RESEARCH ARTICLE

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Trait–micro-environment relationships of forest herb communities across Europe

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Abstract

Aim: The microclimate and light conditions on the forest floor are strongly modified by tree canopies. Therefore, we need to better consider the micro-environment when quantifying trait–environment relationships for forest understorey plants. Here, we quantify relationships between micro-environmental conditions and plant functional traits at the community level, including intraspecific trait variation, and their relationship with microclimate air temperature, light and soil properties.

Location: Deciduous temperate forests across Europe.

Time period: 2018.

Major taxa studied: Herbaceous vegetation.

Methods: We sampled 225 plots across 15 regions along four complementary gradients capturing both macro- and microclimatic conditions including latitude, elevation, forest management and distance to forest edges. We related the community-weighted mean of five plant functional traits (plant height, specific leaf area [SLA], plant carbon [C], plant nitrogen [N] and plant C:N ratio) across 150 vascular plant species to variation in local microclimate air temperature, light and soil properties. We tested the

effect of accounting for intraspecific variation in trait–environment relationships and performed variation partitioning to identify major drivers of trait variation.

Results: Microclimate temperature, light availability and soil properties were all important predictors of community-weighted mean functional traits. When light availability and variation in temperature were higher, the herb community often consisted of taller plants with a higher C:N ratio. In more productive environments (e.g. with high soil nitrogen availability), the community was dominated by individuals with resource-acquisitive traits: high SLA and N but low C:N. Including intraspecific trait variation increased the strength of the trait–micro-environment relationship, and increased the importance of light availability.

Main conclusions: The trait–environment relationships were much stronger when the micro-environment and intraspecific trait variation were considered. By locally steering light availability and temperature, forest managers can potentially impact the functional signature of the forest herb-layer community.

KEYWORDS
community-weighted mean, forest understorey, functional trait, herbaceous layer, intraspecific variation, light availability, microclimate, resource availability, soil properties, trait–environment

1 | INTRODUCTION

Plant functional traits are morpho-, physio- and phenological plant characteristics that affect plant performance through their influence on survival, growth and reproduction (Violle et al., 2007). In addition, plant traits also influence ecosystem functioning (Diaz et al., 2016; Lavorel & Garnier, 2002; Violle et al., 2007; Wright et al., 2004). Trait-based approaches are thus ideal to study the response of plant communities to climate change and other environmental drivers.

Plant communities and their traits shift along environmental gradients, such as light availability, soil properties and temperature (Bjorkman et al., 2018; Depauw et al., 2020; Happonen et al., 2021; Kemppinen et al., 2021; Maes et al., 2020; Zirbel & Brudvig, 2020). These community-level shifts in functional traits are caused by traits varying among (interspecific) and within (intraspecific) species (Bolnick et al., 2011). When the species occurring in communities change or shift in abundance along environmental gradients (also called species turnover), the functional shift can be attributed to interspecific trait variation. However, individual plants of the same species can also have different traits under different environmental conditions. Two complementary factors cause this intraspecific trait variation, that is, phenotypic plasticity as an acclimation strategy to environmental factors, and inherent genetic differences between individuals (Matesanz et al., 2012). As a consequence, intraspecific trait variation can contribute significantly to community-level trait variation (Siefert et al., 2015). Both species turnover (interspecific variation) and intraspecific trait variation thus cause shifts in community-level functional traits. Furthermore, their contributions can change depending on the trait and environmental gradient (Burton

et al., 2017). To understand how traits change along environmental gradients, it is thus highly insightful to assess the separate contributions of species turnover and intraspecific trait variation.

Ecologists often extract environmental data from continental or global databases such as CHELSA (Karger et al., 2017) and TerraClimate (Abatzoglou et al., 2018) to predict changes in plant traits or vegetation structure. As a consequence, environmental heterogeneity inherent to fine spatial scales tends to be ignored. For example, the temperature near the ground can substantially differ from the temperature in the open air due to local shading, soil properties and topography (Lembrechts et al., 2020). Therefore, to accurately predict the effect of climate and anthropogenic changes on plant communities, not only macro-environmental changes but also in situ fine-scale (<1 up to 100 m) variation in the environment should be considered (Lembrechts et al., 2019). Recent research suggests that differences in functional trait composition (both the means and variation) of local plant communities across large geographical extents are indeed for a large part explained by local-scale environmental gradients (Bruelheide et al., 2018; Kemppinen et al., 2021), for example, forest patch-scale factors explained a much larger part of understorey trait variability in temperate forests than macroclimate and landscape-scale factors (Vanneste et al., 2019).

Here, we used a large environmental gradient across Europe to quantify the individual and relative importance of three local environmental factors (soil, light and temperature) affecting functional trait variation of temperate understorey plant communities. Forests are characterized by small-scale heterogeneity in light (Tinya & Odor, 2016) and can have highly variable top-soil chemistry (Falkengrengrerup et al., 1995; Lechowicz & Bell, 1991), both

affecting the distribution of understorey species. In forest understoreys, microclimatic temperatures depend on forest structural complexity, canopy cover and the temperature outside the forest (Meeussen et al., 2021; Zellweger et al., 2019). Understorey plant communities contribute, on average, to more than 80% of total vascular plant species richness in temperate forests and are essential for several ecosystem functions such as nutrient cycling, carbon (C) dynamics and tree regeneration (Gilliam, 2007; Landuyt et al., 2019). Accurate predictions of the effects of air temperature, light and soil properties on the functional signature and functional diversity of the forest understorey community are thus of critical importance. Previous research demonstrated that a higher light availability in forests had a positive effect on the community plant height and a negative effect on SLA (Dubuis et al., 2013; Perring et al., 2018), while soil properties have often been linked to leaf stoichiometric traits such as leaf N content (Chang et al., 2022; Tian et al., 2018).

We studied five key functional traits of 150 forest herb species (plant height, specific leaf area [SLA], plant C, plant nitrogen [N] and plant C:N ratio) in 225 forest plots located along 45 forest edge-to-interior transects and a latitudinal gradient of 2300 km from central Italy (42° N) to central Norway (63° N) (mean annual temperature difference ≈ 13°C). We studied community-weighted means of these traits, with or without accounting for intraspecific trait variation, using four gradients along both broad and small spatial scales across Europe (i.e. latitude, elevation, forest management type and distance to the forest edge). Our general aim was to describe how the functional traits of understorey plant communities throughout temperate European forests are influenced by the separate effects of changes in microclimate temperature, light availability and soil properties. Because we measured these environmental drivers in concert with intraspecific trait variation, we can also investigate two main hypotheses:

> **Hypothesis 1.** We expect that light, temperature and soil properties are all important drivers of the functional signature of herb-layer plant communities, but with different drivers impacting different traits. We hypothesize that increasing light availability will mainly impact plant height and SLA through changed competitive interactions and that soil properties will steer leaf carbon and nitrogen composition (C, N and C:N) through the availability of nutrients;

> **Hypothesis 2.** We hypothesize that matching trait measurements at the intraspecific level to the scale of locally measured environmental drivers leads to better predictions of the trait syndrome of understorey communities than using trait means from across multiple environments, especially for environmental drivers that vary at small spatial scales (light and microclimate temperature) and for plastic traits such as plant height, leaf N and SLA.

2 | METHODS

2.1 | Study design and area

We studied the understorey of broadleaved forests in the temperate forest biome in Europe, including forests at the transition zone with the sub-Mediterranean and boreo-nemoral forest system. Our study design consists of four temperature gradients from the macro- to microscale: a (1) latitudinal; (2) elevational; (3) forest management / structure; and (4) edge to core gradient.

To capture much of the environmental variation across Europe, we selected forest stands across nine regions along a 2300-km-wide latitudinal gradient from Italy (42°N) to Norway (63°N). In Italy, Belgium and Norway, an elevational gradient with three levels (low [mean ± SD: 142 ± 132 m a.s.l.], medium [342 ± 146 m a.s.l.] and high [612 ± 198 m a.s.l.]) was included to capture macroclimatic variation due to elevation. A total of 15 sites were thus selected: six in regions without an elevational gradient and nine in three regions with three levels of elevation. At each site, three forest stands with different forest management and forest structure were selected: The most structurally complex forest type had a well-developed shrub layer and a high basal area. These forests were not managed during the last 10 years and generally not thinned for >30 years. This type of forest will be referred to as *dense forest type*. The most structurally simple forest type was characterized by a high canopy openness and the absence of a well-developed shrub layer due to thinning activities. This type of forest will be referred to as *open forest type*. Forests with an intermediate management regime and structure will be referred to as *intermediate forest* type. The stands, with a minimum forest area of 4 ha, were mainly dominated by oaks (*Quercus robur*, *Q. petraea*, *Q. cerris*), but sometimes also by *Fagus sylvatica*, *Betula pubescens*, *Populus tremula*, *Ulmus glabra*, *Alnus incana* and *Carpinus betulus*. All sites had the same type of land-use history (ancient forest, i.e., continuously forested since the first available land-use maps), were located in a fragmented landscape, as is typical for Western Europe, with forests imbedded in a matrix of agricultural fields and an intermediate level of soil moisture (mesic). In each of the 45 forest stands, we established 100-m transects starting at the south-oriented forest edge and running into the forest in northward direction towards the forest core. Along each transect, five 3 by 3 m plots were installed at an exponentially increasing distance from the forest edge (at 1.5, 4.5, 12.5, 35 and 99.5 m from the edge), resulting in a total of 225 plots. By applying a study design with four nested environmental gradients (latitude, elevation, distance to edge and management intensity) we can partly disentangle the effects of temperature (that varied along all 4 gradients), light (that mostly varied along the local management and edge-to-core gradients) and soil (that mostly varied between regions and less within one forest stand).

The study design, forest structure and site selection is explained and illustrated in detail in Govaert et al. (2020) and Meeussen et al. (2020). More information on the forest stands can be found in Appendix S1.

2.2 | Plant functional traits of the herb layer

Vegetation surveys were conducted at the peak of vegetation biomass from May until early July 2018, following the regional phenology from Italy to Norway (Govaert et al., 2020). All vascular plant species were identified and their percentage ground cover was visually estimated. For our analysis, we focus on the herb layer, which included non-woody vascular plants smaller than 1 m height.

We measured five plant traits: (1) plant height; (2) SLA; the concentration of (3) carbon (C) and (4) nitrogen (N) in the aboveground biomass; and (5) C:N ratio of the aboveground biomass. Plant height is a measure of performance, but is also strongly correlated with ecosystem productivity (Violle et al., 2007). Differences in plant height between individuals can also be an expression of asymmetric competition for light (Blondeel, Perring, De Lombaerde, et al., 2020; DeMalach et al., 2016). SLA is the ratio of total leaf area to total leaf dry mass and represents a trade-off between mass-based photosynthetic capacity and leaf life span (Wright et al., 2004). Species with thick leaves typically have a low SLA, but may have high area-based photosynthetic capacity and long lifespan (Evans & Poorter, 2001). C and N are key elements necessary for plant growth and play pivotal roles in nutrient cycling in ecosystems. Leaf N is an indicator of resource acquisitiveness but is also related to the litter quality and nutrient cycling. Similarly, the C:N ratio is an indicator of N use efficiency (Law, 2013) and resource conservation (Reich, 2014). In addition, plants with low C:N decompose faster (Cornwell et al., 2008). Note that we determined the N and C concentration in all aboveground plant biomass (and not only in the leaves), as is often done in ecological studies (Pérez-Harguindeguy et al., 2013). However, the main focus of this study was the relative comparison of nutrient concentrations of forest understorey communities growing in different micro-environmental conditions. Given the tight correspondence (Pearsons $r = 0.93$) between the leaf economics spectrum and the stem and whole-plant economics spectra (Freschet et al., 2010), higher plant N concentrations—just like higher leaf N concentrations—reflect faster resource acquisition strategies.

Plant height and SLA were measured for five individuals (or ramets in case of clonal plants) of the five most dominant (in terms of percentage cover) herbaceous plant species per plot, if available. A ramet is defined as a recognizably separately rooted, aboveground shoot (Pérez-Harguindeguy et al., 2013). In addition, we collected the aboveground biomass of the same five individuals by harvesting them. We selected healthy plants for the collection of traits and gave priority to seed-producing individuals (that still had green leaves), and then to flower-bearing individuals. Plant height was measured as the distance between the base of the plant and the top of the youngest fully expanded leaf without stretching the plants axis (Pérez-Harguindeguy et al., 2013). The biggest, healthy leaf was collected (or several leaves in case of small-leaved species). Leaves were dried for 3 days at 40°C. Next, the leaf area was measured with a Li-Cor Portable Area Meter Li-3000 (Li-Cor Biosciences, Nebraska, USA). SLA was calculated by dividing the leaf area by the leaf dry mass, measured with an analytical balance (Mettler Toledo, model AG204

delta range). Due to the extensive field campaign across Europe, it was unfeasible to measure SLA on fresh leaves (as recommended by Pérez-Harguindeguy et al., 2013). However, leaf shrinkage due to drying is relatively small in most temperate forest plants and, since we dried all leaves prior to measurement, the comparison of CWM SLA between plots should be relatively unbiased. Finally, we pooled the biomass (excluding the seeds and flowers) per species per plot to obtain sufficient biomass for chemical analysis and dried the samples for 3 days at 60°C. The C- and N-concentration of the biomass was then measured by high temperature combustion at 1150°C using an elemental analyser (Vario MACRO cube CNS, Elementar, Germany) and the C:N ratio calculated.

In total, 276 understorey herb species were identified to species level, and 19 only to the genus level (Appendix S2, and Govaert et al., 2020 for details on the distribution of species richness). We collected trait data of 150 species (6 only identified to the genus level), of which 114 species were sampled in at least two plots (Appendix S2). On average, the proportional cover of the sampled species contributed to 81.2% of the total herb-layer community cover (standard deviation [SD] 19.4). We assessed the robustness of the analysis with an identical analysis excluding plots for which the proportional cover of the sampled species contributed to less than 80% of the total herb-layer community cover (i.e. 84 plots out of 225 removed). These results were very similar and thus confirm the robustness of our findings, but notice that SLA–environment relationships were less significant in the reduced dataset (Appendix S10).

2.3 | Environmental predictors

2.3.1 | Air temperature

We measured hourly *air temperatures* with temperature data loggers (Lascar type EasyLog EL-USB-1, Lascar Electronics, Whiteparish, UK; accuracy at −35 to +80°C: ±0.5°C), which were installed in the centre of all 225 plots, at least 1 month prior to sampling (winter–spring 2018). Air temperature was measured at 1 m above the soil surface, and loggers were covered by a radiation shield to avoid direct incidence of sunlight (Appendix S3; Maclean et al., 2021). For each data logger (225 in total), we computed the daily minimum (as the 5% percentile of the 24 daily measurements), mean and maximum (as the 95% percentile of the 24 daily measurements). To account for missing or incorrect data due to, for example, logger malfunctioning, we used a simple gap filling strategy. If more than 3 hourly values were missing, the daily statistic was not calculated, but replaced by the value of one plot closer to the forest edge, or if also missing, of the plot closer to the forest interior. We then checked for each month how many data loggers were missing more than 10% days per month during the sampling months (May–June). Only the air temperature during the month of May 2018 met these criteria for all sensors. For each plot, we then calculated *the mean* and *standard deviation of the daily minimum, mean and maximum* in the month of May 2018, totalling six temperature variables (Table 1). We assessed the robustness

TABLE 1 Overview of predictor variables used to explain community-weighted mean and variation in functional traits of herbaceous forest plants across a latitudinal gradient in Europe (from Italy to Norway). Temperature variables are based on in situ air temperature during May 2018. The range indicates the minimum and the maximum values. SD stands for standard deviation.

Variable group	Variable name	Description	Min–max (mean)	Unit
Temperature	Mean	Mean of the daily mean temperature	12.3–18.5 (15.5)	°C
	Max	Mean of the daily maximum temperature	13.6–33.7 (22.5)	°C
	Min	Mean of the daily minimum temperature	5.5–13.5 (9.8)	°C
	Variation of mean	Standard deviation (SD) of daily mean temperature	2.1–4.5 (3.4)	°C
	Variation of max	SD of daily maximum temperature	2.1–8.4 (4.8)	°C
	Variation of min	SD of daily minimum temperature	2.2–4.7 (3.2)	°C
Light	Tree cover	Visual estimation of cover of tree layer, summed per species	0–190 (83)	%
	Shrub cover	Visual estimation of cover of shrub layer, summed per species	0–167 (34)	%
	Canopy cover	Visual estimation of cover of shrub and tree layers, summed per species	0–285 (117)	%
	Shade casting	Species-specific shade-casting ability (SCA) based on (Verheyen et al., 2012), community-level mean index weighted by tree and shrub species-specific canopy cover	1–5 (3.0)	/
	Canopy openness	The average percentage of gap fraction across the angle 5–70°	0–0.75 (0.08)	%
Soil	pH	pH-H_2O in topsoil (0–10 cm)	3.8–7.7 (5.2)	/
	Mg	Magnesium in topsoil	12–1482 (245)	mg/kg
	Ca	Calcium in topsoil	43–11,212 (1806)	mg/kg
	K	Potassium in topsoil	33–539 (158)	mg/kg
	Olsen P	Olsen phosphorus in topsoil	1.3–113.1 (15)	mg/kg
	Nitrogen	Total concentration of nitrogen (N) in topsoil	0.12–1.39 (0.41)	%
	Soil C:N	C/N ratio in topsoil	9.5–25.2 (15.5)	/
	Clay	Percentage clay in subsoil (10–20 cm)	0.5–70.2 (21.4)	%
	Sand	Percentage sand in subsoil	1.7–94.2 (42.8)	%

of the analysis based on May temperature with an identical analysis based on temperatures of both the months May and June (period of trait sampling), excluding plots with a high amount of missing data in June. This additional analysis resulted in very similar findings (Appendix S11).

2.3.2 | Light

We quantified light availability using measurements of forest structure, collected at the same time as the trait measurement, as a proxy. *Tree* and *shrub cover* were determined as the sum of the visually estimated ground cover per species in the tree (higher than 7 m) and shrub (1–7 m) layer, respectively. We used the *shade casting ability* (SCA) *index* to account for light transmission differences due to overstorey species identity. The SCA index is a species-specific, expert-based index that varies from one to five, indicating low to high shade casting ability of the canopy species (Verheyen et al., 2012). The SCA of the canopy (the shrub and tree layer combined) was calculated as a cover-weighted mean of SCA scores (see Govaert et al., 2020). Lastly, *canopy openness* was calculated as the average percentage of gap fraction across the full azimuth angle 360° range and the zenith angle range 5–70° (May and July 2018, leaf-on conditions) with a

RIEGL VZ-400 terrestrial laser scanner (LiDAR). More technical details on the terrestrial laser scanning procedure and data processing can be found in Meeussen et al. (2020).

2.3.3 | Soil

In all 225 plots, we collected five soil samples at the same time as the trait measurements and pooled these into a single topsoil aggregate sample (0–10 cm depth) for chemical analyses (*pH* and *soil element concentration*) and into one single subsoil aggregate sample (10–20 cm depth) for texture analysis (% *silt*, *clay* and *sand*) by sieving and sedimentation with a Robinson–Köhn pipette (ISO 11277, 2009). The topsoil samples were dried to constant weight at 40°C for 48 h, ground and sieved over a 2 mm mesh and pH-H_2O was determined by shaking a 1:5 ratio soil/H_2O mixture for 5 min at 300 rpm and measuring with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172 BNWP, Thermo Scientific Orion, USA. Subsamples were combusted at 1200°C. Total N and C concentration was measured by a thermal conductivity detector in a CNS elemental analyser (vario Macro Cube, Elementar, Germany). Bioavailable *phosphorus* (P) which is available for plants within one growing season (Gilbert et al., 2009) was measured by extraction

in $NaHCO_3$ (P_{Olsen}; according to ISO 11263 (1994)) and colorimetric measurement according to the malachite green procedure (Lajtha et al., 1999). Total *calcium* (*Ca*), *potassium* (*K*) and *magnesium* (*Mg*) were measured by atomic absorption spectrophotometry (AA240FS, Fast Sequential AAS) after complete destruction of the soil samples with $HClO_4$ (65%), HNO_3 (70%) and H_2SO_4 (98%) in teflon bombs for 4 h at 150°C.

2.4 | Data analysis

Five out of 225 plots did not contain any herbaceous plant species and were omitted from the analyses. Canopy openness, Olsen-P, K, Mg, Ca and soil N were log-transformed to symmetrize skewed distributions and decrease the influence of potential outliers.

Then we calculated the *community-weighted mean* (*CWM*), that is, mean of the trait values of the sampled species per plot, weighted by the percentage ground cover (Equation 1).

$$\overline{x}_w = \frac{\sum_{i=1}^{N} w_i x_i}{\sum_{i=1}^{N} w_i} \tag{1}$$

where $\overline{x}_w$ is the weighted mean (CWM), N is the number of species, w_i is the weight for observation i and x_i is the trait value of observation i. This statistic was calculated in two ways: (1) excluding intraspecific trait variation—based on a *fixed* mean value per species over all the plots across the entire study area, hereafter called CWM_{fixed}; (2) including intraspecific trait variation—based on a single *specific* trait value per species per plot, hereafter called $CWM_{specific}$. CWM of plant height and SLA were log-transformed prior to the statistical analyses to have a normal error distribution in the linear models. Additionally, the change in CWM due to the inclusion of ITV ($CWM_{intravar}$) was calculated as $CWM_{specific} - CWM_{fixed}$.

To synthesize the environmental variation captured by the predictor variables included in this study, we first performed a principal component analysis (PCA) for each set of variables grouped by temperature ($N=6$ variables), light ($N=5$ variables) or soil ($N=9$ variables) (Table 1). We used the first two axes per group as representative predictor variables in the subsequent analysis. The first two PC axes explained 73.7%, 80.1% and 60.6% of the temperature, light and soil variables respectively (Figure 1). Pearson correlations between the PC axes were below 0.7 (Appendix S4) and variation inflation factors (VIF) were lower than 3, indicating no multicollinearity issues. The greatest Pearson correlation was between the first axes of the soil and temperature PCA (−0.54). We then fitted linear mixed-effects models with the first and second PCA axes of each of the three groups as fixed effects. The response variables were the CWM of the five plant traits, namely plant height, SLA, plant C, plant N and plant C:N (CWM_{fixed}, $CWM_{specific}$, $CWM_{intravar}$, (Table 2). We accounted for the hierarchical structure of the data by selecting the optimal random structure from the beyond optimal model (BOM), which is the full model including all fixed effects, following Zuur et al. (2009). Based on Akaike information criterion (AIC), we
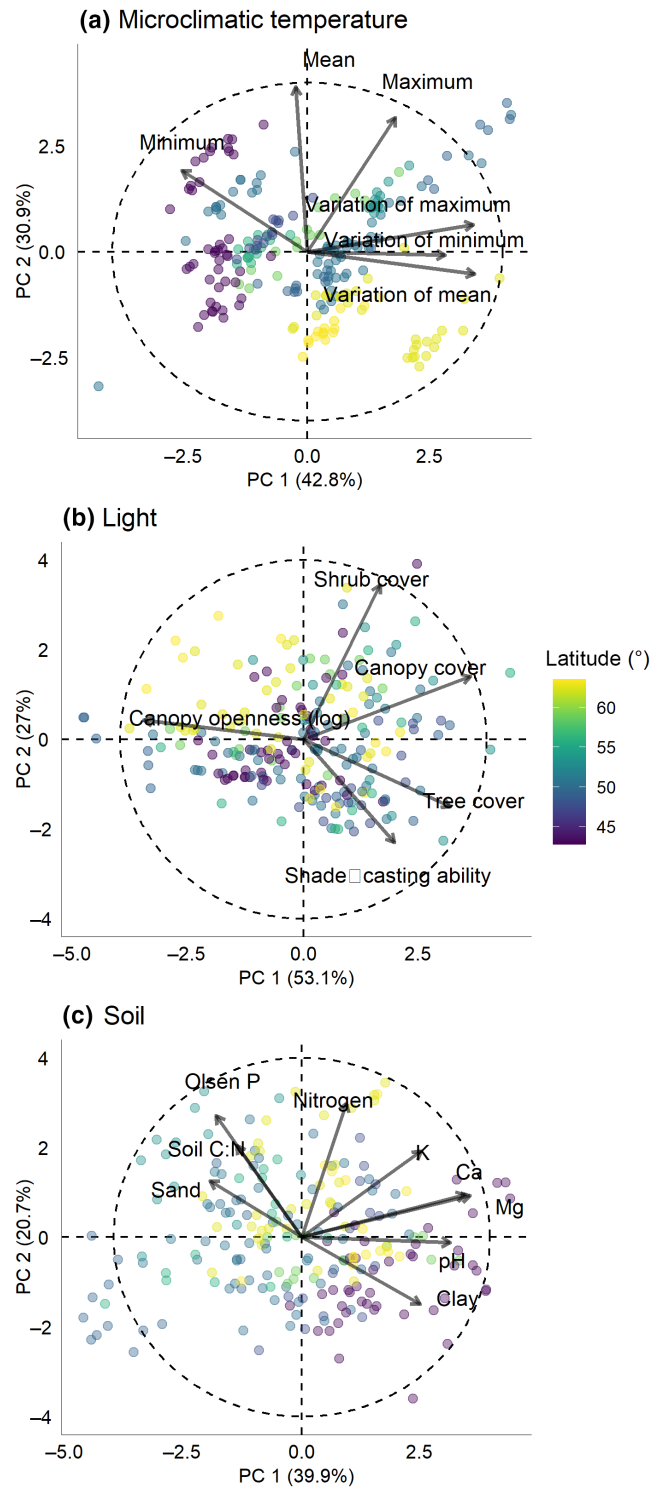
FIGURE 1 Principal components analysis plots for (a) air temperature, (b) light availability and (c) soil properties in temperate forest understoreys across Europe. The arrows indicate the relative loadings of each explanatory variable (scaled to a circle with radius 4 to improve visibility).

compared the following random structures (as random intercept term): 'region', 'forest structure', 'transect ID', 'transect ID' nested within 'region', 'forest structure' nested within 'region', 'transect ID' nested within 'forest structure' and a model without random effect.

TABLE 2 Overview of the five response variables used to explore trait–micro-environment relationships of forest herbs from Norway to Italy. Values indicate the range (mean). C: carbon, N: nitrogen, CWM: community-weighted mean, fixed: based on a single mean per species (turnover), specific: accounted for intraspecific variation in plant traits (turnover+ITV), intravar: CWM$_{specific}$ – CWM$_{fixed}$: changes in CWM solely due to ITV. Plant height and SLA were log-transformed before the analysis.

Trait (unit)	CWM$_{fixed}$	CWM$_{specific}$	CWM$_{intravar}$
Ln(Plant height [cm])	1.74–4.31 (3.28)	1.67–4.65 (3.32)	−1.15–0.73 (−0.024)
Ln(SLA [mm^2/mg])	1.96–4.44 (3.39)	1.70–4.89 (3.39)	−0.98–0.58 (−0.035)
Plant C (mg/g)	396–466 (437)	381–480 (437)	−36.14–20.96 (0.17)
Plant N (mg/g)	14–41.7 (23.8)	10.4–54.5 (24)	−12.92–18.53 (0.15)
Plant C:N ratio	11–33.1 (20.4)	7.6–43.3 (20.5)	−10.45–15.32 (0.05)

For all response variables, 'transect ID' was the best random structure to include, or the difference with the model having the random intercept 'transect ID' nested within 'forest structure' was less than 2 AIC. We finally used 'transect ID' as the random structure for every model, for the sake of uniformity.

First, we investigated how the separate environmental drivers (PC axes) influenced each response variable (CWM$_{fixed}$ and CWM$_{specific}$ of the 5 traits) by testing the significance of the linear relationship with the anova method in the package 'lmerTest' (Kuznetsova et al., 2017). We further explored potential interactions or non-linear responses of traits to the environment by plotting the model residuals against the design variables (region, altitude, management type and plot) and the environmental drivers (PC axes).

Next, to test our first hypothesis, we determined the relative contribution of each environmental driver by performing a variation partitioning among the three groups of explanatory variables (light, temperature and soil) according to Legendre and Legendre (2012). We constructed linear mixed-effects models containing each time the two PC axes of one, two or three groups of fixed-effect variables, while keeping the random structure the same (i.e. 'transect ID') across models, and determined the proportion of variation explained by the fixed factors (marginal R^2; R^2_m) calculated according to Nakagawa and Schielzeth (2013). Subsequently, we calculated the amount of variation explained by the unique and shared contribution of the light, temperature and soil variables, and expressed this relative to the total amount of variation explained by the fixed factors in the global model (containing all three groups of explanatory variables).

Finally, to test our second hypothesis, we assessed the amount of variation in traits explained by species turnover, intraspecific trait variation or covariation based on the sum of squares of the linear mixed-effect models following the method described in Lepš et al. (2011). The covariation is calculated as Total variation—species turnover—ITV. When the covariation is close to zero, turnover and ITV act on the trait CWM independently. When the covariation is positive, they act synergistically, for example, ITV increases in plant C are largest when the community exists of species generally high in C concentrations. When the covariation is negative they act antagonistically.

A protocol for data exploration and model evaluation was carefully followed (Zuur et al., 2010). All statistical analyses were performed in R using the packages 'lme4' (Bates et al., 2015), 'lmerTest' (Kuznetsova et al., 2017), 'FactoMineR' (Lê et al., 2008) and 'eulerr' (Larsson, 2018).

3 | RESULTS

3.1 | Trait–environment relationships

3.1.1 | Environmental variation

The first axis of the PCA on the temperature data was primarily positively correlated to temperature variation, and negatively to minimum temperature and is referred to as TempVar$_{PC}$ hereafter. The second PC axis for temperature increased with the mean and maximum temperature (referred to as MeanTemp$_{PC}$) (Figure 1a). The first PC of the light availability variables, correlated positively with canopy cover and tree cover, and negatively with canopy openness (referred to as CanopyCover$_{PC}$), the second PC axis was positively related to shrub cover and negatively to the shade-casting ability of the overstorey (referred to as ShrubCover$_{PC}$; Figure 1b). The first axis on the PCA of the soil variables correlated positively with Mg, Ca and pH (referred to as SoilpH$_{PC}$); the second soil PC axis increased with soil nitrogen content and Olsen-P (referred to as SoilNP$_{PC}$; Figure 1c).

3.1.2 | Temperature

TempVar$_{PC}$ was an important predictor of CWM plant traits. With increasing temperature variation and decreasing minimum temperatures, plant height and plant C:N increased, while plant N decreased (Figure 3, Appendix S5). These trait–environment relationships were similar whether ITV was considered or not, but the effect was more pronounced when ITV was included. This was often the case in the different trait–environment relationships, so when not explicitly noted, effects were qualitatively similar with and without considering ITV. TempVar$_{PC}$ did not correlate linearly with any of the other plant trait variables, but it did moderately correlate positively with latitude (Pearson $r = 0.53$, $p < 0.001$; Figure 1). Pearson r values were higher and p values were lower for Temp$_{PC1}$ when comparing Temp$_{PC1}$ and

latitude as predictors of the trait statistics (Appendix S6). SLA decreased with increasing $MeanTemp_{PC}$, but only when intraspecific trait variation was accounted for (Figure 3).

3.1.3 | Light conditions

In plots with high light availability (low values for $CanopyCover_{PC}$), CWM of plant C and C:N were greater, and SLA and plant N were lower than in more shaded plots (Figure 3, Appendix S5). However, the patterns of plant height, plant N and C:N only emerged when intraspecific trait variation was accounted for. CWM_{fixed} of plant height and plant C increased with higher $ShrubCover_{PC}$ values (Figure 3). However, when accounting for intraspecific trait variation, this relationship disappeared.

3.1.4 | Soil conditions

When $SoilpH_{PC}$ values were high, CWM of $SLA_{specific}$, plant C and plant N were lower, while $CWM_{specific}$ plant C:N were higher (Figure 3). When $SoilNP_{PC}$ values were high, CWM of SLA and CWM_{fixed} plant N increased, and CWM_{fixed} of plant C:N decreased (Figure 3).

3.2 | Relative importance of the environmental variables

Variation partitioning showed that the three different environmental factors indeed influenced the CWM of plant traits (H1) (Figure 2). When not accounting for intraspecific trait variation (CWM_{fixed}), soil and temperature were the most important predictors of functional traits. More specifically, temperature alone contributed to a large proportion of the explained variation of the CWM_{fixed} of plant height (42.7%) and plant C:N ratio (69.2%). Soil properties also contributed a large proportion of the explained variation of the CWM_{fixed} of SLA (41%), plant C (46.11%) and plant N (61.1%). Contrary to H1, light availability was not the most important predictor of CWM_{fixed} plant height and SLA.

However, when considering intraspecific trait variation ($CWM_{specific}$), light availability became more important (Figure 2). Both the unique fraction of light availability and the shared fraction with temperature gained importance in their relative contribution to the proportion of explained variation. As a consequence, light contributed the most in the proportion of explained variation of $CWM_{specific}$ of plant C (34.6%) and plant N (38.2%). The shared fraction of temperature and light was the most important predictor of $CWM_{specific}$ SLA (41.5%). $CWM_{specific}$ of plant height was best explained by both temperature (39.1%) and the shared fraction of temperature and light (34.8%).

3.3 | Intraspecific trait variation

The R^2_m values of the 15 models (CWM_{fixed}, $CWM_{specific}$ and $CWM_{intravar}$ for the five functional traits) ranged from 0.09 to 0.25. As hypothesized (H2), $CWM_{specific}$ (including intraspecific variation) was better explained by our plot-level micro-environmental data than CWM_{fixed}, for SLA (R^2_m of 0.10 vs. 0.20), plant N (R^2_m of 0.09 vs. 0.17) and plant C:N (R^2_m of 0.12 vs. 0.22), and only marginally for plant height (R^2_m of 0.22 vs. 0.23) and plant C (R^2_m of 0.23 vs. 0.24). Especially light, but also the microclimate air temperature caused intraspecific changes in functional traits (Figure 2). For SLA, plant N and plant C:N ratio, intraspecific trait variability explained most of the variation in CWM (Figures 2 and 4, Appendix S8). Analyses of the residuals of the 15 models showed the absence of interactions and non-linear responses: the residuals of the 15 models showed no significant correlation with the design variables (region, elevation, forest type and distance to the forest edge) nor with the predictor variables (PC axes related to light, temperature and soil) (analysis available in Appendix S12).

4 | DISCUSSION

Here we studied the relationship between functional traits of understorey herb communities in European temperate forests and air temperature, light availability and soil properties. The three environmental factors were important predictors of the different functional traits of the herb community, but the relative importance was different for every trait. Variation in plant height was for instance mostly driven by air temperature, while plant N was mostly explained by soil properties. These trait–environment relationships were often stronger for the community-weighted mean including intraspecific variation (compared to community-weighted means with a fixed trait value per species).

FIGURE 2 The relative contribution of locally measured air temperature, soil characteristics and light availability as predictors of the functional trait signature of understorey herb communities in European temperate forests. The ellipses in the Venn–Euler diagrams show the independent share of explained variation (marginal R^2; R^2_m) for each variable group (i.e. air temperature, light availability and soil properties), in addition to the shared amount of explained variation (intersection of ellipses), as determined by variation partitioning. The sizes of the ellipses are, per subfigure, scaled according to the relative share of R^2_m. The R^2 values below are given below each subfigure for the full models; R^2_m describes the variation explained by fixed factors only, whereas the conditional R^2_c is the variation explained by the fixed and random factors together. Note that negative R^2_m are set to zero, thus the sum of proportions might not be equal to 100. When the R^2_m value of the full model was smaller than 0.1, the subfigure was drawn more transparent. CWM stands for community-weighted means. Fixed: based on a single mean per species (turnover), specific: accounted for intraspecific variation in plant traits (turnover + ITV), intravar: $CWM_{specific} - CWM_{fixed}$: changes in CWM solely due to ITV.
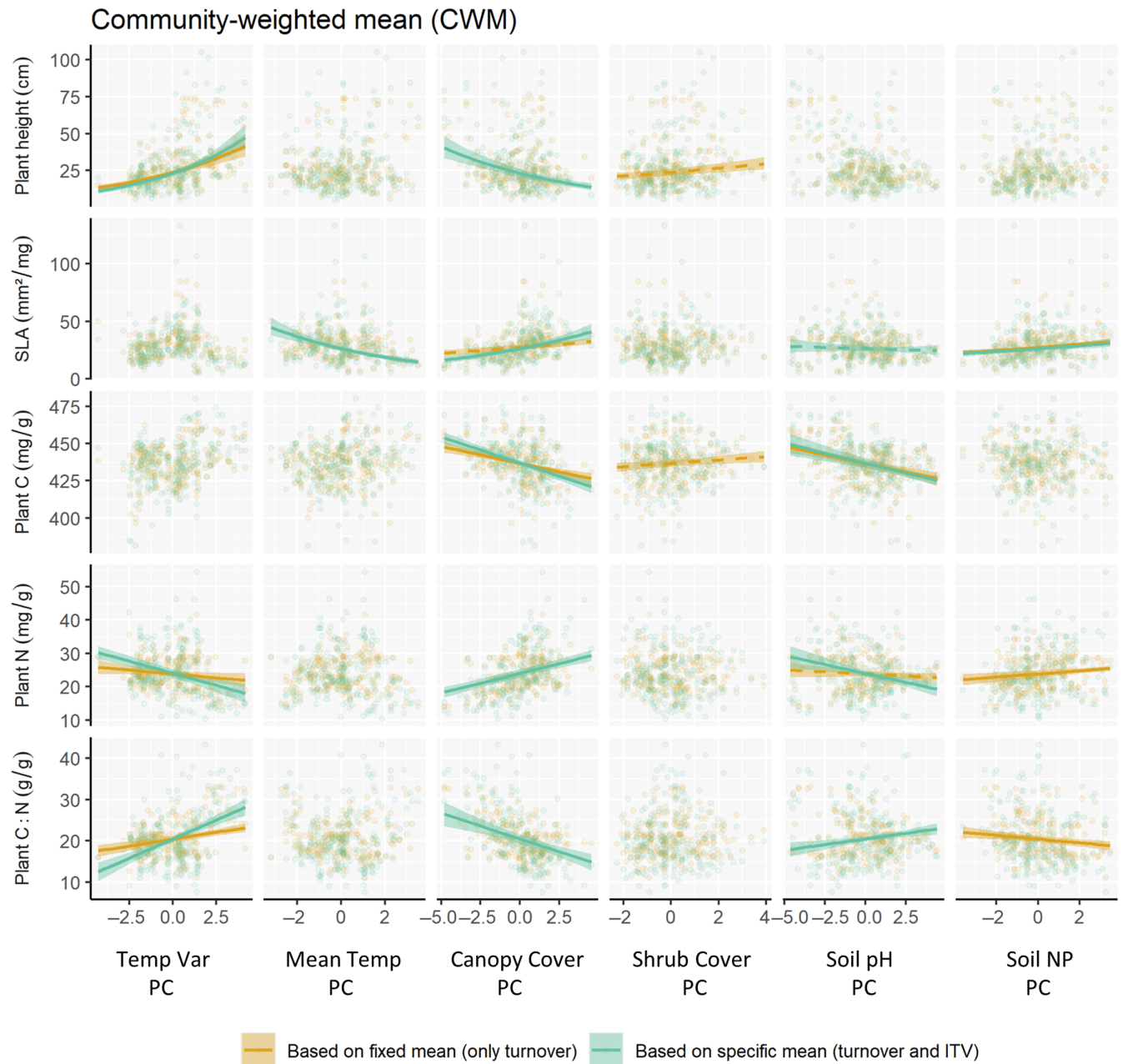
Community-weighted mean (CWM)
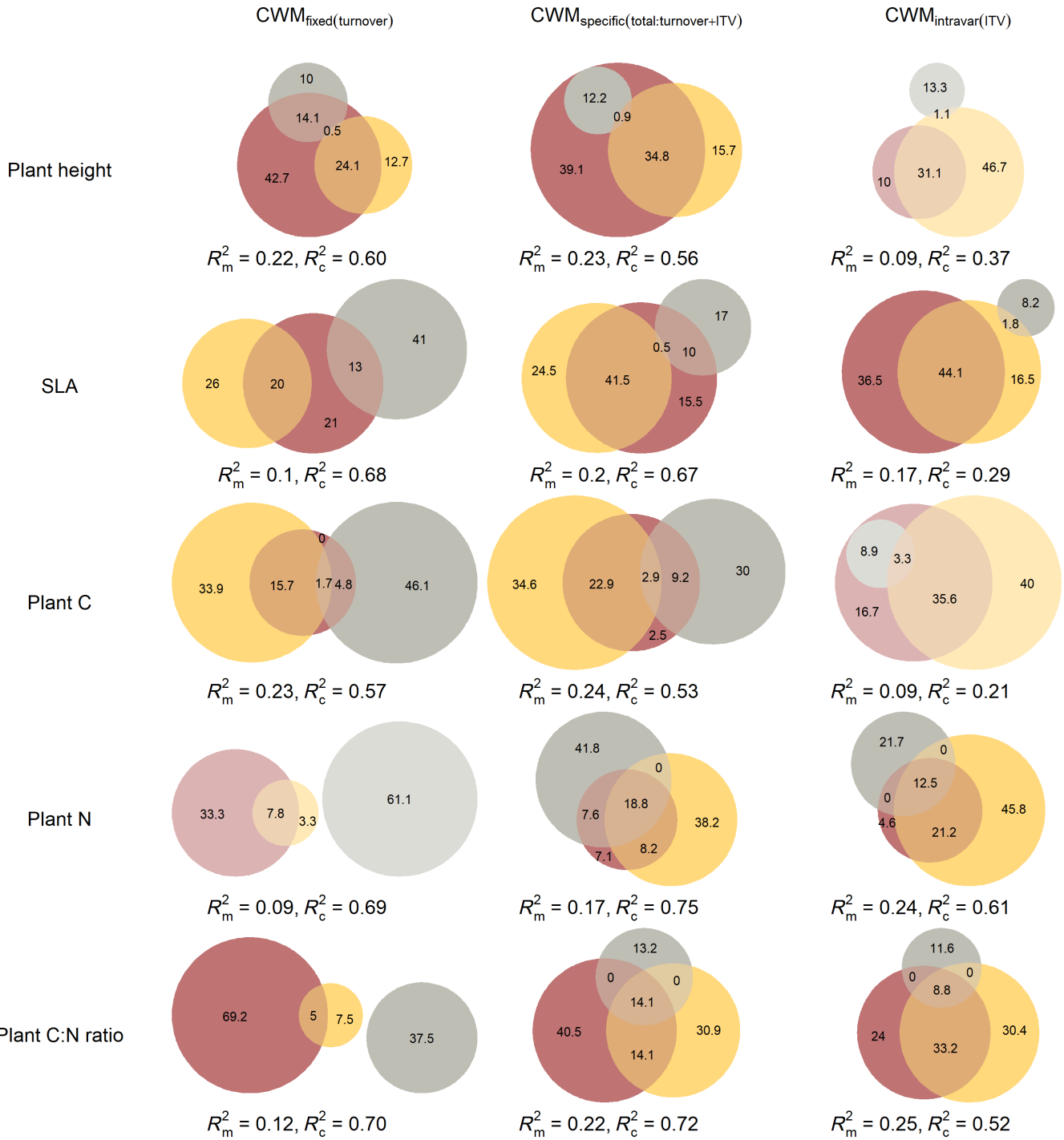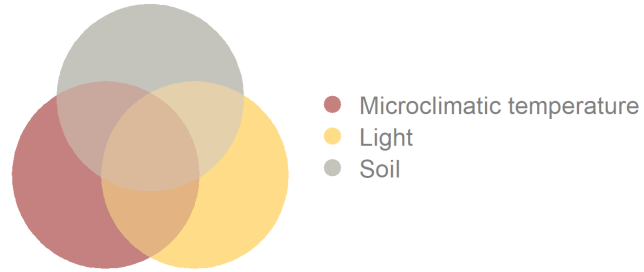
FIGURE 3 Relationship between the six PC axes summarizing variation in the environmental predictors (air temperature, light and soil properties) and the community-weighted means of five functional traits of herbaceous understorey species. Predictions with 95% confidence intervals from the linear mixed-effect models between trait and single environmental driver. Note that on each panel, two different models are plotted: one accounting for intraspecific variation (orange) and one without (green), only when significant in the full model (Appendix S5). Significance in the full model is indicated by solid ($p < 0.01$) and dashed ($p < 0.05$) lines. The mean of plant height, leaf area and SLA were log-transformed for the analysis and back-transformed for visualization purposes. ITV stands for intraspecific trait variation. See Figure 1 for more details on the meanings of the PCs.

4.1 | Intraspecific trait variation plays a crucial role

We showed that the trait–environment relationship models had a higher explanatory power for fine scale trait data (including intraspecific trait variation), compared to a coarser scale of trait measurements (excluding intraspecific variation) with the same environmental data. This supports our second hypothesis that intraspecific trait variation contributes significantly to community-level trait variation of forest herbs (Figures 3 and 4, Appendix S8), confirming previous research (Siefert et al., 2015). Intraspecific trait variation is typically high for SLA, leaf chemical traits and plant height (Burton et al., 2017; Siefert et al., 2014, 2015; Thomas et al., 2020). Our results on SLA and chemical traits are consistent with literature, but not for plant height. Forest herbs showed a much greater variation in plant stature among species than within species (Figure 4). The community's response of traits

FIGURE 4 Decomposition of total variability (sum of squares, see Appendix S8) in functional traits. The black horizontal line shows the total variability, while the orange and green parts of the column give the part of variation due to species turnover and intraspecific variability respectively (values standardized by total variation in $CWM_{specific}$). The space between the black line and the bar shows the covariation effect. When the sum of ITV and turnover approaches or surpasses 100%, the covariation is positive or negative respectively. When the sum of ITV and turnover is 100%, species turnover and ITV affect the CWM independently.
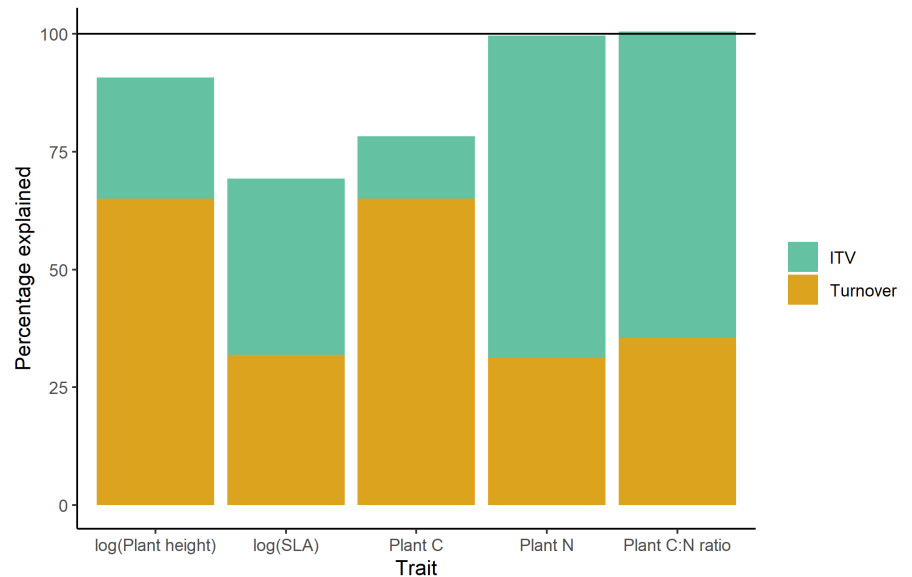
to light could mainly be attributed to intraspecific variation in traits, while responses to temperature and soil nitrogen–phosphorus status were primarily driven by species turnover (Appendix S5). Note that a large proportion of variation in light conditions could be linked to drivers inherent to small spatial scales (among transects with different management intensity and with distance to the forest edge; Appendix S9), while the greatest range in mean temperature was related to the largest scales (among regions and to a smaller extent among elevations; Appendix S9). Naturally, species turnover and thus interspecific trait variation plays a larger role at large scales, while intraspecific trait variation is more important at smaller scales (Siefert et al., 2014). Noteworthy, trait–environment relationships were often (at least once per trait) only significant when intraspecific trait variation was accounted for. Studies using trait data based on one mean value per species, for example, extracted from trait data bases such as LEDA (Kleyer et al., 2008) and BiolFlor (Kühn et al., 2004), might thus underestimate the relationships between plant functional traits and environmental gradients.

4.2 | Air temperature, light and soil conditions are important predictors of plant traits

Locally measured air temperature, soil characteristics and light availability were all important predictors of the functional trait signature of understorey herb communities in European temperate forests, in line with our first hypothesis. Previous studies have found that climate and soil are both important predictors of plant functional traits (Pakeman et al., 2009; Vanneste et al., 2019). However, our results indicate that temperature is most important for plant height and plant C:N ratio, while local light availability and soil properties are more important to explain SLA, plant C and plant N of forest herbs.

Notably, the relative importance of light availability increased strongly when intraspecific trait variation was considered in our

models. Even considering some genetic influence on intraspecific trait variation, this finding indicates that forest herbs are likely to be especially phenotypically plastic towards light conditions. Light conditions in a forest understorey are inherently variable. On the forest floor, the light conditions change daily and seasonally, because of sun position and leaf-out phenology of deciduous trees and shrubs (Hutchison & Matt, 1977; Lei et al., 1997). Many understorey plant species are adapted to tolerate shade, but can respond rapidly to short-term light pulses caused by sunflecks (Chazdon, 1998; Tinya & Odor, 2016). In addition, light conditions can change abruptly by disturbances such as treefalls, tree breakage and harvesting activities. Because plants are immobile organisms, acclimation to these changing light conditions is thus a useful adaptation strategy (Neufeld & Young, 2014). Furthermore, the shared variation between light and temperature was also more important when including intraspecific trait variation. In forests, light and temperature are both related to elevated radiative inputs (Abd Latif & Blackburn, 2010). Therefore, the responses of plant traits to either light or temperature alone might not always be predictable in observational studies because both variables are often correlated. However, due to our study set-up, that involved four different, independent sources of variation in temperature, of which some are strongly correlated with light availability (forest structure and, to some extent, edge-core transect) and some are not (elevation and latitude), we were able to partly disentangle the separate and shared effects of temperature and light.

4.3 | Temperature–trait relationships

When mean and maximum air temperatures were high (High $MeanTemp_{PC}$ values), community SLA values were low and varied less within a plot. This observation is in line with the response of understorey plants to mean annual (macroclimate) temperature found by Maes et al. (2020), but not of grasslands species in the Alps (Rosbakh et al., 2015) and tundra species (Bjorkman et al., 2018).

Community SLA is also lower with higher mean annual temperatures (Moles et al., 2014), because plants grow smaller and have thicker leaves. Likely this is an adaptation to reduce transpiration as a response to drought. Likewise, Poorter et al. (2009) explain low SLA at low temperature as an adaptation to freezing stress, by having a high density of cells per leaf surface. This suggest that the response of SLA to temperature is non-linear, and that a more conservative resource strategy (low SLA) is suitable for both extreme low and high temperatures. This trend could be related to water balance, because little water is available or accessible in both extreme warm and cold conditions. In this context, to further our understanding on the effects of extreme events, explicitly testing non-linear trait responses and tipping points should be considered in further research. Surprisingly, we did not detect any relationships between the other plant traits and mean or maximum temperature. In general, plants are taller in warmer conditions (Blondeel, Perring, Depauw, et al., 2020; Govaert, Vangansbeke, Blondeel, Steppe, et al., 2021; Kemppinen et al., 2021; Maes et al., 2020, but see De Frenne et al., 2011). This, however, was not confirmed by our analyses, possibly because other temperature metrics play a more significant role on the trait community. We here considered May (and May + June in Appendix S11) air microclimate temperatures, but the community functional composition might be shaped by a myriad of microclimatic conditions such as the number of freezing days, thermal sums or the maximum spring temperature (Körner & Hiltbrunner, 2018). More research is necessary to determine which microclimatic temperature metrics have the most significant impact on the investigated traits.

Air temperature variability was negatively correlated with minimum temperature (high TempVar$_{PC}$ values), consistent with recent literature (Kermavnar & Kutnar, 2020; von Oppen et al., 2021). Thus, the colder the minimum temperature, the higher the temperature variability within the month May 2018. This was likely due to colder locations having a less developed canopy in May, causing a larger daily variation in temperature. In these conditions, the forest herb community was taller, with lower concentrations of N and a higher C:N ratio. Note that there was no correlation between light availability and minimum temperature. These results contrast with the findings from other biomes like tundra, where plants get smaller towards harsher climatic conditions while the tundra community also becomes taller as climate is warming (Bjorkman et al., 2018). These opposite responses could possibly be linked to the fact that we only considered herbaceous species, while other studies also included woody species. Not only the share of woody species but also other factors can be confounded with the temperature statistics. For example, precipitation regimes could also explain the trend of taller herbaceous plants towards more variable temperature conditions. The most northern region, Norway, is characterized by high levels of precipitation due to the highly oceanic climate. Furthermore, northern latitudes are not necessarily harsh for the studied communities, because their main growing season is in June–July with long days of plenty of light, while in more southern regions the growing season is in May.

The increase in community height with decreasing temperature was primarily associated with changes in species composition (Figure 3), consistent with observations of Blondeel, Perring, Depauw, et al. (2020). In a study on understorey plants in Slovenia, Kermavnar and Kutnar (2020) detected a trend of less variation in plant height in more stressful conditions (high temperature variability and extreme minimum temperatures), implying an abiotic filter with selection of tall species.

4.4 | Light availability as a key resource

Light availability had, as expected, strong impacts on all five sampled herb traits. When there was plenty of light, and independently from air temperature conditions, the community tended to be taller owing to the asymmetric competition for light (DeMalach et al., 2016; Freckleton & Watkinson, 2001). In these bright conditions, community SLA was lower, because the plants need to invest less in leaf area to capture sufficient sunlight. Due to intraspecific responses to light availability, aboveground N and C concentrations were respectively lower and higher when there is high light availability, resulting in a greater C:N ratio. Nitrogen concentrations typically decrease in response to increasing light availability due to an indirect effect of plant tissue nutrient dilution, because plants grow faster while nutrient uptake remains nearly constant (Blondeel et al., 2019). Our results largely confirm previously reported responses of plant height (Blondeel, Perring, Depauw, et al., 2020; Govaert, Vangansbeke, Blondeel, Steppe, et al., 2021), SLA (Burton et al., 2017; Depauw et al., 2020), leaf nitrogen and C:N ratio (Blondeel et al., 2019; Sanczuk et al., 2021) of temperate forest herb communities and species to light.

Our results underpin the importance of light as a key resource for forest-floor herbs. Light availability drives plant understorey species richness (Govaert et al., 2020; Hofmeister et al., 2009), species composition (Blondeel, Perring, Depauw, et al., 2020; Govaert, Vangansbeke, Blondeel, De Lombaerde, et al., 2021), herb cover (Blondeel, Perring, Depauw, et al., 2020; Depauw et al., 2020) and also functional traits (Burton et al., 2017; Chelli et al., 2021).

4.5 | Soil pH and nitrogen–phosphorus status

Soil pH (SoilpH$_{PC}$) was a strong predictor of the community means of plant traits. In more acidic conditions (low pH), community SLA and plant N were high, but C:N ratio was low. This could be caused by high levels of nitrogen deposition, as observed in large parts of temperate Europe, resulting both in a high nitrogen availability, leading to high N and low C:N in plant tissue, and in soil acidification through depletion of base cations (De Schrijver et al., 2011). Another possible explanation of the strong link with soil pH is due to changes in species composition rather than intraspecific variation in these traits itself (patterns also significant without considering ITV, Figure 2). Indeed, soil pH is a strong predictor of species

occurrences, caused by the (in)tolerance of species to acid soils (Bruelheide & Udelhoven, 2005). In plots with low pH, and thus low concentration of Mg and Ca, the number of species is low (Govaert et al., 2020). Although these species-poorer communities can be higher in phylogenetic diversity, no significant relationship between the soil pH and the functional diversity was found (De Pauw et al., 2021).

On soils containing relatively high levels of nitrogen and phosphorus (high SoilNP$_{PC}$ values), the community was dominated by species having traits related to competitive ability and fast resource acquisition, such as high SLA and N, but low C:N ratio. The trends in SLA and N were caused by changes in species composition over soil gradients, and not by intraspecific variation (Figure 2). However, when four species of this study were analysed separately, the trend of high N and low C:N on soils rich in nitrogen and phosphorus also held for the grass *Deschampsia cespitosa* (Sanczuk et al., 2021). As atmospheric nitrogen deposition levels in many temperate forests remain high and surrounding croplands are fertilized year after year, nutrient-demanding species are favoured in European fragmented forests, resulting in biotic homogenization (Staude et al., 2020). These nutrient-acquisitive species are typically fast-growing, have thinner leaves with a shorter life span and lower C:N ratios (Grime, 2006a; Ordoñez et al., 2009; Zhang et al., 2020). In contrast, on nutrient-poor soils, abiotic stress is relatively high, and the community is dominated by species with traits related to resource conservation (such as *Deschampsia cespitosa*).

4.6 | Conclusions and future research

We here investigated for the first time how locally measured soil properties, light availability and microclimate temperature simultaneously affect five key functional traits of forest understoreys on a continental scale, including the effect of intra-specific variation. Note that we only included above-ground traits, while it is likely that below-ground traits also have a strong relationship with soil properties (Blonder et al., 2018). We also only focused on the community-weighted mean of the trait value and did not include measures of trait variation, that is, the heterogeneity of the traits within one community. Several mechanisms can explain these trait diversity patterns (Czortek et al., 2021). First, based on environmental filtering theory, species within communities are expected to be more functionally similar because of abiotic limitations (Weiher & Keddy, 1995). Typically, harsh environmental conditions such as low resource availability result in lower variation of traits, that is, functional trait convergence (Grime, 2006b). Second, interspecific competitive interactions are predicted to decrease functional similarity, as interspecific trait variation helps fill various available niches (limiting similarity theory; MacArthur & Levins, 1967). Studying trait variation along similar environmental gradients seems a promising future research avenue, but to study trait variation in a reliable way, it is recommended to sample approximately 10 individuals per species, to cover all species in the community and use nonparametric

bootstrapping to infer the moments of trait variation of communities (Maitner et al., 2021).

Overall and as expected, we found many significant trait–environment relationships for understorey communities. Soil properties, light availability and microclimate temperature were all important drivers of the functional signature of the community (Hypothesis 1). Contrary to our expectations, temperature appeared to be most important for plant height and plant C:N ratio, while local light availability and soil properties were more important to explain SLA, plant C and plant N of forest herbs. In sum, while some responses of the herb layer to micro-environmental drivers were caused by species turnover only, many responses were driven by trait variation within species (Hypothesis 2).

Because plant functional traits are indicators of ecosystem functioning, the consequences of anthropogenic factors on ecosystem functions might be underestimated if intraspecific trait variation is not considered. Trait–environment relationships were mainly as expected for soil conditions and light availability. Forest structure, which can be controlled by forest managers, thus emerges as an important determinant of the functional composition of forest understorey communities.

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SUPPORTING INFORMATION

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