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Matching scales of eddy covariance measurements and process-based modeling - Assessing spatiotemporal dynamics of carbon and water fluxes in a mixed forest in Southern Germany

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Abstract. Eddy covariance (EC) measurements are a backbone of ecological research and have provided valuable insights into the variability of carbon and water fluxes in different ecosystems and under varying environmental conditions. Since these measurements are integrative and weighted over changing areas (footprint), species-specific information cannot be easily derived except for extended monocultures. However, EC sites are increasingly established in mixed forest stands which are considered to be more resilient under changing environmental conditions. This imposes the question of how species-specific responses can be derived, and how the magnitude of fluxes originating from temporally varying flux footprints predictions (FFPs) might provide insights into species-specific responses.

At a site in the Black Forest (southwestern Germany), which mainly consists of a mix of mature beech and Douglas fir trees, we investigate how EC flux measurements depend on different FFP areas and how species-specific contributions to gas exchange can be disentangled. We applied an ecosystem model that has been calibrated from EC measurements at various sites with beech- and Douglas fir monocultures, and evaluated it with data of soil water content and soil respiration taken at homogeneous parts of the investigated mixed forest site. Then we compared hourly aggregated measurements of net carbon exchange (NEE) and evapotranspiration (ET) with model simulations under four configurations: (i) pure beech, (ii) pure Douglas fir, (iii) a static weighted average of both species, and (iv) a dynamic weighted average based on footprint variations.

The results show that weighted combinations of the two species generally provide a better match with hourly EC measurements than single-species simulations, while differences between static and dynamic weighting approaches remain relatively small. Nevertheless, specific-species responses to the environment can be significantly different during transitional periods

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such as autumn and spring when physiological differences between Douglas fir and beeches are most pronounced. We demonstrate that considering these differences is particularly important for gap-filling EC measurements and thus for determining annual carbon and water budgets. We herewith demonstrate that EC measurements over mixed forests provide important model evaluation information and that species-specific modeling is essential for untangling and distributing the underlying species-specific ecosystem dynamics.

1. Introduction

Forests play a vital role in regulating both global and national carbon and greenhouse gas (GHG) budgets, generally by acting as significant carbon sinks (Pan et al., 2011). However, the increasing frequency and intensity of extreme climatic events — such as droughts, storms, and heatwaves — poses a substantial threat to this function, potentially diminishing forests' capacity to sequester carbon or even turning them into net GHG sources (Anderegg et al., 2020; Haberstroh et al., 2025; Thum et al., 2025; van der Woude et al., 2023). To better understand and predict how forest ecosystems respond to changing environmental conditions, process-based ecosystem models are often used (e.g. Collalti et al., 2018; Dirnböck et al., 2018; Mäkelä et al., 2023;). Such models need to be calibrated and evaluated with site measurements, for which the eddy covariance (EC) method is a key tool providing data on ecosystem carbon (C) and water (H_2O) exchange (Baldocchi, 2003). However, process-based models require not only net fluxes but also the sink and source terms of fluxes, and often rely on species-specific information, which is not easily derived from EC measurements (Stoy et al., 2019).

Despite these fundamental constraints, EC measurements have been established as a backbone for ecosystem research, particularly serving model calibration and evaluation. Numerous stations have been installed throughout recent decades to investigate carbon and water exchange in grassland, agriculture and forests (Teuling et al., 2010; Baldocchi, 2003). These measurements represent integrated gas exchange fluxes across an area which size depends on wind conditions and sensor height, and is called flux footprint prediction (FFP; Schuepp et al., 1990; Schmid, 1994; Vesala et al., 2008). Thus, ecosystem scale measurements are represented by dynamic FFPs that differ in size and location. Consequently, interpretation of EC measurements is becoming increasingly complex with increasing variation of ecosystem properties in different directions or distance to a respective tower (Fang et al., 2024; Grote et al., 2011b), however the directional bias can also be exploited to extract additional information on fluxes from underlying land cover patches in spatially complex ecosystems (Cassidy et al., 2016; Helbig et al., 2017; Tuovinen et al., 2019; Xu et al., 2020). Thus, in most cases where EC measurements have been used to evaluate ecosystem models, this has been done at sites assumed to be homogeneous or corrected for directional bias. In the case of forested areas these sites are typically even-aged monocultures, and have a similar forest structure in all cardinal directions (e.g. Mahnken et al., 2022). At sites that are less homogenous, it is important to determine the differences in gas exchange rates that can be attributed to different forest structures and compositions in specific FFPs, which might vary not only with wind speed and direction, but also on diurnal or seasonal timescales.

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It should be considered that without a spatial analysis of the flux footprint and its bias, comparison with simulation results can be difficult to interpret. By averaging forest structure over large areas and using this for model initialization, this model might be able to represent eddy-covariance fluxes throughout an evaluation period, but different responses of considered species might still trigger deviations between simulations and measurements in periods that provide specific conditions such as heat-waves (Remy et al., 2019). Similarly, caution is advised for periods where EC data are missing. Such periods that require statistical gap filling in order to derive complete budgets for whole days, seasons, or years often cover substantial periods. Such gap-filling is usually applied without considering differing footprint contributions or species composition, which could lead to biases. In addition, missing knowledge about short-term (Fox et al., 2009) or long-term (Mahecha et al., 2007) ecosystem dynamics may lead to substantial under- or overestimation of fluxes and increases the uncertainty of extrapolations into the future. Along with other issues, this data-related uncertainty has been highlighted as important for model evaluation (Medlyn et al., 2005), but only few approaches have been suggested to investigate it explicitly (Kutsch et al., 2005; Oishi et al., 2008).

In this study we address these questions by i) quantifying hourly varying species contributions based on flux footprint predictions (FFPs) of an EC measurement site located in a heterogeneous forest, and ii) evaluating the impact of FFP-specific species composition on model-measurement comparisons of net CO_2 exchange and latent heat flux. The considered site is a mixed forest dominated by patches of European beech and Douglas fir. The simulations are carried out with the LandscapeD-NDC model (Haas et al., 2013), which has therefore been calibrated at independent sites with pure beech and Douglas fir forests and evaluated with further measurements at the study site. The different species contributions are analyzed on different temporal scales, e.g. to differentiate between growing and non-growing season or different phenological periods.

The objectives are first, to assess the influence of different species composition on evapotranspiration (ET) and net ecosystem exchange (NEE) in a mixed forest. This will in addition allow us to isolate the environmental responses of two forest species that will play a considerably larger role for future German forestry (Brandl et al., 2020; Gribbe et al., 2024). The second objective is to analyze the uncertainty resulting from the assumption of a homogeneous footprint for a temperate mixed forest site. Specifically, we hypothesize that simulations representing species variation in the FFP can provide a complementary perspective to conventional statistical gap-filling procedures, particularly by enabling species-resolved interpretations of missing fluxes.

2. Materials and methods

2.1 Site description

The measurement site (48.2685°N, 7.8782°W, 490 m a.s.l), called ECOSENSE forest, is located in the Black forest close to the town of Ettenheim in Southwest Germany. It is a mixed forest and the area we assumed as potential footprint area is dominated by European beech (*Fagus sylvatica*, 47 %), but holds major shares of Silver fir (*Abies alba*, 25 %) and Douglas fir

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(*Pseudotsuga menziesii*, 21 %) (Fig. 1). Within the ECOSENSE forest, a 46-m tall measurement tower was instrumented with an eddy covariance (EC) system and various measurement devices designated to capture carbon and water fluxes and stress relate responses (Werner et al., 2024). According to the Köppen classification, the climate at this site is temperate oceanic with mild to warm summers and cold winters. The mean annual air temperature is about 9.7°C (ranging from 1.1°C in January to 18.8°C in July) and mean annual precipitation is approximately 1000 mm over the last 20 years using historical data from the nearest meteorological Lahr station (ID 2812) of the German Weather Service (DWD). Geologically, the area lies on Triassic sedimentary rock, predominantly the Plattensandstein Formation — sandstone interbedded with clay layers — with minor outcrops of the Rotton Formation. The soils at the study site are Cambisols with silty loam to loamy clay textures, free of carbonates, and well-developed to depths of 60–120 cm. They exhibit moderate permeability and low stone content (Werner et al., 2024).

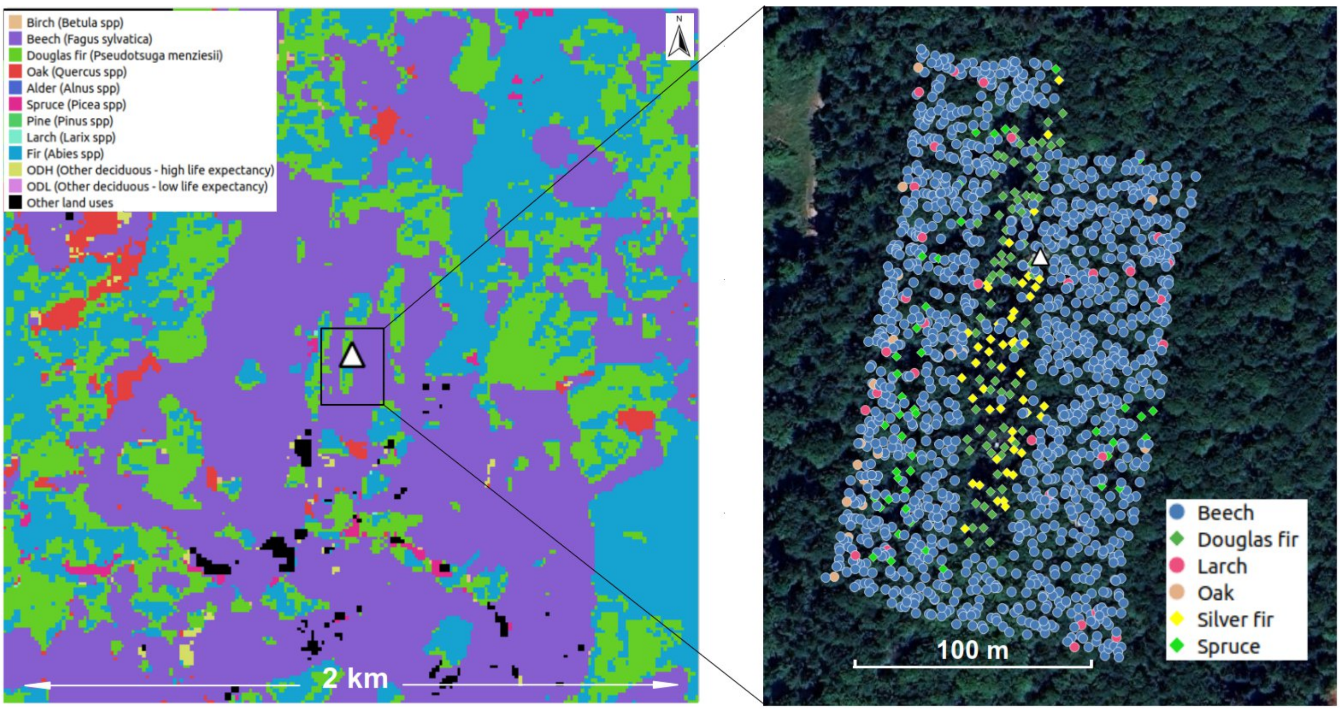

Figure 1: Dominant tree species map within the 2x2km window (left) and the tree inventory in the ECOSENSE experimental site (right). The white triangle shows the location of the eddy covariance (EC) tower. The aerial photo is from Google Earth (© Google Earth 2025).

2.2 Site measurements

2.2.1 Eddy covariance measurements

The EC technique was used to measure the ecosystem CO_2 and water vapor fluxes (evapotranspiration, ET) above the

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ECOSENSE forest (Aubinet et al., 2012; Burba et al., 2013). The EC instrumentation consists of a closed-path infrared gas analyzer (model Li-7200, LI-COR Inc., Lincoln, NE, USA) combined with a three-dimensional sonic anemometer (model CSAT3B, Campbell Scientific Inc., Logan, UT, USA), both measuring at a frequency of 20 Hz. The eddy covariance measurements were performed approximately 20 m above the canopy of the ECOSENSE forest on top of a measurement tower at a height of 46 m above ground level.

EddyPro (version 7.0.9) was used to calculate half-hourly fluxes, which were later averaged to hourly fluxes, from the 20 Hz measurements of the infrared gas analyzer and the three-dimensional sonic anemometer (LI-COR Biosciences, 2022). In this study, only CO_2 fluxes and ET data with quality flags 0 or 1 were used for further analysis, data with quality flag 2 were discarded. The REddyProc software was used for further processing of the EC data (Wutzler et al., 2018), including u_*-filtering according to Papale et al. (2006), gap filling using the marginal distribution sampling (MDS) method (Reichstein et al. (2005)). The MDS method applies look-up tables for similar meteorological conditions, considering shortwave irradiance, air temperature, and vapor pressure deficit, to fill the gaps in the flux data. If no meteorological data are available, the gaps in the flux data are filled using the MDS method with the mean daily course of the fluxes in a moving time window of adjacent days (Reichstein et al., 2005; Wutzler et al., 2018). A flux footprint prediction climatology was created for every hour with available data from the EC system, using the R-code of Kljun et al. (2015). The FFPs were calculated for a domain of 2 x 2 km centered on the tower at a spatial resolution of 1 x 1 m. The input data for the flux footprint predictions were taken from the EddyPro output, except planetary boundary layer height, which was retrieved from the ERA5-Land weather reanalysis dataset (Hersbach et al., 2023). The available EC data from the first year after start of the measurements (15 May 2024 to 15 May 2025) were used for the presented analysis.

2.2.2 Auxiliary measurements

Meteorological data

Several meteorological variables required as input for the LandscapeDNDC model are measured at the study site. Solar irradiance was measured by a heated and ventilated pyranometer (model CNR4, Kipp & Zonen, Delft, Netherland) mounted on the tower above the forest at a height of 47 m. Wind speed and direction was derived from the three-dimensional sonic anemometer integrated in the EC system. Unless data from the EC system were unavailable, data from a propeller anemometer (model Young 05103, R. M. Young Company, Traverse City, Michigan, USA) also mounted on top of the tower were used. Air temperature and relative humidity are taken in the vicinity of the site under open field conditions with sensors mounted at a height of 2 m above ground level inside a passive ventilated radiation shield (model HygroVue 10 and RAD10E, Campbell Scientific Inc., Logan, UT, USA).

Soil moisture

In the ECOSENSE forest permanently installed soil moisture sensors SMT100 (Truebner GmbH, Neustadt, Germany) are

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used to measure dielectric permittivity, soil temperature and volumetric soil water content based on time domain transmission (TDT) principle. A total of 40 sensors were installed in 10 profiles of 4 depths (30, 50, 70 and 90 cm) at the center (plateau) of the observed EC footprint area continuously measuring at a frequency of 15 min. For investigating species influences, two plots were selected influenced only by either purely beech or Douglas fir respectively, each holding seven neighboring trees of similar age and height. Within each of the plots, five soil moisture profiles were arranged in a stratified-random design to ensure a good spatial coverage. First measurements started in October 2023 and are ongoing. All raw data undergo a quality control procedure adapted from Dorigo et al. (2013).

Soil respiration

Soil respiration was measured with an open bottom chamber equipped with a CO_2-Sensor (GMP343, Vaisala Oyj, Finland) at a total of 35 plots (2.25 m^2 per plot). We recorded the tree species for each plot within a vicinity of 5 m and for model evaluation we only chose plots influenced by either European beech (18 plots) or Douglas fir (8 plots) only. Soil respiration was measured on a weekly to bi-weekly basis using two measurement chambers simultaneously during the complete year 2024. From both measurements we calculated a mean value, reporting the respiration for each plot.

2.3 LandscapeDNDC model

2.3.1 Model description

LandscapeDNDC (https://ldndc.imk-ifu.kit.edu, last access: August 15, 2025) is a modular terrestrial ecosystem model (Grote et al., 2011b; Haas et al., 2013). It has been designed to reproduce atmosphere–biosphere exchange processes of carbon, water, and nitrogen, including C and N trace gas exchanges. For this purpose, detailed microclimate, biogeochemical and physical soil process modules are provided to be coupled with vegetation modules (i.e. physiology and structure) that are parameterized at the species level. The LandscapeDNDC model uses air temperature, global radiation, vapor pressure deficit (or relative humidity), and precipitation as meteorological inputs in daily to sub-daily temporal resolution. Soil as well as canopy are 1-d divided into multiple layers, with flexible extensions and properties, depending on available measurements and the initialized ecosystem structure.

Forest carbon uptake and loss are calculated within the physiological simulation model (PSIM) from the basic processes which are photosynthesis and respiration. The latter is differentiated into autotrophic respiration, which in turn consists of growth (fixed fraction of carbon allocated to increase biomass), maintenance (in dependence on temperature and nitrogen concentration, according Cannell and Thornley (2000)) and nitrogen uptake (fixed rate related to nitrate uptake), and heterotrophic respiration related to microbial decomposition of organic matter driven by soil moisture, pH and temperature. Photosynthesis is calculated according to the Farquhar model (Farquhar et al., 1980), which is linked to a soil water-limited stomatal conductance module to optimize gas exchange (Leuning, 1995). Stomatal conductance and soil water availability is thus also

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defining transpiration. Other relevant gaseous water fluxes are evaporation from interception, which is calculated based on leaf area dependent canopy capacity, as well as from snow, open water at the ground and soil. These evaporation terms are driven by potential evaporation determined by a modified Thornthwaite approach (Thornthwaite and Mather, 1957). For more details see descriptions in Holst et al. (2010).

In this configuration, LandscapeDNDC has been previously used to investigate carbon fluxes and budgets in various forested ecosystems in Europe sites (Molina-Herrera et al., 2015; Dirnböck et al., 2020; Cade et al., 2021; Mahnken et al., 2022) and worldwide (Magh et al., 2020; Rahimi et al., 2021).

2.3.2 Model initialization and driving forces

In this study we used hourly climate data for the period from 15 May 2024 to 15 May 2025, corresponding to available eddy covariance time series at the ECOSENSE site (Fig. 2). We considered a spin-up period of 1.5 years starting in January 2023 to allow carbon pools in the soil to equilibrate. Hourly air temperature, global radiation, wind speed, and relative humidity were taken from on-site measurements (see section 2.2.2). Hourly precipitation data from the meteorological station Lahr operated by the German Weather Service (Deutscher Wetterdienst; DWD; https://cdc.dwd.de), located approximately 7 km from the ECOSENSE site.

The soil initialization of the model is based on a vertical profile of soil physicochemical characteristics i.e., humus type, clay and sand content, organic C- and N-content, bulk density, saturated conductivity, stone content, pH, field capacity and wilting point. (Table 1). Only one single on-site soil profile was available for this purpose that we used for all simulations. Regarding the vegetation we initialized two separate forest types, one representative for a beech and one for a Douglas fir forest, each indicating tree species, dominant height, tree diameter at breast height (DBH), and number of trees per hectare. In this initialization, we consider all coniferous trees to be Douglas fir, implicitly assuming that gas exchange responses of Silver fir are sufficiently similar to Douglas fir to be merged. The two initializations are derived from an individual tree inventory which covers an area of 3 hectares surrounding the EC tower (Fig. 1, right). In addition, we used the dominant tree species map at 10 m resolution (Blickensdörfer et al., 2022) to determine the overall shares of coniferous (mostly Douglas fir and Silver fir) and deciduous (mostly beech) within a potential footprint area which is a window of 2x2 km with the ECOSENSE site in the center (Fig. 1, left).

2.3.3 Model parameterization, calibration and evaluation setup

The LandscapeDNDC model in a similar configuration has been used to simulate beech stands already (Grote et al., 2011a; Holst et al., 2010), whereas Douglas fir simulations required a completely new parameterization (see Table S1 for parameters and sources). However, in order to decrease the uncertainty related to literature derived physiological parameters, we calibrated the most sensitive parameters for water and carbon fluxes with Eddy-covariance measurements from various long-term

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observation sites. Therefore, we initialized the model for additional 3 pure beech sites and 2 pure Douglas fir sites, which provided data of latent heat flux and net carbon ecosystem exchange for at least 5 (but mostly more than 10) years. For beech we used three ICOS sites: Leinefelde in Germany (DE-Lnf; Herbst et al. 2015), Soroe in Denmark (DK-Sor; Pilegaard et al. 2003), and Stitna in the Czech Republic (CZ-Stn; McGloin et al. 2018), and for Douglas fir, we used the Speulderbos site in the Netherlands (Van Wijk et al. 2001) and the Campbell River site in Canada (CA-Ca1; Morgenstern et al. 2004). Fluxes were aggregated and compared at daily temporal resolution. We calibrated the most sensitive parameters for transpiration and CO_2 exchange in a stepwise optimization approach for each site as well as for each species separately. The best parameters were selected by minimizing both the root mean square error and the bias between the simulated and measured values. Although the site-specific parameterization in general yielded a closer fit, general species-specific parameterization showed to represent all sites reasonably well and has thus been used for the simulations of the ECOSENSE forest. For details on error and bias of the calibration separated by evapotranspiration and net carbon exchange see supplements (Fig. S1 and S2).
To evaluate the parameterized model's performance at our specific forest site, simulated soil respiration and soil moisture content at specific depths were compared with in situ measurements. Evaluation was carried out separately plots initialized with beech- and Douglas fir, respectively using Nash–Sutcliffe efficiency (NSE) as the main performance metric.

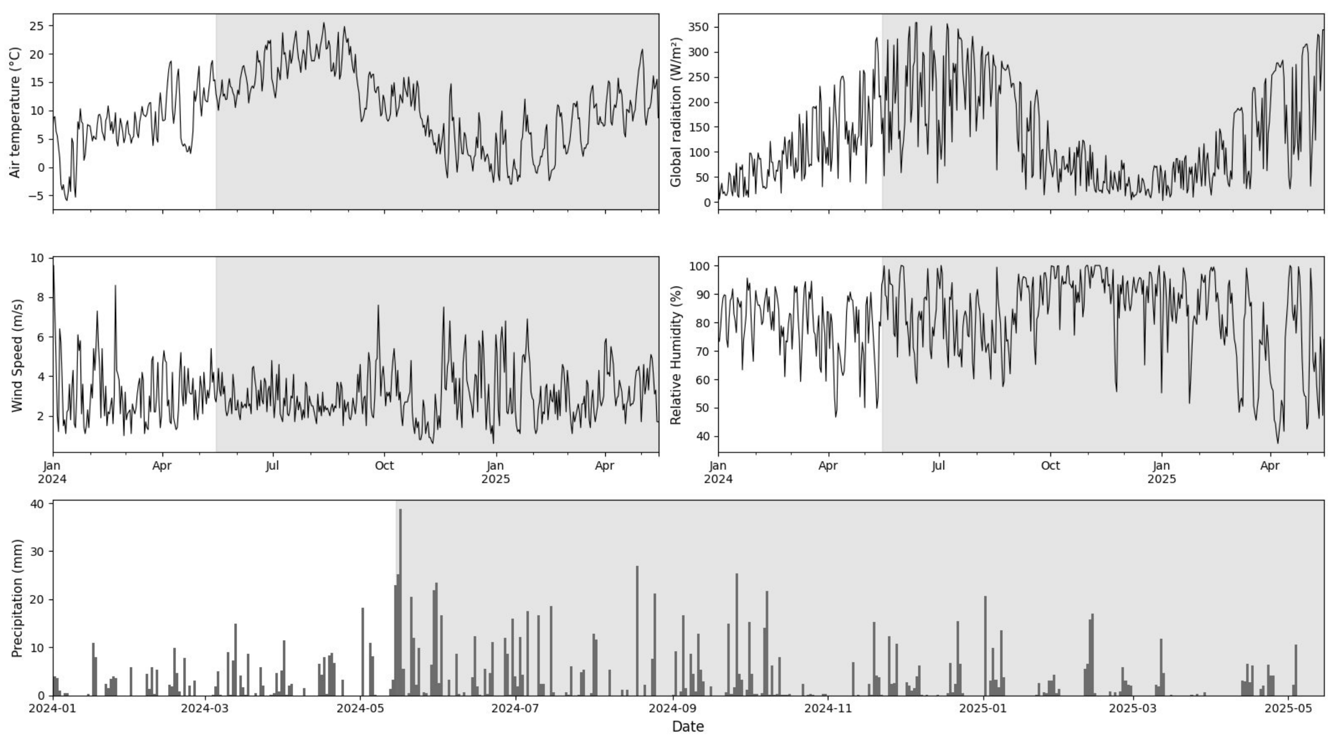

Figure 2: Daily climate variables for the ECOSENSE forest during the period from 1 January 2024 to 15 May 2025. The shaded area represents the study period. Precipitation is from nearby DWD Station Lahr.

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Table 1: Mineral soil properties used for initialization of the LandscapeDNDC model

Soil depth [cm]	Organic C [gC gDW^{-1}]	Total N [gN gDW^{-1}]	pH	Bulk Density [g. cm^{-3}]	Sand Fraction	Clay Fraction	Field Capacity [mm m^{-3}]	Wilting Point [mm m^{-3}]
0-7	0.0216	0.0018	5.1	0.7	0.62	0.14	280	100
7-25	0.0095	0.001	3.5	0.93	0.62	0.16	340	100
25-38	0.0036	0.0007	4.3	1.13	0.61	0.18	350	100
38-50	0.0031	0.0007	3.5	1.19	0.66	0.15	360	150
50-70	0.0019	0.0006	4.5	1.19	0.66	0.15	380	200
70-90	0.0005	0.0005	3.7	1.19	0.66	0.15	380	200

2.4 Estimation of tree species contributions in dynamically changing footprints

To estimate the relative contribution of the different tree species within the footprint area of measured eddy covariance (EC) fluxes, we applied a raster-based spatial convolution approach using high-resolution, hourly footprints and tree species cover data in analogy to Crawford and Christen (2015; Fig. 3). The analysis was restricted to a 2 × 2 km domain centered on the EC tower using only hourly footprints containing more than 80% of the cumulative source contribution in the 2 x 2 km domain. This was needed to minimize inconsistencies of comparisons of EC based measurements with LandscapeDNDC simulations which increase with larger footprint extents (Kljun et al., 2015). Based on a preliminary statistical analysis, this 2 x 2 km domain typically captured the majority (90.7 ± 3.7%) of the sources area for the hourly flux measurements in the ECOSENSE site.

Flux footprints were computed hourly using the analytical model by Kljun et al. (2015), producing a time series of raster layers $F_t(x,y)$ at 1 × 1 m resolution, where each cell represents the percent contribution of that location to the EC flux at time t. To align the spatial resolution of a tree species cover dataset with the footprint raster, the 10 × 10 m dominant tree species grid (see section 2.3.2) was resampled to 1 × 1 m resolution using nearest-neighbor interpolation, preserving a discrete species classification.

For each tree species $s \in S$, a binary mask $B_s(x,y)$ was created, assigning a value of 1 to grid cells where species s was dominant, and 0 elsewhere. Each binary mask was then multiplied element-wise with the corresponding hourly footprint function following Eq. (1):

$$F_{t,s}(x,y) = F_t(x,y) \cdot B_s(x,y) \tag{1}$$

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The resulting raster $F_{t,s}$ retains only the contribution values associated with species s at time t. To obtain the total contribution of species s at each time step, all grid cell values in $F_{t,s}$ were summed following Eq. (2):

$$C_{t,s} = \sum_{(x,y)\in A} F_{t,s}(x,y) \quad (2)$$

where A denotes the 2 × 2 km analysis domain.

This procedure was repeated for each species and each hourly footprint to obtain a time series of species-specific source contributions $C_{t,s}$, expressed as a percentage of the total footprint signal within the 2 x 2 km domain. This raster-based method allowed for a consistent and scalable estimation of the relative contribution of each tree species to the EC measurements, directly linking flux source areas with vegetation composition at high spatial and temporal resolution.

2.5 Data analysis

To explore the vegetation source composition of eddy covariance (EC) carbon and water fluxes, we used simulated net ecosystem exchange (NEE) and evapotranspiration (ET) from the LandscapeDNDC model and compared them with EC observations. The model was run for both, a pure beech and a pure Douglas fir stand representation. These two simulations were then combined in two ways and compared with EC fluxes: (i) using a static weighting (66.5% beech, 33.5% Douglas fir as average of all observed FFPs tree composition), and (ii) using a dynamic, footprint-based weighting, where hourly species contributions were derived by overlapping the EC flux footprint with a high-resolution dominant tree species map (see section 2.3.2) and calculating the proportion of each species contributing at each time step.

Hourly aggregated EC based NEE and ET measurements were compared to the hourly outputs of each individual simulation as well as to the static and dynamic weighted averages for different time periods: the entire year (15 May 2024 – 15 May 2025), and the transitional periods in spring (flushing phase during April) and autumn (senescence during October). For each comparison, we applied simple linear regression and computed the root mean square error (RMSE), Nash–Sutcliffe efficiency (NSE), the bias and the mean absolute error (MAE).

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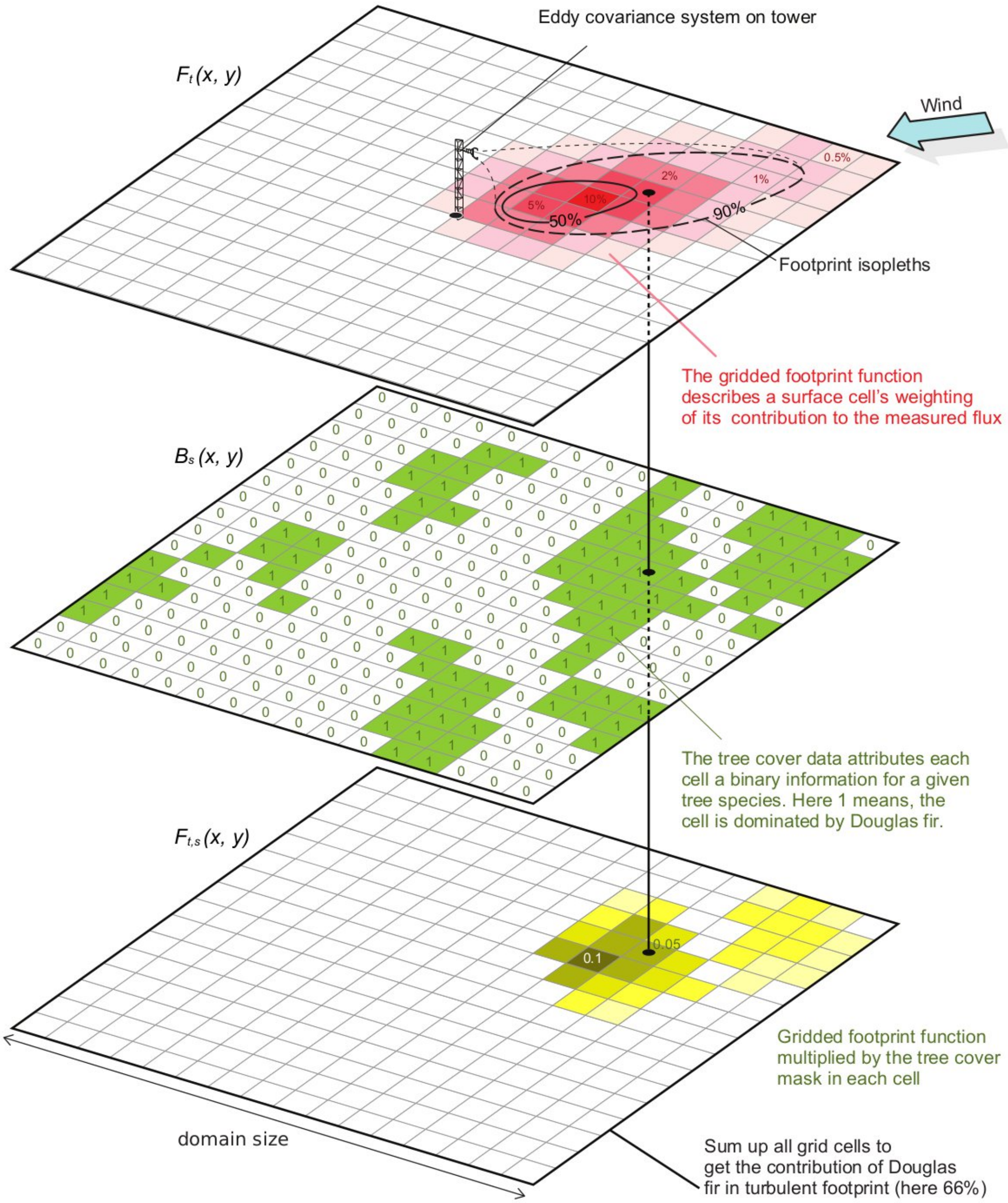

270 **Figure 3: Workflow for estimating tree species contributions to EC flux measurements using raster-based spatial analysis. For each species, a binary presence raster (middle) was generated (1 = species present, 0 = absent). Each binary raster was then multiplied by the corresponding hourly footprint function (top) to retain only the contribution from the target species. The total contribution of each species at each time step was obtained by summing the values of the resulting raster. This process was repeated for each species and each hourly footprint in the analysis period.**

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3. Results

3.1 Model evaluation: Soil moisture and soil respiration

The simulated soil moisture and the simulated soil respiration showed good agreement with observations, capturing both seasonal dynamics and absolute ranges. For soil moisture at 30 cm depth, the simulated time series remained well within the observed range (min–max envelope from the five sensors), yielding NSE values of 0.74 for beech and 0.60 Douglas fir (Fig. 4). Similar results were observed at 50 cm depth with NSE values of 0.60 for beech and 0.65 for Douglas fir (Fig. S3). Soil respiration (sum of below-ground autotrophic and heterotrophic respiration) simulations captured the magnitude and seasonal patterns of measured fluxes, with simulations closely following the observed range derived from multiple daily chamber measurements (18 for beech, 8 for Douglas fir). Model–data agreement was high for both species: beech (NSE = 0.80) and Douglas fir (NSE = 0.79; Fig. 5).

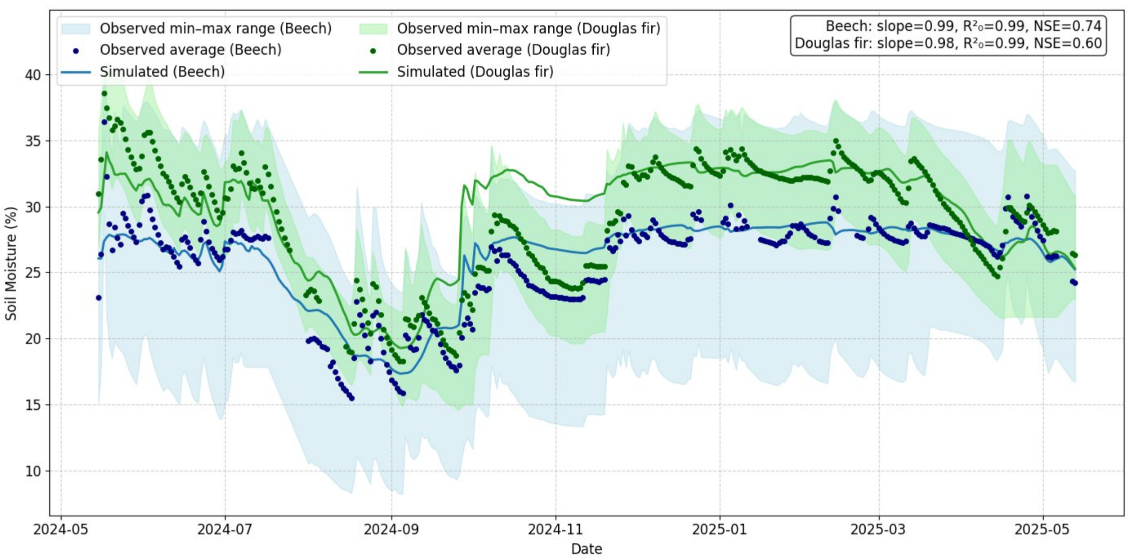

Figure 4: Comparison of simulated and observed soil moisture at 30 cm depth for beech and Douglas fir plots from May 2024 to May 2025 at the ECOSENSE forest. The shaded area represents the observed range (min–max across five sensors in each plot), the dots show the average of the measured flux, while the solid line shows the model simulation.

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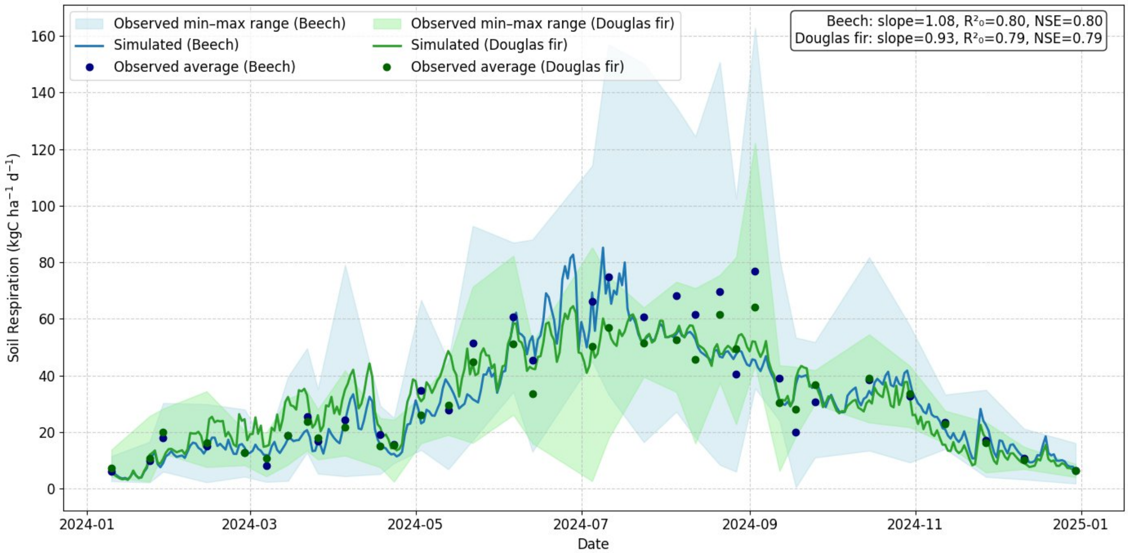

Figure 5: Comparison of simulated and observed soil respiration for beech and Douglas fir stands. The shaded area represents the observed range (min–max across 18 chamber measurements per day for beech and 8 for Douglas fir), the dots shows the average of the measured flux, while the solid line shows the model simulation.

3.2 Spatial pattern of source area contribution

Seasonal and diurnal wind patterns strongly influenced the footprint of the eddy covariance (EC) fluxes at the study site. As shown in Fig. 6a, winds predominantly originated from the south and southwest, with notable frequencies also from the east and northeast, varying by time of day and seasonally. These directional trends shaped the footprint geometry and the relative influence of different vegetation types on the measured fluxes. The species contribution assessed by averaging all footprints from a given wind direction (Fig. 6b) revealed that although beech dominated the source area in any wind direction (average contribution of 66.5%), highest contribution from beech was estimated in the southeast (76.3%) and south (71%), while Douglas fir contributed more substantially at wind directions from the northeast (38.4%), east (35.2%) and southwest (35%).

The spatial distribution of source contributions, aggregated over the full study period, is presented in Fig. 6c. The cumulative footprint shows that 87.1% of the total EC flux signal originated from 80 ha (20% of the 2 x 2 km area) around the EC tower. Due to the frequency distribution of the two dominant wind directions SSW and E, this high-contribution zone forms a distinctive shape resembling an inverted “L”, extending primarily southward and eastward. This spatial alignment underscores the role of wind-driven footprint dynamics and highlights how flux measurements are shaped by a focused, directionally biased region within the 2 × 2 km landscape surrounding the EC tower.

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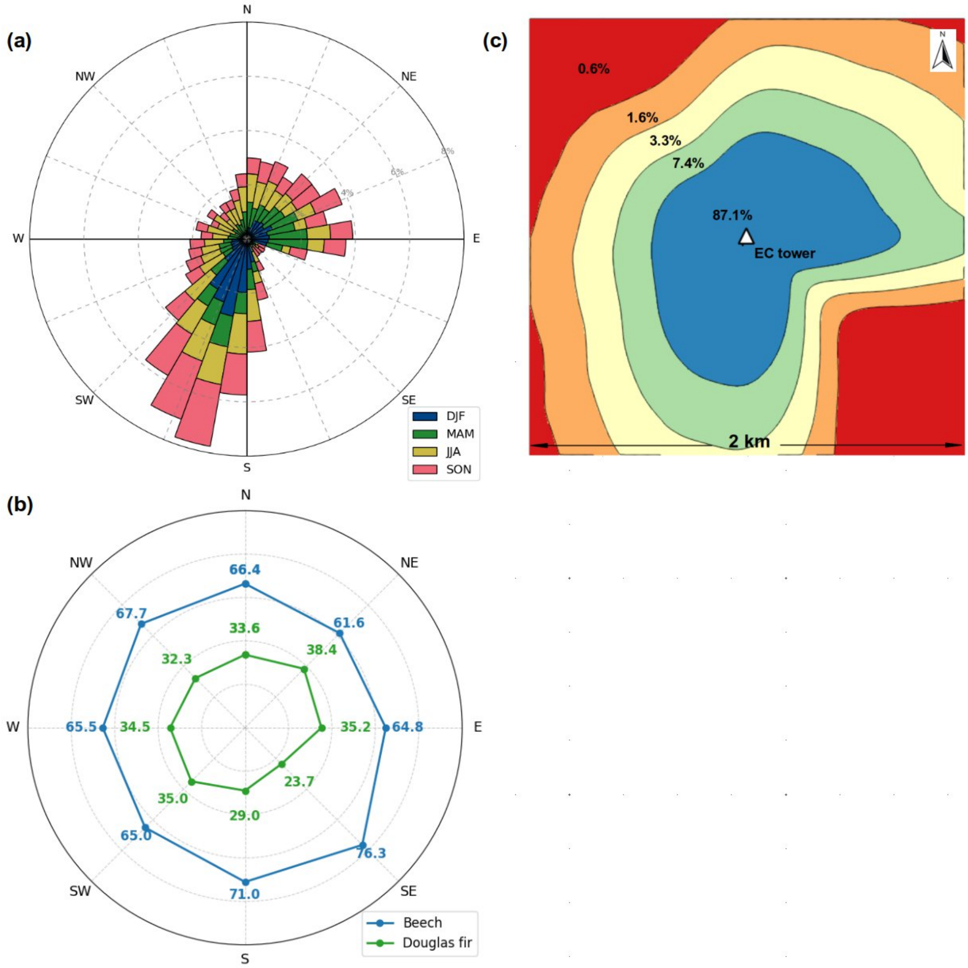

315 **Figure 6: Seasonal wind patterns and their influence on relative species contributions to EC fluxes. The wind rose (a) shows the frequency and direction of winds at the study site from 15 May 2024 to 15 May 2025, with colors indicating different seasons (spring, summer, autumn, winter). The species contribution plot (b) shows the average percentage contribution of beech and Douglas fir to the measured fluxes as a function of wind direction, based on footprint-weighted tree species data across directional bins. The source contribution heat map (c) shows the cumulative footprint-weighted source area around the EC tower, aggregated over the study period.**

3.3 Simulated and measured net ecosystem exchange (NEE)

NEE simulated by the LandscapeDNDC model was compared against eddy covariance (EC) measurements considering four model configurations**:** pure beech (1) and pure Douglas fir (2), dynamically weighted forest types according to the specific footprint in any hour (3), and static footprint (4) with fixed species proportions representing the annual average (66.5% beech and 33.5% Douglas fir). With all configurations the dynamics of NEE could be captured but with some differences in accuracy (Fig. 7). The pure beech simulation aligned slightly better with observations ($R^2 = 0.66$, NSE = 0.63) than the pure Douglas fir simulation ($R^2 = 0.63$, NSE = 0.61), though both exhibited similar mean absolute errors (MAE ≈ 1.94 and 1.99 kgC ha-

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^{1} hr^{-1} respectively) and minimal bias (Table 2). However, the agreement with measured NEE improved when using footprint-weighted mixtures of the two species in the simulation (configurations 3 and 4). The dynamic footprint approach, which integrates hourly adjusted species contributions (configuration 3), achieved the best fit to observed NEE ($R^2 = 0.69$, NSE = 0.68, MAE = 1.74 kgC ha^{-1} hr^{-1}), but the results with the static footprint approach (configuration 4) were almost as good.

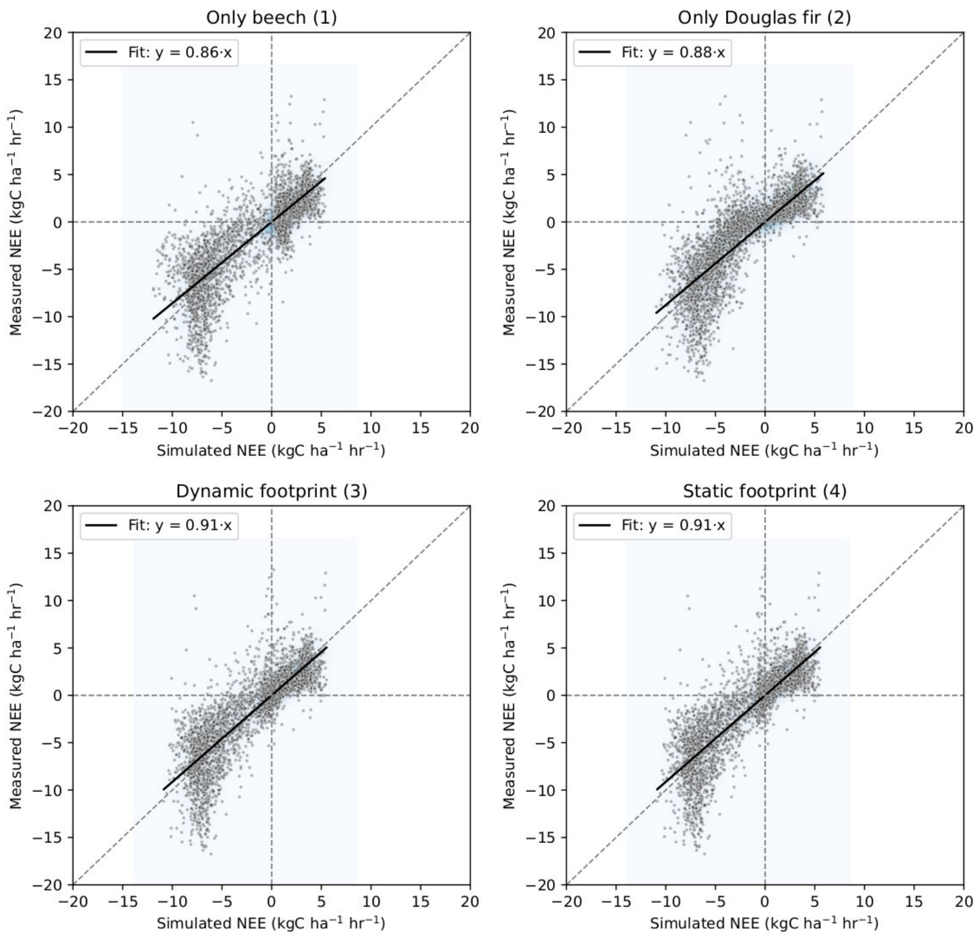

Figure 7: Comparison between hourly measured and simulated net ecosystem exchange (NEE, kgC ha^{-1} hr^{-1}) at the ECOSENSE forest considering the configurations: pure beech (1) and pure Douglas fir (2), dynamically weighted forest types according to the specific hourly footprint (3), and static footprint (4) with fixed species proportions (66.5% beech and 33.5% Douglas fir). The shaded heatmap represents the kernel density estimate of point concentrations.

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Table 2: Summary statistics comparing simulated and measured net ecosystem exchange (NEE) for the four different configurations: pure beech (1) and pure Douglas fir (2), dynamically weighted forest types according to the specific footprint (3), and static footprint (4) with fixed species proportions (66.5% beech and 33.5% Douglas fir). Metrics include coefficient of determination (R^2), slope of linear regression, Nash–Sutcliffe efficiency (NSE), mean absolute error (MAE, $kgC.ha^{-1}.hr^{-1}$), and model bias ($kgC.ha^{-1}.hr^{-1}$) over the period 15 May 2024 to 15 May 2025.

Model configuration	R^2	Slope	NSE	MAE	Bias
1. Pure beech	0.66	0.86	0.63	1.94	-0.12
2. Pure Douglas fir	0.63	0.88	0.61	1.99	-0.39
3, Weighted, dynamic	0.69	0.91	0.68	1.74	-0.21
4. Weighted, static	0.69	0.91	0.68	1.74	-0.21

3.4 Simulated and measured evapotranspiration (ET)

Simulated ET was compared with ET calculated from the EC system for the same four model configurations as for NEE (Fig. 8). The pure beech (1) and pure Douglas fir simulations (2) showed moderate agreement with observed ET based on the eddy covariance measurements, with R^2 values of 0.58 and 0.60 and NSE values of 0.57 and 0.55, respectively (Table 3). Both simulations slightly underestimated peak ET, although linear regression slopes remained close to 1 (0.93 for beech, 0.84 for Douglas fir), and the mean bias was small (–0.01 mm hr^{-1} for all configurations). The footprint-weighted configurations 3 and 4 improved model–measurement alignment slightly. The dynamic footprint approach (3), integrating hourly footprint–land cover contributions, resulted in the highest NSE (0.59) and lowest MAE (0.06 mm day^{-1}), closely matched by configuration 4 with the static footprint case (66.5 % beech, 33.5 % Douglas fir).

3.5 Simulated and measured NEE across phenological periods

Modeled NEE for pure beech, pure Douglas fir, and their dynamic weighted combination reveals species-specific contributions to EC fluxes across phenological phases (Table 4, Fig. S4-6). During the flushing phase (April), both pure species simulations showed limited predictive skill, but the pure Douglas fir simulation performed better than the pure beech simulation (NSE = 0.38 vs. –0.25, MAE = 1.65 vs. 2.38 kgC ha^{-1} hr^{-1}), consistent with its earlier seasonal activity. The dynamic FFP simulation (configuration 3) improved the overall fit compared to pure beech (R^2 = 0.60 vs. 0.55), though its performance fell between the single-species cases, suggesting that mixed contributions complicate model–observation agreement in early spring when Douglas fir is dominating the CO_2 exchange. In the maturity period (from May to September), the simulations of pure species captured observed flux dynamics well, with comparable performance (NSE = 0.63 for beech, 0.67 for Douglas fir). The dynamic FFP simulation produced a similarly strong fit (NSE = 0.66) with a slightly reduced bias (–0.08), indicating that the weighted combination of tree species in the dynamic footprint effectively balances species-specific tendencies during peak productivity. During senescence (October), contrasting behaviors of the species-specific simulations became more ev-

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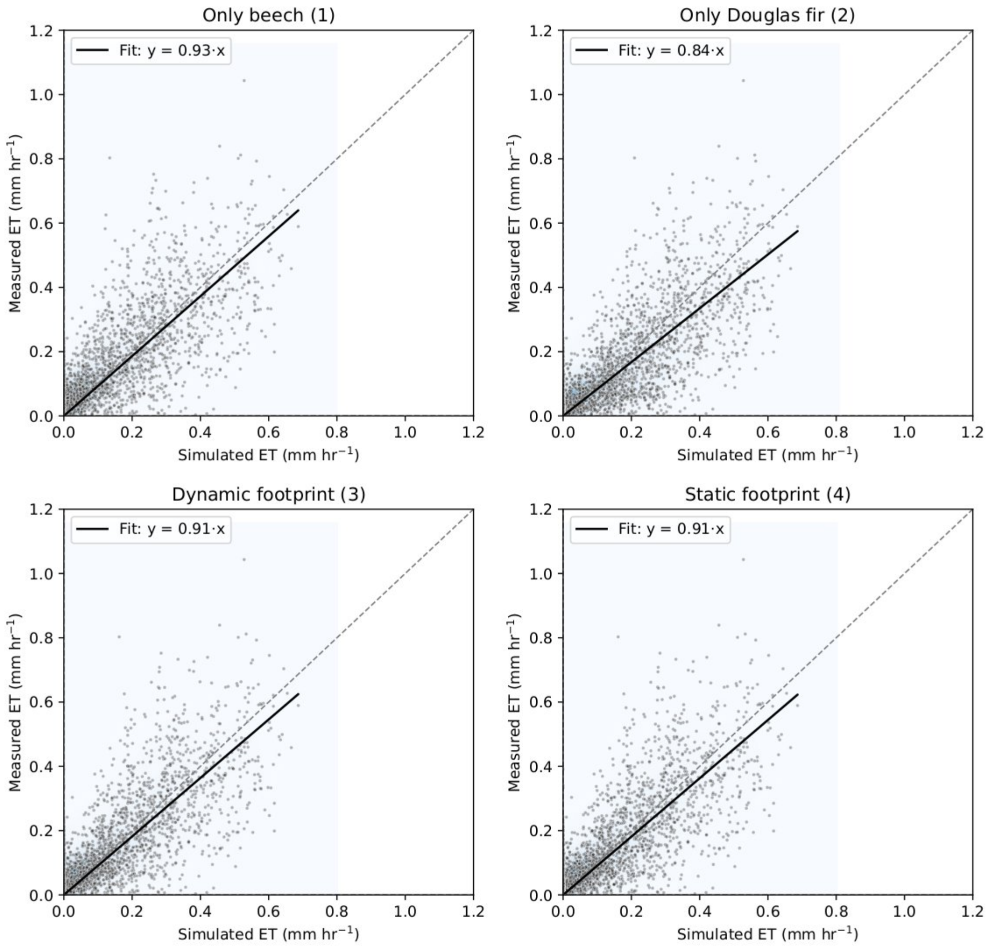
ident. The pure beech simulation maintained high proportionality in line with EC observations (slope = 0.98, NSE = 0.50), while the pure Douglas fir showed weaker predictive skill compared to EC observation (slope = 0.61, NSE = 0.34). The dynamic FFP simulation again yielded the best performance (R^2 = 0.63, NSE = 0.62, MAE = 1.56), capturing the combined late-season activity of both species and reducing the error relative to both single-species simulations.



375 **Figure 8: Comparison between hourly measured and simulated evapotranspiration (ET, mm hr^{-1}) at the ECOSENSE forest for different model configurations: pure beech simulations (1) and pure Douglas fir simulations (2), dynamically weighted simulations according to the hourly footprint (3), and the static footprint (4) with fixed species proportions (66.5% beech and 33.5% Douglas fir). The shaded heatmap represents the kernel density estimate of point concentrations.**

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Table 3: Summary statistics comparing simulated evapotranspiration (ET) from LandscapeDNDC with measured EC-derived ET for different configurations: pure beech (1) and pure Douglas fir (2), dynamically weighted forest types according to the specific footprint (3), and static footprint (4) with fixed species proportions (66.5% beech and 33.5% Douglas fir). Metrics include coefficient of determination (R^2), slope of linear regression, Nash–Sutcliffe efficiency (NSE), mean absolute error (MAE, kgC.ha^{-1}.hr^{-1}), and model bias (kgC.ha^{-1}.hr^{-1}) for the period 15 May 2024 to 15 May 2025.

Model configuration	R^2	Slope	NSE	MAE	Bias
1. Pure beech	0.58	0.93	0.57	0.06	-0.02
2. Pure Douglas fir	0.60	0.84	0.55	0.07	0.00
3. Weighted, dynamic	0.61	0.91	0.59	0.06	-0.01
4. Weighted, static	0.61	0.91	0.59	0.06	-0.01

Table 4. Summary of statistical comparison between EC-measured and simulated NEE across three phenological periods (flushing phase, maturity, senescence). Simulations include pure beech, pure Douglas fir, and their hourly weighted combination based on dynamic flux footprint (Dynamic FFP). Metrics include coefficient of determination (R^2), Nash–Sutcliffe efficiency (NSE), slope, mean absolute error (MAE, kgC.ha^{-1}.hr^{-1}), and model bias (kgC.ha^{-1}.hr^{-1}).

Period	Model configuration	R^2	Slope	NSE	MAE	Bias
Flushing phase (April)	Pure beech	0.55	0.46	-0.25	2.38	-1.65
	Pure Douglas fir	0.57	0.64	0.38	1.65	-1.10
	Weighted, dynamic	0.60	0.54	0.15	1.96	-1.46
Maturity (from May to September)	Pure beech	0.65	0.91	0.63	2.42	-0.31
	Pure Douglas fir	0.67	1.00	0.67	2.26	0.36
	Weighted, dynamic	0.67	0.95	0.66	2.31	-0.08
Senescence (October)	Pure beech	0.50	0.98	0.50	1.93	1.00
	Pure Douglas fir	0.57	0.61	0.34	2.09	-0.93
	Weighted, dynamic	0.63	0.98	0.62	1.56	0.38

3.6 Cumulative Simulated and Measured NEE and Gap Filling Performance

While previous section provided an instantaneous comparison between simulated and measured fluxes, the cumulative NEE curves reveal seasonal dynamics and its influence by species-specific phenology (Fig. 9,10). First, we are comparing only the time periods where measurements are available, therefore neglecting simulated fluxes during periods without evaluation data from the EC tower (Fig. 9). From the start of the analyzed period (15 May 2024) through late September, both beech and Douglas fir simulations accumulate negative values, indicating net carbon uptake during summer. After leaf senescence in beech, its cumulative curve reverses direction and increases (net carbon release), while Douglas fir holds an approximate equilibrium between respiration and carbon assimilation, resulting in a flat winter curve until the end of March. In early spring, Douglas fir resumes carbon uptake earlier in the year compared to beech, causing its cumulative curve to decline sooner. The EC-derived cumulative NEE is closer to the simulation of pure beeches, reflecting the dominance of beech within the flux

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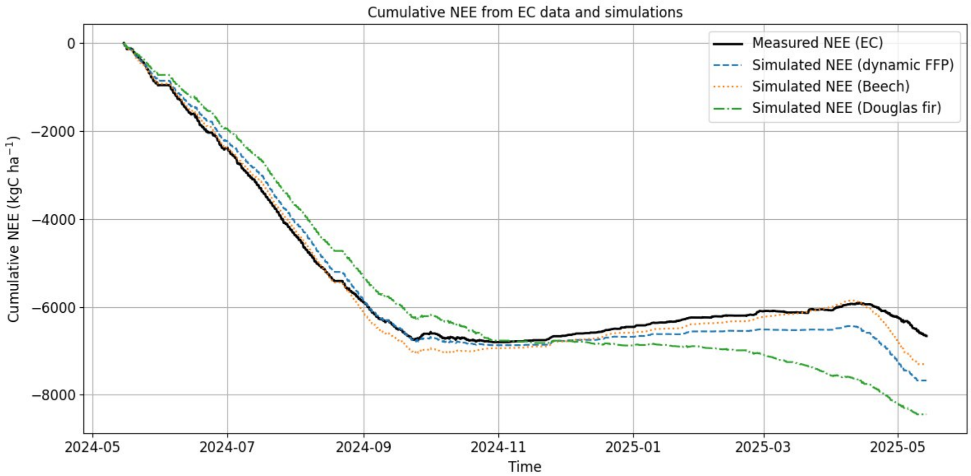
footprint. Overall however, the simulations that consider both species shows the closest agreement with the EC measurements, as the inclusion of Douglas fir improves the seasonal match, particularly during transitional phases.



405 **Figure 9: Cumulative annual NEE from EC measurements and model simulations for May 2024–May 2025, based on periods with available hourly measurement data (without any gap-filling).**

Gap filling of the EC-derived NEE time series based on the fixed footprint distribution simulation, showed comparable performance to the marginal distribution sampling approach used by the REddyProc software (Fig. 10). The process-based gap filling approach based on the simulation model maintains the relative contributions of each species observed during periods with available footprint data, allowing the gap-filled series to reflect species-specific phenological patterns and overall seasonal dynamics as well as representing the annual carbon budget (-1245.3 and -1166.4 kgC.ha^{-1} yr^{-1} estimated by REddyProc and the process-based model approach respectively). This demonstrates that even without dynamic footprint information for gap periods, integrating process-based simulations with realistic species composition estimates can yield accurate and ecologically meaningful gap-filled datasets.

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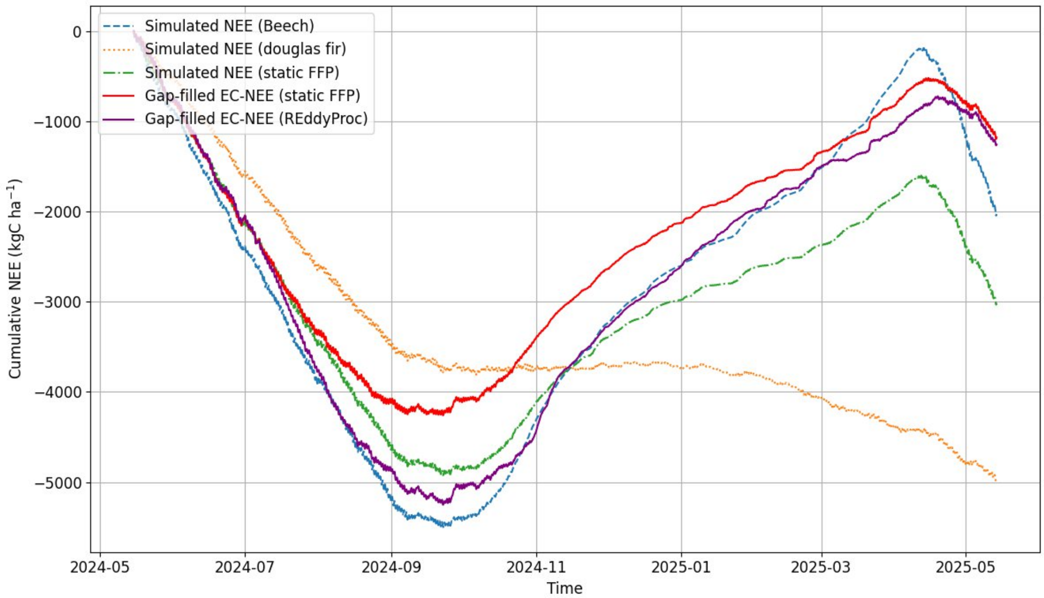

Figure 10: Gap filled cumulative annual NEE from EC measurements and model simulations for the period from May 2024 to May 2025.

4. Discussion

With NSE values above 0.6 for soil moisture and ~0.8 for soil respiration, our simulations are within or above the range reported for site-level model evaluations in comparable forests (e.g. Noh et al., 2024; Zhang et al., 2021). Our results show that the LandscapeDNDC model can capture key hydrological and belowground carbon processes at the ECOSENSE forest independent of the tree species. We are aware that one carbon and one water evaluation term, compared throughout a single year are leaving some room for uncertainty. For example, soil respiration still lumps fluxes from heterotrophic and autotrophic sources (Noh et al., 2024) that the model differentiates using a number of assumptions but respective measurements for corroborating these assumptions were not yet available. Similarly, partitioning between transpiration and surface evaporation does play a role for species differentiation (Bittner et al., 2010) since hydraulic conductance as well as interception capacity will differ by species, which is considered by model parameters not specifically evaluated in the ECOSENSE forest (see table S1). In contrast to other model evaluation studies (Kramer et al., 2002; Morales et al., 2005; Gao et al., 2017; Bergkvist et al., 2023), our evaluation extends beyond EC measurements by also assessing key ecosystem states and fluxes that shape the observed exchange. In other words, it was possible to represent important soil and species-specific properties, enabling a more detailed analysis of the composition of the area integrated footprint flux measurements.

Moreover, the footprint-weighted simulations which considers the temporally changing relative contributions from beech and Douglas fir, enhances the agreement of the simulations with data derived from EC flux measurements. Here, our dynamically footprint weighted mixing approach as well as a fixed-fraction weighted approach performed overall very similar in compar-

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ison to the EC-derived NEE and ET fluxes. This likely follows from the relative homogeneity of species contribution in different cardinal directions where the share of Douglas fir varied between approximately 24 and 38 %, which is in contrast to investigations that discovered a relatively larger contribution of particular directions with specific footprint compositions (Griebel et al., 2016).

Both configurations considering the actual species distribution (configurations 3 and 4) were clearly superior to simulations assuming a pure species forest, reflected in a slope closer to one as well as higher statistical performance measures. The differences between simulations, and hence the added predictive skill, were most clearly found during transitional periods in spring and autumn when species responses diverged most strongly. Simulations only considering beech (configuration 1) underestimated early- and late-season fluxes, when Douglas fir maintained photosynthetic activity. In contrast, simulations that only consider Douglas fir behavior (configuration 2), strongly overestimate the carbon uptake outside the period of the growing season (Fig. S7-8). The cumulative flux analysis underscores the dominant role of beech while the contribution of Douglas fir is still considerable. The important role of species composition, particularly during specific periods has been highlighted before in a mixed conifer-hardwood forest in the US, where inhomogeneities within the flux footprint and species-specific functional traits have strongly influenced the aggregated EC flux signal (Kim et al., 2018). Our results additionally highlight the strong differentiation that originates from a mix of deciduous and evergreen species. With the deciduous species concentrating carbon uptake and evaporation during the growing period but the evergreen species mitigating carbon losses during the non-growing season.

Due to gaps in EC measurements, it is not straightforward to derive annual flux budgets. Data gaps cannot simply be interpolated because of complex interactions with weather (Vekuri et al., 2023) and physiological boundary conditions (Klosterhalfen et al., 2023). Therefore, detangling a lumped EC flux according to its species composition within a footprint is advantageous for reducing the uncertainty and for improving the accuracy of gap-filling, which currently is not the case in current gap-filling approaches (Mahabbati et al., 2021). Our results demonstrate that the lumped flux consists of species-specific contributions that vary in their importance throughout the season. Using an approach that is more related to one of the two – usually the dominating beech flux – thus implies considerable bias in the results. In our case, gap-filling based on the underlying species-specific developments represented in LandscapeDNDC showed comparable performance to the standard REddyProc approach. To ensure that this is not an accidental result, we have compared both approaches by a systematic test, where we created artificial gaps into the NEE measurements (627 hours randomly distributed across the study period) and compared fluxes that have been estimated with either the REddyProc method or the process-based model approach. Both methods achieved broadly comparable performance, with REddyProc showing slightly higher correlation (Fig. S9). Process-based gap-filling approaches have been advocated as a means to reduce biases in annual carbon budgets before (Stoy et al., 2006; Xing et al., 2008). With the current analysis we could corroborate this demand and demonstrate the suitability of process-based models for this task, particularly if deciduous as well as evergreen plants need to be considered. A particular advantage of such an approach is that it not only provides reliable flux estimates but also information about the likely composition of the investigated fluxes that the statistical approach cannot.

5. Conclusions

The integrated, process-based ecosystem model LandscapeDNDC successfully reproduced key hydrological and carbon processes at a mixed forest site, considering soil and tree species-specific properties. Despite inherent uncertainties from limited evaluation metrics, the model reliably captured essential tree species-specific dynamics, enabling a meaningful decomposition of EC fluxes into beech and Douglas fir contributions using flux footprint predictions and tree species maps. Simulations considering both species types - deciduous and evergreen - provided the closest match of simulations to EC measurements, especially during transitional seasons when functional differences driven by the different species physiology were most pronounced. These findings highlight the significance of species composition in interpreting mixed-forest carbon fluxes and demonstrate that combining process-based modeling with a detailed footprint analysis and geospatial data on tree species distribution can reduce biases in flux partitioning and gap-filling. This method therefore has a high potential to effectively improve carbon and water balance assessments in forests where deciduous and evergreen species coexist. This is particularly important when it comes to providing accurate figures on the current and future potential of forests to sequester carbon in the framework of national and global assessments for climate mitigation assessments.

Code and data availability. The LandscapeDNDC model source code for released versions of the model is permanently available online at the Radar4KIT database (https://doi.org/10.35097/438; (Butterbach-Bahl et al., 2021)). The published model version that has been used for the presented simulations can also be freely downloaded upon request from the website: https://ldndc.imk-ifu.kit.edu/download/download-model.php (last access: 25. August 2025). All parameters needed to run the model are provided in the Supplement (soil properties, initial stand properties, and species-specific parameters). Forcing data will be provided on request. Furthermore, the data used for evaluation of beech sites are available from the ICOS data portal (https://www.icos-cp.eu/data-products/ecosystem-release, sites ID CZ-Stn, DE-Lnf, DK-Sor). The Douglas fir data are provided either from the AmeriFlux Network (https://ameriflux.lbl.gov/doi/FLUXNET/CA-Ca1/) or can be directly obtained from the University of Twente, The Netherlands (by request from PK).

Author contributions. MH, KR, and GR designed the conceptual approach, determined the modeling setup, and led the manuscript writing. MH and MS performed the data analysis with additional contributions from CA, and DL, and BJ regarding field site data collection. KP and SL provided additional data for evaluation and LP did the model calibration. All co-authors contributed to writing and revising the manuscript.

Competing interests. The contact author has declared that none of the authors has any competing interests.

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