



RESEARCH PAPER



Simulating functional diversity of European natural forests along climatic gradients

Kirsten Thonicke¹ | Maik Billing^{1,2} | Werner von Bloh¹ | Boris Sakschewski¹ |
Ülo Niinemets³ | Josep Peñuelas^{4,5} | J. Hans C. Cornelissen⁶ | Yusuke Onoda⁷ |
Peter van Bodegom⁸ | Michael E. Schaepman⁹ | Fabian D. Schneider¹⁰ | Ariane Walz²

¹Research Domain 1 “Earth System Analysis”, Potsdam Institute for Climate Impact Research (PIK), Member of the Leibniz Association, Potsdam, Germany

²Institute of Environmental Science and Geography, University of Potsdam, Potsdam-Golm, Germany

³Estonian University of Life Sciences, Tartu, Estonia

⁴National Research Council (CSIC), Global Ecology Unit at Center for Ecological Research and Forestry Applications (CREAF), Universitat Autònoma de Barcelona (UAB), Bellaterra, Catalonia, Spain

⁵Center for Ecological Research and Forestry Applications (CREAF), Bellaterra, Catalonia, Spain

⁶Systems Ecology, Department of Ecological Science, Vrije Universiteit, Amsterdam, the Netherlands

⁷Division of Environmental Science and Technology, Graduate School of Agriculture, Kyoto University, Kyoto, Japan

⁸Institute of Environmental Sciences, Department Environmental Biology, Leiden University, Leiden, the Netherlands

⁹Remote Sensing Laboratories, Dept. of Geography, University of Zurich, Zurich, Switzerland

¹⁰Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA, USA

Correspondence

Kirsten Thonicke, Research Domain 1 “Earth System Analysis”, Potsdam Institute for Climate Impact Research (PIK), Member of the Leibniz Association, Potsdam, Germany. Email: kirsten.thonicke@pik-potsdam.de

Abstract

Aim: We analyse how functional diversity (FD) varies across European natural forests to understand the effects of environmental and competitive filtering on plant trait distribution.

Location: Forest ecosystems in Europe from 11°W to 36°E and 29.5°N to 62°N.

Taxon: Pinaceae, Fagaceae and Betulaceae, Oleaceae, Tiliaceae, Aceraceae, Leguminosae (unspecific).

Methods: We adopted the existing Dynamic Global Vegetation Model Lund-Potsdam-Jena managed Land of flexible individual traits (LPJmL-FIT) for Europe by eliminating both bioclimatic limits of plant functional types (PFTs) and replacing prescribed values of functional traits for PFTs with emergent values under influence of environmental filtering and competition. We quantified functional richness (FR), functional divergence (FDv) and functional evenness (FE) in representative selected sites and at Pan-European scale resulting from simulated functional and structural trait combinations of individual trees. While FR quantifies the amount of occupied trait space, FDv and FE describe the distribution and abundance of trait combinations, respectively, in a multidimensional trait space.

Results: Lund-Potsdam-Jena managed Land of flexible individual traits reproduces spatial PFTs and local trait distributions and agrees well with observed productivity, biomass and tree height of European natural forests. The observed site-specific trait distributions and spatial gradients of traits of the leaf- and stem-resource economics spectra coincide with environmental filtering and the competition for light and water in environments with strong abiotic stress. Where deciduous and needle-leaved trees co-occur, for example, in boreal and mountainous forests, the potential niche space is wide (high FR), and extreme ends in the niche space are occupied (high FDv). We find high FDv in Mediterranean forests where drought increasingly limits tree growth, thus niche differentiation becomes more important. FDv decreases in temperate forests where a cold climate increasingly limits growth efficiency of broad-leaved summer green trees, thus reducing the importance of competitive exclusion. Highest FE

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Funding information

European Union's Horizon 2020 Research and Innovation Programme, Grant/Award Number: 641762; University of Zurich Research Priority Program on Global Change and Biodiversity

Handling Editor: Holger KrefT

was simulated in wet Atlantic and southern Europe which indicated relatively even niche occupation and thus high resource-use efficiency.

Main Conclusions: We find FD resulting from both environmental and competitive filtering. Pan-European FR, FDv and FE demonstrate the influence of climate gradients and intra- and inter-PFT competition. The indices underline a generally high FD of natural forests in Europe. Co-existence of functionally diverse trees across PFTs emerges from alternative (life-history) strategies, disturbance and tree demography.

KEYWORDS

boreal forest, co-existence, competitive filtering, dynamic global vegetation model, environmental filtering, flexible individual traits, mediterranean forest, natural forest, temperate forest

1 | INTRODUCTION

Functional diversity (FD) is a key control of the stability and adaptability of ecosystems under climate change (Yachi & Loreau, 1999). Abiotic conditions (e.g. climate, soil) as well as biotic processes (e.g. competition) determine plant community assembly (Kunstler et al., 2016; Ratcliffe et al., 2017; Ruiz-Benito et al., 2017), and thus the FD of communities (Cadotte, Carscadden, & Mirotchnick, 2011; Lavorel & Garnier, 2002a; Naeem, Duffy, & Zavaleta, 2012). Ecosystem FD has been measured based on the diversity of morphological and/or physiological plant traits (Villegger, Mason, & Mouillot, 2008), which are linked to plant productivity, transpiration or nutrient cycling, and thus to ecosystem functions (cf. Lavorel & Garnier, 2002a). For instance, specific leaf area (SLA) and leaf nitrogen content have been linked to plant productivity, and stem traits such as wood density (WD) to carbon storage and evapotranspiration (Funk et al., 2017) and, among others, determine species tolerance of environmental stresses (Hallik, Niinemets, & Wright, 2009) and control competitive interactions between individual plants (Kunstler et al., 2016).

Climatic conditions are the most important drivers of community assembly and generally constrain the relations between traits globally (Butler et al., 2017; Šimová et al., 2018). Gradients in trait expression, associated with climatic conditions, have been found at global scales (Díaz et al., 2016; Wright et al., 2017) and at the European scale by extrapolating site-specific plant trait data (Butler et al., 2017) and using forest inventories (Ruiz-Benito et al., 2017). Recent studies investigated a mix of globally important physiological traits (e.g. SLA, WD, seed mass and leaf nitrogen content) and morphological traits (including maximum plant height and basal area) (Ratcliffe et al., 2016; Ruiz-Benito et al., 2017), or separate the effects between those trait types (e.g. Madrigal-Gonzalez et al., 2016; Schneider et al., 2017). They advance our understanding of spatial pattern of plant traits at the landscape and continental scale.

Under given climate conditions, the distribution of multiple individual traits results from community assembly rules and opens a multi-dimensional trait space of functionally related traits (Chave et al., 2009; Díaz et al., 2016; Mason, Mouillot, Lee, & Wilson, 2005;

Wright et al., 2004). To quantify how environmental and competitive filtering influence niche complementarity, multidimensional indices of FD are required to quantify occupation and overlap of niches (Mason & de Bello, 2013). In addition, these indices should be scale independent and applicable at regional scale to investigate changes in FD along climatic gradients (Carmona, Bello, Mason, & Leps, 2016).

Many different indices have been used to describe the size of trait spaces, the distribution and the clustering of their trait combinations (e.g. Ratcliffe et al., 2016; Schneider et al., 2017). Villegger et al. (2008) suggested to describe these FD aspects using three independent indices: functional richness (FR), divergence (FDv) and evenness (FE). Whereas FR quantifies the amount of occupied trait space, FDv and FE describe the distribution and abundance of trait combinations in a multidimensional trait space (Mason et al., 2005; Villegger et al., 2008). Whereas FR describes the size of potentially available, functional space, in which niches can be occupied by plants, FDv quantifies the distribution of trait values, thus the degree of niche differentiation, likely the result from competitive exclusion (Garnier, Navas, & Grigulis, 2016; Mason et al., 2005). FE describes the regularity of trait distribution and points to resource-use efficiency within the occupied trait space. Lower FR could relate to lower capability of an ecosystem to buffer environmental stress, whereas lower FE and FDv could indicate reduced ecosystem resilience (Mason et al., 2005).

By dividing FD into richness, divergence and evenness, the mechanisms that link biodiversity to ecosystem functions and describe community assembly can be described (Mason, Bello, Mouillot, Pavoine, & Dray, 2013; Mason et al., 2005). Computing scale-independent FD indices from trait distributions (Carmona et al., 2016) allows investigating FD from community to meta-community scale and extrapolating them to the regional or continental scale. Huge efforts are under way to explore links among plant traits, vegetation composition and climate based on site data (Bruehlheide et al., 2018; Díaz et al., 2016; Wright et al., 2017). They are complemented by dynamic global vegetation models (DGVM) with flexible or adaptive individual traits (e.g. Langan, Higgins, & Scheiter, 2017; Sakschewski et al., 2015) which explore and map the mechanisms between FD and ecosystem functions from local to regional scales. The interplay



between flexible morphological and physiological traits within plant functional types (PFT, Lavorel et al., 2007; Prentice et al., 2007) in combination with the physiology and biogeochemistry of a DGVM allows analysing the effect of community assembly on ecosystem functions, for example, productivity and carbon storage, in forest ecosystems. Because these flexible-trait DGVMs vary plant traits for individual trees that belong to a specific PFT, inter-PFT as well as the intra-PFT trait diversity are captured which allows investigating effects of niche complementarity along climatic gradients.

The overall aim of this study is to investigate the interaction among climate, ecosystem functions and pattern of FD of forest ecosystems. Therefore, we adapted the DGVM Lund-Potsdam-Jena managed Land of flexible individual traits (LPJmL-FIT) to PFTs growing in strongly seasonal European climatic conditions, while the model previously has been successfully applied to tropical rainforests (Sakschewski et al., 2015). We break down the overall aim of the study into the following research questions:

1. What is the role of environmental and competitive filtering on trait distributions and productivity of Mediterranean, temperate and boreal natural forests?
2. How does FD emerge from climate and plant competition at the local and pan-European scale?
3. How does FD vary between and across European natural forests?

We focus on European natural forests ranging from broad-leaved evergreen vegetation in the Mediterranean basin, to temperate forests and to boreal forests in northern Europe. Here, natural forests are defined as potential natural forests whose compositions and ecosystem functions (see Geller et al., 2017; Hooper et al., 2005 for definition) results from climate and soil conditions. Forests and other wooded land are usually defined following the percentage of woody cover (FAO, 2018). However, we denote forests hereafter as vegetation with a significant amount of biomass ($>50 \text{ gC/m}^2$), at least 5% coverage of woody PFTs and a minimum mean tree height of 5 m.

To address these research questions, we check the validity of the adapted LPJmL-FIT model by assessing to what degree the model reconstructs observed (a) productivity and biomass, (b) trait distribution and (c) distribution of PFTs as a result of environmental and competitive filtering. We quantify for selected sites and on a Pan-European scale FR, FDv and FE of simulated physiological and morphological traits (cf. Schneider et al., 2017; Vileger et al., 2008). We expect FD to be relatively high in natural forests as was found in, for example, Schneider et al. (2017) and climatic stressors considered in LPJmL-FIT to be a strong environmental filter (Bernard-Verdier et al., 2012).

Our analysis of FD in natural forests can provide a reference state for restoring highly managed or degraded ecosystems and increase their diversity and stability in face of climate change (Mori, Lertzman, & Gustafsson, 2017). We focus here on the interaction of physiological and morphological plant traits with community assembly processes at the local and Pan-European scale to understand how FD emerges from those interactions.

2 | MATERIALS AND METHODS

We connected the leaf and stem economics approach as implemented in LPJmL-FIT (Sakschewski et al., 2015) with a phenology model (Forkel et al. (2014) to simulate potential natural vegetation in Europe under current climatic conditions. Herbaceous PFTs (C_3 and C_4 grasses) were simulated as in LPJmL (Schaphoff, von Bloh, et al., 2018). To allow for environmental and competitive filtering to take full effect within and across PFTs, we removed the bioclimatic limits that are used in most DGVMs to emulate biogeographic limitations of PFT occurrence (Schaphoff, von Bloh, et al., 2018; Sitch et al., 2008). Phenology, leaf-economics (LES) and stem-economics (SES) traits (cf. Chave et al., 2009; Wright et al., 2004) were assigned to each individual tree sapling at establishment allowing any trait combination (everything-is-everywhere approach, see Figure 1 for trait-selection algorithm) whose competitiveness in a given climate then determines its survival and growth. The implemented LES traits include Specific Leaf Area (SLA, leaf area per unit leaf mass, $\text{mm}^2 \text{ mg}^{-1}$), Leaf Longevity (LL, average life span of leaves, in months), leaf nitrogen content (N_{leaf} , leaf nitrogen content per leaf area, mg/g) and V_{cmax} (maximum carboxylation rate of the RUBISCO enzyme per leaf area at 25°C , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). While the LES traits influence vegetation productivity, the SES trait Wood density (WD, wood dry mass per unit of green volume, g/cm^3) is related to biomass and tree mortality (for more details, see Sakschewski et al., 2015). Physiology, growth and mortality of trees within the forest patch were as described in Sakschewski et al. (2015). Applying this simulation framework to current European climate, environmental and competitive filtering result in site-specific trait distributions, productivity, biomass and in tree height.

LPJmL-FIT combines flexible individual traits with gap dynamics and plant physiology, hydrology and biogeochemistry. Being structured into vertical leaf layers every two meters, trees compete for light and water as they grow in size. The trait combination of each tree determines its competitive strength under given climate conditions at a given site, where several plant strategies can co-exist and form diverse communities in forest ecosystems. The suitability of the trait combinations to the local climate conditions determines trees' competitiveness, and thus which tree strategy is dominant from wet to dry tropical conditions (Sakschewski et al., 2015). In general, the model approach of LPJmL-FIT allows all tree strategies to establish everywhere at any time ("everything is everywhere"). Trees that underperform due to trait combinations less suitable for local climate and/or competitive conditions have a relatively high mortality probability (see Sakschewski et al., 2015 and 2.1 below). Under stable climate conditions, establishment and mortality lead to an equilibrium of tree abundance and community composition in which only those trees occur whose functional traits are suited to the local environmental conditions (climate and soil).

In the following, we describe the adjustments required to apply the LPJmL-FIT model to European natural forests.

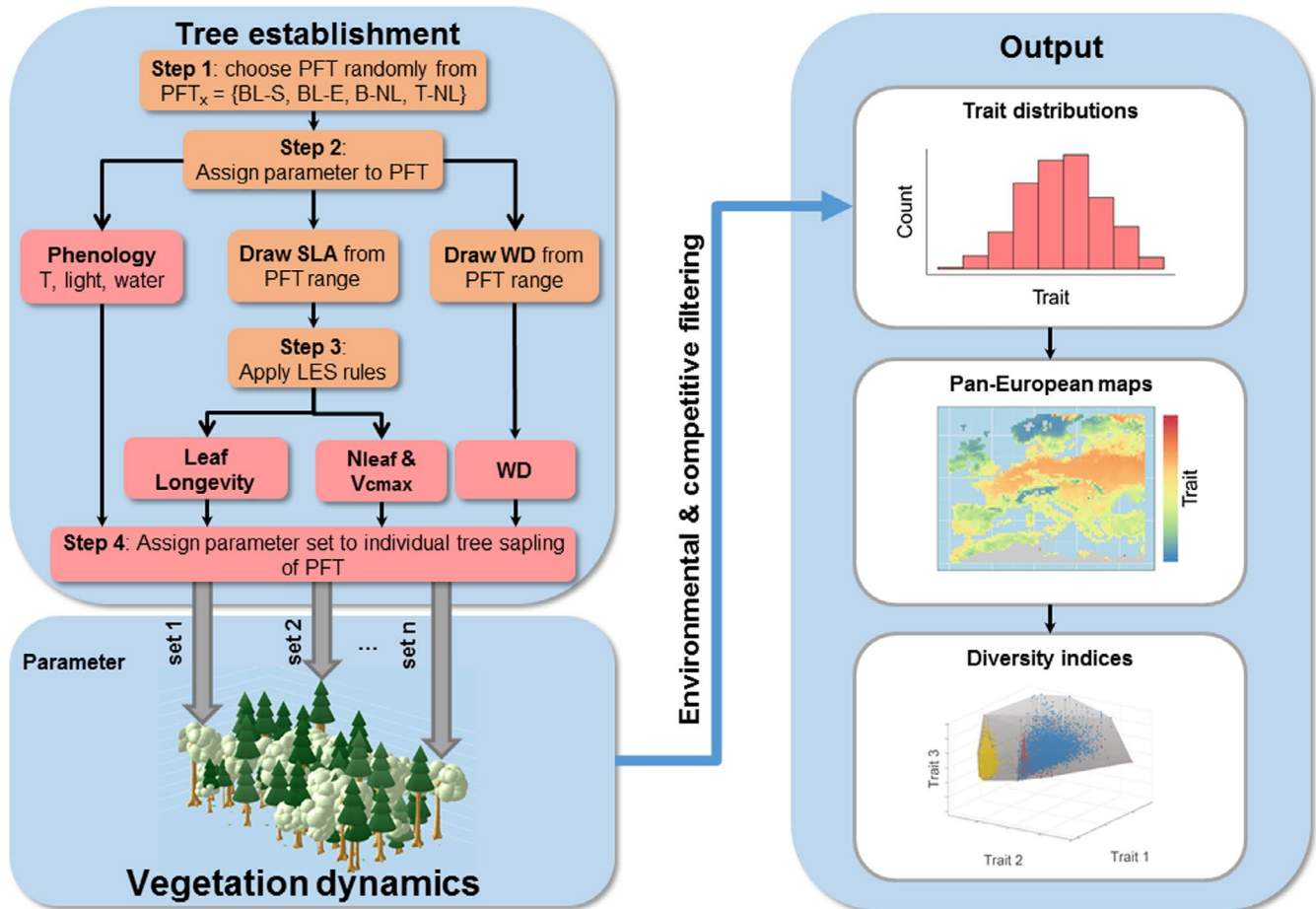


FIGURE 1 Conceptual scheme illustrating how flexible individual parameter are assigned to tree individuals belonging to a specific woody PFT (Steps 2 and 3), including LES (leaf-) and SES (stem economics) plant traits in LPJmL-FIT (SLA – Specific leaf area; WD – Wood density). Parameter sets consist of Phenology (temperature (T), light and water), LES and SES traits (WD) and are assigned to individual tree saplings at model initialization and gap opening (step 4). Climate, soil conditions (environmental filtering) and competition between individual trees within and across PFTs (competitive filtering) result in aggregated grid-cell trait distributions within patches (top-right figure in output panel). They are visualized as trait maps and are used to quantify diversity indices. PFT: BL-S – Broad-leaved summer green tree, BL-E – Broad-leaved evergreen tree, B-NL – Boreal needle-leaved evergreen tree, T-NL – Temperate needle-leaved evergreen tree. LPJmL-FIT, Lund-Potsdam-Jena managed Land of flexible individual traits; PFT, plant functional type

2.1 | Adjusted LPJmL-FIT model

Lund-Potsdam-Jena managed Land of flexible individual traits was originally developed for Amazonian rainforests (Sakschewski et al., 2015). Adapting it to climatic conditions which are strongly seasonal and with a high intra-annual variability requires a number of adaptations and implementations for multiple, co-occurring PFTs to describe Mediterranean, temperate and boreal natural forests in Europe. The LES and SES approach, as implemented in LPJmL-FIT, has therefore been adapted to accommodate four tree PFTs, namely, “broad-leaved summer green” (BL-S), “broad-leaved evergreen” (BL-E), “Temperate needle-leaved evergreen tree” (T-NL) and “Boreal needle-leaved evergreen tree” (B-NL). Each PFT is based on an earlier implementation of these PFTs in LPJmL-4 (Schaphoff, von Bloh, et al., 2018) which has been extensively evaluated (Schaphoff, Forkel, et al., 2018). To account for the phenology of the Mediterranean, temperate and

boreal forests under the influence of light, water and temperature stress, we implemented the phenology model of Forkel et al. (2014) into LPJmL-FIT. This model couples the phenological status of a tree, which ranges between 0 (complete senescence) and 1 (fully leaved), to the local climate. The actual value of the phenology status is determined by the product of four phenology functions, which depend on a set of PFT-specific parameters and the daily temperature, water stress and radiation. We calibrated the phenology parameter (Table S1) to yield a best possible PFT distribution that matches the spatial distribution of European natural vegetation from Bohn et al. (2007). In addition, leaf senescence now occurs immediately if the phenological status of a tree drops below 0.2, forcing a tree to rebuild the complete canopy leaf area in the next simulation year. Given the climate influence on leaf phenology changes along continental climate gradients, a continuous spectrum from summer to winter deciduousness for BL-S trees is captured in the model.



The algorithm to combine the PFT parameter set of the LES- and SES-related traits (WD) with the phenology parameter is implemented as follows: When a new sapling establishes, the selection of the trait combination occurs in three steps. First, the PFT type is randomly chosen out of the four possible PFTs independent of its climate suitability or the present PFT composition (Figure 1). Second, the selected PFT type defines the set of phenology parameters that are assigned to the tree sapling (see Table S1), and it defines the SLA range from which the SLA value is drawn from a uniform distribution. The SLA range differs for BL-E, T-NL, B-NL and BL-S (see Table S2). The functionally related plant traits leaf longevity (LL), leaf N and Vcmax (maximum carboxylation rate of Rubisco per leaf area) are assigned in a third step to the sapling following the LES approach as in Sakschewski et al. (2015), see Figure 1. Both, SLA and WD are drawn from a continuous uniform distribution for each individual tree for which the PFT-specific range is derived from the TRY v4.0 database (see <https://www.try-db.org/> and Kattge et al., 2011) considering only sites located inside our study area. Hence, the parameter set of each newly established sapling in the forest patch contains trait values drawn from the LES and SES as well as the phenology parameters. This approach is applied to the 20 new saplings that are established per patch each year. Grasses are integrated in the model as homogeneous layers using the remaining radiation at the bottom of every forest patch for photosynthesis. C₃ and C₄ grasses compete with trees for water only. The establishment rate of grass is anti-proportional to the actual tree cover and the mortality rate depends on carbon balance by the end of every year (see Schaphoff, von Bloh, et al., 2018 for details). Grasses are assigned phenology parameters (see Table S1), but are simulated without individual trait flexibility following the LPJmL4 modelling approach (Schaphoff, von Bloh, et al., 2018). Therefore, in this study model simulations will be used to evaluate trait distributions and FD regarding trees only.

Different from the LPJmL-FIT version of Sakschewski et al. (2015), the trade-off between SLA and LL has been adopted from LPJmL4 (Schaphoff, von Bloh, et al., 2018):

$$LL = 10^{\frac{\beta_0 - \log_{10}\left(\frac{SLA}{\alpha} \cdot DM_c\right)}{\beta_1}} \quad (1)$$

where DM_c denotes the dry matter carbon content of leaves (DM_c = 0.4763) and the parameter $\alpha = 2 \cdot 10^{-4}$. The parameter β_1 is set to 0.4 and β_0 to 2.2 for broad-leaved PFTs, while $\beta_0 = 2.08$ for both, T-NL and B-NL. All parameters in Equation (1) were obtained from Kattge et al. (2011). The parameters β_1 and α influence the steepness of the SLA-LL relation, whereas β_1 alters the offset.

The mortality $mort_{WD}$ is coupled to its wood density WD by using the equation from King, Davies, Tan, and Noor (2006):

$$mort_{WD} = 10^{\alpha_1 + \alpha_2 / WD} \quad (2)$$

and assigned to each tree individual at establishment (Sakschewski et al., 2015). Because no general mortality-WD relationship for tree species of temperate forests is currently available in the literature, we calibrated α_1 and α_2 to the locally observed biomass. Calibration was carried out

at European sites still containing natural forests (Hainich National Park (NP) and Bialowieza NP) because the model simulates natural vegetation only. Following this calibration, we set the parameter α_1 to -4.5 and α_2 to -2.66 for the broad-leaved trees, and $\alpha_1 = -2.66$ and $\alpha_2 = 0.255$ for needle-leaved trees. The term $mort_{WD}$ is used as the maximum of the growth-efficiency mortality in LPJmL-FIT, meaning that trees with a low growth efficiency resulting from low productivity under unfavourable climate conditions have a higher mortality risk (Sakschewski et al., 2015).

In addition, we reduced the tree allometry parameter k_{ep} to 1.5 (1.6 in Schaphoff, von Bloh, et al., 2018) for needle-leaved trees to simulate realistic tree shapes and growth pattern of needle- in comparison to broad-leaved saplings:

$$CA \sim D^{k_{ep}} \quad (3)$$

where k_{ep} mediates between crown area (CA) and stem diameter (D). The lower k_{ep} , the CA for needle-leaved trees is reduced which then affects LAI:

$$LAI = \frac{C_{leaf} \cdot SLA}{CA}, \quad (4)$$

where C_{leaf} is whole plant carbon investment in leaves (kg per tree) (cf. Sitch et al., 2003). Because of the lower SLA, needle-leaved trees then have to invest more leaf carbon in their first years to reach the same LAI compared with broad-leaved trees.

Fire is an important natural disturbance in European forest ecosystems (Naveh, 1990; Tinner et al., 1999). We applied the simple GlobFIRM model (Thonicke, Venevsky, Sitch, & Cramer, 2001) as embedded in LPJmL4. Here, fire probability depends on soil moisture in the top soil layer and a fuel load threshold modelled by an exponential probability function calculated by the end of every year. We apply this probability to each patch separately. If a patch is burnt, every tree is ignited and survives with a PFT-specific fire resistance probability (cf. Thonicke et al., 2001) which is the same for all individuals that belong to the same PFT. In the patch burnt, all litter carbon is combusted completely.

In boreal forests, evergreen trees exhibit water stress in spring, when relatively high air temperature increases evaporative demand, while the soil is still frozen and thus limits the water availability in the soil. This water stress forces evergreen trees to shed their needles and making them less competitive against BL-S trees which might have their bud burst later in the year. To correctly balance competition between B-NL and BL-S in boreal forests, we increased the root-distribution factor β_{root} for B-NL trees from 0.943 (Schaphoff, von Bloh, et al., 2018) to 0.965, which allows B-NL to reach deeper, non-frozen layers during spring thereby preventing them from leaf senescence.

2.2 | Model input data, simulation protocol and validation sites

To post-process and analyse our simulation data, we used R3.6.0 (R-Core-Team, 2019) and MATLAB 2019 (MATLAB, 2019). All



R-packages used in this study including their citation are listed in Table S6.

2.2.1 | Climate and soil data input

Lund-Potsdam-Jena managed Land of flexible individual traits uses air temperature [°C], precipitation [mm/d] and radiation (short-wave down and long-wave net radiation [W/m^2]) of the combined data set of the WATCH (Weedon et al., 2011) and WFDEI (Weedon et al., 2014) datasets at daily resolution on a $0.5^\circ \times 0.5^\circ$ longitude–latitude grid. This climate data set is based on the reanalysis of ERA-Interim, where precipitation was bias corrected using the Global Precipitation Climatology Centre data set (GPCC, Schneider et al., 2011). The climate data range from 1901 to 2013 with WFD (WATCH Forcing Data) covering 1901 to 1978 and WFDEI-GPCC (WATCH-Forcing-Data-ERA-Interim) is used from 1979 onwards. The atmospheric CO_2 concentration is held constant at 296 ppm over the whole time period.

Soil texture is needed as model input and was taken from the Harmonized World Soil Database version 1.2 (Nachtergaele et al., 2009). The soil depth was kept constant at 2m for all grid cells. Our simulation domain covers Europe from $11^\circ E$ to $36^\circ W$ and $29.5^\circ N$ to $62^\circ N$.

2.2.2 | Simulation protocol

Model simulation starts from bare-ground and simulates a spin-up period of 500 years by recycling the first 30 years of the climate data set (1901–1930) to bring natural vegetation composition (here individual trees with their individual trait combinations) and all living and dead carbon fluxes into equilibrium with the spin-up climate. We then performed a transient run simulating potential natural vegetation until the end of 2013, that is, without land use. For the European simulation domain, 1,000 forest patches being equivalent to 10 ha of forest area are simulated in each grid cell where all patches receive the same climate data and the same soil data as model input. Respective model output is then aggregated over all simulated patches within a grid cell.

To allow for a detailed analysis of plant-trait distribution, FD and productivity, we chose six different sites across Europe with near-natural forest stands and which cover a broad range of climates (Table S4). Site-specific simulations follow the same protocol as described above and were performed with 2,500 patches at each site to ensure a higher spatial coverage.

2.2.3 | Model validation

Simulated seasonal and intra-annual GPP is validated against observed and remotely sensed GPP data at six sites (Table S3) covering a climatic gradient (Table S4). We used monthly MODIS

remote-sensing data (MOD17A2H) for the years 2004–2013 (Running, 2015) at six sites (see Table S1) and respective flux tower measurements from the Euroflux network for the Laegeren (CH-Lae, D'Odorico, 2014; Paul-Limoges, 2018) and Hainich NP (DE-Hai) (for general information, see Papale et al., 2006; Reichstein et al., 2005). Simulated maps of vegetation height and biomass were evaluated against remotely sensed products (Lefsky, 2007; Thurner et al., 2014). Details on the validation of Gross Primary Productivity (GPP), vegetation height and biomass are described in the Data S1. Simulated plant trait distributions were compared against observed plant trait data from the TRY database (Kattge et al., 2011), see Data S1 for methods and data origin.

2.3 | Computation of FD indices

We quantified three complementary indices on multidimensional traits to describe FD, namely, FR, FDv and FE, following Villeger et al. (2008) and Schneider et al. (2017), where each point represents one tree individual (higher than 2 m) with its unique trait combination. In this study, this multidimensional trait space is based on SLA, LL, WD and tree height. While SLA, LL and WD influence productivity and biomass (Reich, 2014) and therefore point to competitive exclusion, tree height is regarded to describe niche differentiation (Garnier et al., 2016). We calculated the FD indices across and within PFTs to capture assembly processes across meta-communities.

Functional richness describes the extent of the occupied trait space and is calculated by the convex hull volume including all points in that trait space, which is normalized by the maximum possible trait volume. However, it implies that FR reacts strongly to outliers. FDv describes how far environmental niches are separated and indicate the intensity of competitive interactions, where $FDv = 0$ indicates convergent trait distribution due to strong environmental and competitive filtering (Mason et al., 2005; Villeger et al., 2008). To measure FDv in a multidimensional trait space, a sphere with radius \bar{d}_G centred in the trait cloud is calculated. FDv then quantifies how points (trait combinations of trees) scatter relative to the surface of the sphere (see eqs. 5–7 in Data S1 and Figure S1). If all points are located on the sphere, FDv becomes unity independent on the respective distribution on the sphere. The more the index decreases, the wider the points are spread around (inside and outside) the sphere. FDv therefore quantifies how the occupied niches are separated. FE describes how regularly points are distributed in the trait space, that is, how efficient available resources are used through niche occupation. FE is based on the minimum spanning tree (MST) linking all points in the trait space in such a way that the sum of all branches becomes minimal (see eqs. 11–13 in Data S1 and Figure S1). Therefore, FE increases when a) the points are evenly distributed, that is, having equal branch length; or b) the trait combinations of the trees are equidistant in the trait space (Villeger et al., 2008). Further details on FE, FDv and FR quantification are provided in Data S1.



Each index was computed by considering all trees as evenly weighted. Before calculation, traits were normalized to their minimum and maximum observable values in the TRY sites in Europe, thus ranging between 0 and 1. For each grid cell we checked that no dimensional reduction was required by using the function “dbFD” of the R-package “FD” performing a principal coordinates analysis (Laliberté et al., 2014). Due to constrained computation capacity, we calculated all FD indices separately in groups of 50 patches in each grid cell (for which 1,000 patches were simulated in total) and aggregated them to the grid level by using the arithmetic mean. To visualize the stochastic uncertainty of the model, we calculated the coefficient of variation (COV) of each index in a grid cell out of the groups of 50 patches ($n = 20$). As all of these groups in a cell received the same climate data, the COV can be seen as a measure for the stochastic uncertainty of the model.

3 | RESULTS

3.1 | Climate influence on trait distribution, productivity and tree height

Environmental and competitive filtering allows those trees to establish and survive whose trait combinations are suitable for local climate conditions in the forest patches simulated by LPJmL-FIT. Unsuitable or less suitable trait combinations lead to a low growth efficiency and are therefore outcompeted. The combination of climate suitability and competitiveness has the effect that the continuous, uniform distribution with which the model is initialized results in a normal trait distribution at the local scale. The resulting trait

distributions therefore emerge from the LPJmL-FIT modelling framework (Figure 1). We compare simulated SLA and WD against TRY observations for BL-S, BL-E trees and needle-leaved evergreen, that is, B-NL and T-NL trees (Figure 2). Simulated mean trait distributions match the TRY observation reasonably well for both, SLA and WD, for BL-S, BL-E and the two needle-leaved PFTs (dashed lines in Figure 2). Simulated ranges of SLA, however, are smaller than the original trait range (see Table S2) and smaller than observed SLA (Figure 2). LPJmL-FIT simulates a mean SLA of 16.11 with a standard deviation of $\pm 1.25 \text{ mm}^2/\text{mg}$ for BL-S compared to 14.95 ± 6.09 documented in TRY. The simulated range for SLA is also smaller for BL-E (LPJmL-FIT: $9.31 \pm 1.13 \text{ mm}^2/\text{mg}$; TRY: $6.95 \pm 2.72 \text{ mm}^2/\text{mg}$) and the needle-leaved evergreen (LPJmL-FIT: $6.11 \pm 0.95 \text{ mm}^2/\text{mg}$; TRY: $6.95 \pm 2.72 \text{ mm}^2/\text{mg}$). Simulated ranges for WD are quite close to observed ranges in TRY for BL-S, slightly smaller for BL-E, but broader for the needle-leaved PFTs (Figure 2, bottom row).

The combined effects of environmental filtering and plant competition for light and water in LPJmL-FIT also result in reasonable seasonal and interannual productivity (GPP) as observed on six selected sites. The model quality is shown by a high Pearson's R (≥ 0.89) and low NMSE (0.03–0.29; see Table S3, Figure S2 and Data S1 for details on the evaluation methods and results, sites are described in Table S4). The simulated competition between tree individuals results in closed forest cover and corresponding high biomass storage in temperate and boreal forests (Figure S3). We found simulated vegetation height and biomass to compare well against remotely sensed observations and local in situ data, although the comparison of natural forest and actual vegetation is limited as remote-sensing products detect properties of actual vegetation cover which are influenced by current land use and forest management (see Data S1

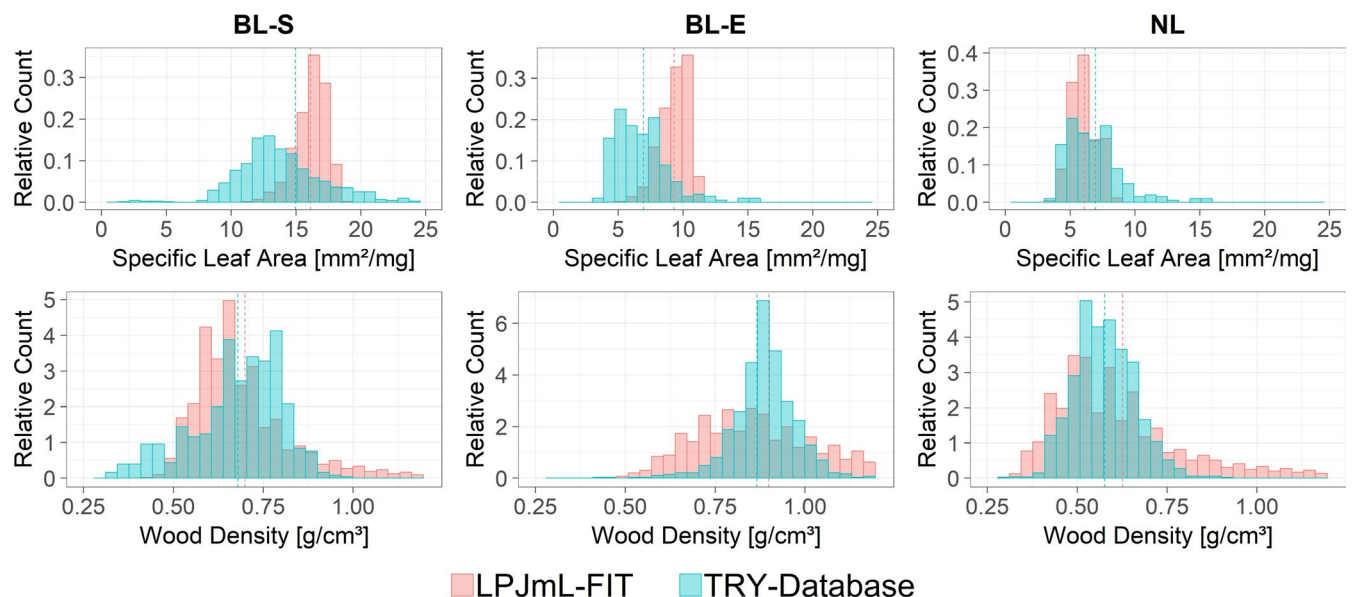


FIGURE 2 Trait distribution of Specific Leaf Area (top panel) and Wood Density (bottom panel) for broad-leaved summer green PFT (BL-S, left column), broad-leaved evergreen PFT (BL-E, central column) and both, boreal and temperate, needle-leaved evergreen PFTs (NL, right column) as simulated by LPJmL-FIT (light red) and observed by TRY database entries (light cyan). Dashed vertical lines show the simulated (light red) and measured (light cyan) average trait values for each PFT. LPJmL-FIT, Lund-Potsdam-Jena managed Land of flexible individual traits. PFT, plant functional type

for details on the evaluation method and results). Centuries of land clearing, agricultural and forestry have greatly changed land cover and reduced natural forests to few remaining small areas (Ellis et al., 2013), which further complicates the evaluation of simulated potential natural vegetation.

3.2 | Climate influence on trait distributions within and across PFTs

Spatial distribution of simulated fractional cover of each PFT result from the PFT-specific phenology and functional trait combinations, which determine the suitability of each parameter set to the climate and soil conditions in a given grid cell (cf. Figure 1). Tree individuals with trait combinations adapted to current climate are the most competitive and most productive in sites with limited environmental stress severity (while their productivity may decrease at stressed sites, Zhang, Niinemets, Sheffield, & Lichstein, 2018), and thus cover larger proportions of a given grid cell (Figure S4). The most suitable combination, to shed leaves under cold and/or dry climate conditions, results in BL-S dominating central Europe, even though it also occurs – albeit at much smaller fractions – in the boreal and the Mediterranean forests. B-NL dominates northern Europe, and T-NL the Mediterranean basin, where it co-occurs with BL-E. Several PFTs co-occur in the Mediterranean forests (three tree PFTs and C_3 grasses), whereas temperate forests in lowland Europe are dominated by just one tree PFT (Figure S4). Note that in all cases, the tree individuals still vary in their trait combination within each PFT.

Abiotic conditions, here aggregated to MAT [°C] and MAP [mm], are strongly linked to tree establishment (Figure 3). The climate space occupied by trees across all PFTs converges towards higher MAT and lower MAP. Intra-PFT variation in SLA values decreases with warmer and drier conditions. Most SLA variation, however, happens between PFTs that occupy different parts of the climate space (Figure 3a). The SLA of BL-S varies from values around 13 mm²/mg under warmer and drier climate conditions to >20 mm²/mg in colder climate conditions (<7°C) with a wide range in precipitation (500 to >2,000 mm MAP). BL-S co-exists with B-NL in cold/wet climate conditions, with BL-E in warmer and increasingly drier climate conditions (>10°C MAT and 300–2,000 mm MAP). Although many trait combinations are possible under the “everything-is-everywhere” approach of LPJmL-FIT, BL-S with SLA values lower than 13 mm²/mg do not occur despite a possible minimum of 7 mm²/mg (see Table S2). BL-E cover a similar temperature range as BL-S, but occur across a wider SLA range between a MAT of 8–17°C, although the possible SLA range of BL-E is among the smallest of all simulated PFTs. Again, this realized trait space separates these PFTs clearly from the two needle-leaved PFTs, T-NL and B-NL, where T-NL increasingly dominates at MAT >10°C and MAP <1,000 mm with SLA ranging from 5 to 8 mm²/mg, whereas B-NL shows lowest SLA values at a MAT below 10°C (see Figure 3a; Figure S5 shows PFT-specific SLA maps, Figure S8 maps the COV of SLA).

Simulated mean WD clearly separates along climate gradients across all PFTs (Figure 3b). Low WDs are simulated in cold climate conditions, and WD increases with increasing MAT and decreasing

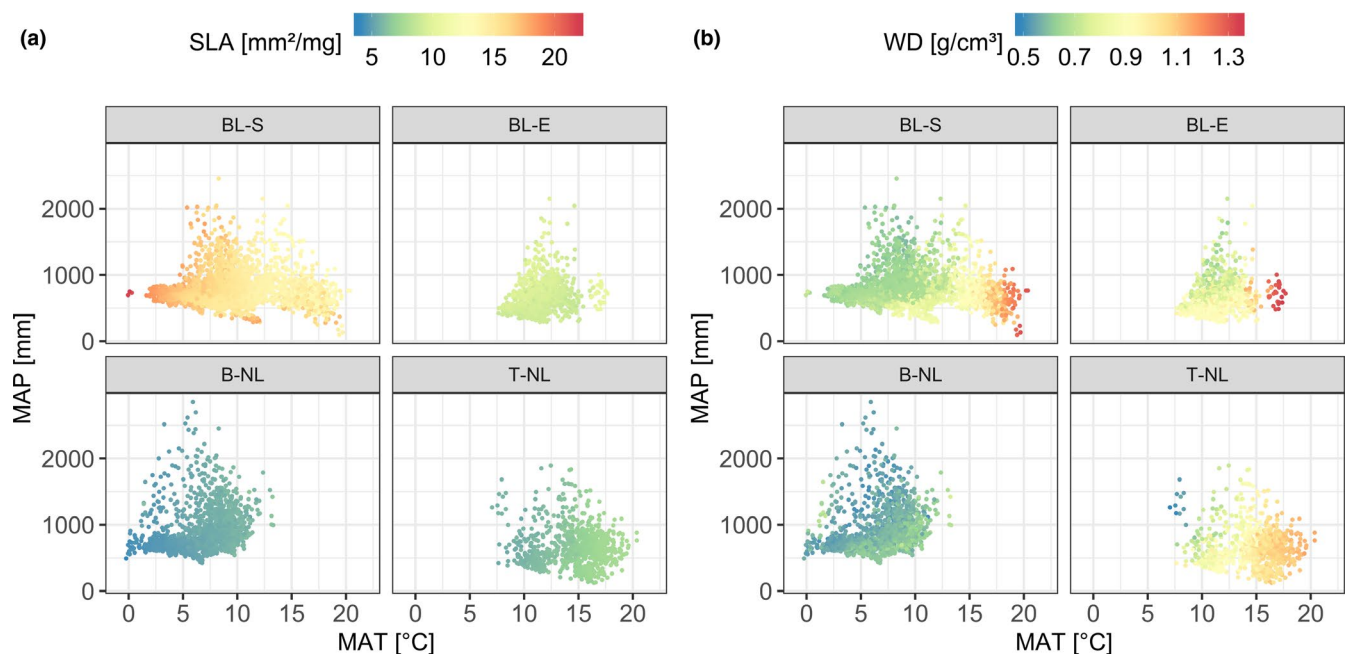


FIGURE 3 Mean Specific Leaf Area (SLA) and Wood Density (WD) distribution for each PFT plotted against mean annual temperature (MAT) and mean annual precipitation (MAP). The colour of each dot represents a mean SLA (a) and WD (b) value and each panel belongs to a woody PFT. (Broad-leaved summer green: BL-S; Broad-leaved evergreen: BL-E; Boreal needle-leaved evergreen tree: B-NL; and Temperate needle-leaved evergreen tree: T-NL) Mean trait values are averaged over the 2004–2013 time period for 1,000 patches per grid cell. PFT, plant functional type

MAP. B-NL and BL-S cover the WD space between 0.5 and $<0.7 \text{ g/cm}^3$ below 10°C MAT. WD around 0.7 g/m^3 are found in cold ($<10^\circ\text{C}$ MAT) and drier climate conditions ($<1,000 \text{ mm}$ MAP), with similar WD values found in warmer ($10\text{--}12^\circ\text{C}$ MAT) and wetter ($>1,000 \text{ mm}$ MAP) climate conditions. Highest WD values ($>1.1 \text{ g/cm}^3$) are simulated for T-NL, BL-S and BL-E with $>15^\circ\text{C}$ MAT and $<1,000 \text{ mm}$ MAP (Figure 3b). Higher WD allows slow plant growth and lowers tree mortality risk (Equation (2) in 2.1) which explains why high WD values are simulated across all PFTs under dry climate conditions (see also Figure S6 for PFT-specific WD maps and Figure S9 for maps displaying the COV of WD).

3.3 | FD emerging from climate and plant competition

The calculation of all diversity indices is based on the initial four-dimensional trait space out of SLA, LL, WD and tree height. However, for visualization, we remapped the trait space from four dimensions to a three-dimensional trait space composed of SLA, WD and tree height. We plot the position of each tree individual in the trait space for the climatologically different sites Seitseminen, Laegern

and Dundo (Figure 4, left column). The occupied trait space forms the hypervolume, that is, the FR (shown in grey-blue in Figure 4, 2nd column) for each site. The sphere around the centre of gravity (grey surface and green cross, respectively, shown in Figure 4, 3rd column) illustrates site-specific FDv, whereas FE is quantified from the MST (Figure 4, last column). Table S4 shows the site-specific FD indices for the six sites.

The wide bi-modal distribution of SLA between BL-S and B-NL trees in Seitseminen increases the trait space, that is, FR, whereas in Laegern and Dundo simulated SLA distributions show narrower bi-modal distributions or even converge (see density distribution in Figure 4, left column). Niche separation (FDv) and regularity of niche occupation (FE) are more comparable across the three sites (Table S4). FDv is highest in Dundo because points in trait space lay closer to the surface of the sphere compared with Seitseminen and Laegern (notice points outside the sphere in Seitseminen and Laegern). Compared with Laegern, we find slightly higher FDv in Seitseminen because of the divergent SLA distribution. Niche occupation is less regularly distributed (FE) in Dundo compared with Seitseminen and Laegern because the trait space of B-NL trees is less occupied in Dundo, leading to larger path length in between points of this PFT (Data S1, Figure S1). This leads to more irregular distances in between points, which lowers FE.

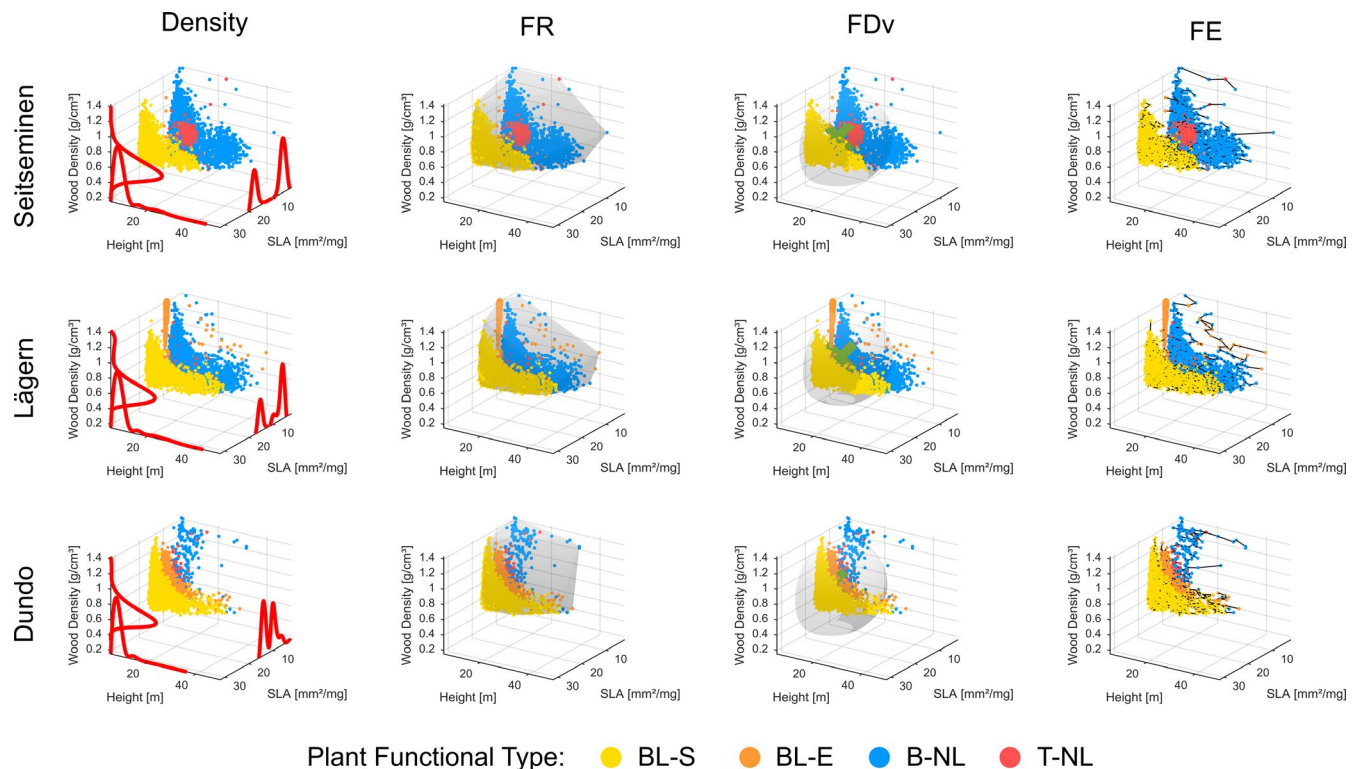


FIGURE 4 Distribution of simulated trees in a three-dimensional trait space (Height, WD and SLA). We plot density (far left) and functional diversity indices for 2,500 simulated patches (FR centre left; FDv centre right and FE (far right) for three sites (Seitseminen (top row), Laegern (middle row) and Dundo (bottom row)). Ranges of the SLA and WD axes correspond to the maximum trait range across all woody PFTs used in the simulation (see Table S2). Seitseminen, Laegern and Dundo represent boreal, mixed temperate and Mediterranean-type forests respectively. Each dot represents a trait combination of one tree larger than 5 m while the colour indicates its PFT type. Plant Functional Types are as followed: Broad-leaved summer green (BL-S), Broad-leaved Evergreen (BL-E), Boreal needle-leaved evergreen tree (B-NL) and Temperate needle-leaved evergreen tree (T-NL). FE, functional evenness; FR, functional richness; PFT, plant functional type; SLA, specific leaf area; WD, wood density

When calculating the FD indices for each PFT trait space separately and for each site, FDv and FE are similar to the corresponding across-PFT values (Table S5 and Data S1 for computation of within-PFT FD indices). Within each PFT, diverse functional strategies co-exist, that is, the intensity of plant competition and regularity of niche occupation are comparable to the one across PFTs. Specifically, FDv is high at Seitseminen for B-NL trees compared with the overall FDv because the point cloud is clearly separated along the tree-height niche axis and shows a wider WD distribution compared with the other sites (Figure 4, left column). However, intra-PFT FR is three orders of magnitude lower than FR across PFTs. This is mainly caused by a much lower realized trait space for LL (e.g. BL-S) and SLA (e.g. B-NL, see Figure 4), whereas the intra-PFT range of tree heights and WDs is similar to that between PFTs. In summary, environmental and competitive filtering influence niche occupation in a similar way within as well as across PFTs.

3.4 | FD at the European scale

At the European scale, spatial gradients in FD indices are relatively small and a few spatially distinct patterns stand out (Figure 5). FR increases with the number of PFTs present through which the size of the trait space increases (Figure 5a, compare Figure S4). Higher FR is found in mountain areas throughout the continent, in boreal forests but also

on the British Isles. Where B-NL and BL-S occupy distant parts of the trait space, FR reaches its maximal values of 0.03–0.04, very much alike in the Seitseminen site (compare Figure 4, top row). In contrast, lowest FR values are computed for areas where one PFT is dominant, especially in the lowland areas of temperate forests which are dominated by BL-S trees (Figure 5a). The COV for FR is high in temperate and alpine forests, where mean FR is low because variability increases where the mean of a variable is close to 0. On the contrary, low values are found in Mediterranean and boreal forests (Figure S7).

Functional divergence is high in natural forests reaching values between 0.68 and 0.82 (Figure 5b). Where needle-leaved and broadleaved trees co-exist (cf. Figure S4), FDv is higher, that is, in boreal and mountain forests, and in southern Mediterranean forests. Where only one PFT dominates, FDv is lower (0.7–0.73 compared to >0.75), for example, in lowland temperate and Mediterranean forests. In the transition zone to boreal forests or mountain forests, trait distributions of BL-S-dominated forests further converges (FDv ~0.68). Here, intensity of filtering increases (FDv converges) when climate conditions reduce growth efficiency of BL-S trees. Further north, growing conditions for B-NL are more suitable, allowing establishment of another plant strategy causing an increase in FDv (Figure 5b). In contrast, in the southern Mediterranean forests, needle-leaved and broad-leaved trees are smaller (Figure S3) and in competition with grasses for water, thus, FDv is higher again

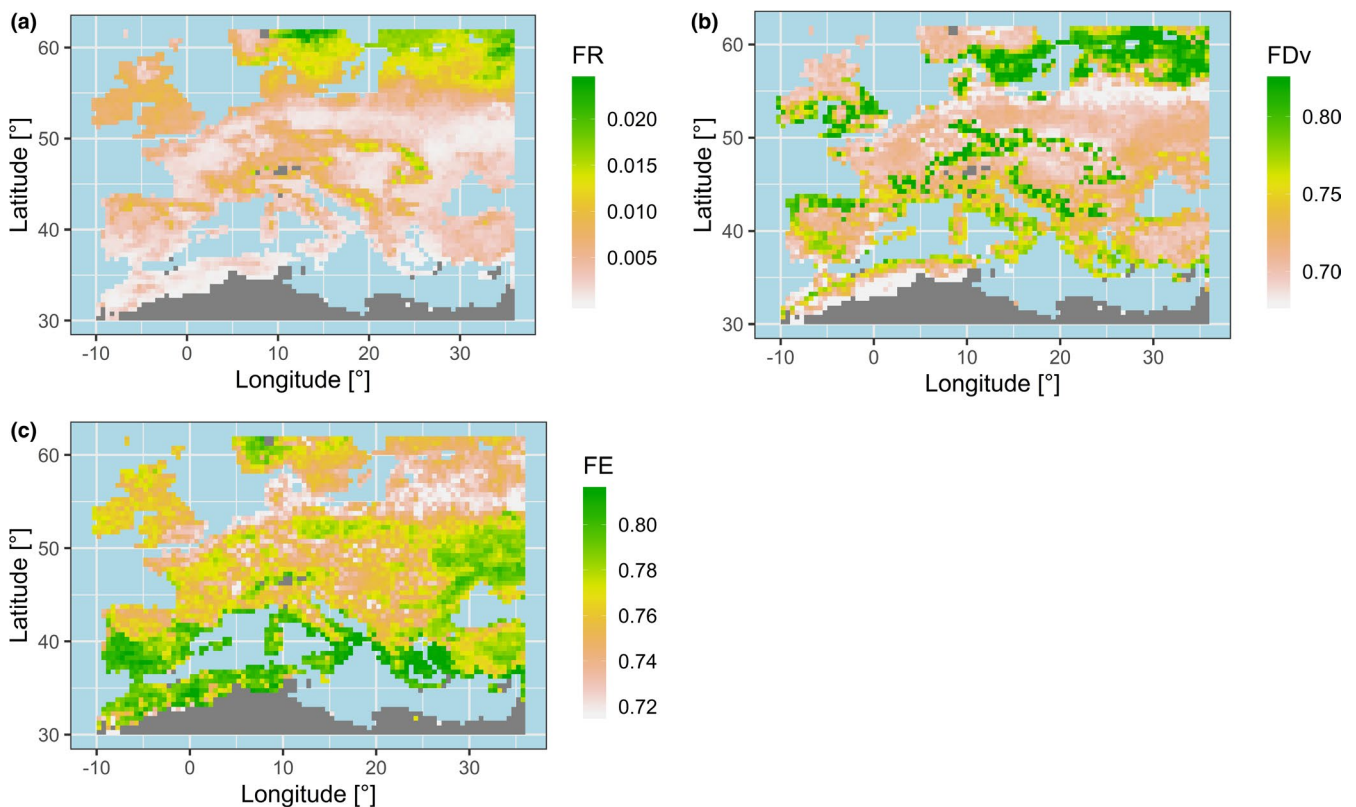


FIGURE 5 Maps of Functional Richness (FR, panel a), Functional Diversity (FDv, panel b) and Functional Evenness (FE, c). All three functional diversity indices are computed from specific leaf area, leaf longevity, wood density and tree height averaged over all individual trees, which are at least 5 m tall. Effects on FR, FDv and FE result from trait variability within and across woody PFTs present in 1,000 patches within a grid cell. PFT, plant functional type



(~0.76, see Figure 5b). COV of FDv is generally very low with maximum values found in some mountainous and boreal transitional areas (Figure S7).

Functional Evenness follows a different spatial pattern across Europe than the other two indices (Figure 5c). Lower FE values (~0.72) are found in lowland temperate forest in central and eastern Europe as well as in the transition zone to the boreal forest in north-eastern Europe, where BL-S dominate but still grow in competition with B-NL trees (Figure S3). FE increases where only one NL-PFT dominates (e.g. British Isles, Norway) and is high in wet Atlantic and in southern Europe, where high environmental stress results in efficient resource use. Here, COV of FE corresponds to the spatial gradient of mean FE, maximum COV is found where mean FE is lower (Figure S7).

4 | DISCUSSION

4.1 | Effect of environmental and competitive filtering on trait distribution and productivity

The adapted LPJmL-FIT model is capable of reproducing observed GPP with a small modelling error and high correlation with observed data (see Data S1). Biomass and plant height follow the spatial distribution of previous publications (Thurner et al., 2014; Healey et al., 2015), although the comparison is limited by the long-term land use history in Europe which restricts the comparability between simulated and observed data and may explain the discrepancy found. Simulated SLA and WD are in close agreement with observed TRY data. These results show that the new version of LPJmL-FIT reproduces the spatial PFT and local trait distributions as well as the productivity and biomass of European natural forests. Even though a preference for measuring short-lived, broad-leaved species can influence measured trait data which could overestimate, for example, SLA (Sandel et al., 2015), such bias is found to be small for European trees and should have little influence on our results because LPJmL-FIT clearly separates between broad-leaved and needle-leaved trees and focuses on trees only. The model is capable of simulating potential natural vegetation without prescribing the spatial extent of PFTs via bioclimatic limits and without prescribing the functional traits in question (e.g. SLA, LL, WD). Therefore, it enables to investigate the interaction between environmental and competitive filtering in European natural forests in an unprecedented manner.

Simulated ranges for SLA (BL-S and BL-E) and WD (BL-E and needle-leaved trees) are smaller than observed (Figure 2 and Table S2). Heat and drought stress as well as light availability (seasonal, vertical canopy structure) influence growing conditions of trees. These climate factors act as environmental filter favouring plant strategies that are adapted to the local climate. Tree growth efficiency influences tree competitiveness and its capacity to reach the top layer in the canopy and gain most light in temperate and boreal forests. Therefore, competitive filtering is the second driver

of trees surviving and growing in a forest patch. Additional processes not yet explicitly captured by LPJmL-FIT might explain the remaining trait variability and include: (a) dispersal and adaptive responses (incl. phenotypic plasticity of traits), (b) nutrient availability (e.g. nitrogen limitation), (c) variable rooting strategies and disturbances other than fire (Van Bodegom et al., 2012; Douma et al., 2012) and (d) trade-offs between different trait combinations and species capacities to tolerate multiple environmental stresses simultaneously (Laanisto & Niinemets, 2015; Niinemets & Valladares, 2006). While the influence of adaptive responses on trait distribution is perhaps difficult to measure, including nutrient availability would introduce another niche axis and perhaps differentiate the trade-off with SLA in the LES better. Variable rooting strategies could alleviate water stress in seasonally dry environments and increase growth efficiency, hence tree height of Mediterranean forests (cf. Figure S3). We have included fire disturbance in LPJmL-FIT, which simulates high fire activity in the Mediterranean forests, less in boreal and low fire activity in temperate forests, but other disturbance agents such as windthrow or frost could also further diversify plant strategies, and thus increase the width of the simulated trait distribution. Implementing these disturbances into LPJmL-FIT would be expected to decrease the competitiveness of the BL-S trees in boreal and mountainous forests, and thus further restrict their spatial extent.

Specific model functions determine the model outcome. The phenology parameter (Table S1) influences GPP, growth efficiency and thus the performance of a tree in the forest patch. In exchange with climate conditions, the phenology parameters determine the spatial distribution of the PFTs, including grasses. The trade-off between SLA and LL defines the carbon cost for leaves (or needles) under specific climate conditions which then determine the length of the growing season, and thus vegetation productivity. With more SLA and LL measurements available for temperate forests, this relationship could be adjusted and contribute to further reduce modelling error of the simulated trait distribution (Figure 2). The WD-dependent mortality function (see Equation (2)) influences simulated biomass, therefore more data on WD and tree mortality would help to improve parameterization of this function. Further reductions in the model error of simulated WD distribution, tree height and biomass could be expected.

Plant-trait validation would profit from more and better resolved plant trait measurements in natural forests in Europe. In this study, we had to aggregate several TRY sites and also to merge T-NL and B-NL to validate simulated trait distributions. Ideally, trait measurements at FLUXNET sites, where we can evaluate both productivity and plant traits, would allow high resolution and in-depth model evaluation. With these consistently measured data available, model evaluation could be extended to water fluxes and biomass as well as stand structure and their related plant traits. Alternatively, remotely sensed traits which are already available at the Laegern site (cf. Schneider et al., 2017) or emerging from global remote-sensing missions (cf. Jetz et al., 2016; Ma et al., 2019) could be used in the future. However, cross-validation experiments are required to

compare spatially continuous traits observed from remote sensing to traits simulated by DGVMs using flexible-individual traits, but approaches are underway (cf. Garonna et al., 2018; Lausch et al., 2018). Simulated trait maps for SLA and WD can be validated against interpolated observed trait maps (Butler et al., 2017; Šímová et al., 2018), even though observed trait distributions include those from highly managed forests. Interpolated trait maps, which combine plant trait data with actual species' presence data, can lead to a potential bias in data-model comparison because species are planted in managed forests. Generating trait maps which use potential natural species distribution would improve such data-model comparison because they would be closer to the spatial trait distribution that would result from environmental and competitive filtering, for example, at local scales (Benavides, Scherer-Lorenzen, & Valladares, 2019). Model-data comparison could be improved with a) more trait data being extracted in natural vegetation and extrapolated using species distribution data to the continental scale; and b) allowing for a better overlap of observed versus simulated plant traits such as leaf N (observation available but simulated map missing) or WD (observation missing, but simulated map available).

4.2 | Community-assembly effects on traits and FD across Europe

Community assembly at a site results from dispersal or migration, environmental filtering of trait combinations adapted to local climate and finally plant competition (Bernard-Verdier et al., 2012). In the adapted LPJmL-FIT model, trait combinations are drawn from observed ranges for SLA and WD. It principally means that any conceivable trait combination can establish everywhere at any time for every PFT without explicitly considering trait inheritance or seed dispersal. Currently, surviving trait combinations in the model represent those trees whose traits are best suited to local climate and the competitive conditions in the established tree community. Therefore, environmental filtering interacts with competitive filtering and reproduces observed trait distributions and productivity of natural forests. Scaling up to the whole study region, SLA and WD gradients emerge along climatic gradients and reflect variability in trait ranges.

Simulated SLA cover a wide temperature and precipitation range, separated by SLA ranges as observed for the four PFTs in Europe. Where cold temperatures and light increasingly limit productivity, that is, in the boreal zone, simulated SLA for BL-S increases, meaning trees with extremely high SLA and short LL survive cold winters and grow in short summers. The shift towards higher WD in southern Europe indicates a local adaptation to seasonally dry Mediterranean-type climate. In general, the increasingly dry climate filters higher WD for BL-E and T-NL which indicates better adaptation to drought.

The identified spatial FD patterns reflect the combined effect of environmental and competitive filtering. The influence of climate on surviving plant strategies and their coexistence are reflected in the occupied trait space. FR is high where trait clusters of different

PFTs are distant and thus cover a large volume of the trait space. In high-elevation areas and the boreal zone, BL-S adapt to high SLA values and lower LL because of shorter vegetation periods leading to a wider functional gap in these two traits between BL-S and B-NL trees. FR is small due to small trait variation, where only BL-S trees dominate the patches of temperate forests (Figure 5). In the Mediterranean region, FR is comparable to temperate forests because lower tree heights limit trait space and counteract the effect of diverse leaf strategies. In the southern Mediterranean, where tree growth reaches its limits, FR decreases because few niches can be occupied under the dry climate conditions.

Functional divergence describes the diversity of co-existing functional strategies. A high FDv illustrates a high degree of niche differentiation, thus high competitive exclusion or intense competitive interaction (Garnier et al., 2016; Mason et al., 2005; Vileger et al., 2008). The larger the influence of environmental filtering through abiotic stress, the more the trait distribution converges (Bernard-Verdier et al., 2012). Maps of FDv (Figure 5) therefore illustrate the relative strength of environmental versus competitive filtering on trait composition. Where climate allows needle- and broad-leaved trees to co-exist (in mountains, boreal forests, wet temperate and Mediterranean forests), FDv is high because of the distant SLA distribution of BL-S and B-NL. In Mediterranean and temperate climates, SLA distributions converge more, and FDv declines (Figure 5b). Interestingly, FDv declines further in the transition from temperate forests to boreal and to mountain forests respectively. Being dominated by BL-S, the performance of these trees declines as climate gets colder, thus the abiotic stress increases which leads to a less divergent distribution. Further north (or at higher elevation) the growing conditions for B-NL improve, thus their dominance increases and increases FDv again. Physiological traits (SLA, WD and LL) converge at the transition from temperate to boreal forests, indicating competitive exclusion. In contrast, in southern Mediterranean forests, increasing drought stress reduces tree height and favours a wide SLA range and higher WD (Figure 3, Figure S5), and thus the trait distributions diverge again, promoting co-occurring alternative strategies (Figure 5b, Figure S3). We find that such bi-modal changes in FDv reflect shifts between competitive exclusion, linked to physiological traits (SLA, WD, and LL), and niche differentiation, linked to morphological traits (tree height).

Functional evenness quantifies the regularity of the distribution in the trait space, that is, niche occupation (cf. Mason et al., 2005; Vileger et al., 2008) and could be interpreted as a lower utilization of resources due to the more irregular occupation of the trait space, that is, environmental niches (cf. Mason et al., 2005). However, there are few studies which have investigated the changes in FE along climatic gradients. Recent studies focussed on changes in FE along disturbance gradients (e.g. Mouillot, Graham, Vileger, Mason, & Bellwood, 2013) and at the local scale (Pakeman, 2011). We find high FE in areas where dry and cold climate conditions limit tree growth and under wet (Atlantic) conditions. Increasing disturbances (fire) and climatic stress (drought) increase resource-use efficiency as suggested by Pakeman (2011). In highly stressed environments,



no strategy can dominate, thus functional traits are more evenly distributed. Low FE is found in mixed temperate forests and in the transition from temperate to boreal forests, where BL-S and B-NL occupy distant parts of the trait space. At the Pan-European scale, FE does not follow a unique climatic gradient which could be interpreted as habitat filtering as suggested by Pakeman (2011). In our study, it is rather a combination of environmental and competitive filtering within and across PFTs.

We computed FR, FDv and FE from four traits following the approach of Vileger et al. (2008) as implemented for the Laegern site in Schneider et al. (2017). The FD indices change with the traits considered and the dimensionality of the trait space. At the Laegern site, we compute FR values one order of magnitude lower than published in Schneider et al. (2017) because we calculate FR for a four- instead of a three-dimensional trait space. In contrast, we derived comparable FDv and slightly lower FE values for the Laegern site (Schneider et al., 2017). A direct comparison between remotely sensed and simulated FD based on three traits is of interest and relies on directly comparable trait spaces and indices. Quantification of FD indices strongly depend on the type of traits (physiological vs. morphological) and the context of their interpretation, for example, niche differentiation or ecosystem functions to which the considered traits relate. Comparing site-specific FD indices based on similar traits where also trait observations are available would be a great step forward to evaluate site-specific FD and its changes along climatic gradients at the regional as well as continental scale. Model-data comparison can help to further investigate the importance of spatial scale or abiotic gradients at the landscape scale, where DGVMs with flexible individual traits such as LPJmL-FIT can be used to test and explore respective FD hypotheses to advance biodiversity-ecosystem functions theory (Hisano, Searle, & Chen, 2018).

Trees occupy trait ranges within each PFT allowing different PFTs to co-exist as a result of FD, tree demography and disturbance in all biomes. Site-specific water availability and temperature have been shown to influence functional composition in temperate forests emphasizing the importance to investigate FD along climate gradients (Zhang et al., 2018).

We find high FD in European natural forests not only for temperate forests as found by Liebergesell et al. (2016) but also for boreal and Mediterranean forests. The simulated community assembly of European biomes can be explained by the interplay between environmental and competitive filtering:

1. In the boreal zone and in high-mountain areas (e.g. Carpathian Mountains, Alps or the Pyrenees) the growing season is short, and needle-leaved trees (low SLA), which keep their leaves longer (high LL) but grow relatively fast due to low WD, are the dominant tree growth strategy mostly as a result of environmental filtering. B-NL trees have high resistance to cold temperatures and their evergreen strategy allows them to fully exploit the short growing season (see Table 1). In contrast, broad-leaved trees (BL-S), which are more prone to cold temperatures and have to unfold their thin, short-lived leaves at the start of

TABLE 1 Overview of the woody PFT characteristics towards phenology, fire sensitivity, leaf and growth strategy, and environment. Plant Functional Types are as follows: Broad-leaved summer green (BL-S), Broad-leaved Evergreen (BL-E), Boreal needle-leaved evergreen tree (B-NL) and Temperate needle-leaved evergreen tree (T-NL)

PFT	Resistance to				Leaf strategy (SLA range, SLA-LL relation)	Growth strategy	Environment
	Cold temperature	Warm temperature	Drought	Fire			
BL-S	Low	Medium	Low	Low	Mostly thin and short-lived leaves	Flexible WD, low WD in north, high WD in south	Very flexible leaf strategy, but less specialized flexible growing strategy, very competitive in temperate zone
BL-E	Low	High	High	Medium	Moderate leaf cost and intermediate leaf longevity	High WD in dry environment lower WD under wet conditions	Less flexible leaf strategy conservative growing strategy competitive in warm temperate zones
B-NL	High	Low	Low	Low	Expensive and long-lived needles	Fast growth, due to lower WD	Conservative leaf strategy, fast growing strategy, specialist in cold climates with short growing season
T-NL	Low	High	High	High	Expensive and long-lived needles	High WD in dry environment, fast-growing under colder climate and thus lower WD	Conservative leaf strategy, conservative growing strategy, specialist in warm, dry and fire-prone environments

Abbreviations: LL, Leaf Longevity; PFT, plant functional type; SLA, specific leaf area; WD, wood density.

the growing season, have a disadvantage under this climate. Nevertheless over a wide range within the boreal zone, B-NL trees are accompanied by BL-S trees. This means, in this range environmental and competitive filtering are not strong enough to select for B-NL trees only and both growing strategies can co-exist. Competitive filtering though pushes BL-S towards lower LL and higher WD as in the temperate zone, which minimizes the overlap of trait values between the two PFTs (Figure 1). Due to the BL-S and B-NL co-existence, a wide trait space (high FR) is covered in which trait combinations are mostly evenly spaced (high FE) and divergent (high FDv), allowing for relatively high resource-use efficiency. The same effect applies further South towards the temperate zone, where B-NL trees can still be found in mixed temperate forests.

2. In the temperate zone, climate supports a longer growing season, higher productivity and biomass. Here, BL-S trees dominate due to competitive filtering. Their tolerance of warmer temperatures together with low carbon investment in short-lived and thin leaves (Table 1) makes this PFT very competitive along a large climate gradient. Moreover, towards warmer and drier climate conditions, the WD of BL-S trees increases to survive this climatic stress keeping this PFT dominant. The clear PFT dominance decreases FR, and leads to intermediate FE and FDv. Towards the Mediterranean zone new tree growth strategies (BL-E, T-NL) enter the forest community with milder winter and drier summer changing environmental filtering effects.
3. In the Mediterranean zone, forests are stressed by drought and warm temperatures, therefore, limitations of growing conditions vary and environmental filtering plays an important role. BL-E and T-NL trees with low SLA and high WD are adapted to seasonally dry summers and can therefore co-exist in complementary and regularly spaced niches which confirms previous findings (Carnicer, Barbeta, Sperlich, Coll, & Penuelas, 2013). Whereas BL-E trees tolerate warm temperatures and drought, T-NL trees are specialists for warm, dry and fire-prone environments (Table 1). Given those dynamic changes in niche occupation, FE and FDv are high in mountainous areas and in the semi-arid southern Mediterranean areas. Where T-NL dominate FDv is slightly lower, that is, niche occupation being less diverse.

5 | CONCLUSION

We introduce a new generation, large-scale vegetation model for Europe allowing to dynamically simulate FD on a continental scale, alongside with productivity and tree demography. Approximating competition of individual trees with randomly selected functional trait combinations has proven successful to reproduce trait patterns, productivity and tree demography of natural forest ecosystems. Whereas some trait ranges are constrained by PFTs (SLA), others follow similar climatic gradients across all PFTs (WD). These results complement the currently available data of trait distributions

derived from Earth observation data, and allow large-scale estimates of FD across Pan-Europe. We demonstrate how FR, FDv and FE vary strongly across Pan-Europe and emerge from environmental and competitive filtering alike. Co-existence of functionally diverse trees results from plant trait diversity, tree demography and disturbance under varying strength of environmental and competitive filtering.

ACKNOWLEDGMENTS

The authors thank three anonymous reviewers for their careful and constructive comments that greatly improved the manuscript. This project has received funding from the European Union's Horizon 2020 Research and Innovation Programme under grant agreement No 641762 (ECOPOTENTIAL). The study has been supported by the TRY initiative on plant traits (<http://www.try-db.org>). The TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Boenisch (MaxPlanck Institute for Biogeochemistry, Jena, Germany) in collaboration with the German Centre for Integrative Biodiversity Research (iDiv). We thank Giovanni Gligora for contributing his data to TRY. TRY is been supported by DIVERSITAS core project bioDISCOVERY, the IGBP, the Global Land Project, the UK Natural Environment Research Council (NERC) through its program QUEST (Quantifying and Understanding the Earth System) and the French programmes 'Climat, Environnement, Societe' and 'Fondation pour la Recherche sur la Biodiversite'. The contribution of M. E. Schaepman is supported by the University of Zurich Research Priority Program on Global Change and Biodiversity (URPP GCB). The research carried out at the Jet Propulsion Laboratory, California Institute of Technology, was under a contract with the National Aeronautics and Space Administration. Government sponsorship is acknowledged.

DATA AVAILABILITY STATEMENT

We have permanently uploaded all relevant data to the public data server at the German Research Centre for Geosciences (GFZ) Potsdam, Germany, to make the research fully reproducible (Billing et al., 2019). Supporting information link: <https://doi.org/10.5880/PIK.2019.022>

ORCID

Kirsten Thonicke  <https://orcid.org/0000-0001-5283-4937>

Werner von Bloh  <https://orcid.org/0000-0002-7399-2704>

Ülo Niinemets  <https://orcid.org/0000-0002-3078-2192>

Fabian D. Schneider  <https://orcid.org/0000-0003-1791-2041>

REFERENCES

- Benavides, R., Scherer-Lorenzen, M., & Valladares, F. (2019). The functional trait space of tree species is influenced by the species richness of the canopy and the type of forest. *Oikos*, 128, 1435–1445. <https://doi.org/10.1111/oik.06348>
- Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A., Garnier, E., & Cornelissen, H. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology*, 100, 1422–1433. <https://doi.org/10.1111/1365-2745.12003>
- Billing, M., von Bloh, W., Sakschewski, B., & Thonicke, K. (2019) LPJmL-FIT in Europe. vol 1.0. GFZ Data Services <https://doi.org/10.5880/PIK.2019.022>, GFZ Potsdam.



- Bohn, U., Zazanashvili, N., & Nakhutsrishvili, G. (2007). The map of the natural vegetation of Europe and its application in the Caucasus Ecoregion. *Bulletin of the Georgia Academy of Science*, 175, 112–121.
- Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., ... Jandt, U. (2018). Global trait-environment relationships of plant communities. *Nature Ecology & Evolution*, 2, 1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>
- Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., ... Reich, P. B. (2017). Mapping local and global variability in plant trait distributions. *Proceedings of the National Academy of Sciences of the United States of America*, 114, E10937–E10946. <https://doi.org/10.1073/pnas.1708984114>
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Carmona, C. P., de Bello, F., Mason, N. W. H., & Leps, J. (2016). Traits without borders: Integrating functional diversity across scales. *Trends in Ecology & Evolution*, 31, 382–394. <https://doi.org/10.1016/j.tree.2016.02.003>
- Carnicer, J., Barbeta, A., Sperlich, D., Coll, M., & Penuelas, J. (2013). Contrasting trait syndromes in angiosperms and conifers are associated with different responses of tree growth to temperature on a large scale. *Frontiers in Plant Science*, 4, 409. <https://doi.org/10.3389/fpls.2013.00409>
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. <https://doi.org/10.1038/nature16489>
- D'Odorico, P., Gonsamo, A., Pinty, B., Gobron, N., Coops, N., Mendez, E., & Schaepman, M. E. (2014). Intercomparison of fraction of absorbed photosynthetically active radiation products derived from satellite data over Europe. *Remote Sensing of Environment*, 142, 141–154. <https://doi.org/10.1016/j.rse.2013.12.005>
- Douma, J. C., Witte, J.-P., Aerts, R., Bartholomeus, R. P., Ordoñez, J. C., Venterink, H. O., ... van Bodegom, P. M. (2012). Towards a functional basis for predicting vegetation patterns; incorporating plant traits in habitat distribution models. *Ecography*, 35, 294–305. <https://doi.org/10.1111/j.1600-0587.2011.07140.x>
- Ellis, E. C., Kaplan, J. O., Fuller, D. Q., Vavrus, S., Goldewijk, K. K., & Verburg, P. H. (2013). Used planet: A global history. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 7978–7985. <https://doi.org/10.1073/pnas.1217241110>
- FAO. (2018). Terms and definitions FRA 2020. In D. P. B. A. Pekkarinen (Ed.), *Forest resources assessment working papers*. Rome, Italy: FAO Forestry Department.
- Forkel, M., Carvalhais, N., Schaphoff, S., von Bloh, W., Migliavacca, M., Thurner, M., & Thonicke, K. (2014). Identifying environmental controls on vegetation greenness phenology through model-data integration. *Biogeosciences*, 11, 7025–7050. <https://doi.org/10.5194/bg-11-7025-2014>
- Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., ... Wright, J. (2017). Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews of the Cambridge Philosophical Society*, 92, 1156–1173. <https://doi.org/10.1111/brv.12275>
- Garnier, E., Navas, M.-L., & Grigulis, K. (2016). *Plant functional diversity. Organisms, traits, community structure, and ecosystem properties*. Oxford, UK: Oxford University Press.
- Garonna, I., de Jong, R., Stöckli, R., Schmid, B., Schenkel, D., David, S., & Schaepman, M. E. (2018). Shifting relative importance of climatic constraints on land surface phenology. *Environmental Research Letters*, 13, 024025. <https://doi.org/10.1088/1748-9326/aaa17b>
- Geller, G. N., Halpin, P. N., Helmuth, B., Hestir, E. L., Skidmore, A., Abrams, M. J., ... Williams, K. (2017). Remote sensing for biodiversity. In M. Walters, & R. J. Scholes (Eds.), *The GEO handbook on biodiversity observation networks* (pp. 187–210). Cham, Switzerland: Springer Nature.
- Hallik, L., Niinemets, Ü., & Wright, I. (2009). Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in Northern Hemisphere temperate woody flora? *The New Phytologist*, 184, 257–274. <https://doi.org/10.1111/j.1469-8137.2009.02918.x>
- Healey, S. P., Hernandez, M. W., Edwards, D. P., Lefsky, M. A., Freeman, E., Patterson, P. L., ... Lister, A. J. (2015). *CMS: GLAS LiDAR-derived Global Estimates of Forest Canopy Height, 2004–2008*. Oak Ridge, Tennessee, USA. <https://doi.org/10.3334/ORNLDAAC/1271>
- Hisano, M., Searle, E. B., & Chen, H. Y. H. (2018). Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biological Reviews*, 93, 439–456. <https://doi.org/10.1111/brv.12351>
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75, 3–35. <https://doi.org/10.1890/04-0922>
- Jetz, W., Cavender-Bares, J., Pavlick, R., Schimel, D., Davis, F. W., Asner, G. P., ... Ustin, S. L. (2016). Monitoring plant functional diversity from space. *Nature Plants*, 2, 16024. <https://doi.org/10.1038/nplants.2016.24>
- Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönsch, G., ... Wirth, C. (2011). TRY - A global database of plant traits. *Global Change Biology*, 17, 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- King, D. A., Davies, S. J., Tan, S., & Noor, N. S. M. (2006). The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology*, 94, 670–680. <https://doi.org/10.1111/j.1365-2745.2006.01112.x>
- Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., ... Westoby, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, 529, 204–207. <https://doi.org/10.1038/nature16476>
- Laanisto, L., & Niinemets, Ü. (2015). Polytolerance to abiotic stresses: How universal is the shade-drought tolerance trade-off in woody species? *Global Ecology & Biogeography*, 24, 571–580. <https://doi.org/10.1111/geb.12288>
- Labiberté, E., Legendre, P., & Shipley, B. (2014). *FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12*.
- Langan, L., Higgins, S. I., & Scheiter, S. (2017). Climate-biomes, pedo-biomes or pyro-biomes: Which world view explains the tropical forest-savanna boundary in South America? *Journal of Biogeography*, 44, 2319–2330. <https://doi.org/10.1111/jbi.13018>
- Lausch, A., Bastian, O., Klotz, S., Leitão, P. J., Jung, A., Rocchini, D., ... Knapp, S. (2018). Understanding and assessing vegetation health by in situ species and remote-sensing approaches. *Methods in Ecology and Evolution*, 9, 1799–1809. <https://doi.org/10.1111/2041-210X.13025>
- Lavorel, S., & Garnier, E. (2002a). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16, 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lavorel, S., Diaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S., ... Urceley, C. (2007). Plant functional types: Are we getting any closer to the Holy Grail? In J. G. Canadell, D. E. Pataki, & L. F. Pitelka (Eds.), *Terrestrial Ecosystems in a Changing World* (pp. 149–160). Berlin, Heidelberg, New York: Springer.
- Lefsky, M. A., Keller, M., Pang, Y., De Camargo, P. B., & Hunter, M. O. (2007). Revised method for forest canopy height estimation from

- Geoscience Laser Altimeter System waveforms. *Journal of Applied Remote Sensing*, 1, 013537–13518. <https://doi.org/10.1117/1.2795724>
- Liebigesell, M., Reu, B., Stahl, U., Freiberg, M., Welk, E., Kattge, J., ... Wirth, C. (2016). Functional resilience against climate-driven extinctions - Comparing the functional diversity of European and North American tree floras. *PLoS ONE*, 11, e0148607. <https://doi.org/10.1371/journal.pone.0148607>
- Ma, X., Mahecha, M. D., Migliavacca, M., van der Plas, F., Benavides, R., Ratcliffe, S., ... Wirth, C. (2019). Inferring plant functional diversity from space: The potential of Sentinel-2. *Remote Sensing of Environment*, 233, 111368. <https://doi.org/10.1016/j.rse.2019.111368>
- Madrigal-González, J., Ruiz-Benito, P., Ratcliffe, S., Calatayud, J., Kändler, G., Lehtonen, A., ... Zavala, M. A. (2016). Complementarity effects on tree growth are contingent on tree size and climatic conditions across Europe. *Scientific Reports*, 6, 10. <https://doi.org/10.1038/srep32233>
- Mason, N. W. H., & de Bello, F. (2013). Functional diversity: A tool for answering challenging ecological questions. *Journal of Vegetation Science*, 24, 777–780. <https://doi.org/10.1111/jvs.12097>
- Mason, N. W. H., Moullot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, 111, 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Mason, N. W. H., de Bello, F., Moullot, D., Pavoine, S., & Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24, 794–806. <https://doi.org/10.1111/jvs.12013>
- MATLAB. (2019). *version 9.6 (R2019a)*. The MathWorks Inc.
- Mori, A. S., Lertzman, K. P., & Gustafsson, L. (2017). Biodiversity and ecosystem services in forest ecosystems: A research agenda for applied forest ecology. *Journal of Applied Ecology*, 54, 12–27. <https://doi.org/10.1111/1365-2664.12669>
- Moullot, D., Graham, N. A. J., Villeger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28, 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>
- Nachtergaele, F., van Velthuizen, H., Verelst, L., Batjes, N., Dijkshoorn, K., van Engelen, V., ... Petri, M. (2009). *Harmonized world soil database, Food and Agriculture Organization of the United Nations*. Retrieved from <http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/>, Rome.
- Naeem, S., Duffy, J. E., & Zavaleta, E. S. (2012). The functions of biological diversity in an Age of Extinction. *Science*, 336, 1401–1406. <https://doi.org/10.1126/science.1215855>
- Naveh, Z. (1990) Fire in the Mediterranean - A landscape ecological perspective. In J. G. Goldammer, & M. J. Jenkins (Eds.), *Fire in ecosystem dynamics: Mediterranean and Northern perspectives*. The Hague, the Netherlands: SPB Academic Publ.
- Niinemets, Ü., & Valladares, F. (2006). Tolerance to shade, drought and waterlogging in the temperate dendroflora of the Northern hemisphere: Tradeoffs, phylogenetic signal and implications for niche differentiation. *Ecological Monographs*, 76, 521–547.
- Pakeman, R. J. (2011). Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology*, 99, 1143–1151. <https://doi.org/10.1111/j.1365-2745.2011.01853.x>
- Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., ... Yakir, D. (2006). Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: Algorithms and uncertainty estimation. *Biogeosciences*, 3, 571–583. <https://doi.org/10.5194/bg-3-571-2006>
- Paul-Limoges, E., Damm, A., Hueni, A., Liebisch, F., Eugster, W., Schaeppman, M. E., & Buchmann, N. (2018). Effect of environmental conditions on sun-induced fluorescence in a mixed forest and a cropland. *Remote Sensing of Environment*, 219, 310–323. <https://doi.org/10.1016/j.rse.2018.10.018>
- Prentice, I., Bondeau, A., Cramer, W., Harrison, S., Hickler, T., Lucht, W., Sykes, M. (2007) Dynamic global vegetation modelling: quantifying terrestrial ecosystem responses to large-scale environmental change. In J. G. Canadell, D. E. Pataki, & L. F. Pitelka (Eds.). *Terrestrial ecosystems in a changing world*. Berlin, Heidelberg, New York: Springer.
- R-Core-Team. (2019) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>.
- Ratcliffe, S., Liebigesell, M., Ruiz-Benito, P., Madrigal González, J., Muñoz Castañeda, J. M., Kändler, G., ... Wirth, C. (2016). Modes of functional biodiversity control on tree productivity across the European continent. *Global Ecology and Biogeography*, 25, 251–262. <https://doi.org/10.1111/geb.12406>
- Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., ... Baeten, L. (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, 20, 1414–1426. <https://doi.org/10.1111/ele.12849>
- Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102, 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., ... Valentini, R. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change Biology*, 11, 1424–1439. <https://doi.org/10.1111/j.1365-2486.2005.001002.x>
- Ruiz-Benito, P., Ratcliffe, S., Jump, A. S., Gómez-Aparicio, L., Madrigal-González, J., Wirth, C., ... Zavala, M. A. (2017). Functional diversity underlies demographic responses to environmental variation in European forests. *Global Ecology and Biogeography*, 26, 128–141. <https://doi.org/10.1111/geb.12515>
- Running, S. (2015). *MODIS/TERRA Gross Primary Productivity 8-Day L4 Global 500 m SIN Grid V006*. Sioux Falls, South Dakota. Retrieved from <https://lpdaac.usgs.gov>.
- Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., ... Thonicke, K. (2015). Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology*, 21, 2711–2725. <https://doi.org/10.1111/gcb.12870>
- Sandel, B., Gutierrez, A. G., Reich, P. B., Schrodt, F., Dickie, J., & Kattge, J. (2015). Estimating the missing species bias in plant trait measurements. *Journal of Vegetation Science*, 26, 828–838. <https://doi.org/10.1111/jvs.12292>
- Schaphoff, S., Forkel, M., Müller, C., Knauer, J., von Bloh, W., Gerten, D., ... Waha, K. (2018). LPJmL4 - A dynamic global vegetation model with managed land - Part 2: Model evaluation. *Geoscientific Model Development*, 11, 1377–1403. <https://doi.org/10.5194/gmd-11-1377-2018>
- Schaphoff, S., von Bloh, W., Rammig, A., Thonicke, K., Biemans, H., Forkel, M., ... Waha, K. (2018). LPJmL4 - A dynamic global vegetation model with managed land - Part 1: Model description. *Geoscientific Model Development*, 11, 1343–1375. <https://doi.org/10.5194/gmd-11-1343-2018>
- Schneider, F. D., Morsdorf, F., Schmid, B., Petchey, O. L., Hueni, A., Schimel, D. S., & Schaeppman, M. E. (2017). Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nature Communications*, 8, 1441. <https://doi.org/10.1038/s41467-017-01530-3>
- Schneider, U., Becker, A., Finger, P., Meyer-Christoffer, A., Rudolf, B., & Ziese, M. (2011) GPCC Full Data Reanalysis Version 6.0 at 0.5°: Monthly Land-Surface Precipitation from Rain-Gauges built on GTS-based and Historic Data. https://doi.org/10.5676/DWD_GPCC/FD_M_V6_050.



- Šímová, I., Violle, C., Svenning, J.-C., Kattge, J., Engemann, K., Sandel, B., ... Enquist, B. J. (2018). Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *Journal of Biogeography*, 45, 895–916. <https://doi.org/10.1111/jbi.13171>
- Sitch, S., Smith, B., Prentice, I. C., Arneeth, A., Bondeau, A., Cramer, W., ... Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. *Global Change Biology*, 9, 161–185. <https://doi.org/10.1046/j.1365-2486.2003.00569.x>
- Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., ... Woodward, F. I. (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, 14, 2015–2039. <https://doi.org/10.1111/j.1365-2486.2008.01626.x>
- Thonicke, K., Venevsky, S., Sitch, S., & Cramer, W. (2001). The role of fire disturbance for global vegetation dynamics: Coupling fire into a dynamic global vegetation model. *Global Ecology and Biogeography*, 10, 661–677. <https://doi.org/10.1046/j.1466-822X.2001.00175.x>
- Turner, M., Beer, C., Santoro, M., Carvalhais, N., Wutzler, T., Schepaschenko, D., ... Schmullius, C. (2014). Carbon stock and density of northern boreal and temperate forests. *Global Ecology and Biogeography*, 23, 297–310. <https://doi.org/10.1111/geb.12125>
- Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B., & Conedera, M. (1999). Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology*, 87, 273–289. <https://doi.org/10.1046/j.1365-2745.1999.00346.x>
- Van Bodegom, P. M., Douma, J. C., Witte, J. P. M., Ordoñez, J. C., Bartholomeus, R. P., & Aerts, R. (2012). Going beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes: Exploring the merits of traits-based approaches. *Global Ecology and Biogeography*, 21, 625–636. <https://doi.org/10.1111/j.1466-8238.2011.00717.x>
- Villeger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301. <https://doi.org/10.1890/07-1206.1>
- Weedon, G. P., Balsamo, G., Bellouin, N., Gomes, S., Best, M. J., & Viterbo, P. (2014). The WFDEI meteorological forcing data set: WATCH Forcing Data methodology applied to ERA-Interim reanalysis data. *Water Resources Research*, 50, 7505–7514. <https://doi.org/10.1002/2014WR015638>
- Weedon, G. P., Gomes, S., Viterbo, P., Shuttleworth, W. J., Blyth, E., Österle, H., ... Best, M. (2011). Creation of the WATCH forcing data and its use to assess global and regional reference crop evaporation over land during the twentieth century. *Journal of Hydrometeorology*, 12, 823–848. <https://doi.org/10.1175/2011JHM1369.1>
- Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., ... Wilf, P. (2017). Global climatic drivers of leaf size. *Science*, 357, 917–921. <https://doi.org/10.1126/science.aal4760>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827. <https://doi.org/10.1038/nature02403>
- Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *PNAS*, 96, 1463–1468.
- Zhang, T., Niinemets, U., Sheffield, J., & Lichstein, J. W. (2018). Shifts in tree functional composition amplify the response of forest biomass to climate. *Nature*, 556, 99–102. <https://doi.org/10.1038/nature26152>

BIOSKETCHES

Kirsten Thonicke is interested in plant trait ecology and its link to ecosystem function and ecosystem services. She approaches this by developing and applying a flexible-trait DGVM. She is also interested in developing the concept of functional diversity based on simulated plant traits from the local to the regional scale. She works on the stabilizing role of biodiversity for ecosystem functioning under climate change.

Maik Billing works on disentangling the relations among functional diversity, plant traits, ecosystem functions and their effect on ecosystem stability. He therefore combines process-based models and machine learning techniques to further understand what makes forests resistant towards the approaching climate crisis.

Ariane Walz works in the broad field of landscape ecology, on impact of climate change to ecosystems, their services and their adaptive potential. She approaches these questions by ecosystem modelling and seeking solutions that are ecologically as well as socially feasible.

Boris Sakschewski is interested in the adaptive capacity of forest ecosystems to environmental change. He approaches this by developing a flexible-trait DGVM which reflects the diversity of functional plant traits and their plasticity.

Michael E. Schaepman specializes in Earth Observation using imaging spectroscopy combined with forward and inverse physical modelling. His interest is to retrieve morphological and physiological traits from remotely sensed data for biodiversity mapping.

Author contributions: KTh and MB jointly designed the study and jointly conducted the main analyses. KTh, MB, BS, WvB and AW adapted the LPJmL-FIT model to European natural forests. MB and WvB performed the simulation experiments. KTh, MB, BS, FS and MS analysed the simulated trait data and worked on the computation of the functional diversity indices. KTh wrote the first paper draft. ÜN, JP, HC, YO and PvB contributed TRY data to the study. All authors contributed to the analyses and interpretation of the data, and the final paper draft.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Thonicke K, Billing M, von Bloh W, et al. Simulating functional diversity of European natural forests along climatic gradients. *J Biogeogr*. 2020;47:1069–1085. <https://doi.org/10.1111/jbi.13809>