

1 **Title: “Accuracy, realism and general applicability of European**
2 **forest models”**

3 *Running head: “Forest Model Evaluation”*

4 M. Mahnken* (1,2), M. Cailleret (3,4), A. Collalti (5,6,7), C. Trotta (6,7), C. Biondo (6,7), E. D’Andrea (5),
5 D. Dalmonech (5), G. Marano (5,8), A. Mäkelä (9), F. Minunno (9), M. Peltoniemi (10), V. Trotsiuk (4), D.
6 Nadal-Sala (11, 12), S. Sabaté (12, 13), P. Vallet (14), R. Aussenac (14), D.R. Cameron (15), F.J. Bohn (16),
7 R. Grote (11), A.L.D. Augustynczyk (17), R. Yousefpour (18,19), N. Huber (8,20), H. Bugmann (8), K. Mer-
8 ganicova (21,22), J. Merganic (23), P. Valent (23), P. Lasch-Born (1), F. Hartig (24), I.D. Vega del Valle
9 (1), J. Volkholz (1), M. Gutsch (1), G. Matteucci (5), J. Krejza (25,26), A. Ibrom (27), H. Meesenburg (28),
10 T. Rötzer (29), M. van der Maaten-Theunissen (2), E. van der Maaten (2), C.P.O. Reyer (1)

11 **Affiliations:**

12 (1) Potsdam Institute for Climate Impact Research (PIK), Member of the Leibniz Association, Telegrafenberg,
13 14473 Potsdam, Germany

14 (2) Chair of Forest Growth and Woody Biomass Production, TU Dresden, 01737 Tharandt, Germany

15 (3) INRAE, Aix-Marseille University, UMR RECOVER, 13182 Aix-en-Provence, France

16 (4) Forest Dynamics Unit, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

17 (5) Forest Modelling Lab., National Research Council of Italy, Institute for Agriculture and Forestry Systems in
18 the Mediterranean (CNR-ISAFOM), 06128, Perugia, Italy

Forest Model Evaluation

- 19 (6) University of Tuscia, Department of Innovation in Biological, Agro-food and Forest Systems (DIBAF),
20 01100, Viterbo, Italy
- 21 (7) Foundation Euro-Mediterranean Centre on Climate Change, Division Impacts on Agriculture, Forests and
22 Ecosystem Services (CMCC-IAFES), 01100, Viterbo Italy
- 23 (8) Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH
24 Zurich, 8092 Zurich, Switzerland
- 25 (9) Department of Forest Sciences, Institute for Atmospheric and Earth System Research (INAR) & Faculty of
26 Agriculture and Forestry. P.O. Box 27, 00014 University of Helsinki, Finland
- 27 (10) Natural Resources Institute Finland (Luke), Latokartanonkaari 9, FIN-00790 Helsinki, Finland
- 28 (11) Institute of Meteorology and Climate Research – Atmospheric Environmental Research (IMK-IFU), Karls-
29 ruhe Institute of Technology (KIT), Kreuzeckbahnstr. 19, 82467 Garmisch-Partenkirchen, Germany
- 30 (12) Ecology section. Department of Evolutionary Biology, Ecology and Environmental Sciences, University of
31 Barcelona (UB), Barcelona 08028, Spain
- 32 (13) CREAM (Center for Ecological Research and Forestry Applications), Cerdanyola del Vallès 08193, Spain
- 33 (14) Univ. Grenoble Alpes, INRAE, LESSEM, F-38402 St-Martin-d'Hères, France
- 34 (15) UK Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK
- 35 (16) Helmholtz Centre for Environmental Research - UFZ, Permoserstraße 15, Leipzig 04318, Germany
- 36 (17) International Institute for Applied Systems Analysis (IIASA), Schlossplatz 1, A-2361 Laxenburg, Austria
- 37 (18) Chair of Forestry Economics and Forest Planning, University of Freiburg, Tennenbacherstr. 4, 79106 Frei-
38 burg, Germany
- 39 (19) Institute of Forestry and Conservation, John Daniels Faculty of Architecture, Landscape and Design, Uni-
40 versity of Toronto, 33 Willcocks St., Toronto, ON M5S 3B3, Canada
- 41 (20) Remote Sensing, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

Forest Model Evaluation

42 (21) Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 6-Such-
43 dol, 16500 Praha, Czech Republic

44 (22) Department of Biodiversity of Ecosystems and Landscape, Institute of Landscape Ecology, Slovak Acad-
45 emy of Sciences, Akademická 2, 949 01 Nitra, Slovakia

46 (23) Faculty of Forestry, Technical University in Zvolen; T. G. Masaryka24, 96001 Zvolen, Slovak Republic

47 (24) Theoretical Ecology, University of Regensburg, Regensburg, Germany

48 (25) Global Change Research Institute CAS, Bělidla 986/4a, CZ-603 00, Brno, Czech Republic

49 (26) Department of Forest Ecology, Mendel University in Brno, Zemědělská 3, Brno 6130, Czech Republic

50 (27) Department of Environmental Engineering, Technical University of Denmark (DTU), 2800 Kgs. Lyngby,
51 Denmark

52 (28) Northwest German Forest Research Institute, Grätzelstr. 2, 37079 Göttingen, Germany

53 (29) Chair for Forest Growth and Yield Science, TU München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freis-
54 ing, Germany

55 *Corresponding author: Mats Mahnken, mahnken@pik-potsdam.de

56 **Keywords: model evaluation; gap model; process-based modeling; eddy-covariance; terrestrial**
57 **carbon dynamics; model ensemble**

58 **Abstract**

59 Forest models are instrumental for understanding and projecting the impact of climate change on for-
60 ests. A considerable number of forest models have been developed in the last decades. However, few
61 systematic and comprehensive model comparisons have been performed to date to compare model
62 agreement with field data and evaluate structural uncertainties. Here, we evaluate 13 widely-used,

63 state-of-the-art, stand-scale forest models against field measurements of forest structure and eddy-co-
64 variance data of carbon and water fluxes over multiple decades across an environmental gradient at
65 nine typical European forest stands. We test the models' performance in three dimensions: *accuracy of*
66 *local predictions* (agreement of simulated and observed annual data), *realism of environmental responses*
67 (agreement of modelled and observed responses of daily gross primary productivity to temperature,
68 radiation and vapor pressure deficit) and *general applicability* (proportion of European tree species
69 covered). We find that multiple models are available that excel according to our three dimensions of
70 model performance. For the accuracy of local predictions, variables related to forest structure have
71 lower random and systematic errors than annual carbon and water flux variables. Moreover, the multi-
72 model ensemble mean provided overall more realistic daily productivity responses to environmental
73 drivers across all sites than any single individual model. The general applicability of the models is high,
74 as almost all models are currently able to cover Europe's common tree species. We show that forest
75 models complement each other in their response to environmental drivers and that there are several
76 cases in which individual models outperform the model ensemble. Our framework provides a first step
77 to capturing essential differences between forest models that go beyond the most commonly used ac-
78 curacy of predictions. Overall, this study provides a point of reference for future model work aimed at
79 predicting climate impacts and supporting climate mitigation and adaptation measures in forests.

80 **Introduction**

81 Forest models are widely used to assess the impacts of changing environmental conditions such as cli-
82 mate, atmospheric CO₂ concentration and nitrogen deposition on forest functioning, dynamics and
83 structure (e.g. Reyer et al. 2013). Yet, because of our incomplete understanding of forest ecosystems
84 and computational constraints, these models differ in the way specific processes are represented, lead-
85 ing to differences in their predictions (Bugmann et al. 2019; Collalti et al. 2019; Huber et al. 2021).
86 Hence, models need to be comprehensively evaluated using different data types at different spatio-tem-
87 poral scales before we can judge their structural uncertainties and suitability for answering specific
88 questions (Maréchaux et al. 2021; Oberpriller et al. 2021).

89 Model simulations need to be in adequate agreement with independent observations. Moreover, models
90 have to be sensitive to environmental drivers to ensure that system responses are realistically predicted
91 under a wide range of environmental and climatic conditions (Collalti et al. 2016). Additionally, for spa-
92 tially comprehensive assessments of climate impacts it is also required that the models have a large
93 range of applicability covering different ecological conditions. Ideally, models meet all these require-
94 ments.

95 Levins (1966) categorized these requirements as trade-offs between three dimensions: model accuracy,
96 realism and generality. Accuracy indicates the goodness-of-fit between prediction and observation, re-
97 alism refers to causally correct internal model processes, and generality represents robust applicability
98 across space and time (Kramer et al. 2002). While it is difficult to maximize accuracy, realism and gen-
99 erality simultaneously, model developers have to identify an optimal point on the trade-off according
100 to the overall aim of the model.

Forest Model Evaluation

101 Many climate sensitive forest models have been developed in Europe for different applications, regions
102 and species (e.g., Fontes et al. 2010; Pretzsch et al. 2015). Yet, it is unknown how they perform relative
103 to the same benchmark conditions, and how their structure leads to trade-offs between accuracy, real-
104 ism and generality since model inter-comparisons across large numbers of complex models are missing.
105 Earlier model evaluations have either focused on selected processes (e.g., NPP: Morales et al. 2005;
106 mortality: Bugmann et al. 2019), relied on short time series of observed data (Kramer et al. 2002), or
107 investigated only few models and sites (Horemans et al. 2017). Yet, the increasing amount of harmo-
108 nized data recently becoming available across Europe (e.g. Reyer et al. 2020a,b) allows for a rigorous
109 evaluation of the state-of-the-art in forest modeling across different biogeographical regions, forest
110 types and types of data. Such an evaluation may provide a deeper understanding of model differences
111 and structural uncertainties, and provide crucial guidance for designing ensemble studies of climate
112 impacts on forests.

113 The objective of this paper is to evaluate and compare 13 widely applied forest models in managed
114 forests across an environmental gradient in Europe. The models range in complexity from empirically-
115 based to highly mechanistic approaches, while the evaluation data types range from ground-based in-
116 ventories to tower-based eddy-covariance measurements. To achieve this objective, we: (i) compare
117 model outputs to observations to quantify the accuracy of local predictions by deriving the statistical fit
118 between observations and model output of important forest variables; (ii) determine the realism of en-
119 vironmental responses by assessing the agreement of observed and modeled relationships between
120 stand productivity and climatic drivers; (iii) describe the general applicability by deriving the propor-
121 tion of European forest stands that a model is able to cover; and (iv) integrate these three dimensions
122 in a model performance framework. We hypothesize that trade-offs in our ensemble of forest models
123 can be traced back to differences in accuracy, realism and generality as described by Levins (1966).

124 **Methods**

125 **Vegetation models and simulation protocol**

126 We used simulation outputs from 13 state-of-the-art, structurally different, forest models (3D-CMCC-
127 FEM LUE, 3D-CMCC-FEM BGC, 3PG, 3PGN-BW, 4C, BASFOR, ForClim v.3.3, FORMIND, GOTILWA+, Land-
128 scapeDNDC, PREBAS, SALEM, SIBYLA) that participated in the Inter-Sectoral Impact Model Intercom-
129 parison Project (ISIMIP, Frieler et al. 2017). The key assumptions and formulations for simulating pro-
130 cesses or variables between models as well as their differences are described in Tab. 1. All models are
131 designed to predict long-term (multiple decades) forest growth and forest dynamics. Empirical models
132 are geared towards one full stand rotation while gap models focus on describing successional dynamics
133 in multi-species stands. Mechanistic models describe forest dynamics based on the dynamics of plant
134 carbon and water exchange at a high temporal resolution. Ten of the models describe the ecosystem-
135 atmosphere exchange of carbon, and nine of them the exchange of water in forest stands at a daily to
136 annual time step. All 13 models have been applied as research tools to study climate impacts on man-
137 aged forests.

138 The simulations followed the ISIMIP phase 2a simulation protocol (<https://www.isimip.org/protocol/>),
139 which provides a consistent simulation setup based on common, harmonized data for initializing, driv-
140 ing and evaluating models from the PROFOUND database (Reyer et al. 2020a,b). The models were ini-
141 tialized with observed stand characteristics (e.g. stem diameter at breast height, tree height, stand den-
142 sity, stand age) and then driven with locally measured weather data (e.g. surface air temperature, pre-
143 cipitation, vapor pressure deficit), atmospheric CO₂ concentration and nitrogen deposition data, as well
144 as historically observed forest management interventions. Simulated management was based on ob-

Forest Model Evaluation

145 served stem numbers and thinning regimes, i.e. thinning from above (higher diameter classes preferen-
146 tially removed) or from below (lower diameter classes preferentially removed). Forest management
147 was the only explicitly simulated disturbance. Drought effects were implicitly included by the driving
148 weather data. The models were run for 13 to 63 years on nine forest stands across Europe that are
149 contrasting in climate, species composition, phenology, management type and age (Tab. 2). Not all sites
150 were simulated by all models due to incomplete parameterization for species. Site-specific parameter
151 calibration on the observed data was not permitted.

Forest Model Evaluation

152 *Tab. 1: Overview of main processes implemented in all forest models as well as examples of model applications. NSC: non-structural carbon;*
 153 *GPP: gross primary productivity; VPD: vapor pressure deficit; DBH: diameter at breast height; NA: not included explicitly. Models are classified*
 154 *according to their complexity into empirical (E), hybrid (H) and process-based (P) types. This classification is based on expert judgment to*
 155 *provide a rough overview of model complexity; in reality these models align along a continuum from more empirical to more process-based*
 156 *models. References are indicated by numbers.*

model	photosynthesis	stomatal conductance	aut. respiration	evapo-transpiration	soil water balance	phenology	carbon allocation	structure development			example applications	model class
								height	diameter	mortality		
SALEM	NA	NA	NA	NA	NA	NA	NA	allometric equations (1)	Diameter, density, and site index specific stand level-dependent increment model (1,2)	diameter-dependent specific self thinning (1)	1,3,4	E
SIBYLA	NA	NA	NA	NA	NA	NA	NA	empirical: based on tree age, site specification, tree vitality and competition	empirical: based on site specification, tree vitality and competition	empirical: based on tree dimensions, growth and stand density	5,6,7	E
ForClim v.3.3	NA	NA	NA	8 based on 9	Single layer bucket model (10)	temperature sensitive and species specific	NA	derived from diameter increment under consideration of light availability and climate specific maximum tree height	modified carbon budget model (11) considering environmental constraints	age-related, stress-related	v.3.3: 12; for most recent version v.4.0.1 see 13,14	H
FORMIND	Light-use efficiency (15)	NA	Maintenance respiration + dynamic growth respiration	Water-use efficiency as a function of GPP	Single layer bucket model	Degree day sum approach (16)	dynamic allocation based on phenology, temperature, light and water availability	allometric equations	Dependent on carbon allocation to stem mass and current DBH of the tree	carbon-based stress mortality	17,18,19	H

Forest Model Evaluation

3PG	Light-use efficiency (20)	NA	Constant fraction of GPP	Penman-Monteith	Single-layer soil-water-balance	Fixed species-specific growing season	Dynamic allocation based on age, size, soil water, VPD	allometric equation from dbh, competition, etc.	Dependent on carbon allocation to stem mass and current DBH of the tree	age-dependent + stress-related + self-thinning	21,22,23	H
3PGN-BW	Light-use efficiency (20)	NA	Maintenance respiration + dynamic growth respiration	Penman-Monteith	Single-layer soil-water-balance	species-specific based on minimum monthly temperature	dynamic allocation based on environmental modifiers	allometric equations	dependent on carbon allocation to stem mass and current DBH of the tree	age-dependent + stress-related + self-thinning with stochastic component	24,25	H
BASFOR	Light-use efficiency	NA	Fixed ratio NPP/GPP	Penman	Single layer bucket model	Function of temperature, chilling days, day length	Branch and stem fractions constant, leaf and root fractions functions of water- and N-status	Function of stem dry matter	Function of stem dry matter and height	NA	26,27	H
PREBAS	Light-use efficiency (28)	NA	Maintenance respiration + growth respiration (29)	Empirical formulation based on daily photosynthesis, VPD, and Priestley-Taylor (30)	Bucket model (30)	Photosynthesis: Reversible temperature based model (31) Deciduous:, additionally a temperature sum based on (32)	dynamic allocation based on pipe-model and functional balance and crown allometry	Follows from carbon allocation	Follows from carbon allocation	competition	33,34,35,36	H
3D-CMCC-FEM LUE	Light-use efficiency (20)	37,38	Maintenance respiration + dynamic growth respiration (39,40)	Penman-Monteith	Single-layer soil-water-balance	species-specific temperature (i.e. Thermic sum), eliphany, LAI and others	dynamic allocation based on phenology, light and water availability (<i>sensu</i> 41)	allometric equations from dbh	allometric equations from stem biomass	age-dependent + self-thinning + NSC pool depletion + stochastic component	42,43,44,45	H
3D-CMCC-FEM BGC	Farquhar, von Caemmerer and Berry (46,47)										48,49	P
4C	Light-use efficiency (15,50)	NA	Constant fraction of GPP	Turc-Ivanov/Penman-Monteith/Priestley-Taylor	Dynamic multi-layered bucket model	inhibitor-promotor system (51)	dynamic allocation based on pipe-model and functional balance theory	function of foliage mass and crown architecture	dependent on carbon allocation	self-thinning + carbon starvation + age-related (52)	53	P
GOTILWA+	Farquhar (46)	Stomatal conductance after 54	Maintenance respiration + dynamic growth respiration	Penman-Monteith. Transpiration calculated from stomatal conductance, leaf area and vapor pressure deficit.	Two layer bucket model	Temperature sensitive (55)	dynamic allocation based on pipe-model and functional balance	allometric equations from dbh	allometric equations from dbh	NSC pool depletion + loss of active sapwood	56,57,58	P

Forest Model Evaluation

Landscape-DNDC (PSIM)	Farquhar (46)	Optimization scheme after 59 (considering soil water influence)	Maintenance respiration (60) + Growth respiration (fixed fraction)	61, stomatal conductance after 59	Multi-layer model	Cumulative temperature approach (62)	sink-source approach driven by phenology (63)	based on stem carbon allocation and density-dependent height:diameter relations (64)	based on stem carbon allocation and density-dependent height:diameter relations (64)	fixed fraction + density related limits (65)	66,67,68	P
-----------------------	---------------	---	--	-----------------------------------	-------------------	--------------------------------------	---	--	--	--	----------	---

157
158
159
160
161
162
163
164
165

References 1: Aussenac et al. 2021; 2: Toigo et al 2015; 3: Vallet et al 2018; 4: Toigo et al. 2018; 5: Fabrika and Ďurský 2005; 6: Hlásny et al. 2014; 7: Merganič et al. 2020; 8: Bugmann and Cramer 1998; 9: Thornthwaite and Mather 1957; 10: Bugmann and Solomon 2000; 11: Moore 1989; 12: Mina et al. 2015; 13: Huber et al. 2020; 14: Huber et al. 2021; 15: Haxeltine and Prentice 1996a; 16: Sato et al. 2007; 17: Bohn et al. 2014; 18: Rödiger et al 2017; 19: Bohn et al. 2018; 20: Monteith et al. 1977; 21: Landsberg and Waring 1997; 22: Gupta and Sharma 2019; 23: Trotsiuk et al. 2020; 24: Xenakis et al. 2008; 25: Augustynczyk and Yousefpour 2021; 26: van Oijen et al. 2014; 27: Cameron et al. 2013; 28: Mäkelä et al. 2008; 29: Mäkelä 1997; 30: Peltoniemi et al. 2015; 31: Mäkelä et al., 2004; 32: Linkosalo et al. 2008; 33: Kalliokoski et al. 2018; 34: Kalliokoski et al. 2020; 35: Holmberg et al. 2019; 36: Forsius et al. 2021; 37: Jarvis 1976; 38: Jarvis and Davies 1998; 39: McCree and Setlick 1970; 40: Thornley 1970; 41: Friedlingstein et al. 1999; 42: Collalti et al. 2014; 43: Collalti et al. 2016; 44: Collalti et al. 2018; 45: Marconi et al. 2017; 46: Farquhar et al. 1980; 47: De Pury and Farquhar 1997; 48: Collalti et al. 2019; 49: Collalti et al. 2020; 50: Haxeltine and Prentice, 1996b; 51: Schaber and Badeck 2003; 52: Botkin 1993; 53: Gutsch et al. 2018; 54: Leuning et al. 1995; 55: Leinonen 1996; 56: Sabaté et al. 2002; 57: Keenan et al. 2011; 58: Nadal-Sala et al. 2019; 59: Leuning 1995; 60: Cannell and Thornley 2000; 61: Thornthwaite 1948; 62: Grote 2007; 63: Grote 1998; 64: Grote et al. 2020; 65: Grote et al. 2011; 66: Lindauer et al. 2014; 67: Schweier et al. 2017; 68: Dirnböck et al. 2020.

166 **Evaluation data**

167 The PROFOUND database (Reyer et al. 2020a,b) hosts observed data from nine boreal and temperate
 168 forest stands located across Europe (Tab. 2). The database provides measurements of forest structure
 169 including basal area (*BA*), arithmetic mean diameter at breast height (*DBH*) and arithmetic mean tree
 170 height (*H*). On a subset of five sites, carbon and water fluxes measured at eddy-covariance towers are
 171 available (Tab. 2) including gross primary productivity (*GPP*), ecosystem respiration (*Reco*), net ecosys-
 172 tem exchange (*NEE*) and actual evapotranspiration (*AET*).

173 *Tab. 2: Features of evaluation sites in the PROFOUND database used in this study. MAP: mean annual pre-*
 174 *cipitation (mm/year); MAT: mean annual temperature (°C); lat.: latitude; long.: longitude; structure:*
 175 *structure variable time coverage; flux: flux variable time coverage.*

site	dom. spe- cies	forest type	MAP	MAT	elevation (m a.s.l)	country	lat.	long.	structure	flux
Hyytiälä	<i>Pinus sylvestris</i>	even-aged	604	4.4	185	FI	61.8 5	24.23	1995-2011	1996- 2014
Solling beech	<i>Fagus sylvatica</i>	even-aged	1113	6.8	500	DE	51.7 7	9.57	1967-2014	NA
Solling spruce	<i>Picea abies</i>	even-aged	1113	6.8	508	DE	51.7 7	9.57	1967-2014	NA
Collelongo	<i>Fagus sylvatica</i>	even-aged	1179	7.2	1560	IT	41.8 5	13.59	1992-2012	1996- 2014
Bily Kriz	<i>Picea abies</i>	even-aged	1434	7.4	875	CZ	49.3 0	18.32	1997-2015	2000- 2008
Kroof	<i>Fagus sylvatica</i> , <i>Picea abies</i> , de- cid. species	mixed	849	8.2	502	DE	48.2 5	11.4	1997-2010	NA
Sorø	<i>Fagus sylvatica</i>	even-aged	774	9.0	40	DK	55.4 9	11.65	1997-2013	1996- 2012
Peitz	<i>Pinus sylvestris</i>	even-aged	608	9.2	50	DE	51.9 2	14.35	1948-2011	NA
Le Bray	<i>Pinus pinaster</i>	even-aged	920	13.4	61	FR	44.7 2	-0.77	1986-2009	1996- 2008

176

177 For the carbon flux data, there are multiple products available for the same variable due to varying
 178 underlying estimation techniques (Pastorello et al. 2020). We used the data derived with constant fric-

tion velocity (USTAR) threshold where the reference is selected based on model efficiency for processing *NEE* (NEE_CUT_REF; <https://fluxnet.org/data/fluxnet2015-dataset/data-processing/>, Pastorello et al. 2020) and the daytime (DT) method (Lasslop et al. 2010) for partitioning *NEE* into *GPP* and *Reco*. The first year of carbon flux measurements at each site was discarded since the majority of data points had a quality flag of “poor”. Daily *AET* was derived from measured latent heat flux (*LE*) to the atmosphere by $AET = LE/\lambda$, with $\lambda = (2.501 - 0.00237 * T_{air}) * 10^6$, where T_{air} is the mean daily temperature (Foken 2008). Annual *AET* was aggregated as the sum of daily *AET* derived from the measured daily latent heat flux.

Evaluation framework

We evaluated the models in three dimensions based on the framework by Levins (1966) and further specified by Kramer et al. (2002): accuracy of local predictions, realism of environmental responses and general applicability. We defined the *accuracy of local predictions* as the agreement between observed and predicted data of relevant forest variables at the annual time scale; the *realism of environmental responses* as the agreement of simulated to observed relationships between daily climatic drivers and gross primary productivity; and the *general applicability* as the proportion of European forests a model can represent based on parameterized tree species. In addition to the individual models, we evaluated the model ensemble as the arithmetic mean time series of all individual model predictions available for a given site and variable. We used the statistical computing language R (R Core Team 2020) for all analyses.

Uncertainty in model predictions arises from model structural uncertainty, parameter uncertainty and input data uncertainty (Lindner et al. 2014; Collalti et al. 2019). Here we focused on evaluating compound model uncertainty originating from all uncertainty sources except for input data uncertainty

which is shared across all models. The coverage of sites and variables is model-specific and the temporal resolution of model predictions varies from daily to monthly to annual. The models used their individual default species-specific parameter settings for the simulations.

Accuracy of local predictions

The accuracy of local predictions was quantified for the primary variables of interest on an annual resolution: *BA*, *DBH increment (DBHinc)*, *H increment (Hinc)*, *GPP*, *Reco*, *NEE*, *AET*. *DBHinc* and *Hinc* were evaluated instead of *DBH* and *H* to eliminate the temporal autocorrelation that is associated with these variables, resulting from the incremental nature of diameter and height growth. In this way, we covered increments as well as the structure through *BA* (which is strongly dominated by temporal autocorrelation). *DBHinc* and *Hinc* were computed as the average annual change of stand scale mean *DBH* and *H*, respectively, for the period between two consecutive observations, since there were no measurements available for every year at all sites and the uncertainty in single year increment measurements is high. The same approach was applied to derive increments from the simulated data. *DBHinc* and *Hinc* integrate individual tree increments related to growth as well as changes of the stand scale mean *DBH* and *H* resulting from the removal of certain trees during management interventions and/or natural tree mortality.

Following Gauch et al. (2003), we computed multiple metrics describing different aspects of the disagreement between predictions and observations. The mean squared deviation (*MSD*) and its components squared bias (*SB*), lack of correlation (*LC*) and non-unity slope (*NU*) were computed for each model-site-variable combination. These metrics describe three sources of error: a systematic error (*SB*), random errors (*LC*) and linear patterns in the residuals (*NU*):

$$MSD = \frac{\sum_{n=1}^N (X_n - Y_n)^2}{N} = SB + NU + LC \quad (1)$$

Forest Model Evaluation

223 with X = simulated data, Y = observed data and $n = \{1, 2, \dots, N\}$, with N = number of data pairs.

$$224 \quad SB = (\bar{X} - \bar{Y})^2 \quad (2)$$

$$225 \quad NU = (1 - b)^2 * \left(\frac{\sum_{n=1}^N x_n^2}{N} \right) \quad (3)$$

226 with $b = \frac{\sum_{n=1}^N x_n y_n}{\sum_{n=1}^N x_n^2}$ which is the slope of the least-square-regression between Y and X . The
227 deviations from the mean are described by $y_n = Y_n - \bar{Y}$ (analogous: $x_n = X_n - \bar{X}$).

$$228 \quad LC = (1 - r^2) * \left(\frac{\sum_{n=1}^N y_n^2}{N} \right) \quad (4)$$

229 with $r^2 = \frac{(\sum_{n=1}^N x_n y_n)^2}{\sum_{n=1}^N x_n^2 \sum_{n=1}^N y_n^2}$ which is the square of the correlation between Y and X .

230 The quantification of these three completely independent components of the *MSD* allowed us to derive
231 which components drive the inaccuracies most strongly.

232 For cross-variable and cross-site comparability, we normalized the *MSD* (*norm. MSD*; and analogous *SB*,
233 *LC*, and *NU*) with the observed variance of a given variable at a specific site:

$$234 \quad \text{norm. MSD} = \frac{MSD}{\frac{1}{N} \sum_{n=1}^N (Y_n - \bar{Y})^2} \quad (5)$$

$$235 \quad \text{norm. SB} = \frac{SB}{\frac{1}{N} \sum_{n=1}^N (Y_n - \bar{Y})^2} \quad (6)$$

$$236 \quad \text{norm. LC} = \frac{LC}{\frac{1}{N} \sum_{n=1}^N (Y_n - \bar{Y})^2} \quad (7)$$

$$237 \quad \text{norm. NU} = \frac{NU}{\frac{1}{N} \sum_{n=1}^N (Y_n - \bar{Y})^2} \quad (8)$$

238 Then we aggregated the *norm. MSD* over all sites by computing the arithmetic mean of *norm. MSD* for a
239 given model-variable combination. To derive a unique accuracy of local predictions score (*A*) for each
240 model, we first computed the coefficient of determination as $R^2 = 1 - \text{norm. MSD}$ for each variable (cf.
241 Moffat et al. 2010). Then we calculated the arithmetic mean of the R^2 values across all structure varia-
242 bles and all carbon and water variables ($R^2_{structure}$ and $R^2_{carbon\ and\ water}$) and re-projected the result-
243 ing values to the range from 0.1 to 1 to derive $A_{structure}$ and $A_{carbon\ and\ water}$. Overall *A* was then derived
244 analogous to $A_{structure}$ and $A_{carbon\ and\ water}$ but with all variables available for a model. The predictive
245 skill of a forest model was higher than the predictive skill of the observed mean in terms of the overall
246 absolute error if *norm. MSD* < 1.

247 **Realism of environmental responses**

248 The realism of environmental responses was derived by quantifying the agreement of simulated to ob-
249 served relationships between climatic drivers and productivity, i.e., *GPP*, since *GPP* is sensitive to several
250 interacting climatic drivers (Zhang et al. 2017, Zhang et al. 2019, Zhou et al. 2021). Only those models
251 that output daily *GPP* could be evaluated for their realism of environmental responses. We considered
252 mean daily temperature (*temp*), daily global incoming radiation (*rad*) and daily mean vapor pressure
253 deficit (*vpd*) as forcing variables on the daily *GPP*. For each of the five FLUXNET sites, we assessed the
254 realism of the environmental responses for the relation of *GPP* to *temp*, *rad* and *vpd* of every model. The
255 observations were filtered for FLUXNET quality flags 0 (measured) and 1 (good quality gap-filled). Ad-
256 ditionally, the data was filtered for days with *temp* > 5 °C (cf. Franklin et al. 2013, Rehfeld et al. 2006) to
257 ensure that the bulk of the data lie within the growing season, because this is the most important period
258 in which the model needs to exhibit realistic responses of productivity to environmental drivers.

259 First, we visually compared the form of the observed and simulated relationships between *GPP* and the
 260 three forcing variables including their interactions by deriving general additive models (GAMs) for the
 261 0.5 quantile. The computation was done using the R library *qgam* (Fasiolo et al. 2017). The quantile
 262 GAMs have the form

$$263 \quad GPP = f_1(temp) + f_2(rad) + f_3(vpd) + f_4(temp, rad) + f_5(temp, vpd) + f_6(rad, vpd) +$$

$$264 \quad f_7(temp, rad, vpd) \quad (9)$$

265 using tensor product (te) smooth functions f_i .

266 Second, to formally compute model scores for the realism of environmental responses, the residuals
 267 between daily simulated and observed *GPP* were derived from the GAMs. We computed simple linear
 268 regression models relating the residual daily *GPP* from the GAMs to each of the three forcing variables.
 269 The GAM predictions were obtained by fixing two of the three independent variables to their arithmetic
 270 mean value. The linear regressions take the form

$$271 \quad GPP_{sim, rad_{fixed}, vpd_{fixed}} - GPP_{obs, rad_{fixed}, vpd_{fixed}} = \beta_1 + \alpha_1 * temp \quad (10)$$

$$272 \quad GPP_{sim, temp_{fixed}, vpd_{fixed}} - GPP_{obs, temp_{fixed}, vpd_{fixed}} = \beta_2 + \alpha_2 * rad \quad (11)$$

$$273 \quad GPP_{sim, temp_{fixed}, rad_{fixed}} - GPP_{obs, temp_{fixed}, rad_{fixed}} = \beta_3 + \alpha_3 * vpd \quad (12)$$

274 Similar *GPP*-environment relationships in observed and simulated data were characterized by small
 275 residuals, or at least by a lack of patterns in the residuals across the environmental drivers. Hence, small
 276 absolute slopes in the linear regression of the residuals indicated an agreement of observed to simu-
 277 lated relationships. For each environmental variable we re-projected the mean absolute slope across all
 278 models and sites $|\overline{\alpha_i}|$ to the range between 0 and 1 ($|\overline{\alpha_i}'|$) to account for differences in the magnitude
 279 of the variable units (*temp*: °C; *rad*: J/cm²; *vpd*: kPa). Then we derived the realism of environmental

280 responses for each model as the mean of the re-projected slope ($\frac{|\alpha_1|' + |\alpha_2|' + |\alpha_3|'}{3}$) of these linear regres-
281 sions.

282 **General applicability**

283 We interpreted the general applicability of the models as the application range across tree species. As
284 opposed to the accuracy of local predictions and the realism of environmental responses, this quantifi-
285 cation was independent of the actual simulations and solely based upon the tree species represented in
286 the models. We computed the share of European forests covered by dominant tree species each model
287 is currently parameterized for. Data on tree species group coverage across Europe were derived from
288 Brus et al. (2011). In case a model covered only subsets of a tree species group (e.g. only *Larix decidua*
289 and not *Larix kaempferi* for genus *Larix*), we assumed the forest area of that species group to be covered
290 fully by the model. We only expect a minor overestimation of the area covered by a model because the
291 tree species groups with many species are the ones that are less dominant in Europe. In this way, we
292 derived a rough approximation of the share of European forests where a given model could be applied
293 without considering the actual predictive skill that the model would have in these forests.

294 **Standardization and aggregation**

295 The results for the accuracy of local predictions, the realism of environmental responses and the general
296 applicability were projected back to a range from 0.1 to 1, which can be interpreted as relative differ-
297 ences across models. We would like to stress that the designation of 0.1 to a model does not indicate a
298 failure or lack of performance but rather that the model had the lowest metric value (relative perfor-
299 mance) across the models that were investigated here. We selected 0.1 as the lower boundary simply
300 to avoid misinterpretation that may be intuitively associated with the number zero.

301 Results

302 Accuracy of local predictions

303 There was no model that was able to predict all variables at all sites with high accuracy and only few
304 models showed a high accuracy of local predictions for all variables at one site (SALEM at Bily-Kriz, 3PG
305 at Solling-spruce and 3D-CMCC-FEM BGC at Solling-beech). At the same time, every model predicted at
306 least one variable at one site with an adequate accuracy of local predictions except for 3PGN-BW which
307 showed consistently lower predictive skill than the average of observations. (Fig. 1)

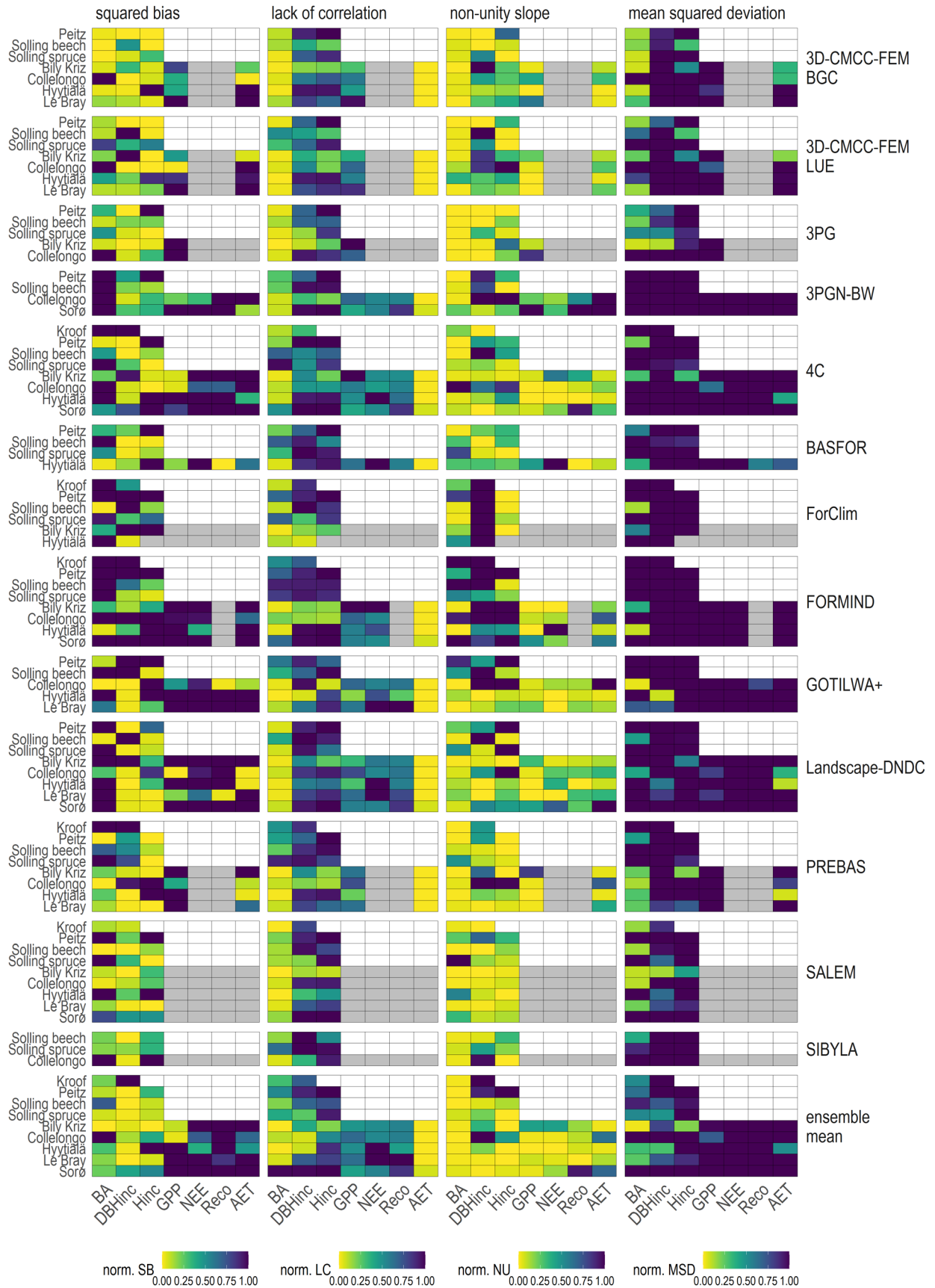
308 Partitioning the accuracy differences between models into the three *MSD* components showed that the
309 offset between model prediction and observed data had varying origins (Fig. 1). Random errors (*LC*)
310 made up the largest share of the overall error except for *BA* and *AET*. Systematic errors (*SB*) of the struc-
311 ture variables may have been a result of offsets in model initialization from the reference data (see Figs.
312 S4-S9 in the supplementary material). Flux variables were also prone to *SB* due to systematic over- or
313 underestimation. Persistent underestimation of *GPP* was evident in GOTILWA+ and FORMIND as well
314 as for a range of models at Hyytiälä, while 3PG persistently overestimated *GPP* and Landscape-DNDC
315 overestimated *GPP* at Bily Kriz. Most models underestimated *AET* in Le Bray, while overestimation was
316 evident at Bily Kriz (see Figs. S10-S17 in the supplementary material). Predicted-observed offsets from
317 linear patterns in the residuals (*NU*) were generally low except for *BA* and *DBHinc* simulated by FOR-
318 MIND, *DBHinc* simulated by ForClim v.3.3 as well as *Reco* and *AET* for 3PGN-BW.

319 Forest structure variables displayed a higher overall accuracy of local predictions than the carbon and
320 water variables. On average, simulated *BA* showed the highest accuracy of local predictions. This is
321 partly related to the temporal autocorrelation of the variable. Annual carbon variables had the lowest
322 accuracy of local predictions, while *NEE* had the lowest accuracy of the annual carbon variables. No

Forest Model Evaluation

323 model had a better predictive skill at any site than the observed mean *NEE*. None of the sites' observed
324 data could be predicted with a high accuracy of local predictions for all carbon and water variables sim-
325 ultaneously by any given model.

Forest Model Evaluation

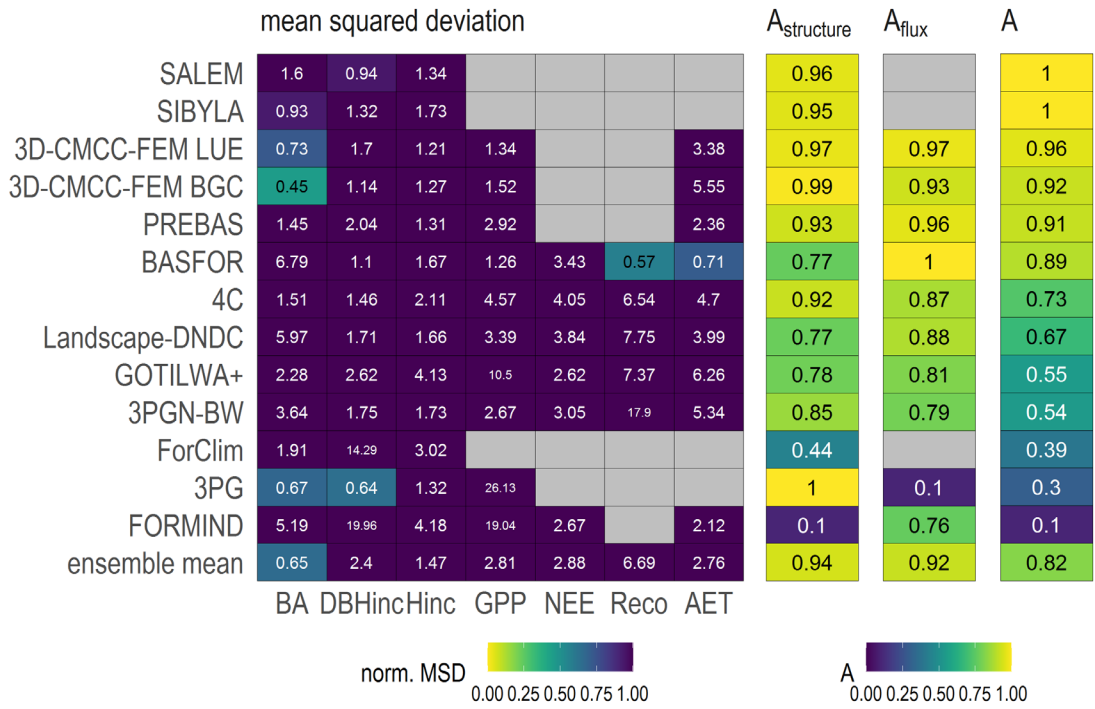


Forest Model Evaluation

327 *Fig. 1: Metrics for the accuracy of local predictions for all site-model-variable combinations. On the y-axis*
328 *are the sites, the x-axis shows variables, vertical panels are different models and horizontal panels show*
329 *the different metrics. Colors visualize the normalized metric values, where yellow indicates high agreement*
330 *and blue indicates low agreement of observed and predicted data. Cells in the column for mean squared*
331 *deviation (right) in dark blue ($norm. MSD \geq 1$) indicate cases where the observed average has a higher*
332 *predictive skill than the model predictions. White cells indicate cases with no evaluation data available*
333 *whereas grey cells indicate cases that are not provided by the model. The model coverage of sites and var-*
334 *iables depends on the model application range. norm. SB: normalized squared bias; norm. LC: normalized*
335 *lack of correlation; norm. NU: normalized non-unity slope; norm. MSD: normalized mean squared devia-*
336 *tion.*

337 The models varied regarding the overall accuracy of local prediction score (A, Fig. 2). Only few models
338 had a consistently better predictive skill for single variables than the observed mean ($norm. MSD < 1$):
339 SALEM for *DBHinc*, 3D-CMCC-FEM BGC, 3D-CMCC-FEM LUE and SIBYLA for *BA*, 3PG for *BA* and *DBHinc*
340 and BASFOR for *Reco* and *AET*. Although 3PG had a high predictive skill for structure variables, the pre-
341 dictions for *GPP* had the lowest predictive skill of any model. While some models performed consistently
342 well for one or two variables over multiple sites, other models performed worse than the observed
343 mean for all variable-site combinations. The ensemble mean ranked sixth for accuracy of local predic-
344 tions of forest structure variables and fourth for carbon and water fluxes. Overall, the ensemble mean
345 had a higher accuracy of local predictions than eight of the individual models.

Forest Model Evaluation



346

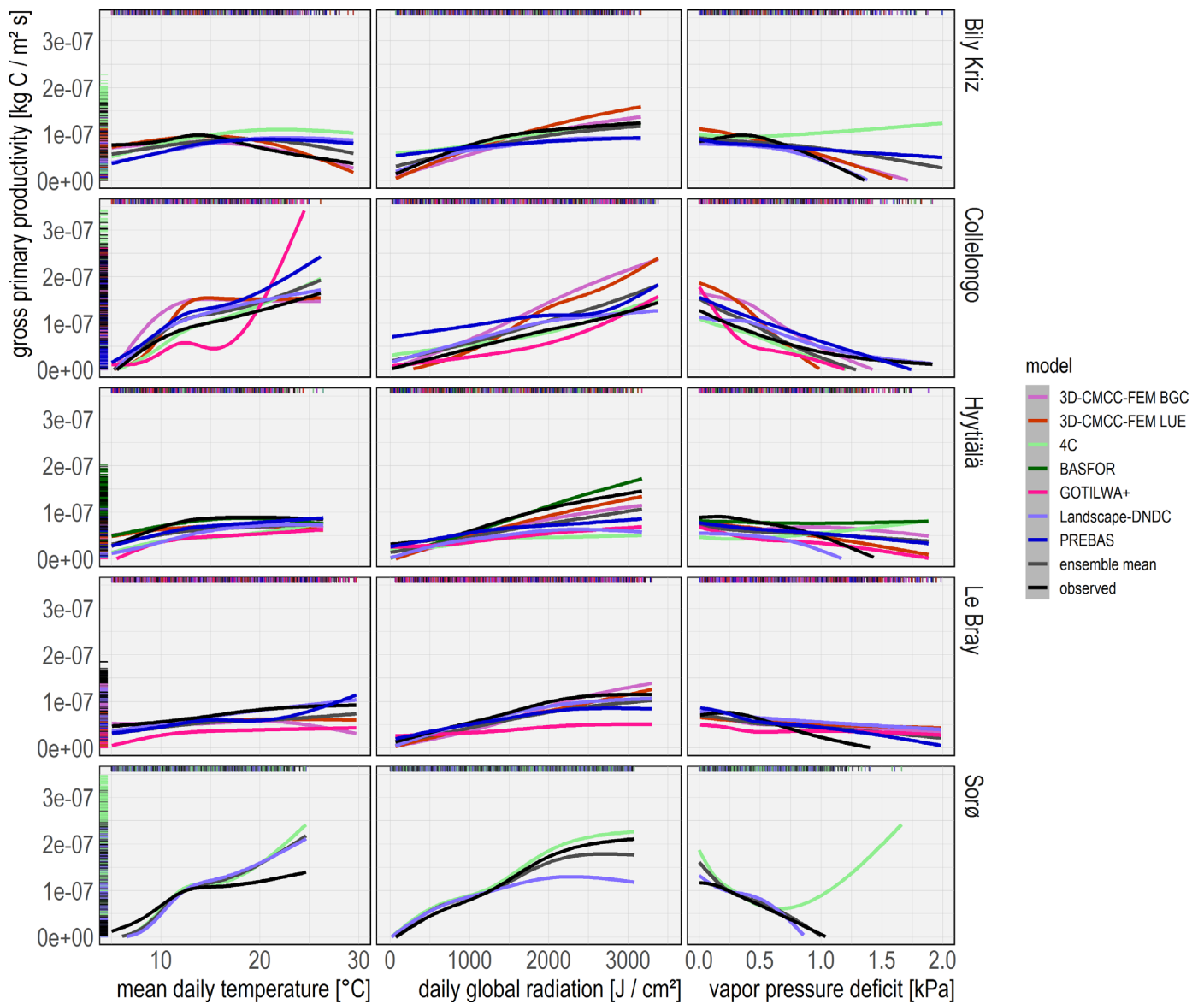
347 *Fig. 2: Aggregated metrics for accuracy of local predictions for all model-variable combinations assessed*
 348 *(aggregated across sites). Numbers indicate the metric value and colors visualize the normalized metric*
 349 *values, where yellow indicates high agreement and blue indicates low agreement of observed and predicted*
 350 *data.*

351

352 Realism of environmental responses

353 Observed relationships of daily *GPP* to *temp*, *rad* and *vpd* followed plausible patterns for all models
354 while the distinct patterns differed from site to site (Fig. 3). Increasing *temp* and increasing *rad* were
355 related to increasing daily *GPP*, except for *temp* relationship at higher *temp* values in Bily Kriz, while an
356 increase in *vpd* was related to decreasing daily *GPP*. Most models were able to reproduce these observed
357 patterns. Distinct site-specific patterns however were not predicted well at all sites by all models. Strong
358 non-linear patterns were observed for the *temp* relationship in GOTILWA+ at Collelongo and for the *vpd*
359 relationship of 4C at Sorø, which may be artifacts of the model fitting procedure or model responsive-
360 ness to other drivers such as water availability, which was not analyzed here due to the lack of observed
361 data at the sites. For *vpd*, models overestimated daily *GPP* at high *vpd*. High daily *GPP* at high levels of
362 *vpd* for 4C at Bily-Kriz and Sorø and many models at Le Bray and Hyytiälä indicated unrealistic produc-
363 tivity responses.

Forest Model Evaluation



364

365 *Fig. 3: Relationship between climate variables and simulated and observed gross primary productivity*
 366 *(GPP). Quantile general additive models are displayed (as lines) by fixing two of the three independent*
 367 *variables to their arithmetic mean value. Small indicators along the axes display individual simulated and*
 368 *observed daily GPP data and observed data on temp, rad and vpd.*

369 The slopes of the linear regressions of the daily GPP residuals (sim. GPP - obs. GPP) to environmental
 370 variables indicated varying agreement of observed and simulated environmental responses across
 371 models and sites (Tab. 3; Fig. S2 in the supplementary material). The *temp* and *rad* response had the

Forest Model Evaluation

372 lowest average absolute slope at Le Bray and Sorø had the lowest average absolute slope for *vpd* (see
373 Tab. S2 in the supplementary material).

374 On average, the ensemble mean showed the most realistic environmental responses while Landscape-
375 DNDC and 3D-CMCC-FEM BGC also show highly realistic responses of daily *GPP* to different environ-
376 mental drivers. Yet, there is no individual model that shows the most realistic responses of *GPP* to all
377 three environmental variables at all sites. Some models feature intermediate realism of environmental
378 responses to all environmental variables, e.g. 3D-CMCC-FEM LUE. The most realistic response to *rad*
379 was obtained by the ensemble mean. Landscape-DNDC had the most realistic *GPP* response to *vpd*, while
380 GOTILWA+ had the most realistic *GPP* response to *temp*. At the same time GOTILWA+ had the least
381 realistic *GPP* response to *rad*, 4C had the least realistic *GPP* response to *temp* and BASFOR had the least
382 realistic *GPP* response to *vpd*.

383

384 *Tab. 3: Realism of environmental responses per model and environmental variable derived from multiple*
 385 *linear regression slopes of residuals from simulated to observed daily GPP. The overall realism of the envi-*
 386 *ronmental response score is the average of the variable-specific realism of environmental responses re-*
 387 *projected to the range 0.1 to 1. Note that for the models not listed here realism of environmental responses*
 388 *was not derived because of missing representation of daily GPP.*

model	Mean absolute slope (re-projected mean absolute slope)			Realism of environ- mental re- sponses
	temp	rad	vpd	
ensemble mean	$1.887 * 10^{-9}$ (0.601)	$0.913 * 10^{-11}$ (0.000)	$4.488 * 10^{-8}$ (0.511)	1.00
Landscape-DNDC	$2.121 * 10^{-9}$ (0.716)	$1.587 * 10^{-11}$ (0.677)	$1.686 * 10^{-8}$ (0.000)	0.70
3D-CMCC-FEM BGC	$1.376 * 10^{-9}$ (0.352)	$1.396 * 10^{-11}$ (0.485)	$3.847 * 10^{-8}$ (0.612)	0.63
GOTILWA+	$0.654 * 10^{-9}$ (0.000)	$1.909 * 10^{-11}$ (1.000)	$3.856 * 10^{-8}$ (0.615)	0.45
PREBAS	$1.602 * 10^{-9}$ (0.462)	$1.908 * 10^{-11}$ (0.998)	$2.631 * 10^{-8}$ (0.268)	0.33
BASFOR	$1.351 * 10^{-9}$ (0.340)	$1.319 * 10^{-11}$ (0.408)	$5.215 * 10^{-8}$ (1.000)	0.31
3D-CMCC-FEM LUE	$1.865 * 10^{-9}$ (0.590)	$1.412 * 10^{-11}$ (0.501)	$4.412 * 10^{-8}$ (0.772)	0.18
4C	$2.705 * 10^{-9}$ (1.000)	$1.198 * 10^{-11}$ (0.286)	$3.995 * 10^{-8}$ (0.654)	0.10

389

390 **General applicability**

391 The most common tree species and species groups in Europe are *Pinus sylvestris*, *Picea* spp., *Fagus syl-*
 392 *vatica* and *Quercus robur* and *Quercus petraea*, which dominate around 75 % of Europe's forests (Brus
 393 et al. 2011). Almost all models covered these species with species-specific parameterizations. Only
 394 PREBAS and BASFOR were missing *Quercus robur* and *Quercus petraea*, whereas GOTILWA+ was miss-
 395 ing *Picea* spp. and *Quercus robur* and *Quercus petraea*. Additionally, most models covered other species
 396 that are less common in Europe, hence most models had species parameterized that represented the

Forest Model Evaluation

397 dominant tree species on 73 - 98 % of Europe's forest cover. The two models covering the least of
398 Europe's forest cover are BASFOR and GOTILWA+ with 66 % and 54 %. The ensemble mean had the
399 highest general applicability because it combined the species covered by all models. (Tab. 4)

Forest Model Evaluation

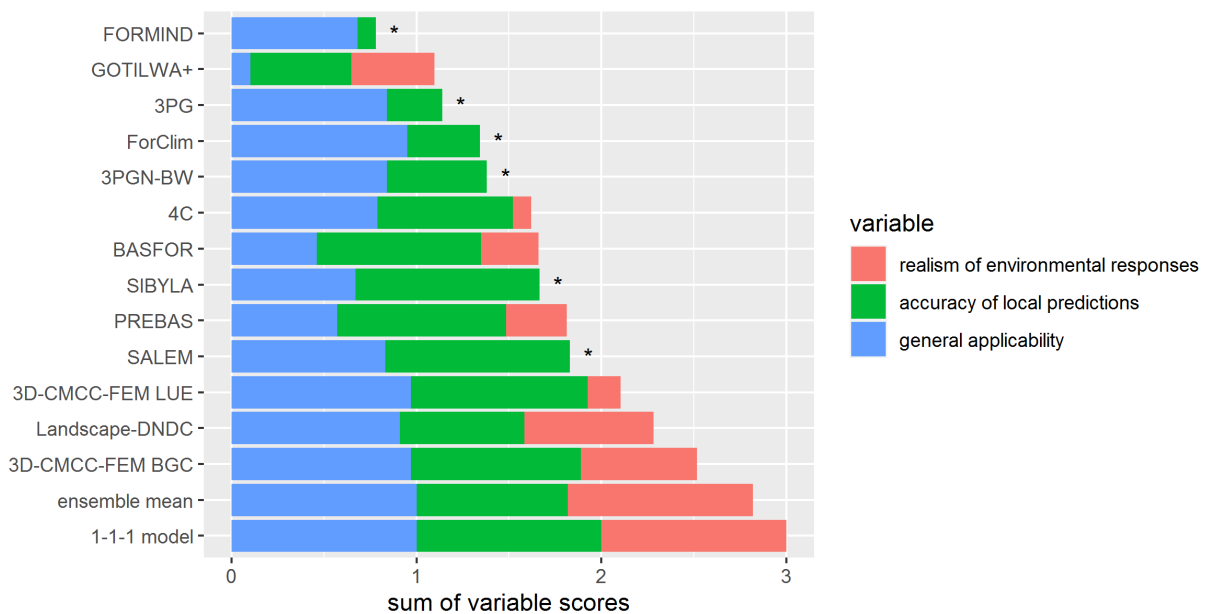
400 *Tab. 4: Tree species groups parameterized in complex forest models as an indicator for the general applicability across European tree species*
 401 *groups. Tree species group cover ("cover Europe") is according to Brus et al. (2011). The general applicability per model is the coverage of*
 402 *European forests re-projected to a range of 0.1 to 1.*

403

	<i>Abies</i> spp.	<i>Alnus</i> spp.	<i>Betula</i> spp.	<i>Carpinus</i> spp.	<i>Castanea</i> spp.	<i>Eucalyptus</i> spp.	<i>Fagus</i> spp.	<i>Fraxinus</i> spp.	<i>Larix</i> spp.	other broadleaves	other conifers	<i>Pinus</i> spp.	other <i>Quercus</i> spp.	<i>Picea</i> spp.	<i>Pinus pinaster</i>	<i>Pinus sylvestris</i>	<i>Populus</i> spp.	<i>Pseudotsuga menziesii</i>	<i>Quercus robur</i> , <i>Q. petraea</i>	<i>Robinia</i> spp.	cover Europe [%]	General applicability
ensemble mean	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100.0	1.00
3D-CMCC-FEM BGC	X		X		X		X		X	X	X	X	X	X	X	X			X		97.34	0.97
3D-CMCC-FEM LUE	X		X		X		X		X	X	X	X	X	X	X	X			X		96.93	0.95
ForClim v.3.3	X	X	X	X	X		X	X	X	X	X	X	X	X		X	X	X	X	X	97.29	0.91
Landscape-DNDC	X		X			X	X	X	X	X		X	X	X	X	X	X	X	X	X	90.02	0.84
3PG	X		X				X	X	X	X		X	X	X		X	X	X	X	X	90.02	0.84
3PGN-BW	X		X				X	X	X	X		X		X		X		X	X	X	88.88	0.83
SALEM	X						X					X	X	X	X	X		X	X	X	86.97	0.79
4C	X		X			X	X					X		X		X	X	X	X	X	80.16	0.68
FORMIND			X				X	X						X		X	X	X	X	X	78.87	0.67
SIBYLA	X						X							X		X	X	X	X	X	73.38	0.57
PREBAS			X			X	X							X	X	X	X			X	66.04	0.46
BASFOR							X							X		X				X	54.11	0.1
GOTILWA+						X	X	X				X	X		X	X				X		
cover Europe [%]	3.59	1.05	4.12	0.35	0.97	0.44	10.55	0.45	0.20	3.05	0.28	3.17	4.11	22.73	2.57	32.75	0.15	0.16	9.24	0.06		

404 **Model performance along the three dimensions of the model performance frame-**
 405 **work**

406 Besides the analysis of model performance, accuracy of local predictions, realism of environmental re-
 407 sponses and general applicability in isolation, we also analyzed the relations between the three dimen-
 408 sions. Figure 4 shows that the ensemble mean had the highest overall score across the three dimen-
 409 3D-CMCC-FEM BGC, Landscape-DNDC and 3D-CMCC-FEM LUE performed best across the three dimen-
 410 sions, followed by PREBAS, BASFOR, 4C, and GOTILWA+. The models covering only two dimensions of
 411 model performance ranked as follows: SALEM, SIBYLA, 3PGN-BW, ForClim v.3.3, 3PG and FORMIND.



412
 413 *Fig. 4: Model performance along with accuracy of local predictions, realism of environmental responses*
 414 *and general applicability. The highest theoretical total score along three dimensions is 1-1-1 (“1-1-1*
 415 *model”). *note that for SALEM, SYBILA, 3PGN-BW, ForClim v.3.3, 3PG and FORMIND realism of environ-*
 416 *mental responses could not be calculated. For further information regarding the interpretation of individ-*
 417 *ual metrics cf. the methods section.*

418 **Discussion**

419 This study evaluates a large number of complex forest models in an unprecedented model comparison
420 study against a large number of observations: 72 (carbon and water variables) to 128 (forest structure
421 variables) site-years with multiple data sources covering forest structure, carbon and water variables.
422 We developed a model performance framework based on Levin's (1966) concept to evaluate accuracy,
423 realism and general applicability of the participating models against this data. Overall, we find that no
424 individual model outperforms the others across all three dimensions, and that the model ensemble
425 performs mostly well.

426 **Model performance**

427 **Accuracy of local predictions**

428 3PG and 3D-CMCC-FEM BGC simulate the structure variables most accurately, while BASFOR and 3D-
429 CMCC-FEM LUE do so for the carbon and water variables. The main difference between 3D-CMCC-FEM
430 BGC and 3D-CMCC-FEM LUE is the representation of photosynthesis (see Tab. 1), with the BGC version
431 featuring a more process-based approach. The BGC version performs better for the structure variables
432 than the LUE version, while the LUE version is more accurate than the BGC version regarding carbon
433 flux variables at the annual scale. This unexpected trade-off cannot be explained in a straight-forward
434 manner by the differences in the model versions, but indicates that more empirical photosynthesis mod-
435 els (LUE version) do not necessarily produce less accurate predictions of annual flux variables than
436 more process-based approaches (BGC version). 3PG is rather simple compared to the other models ap-
437 plied here (Tab. 1), but it still produces accurate predictions of *DBHinc* for the subset of sites in this
438 study that are truly monospecific and even-aged. Apparently, less detailed but more robust model for-
439 mulations are an advantage when simulating these types of forests. Likewise, the other models that

440 focus on forest dynamics alone rather than also simulating biogeochemical fluxes, such as SALEM and
441 SIBYLA, also show a high accuracy of local predictions for structure variables. ForClim v.3.3 and FOR-
442 MIND show a lower accuracy of local predictions for structure variables mainly because the predictions
443 of *DBHinc* have a large offset to observations. These offsets result from the simulated thinning regime
444 and, in the case of ForClim v.3.3, a bias in the allocation (which has been addressed in v4.01, Huber et
445 al. 2020). Low accuracy of *BA* among all models may be explained by simulated mortality reducing stand
446 density below the observed stem numbers (see Fig. S9 in the supplementary material). BASFOR, which
447 is also among the less complex models of our ensemble, produces accurate predictions of carbon and
448 water variables while it predicts the structure variables with low accuracy. Such systematic errors re-
449 garding structure variables may also result from specifics in model initialization (see Figs. S4-S9 in the
450 supplementary material), e.g. BASFOR initialized trees with a planting procedure while most models
451 were initialized with observed data of adult stands. In models that operate at the forest stand-scale
452 rather than the tree level, systematic errors may also arise from the underestimation of *BA* if it is calcu-
453 lated internally from a multimodal *DBH* distribution and stem number. For example, Landscape-DNDC
454 and 3PGN-BW initialized mean *DBH* assuming a mean weighted by basal area and not an arithmetic
455 mean, leading to systematically higher *BA*, *DBH* and *H* (but not growth) at sites with a heterogenous
456 diameter distribution as is the case in particular in Sorø. Finally, the systematic over- as well as under-
457 estimation of flux variables shown by most models at least for some sites may be an effect of an insen-
458 sitivity for specific environmental conditions defined by either model structure or the generic parame-
459 ter sets used in this study.

460 Generally, the models predicted structure variables more accurately than annual carbon and water var-
461 iables, except for BASFOR and FORMIND. Earlier findings by Kramer et al. (2002) and Morales et al.
462 (2005) suggested that forest models have an adequate accuracy regarding daily carbon and water

463 fluxes. Yet, on the multi-annual time scale, Horemans et al. (2017) found larger uncertainties for *NEE*
464 than on the daily time scale. Our findings using a much larger ensemble of models confirm these earlier
465 findings. Carry-over effects from preceding years, which are usually not well represented in models,
466 may be a reason for the inaccurate year-to-year variation of carbon fluxes in the models (Aubinet et al.
467 2018).

468 Moreover, besides the reasons for individual model-data mismatches discussed above, the quality of the
469 observed data may affect all models collectively. Systematic and unsystematic observation errors affect
470 the reference data the models are compared to, e.g. uncertainty from the method used to partition *NEE*
471 into *GPP* and *Reco* (Oikawa et al. 2017). Checking the agreement of estimates from these different meth-
472 ods, we found that *GPP* estimated with the DT partitioning method (Lasslop et al. 2010) is highly corre-
473 lated with *GPP* estimated with the nighttime method (NT, Reichstein et al. 2005) in the evaluation data
474 with no apparent bias (see Fig. S3 in the supplementary material). Consequently, using DT- or NT-based
475 *GPP* estimates led to only minor changes in the results. Moreover, abiotic or biotic disturbances that
476 affect the reference data but are not represented in model simulations may affect model accuracy (Finzi
477 et al. 2020, Trugman et al. 2021). Furthermore, the understory contribution to the carbon balance was
478 not assessed in any of the models but contributes to the measured carbon balance (Dirnböck et al.
479 2020).

480 Additionally, uncertainties in model forcing data may contribute to model-data mismatches. For exam-
481 ple, the climate data used to drive the simulations was sometimes observed at or close to the forest
482 stand, but in some cases only inferred from the nearest climate station (Reyer et al. 2020a), which may
483 introduce additional uncertainties, e.g. due to orographic effects. Likewise, even though the stands are
484 managed using standard silvicultural treatments (Reyer et al. 2020a), specific, local forest management
485 actions may not be perfectly covered by the models' approximation of the management.

486 Overall, we find that simpler models, like SALEM, SIBYLA, 3PG, BASFOR and PREBAS did not necessarily
487 perform worse than more complex models like 3D-CMCC-FEM BGC, 3D-CMCC-FEM LUE, 4C, Landscape-
488 DNDC or GOTILWA+. The ensemble mean has an intermediate overall accuracy. Hence, in most cases
489 there are more accurate individual models available for each site-variable combination. Moreover, the
490 range of annual model predictions did not always overlap with observations. Hence, assessing the range
491 of the model ensemble and assuming that the “true” value lies within that range is not always advisable.
492 This was most pronounced for *Hinc* at Hyytiälä, Le-Bray, Solling-beech, Solling-spruce and Sorø, *Reco* at
493 Collelongo and Sorø, *NEE* at Collelongo, Bily-Kriz and Sorø as well as *DBHinc*, *GPP* and *AET* at Le Bray.
494 Hence, in some cases all models overestimate or underestimate the observed data, which points either
495 to general issues in model structure and/or parameterization across all models, or it may relate to is-
496 sues with the reference data outlined above.

497 **Realism of environmental responses**

498 Earlier findings by Kramer et al. (2002) showing realistically simulated relationships of daily *GPP* to
499 daily mean temperature and global radiation can be confirmed by our large ensemble. In addition, we
500 find that models exhibit also realistic responses of *GPP* to vapor pressure deficit (*vpd*). Properly captur-
501 ing *GPP* responses to *vpd* has proven to be fundamental to reproduce annual productivity patterns
502 (Medlyn et al., 2011), especially in stands where the most limiting environmental driver for *GPP* shifts
503 from water availability to *vpd* along the year (e.g. Nadal-Sala et al., 2021), and given that *vpd*-driven
504 limitation of productivity is expected to increase under global warming (e.g. Novick et al., 2016). In this
505 regard, our lumped GAM analysis is not able to fully determine the exact driver that is limiting *GPP* at a
506 given moment, and therefore interactive effects of constraining environmental drivers cannot be fully
507 discarded. Hence, the impact of *vpd* on *GPP* for each individual model remains unassessed, with the

508 realism of this key response potentially being masked by its positive correlation with temperature and
509 radiation.

510 While 3D-CMCC-FEM BGC shows relatively realistic daily *GPP* response, the closely related model 3D-
511 CMCC-FEM LUE has the second least realistic *GPP* response. The single difference between these two
512 models is the description of photosynthesis that is more process-based for 3D-CMCC-FEM BGC which
513 used the Farquhar, von Caemmerer and Berry biochemical photosynthesis model (Farquhar et al. 1980)
514 and the 3D-CMCC-FEM LUE which uses the Monteith empirical approach (Monteith et al. 1977). While
515 the BGC version shows more realistic daily environmental responses of *GPP* the LUE version is more
516 accurate at the annual scale. Since the BGC version was constructed to provide daily estimates of
517 productivity while the LUE version was originally constructed to provide estimates at the monthly time
518 scale, and compensating for possible over and under estimations, this performance relation can be ex-
519 pected. Biases originating from missing site-specific calibration and, given the higher number of param-
520 eters in biochemical photosynthesis models, increased uncertainty in the daily outputs of the BGC ver-
521 sion could explain the worse performance at the annual scale. The issue related to the temporal scale in
522 modeling *GPP* has already been discussed by Collalti et al. (2016) and Lasch-Born et al. (2020).

523 Overall, the individual models complemented each other with regard to the realism of environmental
524 responses of productivity. On average, the ensemble mean produced more realistic daily *GPP* responses
525 to environmental variables than any of the individual models. This is due to overestimating and under-
526 estimating individual models that cancel out when aggregated into an ensemble mean. Nevertheless,
527 the ensemble mean's performance relative to individual models strongly depends on whether the un-
528 derlying models are balanced (over- as well as underestimation) and represent different model struc-
529 tures.

530 **General applicability**

531 Following our rather simple definition of the general applicability of models, we find that most of the
532 models are able to simulate a relatively large share of European forests. However, having a tree species
533 parameterized does not necessarily mean that the models can really cover all potential mixtures in
534 which that species might grow. Still, it is encouraging to see that the models generally cover the main
535 species that are of commercial and ecological relevance in Europe, and hence from this point of view
536 most models are suitable to be applied in climate impact studies covering different European forests.
537 However, the focus of forest policies on adapting forests by generating more complex and species rich
538 forests will challenge the general applicability of the models. Finally, the ensemble covers almost all
539 European forest tree species because the individual models complement each other especially for the
540 less common tree species.

541 **Trade-offs between the three dimensions of the model performance framework**

542 Even though our framework of model performance does not theoretically prevent models from scoring
543 high in all three dimensions, we did not expect that any model would do so, but that trade-offs between
544 accuracy of local predictions, realism of environmental responses and general applicability were pre-
545 sent. While our results confirm that there is no “silver bullet”, we could not find explicit trade-offs such
546 as a systematic negative relation between general applicability and accuracy of local predictions either.
547 Models that have a high general applicability score such as 3D-CMCC-FEM BGC also perform well in
548 terms of accuracy of local predictions and realism of environmental responses. In general, the scores of
549 the three dimensions of model performance seem to be more or less balanced for most models although
550 at different overall levels. One of the exceptions is the model GOTILWA+ which has a relatively low score
551 for accuracy of local predictions but a comparably high score for realism of environmental responses.

552 Such results may originate from parameter uncertainties in the initial model setup, as physiological and
553 allometric parameters for a given species have not been calibrated, though they have been observed to
554 be highly site-dependent (e.g. allometric and photosynthetic parameters) and varying also with forest
555 developmental stages (Collalti et al. 2019). Also, the lack of trade-offs between accuracy of local predic-
556 tions, realism of environmental responses and general applicability may be an artifact of the way we
557 derived the realism of environmental responses. The potential trade-off in the framework provided by
558 Levins (1966), and further elaborated by Weisberg (2006), may not be apparent in the suggested frame-
559 work here, because we did not strictly follow the definitions of accuracy, realism and generality since
560 they are inherently difficult to assess and not meant to be operationalized for actual simulation models.
561 Operationalizing the framework for complex forest models may have distorted the relation between the
562 three dimensions as defined by Levins (1966). Furthermore, although a balance between the three di-
563 mensions is advisable, it may not always be necessary. For example, qualitatively correct insights about
564 forest growth and dynamics under global change may be sufficient to guide adaptation planning, e.g.
565 insights about the growth dominance of one species over the other, indicating that realism and gener-
566 ality may be more important for this purpose than accuracy.

567 Another key aspect that might explain the differences in performance among models is that some mod-
568 els were initially developed for other scopes. Some models have been developed to simulate forest
569 growth and fluxes in the short-term (i.e. the variables of interest here), but others to simulate forest
570 growth and demography over the medium- to long-term (decadal to centennial) and, thus, focusing
571 more on processes such as reproduction and mortality (not analyzed here). For instance, a specific strat-
572 egy for model development in ForClim is that each model development step should lead to better pre-
573 dictions of long-term (centennial) forest dynamics and/or of potential natural vegetation (simulations
574 over >1000 years) (Didion et al. 2009). Testing for these model capabilities would probably lead to a

575 different model ranking than presented here. Furthermore, some models have been developed with the
576 primary aim to capture multi-decadal dynamics in complex multi-species stands (e.g. SIBYLA, FOR-
577 MIND, ForClim), but eight of the nine stands used here were rather homogenous single-species stands
578 (see Tab. 2), which may be, in theory, easier to simulate using mechanistic biogeochemistry models.

579 **Limitations of the model performance framework**

580 Most model evaluation studies to date have assessed the accuracy of local predictions (e.g., Irauschek et
581 al. 2021). Yet, in addition to the agreement of predicted and observed variables of primary interest, also
582 realistic secondary patterns, like the responses of productivity to environmental drivers are important,
583 especially when assessing models that are being used for climate impact studies. Likewise, given the
584 rapid expansion of model uses and users, the general applicability is important to help the latter to as-
585 sess whether the model is likely to be useful for comprehensive impact studies across a large range of
586 tree species. Our model performance framework is a first attempt to operationalize Levins' (1966) ideas
587 within the context of climate impact assessments with complex vegetation models.

588 We quantified the accuracy of local predictions by deriving the average differences between predicted
589 and observed data for forest variables of primary interest at multiple sites on an annual time scale. The
590 approach is a robust way for assessing the agreement of predicted-observed data for models with dif-
591 ferent numbers of variable outputs. Models that provide more output variables for assessment in the
592 performance framework are not necessarily less accurate. Nevertheless, those models that assess vari-
593 ables which are generally more difficult to accurately predict will have lower levels of accuracy than
594 those models only assessing variables that are less difficult to predict. Future applications of the frame-
595 work could explore different weightings of the variables depending on the difficulty in predicting them
596 and the availability of data to test them. Furthermore, we acknowledge that model predictions are also

597 useful if they have less predictive skill than the observed mean because there are many instances where
598 no data are available to derive the mean for a given variable. Here, we used the observed mean as
599 threshold to identify especially well performing models and not to penalize poorly performing models.

600 Besides an accurate representation of historical data, forest models should be characterized by a real-
601 istic response of productivity to environmental drivers under varying climatic conditions. However, to
602 assess model realism more comprehensively all processes represented in the model need to be as-
603 sessed, rather than only the productivity response (see also Huber et al. 2020). Therefore, even though
604 we test the models with carbon and water variables, further refinements of the model performance
605 framework should include testing other variables for their realism to environmental responses such as
606 structure and mortality variables or autotrophic and soil respiration to test model realism across a
607 broader range of processes. Likewise, model comparisons in which the models have been forced to
608 mimic experimental changes in environmental variables such as shifting of atmospheric CO₂ concentra-
609 tions in FACE experiments (Zaehle et al. 2014, Walker et al. 2021) or rainfall manipulation experiments
610 (Paschalis et al. 2020) could help us to learn further about the model's realism of environmental re-
611 sponses. Whether the model includes flexible traits (Berzaghi et al. 2019) and whether it is able to mimic
612 natural adaptive processes (Collalti et al. 2020) could be a further element of testing the realism of en-
613 vironmental response.

614 Moreover, restricting the quantification of realism to periods when the environmental driver analyzed
615 (e.g. temperature, radiation or vapor pressure deficit) is actually the one that is driving the process
616 should be included in the evaluation of the *GPP* response (e.g. Nadal-Sala et al., 2021). Additionally,
617 model parameterization is important. For instance, if a model assumes the same allometric relationship
618 for a single species regardless of environmental conditions, we expect it to be less accurate than other
619 models that account for site differences by using either different allometric coefficients in different

620 stands or incorporating environmental drivers (Cysneiros et al. 2021), or if models, and their parame-
621 terizations, account for changes in tree growth and carbon allocation and acclimation in response to
622 environmental stressors as well as during different stages of forest development (Collalti et al. 2019;
623 Merganičová et al. 2019). These considerations also hold for other structural aspects such as leaf distri-
624 bution or process parametrization, e.g. regarding photosynthesis. Evaluating process rates (e.g. *GPP*) in
625 contrast to model states (e.g. *BA*) requires a higher realism of environmental responses to produce ac-
626 curate predictions, because model states are dominated more strongly by long-term model assumptions
627 on stand dynamics (such as mortality definitions, carbon allocation, allometric relationships, manage-
628 ment regime). Overall, to test realism properly, one should test the response of the models to different
629 forcing conditions, and compare the (qualitative) responses of the models to our general understanding
630 of the processes and observed data describing these responses.

631 Also, it is noteworthy that even though we interpret the results along three dimensions, the quantifica-
632 tion of the accuracy of local predictions and the realism of environmental responses are not fully inde-
633 pendent of each other. These two dimensions are both based on the comparison of predicted to ob-
634 served data, therefore there is no trade-off *sensu stricto* to be expected. Furthermore, the quantification
635 of realism of environmental responses does not consider other non-linear patterns in the residuals of
636 simulated to observed values which may overestimate the agreement of simulated to observed re-
637 sponses of *GPP* to climatic drivers. Thus, in this respect future studies could refine the relationship be-
638 tween the computation of accuracy of local predictions and realism to environmental responses.

639 Generality, as the robust model applicability across space and time, is challenging to assess since exten-
640 sive data are needed to apply and evaluate models across large spatial and temporal scales. We did not
641 derive the general applicability across time but focused on the general applicability in space. However,
642 simply being able to simulate tree species or plant functional types does not warrant that models area

643 able simulate for example complex forest mixtures or management systems (Grote et al. 2011, Pretzsch
644 et al. 2015, Bravo et al. 2019). Information on whether the models are able to simulate mixed forests
645 with a complex structure, comprising both managed and natural dynamics, could be used to widen the
646 general applicability metric which is important since the structural complexity of forests may increase
647 in the future as part of forest adaptation to climate change (Huber et al. 2020, Pardos et al. 2021, de
648 Wergifosse et al. 2022).

649 Finally, because we investigated the model performance based on current model parameterization
650 without further site specific parameter calibration, the resulting uncertainty is originating from both
651 model structure and model parameterization. The model performance is reflecting the current state of
652 the model only. However, model parameterization and calibration have the potential to increase the
653 performance along all three dimensions of the model performance framework. In theory, if a model is
654 general in its structure (i.e., more process-based models), it would need less data to be parameterized
655 to different environments or species, if it is less general (i.e., more empirical models) it would need more
656 data. Hence, the effort that is needed for calibrating a model to specific environments is model specific
657 and different calibration efforts would lead to varying levels of improvement of the three dimensions of
658 model performance. But not all three dimensions are dependent on model structure and parameteriza-
659 tion to the same extent. The realism of environmental responses is mostly driven by model structure,
660 accuracy of local predictions is affected by both model structure and parameterization while the general
661 applicability is mostly dependent on the model parametrization effort. In summary, the current model
662 performance can be improved not only by development of the model structure itself but also by model
663 parameter calibration.

664 Conclusions and implications for model applications

665 We performed the, to our knowledge, largest forest model comparison with a wide range of multi-
666 source evaluation data in an innovative model performance framework. We found that the accuracy of
667 local predictions in the historical period is not related to the level of complexity of a model, i.e. empirical
668 models do not necessarily provide less accurate predictions than hybrid or process-based models under
669 current climate conditions. Furthermore, accurate predictions of carbon variables at annual scale are
670 more difficult to obtain than accurate predictions of structure variables. The realism of environmental
671 responses in model simulations provides an approximation how well relationships that are crucial to
672 assessing climate impacts are covered. We showed that the model ensemble mean has the most realistic
673 daily *GPP* responses to environmental variables. General applicability, in terms of the coverage of Euro-
674 pean tree species is high for most models but less common species that may become more important
675 under climate change are only partly covered by models.

676 We conclude that, if accuracy is the objective, individual models may provide the best results at single
677 specific locations. Which model will provide optimal results depends on the environmental conditions,
678 structural properties, disturbances, etc. of those locations. Moreover, most individual models cover the
679 most relevant European tree species, but to cover all and particularly the less abundant species, multi-
680 ple models need to be applied. Finally, we highlight the importance to evaluate several model output
681 variables with a wide range of data, because models struggle to achieve high accuracies for several var-
682 iables at the same time. Because already multiple models exist to study climate impacts on forests we
683 expect that our study will provide a common benchmark to test whether new modelling efforts outper-
684 form the models presented here to add value to the existing set of tools.

685 **Acknowledgements**

686 MM, MG, PV, RA acknowledge financial support from I-Maestro (Innovative forest management strate-
687 gies for a resilient bioeconomy under climate change and disturbances, grant nos. 773324 and
688 22035418, 2019–2022) funded by the ERA-NET Cofund ForestValue. AC, CB, CT, GM and DD thank
689 Foundation Euro-Mediterranean Centre on Climate Change and the ALForLab (PON03PE_00024_1)
690 project co-funded by the Italian National Operational Program for Research and Competitiveness (PON
691 R&C) 2007–2013, through the European Regional Development Fund (ERDF) and national resource
692 (Revolving Fund - Cohesion Action Plan (PAC)) MIUR, for their support in model development and data
693 analysis. This article is further based upon work from COST Action CA19139 PROCLIAS (PROcess-based
694 models for CLimate Impact Attribution across Sectors), supported by COST (European Cooperation in
695 Science and Technology; <https://www.cost.eu>), the ERA4CS Joint Call on Researching and Advancing
696 Climate Services (ISIpedia; BMBF grant 01LS1711A) and the German Federal Ministry of Education and
697 Research (BMBF) under the research project ISIAccess (BMBF grant 16QK05). FH acknowledges fund-
698 ing by the Bavarian Ministry of Science and the Arts in the context of Bavarian Climate Research Net-
699 work (bayklif). We are further grateful to all the researchers providing data to the PROFOUND Database
700 and for long-term funding of the stations from national and international sources and networks. In ad-
701 dition, thanks are given to Dario Papale for initiating and continually supporting the post-processing
702 and harmonization of the legacy flux and meteorological data provided by the international flux data
703 base FLUXNET. Finally, we want to thank Dr. Felicitas Suckow and Dr. Chris Kollas for help with 4C
704 development and application, and all data providers for establishing a database that enables thorough
705 model evaluations.

706 **References**

707 Aubinet, M., Hurdebise, Q., Chopin, H., Debacq, A., De Ligne, A., Heinesch, B., Manise, T., & Vincke, C. (2018).
708 Inter-annual variability of Net Ecosystem Productivity for a temperate mixed forest: A predominance of
709 carry-over effects? *Agricultural and Forest Meteorology*, 262, 340-353.

710 <https://doi.org/10.1016/j.agrformet.2018.07.024>

711 Augustynczyk, A. L. D., & Yousefpour, R. (2021). Assessing the synergistic value of ecosystem services in Eu-
712 ropean beech forests. *Ecosystem Services*, 49(C), S221204162100022X. <https://EconPa->

713 <pers.repec.org/RePEc:eee:ecoser:v:49:y:2021:i:c:s221204162100022x>

714 Aussenac, R., Pérot, T., Fortin, M., de Coligny, F., Monnet, J., & Vallet, P. (2021). The Salem simulator version
715 2.0: a tool for predicting the productivity of pure and mixed forest stands and simulating management op-
716 erations [version 2; peer review: 2 approved]. *Open Research Europe*, 1(61). <https://doi.org/10.12688/open->

717 <reseurope.13671.2>

718 Berzaghi, F., Wright, I. J., Kramer, K., Oddou-Muratorio, S., Bohn, F. J., Reyer, C. P. O., Sabate, S., Sanders, T.
719 G. M., & Hartig, F. (2019). Towards a New Generation of Trait-Flexible Vegetation Models. *Trends Ecol Evol*.

720 <https://doi.org/10.1016/j.tree.2019.11.006>

721 Bohn, F. J., Frank, K., & Huth A. (2014). Of climate and its resulting tree growth: Simulating the productivity
722 of temperate forests. *Ecological Modelling*. <https://doi.org/10.1016/j.ecolmodel.2014.01.021>

723 Bohn, F. J., May, F., & Huth, A. (2018). Species composition and forest structure explain the temperature
724 sensitivity patterns of productivity in temperate forests. *Biogeosciences*, 15(6), 1795-1813.

725 <https://doi.org/10.5194/bg-15-1795-2018>

Forest Model Evaluation

- 726 Botkin, D. B., Janak, J., & Wallis, J. R. (1972). Some ecological consequences of a computer model of forest
727 growth. *Journal of Ecology*, 60, 849-872.
- 728 Bravo, F., Fabrika, M., Ammer, C., Barreiro, S., Bielak, K., Coll, L., Fonseca, T., Kangur, A., Löf, M., Merganičová,
729 K., Pach, M., Pretzsch, H., Stojanović, D., Schuler, L., Peric, S., Rötzer, T., Río, M. d., Dodan, M., & Bravo-
730 Oviedo, A. (2018). Modelling approaches for mixed forests dynamics prognosis Research gaps and opportu-
731 nities. *Forest Systems (Online)*, 28(1), 18. <https://doi.org/105424/fs/2019281-14342>
- 732 Brus, D. J., Hengeveld, G. M., Walvoort, D. J. J., Goedhart, P. W., Heidema, A. H., Nabuurs, G. J., & Gunia, K.
733 (2011). Statistical mapping of tree species over Europe. *European Journal of Forest Research*, 131(1), 145-
734 157. <https://doi.org/10.1007/s10342-011-0513-5>
- 735 Bugmann, H. & Cramer W. (1998). Improving the behaviour of forest gap models along drought gradients.
736 *Forest Ecology and Management* 103(2): 247-263.
- 737 Bugmann, H., Seidl, R., Hartig, F., Bohn, F., Bruna, J., Caillaret, M., Francois, L., Heinke, J., Henrot, A.-J., Hickler,
738 T., Hülsmann, L., Huth, A., Jacquemin, I., Kollas, C., Lasch-Born, P., Lexer, M. J., Merganic, J., Merganicová, K.,
739 Mette, T., Miranda, B. R., Nadal-Sala, D., Rammer, W., Rammig, A., Reineking, B., Roedig, E., Sabaté, S., Stein-
740 kamp, J., Suckow, F., Vacchiano, G., Wild, J., Xu, C., & Reyer, C. P. O. (2019). Tree mortality submodels drive
741 simulated long-term forest dynamics: assessing 15 models from the stand to global scale. *Ecosphere*, 10(2).
- 742 Bugmann, H. & Solomon A. M. (2000). Explaining Forest Composition and Biomass across Multiple Biogeo-
743 graphical Regions. *Ecological Applications* 10(1): 95-114.
- 744 Cameron, D. R., Van Oijen, M., Werner, C., Butterbach-Bahl, K., Grote, R., Haas, E., Heuvelink, G. B. M., Kiese,
745 R., Kros, J., Kuhnert, M., Leip, A., Reinds, G. J., Reuter, H. I., Schelhaas, M. J., De Vries, W., & Yeluripati, J.

Forest Model Evaluation

- 746 (2013). Environmental change impacts on the C- and N-cycle of European forests: a model comparison study.
747 *Biogeosciences*, 10(3), 1751-1773. <https://doi.org/10.5194/bg-10-1751-2013>
- 748 Collalti, A., Ibrom, A., Stockmarr, A., Cescatti, A., Alkama, R., Fernández-Martínez, M., Matteucci, G., Sitch,
749 S., Friedlingstein, P., Ciais, P., Goll, D. S., Nabel, J. E. M. S., Pongratz, J., Arneeth, A., Haverd, V., & Prentice, I.
750 C. (2020). Forest production efficiency increases with growth temperature. *Nature Communications*, 11(1),
751 5322. <https://doi.org/10.1038/s41467-020-19187-w>
- 752 Canell, M.G.R. & Thornley, J.H.M. (2000). Modelling the Components of Plant Respiration: Some Guiding
753 Principles. *Annals of Botany* 85(1): 45-54.
- 754 Collalti, A., Marconi, S., Ibrom, A., Trotta, C., Anav, A., amp, apos, Andrea, E., Matteucci, G., Montagnani, L.,
755 Gielen, B., Mammarella, I., Grünwald, T., Knohl, A., Berninger, F., Zhao, Y., Valentini, R., & Santini, M. (2016).
756 Validation of 3D-CMCC Forest Ecosystem Model (v.5.1) against eddy covariance data for 10 European forest
757 sites. *Geoscientific Model Development*, 9(2), 479-504. <https://doi.org/10.5194/gmd-9-479-2016>
- 758 Collalti, A., Perugini, L., Santini, M., Chiti, T., Nolè, A., Matteucci, G., & Valentini, R. (2014). A process-based
759 model to simulate growth in forests with complex structure: Evaluation and use of 3D-CMCC Forest Ecosys-
760 tem Model in a deciduous forest in Central Italy [Article]. *Ecological Modelling*, 2014 v.272, pp. 362-378.
761 <https://doi.org/10.1016/j.ecolmodel.2013.09.016>
- 762 Collalti, A., Thornton, P. E., Cescatti, A., Rita, A., Borghetti, M., Nolè, A., Trotta, C., Ciais, P., & Matteucci, G.
763 (2019). The sensitivity of the forest carbon budget shifts across processes along with stand development and
764 climate change. *Ecological Applications*, 29(2), e01837. <https://doi.org/10.1002/eap.1837>

Forest Model Evaluation

- 765 Collalti, A., Tjoelker, M. G., Hoch, G., Mäkelä, A., Guidolotti, G., Heskell, M., Petit, G., Ryan, M. G., Battipaglia,
766 G., Matteucci, G., & Prentice, I. C. (2020). Plant respiration: Controlled by photosynthesis or biomass? *Global*
767 *Change Biology*, 26(3), 1739-1753. <https://doi.org/10.1111/gcb.14857>
- 768 Collalti, A., Trotta, C., Keenan, F. K., Ibrom, A., Bond-Lamberty, B., Grote, R., Vicca, S., Reyer, C. P. O.,
769 Migliavacca, M., Veroustraete, F., Anav, A., Campioli, M., Scoccimarro, E., Sigut, L., Gioco, E., Cescatti, A., &
770 Matteucci, G. (2018). Thinning can reduce losses in carbon use efficiency and carbon stocks in managed for-
771 ests under warmer climate. *Journal of Advances in Modeling Earth Systems*, 10.
772 <https://doi.org/10.1002/2018MS001275>
- 773 Cysneiros, V. C., de Souza, F. C., Gai, T. D., Pelissari, A. L., Orso, G. A., Machado, S. D., de Carvalho, D. C., &
774 Silveira, T. B. (2021). Integrating climate, soil and stand structure into allometric models: An approach of site-
775 effects on tree allometry in Atlantic Forest. *Ecological Indicators*, 127, Article 107794.
776 <https://doi.org/10.1016/j.ecolind.2021.107794>
- 777 de Pury, D. G. G., & Farquhar, G. D. (1997). Simple scaling of photosynthesis from leaves to canopies without
778 the errors of big-leaf models. *Plant, Cell & Environment*, 20(5), 537-557. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-3040.1997.00094.x)
779 [3040.1997.00094.x](https://doi.org/10.1111/j.1365-3040.1997.00094.x)
- 780 de Wergifosse, L., André, F., Goosse, H., Boczon, A., Cecchini, S., Ciceu, A., Collalti, A., Cools, N., D'Andrea, E.,
781 De Vos, B., Hamdi, R., Ingerslev, M., Knudsen, M. A., Kowalska, A., Leca, S., Matteucci, G., Nord-Larsen, T.,
782 Sanders, T. G. M., Schmitz, A., Termonia, P., Vanguelova, E., Van Schaeybroeck, B., Verstraeten, A., Vesterdal,
783 L., & Jonard, M. (2022). Simulating tree growth response to climate change in structurally diverse oak and
784 beech forests. *Science of the Total Environment*, 806, 150422. [https://doi.org/10.1016/j.sci-](https://doi.org/10.1016/j.scitotenv.2021.150422)
785 [totenv.2021.150422](https://doi.org/10.1016/j.scitotenv.2021.150422)

Forest Model Evaluation

- 786 Didion, M., Kupferschmid, A. D., Zingg, A., Fahse, L., & Bugmann, H. (2009). Gaining local accuracy while not
787 losing generality — extending the range of gap model applications. *Canadian Journal of Forest Research*,
788 39(6), 1092-1107. <https://doi.org/10.1139/x09-041>
- 789 Dirnböck, T., Kraus, D., Grote, R., Klatt, S., Kobler, J., Schindlbacher, A., Seidl, R., Thom, D., & Kiese, R. (2020).
790 Substantial understory contribution to the C sink of a European temperate mountain forest landscape. *Land-*
791 *scape Ecology*, 35(2), 483-499. <https://doi.org/10.1007/s10980-019-00960-2>
- 792 Fabrika, M., & Ďurský, J. (2005). Algorithms and software solution of thinning models for SIBYLA growth sim-
793 ulator [Article]. *Journal of Forest Science*, 51(10), 431-445. <https://doi.org/10.17221/4577-jfs>
- 794 Farquhar, G. D., von Caemmerer, S., & Berry, J. A. (1980). A biochemical model of photosynthetic CO₂ assim-
795 ilation in leaves of C₃ species. *Planta*, 149(1), 78-90. <https://doi.org/10.1007/BF00386231>
- 796 Fasiolo M, Goude Y, Nedellec R, Wood S. N. (2017). Fast calibrated additive quantile regression.
797 <https://arxiv.org/abs/1707.03307>.
- 798 Finzi, A. C., Giasson, M.-A., Barker Plotkin, A. A., Aber, J. D., Boose, E. R., Davidson, E. A., Dietze, M. C., Ellison,
799 A. M., Frey, S. D., Goldman, E., Keenan, T. F., Melillo, J. M., Munger, J. W., Nadelhoffer, K. J., Ollinger, S. V.,
800 Orwig, D. A., Pederson, N., Richardson, A. D., Savage, K., Tang, J., Thompson, J. R., Williams, C. A., Wofsy, S.
801 C., Zhou, Z., & Foster, D. R. (2020). Carbon budget of the Harvard Forest Long-Term Ecological Research site:
802 pattern, process, and response to global change. *Ecological Monographs*, 90(4), e01423.
803 <https://doi.org/10.1002/ecm.1423>
- 804 Foken, T (2008). *Micrometeorology*. Springer, Berlin, Germany.

Forest Model Evaluation

- 805 Fontes, L., Bontemps, J.-D., Bugmann, H., Van Oijen, M., Gracia, C., Kramer, K., Lindner, M., Rötzer, T., &
806 Skovsgaard, J. P. (2010). Models for supporting forest management in a changing environment. *Forest Sys-*
807 *tems*, 19.
- 808 Forsius, M., Kujala, H., Minunno, F., Holmberg, M., Leikola, N., Mikkonen, N., Autio, I., Paunu, V.-V., Tanhuan-
809 pää, T., Hurskainen, P., Mäyrä, J., Kivinen, S., Keski-Saari, S., Kosenius, A.-K., Kuusela, S., Virkkala, R., Viinikka,
810 A., Vihervaara, P., Akujärvi, A., Bäck, J., Karvosenoja, N., Kumpula, T., Kuzmin, A., Mäkelä, A., Moilanen, A.,
811 Ollikainen, M., Pekkonen, M., Peltoniemi, M., Poikolainen, L., Rankinen, K., Rasilo, T., Tuominen, S., Valkama,
812 J., Vanhala, P., & Heikkinen, R. K. (2021). Developing a spatially explicit modelling and evaluation framework
813 for integrated carbon sequestration and biodiversity conservation: Application in southern Finland. *Science*
814 *of the Total Environment*, 775, 145847. <https://doi.org/10.1016/j.scitotenv.2021.145847>
- 815 Franklin, J., Davis, F. W., Ikegami, M., Syphard, A. D., Flint, L. E., Flint, A. L., & Hannah, L. (2013). Modeling
816 plant species distributions under future climates: how fine scale do climate projections need to be? *Global*
817 *Change Biology*, 19(2), 473-483. <https://doi.org/10.1111/gcb.12051>
- 818 Friedlingstein, P., Joel, G., Field, C. B., & Fung, I. Y. (1999). Toward an allocation scheme for global terrestrial
819 carbon models. *Global Change Biology*, 5(7), 755-770. <https://doi.org/10.1046/j.1365-2486.1999.00269.x>
- 820 Frieler, K., Lange, S., Piontek, F., Reyer, C. P. O., Schewe, J., Warszawski, L., Zhao, F., Chini, L., Denvil, S.,
821 Emanuel, K., Geiger, T., Halladay, K., Hurtt, G., Mengel, M., Murakami, D., Ostberg, S., Popp, A., Riva, R.,
822 Stevanovic, M., Suzuki, T., Volkholz, J., Burke, E., Ciais, P., Ebi, K., Eddy, T. D., Elliott, J., Galbraith, E., Gosling,
823 S. N., Hattermann, F., Hickler, T., Hinkel, J., Hof, C., Huber, V., Jägermeyr, J., Krysanova, V., Marcé, R., Müller
824 Schmied, H., Mouratiadou, I., Pierson, D., Tittensor, D. P., Vautard, R., van Vliet, M., Biber, M. F., Betts, R. A.,
825 Bodirsky, B. L., Deryng, D., Frohking, S., Jones, C. D., Lotze, H. K., Lotze-Campen, H., Sahajpal, R., Thonicke, K.,

Forest Model Evaluation

- 826 Tian, H., & Yamagata, Y. (2017). Assessing the impacts of 1.5 °C global warming – simulation protocol of the
827 Inter-Sectoral Impact Model Intercomparison Project (ISIMIP2b). *Geoscientific Model Development*, 10(12),
828 4321-4345. <https://doi.org/10.5194/gmd-10-4321-2017>
- 829 Gauch, H. G., Hwang, J. T. G., & Fick, G. W. (2003). Model evaluation by comparison of model-based predic-
830 tions and measured values. *Agronomy Journal*, 95.
- 831 Grote, R. (1998). Integrating dynamic morphological properties into forest growth modelling: II Allocation
832 and mortality. *Forest Ecology and Management*, 111(2), 193-210. [https://doi.org/10.1016/S0378-
833 1127\(98\)00328-4](https://doi.org/10.1016/S0378-1127(98)00328-4)
- 834 Grote, R. (2007). Sensitivity of volatile monoterpene emission to changes in canopy structure: a model-based
835 exercise with a process-based emission model. *New Phytologist*, 173(3), 550-561.
836 <https://doi.org/10.1111/j.1469-8137.2006.01946.x>
- 837 Grote, R., Korhonen, J. & Mammarella, I. (2011). Challenges for evaluating process-based models of gas ex-
838 change at forest sites with fetches of various species. *For. Syst.* 20, 389-406.
839 <https://doi.org/10.5424/fs/20112003-11084>
- 840 Grote, R., Kraus, D., Weis, W., Ettl, R., & Göttlein, A. (2020). Dynamic coupling of allometric ratios to a pro-
841 cess-based forest growth model for estimating the impacts of stand density changes. *Forestry: An Interna-
842 tional Journal of Forest Research*, 93(5), 601-615. <https://doi.org/10.1093/forestry/cpaa002>
- 843 Gupta, R., & Sharma, L. K. (2019). The process-based forest growth model 3-PG for use in forest management:
844 A review. *Ecological Modelling*, 397, 55-73. <https://doi.org/10.1016/j.ecolmodel.2019.01.007>

Forest Model Evaluation

- 845 Gutsch, M., Lasch-Born, P., Kollas, C., Suckow, F., & Reyer, C. P. O. (2018). Balancing trade-offs between
846 ecosystem services in Germany's forests under climate change. *Environmental Research Letters*, 13(4).
847 <https://doi.org/10.1088/1748-9326/aab4e5>
- 848 Haxeltine, A., & Prentice, I. C. (1996a). A General Model for the Light-Use Efficiency of Primary Production.
849 *Functional Ecology*, 10(5), 551-561.
- 850 Haxeltine, A., & Prentice, I. C. (1996b). BIOME3: An equilibrium terrestrial biosphere model based on eco-
851 physiological constraints, resource availability, and competition among plant functional types. *Global Biogeo-*
852 *chemical Cycles*, 10(4), 693-709. <https://doi.org/10.1029/96GB02344>
- 853 Hlásny, T., Barcza, Z., Barka, I., Merganičová, K., Sedmák, R., Kern, A., Pajtík, J., Balázs, B., Fabrika, M., &
854 Churkina, G. (2014). Future carbon cycle in mountain spruce forests of Central Europe: Modelling framework
855 and ecological inferences. *Forest Ecology and Management*, 328, 55-68.
856 <https://doi.org/10.1016/j.foreco.2014.04.038>
- 857 Holmberg, M., Aalto, T., Akujärvi, A., Arslan, A. N., Bergström, I., Böttcher, K., Lahtinen, I., Mäkelä, A., Mark-
858 kanen, T., Minunno, F., Peltoniemi, M., Rankinen, K., Vihervaara, P. & Forsius, M. (2019) Ecosystem Services
859 Related to Carbon Cycling - Modeling Present and Future Impacts in Boreal Forests. *Frontiers in plant sci-*
860 *ence*, 10, 343-351.
- 861 Horemans, J. A., Henrot, A., Delire, C., Kollas, C., Lasch-Born, P., Reyer, C., Suckow, F., François, L., &
862 Ceulemans, R. (2017). Combining multiple statistical methods to evaluate the performance of process-based
863 vegetation models across three forest stands. *Central European Forestry Journal*, 63(4), 153-172.
864 <https://doi.org/10.1515/forj-2017-0025>

Forest Model Evaluation

- 865 Huber, N., Bugmann, H., Cailleret, M., Bircher, N., & Lafond, V. (2021). Stand-scale climate change impacts
866 on forests over large areas: transient responses and projection uncertainties. *Ecological Applications*, 31(4).
- 867 Huber, N., Bugmann, H., & Lafond, V. (2020). Capturing ecological processes in dynamic forest models: why
868 there is no silver bullet to cope with complexity. *Ecosphere*, 11(5).
- 869 Irauschek, F., Barka, I., Bugmann, H., Courbaud, B., Elkin, C., Hlásny, T., Klopčič, M., Mina, M., Rammer, W.,
870 & Lexer, M. J. (2021). Evaluating five forest models using multi-decadal inventory data from mountain for-
871 ests. *Ecological Modelling*, 445, 109493. <https://doi.org/10.1016/j.ecolmodel.2021.109493>
- 872 Jarvis, A. J., & Davies, W. J. (1998). The coupled response of stomatal conductance to photosynthesis and
873 transpiration. *Journal of Experimental Botany*, 49(Special_Issue), 399-406.
874 https://doi.org/10.1093/jxb/49.Special_Issue.399
- 875 Jarvis, P. G., Monteith, J. L., & Weatherley, P. E. (1976). The interpretation of the variations in leaf water
876 potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal
877 Society of London. B, Biological Sciences*, 273(927), 593-610. <https://doi.org/doi:10.1098/rstb.1976.0035>
- 878 Kalliokoski, T., Heinonen, T., Holder, J., Lehtonen, A., Mäkelä, A., Minunno, F., Ollikainen, M., Packalen, T.,
879 Peltoniemi, M., Pukkala, T., Salminen, O., Schelhaas, M-J., Seppälä, J., Vauhkonen, J. & Kanninen, M. (2019).
880 Scenario analysis of similarities and differences between forest growth model projections (in Finnish). *Finnish
881 Climate Change Panel*. 88 pp.
- 882 Kalliokoski, T., Mäkelä, A., Fronzek, S., Minunno, F., & Peltoniemi, M. (2018). Decomposing sources of uncer-
883 tainty in climate change projections of boreal forest primary production. *Agricultural and Forest Meteorol-
884 ogy*, 262, 192-205. <https://doi.org/10.1016/j.agrformet.2018.06.030>

Forest Model Evaluation

- 885 Keenan, T., Maria Serra, J., Lloret, F., Ninyerola, M., & Sabate, S. (2011). Predicting the future of forests in
886 the Mediterranean under climate change, with niche- and process-based models: CO2 matters! *Global*
887 *Change Biology*, 17(1), 565-579. <https://doi.org/10.1111/j.1365-2486.2010.02254.x>
- 888 Kramer, K., Leinonen, I., Bartelink, H. H., Berbigier, P., Borghetti, M., Bernhofer, C., Cienciala, E., Dolman, A.
889 J., Froer, O., Gracia, C. A., Granier, A., Grünwald, T., Hari, P., Jans, W., Kellomäki, S., Loustau, D., Magnani, F.,
890 Markkanen, T., Matteucci, G., Mohren, G. M. J., Moors, E., Nissinen, A., Peltola, H., Sabaté, S., Sanchez, A.,
891 Sontag, M., Valentini, R., & Vesala, T. (2002). Evaluation of six process-based forest growth models using
892 eddy-covariance measurements of CO2 and H2O fluxes at six forest sites in Europe. *Global Change Biology*,
893 8(3), 213-230. <https://doi.org/10.1046/j.1365-2486.2002.00471.x>
- 894 Landsberg, J. J., & Waring, R. H. (1997). A generalised model of forest productivity using simplified concepts
895 of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, 95(3), 209-
896 228. [https://doi.org/10.1016/S0378-1127\(97\)00026-1](https://doi.org/10.1016/S0378-1127(97)00026-1)
- 897 Lasch-Born, P., Suckow, F., Reyer, C. P. O., Gutsch, M., Kollas, C., Badeck, F. W., Bugmann, H. K. M., Grote, R.,
898 Fürstenau, C., Lindner, M., & Schaber, J. (2020). Description and evaluation of the process-based forest
899 model 4C v2.2 at four European forest sites. *Geosci. Model Dev.*, 13(11), 5311-5343.
900 <https://doi.org/10.5194/gmd-13-5311-2020>
- 901 Lasslop, G., Reichstein, M., Papale, D., Richardson, A. D., Arneth, A., Barr, A., Stoy, P., & Wohlfahrt, G. (2010).
902 Separation of net ecosystem exchange into assimilation and respiration using a light response curve ap-
903 proach: critical issues and global evaluation. *Global Change Biology*, 16(1), 187-208.
904 <https://doi.org/10.1111/j.1365-2486.2009.02041.x>

Forest Model Evaluation

- 905 Leinonen, I. (1996). A Simulation Model for the Annual Frost Hardiness and Freeze Damage of Scots Pine.
906 *Annals of Botany*, 78(6), 687-693. <https://doi.org/10.1006/anbo.1996.0178>
- 907 Leuning, R. (1995). A critical appraisal of a combined stomatal-photosynthesis model for C3 plants. *Plant, Cell*
908 *& Environment*, 18(4), 339-355. <https://doi.org/10.1111/j.1365-3040.1995.tb00370.x>
- 909 Leuning, R., Kelliher, F. M., De Pury, D. G. G., & Schulze, E.-D. (1995). Leaf nitrogen, photosynthesis, conduct-
910 ance and transpiration: scaling from leaves to canopies. *Plant, Cell & Environment*, 18(10), 1183-1200.
911 <https://doi.org/10.1111/j.1365-3040.1995.tb00628.x>
- 912 Levins, R. (1966). The strategy of model building in population biology. *American Scientist*, 54(4).
- 913 Lindauer, M., Schmid, H. P., Grote, R., Mauder, M., Steinbrecher, R., & Wolpert, B. (2014). Net ecosystem
914 exchange over a non-cleared wind-throw-disturbed upland spruce forest—Measurements and simulations.
915 *Agricultural and Forest Meteorology*, 197, 219-234. <https://doi.org/10.1016/j.agrformet.2014.07.005>
- 916 Lindner, M., Fitzgerald, J. B., Zimmermann, N. E., Reyer, C., Delzon, S., van der Maaten, E., Schelhaas, M. J.,
917 Lasch, P., Eggers, J., van der Maaten-Theunissen, M., Suckow, F., Psomas, A., Poulter, B., & Hanewinkel, M.
918 (2014). Climate change and European forests: what do we know, what are the uncertainties, and what are
919 the implications for forest management? *Journal of Environmental Management*, 146, 69-83.
920 <https://doi.org/10.1016/j.jenvman.2014.07.030>
- 921 Linkosalo, T., Lappalainen, H. K., & Hari, P. (2008). A comparison of phenological models of leaf bud burst
922 and flowering of boreal trees using independent observations. *Tree Physiology*, 28(12), 1873-1882.
923 <https://doi.org/10.1093/treephys/28.12.1873>

Forest Model Evaluation

- 924 Luysaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E. D.,
925 Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond,
926 J. M., Chambers, J., Ciais, P., Cook, B., Davis, K. J., Dolman, A. J., Gielen, B., Goulden, M., Grace, J., Granier,
927 A., Grelle, A., Griffis, T., GrÜNwald, T., Guidolotti, G., Hanson, P. J., Harding, R., Hollinger, D. Y., Hutyra, L. R.,
928 Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A., Loustau, D.,
929 Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J. W.,
930 Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Rouspard, O., Saigusa, N., Sanz, M. J., Seufert, G., Sierra,
931 C., Smith, M. L., Tang, J., Valentini, R., Vesala, T., & Janssens, I. A. (2007). CO2 balance of boreal, temperate,
932 and tropical forests derived from a global database. *Global Change Biology*, 13(12), 2509-2537.
933 <https://doi.org/10.1111/j.1365-2486.2007.01439.x>
- 934 Mäkelä, A. (1997). A Carbon Balance Model of Growth and Self-Pruning in Trees Based on Structural Rela-
935 tionships. *Forest Science*, 43(1), 7-24. <https://doi.org/10.1093/forestscience/43.1.7>
- 936 Mäkelä, A., Hari, P., Berninger, F., Hänninen, H., & Nikinmaa, E. (2004). Acclimation of photosynthetic capaci-
937 ty in Scots pine to the annual cycle of temperature. *Tree Physiology*, 24(4), 369-376.
938 <https://doi.org/10.1093/treephys/24.4.369>
- 939 Mäkelä, A., Pulkkinen, M., Kolari, P., Lagergren, F., Bergibier, P., Lindroth, A., Loustau, D., Nikinmaa, E.,
940 Vesala, T., & Hari, P. (2008). Developing an empirical model of stand GPP with the LUE approach: analysis of
941 eddy covariance data at five contrasting conifer sites in Europe. *Global Change Biology*, 14(1), 92-108.
942 <https://doi.org/10.1111/j.1365-2486.2007.01463.x>

Forest Model Evaluation

- 943 Marconi, S., Chiti, T., Nolè, A., Valentini, R., & Collalti, A. (2017). The Role of Respiration in Estimation of Net
944 Carbon Cycle: Coupling Soil Carbon Dynamics and Canopy Turnover in a Novel Version of 3D-CMCC Forest
945 Ecosystem Model. *Forests*, 8(6), 220. <https://www.mdpi.com/1999-4907/8/6/220>
- 946 Marechaux, I., Langerwisch, F., Huth, A., Bugmann, H., Morin, X., Reyer, C. P. O., Seidl, R., Collalti, A., Dantas
947 de Paula, M., Fischer, R., Gutsch, M., Lexer, M. J., Lischke, H., Rammig, A., Rodig, E., Sakschewski, B., Taubert,
948 F., Thonicke, K., Vacchiano, G., & Bohn, F. J. (2021). Tackling unresolved questions in forest ecology: The past
949 and future role of simulation models. *Ecology and Evolution*, 11(9), 3746-3770.
950 <https://doi.org/10.1002/ece3.7391>
- 951 McCree, K., & Setlick, I. (1970). Prediction and measurement of photosynthetic productivity. Proceedings of
952 the IBP/PP Technical Meeting, Trebon, 14-21 September 1969,
- 953 Medlyn, B. E., Duursma, R. A., & Zeppel, M. J. B. (2011). Forest productivity under climate change: a checklist
954 for evaluating model studies. *Wiley Interdisciplinary Reviews: Climate Change*, 2(3), 332-355.
955 <https://doi.org/10.1002/wcc.108>
- 956 Merganic, J., Merganicova, K., Vybostok, J., Valent, P., Bahyl, J., & Yousefpour, R. (2020). Searching for Pareto
957 Fronts for Forest Stand Wind Stability by Incorporating Timber and Biodiversity Values. *Forests*, 11(5), 583.
958 <https://www.mdpi.com/1999-4907/11/5/583>
- 959 Merganicova, K., Merganic, J., Lehtonen, A., Vacchiano, G., Sever, M. Z. O., Augustynczyk, A. L. D., Grote, R.,
960 Kyselova, I., Makela, A., Yousefpour, R., Krejza, J., Collalti, A., & Reyer, C. P. O. (2019). Forest carbon allocation
961 modelling under climate change. *Tree Physiol.* <https://doi.org/10.1093/treephys/tpz105>

Forest Model Evaluation

- 962 Mina, M., Bugmann, H., Klopčič, M., & Cailleret, M. (2015). Accurate modeling of harvesting is key for pro-
963 jecting future forest dynamics: a case study in the Slovenian mountains. *Regional Environmental Change*,
964 17(1), 49-64. <https://doi.org/10.1007/s10113-015-0902-2>
- 965 Moffat, A. M., Beckstein, C., Churkina, G., Mund, M., & Heimann, M. (2010). Characterization of ecosystem
966 responses to climatic controls using artificial neural networks. *Global Change Biology*, 16(10), 2737-2749.
967 <https://doi.org/10.1111/j.1365-2486.2010.02171.x>
- 968 Monteith, J. L., Moss, C. J., Cooke, G. W., Pirie, N. W., & Bell, G. D. H. (1977). Climate and the efficiency of
969 crop production in Britain. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*,
970 281(980), 277-294. <https://doi.org/doi:10.1098/rstb.1977.0140>
- 971 Moore, A. D. (1989). On the maximum growth equation used in forest gap simulation models. *Ecological*
972 *Modelling*, 45, 63-67.
- 973 Morales, P., Sykes, M. T., Prentice, I. C., Smith, P., Smith, B., Bugmann, H., Zierl, B., Friedlingstein, P., Viomy,
974 N., Sabate, S., Sanchez, A., Pla, E., Gracia, C. A., Sitch, S., Arneth, A., & Ogee, J. (2005). Comparing and evalu-
975 ating process-based ecosystem model predictions of carbon and water fluxes in major European forest bi-
976 omes. *Global Change Biology*, 11(12), 2211-2233. <https://doi.org/10.1111/j.1365-2486.2005.01036.x>
- 977 Nadal-Sala, D., Grote, R., Birami, B., Lintunen, A., Mammarella, I., Preisler, Y., Rotenberg, E., Salmon, Y., Ta-
978 tarinov, F., Yakir, D., & Ruehr, N. K. (2021). Assessing model performance via the most limiting environmental
979 driver in two differently stressed pine stands. *Ecological Applications*, 31(4), e02312.
980 <https://doi.org/10.1002/eap.2312>

Forest Model Evaluation

- 981 Nadal-Sala, D., Hartig, F., Gracia, C. A., & Sabaté, S. (2019). Global warming likely to enhance black locust
982 (*Robinia pseudoacacia* L.) growth in a Mediterranean riparian forest. *Forest Ecology and Management*, 449,
983 117448. <https://doi.org/10.1016/j.foreco.2019.117448>
- 984 Novick, K. A., Ficklin, D. L., Stoy, P. C., Williams, C. A., Bohrer, G., Oishi, A. C., Papuga, S. A., Blanken, P. D.,
985 Noormets, A., Sulman, B. N., Scott, R. L., Wang, L., & Phillips, R. P. (2016). The increasing importance of at-
986 mospheric demand for ecosystem water and carbon fluxes. *Nature Climate Change*, 6(11), 1023-1027.
987 <https://doi.org/10.1038/nclimate3114>
- 988 Oberpriller, J., Cameron, D. R., Dietze, M. C., & Hartig, F. (2021). Towards robust statistical inference for
989 complex computer models. *Ecol Lett*, 24(6), 1251-1261. <https://doi.org/10.1111/ele.13728>
- 990 Oikawa, P. Y., Sturtevant, C., Knox, S. H., Verfaillie, J., Huang, Y. W., & Baldocchi, D. D. (2017). Revisiting the
991 partitioning of net ecosystem exchange of CO₂ into photosynthesis and respiration with simultaneous flux
992 measurements of ¹³CO₂ and CO₂, soil respiration and a biophysical model, CANVEG. *Agricultural and Forest
993 Meteorology*, 234-235, 149-163. <https://doi.org/10.1016/j.agrformet.2016.12.016>
- 994 Pardos, M., del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defosse, E., Engel, M.,
995 Godvod, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M.,
996 Riofrío, J., Ruíz-Peinado, R., Tomao, A., Uhl, E., & Calama, R. (2021). The greater resilience of mixed forests
997 to drought mainly depends on their composition: Analysis along a climate gradient across Europe. *Forest
998 Ecology and Management*, 481. <https://doi.org/10.1016/j.foreco.2020.118687>
- 999 Paschalis, A., Fatichi, S., Zscheischler, J., Ciais, P., Bahn, M., Boysen, L., Chang, J., De Kauwe, M., Estiarte, M.,
1000 Goll, D., Hanson, P. J., Harper, A. B., Hou, E., Kigel, J., Knapp, A. K., Larsen, K. S., Li, W., Lienert, S., Luo, Y.,

Forest Model Evaluation

- 1001 Meir, P., Nabel, J. E. M. S., Ogaya, R., Parolari, A. J., Peng, C., Peñuelas, J., Pongratz, J., Rambal, S., Schmidt, I.
- 1002 K., Shi, H., Sternberg, M., Tian, H., Tschumi, E., Ukkola, A., Vicca, S., Viovy, N., Wang, Y.-P., Wang, Z., Williams,
- 1003 K., Wu, D., & Zhu, Q. (2020). Rainfall manipulation experiments as simulated by terrestrial biosphere models:
- 1004 Where do we stand? *Global Change Biology*, 26(6), 3336-3355. <https://doi.org/10.1111/gcb.15024>
- 1005 Pastorello, G., Trotta, C., Canfora, E., Chu, H., Christianson, D., Cheah, Y.-W., Poindexter, C., Chen, J., El-
- 1006 bashandy, A., Humphrey, M., Isaac, P., Polidori, D., Reichstein, M., Ribeca, A., van Ingen, C., Vuichard, N.,
- 1007 Zhang, L., Amiro, B., Ammann, C., Arain, M. A., Ardö, J., Arkebauer, T., Arndt, S. K., Arriga, N., Aubinet, M.,
- 1008 Aurela, M., Baldocchi, D., Barr, A., Beamesderfer, E., Marchesini, L. B., Bergeron, O., Beringer, J., Bernhofer,
- 1009 C., Berveiller, D., Billesbach, D., Black, T. A., Blanken, P. D., Bohrer, G., Boike, J., Bolstad, P. V., Bonal, D.,
- 1010 Bonnefond, J.-M., Bowling, D. R., Bracho, R., Brodeur, J., Brümmer, C., Buchmann, N., Burban, B., Burns, S.
- 1011 P., Buysse, P., Cale, P., Cavagna, M., Cellier, P., Chen, S., Chini, I., Christensen, T. R., Cleverly, J., Collalti, A.,
- 1012 Consalvo, C., Cook, B. D., Cook, D., Coursolle, C., Cremonese, E., Curtis, P. S., D'Andrea, E., da Rocha, H., Dai,
- 1013 X., Davis, K. J., Cinti, B. D., Grandcourt, A. d., Ligne, A. D., De Oliveira, R. C., Delpierre, N., Desai, A. R., Di Bella,
- 1014 C. M., Tommasi, P. d., Dolman, H., Domingo, F., Dong, G., Dore, S., Duce, P., Dufrêne, E., Dunn, A., Dušek, J.,
- 1015 Eamus, D., Eichelmann, U., ElKhidir, H. A. M., Eugster, W., Ewenz, C. M., Ewers, B., Famulari, D., Fares, S.,
- 1016 Feigenwinter, I., Feitz, A., Fensholt, R., Filippa, G., Fischer, M., Frank, J., Galvagno, M., Gharun, M., Gianelle,
- 1017 D., Gielen, B., Gioli, B., Gitelson, A., Goded, I., Goeckede, M., Goldstein, A. H., Gough, C. M., Goulden, M. L.,
- 1018 Graf, A., Griebel, A., Gruening, C., Grünwald, T., Hammerle, A., Han, S., Han, X., Hansen, B. U., Hanson, C.,
- 1019 Hatakka, J., He, Y., Hehn, M., Heinesch, B., Hinko-Najera, N., Hörtnagl, L., Hutley, L., Ibrom, A., Ikawa, H.,
- 1020 Jackowicz-Korczynski, M., Janouš, D., Jans, W., Jassal, R., Jiang, S., Kato, T., Khomik, M., Klatt, J., Knohl, A.,
- 1021 Knox, S., Kobayashi, H., Koerber, G., Kolle, O., Kosugi, Y., Kotani, A., Kowalski, A., Kruijt, B., Kurbatova, J.,
- 1022 Kutsch, W. L., Kwon, H., Launiainen, S., Laurila, T., Law, B., Leuning, R., Li, Y., Liddell, M., Limousin, J.-M., Lion,

Forest Model Evaluation

- 1023 M., Liska, A. J., Lohila, A., López-Ballesteros, A., López-Blanco, E., Loubet, B., Loustau, D., Lucas-Moffat, A.,
1024 Lüers, J., Ma, S., Macfarlane, C., Magliulo, V., Maier, R., Mammarella, I., Manca, G., Marcolla, B., Margolis, H.
1025 A., Marras, S., Massman, W., Mastepanov, M., Matamala, R., Matthes, J. H., Mazzenga, F., McCaughey, H.,
1026 McHugh, I., McMillan, A. M. S., Merbold, L., Meyer, W., Meyers, T., Miller, S. D., Minerbi, S., Moderow, U.,
1027 Monson, R. K., Montagnani, L., Moore, C. E., Moors, E., Moreaux, V., Moureaux, C., Munger, J. W., Nakai, T.,
1028 Neiryneck, J., Nestic, Z., Nicolini, G., Noormets, A., Northwood, M., Noretto, M., Nouvellon, Y., Novick, K.,
1029 Oechel, W., Olesen, J. E., Ourcival, J.-M., Papuga, S. A., Parmentier, F.-J., Paul-Limoges, E., Pavelka, M., Peichl,
1030 M., Pendall, E., Phillips, R. P., Pilegaard, K., Pirk, N., Posse, G., Powell, T., Prasse, H., Prober, S. M., Rambal, S.,
1031 Rannik, Ü., Raz-Yaseef, N., Reibmann, C., Reed, D., Dios, V. R. d., Restrepo-Coupe, N., Reverter, B. R., Roland,
1032 M., Sabbatini, S., Sachs, T., Saleska, S. R., Sánchez-Cañete, E. P., Sanchez-Mejia, Z. M., Schmid, H. P., Schmidt,
1033 M., Schneider, K., Schrader, F., Schroder, I., Scott, R. L., Sedlák, P., Serrano-Ortíz, P., Shao, C., Shi, P., Shironya,
1034 I., Siebicke, L., Šigut, L., Silberstein, R., Sirca, C., Spano, D., Steinbrecher, R., Stevens, R. M., Sturtevant, C.,
1035 Suyker, A., Tagesson, T., Takanashi, S., Tang, Y., Tapper, N., Thom, J., Tomassucci, M., Tuovinen, J.-P., Urban-
1036 ski, S., Valentini, R., van der Molen, M., van Gorsel, E., van Huissteden, K., Varlagin, A., Verfaillie, J., Vesala,
1037 T., Vincke, C., Vitale, D., Vygodskaya, N., Walker, J. P., Walter-Shea, E., Wang, H., Weber, R., Westermann, S.,
1038 Wille, C., Wofsy, S., Wohlfahrt, G., Wolf, S., Woodgate, W., Li, Y., Zampedri, R., Zhang, J., Zhou, G., Zona, D.,
1039 Agarwal, D., Biraud, S., Torn, M., & Papale, D. (2020). The FLUXNET2015 dataset and the ONEFlux processing
1040 pipeline for eddy covariance data. *Scientific Data*, 7(1), 225. <https://doi.org/10.1038/s41597-020-0534-3>
1041 Peltoniemi, M., Pulkkinen, M., Aurela M., Pumpanen, J., Kolari, P. & Mäkelä, A. 2015. A semi-empirical model
1042 of boreal forest gross primary production, evapotranspiration, and soil water – calibration and sensitivity
1043 analysis. *Boreal Environment Research*, 20, 151–171. <http://hdl.handle.net/10138/228031>

Forest Model Evaluation

- 1044 Pretzsch, H., Forrester, D. I., & Rötzer, T. (2015). Representation of species mixing in forest growth models.
1045 A review and perspective. *Ecological Modelling*, 313, 276-292.
1046 <https://doi.org/10.1016/j.ecolmodel.2015.06.044>
- 1047 R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical
1048 Computing, Vienna, Austria. <https://www.R-project.org/>.
- 1049 Rehfeldt, G. E., Crookston, N. L., Warwell, M. V. & Evans, J. S. (2006). Empirical analyses of plant-climate
1050 relationships for the western United States. *International Journal of Plant Sciences*. 167(6), 1123-1150.
- 1051 Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N.,
1052 Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila,
1053 A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg,
1054 E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., & Valentini, R. (2005). On the separa-
1055 tion of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm.
1056 *Global Change Biology*, 11(9), 1424-1439. <https://doi.org/10.1111/j.1365-2486.2005.001002.x>
- 1057 Reyer, C. P. O., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A., & Pilz, T. (2013). Projections of regional
1058 changes in forest net primary productivity for different tree species in Europe driven by climate change and
1059 carbon dioxide. *Annals of Forest Science*, 71(2), 211-225. <https://doi.org/10.1007/s13595-013-0306-8>
- 1060 Reyer, C. P. O., Silveyra Gonzalez, R., Dolos, K., Hartig, F., Hauf, Y., Noack, M., Lasch-Born, P., Rötzer, T.,
1061 Pretzsch, H., Meesenburg, H., Fleck, S., Wagner, M., Bolte, A., Sanders, T. G. M., Kolari, P., Mäkelä, A., Vesala,
1062 T., Mammarella, I., Pumpanen, J., Collalti, A., Trotta, C., Matteucci, G., D'Andrea, E., Foltýnová, L., Krejza, J.,

Forest Model Evaluation

- 1063 Ibrom, A., Pilegaard, K., Loustau, D., Bonnefond, J.-M., Berbigier, P., Picart, D., Lafont, S., Dietze, M., Cam-
1064 eron, D., Vieno, M., Tian, H., Palacios-Orueta, A., Cicuendez, V., Recuero, L., Wiese, K., Büchner, M., Lange,
1065 S., Volkholz, J., Kim, H., Horemans, J. A., Bohn, F., Steinkamp, J., Chikalanov, A., Weedon, G. P., Sheffield, J.,
1066 Babst, F., Vega del Valle, I., Suckow, F., Martel, S., Mahnken, M., Gutsch, M., & Frieler, K. (2020a). The PRO-
1067 FOUND Database for evaluating vegetation models and simulating climate impacts on European forests.
1068 *Earth System Science Data*, 12(2), 1295-1320. <https://doi.org/10.5194/essd-12-1295-2020>
- 1069 Reyer, C., Silveyra Gonzalez, R., Dolos, K., Hartig, F., Hauf, Y., Noack, M., Lasch-Born, P., Rötzer, T., Pretzsch,
1070 H., Meesenburg, H., Fleck, S., Wagner, M., Bolte, A., Sanders, T., Kolari, P., Mäkelä, A., Vesala, T., Mamma-
1071 rella, I., Pumpanen, J., Matteucci, G., Collalti, A., D'Andrea, E., Foltýnová, L., Krejza, J., Ibrom, A., Pilegaard,
1072 K., Loustau, D., Bonnefond, J.-M., Berbigier, P., Picart, D., Lafont, S., Dietze, M., Cameron, D., Vieno, M., Tian,
1073 H., Palacios-Orueta, A., Cicuendez, V., Recuero, L., Wiese, K., Büchner, M., Lange, S., Volkholz, J., Kim, H.,
1074 Weedon, G., Sheffield, J., Vega del Valle, I., Suckow, F., Horemans, J., Martel, S., Bohn, F., Steinkamp, J.,
1075 Chikalanov, A., Mahnken, M., Gutsch, M., Trotta, C., Babst, F., & Frieler, K. (2020b). The PROFOUND database
1076 for evaluating vegetation models and simulating climate impacts on European forests Version V. 0.3. GFZ
1077 Data Services. <https://doi.org/10.5880/PIK.2020.006>
- 1078 Rödig, E., Huth, A., Bohn, F., Rebmann, C., & Cuntz, M. (2017). Estimating the carbon fluxes of forests with
1079 an individual-based forest model. *Forest Ecosystems*, 4(1), 4. <https://doi.org/10.1186/s40663-017-0091-1>
- 1080 Sabaté, S., Gracia, C. A., & Sánchez, A. (2002). Likely effects of climate change on growth of *Quercus ilex*,
1081 *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region.
1082 *Forest Ecology and Management*, 162, 23-37.

Forest Model Evaluation

- 1083 Sato, H., Itoh, A., & Kohyama, T. (2007). SEIB-DGVM: A new dynamic global vegetation model using a spatially
1084 explicit individual-based approach. *Ecological Modelling*, 200(3-4), 279-307.
1085 <https://doi.org/10.1016/j.ecolmodel.2006.09.006>
- 1086 Schaber, J., & Badeck, F.-W. (2003). Physiology-based phenology models for forest tree species in Germany.
1087 *International Journal of Biometeorology*, 47(4), 193-201. <https://doi.org/10.1007/s00484-003-0171-5>
- 1088 Schweier, J., Molina-Herrera, S., Ghirardo, A., Grote, R., Díaz-Pinés, E., Kreuzwieser, J., Haas, E., Butterbach-
1089 Bahl, K., Rennenberg, H., Schnitzler, J.-P., & Becker, G. (2017). Environmental impacts of bioenergy wood
1090 production from poplar short-rotation coppice grown at a marginal agricultural site in Germany. *GCB Bioen-
1091 ergy*, 9(7), 1207-1221. <https://doi.org/10.1111/gcbb.12423>
- 1092 Thornley, J. H. M. (1970). Respiration, Growth and Maintenance in Plants. *Nature*, 227(5255), 304-305.
1093 <https://doi.org/10.1038/227304b0>
- 1094 Thornthwaite, C. W. (1948). An Approach toward a Rational Classification of Climate. *Geographical Review*,
1095 38(1), 55-94. <https://doi.org/10.2307/210739>
- 1096 Thornthwaite, C. W. & Mather J.R. (1957). Instructions and tables for computing potential evapotranspira-
1097 tion and the water balance. *Publ. Climatol*, 10, 183-311.
- 1098 Toïgo, M., Perot, T., Courbaud, B., Castagneyrol, B., Gégout, J.-C., Longuetaud, F., Jactel, H., & Vallet, P.
1099 (2018). Difference in shade tolerance drives the mixture effect on oak productivity. *Journal of Ecology*,
1100 106(3), 1073-1082. <https://doi.org/10.1111/1365-2745.12811>

Forest Model Evaluation

- 1101 Toïgo, M., Vallet, P., Perot, T., Bontemps, J.-D., Piedallu, C., Courbaud, B., & Canham, C. (2015). Overyielding
1102 in mixed forests decreases with site productivity. *Journal of Ecology*, 103(2), 502-512.
1103 <https://doi.org/10.1111/1365-2745.12353>
- 1104 Trotsiuk, V., Hartig, F., Cailleret, M., Babst, F., Forrester, D. I., Baltensweiler, A., Buchmann, N., Bugmann, H.,
1105 Gessler, A., Gharun, M., Minunno, F., Rigling, A., Rohner, B., Stillhard, J., Thurig, E., Waldner, P., Ferretti, M.,
1106 Eugster, W., & Schaub, M. (2020). Assessing the response of forest productivity to climate extremes in Swit-
1107 zerland using model-data fusion. *Glob Chang Biol.* <https://doi.org/10.1111/gcb.15011>
- 1108 Trugman, A. T., Anderegg, L. D. L., Anderegg, W. R. L., Das, A. J., & Stephenson, N. L. (2021). Why is Tree
1109 Drought Mortality so Hard to Predict? *Trends in Ecology & Evolution*, 36(6), 520-532.
1110 <https://doi.org/10.1016/j.tree.2021.02.001>
- 1111 Vallet, P., & Pérot, T. (2018). Coupling transversal and longitudinal models to better predict *Quercus petraea*
1112 and *Pinus sylvestris* stand growth under climate change. *Agricultural and Forest Meteorology*.
- 1113 van Oijen, M., Balkovi, J., Beer, C., Cameron, D. R., Ciais, P., Cramer, W., Kato, T., Kuhnert, M., Martin, R.,
1114 Myneni, R., Rammig, A., Rolinski, S., Soussana, J. F., Thonicke, K., Van der Velde, M., & Xu, L. (2014). Impact
1115 of droughts on the carbon cycle in European vegetation: a probabilistic risk analysis using six vegetation
1116 models. *Biogeosciences*, 11(22), 6357-6375. <https://doi.org/10.5194/bg-11-6357-2014>
- 1117 Walker, A. P., De Kauwe, M. G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R. F., McMahon, S. M.,
1118 Medlyn, B. E., Moore, D. J. P., Norby, R. J., Zaehle, S., Anderson-Teixeira, K. J., Battipaglia, G., Brien, R. J.
1119 W., Cabugao, K. G., Cailleret, M., Campbell, E., Canadell, J. G., Ciais, P., Craig, M. E., Ellsworth, D. S., Farquhar,
1120 G. D., Fatichi, S., Fisher, J. B., Frank, D. C., Graven, H., Gu, L., Haverd, V., Heilman, K., Heimann, M., Hungate,

Forest Model Evaluation

- 1121 B. A., Iversen, C. M., Joos, F., Jiang, M., Keenan, T. F., Knauer, J., Körner, C., Leshyk, V. O., Leuzinger, S., Liu,
1122 Y., MacBean, N., Malhi, Y., McVicar, T. R., Penuelas, J., Pongratz, J., Powell, A. S., Riutta, T., Sabot, M. E. B.,
1123 Schleucher, J., Sitch, S., Smith, W. K., Sulman, B., Taylor, B., Terrer, C., Torn, M. S., Treseder, K. K., Trugman,
1124 A. T., Trumbore, S. E., van Mantgem, P. J., Voelker, S. L., Whelan, M. E., & Zuidema, P. A. (2021). Integrating
1125 the evidence for a terrestrial carbon sink caused by increasing atmospheric CO₂. *New Phytologist*, 229(5),
1126 2413-2445. <https://doi.org/10.1111/nph.16866>
- 1127 Weisberg, M. (2007). Forty Years of 'The Strategy': Levins on Model Building and Idealization. *Biology & Phi-*
1128 *losophy*, 21(5), 623-645. <https://doi.org/10.1007/s10539-006-9051-9>
- 1129 Xenakis, G., Ray, D., & Mencuccini, M. (2008). Sensitivity and uncertainty analysis from a coupled 3-PG and
1130 soil organic matter decomposition model. *Ecological Modelling*, 219(1), 1-16.
1131 <https://doi.org/10.1016/j.ecolmodel.2008.07.020>
- 1132 Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hickler, T., Luo, Y., Wang, Y.-P., El-
1133 Masri, B., Thornton, P., Jain, A., Wang, S., Warlind, D., Weng, E., Parton, W., Iversen, C. M., Gallet-Budynek,
1134 A., McCarthy, H., Finzi, A., Hanson, P. J., Prentice, I. C., Oren, R., & Norby, R. J. (2014). Evaluation of 11 ter-
1135 restrial carbon–nitrogen cycle models against observations from two temperate Free-Air CO₂ Enrichment
1136 studies. *New Phytologist*, 202(3), 803-822. <https://doi.org/10.1111/nph.12697>
- 1137 Zhang, Q., Ficklin, D. L., Manzoni, S., Wang, L., Way, D., Phillips, R. P., & Novick, K. A. (2019). Response of
1138 ecosystem intrinsic water use efficiency and gross primary productivity to rising vapor pressure deficit. *Envi-*
1139 *ronmental Research Letters*, 14(7). <https://doi.org/10.1088/1748-9326/ab2603>

Forest Model Evaluation

- 1140 Zhang, Z., Zhang, R., Cescatti, A., Wohlfahrt, G., Buchmann, N., Zhu, J., Chen, G., Moyano, F., Pumpanen, J.,
1141 Hirano, T., Takagi, K., & Merbold, L. (2017). Effect of climate warming on the annual terrestrial net ecosystem
1142 CO₂ exchange globally in the boreal and temperate regions. *Sci Rep*, 7(1), 3108.
1143 <https://doi.org/10.1038/s41598-017-03386-5>
- 1144 Zhou, H., Yue, X., Lei, Y., Zhang, T., Tian, C., Ma, Y., & Cao, Y. (2021). Responses of gross primary productivity
1145 to diffuse radiation at global FLUXNET sites. *Atmospheric Environment*, 244, 117905.
1146 <https://doi.org/10.1016/j.atmosenv.2020.117905>