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# Remote sensing-based forest modeling reveals positive effects of functional diversity on productivity at local spatial scale

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## Key Points:

- We explored forest functional diversity-productivity relationships using a terrestrial biosphere model initialized with remote sensing
- Higher functional diversity at 20×20-m to 30×30-m scale was associated with higher productivity ( $p < 0.001$ ) across all simulations
- Soil depth and texture were the main drivers of productivity at the hectare scale, while functional diversity saturated at coarser scales

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## Abstract

Forest biodiversity is critical for many ecosystem functions and services. Yet, it remains uncertain how plant functional diversity influences ecosystem functioning across environmental gradients and contiguous larger areas. We integrated remote sensing and terrestrial biosphere modeling to explore functional diversity–productivity relationships at multiple spatial scales for a heterogeneous forest ecosystem in Switzerland. We initialized forest structure and composition in the ecosystem demography model (ED2) through a combination of ground-based surveys, airborne laser scanning and imaging spectroscopy for forest patches at 10×10-m spatial grain. We derived morphological and physiological forest traits and productivity from model simulations at patch-level to relate morphological and physiological aspects of functional diversity to the average productivity from 2006–2015 at 20×20-m to 100×100-m spatial extent. We did this for model simulations under observed and experimental conditions (mono-soils, mono-cultures and mono-structures). Functional diversity increased productivity significantly ( $p < 0.001$ ) across all simulations at 20×20-m to 30×30-m scale, but at 100×100-m scale positive relationships disappeared under homogeneous soil conditions potentially due to the low beta diversity of this forest and the saturation of functional richness represented in the model. Although local functional diversity was an important driver of productivity, environmental context underpinned the variation of productivity (and functional diversity) at larger spatial scales. In this study, we could show that the integration of remotely-sensed information on forest composition and structure into terrestrial biosphere models is important to fill knowledge gaps about how plant biodiversity affects carbon cycling and biosphere feedbacks onto climate over large contiguous areas.

## Plain Language Summary

We explored relationships between forest biodiversity and productivity at multiple spatial scales to better understand how plant traits and their diversity influence the functioning of forest ecosystems. To do this across large contiguous areas, we simulated a temperate mixed forest by combining process-based terrestrial biosphere modeling with remotely sensed information about forest structure and composition. We found that higher functional diversity was associated with higher productivity at local spatial scale (tens of meters), while soil depth and texture were the main drivers of productivity at the hectare scale. At this larger scale, functional diversity tended to be saturated due to the low turnover of species and functional traits of the temperate mixed forest and the limited representation of physiological diversity in the model.

## 1 Introduction

Biodiversity is a key property of forests that affects important ecosystem services, including provisioning services such as timber supply or water purification, cultural services of recreational and spiritual value, and regulating services such as carbon sequestration (Hooper et al., 2005; Cardinale et al., 2012; Chamagne et al., 2017; Aerts et al., 2018; Isbell et al., 2017). Biodiversity also plays an important role in the carbon cycle and influences vegetation–atmosphere interactions and feedbacks (Schimel et al., 2015). For example, higher biodiversity may increase the resistance and resilience of ecosystems to climate change and increase carbon sequestration contributing to climate change mitigation (Isbell et al., 2015; Liang et al., 2016; J. Liu et al., 2018; Huang et al., 2018). However, earth’s biodiversity is declining rapidly with negative consequences for ecosystem functions and services (Cardinale et al., 2012; Ceballos et al., 2015; Díaz et al., 2019a). Thus, losses in biodiversity may contribute to accelerating impacts of climate change on forest ecosystems (Mori, 2020), triggering potentially additional species losses (Trisos et al., 2020; Arneeth et al., 2020). Despite recognized importance of plant diversity to help ecosystems provide multiple functions and services (Hautier et al., 2018; Díaz et al., 2019b),

there is still considerable uncertainty in understanding and predicting the mechanistic relationship between biodiversity and ecosystem functioning, such as productivity or biomass production, (BEF) and the role of different aspects of biodiversity such as functional, genetic, phylogenetic or taxonomic diversity. Specifically, there is a need to improve our understanding of how BEF relationships scale up from plot-level to large contiguous areas of forest, how BEF relationships may be modified by environmental variation and change, which measures of biodiversity can be used for large-scale assessments, and how biodiversity effects are represented in mechanistic demographic modeling of forest dynamics that can be used for predicting future scenarios and changes.

Positive effects of species richness on ecosystem functioning and stability have been reported widely at plot scale, while mostly focusing at biomass production as an indicator of ecosystem functioning and stability. Initially, results were published mainly from experimental studies (Balvanera et al., 2006; Cardinale et al., 2011; Tilman et al., 2014) but recently also from observational studies (e.g. Grace et al., 2016; Liang et al., 2016; Duffy et al., 2017; van der Plas, 2019). Jochum et al. (2020) showed that results from grassland experiments represent realistic species compositions and Liang et al. (2016); Oehri et al. (2020) found positive effects when controlling for differences in climate across sites, but it is unclear whether the relationships will hold within natural ecosystems that extend beyond the typical plot-scale (Gonzalez et al., 2020), and very few studies explicitly test plot-size effects (e.g. Huang et al., 2018; Chisholm et al., 2013; Poorter et al., 2015). Therefore, scaling up BEF relationships remains a major challenge. We expect BEF relationships to span multiple scales, but the form and strength of the relationship might change across scales, biomes and diversity metrics (Gonzalez et al., 2020). There have been a number of studies addressing environmental context in BEF studies (see Hong et al., 2022, for a recent meta-analysis), but few focused on forests. Paquette and Messier (2011), Ratcliffe et al. (2017), and Mina et al. (2017) found that the mechanisms and BEF effects varied with environmental conditions and stress. Yet, whether or not forests will remain a carbon sink under future climate remains uncertain (Brienen et al., 2015; Sabatini et al., 2019; Arora et al., 2020; Hubau et al., 2020), and this uncertainty may be at least partially attributable to BEF.

Previous BEF literature explored which components of biodiversity are most predictive for ecosystem functioning, but no single component is consistently the best (Craven et al., 2018). Functional diversity is often considered promising (Loreau, 2000; Hooper et al., 2005), and in a review of 258 BEF studies of naturally assembled communities, van der Plas (2019) found that, while most studies focused on the effects of taxonomic diversity, metrics of functional diversity were generally stronger predictors of ecosystem functioning. This is in line with early findings from grassland experiments. For example, Tilman, Knops, et al. (1997) found that functional composition and functional diversity were the principal factors explaining plant productivity and Petchey et al. (2004) found that functional diversity explained greater variation in biomass production than species richness. Yet, forest functional diversity is rarely assessed explicitly and independent of taxonomy (but see Schneider et al., 2017; Guillén-Escribà et al., 2021). Most plant studies thus far have focused on the effects of species richness (as a measure of biodiversity) on biomass (as a measure of ecosystem function) in grassland ecosystems, mostly under uniform abiotic conditions. Therefore, little is known about other dimensions of diversity and function, and their relationships in forests across a larger range of environmental gradients and spatial scales (Sheil & Bongers, 2020).

Regarding underlying mechanisms behind BEF relationships, the theoretical reasoning suggests that niche complementarity (complementary traits lead to better resource use of a community as a whole), selection probability (higher likelihood to have highly productive individuals), and ecological insurance (higher likelihood to adapt to or recover from fluctuating environmental conditions or disturbance) underpin biodiversity effects on ecosystem functioning and stability (Tilman, Lehman, & Thomson, 1997; Yachi &

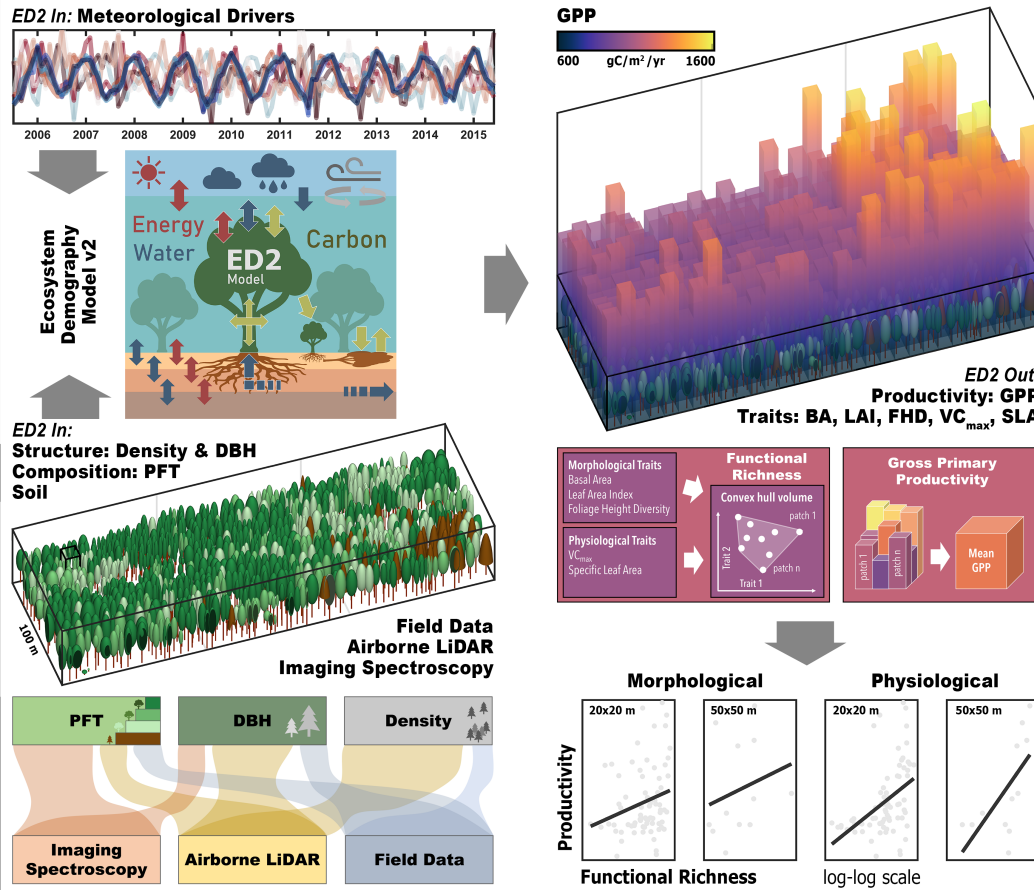
Loreau, 1999; Loreau, 2000). However, integration of observed biodiversity patterns into terrestrial biosphere models and direct demographic modeling of these mechanisms still represents a challenge, but it is critically important.

Simulations and model experiments using process-based models can help fill some of these knowledge gaps, especially since diversity experiments and measurements of plant functional traits, diversity and functioning are difficult to conduct in forest ecosystems. Morin et al. (2011), for example, used a process-based dynamic vegetation model to simulate biodiversity experiments for a range of sites and species in Europe, finding consistent positive effects of biodiversity on productivity due to complementarity. Extending this approach to larger scales, Levine et al. (2016), Sakschewski et al. (2016) and Longo et al. (2018) found that ecosystem heterogeneity and diversity were important to predict forest resilience to climate change including extreme drought events in the Amazon. Many terrestrial biosphere models, however, are not able to resolve this level of detail, or only allow to simulate potential vegetation, which can lead to uncertainties in the prediction of the carbon cycle (Braghiere et al., 2019) and climate change feedbacks (Schimel et al., 2019; Fisher & Koven, 2020). The integration of remote observations of forest composition and structure, such as from imaging spectroscopy and lidar, into models holds great promise to improve our understanding of patterns and drivers of forest diversity and productivity. Previous studies have shown that incorporating such measurements into biosphere models, such as the ecosystem demography model version 2 (ED2), substantially improved their predictions of forest carbon fluxes (A. Antonarakis, 2014; A. S. Antonarakis et al., 2022; Rödiger et al., 2018).

In this study, we investigate the relationship between forest functional diversity, as a measure of biodiversity, and productivity, as a measure of ecosystem functioning, across spatial scales and environmental gradients by integrating remotely sensed measures of forest structure and composition in the terrestrial biosphere model ED2 (Fig. 1). Analyses of the model outputs enabled us to address the two main research questions: (1) What is the relationship between functional diversity and productivity at different spatial scales? (2) How does the relationship between diversity and productivity vary across environmental and ecological gradients involving different soil types, plant functional types (PFTs) and canopy structural types? We expect a positive relationship between functional diversity and productivity over longer time scales, since diversity promotes spatial and temporal complementarity and stability in light and water use as simulated among different plant functional and structural types in ED2 (Longo et al., 2020; Meunier et al., 2021; A. S. Antonarakis et al., 2022). We also expect differences in soil types to influence both diversity and productivity, especially if water availability is limited. For example, simulations by Longo et al. (2018) showed that forests on sandier soils were more resilient to drought, and Medvigy et al. (2019) found that variation in soil properties caused variation in biomass and ecosystem composition in simulations of forest succession. Based on Chisholm et al. (2013), we would expect sampling effects and niche complementarity to dominate at small scales, while environmental gradients should drive patterns at large scales. However, this has not been tested in terrestrial biosphere models and in observational studies it is often difficult to disentangle effects of composition and environment.

## Materials and methods

We combine field data with high-spatial resolution airborne laser scanning and imaging spectroscopy measurements to derive estimates of temperate forest structure (i.e. stem density and diameter at breast height) and composition (i.e. plant functional types) that we use as initial conditions in the process-based terrestrial biosphere model ED2 (Fig. 1, Longo, Knox, Medvigy, et al., 2019). ED2 models dynamic interactions, niche complementarity and competition for resources (light and water) (Longo, Knox, Medvigy, et al., 2019; Longo, Knox, Levine, et al., 2019). We simulate gross primary productiv-



**Figure 1.** Forest modeling approach to derive forest diversity and productivity relationships in a temperate mixed forest. We used airborne imaging spectroscopy and light detection and ranging (LiDAR) together with field inventory data to derive stem density, tree diameters at breast height (DBH) and plant functional types (PFT). These variables were used to represent the forest in the ED2 terrestrial biosphere model in  $10 \times 10$  m patches and vertically resolved cohorts within patches, on different soil types. Forest productivity was then simulated as gross primary productivity (GPP) based on hourly meteorological drivers and averaged over 10 years. Together with traits retrieved from the model (morphological: basal area (BA), leaf area index (LAI), foliage height diversity (FHD), and physiological:  $VC_{max}$ , specific leaf area (SLA)), this allowed us to relate the morphological and physiological diversity to the simulated long-term forest productivity. The visualization shows an example based on data and simulations conducted in this study.

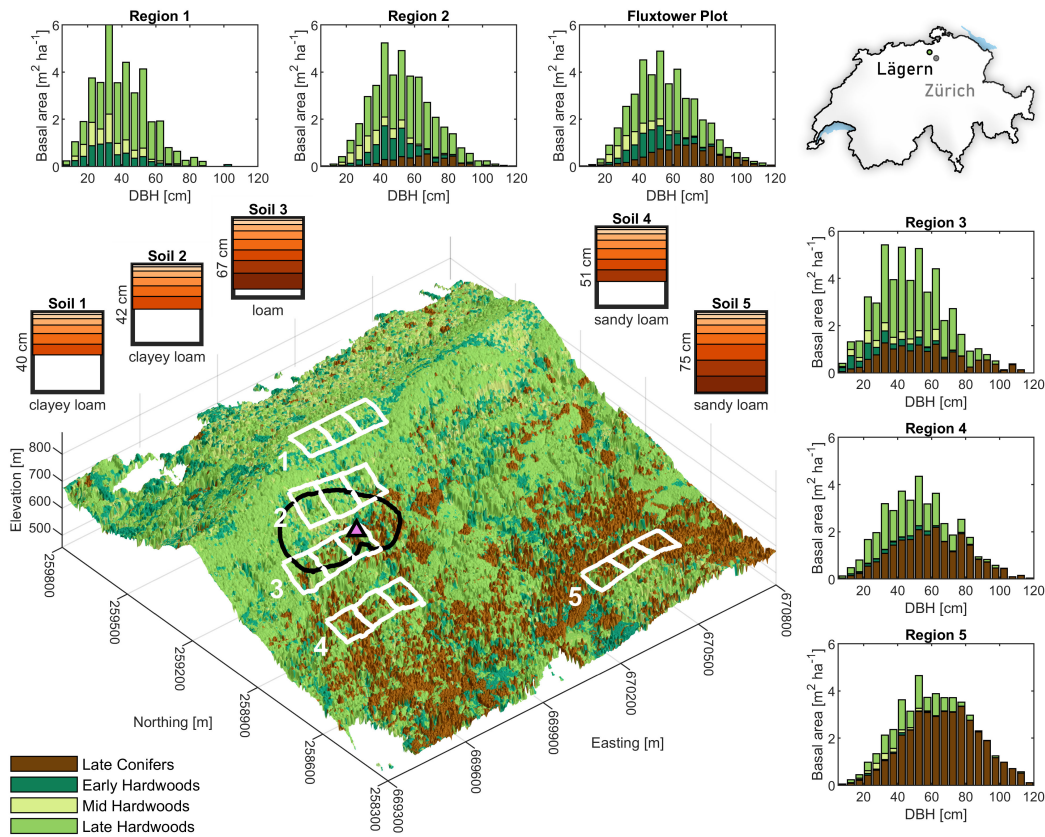
ity (GPP) under observed meteorological boundary conditions from 2006 to 2015 (Fig. 1) for forests across a range of observed soil depths and textures (Fig. 2). We evaluate the model's ability to simulate carbon dynamics and seasonality of the studied temperate mixed forest as measured at the eddy covariance flux tower at the Laegern forest in Switzerland. To explore what is driving the spatial variation in forest GPP at  $20 \times 20$  to  $100 \times 100$ -m spatial scale, we run and analyze simulations based on observed soil, forest structure and composition as well as model experiments where we test combinations of homogenized soil types (mono-soils), plant functional types (mono-cultures), and canopy structural types (mono-structures). We then use the model simulation outputs to investigate the role of different aspects of forest functional diversity on spatial patterns of forest productivity at local to landscape scales (Fig. 1). For this, we analyzed the simulated diversity–productivity relationships using general linear models and random forest models. In terms of functional diversity metrics, we investigate the role of richness, divergence and evenness (see Schneider et al., 2017) derived from morphological traits, namely leaf area index (LAI), basal area (BA) and foliage height diversity (FHD), and physiological traits, namely maximum leaf Rubisco carboxylation rate ( $V_{C_{max}}$ ) and specific leaf area (SLA), modeled at cohort-level. In the following sections, we provide a detailed description and methodology of the study area, the terrestrial biosphere model, the integration of remote sensing data into the model, model evaluation and simulations, and how we derived and analyzed the model outputs with regard to morphological and physiological diversity and productivity.

### Study area

We conducted this study at the Laegern temperate mixed forest in Switzerland ( $47^{\circ}28'43.0$  N,  $8^{\circ}21'53.2$  E), which is located on a mountain range representing broad ecological and environmental gradients (Fig. 2). The study area is characterized by increasing soil depth (40 to 75 cm) and soil grain size (clayey to sandy loam), and mean tree stem diameter and abundance of conifers from high to low elevation (850–450 m above sea level). The vegetation consists of diverse beech forests with a total of 13 tree species and about 70% deciduous broadleaf and 30% evergreen coniferous tree individuals. The dominant deciduous species are common beech (*Fagus sylvatica* L.), European ash (*Fraxinus excelsior* L.), and sycamore maple (*Acer pseudoplatanus* L.). The dominant coniferous species are Norway spruce (*Picea abies* (L.) H. Karst) and silver fir (*Abies alba* Mill.).

Laegern is a key ecological and remote sensing site in central Europe (Morsdorf et al., 2020), which has been studied extensively in terms of 3D structure and radiative transfer (Schneider et al., 2014; Fawcett et al., 2018; Schneider et al., 2019; Kükenbrink et al., 2021), functional and genetic diversity (Schneider et al., 2017; Czyz et al., 2020; Guillén-Escribà et al., 2021; Helfenstein et al., 2022; Czyz et al., 2023), and carbon and water fluxes (Paul-Limoges et al., 2018; Damm et al., 2020; Paul-Limoges et al., 2020). The study area has a fluxtower (CH-LAE; Paul-Limoges et al., 2020) equipped with eddy-covariance instruments and a meteorological station, as well as a 5.5-ha field plot, where 1307 canopy trees were mapped by stem location, crown extent, diameter at breast height (DBH) and species identity (Morsdorf et al., 2020; Guillén-Escribà et al., 2021).

We selected five regions to study diversity–productivity relationships, covering the range of soil characteristics and the ecological gradient from shorter deciduous broadleaf forest on top of the ridge to taller mixed communities in lower elevations. Each region was sub-divided into three  $100 \times 100$ -m sites, selected to minimize environmental heterogeneity within regions and maximize the range of abiotic and biotic variation between regions and sites, respectively (Fig. 2).



**Figure 2.** Study regions at the Laegern mountain, Switzerland, covering a gradient in soil, structure, composition and diversity of the temperate mixed forest. The three-dimensional surface topography is colored by the four plant functional types: late-successional conifers, early-, mid- and late-successional hardwoods. Regions 1–5 are each comprised of three 1-ha sites (white boxes) and show a shift from shorter deciduous broadleaf forest on top of the mountain (1) to taller evergreen coniferous forest at lower elevation (5) following a gradient in soils from shallow clayey loam (1) to deeper sandy loam (5). The histograms show the distribution of basal area per tree diameter at breast height (DBH) for the four plant functional types. The Laegern fluxtower is located at the north-east corner of region three (pink triangle). Model evaluation was performed using forest composition and structure representative of the fluxtower footprint, shown as black outline at 70% flux density. The map (top-right) shows the location of Laegern north-west of Zurich, with respect to the country border of Switzerland.



## Model description

The ED2 model is a process-based terrestrial biosphere model that represents individual plant-level dynamics (growth, mortality and recruitment), and associated ecosystem-level carbon, water and energy fluxes over time scales ranging from hours to centuries (Fig.1; Longo, Knox, Medvigy, et al., 2019). In contrast to conventional ‘ecosystem as big leaf’ models that represent the canopy in a highly aggregated manner, the ecosystem demography (ED) model utilizes the concept introduced by Moorcroft et al. (2001), in which vegetation is represented as cohorts of plants of similar height and plant functional type, grouped in patches that can be initialized with spatially explicit remote observations, within a site of homogeneous environmental conditions with regard to soil, topography and meteorology (Longo, Knox, Medvigy, et al., 2019). Forest patches and cohorts are initialized by PFTs, which have constant plant functional traits associated to them that do not vary within PFT, and DBH and stem density, which vary dynamically over time. Plant growth, mortality and recruitment dynamics are simulated as part of vegetation dynamics. The model can be run with vegetation dynamics off, where only phenological and physiological dynamics are simulated.

The size- and age-structured representation allows us to incorporate fine-scale spatial variation in canopy structure and composition arising from disturbance processes and spatially-localized, size-dependent competition for light within the above-ground plant canopy and below-ground for water (bigger trees have deeper roots and thus can access water in deeper soil layers). To improve vegetation dynamics regarding canopy structure and light availability compared to previous ED modeling schemes, heterogeneity in horizontal and vertical micro-climate environments has been introduced in ED2 (Medvigy et al., 2009; Longo, Knox, Medvigy, et al., 2019). The ED2 biosphere model has shown good conservation of energy, water and carbon (Longo, Knox, Medvigy, et al., 2019; Longo, Knox, Levine, et al., 2019) and has been successfully run with initial conditions from forest-stand data as observed from remote sensing (Longo et al., 2020), field plots (Meunier et al., 2021) or a combination of both (Bogan et al., 2019; Meunier et al., 2022).

## Integration of remote sensing data into the model

The ED2 model can be initialized by prescribing the plant functional types (PFTs), tree stem diameter (DBH) and stem density organized as tree cohorts within forest patches. We derived forest composition (PFTs) and structure (DBH and stem density) using a combination of field data, airborne imaging spectroscopy, and laser scanning (ALS) at high spatial resolution of  $2\times 2$ -m (Fig. S1). We then integrated these empirical data into the model as initial conditions of tree cohorts within forest patches of  $10\times 10$ -m (Figs. S2, S3).

*Forest composition* was integrated into the model based on a classification of ED2-PFTs originally defined for Harvard forest (Medvigy et al., 2009), namely: late-successional conifers and early-, mid-, and late-successional hardwoods (LCf, EHw, MHw, LHw, respectively). These four ED2-PFTs and corresponding physiological traits have been extensively used and tested in temperate forests in North America and Europe (e.g. Medvigy et al., 2009, 2010; A. Antonarakis, 2014; Jin et al., 2017; Paul-Limoges et al., 2020). A. Antonarakis (2014) noted the importance of high-resolution PFT classification and forest structure estimates to capture fine-scale ( $<10\times 10$ -m) PFT-specific variation in forest canopy composition and structure. In this study, we address this requirement by performing the PFT classification at high ( $2\times 2$ -m) spatial resolution using a random forest classifier with remotely sensed input features, trained and validated based on field data of 1307 identified trees (Morsdorf et al., 2020; Guillén-Escribà et al., 2021) and 73 forest stand polygons (Schneider et al., 2017). From 81 possible input features, we selected 27 relevant features (see Table 1) that yielded the best model results, including physiological and morphological forest traits (leaf chlorophylls, carotenoids, water and

**Table 1.** Remote sensing input features used for the random forest classification of plant functional types. We used three morphological and three physiological forest traits from Schneider et al. (2017), and their filtered version applying a median filter with a window size of  $7 \times 7$  pixels. We also used selected principal components of surface reflectance and continuum-removed reflectance from APEX, data described in Supporting Note 1 and Helfenstein et al. (2022).

Random forest feature	Remote Sensing
Canopy height (CH)	Airborne Laser Scanning
CH $7 \times 7$ median filtered	Airborne Laser Scanning
Plant Area Index (PAI)	Airborne Laser Scanning
PAI $7 \times 7$ median filtered	Airborne Laser Scanning
Foliage Height Diversity (FHD)	Airborne Laser Scanning
FHD $7 \times 7$ median filtered	Airborne Laser Scanning
Leaf Chlorophylls (CHL)	Imaging Spectroscopy
CHL $7 \times 7$ median filtered	Imaging Spectroscopy
Leaf Carotenoids (CAR)	Imaging Spectroscopy
CAR $7 \times 7$ median filtered	Imaging Spectroscopy
Leaf Water (LWC)	Imaging Spectroscopy
LWC $7 \times 7$ median filtered	Imaging Spectroscopy
Reflectance principal components 1-9, 13, 18	Imaging Spectroscopy
Continuum-removed reflectance principal components 1, 2, 4, 10	Imaging Spectroscopy

canopy height, plant area index, foliage height diversity, see Schneider et al., 2017), principal components of surface reflectance and continuum-removed reflectance acquired by the airborne imaging spectrometer APEX (Schaepman et al., 2015). The imaging spectroscopy data was processed following Hueni et al. (2009, 2013) and geometrically corrected following Schläpfer and Richter (2002), for more details see Supporting Note 1. The classifier had an overall accuracy of 74% and a Cohen’s kappa coefficient of 61% for the classification of plant functional types over the whole forest. Further details are provided on data in Supporting Note 1, Schneider et al. (2017); Helfenstein et al. (2022), on the classification approach in Supporting Note 2, on the remote sensing workflow in Fig. S1, and on the random forest classification accuracy in Fig. S4. The classified map of plant functional types is shown in Fig. S5.

*Forest structure* was integrated into the model as initial conditions of DBH and stem density estimated from ALS and field data. DBH values were estimated from ALS-derived canopy height using an exponential model that was fitted to field inventory data of 159 late conifers, 253 early hardwoods, 328 mid hardwoods and 566 late hardwoods:

$$\text{DBH} = a \cdot \text{CH}^b + \epsilon(\sigma, \gamma, \kappa), \quad (1)$$

where CH is canopy height,  $a$  and  $b$  are coefficients and  $\epsilon$  is the residual distribution around the mean. To predict not only the mean but a realistic DBH distribution, we derived the standard deviation  $\sigma$ , skewness  $\gamma$  and kurtosis  $\kappa$  of the distribution to model  $\epsilon$  (Matlab R2017a, `pearsrnd`). The resulting values for  $a$ ,  $b$ ,  $\sigma$ ,  $\gamma$  and  $\kappa$  are summarized in Table S1. We applied this approach to predict a DBH value for each  $2 \times 2$ -m pixel based on its

remotely sensed canopy height. Single-tree delineation was applied to the ALS point cloud to estimate the density of stems of different sizes (i.e. canopy height classes) across each 1-ha site (Morsdorf et al., 2004; Kaartinen et al., 2012; Y. Wang et al., 2016). The method had a detection rate of 79% overall, 83% for trees  $\geq 35$  m and 76% for trees  $< 35$  m. We show a comparison between the field data and predicted stem density and DBH in Figures S6 and S7. We then assigned stem density to each  $2 \times 2$ -m pixel based on canopy height, by assigning the average density estimate per 1-m canopy height class derived at each study region. For more information on the forest structure estimation, see Supporting Note 1 and Kükenbrink et al. (2017) for the underlying lidar data, see Supporting Note 3 for more details on the stem segmentation and basal area calculation, and see Figure S1 for a workflow overview.

Finally, values were aggregated as cohorts in discrete  $10 \times 10$ -m forest patches across each  $100 \times 100$ -m site by averaging DBH and stem density for each plant functional type and 10-cm DBH class (Fig. S2), which were used as initial conditions in the model (Fig. S3). This approach reduces the number of cohorts to simulate in the model, reduces computational expenses, and better approximates the individual tree scale of the forest while preserving plant functional type distributions within patches. The cohort-based nature of the ED2 model means that forest canopy structure can be prescribed from spatially-resolved field or remote sensing measurements of DBH and stem density. Therefore, the current state of the forest's morphological diversity can be directly incorporated into the model simulation, thereby accounting for impacts of past disturbances and forest management on canopy structure. All other structural attributes, such as tree height, leaf area index (LAI) and biomass, are then calculated by ED2 using the model's allometric relationships that are part of the definition of each PFT (Fig. S3).

*Meteorological drivers* should reflect short-term (hourly-to-weekly) meteorological variability, which has an important effect on ecosystem functioning such as carbon sequestration, and, over decadal timescales, can drive shifts in forest structure and composition (Medvigy et al., 2010). Therefore, we used hourly meteorological variables measured between 2006 and 2015 as boundary conditions. Atmospheric pressure at field elevation (hPa), air temperature ( $^{\circ}\text{C}$ ), relative humidity (%), average wind speed ( $\text{m s}^{-1}$ ), and precipitation (mm) were measured at 10-minute intervals on the Laegern fluxtower as part of the national air pollution monitoring network (NABEL) of Switzerland. Incoming shortwave ( $\text{W m}^{-2}$ ) and longwave radiation fluxes ( $\text{W m}^{-2}$ ) were measured at 1-minute intervals. For gap filling of missing values ( $< 2\%$ ), we used meteorological data from nearby meteorological stations (Supporting Note 4, Fig. S8). All meteorological variables were averaged to one hour for input into the ED2 model. Atmospheric  $\text{CO}_2$  was assumed constant at  $391 \mu\text{mol mol}^{-1}$ , consistent with the average background values observed at Mauna Loa between 2006 and 2015 (Tans & Keeling, 2020).

*Soil* information was used from FOAG (1996) to specify spatial variation in soil depth and texture (relative sand, loam, clay content) as the main ED2 inputs (Fig. 2).

### Model evaluation

We evaluated the model's carbon flux predictions for the period 2006–2015 against corresponding estimates from eddy-covariance fluxes (Baldocchi, 2003) measured continuously at the Laegern flux tower. Flux quality post-processing was done following Vickers and Mahrt (1997). Standardized gap filling and partitioning of the net ecosystem  $\text{CO}_2$  exchange into GPP and ecosystem respiration were done using the method from Barr et al. (2004). We ran the flux footprint prediction model FFP (Kljun et al., 2015) to estimate the average proportions of PFTs, DBH and stem density within the footprint based on the  $2 \times 2$ -m remote sensing maps (Fig. S1). The predicted average daytime fluxtower footprint is shown in Figure S9. We then selected a sample of 200 representative forest

**Table 2.** Model simulations under observed initial conditions and experiments run using ED2 on five regions each comprised by three 1-ha sites (15 total) to produce monthly outputs for the years 2006–2015. Multiple entries separated by | represent multiple simulations in a set. Mono-soils were simulated at three depths (40, 51, 75 cm) and three textures (-clayey loam, o-loam, O-sandy loam), and the combinations thereof. Monocultures were simulated for early-, mid- and late-successional hardwoods (EHw, MHw, LHw) and late-successional conifers (LCf). Mono-structures were simulated for sparse, medium and dense canopies.

Simulation	Composition	Structure	Soil	Vegetation dynamics
Observed	as observed	as observed	as observed	on   off
Experiment Mono-soil	as observed	as observed	40 .   40 o   40 O	off
			51 .   51 o   51 O	
			75 .   75 o   75 O	
Experiment Mono-culture	EHw   MHw	as observed	40 .   51 o   75 O	off
	LHw   LCf			
Experiment Mono-structure	as observed	sparse   medium dense	40 .   51 o   75 O	off

patches for simulation in ED2 and comparison to fluxtower estimates that resembled the average forest composition within the footprint as shown in Figure S10.

We ran a 10-year spin-up phase using the 200 patches as initial condition before simulating the years 2006–2015 including vegetation dynamics. Longo, Knox, Levine, et al. (2019) tested the sensitivity of the model with regard to different spin up times from 5 to 60 years and found that the effect was relatively small if the spin up time was at least 5 years. Demographic rates showed low sensitivity. Also, GPP and the dynamic of the living trees is not influenced by soil carbon pools, which would take longer to reach equilibrium. Other studies used similar spin up times. For example, A. S. Antonarakis and Guizar Coutino (2017) used a 10 year period and Medvigy et al. (2009) used a spin up of 3 years for grasses.

We also assessed the predicted phenology by comparing ED2’s monthly simulated LAI with satellite-based LAI estimated using the data assimilation model PhenoAnalysis (Stöckli et al., 2011). We ran the PhenoAnalysis model in the data assimilation mode to fit an LAI time series to the noisy Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data taking into account the gap filled meteorological variables from the fluxtower (Fig. S11).

### Model simulations and experiments

For all simulations, we ran the model over a 20-year period by cycling through the meteorological drivers time series twice. The first 10-year cycle was considered spin-up, so that the soil moisture and the vegetation dynamics could stabilize after integrating initial conditions of the forest, and only the second 10-year cycle was considered in the analyses.

To address the two research questions and disentangle the effects of forest structure, composition and soil on productivity, we ran five sets of simulations on the 15 ( $5 \times 3$ )  $100 \times 100$ -m sites, summarized in Table 2. The first set of simulations were run with the observed composition, structure, and soil information for the 15 sites, with both vegetation dynamics on and off. Note that with vegetation dynamics off, phenological and physiological dynamics are still simulated, but the dynamics of mortality, growth and recruitment are only simulated when vegetation dynamics are on. We then ran three experimental simulations to which we refer as mono-soils, mono-cultures and mono-structures. In the mono-soil simulations, the 15 sites were run with observed stand composition and structures on nine uniform soils ( $3$  soil depths  $\times$   $3$  soil textures). In the mono-culture simulations, the 15 sites were run with four different uniform PFTs, each on 3 soils (i.e.  $4$  PFTs  $\times$   $3$  soils  $\times$   $15$  sites). Finally, the mono-structure simulations were run with the observed composition across the 15 sites, but using three different uniform canopy structures, each on 3 soils ( $3$  structures  $\times$   $3$  soils  $\times$   $15$  sites). Canopy structure types were created by replicating the vegetation structure of forest patches that had low ( $19 \text{ m}^2 \text{ ha}^{-1}$ ), medium ( $39 \text{ m}^2 \text{ ha}^{-1}$ ) and high ( $83 \text{ m}^2 \text{ ha}^{-1}$ ) basal area across all 15 sites, while keeping the PFT-composition as observed. The model experiments were run with vegetation dynamics off to maintain the specified canopy composition, structure and soil type combinations, which might not naturally occur.

### Forest functional traits, diversity and productivity

Forest functional traits were calculated as patch-averages at  $10 \times 10$ -m spatial grain from cohort-level ED2 model outputs. Traits and diversity remained constant in simulations with vegetation dynamics off, but can vary when vegetation dynamics are simulated. To improve the comparability and interpretation of the various results, we related productivity to initial functional diversity of summer 2006. This marks the first peak growing season of the time series and the initial condition as prescribed by remote sensing and field data, thus providing valuable insights into how initial diversity predicts productivity over time (Hagan et al., 2021). The selected traits represent important ecological and model variables for ecosystem functioning, relating to the distribution of leaf area (LAI), tree diameter and density (basal area, BA), vertical canopy layering (foliage height diversity, FHD), maximum leaf Rubisco carboxylation rate ( $VC_{\max}$ ) and specific leaf area (SLA). The physiological traits  $VC_{\max}$  and SLA were derived from the model values assigned to each PFT and within-patch PFT-mixtures by calculating weighted averages based on the cohort leaf area index and leaf biomass, respectively (Fig. S3). This means that the resulting values of  $VC_{\max}$  and SLA per forest patch were restricted to the mixtures of four PFTs and their trait values, which are constant in the model. The morphological traits were also derived based on the cohorts within each forest patch, with the difference that they can vary within and between PFTs (based on remotely sensed tree diameter and density, and PFT-specific model allometries to LAI and height) and dynamically over time (if vegetation dynamics is simulated). BA and LAI were derived as cohort averages per patch, and FHD was calculated from the vertical distribution of cohort LAI values within each patch following Schneider et al. (2017). We then calculated multi-dimensional functional diversity metrics from those traits (see Fig. S3), specifically morphological and physiological richness, divergence and evenness at  $20 \times 20$ ,  $30 \times 30$ ,  $40 \times 40$ ,  $50 \times 50$  and  $100 \times 100$ -m spatial extent following Schneider et al. (2017). We defined functional richness as the average of morphological and physiological richness, since both should receive equal weight but they were calculated with a different number of traits. For forest productivity, we used cohort-level outputs to calculate monthly GPP per  $10 \times 10$ -m forest patch and average annual and decadal GPP of 2006–2015. We also calculated GPP normalized by leaf area, for comparison of leaf-level productivity.

## Statistical analyses

To study the effects of morphological and physiological diversity on GPP, we fitted a linear model (Matlab 2019a, fitlm) with functional diversity metrics (log(richness), divergence, evenness) as explanatory variables and log(GPP) as the response variable; and a general linear model (Matlab 2019a, fitglm) with soil depth\*texture combinations and functional diversity metrics as fixed effects. We also analyzed the model outputs with a random forest model to show the relative feature importance of average functional traits and diversity for predicting GPP at 20×20 and 100×100-m spatial resolution. The analysis with and without including average plant functional traits in the random forest model indicates contributions of functional diversity for predicting GPP in a direct (additional to mean traits) and indirect (due to correlations to mean traits) way. Predictor importance was estimated from permutations of out-of-bag predictor observations of 1000 regression trees (Matlab 2019a, fitensemble, oobPermutedPredictorImportance; Schneider et al., 2020), and scaled relative to the fraction of variance explained ( $r^2$ ) by the model.

We analyzed the effects of morphological and physiological richness on productivity in model experiments (mono-soil, mono-culture, mono-structure). We fitted general linear models (Matlab 2019a, fitglm) with log(GPP) as response variable, and soil depth\*texture combinations and log(richness) as fixed effects in mono-soil, soil depth\*texture, PFT and log(richness) in monoculture, and soil depth\*texture, structure and log(richness) in mono-structure experiments, respectively.

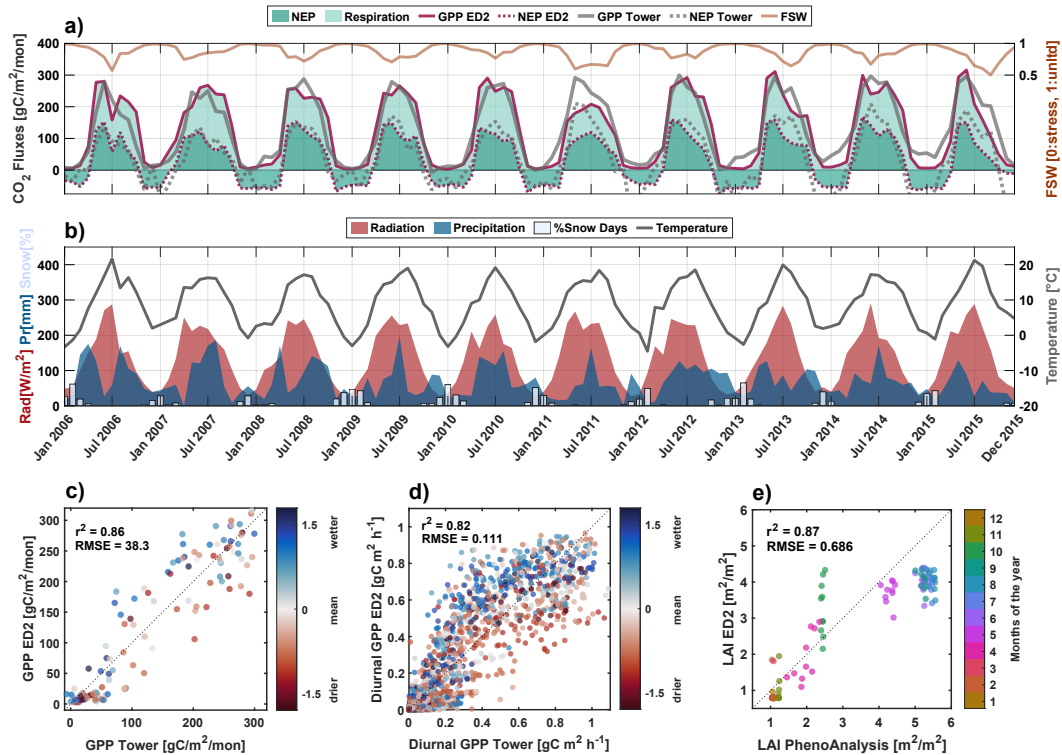
## Results

Integrating high-resolution remote observations of forest composition and structure into the terrestrial biosphere model ED2 allowed us to predict the field-measured size-structure as basal area per diameter class with an  $r^2$  of 0.94, ranging from 0.70 to 0.93 for individual plant functional types at the flux tower plot. Figure S12 shows that we were able to capture the distribution of basal area per DBH and PFT in the model, and Figure S13 shows the scatter plots and linear model results compared to the field-based estimates. This allowed us to study the relationships between morphological and physiological diversity and forest productivity at various spatial scales (20–100-m) along an environmental gradient (5 soil types) in simulations of observed conditions and model experiments. We first evaluated the model performance by comparing simulated carbon fluxes with eddy covariance-based estimates at the temperate mixed forest's fluxtower over the course of ten years, which built the basis for the subsequent diversity–productivity analyses.

### Model evaluation

We found that the model was able to accurately predict the carbon dynamics and seasonality of the Laegern temperate mixed forest averaged across the flux tower footprint, explaining 86% and 82% of monthly and diurnal variations in GPP as estimated at the flux tower using eddy-covariance data from 2006 to 2015. Figure 3 shows the simulated carbon dynamics with respect to the most important meteorological drivers and flux tower estimates. The model captured the seasonality of monthly GPP, but was sensitive to water available to the plants, potentially overestimating their physiological response.

For example, annual GPP of the year 2011 was underestimated by 27% (Fig. 3a) following an exceptionally dry spring with precipitation 63% below the decadal average (Fig. 3b). The increased water stress was also reflected by the model parameter FSW (ecosystem-scale down-regulation factor for photosynthesis due to limited soil water availability; FSW = 1 means no soil water stress), which showed values 13% below the growing season average, indicating increased drought stress. Similar effects of reduced GPP



**Figure 3.** ED2 model evaluation of monthly and diurnal carbon fluxes and monthly leaf area index (LAI) against eddy covariance tower-based and satellite-based estimates in the context of meteorological drivers. The panels show (a) monthly simulated gross primary productivity (GPP, solid red line), heterotrophic and plant respiration (light green area), net ecosystem productivity (NEP, dark green area, dotted red line), the flux tower estimates of GPP (solid gray line) and NEP (dotted gray line); (b) monthly radiation (red area), precipitation (blue area), percent days with snow cover (white bars), and air temperature (solid gray line); (c) modeled GPP (ED2) against flux tower estimates (Tower) per month and (d) as monthly average diurnal cycle per hour; (e) modeled LAI (ED2) as monthly average of site-level LAI against satellite-based LAI using PhenoAnalysis to retrieve LAI from Moderate Resolution Imaging Spectroradiometer (MODIS). The colorscale of wetter to drier months is based on a z-score transformation of monthly precipitation values from 2006–2015 to a mean of 0 and a standard deviation of 1 for each month.

and FSW were observed for dry summer months in 2006, 2008 and 2014, and an early GPP drop-off in dry and hot summers of 2013 and 2015. In 2006, the wet spring and fall (115% and 24% above average precipitation) led to 23% higher annual GPP than estimated by the tower despite hot and dry June and July. In summary, the model overestimated tower GPP under wetter conditions and underestimated it under drier conditions, at both monthly (Fig. 3c) and diurnal scales (Fig. 3d), but generally captured the dynamics with little overall bias. Seasonality was generally well predicted, with a slight tendency to an extended productivity at the end of season. This is also reflected in a higher LAI in October in most years due to ED2 predicting delayed leaf fall in comparison with satellite-based LAI (Fig. 3e).

Here, we focus on GPP, but the model shows a good overall performance in simulating carbon fluxes including net ecosystem productivity as estimated by the flux tower ( $r^2 = 0.76$ ), even though respiration is difficult to estimate from fluxes at this particular site due to the steep slope, dense upper canopy and potential below canopy CO<sub>2</sub> drainage (Paul-Limoges et al., 2017; Etzold et al., 2010).

### Diversity–productivity across sites

We found generally positive relationships between functional diversity and productivity across sites, spatial scales, and functional diversity indices when modeling GPP with vegetation dynamics and observed soil types. A general linear model showed highly significant effects of local morphological and physiological richness ( $p < 0.001$ ) and soil types ( $p < 0.001$ ) on average GPP at 20×20-m to 50×50-m scale, when controlling for different soils between regions (Fig. 4a,b,d,e, Fig. S14; Tab. S2, S3). There is a strong separation in GPP between regions 1-2 and the rest, following differences in soil matric potential and depth (Fig. 4i). Functional divergence and evenness effects were less strong and more variable from positive to neutral (Figs. S15, S16, Tabs. S4, S5, S6, S7).

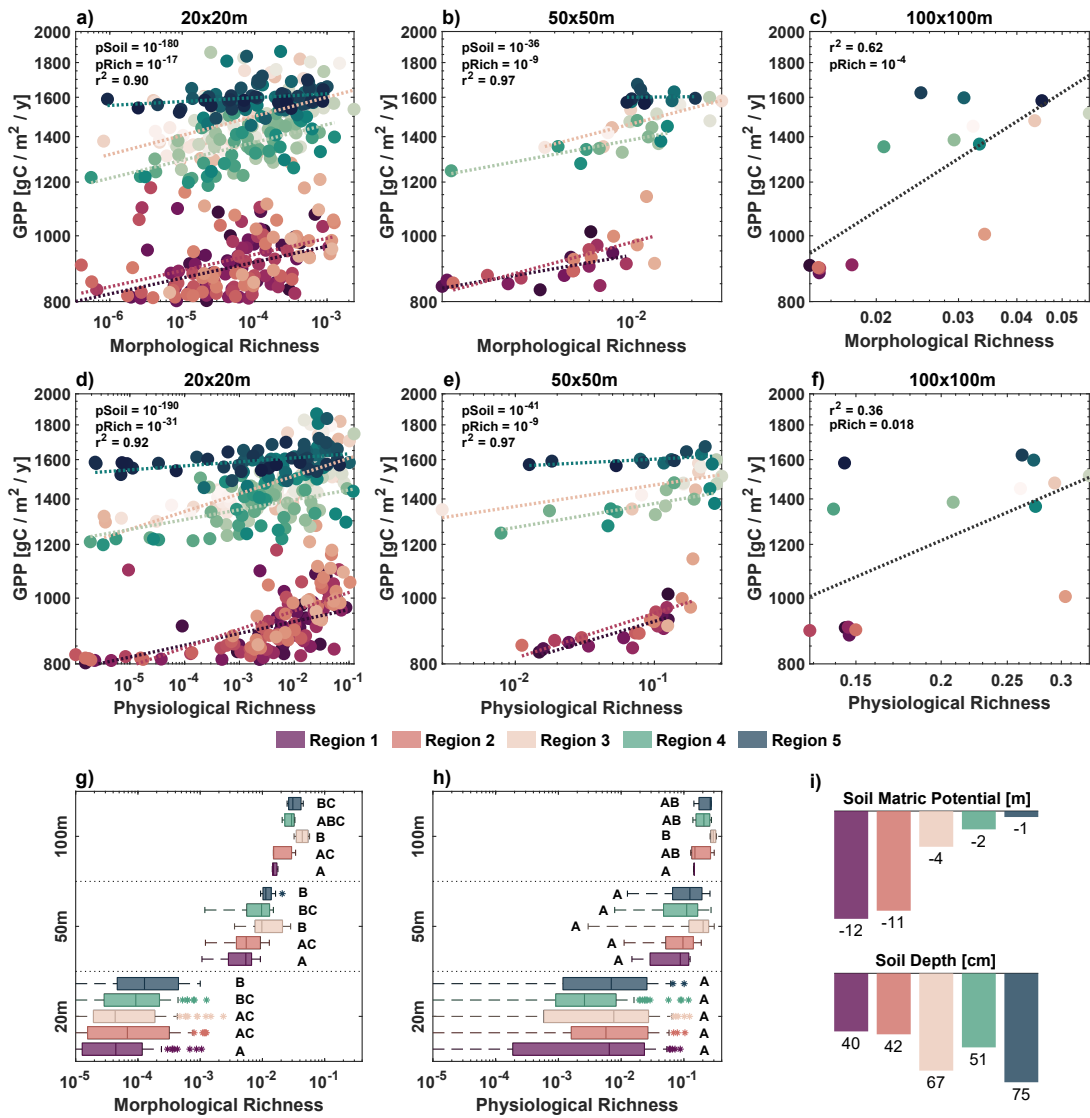
At 100×100-m scale, we found significant positive relationships with productivity across sites for morphological ( $p < 0.001$ ) and physiological ( $p < 0.05$ ) richness (Fig. 4c,f). Figure 4g and h show the increase of functional richness and narrowing of the range with spatial extent. Morphological richness was significantly different between regions with the shallowest and deepest soils (Fig. 4g), while physiological richness did not differ significantly except between region 1 and 3 at 100×100-m (Fig. 4h).

A random forest model analysis showed that environmental variables related to soil water were the dominant predictors of GPP at 100×100-m scale, but functional diversity still showed a relative importance of 9–18% and up to 17–20% for predicting GPP when considering indirect effects through correlation to other functional traits (Fig. 5). At local scale, community-weighted average physiological traits had the highest relative importance (51%) when predicting GPP with vegetation dynamics enabled, whereas community-weighted average morphological traits were most important (27%) when vegetation dynamics was disabled (Fig. 5). In both cases, the importance of functional diversity strongly increased when both direct and indirect effects were considered (11–55% with vegetation dynamics on, 9–26% with vegetation dynamics off). Functional richness was the overall most important diversity metric, and both morphological and physiological richness were important and varied significantly with GPP (Figs. 4, 5).

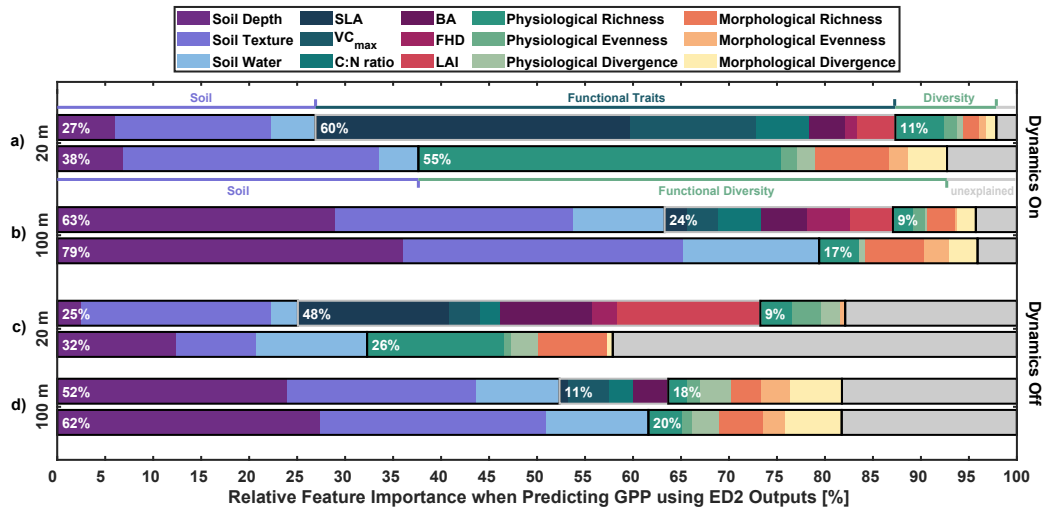
### Diversity–productivity model experiments

In natural ecosystems, co-varying drivers of diversity and productivity, such as different soil characteristics, make it difficult to draw conclusions about diversity effects on productivity (Loreau, 2000; Grace et al., 2016). The model environment enabled us to run experiments with homogeneous soils (mono-soils), plant functional types (mono-cultures)





**Figure 4.** Relationship between (a-c) morphological and (d-f) physiological richness and productivity as average annual gross primary productivity (GPP), simulated across five regions over the course of a decade with vegetation dynamics at (a,d) 20x20-m, (b,e) 50-50-m, and (c,f) 100x100-m scale. Statistics in (a,b,d,e) are based on a general linear model controlling for different soils between regions, while (c,f) shows a linear regression across all sites. Panels (g,h) show the overlap of richness for each region across spatial scales. Significant differences between the regions within three spatial scales are indicated by the compact letter display based on Fisher's least significant difference test. Panel (i) shows soil matric potential as indicator of soil water available to the plants (more negative numbers mean more strength required to extract water), and corresponding soil depth of the five regions. Colors are consistent across panels and refer to the five different regions and their unique soil properties.



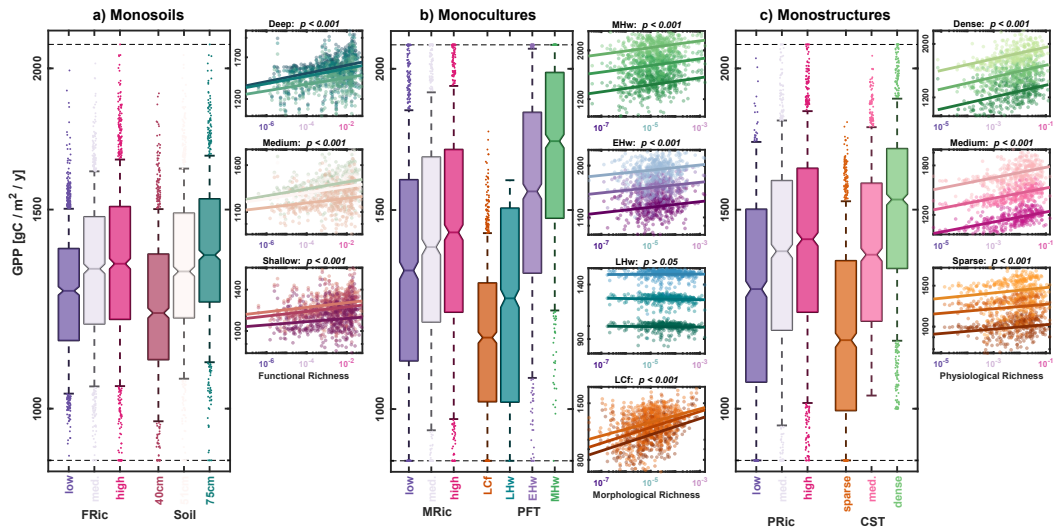
**Figure 5.** Random forest feature importance to predict average annual gross primary productivity, based on simulation outputs with vegetation dynamics on (a,b) and off (c,d) at 20 m (a,c) and 100 m (b,d) spatial scale, scaled by the total variation explained ( $r^2$ ) by the model. The gray bars indicate unexplained variance. The white numbers indicate the relative importance of a group of variables, while the partitioning within the group has to be interpreted with care due to possibly stronger correlations among the different explanatory variables in a group than between the groups. By including (top of each spatial scale) and excluding (bottom of each spatial scale) average functional traits, we can see direct and indirect effects of functional diversity on productivity.

and canopy structural types (mono-structures) to disentangle the effects of soil, morphological and physiological richness on long-term productivity.

We found that functional richness, as average of morphological and physiological richness, on mono-soils had a significant positive effect on GPP ( $p < 0.001$ ) at local scale (20–30 m, see Fig. 6a, Tab. S8). Only when considering productivity per leaf area, the richness effect remained strongly positive among all scales ( $p < 0.001$  at 20–100 m, Fig. S17, Tab. S9). Evenness and divergence showed mixed results from positive to negative and highly to non-significant relationships without clear patterns (Fig. S18).

The mono-culture simulations further showed that the effect of morphological richness on productivity was highly significant at local scales ( $p < 0.001$  at 20–40 m, Tab. S10), but the effect varied by PFT, with no effect for late-successional hardwoods and the most positive effect for late-successional conifers (Figs. 6b, Fig. S19). A positive effect was also found for physiological richness across canopy structures (Fig. 6c; Tab. S11), with strongest positive effect for tall and dense canopies at scales from 20–50 m (Fig. S20).

In all three experiments, the maximum difference in productivity between the lowest and highest productivity soils, plant functional types and canopy structures, respectively, was larger than between lowest and highest forest functional diversity (Fig. 6). Also, there was no diversity effect at 100×-m scale in the experiments (Figs. S17, S19, S20), indicating that morphological and physiological diversity were especially important at local scale.



**Figure 6.** Boxplots comparing low, medium and high (a) functional (FRic), (b) morphological (MRic) and (c) physiological richness (PRic) with (a) shallow, medium and deep soil, (b) late-successional conifers (LCf), late-, early- and mid-successional hardwoods (LHw, EHw, MHw) plant functional types (PFT), and (c) sparse, medium and dense canopy structural types (CST), respectively, at  $20 \times 20$ -m spatial extent. Diversity values were split into low, medium and high based on percentiles at 1/3 and 2/3 of the distributions. Simulations were run with single soil type (mono-soil, each 375 areas at  $20 \times 20$  m), single PFTs (monoculture,  $375 \times 3$  soils), and CSTs (mono-structure,  $375 \times 3$  soils). The scatter plots show all data points and linear regression lines for (a) three soil textures (clayey loam, loam, sandy loam) per soil depth, (b) three soils per PFT and (c) three soils per CST. The three soils were clayey loam at 40 cm, loam at 51 cm, and sandy loam at 75 cm depth. P-values are shown based on general linear models controlling for soil.

## Discussion

Our modeling results show that there are significant positive effects of morphological and physiological diversity on average annual forest productivity in the 2006–2015 period at local spatial scales (tens of meters), and that this phenomenon holds both within soil types and across an environmental gradient. Among diversity indices, we found the strongest and most consistent relationship between functional richness and productivity, while evenness and divergence showed weaker and less consistent results. Functional richness is a measure of the total niche space covered in the multivariate trait space, which can indicate resource use efficiency and utilization through the range of functional strategies and growth forms (Cadotte et al., 2011; Schneider et al., 2017). Therefore, we expect it to be a good predictor of productivity (Durán et al., 2019). Since evenness and divergence describe the distribution within the occupied niche, they are less informative in small niches or with small sample sizes but they can contribute to explaining variation in forest productivity if richness is large (Fig. 5). These positive diversity effects are likely stronger in reality, because terrestrial biosphere models do not include all processes and interactions between species and forest patches, such as the plastic responses of species traits to environmental conditions and stand diversity (Roscher et al., 2018).

At larger spatial scales ( $100 \times 100$ -m), we found overall positive correlations between functional diversity and productivity along the environmental gradient of differing soil

textures and depth, comparable to Durán et al. (2019). This effect is more complex, however, because soils may act as confounding factors as evidenced by the loss of the hectare-scale diversity–productivity relationship when simulating uniform soil types. In the following sections, we discuss the processes and mechanisms in the terrestrial biosphere model that drive the influence of morphological, physiological and environmental aspects of the forest ecosystem on its functioning.

### **Morphological diversity and productivity**

Morphological diversity of the plant canopy structure controls the radiative transfer and light distribution throughout the canopy, with higher diversity in canopy structure leading to a more even distribution of light throughout the canopy and higher light use efficiency and productivity (Ishii et al., 2004; Williams et al., 2017; Kükenbrink et al., 2021). In the ED2 model, higher morphological diversity also relates to higher complementarity in soil water use, as plant size (i.e. tree diameter and height) determines the plant rooting depth. High local variability in plant size means high variability in rooting depth, thus reducing competition for water in the same soil layer, increasing complementarity and overall productivity through reduced stress (Loreau et al., 2001).

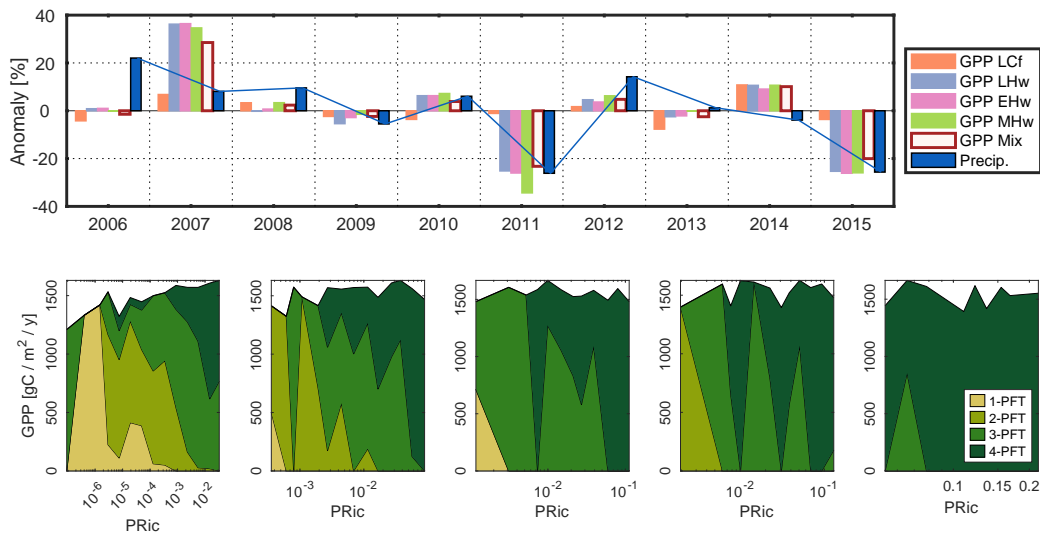
The effect of morphological diversity on productivity is likely underestimated in the model, since interactions between forest patches, such as changed radiative transfer through shading or sun exposure from neighboring patches, were not modeled. However, the remotely sensed structural information that we used as initial conditions in the model likely did integrate processes that are not modeled explicitly, such as nutrient cycles, wind throw disturbance or forest management. Morphological diversity effects in the model are therefore mostly stemming from observed relationships between diversity and other stand-level structural properties that influence model productivity, such as increased stem density and basal area in structurally more diverse forest areas as observed in other studies (Barrufol et al., 2013; Morton et al., 2016). Such a limitation is common in terrestrial biosphere models (Fisher & Koven, 2020) and shows the importance of integrating empirical observations of forest structural variability into the models (e.g., Caylor et al., 2004; Hurtt et al., 2010; Fischer et al., 2016; Levine et al., 2016; Longo et al., 2018; Braghiere et al., 2019). Additional efforts are needed to map forest structure and composition repeatedly and to operationalize data-model integration and model benchmarking over time.

Finally, while tree diameters and density can vary freely and they can be integrated into the model as initial conditions, other structural variables such as height or biomass are defined by static PFT-specific allometric relationships. ALS measurements show, however, a high degree of variability in diameter-height relationships. Incorporating plastic allometry is an interesting area for future model development, since tree heights (and many other variables of canopy structure) can be derived from laser scanning at different spatial scales (e.g. Schneider et al., 2014, 2019, 2020).

### **Physiological diversity and productivity**

The diversity of physiological traits (here only between PFTs, within PFTs these traits are assumed to be constant) represents the variety of functional strategies and life forms (Reich et al., 2003; Díaz et al., 2015), influencing an ecosystem’s ability for adaptation, defense and recovery that will determine its long-term stability and productivity (Díaz & Cabido, 2001; Mason & de Bello, 2013). There are two main effects causing productivity to increase as physiological diversity increases that are captured in the model: (1) a temporal stability and insurance effect, and (2) a selection and dominance effect driven by the physiological properties of the model PFTs.

With respect to (1), the temporal asynchrony of plant communities, species or functional types has been shown to positively influence ecosystem productivity and stability (Tilman et al., 2014; Loreau & de Mazancourt, 2013; Craven et al., 2018), and this effect is also represented by ED2. For example, late-successional conifers can photosynthesize earlier and later in the growing season during leaf development and senescence of deciduous species, and their productivity is more stable due to lower stomatal conductance that leads to lower drought sensitivity (Fig. 7a). In contrast, deciduous hardwoods are more productive during peak greenness, but react more strongly to meteorological variability (Fig. 7a). The ED2 model's plant functional types represent the different seasonal dynamics and stress responses that can explain positive diversity-effects at decadal temporal scales, consistent with previous ecological modeling experiments (Cardinale et al., 2004).



**Figure 7.** Annual variability in gross primary productivity (GPP) of plant functional type (PFT) monocultures and mixtures, and contributions of PFT-mixing to physiological richness (PRic) and GPP at different spatial scales. a) Annual relative anomaly compared to the decadal mean GPP of late-successional conifers (LcF), late-, early- and mid-successional hardwoods (LHw, EHw, MHw), simulated in monocultures, compared to simulations using observed PFT-mixtures (Mix) on a 51-cm loamy soil. The blue bars and connecting lines show annual precipitation anomalies for context. b) Cumulative contributions of mixtures of 1-4 PFTs to GPP by physiological richness across spatial scales from 20×20-m to 100×100-m extent. PRic shows saturation towards larger scales, where almost all PFTs are present at all sites, even though in different abundances.

With regard to (2), there can be a selection and dominance effect in which dominance by species or plant functional types with particular traits affects ecosystem functioning (selection effect; Loreau et al., 2001). As in most central European temperate forests, in our study area beech is the dominant late-successional hardwood species. We modeled late-successional hardwoods with lower  $VC_{max}$  and higher SLA to represent their lower maximum productivity and higher shade tolerance compared to early- or mid-successional hardwoods (Peters, 1992; Heiri et al., 2009, see also Fig. 6). The consequence is that early- and mid-successional hardwoods have higher productivity if enough light is available but cannot maintain high leaf area and productivity in dense canopies or understory, while late-successional hardwoods can maintain dense, tall canopies and productivity under lower light conditions, but with lower maximum productivity. Therefore, lower-diversity

beechn forests will have lower productivity than mixed forests with local disturbance and location-specific growing conditions that allow early and mid-successional species to compete, co-exist and be highly productive. This diversity of plant community and structure was captured by the integration of remote observations into the model that capture different development stages and the effect of local disturbance processes, which is characteristic of productive and sustainable forests over time (Cardinale et al., 2004; Silva Pedro et al., 2016; Dolezal et al., 2020).

Overall, physiological diversity effects may also be underestimated in the model, since physiological complementarity in nutrient use, complementarity in soil microbial communities and related co-benefits of microbial diversity, or complementarity in insect defence strategies were not included in the model formulation. In addition, physiological traits were defined by the plant functional type of each tree species, which limits functional diversity in physiological traits to mixtures of typically three to four PFTs, even when the total species richness may be considerably higher (13 tree species at our study site). Opportunities exist to implement more flexible traits, for example in terms of within-canopy trait plasticity with light availability (Berzaghi et al., 2020; Xu et al., 2021). Further development is needed, for example towards flexible traits such as leaf mass per area, nitrogen or  $V_{cmax}$ , as proposed by Sakschewski et al. (2015) and adapted to European forests by Thonicke et al. (2020). The combined ability to represent plastic trait variation and integrate it from remote sensing could greatly advance the representation of forest functional diversity (e.g. Schneider et al., 2017; Durán et al., 2019; Z. Wang et al., 2020) and the modeling of carbon fluxes and responses to climate change (Schimel et al., 2019).

### Spatial scale and environmental drivers

Our results showed that the diversity effects discussed above primarily act at the local (sub-hectare) spatial scale, where functional diversity varies within a large range from low to medium diversity (Fig. 4g,h). This is related to the community structure of the temperate mixed forest, which has high alpha- and low beta-diversity (Schneider et al., 2017), a situation that is typical for most temperate forests (Swenson, 2012). Additionally, most plant interactions in forests happen at the scale of tens of meters (X. Wang et al., 2015), and thus our results are consistent with findings from field-based studies (Chisholm et al., 2013; Poorter et al., 2015; X. Liu et al., 2018). At larger spatial scales, diversity can be saturated when beta-diversity is low. This can lead to functional redundancy (Rosenfeld, 2002) and a weakening of the diversity–productivity relationship (Jochum et al., 2020). In our study, a saturation of physiological diversity with increasing spatial extent might have occurred earlier than in reality due to the limited number of plant functional types (Fig. 7b) and negligence of intraspecific physiological diversity present at this site (Guillén-Escribà et al., 2021).

The positive correlation between diversity and productivity at the hectare-scale was considerably weakened when the sites were simulated with uniform environmental conditions, indicating co-variation of soil properties with plant diversity and productivity. This suggests that the environmental gradient, characterized by variations in soil depth and texture in the model, was the main driver of productivity at this larger scale, limiting plant productivity through limiting resources such as water availability, while functional diversity was saturated. The effect of soil texture and depth on forest productivity may be overestimated because the model shows a higher-than-observed sensitivity of productivity to plant water availability, which is indicated by monthly and diurnal comparisons to the fluxtower (Fig. 3) and annual GPP anomalies following precipitation (Fig. 7a). The steep, fractured limestone bedrock might offer the trees opportunities to access water below the average soil depth, and this currently cannot be represented by ED2. Longo et al. (2018) also noted that ED2 might overestimate the compactness of clay-rich soils, which could exaggerate water limitation in clayey soils. Therefore, the actual trees

at Laegern may exhibit more resistance to water stress than our analysis implies (Paul-Limoges et al., 2020).

## Conclusions and outlook

Functional diversity had a significant positive effect on decadal forest productivity at local spatial scales (tens of meters) in terrestrial biosphere simulations in a temperate mixed forest. This result was found across all soil types and including morphological and physiological diversity, with strongest effects for functional richness. This implies that local functional richness, which can be measured with remote sensing across large spatial extents and in remote ecosystems, is an important driver of productivity in temperate mixed forests. This finding is in line with studies that analyzed species richness-productivity relationships in field plots (Chisholm et al., 2013; Poorter et al., 2015).

At larger spatial scales (hectare-scale and above), our model experiments showed that diversity's influence on productivity saturated and that soil depth and texture appeared to be the main drivers of spatial variation in forest productivity at this scale. We note that the influence of soil properties may be overestimated due to the challenge of modeling soil water availability to the plants in this complex terrain. The diversity saturation may in part be due to the community structure of this temperate forest and the limited representation of functional diversity in the model, i.e. physiological diversity being limited to mixtures of plant functional types. We also note that the saturation of biodiversity-ecosystem functioning relationship at the larger scale does not imply that this relationship is not important in driving global forest productivity. That is, if diversity is low at the smaller scale, this also leads to lower productivity at the large scale.

The integration of spatially explicit remotely-sensed trait information in Earth system models is crucial to study the role of biodiversity in carbon cycling and to predict impacts and feedbacks of climate change. The advancement of spaceborne remote sensing will help to characterize plant functional traits and diversity globally, for example morphological diversity using lidar (Schneider et al., 2020) and radar (Bae et al., 2019) or physiological diversity using imaging spectroscopy (Cawse-Nicholson et al., 2021), and will provide new measurements of ecosystem functioning (Schimel et al., 2019) to initialize and benchmark global terrestrial biosphere models that represent structurally and functionally diverse ecosystems (Fisher et al., 2018).

## 2 Open Research

The datasets that support the findings of this study are available online at figshare (Schneider et al., 2023): <https://doi.org/10.6084/m9.figshare.22705024.v1>. The most up-to-date ED2 source code is available at <https://github.com/EDmodel/ED2>, and the version used for this study is permanently deposited on <https://dx.doi.org/10.5281/zenodo.3365659>.

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