MEDFATE 2.8.1: A trait-enabled model to simulate Mediterranean forest function and dynamics at regional scales

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Abstract. Regional-level applications of dynamic vegetation models are challenging because they need to accommodate the variation in plant functional diversity, which requires moving away from broadly-defined functional types. Different approaches have been adopted in the last years to incorporate a trait-based perspective into modeling exercises. A common parametrization strategy involves using trait data to represent functional variation between individuals while discard taxonomic identity, but this strategy ignores the phylogenetic signal of trait variation and cannot be employed when predictions for specific taxa are needed, as in applications to inform forest management planning. An alternative strategy involves adapting the taxonomic resolution of model entities to that of the data source employed for large-scale initialization and estimating functional parameters from available plant trait databases while adopting alternative solutions for missing data and non-observable parameters. Here we report the advantages and limitations of this second strategy according to our experience in the development of MEDFATE (v. 2.8.1), a novel cohort-based and trait-enabled model of forest dynamics, for its application over a region in the Western Mediterranean Basin. First, 217 taxonomic entities were defined according to woody species codes of the Spanish National Forest Inventory. While forest inventory data were used to obtain some empirical parameter estimates, a large proportion of physiological, morphological, and anatomical parameters were mapped to measured plant traits, with estimates extracted from multiple databases and averaged at the required taxonomic level. Estimates for non-observable key parameters were obtained using meta-modeling and calibration exercises. Missing values were filled using imputation procedures based on trait coordination, taxonomic averages or both. The model properly simulated observed historical basal area changes, with a performance similar to an empirical model trained for the same region. While strong efforts are still required to parameterize trait-enabled models for multiple taxa, estimation procedures can be progressively refined, transferred to other regions or models and iterated following data source changes by employing automated workflows. We advocate for the adoption of trait-enabled population-structured models for regional-level projections of forest function and dynamics.

1. Introduction

Dynamic vegetation models are essential tools to anticipate future function and dynamics of terrestrial ecosystems. However, forest responses to changes in climate and disturbance regimes are complex and non-linear, as they involve multiple processes operating at various scales, which makes forecasting a challenging task (Adams et al., 2013). Global-scale assessments of the effects of climatic changes on terrestrial ecosystems and their feed-backs require physically-based
50 mechanistic approaches, given the need to evaluate energy, water and carbon exchanges between the biosphere and the atmosphere (Prentice and Cowling, 2013). At the regional-scale, however, climate change impact assessments on forest function and dynamics often do not include feed-backs to the atmosphere system and can be conducted using a much broader range of modeling approaches, with differences in the way vegetation structure is represented and different degrees of mechanistic detail of process representation (Bugmann and Seidl, n.d.; Maréchaux et al., 2021; Blanco et al., 2020). Some
55 models are very detailed in terms of biophysical, biogeochemical and physiological processes, but have a missing or limited representation of vegetation structure and demographic processes (Running and Coughlan, 1988; Dufrêne et al., 2005; Gracia et al., 2004). These models are better suited for predicting vegetation function than structural and/or compositional forest dynamics. At the opposite end, growth and yield models calibrated using empirical individual data allow simulating forest structural and compositional dynamics arising from the birth, growth and death of tree individuals (Dixon, 2013;
60 Stadelmann et al., 2019; Trasobares et al., 2022), but are unable to predict vegetation function and often lack sufficient responsiveness to changing climatic conditions. Forest gap models combine an individual- or cohort-based representation of vegetation with an intermediate level of mechanistic detail, where demographic processes depend on competition for light, water, and nutrients, but the impact these factors on demographic processes is modeled with a low degree of mechanistic detail (Bugmann, 2001; Morin et al., 2021; Thrippleton et al., 2020; García-Valdés et al., 2020). Finally, hybrid models exist
65 combining a detailed mechanistic approach to energy, water and carbon balances with a sufficient treatment of vegetation structure and demographic processes (Fisher et al., 2018; Maréchaux and Chave, 2017; Liu et al., 2021). These kind of models have the advantage of allowing a better representation of the interaction between vegetation function and dynamics, often at the cost of increased computational requirements.

Regardless of the model type, one of the common challenges when modeling forest function and dynamics at large scales is
70 to appropriately represent plant functional diversity into model parameters (Maréchaux and Chave, 2017), while it is known that functional traits display a wide spectrum of variation at multiple spatial scales (Funk et al., 2017). First, not all vegetation models are 'trait-enabled', in the sense that their design and formulation has not been conducted taking into account that model parameters should preferably be matched with observable plant traits, which hinders parameter estimation of complex models. Second, it is common in many models to reduce functional diversity into a manageable set of
75 dominant tree species or a lumped set of plant functional types (Vanderwel et al., 2013; Morin et al., 2021; Prentice and Cowling, 2013; Dufrêne et al., 2005), with the corresponding decrease in ecological realism. Nowadays, comprehensive

global trait databases represent a key source of information to boost parameter estimation (Kattge et al., 2020) and including functional trait variation has been proven to substantially impact simulation outcomes (Verheijen et al., 2015). Different strategies have been adopted to incorporate plant functional diversity into vegetation modeling exercises (Zakharova et al.,

80   2019; Berzaghi et al., 2020). One possibility is to sample individual-level trait values from the distribution observed in a given forest area (Fyllas et al., 2014). This stochastic sampling of trait combinations can preserve trait coordination and relies on competition processes implemented in the model to filter trait distributions in each simulated patch (Sakschewski et al., 2015; Thonicke et al., 2020; Pavlick et al., 2013). Another approach consists in combining a trait-based description of individuals with genetic and demographic processes included in the model to simulate trait inheritance and, hence, eco-

85   evolutionary processes (Scheiter et al., 2013; Scheiter and Higgins, 2009). For simulations over large extents, yet another possibility is to use climate-trait relationships, calibrated using global trait databases, to prescribe the variation across space of parameter values (Verheijen et al., 2013, 2015). All these approaches ignore taxonomic information, or continue to use broadly-defined functional types, and focus on representing the continuum of traits at the individual level. Even though models implementing these approaches are valuable tools, disregarding taxonomic information entails some limitations.

90   Importantly, many plant traits exhibit a phylogenetic signal (Sanchez-Martinez et al., 2020; Anderegg et al., 2022) and trait coordination frequently differs within- and among-species (Rosas et al., 2019; Anderegg et al., 2018). Hence, it is unclear how a model without explicitly treating taxonomic entities can deal with functional diversity in a realistic way, which explains why recent approaches sample parameter combinations within species-defined boundaries (Buotte et al., 2021). In addition, there are many applications at local to regional scales that require species identity. An example would be the

95   evaluation of future climatic and socioeconomic scenarios for forest management and planning purposes (Morán-Ordóñez et al., 2020). Accounting for taxonomy in trait-enabled model simulations requires using as many trait data sources as possible to obtain taxon-specific estimates of model parameters (Maréchaux and Chave, 2017; Schmitt et al., 2020; Morin et al., 2021; Ruffault et al., 2022). This taxon-based parameter estimation strategy can be employed in large-scale simulation exercises if combined with systematic forest inventory data, which defines the maximum resolution of taxonomic entities

100   and provides empirical data to estimate parameters modulating forest dynamics (Vanderwel et al., 2013; Caspersen et al., 2011; Dijak et al., 2017; Morin et al., 2021). To date, however, there are few examples of trait-enabled models of vegetation dynamics being extensively parameterized for a large number of taxa using plant trait databases (Christoffersen et al., 2016). Hence, it is important to appropriately address the different challenges to overcome if this approach is adopted because, even with the current wealth of plant trait data sources, information is still insufficient for less common species that have not

105   received much attention; and for key model parameters that are difficult to measure or cannot be matched to any observable trait.

The main objectives of this manuscript are: (1) to present MEDFATE (ver. 2.8.1), a cohort-based and trait-enabled model of forest function and dynamics designed for regional applications; and (2) to illustrate the challenges encountered in the process of estimating parameter values for multiple-taxa in trait-enabled models. We begin by describing the design and

110 formulation of MEDFATE, focusing on new processes that have been added to two preceding models (De Cáceres et al., 2015, 2021) that are now considered as alternative sub-models. We then detail the different procedures we employed to estimate taxon parameter values for the application of MEDFATE over a target region in the Mediterranean Basin, including the imputation procedures used to address missing values. Once fully parameterized, we evaluate the model in terms of predicted forest dynamics at the regional level and compare its performance with that of an alternative empirical model

115 (García-Callejas et al., 2017) calibrated for the main species in the target region. We then illustrate the potential of MEDFATE to assess the impact of expected climate changes on forest function and dynamics of the target region. We finish by discussing the challenges that we encountered, the transferability of the adopted parameter estimation procedures and the overall value of trait-enabled forest models for regional applications.

2. Model description

120 MEDFATE simulates energy, water and carbon balances and ultimately forest dynamics for a set of woody plants (i.e. trees or shrubs) in a given forest stand using daily weather data as input. The above- and below-ground vertical structure of the stand is explicitly represented, but the horizontal location of plants within the stand is not considered. Importantly, the model is cohort-based, meaning that plants considered similar (e.g., in size and taxonomic identity) are represented using a single entity with average characteristics (e.g., tree height and diameter, or shrub height), and a density variable is used to upscale

125 quantities from the individual to the cohort level. Fig. 1 summarizes the main processes in the model. Most of the processes involved in water and energy balances are implemented at the stand level, whereas transpiration, photosynthesis, mortality and recruitment are implemented at the cohort level; and labile carbon balance, structural growth and senescence are implemented at the individual level. Hydrological processes (rainfall interception, soil infiltration, percolation and evaporation from bare soil) are simulated at daily time steps and were already described in De Cáceres et al. (2015).

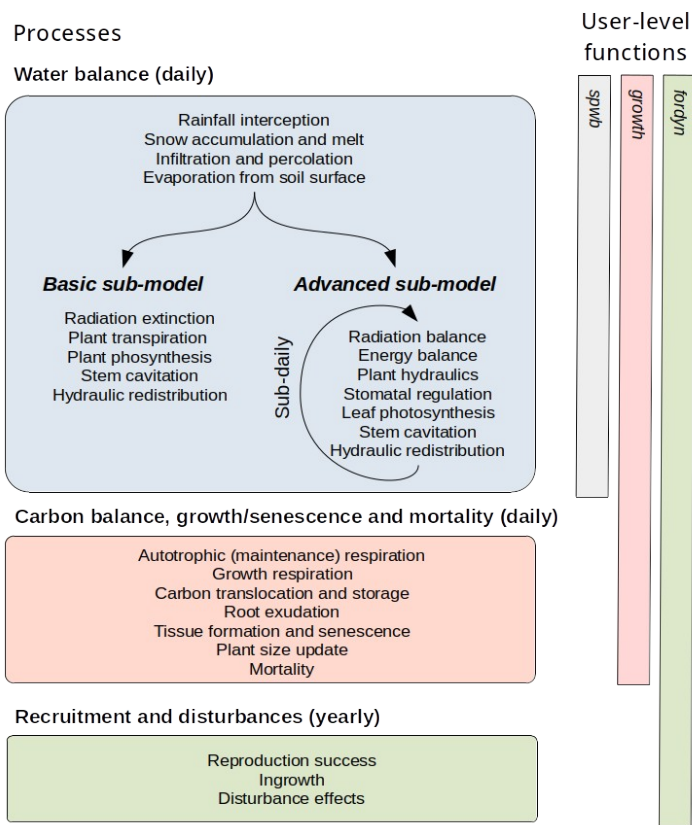
130 MEDFATE can be run using two different levels of complexity, depending on the sub-model employed to estimate plant transpiration and photosynthesis (De Cáceres et al., 2015, 2021), hereafter referred to as the "basic" and "advanced" sub-models (Fig. 1). Although the basic sub-model is limited in its assumptions and includes key parameters that cannot be matched to plant traits, the finer time step and detail in process representation of the advanced sub-model easily leads to computational limitations when processing thousands of stands. Hence, the two sub-models have their context of application.

135 Sub-sections 2.1 and 2.2 briefly describe the design of the two sub-models. We then present the design and formulation of the carbon balance, growth, mortality and recruitment processes with some more detail, because they are new to MEDFATE. Table 1 includes a description of all symbols mentioned in the text. MEDFATE is implemented in a modular way, so that different R functions can be used to execute different sub-models (Fig. 1). A full model description, including process formulation, can be found at https://emf-creaf.github.io/medfatebook/.

Symbol	Description	Units/range	Sub-model
LAI	Leaf area index of the stand	$m^2 \cdot m^{-2}$	

BA	Total basal area of the stand	m²·ha⁻¹	
H	Height of an "average" individual	m	
SA	Sapwood area of an "average" individual	cm²	
DBH	Diameter at breast height for an "average" individual	cm	
FBR_s	Fine root biomass in soil layer s	g dry	
PET	Potential evapo-transpiration according to Penman (1948)	mm	
T	Air temperature	ºC	
T_s	Temperature of soil layer s	ºC	
$FPAR_i$	Fraction of photosynthetically active radiation (PAR) for cohort i	[0-1]	
$[CO_2]$	Air carbon dioxide concentration	ppm	
VPD	Vapor pressure deficit	kPa	
$E_{max,stand}$	Maximum daily stand transpiration	l·m⁻²	basic
$E_{max,stand(i)}$	Maximum daily stand transpiration according to species of cohort i	l·m⁻²·d⁻¹	basic
a_{Tmax}, b_{Tmax}	Species-specific parameters relating LAI with the ratio $E_{max,stand(i)}$/PET		basic
$E_{max,i}$	Maximum daily transpiration for plant cohort i	l·m⁻²·d⁻¹	basic
E_i	Actual daily transpiration for plant cohort i	l·m⁻²·d⁻¹	
$A_{g,i}$	Daily gross photosynthesis of plant cohort i	g C·m⁻²·d⁻¹	
NPP	Annual net primary production	g C·m⁻²·yr⁻¹	
$\Psi_{extract}$	Plant water potential corresponding to 50% of transpiration	MPa	basic
Ψ_{critic}	Plant water potential corresponding to 50% of cavitation	MPa	basic
Ψ_{plant}	Plant water potential	MPa	basic
Ψ_{leaf}	Leaf water potential	MPa	advanced
Ψ_{stem}	Stem water potential	MPa	advanced
Ψ_s	Water potential in soil layer s	MPa	
PLC	Proportion of stem xylem conductance lost due to cavitation	[0-1]	
WUE_{max}	Water use efficiency assuming no light, water or CO₂ limitations	g C·l⁻¹	basic
WUE_{PAR}, WUE_{CO2}, WUE_{VPD}	Coefficients regulating the dependency of WUE on light availability, CO₂ concentration and VPD		basic
$r_{cell}(\Psi, T)$	Relative cell expansion rate, depending on water potential (Ψ) and temperature (T)		
$r_{cellmax}$	Maximum relative cell expansion rate (at T = 30ºC and Ψ = 0)		
$RER_{sapwood}$	Sapwood (parenchima) maintenance cost per dry mass unit	g gluc·g dry⁻¹·d⁻¹	
$RGR_{leafmax}$	Maximum daily leaf area growth rate per unit sapwood area	m²·cm⁻²·d⁻¹	
$RGR_{cambiummmax}$	Maximum daily (tree) sapwood area growth rate per unit cambium length	cm²·cm⁻¹·d⁻¹	
$RGR_{sapwoodmax}$	Maximum daily (shrub) sapwood area growth rate per unit sapwood area	cm²·cm⁻²·d⁻¹	
$RGR_{finerootmax}$	Maximum daily fine root biomass relative growth rate	g dry·g dry⁻¹·d⁻¹	

$SR_{sapwood}$	Daily relative rate of sapwood area senescence at 25ºC	cm²·cm⁻²·d⁻¹
$SR_{fineroot}$	Daily relative rate of fine root biomass senescence at 25ºC	g dry·g dry⁻¹·d⁻¹
ΔLA_{growth}	Daily leaf area increase due to growth	m²·d⁻¹
ΔSA_{growth}	Daily sapwood area increase due to growth	cm²·d⁻¹
$\Delta SA_{senescence}$	Daily sapwood area decrease due to senescence	cm²·d⁻¹
$\Delta FRB_{growth,s}$	Daily increase in fine root biomass in soil layer s due to growth	g dry·d⁻¹
$\Delta FRB_{senescence,s}$	Daily decrease in fine root biomass in soil layer s due to senescence	g dry·d⁻¹
$RSSG$	Minimum relative storage for sapwood growth	[0-1]

140 **Table 1**: Description and units of input variables, state variables and model parameters mentioned in the text and in Appendix C. Column 'sub-model' indicates when a given state variable or parameter is specific to one of the two sub-models. A complete list of model parameter definitions and units is given in Table B1.

145 **Fig. 1**: MEDFATE (ver. 2.8.1) model processes, with their temporal resolution, and user-level R simulation functions.

2.1. Transpiration, photosynthesis and drought impacts in the basic sub-model

The basic sub-model was first described in (De Cáceres et al., 2015), but has recently undergone modifications that are detailed in Appendix C.1. All processes are represented at daily time steps. Extinction of short-wave radiation and photosynthetically-active radiation through the canopy follows Beer-Lambert's equation. The model first derives a separate

150   estimate of whole-stand maximum transpiration – i.e. before accounting for soil water deficit – for each taxon present, which accounts for atmospheric evaporative demand and requires two taxon-specific parameters (see eq. (C.2)). Actual cohort transpiration depends on stand's maximum transpiration calculated for the corresponding taxon and the fraction of short-wave radiation absorbed by the plant cohort (Korol et al., 1995). It also depends on the vertical distribution of its fine roots, soil moisture and $\Psi_{extract}$, a taxon-specific parameter indicating the soil water potential corresponding to 50% of maximum

155   transpiration (De Cáceres et al., 2015). The sub-model also simulates hydraulic redistribution of water among soil layers via circulation through plant roots (Neumann and Cardon, 2012). The sub-model assumes a linear relationship between plant transpiration and gross photosynthesis, but accounts for the dependency of water use efficiency on the fraction of photosynthetically-active radiation, air CO_2 concentration and vapor pressure deficit. Overall, the estimation of gross photosynthesis requires four taxon-specific coefficients (see eq. (C.3)). Plant water status is represented by a plant water

160   potential, Ψ_{plant}, calculated as an "average" of soil water potential in the rhizosphere. The sub-model keeps track of drought legacies using *PLC*, the proportion of conductance lost due to stem cavitation. Increases in *PLC* occur whenever Ψ_{plant} decreases, following a whole-plant vulnerability curve described by a single taxon-specific parameter, Ψ_{critic}. *PLC* limits actual transpiration rates and does not decrease following increases in Ψ_{plant}. Cavitation effects can only be reversed (i.e. *PLC* decreased) via new sapwood formation (Choat et al., 2018).

165   *2.2. Transpiration, photosynthesis and drought impacts under the advanced sub-model*

The advanced sub-model simulates radiation balance, canopy, soil and leaf energy balances, plant hydraulics, stomatal regulation and photosynthesis at hourly time steps. We provide a brief description here, but a more complete description can be found in De Cáceres et al. (2021). Radiation balance and sunlit/shade leaf energy balance are estimated assuming a multi-layer canopy (Anten and Bastiaans, 2016), but canopy energy balance equations are evaluated assuming a single layer that

170   exchanges energy with the atmosphere and the soil (Best et al., 2011). The 'supply function' approach of (Sperry and Love, 2015) is used to model the relationship between steady-state instantaneous water flow and water status along the soil-plant-atmosphere hydraulic network, which includes rhizosphere, root, stem and leaf segments (Sperry et al., 1998). The advanced sub-model, thus, requires parameters describing maximum hydraulic conductance and hydraulic vulnerability curves for these three plant segments. Gross photosynthesis is approximated following the sunlit/shade model of De Pury and Farquhar

175   (1997), which requires estimates for the usual photosynthetic parameters, namely, the maximum Rubisco carboxylation rate and the maximum electron transport rate, which are considered taxon-specific. Stomatal regulation follows the "profit maximization" approach of Sperry et al. (2017), where an optimum stomatal conductance is determined by comparing the risks associated to hydraulic damage against photosynthetic gains, subject to the limits imposed by minimum and maximum

stomatal conductance. Hydraulic redistribution of soil water is an emergent outcome in the advanced sub-model, derived
from its formulation of plant hydraulics. Like the basic sub-model, the advanced sub-model keeps track of drought legacy
effects through their cumulative effects on stem *PLC*, which feed-backs on stem vulnerability curves and, as before, its
effects are only reversed via sapwood area growth.

2.3. C pools and labile C balance

Three different carbon compartments are represented in MEDFATE: *leaves*, *sapwood* – which includes stem, branches and
coarse roots – and *fine roots*. We differentiate two main forms of C pools, *structural* and *labile*. Structural C corresponds to
membranes, walls, and the cytosolic organelles of living cells, whereas labile C occurs in leaves and sapwood compartments
only, and it is divided between *metabolic* and *storage* (Richardson et al., 2013; Dietze et al., 2014). Metabolic C is assumed
to correspond to dissolved sugars (e.g., glucose or fructose) that are used to directly sustain cell functioning, whereas storage
C is assumed to correspond to starch. We chose this design because structural growth and photosynthesis are frequently
uncoupled (Dietze et al., 2014; Fatichi et al., 2014; Cabon et al., 2022), which points to the need to include storage
compartments when modeling tree growth at daily to seasonal resolution (Richardson et al., 2013; Jones et al., 2020).

Initial values of leaf structural C are obtained dividing leaf area by specific leaf area, whereas sapwood structural C depends
on sapwood area, plant height, coarse root length and wood density. Finally, fine root structural C is estimated assuming a
constant relationship between leaf area and fine root area. Leaf/sapwood C storage capacity is determined by tissue volume
and density, assuming that a maximum of 50% of cell volume is available for starch accumulation. Sapwood storage
conforms the largest C pool, depending on sapwood volume and the fraction of sapwood corresponding to xylem
parenchyma.

The balance of leaf labile C includes gross photosynthesis, leaf maintenance respiration, sugar-starch conversion and phloem
transport processes. Sapwood labile C balance includes phloem transport, sugar-starch conversion, maintenance respiration
of sapwood and fine roots, growth costs, senescence and root exudation. Sapwood maintenance applies to the xylem
parenchyma only, because dead xylem conduits are assumed to be inexpensive. Maintenance respiration rates per dry mass
unit are estimated from nitrogen content in the case of leaves and fine roots (Reich et al., 2008), but not for sapwood because
of the lower knowledge in the factors affecting wood respiration, which results in a species-specific parameter ($RER_{sapwood}$) to
be calibrated. Maintenance respiration is temperature-dependent and is subtracted from metabolic C pools, whereas C used
for growth is withdrawn from sapwood storage C pool. Storage accumulation is considered a passive consequence of sugar-
starch dynamics and reduced C use by other sinks (Palacio et al., 2014; Le Roux et al., 2001). Sugar-starch dynamics are
modeled with the aim to maintain a constant metabolic C concentration in leaves and sapwood tissues, whereas phloem
transport decreases leaf-vs-sapwood differences in sugar concentration. Root exudation is not modeled as an active process
competing for metabolic C, but a consequence of plant C storage capacity being surpassed (Prescott et al., 2020) (but see
Williams and de Vries, 2020), which can happen when temperature or plant water status limit growth more than

photosynthesis. During leaf senescence, labile C pools are recycled and relocated to sapwood storage. Analogously, when sapwood is converted into heartwood, labile C in the protoplasm of parenchyma cells is assumed to be re-absorbed by neighboring living cells as storage.

2.4. Growth and senescence

215   In many mechanistic dynamic vegetation models growth is proportional to the amount of C fixed by photosynthesis or is determined from the difference of photosynthesis and respiration (Körner, 2015; Fatichi et al., 2019). Following the C sink limitation hypothesis, which posits that for trees growing under environmental constraints direct restrictions on tissue formation can occur before any C shortage comes into play (Körner, 2003), formation of new plant tissues in MEDFATE also considers biophysical constraints on plant tissue expansion (Schiestl-Aalto et al., 2015; Lempereur et al., 2015; Hayat et

220   al., 2017; Potkay et al., 2021; Eckes-Shephard et al., 2021). Specifically, temperature and turgor limitations on cell expansion are implemented following Cabon et al. (2020a, b) Although these authors developed their approach for tracheid production and enlargement and we apply it to model growth in all kinds of tissues.

A leaf phenology sub-model controls the duration of phenophases corresponding to budburst, leaf development and senescence (Chuine et al., 2013; Delpierre et al., 2009). During bud formation periods, the model updates the maximum leaf

225   area that can be achieved, as the product of current sapwood area and a target leaf area to sapwood area ratio, following the pipe model (Shinozaki et al., 1964). Assuming no allocation or C limitations, daily leaf area increase due to growth is estimated using:

$$\Delta LA_{growth} = SA \cdot RGR_{leafmax} \cdot \frac{r_{cell}(\Psi_{leaf}, T)}{r_{cellmax}}$$ (1)

where $RGR_{leafmax}$ is the maximum daily leaf area growth rate per unit sapwood area, r_{cell} is the relative cell expansion rate,

230   depending on leaf water potential (Ψ_{leaf}) and temperature (T) (Cabon et al., 2020a), and $r_{cellmax}$ is a reference cell expansion rate at T = 30ºC and Ψ_{leaf} = 0. Leaf senescence occurs due to leaf aging in evergreen species, programmed leaf senescence in deciduous species or as defoliation triggered by cavitation (i.e. following increases in *PLC*).

The maximum fine root biomass that a given individual can have depends on its leaf area target, the root area to leaf area ratio and specific root surface area. Thus, fine root biomass is constrained by allocation parameters in a similar way as leaf

235   area. Assuming no allocation or C limitations, daily fine root biomass increment in a given soil layer s ($\Delta FRB_{growth,s}$) is modeled analogously to eq. (1):

$$\Delta FRB_{growth,s} = FRB_s \cdot RGR_{finerootmax} \cdot \frac{r_{cell}(\Psi_s, T_s)}{r_{cellmax}}$$ (2)

where FRB_s is the current fine root biomass in layer s, $RGR_{finerootmax}$ is the maximum daily relative growth rate for fine roots, and r_{cell} depends here on the water potential (Ψ_s) and temperature (T_s) in soil layer s. Fine root senescence is estimated

240   assuming a linear temperature dependence:

$$\Delta FRB_{senescence,s} = FRB_s \cdot SR_{fineroot} \cdot \frac{max(T_s - 5, 0)}{20} \tag{3}$$

where $SR_{fineroot}$ is the daily relative rate of fine root senescence at 25 ºC.

Unlike leaves and fine roots, formation of new sapwood area is not constrained by allocation parameters. On the contrary, sapwood growth and senescence are the processes that constrain the target biomass of the other organs. This lack of an

245   explicit allocation rule does not imply continuous sapwood growth, because it is regulated by sink limitations and two additional constraints: First, formation of sapwood area can only occur if unfolded leaves are present, assuming that hormonal signals controlling cambium division and sapwood development are mainly synthesized within leaves. Second, sapwood formation does not occur if C storage levels are below a given threshold, so that the maintenance of metabolic functioning and replacement of leaves/fine roots are prioritized over plant growth whenever C storage levels are low

250   (Martínez-Vilalta et al., 2016), helping to maintain a safety margin against the risk of carbon starvation (Huang et al., 2019). This threshold is specified in relative terms via species parameter $RSSG$, the minimum relative starch for sapwood growth. Assuming the former two constraints do not operate, daily sapwood area increases (ΔSA_{growth}) are modeled analogously to the other tissues:

$$\Delta SA_{growth} = \pi \cdot DBH \cdot RGR_{cambiummax} \cdot \frac{r_{cell}(\Psi_{stem}, T)}{r_{cellmax}} \text{ for tree cohorts, and} \tag{4a}$$

255    $$\Delta SA_{growth} = SA \cdot RGR_{sapwoodmax} \cdot \frac{r_{cell}(\Psi_{stem}, T)}{r_{cellmax}} \text{ for shrub cohorts,} \tag{4b}$$

where DBH is the current diameter at breast height (for a tree cohort), SA is the current sapwood area (for a shrub cohort), r_{cell} now depends on stem water potential (Ψ_{stem}) and temperature (T), $RGR_{cambiummax}$ is the maximum daily growth rate relative to the current cambium perimeter and $RGR_{sapwoodmax}$ is the maximum daily growth rate relative to the current area of sapwood (note that diameter is not available in multi-stemmed shrubs). Unlike other models where height-to-diameter variations arise

260   from an explicit regulation of the activity of apical and lateral (i.e. cambium) meristems (e.g., Hayat et al., 2017), in MEDFATE tree height increases are estimated as function of diameter increases and a variable height-to-diameter ratio depending on $FPAR$ (Rasche et al., 2012).

Sapwood area senescence (i.e., conversion to heartwood) is assumed to occur with aging, although evidence points towards a plant-controlled developmental process (Spicer, 2005). Most process-based forest models assume a fixed rate of sapwood

265 turnover (Collalti et al., 2020). Like in eq. (3), we assume the rate of conversion to heartwood is faster under warmer

conditions and, similarly to 3-PG (Landsberg and Waring, 1997), we assume that the relative turnover rate of sapwood is

smallest for young plants, and it progressively increases with size:

$$\Delta SA_{senescence} = SA \cdot \frac{SR_{sapwood}}{1 + 15 \cdot e^{-H}} \cdot \frac{max(T - 5, 0)}{20} \tag{5}$$

where $SR_{sapwood}$ is the daily rate of sapwood conversion to heartwood at 25 ºC and H is plant height (m).

270 When using the advanced sub-model, leaf, stem and soil water balances provide the water status for eqs. (1)-(5); while the

soil and canopy energy balances provide temperature values. Leaf and sapwood area changes feedback on maximum stem

hydraulic conductance and fine root biomass changes feedback on rhizosphere conductance. Moreover, recovery from stem

embolism is assumed to be the result of new xylem formation (Choat et al., 2018; Rehschuh et al., 2020). Specifically,

formation of new sapwood reduces the proportion of conductance loss (*PLC*) between time steps t and t+1:

275 $$PLC_{t+1} = min\left[PLC_t - \frac{\Delta SA_{growth}}{SA}, 0\right] \tag{6}$$

When using the basic sub-model, it is assumed that $T_s = T$ and $\Psi_s = \Psi_{stem} = \Psi_{leaf} = \Psi_{plant}$. In this case, changes in sapwood

area affect maximum transpiration rates per unit of leaf area via reduction of *PLC* only.

2.5. Mortality and recruitment

Dynamic vegetation models implement mortality in very different ways, from purely-empirical to mechanistic approaches

280 (Hawkes, 2000; Keane et al., 2001; Bugmann et al., 2019). In MEDFATE, woody plants are assumed to die at a constant

basal rate due to processes not explicitly included in the model (e.g. biotic attacks or windstorms), but mortality rates

increase whenever physiological stress thresholds presumed to lead to plant mortality are surpassed (McDowell et al., 2022).

The model allows plants to die explicitly from either *starvation* (if metabolic carbon is exhausted) or *desiccation* (extreme

tissue dehydration) (McDowell et al., 2008, 2011). Starvation is assumed to occur whenever the size of the sapwood

285 metabolic C pool decreases below 30% of its maximum value (Martínez-Vilalta et al., 2016). Plant desiccation occurs when

stem symplastic relative water content decreases below 30% (Mantova et al., 2021; Kursar et al., 2009). Although the two

thresholds are applied independently, the associated processes are strongly coupled, because water potential decreases cause

stomatal closure and cavitation-induced defoliation, both reducing carbon assimilation and, conversely, reduced carbon

storage impacts the capacity of plants to produce new tissues and, hence, recover hydraulic conductance and normal gas

290 exchange rates (McDowell et al., 2022).

Although recruitment is known to be the result of a number of processes (flowering and pollination, fruit/seed production, dispersal, storage, seed predation, germination, seedling establishment and survival until the sapling stage), but they are challenging to include in models (Price et al., 2001; König et al., 2022). Recruitment in MEDFATE is hence modeled using a single aggregated process that estimates the appearance of young plants, as done in other models (Hanbury-Brown et al.,

295 2022). Dispersal is not considered and local seed production is considered as a binary process, where plants are considered fertile and able to produce viable seeds if they reach a given taxon-specific height (different for shrubs and trees). Recruitment of species with available seeds is further constrained by three species-specific thresholds (minimum temperature, maximum aridity and minimum *FPAR*) that are used to determine whether recruitment (actually, ingrowth into an initial plant size) is possible, similarly to FORCLIM (Bugmann, 1996). A constant probability of recruitment determines

300 actual recruitment within these bioclimatic limits.

3. Study area, forest, soil and historic weather data

Our target region for parameter estimation, model evaluation and application was Catalonia (32,108 km^2, NE Spain). Most of the region has a Mediterranean climate, with hot and dry summers, but it includes a strong climatic variation due to its complex relief. Mean annual temperature ranges between 3 ºC and +17 ºC (average +12.3 ºC) and annual rainfall ranges

305 between 344 and 1587 mm (average 684 mm). Abandonment of rural areas during the second half of the 20th century led to a remarkable increase in the area covered by forests. Nowadays, forests cover around 47% of Catalonia and keep increasing in density and wood volume stock. Among forested areas, 52% are dominated by conifers, 36% by broadleaves, and 13% are considered mixed forests (Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente, 2017).

Three different surveys of Spanish National Forest Inventory (SNFI) are available for the region (SNFI2, 1989-1991; SNFI3,

310 2000-2001; and SNFI4, 2013-2016). These were conducted using a systematic sampling scheme, with 11,314 plots in SNFI3 (average density of 1 plot/km^2) and 5,500 plots in SNFI4 (0.5 plot/km^2). Plot sampling involves a variable radius with circular nested subplots, where trees of different diameter classes are identified to the species level and their DBH and height is measured. Shrub sampling consists in determining mean height and percent cover by species. Since field soil data is absent in forest inventory plots, soil physical properties (texture, bulk density, organic matter content) corresponding to plot

315 locations were drawn from the global database SoilGrids (Hengl et al., 2017), complemented by rock fragment content estimates derived from surface stoniness measurements during SNFI surveys. Soil water retention and conductivity curves followed the van Genuchten (1980) model, with parameters estimated following Tóth et al. (2015). Historical daily weather data used for parameter estimation and model evaluation exercises was obtained via interpolation of weather records from Catalan and Spanish surface station networks on forest plot locations using the R package 'meteoland' (De Cáceres et al.,

320 2018).

4. Parameter estimation

We reduced the tree and shrub species classification codes included in the SNFI to 217 taxon entities. 144 taxa were at the species level, whereas 73 were aggregated at the genus level based on their frequency and the availability of species-specific data. Upper taxonomic levels (genus, family, order) were filled using R package 'taxize' (Chamberlain and Szocs, 2013).

325   MEDFATE (ver. 2.8.1) requires taxon-specific estimates for 117 different parameters (including qualitative variables and allometric coefficients) to be run. The different procedures employed for parameter estimation are summarized in Table 2.a and are detailed in the following subsections. Table B1 includes the strategy used to estimate taxon values for each parameter. The final taxon parameter estimates are given in Table B3.

a) Estimation procedures	Num. Params.	%
Forest Inventory Data (section 4.1)	12	10.3%
Plant trait databases (section 4.2)	49	41.9%
Allometry databases (section 4.2)	19	16.2%
Meta-modelling exercise (section 4.3)	6	5.1%
Calibration exercise (section 4.4)	3	2.6%
None (always requiring imputation)	28	23.9%
b) Imputation procedures (section 4.5)	**Num. Params.**	**%**
Quantitative trait relationship	17	14.5%
Qualitative trait relationship	31	26.5%
Family means / Qualitative trait relationship	4	3.4%
Family means / Default value	11	9.4%
Default value	44	37.6%
None (completely specified from databases)	10	8.5%

Table 2: Summary of procedures used for taxon parameter estimation (a) and imputation of missing values (b). The number
330   of parameters are indicated as well as the percentage with respect to the 117 parameters in MEDFATE.

4.1 Parameter estimates obtained from forest inventory data

We used SNFI data from the whole Spanish territory to find suitable values for twelve parameters. A number of quantitative traits, such as maximum and median plant heights and tree diameter-height relationships under shade/sunlit conditions, were directly calculated from SNFI shrub/tree records (Morin et al., 2021). We also used permanent forest inventory plot data
335   (SNFI2-3 and SNFI3-4) to estimate tree mortality and recruitment parameters. Initial values for basal mortality rates were estimated using observed tree mortality rates in permanent inventory plots, excluding those where management effects (i.e. stumps) were detected. Since the model incorporates mortality due to carbon starvation and desiccation explicitly, using observed mortality rates as basal rates leads to overestimation of mortality. Following preliminary tests, we defined tree basal mortality rates for all species as one third of observed mortality rates. We then manually modified basal mortality rates
340   for the main tree species to obtain an acceptable bias in basal area mortality predictions when evaluating the model at the regional level (see section 5.1). To obtain suitable recruitment parameter estimates we first calculated three bioclimatic

variables (minimum monthly temperature, moisture index and ground *FPAR*) for each forest plot. For tree taxa, we fitted a non-linear model by maximum likelihood for the probability of ingrowth into the $7.5 < DBH < 12.5$ cm class between inventory surveys based on plots where the species was present in the initial survey. For shrub taxa, bioclimatic limits were

345   determined using 1% percentiles of the same bioclimatic variables among those plots where the species was found and we assumed a constant 5% probability of annual recruitment within these limits.

4.2 Parameter estimates obtained from allometric and plant trait databases

We used available allometric relationships for shrub/tree leaf biomass and crown base height assembled from multiple sources (Hasenauer, 1997; Burriel et al. 2004; De Cáceres et al., 2019) to populate 19 (16%) of model parameters. In turn, 49

350   (42%) model parameters were mapped to plant trait definitions from existing plant trait databases (see Table B1). Among those, 23 (47%) model parameters were matched to plant traits drawn from TRY public data sets (ver 5.0; https://www.try-db.org/) (Kattge et al., 2020). TRY data sets were complemented with additional data bases, global analysis papers and personal compilations for phenology, anatomy and morphology (Tavşanoğlu and Pausas, 2018; Zanne et al., 2009; Morris et al., 2016), plant hydraulics (Mencuccini et al., 2019; Sanchez-Martinez et al., 2020; Martin-StPaul et al., 2017; Choat et al.,

355   2012), tissue water content (Bartlett et al., 2012) and stomatal or cuticular conductance (Hoshika et al., 2018; Duursma et al., 2018) (see Table B.2). Transpiration and photosynthesis functions of the advanced sub-model were readily parameterizable with measured traits, although hydraulic parameters were often missing for leaf and root segments. In the case of the basic sub-model, $\Psi_{extract}$ was estimated from the water potential at turgor loss point and Ψ_{critic} was estimated from the water potential corresponding to 50% stem PLC, but six other parameters regulating transpiration and photosynthesis (eqs. (C.2)

360   and (C.3)) could not be matched to plant traits.

Most plant traits were mapped directly, sometimes requiring homogenizing measurement units, whereas others required the use of transforming functions. For example, *RGGS* was estimated by monotonically re-scaling an ordinal (0-5) shade tolerance index (Niinemets and Valladares, 2006) to a proportion [0-1], assuming that a higher degree of shade tolerance implied a stronger prioritization of leave/fine root maintenance over stem growth. Parameters for plant taxa were estimated

365   using species-level averages or genus-level averages (for genus taxa or when the target species was not found in the data base).

4.3 Estimation of transpiration and photosynthesis parameters of the basic sub-model

As indicated above, six key parameters regulating transpiration and photosynthesis in the basic sub-model (eqs. (C.2) and (C.3)) could not be estimated from plant trait databases. With the aim make transpiration, gross photosynthesis and growth

370   predictions obtained by the basic sub-model as similar as possible to those produced by the advanced sub-model, we conducted a meta-modelling exercise in which the results of simulations with the advanced sub-model were used to provide estimates for the six parameters of the basic sub-model. The meta-modelling exercise was conducted separately for each of

twelve prioritized species on the basis of their importance in the study area. These were *Pinus halepensis* Mill. (Aleppo pine), *Pinus nigra* spp. *salzmannii* J. F. Arnold (black pine), *Pinus sylvestris* L. (Scots pine), *Pinus pinea* L. (stone pine),

375 *Pinus uncinata* Ramond ex *A. DC.* (mountain pine), *Fagus sylvatica* L. (European beech), *Abies alba* (white fir), *Quercus ilex* L. (holm oak), *Quercus faginea* Lam. (Portuguese oak), *Quercus pubescens* Mill. (downy oak) and *Quercus suber* (cork oak), which altogether represent 87% of the total number of stems (Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente, 2017). Details of the procedure and results are provided in Appendix C.2. The same exercise could in principle be conducted on the remaining target taxa, provided confidence exists on the estimates of transpiration and photosynthesis

380 parameters of the advanced sub-model for those taxa.

4.4 Calibration of sapwood respiration, growth and senescence parameters

We conducted calibration exercises to obtain suitable estimates for three key parameters regulating sapwood respiration, growth and senescence. Given the large amount sapwood biomass in trees, the daily maintenance respiration rate of sapwood parenchyma ($RER_{sapwood}$) is an important parameter determining C availability for growth. Maximum daily sapwood growth

385 rates relative to cambium perimeter ($RGR_{cambiummax}$) represents optimum growth rates and, since leaf and fine root allocation targets depend on sapwood area, it determines whole-tree growth rates. Finally, daily sapwood senescence rate ($SR_{sapwood}$) defines the rate of sapwood-to-heartwood conversion and contributes to modulate sapwood biomass and its maintenance costs. Parameters regulating the maximum growth rates leaves and fine roots were deemed less important, given the allocation constraints to the formation of these organs. Tree ring data has been previously used for the calibration of growth

390 parameters in other models (Fyllas et al., 2017), so we adopted the same approach. The tree ring data set used for the calibration exercise was sampled in 75 SNFI plots, located in pure stands whose dominant species are *F. sylvatica*, *P. halepensis*, *P. nigra*, *P. sylvestris* or *Q. pubescens*, and selected to encompass a range of climatic aridity (Rosas et al., 2019). We took annual basal area increments of each tree as the observations to be matched by model predictions of sapwood growth. Simulations of the calibration exercise were performed using the basic sub-model only, for computational reasons.

395 Further details of the calibration procedure and results are given in Appendix C.3. We did not found any significant relationship between calibrated estimates and species identity for $RGR_{cambiummax}$, $SR_{sapwood}$ and $RER_{sapwood}$. In contrast, plots where the target species grew faster resulted in larger calibrated values of $RGR_{cambiummax}$ and $SR_{sapwood}$, indicating faster sapwood area dynamics (Table C4). This result allowed us to devise a strategy to obtain estimates of these two parameters for all tree species. Assuming that the $RGR_{cambiummax}$ and $SR_{sapwood}$ should scale proportionally to observed growth rates, we

400 fitted a regression through the origin for the observed relationship between observed mean annual relative growth rates and each of these parameters (Fig. 2a-b). We then estimated mean annual growth rates relative to cambium perimeter for all tree species using re-measured tree records in SNFI permanent plots (by solving for the annual rate leading to the observed diameter increment between consecutive surveys). We obtained estimates of $RGR_{cambiummax}$ and $SR_{sapwood}$ for all tree taxa by

using the calculated mean annual relative growth rates as input in the fitted linear models, whereas we took the average of
405 calibrated $RER_{sapwood}$ values as default for all taxa.

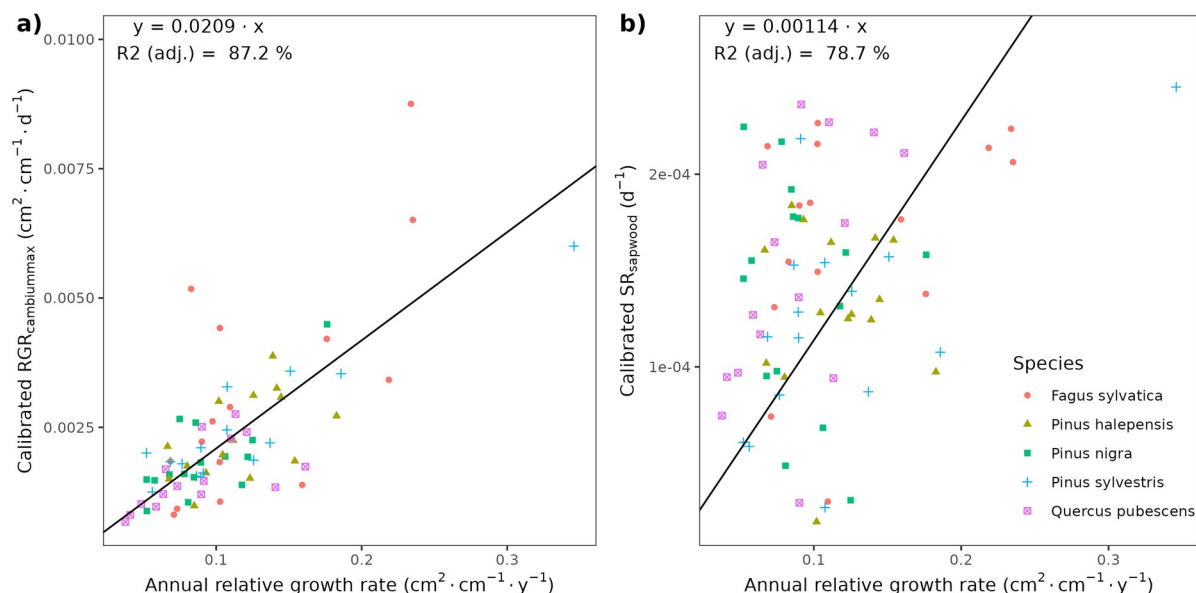



Fig. 2. Linear relationships, fitted using regression through the origin, between observed mean annual relative growth rates
in calibration plots and calibrated $RGR_{cambiummax}$ values (a) or calibrated $SR_{sapwood}$ values (b). Symbols represent individual
forest plots. Note that adjusted R^2 values of regressions through the origin cannot be compared to those of ordinary linear
410 regression models.

4.5 Inbuilt parameter estimation procedures

Altogether, the previous estimation procedures provided suitable values for 89 parameters, still leaving 28 (24%) model
parameters to be populated (Table 2). Moreover, only for 10 (8.5%) parameters estimates were obtained for all 217 taxa.
Therefore, large amounts of missing values remained after previous estimation procedures (Tables B1 and B3). Different
415 imputation strategies were adopted to address this issue (Table 2.b; Table B1). Trait-trait relationships are frequently
employed for parameter estimation, most often following functional syndromes (Maréchaux and Chave, 2017; Sakschewski
et al., 2015). Following this strategy, we defined trait-to-trait mappings between parameters with low missing rates and
parameters with higher missing rates (see Fig. A1). Quantitative trait-trait relationships were adopted for 17 (15%) of
parameters, on the basis of functional spectra, mainly to estimate parameters of hydraulic conductivity curves, pressure-
420 volume curves, photosynthetic parameters and tissue respiration rates. Relationships with qualitative traits were adopted to
populate 31 (26.5%) quantitative parameters, with average values for combinations of leaf shape, life size and/or life form
being frequently used as source for the estimation of other parameters. For 15 (13%) parameters we estimated family-level
averages, but combined this strategy with other imputation strategies whenever family-level values are missing. Finally, we
provided single value defaults for 44 (38%) parameters where we felt that taxonomic resolution was not critical. Among

425 them, 13 parameters had not been estimated by any procedure and, therefore, can be considered as constants in the current model version. Instead of filling imputed values in the taxon parameter table, we implemented inbuilt parameter imputation procedures within MEDFATE initialization routines.

5. Evaluation and application at the regional level

5.1 Evaluation with SNFI data

430 While complex models can be applied to a range of purposes, model suitability should be assessed with respect to intended application (Planque et al., 2022). Our aim to use MEDFATE to project forest dynamics at the regional level required evaluating the capacity of the model to reproduce observed changes in forest dynamics. We therefore compared simulated forest dynamics between the third and fourth surveys of the SNFI in Catalonia against observations from repeated SNFI plots. Specifically, we selected 2,949 permanent plots (between SNFI3 and SNFI4) without signs of recent management and

435 avoiding large decreases in stand basal area, which could indicate the effect of disturbances. Both the basic and advanced sub-models were tested, taking 5h and 120h of computation on 20 parallel threads, respectively. Evaluation focused on predictions of: (a) changes in stand basal area due to growth of surviving trees; (b) stand basal area losses due to tree mortality; (c) stand basal area increases due to recruitment (ingrowth) into the first diameter class (ingrowth into large size classes can occur in the observed data due to the variable radius sampling, but these are not included); and (d) overall

440 changes in stand basal area (this is growth + ingrowth - mortality). With the aim to compare the performance of MEDFATE with that of an empirical alternative, we took an Integral Projection Model (IPM) calibrated using SNFI data for the whole of Spain and evaluated its predictive performance over the same target region. Unlike matrix-based models, the Integral Projection Model (IPM) methodology does not classify the population of trees into discrete stage classes. Rather, each tree population is described by a continuous distribution as a function of a continuous variable like size (Easterling et al., 2000).

445 A brief description of the IPM implemented in this work is given in Appendix C.4. For further details, see García Callejas et al. (2017).

Overall changes in stand basal area had a mean bias of +0.4 $m^2 \cdot ha^{-1}$ (+7.5%) for the basic sub-model, and +0.9 $m^2 \cdot ha^{-1}$ (+17.4%) for the advanced sub-model, whereas the empirical IPM over the same region had a mean bias of +0.7 $m^2 \cdot ha^{-1}$ (+11.1%) (Table 3). RMSE was 4.9 $m^2 \cdot ha^{-1}$ (95%) for the basic sub-model and 5.0 $m^2 \cdot ha^{-1}$ (97%) for the advanced sub-

450 model. These average error rates were higher than the 4.8 $m^2 \cdot ha^{-1}$ (82%) of IPM, reflecting a slightly lower prediction capacity of MEDFATE at the plot level. When inspecting the error distribution of overall basal area change predictions we a small tendency to over-predict basal area changes for stands with large initial basal area and to under-predict them for stands cold areas (Figs. A.2 and A.3). Predicted stand basal area increments due to growth had a larger positive bias when using the advanced sub-model than when using the basic sub-model and, conversely, basal area reductions due to mortality had a more

455 negative bias, which explains the larger positive bias for overall basal area changes (Table 3). Despite having larger biases,

the advanced sub-model yielded more accurate predictions of mortality than the basic sub-model. Both sub-models produced a ~25% overestimation of ingrowth.

	Sub-model	Mean observed ($m^2 \cdot ha^{-1}$)	Mean predicted ($m^2 \cdot ha^{-1}$)	Bias ($m^2 \cdot ha^{-1}$)	Bias (%)	RMSE ($m^2 \cdot ha^{-1}$)	RMSE (%)	R^2
BA increment for surviving trees	basic	4.896	4.972	+0.077	+1.6	3.474	70.9	0.30
	advanced	4.936	5.435	+0.364	+7.37	3.942	79.9	0.28
BA corresponding to tree mortality	basic	0.966	0.938	-0.028	-2.9	2.534	262.3	0.03
	advanced	0.967	0.754	-0.212	-21.9	1.576	163.0	0.10
BA corresponding to ingrowth	basic	1.263	1.551	+0.287	+22.7	2.455	194.4	0.008
	advanced	1.260	1.592	+0.332	+26.4	2.562	203.5	0.003
Overall changes in stand BA	basic	5.193	5.585	+0.391	+7.5	4.915	94.6	0.11
	advanced	5.229	6.138	+0.909	+17.4	5.056	96.7	0.13
Overall changes in stand BA (IPM)		5.895	6.552	+0.656	+11.1	4.806	81.5	0.26

Table 3: Results of model evaluation at the regional level in terms of basal area (BA) changes predicted for different processes and overall stand changes. The last row presents the results of an evaluation over the target region of an Integral Projection Model (IPM) calibrated using SNFI data. Bias % and RMSE % result from expressing mean bias and root mean squared error (RMSE) as percentage of the mean observed value. While overall changes in BA are the sum independent processes in the evaluation of MEDFATE, the evaluation of IPM predictions was conducted between the original and final states. This fact, and the variable-radius sampling of SNFI, explain the slightly higher mean observed BA value for IPM.

5.2 Application

To illustrate the potential of the fully-parameterized model to project future forest functioning and dynamics at the regional level, we took all forest plots surveyed in Catalonia during SNFI3 (yr. ~ 2000) and projected them for the 21st century. We took interpolated historical records for the 2001-2020 period and climate projections for the 2021-2100 period, corresponding to the 5th phase of the Coupled Model Intercomparison project (CMIP5) under Representative Concentration Pathways (RCPs) 4.5 and 8.5. We obtained daily weather projections from the EURO-CORDEX project (Kotlarski et al., 2014), corresponding to a single global/regional climate model couple (i.e. MPI-ESM/RCA4), which has been deemed appropriate to describe future climate change in Catalonia (Altava-Ortiz and Barrera-Escoda, 2020). Since the spatial resolution of climate model predictions was 0.1º (~ 9km), we used empirical quantile mapping to bias-correct and downscale weather to the forest plot scale, taking interpolated historical records (1976-2005 period) as reference data (De Cáceres et al., 2018). Annual [CO_2] series under RCP 4.5 and RCP 8.5 scenarios were obtained from Meinshausen et al (2011). A climate scenario assuming constant climate (No CC) was also evaluated for comparison with RCP scenarios, by repeating historical 2001-2020 weather over the century and assuming [CO_2] = 386 ppm. Forest management and natural disturbances such as wildfires or biotic attacks were not considered for simplicity. MEDFATE runs were conducted using the basic sub-model,

which nevertheless required 72h of computation on 20 parallel threads to process each scenario (we estimate 1728h would be required with the advanced model).

480   Climate projections for Catalonia include a steady increase in temperature (+3.5ºC under RCP8.5) and, while much more uncertain, a 40% reduction in annual precipitation during the second half of the 21st century under RCP 8.5 (Fig. 3a) (Altava-Ortiz and Barrera-Escoda, 2020). Despite these trends, the most important regional-level pattern predicted the model was a steady increase in wood volume stock throughout the century under all three scenarios and for all the main species (Figs. 4d and A.4). This is largely because most forests in Catalonia are relatively young as a consequence of abandonment of

485   agricultural lands and reduction of forest management during the second half of the 20th century (Vilà-Cabrera et al., 2017). Net primary production (*NPP*) was always positive (Fig. 3b), but decreased steadily along the century under a stable climate due to the increase in respiration costs needed to sustain an increasing forest biomass. Under two climate change scenarios, however, the progressive increase in temperatures and air [CO_2] resulted in higher *NPP* and slightly larger timber accumulation during the central part of the 21st century, compared to predictions under stable climate. The continuation of

490   ongoing forest densification caused *LAI* to increase asymptotically under stable climate (Fig. 3c). Nevertheless, strong decreases in *NPP* and *LAI* were predicted between 2070 and 2100 under RCP 8.5, as a result of years with very low rainfall which, together with the increased VPD, caused widespread drought-induced defoliation. Increased mortality rates were also predicted under RCP 8.5 for this last period, as shown by the lower rates of wood volume stock accumulation (Figs. 3d and A.4).

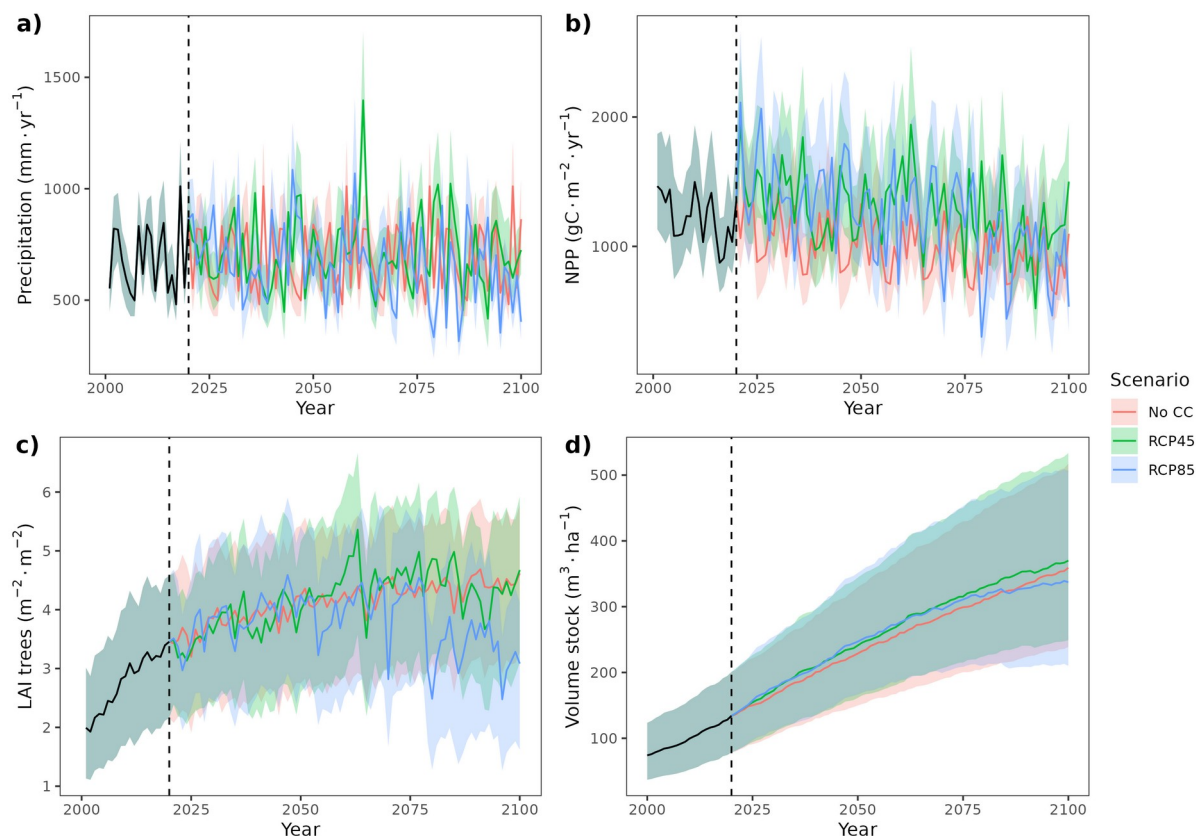



Fig. 3. Precipitation input (a) and model predictions regarding net primary production (b), canopy leaf area index (c) and wood volume stock (d) under a scenario without climate change (No CC) and two climate change scenarios (RCP4.5 and RCP8.5) in Catalan forests. Results for period 2000-2020 correspond to historic climate. Continuous lines correspond to median values and shaded areas indicate the 25%-75% quantile range, all of them estimated across all forest plots. Results of regional levels of timber stock by species are shown in Fig. A4, and a comparison of projected wood volume between MEDFATE and IPM is given in Fig. A.5.

6. Discussion

6.1 Accounting for functional diversity in regional-level forest models

Species-specific parameter estimation in complex dynamic vegetation models is often done by focusing on one species at a time (e.g., Davi and Cailleret, 2017; Guillemot et al., 2017), but this becomes impractical when the number of taxonomic entities increases. Resorting on plant trait databases and forest inventory data facilitates dealing with functional diversity, but our experience shows that it has its own challenges. First, this strategy becomes more useful the larger the fraction of taxon-specific parameters that can be conceptually matched to observable traits, which needs to be accounted during model design and formulation. In other words, the model should be 'trait-enabled'. The design of MEDFATE allowed us to match up to 49 parameters with functional trait definitions (50% of parameters if we exclude allometric coefficients). Even in 'trait-enabled'

models there will always be parameters that are not observable or are only seldom measured, even for the most common species, which requires adopting alternative parameter estimation procedures. For regional applications, structural (e.g. maximum size) and demographic parameters (e.g. recruitment and mortality rates) can often be empirically estimated using forest inventory data (Morin et al., 2021). Calibration of key, but non-observable, parameters using observations on

515   particular stands is another alternative. For example, we used calibration and tree ring series in 75 SNFI plots to address the estimation of growth/senescence parameters. However, if this approach is followed there is always the possibility that taxon-average estimates across calibration plots produce biased predictions in the application at the regional level. Moreover, it is unlikely to have the appropriate calibration data (e.g. tree ring series) for all woody taxa occurring in the target region. We circumvented these problems by fitting a relationship between calibrated growth or senescence rates ($RGR_{cambiummax}$ and

520     $SR_{sapwood}$) and observed annual growth rates relative to cambium perimeter, which can be empirically estimated using resampled plot data for all species included in the forest inventory. Another alternative estimation procedure that we adopted to populate non-observable key parameters was meta-modeling. Computational limitations of the "advanced" sub-model for regional applications led us to conduct improvements in the "basic" sub-model, including increased sensitivity to environmental variables, and a meta-modeling exercise to obtain estimates for non-observable transpiration and

525   photosynthesis parameters for the "basic" sub-model. This estimation procedure can be applied to any taxon, but requires confidence on the trait parameter estimates of the model used as reference (here, the "advanced" sub-model), which we partially got from stand-level evaluation exercises (De Cáceres et al., 2021). Developers should always avoid manual tuning, due to its non-reproducibility, and it is a slow process for multiple taxa. We only resorted on this procedure for baseline mortality rates, forced by the mixture of mechanistic and empirical design in mortality modeling, although we acknowledge

530   that calibration exercises could be used instead (e.g. Hartig et al., 2012).

Another important limitation when estimating parameters for multiple taxa is, obviously, plant trait data availability. Even though plant trait databases continue to increase in size (Kattge et al., 2020), the finer the taxonomic resolution is, the less information is available, which leads to a trade-off between the taxonomic resolution in the model entities vs. the amount of missing parameter values in the final parameter table. When parsing trait databases we took both species- or genus-level

535   averages as valid estimates to reduce the frequency of missing values in the parameter table, but this entails a potential loss of accuracy at the species level. Regardless of this decision, and no matter how much effort is put in parameter estimation procedures, parameter imputation will always be needed to fill information gaps in models representing multiple taxa. We recommend implementing imputation procedures in initialization routines, keeping them separated from taxon parameter tables because the large number of missing values in the table reveals information gaps to be addressed with additional data

540   gathering. A range of parameter imputation procedures are possible for observable traits. Models often use quantitative-quantitative trait relationships from functional syndromes and averages across levels of qualitative traits to obtain suitable species parameter estimates (Thonicke et al., 2020; Sakschewski et al., 2015). Assuming taxonomic families bear a trait phylogenetic signal, we complemented the information provided by functional covariation with family-level averages

(Anderegg et al., 2022), but more sophisticated phylogenetically-informed approaches would also be possible (Sanchez-
545 Martinez et al., 2020). Note that models can also use known relationships between measured traits and demographic rates for
the imputation of the latter, as between wood density and mortality rates (Fyllas et al., 2017; Thonicke et al., 2020). In our
opinion more research is needed around the imputation procedures to fill missing taxon parameter values. For example,
future research could evaluate the phylogenetic signal of multiple traits; or compare the relative performance of different
imputation alternatives, analogously to the comparison of alternative biomass allometries (Ameztegui et al., 2022); or
550 evaluate the loss of accuracy of model predictions caused by imputations. In the same way that there are databases of
biomass or volume allometric relationships, the development of databases documenting bi- or multivariate trait relationships
and their domain of application could help modelers to implement sound imputation strategies.

We addressed specific- and supra-specific trait variability in our study, but did not consider intra-specific variability, which
can account to 25% of overall phenotypic variation (Funk et al., 2017; Siefert et al., 2015). Berzaghi et al. (2020) describe
555 three main strategies to accounting for intra-specific trait variability in vegetation models, among-which the first two could
be combined with our parameter estimation approach. First, prescribed (i.e. non-plastic) intra-specific trait variation may be
approximated in models using within-species environmental-trait relationships or trait coordination (Rosas et al., 2019;
Poyatos et al., 2007). To implement this strategy, intra-specific functional trait databases are needed, but are presently scarce
(López et al., 2021). These relationships may be implemented as inbuilt estimation rules to be applied at the time of
560 initialization. Second, intra-specific can be considered in vegetation models by dynamically changing parameter values (e.g.
photosynthesis) depending on transient environmental conditions (i.e. nitrogen content, average temperature or light
availability) (Prentice et al., 2014; Crous et al., 2022). This strategy can also be combined with our parameter estimation
approach, but requires implementing equations internally, while acknowledging trade-offs between traits and limits to
phenotypic plasticity. Finally, trait inheritance and hence eco-evolutionary dynamics can be simulated (Oddou-Muratorio
565 and Davi, 2014), but we estimate this approach computationally too demanding for regional-level applications.

6.2 Reproducibility and transferability of parameter estimation strategies

Given the iterative nature of model development, taxon-specific model parameters need to be re-estimated (and model
performance re-evaluated) in many situations, such as whenever the design or mathematical formulation of the model is
modified; taxonomic entities are redefined; updates of existing trait data sources occur. Unlike models developed for single
570 or few species, parameter re-estimation for multiple-taxa requires that procedures be reproducible and automated. All the
procedures mentioned in the previous section, except manual tuning, are reproducible and were repeated several times during
the development of MEDFATE. The code to implement parameter estimation and evaluation procedures should be
continuously integrated into workflows coupled to modeling development cycles, in the same way as model evaluation
procedures for all the key outputs related to the most important applications. In our opinion, this aspect of trait-enabled

575   model development deserves more attention and should be one of the focus of collaboration efforts between modelers, with the long-term aim of achieving community modeling cyber-infrastructures (Fer et al., 2021).

Another practical issue is the transferability of parameter estimates and estimation procedures, initially developed for a given trait-enabled model and region, to new target regions and/or other models. Even though intra-taxon variability is neglected, taxon-average estimates derived from global plant trait databases are, in principle, as valid for a given region as they are for

580   other regions. Moreover, trait-enabled forest models could share databases of taxon-based parameter estimates thanks to parameter definitions being matched to the same measurable entities. Being derived from global data, imputation procedures based on among-species trait coordination or family-level averages should be equally valid in different regions. Procedures for extracting taxon-specific parameter estimates from (global) trait databases can also be used for new taxa or other models, which points to the possibility of sharing these procedures among developers, although the information available will differ

585   widely depending on the target region. In contrast, empirical parameters obtained from forest inventory data are unlikely to be valid in different areas (Thonicke et al., 2020), and the procedures to derive them may need to be tailored to idiosyncratic aspects of national forest inventories (plot spatial arrangement and temporal replication, taxonomic treatment, field sampling protocols), unless harmonized forest inventory data is used. Calibration and meta-analyses procedures, or relationships between growth/senescence parameters and observed annual relative growth rates, can be applied to other target regions but

590   they are specific to MEDFATE.

6.3 The value of trait-enabled models for the projection of forest dynamics at the regional level

Mechanistic models are often regarded as having a larger degree of uncertainty than empirical models – due to their larger number of parameters (Adams et al., 2013), but mechanistic models of vegetation dynamics can achieve good performance when calibrated for specific stands and parameter estimates are carefully chosen for target species (de Wergifosse et al.,

595   2022; Forrester et al., 2021). In the case of mechanistic trait-enabled models, one can expect substantial biases with respect to the prediction forest dynamics because key parameters of demographic processes are unlikely to be matched by observable database traits. In contrast, we achieved a small bias in overall basal area changes by introducing key empirical elements in the model design and parameter estimation – annual relative growth rates, mortality rates, bioclimatic limits and probabilities of ingrowth –, all of them from SNFI data. The relatively small bias increases our confidence on MEDFATE

600   for applications like projecting regional standing timber volume, at the cost of requiring empirical inventory data for its application in other regions. Indeed, the projected changes in wood volume stocks are similar for simulations with the Integral Projection Model (IPM) and MEDFATE (see Fig. A5). The accuracy of MEDFATE was somewhat lower than that of the IPM over Catalonia, but similar to that reported in Trasobares et al. (2022) for an empirical forest projection system developed for the whole Spanish territory. A number of factors can increase model errors at the stand level. The use of a

605   global soil product for soil properties, as opposed to regional data sources, and the lack for information on rock content and the topographic context of forest plots surely contributes to larger errors. The fact that rock fragment content estimates

obtained in the calibration exercise were different across species (Fig. C3.d and Table C4) is an indication of the importance of these factors for accurate growth (and mortality) predictions. We did not account for spatial variation in nutrient availability either, which is known to influence growth rates. At present, MEDFATE is fairly unbalanced in the detail

610   accorded to water, carbon and growth processes, with respect to mortality and recruitment. The approach taken to model baseline mortality rates and ingrowth was even simpler than many forest gap models (Bugmann and Seidl, n.d.), which may explain the poor results regarding those processes and points to future development efforts. For example, mortality predictions could be improved by fitting more complex empirical models that account for tree size or recent growth (Vanoni et al., 2019). However, this equations are difficult to parameterize in a model that also includes explicit mortality

615   mechanisms based on water and carbon levels (i.e. dessication and carbon starvation). Mechanistic modelling of drought-induced mortality is an active field of research (Venturas et al., 2020; Liu et al., 2021; Trugman et al., 2021; McDowell et al., 2022), but important developments are still required to address multiple interactions between drivers. In our opinion, hybrid mechanistic and empirical approaches are thus needed to produce unbiased predictions of tree mortality currently. Recruitment prediction could benefit from considering additional refinements, such as accounting for resprouting capacity or

620   mechanistically dealing with seedling and sapling mortality (König et al., 2022), at the potential cost of increasing the number of non-observable model parameters.

In addition to the comparison with empirical models, it is also interesting to discuss the differences between MEDFATE simulations conducted using the basic vs. advanced sub-models. Mechanistic models are expected to perform under novel environmental conditions, due to their ability to separate the causal effect of different climatic variables. MEDFATE with the

625   advanced sub-model is clearly a better choice than with the basic sub-model in this respect, but the advanced sub-model is still computationally very demanding for large-scale application. Like other models before (e.g., Landsberg and Sands, 2011), the modifications made to the basic, yet faster, sub-model show that it is possible to design and parameterize simpler approaches while fully retaining the ecophysiological responsiveness to key climate change variables such as [CO_2] or *VPD*. However, further work would be necessary to compare the performance of the two sub-models in terms of key stand-level *E*,

630   *GPP* or *NPP* fluxes under different conditions. In terms of forest dynamics, the advanced sub-model produced more biased growth estimates than the basic sub-model, but yielded more accurate mortality predictions. We attribute this different performance to the fact that calibration of growth parameters was conducted using the basic sub-model, and to differences in the predictions of soil moisture and plant water status yielded by the two sub-models. Although conducted using the basic sub-model, we have illustrated in our application that a trait-enabled model with hybrid model design allows the projection

635   of structural variables of interest for forest management planning (such as basal area, density or volume stock per tree species) as well as variables directly related to ecosystem function (such as *LAI*, *E*, *GPP* or *NPP*). This advantage comes at the cost of large parametrization efforts, like the one conducted here. Nevertheless, both parameter estimation procedures and the resulting taxon-estimates estimates can be profited by developers of other models having similar parameter

definitions. For all these reasons, in our opinion population-structured trait-enabled models such as MEDFATE may have an

640   important role to play for predictions of forest function and dynamics at regional scales.

7. Conclusion

Here we presented the design, parameter estimation and evaluation of MEDFATE, coupled to forest inventory data, for its

application at the regional level in Catalonia. Our model is similar to many forest gap models in terms of its representation of

population structure, but it has a higher degree of detail in the representation of water and carbon processes, an hybrid design

645   shared with other models (Fisher et al., 2018; Liu et al., 2021). Models that are similar to MEDFATE have been previously

developed to simulate regional forest dynamics in the Mediterranean Basin (Fyllas et al., 2007; Mouillot et al., 2001; Fyllas

and Troumbis, 2009). However, the detail on plant hydraulics of the advanced sub-model is similar to more specialized

models focusing on drought-induced plant dessication (Cochard et al., 2021; Ruffault et al., 2022). MEDFATE has some

unique features (i.e. the link between xylem cavitation and leaf defoliation, together with the need to build new sapwood

650   tissue to recover water transport capacity) that make it suitable to study drought legacy effects. Overall, we think MEDFATE

can be an attractive tool to study forest function and dynamics under increasing water limitations, such as those of

Mediterranean climate. Besides the value of the model, we illustrated the process of determining parameter estimates for a

large number of taxa in trait-enabled models by extensively using plant trait databases. Hence, our efforts allow illustrating

challenges that arise when adopting this approach and provide potential strategies to address them, which can be useful for

655   the parametrization of other trait-enabled models.

Appendix A: Supplementary Figures

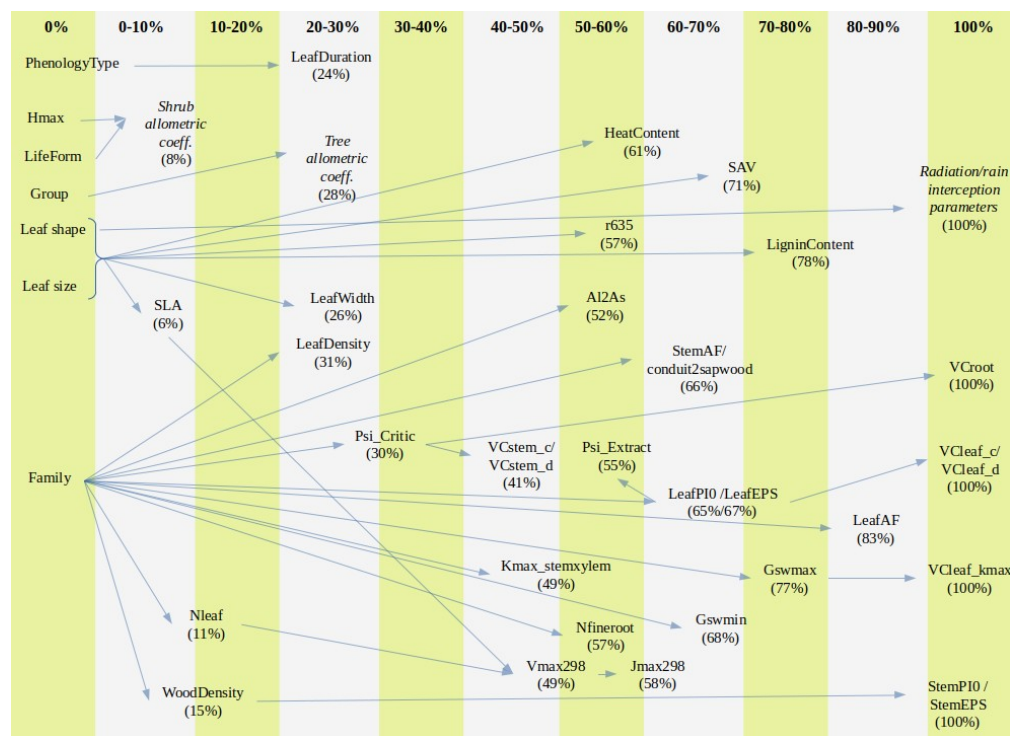
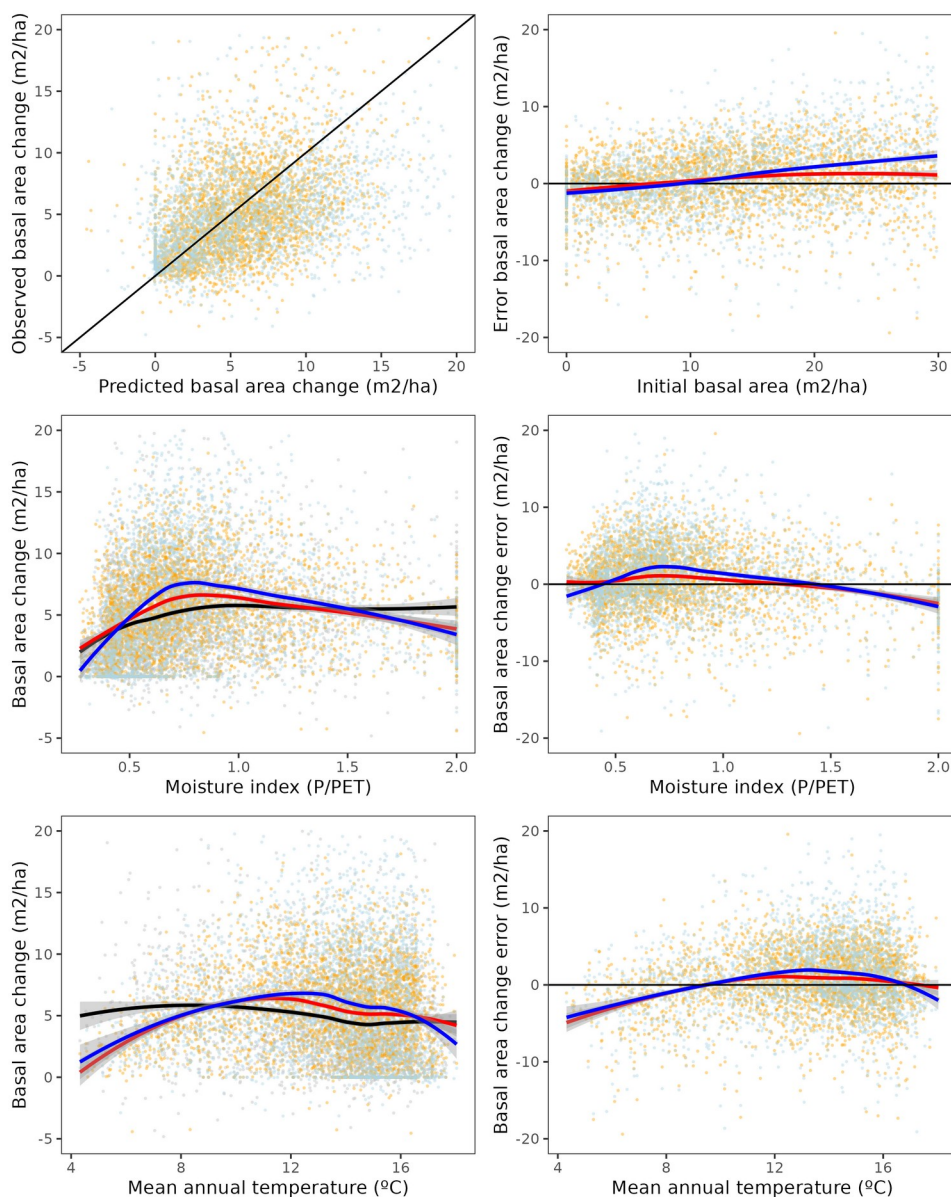



Fig. A1. Percentage of missing values for model parameters across species and parameter relationship (arrow) from which imputation is performed (trait-trait quantitative relationship, averages for combinations of categorical traits or imputation from family means). Parameters that are given constant values when missing are not shown. Definition of parameters is given in Table B1.

665 **Fig. A2**. Comparison of predicted vs observed overall basal area changes and the distribution of model errors depending on initial basal area, moisture index and mean annual temperature. Gray dots and black lines correspond to observations; orange dots and red lines to predictions with the basic sub-model; and light blue dots and blue lines to predictions with the advanced sub-model.

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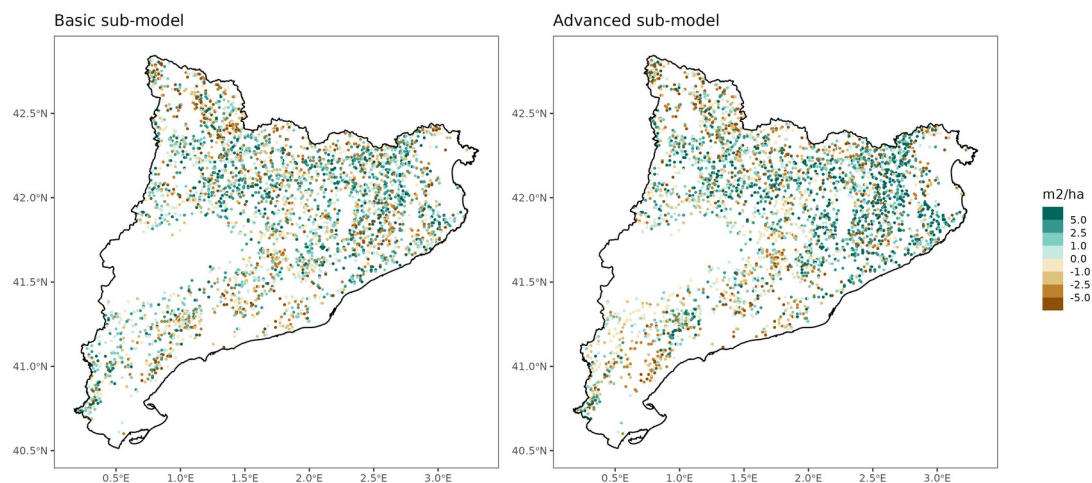
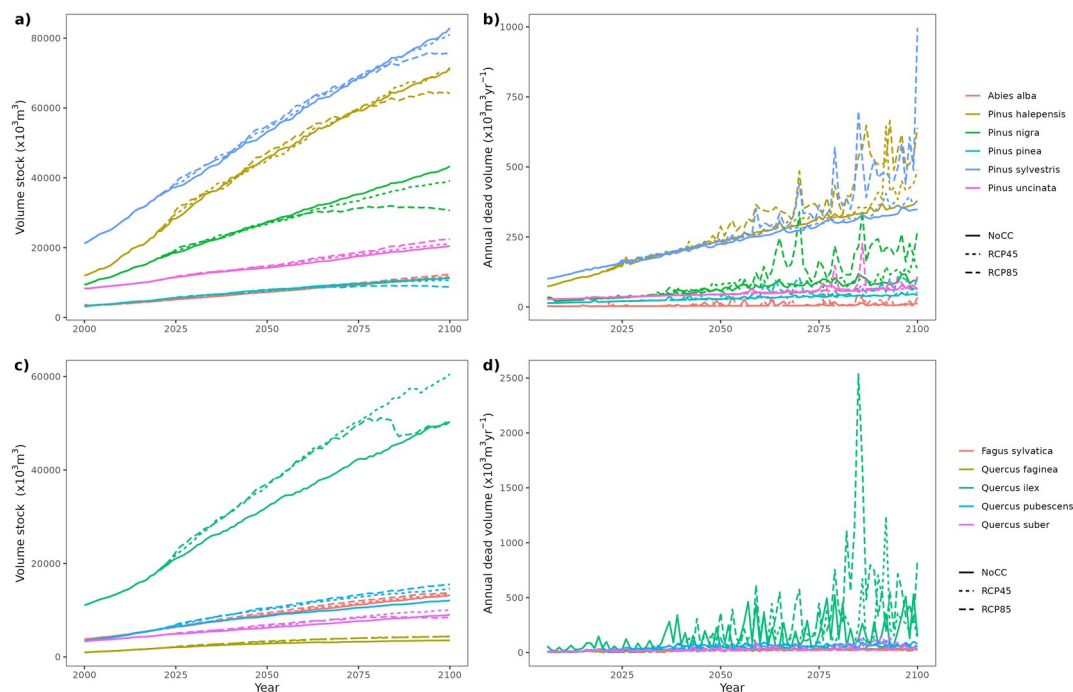

670 **Fig. A3**. Spatial distribution of prediction errors in overall basal area changes for simulations using the basic sub-model (left) or the advanced sub-model (right).

675
Fig. A4. Regional-level timber accumulation (left panels) and annual mortality loss (right panels) predicted by MEDFATE under a scenario of constant climate (No CC) and two climate change scenarios (RCP4.5 and RCP8.5) for the ten main tree species in Catalonia, grouped into conifer (upper panels) and broad-leaf species (lower panels). Results for period 2000-2020 correspond to historic climate.

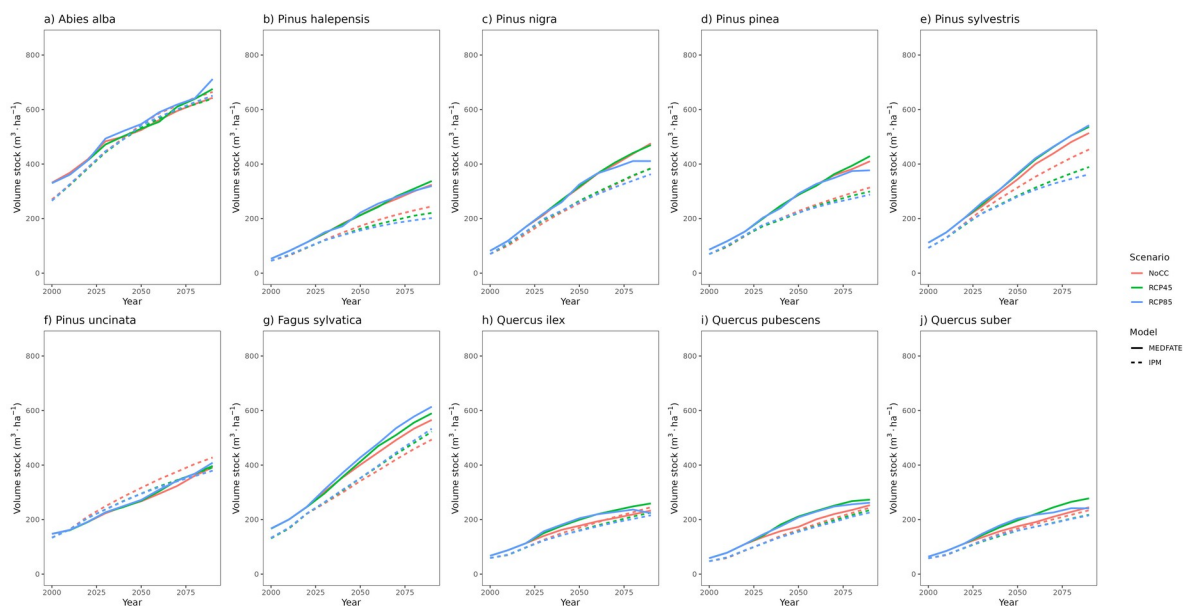



Fig. A5. Comparison of the wood volume stock predicted by the Integral Projection Model (IPM) and MEDFATE under a scenario of constant climate (No CC) and two climate change scenarios (RCP4.5 and RCP8.5) for the ten main tree species in Catalonia. Continuous lines correspond to median values and shaded areas indicate the 25%-75% quantile range, estimated across all forest plots. Volumes correspond to the average across forest plots where the species occurs and are indicated in 10 yr-steps because IPM has this temporal resolution.

Appendix B: Supplementary Tables

Supplementary file: 'Appendix_B_SupplementaryTables.xlsx'

Appendix C: Details of the design of the basic sub-model and parameter estimation procedures

All mathematical symbols used here are described in Table 1 of the main text. Parameter definitions and units are given in Table B1.

C.1 Transpiration and photosynthesis in the basic sub-model

We describe here the modifications of transpiration and photosynthesis processes included in recent versions of the sub-model, with respect to the description given in De Cáceres et al. (2015). Radiation extinction, transpiration and photosynthesis processes are represented at a daily time-scale in the basic sub-model. Extinction of short-wave radiation (SWR) and photosynthetically-active radiation (PAR) through the canopy follows Beer-Lambert's equation. Maximum transpiration – i.e. before accounting for soil water deficit – for the whole stand ($E_{max, stand}$) is estimated using daily Penman's potential evapotranspiration (PET) and an empirical relationship developed by Granier et al. (1999):

$$\frac{E_{max,stand}}{PET} = 0.036 + 0.134 \cdot LAI - 0.006 \cdot LAI^2 \tag{C.1}$$

where LAI is the leaf area index of the stand. While Granier et al. (1999) estimated the coefficients of the eq. (C.1) by pooling empirical data from different forest stands, species differ in the relationship between leaf area and maximum transpiration. Hence, we modified the estimation of $E_{max, stand}$ implemented in the original sub-model (De Cáceres et al., 2015) as follows. If one neglects the intercept (so that transpiration is zero for a bare stand) and assumes that all leaf area of a stand corresponds to a single cohort i, eq. (C.1) becomes:

$$\frac{E_{max,stand(i)}}{PET} = a_{Tmax} \cdot LAI + b_{Tmax} \cdot LAI^2 \tag{C.2}$$

where a_{Tmax} and b_{Tmax} are species-specific parameters for cohort i. Assuming that reasonable species-specific estimates are available for a_{Tmax} and b_{Tmax}, eq. (C.2) can be used to estimate $E_{max,stand(i)}$, the maximum stand transpiration if dominated by the species of cohort i. Once $E_{max,stand(i)}$ has been estimated for each species in the stand, the fraction of SWR absorbed by a given cohort i is used to estimate its maximum transpiration ($E_{max,i}$) from $E_{max,stand(i)}$ (Korol et al., 1995). Actual cohort transpiration (E_i) is a function of $E_{max,i}$, the vertical distribution of its fine roots, soil layer moisture and $\Psi_{extract}$, a species-specific parameter indicating the soil water potential corresponding to 50% of maximum transpiration (De Cáceres et al., 2015). In contrast with the original formulation of the basic sub-model, actual transpiration does not decrease to zero under drought conditions, since water losses can still occur via leaf cuticular conductance and incomplete stomatal closure (Duursma et al., 2018).

The basic sub-model assumes a linear relationship between plant transpiration and gross photosynthesis. However, it accounts for the dependency of water use efficiency on light availability, air CO_2 concentration ($[CO_2]$) and vapor pressure deficit (VPD):

$$A_{g,i} = E_i \cdot WUE_{max} \cdot f_1(FPAR_i) \cdot f_2(CO_2) \cdot f_3(VPD), \text{ with}$$

$$f_1\big(FPAR_i\big) = FPAR_i^{WUE_{PAR}}, f_2\big(CO_2\big) = 1 - e^{-WUE_{CO2} \cdot [CO_2]}, f_3\big(VPD\big) = VPD^{WUE_{VPD}}. \tag{C.3}$$

720 where $FPAR_i$ is the fraction of PAR at the mid-crown level of cohort i; and WUE_{PAR}, WUE_{CO2} and WUE_{VPD} are empirical parameters modulating WUE depending on environmental conditions, i.e. $FPAR$, $[CO_2]$ and VPD, respectively. Given the formulation of eq. (C.3), WUE_{max} is interpreted as the water use efficiency of the species at VPD = 1kPa and without air $[CO_2]$ or light limitations to photosynthesis.

C.2 Details of the estimation of transpiration and photosynthesis parameters of the basic sub-model

725 The six key parameters regulating transpiration (a_{Tmax}, b_{Tmax}; eq. (C.2)) and photosynthesis (WUE_{max}, WUE_{PAR}, WUE_{CO2} and WUE_{VPD}; eq. (C.3)) in the basic sub-model cannot be estimated from plant trait databases. Assuming transpiration (E) and gross photosynthesis (A_g) predictions of the advanced sub-model are more accurate, we adopted a meta-modelling approach make A_g predictions obtained by the basic sub-model as similar as possible to those produced by the advanced sub-model (both for present-day and projected climate). For each target species, we first revised the parameters of the advanced sub-

730 model that regulated plant transpiration and photosynthesis (Table C1):

Species	Gswmin	Gswmax	VCleaf_kmax	VCleaf_c	VCleaf_d	Kmax_stemxylem	VCstem_c	VCstem_d	VCroot_c	VCroot_d	Vmax298	Jmax298
Abies alba	0.004	0.23	6.00			1.30	6.71	-3.93			58.09	103.28
Fagus sylvatica	0.004	0.34	8.00	1.87	-1.74	0.90	7.31	-3.31	1.87	-1.05	94.50	159.90
Pinus halepensis	0.003	0.29	4.00	11.14	-2.38	0.15	12.71	-5.29	11.14	-3.07	72.20	124.17
Pinus nigra	0.003	0.24	5.00	2.24	-2.25	0.41	3.14	-3.37	2.24	-2.16	68.50	118.77
Pinus pinea	0.003	0.24	4.00	11.14	-2.38	0.25	7.11	-4.43	11.14	-3.07	72.42	124.50
Pinus sylvestris	0.003	0.24	5.00	2.45	-2.05	0.45	10.24	-3.20	2.45	-2.08	83.00	143.00
Pinus uncinata	0.003	0.24	5.00	2.45	-2.05	0.69	17.26	-4.27	2.45	-2.08	73.41	125.94
Quercus pubescens	0.004	0.28	6.00	2.18	-2.32	0.70	10.27	-4.98	2.18	-1.37	57.34	102.15
Quercus ilex	0.004	0.20	4.00	1.34	-2.58	0.40	3.56	-7.72	1.34	-2.21	68.52	118.79
Quercus faginea	0.006	0.28	6.00	2.18	-2.32	0.70	3.54	-4.13	2.18	-1.37	71.22	122.74
Quercus suber	0.006	0.29	4.00	1.34	-2.58	0.40	4.97	-5.60	1.34	-2.21	70.28	121.37

Table C1: Revised estimates of the parameters regulating photosynthesis and transpiration in the advanced sub-model, for the set of twelve prioritized species. Parameter definitions and units are provided in Table B1.

After that, we randomly selected up to 60 SNFI3 plots with a minimum stand basal area of 3 m²·ha⁻¹ and where the target species was dominant (> 80% in basal area). Plot records corresponding to species different than the target species were

735 discarded. Using daily weather corresponding to a single year (yr. 2001), we ran the two sub-models with unlimited water supply, so that transpiration and photosynthesis estimates were not affected by soil water deficit. The basic sub-model was run with default values for a_{Tmax} and b_{Tmax}, i.e., using coefficients of eq. (C.1). We found that the cohort's annual $E_{basic}/E_{advanced}$

ratio was rather unaffected by *FPAR*, on average, but we found substantial differences across species in the this ratio (Fig. C1.a). We used the $E_{basic}/E_{advanced}$ ratio, averaged across cohorts and plots, to scale a_{Tmax} and b_{Tmax} for each species with respect

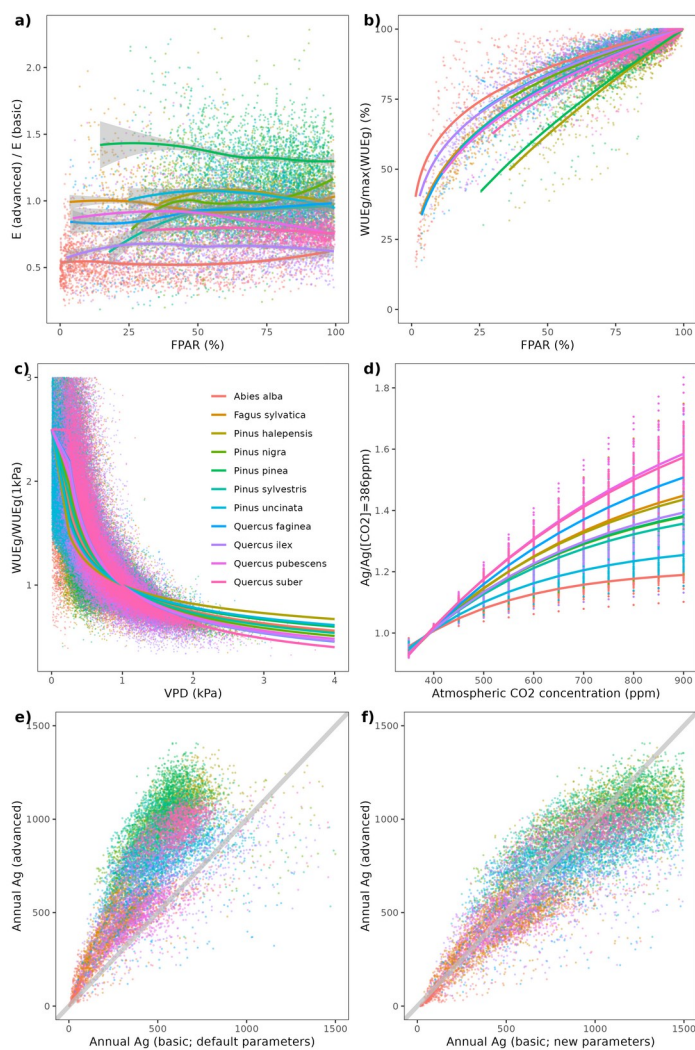
740   to coefficients of eq. (C.1). With the aim to estimate parameter WUE_{PAR}, we began by calculating annual WUE_g (i.e. annual A_g over annual E) for each cohort under the advanced sub-model. We then calculated the ratio between WUE_g of each cohort and the plot's maximum WUE_g value. For each species, we fitted a model of this ratio as a power function of *FPAR*, and took the exponent as estimate of WUE_{PAR} (Fig. C1.b).

745

Fig. C1. (a) Cohort $E_{basic}/E_{advanced}$ values against their available *FPAR*; (b) Annual WUE_g values (relative to the maximum WUE_g value obtained for each plot) against available *FPAR*; (c) Daily WUE_g values (relative to WUE_g at VPD = 1kPa) against *VPD*; (d) Plot-level ratios between gross photosynthesis under increasing $[CO_2]$ values and gross photosynthesis under $[CO_2]$ = 386 ppm; (e-f) Comparison of annual A_g predictions (g C · m^2 · yr^{-1}) obtained by the basic sub-model using

750 the default parameter values (e) and the new parameter values (f), against A_g predictions of the advanced sub-model. Lines of panel (a) correspond to smoothed splines, whereas those of panels (b-d) indicate the models fitted for each species.

We then analyzed the relationship between daily WUE_g values and *VPD* under the advanced sub-model. Specifically, a power relationship was fitted between *VPD* and WUE_g relative to its value at VPD = 1kPa, except for 0 < *VPD* < 0.25 kPa range, where a linear relationship was assumed to avoid unrealistic values (Fig. C1.c). To estimate WUE_{CO2} we conducted

755 additional sets of simulations with the advanced model under increasing values of $[CO_2]$, from 350 to 900 ppm, and fitted

negative exponential models to the ratio between A_g at each given $[CO_2]$ and of A_g under $[CO_2]$ = 386 ppm (Fig. C1.d). Finally, WUE_{max} estimates were obtained by dividing annual A_g estimates over those obtained from the sum of daily E values multiplied by $f_1(FPAR)$, $f_2(VPD)$ and $f_3([CO_2])$ terms of eq. (C.3).

Species	a_{Tmax}	b_{Tmax}	WUE_{max}	WUE_{PAR}	WUE_{CO2}	WUE_{VPD}
Abies alba	0.072	-0.0032	7.80	0.216	0.0044	-0.413
Fagus sylvatica	0.129	-0.0056	7.95	0.320	0.0024	-0.444
Pinus halepensis	0.138	-0.0062	8.53	0.683	0.0025	-0.303
Pinus nigra	0.134	-0.0060	7.48	0.278	0.0028	-0.505
Pinus pinea	0.178	-0.0080	6.71	0.632	0.0028	-0.359
Pinus sylvestris	0.125	-0.0056	7.77	0.321	0.0030	-0.458
Pinus uncinata	0.138	-0.0062	5.56	0.253	0.0038	-0.325
Quercus faginea	0.123	-0.0055	7.91	0.330	0.0021	-0.560
Quercus ilex	0.088	-0.0039	8.60	0.257	0.0027	-0.578
Quercus pubescens	0.114	-0.0051	8.40	0.333	0.0018	-0.520
Quercus suber	0.104	-0.0046	9.98	0.384	0.0019	-0.633

Table C2: Parameter estimates obtained from the meta-modeling exercise, corresponding to equations (C.2) and (C.3), for the twelve prioritized species.

When replacing default parameter values (i.e. coefficients of eq. (C.1), WUE_{max}= 5 and $f_1 = f_2 = f_3 = 1$) by those resulting from the meta-modeling exercise, annual A_g estimates produced by the basic sub-model resembled more closely those produced by the advanced sub-model (Figs. C1.e-f). Final parameter estimates resulting from the meta-modeling exercise are shown in Table C2.

C.3 Details of the calibration of growth and senescence parameters

The tree ring data set used for the calibration exercise was sampled in 75 SNFI plots, located in pure stands whose dominant species are *F. sylvatica*, *P. halepensis*, *P. nigra*, *P. sylvestris* or *Q. pubescens,* and selected to encompass a range of climatic aridity (Rosas et al., 2019). Tree ring series were available for 5 trees per plot, with samples taken in December 2015. More information on tree-ring methods can be found in Serra-Maluquer et al. (2018) and González de Andrés et al (2021). We took annual basal area increments of each tree as the observations to be matched by model predictions of sapwood growth. Simulations were performed using the basic sub-model and daily weather data for each target plot for the 2001 - 2015 period. We calibrated the three target parameters for the dominant species and rock fragment content in each plot using a genetic algorithm implemented in R package 'GA' (Scrucca, 2013). The objective function to be minimized was the average, across cohorts with tree ring data, of the relative mean absolute error resulting from comparing observed and predicted annual *BAI* series. Population size for the genetic algorithm was set to 40 individuals, a maximum of 25 iterations were allowed, and the procedure stopped if the best parameter combination did not change during 5 consecutive iterations. The

distribution of final values of the objective function is shown in Fig. C2. We did not find significant correlations between pairs of calibrated parameters, except for a weak relationship between $SR_{sapwood}$ and rock fragment content (Table C3). Estimates for $RER_{sapwood}$, $RGR_{cambiummax}$ and $SR_{sapwood}$ were not statistically different across species (Table C4; Fig. C3).

780 However, we found the calibrated rock fraction to differ across tree species, indicating differences in soil characteristics of the habitat were the species grow (Fig. C3). With the aim to obtain growth and senescence parameter estimates for all tree species in the region, we examined the relationship between calibrated values and the mean annual growth rates relative to cambium perimeter, a variable that is easy to derive using data from permanent plots. The relationship turned out to be strongly significant for $RGR_{cambiummax}$ and, to a lower extent, for $SR_{sapwood}$ (Table C4).

785

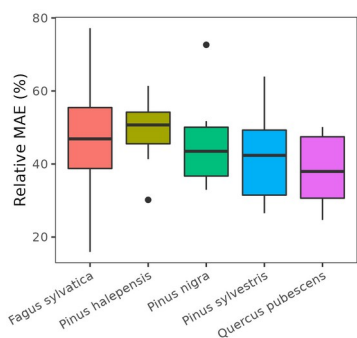



Fig. C2. Distribution of the minimum value of relative mean absolute error (MAE) obtained by calibration against tree ring data for the 15 plots of each species.

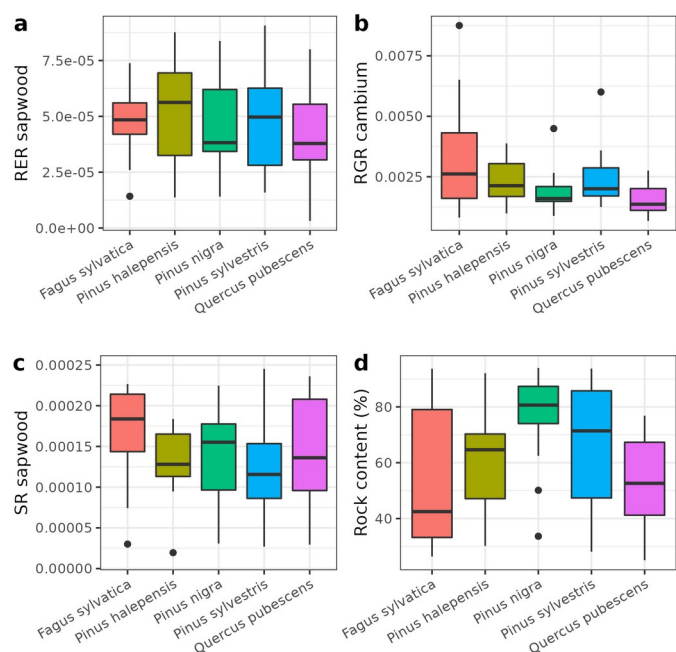



Fig. C3. Distribution of the calibrated parameters across the 15 plots of each species.

Parameter	$RER_{sapwood}$	$RGR_{cambium,max}$	$SR_{sapwood}$	Fraction of rocks
$RER_{sapwood}$		**+0.132**	**+0.084**	**-0.040**
$RGR_{cambium,max}$	*0.259*		**+0.165**	**+0.079**
$SR_{sapwood}$	*0.473*	*0.158*		**-0.289**
Fraction of rocks	*0.735*	*0.502*	*0.012*	

Table C.3: Linear correlation between calibrated parameters across the 75 forest plots. Upper right triangle contains Pearson's r statistics (in bold) and the lower left triangle contains p-values (in italics).

Parameter	Mean annual RGR			Species			Interaction		
	df	F	P-value	df	F	P-value	df	F	P-value
$RER_{sapwood}$	1	1.548	0.218	4	0.280	0.890	4	0.319	0.864
$RGR_{cambium,max}$	1	87.20	**1.26e-13**	4	1.784	0.143	4	1.490	0.216
$SR_{sapwood}$	1	8.260	**0.005**	4	1.579	0.190	4	1.579	0.190
Fraction of rocks	1	1.004	0.320	4	2.776	**0.034**	4	0.652	0.627

Table C.4: Results of an Analysis of Covariance (ANCOVA) for the four calibrated parameters, using the mean annual relative growth rate, species identity and their interaction as tested effects. Significant relationships are highlighted in bold.

C.4 Details of the Integral Projection Model (IPM)

The formulation of the IPM used in this work followed closely that of Easterling et al. (2000) with regard to adult trees, whereas it differed substantially for ingrowth and small trees. Below we will briefly describe the main characteristics of the methodology as we implemented it. For further details, see García-Callejas et al. (2017).

Models were developed for 16 main species and 5 functional types, the latter including species less abundant in the target area. We determined, for each target species or functional type, the number of adult individual trees at a future time $t+\Delta$ from the number of adult individual trees at a previous time t plus tree ingrowth from saplings. In our simulations, time interval $\Delta=10$ years, which approximately corresponded to the mean time difference between SNFI2 and SNFI3.

In the model, the number of adult trees at any time $t+\Delta$, $N_{Adult}(y,t+\Delta)$, was determined by two contributions: a) the dynamics of adult trees that survived and growth from t to $t+\Delta$, and b) the ingrowth of saplings (i.e. DBH < 7.5cm) into the adult tree class:

$$N_{Adult}(y,t+\Delta)=\int N_{Adult}(x,t)\cdot S(x,\ldots)\cdot G(x,y,\ldots)\cdot dx + N_{Ingrowth}(y,t+\Delta) \tag{C.4}$$

Contribution a) is represented by the integral term on the right-hand-side, whereas contribution b) consists of an additional term $N_{Ingrowth}$. In eq. (C.4), variables x and y indicate the DBH of adult trees at t and $t+\Delta$, respectively. Functions

$S(x,\dots)$ and $G(x,y,\dots)$ correspond to tree survival and tree growth, respectively. They were calculated independently for each target tree species or functional type with data from SNFI2 and SNFI3. Their dependence on variables other than DBH (i.e. annual mean temperature, total annual precipitation, anomalies of temperature and precipitation, and basal area of the stand) is expressed in eq.(C.4) with an ellipsis (...).

Tree ingrowth was not included within the IPM integral, unlike the formulation in Easterling et al. (2000), due to limitations imposed by the SNFI sampling methodology. Instead, we assumed that $N_{Ingrowth}$ did not depend on DBH at time t and took it out of the integral. We then expressed it as:

$$N_{Ingrowth}(t+\Delta)=I(\dots)\cdot\varphi(y) \tag{C.5}$$

Here, I indicates the number of new adult trees. It depended on the number of saplings at t, the basal area of the stand and the climatic variables described above, but not on previous size. In turn, term $\varphi(y)$ consisted of a truncated (i.e. $y\geq7.5$ cm) exponential distribution that determined the size distribution of the new cohort of adult trees. Finally, modeling of smaller trees (DBH < 7.5 cm) was carried out by means of a zero-inflated Poisson linear regression with the same predictor variables as I above.

Code availability

Core model functions are coded in C++ and linked to a R user interface. MEDFATE is distributed via the R package 'medfate', which is available at CRAN (https://cran.r-project.org/package=medfate) and GitHub (https://github.com/emf-creaf/medfate). The model code to run MEDFATE (ver. 2.8.1) is available at https://doi.org/10.5281/zenodo.7129635 (De Cáceres et al., 2022).

Data availability

Weather simulation data of simulation model used in this study is available from the EURO-CORDEX initiative at https://www.euro-cordex.net/index.php.en for noncommercial research and educational purposes. Spanish forest inventory data is available at https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/.

Author contributions

MCA designed and implemented the model, with contributions from AC, and led the writing of the manuscript, with input from all authors. RMH conducted model simulations. AC, JMV, MM, NMS, AA, RGV, DNS and SS contributed to model design. All authors read and approved the manuscript.

Competing interests

835   The corresponding author has declared no competing interests.

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