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Research

The leaf economic and plant size spectra of European forest understory vegetation

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Forest understories play a vital role in ecosystem functioning and the provision of ecosystem services. However, the extent to which environmental conditions drive dominant ecological strategies in forest understories at the continental scale remains understudied. Here, we used ~29 500 forest vegetation plots sampled across Europe and classified into 25 forest types to explore the relative role of macroclimate, soil pH and tree canopy cover in driving abundance-weighted patterns in the leaf economic spectrum (LES) and plant size spectrum (PSS) of forest understories (shrub and herb layers). We calculated LES using specific leaf area (SLA) and leaf dry matter content (LDMC) and PSS using plant height and seed mass of vascular plant species found in the understories. We found that forest understories had more conservative leaf economics in areas with more extreme mean annual temperatures (mainly Fennoscandia and the Mediterranean Basin), more extreme soil pH and under more open canopies. Warm and summer-dry regions around the Mediterranean Basin and areas of Atlantic Europe also had taller understories with heavier seeds than continental temperate or boreal areas. Understories of broadleaved deciduous forests, such as *Fagus* forests on non-acid soils, or ravine forests, more commonly hosted species with acquisitive leaf economics. In contrast, some coniferous forests, such as *Pinus*, *Larix* and *Picea* mire forests, or *Pinus sylvestris* light taiga and sclerophyllous forests, more commonly hosted species with conservative leaf economics. Our findings highlight the importance of macroclimate and soil factors in driving trait variation of understory communities at the continental scale and the mediator effect of canopy cover on these relationships. We also provide the first maps and analyses of LES and PSS of forest understories across Europe and give evidence that the understories of European forest types are differently positioned along major axes of trait variation.

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Introduction

Determining the mechanisms driving plant community functions has been a central goal in vegetation ecology during the last decades (Ackerly and Cornwell 2007, Violle et al. 2007). These mechanisms have usually been investigated using plant functional traits, defined as any morphological, physical or phenological features of individuals that affect their fitness (Violle et al. 2007). Plant traits are known to provide deeper insights into ecosystem functioning than approaches based only on plant species identity (Díaz and Cabido 2001, McGill et al. 2006). As such, plant functional traits serve as indicators of different community assembly processes and have important implications for understanding global, regional and local plant species distributions.

Researchers have globally identified two main plant trait spectra at the species level that represent the trade-offs between resource economics and the size of plants and their organs (Wright et al. 2004, Moles et al. 2009, Adler et al. 2014, Reich 2014, Díaz et al. 2016). On the one hand, the leaf economic spectrum (LES) runs from species with an acquisitive resource-use strategy (i.e. rapid resource capture and a high relative growth rate) to those with a more conservative resource-use strategy (i.e. long-lived leaves and a low photosynthetic rate) (Wright et al. 2004, Reich 2014). On the other hand, the plant size spectrum (PSS) runs from shorter species with smaller organs to taller species with larger organs. In temperate zones, taller species tend to have larger canopies, larger leaves and a deeper and longer root system, which allow them greater access to light, water and soil nutrients (Cornelissen 1999, Poorter et al. 2005, Padilla and Pugnaire 2007, Díaz et al. 2016). However, the cost of maintaining non-photosynthetic support tissues increases with height (King 1990). Larger plants also tend to have heavier seeds and seed size is known to affect plant regeneration, for example, through seed production (Jakobsson and Eriksson 2000), seed survival in the soil (Thompson et al. 1993) or seed dispersal distance (Thomson et al. 2011).

Scaling up from individual plant species traits to communities has confirmed that half of the global trait variation at the community level also reflects the trade-offs in LES and PSS (Bruelheide et al. 2018). These community trade-offs are weakly associated with macroclimatic and coarse-grain soil conditions globally, although with differences across habitats, suggesting that trait combinations are mainly filtered by more regional- and local-scale processes (Bruelheide et al. 2018). Indeed, studies conducted at regional scales have found variables related to climate harshness (minimum/maximum temperature and precipitation) and seasonality (temperature and precipitation seasonality) to be the primary macro-filters acting on the functional trait structure of tree communities (Swenson and Weiser 2010, Shiono et al. 2015). Local soil properties, such as soil fertility or pH, are also important determinants of leaf, root and seed traits in tree species of temperate forests (Simpson et al. 2016). Therefore, assessing the extent to which climate and soil control the variation in key plant functional traits at large spatial scales can provide new insights for the interpretation of trait variation within plant communities.

In Europe, forests currently represent over 40% of the land surface (European Environment Agency 2016) and most of their species occur in the understory (i.e. in the space beneath the forest canopy and above the forest floor). From an ecological perspective, mature forest understories can be seen as highly selective environments adapted to stable environmental conditions where shade tolerance affects plants' ability to cope with other stressors (Verheyen et al. 2003, Su et al. 2019). Trait variation across European forest understories, like across their tree layers, is strongly shaped by macroclimate (Chelli et al. 2019, Vanneste et al. 2019, Maes et al. 2020) and soil nutrient availability at regional scales (Gilliam 2006, Hedwall and Brunet 2016, Chelli et al. 2019). Furthermore, tree canopy cover and structure can also partially buffer climate variability (Zellweger et al. 2020) and influence patterns of light availability (Dahlgren 2006), thus affecting understory traits related to resource acquisition and competition. Although some large-scale studies have examined trait–environment relationships either for the woody layer of forest communities (Swenson and Weiser 2010, Shiono et al. 2015, Simpson et al. 2016, Wieczynski et al. 2019) or across all vegetation layers (Bruelheide et al. 2018), no studies have assessed the combined effect of climate, soil conditions and tree canopy cover on trait variation of forest understories at the continental scale or examined how this variation differs from random expectation among forest types. Exploring these relationships and patterns is essential because understory species may respond differently to environmental fluctuations than species in the woody layer (Šímová et al. 2018) and play a vital role in ecosystem functioning (e.g. litter decomposition and nutrient cycling; Gilliam 2007) and the provision of ecosystem services (e.g. habitat provisioning, tree regeneration and pollination; Nilsson and Wardle 2005).

In this study, we used ~29 500 forest vegetation plots sampled across Europe and classified into 25 different forest types to address the relative role of macroclimatic and soil factors and tree canopy cover in driving abundance-weighted patterns in LES and PSS of forest understories. These two mostly independent principal functional trait spectra were computed from four plant functional traits: specific leaf area (SLA) and leaf dry matter content (LDMC) for LES and plant height and seed mass for PSS. Based on previous regional studies from European temperate and boreal forests (Perring et al. 2018, Chelli et al. 2019, Vanneste et al. 2019, Maes et al. 2020), we expected environmental harshness (i.e. more extreme temperatures and soil pH, increased climatic seasonality and reduced precipitation) to be associated with a more conservative resource-use strategy of forest understory plants, and to a lower variation in leaf resource-use strategies. We expected this because areas with harsher environmental conditions are often poorer in resources such as water or nutrients. Similarly, we expected denser canopy to favor more conservative understories due to limited light availability. Furthermore, we expected temperature and precipitation to be positively related and climatic seasonality negatively related to the size of forest understories and to greater variation in understory plant sizes because stronger abiotic constraints can limit the growth of plants and their organs. We also expected canopy openness to favor taller species with heavier seeds and promote greater variation of these traits in the understory because increased light availability reduces competition for this resource and allows species to grow taller and have a wide range of sizes. Nonetheless, we also expected tree canopy cover to mediate the effect of macroclimate and soil conditions on trait variation in the understory since abiotic constraints, particularly low temperatures and limited soil nutrient and water availability, can also limit the formation of dense canopies (Tang et al. 2019), and in turn, affect the function of the understory. Among forest types, we expected that those in more resource-limited environments, such as forests in mires, bogs or on acidic soils, would present more conservative understories. In contrast, those in more resource-rich and humid environments, such as ravine or riparian forests, would show more acquisitive understories (Wright et al. 2004, Reich 2014). We also expected thermophilous forests at southern latitudes to contain larger (i.e. taller species with heavier seeds) understories.

Specifically, we aimed at: 1) exploring geographical patterns in LES and PSS of forest understories across Europe; 2) determining the relative contribution of current macroclimatic factors, soil pH and tree canopy cover in explaining abundance-weighted patterns in LES and PSS of European forest understories, and; 3) assessing how understory communities of European forest types differ in their LES and PSS.

Material and methods

Vegetation data

We retrieved georeferenced vegetation-plot records from the European Vegetation Archive (EVA; Chytrý et al. 2016). This database contains more than 1.7 million vegetation plots sampled across Europe (see Supporting information for an overview of contributing databases). We selected plots with areas ranging between 100 and 1000 m^2, the most common sizes of forest plots in the database, and removed plots sampled before 1970. We also removed plots with the location uncertainty of coordinates larger than 10 km. However, we retained plots where this information was not available because some countries were represented only by such data.

We classified vegetation plots into different forest types according to the EUNIS classification of European habitats using the expert system EUNIS-ESy ver. 2020-06-08 (Chytrý et al. 2020) run in the JUICE 7.1 software (Tichý 2002). We then retained vegetation plots belonging to natural forest types and containing at least five vascular plant species (n = 123 682). To reduce the disproportionately high sampling density in some areas, we conducted, separately for each forest type, heterogeneity-constrained random (HCR) resampling (Lengyel et al. 2011) with the R package 'vegclust' (De Cáceres et al. 2010). The HCR resampling procedure maximizes the mean and minimizes the variance of the compositional dissimilarity between pairs of plots. To perform the HCR resampling, we initially assigned each vegetation plot to a geographical grid of 1° × 1° and calculated the median number of plots per grid cell. For those grid cells where the number of plots exceeded the median, we performed HCR by calculating the compositional dissimilarity between vegetation plots co-occurring in the same grid cell with the turnover component of the Sørensen's index (Baselga 2010) and running 1000 iterations. For those grid cells where the number of plots was lower than the median, we retained all plots. We then discarded forest types with less than 100 plots to guarantee an optimum representation of the vegetation in each forest type (Supporting information). The total final number of plots included in our study was 29 668 (see Supporting information for the spatial distribution of plots in the study area).

We standardized the species names according to The Plant List using the R package 'Taxonstand' (Cayuela et al. 2017). We discarded from subsequent analyses the species present in < 1% of the plots in all forest types where they had been recorded. We discarded these rare species because most of them had limited trait data availability in the databases and their effect on the calculation of community weighted means (CWM) and variances (CWV) was presumably negligible (below). For each plot, we obtained the relative abundance of all vascular plant species.

Plant functional traits

We obtained data on specific leaf area (SLA), leaf dry-matter content (LDMC), plant height and seed mass from the TRY database (<www.try-db.org/>; Kattge et al. 2020; accessed on July 2020) (see Supporting information for specific references). SLA and LDMC are related to LES, with leaves with high SLA and low LDMC being more acquisitive (i.e. cheap to build and returning a high photosynthetic revenue for a short time) and leaves with low SLA and high LDMC being more conservative (i.e. requiring a higher initial investment of biomass and yielding a low photosynthetic income over many years) (Wright et al. 2004, Moles et al. 2009, Reich 2014). Plant height and seed mass are positively related to PSS (Díaz et al. 2016, Bruelheide et al. 2018). These traits are amongst the most widely available in TRY (Kattge et al. 2020).

Pteridophytes do not produce seeds, but they can be an essential component of European forest understories, particularly in humid environments. To retain pteridophytes in our analysis, we used the lowest seed mass value found across all spermatophytes included in the study as the seed mass for all pteridophytes. We also repeated the analysis excluding all pteridophytes to test for the effect of this group of species on the results.

We also obtained TRY data on leaf area, leaf length, leaf N content, leaf C content and leaf P content. These traits, together with plant taxonomy (species, genus and family), were used to estimate missing trait values (Supporting information) for plant height, seed mass, SLA and LDMC using the Bayesian hierarchical matrix factorization (BHPMF) gap-filling method (Schrodt et al. 2015). Although leaf N and P contents are also commonly associated with LES (Wright et al. 2004, Reich 2014), we did not use these traits to quantify LES in our study because a large fraction of our species had no TRY data for these traits (Supporting information). Before performing BHPMF, we excluded TRY trait records with a distance > 4 standard deviations from the mean of species to avoid potential outlier effects (Díaz et al. 2016) and $\log_e$-transformed all trait variables. To assess the gap-filling quality, we used the prediction uncertainties provided by BHPMF for each imputation and removed all imputations with a coefficient of variation > 1 (Fazayeli et al. 2014, Bruelheide et al. 2018). For the taxa that were recorded at the genus level only, we calculated estimates of genus means. We removed 68 taxa out of the total of 2037 included in our dataset due to trait data incompleteness.

In this study, we defined forest understory as the layer of vegetation growing beneath the tree canopy and above the forest floor. We obtained the growth form of all taxa from TRY, BIEN (Maitner 2020) and specialized literature and removed all species classified as ‘trees’ from our list of understory taxa. We also removed tree seedlings in forest understories because they could not be distinguished from adult trees in our dataset. We also removed species considered ‘cryptic trees’ (i.e. usually with a shrubby form) in the Mediterranean region of Europe (Médail et al. 2019). As a result, we generated a list of forest understory taxa with 1802 species. We also repeated the analysis excluding all shrubs (irrespectively of their size) and lianas, independently and jointly and including as part of the understory ‘cryptic trees’, to explore the effect of these species groups on our results.

Environmental data

We obtained current climatic data for mean annual temperature (°C), temperature seasonality (standard deviation × 100), total annual precipitation (mm) and precipitation seasonality (coefficient of variation) at a resolution of 30 arc seconds from the WorldClim ver. 2.1 database (<www.worldclim.org>; Fick and Hijmans 2017). We also obtained the Global Aridity Index (hereafter ‘Aridity index’) at a resolution of 30 arc seconds from Trabucco and Zomer (2019). This variable reflects moisture availability for the potential growth of reference vegetation, excluding the impact of soil mediating water runoff events. Aridity index values increase towards more humid conditions and decrease with more arid conditions. Finally, we also obtained data for soil pH (at 15 cm depth) at a resolution of ~ 250 m (rescaled to 30 arc seconds) from the SoilGrids database (<https://soilgrids.org/>; Hengl et al. 2017).

To extract environmental data for each plot, we delimited a circular buffer with a fixed radius of 2.5 km around each plot and calculated the mean value of all cells within the buffer zone. The buffering approach smoothed potentially extreme values of environmental variables from point extractions and reduced biases derived from the inaccuracy in the coordinates.

Tree canopy cover

We derived the proportion of tree canopy cover in each plot using the Jennings–Fischer’s formula (Jennings et al. 2009, Fischer 2015), which combines the percentage cover of all trees in the tree layer into a single value that does not exceed 100%. We provide the code to implement the Jennings–Fischer’s formula in R in the Supporting information. Correlations among environmental variables and tree canopy cover can also be found in the Supporting information.

Statistical analyses

We performed principal component analysis (PCA) on SLA, LDMC, plant height and seed mass of plant species with Varimax rotation applied to the first two axes with centered and standardized data. The first principal component explained 38% of the variation and defined a gradient ranging from more acquisitive to conservative leaves (Supporting information). In contrast, the second principal component explained 30% of the variation and defined a gradient ranging from shorter understory plants with lighter seeds to taller understory plants with heavier seeds (Supporting information). We labeled the first and second factors as leaf economic spectrum (LES) and plant size spectrum (PSS), respectively.

For each plot, we calculated the community weighted mean (CWM; Garnier et al. 2004, Enquist et al. 2015) for both LES and PSS factors using the *functcomp* function in R package ‘FD’ (Laliberté and Legendre 2010). Furthermore, we also calculated the community weighted variance (CWV; Garnier et al. 2004, Enquist et al. 2015) with customization of the *functcomp* function in the same package. We then calculated the standardized effect size (SES) of CWM (CWM.ses) and CWV (CWV.ses) to assess how plot-level means and within-plot trait variances departed from random expectation. We obtained CWM.ses and CWV.ses by randomizing 999 times LES and PSS values across all species in our dataset. In each run, we maintained species abundances in the plots and shuffled trait values. We calculated SES values as (observed value – expected value)/standard deviation of the expected value. Standardized effect sizes of CWM.ses of LES and PSS < -1.96 indicate that forest understories are significantly more acquisitive and smaller than random, respectively. In contrast, standardized sizes of CWM.ses of LES and PSS > 1.96 indicate that forest understories are significantly more conservative and larger than random, respectively.

To map CWM.ses of LES and PSS of forest understory communities across Europe comprehensively, we created a grid of 1° × 1°. We reclassified all forest vegetation plots inside each grid cell as follows: −1 if the plot had significantly lower LES (i.e. more acquisitive species) and PSS (i.e. smaller species) than random, 0 if the plot had LES and PSS that did not differ from random and 1 if the plot had significantly higher LES (i.e. more conservative species) and PSS (i.e. larger species) than random. Then, we calculated the overall value of each grid cell as the average of all plots included in the cell. We mapped only grid cells with a minimum of five plots to reduce biases associated with very low sample sizes and, at the same time, maximize the representation of forest understories across the continent. The observed spatial patterns were robust despite differences in sampling intensity across the continent (Supporting information). We repeated this same approach to map CWV.ses of LES and PSS. In this case, we reclassified all forest vegetation plots inside each grid cell as follows: −1 if the plot had significantly lower variation in LES and PSS than random, 0 if the plot had a variation of LES and PSS that did not differ from random and 1 if the plot had a significantly higher variation in LES and PSS than random.

To test for the relative influence of environmental variables and tree canopy cover on plot-level CWM.ses and CWV.ses, we used boosted regression trees (BRTs; Elith et al. 2008) implemented in the R package 'dismo' (Hijmans et al. 2017). We used BRTs with Gaussian distribution rather than traditional regression because of the ability of BRTs to handle complex non-linear relationships and account for collinearity. We obtained the optimum number of regression trees using a 10-fold cross-validation procedure (Supporting information). We calculated pseudo-R^2 for each model based on the correlation between observed and predicted values. We obtained the contribution score (in %) of each environmental variable as a measure of its relative importance in BRTs models. We used partial dependence plots to visualize the shape of the relationships between response and predictor variables. Furthermore, we tested for spatial autocorrelation in the residuals of each model using Moran's I statistics for distance classes defined using Sturge's rule. Because we were interested in spatial autocorrelation at short spatial distances, we randomly selected 200 plots and calculated the spatial correlogram for all plots located within 2° (~225 km) of the target plot (Supporting information). In the main text, we focus on the results for CWM.ses, but we also refer to the results for CWV.ses in the Supporting information.

We additionally used structural equation models (SEMs; Grace 2006) to quantify the causal relationships between environmental variables, tree canopy cover and LES and PSS of forest understories. We fitted SEMs using a piecewise approach to overcome the limitations of traditional variance–covariance SEMs (Lefcheck 2016). Because our data were spatially structured, we implemented SEMs using spatial simultaneous autoregressive (SAR; Kissling and Carl 2007) models, which supplement ordinary least squares (OLS) regressions with a spatial weight matrix that accounts for spatial autocorrelation in model residuals. Spatial weight matrices were defined by successively fitting a SAR model and testing several distances between neighbors, ranging from 100 to 200 km away from a given grid cell at intervals of 50 km. We finally selected the model that minimized spatial autocorrelation among the first distance classes and had the lowest Akaike information criterion (AIC) (i.e. 100 km; Supporting information). We included quadratic terms calculated as $[x - \text{mean}(x)]^2$ (Maureaud et al. 2019) for mean annual temperature and soil pH in our SEMs to account for the non-linear effect of these factors on our response variables (Supporting information). We also removed the Aridity index from this part of the analysis because it was highly correlated with annual precipitation (Supporting information) and notably increased the levels of multicollinearity in our models when measured using variance inflation factors (VIF > 2.5; Legendre and Legendre 2012). We report Nagelkerke pseudo-R-squared (R^2) of final SAR models as a measure of the coefficient of determination. We ran SEMs with the R package 'piecewiseSEM' (Lefcheck 2016) and SAR models with the R package 'spatialreg' (Bivand and Piras 2015).

We established significance at $\alpha < 0.05$ and performed all the analyses in R ver. 3.5.3 (<www.r-project.org>).

Results

Spatial patterns of LES and PSS of European forest understories

Forest understories consisting of species with a conservative resource use occurred mainly in Fennoscandia and the Mediterranean Basin (Fig. 1). In contrast, communities of species with more acquisitive leaves tended to occur in the temperate zone of Europe. Taller plants with heavier seeds tended to occur in the Mediterranean Basin, France and Ireland, while plants significantly shorter than under random expectation rarely dominated forest understories, occurring sporadically at latitudes higher than 50°N. The variance in LES tended to be higher in the central parts of Europe. In contrast, the variance in PSS was particularly high along the Atlantic seashore of France, England, Ireland, Spain and Portugal (Supporting information). Results considering only species occurrences in communities tended to maximize these patterns (Supporting information).

When we removed all shrubs and lianas from the analysis, the strong patterns towards more conservative forest understories in Fennoscandia and, to a lower extent, the Mediterranean Basin tended to dilute (Supporting information). We also found that forest understories with plants or seeds significantly larger than under random expectations decreased in several areas in the Mediterranean Basin, France and Ireland when we removed shrubs and

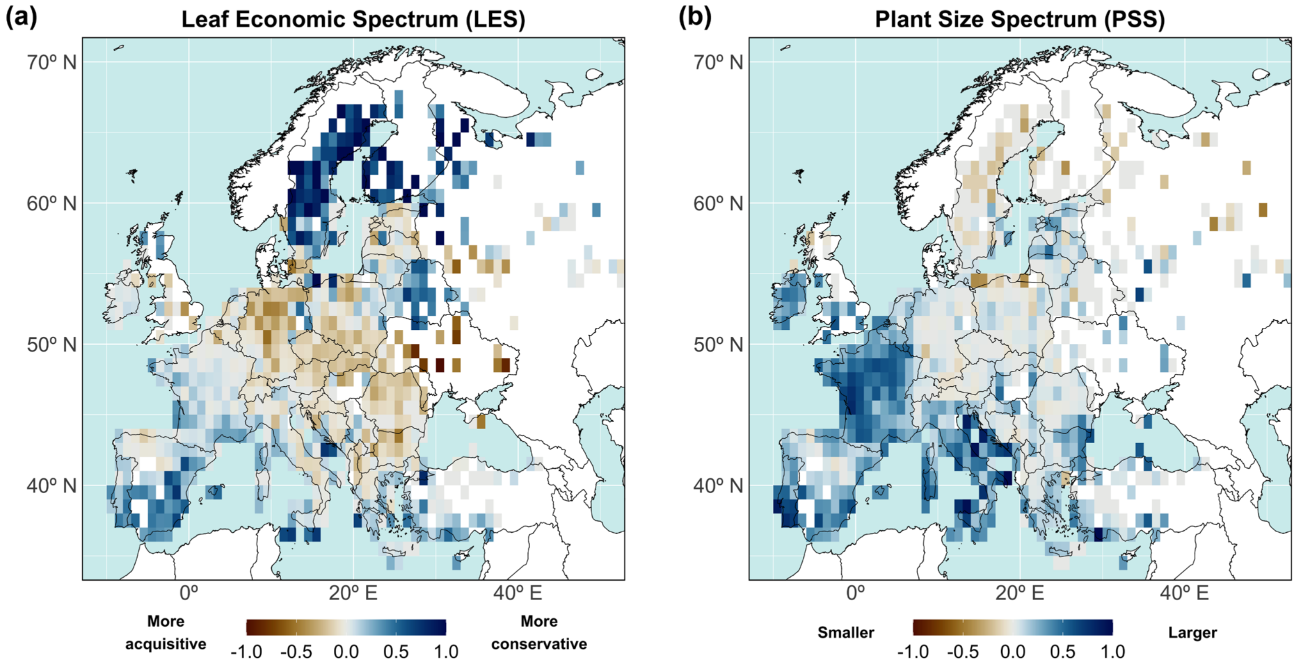

Figure 1. Spatial patterns in the (a) leaf economic spectrum (LES) and (b) plant size spectrum (PSS) of European forest understory vegetation calculated as CWM.ses. Values of −1 indicate that all vegetation plots in the given cell had (a) more acquisitive leaves or (b) smaller species than under random expectation. Values of 1 indicate that all vegetation plots in the given cell had (a) more conservative leaves or (b) larger species than under random expectation. Values of 0 indicate that plots in the given cell did not differ from the random expectation for LES and PSS. Only grid cells with at least five plots containing at least five species were mapped.

lianas. Results did not differ substantially when we removed ferns (Supporting information).

Environmental drivers of LES and PSS of European forest understories

The BRTs explained 36% and 43% of the variation in CWM.ses of LES and PSS, respectively. The most important variables for LES included mean annual temperature (34.8%), the proportion (%) of tree canopy cover (20.4%) and temperature seasonality (14.2%) (Fig. 2; Supporting information). LES showed a negative quadratic relationship with mean annual temperature and was negatively linearly related to the % of canopy cover and temperature seasonality. The most important variables for PSS included mean annual temperature (58.6%) and, to a lower extent, the % of canopy cover (12.2%) and precipitation seasonality (8.7%) (Fig. 2; Supporting information). PSS showed a positive linear relationship with mean annual temperature, although it tended to stabilize at high and low temperatures. PSS also showed a positive and negative linear relationship with the % of canopy cover and precipitation seasonality, respectively.

The BRT models also explained 18% and 28% of the variation in CWV.ses of LES and PSS, respectively. The variances in LES were best predicted by mean annual temperature and temperature and precipitation seasonality. In contrast, the variances in PSS were best predicted by mean annual temperature, temperature seasonality and the % of canopy cover (Supporting information).

Causal relationships

Our SEMs suggested multiple causal relationships between environmental variables, tree canopy cover and LES and PSS of European forest understories (Fig. 3; Supporting information). Mean annual temperature and soil pH had direct and indirect effects through tree canopy cover on LES and PSS. Precipitation seasonality also had direct and indirect effects on PSS, but only an indirect effect on LES. In contrast, temperature seasonality also had direct and indirect effects on LES but only an indirect effect on PSS. Annual precipitation only had a significant direct effect on PSS. More extreme mean annual temperatures and soil pH and higher climatic seasonality induced more open canopies, which in turn were associated with more conservative and smaller (i.e. shorter plants with lighter seeds) understories. Tree canopy cover and mean annual temperature had the strongest direct effects on LES, while mean annual temperature disproportionately had the strongest direct effect on PSS.

Characterization of European forest types based on LES and PSS of their understories

In general, forest types with a higher proportion of more conservative plant understories than under random expectation were coniferous or sclerophyllous (Fig. 4a, 5). Coniferous forests were mainly represented by *Pinus* and *Larix* mire forest, Mediterranean lowland to submontane *Pinus* forest, *Picea*

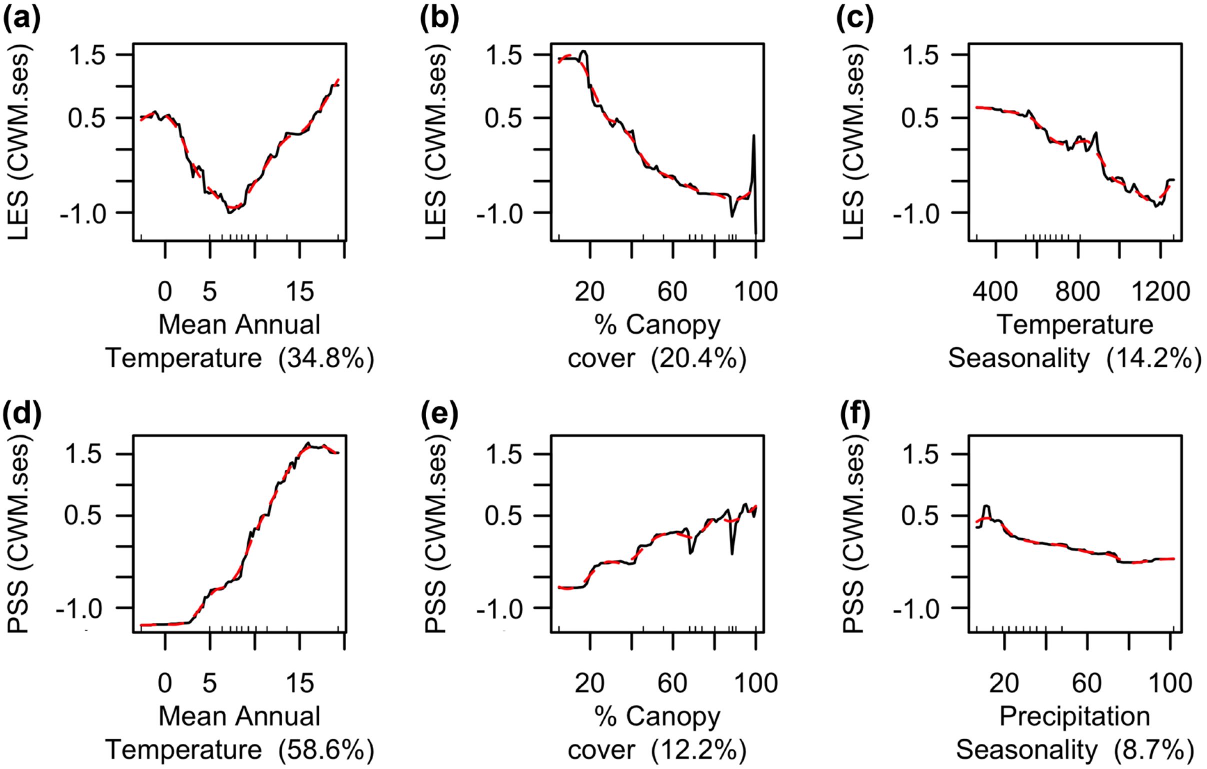

Figure 2. Effects of the three top-ranked predictor variables on CWM.ses of the (a–c) leaf economic spectrum (LES) and (d–f) plant size spectrum (PSS) of European forest understory vegetation (partial dependence plots). The integrated importance scores are shown in parentheses. LES defines a gradient ranging from more acquisitive to conservative leaves of forest understories. PSS defines a gradient ranging from smaller plants with lighter seeds to larger plants with heavier seeds in the understory. Smoothed versions of the fitted functions (red dashed curves) were calculated using local polynomial regression. Vertical ticks on the x-axis indicate deciles of the response variable. Note than the y-axis represents the fitted function and has a zero mean over the data distribution. The effects of lower-ranked predictors can be found in the Supporting information.

mire forest, *Pinus sylvestris* light taiga and temperate subalpine *Larix*, *Pinus cembra* and *Pinus uncinata* forests. Sclerophyllous forests were represented by Mediterranean evergreen *Quercus* forests. Deciduous forest types with the highest proportion of plots with a more conservative resource-use strategy than random included broadleaved mire forest on acid peat. In contrast, forest types with a more acquisitive resource-use strategy corresponded to ravine forest, *Fagus* forest on non-acid soil, *Carpinus* and *Quercus* mesic deciduous forest, dark taiga and temperate mountain *Picea* and *Abies* forests.

Forest types with a higher proportion of larger (i.e. taller and with heavier seeds) understory plants than under random expectation were generally deciduous. They included Mediterranean and Macaronesian riparian forest, ravine forest or temperate and submediterranean thermophilous deciduous forest (Fig. 4a, 5). Moreover, Mediterranean evergreen *Quercus* forests showed the highest proportion of larger plants in understory communities than under random expectation. We found no major patterns in the variance of LES among forest types. Still, we found a tendency of broadleaved deciduous and evergreen forests to be more variable in PSS than coniferous forests (Supporting information).

When we considered 'cryptic trees' as part of the understory, the proportion of Mediterranean and submediterranean forest plots with more conservative and taller understories slightly increased, but the overall observed patterns remained identical (Supporting information). The list of species with the highest contributions to LES and PSS of each forest type can be found in the Supporting information.

Discussion

Geographical patterns and drivers of LES and PSS in forest understories

Our study quantified the functional trait variation in the leaf economic (LES) and plant size (PSS) spectra of forest understories and related the observed patterns to the underlying effects of macroclimate, soil variables and tree canopy cover across Europe. Climate, particularly mean annual temperature, exerted the greatest effect on both LES and PSS. This result is in line with recent studies conducted in forest ecosystems at more regional scales (Perring et al. 2018, Chelli et al. 2019, Vanneste et al. 2019, Maes et al. 2020). It confirms the role of climate as a primary macro-filter shaping community mean plant traits and their variation at the continental scale. It also shows that the effect of climate and soil characteristics

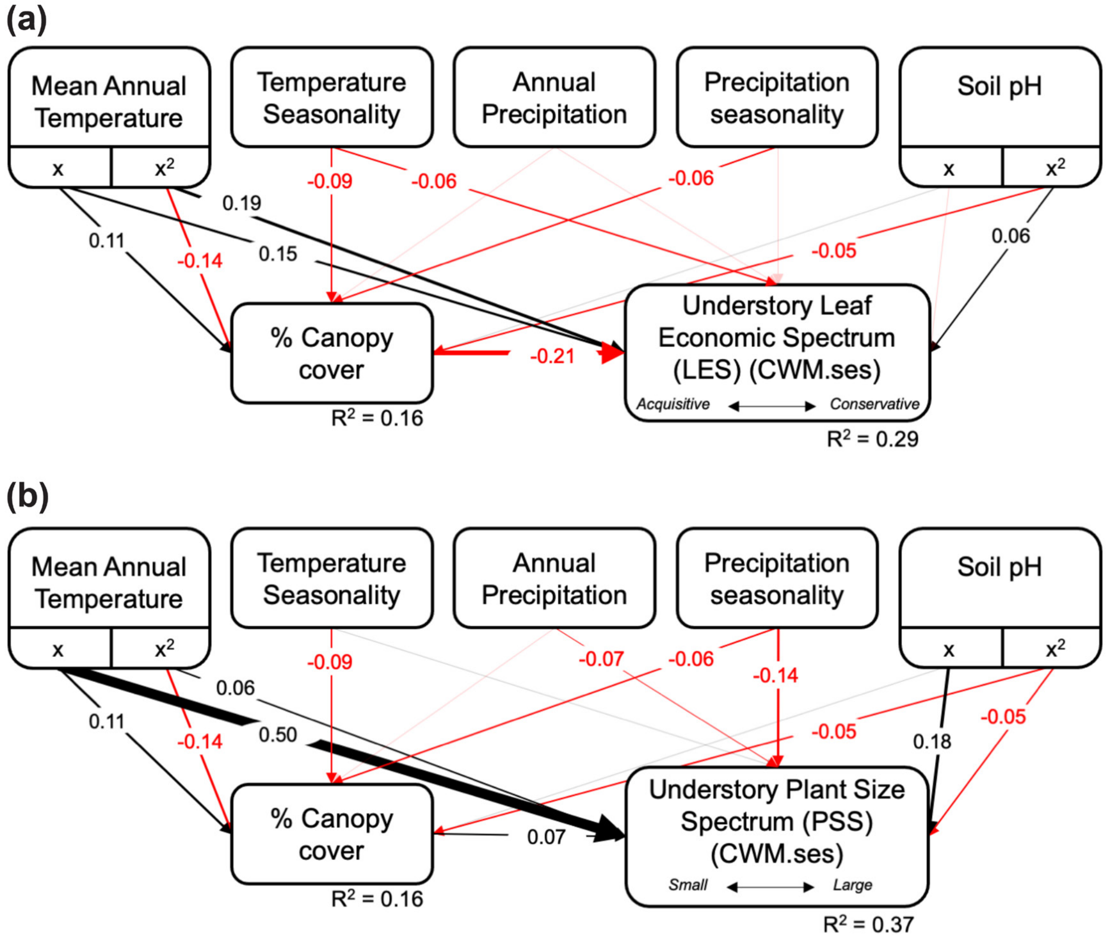

Figure 3. Structural equation models (SEMs) explaining CWM.ses of the (a) leaf economic spectrum (LES) and (b) plant size spectrum (PSS) of European forest understories. Black and red arrows represent positive and negative relationships, respectively. Path thickness reflects the strength of the relationship (i.e. values of standardized β coefficients). Arrows for non-significant paths ($p \geq 0.05$) are semi-transparent. Standardized β coefficients and Nagelkerke pseudo-R-squared values (R^2) for the dependent variables are also shown. 'x^2' indicates if the variable was transformed following: $[x - \text{mean}(x)]^2$. Total effects of predictor variables can be found in the Supporting information.

on trait variation of European forest understories is partly mediated by tree canopy cover.

Forest understories located in areas with the lowest and highest temperatures were characterized by more conservative leaf strategies (i.e. high LDMC and low SLA). These areas were mainly located in Fennoscandia and around the Mediterranean Basin, particularly in the eastern Iberian Peninsula, southern Italy and Anatolia. The prevailing environments of these regions are stressful for the plants: Fennoscandia due to low temperature and short growing season and the Mediterranean due to summer drought. Species in these stressed environments focus on resource conservation through thicker leaves with a longer life span (Westoby et al. 2002, Wright et al. 2004, Reich 2014). The observed tendency towards more conservative forest understories at colder northern latitudes was primarily driven by Ericaceae dwarf shrubs such as *Vaccinium* spp., *Calluna vulgaris* or *Ledum* spp. (Supporting information), which have adaptations to nutrient-poor habitats, including tough evergreen leaves or ericoid mycorrhiza (Cairney and Meharg 2003). In warmer and drier regions, producing conservative evergreen leaves is probably a water-conserving rather than nutrient-conserving strategy. Accordingly, species with the highest contributions to more conservative resource-use strategies of understories in warm and dry areas included several Mediterranean evergreen shrubs that thrive in dry conditions, such as *Cistus* spp., *Erica* spp. or *Rosmarinus* spp. In contrast, forest understories with more resource-acquisitive strategies occurred in temperate and more mesic areas of central and eastern Europe. They were dominated by species with more inexpensive, thinner and short-lived leaves that perform well in nutrient-rich environments (e.g. *Oxalis acetosella*, *Galium* spp. or *Lactuca muralis*; Supporting information).

Plant understories in warmer regions were not only more conservative but also composed of taller species with heavier seeds. Moreover, they showed a larger variation in plant sizes than those in more temperate regions (Moles et al. 2009, De Frenne et al. 2013, Vanneste et al. 2019). However, we found this pattern to be connected to the relatively high abundance of shrubs and lianas in the understories of these regions. These

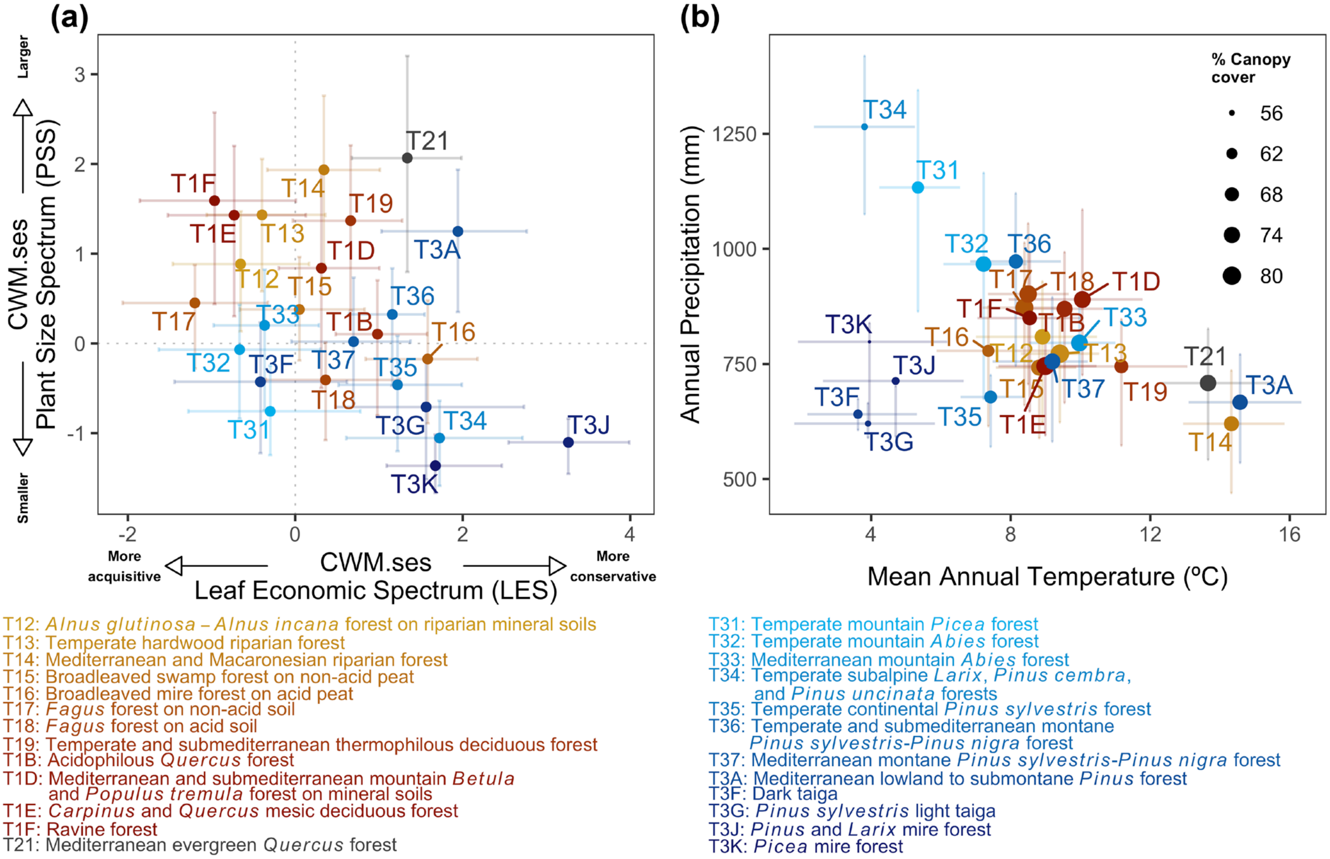

Figure 4. (a) Mean CWM.ses of the leaf economic spectrum (LES) and plant size spectrum (PSS) of forest understory communities in European forest types. We also show (b) the average position of European forest types along two major axes of climate variation ('mean annual temperature' and 'annual precipitation') for a better interpretation of (a). The size of the points in (b) reflects the average proportion (%) of tree canopy cover in each forest type. In both plots, bars represent the 25% and 75% quantiles. Broadleaved deciduous forests (T1) are colored with warm red colors, sclerophyllous forests (T2) are dark grey and coniferous forests (T3) are cold blue.

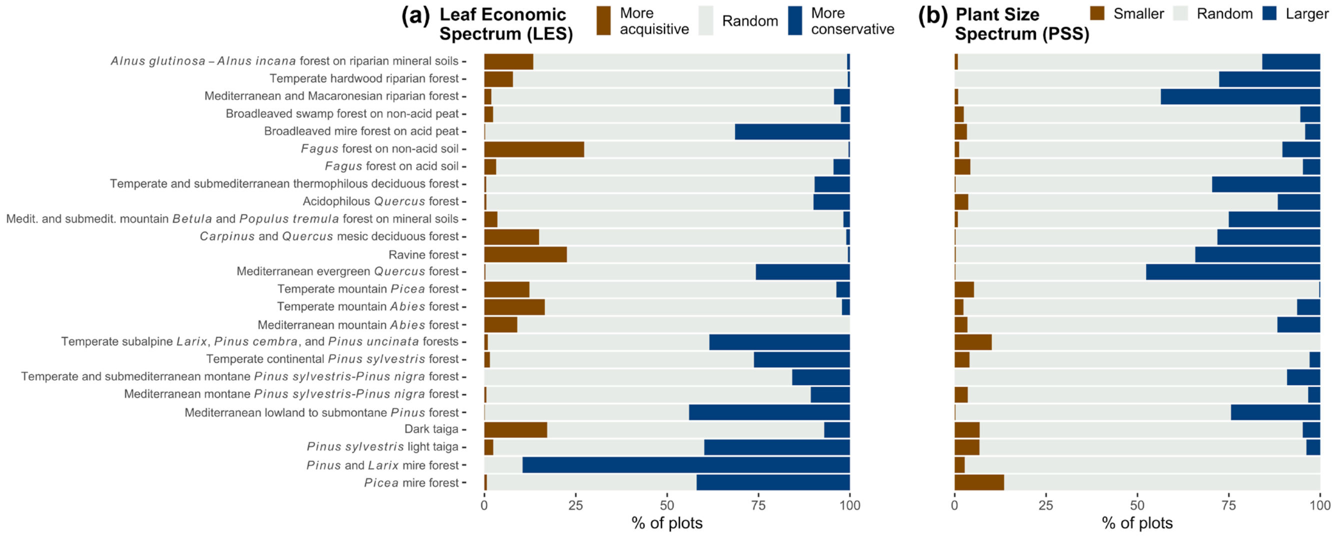

Figure 5. Proportion of plots from forest types with understories containing plant species with (a) more acquisitive (brown) and conservative (blue) leaf economics than under random expectation, and with (b) smaller (brown) and larger (blue) plant and seed sizes than under random expectation, based on CWM.ses of the leaf economic spectrum (LES) and plant size spectrum (PSS), respectively. The proportion of plots with random LES and PSS are shown in light grey.

groups of woody plants are generally taller and have a slower growth rate than herbaceous plants due to the large energy requirements for the formation of woody structures (Poorter and Evans 1998, Šímová et al. 2018). Nonetheless, future warming could lead to the expansion of forest understories with taller species and more resource-conservative leaves across the investigated climatic gradients (Maes et al. 2020). These changes could be influenced by changes in the composition and structure of the tree layer, as we found that climate variability also affected tree canopy cover across Europe.

Contrary to our expectations, we found denser forest canopies to be associated with more acquisitive understories. Ecological traits such as lower transpiration rates, thinner leaves or short leaf turnover time have been proposed to explain why plants respond to low levels of light with an increase in SLA (Givnish et al. 2004). Further, while the effect of tree canopy cover on understory trait variation was significant once macroclimatic factors and soil pH were held constant, it is possible that this effect indirectly reflects other unmeasured environmental variables, such as soil depth or water and nutrient availability and their interactions. In this regard, tree canopy cover mediated the effect of our environmental variables on trait variation in the understories so that harsher climate, particularly low temperatures and poorer soils induced more open canopies (Tang et al. 2019), which in turn favored more conservative understories. More open canopies were also associated with shorter understory species with lighter seeds, which could partially be explained by an indirect effect of limited soil nutrient availability on the understory through tree canopy cover. Nonetheless, using alternative measures of light transmission in forest understories, such as the leaf area index (LAI) or site-specific measurements of nutrient concentrations, could help refine these interpretations (Horvat et al. 2017).

Taller understory species also occurred in areas with a more regular precipitation distribution, confirming the importance of regular water availability in supporting understories with greater biomass (Moles et al. 2009). However, temperature seasonality showed no consistent direct effect on the size of forest understories, although it directly favored more acquisitive species in the understories. It is possible that areas under strong temperature seasonality – mainly in continental Europe – support faster growth to compensate for shorter growing seasons (Kikuzawa et al. 2013) and that forest understories in these areas do not suffer from the effect of extreme winter temperatures but benefit from the relatively warm summers.

Our findings also revealed that forests on soils with more extreme pH harbored more conservative understory species that can survive in low-nutrient environments (Westoby et al. 2002, Simpson et al. 2016). Several non-exclusive mechanisms could help explain this pattern. For example, limited nutrient acquisition in low pH soils could partially be explained by the release of toxic aluminum cations. In contrast, in soils with high pH, it is generally associated with limited availability of phosphorus, which is commonly bound to calcium (Tyler 2003). Furthermore, more extreme soil pH also induced greater canopy openness, which increased light availability and favored more conservative species in the understory. Nonetheless, the strength of the relationship between LES and soil pH could have been limited by the scale mismatch between the fine-scale effect of soil factors on plant distribution and the broad-scale soil pH data we used here (Bruelheide et al. 2018). It is also possible that other soil factors not included in our study and related to soil fertility, such as soil total N, soil C:N and soil total P, can influence the leaf economic spectrum of plant communities as they modulate leaf-level photosynthetic properties (Ordoñez et al. 2009, Weigel et al. 2019).

Our study relied on mean species trait values collated from global databases, which excludes the possibility of accounting for intraspecific trait variance. However, at extensive spatial scales, intraspecific trait variation is minimized and likely does not have a strong effect on community-level trait values (Albert et al. 2011). Furthermore, the traits used in our study are usually measured in standardized and optimum conditions. Therefore, our interpretations could be complemented by considering traits measured under fluctuating environmental conditions, such as traits accounting for seasonal adaptation, responses to biotic or abiotic stress, or perturbation, suitable for inferring ecological processes (Volaire et al. 2020). It should also be noted that SLA can be unrelated to the species' photosynthetic capacity and growth rates, especially in soils with low fertility, as shown in tropical forest understories (van der Sande et al. 2018, Modolo et al. 2021).

The unexplained variation in our models could be driven by other fine-scale environmental factors, which we did not measure in our study. Previous studies have reported that microclimate (Stark et al. 2017), abiotic heterogeneity (Vanneste et al. 2019) or biotic interactions (Moles et al. 2009) might have played an important role in structuring the functional composition and the diversity of understory plant communities across Europe. Human-induced disturbances, such as clearcutting or partial harvesting, are also likely to modify the abundance and composition of understory species by altering resource availability and heterogeneity (Su et al. 2019). Therefore, further research should evaluate the effects of multiple environmental drivers measured at various spatial scales to improve our predictions on how forest understories respond to the environment.

The LES and PSS of forest types in Europe

Our study is the first that examined how understory communities of European forest types differ from LES and PSS under a random expectation. In general, our results corroborate that more conservative leaf strategies prevail in forests at more resource-poor sites, whereas more acquisitive leaf strategies succeed at more productive (warm and moist) sites (Wright et al. 2004, Reich 2014). For example, several coniferous forest types, such as *Pinus* and *Larix* mire forests, Mediterranean lowland to submontane *Pinus* forests, *Pinus sylvestris* light taiga, *Picea* mire forests and broadleaved mire forest on acid peat included relatively high proportions of plots with more conservative understories than under random expectation. These forest types, which mainly occur under harsher environmental conditions at higher latitudes or in other resource-poor environments, frequently have thick litter layers that can reduce the light transmission and cause topsoil acidification, further inhibiting the nutrient-demanding vascular plants (Chen et al. 2018, Kumar et al. 2018). We also revealed that most of these forest types form relatively open canopies, which can, in turn, prevent the tree layer from acting as a thermal insulator and allow the growth of light-demanding species with low SLA (Dahlgren 2006). In contrast, other coniferous forest types, such as dark taiga or temperate mountain *Picea* and *Abies* forests, occur on more fertile soils and have a greater proportion of acquisitive understories. These forest types usually have shallow roots that allow them to outcompete *Pinus* forests in moist and fertile soils (Morén et al. 2000), while the latter tend to have deep roots that give them a competitive advantage on dry, acidic, nutrient-poor sites (Sutinen et al. 2005).

Some broadleaved deciduous forests, such as *Fagus* forests on non-acid soil, *Carpinus* and *Quercus* mesic deciduous forests, ravine forests or *Alnus* forests on riparian mineral soils, presented a relatively high fraction of plots with more acquisitive understories than under random expectation. *Carpinus* and *Fagus* form dense canopies and are considered superior competitors, eliminating other tree species at mesic and fertile sites (Ellenberg 1988, Backes and Leuschner 2000) and allowing shade-tolerant and nutrient-acquisitive species to thrive in their herb layer. Also, higher levels of soil moisture in ravine forests dominated by *Acer*, *Tilia* or *Ulmus* (Zhang et al. 2014, Su et al. 2019), coupled with a relatively fast decomposition of their nutrient-rich leaf litterfall (Hobbie et al. 2006, Zhang et al. 2014), or high soil pH (Simpson et al. 2016), could favor the growth of nutrient-demanding understory vegetation at these sites. Moreover, mild climatic conditions and the extended growing season in Mediterranean and Macaronesian riparian forests, Mediterranean evergreen *Quercus* forests or Mediterranean lowland to submontane *Pinus* forests, could help explain why these forest types present a higher fraction of taller understories with associated heavier seeds, as well as a vertically well-structured mixture of plants with different statures and growth forms (Moles et al. 2009, Vanneste et al. 2019). Altogether, our findings underscore the importance of examining trait variation between forest habitat types for inferring the underlying mechanisms responsible for shaping understory plant assemblages.

Conclusions

Using a large dataset of forest vegetation plots spanning from the Mediterranean to the boreal region in Europe, we have demonstrated that the variation in the leaf economic and plant size spectra of forest understories is largely influenced by current macroclimatic and soil conditions and tree canopy cover. In particular, forest understories in areas with more extreme temperatures and soil pH, and located under more open canopies, have a more conservative resource use. Also, forest understories in areas with higher temperatures and under denser canopies have understories composed of taller species with heavier seeds. Our findings suggest that future warming could lead to forest understories with taller species and more resource-conservative leaves in temperate and boreal Europe, both directly and indirectly through the structure of the tree layer. Furthermore, our study also shows that examining trait variation between different forest types with contrasting ecological requirements can help infer the effect of local environmental conditions in shaping forest understories. Future studies should consider the interactive effect of multiple environmental drivers on the main functional strategies of forest understories and how these changes impact the provision of ecosystem services.

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Conflicts of interest – The authors have no conflicts of interest to declare.

Author contributions

Josep Padullés Cubino: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Idoia Biurrun**: Resources (equal); Writing – review and editing (equal). **Gianmaria Bonari**: Resources (equal); Writing – review and editing (equal). **Tatiana Braslavskaya**: Resources (equal); Writing – review and editing (equal). **Xavier Font**: Resources (equal); Writing – review and editing (equal). **Ute Jandt**: Resources (equal); Writing – review and editing (equal). **Florian Jansen**: Resources (equal); Writing – review and editing (equal). **Valerijus Rašomavičius**: Resources (equal); Writing – review and editing (equal). **Željko Škvorc**: Resources (equal); Writing – review and editing (equal). **Wolfgang Willner**: Resources (equal); Writing – review and editing (equal). **Milan Chytrý**: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Project administration (lead); Resources (equal); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Transparent Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.05598>.

Data availability statement

We obtained all the data used in this study from the European Vegetation Archive (EVA) (project no. 82). Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mkkwh710j (Padullés Cubino et al. 2021).

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