Biogeochemical model Biome-BGCMuSo v6.2 provides plausible and accurate simulations of carbon cycle in Central European beech forests

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Abstract. Process-based ecosystem models are increasingly important for predicting forest dynamics under future
environmental conditions, which may encompass non-analogous climate coupled with unprecedented disturbance regimes.
However, challenges persist due to the extensive number of model parameters, scarce calibration data, and the trade-offs
between the local precision and the model wide-ranging applicability. In this paper, we describe a protocol that allows a
modeller to collect transferable ecosystem properties based on ecosystem characteristic criteria and to compile the parameters
that need to be described in the field.

We applied the procedure to develop a new parameterization for the European beech (*Fagus sylvatica* L.) for the Biome-
BGCMuSo model, the most advanced member of the Biome-BGC family. For model calibration and testing, we utilized
multiyear forest carbon data from 87 plots distributed across five European countries. The initial values of 48 new
ecophysiological parameters were defined based on the literature review. The final values of 6 calibrated parameters were
optimised for single sites as well as for multiple sites using the Generalised Likelihood Uncertainty Estimation and model
output conditioning that ensured plausible simulations based on user-defined ranges of carbon stock output variables (carbon
stock in aboveground wood biomass, soil, and litter) and finding the intersections of site-specific plausible parameter
hyperspaces. To support the model use, we tested the model performance in simulating tree aboveground wood, soil, and litter
carbon across a large geographical gradient of Central Europe and evaluated the trade-offs between parameters tailored to
single plots and parameters estimated using multiple sites.

Our findings indicated that parameter sets derived from single sites provided an improved local accuracy of simulations of
aboveground wood, soil, and litter carbons stocks by 35 %, 55 %, and 11 % in comparison to the a priori parameter set.
However, their broader applicability was very limited. A multi-site optimised parameter set, on the other hand, performed
satisfactorily across the entire geographical domain studied here, including sites not involved in the parameter estimation, but
the errors were on average by 26 %, 35 % and 9 % greater for the aboveground wood, soil, and litter carbons stocks than those
obtained with the site-specific parameter sets. Importantly, model simulations demonstrated plausible responses across large-
scale environmental gradients, featuring a clear production optimum of beech that aligns with empirical studies. These findings
suggest that the model is capable of accurately simulating the dynamics of the European beech across its range and can be
used for more comprehensive experimentations.

1   Introduction

Forests are dynamic long-lived ecosystems, with the life span of single trees potentially exceeding several centuries (Di Filippo et al., 2015). Forests longevity and ecological complexity make studies of their dynamics challenging, mainly under unstable environmental conditions, changing ecological interactions and management (Mouquet et al., 2015), due to limited options of

55   research repeatability in empirical studies (Schnitzer and Carson, 2016). Computer models have become indispensable in overcoming these problems since they account for complex interactions, feedback loops, and dependencies between ecosystem components (Bugmann and Seidl, 2022; Geary et al., 2020). The development of models was considerably accelerated by advances in computer science and the progress in ecophysiological and ecological research, which helped define different model structures and parameters (Minunno et al., 2019; Augustynczik et al., 2017). Hence, currently a great number of different

60   models using varying methodological approaches, different temporal and spatial scales, and focusing on answering different primary questions is available (for an overview see e.g. Fabrika et al., 2019; Bosela et al., 2022).

Over time, the objectives of vegetation dynamics modelling have shifted from supporting practical decision-making towards providing novel insights into ecological patterns and processes, ecosystem transformations driven by climate change, and complex scenario and effect attribution studies (Geary et al., 2020). An urgency of informing ecosystem management and

65   policies about the impacts of climate change and effects of management actions has become a prominent use of ecosystem models (Pecl et al., 2017). Rapid environmental changes have increasingly favoured process-based ecosystem models (PBM) over the empirical ones (Adams et al., 2013), because they incorporate a mechanistic description of physical and biological processes and interactions between plants and the environment (Waring and Running, 1998). Hence, they should possess the capacity to better address novel and non-analogous conditions, which could occur in the future but were not observed in the

70   past (Adams et al., 2013).

Complex PBMs typically contain many parameters specifying physiology, biochemistry, phenology, and allocation patterns of different vegetation types or species (Cameron et al., 2013; van Oijen, 2017). Parameter values are estimated based on different field or laboratory measurements, trial-and-error parameter adjustments or probabilistic methods (Forrester et al., 2021; Hollós et al., 2022). Thereby, each measurable parameter has its intrinsic variability that emerges from environmental

75   conditions, sampling and measurement errors. Such a value range can be interpreted as a probability distribution or parameter uncertainty (van Oijen, 2017). Calibration is often applied to narrow the initial parameter ranges and capture regional or local peculiarities. A selection of most influential variables to be calibrated using a sensitivity analysis (SA) and coping with the calibration equifinality, i.e. a situation when various combinations of parameter values produce the same results (Beven, 2006), can challenge calibration efforts. To this end, different calibration approaches, such as trial-and-error parameter adjustments

80   or probabilistic methods (Forrester et al., 2021; Hollós et al., 2022) including Bayesian methods (van Oijen, 2017; Fer et al., 2018) or the Generalized Likelihood Uncertainty Estimation (GLUE) (Beven and Binley, 2014) have been proposed. The calibration can focus on one or several variables simultaneously. Multivariate approaches are generally preferred as they aim to identify parameter values that minimize the differences between simulated and observed values of multiple variables

(Wöhling et al., 2013; Kamali et al., 2022). The spatial aspect may be dealt with in a similar manner. The model calibrated for
single sites provides model outputs with a high local accuracy, but loses the ability to generalize outside the calibration data
(Levins, 1966; Kramer et al., 2002; Blyth et al., 2011). Therefore, advanced calibration designs maintaining a balance between
the local accuracy and generality, and providing good performance across multiple variables, have been developed (Keenan et
al., 2011; Wallach et al., 2021).

In this study, we addressed the process-based model Biome-BGCMuSo (BBGCMuSo, Hidy et al., 2016, 2022, 2012), which
is the most rapidly developing member of the Biome-BGC model family (Thornton, 1998). It simulates storages and fluxes of
these elements within and between the pools. The model has been extensively used in the research of forest ecosystems
concerning their productivity (Kimball et al., 1997; Sever et al., 2017), carbon (Churkina et al., 2003; Ostrogović Sever et al.,
2021; Yan et al., 2016), water (Pietsch et al., 2003), and nitrogen dynamics (Pietsch et al. 2003; Merganičová, Pietsch, a
Hasenauer 2005), including effects of climate change (White et al., 1999; Jager et al., 2000; Churkina and Running, 2000;
Hlásny et al., 2011). The recent developments of BBGCMuSo included a multilayer soil profile; complex water cycling
between soil, vegetation, and atmosphere; intra-annual phenology; and complex management operations (Hidy et al., 2022,
2016, 2012). However, robust testing of ecological plausibility and model performance in forest ecosystems as well as the
regionally calibrated species-specific parameter sets are still lacking. These tasks are challenging given the substantial increase
in model structural complexity and the number of parameters, which limits the use of former parameter sets (Pietsch et al.,
2005).

The aim of this study is to develop a multi-objective calibration procedure of model parameters that considers balancing the
trade-off between the local precision of model outputs and a broad applicability of parameters, and to perform a comprehensive
model benchmarking of the ecological plausibility of model results across large environmental gradients. We hypothesise that
parameter estimates optimized for single sites are not sufficiently robust to be applied across large geographical space, while
the multi-site optimisation reduces the ability of model output to capture the phenotypical plasticity. The proposed method
was applied to calibrate ecophysiological parameters of BBGCMuSo v6.2 for the European beech (*Fagus sylvatica* L.) to
facilitate a large-scale utilization of the model in addressing research questions related to alterations in species productivity
and carbon cycle under different climatic and management scenarios. The findings should serve as a reference for calibrating
other tree species and/or models.

2. Data and Methods

2.1. Model

Biome-BGCMuso (Hidy et al., 2022, 2016, 2012) is a descendant of Biome-BGC model (Thornton, 1998). It is a
biogeochemical model that simulates cycling of carbon, water, nitrogen, and energy in terrestrial ecosystems (Thornton, 1998).
Biome-BGC was one of the earliest biogeochemical models that included explicit carbon, water and nutrient cycles. The

115 represented processes include photosynthesis, evapotranspiration, allocation, respiration, litterfall, and decomposition (Thornton et al., 2002). These processes are defined for a unit ground area that is considered homogeneous. A so-called „two-leaf" representation is used to simulate radiation interception, evapotranspiration, and gross primary production for the sunlit and shaded canopy fractions (Thornton and Rosenbloom 2005). The modelled ecosystem consists of several components representing different plant parts (leaf, stem, roots), litter, soil, and coarse woody debris. The ecosystem status and dynamics

120 are represented by carbon (C), nitrogen (N) and water (W) pools and fluxes between the pools. The main pools represent leaf (C, W, N), aboveground wood (C, N), coarse root (C, N), fine root (C, N), coarse woody debris (C, N), litter (C, N), soil (C, W, N), yield (C, N), standing-dead-biomass (C, N) cut-down biomass (C, N). BBGCMuSo contains a number of new features including a multilayer soil representation that allows simulating a more realistic dynamics of water, carbon and nitrogen across the soil profile; a possibility of using a dynamic annual mortality rates; adjustable intra-annual allocation driven by phenology;

125 improved representation of transpiration, soil evaporation, and inorganic nitrogen; and flexible simulation of management operations, including forest thinning and harvesting (Hidy et al., 2012, 2016, 2022). It can also simulate acclimation to temperature and short-term temperature dependence of maintenance respiration, drought legacy effects through reduction of non-structural carbohydrate storages, and a CO2 concentration-dependent stomatal conductance (Hidy et al., 2016). The model version 6.2 uses 53 soil-related and 105 ecophysiological parameters (Hidy et al., 2021), of which some are site-specific (e.g.

130 soil depth, soil texture), while others, such as C:N ratio in different tree compartments, are species-specific. The number of parameters in BBGCMuSo has been tripled in comparison to the original model Biome-BGC mostly thanks to the fact that the model was also made suitable for simulations of the crop functioning. The model, including its source code, is available at https://nimbus.elte.hu/bbgc/.

2.2. Data

135 The dendrometric and environmental data represented 87 forest sites distributed across Central Europe within the distributional range of European beech (Figure 1). The dataset includes sites from the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests, Michel et al., 2018) long-term forest research plots from thinning trials supervised by different national institutions, and highly-instrumented intensively monitored plots equipped with weather stations, dendrometers, instruments measuring sap flow, soil water content, etc. (Table A2). The plots are located in

140 Croatia, Hungary, Slovakia, the Czech Republic, and Poland along an elevation gradient from 20 to 1,325 m a.s.l. Their mean annual precipitation totals vary from 419 to 1,883 mm, mean annual temperatures range from 3.5 to 13.3°C, and soil depths vary between 0.4 and 2 m (Table 1). Most plots were of a circular shape with a size from 0.09 to 1.05 ha. Forest stands were established between 1787 and 1984, i.e. their age in the year 2022 varied from 38 to 235 years. Both managed and unmanaged forest stands that originated either from natural or artificial regeneration or a combination of both, are represented. Time series

145 lengths and the number of observations differed between the sites depending on the year of plot establishment, and the

frequency of re-measurements of tree dimensions. The maximum time series length was 60 years, and the maximum number

of observations in a single time series was 30.

(a)   (b)
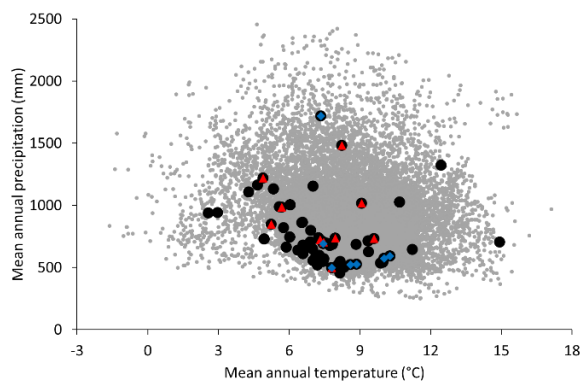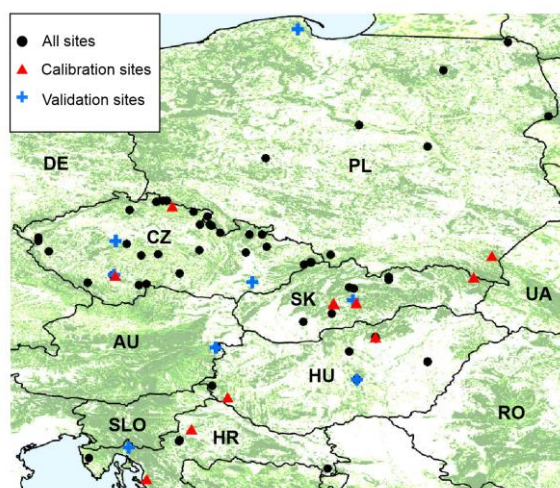
Figure 1 Distribution of used forest sites across Europe with the forest cover displayed in the background (CORINE Land Cover, 2023), a), and in the climatic space of European beech in Europe derived from Caudullo et al. (2017) and indicated by grey dots, b).
150 **Black dots indicate 87 research sites used for testing model plausibility (realism), red triangles indicate eleven data-rich sites used for the calibration of the BBGCMuSo model for simulating European beech forests, and blue crosses and diamonds represent eight validation sites.**

Out of the whole data set, 11 beech-dominated sites with the most comprehensive data and balanced geographical coverage,

ensuring that each country was represented by at least one site, were used for model calibration (hereafter referred as calibration

155   sites). Eight beech-dominated sites with repeated stand measurements representing all included countries were selected to

perform an independent model validation (hereafter as validation sites). All 87 sites were used for testing the plausibility

(realism) of simulated model output using the calibrated parameter set across an extended geographical gradient.

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Table 1 Summary of site and forest stand characteristics for the whole data set (All), calibration and validation sets. Climate data represent a period from 1950 to 2018.

Data set	All	Calibration	Validation
Number of sites	87	11	8
Dominant tree species	*Fagus sylvatica, Picea abies, Pinus sylvestris, Quercus spp.*	*Fagus sylvatica*	*Fagus sylvatica*
Site variables	mean (min - max)		
Years with observations	(1990 - 2018)	(1949 - 2018)	(1990 - 2018)
Latitude (°)	(N 45.4814 - N 54.559)	(N 44.8164 - N 50.7349)	(N 45.4814 - N 54.5592)
Longitude (°)	(E 14.2736 - E 23.72)	(E 14.3000 - E 22.4917)	(E 14.2736 - E 19.4701)
Elevation (m a.s.l.)	544.2 (20 - 1325)	686.8 (240 - 1325)	502.5 (120 - 1180)
Annual precipitation (mm)	789 (419 – 1884)	1018 (663 – 1884)	784 (458 - 1592)
Mean temperature (°C)	7.75 (3.52 - 13.28)	7.34 (4.86 - 10.3)	8.37 (6.41 - 11.11)
Soil depth (m)	0.99 (0.4 - 2)	0.92 (0.45 - 2)	0.99 (0.5 - 1.8)
Plot size (ha)	0.31 (0.09 - 1.05)	0.45 (0.25 - 1.05)	0.28 (0.09 - 0.84)
Stand age (yr)	84 (35 - 232)	118 (64 - 232)	79 (41 - 122)
Aboveground wood carbon (kgC m^{-2})	8.62 (0.01 - 36.87)	16.92 (0.03 - 35.87)	16.89 (4.30 - 33.74)
Soil carbon (kgC m^{-2})	13.31 (1.13 - 16.24)	13.21 (1.13 - 16.24)	NA
Litter carbon (kgC m^{-2})	0.256 (0.086 - 0.344)	0.256 (0.086 - 0.344)	NA

The plot data contain information on site, forest stand structure and development, soil, climate, nitrogen deposition, and
170 physiological processes (Table A2). Site description data comprise plot coordinates (latitude, longitude), elevation, aspect, and slope. Forest stand data comprise information on tree species composition, stand age, stand structure, data on individual tree dimensions or mean stand characteristics (e.g. mean diameter at breast height (DBH), mean tree height (H)), mortality, the applied management and damages. Soil data contain soil depth, texture, pH, nutrient stocks, and indicators of water regime. If soil information was not available, it was obtained from the Harmonized World Soil Database (HWSD v 1.21) (FAO, 2012)
175 that provides soil attributes, such as soil depth, soil texture, pH, etc., at a grid cell size of approximately 1km.

Climate data include daily values of minimum and maximum temperature, solar radiation, precipitation, water vapour deficit, wind speed and direction observed at individual sites, nearby meteorological stations, or taken from the E-OBS gridded dataset providing daily minimum, maximum temperature, and precipitation with 0.1 deg. resolution (Cornes et al., 2018). The climate data cover a period from 1950 to 2018. To cope with the varying climate data availability on the sites, we combined the on-
180 site measurements with the E-OBS data. The MTClim model (Hungerford et al., 1989) was used to extrapolate the climate time series from the nearest E-OBS grid cell and to calculate daylight values of mean temperature, vapour pressure deficit (VPD), solar radiation, and daylength.

Annual CO2 data were taken from Mauna Loa observations (Keeling et al., 1976). While nitrogen deposition data were directly available only for ICP Forests plots, they were taken from Tian et al. (2018) for the remaining sites.

185   Data about site, soil texture, pH, stand age, management, nitrogen deposition, CO2 concentration and daily climate data were used as model input to run site-specific simulations. Model calibration and validation was based on carbon stocks in aboveground wood, litter and soil (AbgwC, SoilC, LitterC). AbgwC was derived from dendrometric characteristics of individual trees by calculating the total aboveground wood volume using species-specific two-parameter regressions by Petráš and Pajtík (1991) that was subsequently converted to carbon stock using the species-specific basic wood density from Merganič

190   et al. (2017, 570 kg m^{-3} for beech) and 50 % carbon content in biomass (IPCC, 2003).

2.3 Simulation design

Simulations of forest ecosystem dynamics at each site were performed with BBGCMuSo v6.2 in three steps: (1) spin-up run, (2) transient run, and (3) normal run (Hidy et al., 2021). Spin-up was performed with a constant CO2 concentration and nitrogen deposition equal to the pre-industrial values of 277.15 ppm and 0.002 kgN m^{-2} year^{-1}, respectively. During the transient run,

195   annual values of CO2 concentration and nitrogen deposition increased from their pre-industrial to the current values. The transient run started in 1850 and lasted until the year preceding the establishment of the current stand. Hence, the length of the transient run varied between sites, and it was used only for the simulations of the stands established after 1850, while the maximum length of the transient run was 134 years. Both spin-up and transient runs were performed with no management, no fire-induced mortality, and constant natural (background) mortality.

200   The normal run was driven by the temporally varying CO2 and N-deposition, and included management reconstructed based on forest inventory records or yield tables, if no site-specific information on management interventions was available. The normal run simulations started at stand age 0 (i.e., the year of stand establishment) and continued to the present day; i.e. the simulation length equalled the actual stand age. In simulation year 1, a clearcut was applied followed by the removal of 90 % of the aboveground woody biomass accumulated during the spin-up and transient runs, with all non-woody biomass, i.e.

205   foliage, remaining in the stand. Natural mortality was changing annually (Fig. A1). In the first 30 years after the stand establishment, natural mortality rates followed a decreasing exponential function with the highest annual mortality rate one year after the stand establishment and subsequent gradual reduction over time, resembling the survival rates of regeneration from experimental studies focusing on beech (Hülsmann et al., 2018; Barna et al., 2011). After 30 years, we used a constant annual mortality rate of 0.9 % (Pajtík et al. 2018; Vanoni et al. 2019) to simulate managed forests, while unmanaged sites were

210   simulated using the dynamic natural mortality rates that fluctuated between 0.76 and 4.1 % during a cycle of 300 years and followed the elliptical function (Merganičová and Merganič, 2014).

2.4. Parameter estimation

The estimation of model parameters (i.e. model calibration) consisted of several phases (Figure 2) described below.
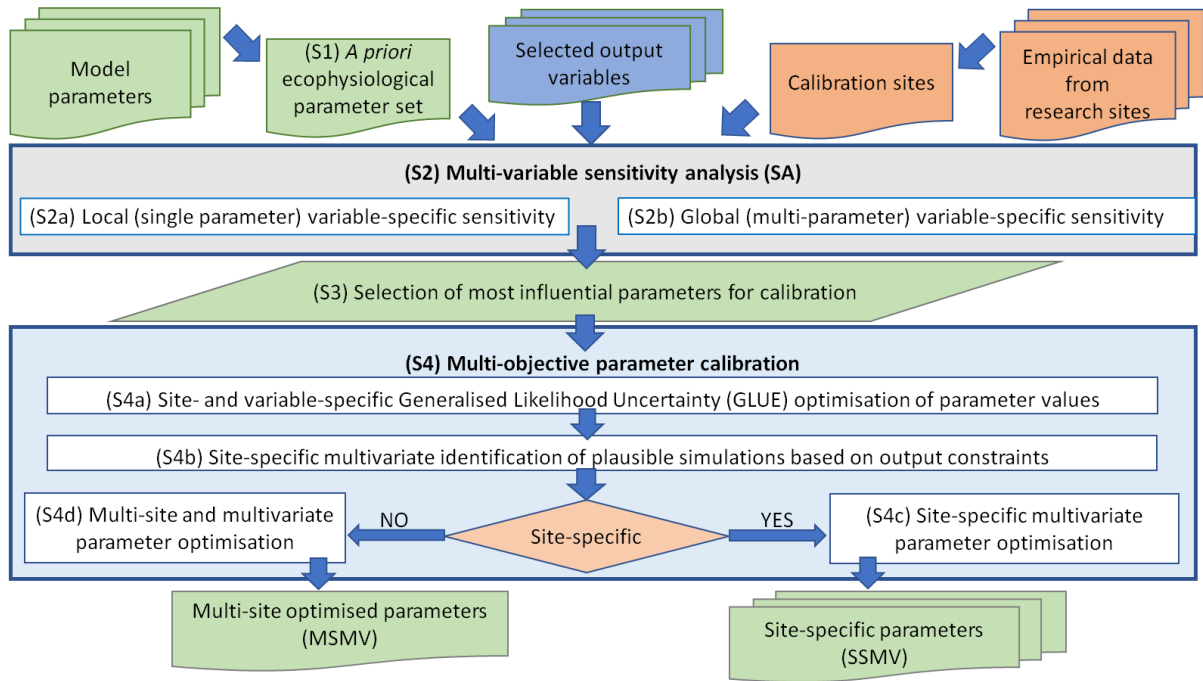
Figure 2 A general workflow used for optimising values of ecophysiological parameters of BBGCMuSo for the European beech using the multi-objective calibration approach.

2.4.1. A priori parameter setting

Prior to the calibration of model parameters, the default or a priori parameter values were set (S1 phase in Figure 2). The initially defined set (called "First" in Table 2) was defined based on values of 40 ecophysiological parameters included in previous model versions taken from Pietsch et al. (2005) and the values of new 48 parameters, which were introduced in the latest model version, were set based on the literature review and the TRY database (Kattge et al., 2020). This set was used for first simulations of all 87 sites to examine the successfulness of simulated development. Under a successful simulation we understand a simulation from spin-up until the end of normal run, during which the ecosystem existence was maintained, i.e. during the spin-up run, carbon stock in vegetation and soil was accumulated until they reached a balanced state, and the development during the normal run simulation maintained the ecosystem existence in the model. Based on the results of unsuccessful simulations at specific sites, we identified potential causes of the problems, such as insufficient water or nitrogen supply, and changed respective parameters using the trial-and-error approach until we obtained 100 % successfulness rate of simulations and an a priori parameter set (called "A priori" in Table 2).

Table 2 List of parameters that were tested and modified during the calibration of Biome-BGCMuSo for *Fagus sylvatica* L. Min = Minimum and Max = maximum values represent parameter ranges used for sensitivity analysis and optimisation, Local Sensitivity presents the values of the sensitivity index per output variable (carbon stock in aboveground wood, soil, and litter labelled as AbgwC, SoilC, and LitterC) calculated following Hoffman and Gardner (1983), the column named "First" is the very first setting for beech that we used based on the species-specific values derived for Biome-BGC by Pietsch et al. (2005) in italics and the literature review, while "A priori" is the setting that led to successful simulations of all 87 sites in the database before parameter optimisation (result of S1 phase in Figure 2), "MSMV optimised" is the multi-site multivariate calibrated parameter set (result of S4d phase in Figure 2) based on 11 calibration sites and 3 output variables. Calibrated parameters are indicated with grey background.

Parameter			Tested range		Local sensitivity			Parameter set		
Name	Abbreviation	Unit	Min	Max	AbgwC	SoilC	LitterC	First	A priori	MSMV
Transfer growth period as fraction of growing season	GP	dim	0.05	0.3	0.005	0.073	0.003	0.2	0.2	0.2
Litterfall as fraction of growing season	LP	dim	0.2	0.6	0.002	0.027	0.001	0.2	0.2	0.2
Base temperature	T_base	°C	0	7	0	0	0	5	5	5
Annual live wood turnover fraction	WTF	dim	0.5	1	0.00002	0.00026	0.00001	0.7	0.7	0.7
Annual fire mortality fraction	FM	dim	0	1	0.078	0.716	0.008	0	0	0
Whole-plant mortality fraction in vegetation period	WPM	dim	0	0.1	0.996	0.493	0.006	0.005	0.005	0.005
C:N of leaves	CN_lv	kgC kgN⁻¹	16.5	40	0.017	0.183	0.004	26.9	26.9	26.9
C:N of leaf litter, after retranslocation	CN_li	kgC kgN⁻¹	10	114	0.0002	0.015	0.178	44	44	44
C:N of fine roots	CN_ro	kgC kgN⁻¹	10	75.8	0.005	0.054	0.007	47.6	47.6	47.6
C:N of live wood	CN_lw	kgC kgN⁻¹	17	100	0.004	0.041	0.001	50	50	50
C:N of dead wood	CN_dw	kgC kgN⁻¹	300	819	0.00002	0.0002	0.005	550	550	550
Leaf litter labile proportion	LLaP	dim	0.1	0.6	0.00002	0.111	0.004	0.124	0.124	0.124
Leaf litter cellulose proportion	LCeP	dim	0.1	0.7	0.00002	0.157	0.004	0.561	0.561	0.561
Fine root labile proportion	RLaP	dim	0.1	0.6	0.00002	0.067	0.003	0.34	0.34	0.34
Fine root cellulose proportion	RCeP	dim	0.1	0.6	0.00003	0.080	0.002	0.44	0.44	0.44
Dead wood cellulose proportion	WCeP	dim	0.5	0.9	0.00004	0.361	0.376	0.77	0.77	0.77
Canopy water interception coefficient	CWIC	mm LAI⁻¹ d⁻¹	0.01	0.063	0.003	0.017	0.011	0.034	0.034	0.034
Canopy light extinction coefficient	CLEC	dim	0.3	0.7	0.012	0.136	0.004	0.6	0.6	0.6616
All-sided to projected leaf area ratio	SLA:PA	dim	1.5	2.5	0.0007	0.001	0.00002	2	2	2
Ratio of shaded SLA:sunlit SLA	shSLA:suSLA	dim	0.2	5	0.073	0.568	0.004	2	2	2
Fraction of leaf N in Rubisco	FLNR	dim	0.1	0.3	0.008	0.087	0.003	0.162	0.162	0.1383
Maximum stomatal conductance (projected area basis)	MSC	m s⁻¹	0.001	0.009	0.088	0.925	0.020	0.006	0.005	0.0051
Cuticular conductance (projected area basis)	CC	m s⁻¹	0.00001	0.0001	0.001	0.011	0.000	0.00006	0.00006	0.00006
Boundary layer conductance (projected area basis)	BLC	m s⁻¹	0.01	0.09	0.005	0.076	0.002	0.01	0.01	0.01
Maximum depth of rooting zone	MRD	m	0.2	4.1	0.001	0.021	0.003	2	2	2
Root distribution parameter	rootDistr	dim	0.5	4	0.001	0.088	0.123	3.67	1.5	1.5
Growth resp per unit of C grown	GRC	dim	0.1	0.5	0.020	0.216	0.016	0.3	0.3	0.3
Maintenance respiration in kgC/day per kg of tissue N	MRperN	kgC kgN⁻¹ d⁻¹	0.1	0.4	0.091	0.902	0.023	0.218	0.218	0.218
Theoretical maximum proportion of non-structural and structural carbohydrates	NSC:SCmax	dim	0.05	0.3	0.0001	0.0004	0.00001	0.1	0.1	0.1
Proportion of non-structural carbohydrates available for maintanance respiration	NSC2MR	dim	0.1	0.5	0.00002	0.00011	0.00008	0.3	0.3	0.3
Symbiotic+asymbiotic fixation of N	Nfix	kgN m⁻² yr⁻¹	0.0001	0.01	0.046	0.494	0.991	0.0005	0.01	0.0091
Time delay for temperature in photosynthesis acclimation	tau	day	0	50	0.0003	0.0035	0.0001	10	10	10
Volumetric water content ratio to calculate soil moisture limit 1	VWCratio_lim1	dim	0.1	0.9	0.004	0.067	0.002	0.99	0.1	0.1
Volumetric water content ratio to calculate soil moisture limit 2	VWCratio_limit2	dim	0.5	1	0.0001	0.0049	0.0021	0.99	0.99	0.99
Minimum of soil moisture limit2 multiplicator (full anoxic stress value)	min_soilstress2	dim	0	1	0	0	0	0.4	0.4	0.4
Vapor pressure deficit: start of conductance reduction	VPDS	Pa	500	1500	0.005	0.079	0.003	600	600	600
Vapor pressure deficit: complete conductance reduction	VPDC	Pa	1500	3500	0.080	0.783	0.009	3000	3000	2910
Maximum senescence mortality coefficient of aboveground plant material	SMCA	dim	0	0.01	0	0	0	0.001	0	0
Maximum senescence mortality coefficient of belowground plant material	SMCB	dim	0	0.01	0.0001	0.001	0.00002	0.001	0	0
Maximum senescence mortality coefficient of non-structured plant material	SMCL	dim	0	0.01	0.003	0.079	0.004	0.0001	0	0
Lower limit extreme high temperature effect on senescence mortality	SNSC_ext1	°C	30	40	0	0	0	30	30	30
Upper limit extreme high temperature effect on senescence mortality	SNSC_ext2	°C	30	50	0	0	0	40	40	40
Turnover rate of wilted standing biomass to litter	TRWB	dim	0.01	0.1	0	0	0	0.01	0.01	0.01
Turnover rate of non-woody cut-down biomass to litter	TRCN	dim	0.01	0.1	0	0	0	0.05	0.01	0.01
Turnover rate of woody cut-down biomass to litter	TRCW	dim	0.0001	0.1	0	0	0	0.01	0.0009	0.0009
Drought tolerance parameter	DSWScirt	nday	0	100	0	0	0	30	100	100
Effect of soilstress factor on photosynthesis	Sseff	dim	0	0.4	0.006	0.066	0.002	0	0	0
Leaf carbon allocation proportion		dim	-	-	-	-	-	0.173	0.173	0.173
Fine root carbon allocation proportion		dim	-	-	-	-	-	0.094	0.094	0.094
Live woody stem carbon allocation proportion		dim	-	-	-	-	-	0.101	0.101	0.101
Dead woody stem carbon allocation proportion		dim	-	-	-	-	-	0.556	0.556	0.556
Live coarse root carbon allocation proportion		dim	-	-	-	-	-	0.012	0.012	0.012
Dead coarse root carbon allocation proportion		dim	-	-	-	-	-	0.064	0.064	0.064
Canopy average specific leaf area (projected area basis)		m2 kgC⁻¹	-	-	-	-	-	48	34.5	34.5
Canopy growth proportion		dim	-	-	-	-	-	0.5	0.5	0.5

2.4.2. Sensitivity analysis

The sensitivity analysis (S2 phase in Figure 2) was performed to identify the impact of parameters on the carbon stock in
245 aboveground wood, soil, and litter (AbgwC, SoilC, LitterC) using BBGCMuSo simulations of calibration sites (Table 1). First,
we performed a local, i.e. single parameter, SA (S2a in Figure 2) using regular sampling of parameter values from their pre-
defined ranges based on the literature review. The sensitivity of variable *i* to parameter *P* was quantified with the sensitivity
index (*SI*) using the equation of Hoffman and Gardner (1983):

$$SI_{Pi} = \frac{Vmax_{Pi} - Vmin_{Pi}}{Vmax_i} \tag{1}$$

250 where $Vmax_{Pi}$ and $Vmin_{Pi}$ are the maximum and minimum values of the simulated output variable *i* when testing parameter *P*,
and $Vmax_i$ is the absolute maximum value of the output variable obtained from the tests of all parameters.

Afterwards, a global, i.e. multi-parameter, SA (S2b in Figure 2) was performed following the approach by (Verbeeck et al.,
2006). The sampling of values of the selected model parameters from their ranges was done with Monte Carlo simulations,
while assuming a multivariate uniform distribution. The simulated output was examined with regard to parameter deviations
255 from the mean using the least square linearisation method. This allowed us to estimate the contribution of each tested parameter
to the analysed model output uncertainty and identify the parameters that affected AbgwC, SoilC, and LitterC most. The results
of SA were used to select the parameters to be calibrated (S3 phase in Figure 2). The SA was performed using the musoMonte
and musoSensi functions implemented in the RBBGCMuSo package (Hollós et al., 2023).

2.4.3. Parameter calibration

Within the parameter optimisation we first performed a site- and variable-specific calibration (S4a phase in Figure 2) using
GLUE method (Beven and Binley, 2014) implemented in the calibMuso function of the RBBGCMuSo package (Hollós et al.,
2023). With this procedure, a selected parameter set was optimised using the least squares likelihood function based on the
comparison of the simulated values of the selected output variable with its observations in the pre-defined parameter space:

265

$$L = e^{-\sqrt{\frac{(Vobs - Vsim)^2}{n}}} \tag{2}$$

where *L* is the estimated likelihood, *Vobs* and *Vsim* are the observed and the simulated values of the output variable, and *n* is
the number of observations.

For every site, we performed 100,000 Monte Carlo simulations, each with a unique combination of parameter values randomly
generated from the predefined parameter ranges (Table 2). The results of all simulations were used in the subsequent
270 optimisation steps.

First, we evaluated the plausibility (i.e. the realism) of simulated AbgwC, LitterC, and SoilC (S4b phase in Figure 2) at the
end of spin-up and in individual years of normal run simulations. The plausibility check is a form of output data streams

conditioning similar to the CIRM method proposed by Hollós et al. (2022). We applied the following constraints derived from literature to evaluate the plausibility of simulated values: carbon stock in aboveground wood below 70 kgC m^{-2} (Barna et al.,
275 2011; Georgi et al., 2018; Standovár and Kenderes, 2003; Trotsiuk et al., 2012), soil carbon in the whole soil profile between 5 and 25 kgC m^{-2}, and litter carbon amount between 0.1 to and 4 kgC m^{-2} (De Vos and Cools, 2011; Pavlenda and Pajtík, 2010; Wellbrock et al., 2016; Wellbrock and Bolte, 2019). A simulation was identified as plausible if all three examined output variables fulfilled the above-listed constraints at the end of the spin-up and in all simulated years of the normal run.

The site-specific multivariate optimised parameter values (SSMV parameter sets resulting from S4c phase in Figure 2) were
280 derived from subsets of plausible simulations selected for each calibration site as those minimising estimation errors of AbgwC, SoilC, and LitterC, and maximizing the joint-likelihood function. We used the normal likelihood function and calculated the sum of loglikelihood values for each timestamp (year) assuming that the estimation errors are independent from each other.

Next, we performed an optimisation of parameters across the studied geographical domain (S4d phase in Figure 2) by processing the plausible subsets of outputs from all calibration sites together. First, we identified feasible ranges for each
285 parameter and site by overlapping the results of the three output variables (Fig. A2a). Then, we derived the multi-site feasible parameter ranges as an intersection of site-specific feasible parameter ranges. Afterwards, we divided the multi-site ranges of each parameter into five equally wide sub-intervals defining 5 discrete steps on each dimension (Fig. A2b) of the multi-dimensional parameter space. This categorisation was required because the applied parameter values in site-specific Monte Carlo simulations differed between the sites. In the hyperspace, we identified ten cells with the highest number of allocated
290 sites and simulations and the smallest arithmetic mean errors of AbgwC, SoilC, and LitterC, and calculated mean values of parameters per cell. The final multi-objective optimal parameter set was the one that led to successful simulations of all calibration sites and smallest errors.

2.5. Robustness, validation and plausibility tests

2.5.1. Robustness of calibrated parameter values

295 The robustness of the site-specific (SSMV) and multi-site (MSMV) optimised values of parameters was tested by simulating all calibration sites with all derived parameter sets and calculating root mean square errors (RMSE) of simulated output variables. This test allowed us to examine the problem of overfitting and the applicability of site-specific parameter sets outside the specific site conditions. The results were presented with heatmaps produced using ggplot2 R package (Wickham, 2016).

Next, we applied the machine learning method of decision trees (DT) to identify the problems due to the trade-off between
300 variables and/or sites based on the evaluation of the entropy. With the DT method we determined parameter ranges, within which plausible simulations can be expected. This was done by deriving classification decision trees for each site and output variable using all 100,000 Monte Carlo simulations per calibration site that were split into 2 groups of plausible and implausible ones based on the constraints for the three tested variables (see Sect. 2.4.3.). In total we derived 33 decision trees (11 sites x 3 variables) using the rpart R package (Therneau et al., 2023). From the DT results, we obtained plausible ranges for each

305 parameter, site and variable. Then, we searched for intersections of these ranges to obtain the final parameter-wise plausible ranges for a specific site and multi-site ranges for all calibration sites and variables together. The SSMV and MSMV optimised parameter values were considered robust if they occurred within the respective DT parameter ranges.

The next test was aimed at analysing if SSMV parameter values followed any trends along specific gradients. Specifically, we examined the interdependencies between the pairs of parameters, and the trends along stand and site gradients, namely age,

310 elevation, latitude, climate and soil characteristics. Any significant trend may indicate that the respective parameter should not be handled as a constant but should vary with specific conditions. The analyses were based on Spearman correlations, and linear regressions performed in R environment (R Core Team, 2018). We examined the physiological meaningfulness of revealed trends and relationships using the empirical evidence collected from the scientific literature.

315 2.5.2. Model performance with parameter values optimised for multiple sites

The MSMV parameter set of BBGCMuSo derived in S4d calibration phase (Figure 2) was validated using an independent dataset from 8 European beech dominated sites located within the studied geographical domain (Table 1, Figure 1), each represented by at least two repeated observations of aboveground wood carbon. The simulations consisted of spin-up, transient run and normal run as described above. The validation was based on the comparison of modelled and observed carbon stock

320 in aboveground wood at specific time points, for which we calculated the bias defined as an arithmetic mean of differences between modelled and observed values of the respective variable, mean absolute error (MAE), mean percentage error (MPE), and root mean square error (RMSE). SoilC and LitterC were compared to plausible ranges derived from literature (De Vos and Cools, 2011; Pavlenda and Pajtík, 2010; Wellbrock et al., 2016; Wellbrock and Bolte, 2019) since no observed data on soil and litter carbon were available for validation sites.

325 2.5.3. Robustness and plausibility of simulated output at a large scale

To evaluate the broad applicability of the derived multi-objective parameter set, we simulated forest development across 87 sites, encompassing the main climatic and soil gradients in the study area (Figure 1). We specifically assessed the plausibility of absolute values of AbgwC, LitterC, and SoilC by comparing them with values documented in the literature (e.g. Barna et al., 2011; Pavlenda and Pajtík, 2010). We also examined the responses of simulated carbon stocks to environmental conditions

330 and compared their shapes to the patterns published from empirical studies. We analysed the responses of simulated outputs using Spearman correlations, linear and quadratic regressions, and generalised additive models (GAM). When explaining the patterns of the main three variables along environmental gradients we examined also other stocks, such as carbon stock in roots, leaves, as well as some carbon fluxes, particularly heterotrophic respiration, to reveal the mechanisms driving the model response. All tests were performed in R environment (R Core Team, 2018).

3. Results

3.1 Parameter sensitivity analysis

The local (single parameter) sensitivity analysis (S2a in Figure 2) focusing on evaluating the effects of individual parameters revealed that the aboveground wood carbon stock was most affected by the whole plant mortality rate (WPM). Soil and litter carbon stocks were most sensitive to the maximum stomatal conductance (MSC) and nitrogen fixation (Nfix), respectively (Table 2). The analysis of trends in variable changes due to modifications of parameter values clarified how the increase of the parameter value affected the values of the respective output variable, e.g. the increase of MSC caused an increase of all tested output variables (AbgwC, SoilC, LitterC) in the whole parameter range (Fig. A5). The impact of other parameters was more complex, as we revealed both positive and negative trends, while in the case of the increase of e.g. Nfix the positive ones prevailed in AbgwC and SoilC, and negative ones in LitterC. A more detailed analysis identified the changes of output variables along the parameter range, e.g. the increase of Nfix caused an initial increase of LitterC, which was followed by its gradual reduction as Nfix was increasing (Fig. A3a).

The global (multi-parameter) sensitivity analysis (S2b in Figure 2) showed that Nfix had the highest impact on all three analysed carbon pools (Figure 3). The subsequent parameters were MSC, growth respiration per unit of carbon allocation (GRC), maintenance respiration in kgC day^{-1} per kg of tissue nitrogen (MRperN), fraction of leaf nitrogen in Rubisco (FLNR). However, the ranking of parameters differed between the individual output variables (Figure 3).
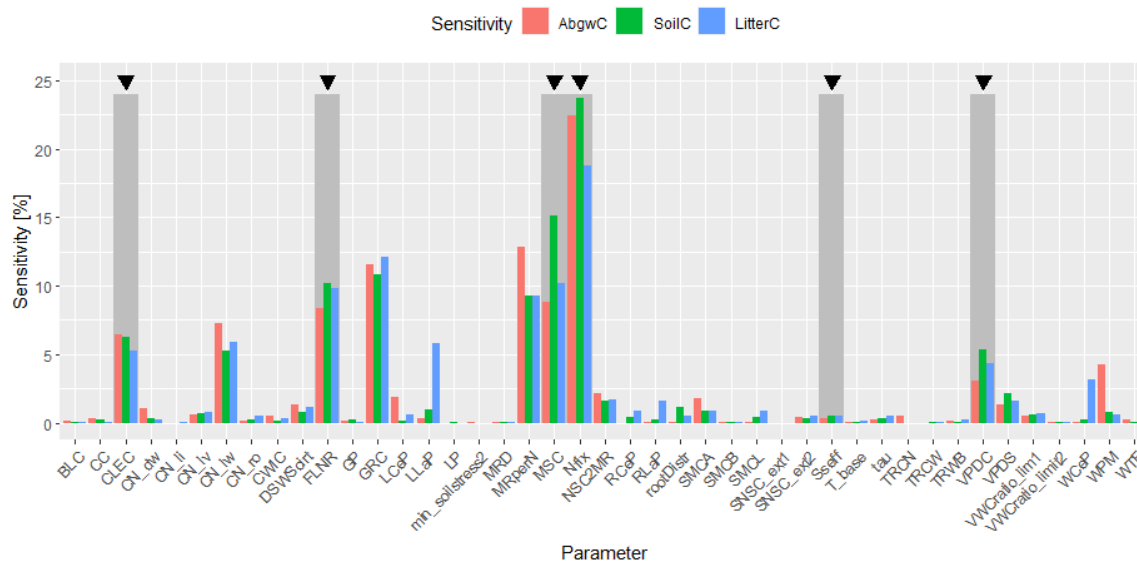
Figure 3 Results of global (multi-parameter) sensitivity analysis (S2b in Figure 2) of simulated carbon stock in aboveground wood, soil and litter (AbgwC, SoilC, LitterC) to ecophysiological parameters of BBGCMuSo. Parameter abbreviations are given in Table 2. Dark grey rectangles with black arrows above indicate parameters selected for the calibration procedure: canopy light extinction coefficient (CLEC), fraction of leaf nitrogen in rubisco (FLNR), maximum stomatal conductance (MSC), nitrogen fixation (Nfix), effect of soil stress factor on photosynthesis (Sseff), and vapour pressure deficit for complete conductance reduction (VPDC).

Based on the results of the sensitivity analysis we selected six parameters to be calibrated: canopy light extinction coefficient (CLEC), FLNR, MSC, Nfix, vapour pressure deficit for complete conductance reduction (VPDC), and effect of soil stress factor on photosynthesis (Sseff), as they had a substantial effect on carbon stock in aboveground wood, soil, and litter (Figure 360   3). Other parameters with a high influence on the simulated C pools (such as C:N ratio in leaves, Fig. A3b) were not to selected for calibration due to a strong support of their actual values from the literature (e.g. Fig. A4).

3.2 Parameter estimation

The site-specific multivariate (SSMV) optimised values of all 6 calibrated parameters for 11 calibration sites differed from the a priori ones, varied within the whole tested ranges (Table 2) and strongly differed between the sites (Figure 4). Two parameters 365   (FLNR, VPDC) showed a gradual change of SSMV values across the whole tested range, while the SSMV values of others, especially CLEC and Sseff, were clustered. In comparison to a priori values, SSMV values of individual parameters changed by 41 % on average, while Nfix was modified most substantially (67 % on average).
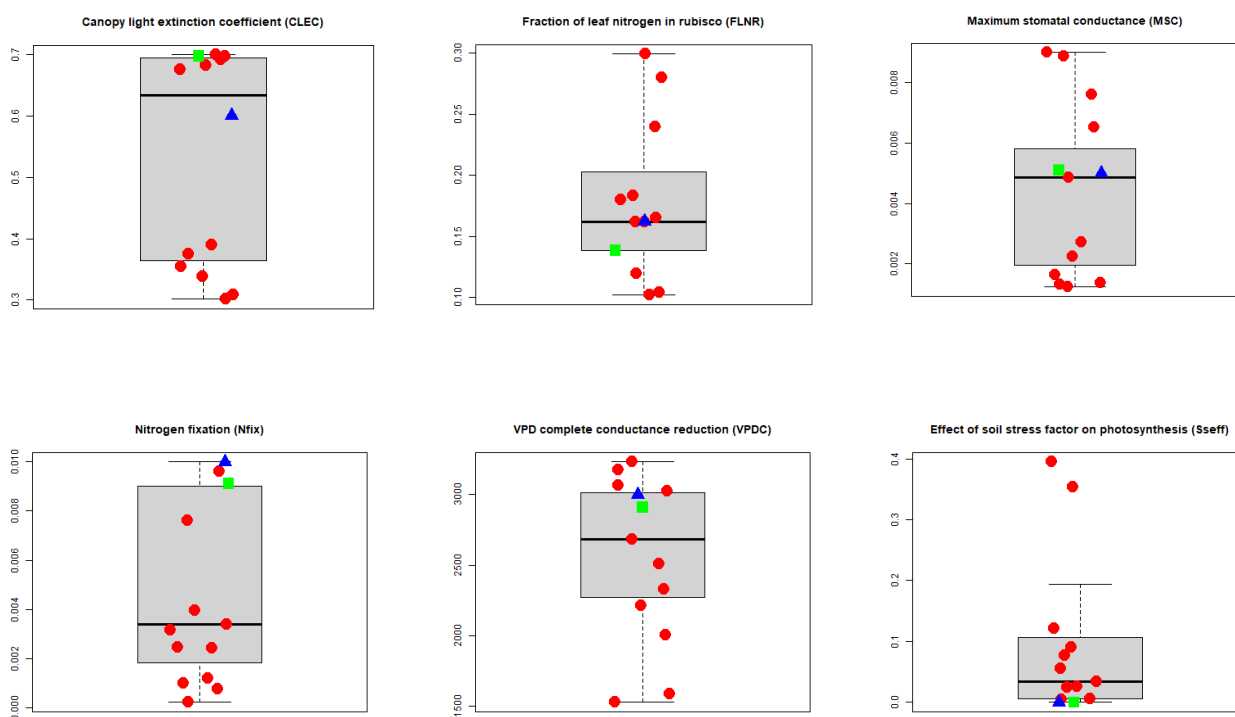
Figure 4 A priori (blue triangles), site-specific (SSMV, red dots) and multi-site (MSMV, green squares) optimised values of calibrated ecophysiological parameters selected based on the multi-objective sensitivity analysis (S4 in Figure 2). The thick horizontal lines 370   **represent medians, boxes represent the interquartile ranges (IQR), and the whiskers represent ±1.5IQR.**

The median reduction of model errors at calibration sites simulated with SSMV parameter sets in comparison to the a priori set was 35 %, 55 %, and 11 % for AbgwC, SoilC, and LitterC, respectively, and 26 %, 35 % and 9 % in comparison to the simulation output obtained with the MSMV parameter set (Figure 5).
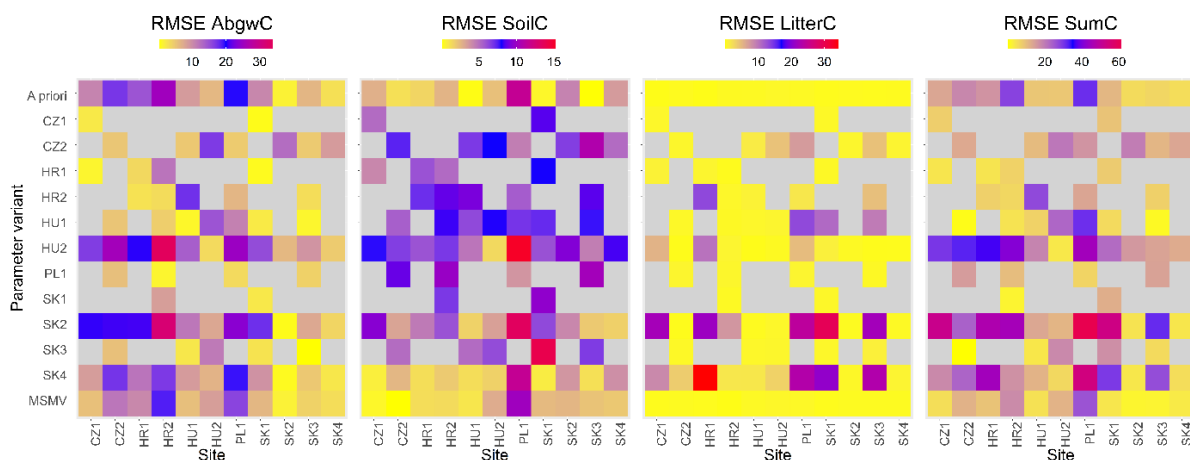
Figure 5 Heatmaps of root mean square errors (RMSEs) for carbon stock in aboveground wood, soil, and litter (AbgwC, SoilC, LitterC) and their sum (SumC) for individual calibration sites (presented on x axis) and 13 different variants of parameter sets (presented on y axis): one a priori set, 11 site-specific (SSMV) optimised ones identified by site abbreviations, and one multi-objective (multi-site and multivariate, MSMV) optimised set. The red colour indicates the largest RMSEs, while the yellow one indicates the smallest RMSEs, the grey colour indicates unsuccessful simulations, which ended with zero or close to zero values of carbon state variables.

Parameter values obtained from the multi-site optimisation (S4d in Figure 2) changed by 2 to 15 % of their a priori estimates except for the Sseff, which remained unchanged (Figure 4, Table 2). Simulation results using the MSMV parameter set showed reduced mean errors of all three tested output variables, i.e. AbgwC, SoilC and LitterC, in comparison to the results obtained with the a priori set by 10, 26, and 5 %, respectively (Table 3, Figure 5).

Table 3 Evaluation of model performance based on simulations of beech ecosystems at 11 calibration sites using the a priori parameter set and the optimised parameter sets optimised with respect to measured sets of carbon stock in the aboveground wood, soil, and litter (AbgwC, SoilC, and LitterC in kgC m⁻²). "Site-specific" refers to parameter sets derived for single sites using a multivariate approach (SSMV, S4c phase in Figure 2). "Multi-site" refers to multi-site and multivariate (MSMV) parameter values
400 **derived collectively for all calibration sites (S4d in Figure 2). RMSE = root mean square error, Bias = arithmetic mean of differences between modelled and observed values of the respective variable, MAE = mean absolute error, MPE = mean percentage error, MinDif and MaxDif are minimum and maximum differences between the modelled and observed values of the respective variable.**

Parameter set	Variable	N	RMSE	Bias	MAE	MPE	MinDif	MaxDif
A priori		96	9.7727	7.3911	7.8366	29.502	-8.1569	27.007
Site-specific	AbgwC	96	2.0698	-0.2887	1.4873	0.012	-5.4830	5.7422
Multi-site		96	6.8718	4.1734	5.4798	19.246	-9.5527	27.756
A priori		72	3.5242	2.2276	2.2630	58.329	-0.2268	11.729
Site-specific	SoilC	72	6.8068	-2.7876	6.3782	-0.408	-9.7400	4.7630
Multi-site		72	3.0803	0.1167	2.6423	38.068	-2.4427	10.243
A priori		10	0.2424	0.2117	0.2117	121.774	0.0611	0.4651
Site-specific	LitterC	10	0.2035	0.0030	0.1653	42.005	-0.2894	0.4382
Multi-site		10	0.1849	0.1417	0.1419	91.327	-0.0007	0.4185

The simulations performed with site-specific and multi-site optimised parameter sets produced more accurate estimates of
405 carbon stock in aboveground wood, soil and litter than the a priori set. The Wilcoxon signed rank test with the continuity correction data confirmed insignificant differences between observed and modelled carbon stock in aboveground wood and litter simulated with SSMV parameter sets (V = 1807, p = 0.14 for AbgwC, and V = 26, p = 0.92 for LitterC), while the differences for soil carbon were significant (V = 528, p = 1.04e-05, see Sect. 4.2 for explanation). The use of MSMV parameter set resulted in insignificant differences of SoilC (V = 1396, p = 0.64), while the estimates of AbgwC and LitterC were
410 significantly different from observations (V = 4094, p = 1.10e-10, and V = 54, p = 0.004, respectively). Nevertheless, the magnitudes of their mean errors calculated for the whole set of calibration sites as well as for most of individual sites were substantially reduced (Table 3, Figure 5).

3.3 Robustness, validation, and plausibility tests

3.3.1 Robustness of calibrated parameter values

415 When simulating the development of calibration sites with the site-specific parameter sets (SSMV) optimised for other sites, we revealed a high variation in modelled outputs per site (Figure 5 and Fig. A6). In 47 % of cases we encountered unsuccessful simulations, during which the modelled forests did not survive. Only three SSMV parameter sets led to successful simulations of all calibration sites, but their errors exceeded those obtained with the a priori, respective SSMV or MSMV optimised sets (MPE of AbgwC, SoilC, and LitterC were 39 %, 296 %, and 570 %, respectively).

420 The robustness test of SSMV and MSMV optimised parameter values using the method of decision trees (DT) revealed that

in 78 % of cases site-specific and muti-site parameter values occurred within the parameters ranges derived from decision trees

for individual output variables and sites (Table 4, Fig. A9). The discrepancies between the optimised parameter values and DT

ranges occurred for the variables and sites with lower proportions of plausible simulations (Fig. A16) or in the cases when DT

parameter ranges derived for individual output variables did not overlap (e.g. the ranges derived for FLNR and site CR2015,

425 Fig. A9).

Table 4 Robustness of site-specific (SSMV) and multi-site (MSMV) parameter values based on the analysis if the optimised parameter value occurred inside the parameter ranges derived for individual calibration sites and carbon stock variables (aboveground wood, soil and litter carbon labelled as AbgwC, SoilC, LitterC) using the method of decision trees (DT, Sect. 2.5.1).
430 **The values for SSMV represent the mean from 11 calibration sites. The value 1 indicates that the MSMV value or all SSMV optimised parameter values occurred within the DT ranges. The abbreviations of parameters are CLEC = canopy light extinction coefficient, FLNR = fraction of leaf nitrogen in rubisco, MSC = maximum stomatal conductance, Nfix = nitrogen fixation, VPDC = vapour pressure deficit for complete conductance reduction, Sseff = effect of soil stress factor on photosynthesis.**

		Proportion of optimised parameter values inside parameter ranges derived using decision tree method					
Output variable		AbgwC		SoilC		LitterC	
Parameter set		SSMV	MSMV	SSMV	MSMV	SSMV	MSMV
Parameter	CLEC	1.00	1	0.91	1	0.91	1
	FLNR	0.73	1	0.64	0	0.64	0
	MSC	1.00	1	0.55	1	0.36	0
	Nfix	0.91	0	1.00	0	0.36	1
	VPDC	1.00	1	1.00	1	1.00	1
	Sseff	1.00	1	1.00	1	1.00	1
Mean of All		0.94	0.83	0.85	0.67	0.71	0.67

435 The analysis of interdependencies between the site-specific optimised parameter values revealed the only significant Spearman

correlation between CLEC and MSC, which were negatively correlated at 95 % significance level (r=-0.6, p=0.04, Figure 6a).

The highest, although non-significant, correlation was found between Nfix and FLNR (r=0.7, p=0.37) suggesting that if Nfix

increases FLNR should also increase.

Spearman correlations between parameters and site characteristics revealed that the site-specific optimised values of two

440 calibrated parameters (CLEC, VPDC) were significantly related to elevation (r=0.5 and -0.7, p=0.04, respectively). Significant

relationships were also found between CLEC and several climatic variables (Figure 6). The highest positive correlation (r=0.9,

p=0.01) of CLEC was with the long-term mean annual precipitation total (AMPRCP), and the highest negative correlation (r=-

0.8, p=0.01) with the long-term mean annual vapour pressure deficit (AMVPD). The increasing AMVPD was positively

significantly related to the values of MSC (r=0.7, p=0.05). For other parameters we did not reveal any significant relationships

445 with climate conditions, nor could we confirm any significant correlations of parameter values to soil conditions (Fig. A10),

although positive or negative trends with several environmental characteristics were visible for some parameters, mainly for MSC and VPDC (Figure 6b, Fig. A10).
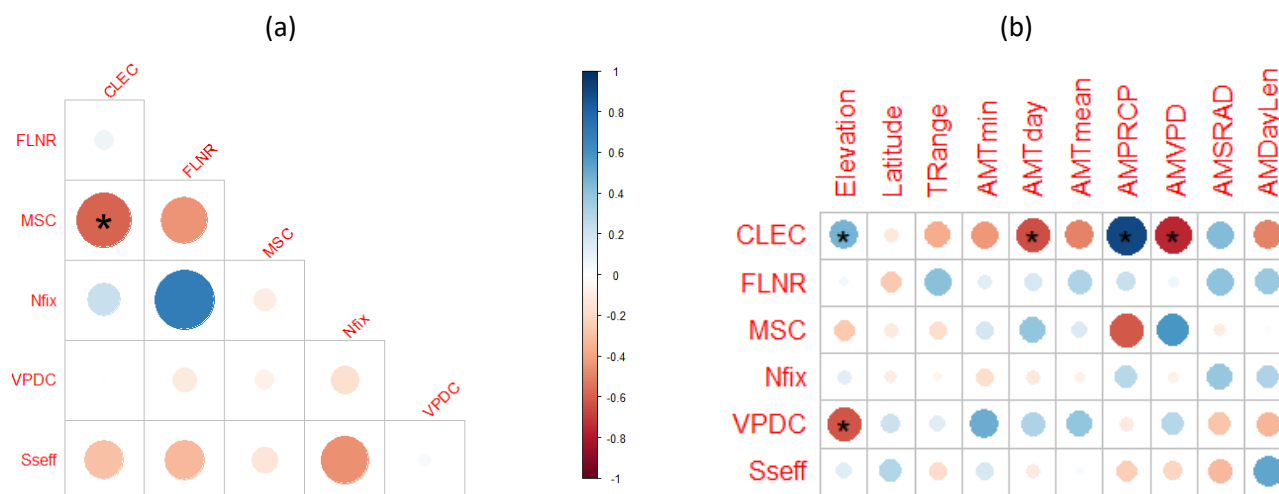
Figure 6 Spearman correlations between site-specific optimised values of calibrated parameters (a) and between site-specific
450 **optimised parameter values and site characteristics (b). The colour and the size of the circles indicate the value of the correlation coefficient, and the stars indicate the significance of the correlation (1 star for 95 % significance level, 2 stars for 99 % significance level). The abbreviations of parameters are: CLEC = canopy light extinction coefficient, FLNR = fraction of leaf nitrogen in Rubisco, MSC = maximum stomatal conductance, Nfix = nitrogen fixation, VPDC = vapour pressure deficit for complete conductance reduction, and Sseff = effect of soil stress factor on photosynthesis. Climate characteristics represent long-term annual averages:**
455 **TRange = Temperature range, AMTmin = Minimum temperature, AMTday = Daylight temperature, AMTmean = Mean temperature, AMPRPCP= Precipitation total, AMVPD = Vapour pressure deficit, AMSRAD = Daily solar radiation, AMDayLen = Daylength.**

3.3.2 Model performance with parameter values optimised for multiple sites

460 The mean absolute error (MAE) between the simulated and observed aboveground wood carbon of 8 validation sites was 0.26 kgC m^{-2} with a 95 % confidence interval from -0.025 to 0.56 kgC m^{-2}, while the individual absolute differences varied between -2.06 and 5.11 kgC m^{-2} (Figure 7). The root mean square error was 1.22 kgC m^{-2}. The non-parametric Wilcoxon signed rank test with continuity correction indicated non-significant differences between simulations and observations of aboveground wood carbon (V = 1385, p-value = 0.1962). The mean percentage error of AbgwC was 1.25 % of the observed carbon stock
465 in the aboveground wood. Hence, both absolute and relative differences were of negligible magnitudes.

Since no observed data on soil and litter carbon were available for validation sites, the simulated SoilC and LitterC were tested against their ranges reported in the literature. The results showed that both variables occurred within the plausible ranges (Fig. A 12).
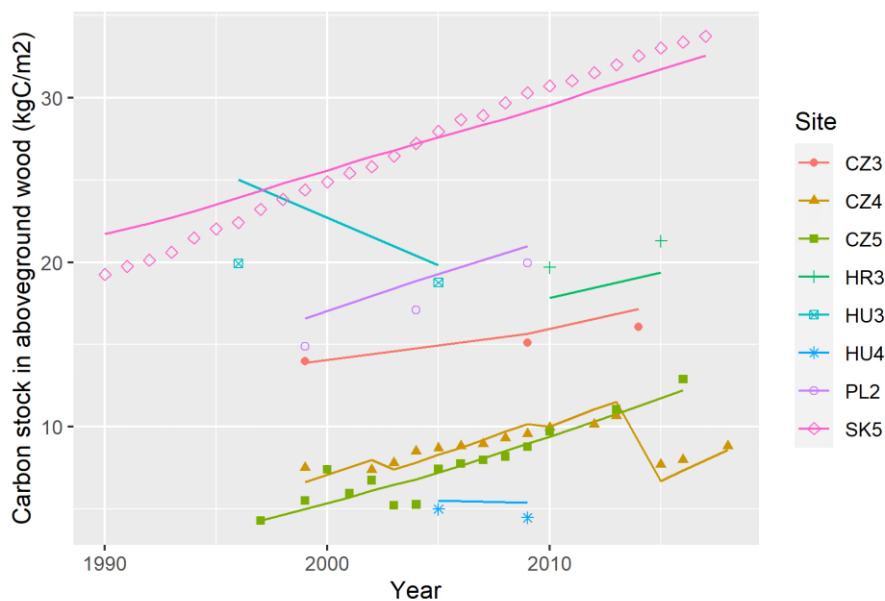
Figure 7 Comparison of the temporal development of observed (points) carbon stock in aboveground wood (AbgwC) and simulated AbgwC (lines) using the multi-site multivariate optimised (MSMV) parameter set at 8 validation research sites.

3.3.3 Robustness and plausibility of simulated output at a large scale

The simulations of all 87 research sites using the multi-site optimised (MSMV) parameter values were successful and the simulated values of the three output variables (i.e. AbgwC, SoilC, and LitterC) at the end of the spin-up run were well-aligned with the plausible ranges indicated in the literature (Fig. A 13).

The simulated values of output variables were significantly correlated with multiple site characteristics (Figure 8, Fig. A17, Fig. A18). The modelled aboveground wood carbon exhibited distinct unimodal responses along the gradients of elevation, long-term mean air temperature, and vapour pressure deficit (VPD). The results manifested a production optimum of beech in Central Europe at elevations of 500 - 600 m a.s.l., mean annual air temperature of 9°C, and VPD of 530 Pa. The SoilC and LitterC demonstrated an increasing trend along the elevation gradient and decreasing trends along the climatic gradients. The responses of carbon stocks to soil properties generally followed a linear pattern, while SoilC and LitterC significantly decreased with the increasing clay content and increased with the increasing sand content in soil. Aboveground wood carbon was found to be significantly correlated with the proportion of clay in the first and second soil layers, and with the proportion of silt in the fifth layer (Fig. A18). The highest levels of simulated aboveground wood carbon were observed on loamy or sandy-loamy soils (Fig. A20).
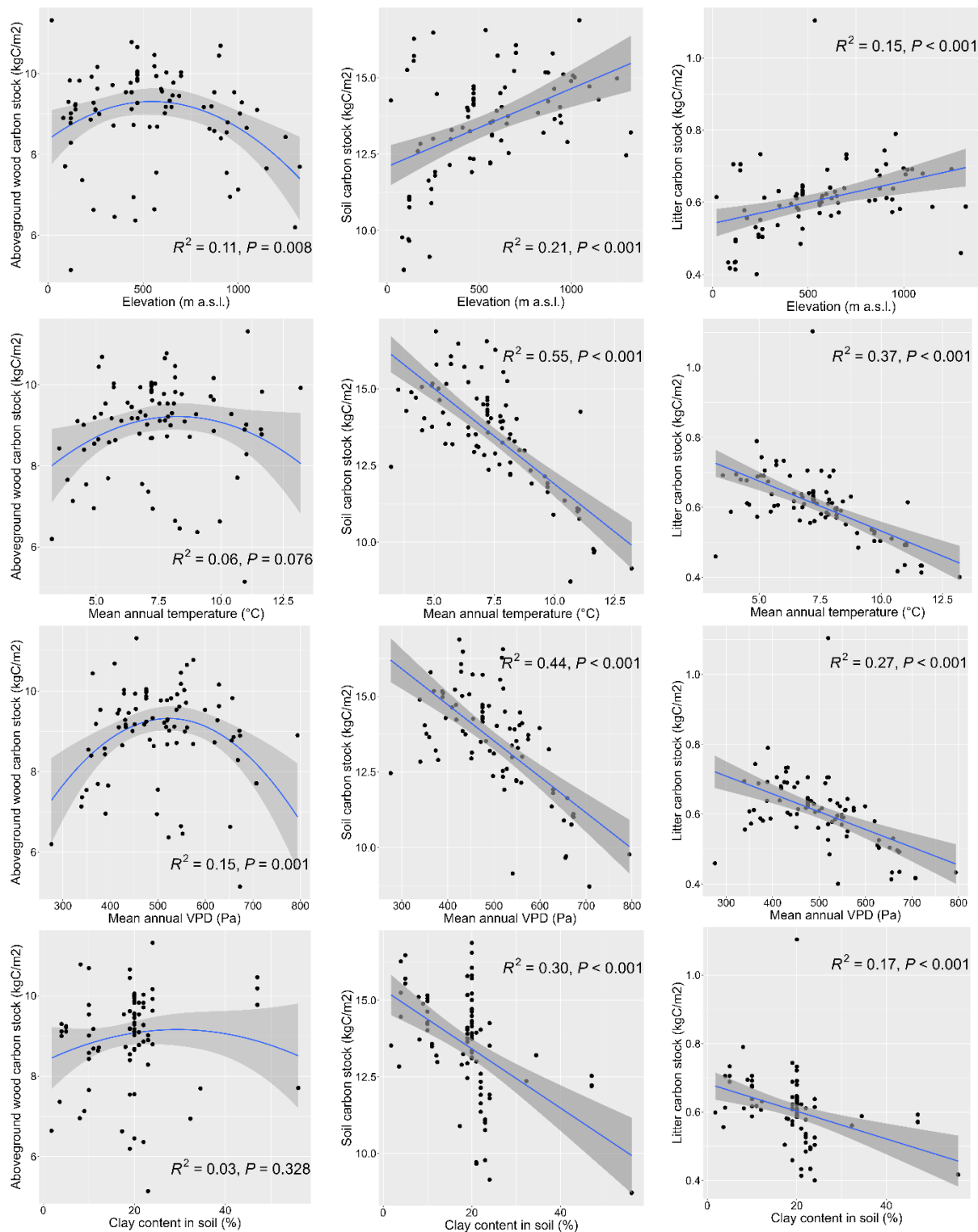
Figure 8 Responses of modelled carbon stocks in the aboveground wood at the standardised stand age of 35 years (left), soil (middle) and litter (right) carbon stocks to selected environmental variables. The simulations with BBGCMuSo were conducted for 87 sites distributed across central Europe (see Figure 1). Linear or quadratic regressions were fitted to the data. R2 represents the squared regression coefficient, and P is the p-value for the F-test of the fitted model.

490 **4. Discussion**

4. 1. Selection of parameters for calibration

The sensitivity analysis identified the parameters with the highest impact on the selected model output (Table 2, Figure 3). Several highly influential parameters identified by SA were excluded from the calibration for different reasons. Growth respiration per unit of carbon allocation (GRC), and maintenance respiration per kg of tissue nitrogen (MRperN), were not

495 calibrated because they were already used in previous model versions (White et al., 2000), and we could not support the modification of their values by observations. Other parameters were not included in calibration because the data from literature supported their current values and/or because of the adverse impact on the variables of interest. For example, C:N ratio in leaves was found to have a substantial effect on all examined carbon pools (Figure 3), but to obtain a desired reduction of carbon stock in aboveground wood we would need to increase this parameter from its a priori value (Fig. A3). However, the

500 analysis of the values obtained from site-specific measurements performed on some of our sites and the data from the TRY database (Kattge et al., 2020) revealed that increasing the value of C:N ratio in leaves would cause its significant deviation from the mean or median of experimental observations (Fig. A4). Similarly, the parameter representing the natural whole plant mortality was not calibrated since instead of the temporarily constant mortality we applied dynamic mortality rates during the normal run simulations that depend on the applied forest management and were derived from published field observations

505 (Barna et al., 2011; Hülsmann et al., 2018; Pajtík et al., 2018; Vanoni et al., 2019). The possibility of using dynamic mortality rates in BBGCMuSo is a major improvement in comparison to the original Biome-BGC model, as mortality has been found to be a driving process of vegetation dynamics in forest growth models (Hlásny et al., 2014; Bugmann et al., 2019).

The identification of influential parameters is crucial not only for model calibration, but also for future local studies as it provides valuable information about the key parameters, the values of which should be collected in the field, since applying

510 site-specific values obtained from experimental data may substantially reduce the uncertainty of model simulations. Already (Thornton et al., 2002) presented that some parameters, such as C:N ratio in leaves, should be treated as site-specific. However, such data were not available for most of our sites, and thus, we used a generalised value of this parameter.

4.2. Parameter estimation

The mean error metrics (root mean square errors, mean absolute and percentage errors) showed the increased accuracy of

515 modelled output obtained using single-site (SSMV) and multi-site (MSMV) optimised parameter sets in comparison with those obtained with the a priori parameter set (Table 3). Greater errors of soil carbon for SSMV parameter sets resulted from very tight positive relationship between the simulated AbgwC and SoilC revealed when analysing Monte Carlo simulations. Due to

this, even the high number of performed simulations (100,000 simulations per site) generally covered only a small portion of the 2D space defined by AbgwC and SoilC (Fig. A7). Hence, improving the results for one of these two carbon pools caused

520 the increase of the error of the other pool within the tested space of six calibrated parameters (Fig. A8). Although some empirical studies reported the positive correlation between aboveground wood and soil carbon stock, particularly of the top soil, the relationship is less strong (R2=0.24, (Woollen et al., 2012), frequently insignificant (Osei et al., 2022), as SoilC primarily depends on climate, topography, soil mineralogy and soil texture, especially the content of clay (Powers and Schlesinger, 2002) or sand (Devi, 2021). Our results indicated that different or additional parameters may need to be included

525 in the calibration or the model to increase the accuracy of model estimates of both variables and/or the spatial coverage defined by observations.

The application of site-specific calibrated parameter sets outside the respective sites pointed out at the contradiction between their generality and the local accuracy of model estimations. SSMV optimised parameters were not generally applicable, as 47 % of simulations of calibration sites with SSMV parameter sets optimised for different sites collapsed (Figure 5). Calibrating

530 models for individual sites may often result in model overfitting due to the small amount of available data (Tsai et al., 2021), which may lead to completely different parameter sets in the case of a recalibration, and hence a high variance in calibrated values, reducing thus the reusability of calibrated parameter values.

As expected based on similar calibration works of forest growth models that used comprehensive data sources (Forrester et al., 2021; Minunno et al., 2019), the multisite and multivariate calibration increased the generality and robustness of the model

535 application by finding a parameter set that worked across all calibration sites (Figure 5), and the validation set (Figure 7). Nevertheless, differences in data quality and availability across space can substantially influence the calibration results. Although this problem can be mitigated using Bayesian calibration techniques and by choosing the appropriate likelihood function in frequentist calibrations, the data quality at individual sites is not always independent from each other, since there is often a significant spatial autocorrelation. The extent of this interdependence is rarely quantifiable, therefore the error-

540 covariance matrix used for the likelihood functions is usually incorrect, which can mislead the calibration process.

In addition, the multi-site calibration can also reduce spatial heterogeneity due to the "averaging out effect" causing that the average model performance will be good, but at specific sites it can be completely wrong. This could be overcome by applying a hybrid approach that combines the site-specific and multisite calibration. Thus, the overall correctness can be ensured by multisite calibration, while spatial heterogeneity by site-specific calibration.

545 **4.3. Trends in parameters**

The analysis of the variation of the optimised site-specific values of parameters across environmental gradients revealed some significant trends (see Figure 6, Fig. A10). This may indicate that a specific parameter should not be kept as a constant but rather as a characteristic that changes depending on driving conditions. An example of such a parameter is the canopy light extinction coefficient (CLEC) that specifies the proportion of solar radiation intercepted in the canopy. A number of process-

550 based models that use this parameter set its value around 0.5, while some models differentiate values between different species (Zhang et al., 2014). Based on our multi-objective optimisation for beech ecosystems we set the MSMV value of CLEC to 0.66, which is by 10 % higher than the value used by Pietsch et al. (2005) in the original Biome-BGC model for beech (0.6), but it is within the range for broadleaved forests reported by Zhang et al. (2014).

Although most models keep this parameter constant across sites and throughout their simulations (Liu et al., 2021; Zhang et
555 al., 2014), in reality its value changes during a day as well as during a year as it depends on the solar zenith angle, leaf area, leaf inclined angle, and leaf clumping (Zhang et al., 2014; Wang et al., 2004; Parker, 2020). It also changes with stand age, while it reaches its maximum in young stands (Brown and Parker, 1994). A constant value of CLEC causes intra-annual errors in estimations of plant transpiration and soil evaporation during a year (Tahiri et al., 2006). Due to this, a variable CLEC seems to be a more appropriate option. Our analysis revealed significant trends in the SSMV optimised values of CLEC with multiple
560 environmental characteristics, while the trends with elevation and precipitation were positive, and with temperature and VPD negative (Figure 6). Such patterns were not observed in other studies analysing measured data of CLEC, but the number of tested observations was low (Zhang et al., 2014) as it was also in our case. Nevertheless, the empirical data showed that CLEC increases with the decreasing plant density (Timlin et al., 2014) and LAI (Zhang et al., 2014). Since our model operates at a stand level, stand biomass can be considered as a proxy of stand density. Our results showed the decreasing trend of CLEC
565 with the increasing aboveground wood carbon stock (Fig. A11), which is in agreement with (Timlin et al., 2014). Moreover, the simulated AbgwC of calibration sites decreased along the elevational gradient (Fig. A11) explaining the positive correlation of CLEC to elevation, which can be considered as a side effect of stand density that is lower at high elevations.

Tahiri et al. (2006) successfully applied a simple empirical approach using a linear regression with leaf area. Parker (2020) calculated CLEC as a ratio between the effective LAI and the total LAI. CLEC is usually calculated following the simplified
570 Beer Lambert law as a function of above- and below-canopy solar radiation and leaf area (Zhang et al., 2014). A more sophisticated approach includes the solar zenith angle and the clumping index. Some models also use the inclination angle of leaves, while most commonly the spherical distribution of leaves is assumed (Liu et al., 2021), although Pisek et al. (2013) found that tree species in temperate and boreal regions are usually characterised by planophile or plagiophile leaf angle distribution.

575 Although we derived several multiple linear regressions explaining the variation in site-specific CLEC values using different combinations of environmental predictors (Fig. A15), the simulations with varying CLEC based on environmental conditions did not produce satisfactory results (33 % and 27 % of all and calibration sites collapsed if simulated with CLEC derived from its regression to annual precipitation, respectively). The possible reason is the existence of interdependences between parameters. We revealed a significant negative linear relationship between site-specific CLEC and the maximum stomatal
580 conductance (MSC, Figure 6), suggesting that low values of CLEC should be coupled with high values of MSC and vice versa. Hence, changing the value of one parameter should be coupled with the modification of the value of another parameter. However, we have not found any empirical evidence in the literature to confirm or refute the revealed relationship between

CLEC and MSC, and therefore it is not clear if the revealed pattern is realistic, or if it is only a side effect of the calibration procedure.

585   Moreover, we found that MSC was also significantly related to environmental conditions, namely VPD (Figure 6). MSC specifies the highest possible rate at which stomata can open and allow the exchange of gases between the plant and the environment under present-day CO_2 concentration and optimal environmental conditions, i.e. maximum radiation, and unlimited water availability, when VPD is zero, and there is no soil water stress. Such conditions rarely occur in the field, and hence, the observed maximum conductance, which represents the highest conductance on fully expanded leaves that was

590   measured during the summer growing season (Murray et al., 2019), does not usually reach the theoretical maximum (McElwain et al., 2016). The theoretical MSC can be derived from leaf anatomy, namely stomatal density, maximum stomatal pore area and stomatal pore depth (Murray et al., 2020; McElwain et al., 2016). The SSMV optimised values of MSC were found to be positively related to the long-term mean VPD (Figure 6), which decreases with elevation, whereas the stomatal conductance as well as stomatal characteristics specifying MSC usually increase with elevation (Petrik et al., 2022; Bresson et al., 2011).

595   In line with this, the studies from temperate European ecosystems reported an inverse relationship between the stomatal conductance and VPD (Körner, 1995; Urban et al., 2017). Similarly, the site-specific values of another ecophysiological parameter representing the stomata closure (VPDC, i.e. the vapour pressure deficit causing the complete conductance reduction) were found to be significantly negatively related to elevation (Figure 6), while the empirical studies did not reveal any differences in the onset of stomatal closure along an elevational gradient (Körner and Cochrane, 1985). Hence, we assume

600   that the revealed correlations in our data are by-products of the site-specific calibrations.

Due to the above above-stated inconsistencies, and the lack of data and supporting information, we decided not to apply the dynamically changing CLEC, MSC and/or VPDC along environmental gradients. However, this approach may be considered as a potential way forward in a future model development when more scientific knowledge becomes available. Nonetheless, our results pointed out that for simulations at a local level, some parameters may need site-specific values. Such a hybrid

605   approach of using a combination of general and site-specific parameters, which was already applied by e.g. (Thornton et al., 2002), may be beneficial to reduce the uncertainty of local predictions. Since the values of many of the parameters are usually not measured at research plots, global trait databases, such as TRY (Kattge et al., 2020) or the ones by Liu et al. (2023); Maire et al. (2015); Lin et al. (2015), might be useful to estimate the local values for a specific site and species.

610   **4.4. Robustness and plausibility tests of simulated outputs at a large scale**

Soil carbon represents a large storage of terrestrial carbon (Amundson, 2001) accounting for approximately a half of total forest ecosystem carbon (Domke et al., 2017; Jobbágy and Jackson, 2000). A similar proportion was also revealed in the output of our simulations (median= 47.7 %, mean=51.5 %, 1st Qu.= 32.6%, 3rd Qu.=69.9 %). The absolute values of simulated carbon stock in soil per unit area occurred within the range of soil organic carbon (SOC) reported by empirical studies (De

615 Vos and Cools, 2011; 2010; Wellbrock et al., 2016; Wellbrock and Bolte, 2019), although the variability of simulated values was lower (Fig. A 13). The mean value of the simulated SoilC (Min.=7.9, 1st Qu.=12.1, Median = 13.3, Mean = 13.1, 3rd Qu. = 14.4, Max. =17.0 kgC m^{-2}) was similar to the mean values observed in European beech forest stands (e.g. Meier and Leuschner, 2010; Mund, 2004).

The site-specific simulated SoilC significantly decreased with the increasing air temperature (Figure 8), which is consistent
620 with the observed patterns in soil carbon stocks from soil profile data along temperature gradients (Hartley et al., 2021; Jobbágy and Jackson, 2000; Sun et al., 2019; Post et al., 1982; Wang et al., 2013). The impact of temperature was also apparent in the relationships between the simulated SoilC and elevation or latitude, both of which were significantly positive (Fig. A17). The increasing trend of SoilC with latitude matched the trend of soil carbon stock found in temperate regions of the northern hemisphere (Minasny et al., 2014). These trends result from the faster decomposition (Wang et al., 2013) and hence the
625 microbial soil respiration as the temperature increases (Cao et al., 2019; Rodeghiero and Cescatti, 2005; Sun et al., 2019), the pattern that was found significant (r=0.33, t = 3.15, p-value = 0.002, 95 % CI = 0.12, 0.51) also in our simulated output (Fig. A19a).

Unlike the increasing trend of SOC with the increasing precipitation reported in the literature (Jobbágy and Jackson, 2000; Post et al., 1982), the simulated SoilC was not significantly related to the precipitation amount (Fig. A19b). In general, the
630 impact of precipitation on SOC changes depending on whether the examined ecosystems are water-limited (Wiesmeier et al., 2019). The small-scale study of SOC in beech forests in Germany revealed its significant correlation to precipitation (Meier and Leuschner, 2010), while at high-latitude ecosystems precipitation has only a minor impact on SOC stock (Devos et al., 2022). Our study includes a much wider variety of environmental conditions including different temperature ranges, soil depths, and soil textures than the study of Meier and Leuschner (2010), which may mask the relationship between SoilC and
635 precipitation. Unfortunately, we could not derive the regional relationships between measured SOC and environmental characteristics from our dataset due to the lack of data on soil carbon stock at all plots. Hence, we performed only plausibility tests with modelled values and compared the revealed trends with those reported in published papers from elsewhere.

When we checked the relationship of simulated SoilC to soil characteristics, we found the opposite trend of SoilC with the increasing clay content (Figure 8) to the one reported in the literature based on soil measurements (Jobbágy and Jackson, 2000;
640 Hartley et al., 2021). The fine mineral fraction composed of medium to fine silt particles and clay is known to have a stabilisation effect on SOC (Hartley et al., 2021), due to which it is often used as an indicator for SOC storage (Wiesmeier et al., 2019). However, our model results showed that SoilC decreased with the increasing content of fine particles (clay or silt) and increased as sand fraction dominated (Figure 8). Under real conditions, higher clay content supports the formation of soil aggregates that can save organic matter from decomposers and sequester SOC (Schmidt et al., 2011; Angst et al., 2018). In
645 BBGCMuSo this mechanism is not accounted for, as SOC formation is driven solely by temperature and SWC, and the litter input (Hidy et al., 2022). Moreover, the data used for our model simulations did not include the full range of clay content, since the maximum in our database was 56 %, and most site-specific values did not exceed 30 % (median=20 %, mean=19.6

%, 3rd quartile = 22 %). When we experimentally increased the clay content in soils of some sites to the maximum value (i.e. clay content =100 %), we could see the reversed pattern in the relationship (Fig. A19c).

650 Soil acidity enhances the storage of SOC by reducing soil microbial activities driving the decomposition of soil organic matter (Funakawa et al., 2014). The new BBGCMuSo model includes soil pH as a factor affecting the process of nitrification in soil layers (Hidy et al., 2022). The observed decreasing trend in the simulated output of SoilC with the increasing pH (Fig. A19d) is consistent with the experimental results (Funakawa et al., 2014) confirming the correct implementation of pH impact on soil processes in the model.

655 Soil carbon is the result of carbon inputs from vegetation followed by decomposition processes. In the model, decomposition is driven by soil temperature and soil water content, which is dependent on the precipitation amount, and water infiltration driven by soil texture (Hidy et al., 2022). In nature, around 60 % of the variability in soil respiration is explained by soil temperature and precipitation (Čater and Ogrinc, 2011). Our simulated output also showed a significantly increasing trend of heterotrophic soil respiration with the increasing temperature (Fig. A19g), but the trends with the soil water content or 660 precipitation were insignificant (Fig. A19h,i). Nevertheless, the increase of the simulated soil water content with the increasing fraction of clay and the decreasing fraction of sand in soil (Fig. A20) was consistent with the general knowledge about the impact of soil texture on soil moisture (Kaufmann and Cleveland, 2008). However, the simulated soil microbial respiration was found to have an increasing though insignificant trend with the increasing clay proportion (Fig. A19e), and a significant decreasing trend with the sand proportion (Fig. A19f). Although these results explain the negative correlation between SoilC 665 and clay content, they contradict our expectations based on the evidence from empirical studies that suggest that decomposition should be faster in coarse-sized soils (Hartley et al., 2021). In addition, soil respiration is strongly driven by root biomass (Čater and Ogrinc, 2011), which was also detected in our simulations (Fig. A19j, significant Pearson's product-moment correlation between the carbon stock in fine roots and heterotrophic respiration with r=0.53, t = 5.74, p-value = 1.45e-07, 95 % CI = (0.36, 0.67)).

670 Similarly to the reported positive relationship of soil carbon to organic carbon input (Cao et al., 2019; Jobbágy and Jackson, 2000), our outputs showed that SoilC increased with the increasing vegetation carbon stock (Fig. A19k), although the correlation was not significant (Pearson's product-moment correlation r=0.15, t = 1.43, p-value = 0.16, 95 % CI= (-0.06, 0.36)). In the model direct carbon inputs into soil storage come from the litter (Hidy et al., 2022). The significant positive correlation (r=0.89, t=16.79, p-value < 2.2e-16, 95 % CI= (0.82, 0.92)) between the simulated litter and soil carbon stocks (Fig. A19l), 675 confirmed that the model captured the carbon flow from vegetation to the soil according to expectations based on published field data (Hilli et al., 2010). In the model, litter is formed by leaf fall, fine root mortality, and defragmentation of coarse woody debris (CWD, Hidy et al., 2022). Surprisingly, the relationships of simulated SoilC to the annual amount of carbon in leaves or fine roots were insignificant (Fig. A19m,n), while the correlation of SoilC with CWD was significantly positive (Fig. A19o). These results were caused by a much higher amount of accumulated CWD in the simulated ecosystem in comparison 680 to the input from leaves or fine roots. Hence CWD represents the main source of carbon for soil. In the current model version,

the actual amount of CWD results from the accumulation over the whole simulation that cannot be reduced by a user, although the usual practice in managed forests has been to remove dead trees during logging operations for sanitary reasons (Kirby et al., 1998; Paletto et al., 2012). Hence, the actual amount of CWD found in managed forests normally represents only a small fraction of the CWD stock of what can be found in nature reserves (Christensen et al., 2005). To make the ecosystem

685   development under the human influence more realistic, the future model version will include the possibility to simulate the extraction of CWD or its part from the system at any time during the normal run simulation.

The absolute values of simulated carbon stock in litter (Min.= 0.33, 1st Qu.= 0.53, Median= 0.59, Mean = 0.61, 3rd Qu. = 0.68, Max. = 1.07 kgC m^{-2}) were consistent with the litter carbon stock reported from beech forests in Europe (Meier and Leuschner, 2010; Mund, 2004; Vesterdal et al., 2008). The litter amount represented approximately 2.5 % of the total

690   ecosystem carbon (Min.= 0.6, 1st Qu.= 1.4, Median = 2.2, Mean= 2.5, 3rd Qu.= 3.7, Max.=9.8 %), which is lower than the relative mean litter C stock reported globally (5 % based on Pan et al. (2011)) or for the U.S.A. (7 %, Domke et al., 2016). Such a relatively small amount of organic litter is typical for temperate hardwood forests on fertile soils (BMELF, 1997).

We revealed similar trends of LitterC along environmental gradients as for SoilC, e.g. the simulated carbon stock in litter significantly decreased with the increasing temperature since the heterotrophic respiration also increases along the temperature

695   gradient (Sun et al., 2019). Similar trends were also found with elevation, and latitude, as well as with soil characteristics (Fig. A17 and Fig. A18). The decreasing trends of simulated LitterC with the increasing pH, clay and silt proportion in soil and with the decreasing content of coarse sand were consistent with the trends derived from field measurements (Vesterdal and Raulund-Rasmussen, 1998). Based on the empirical evidence by Meier and Leuschner (2010), fine root biomass is the major factor affecting carbon stock in litter. However, our analysis did not reveal a significant relationship between carbon stock in fine

700   roots and litter (Fig. A19p) probably due to the differences in the perception of the term "litter" in the model and in empirical studies. Vesterdal and Raulund-Rasmussen (1998) also found significant correlations of LitterC to the soil content of other chemical elements (P, Ca, K, Mg), which are not included in our model and in most available models of vegetation dynamics (Merganičová et al., 2019). Nevertheless, due to the ongoing climate change including the dynamics of other nutrients in models may become more important especially if they represent limiting factors for ecosystems (Zaehle, 2013).

705   The accumulated carbon stock in wood biomass strongly depends on the forest age or the forest developmental phase. Due to this we first compared the absolute values of AbgwC at the end of spinup simulations to the stock observed in over-aged and old-growth beech forests (Barna et al., 2011). The absolute values occurred within the reported range, although the variability of simulated values was substantially lower than in the observed ones (Fig. A 13). On average, around 40 % of total ecosystem carbon was fixed in simulated AbgwC (1st Qu.=21.6, Median=43.5, Mean=39.9, 3rd Qu.=57.9, Max.=78.7 %), similarly as

710   reported from temperate European forest ecosystems (Wellbrock et al., 2017).

Simulated values of AbgwC exhibited a parabolic relationship to elevation and temperature, with maximum values at elevations of around 500 - 600 m a.s.l., and a mean annual air temperature of approximately 9°C (Figure 8). These results coincide with optimum growth conditions for beech reported in the literature, based on which beech growth optimum occurs

between 450 and 900 m a.s.l. (Schieber et al., 2013), and at sites with a mean annual temperature of 7 to 10°C (Czajkowski et al., 2006; Pagan, 1996; Paule, 1995). The literature also suggests the optimum annual precipitation total for beech from 700 to 1,000 mm (Czajkowski et al., 2006; Paule, 1995), but the relationship of the simulated AbgwC with precipitation explained only 5 % of AbgwC variability. Nevertheless, the unimodal relationship of AbgwC with VPD revealed the maximum AbgwC at around 530 Pa of VPD (Figure 8), which falls within the optimum VPD range for plant growth (500 to 1,200 Pa) (Noh and Lee, 2022). Although empirical studies reported an inverse relationship of beech production to VPD (Lendzion and Leuschner, 2008; Tumajer et al., 2022; Roibu et al., 2022), they focus on short-term changes, whereas in our analysis we used a long-term mean VPD characterising overall site conditions. Already Leuschner (2002) showed in his experiment that the prevailing VPD during the plant development determines the growth potential of plants under the conditions of Central Europe. The laboratory experiment by Lihavainen et al. (2016) revealed that the effect of VPD changes in time. While the initial reduction of VPD to low values caused an acceleration in the growth rate of silver birch, the effect diminished in time due to nitrogen limitation (Lihavainen et al., 2016). Since VPD seems to have a more profound effect on an intra-annual growth of broadleaved tree species than temperature (Tumajer et al., 2022), more research is required to clarify the impacts at different temporal levels.

The simulated AbgwC trend along the soil gradient was consistent with the empirical knowledge about optimum soil conditions for beech. Beech prefers well-drained soils and does not tolerate wet clay soils. It frequently occurs on loamy or sandy-loamy soils (Packham et al., 2012), on which the simulated AbgwC was the highest (Fig. A20). Loams are the most productive soils because of their moderate soil texture due to which they are able to hold a large amount of water available for plants Kolb, 2022). Soil texture also affects fine root production, e.g. Weemstra et al. (2017) observed significantly higher fine root biomass on sand than on clay. We did not reveal such a trend in our simulation outputs (Fig. A19q, Pearson's product-moment correlation r=0.11, t = 1.0, df = 82, p-value = 0.32, 95 % CI= (-0.11, 0.32)) because C allocation in the model is fixed and does not depend on soil texture. Although beech forests grow on soils with a large range of pH from 3.5 to 8.5 (Packham et al., 2012), the optimum values at which the maximum biomass production is achieved fluctuate between 5.5. and 6 (Pagan, 1994). The pH of the plots in our database varied between 3.69 and 7.5 (1st Qu.= 5.1, Median = 5.2, Mean = 5.6, 3rd Qu. = 6.4), but we did not reveal a significant trend in AbgwC with pH in the simulated output (Fig. A19r).

The variability in output data along the gradients of individual characteristics indicates the complex nature of the model and the combined impact of multiple environmental and ecosystem conditions on the final state of the system. In general, we can say that the model output behaves according to well-known natural rules along environmental gradients. The revealed discrepancies are of lesser importance and point out at the issues in the model that should be dealt with in the future model development. Water seems to play a minor role in modifying the simulated carbon-related output. The impact of soil texture might need to be examined in more detail. Moreover, there are environmental characteristics which are not accounted for in the current model but may explain the differences between the observed and modelled trends in soil carbon stock, e.g. parent rock material (Wiesmeier et al., 2019), or the proportion of coarse rock fragments in soil, which may substantially influence

5. Conclusion

750 The work presents a novel multi-objective calibration approach that uses the generalised likelihood estimation method, plausibility checks of output variables, and intersection principles. The proposed multi-objective calibration approach solves the problems of model overfitting, calibration efficiency, spatial heterogeneity, and quantity and quality of available data. The integration of the plausibility checks of model outputs ensures the realism of simulated ecosystems. The solution may be generally applicable to any process-based models of ecosystem dynamics. Such models heavily rely on how they characterize

755 the underlying ecosystem. The process is crucial for every modelling application, and it is considered as one of the main challenges, because of its vast computational, and data need.

The method includes the multi-dimensional sensitivity analysis used as a basis for the selection of parameters for calibration. The sensitivity results highlighted the need for the multivariate approach, as the impact rates of parameters and the trends of changes differed between the selected output variables. In addition, the analysis also documented the importance of plausibility

760 range checks for parameters, for which global databases on plant traits, such as TRY, play a crucial role.

The calibration of the model performed at individual sites (SSMV) and multiple sites (MSMV) revealed pros and cons of both approaches. Site specific parameter values improved the accuracy of the simulated outputs of aboveground wood, soil, and litter carbons stocks for the specific sites by 35 %, 55 %, and 11 % in comparison to the a priori parameter set. However, when using them for different locations, we observed the collapse of the simulations in 47 % of the cases. When applying the MSMV

765 parameter values obtained from the multi-site calibration, all simulations were successful, but the errors were on average by 26 %, 35 % and 9 % greater for the aboveground wood, soil, and litter carbons stocks than those obtained with the SSMV parameter sets. Thus, for local simulation studies, site-specific values of the parameters may be more suitable than the generalised parameter set, which is more appropriate for studies covering a larger spatial scale. On the other hand, the multi-site calibration reduces the spatial heterogeneity due to the "averaging out effect" causing that the average model performance

770 will be good, but at specific sites it can be completely wrong. This could be overcome by applying a hybrid approach that combines the site-specific and multisite calibration.

The independent validation, robustness and plausibility tests confirmed the robustness of the multi-site and multivariate calibrated set of ecophysiological parameters for the European beech at a regional level. In general, the examined model output followed well-known natural rules along environmental gradients. The revealed discrepancies were of lesser importance and

775 pointed out at the issues in the model structure that can be improved in the future model development. The study also highlighted the gaps in the empirical data and knowledge explaining the relationships between parameters, or between parameters and environmental conditions, which should be addressed by future research. For future applications, additional parameters that were not considered in this study, such as parameters specifying drought-induced mortality, may need to be

calibrated with additional empirical data since the occurrence of extreme events and disturbances has been increasing due to

780 the climate change.

Code and data availability. The current version of Biome-BGCMuSo, together with sample input files and a detailed user guide, is available from the website of the model at http://nimbus.elte.hu/bbgc/download.html under the GPL-2 license. Biome-BGCMuSo v6 is also available at GitHub: https://github.com/bpbond/Biome-BGC/tree/Biome-BGCMuSo_v6. The exact
785 version of the model (v6.2 alpha) used to produce the results in this paper is archived on Zenodo (https://doi.org/10.5281/zenodo.5761202; Hidy and Barcza, 2021). Experimental data used in the study are available from ICP Forests (http://icp-forests.net/) and from authors that provided the data upon request.

Supplement. The supplement related to this article is available online.

Author contributions. KM and TH conceived and designed the study and KM carried the experiments with the assistance
790 from JM, LD, and RH. DH developed Biome-BGCMuSo, and maintained the source code. RH developed RBBGCMuSo. KM and DK performed the literature review. KM executed simulations, and KM and JM performed the analyses. LD and JM contributed with model benchmarking. ZS, PP, HM, JN, MB, DB, MO, P and F contributed with experimental data. KM prepared the paper and the Supplement with contributions from all co-authors. All authors reviewed and approved the present article and the Supplement.

795 **Competing interests.** The authors declare that they have no conflict of interest.

Acknowledgements

The study was supported by COST PROCLIAS CA19139, grant "EVA4.0", No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDEEVA4.0, and the Slovak Research and Development Agency, projects No. APVV-21-0412 (KM, PF), APVV-18-0305, APVV-22-0001 (JM), APVV-19-0183 (MB). HM, MO, and DB were supported by the project MODFLUX (HRZZ IP-
800 2019-04-6325) and by the Croatian Science Foundation National Multidisciplinary Laboratory for Climate Change, RRF-2.3.1-21-2022-00014 project. PP was supported by „TreeAdapt" funded on the base of contract between the National Forest Centre and Ministry of Agriculture and Rural Development of the Slovak Republic.

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