



RESEARCH PAPER

Plant functional trait response to environmental drivers across European temperate forest understorey communities

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ABSTRACT

- Functional traits respond to environmental drivers, hence evaluating trait–environment relationships across spatial environmental gradients can help to understand how multiple drivers influence plant communities. Global-change drivers such as changes in atmospheric nitrogen deposition occur worldwide, but affect community trait distributions at the local scale, where resources (e.g. light availability) and conditions (e.g. soil pH) also influence plant communities.
- We investigate how multiple environmental drivers affect community trait responses related to resource acquisition (plant height, specific leaf area (SLA), woodiness, and mycorrhizal status) and regeneration (seed mass, lateral spread) of European temperate deciduous forest understoreys. We sampled understorey communities and derived trait responses across spatial gradients of global-change drivers (temperature, precipitation, nitrogen deposition, and past land use), while integrating in-situ plot measurements on resources and conditions (soil type, Olsen phosphorus (P), Ellenberg soil moisture, light, litter mass, and litter quality).
- Among the global-change drivers, mean annual temperature strongly influenced traits related to resource acquisition. Higher temperatures were associated with taller understoreys producing leaves with lower SLA, and a higher proportional cover of woody and obligate mycorrhizal (OM) species. Communities in plots with higher Ellenberg soil moisture content had smaller seeds and lower proportional cover of woody and OM species. Finally, plots with thicker litter layers hosted taller understoreys with larger seeds and a higher proportional cover of OM species.
- Our findings suggest potential community shifts in temperate forest understoreys with global warming, and highlight the importance of local resources and conditions as well as global-change drivers for community trait variation.

INTRODUCTION

Global environmental changes are causing shifts in the composition and functioning of plant communities (Sala *et al.*,

2000; Hansen *et al.*, 2001; Walther, 2010; De Frenne *et al.*, 2011; Bernhardt-Römermann *et al.*, 2015; Bjorkman *et al.*, 2018). Important global change drivers affecting temperate plant communities include increased temperatures, changes in

precipitation and in atmospheric nitrogen and sulphur deposition, as well as land-use changes (Skov & Svenning, 2004; Millennium Ecosystems Assessment, 2005; Dentener *et al.*, 2006; Pereira *et al.*, 2012; Fowler *et al.*, 2013). If we are to accurately predict the effects of future environmental changes on these communities, we need a thorough understanding of whether and how these drivers shape plant communities (Bjorkman *et al.*, 2018; Bruelheide *et al.*, 2018; Landuyt *et al.*, 2018; Van Neste *et al.*, 2018).

Functional traits, *i.e.* measurable characteristics of organisms that ultimately influence their fitness through effects on growth, reproduction and establishment, show great potential to investigate trait–environment relationships (Suding *et al.*, 2008; Šimová *et al.*, 2018). Community-weighted traits depend on the species composition of communities and relate to ecosystem functions, while they may also be related to environmental drivers, thus connecting ecosystem patterns to ecosystem processes (Weiher *et al.*, 1999; Suding *et al.*, 2008; Laughlin, 2014). Unravelling community trait responses across environmental gradients can therefore advance our understanding of which drivers shape plant communities (Dubuis *et al.*, 2013; Bjorkman *et al.*, 2018; Bruelheide *et al.*, 2018; Van Neste *et al.*, 2018).

Community composition and hence trait properties are influenced by environmental drivers acting over different spatial extents (Vilà-Cabrera *et al.* 2015; Perez-Ramos *et al.*, 2017; Bruelheide *et al.*, 2018). Global change drivers, such as changes in atmospheric deposition, are being altered on a global scale, but they affect community trait distributions locally, at which scale other resources (*e.g.* light availability) and conditions (*e.g.* soil pH) also strongly influence plant communities (Smith *et al.* 2009; Naaf & Kolk, 2016; Bruelheide *et al.*, 2018). Furthermore, global change drivers can drive changes in plant communities through altering local resource availabilities, *e.g.* soil nitrogen or phosphorus; and local resources and conditions can, *vice versa*, determine whether and how global change drivers affect plant communities (Smith *et al.*, 2009; Perring *et al.* 2018b). Studies evaluating the functional response of communities to global change drivers should therefore aim to incorporate effects of local resources and conditions (Bruelheide *et al.*, 2018).

In this study, we investigate how concurrent global change drivers, along with local resources and conditions, are linked with understorey community traits in European temperate deciduous forests. Temperate forest understoreys: (i) constitute the majority of plant diversity in temperate forests, thus playing a key role in their functioning (Gilliam, 2006; Landuyt *et al.*, 2019), and (ii) are very vulnerable to environmental changes because they are adapted to stable environmental forest conditions (Verheyen *et al.* 2003; Van Der Veken *et al.*, 2004; De Frenne *et al.*, 2012). Because of the low colonization capacity, specific habitat requirements and long generation times of many perennial understorey plants (in contrast to *e.g.* annual grassland plant species), these communities may be hampered in their abilities to track moving climate boundaries or colonize new forest sites. For example, forests on post-agricultural sites may have a different understorey community composition as compared to apparently similar forest sites (*e.g.* in overstorey composition) but without an agricultural legacy (Baeten *et al.* 2010). A better understanding of the relative importance of environmental factors for community trait

distributions may improve projections of future changes in understorey community responses. To achieve this, we sampled understorey communities and derived trait responses across spatial environmental gradients of global change drivers, while also integrating *in-situ* measurements on the resources and conditions that may affect these communities.

Specifically, we evaluate the relationship between community-weighted mean (CWM) trait values and environmental drivers including: (i) four global change drivers (mean annual temperature and precipitation, nitrogen deposition and past land cover), and (ii) six local resources and conditions (soil type, bio-available phosphorus, Ellenberg soil moisture, light availability, litter mass and litter quality). We examine traits related to two fundamental strategies for plant growth and performance: (i) resource acquisition (plant height, specific leaf area (SLA), woodiness and mycorrhizal status), and (ii) regeneration (seed mass, lateral spread) (Cornelissen *et al.*, 2003; Diaz *et al.*, 2004; Thomson *et al.* 2011; Garnier *et al.*, 2016).

We hypothesize that understorey community traits may be affected by both the global change drivers as well as the local resources and conditions in the plots (Verheyen *et al.*, 2003; Bruelheide *et al.*, 2018; Perring *et al.*, 2018a). Community plant height as well as SLA were expected to be higher in plots with higher nitrogen deposition, Ellenberg soil moisture and temperature. Community plant height was expected to be higher in plots with more light, while SLA was expected to be lower in plots with more light (Dubuis *et al.*, 2013; Garnier *et al.*, 2016; Perring *et al.*, 2018a). The proportion of woody and of obligate mycorrhizal plants in understorey communities might also be related to environmental drivers (*e.g.* nitrogen deposition), given the demonstrated differences in resource acquisition between woody *versus* non-woody as well as non-mycorrhizal *versus* mycorrhizal plants (Ryser, 1996; Graves *et al.* 2006; Kleyer *et al.*, 2008; Hempel *et al.*, 2013; Bardgett *et al.* 2014; Valverde-Barrantes *et al.* 2017). Finally, higher community seed mass was expected to be associated with lower moisture or nutrient levels (Westoby *et al.* 1996; DeMalach *et al.* 2018), while the mean lateral spread of an understorey community could be higher in plots with a differing land-use history, *i.e.* recent (RF) *versus* ancient forests (AF), because of potentially higher colonization capacities of plant species in RF (Verheyen *et al.*, 2003; Flinn & Vellend, 2005; Baeten *et al.*, 2010).

MATERIAL AND METHODS

Study regions

We selected 19 regions along spatial environmental gradients of atmospheric nitrogen deposition and climate conditions (temperature, precipitation) within the Central-Western European temperate deciduous forest biome (Fig. 1, Table S1a). The plots used were selected as part of a vegetation resurvey project investigating land-use history and global change effects on understorey communities across European forests (ERC project Pastforward-team 2018, <http://www.pastforward.ugent.be/>).

Mean annual temperature and precipitation (MAT, MAP, respectively) and nitrogen deposition (Ndep) at the study regions ranged from 6.1 to 11.9 °C, from 526 to 1586 mm·year^{−1} and from 7 to 30 kg·ha^{−1}·year^{−1}, respectively (Fig. 1a; long-term average values from 1980 to 2015 for MAT

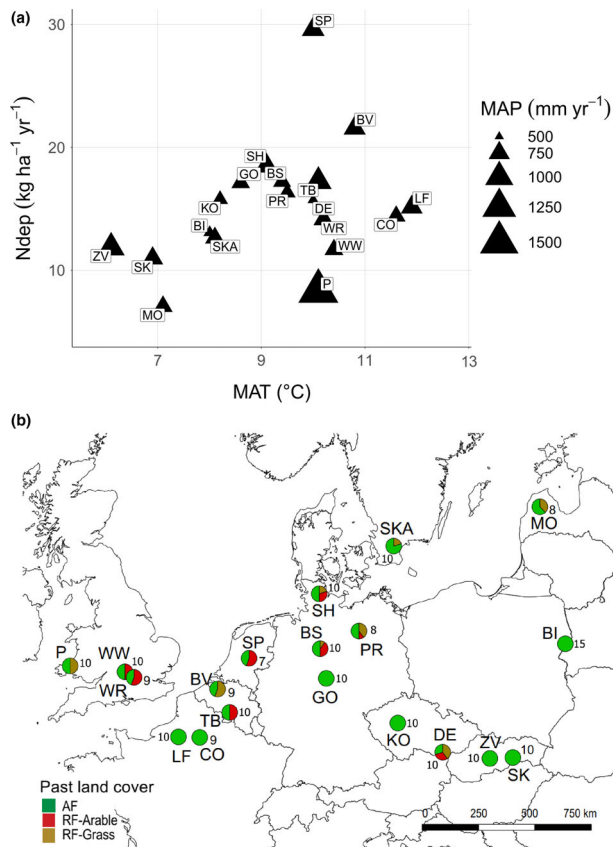


Fig. 1. (a) Environmental gradients covered by the 19 forest regions where plots were sampled: nitrogen deposition (Ndep – kg·ha⁻¹·year⁻¹) versus mean annual temperature (MAT – °C) is plotted, with the symbol size reflecting the total annual precipitation (MAP – mm·year⁻¹) in that region. Values from the year 2000 were used for Ndep, and average values for 1980–2015 were used for MAT and MAP. (b) Geographic distribution of the 19 forest regions where plots were sampled. Per region, the pie chart visualizes the proportion of ancient forest (AF: green) versus recent forest plots with past arable land use (RF-Arable: red) versus recent plots with past heathland/grassland as past land use (RF-Grass: brown). The Region code and total number of plots used per region is indicated next to the pie charts. Note: the 185 plots that were used in the analyses (out of 192 initially sampled) are shown in this figure.

and MAP, values for the year 2000 for Ndep). We aimed at maximizing differences in land-use history between plots (within regions; Fig. 1b) by sampling in ancient *versus* recent forest. We classified ancient forest (AF) plots here as plots that have been continuously forested since at least 1850, whereas recent forest (RF) plots were afforested after 1850 (Hermy *et al.* 1999).

In each region, we selected ten 400-m² forest plots (except for eight plots in Moricsala, nine plots in Binnen-Vlaanderen and 15 plots in Białowieża), resulting in a total sample size of 192 plots. Each 400-m² plot contained a nested 100-m² sub-plot. We tried to minimize differences in parent material and topography between plots and regions. However, plot selection was also constrained by the existence of a prior understorey vegetation survey (not relevant within this spatial study) and information on land-use history.

All plots comprised closed canopy forests with a variable tree and shrub layer composition, but we focused on plots

predominantly composed of broadleaved species, although a higher occurrence of coniferous species in the easternmost regions with a hemiboreal climate (Białowieża (BI), Moricsala (MO)) was unavoidable. The canopies consisted mainly of *Fagus sylvatica* (present in 65 of the 192 plots), *Fraxinus excelsior* (64/192 plots), *Quercus robur* (60/192 plots), *Carpinus betulus* (52/192 plots), *Quercus petraea* (41/192 plots) and *Acer pseudoplatanus* (35/192 plots).

Data collection

In May–June 2015 and 2016, we characterized resources and conditions by sampling the mineral topsoil (0–20 cm) and organic forest floor layer, and by taking light measurements, at eye level, with a spherical densiometer in the 100-m² sub-plots. In the 400-m² plots, we took basal area measurements to characterize the overstorey structure and composition based on all trees and shrubs with DBH > 7.5 cm. Global change drivers were estimated from online databases (temperature, precipitation and atmospheric deposition) and plot-level information searches (land-use history). We derived understorey community response variables by conducting standardized vegetation surveys in the 100-m² plots and used trait databases to derive community-level descriptors of trait properties based on species' percentage cover. We also derived the Ellenberg index of moisture availability from these vegetation surveys, using species scores from Ellenberg & Leuschner (2010) (Diekmann, 2003; Bartelheimer & Poschlod, 2016; Scherrer & Guisan, 2019).

Functional trait response

Understorey community composition

We recorded the species composition and cover through 10 × 10 m plot-level vegetation surveys to calculate descriptors of community trait distributions. Trait values were sourced from several literature databases including *e.g.* ECOFLORA (Fitter & Peat, 1994) and LEDA (Kleyer *et al.*, 2008) (full list see Table S2). We included herbaceous species and low-growing woody species that are structurally and functionally part of the understorey layer (*e.g.* *Vaccinium myrtillus*) but excluded tree and shrub seedlings and some climber species present in the understorey for two reasons. First, many recorded trait values (plant height, SLA, lateral spread) are representative for adult trees, shrubs and climbers rather than the juvenile state found in the understorey. Second, we wanted to focus on the species that remain structurally part of the understorey throughout their life cycle, as opposed to those that are only 'passing through' (*cf.* Perring *et al.*, 2018a). See Table S3 for a detailed species list.

Trait data

Previous studies have identified traits that strongly influence plant growth and survival (Westoby, 1998; Westoby *et al.* 2002; Cornelissen *et al.*, 2003; Diaz *et al.*, 2004; Bardgett *et al.*, 2014; Laughlin, 2014; Laliberté, 2017). Based on these studies, we focused on six key traits that capture fundamental trade-offs for plants related to regenerative and resource acquisition strategies: (i) SLA (mm²·mg⁻¹), (ii) plant height (m), (iii) seed mass (mg), (iv) woodiness, (v) mycorrhizal status and (vi) lateral spread (m). We first selected three key traits capturing

fundamental trade-offs for plants that are incorporated within the ‘leaf–height–seed’ scheme, *i.e.* SLA or light-capturing area per allocated leaf dry mass, plant height or vegetative height of the plant’s canopy at maturity, and seed mass (Westoby, 1998). Note that in the trait databases from where most of the seed mass records used in our analyses originate, usually the mass of the diaspore is given, but we use the term ‘seed mass’ instead of ‘diaspore mass’ for the sake of simplicity (cf. Sonkoly *et al.* 2017).

We then added three additional traits in which we expected to find relationships with several of the environmental drivers. Woodiness and mycorrhizal status were included based on the demonstrated differences in resource acquisition between woody/non-woody or herbaceous, as well as between non-mycorrhizal/mycorrhizal plants (Ryser, 1996; Graves *et al.*, 2006; Kleyer *et al.*, 2008; Hempel *et al.*, 2013; Bardgett *et al.*, 2014; Valverde-Barrantes *et al.*, 2017). Lateral spread, or the increment of vegetative growth organs in a horizontal direction, was included because of the importance of vegetative growth for many understorey species and the potential response to land-use legacies (Klimešová *et al.* 2009; Baeten *et al.*, 2010).

For each of the four continuous plant traits, *i.e.* adult plant height, SLA, seed mass and lateral spread, we calculated the CWM, which was weighted by relative percentage cover (Fig. 2). To gain additional information on the community trait distributions and their response to environmental drivers, the coefficient of variation (CV) was calculated for each of the four continuous traits as SD/CWM. We show these results in the supplementary data (Table S4, Figure S6) and focus on the CWM results in the main text. The categorical traits woodiness and mycorrhizal status were included as the proportional cover of woody species (excluding tree, shrub and climber species), and species with obligate mycorrhizal (OM) associations in the plots, respectively (Moora, 2014; Bjorkman *et al.*, 2018) (Fig. 2).

We used ‘mean’ species values for traits here (following Albert *et al.* 2011; Kazakou *et al.*, 2014), and did not take into account intraspecific trait variation, which also responds to environmental factors (Violle *et al.*, 2012). We followed a two-step procedure to ensure that we had adequate trait data representative of the plot understorey communities. We first checked that trait attributes were present for the most abundant species (present in >5% of the plots and with mean cover >1%) and then ensured that 80% of the plot cover was represented by trait values (Table S2) (Pakeman, 2014). An overview of the regional trait variation and distributions is shown in Table S1b, c and Figure S1. We also checked pairwise correlations among the traits (Figure S2).

Global change drivers

We included two climate and two atmospheric deposition variables, estimated at the regional scale, to quantify potential drivers of understorey trait variation. These were (i) mean annual temperature (MAT, °C), (ii) mean annual precipitation (MAP, mm·year^{−1}), (iii) atmospheric nitrogen deposition (Ndep, kg·ha^{−1}·year^{−1}) and (iv) acidification rate (AcidRate, keq·ha^{−1}·year^{−1}) (Fig. 2). For the climate variables, we extracted monthly climate data from the gridded CRU TS3.24 dataset (Climate Research Unit; 0.1° resolution, ca. ±40 km):

Harris *et al.* 2014) and calculated annual temperature and precipitation values. We used mean annual temperature and precipitation for the time period 1980–2015. Microclimatic buffering effects on below-canopy temperatures were not considered due to the lack of available data, thus the results could differ when using actual measured temperatures at the forest floor (De Frenne *et al.*, 2013b; Bhatta & Vetaas, 2016; Vanneste *et al.*, 2018).

To evaluate potentially eutrophying *versus* acidifying effects of increased deposition, we included Ndep as a measure of eutrophication and AcidRate as a measure of acidification. We extracted total nitrogen deposition (NH₃ + NO_x) and sulphur deposition (SO_x) for the year 2000 based on interpolated model results from the European Monitoring and Evaluation Programme (version 2013, <http://www.emep.int/>) and calculated the acidification rate based on nitrogen and sulphur deposition as (cf. Verheyen *et al.*, 2012):

$$\text{AcidRate} = \frac{\text{N}_{\text{dep}}}{14} + 2 \times \frac{\text{S}_{\text{dep}}}{32.06}$$

Cumulative deposition values would have been based on backcasting from deposition patterns for the year 2000 (as in Duprè *et al.* 2010), and thus highly correlated with the 2000 values, leading to high similarity in model results (Henrys *et al.*, 2011). To minimize the number of assumptions in our analysis, we used 2000 values rather than estimated cumulative deposition. We assumed homogeneous environmental conditions within a region, so we extracted all climate and deposition variables on a plot level, and then calculated the mean of all plots for each region.

We reconstructed the land-use history of each plot between 1850 and 2015 in a standardized way based on a combination of expert knowledge of our local contact person in each region, a thorough search of region-specific maps and literature and oral interviews. We tried to maximize differences in past land cover within regions, but it was not always possible to find a perfectly even distribution of past land-cover categories within each region from the available datasets.

We distinguished between ancient forest (AF) plots (*n* = 131), *i.e.* plots that have been continuously forested since at least 1850, *versus* recent forest (RF) plots (*n* = 54), *i.e.* plots that were afforested after ca. 1850. The majority of the recent plots were afforested after 1850, while several were afforested between 1800 and 1850. The previous land-cover categories of these recent forest plots were heathland (three), grassland (21) and arable land (30), and they transitioned into forest between 1810 and 1900 for the heathland plots, between 1860 and 1912 for former grassland plots and between 1820 and 1970 for the former arable plots. The past land cover of the recent forest plots may have influenced current understorey communities differently, so we distinguished between the 30 post-arable recent forest plots, on the one hand, and the 21 post-grassland plus three post-heathland plots, on the other hand (Fig. 1b). Nutrient enrichment practices, such as fertilization and liming, and soil disturbance practices (*e.g.* soil tilling or ploughing) are more likely to have taken place in the post-arable plots *versus* more nutrient-depleting practices in the grassland/heathland plots (*e.g.* burning or sod-cutting). This may have differently altered soil fertility and microbial communities, and potentially

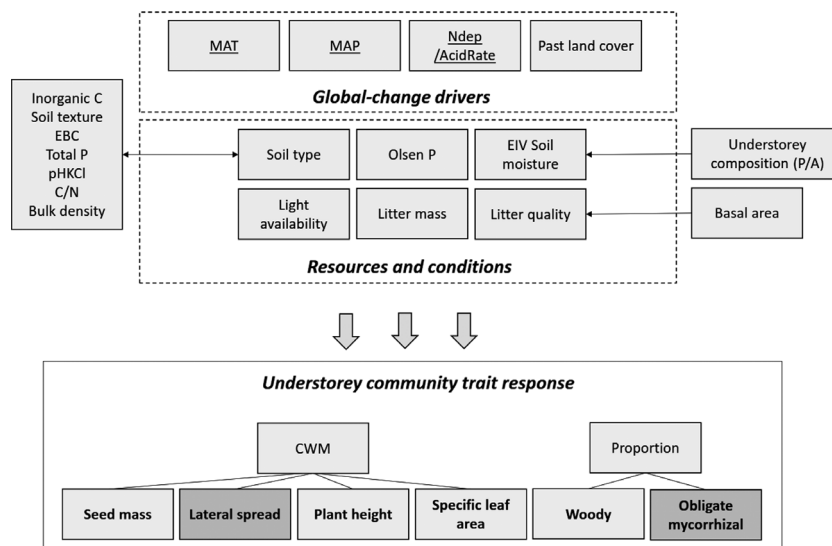


Fig. 2. Graphical representation of the predictors, including global change drivers and resources and conditions, and investigated understorey community trait responses (*left*: community-weighted means (CWM), *right*: proportional cover of species). Underlined predictor variables were calculated at the regional scale, while all others were calculated at the plot scale. Aboveground traits are shaded in light grey, while belowground traits are in dark grey. Variables outside the boxes have been used to calculate other variables inside the box (i.e. basal area-weighted litter quality score and presence–absence based mean Ellenberg Indicator Value for soil moisture) or reflect variation in other topsoil physicochemical variables (soil type). Abbreviations used in the figure represent mean annual temperature and precipitation (MAT – °C, MAP – mm·year^{−1}), nitrogen deposition (Ndep – kg·ha^{−1}·year^{−1}), acidification rate (AcidRate – keq·ha^{−1}·year^{−1}), Olsen phosphorus (Olsen P – mg·kg^{−1}), Presence/Absence (P/A), Inorganic carbon content (Inorganic C – %), proportion of exchangeable base cations (EBC), total phosphorus (Total P – mg·kg^{−1}), and organic carbon/total nitrogen ratio (C/N). Note that (i) Olsen P is included as a separate predictor here as it is an important nutrient for plant growth and was not correlated with soil type, and (ii) lateral spread is ‘mainly’ a belowground trait (e.g. rhizomes), but understorey species also have aboveground characteristics for lateral spread (e.g. stolons).

influenced understorey trait responses (Matson *et al.* 1997; Buckley & Schmidt, 2001; Fichtner *et al.* 2014).

Resources and conditions

We clustered our plots into three ‘Soil type’ groups (Fig. 2) based on soil texture (% Clay, % Silt, % Sand) and carbonate or inorganic carbon concentration (%) using the *hclust* function in R (stats package, Ward.D method, Euclidean distances; R Core Team 2016). See Maes *et al.* (2019) for details on the soil sampling. The ClayCarbonate soils (21 plots) represent silty-clay-carbonate soils with high inorganic carbon concentration, whereas the ClayNoCarbonate soils (82 plots) represent silty-clay soils without the presence of carbonates (low inorganic carbon concentration), and the Sand soils (82 plots) represent sandy soils with a low inorganic carbon concentration. These clusters represented differences in other topsoil conditions. From the poorer sandy soils to the intermediate clay-no-carbonate to the richer clay-carbonate soils, we observed an increase in proportion of exchangeable base cations (EBC), pH (pH_{KCl}) and total phosphorus content (TotP), and a decrease in litter mass, bulk density and C/N ratio (details see Maes *et al.* (2019)). Since Olsen P was not correlated with the soil type groups, and because it is an important nutrient for plant growth, we included it as a separate predictor here (Fig. 2).

We expected soil moisture to influence community trait responses (Riegal *et al.*, 1991; Schaffers & Sýkora, 2000). We used a proxy that integrates the moisture conditions typically experienced in the plot, since *in situ* measurements are subject to fluctuation from local weather conditions and fine-scale

spatio-temporal variation (Kopecký & Čížková, 2010; Korres *et al.*, 2015; Peng *et al.*, 2016). We calculated a presence/absence-based mean community Ellenberg Indicator Value (EIV) score from all the vegetation, including tree, shrub and understorey species, in the plot (*i.e.* an ordinal score between 1 = species typically growing on dry soils, and 9 = species growing on wet soils) – further referred to as ‘Ellenberg soil moisture’ (Fig. 2). EIV indicate species preferences in their realized niche, which may characterize the environment in the absence of directly measured variables (Schaffers & Sýkora, 2000; Diekmann, 2003; Bartelheimer & Poschlod, 2016). Although this might be regarded as circular reasoning because both this predictor and the trait responses were based on compositional data (*sensu* Zelený & Schaffers, 2012), we think that using the EIV for soil moisture is justified here. First, the EIV for soil moisture ignored species abundance while this *was* considered to calculate the CWM trait responses (weighted by relative abundance). Second, EIV for soil moisture was calculated based on *all* the vegetation cover in the plot (*i.e.* understorey, shrub and tree species), while the trait responses were calculated for understorey species only. Nevertheless, we should treat our results for soil moisture with some caution, given the potential bias that could be related to the use of this species-derived Ellenberg variable.

The overstorey might also influence understorey trait variation across our plots through modifying the leaf litter (quantity and quality) as well as the light availability that reaches the forest floor. We recorded the dry weight of the organic layer as the ‘Litter mass’ (g) for each plot after drying the forest floor samples for 24 h at 65 °C and included a plot-scale average

‘Litter quality’ score (LQ; Fig. 2). This was calculated as a weighted average (by basal area – $\text{m}^2\cdot\text{ha}^{-1}$) of litter quality indices of individual canopy species (trees and shrubs with DBH >7.5 cm) present within the plot. These species scores reflect the rate of leaf litter decomposition and were obtained from the literature (details see Maes *et al.*, 2019). Finally, we took the average of five densiometer measurements in each plot to attain a canopy openness estimate (%), reflecting the light that reaches the understorey (taken in four plot corners + centre, at eye level, *i.e.* 1.6–1.8 m height, further referred to as ‘Light’) (Fig. 2) (Lemmon, 1957; Baudry *et al.* 2014). To take into account potential confounding effects of canopy development among the different forest regions at the times of sampling, we sampled the regions from west to east, capturing the understorey communities as much as possible at similar stages of canopy development or phenology (when canopy leaf-out was complete).

For an overview of the regional variation in predictor values and their distribution across all regions, refer to Table S1a and Figure S3, respectively.

Data analysis

We used 185 plots for the analyses from the 192 sampled plots, excluding two plots with very high soil organic matter content and five plots because they had no understorey species. For the analysis of seed mass, Monilophyta species (12 fern and two *Equisetum* species) were excluded because their very low ‘diaspore’ mass caused a bias in the results (0.000034 mg for ferns; Gómez-Noguez *et al.* 2016)). Table S5 shows results when including these species. Three additional plots were excluded from the analyses of seed mass because they only comprised fern species, resulting in a final sample size of 182 plots.

We evaluated the CWM of the response traits Plant height, SLA, Seed mass and Lateral spread, and the proportional cover of the response traits Woodiness and Obligate mycorrhizal status in each plot in relation to the global change drivers and the resources and conditions (Table S6). We included Ndep in the global model as a (potential) quadratic effect, because we expected that the effect of deposition on understorey trait responses in our plots might not be linear because of N saturation effects in several regions where the critical N load for understorey communities was exceeded ($>15\text{--}20\text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$; Table S1a; Bobbink *et al.*, 2017, 2010; Gilliam, 2006).

Several predictors and response variables required a transformation prior to the analysis to linearize relationships (Figures S1 and S3): LitterMass (square root), OlsenP (log), Light (log) and the response CWM Plant height (log), CWM Seed Mass (log). We checked for potential confounding and collinearity issues between the predictor variables by means of boxplots and correlograms (Figure S4). Soil type was slightly correlated with the litter mass as well as litter quality, which should be kept in mind when interpreting the results. Otherwise, only N deposition and acidification rate were highly correlated ($R_p = 0.94$), which led to separate models being built using one or the other. All continuous predictors were standardized (scaled and centred) prior to analysis to enable comparison of their effect sizes.

We built a model for each trait including all possible combinations of our predictors as main effects. We adopted an AIC-based multi-model inference approach to derive the best-

supported models by weighing and ranking all possible models based on a small sample information criterion (AIC_c). We derived ‘full’ average parameter estimates and 95% CI (‘zero-method’ *sensu* Grueber *et al.* 2011) based on a reduced set of models with good empirical support ($\Delta\text{AIC}_c \leq 3$ from lowest AIC_c model (Burnham & Anderson, 2002)). Models were run using the MuMIn package in R (Barton, 2017).

To take into account the hierarchical structure of our data (plots within regions), we included the random intercept Region in the models. We used linear mixed effect models (LMM) and generalized linear mixed effect models (GLMM) for the CWM response traits (Plant height, SLA, Seed mass and Lateral spread) and the proportional cover response traits (Woodiness, Obligate mycorrhizal status), respectively. We modelled Woodiness and Obligate mycorrhizal status with a gamma distribution and a log link function because there were several zeroes in the proportional cover data, and this provided the best model fit. Because the results of the acidification models largely overlap with the results of the N deposition models, we report them in the supplementary data (Tables S4 and S7), and only highlight new results compared to the deposition models in the main text.

We discuss effects where zero was not included in the 95% CI of its parameter estimate (Burnham & Anderson, 2002). We evaluated the global models’ performance graphically by looking at plots of the residuals *versus* fitted values, and of the fitted *versus* observed values (*i.e.* ‘goodness-of-fit’). For the GLMM, we additionally checked for heteroscedasticity by evaluating the scaled residual plots, as well as tested for overdispersion by means of the R package ‘DHARMa’. We also calculated the marginal and conditional R^2 (proportion of variance explained by fixed factors – R^2_m , and by both fixed and random factors – R^2_c) of the global and selected models following Nakagawa & Schielzeth (2013). All statistical analyses and visualizations were performed in R (version 3.3.3; R Core Team 2016) with the packages ‘STATS’, ‘MUMIN’, ‘LME4’, ‘DHARMa’ and ‘GGPLOT2’ (Wickham, 2009; Pinheiro *et al.* 2016; Barton, 2017; Hartig, 2018, respectively).

RESULTS

Some global change drivers (MAT, Ndep/AcidRate), as well as several resources and conditions (Ellenberg soil moisture, litter mass and OlsenP), were correlated with variation in trait CWM in the plots [Table 1 (models with Ndep), Table S7 (models with AcidRate)]. We did not observe any effects of past land cover, soil type, litter quality or light availability on the investigated traits (Tables 1 and S7). Overall, lateral spread was much less influenced by the predictors than the other traits (Table 1, Figs 3, 4).

Significant trait–environment relationships were found between mean annual temperature (MAT) and CWM of various traits (Table 1). The CWM plant height, proportional cover of woody and OM species showed a positive relationship, while SLA had a negative relationship with MAT (Fig. 4). Furthermore, we found a quadratic effect of Ndep as well as AcidRate on CWM SLA (Tables 1 and S7, Fig. 4).

Ellenberg soil moisture and litter mass also appeared to be important predictors of understorey trait variation in our plots (Table 1). A higher Ellenberg soil moisture was associated with a lower proportional cover of woody and OM species (Fig. 4),

Table 1. Parameter estimates (*i.e.* effect sizes) and directions (increase↑ or decrease↓) of the main effects in the average models for the response variables: CWM (first four columns) and proportional cover (last two columns). The last four rows provide information on the selected models that make up the average model: the maximum R^2 explained with the models by fixed factors only (R_m^2) and by fixed and random factors (R_c^2), the relative weight of the ‘best-ranked’ model based on an AIC cut off of 3 (max weight) and the number of models used to derive weighted parameter estimates.

	CWM/Proportional cover					
	Regeneration		Resource acquisition			
	Seed mass	Lateral spread	Plant height	SLA	Woody	OM
Intercept	1.82	0.15	−0.71	28.88	−2.96	−1.40
Global-change drivers						
MAT	−0.07↓	0.00	0.30↑	−4.22↓	1.01↑	0.35↑
MAP	−0.23↓	0.00	0.00	0.02↑	0.01↑	0.26↑
Ndep	−0.08↓	0.00	0.00	1.26↑	−0.01↓	0.07↑
Ndep ²	0.00*	0.00	0.00	−0.80↓	0.00	0.01↑
AFRF [RF-Grass]	−0.01↓	NA	NA	−0.08↓	0.03↑	0.03↑
AFRF [RF-Arable]	−0.09↓	NA	NA	−0.34↓	0.05↑	0.03↑
Resources and conditions						
Soil type [ClayNoCarb]	NA	−0.02↓	0.02↑	NA	NA	0.00
Soil type [Sand]	NA	−0.02↓	0.01↑	NA	NA	−0.01↓
Olsen P	−0.05↓	0.00	0.03↑	−0.39↓	−0.35↓	−0.11↓
Soil moisture (EIV)	−0.29↓	0.00	0.00	0.07↑	−0.51↓	−0.26↓
Litter mass	0.24↑	0.00	0.14↑	−0.06↓	0.32↓	0.28↑
Litter quality	0.02↑	0.00	0.00	0.13↑	−0.30↓	0.01↑
Light	0.00	0.00	0.06↑	−0.19↓	0.30↑	0.00
Max R_m^2	0.28	0.13	0.37	0.41	0.22	0.25
Max R_c^2	0.48	0.42	0.53	0.44	0.44	0.33
Max weight	0.06	0.05	0.15	0.08	0.29	0.11
No models	41	51	16	33	8	22

The abbreviated response variables are SLA (specific leaf area), Woody (proportional cover of woody species) and OM (proportional cover of obligate mycorrhizal species) per plot. The abbreviated predictors (first column) are MAT (mean annual temperature), MAP (mean annual precipitation), Ndep (N deposition), AFRF[RF-Grass] (recent post-grassland/heathland), AFRF[RF-Arable] (recent post-arable forest plots), Soil type[ClayNoCarb] (clayey soils without carbonate), Soil type[Sand] (sandy soils) and OlsenP. Effect sizes are in bold if the 95% CI does not include zero. NA: the predictor did not occur in any of the selected models that make up the average model. *An effect size of 0.00 implies that the predictor occurred in the selected models, but with a very small effect size (rounded to 0.00).

as well as a lower CWM seed mass (Fig. 3). Plots with a higher litter mass had higher CWM plant height, a higher proportional cover of OM species (Fig. 4), as well as higher CWM seed mass (Fig. 3). Finally, plots with a higher bioavailable phosphorus (Olsen P) also contained lower proportional cover of woody species (Fig. 4).

Overall, the R^2 values (R_m^2 between 13% and 41%) suggested that the predictors explained a medium amount of the variation in our response traits. Among the response traits, we observed a positive correlation between woodiness and CWM plant height ($r = 0.70$) as well as between woodiness and proportional cover of OM species ($r = 0.57$), while CWM plant height and SLA were negatively correlated ($r = -0.60$).

DISCUSSION

Regeneration traits

Lateral spread showed no relationship with environmental drivers, while seed mass was related to some of the resources and conditions, *i.e.* Ellenberg soil moisture and litter mass. Communities in moister plots having on average lower seed mass is in accordance with other studies on the relationship between seed mass and Ellenberg soil moisture (Baker, 1972; Westoby

et al. 1992; Dubuis *et al.*, 2013; Sonkoly *et al.*, 2017). Larger seed mass has been linked with a higher resilience to various seedling disturbances, such as drought, likely due to the tendency of larger seeds to retain more metabolic reserves (Westoby *et al.*, 1996; Westoby, 1998; DeMalach *et al.*, 2018).

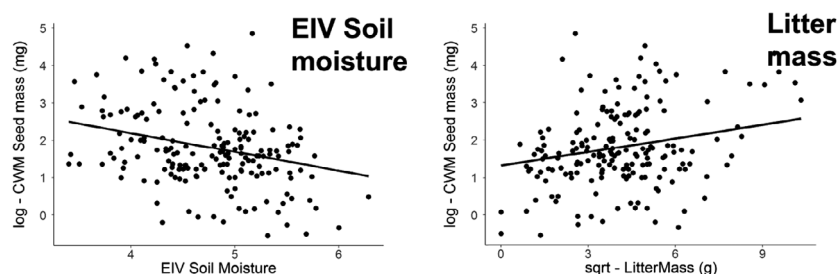
Communities in plots with more litter had, on average, larger seeds. This may be because more seed reserves enable the initial seedlings to penetrate these thicker litter layers (Kidson & Westoby, 2000; Baltzinger *et al.* 2012). Reduced light availabilities beneath litter layers may also prevent small seeds from germinating, whereas large-seeded species are less dependent on light for germination success (Milberg *et al.* 2000; Simpson, Richardson *et al.* 2016; Zhang *et al.* 2017).

Resource acquisition traits

Mean annual temperature (MAT) showed a relationship to all resource acquisition traits in our plots. This result agrees with findings from previous trait studies showing that temperature is a key factor for understorey composition and functioning (Murray *et al.* 2004; Reich & Oleksyn, 2004; Wright *et al.*, 2004; De Frenne *et al.*, 2013a; Moles *et al.*, 2014; Lu *et al.*, 2017; Bjorkman *et al.*, 2018). Besides temperature, a strong link between Ellenberg soil moisture and several traits was also

Resources and conditions

Fig. 3. Trait–environment relationships for the regeneration trait seed mass. Effects of EIV soil moisture (left) and litter mass (right) on the community-weighted mean seed mass (CWM seed mass). Actual data points (dots) and average model estimates of the effects (full lines), in which the values of the other continuous variables were set at their observed mean, are shown.



found in our plots (Riegal *et al.*, 1991; Schaffers & Sýkora, 2000).

Understoreys were taller and had leaves with a lower CWM SLA in warmer regions (Moles *et al.*, 2009; De Frenne *et al.*, 2013a; Vanneste *et al.*, 2018). Specific leaf area represents a trade-off between potential carbon gain (biomass production) and resource conservation (Wright *et al.*, 2004). Species in resource-rich environments (*i.e.* resources such as water or nutrients) tend to have a larger SLA, *i.e.* focus on rapid resource acquisition through thinner leaves with a shorter life span than those in resource-stressed environments, which focus on resource conservation through thicker leaves with a longer life span (Westoby *et al.*, 2002; Wright *et al.*, 2004; Ordoñez *et al.*, 2009). Producing leaves with a lower SLA (sclerophyllous) in warmer regions with higher potential evapotranspiration rates might be more an (indirect) water-conserving rather than a nutrient-conserving strategy. This could become increasingly important in regions with increasing temperatures without concurrent increases in precipitation (Soudzilovskaia *et al.*, 2013). If so, we could also expect to find an effect between CWM SLA and MAP, which was not the case. On the other hand, the lower CWM SLA in warmer regions might be linked to the higher proportions of woody species cover in those regions, since woody plants have a lower SLA and growth rates than herbaceous plants due to the large energy requirements for formation of woody structures (Jarvis & Jarvis, 1964; de Vries, Brunsting, & Van Laar, 1974; Poorter & Evans, 1998).

The CWM SLA had a quadratic hump-shaped relationship with N deposition as well as acidification rate, although this was weaker than the negative linear relationship with temperature. Higher N availability from increased atmospheric deposition can increase SLA (and growth rates) through favouring highly resource-competitive species over more N-efficient species (Reich, Walters, & Ellsworth, 1997; Westoby *et al.*, 2002; Poorter, Niinemets, Poorter, Wright, & Villar, 2009; Boutin *et al.*, 2017), while beyond a certain threshold or critical load of deposition (here ca. 18 kg·ha⁻¹·year⁻¹), growth reductions from N saturation and potential acidification may occur, as suggested by these results (Aber, 1992, 1998; Bobbink *et al.*, 2017). Due to potential confounding effects with the topsoil conditions in this result, we should not over-interpret this. That is, the Speulderbos (NL) region receiving the highest Ndep also had poorer topsoil properties (sandy soil type, lower pH) and lower species numbers.

Interestingly, both the proportional cover of woody and of OM species was positively related to temperature, and negatively to Ellenberg soil moisture. A higher abundance of woody plant species (not counting tree and shrub seedlings, which

were excluded from the analysis) in the understorey may result in a stronger mycorrhizal fungal network, leading to higher occurrences of species forming mycorrhizal associations (Wang *et al.*, 2006; Hempel *et al.*, 2013; Veresoglou, Wulf, & Rillig, 2017). This might also explain the positive correlation between proportional cover of woody and OM species ($R_p = 0.57$). Species forming mycorrhizal associations appeared to thrive better (*i.e.* they had larger relative cover) in plots with lower Ellenberg soil moisture as compared to species that do not, as fungal associations aid water uptake (Wang *et al.*, 2006; Bennett & Klironomos, 2018). The decrease in woody species cover with higher Ellenberg soil moisture (and also with bioavailable P) seems in line with the hypothesis that higher available resources promote herbaceous but constrain woody understorey species growth because of the higher resources per unit biomass required for herbaceous species development (Graves *et al.*, 2006).

Besides temperature and Ellenberg soil moisture, litter mass also affected CWM of some resource acquisition traits, with communities in plots with more litter being taller, having larger seeds and harbouring more OM species (cover). These results support previous studies demonstrating the importance of (deciduous) litter in structuring understorey communities, through forming a chemical, physical and biological barrier for seeds, seedlings and adult plants (Xiong & Nilsson, 1999; Baltzing *et al.*, 2012; Maes *et al.*, 2019).

Lack of effects of light availability and past land cover

The lack of effects of light availability on the investigated traits is surprising, as light is considered a key driver of the functional composition and dynamics of understorey communities (Liefers *et al.* 1999; Bartemucci *et al.* 2006; Bartels & Chen, 2009; Bernhardt-Römermann *et al.*, 2015; De Frenne *et al.*, 2015; Sercu *et al.*, 2017). We sampled in quite closed mature forests with a mean canopy openness of 18.3% (min. 1.4%, max. 69.8%), so perhaps there was too little variation in light availability to result in functional trait variation. Other explanations could be that light heterogeneity, rather than availability, is more important for understorey functioning (Valladares & Niinemets, 2008; Bartels & Chen, 2009; Burton *et al.* 2017), or that we missed community trait responses to light here by using single trait values per species. Intraspecific trait variation or plasticity to light may be particularly strong because of the asymmetric nature of competition for light (Roscher *et al.* 2015; Valladares *et al.* 2016). Finally, although several studies have demonstrated the reliability of densiometer measurements as an alternative for estimating light availability below the canopy (*e.g.* compared to hemispherical photography) (Bellow & Nair, 2003; Parker,

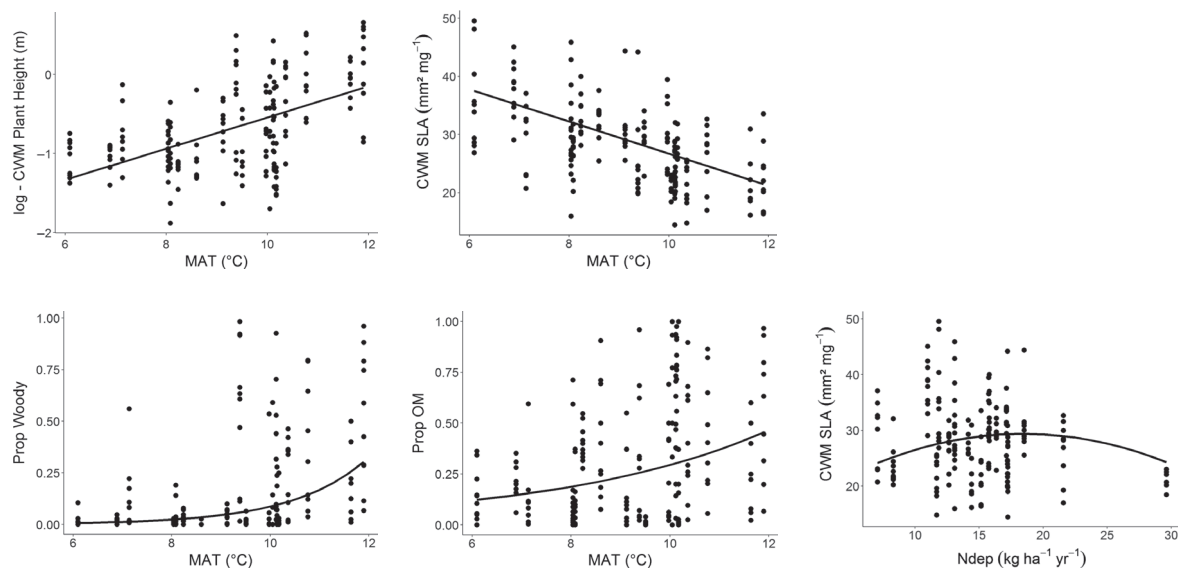
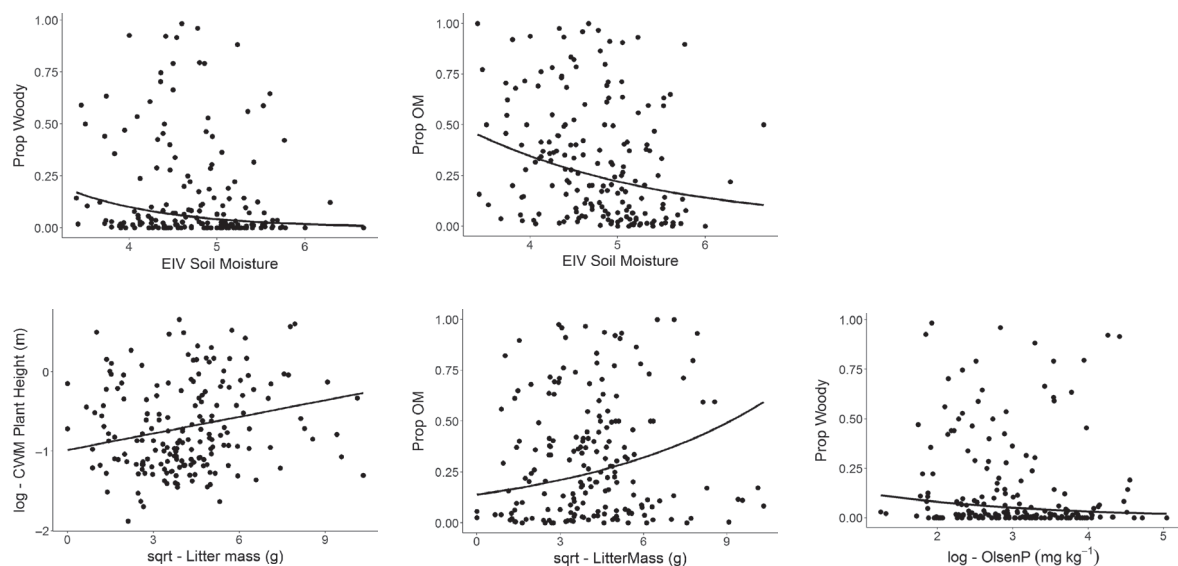
(a) Global-change drivers**(b) Resources and conditions**

Fig. 4. Trait–environment relationships for resource acquisition traits. (a) Effects of global change drivers: of MAT (°C) on community-weighted mean plant height (CWM plant height – m), CWM specific leaf area (CWM SLA – mm²·mg^{−1}), proportional cover of woody species (Prop Woody) and proportional cover of obligate mycorrhizal species (Prop OM, (left); and of Ndep (kg·ha^{−1}·year^{−1}) on CWM SLA (right). (b) Effects of local resources and conditions: of EIV soil moisture on Prop Woody and Prop OM (top left); of litter mass (g) on CWM plant height and Prop OM (bottom left); and of OlsenP on Prop Woody (bottom right).

2014), using this ‘indirect’ method to estimate light availability could still be partly responsible for the lack of effects here (Jennings, 1999; Engelbrecht & Hertz, 2001).

We also expected to find land-use legacies in the functional signature (*e.g.* lateral spread) of the present-day understorey communities (Verheyen *et al.*, 2003; Flinn & Vellend, 2005; Holmes & Matlack, 2018), but past land cover did not affect any of the traits. This could suggest that land-use legacies do not necessarily affect the functional signature of understorey communities, even if compositional shifts from land-use legacies might occur.

Implications for future understorey communities

Community-level resource acquisition traits in temperate forest understoreys seemed driven by both global change drivers and local resources and conditions. Considering the local context is not always straightforward, as *in situ* measurements of local resources and conditions can be laborious, costly and logistically challenging, especially across larger-scale environmental gradients. Global change drivers may affect forests *through* (indirectly) altering other local conditions, as well as these local conditions may influence how forests respond to

global changes (Smith *et al.*, 2009; Naaf & Kolk, 2016; Simpson *et al.*, 2016; Landuyt *et al.*, 2018). Because of this, it will be crucial to also evaluate interactive effects among environmental drivers, not only among global change drivers or among local resources and conditions, but also between these two, *e.g.* by performing structural equation modelling and evaluating interactive effects.

Among the studied global change drivers, MAT appeared more important than N deposition, MAP or past land cover. Based on our findings, future warming could lead to understorey community changes benefiting taller species with more resource-conservative leaves (lower SLA) across the investigated environmental gradients. Future warming may also benefit woody species and species forming mycorrhizal associations residing in understorey communities. Future studies should consider microclimatic buffering effects on below-canopy temperatures by including measured temperatures at the forest floor, since this buffering effect (*i.e.* likely reduced temperature ranges) may confound the temperature–trait relationships found here (Zellweger *et al.*, 2019). That is, our plots comprised closed canopy forests that have not had much disturbance in the recent past, and where canopy cover has increased over time. Thus, we might expect even stronger temperature effects on the understorey trait responses if this buffering was not to occur or was altered, *e.g.* through opening up of the canopy. Note that we excluded tree and shrub seedlings in this study, since these do not remain part of the understorey, so these results do not consider effects on tree regeneration. Furthermore, future responses may also depend on other local resources and conditions, such as *e.g.* the size of the litter layer or P availability. Due to the heterogeneous nature of these resources and conditions below the forest canopy, they can differ considerably among sites, and potentially confound the expected understorey responses to global change.

Spatial environmental gradients only allowed us to hint at potential future changes in understorey community trait composition and functioning (Kratz *et al.* 2003; Blois *et al.* 2013; Elmendorf *et al.*, 2015; De Lombaerde *et al.*, 2018). Future studies using plot resurveys should also investigate temporal changes, to test the validity of our results (Hedwall & Brunet, 2016; Perring *et al.*, 2016; Verheyen *et al.*, 2016; Perring *et al.*, 2018a). More work is needed to take into account biotic influences on understorey communities (*e.g.* herbivory pressure) (Morecroft *et al.* 2001; Rooney, 2009; Bernhardt-Römermann *et al.*, 2015; de la Peña *et al.*, 2016), as well as more in-depth analysis of individual species responses. We also did not take into account potential effects of forest size/fragmentation here, because most of our regions comprised medium- to large-sized forests. Future studies should consider this, since potential time lags in composition turnover from fragmentation effects, and even potential extinction debts, could have an influence on the composition of the understorey, indirectly affecting trait responses (Vanneste *et al.*, 2018). Given the broad environmental gradients covered here, we expected trait variation to be dominated by interspecific differences rather than intraspecific variation (Auger & Shipley, 2013). However, for certain traits such as SLA, intraspecific trait variation (ITV) might play a more important role in driving trait variation, hence considering ITV is also a necessary priority for future research. Furthermore, ITV has been suggested as a useful early-warning signal

where changes in traits at the individual level may forecast future shifts at community level, reiterating the importance of evaluating ITV as well (Smith *et al.*, 2009).

CONCLUSION

To conclude, warmer temperatures were associated with, on average, taller understoreys producing leaves with lower SLA, and a higher relative cover of woody and obligate mycorrhizal species. These findings may hint at community shifts in temperate forest understoreys with (future) global warming. Furthermore, local resources and conditions including Ellenberg soil moisture, litter mass and, to a lesser extent, P availability, were also associated with community trait variation across the spatial environmental gradients. Based on these findings, we recommend that studies investigating global environmental (change) effects on understorey communities should consider the local environmental context. Further investigations should evaluate interactive effects among the different environmental drivers, incorporate intraspecific trait variation, as well as perform temporal studies to validate how understoreys are already changing in response to changing environments.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

SLM, MPP and KV conceived and designed the study with significant contributions from SG, DL, LD, and HB. GB, JB, GD, JDO, WH, RH, TH, SH, BJ, KK, MK, FM, MW, and KV assessed historical land-use information for the study regions and participated in the field campaign (as well as MPP, SG, DL, LD and HB). SLM, MBR and SG compiled the trait information from various literature sources. SLM, with input from

MPP, DL, LH, TV and KV performed data quality checks, and subsequent statistical analyses on the data. SLM wrote the first draft of the paper. All co-authors provided revisions and comments.

DATA AVAILABILITY STATEMENT

We intend to archive all data used in this paper on our public website: www.pastforward.ugent.be.

SUPPORTING INFORMATION

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

Figure S1. Histograms (data distributions) of the raw (un-transformed) trait response data.

Figure S2. Pairwise correlogram of the community trait responses (trait names on diagonal) used in the analyses.

Figure S3. Histograms (data distributions) of the raw predictor data.

Figure S4. Pairwise correlogram of the continuous predictor variables (names on diagonal) used in the analyses.

Figure S5. Boxplots evaluating the potential confounding between the categorical variable soil type and the continuous variables litter mass (g) and litter quality.

Figure S6. Trait–environment relationships for the resource acquisition traits (additional analysis on the coefficients of variation (CV) – Table A4).

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