protocol and plot network design. The more targeted and detailed measurements, as carried out in the orthogonally distributed resurvey, should have reduced the amount of noise in the data and definitely reduced confounding among global-change drivers, in comparison to the database study. Our analysis, however, suggests that this investment in data quality does not always compensate for the loss in terms of data quantity. Indeed, many of the trends that emerged from the opportunistic database could not be detected based on the data from the orthogonally distributed resurvey. The latter approach is probably more suitable to investigate hypotheses that require very specific plot network designs and measurement protocols.

5 | CONCLUSION

Our findings suggest that small-scale forest disturbances or management activities (e.g., single tree mortality or harvest) will probably not intensify functional understorey responses to global change in contrast to what has been found in previous studies focusing on compositional responses. Irrespective of global change, however, these small-scale disturbances will affect the functional composition of the understorey, by altering resources and growing conditions at the forest floor. Whether our findings also hold for more severe canopy disturbances remains to be studied. By combining evidence from multiple investigative approaches, we found that large datasets are needed to detect understorey responses to regional-scale drivers of change and that increasing data quality at the expense of data quantity does not necessarily increase our ability to detect potential drivers of change. Given that experimental findings deviated from observational findings, our analysis also demonstrates that understorey responses to regional-scale warming and changes in N deposition (as detected by resurvey studies) may be different from understorey responses to these drivers at the forest floor (as detected by experiments).

AUTHOR CONTRIBUTIONS

Dries Landuyt: Conceptualization; formal analysis; funding acquisition; investigation; visualization; writing – original draft. **Michael P. Perring:** Conceptualization; data curation; investigation; writing – original draft. **Haben Blondeel:** Conceptualization; data curation; investigation; writing – review and editing. **Emiel De Lombaerde:** Conceptualization; investigation; writing – review and editing. **Leen Depauw:** Conceptualization; data curation; investigation; writing – review and editing. **Eline Lorer:** Conceptualization; data curation; investigation; writing – review and editing. **Sybryn L. Maes:** Conceptualization; data curation; investigation; writing – review and editing. **Lander Baeten:** Investigation; writing – review and editing. **Laurent Bergès:** Investigation; writing – review and editing. **Markus Bernhardt-Römermann:** Investigation; writing – review and editing. **Guntis Brūmelis:** Investigation; writing – review and editing. **Jörg Brunet:** Investigation; writing – review and editing. **Markéta Chudomelová:** Investigation; writing – review and editing. **Janusz Czerepko:** Investigation; writing – review and editing. **Guillaume Decocq:** Investigation; writing – review and editing. **Jan den Ouden:** Investigation; writing – review and editing. **Pieter De Frenne:** Investigation; writing – review and editing. **Thomas Dirnböck:** Investigation; writing – review and editing. **Tomasz Durak:** Investigation; writing – review and editing. **Andreas Fichtner:** Investigation; writing – review and editing. **Radosław Gawryś:** Investigation; writing – review and editing. **Werner Härdtle:** Investigation; writing – review and editing. **Radim Hédl:** Investigation; writing – review and editing. **Steffi Heinrichs:** Investigation; writing – review and editing. **Thilo Heinken:** Investigation; writing – review and editing. **Bogdan Jaroszewicz:** Investigation; writing – review and editing. **Keith Kirby:** Investigation; writing – review and editing. **Martin Kopecký:** Investigation; writing – review and editing. **František Máliš:** Investigation; writing – review and editing. **Martin Macek:** Investigation; writing – review and editing. **Fraser J. G. Mitchell:** Investigation; writing – review and editing. **Tobias Naaf:** Investigation; writing – review and editing. **Petr Petřík:** Investigation; writing – review and editing. **Kamila Reczyńska:** Investigation; writing – review and editing. **Wolfgang Schmidt:** Investigation; writing – review and editing. **Tibor Standovár:** Investigation; writing – review and editing. **Krzysztof Swierkosz:** Investigation; writing – review and editing. **Simon M. Smart:** Investigation; writing – review and editing. **Hans Van Calster:** Investigation; writing – review and editing. **Ondřej Vild:** Investigation; writing – review and editing. **Donald M. Waller:** Investigation; writing – review and editing. **Monika Wulf:** Investigation; writing – review and editing. **Kris Verheyen:** Funding acquisition; investigation; supervision; writing – review and editing.

AFFILIATIONS

[1]Forest&Nature Lab, Department of Environment, Ghent University, Melle, Belgium
[2]UK Centre for Ecology and Hydrology (UKCEH), Bangor, UK
[3]The UWA Institute of Agriculture, The University of Western Australia, Perth, Western Australia, Australia
[4]Division of Forest, Nature and Landscape, Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium

[5]Laboratoire ecosystèmes et sociétés en montagne (LESSEM), National Research Institute for Agriculture, Food and the Environment (INRAE), St-Martin d'Hères, France
[6]Institute of Ecology and Evolution, Friedrich Schiller University Jena, Jena, Germany
[7]German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany
[8]Faculty of Biology, University of Latvia, Riga, Latvia
[9]Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Lomma, Sweden
[10]Institute of Botany, Czech Academy of Sciences, Brno, Czech Republic
[11]Forest Research Institute, Raszyn, Poland
[12]Jules Verne University of Picardie, Amiens, France
[13]Forest Ecology and Forest Management Group, Wageningen University & Research, Wageningen, The Netherlands
[14]Environment Agency Austria, Vienna, Austria
[15]Institute of Biology, University of Rzeszów, Rzeszów, Poland
[16]Institute of Ecology, Leuphana University Lüneburg, Lüneburg, Germany
[17]Department of Botany, Faculty of Science, Palacký University in Olomouc, Olomouc, Czech Republic
[18]Department Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Göttingen, Germany
[19]General Botany, Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany
[20]Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Białowieża, Poland
[21]Department of Plant Sciences, University of Oxford, Oxford, UK
[22]Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic
[23]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic
[24]Technical University in Zvolen, Zvolen, Slovakia
[25]Botany Department, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland
[26]Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany
[27]Faculty of Environmental Sciences, Czech University of Life Sciences, Prague, Czech Republic
[28]Department of Botany, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland
[29]Department of Plant Systematics, Ecology and Theoretical Biology, ELTE Eötvös Loránd University, Budapest, Hungary
[30]Museum of Natural History, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland
[31]UK Centre for Ecology & Hydrology (UKCEH), Lancaster University, Bailrigg, UK
[32]Research Institute for Nature and Forest, Brussels, Belgium
[33]Department of Botany, University of Wisconsin–Madison, Madison, Wisconsin, USA

ACKNOWLEDGEMENTS

All field data collection campaigns (coordinated by HB, SLM, LD, MPP, and KV), lab analyses (performed by Greet De bruyn and Luc Willems) and preliminary statistical analyses (coordinated by MPP and KV) have been funded by ERC consolidator project PASTFORWARD (614839, funding obtained by KV). Further statistical analyses have been performed within the frame of a postdoctoral fellowship of the Flemish Research Foundation FWO (funding obtained by DL, 1200321N). LD, SLM, and EL are currently being funded by two FWO postdoctoral fellowships (1221523N, 12ZZV21N) and a FWO research project (G078921N), respectively. EDL is being funded by a BOF postdoctoral fellowship. FM was supported by Slovak Research and Development Agency grant APVV-19-0319. MK, MM, MC, PP, OV, and RH are supported by long-term research development project No. RVO 67985939 of the Czech Academy of Sciences, the grant 21-11487S by the Czech Science Foundation, and postdoctoral fellowship L200052302 (to MC). TD is supported by EU Horizon 2020 INFRAIA project eLTER-PLUS (871128). Historical vegetation surveys in Białowieża Forest were funded by the Directorate-General of the State Forests in Poland (grant no. BLP-370).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.24598458 (Landuyt et al., 2023).

ORCID

Dries Landuyt https://orcid.org/0000-0001-8107-5546
Michael P. Perring https://orcid.org/0000-0001-8553-4893
Haben Blondeel https://orcid.org/0000-0001-9939-5994
Emiel De Lombaerde https://orcid.org/0000-0002-0050-2735
Leen Depauw https://orcid.org/0000-0001-5703-6811
Eline Lorer https://orcid.org/0000-0003-3957-7969
Sybryn L. Maes https://orcid.org/0000-0002-7168-2390
Lander Baeten https://orcid.org/0000-0003-4262-9221
Laurent Bergès https://orcid.org/0000-0003-0408-7900
Markus Bernhardt-Römermann https://orcid.org/0000-0002-2740-2304
Guntis Brūmelis https://orcid.org/0000-0002-8385-2553
Jörg Brunet https://orcid.org/0000-0003-2667-4575
Markéta Chudomelová https://orcid.org/0000-0001-7845-4000
Janusz Czerepko https://orcid.org/0000-0002-7485-0134
Guillaume Decocq https://orcid.org/0000-0001-9262-5873
Jan den Ouden https://orcid.org/0000-0003-1518-2460
Pieter De Frenne https://orcid.org/0000-0002-8613-0943
Thomas Dirnböck https://orcid.org/0000-0002-8294-0690
Tomasz Durak https://orcid.org/0000-0003-4053-3699
Andreas Fichtner https://orcid.org/0000-0003-0499-4893
Radosław Gawryś https://orcid.org/0000-0003-3432-3097
Werner Härdtle https://orcid.org/0000-0002-5599-5792
Radim Hédl https://orcid.org/0000-0002-6040-8126
Steffi Heinrichs https://orcid.org/0000-0003-3146-031X
Thilo Heinken https://orcid.org/0000-0002-1681-5971
Bogdan Jaroszewicz https://orcid.org/0000-0002-2042-8245
Keith Kirby https://orcid.org/0000-0003-0276-4496
Martin Kopecký https://orcid.org/0000-0002-1018-9316
František Máliš https://orcid.org/0000-0003-2760-6988
Martin Macek https://orcid.org/0000-0002-5609-5921
Fraser J. G. Mitchell https://orcid.org/0000-0002-9857-5632
Tobias Naaf https://orcid.org/0000-0002-4809-3694
Petr Petřík https://orcid.org/0000-0001-8518-6737
Kamila Reczyńska https://orcid.org/0000-0002-0938-8430
Wolfgang Schmidt https://orcid.org/0000-0001-5356-4684

Tibor Standovár https://orcid.org/0000-0002-4686-3456
Krzysztof Swierkosz https://orcid.org/0000-0002-5145-178X
Simon M. Smart https://orcid.org/0000-0003-2750-7832
Hans Van Calster https://orcid.org/0000-0001-8595-8426
Ondřej Vild https://orcid.org/0000-0002-0728-2392
Donald M. Waller https://orcid.org/0000-0001-5377-3929
Monika Wulf https://orcid.org/0000-0001-6499-0750
Kris Verheyen https://orcid.org/0000-0002-2067-9108

REFERENCES

Axmanová, I., Zelený, D., Li, C., & Chytrý, M. (2011). Environmental factors influencing herb layer productivity in Central European oak forests: Insights from soil and biomass analyses and a phytometer experiment. *Plant and Soil*, *342*, 183–194. https://doi.org/10.1007/s11104-010-0683-9

Baeten, L., Hermy, M., & Verheyen, K. (2009). Environmental limitation contributes to the differential colonization capacity of two forest herbs. *Journal of Vegetation Science*, *20*(2), 209–223. https://doi.org/10.1111/j.1654-1103.2009.05595.x

Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., Jaroszewicz, B., Selvi, F., Valladares, F., Allan, E., Ampoorter, E., Auge, H., Avăcăriei, D., Barbaro, L., Bărnoaiea, I., Bastias, C. C., Bauhus, J., Beinhoff, C., Benavides, R., … Scherer-Lorenzen, M. (2013). A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics*, *15*(5), 281–291. https://doi.org/10.1016/j.ppees.2013.07.002

Bates, D., Mächler, M., Bolker, M. B., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*(7725), 57–62. https://doi.org/10.1038/s41586-018-0563-7

Blondeel, H., Perring, M. P., Depauw, L., De Lombaerde, E., Landuyt, D., De Frenne, P., & Verheyen, K. (2020). Light and warming drive forest understorey community development in different environments. *Global Change Biology*, *26*(3), 1681–1696. https://doi.org/10.1111/gcb.14955

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J. W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., & De Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*(1), 30–59. https://doi.org/10.1890/08-1140.1

Chelli, S., Simonetti, E., Wellstein, C., Campetella, G., Carnicelli, S., Andreetta, A., Giorgini, D., Puletti, N., Bartha, S., & Canullo, R. (2019). Effects of climate, soil, forest structure and land use on the functional composition of the understory in Italian forests. *Journal of Vegetation Science*, *30*(6), 1110–1121. https://doi.org/10.1111/jvs.12792

De Frenne, P., De Schrijver, A., Graae, B. J., Gruwez, R., Tack, W., Vandelook, F., Hermy, M., & Verheyen, K. (2010). The use of open-top chambers in forests for evaluating warming effects on herbaceous understorey plants. *Ecological Research*, *25*(1), 163–171. https://doi.org/10.1007/s11284-009-0640-3

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *PNAS*, *110*(46), 18561–18565. https://doi.org/10.1073/pnas.1311190110

De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. A., Hermy, M., Vangansbeke, P., & Verheyen, K. (2015). Light accelerates plant responses to warming. *Nature Plants*, *1*(9), 15110. https://doi.org/10.1038/nplants.2015.110

De Lombaerde, E., Baeten, L., Verheyen, K., Perring, M. P., Ma, S., & Landuyt, D. (2021). Understorey removal effects on tree regeneration in temperate forests: A meta-analysis. *Journal of Applied Ecology*, *58*(1), 9–20. https://doi.org/10.1111/1365-2664.13792

De Pauw, K., Sanczuk, P., Meeussen, C., Depauw, L., De Lombaerde, E., Govaert, S., Vanneste, T., Brunet, J., Cousins, S. A. O., Gasperini, C., Hedwall, P., Iacopetti, G., Lenoir, J., Plue, J., Selvi, F., Spicher, F., Uria-Diez, J., Verheyen, K., Vangansbeke, P., & De Frenne, P. (2022). Forest understorey communities respond strongly to light in interaction with forest structure, but not to microclimate warming. *New Phytologist*, *233*(1), 219–235. https://doi.org/10.1111/nph.17803

Depauw, L., Perring, M. P., Landuyt, D., Maes, S. L., Blondeel, H., De Lombaerde, E., Brūmelis, G., Brunet, J., Closset-Kopp, D., Czerepko, J., Decocq, G., Den Ouden, J., Gawryś, R., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., … Verheyen, K. (2020). Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities. *Journal of Ecology*, *108*(4), 1411–1425. https://doi.org/10.1111/1365-2745.13339

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., & Werner, W. (2001). Zeigerwerte van Pflanzen in Mitteleuropa. *Scripta Geobotanica*, *18*, 1–262.

Erisman, J. W., & Draaijers, G. (2003). Deposition to forests in Europe: Most important factors influencing dry deposition and models used for generalisation. *Environmental Pollution*, *124*(3), 379–388. https://doi.org/10.1016/S0269-7491(03)00049-6

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E. K. V., Linsenmair, K. E., Schulze, E. D., & Weisser, W. W. (2010). Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology*, *11*(6), 473–485. https://doi.org/10.1016/j.baae.2010.07.009

Gilliam, F. S. (2006). Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology*, *94*(6), 1176–1191. https://doi.org/10.1111/j.1365-2745.2006.01155.x

Gilliam, F. S. (2007). The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience*, *57*(10), 845–858. https://doi.org/10.1641/B571007

Gilliam, F. S., Welch, N. T., Phillips, A. H., Billmyer, J. H., Peterjohn, W. T., Fowler, Z. K., Walter, C. A., Burnham, M. B., May, J. D., & Adams, M. B. (2016). Twenty-five-year response of the herbaceous layer of a temperate hardwood forest to elevated nitrogen deposition. *Ecosphere*, *7*(4), 1–16. https://doi.org/10.1002/ecs2.1250

Hedwall, P. O., Uria-Diez, J., Brunet, J., Gustafsson, L., Axelsson, A. L., & Strengbom, J. (2021). Interactions between local and global drivers determine long-term trends in boreal forest understorey vegetation. *Global Ecology and Biogeography*, *30*(9), 1765–1780. https://doi.org/10.1111/geb.13324

Heinrichs, S., Bernhardt-Römermann, M., & Schmidt, W. (2010). The estimation of aboveground biomass and nutrient pools of understorey plants in closed Norway spruce forests and on clearcuts. *European Journal of Forest Research*, *129*(4), 613–624. https://doi.org/10.1007/s10342-010-0362-7

Hermy, M. (1985). *Ecologie en fytosociologie van oude en jonge bossen in binnen-Vlaanderen*. University of Ghent.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Lai, M., He, S., Yu, S., & Jin, G. (2018). Effects of experimental N addition on plant diversity in an growth temperate forest. *Ecology and Evolution*, *8*(11), 5900–5911. https://doi.org/10.1002/ece3.4127

Landuyt, D., De Lombaerde, E., Perring, M. P., Hertzog, L. R., Ampoorter, E., Maes, S. L., De Frenne, P., Ma, S., Proesmans, W., Blondeel, H., Sercu, B. K., Wang, B., Wasof, S., & Verheyen, K. (2019). The functional role of temperate forest understorey vegetation in a changing world. *Global Change Biology*, *25*(11), 3625–3641. https://doi.org/10.1111/gcb.14756

Landuyt, D., Maes, S. L., Depauw, L., Ampoorter, E., Blondeel, H., Perring, M. P., Brūmelis, G., Brunet, J., Decocq, G., den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kirby, K. J., Kopecký, M., Máliš, F., Wulf, M., & Verheyen, K. (2020). Drivers of aboveground understorey biomass and nutrient stocks in temperate deciduous forests. *Journal of Ecology*, *108*(3), 982–997. https://doi.org/10.1111/1365-2745.13318

Landuyt, D., Perring, M., Blondeel, H., De Lombaerde, E., Depauw, L., Lorer, E., Maes, S., & Verheyen, K. (2023). Changes in the functional composition of the understorey across European temperate forests, in relation to changes in canopy openness, changes in N deposition rates and climate warming. *Figshare*. Dataset. https://doi.org/10.6084/m9.figshare.24598458

Lemmon, P. E. (1956). A spherical densiometer for estimating forest overstory density. *Forest Science*, *2*(4), 314–320. https://doi.org/10.1093/forestscience/2.4.314

Lüdecke, D. (2022). *sjPlot: Data visualization for statistics in social science*. https://cran.r-project.org/package=sjPlot

Luo, Y., Melillo, J., Niu, S., Beier, C., Clark, J. S., Classen, A. T., Davidson, E., Dukes, J. S., Evans, R. D., Field, C. B., Czimczik, C. I., Keller, M., Klimball, B. A., Kueppers, L. M., Norby, R. J., Pelini, S. L., Pendall, E., Rastetter, E., Six, J., … Torn, M. S. (2011). Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology*, *17*(2), 843–854. https://doi.org/10.1111/j.1365-2486.2010.02265.x

Maes, S. L., Blondeel, H., Perring, M. P., Depauw, L., Brūmelis, G., Brunet, J., Decocq, G., den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kirby, K., Kopecký, M., Máliš, F., Wulf, M., & Verheyen, K. (2019). Litter quality, land-use history, and nitrogen deposition effects on topsoil conditions across European temperate deciduous forests. *Forest Ecology and Management*, *433*, 405–418. https://doi.org/10.1016/j.foreco.2018.10.056

Malhi, Y., Franklin, J., Seddon, N., Solan, M., Turner, M. G., Field, C. B., & Knowlton, N. (2020). Climate change and ecosystems: Threats, opportunities and solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190104. https://doi.org/10.1098/rstb.2019.0104

Maskell, L. C., Smart, S. M., Bullock, J. M., Thompson, K., & Stevens, C. J. (2010). Nitrogen deposition causes widespread loss of species richness in British habitats. *Global Change Biology*, *16*(2), 671–679. https://doi.org/10.1111/j.1365-2486.2009.02022.x

Mazalla, L., & Diekmann, M. (2022). Regression to the mean in vegetation science. *Journal of Vegetation Science*, *33*(2), 1–8. https://doi.org/10.1111/jvs.13117

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*, 37–42. https://doi.org/10.1038/nature01286

Perring, M. P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L., Landuyt, D., Maes, S. L., De Lombaerde, E., Carón, M. M., Vellend, M., Brunet, J., Chudomelová, M., Decocq, G., Diekmann, M., Dirnböck, T., Dörfler, I., Durak, T., De Frenne, P., … Verheyen, K. (2018). Global environmental change effects on plant community composition trajectories depend upon management legacies. *Global Change Biology*, *24*(4), 1722–1740. https://doi.org/10.1111/gcb.14030

R Core Team. (2022). *R: A language and environment for statistical computing*. https://www.r-project.org/

Richard, B., Dupouey, J. L., Corcket, E., Alard, D., Archaux, F., Aubert, M., Boulanger, V., Gillet, F., Langlois, E., Macé, S., Montpied, P., Beaufils, T., Begeot, C., Behr, P., Boissier, J. M., Camaret, S., Chevalier, R., Decocq, G., Dumas, Y., … Lenoir, J. (2021). The climatic debt is growing in the understorey of temperate forests: Stand characteristics matter. *Global Ecology and Biogeography*, *30*(7), 1474–1487. https://doi.org/10.1111/geb.13312

Rustad, L. E. (2008). The response of terrestrial ecosystems to global climate change: Towards an integrated approach. *Science of the Total Environment*, *404*(2–3), 222–235. https://doi.org/10.1016/j.scitotenv.2008.04.050

Segar, J., Pereira, H., Baeten, L., Bernhardt-Römermann, M., De Frenne, P., Fernández, N., Gilliam, F., Lenoir, J., Ortmann-Ajkai, A., Verheyen, K., Waller, D., Teleki, B., Berki, I., Brunet, J., Chudomelová, M., Decocq, G., Dirnböck, T., Hédl, R., Heinken, T., … Staude, I. (2022). Divergent roles of herbivory in eutrophying forests. *Nature Communications*, *13*, 7837. https://doi.org/10.1038/s41467-022-35282-6

Spicer, M. E., Mellor, H., & Carson, W. P. (2020). Seeing beyond the trees: A comparison of tropical and temperate plant growth forms and their vertical distribution. *Ecology*, *101*(4), 1–9. https://doi.org/10.1002/ecy.2974

Staude, I. R., Waller, D. M., Bernhardt-Römermann, M., Bjorkman, A. D., Brunet, J., De Frenne, P., Hédl, R., Jandt, U., Lenoir, J., Máliš, F., Verheyen, K., Wulf, M., Pereira, H. M., Vangansbeke, P., Ortmann-Ajkai, A., Pielech, R., Berki, I., Chudomelová, M., Decocq, G., … Baeten, L. (2020). Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome. *Nature Ecology and Evolution*, *4*(6), 802–808. https://doi.org/10.1038/s41559-020-1176-8

Stevens, J. T., Safford, H. D., Harrison, S., & Latimer, A. M. (2015). Forest disturbance accelerates thermophilization of understory plant communities. *Journal of Ecology*, *103*(5), 1253–1263. https://doi.org/10.1111/1365-2745.12426

Strengbom, J., Näsholm, T., & Ericson, L. (2004). Light, not nitrogen, limits growth of the grass *Deschampsia flexuosa* in boreal forests. *Canadian Journal of Botany*, *82*(4), 430–435. https://doi.org/10.1139/b04-017

Van Calster, H., Baeten, L., Verheyen, K., De Keersmaeker, L., Dekeyser, S., Rogister, J. E., & Hermy, M. (2008). Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. *Forest Ecology and Management*, *256*(4), 519–528. https://doi.org/10.1016/j.foreco.2008.04.042

van de Waal, D. B., & Litchman, E. (2020). Multiple global change stressor effects on phytoplankton nutrient acquisition in a future ocean. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1798), 1–8. https://doi.org/10.1098/rstb.2019.0706

Vanneste, T., Valdés, A., Verheyen, K., Perring, M. P., Bernhardt-Römermann, M., Andrieu, E., Brunet, J., Cousins, S. A. O., Deconchat, M., De Smedt, P., Diekmann, M., Ehrmann, S., Heinken, T., Hermy, M., Kolb, A., Lenoir, J., Liira, J., Naaf, T., Paal, T., … De Frenne, P. (2019). Functional trait variation of forest understorey plant communities across Europe. *Basic and Applied Ecology*, *34*, 1–14. https://doi.org/10.1016/j.baae.2018.09.004

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petřík, P., Pfadenhauer, J., Van Calster, H., … Verstraeten, G. (2012). Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology*, *100*(2), 352–365. https://doi.org/10.1111/j.1365-2745.2011.01928.x

Verheyen, K., De Frenne, P., Baeten, L., Waller, D. M., Hédl, R., Perring, M. P., Blondeel, H., Brunet, J., Chudomelová, M., Decocq, G., De Lombaerde, E., Depauw, L., Dirnböck, T., Durak, T., Eriksson, O., Gilliam, F. S., Heinken, T., Heinrichs, S., Hermy, M., … Bernhardt-Römermann, M. (2017). Combining biodiversity resurveys across regions to advance global change research. *Bioscience*, *67*(1), 73–83. https://doi.org/10.1093/biosci/biw150

Von Arx, G., Graf Pannatier, E., Thimonier, A., & Rebetez, M. (2013). Microclimate in forests with varying leaf area index and soil moisture: Potential implications for seedling establishment in a changing climate. *Journal of Ecology*, *101*(5), 1201–1213. https://doi.org/10.1111/1365-2745.12121

von Liebig, J. (1855). *Die Grundsätze der Agricultur-Chemie mit Rücksicht auf die in England angestellten Untersuchungen*. Vieweg.

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*(2), 213–227. https://doi.org/10.1023/A:1004327224729

Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., Kirby, K. J., Brunet, J., Kopecký, M., Máliš, F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K., & De Frenne, P. (2019). Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, *28*(12), 1774–1786. https://doi.org/10.1111/geb.12991

Zellweger, F., de Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., … Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*(6492), 772–775. https://doi.org/10.1126/science.aba6880

Zhang, S., Landuyt, D., Verheyen, K., & De Frenne, P. (2022). Tree species mixing can amplify microclimate offsets in young forest plantations. *Journal of Applied Ecology*, *59*(6), 1428–1439. https://doi.org/10.1111/1365-2664.14158

Zhang, S., Verheyen, K., De Frenne, P., & Landuyt, D. (2022). Tree species mixing affects throughfall in a young temperate forest plantation. *Agricultural and Forest Meteorology*, *327*, 109220. https://doi.org/10.1016/j.agrformet.2022.109220

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Landuyt, D., Perring, M. P., Blondeel, H., De Lombaerde, E., Depauw, L., Lorer, E., Maes, S. L., Baeten, L., Bergès, L., Bernhardt-Römermann, M., Brūmelis, G., Brunet, J., Chudomelová, M., Czerepko, J., Decocq, G., den Ouden, J., De Frenne, P., Dirnböck, T., Durak, T. … Verheyen, K. (2023). Combining multiple investigative approaches to unravel functional responses to global change in the understorey of temperate forests. *Global Change Biology*, *30*, e17086. https://doi.org/10.1111/gcb.17086