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Unravelling the effect of species mixing on water use and drought stress in Mediterranean forests: A modelling approach

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Understanding how water use and drought stress in woody plants change in relation to compositional, structural and environmental variability of mixed forests is key to understand their functioning and dynamics. Observational and experimental studies have so far shown a complex array of water use and drought stress responses to species mixing, but progress is hampered by the costs of replicating measurements. A complementary approach consists in using in silico experiments with trait-based forest ecosystem models, which have the advantage of allowing the interpretation of the net mixing effect as the result of specific combinations of trait differences. We explore the potential of such an approach using a novel trait-based forest ecosystem model with a strong focus on plant hydraulics and data from 186 mixed forest inventory plots including holm oak (Quercus ilex L.) and eight co-occurring species. Sensitivity analyses focusing on the effect of differences in individual plant traits indicate that water use and summer drought stress of holm oak trees respond primarily to the variation in competitor's height, root distribution and xylem hydraulic efficiency and safety. Simulations of pure and mixed stands across different combinations of climate aridity and stand leaf area index indicate that differences in traits may compensate for one another, so that the influence of a given trait (e.g. tree height) on water use or drought stress can be decreased or offset by the influence of another one (e.g. hydraulic efficiency). Importantly, we show that species mixing does not always have positive effects at the stand level. Overall, our simulation study shows that the complexity of species- and stand-level mixing effects on water use and drought stress arises primarily as the result of differences in key functional traits of the competitor, although stand structure and climate aridity may modulate mixing effects.

1. Introduction

Terrestrial plants lose water when their stomata are opened to acquire CO_2 and need to extract water from the soil to replace the water lost and avoid desiccation. Although water availability is largely determined by abiotic factors such as climate and soil, stand structure also plays a key role in plant water use and drought responses, including drought-induced vegetation mortality (Bradford and Bell, 2017). Interactions among co-occurring plants for the acquisition and use of water resources may be positive under certain situations (Neumann and Cardon, 2012), but they are most often competitive, leading to an increase in water use and a relief in drought stress when competitors are excluded (Giuggiola et al., 2018). Water-related interactions among woody plants are particularly complex in mixed forests, where not only

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stand structure but also species composition plays a relevant role (Forrester and Pretzsch, 2015). Understanding how water use and drought stress of woody plants change in relation to compositional, structural and environmental variability of mixed forests is key to understand their functioning and dynamics, as well as to design appropriate management practices (Grossiord, 2019).

The huge variation of water use and drought response strategies across and within species (Bréda et al., 2006; Brodribb, 2009; Maherali et al., 2004), together with the enormous spatial and temporal variation of water availability, make the study of interactions for water use in mixed forests a challenging task. Plant water use and drought responses are determined by the whole-plant integration of multiple traits including root traits, water transport efficiency and safety (Choat et al., 2018), allocation between transpiring and conducting surfaces (i.e. the Huber value, the ratio of xylem sapwood area to leaf area, Mencuccini et al., 2019b), leaf traits involved in gas exchange (Collatz et al., 1991), water storage (Martin-StPaul et al., 2017) and phenology of fine roots and leaves. Moreover, selective pressures modify traits in a coordinated fashion and hence their variation is often correlated (McCulloh et al., 2019). In mixed forests, differences in the amount and distribution of fine roots imply different access to soil water pools and different levels of drought stress (Jonard et al., 2011; Schume et al., 2004; Zapater et al., 2013), whereas crown height differences may also mediate water interactions by leading to unequal transpiration rates per unit leaf area (Manoli et al., 2017). While trait differences have primarily a phylogenetic origin (Maherali et al., 2004; Sanchez-Martínez et al. 2020), they are modulated by acclimation to local environmental conditions (Limousin et al., 2012, 2010; Martin-StPaul et al., 2013; Ogaya and Peñuelas, 2003) and by plant-to-plant interactions (e.g., changing their rooting patterns under mixtures; Rolo and Moreno, 2012; Schmid and Kazda, 2001; Schume et al., 2004).

Species differences in water use and their responses to drought are often studied by comparing their performance (e.g. growth rate, transpiration rate, water use efficiency or drought stress) in a mixed forest stand where they co-occur (Hölscher et al., 2005; Zapater et al., 2013). However, this comparison does not properly address the effect of species mixing in species- or stand-level functioning. By mixing effect, we refer to any difference in the stand-level performance of mixtures compared with the mean of the corresponding performance of pure stands, or the performance of a given species in a mixture compared to its performance in monoculture (Forrester and Pretzsch, 2015). The empirical study of mixing effects may involve: (i) comparing pure and mixed stands on the same site (Gebauer et al., 2012; Grossiord et al., 2015; Jonard et al., 2011; Schume et al., 2004; Steckel et al., 2020); (ii) comparing alternative mixing treatments in experimental plantations (Bello et al., 2019; Forrester et al., 2010; Kunert et al., 2012); or (iii) comparing sites with different degrees of mixture and environmental conditions (Lebourgeois et al., 2013). Empirical studies have shown that water-related mixing effects are complex and strongly dependent on the species composition, structure and environmental conditions of the target stands (Forrester et al., 2016; Grossiord, 2019). To start with, mixing effects on water use and drought stress can be different at species- and stand levels (Forrester and Pretzsch, 2015). Species mixing has been found to increase stand-level transpiration in plantations, mostly as a result of larger diameters and sapwood areas (Kunert et al., 2012), but studies in natural forests and sapling experiments indicate that increased stand-level transpiration rates are mainly caused by species identity effects (Gebauer et al., 2012; Lübbe et al., 2016). Horizontal heterogeneity in soil moisture has been shown to be larger in mixed than in pure stands; and the effect of mixing on the temporal pattern of soil water depletion and recharge has been reported to be non-additive with respect to that of monospecific stands (Schume et al., 2004). Changes in rooting patterns and/or water uptake profiles under mixtures have been shown to enhance niche complementarity (Bello et al., 2019; del Castillo et al., 2016; Schume et al., 2004), but to have potentially negative effects to cope with summer drought as a result of an accelerated soil water

depletion driven by the more extractive species (Goisser et al., 2016). Clearly, drought sensitivity may be affected by mixing in different ways, depending on the identity of competitors (Grossiord et al., 2015; Jonard et al., 2011). In particular, species with high water use may increase drought stress of co-occurring species during dry years (Gebauer et al., 2012; Grossiord et al., 2013), contrary to the common belief that mixing is beneficial to withstand drought stress (Forrester et al., 2016).

Given the complexity of species mixing effects on water relations and the costs of replication in observational and experimental studies, empirical evidence may be complemented using forest ecosystem models (FEMs), provided they adequately represent the interaction between woody plants for above- and belowground resources (Pretzsch et al., 2017; Rötzer et al., 2017; Simioni et al., 2016). For example, using FEM simulations González de Andrés et al. (2017) found that beech-pine mixtures relieved the strong beech intraspecific competition for water and increased light interception for pines. FEM-based assessments of plant interactions have the great advantage of allowing the evaluation of fully-balanced in silico experiments including multiple species combinations, stand structures and environmental conditions (Forrester et al., 2018; Forrester and Tang, 2015; Morin et al., 2011). Most importantly, when parameterized using measurable traits, FEMs can account for intraspecific trait variability and can be used to analyze the net effect of trait trade-offs and compensations (Christoffersen et al., 2016; Fauset et al., 2019), although parametrizing models to appropriately account for all sources of trait variability remains challenging.

While FEMs have already been used to study water-related interactions between particular species pairs (e.g. González de Andrés et al., 2017), we evaluate here their usefulness to understand water-driven mixing effects on the basis of plant trait differences. Specifically, we use a novel trait-based FEM with a strong emphasis on plant hydraulics to ask: (a) What plant traits are most relevant in determining mixing effects on water use and drought stress? (b) Can the influence of a given trait on the outcome of species mixing be decreased or offset by the influence of another one? (c) To what extent are species- and stand-level mixing effects on water use and drought stress modulated by the forest environmental and structural context? As a case study, we take Mediterranean holm oak (Quercus ilex L.; hereafter QI) forests, where competition for soil water is particularly severe during summer months. We use model sensitivity analyses to determine which plant traits have a stronger influence on water-related interactions between competing species and holm oak. We then evaluate species mixing effects on transpiration, photosynthesis and summer drought stress in forest inventory plots of Catalonia (NE Spain) co-dominated by holm oak and eight different companion species, where the set of plots selected for each competitor species includes a range of combinations of climatic aridity and stand leaf area index (LAIstand). Given previous empirical evidence on mixing effects and knowledge on plant hydraulics, our a priori expectations were that (i) water-driven mixing effects at the species level have different sign for the two interacting species (e.g. an increase in transpiration per unit leaf area for QI under mixture should correspond to a decrease in transpiration for the competing species, in both cases relative to monospecific stands); (ii) the outcome of mixing on species level water use and drought stress can be mainly explained by the differences in traits involved in the acquisition of resources and in traits determining hydraulic efficiency and safety, including the possibility of compensations; (iii) mixing effects on stand-level transpiration should be generally low in mixed holm oak forests, because the water not used by one species should be used by the other; (iv) while variations in climatic aridity or LAIstand are highly relevant to determine water use and drought stress in general, we did not expect them to be key for species- or stand-level mixing effects, since these are defined with respect to monospecific stands under the same conditions.

2. Material and methods

2.1. Model description

MEDFATE, the FEM used in this study, has been designed to simulate soil and plant water balances in structurally and compositionally heterogeneous forest stands. The model extends the soil water balance model presented in De Cáceres et al. (2015) by increasing the detail in processes determining plant transpiration (i.e., plant hydraulics, photosynthesis, stomatal regulation, radiation extinction and energy balance). As in De Cáceres et al. (2015), aboveground stand structure is represented in terms of total height (H), leaf area index (LAI) and crown ratio (CR) of a set of woody plant cohorts. The soil is represented using a set of vertical layers and each cohort may have a different root distribution, specified using the depth corresponding to cumulative 50% and 95% of fine roots (Z_{50} and Z_{95} , respectively). MEDFATE requires daily weather as input and most hydrological processes are simulated at daily time steps. However, radiation extinction, energy balance equations and water flows mediated by plant hydraulics (i.e., soil water uptake, transpiration and hydraulic redistribution) are evaluated at hourly time steps. Even though radiation extinction and sunlit/shade leaf energy balances are estimated dividing the canopy into 1 m layers (Anten and Baastians 2016), canopy-level energy balance equations are evaluated assuming a single layer that exchanges energy with the atmosphere and

the soil (Best et al., 2011). The 'supply function' approach of Sperry and Love (2015) is used to represent the correspondence between steady-state instantaneous flow rates and water potentials across the soil-plant-atmosphere hydraulic network, which includes rhizosphere, root, stem and leaf segments. Water storage is considered by including two (leaf and stem) symplastic compartments and one stem apoplastic (i. e., xylem) compartment. The stem apoplastic compartment is coupled to water flows via two supply functions representing the soil-to-plant and the plant-to-atmosphere pathways, respectively (Fig. 1). Cohort's gross photosynthesis is approximated using the sunlit/shade model of De Pury and Farquhar (1997). Stomatal regulation for sunlit/shade leaves 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 potential photosynthetic gains. While hydraulic conductance of roots and leaves is completely recovered when autumn rains restore soil water availability (i.e., no hysteresis), the recovery of stem conductance is progressive, through the formation of new xylem conduits as a function of the water potential in the stem symplastic compartment (Cabon et al., 2020). Model outputs include daily soil water balance components, as well as hourly values of transpiration (E), net photosynthesis (A_n) and drought stress for each plant cohort. The latter is quantified by the relative water content (*RWC*) in plant compartments and the relative whole-plant conductance (k_{plant} . rel). Appendix S1 in Supporting Information presents further details of



Fig. 1. Schematic representation of the hydraulic submodel in MEDFATE. Black arrows represent the soil-to-plant hydraulic pathway and the red arrow represents the plant-to-atmosphere pathway. Notation for water potentials in nodes (circles) and water compartments (boxes), transpiration flows and lateral flows (double-head arrows) are explained in Appendix S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

model design and includes the definition and units of all model parameters and output variables. A detailed formulation of processes can be found at https://vegmod.ctfc.cat/frames/medfatebook/. Core model functions were programmed in C++ and linked to a R user interface within the package 'medfate' (De Cáceres et al. 2015), which is available at CRAN (https://cran.r-project.org/package=medfate) and GitHub (https://github.com/vegmod/medfate).

2.2. Target species

Quercus ilex L. (holm oak) is a common and widespread evergreen tree species in the western Mediterranean Basin, with large ecological and economic importance (Barbero et al., 1992). QI is found under a wide range of environmental conditions and forest structures co-occurring with several other woody species. The following are the most common cases: (i) Given its slow growth and shade tolerance, QI is frequently found as understory or sub-canopy of pine-dominated forests (Zavala et al., 2000); (ii) QI also frequently co-occurs with other (sub-) Mediterranean oak species having similar tree size, rooting pattern and shade tolerance; (iii) QI forests often include smaller trees and shrubs, some of these being less drought resistant than QI, but others being able to outcompete it when climate is too arid or soils are shallow (Ogava and Peñuelas, 2007a). We study here the water-related interactions between QI and eight species representatives of the three situations mentioned above: Pinus halepensis Mill. (Aleppo pine), Pinus nigra ssp. salzmannii J. F. Arnold (black pine) and Pinus sylvestris L. (Scots pine) for case (i); Quercus pubescens Mill. (downy oak) and Quercus faginea Lam. (Portuguese oak) for case (ii); Arbutus unedo L. (strawberry tree), Phillyrea latifolia L. (green olive tree) and Buxus sempervirens L. (European boxwood) for case (iii).

The eight selected species differ from QI in several traits related to water use and drought responses. For a similar age, pines are normally taller and more shallowly rooted than QI. The three pines can be regarded as relatively isohydric and water-saving species, because their needles have lower hydraulic safety and exhibit a tighter stomatal control than QI (Borghetti et al., 1998; Irvine et al., 1998). Regarding trait differences among them, Pinus halepensis has denser wood and lower wood-specific hydraulic conductivity than P. nigra and P. sylvestris (Froux et al., 2002; Martínez-Vilalta et al., 2004). Quercus pubescens and Q. faginea are deep-rooted species like QI. Both species are winter-deciduous and have higher wood-specific conductivity than QI (Tognetti et al., 1998), but their leaves are more hydraulically vulnerable (Corcuera et al., 2002). Hence, their strategy involves maximizing gas exchange and productivity during a shorter growing season (Baldocchi et al., 2010). Among the smaller trees, Phillyrea latifolia and Arbutus unedo also have dimorphic root systems and rely on deep water uptake during summer drought (Barbeta et al., 2015). In addition, P. latifolia exhibits little stomatal regulation and has less vulnerable stem and root xylem than A. unedo and QI. Therefore, it is able to maintain water transport at more negative water potentials during summer drought (Barbeta et al., 2012; Martínez-Vilalta et al., 2003, 2002). Finally, Buxus sempervirens is a slow-growing, shade and drought-tolerant evergreen species that has less efficient but also less vulnerable hydraulic system compared to QI (Aussenac and Valette, 1982; Rodríguez-Calcerrada et al., 2013).

2.3. Forest inventory plots

In order to study mixing effects on water use and summer drought stress of holm oak forests while accounting for environmental and structural variation, we selected plots of the Third Spanish National Forest Inventory (SFI3) (Villanueva, 2004) within the Mediterranean region of Catalonia (NE Spain). For each of the eight species presented in the previous section, we first selected the set of SFI3 plots where both QI and the competitor species occurred with mean H > 1.5 m and together accounted for at least 50% of the leaf area index of the stand (*LAI*_{stand}).

We required QI and the competitor species to be present in the stand but not necessarily dominant, because we artificially modified dominance in our simulations (see Section 2.6). With the aim to sample uniformly over environmental and stand structural gradients, we conducted a stratified random resampling of the initial plot selection over a two-dimensional space defined by the summer moisture index (MI_{summer}) as indicator of climatic variation, and LAI_{stand} as a stand structural variable determining resource use intensity. MI_{summer} was estimated as the ratio of mean summer (June, July, August) precipitation and mean summer potential evapotranspiration for a 30-yr (1986–2015) period, with daily values calculated using Penman's (1948) equation. We used combinations of stand LAI_{stand} bins (i.e., 0–1, 1–2, ...) and MI_{summer} bins (i.e., 0.1–0.2, 0.2–0.3, ...) to define strata and sampled one random plot per stratum. The geographic distribution of the final set of 186 SFI3 plots selected is shown in Fig. 2.

2.4. Model parametrization and evaluation

Physical soil properties on SFI3 plot coordinates were obtained from SoilGrids database (Hengl et al., 2017). For all plots we initially considered four soil layers down to a total depth of 4 m, but the deepest layers were merged into a rocky layer (95% of rocks) following the depth of the R horizon. A monotonous increase in rock fragment content across soil layers from the surface to the rocky layer was defined on the basis of surface stoniness classes determined in SFI3 plot surveys.

The eight woody species presented in Section 2.2 were selected because of the availability of data from five experimental forest plots codominated by QI and located in Spain and south-eastern France (see Table S3.1 in Appendix S3). As SFI3 sampling protocols did not include physiological parameters, we used data from experimental plots to obtain plant trait estimates - complementing other sources - and to evaluate the predictive capacity of MEDFATE. A detailed description of parametrization of plant traits is provided in Appendix S2. A number of traits were estimated at species level (i.e. had different values for different species but the same values in all plots), including wood density (WD), maximum photosynthetic rates of carboxylation and electron transport at 25 °C (Vmax298 and Jmax298, respectively), maximum leaf hydraulic conductance ($k_{leaf,max}$), maximum stem xylem hydraulic conductivity (Kstem,max), maximum leaf conductance to water vapour (Gw,max) and Weibull parameters of leaf/stem/root hydraulic vulnerability curves (i.e., c_{leaf} , c_{stem} , c_{root} , d_{leaf} , d_{stem} and d_{root}). Values for all these species-specific parameters were obtained from available trait databases and bibliographic sources (see Table S2.1). Specific leaf area (SLA) and Huber value (H_{ν}) were also species-specific for SFI3 plots, but estimates were obtained from on-site measurements in experimental plots. For another set of parameters, estimates were given specific to each species in each SFI3 or experimental plot. Forest inventory measurements included tree height (H) and tree diameter at breast height, which was used to obtain estimates of foliar biomass (hence leaf area after multiplying by SLA) and crown ratio (CR) via species-specific allometries (see Appendix S2). Depths corresponding to cumulative 50% and 95% of fine roots (Z_{50} and Z_{95}) were derived from empirical relationships based on LAIstand, soil properties, summer climate and species identity (Cabon et al., 2018), but did not account for species interaction effects. Among hydraulic plant traits, maximum hydraulic conductances (kroot, max, $k_{stem,max}$ and $k_{rhizo,max}$) and stem water storage capacity (W_{stem}) also varied from one forest plot to another as a result of a modelled dependency on plant size (see Appendix S2). Overall, we acknowledge that our trait parametrization contains a substantial degree of expert-based decisions and did not include an explicit assessment of uncertainty in parameter estimates, but addressing these shortcomings was unfeasible at the scale of the study, as data for model calibration/validation was lacking for SFI3 plots.

We purposely avoided model calibration exercises on the five experimental plots so that model performance in SFI3 plots could be considered similar to the evaluation results, despite the fact that some



Fig. 2. Distribution of selected forest inventory (SFI3) plots within Catalonia (NE Spain) for each of the eight competitor species. The summer moisture index (*MI*_{summer}), calculated as the ratio of mean summer precipitation over mean summer potential evapotranspiration for 1 km grid cells, is indicated using a gray scale, where darker tones indicate lower *MI*_{summer} values and, hence, stronger summer aridity.

traits had been measured in situ for experimental plots, which reduced parameter uncertainty compared to SFI3 plots. Appendix S3 contains the description of experimental sites, plot- and species- specific parameter values and model evaluation results. The model generally showed a reasonably good predictive capacity for soil moisture dynamics on experimental plots (MAE 0.135 \pm 0.058 in relative extractable water). The ability of the model to predict transpiration rates from sapflow data was also acceptable (MAE 0.178 \pm 0.083 lom⁻²od⁻¹), but model predictions of water status were less satisfying when compared to measured leaf water potentials (MAE 0.805 \pm 0.178 MPa), including substantial (but less than 1 MPa) biases in some cases.

2.5. Sensitivity analyses

We used sensitivity analyses to assess the role of individual traits in determining the outcome of interactions between *Quercus ilex* (QI) and a competitor on transpiration, photosynthesis and drought stress. To this aim, we took the parametrization of one of the experimental plots (Puéchabon, France) and defined two cohorts of LAI = 1 with the remaining trait parameters initially set equal to those of QI. Parameter values of the first cohort (QI) were kept the same in all simulations, while for the second cohort (i.e., hereafter the competitor) we modified the value of specific traits and evaluated the effect of the trait difference on model predictions. We evaluated the sensitivity to traits related to resource access and resource use. For traits determining access to

resources, we focused on total plant height (H) and fine root distribution $(Z_{50} \text{ and } Z_{95})$. For traits related to resource use we studied the effect of maximum whole-plant hydraulic conductance ($k_{plant,max}$), xylem's hydraulic safety (Weibull d parameters), maximum leaf conductance to water vapour ($G_{w,max}$), maximum photosynthetic capacity (V_{max298} and J_{max298}) and water storage capacity (W_{leaf} and W_{stem}). Parameter values of the competitor were varied between -80% and +80% of the original QI value (see values in Table S4.1 of Appendix S4, including a comparison with the range of values in experimental plots). Changes in fine root distribution were applied proportionally to both Z₅₀ and Z₉₅, and these changes affected the partitioning of $k_{root,max}$ and $k_{rhizo,max}$ among soil layers. When varying whole-plant $k_{plant,max}$ we assumed proportional variations in leaf, stem and root hydraulic conductances ($k_{leaf,max}$, $k_{stem.max}$ and $k_{root.max}$), i.e., we assumed constant relative contribution to whole-plant resistance. Since, kplantmax was defined as conductance per unit leaf area, alterations of this parameter can be interpreted either as a modification of tissue conductivities or, equivalently, as a modification of H_{ν} . When evaluating the sensitivity to hydraulic safety, we proportionally modified *d* values of the leaf/stem/root vulnerability curves (i. e., *d_{leaf}*, *d_{stem}* and *d_{root}*). Likewise, sensitivity to photosynthetic capacity was examined applying the same proportional changes to V_{max298} and J_{max298} , and changes in storage capacity were applied proportionally to W_{leaf} and W_{stem} . All simulations were conducted using the soil definition and 4 years of weather data at Puéchabon.

Average values of annual of transpiration per unit leaf area (E) and

net photosynthesis per unit leaf area (A_n) were calculated to evaluate the performance of QI and its competitor in terms of water use and carbon assimilation, respectively. Summer drought stress was evaluated using summer (Jun-Jul-Aug) averages of relative whole-plant conductance $(k_{plant,rel})$ and leaf relative water content (RWC_{leaf}) , representing the decrease in hydraulic conductance and plant water status, respectively.

2.6. Model simulations in SFI3 plots

We used model simulations on SFI3 plots to study mixing effects on water use and summer drought stress of holm oak forests while accounting for variation in trait differences, climatic aridity and stand structure. We ran MEDFATE on each selected SFI3 plot using daily weather data corresponding to a 10-yr period (1996-2005), centered on the dates of SFI3 sampling (2000-2001), and obtained by interpolation from surface weather station data with the R package 'meteoland' (De Cáceres et al., 2018). For each SFI3 plot, we simulated three stands where LAI proportions of QI and its competitor were set to either 100-0% (pure QI stand), 50-50% (mixed stand) or 0-100% (pure competitor stand), but where the LAIstand was held equal to the value estimated from forest inventory data. Response variables were the same as in sensitivity analyses – i.e., mean annual sums for E and A_n ; and summer means for $k_{plant,rel}$ and RWC_{leaf} – but included both species-level (QI and its competitor) and stand-level responses in the three simulated stands. As before, species-level E and A_n values were expressed per leaf area unit, but stand-level values were expressed per ground area unit. The effect of mixing at the species-level was defined as the difference in the response variable in the mixed stand with respect to the value in the pure stand of the same species. We quantified the mixing effects at the stand level using (Forrester and Pretzsch, 2015):

 $ME = p_{1,2} - 0.5 \cdot (p_1 + p_2)$

where p_1 and p_2 are the stand-level response values for pure stands of species 1 and 2, respectively, and $p_{1,2}$ is the corresponding value for the mixed stand. When ME = 0, the performance of the mixture is exactly as the mean of values in pure stands (i.e., pure additive effects), and would indicate no complementarity effect at the stand level. If ME > 0 the response is higher than expected from pure additive effects, with units depending on the response variable, whereas the opposite occurs if ME < 0.

2.7. Statistical analyses

Simulation results for individual SFI3 plots (responses in pure stands and mixed stands, as well as the resulting mixing effects) were first represented on scatter diagrams with LAIstand and MIsummer axes for each competitor species. We then averaged mixing effects for each competitor species, to focus on the variation due to the identity of the QI competitor, and represented these means on the axes of a principal components ordination diagram of trait differences. Finally, we used linear models to estimate how much of QI and stand-level simulated responses to species mixing were explained by plant trait differences, climatic aridity (MIsummer) and stand structure (LAIstand). Linear models were fit to both the ('absolute') response in mixed stands and to the mixing effect, using as explanatory factors the difference in each plant trait, MIsummer, LAIstand, and the LAIstand / MIsummer ratio representing their interaction. We partitioned R² of linear models into the contribution of each factor using the 'lmg' metric developed by Lindeman et al. (1980) and available in R package 'relaimpo'.

3. Results

3.1. Sensitivity to competitor's specific traits

The alteration of specific traits of the plant cohort competing with QI

resulted in species-level water use, photosynthesis and drought stress being affected in multiple ways (Fig. 3). Transpiration per unit leaf area (E) and net photosynthesis per unit leaf area (A_n) of QI and its competitor were sensitive to alterations of the height (H) of the competitor, the tallest cohort being the one with higher annual E and A_n (Fig. 3a-b). A shallower root distribution (Z_{50} and Z_{95}) of the competitor led to lower E and A_n for the competitor (Fig. 3a-b), increased drought stress for the competitor and allowed a small stress release for QI (Fig. 3c-d). Higher hydraulic efficiency $(k_{max,plant})$ of the competitor increased E and A_n for the competitor, as expected, but also decreased Eand A_n for QI (Fig. 3a-b). Summer drought stress variables were very sensitive to the hydraulic efficiency of competitor's xylem, with stress increasing along with $k_{max,plant}$ for both plant cohorts (Fig. 3c-d). The competitor's hydraulic resistance to embolism strongly affected E of QI (Fig. 3a) and was also the plant trait most significantly affecting drought stress of QI, with higher competitor's resistance (i.e. more negative d values) leading to increased QI stress (Fig. 4C-d). Stress of the competitor was increased by either very high or very low resistance values, the former because of increased transpiration under non-limiting soil water. Moderate to large reductions in competitor's maximum leaf conductance to water vapor $(G_{w,max})$ decreased E for the competitor, increased E for QI and reduced drought stress for both cohorts (Fig. 3cd). A_n of the competitor responded strongly to variation in photosynthetic capacity (V_{max298} and J_{max298}), but A_n of QI was little affected (Fig. 4b). Finally, we did not observe significant effects of water storage capacity (Wleaf and Wstem) on water use or drought stress variables.

3.2. Plant trait differences in SFI3 plots

Fig. 4 shows the biplot of a principal component analysis (PCA) conducted on the matrix of trait differences between the competitor and QI in SFI3 plots (see average trait value differences for each species pair in Table S4.2). The first axis (34.5% var.) is defined by higher xylem hydraulic safety (compared to QI), lower plant height and lower storage capacity, whereas the second axis (28.4% var.) is defined by higher hydraulic conductance and higher maximum stomatal conductance. Much of the variation in trait differences comes from the identity of the competitor species, but within-species dispersion can be observed because of differences in those traits that include plot-level variation.

3.3. Responses and mixing effects at species and stand levels

Fig. 5. shows the simulated species- and stand-level transpiration, photosynthesis, and drought stress in pure and mixed stands of QI and *Pinus halepensis* (results for the remaining competitor species are included in Figs. S5.1–16 of Appendix S5). The four response variables (*E*, *A*_n, *k*_{plant,rel} and *RWC*_{leaf}) were strongly affected by *LAI*_{stand}, both in pure and mixed stands, whereas climatic aridity became influential in combination with high values of *LAI*_{stand}. The mixing effects corresponding to Fig. 5 are shown in Fig. 6, where we found that the mixture with *P. halepensis* increased annual transpiration (*E*) for QI, with respect to monospecific stands (Fig. 6a), while it decreased its net photosynthesis (*A*_n; Fig. 6b) and summer stress (*k*_{plant,rel} and *RWC*_{leaf}; Fig. 6c-d), with *LAI*_{stand} modulating the intensity of the mixing effect. Opposite mixing effects were observed for *P. halepensis*, with respect to pure pine stands. Stand-level mixing effects on *E* and *A*_n were qualitatively similar to the corresponding species-level effects on QI (Fig. 6a-b).

While Figs. 5 and 6 show the simulation results for the interaction between QI and *P. halepensis*, Fig. 7 represents the average mixing effects for each species pair using symbols located on the mean coordinates in the PCA ordination space of trait differences (cf. Fig. 4). Annual transpiration (*E*) increased for QI (with opposite effects on the competitor) under mixing (relative to pure QI stands) with all competitor species except with the two oaks (*Q. faginea* and *Q. pubescens*), although milder positive effects were obtained with the three pines (Fig. 7a). Net photosynthesis (A_n) for QI increased or decreased under mixing as a

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Fig. 3. Variation of *Quercus ilex* (QI) and competitor's annual transpiration per unit leaf area (*E*), net photosyntesis per unit leaf area (*A_n*), relative whole-plant conductance ($k_{plant,rel}$) and leaf relative water content (RWC_{leaf}) with respect to changes in competitor's individual plant traits in the experimental plot of Puéchabon. Traits analyzed are plant height (*H*), fine root distribution (Z_{50} and Z_{95}), maximum whole-plant hydraulic conductance ($k_{plant,max}$), hydraulic vulnerability (Weibull *d* parameter), maximum leaf conductance to water vapor ($G_{w,max}$), maximum photosynthetic capacity (V_{max298} and J_{max298}) and water storage capacity (W_{leaf} and W_{stem}). Central (0%) change values correspond to simulated water use and drought stress for pure QI stands. Dashed line segments correspond to parameter estimates outside the range of trait values found across experimental plots (see Table S4.1).

result of differences in crown position within the canopy, i.e. it increased when mixing with shorter trees and decreased when mixing with taller trees (i.e., the other oaks and pines) (Fig. 7b). The response patterns of the two drought stress indicators (k_{plant,rel} and RWC_{leaf}) were similar at the species level (Fig. 7c-d): drought stress decreased (i.e., k_{plant,rel} and RWCleaf increased) for QI in mixtures with the three pines, Buxus sempervirens and Arbutus unedo; whereas it increased in mixtures with oaks and Phillyrea latifolia. The effect of mixing on drought stress of the competitor species was always opposite in sign to that of QI. At stand level, a positive average mixing effect was always predicted on E per unit ground area, ranging between +4.8 mm•yr⁻¹ (+1.6%) with P. nigra and $+26.0 \text{ mm} \cdot \text{yr}^{-1}$ (+8.2%) with *B. sempervirens* (Fig. 7a). Mixing effects on stand-level A_n per unit ground area had different sign depending on the specific mixture, ranging from $-66.1 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (-4.7%) with *P. latifolia* to $+88.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (+7.7%) with *Q. faginea* (Fig. 7b). Standlevel mixing effects on summer drought stress were rather small (effects on RWC_{leaf} between -4.6% and +1.8%; effects on $k_{plant,rel}$ between -4.0% and +4.5%) (Figs. 7c-d).

3.4. Importance of trait differences vs. climatic aridity and structure

Fig. 8 shows the proportion of variation of simulation results explained by trait differences, stand structure and climatic aridity, where the R² of linear models is divided into the contribution of individual factors or two factor groups ('trait differences' and 'structure and aridity'). As could be expected, QI and stand-level 'absolute' water use, photosynthesis and drought stress in mixed stands strongly depended on stand structure, climatic aridity and its interaction, although differences in traits were also relevant (Fig. 8a). In contrast, mixing effects were

explained to a very large degree by trait differences (Fig. 8b). At specieslevel, differences in xylem's hydraulic safety appeared most important for mixing effects on all four response variables, whereas differences in hydraulic efficiency also highly influential for *E*, differences in height were important for A_n and differences in storage capacity for drought stress. Mixing effects on *E* at the stand level were also influenced by differences in xylem's hydraulic efficiency and safety. LAI_{stand} and climatic aridity were also relevant to modulate stand-level mixing effects for *E* and A_n (i.e., a decrease in the mixing effect for plots with higher LAI_{stand} is apparent for some species pairs, but not all, in Figs. S5.1–16). Stand structure and climatic aridity had almost no influence on standlevel (or species-level) mixing effects on drought stress (Fig. 8b).

4. Discussion

4.1. Effects of individual traits on water-related interactions with holm oak

According to the results of our sensitivity analyses, differences in plant height (*H*) between QI and a given competitor have an effect not only on net photosynthesis (A_n) but also on transpiration per unit leaf area (*E*) (Fig. 3a-b). We interpret these crown position effects as derived from corresponding differences in the leaf energy balance and gas exchange, and reflecting a size-asymmetric competition for water resources (Schwinning and Weiner, 1998; Forrester 2019). Differences in root distribution (Z_{50} and Z_{95}) did not strongly influence *E* or A_n , except for very shallow rooting of the competitor, but they did influence drought stress. Species differences in rooting depth are known to lead to differences in water uptake, leaf water potential, stem hydraulic



Fig. 4. Principal component analysis biplot of trait value differences between QI and its competitor on each SFI3 plot (mean differences are included in Table S4.2). Trait difference loadings are represented by arrows and SFI3 are represented by points. Au - *Arbutus unedo*; Bs - *Buxus sempervirens*; Ph - *Pinus halepensis*; Ps - *P. sylvestris*; Pn - *P. nigra*; Pl - *Phillyrea latifolia*; Qp - *Quercus pubescens*; Qf - *Q. faginea*.

conductivity and stress under drought (del Castillo et al., 2016; Nardini et al., 2016; Zapater et al., 2013), but we are unaware of empirical studies showing how the root distribution of neighbors influences the drought stress of a target tree. As expected, differences in xylem's hydraulic efficiency and safety had a strong effect on water use and drought stress. Either increasing $k_{max,plant}$ or increasing d (i.e., increasing xylem's hydraulic safety) reduces the cost of water for the target plant cohort in the profit maximization approach to stomatal regulation of Sperry et al. (2017). The former because the same transpiration and photosynthesis rates imply a smaller water potential drop, and hence a lower decrease of conductance. The latter because more negative water potentials can be attained without decreasing hydraulic conductance. At larger temporal scales, increasing either $k_{max,plant}$ or d of the competitor led to increased transpiration and either earlier soil water depletion and/or lower moisture levels, both causing an increase in summer drought stress. Mixing with water demanding species has been found to cause earlier exhaustion of soil water reserves and increased drought stress on neighbors (Gebauer et al., 2012). While there is ample empirical evidence of xylem's hydraulic safety mediating species responses to drought stress, with higher resistance to embolism being correlated with lower drought-related damage (Martin-StPaul et al., 2017), less is known about how mixing species with different hydraulic safety levels affects drought stress, compared to pure stands. Our modeling results support the idea that species with higher resistance to embolism may cause an increase in drought stress to their neighbors exhibiting lower resistance, which could lead to competitive exclusion under increasingly arid conditions.

Compared to the previous traits, we found relatively mild effects of differences in photosynthetic capacity (V_{max298} and J_{max298}), maximum stomatal conductance ($G_{w,max}$) and plant water storage capacity (W_{leaf} and W_{stem}) on QI water-related interactions. Stronger impacts of V_{max298} and J_{max298} on mixing effects should be expected if we had modelled longer-term increased growth associated to higher photosynthetic capacity of the competitor. The model was only sensitive to $G_{w max}$ if strong decreases were applied, reflecting the coordination between hydraulic efficiency and stomatal conductance (Manzoni et al., 2014; Anderegg et al., 2018). The minor importance of differences in water storage obtained in our sensitivity analyses (larger relevance was obtained in SFI3 simulations; see Fig. 8b) may be explained by the fact that the initial stem storage capacity was relatively low for QI (1.4 lom⁻²) and so were the values assigned to its competitor. Storage capacity is nevertheless important at daily scale, and Salomón et al. (2017) have found that stem storage water can contribute between 2% and 5% to daily transpiration for QI at Puéchabon.

4.2. Species-level mixing effects

The outcome of mixing at the species level had often opposite effects for QI and the competitor species, as we hypothesized. Negative or positive effects strongly depended on the species identity of the competitor, in agreement with empirical evidence that the species identity of neighbors is an important factor modulating tree water use and drought stress (Grossiord et al., 2015; Grossiord, 2019). Our modelling approach allowed us to link competitor species identity to



Fig. 5. Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50-50% LAI) stands of QI and Pinus halepensis: (a) annual transpiration (*E*), (b) annual net photosynthesis (*A_n*), (c) relative whole-plant conductance (*k_{plant,rel}*) and (d) leaf relative water content (*RWC_{leaf}*). Specieslevel E and A_n values are calculated per unit leaf area, whereas stand-level values are presented per unit soil area. Plot axes are the leaf area index of the stand (LAIstand) and summer moisture index (MIsummer). Point size and color indicate the magnitude of the response. The corresponding mixing effects are shown in Fig. 6.

trait differences, illustrating how different combinations of crown position, hydraulic efficiency and safety differences can lead to a range of mixing outcomes.

We obtained relatively small species-level mixing effects when mixing QI with the other oaks (Q. faginea and Q. pubescens), because the three species shared similar values for several key traits. Nevertheless, the higher hydraulic conductance of deciduous oaks and their somewhat taller crowns (Table S4.2) led to a small decrease in E and to an increase in drought stress for QI. Mixing effects of QI with pines (P. halepensis, P. nigra and P. sylvestris) illustrate cases where differences in one trait can override the effect of differences in another. All three pines have crowns usually taller than those of QI, so their better position to harvest light caused a decrease in A_n for QI under mixing and, taking height differences alone, one would also expect a decrease in *E* for QI (see Fig. 4a). However, the more efficient and less vulnerable hydraulic system of QI increased E for QI under mixtures with pines, compared to monospecific stands, overriding the effect of crown position differences. Moreover, the higher extractive capacity of QI lead to an increase in drought stress for pines compared to monospecific pine stands. This is in apparent contradiction with observed positive oak-mixing effects on growth of Pinus pinea L. (stone pine) resulting from a reduction of intraspecific competition (de-Dios-García et al., 2015), but we also observed a



Fig. 6. Species- and stand-level effects of mixing QI with *Pinus halepensis* on (a) annual transpiration (*E*), (b) annual net photosynthesis (A_n), (c) relative whole-plant conductance ($k_{plant,rel}$) and (d) leaf relative water content (RWC_{leaf}). Species-level *E* and A_n values are calculated per unit leaf area, whereas stand-level values are presented per unit soil area. Plot axes are the leaf area index of the stand (LAI_{stand}) and summer moisture index (MI_{summer}). Point size and color indicate the magnitude and sign of the mixing effect.



Fig. 7. Average species- and stand-level mixing effects on (a) annual transpiration (*E*), (b) annual net photosynthesis (A_n), (c) relative whole-plant conductance ($k_{plant,rel}$) and (d) leaf relative water content (RWC_{leaf}), depending on the species identity of the competitor (Au - *Arbutus unedo*; Bs - *Buxus sempervirens*; Ph - *Pinus halepensis*; Ps - *P. sylvestris*; Pn - *P. nigra*; Pl - *Phillyrea latifolia*; Qp - *Quercus pubescens*; Qf - *Q. faginea*). Points are located at the mean coordinates of the competitor species in the ordination space of trait differences (Fig. 4) whereas point size and color indicate the magnitude and sign of the average mixing effect. Species-level mixing effects were estimated as the difference between the response in the 50–50% mixed stand and a pure stand of the same species. Stand-level mixing effects were estimated in the text. In both cases, values shown are means calculated across SFI plots (see Figs. S5.1–16).



Fig. 8. (a) Percentage of variation (R^2) of species-level (QI) and stand-level performance in mixed stands – in terms of transpiration, photosynthesis, whole-plant relative conductance and leaf relative water content – explained by differences in traits, stand structure (*LAI_{stand}*) and climatic aridity (*MI_{summer}*); (b) Percentage of variation of species-level and stand-level mixing effects explained by the same factors. Left panels indicate the variation explained by individual factors, whereas right panels indicate the variation explained by the two groups of factors.

positive mixing effect on A_n for pines, which would be compatible with positive effects on growth. Overall, our results combined with the shade tolerance of QI, are in agreement with the traditional successional relationship between QI and pines and the differential impacts of severe droughts on coexisting oaks and pines (Aguadé et al., 2015; Galiano et al., 2010; Grossiord et al., 2015).

We found complex interactions between hydraulic trait effects in mixtures of QI with smaller trees: Buxus sempervirens, Phillyrea latifolia and Arbutus unedo. Species mixing in the three cases yielded an increase in E and A_n for QI, explained by crown height differences and the resulting self-shading relief of QI under mixing. In contrast with pine species mixtures, the effect of crown height differences was reinforced by a less efficient hydraulic system in the case of B. sempervirens and, even if this species has a more resistant xylem than QI, the faster soil water depletion led to an increase in drought stress for B. sempervirens, compared to monospecific stands of this species. Nevertheless, absolute drought stress levels were still rather low for B. sempervirens in mixed stand simulations (Fig. S5.15), in agreement with the ability of this species to withstand intense drought (Rodríguez-Calcerrada et al., 2013). The higher leaf vulnerability and shallower root distribution of A. unedo also led our model to predict higher drought stress of this species under mixture with QI. Higher rates of leaf senescence of A. unedo than QI have been observed in mixed stands under severe drought (Sperlich et al., 2015), although these values should be relativized to monospecific stands in order to compare them to our simulation results. Whole-plant hydraulic efficiency of P. latifolia was similar to QI but its xylem was more resistant. In this case, even if mixing with QI decreased *E* for *P*. *latifolia*, as a result of differences in crown height, soil water uptake continued for longer during summer (as also shown empirically; Barbeta et al., 2012), with respect to monospecific QI stands, leading to an increase in drought stress for QI. Our results qualitatively agree with empirical evidence of the differential leaf shedding, growth and mortality responses of A. unedo, P. latifolia and QI to experimental drought (Ogaya and Penuelas, 2006; Ogaya and Peñuelas, 2007a), although again empirical values should be relativized to monospecific stands to be fully comparable.

4.3. Stand-level mixing effects

At the stand level, we found average mixing effects to be positive for stand transpiration (per unit ground area) in all species pairs, which would indicate complementarity in resource use. However, when compared to sapling experiments using temperate species (Lübbe et al., 2016), our mixing effects appear relatively modest, our mixing effects appear relatively modest in relative terms (an average of +4.0% in our study vs. an average of +8% and +11% under dry and moist treatments in theirs). This difference can be attributed to summer drought limiting transpiration in Mediterranean climate regardless of species composition. In accordance with this idea, complementarity in light use strategies has been found to underlie increases in stand-level productivity of mixed forests in both empirical (Pretzsch, 2014) and modelling studies (Morin et al., 2011; Forrester et al., 2018), but that this effect may be severely reduced under increased competition for water (Jucker et al., 2014; but see Sheil and Bongers 2020). In our case, stand-level mixing effects for A_n had different sign depending on the species pair considered, and in some cases such as oak-pine mixtures the positive effects vanished in forests with higher LAIstand. If we add to these results the fact that average stand-level mixing effects on $k_{plant,rel}$ and RWC_{leaf} were often negative (Fig. 7), our simulation study globally supports the idea that species mixing does not always have positive effects at the stand level if water is a limiting factor and hence forest managers should carefully choose accompanying species (Grossiord, 2019).

4.4. Relative importance of factors determining water-driven mixing effects

When analyzing the relative importance of different factors on mixing effects (Fig. 8), we found that differences in traits, particularly xylem's hydraulic safety and efficiency, had a dominant influence on both species-level and stand-level mixing effects for the four performance variables considered. Stand structure and climatic conditions have a key role in determining productivity, transpiration rates and drought stress in forests (De Cáceres et al., 2015; Gleason et al., 2017) and this was also the case in our simulations (Fig. 8a). However, we did not find stand structure or climatic aridity to have a relevant role on modulating mixing effects, in agreement with Forrester et al. (2016), even though higher LAIstand values decreased the magnitude of positive mixing effects on E and A_n for some species pairs. Nevertheless, the relative importance of the different groups of traits in determining mixing effects, while informative, should be interpreted with caution, because of the relatively low number of species pairs tested and the limitations of our modelling approach.

4.5. Limitations of the study

Our results may have been affected by untested assumptions, inadequate process representation and/or unaccurate parametrization inherent to any modelling exercise. MEDFATE accounts for vertical (1-D) interactions for light and water resources, but the current canopy energy balance does not allow simulating temperature and humidity gradients within the canopy as in multi-layer canopy models (e.g. Ma and Liu, 2019), which may result in over- or under- estimations of transpiration and drought stress depending on crown positions within the canopy. Furthermore, plant cohorts were assumed to extend their root systems horizontally across the entire plot, whereas FEMs allowing 3-D interactions for water have shown distinct soil moisture dynamics under trees of different species and sizes (Manoli et al., 2017; Rötzer et al., 2017). Neglecting below-ground horizontal interaction for water resources may have led us to overestimate mixing effects, especially at the species level, as empirical studies suggest that group-wise mixtures may reduce negative effects of mixing (Goisser et al., 2016). Regarding parametrization, our study avoided calibration exercises and relied on trait measurements. One limitation of this approach is the challenge to appropriately scale tissue-level traits to whole-plant hydraulic parameters (Mencuccini et al., 2019a). Some traits are particularly difficult to measure and we addressed the parametrization of root and rhizosphere resistances by making them proportional to aboveground resistances, neglecting that differences in root biomass allocation exist even among oaks (Cotillas et al., 2016). We addressed intraspecific variability of some traits in relation to local environmental conditions and stand density, but omitted the known variability in others, such as specific leaf area (Ogaya and Peñuelas, 2007b) or Huber value (Rosas et al., 2019). Accounting for these sources of trait variation would increase the relative importance of trait differences in determining mixing effects, although indirectly reflecting environmental influences. Another potential limitation is that we assumed that plant traits were constant over time. Particular, root distribution was assumed equal in simulations of monospecific and mixed stands, while trees are known to dynamically adapt root systems (e.g., Mackay et al., 2019). We also calculated crown ratios (CR) from inventory plot data and the same values were used for both mixed and pure stand simulations, neglecting variations in crown morphology derived from mixtures (Pretzsch, 2014).

4.6. Concluding remarks

MEDFATE has several features that make it appropriate to test the role of composition and structure on water-related interactions and drought impacts in forest stands (Choat et al., 2018; Matheny et al., 2017; Mencuccini et al., 2019a). Its predictions in the case of holm oak

forests generally matched the existing knowledge of water-related interactions among the species involved. Moreover, we showed that water use and drought stress in water-limited mixed forests is strongly determined by differences in multiple plant traits of competitors, with a prominent role of xylem's hydraulic efficiency and safety. However, the complex outcome of species mixing depends on compensating effects driven by multiple trait differences and may be modulated by stand structure and climatic aridity. Further developments in process-based forest modelling should allow revisiting this issue while accounting for additional processes, such as carbon balance, growth and acclimation. In any case, we have shown that trait-based FEMs like MEDFATE are a useful complement to empirical approaches in studies aiming at understanding the effect of species composition on the functioning and dynamics of water-limited mixed forests.

Declaration of Competing Interest

None.

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Appendix S1. Details of model description

Here we describe the overall design of the forest ecosystem model MEDFATE used in this study (a complete detailed description can be found at <u>https://vegmod.ctfc.cat/frames/medfatebook/</u>).

Soil water balance - Soil water balance is performed daily and similarly to De Cáceres et al. (2015). Precipitation can be in the form of rainfall or snowfall, and the model includes a simplified submodel of snow pack dynamics (Kergoat 1998). During rainfall events, the model calculates evaporation due to rainfall interception, surface runoff and snow melt to determine infiltration (Boughton 1989, Gash et al. 1995). When refilling a given soil layer, a fraction of water is assumed to directly percolate through macropores to the layer below (Granier et al. 1999). Water exceeding field capacity or percolating from the deepest layer is assumed to become unavailable to plant roots and exported as deep drainage. After potentially refilling soil layers, the model determines evaporation from the soil surface following Ritchie (1972) (litter moisture dynamics are thus neglected). Plant water extraction, transpiration and hydraulic redistribution processes are modelled at hourly time steps and involve detailed calculations of hydraulics and photosynthesis (see below).

Radiation extinction and energy balances - Diurnal above-canopy air temperature variations are determined assuming a sinusoidal pattern (McMurtrie et al. 1990), whereas diurnal variations of instantaneous direct and diffuse shortwave radiation values are derived from daily insolation following Spitters et al. (1986). The amount of short- and longwave radiation absorbed by sunlit and shade leaves follows the multilayer canopy model of Anten and Bastiaans (2016), with the forest stand being divided into 1m layers and leaf area density in each layer being determined by a Gaussian distribution truncated between crown base height and *H*. However, canopy-level energy balance is performed considering that the canopy conforms a single layer that exchanges energy with the atmosphere and the soil. Canopy and soil energy balance equations include short- and longwave radiation, convective and latent heat energy exchanges (Best et al. 2011). Latent heat exchanges are coupled to several water flows: plant transpiration, evaporation of intercepted rainfall, snow melt and evaporation from bare soil.

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Hydraulics - Plant hydraulics can be represented with or without water storage compartments. When storage compartments are not considered, soil-plant hydraulic pathways are represented using a network of $2 \cdot S + 3$ resistance elements, where *S* is the number of soil layers (Fig. S1.1a). For each soil layer, there is a rhizosphere element in series with a root xylem element. These are connected in parallel up to the root crown, which in turns connects to leaf evaporation sites via two stem xylem elements (with the same hydraulic parameters) plus a leaf resistance element in series. Steady-state configuration of water potentials (Ψ) across the whole hydraulic network are determined for a range of instantaneous leaf transpiration (E_{leaf}) values using the water 'supply function' approach of Sperry & Love (2015) and Sperry et al. (2017). Given known values of soil water potential and a soil-plant hydraulic network, the 'supply function' describes the theoretical steady-state relationship between E_{leaf} and Ψ_{leaf} (and the water potential of any intermediate node within the network). **Fig. S1.1**: Schematic representation of the hydraulic submodel of MEDFATE, with or without considering water storage compartments (submodel 'b' is used in this manuscript, Fig. 1). Notation for water potentials in nodes (circles) and water compartments (boxes), transpiration flows and lateral flows is explained in the text.



Supply functions for a segmented hydraulic network such as that of Fig. S1.1a are calculated from soil and xylem vulnerability curves, which describe how hydraulic conductance (k) of each segment declines from its maximum value (k_{max}) in response to water pressure (Ψ) (see example in Fig. S1.2). The dependence of xylem conductance on water potential (i.e. vulnerability curves) is modelled using Weibull functions for root, stem or leaf segments:

$$k(\Psi) = k_{max} \cdot \exp\left(-(\Psi/d)^{c}\right)$$

where Ψ is the water potential, k_{max} is the maximum conductance of the segment (hydraulic efficiency) and *c* and *d* define the shape of its decline (hydraulic vulnerability). Rhizosphere elements have their vulnerability (i.e. unsaturated conductivity) curves dictated by van Genuchten (1980) functions. Steady-state flows between specific nodes are calculated using a linearized version of the Richards' equation via the Kirchhoff integral transform (Ross and Bristow 1990), with incomplete Gamma integrals calculated following Sperry et al. (1998) and integrals of van Genuchten functions calculated following van der Lier et al. (2009). For each value of E_{leaf} and given current soil layer water potentials, flows and water potentials up to the root crown are solved using a Newton-Raphson routine (Sperry et al. 1998) and water potential drops across stem and leaf elements are determined by inverting incomplete Gamma integrals (Gil et al. 2012). Calculation of supply functions without water compartments is done once per day, following the update of soil moisture.

Fig. S1.2: Examples of segment vulnerability curves (a-c) and the supply function (d) for two species (assuming zero water potential for all soil layers).



When considering water storage compartments, the model uses two supply functions (Fig. S1.1b): the first supply function has $2 \cdot S + 1$ resistance elements (black arrows in Fig. S1.1b) and defines the steady-state water supply from soil to the stem xylem compartment ($E_{stem,in}$); the second (red arrow in Fig. S1.1b) has four resistance elements and defines water supply to the leaves (E_{leaf}). The two supply functions interact via $\Psi_{stem,1}$, the water potential of an explicit stem xylem compartment from which water flows towards the leaves ($E_{stem,out}$) and where soil water is poured ($E_{stem,in}$). Two symplasmic compartments exchange water with the xylem (Steppe et al. 2006). The stem xylem compartment ($\Psi_{symp,stem}$). Another symplasmic compartment is considered at the leaf level ($\Psi_{symp,leaf}$) that adds or withdraws water from the transpiration stream, modifying the water demand from the stem (i.e., making $E_{stem,out}$ different from E_{leaf}). Although interaction of the two supply functions is done via $\Psi_{stem,1}$, the second

supply function still requires a complete description of resistances along the plant pathway in order to correctly determine steady-state water potential drops and flows, which explains why two 'virtual' nodes $\Psi_{rootcrown}$ and $\Psi_{rootsurf}$ need to be defined for the second supply function. Instantaneous flows from/to symplasmic compartments (Flat,stem and Flat,leaf) are modelled using Darcy's law. Following Hölttä et al. (2009), changes in stem water volume are composed of two terms, one arising from the balance of flows in and out of the stem (i.e. $E_{stem,in} - E_{stem,out} + F_{lat,stem}$) and the other arising from stem xylem embolism, where the relationship between the proportion of embolized xylem and stem water potential is assumed to follow the function as the conductance vulnerability curve. Relationship between water content and water potential of symplastic compartments follows pressure-volume curves (Bartlett et al. 2012) whereas in the case of stem apoplastic compartment an elastic modulus of 1000 Mpa is assumed. The dynamic system is solved by time discretization: Flat.stem, Flat.leaf, Estem.in, water balance equations and water potentials ($\Psi_{stem,1}$, $\Psi_{symp,stem}$ and $\Psi_{symp,leaf}$) are re-calculated using onesecond time steps, whereas E_{leaf} is updated hourly (see below). The first supply function is updated daily following variations in soil moisture. The second supply function is recalculated at hourly time steps following variations in $\Psi_{stem,1}$, after updating the 'virtual' nodes $\Psi_{rootsurf}$ and $\Psi_{rootcrown}$ according to E_{leaf} of the previous step. Recovery from stem xylem embolism (and hence, recovery of stem conductance) is evaluated daily, assuming the formation of new vessels and being modelled as a function of a maximum rate of sapwood area increase and stem symplastic water potential (Cabon et al. 2020). Reduction of xylem hydraulic conductance due to embolism is assumed completely reversible for rhizosphere, root and leaf segments.

Photosynthesis and stomatal regulation - For any given E_{leaf} value of the supply function, gross photosynthesis (A_{leaf}) is calculated at hourly time steps for sunlit and shade leaves separately, using the following sequence (Sperry et al. 2017, Venturas et al. 2018): (a) leaf temperature is calculated from E_{leaf} , absorbed radiation, canopy air temperature (determined in the canopy energy balance) and leaf width via a leaf energy budget equation (Campbell and Norman 1998); (b) leaf-air vapor pressure deficit is calculated from temperature and atmospheric vapor pressure, which is assumed constant during the day; (c) conductance to water vapor (G_w) is calculated from E_{leaf} , leaf-air vapor pressure deficit and atmospheric pressure; (d) conductance to CO₂ is estimated from G_w assuming a 1.6 constant ratio of the two conductances (Tuzet et al. 2003); and (e) A_{leaf} is calculated following a Farquhar-type model (Collatz et al. 1991, Medlyn et al. 2002). Temperature dependence of maximum carboxylation rates and maximum electron transport rates follows Bernacchi et al (2001). Plant photosynthesis is approximated using a sun-shade model of de Pury and Farquhar (1997), which involves: (i) aggregating leaf area of sunlit/shade leaves across the crown; (ii) aggregating the light absorbed by sunlit/shade leaves across the crown; (iii) aggregating maximum carboxylation and electron transport at 25°C (V_{max298} and J_{max298}), which are assumed highest at the top of the crown and to exponentially decrease towards the crown base (de Pury and Farquhar 1997). Stomatal regulation in sunlit and shade leaves is determined following the 'profit maximization' approach of Sperry et al. (2017), where the costs associated to an increasing hydraulic damage from cavitation are compared against photosynthetic gains, while taking into account minimum and maximum stomatal conductances ($G_{w,min}$ and $G_{w,max}$). The hydraulic cost function is equal to the derivative $dE_{leaf}/d\Psi_{leaf}$ of the whole-plant supply function normalized to the [0-1] interval, whereas the photosynthetic gain function is obtained by dividing A_{leaf} (gross photosynthesis) by its maximum value across the Ψ_{leaf} range. Profit maximization is conducted for the two types of leaves separately. The corresponding transpiration flows are averaged to the cohort level using the leaf area of sunlit and shade leaves as weights, and the resulting E_{leaf} value is compared to the supply function to determine all water potentials along the hydraulic pathway. Daily transpiration for the plant cohort per unit leaf area (E) is the sum of instantaneous transpiration across hourly steps divided by cohort's LAI, and daily net photosynthesis per unit leaf area (A_n) is the sum of instantaneous photosynthesis for sunlit and shade leaves, after accounting for leaf autotrophic respiration, also divided by cohort's LAI. Drought stress, cavitation and recovery - Plant drought stress is assessed at hourly time steps via different indicators: (a) relative whole-plant conductance $(k_{plant,rel})$, measured as the ratio between the slope of the supply function $(dE_{leaf}/d\Psi_{leaf})$ and maximum whole-plant hydraulic conductance $(k_{plant,max})$; (b) Leaf and stem relative water content (RWC_{leaf} and RWC_{stem}), each of them calculated using pressure-volume curves for the water content in symplastic tissues and xylem (apoplastic) tissues; (d) Percentage of stem conductance lost (PLC_{stem}) as a result of cavitation (conductivity losses are assumed completely reversible for root and leaf segments).

Symbol	Definition	Units
S		
Н	Number of soil layers	cm
	Average tree or shrub height	•
LAI	Leaf area index (one-side)	$m^2 \cdot m^{-2}$
LAIstand		m ² ·m ⁻²
CR	Leaf area index (one-side) of the whole stand	
	Crown ratio (i.e. ratio between crown length and plant height)	
Z_{50}	Depth above which 50% of the fine root mass is located	cm
Z_{95}	-	cm
WD	Depth above which 95% of the fine root mass is located	g·cm ⁻³
	Wood density	
Al2As	Leaf area to sapwood area ratio (i.e. the inverse of H_{ν} value)	m²·m²
SLA		mm ² ·mg ⁻¹
lw	Specific leaf area	cm
11 1	Leaf width	
albeao	Short-wave radiation leaf reflectance (albedo)	
<i>k</i> _{swr}	Short-wave radiation extinction coefficient	
g	Short-wave radiation extinction coefficient	mm·LAI ⁻¹
C	Crown water storage capacity	$mal H O c^{-1} m^{-2}$
\mathbf{U}_{w}	Stomatal conductance to water vapour	
$G_{w,min}$	Minimum stomatal conductance to water vapour	mol $H_2O \cdot s^{-1} \cdot m^{-2}$
$G_{w,max}$		mol $H_2O\cdot s^{-1}\cdot m^{-2}$
V	Maximum stomatal conductance to water vapour	umol CO-s ⁻¹ ·m ⁻²
• max298	Maximum rate of electron transport at 298K	
J_{max298}	Rubisco's maximum carboxylation rate at 298K	μ mol electron·s ⁻¹ ·m ⁻²
K _{stem,max}		$kg H_2 O \cdot s^{-1} \cdot m^{-1} \cdot MPa^{-1}$
Ψ	Maximum stem sapwood conductivity	MPa
	Water potential	

Table S1.1: Definition and units of symbols.

Ψ_{leaf}		MPa
	Leaf water potential	
Ψ_{stem}		MPa
	Stem water potential	
$\Psi_{rootcrown}$		MPa
	Water potential at the root crown	
$\Psi_{rootsurf}$		MPa
	Water potential inside fine roots	
Ψ_{soil}		MPa
	Soil water potential	
$\Psi_{symp,leaf}$		MPa
	Water potential of leaf symplastic compartment	
$\Psi_{symp,stem}$		MPa
	water potential of stem symplastic compartment	
k	Undraulia conductorica	mmol $H_2O \cdot s^{-1} \cdot m^{-2} \cdot MPa^{-1}$
1	Hydraune conductance	1110
K _{max}	Maximum hydraulic conductance	mmol H ₂ O·S ·m ·MPa
k.	Waxinian nyuraune conductance	mmol H.O.s ⁻¹ .m ⁻² .MPa ⁻¹
N leaf,max	Maximum leaf hydraulic conductance	
Ψ_{π} , p i.e. (MPa
1 ILP, leaf	Leaf water potential corresponding to turgor loss	ivii u
$\Psi_{50PLC \ leaf}$		MPa
	Leaf water potential corresponding to 50% of conductance loss	
$\Psi_{50PLC,stem}$		MPa
	Stem water potential corresponding to 50% of conductance loss	
$\Psi_{50PLC,root}$		MPa
	Root water potential corresponding to 50% of conductance loss	
Cleaf		
	Weibull parameter c of the vulnerability curve for leaves	
d_{leaf}		MPa
	Weibull parameter d of the vulnerability curve for leaves	
k _{stem,max}		mmol $H_2O \cdot s^{-1} \cdot m^{-2} \cdot MPa^{-1}$
	Maximum stem hydraulic conductance	
C _{stem}	Waihull percentar a of the universality surve for store	
d	weroun parameter c'or the vulneraonity curve for stem	MDa
<i>U</i> _{stem}	Weibull parameter d of the vulnerability curve for stem	MIFa
k	worden parameter a of the valueraonity curve for stem	mmol H2O·s ⁻¹ ·m ⁻² ·MPa ⁻¹
wroot,max	Maximum root hydraulic conductance	
Croot	-	
	Weibull parameter c of the vulnerability curve for roots	
d _{root}		MPa
	Weibull parameter d of the vulnerability curve for roots	
k _{rhizo,max}		mmol H ₂ O·s ⁻¹ ·m ⁻² ·MPa ⁻¹
	Maximum rhizosphere hydraulic conductance	
k _{plant,max}	Maximum whole-plant hydraulic conductance	mmol $H_2O \cdot s^{-1} \cdot m^{-2} \cdot MPa^{-1}$

$\Pi_{0,leaf}$		MPa
Eleaf	Osmotic potential at full turgor of leaves	MPa
- 100	Modulus of elasticity of leaves	
AF_{leaf}	Amonhastic fraction of looves	
W_{leaf}	Apoptastic fraction of leaves	l⋅m ⁻²
v	Leaf water storage capacity per leaf area unit	
$\Pi_{0,stem}$	Osmotic potential at full turger of stem	MPa
\mathcal{E}_{stem}	Osmotic potential at full targot of stem	MPa
	Modulus of elasticity of stem	
AF_{stem}	Apoplastic fraction of stem	
Wstem		l⋅m ⁻²
	Stem water storage capacity per leaf area unit	
E_{leaf}	Instantaneous transpiration per leaf area	mmol H ₂ O·s ⁻¹ ·m ⁻²
$E_{stem,in}$		mmol H ₂ O·s ⁻¹ ·m ⁻²
	Instantaneous vertical flow into the stem water compartment	
Estem,out	Instantaneous vertical flow out of the stem water compartment	mmol H_2O s \cdot m 2
$F_{lat,stem}$	Instantaneous lateral flow between stem symplastic and xylem compartments	mmol $H_2O \cdot s^{-1} \cdot m^{-2}$
$F_{\it lat, \it leaf}$	Instantaneous lateral flow between leaf symplastic and xylem compartments	mmol $H_2O \cdot s^{-1} \cdot m^{-2}$
A_{leaf}		$\mu mol \ CO_2 \cdot s^{-1} \cdot m^{-2}$
F	Gross instantaneous photosynthesis per leaf area	l·m ⁻² ·dav ⁻¹
L	Daily cohort transpiration per leaf area	i iii duy
A_n	Deile ach ert act als the term there is a set last anot	$gC \cdot m^{-2} \cdot day^{-1}$
WUE	Daily conort net photosynthesis per leaf area	$gC \cdot l^{-1}$
	Cohort water use efficiency	C
RWC _{leaf}	Leaf relative water content	0⁄0
RWC _{stem}		%
	Stem relative water content	
PLC_{stem}	Stem percent lost conductance	%
$dE_{leaf}/d\Psi_{leaf}$	2 percente rost conductantee	mmol H ₂ O·s ⁻¹ ·m ⁻² ·MPa ⁻¹
k	Slope of the supply function	0/
K _{plant,rel}	Relative whole-plant conductance (i.e. the ratio between $dE_{leaf}/d\Psi_{leaf}$ and $k_{plant,max}$).	70

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Appendix S2. Details of species parametrization

In the following we describe the procedures employed to determine parameter values for species within each simulated stand, including the forest inventory plots and the five experimental plots used for model evaluation (Appendix S3).

S2.1 Species-specific parameters

Several plant parameters were given the same species-specific values for all plots to be simulated (see Table S2.1). The following describes the sources employed in each case:

- *Wood density* (*WD*) Wood density values were obtained from Borràs & Gené (2012),
 Voulgaridis & Passialis (1995), Knapic et al. (2011) and Rodriguez-Calcerrada et al. (2013).
- *Leaf width* (*lw*) Values were set according to the average leaf size of each species.
- *Albedo* and *light extinction* (k_{swr}) Values were drawn from Geiger et al. (2009), Aubin et al.
 (2000) and Bréda et al. (2003), after classifying species into functional groups.
- *Canopy water storage capacity per LAI unit* (g) Storage capacity was measured for *Quercus ilex* canopies in Puéchabon (Limousin et al. 2008), and we used the same values for all broadleaved species. We set g = 1 for all three pines, according to De Cáceres (2015).
- Stomatal conductance ($G_{w,min}$ and $G_{w,max}$) Values for minimum stomatal conductance ($G_{w,min}$) were taken from Duursma et al. (2018), including averages for phylogenetic orders and an overall mean value of 0.0045 mol H₂O·s⁻¹·m⁻² for missing data. Species maximum stomatal conductance values ($G_{w,max}$) were drawn from multiple bibliographic sources (Ogaya and Peñuelas 2003, Limousin et al. 2010, Rodríguez-Calcerrada et al. 2013, Sperlich et al. 2015, Hoshika et al. 2018).
- *Photosynthetic capacity* (V_{max298} and J_{max298}) Species values for Rubisco's maximum carboxylation rate (V_{max298}) and maximum rate of electron transport (J_{max298}), both at 25°C, were compiled from bibliography (Dreyer et al. 2001, Jones et al. 1995, Maroco et al. 2002,

Medlyn et al. 1999, Kuusk et al. 2018). Missing values for J_{max298} were estimated from V_{max298} following the relationship established in Walker et al. (2014).

- *Leaf maximum conductance* (k_{leaf, max}) Leaf maximum hydraulic conductance was empirically determined for *Quercus ilex* at Puéchabon (Limousin et al., in prep.); the remaining values were taken from Sack et al. (2003).
- Leaf hydraulic vulnerability (c_{leaf} and d_{leaf}) Values for the leaf water potential corresponding to 50% PLC ($\Psi_{50PLC, leaf}$) were taken for *Quercus ilex*, *Pinus nigra* and *Q. pubescens* from Bartlett et al. (2016). *P. sylvestris* and *P. halepensis* were assumed to have the same leaf vulnerability as *P. nigra*, whereas $\Psi_{50PLC, leaf}$ of the remaining species was estimated from an empirical relationship with water potential corresponding to leaf turgor loss point ($\Psi_{50PLC, leaf} =$ $0.99 \cdot \Psi_{TLP, leaf} + 0.248$; R²=0.43). $\Psi_{88PLC, leaf}$ values were estimated from $\Psi_{50PLC, leaf}$ (see stem vulnerability) and Weibull parameters (c_{leaf} and d_{leaf}) were calculated from them.
- Maximum sapwood reference conductivity (K_{stem, max}) Species-specific values for K_{stem, max}
 were obtained from several sources (Oliveras et al. 2003, Maherali et al. 2004; Rosas et al. 2019; Martin-StPaul unpubl.).
- Stem hydraulic vulnerability (c_{stem} and d_{stem}) Water potential corresponding to 12%, 50% and 88% PLC for stems (Ψ_{12PLC,stem}, Ψ_{50PLC, stem} and Ψ_{88PLC, stem}, respectively) were compiled from Lobo et al. (2018), Lens et al. (2016) and Martin-StPaul et al. (2017). When Ψ_{88PLC, stem} were missing, we used an empirical relationship calibrated from Choat et al. (2012) (Ψ_{88PLC, stem} = 1.2593 · Ψ_{50PLC, stem} -1.4264). Weibull parameters (c_{stem} and d_{stem}) were then calculated from Ψ_{50PLC, stem} and Ψ_{12PLC,stem} or Ψ_{88PLC, stem} values.
- *Root hydraulic vulnerability* (*c_{root}* and *d_{root}*) Values for root Ψ_{50PLC, root} were taken from Bartlett et al. (2016), either directly or estimated from Ψ_{50PLC, stem} using an empirical relationship calibrated from the same source (Ψ_{50PLC, root} = 0.742·Ψ_{50PLC, stem} + 0.4892; R² = 0.7467). Ψ_{88PLC, root} values were estimated from Ψ_{50PLC, root} (see stem vulnerability) and Weibull

parameters (c_{root} and d_{root}) were calculated from them. Root vulnerability of *Pinus sylvestris* and *P. nigra* was assumed equal to *P. halepensis*.

- Leaf pressure volume curves (Π_{0,leaf}, ε_{leaf} and AF_{leaf}) Parameters of the pressure-volume curves for leaves were taken from Bartlett et al. (2012), Serrano et al. (2005) and Limousin et al. (in prep.). Values for pines were taken from *Pinus ponderosa* and those of *Buxus sempervirens* were assumed to be equal to average values for Mediterranean species.
- Stem pressure volume curves (π_{0,stem}, ε_{stem} and Af_{stem}) Pressure-volume curve parameters for stems (π_{0,stem} ε_{stem}) were calculated using empirical relationships with wood density (Christoffersen et al. 2016):

 $\pi_{0,stem} = 0.52 - 4.16 \cdot WD$

$$\varepsilon_{stem} = \sqrt{1.02 \cdot e^{8.5 \cdot WD} - 2.89}$$

whereas stem apoplastic fraction was assumed equal to $AF_{stem} = 0.8$ for all species.

Table S2.1: Species-specific parameters values with source reference numbers in parentheses. Parameter definition and units can be found in Table S1.1. Water potentials corresponding to 50% of conductance loss for leaves, stems and roots (i.e., $\Psi_{50PLC, leaf}$, $\Psi_{50PLC, stem}$ and $\Psi_{50PLC, root}$) are included for comparability.

Parameter	Quercus ilex	Pinus sylvestris	Pinus nigra	Pinus halep.	Quercus pubesc.	Quercus faginea	Arbutus unedo	Phill. latifolia	Buxus sempervirens
WD	0.90 (1)	0.51 (2)	0.53 (2)	0.55(2)	0.86 (2)	0.85 (3)	0.82 (1)	0.76 (1)	0.85 (4)
lw	3.0	0.1	0.1	0.1	5.0	4.0	4.0	2.0	1.0
albedo	0.18 ⁽⁵⁾	0.14 (5)	0.14 ⁽⁵⁾	0.14 ⁽⁵⁾	0.18 (5)	0.18 (5)	0.15 (5)	0.15 (5)	0.15 ⁽⁵⁾
k _{swr}	0.55 ⁽⁶⁾	0.50 (6)	0.50 (6)	0.50 (6)	0.55 (6)	0.55 (6)	0.40 ⁽⁷⁾	0.40 (7)	0.55 (7)
g	0.8 (8)	1.0 ⁽⁹⁾	1.0 (9)	1.0 (9)	0.8 (8)	0.8 (8)	0.8 ⁽⁸⁾	0.8 (8)	0.8 (8)
$G_{w,min}$	0.0045 (10)	$0.00316^{(10)}$	0.003 (10)	0.00203 (10)	$0.0045^{(10)}$	$0.0045^{(10)}$	0.004 ⁽¹⁰⁾	0.0055 (10)	$0.0049^{(10)}$
$G_{w,max}$	0.21 (11)	0.22 (12)	0.22 (12)	0.190 (13)	0.20 ⁽¹⁴⁾	0.26 (12)	$0.17^{(12)}$	0.085 (15)	0.052 (4)
V_{max298}	66.2 (16)	60.3 (16)	93 (17)	62.5 (17)	66 ⁽¹⁷⁾	90 (18)	66 ⁽¹⁹⁾	64.7 ⁽¹⁶⁾	71.5 (20)
J_{max298}	130 (16)	118 (16)	115 (17)	129.5 (17)	150 (14)	157 (18)	187 (19)	136 (16)	123.1 (20)
K _{stem,max}	0.4 (21)	0.45 ⁽²²⁾	0.41(22)	0.15 ⁽²³⁾	0.7 ⁽²¹⁾	0.7 ⁽²¹⁾	0.54 (22)	0.408 ⁽²²⁾	0.15 ⁽³²⁾
$k_{leaf,max}$	2.63 ^(24a)	4 ^(24b)	4 ^(24b)	4 ^(24b)	3 ^(24b)	5 ^(24b)	4 ^(24b)	3 ^(24b)	3 ^(24b)
$\Psi_{50PLC,leaf}$	-3.90 ^(24a)	-1.52 (25)	-1.52 (25)	-1.52 ⁽²⁵⁾	-2.83 (25)	-2.63 (26)	-1.42 (26)	-2.77 (26)	-2.15 ⁽²⁶⁾
Cleaf	5.41 ^(24a)	1.42 (25)	1.42 (25)	1.42 (25)	1.97 (25)	1.90 (26)	1.37 (26)	1.95 (26)	1.71 (26)
d _{leaf}	-4.18 ^(24a)	-1.97 (25)	-1.97 ⁽²⁵⁾	-1.97 ⁽²⁵⁾	-3.42 (25)	-3.19 ⁽²⁶⁾	-1.86 (26)	-3.34 ⁽²⁶⁾	-2.66 ⁽²⁶⁾
$\Psi_{50PLC,stem}$	-7.13 ^(27a)	-3.09 ^(27b)	-3.00 ^(27b)	-5.14 ^(27b)	-4.81 ^(27c)	$-4.74^{(27a^*)}$	-7.84 ^(27b)	-9.53 ^(27b+)	-8.00 ^(27b)
C _{stem}	3.56 ^(27a)	10.24 ^(27b)	3.14 ^(27b)	12.71 ^(27b)	10.27 ^(27c)	$7.74^{(27a^*)}$	13.70 ^(27b)	17.32 ^(27b+)	3.56 ^(27b)
d _{stem}	-7.72 ^(27a)	-3.20 ^(27b)	-3.37 ^(27b)	-5.29 ^(27b)	-4.98 ^(27c)	$-4.96^{(27a^*)}$	-8.05 ^(27b)	-9.73 ^(27b+)	-8.87 ^(27b)
¥ 50PLC,root	-1.67 ⁽²⁵⁾	-0.88 (25)	-0.88 (25)	-0 .88 ⁽²⁵⁾	-1.96 ⁽²⁹⁾	-1.25 (29)	-1.20 ⁽²⁵⁾	-5.30 ⁽²⁵⁾	-5.44 (29)
Croot	1.49 ⁽²⁵⁾	1.06 ⁽²⁵⁾	1.06 (25)	1.06 (25)	1.63 (29)	1.28 (29)	1.25 (25)	2.64 (25)	2.66 ⁽²⁹⁾
u _{root}	-2.13 (25)	-1.24 (25)	-1.24 (25)	-1.24 ⁽²⁵⁾	-2.45 ⁽²⁹⁾	-1.66 ⁽²⁹⁾	-1.61 (25)	-6.09 ⁽²⁵⁾	-6.24 ⁽²⁹⁾
11 _{0,leaf}	-2.66 ⁽²⁴⁾	-2.11 (30)	-2.11 (30)	-2.11 (30)	-2.07 (30)	-2.14 (30)	-0.74 (30)	-3.10 ⁽³¹⁾	-2.12 ⁽³²⁾
č leaf	10.57 ⁽²⁴⁾	12.18 ⁽³⁰⁾	12.18 (30)	12.18 (30)	12.33 (30)	14.53 (30)	7.00 ⁽³⁰⁾	11.04 ⁽³¹⁾	19.01 (32)
AF_{leaf}	0.43 (24)	$0.16^{(30)}$	$0.16^{(30)}$	$0.16^{(30)}$	0.10 (30)	$0.19^{(30)}$	0.29 (33)	0.20 (31)	0.29 (33)

	0.80(33)	0.80 (33)	0.80 (33)	0.80(33)	0.80 (33)	0.80 (33)	0.80 (33)	0.80 (33)	0.80 (33)
AFstern	46.26 ⁽³⁴⁾	8.50 (34)	9.58 (34)	10.43 (34)	39.71 ⁽³⁴⁾	37.07 (34)	32.90 ⁽³⁴⁾	25.47 ⁽³⁴⁾	37.39 (34)
E	-3.22 ⁽³⁴⁾	-1.58 (34)	-1.70 ⁽³⁴⁾	-1.78 ⁽³⁴⁾	-3.07 ⁽³⁴⁾	-3.01 (34)	-2.89 ⁽³⁴⁾	-2.64 ⁽³⁴⁾	-3.02 (34)

References: ¹Voulgaridis & Passialis (1995); ²Borràs & Gené (2012); ³Knapic et al. (2011); ⁴ Rodriguez-Calcerrada et al. (2013); ⁵ Geiger et al. (2009); ⁶Bréda et al. (2003); ⁷Aubin et al. (2000); ⁸Limousin et al. (2008); ⁹De Cáceres et al. (2015); ¹⁰Duursma et al. (2018); ¹¹Limousin et al. (2010b); ¹²Hoshika et al. (2018); ¹³Morte et al. (2001); ¹⁴Sperlich et al. (2015); ¹⁵Ogaya & Peñuelas (2003); ¹⁶Medlyn et al. (1999); ¹⁷Nadal-Sala et al. (2013); ¹⁸Dreyer et al. (2001); ¹⁹Jones et al. (1995); ²⁰Regressions from Walker et al. (2004); ²¹Rosas et al. (2019); ²²Maherali et al. (2004); ²³Oliveras et al. (2003); ^{24a}Limousin et al. (2016); ^{27a}Lobo et al. (2018); ^{27b}Lens et al. (2016); ^{27c}Martin-StPaul et al. (2017); ²⁸Choat et al. (2012); ²⁹Relationship with $\Psi_{50,stem}$ from Bartlett et al. (2016); ³⁰Bartlett et al. (2012); ³¹Serrano et al. (2005); ³²Martin-StPaul (unpubl.); ³³Default value in MEDFATE; ³⁴from wood density, following Christoffersen et al. (2016); ^{*}Values for *Quercus robur*; ⁺ Values for *P. angustifolia*.

S2.2. Plot- and species-specific parameters

Here we describe the parametrization of plot- and species-specific plant parameters (exceptions were values were only species-specific are indicated):

- Average height (H) Tree height was measured in all IFN plots and experimental plots except Armallones, where H values were derived from diameter-height allometries (Burriel et al. 2004).
- Specific leaf area (SLA) Specific leaf area was measured in situ for each species in Prades, Puéchabon and Armallones experimental plots; the remaining values were obtained from Burriel et al. (2004). SLA values for IFN plots were species-specific, taking the values of the corresponding species in experimental plots (SLA for *P. halepensis* was taken FontBlanche).
- Huber values (H_v = 1/Al2As) Huber values for Puéchabon, Prades, Can Balasc and Armallones, were measured on excised branches, whereas values for FontBlanche were measured from the same species at other locations (Martin-StPaul unpubl.). As for SLA, H_v values for IFN plots were species-specific, taking the values of the corresponding species in experimental plots.

- Leaf area index (LAI) LAI values were obtained in experimental plots from plot-specific leaf biomass allometries or optical measurements. In the case of Armallones, measured LAI_{stand} was partitioned among species according to foliar biomass proportions derived from tree data using allometries. For IFN plots, LAI estimates were derived from tree data using foliar biomass allometries and *SLA*. Foliar biomass allometries were calibrated using data from (Burriel et al. 2004) and the leaf biomass of a given tree cohort (B_{leaf}) followed the equation (Ameztegui et al. 2017) $B_{leaf} = N \cdot a \cdot DBH^b \cdot e^{c \cdot BAL} \cdot DBH^{d \cdot BAL}$, where N is the density of the tree cohort, DBH is diameter at breast height (DBH) and BAL is the basal area of larger trees in the same stand.
- *Crown ratio* (*CR*) Crown ratio estimates were obtained using available allometries based on tree diameter data (Hasenauer and Monserud 1996).
- *Root distribution* (*Z*₅₀ and *Z*₉₅) Depths corresponding to cumulative 50% and 95% of fine roots (*Z*₅₀ and *Z*₉₅) were derived for each plot and species from empirical relationships obtained by Cabon et al (2018), based on soil properties, *LAI*_{stand}, species hydraulic vulnerability and climatic variables.
- Stem maximum hydraulic conductance (k_{s, max}) Estimation of stem maximum hydraulic conductance followed the work of Savage et al. (2010), Olson et al. (2014) and Christoffersen et al. (2016). Calculations are based on tree/shrub height (*H*), maximum sapwood reference conductivity (K_{s, max, ref}), and Huber value (H_v).
- Root maximum hydraulic conductance $(k_{root,max})$ Maximum root conductances were estimated assuming that roots represented 40% of total whole-plant resistance, even though empirical evidence suggests that this proportion is species-dependent and varies with tree height/age (Sperry et al. 1998, Martínez-Vilalta et al. 2007). Following Sperry et al. (2016), we divided total root system maximum conductance among soil layers in proportion to the

inverse of the transport distance to each layer (i.e. depth to the center of layer plus the radial spread or roots within each layer).

- Maximum whole-plant conductance (k_{plant, max}) Whole-plant conductance was calculated from maximum conductance values of leaf, stem and root segments.
- *Rhizosphere conductance* (*k_{rhizo, max}*) Following Sperry et al. (2016), maximum rhizosphere conductance (*k_{rhizo, max}*) is determined from an expected 'average percentage rhizosphere resistance' (15%) after all other continuum elements are parametrized. The average resistance for a given estimate of *k_{rhizo, max}* is found by evaluating the percentage of continuum resistance corresponding to the rhizosphere for a range of soil water potential values.
- Stem storage capacity (W_{stem}) Water storage capacity of sapwood tissue per leaf area unit (in L·m⁻²) was estimated from tree height and Huber value, following $W_{stem} = 10^3 \cdot H \cdot H_v \cdot \Theta$, where Θ is sapwood porosity and was estimated from wood density, $\Theta = 1 (WD/1.54)$, assuming a fixed density of wood substance.
- *Leaf storage capacity* (*W*_{*leaf*}) Leaf storage capacity (l·m⁻²) was estimated from *SLA* (m²·kg⁻¹) assuming a leaf density of 0.7 g/cm³ and a porosity of 0.545 cm³/cm³:

$$W_{leaf} = \frac{0.545}{SLA \cdot 0.7}$$

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Appendix S3. MODEL EVALUATION IN EXPERIMENTAL PLOTS

S3.1 Experimental plots

In order to evaluate the predictive capacity of MEDFATE in holm oak mixed forests, we compiled data from five experimental forest plots co-dominated by *Quercus ilex* (Holm oak) and located in Spain and south-eastern France (Table S3.1):

- Prades plot is placed on a dense mixed forest whose upper canopy is dominated by *P*. sylvestris trees and an underlying story dominated by QI. The plot is located in the Titllar valley of the Poblet Forest Natural Reserve (NE Spain). Soils are mostly Xerochrepts with fractured schist and clay loam texture and a relatively high gravel content, although outcrops of granitic sandy soils are also present (Poyatos et al., 2013).
- Puéchabon plot is a dense evergreen forest dominated by *Q. ilex*, managed as a coppice for centuries and clear cut for the last time in 1942. Understorey species are *Buxus sempervirens*, *Phillyrea latifolia*, *Pistacia terebinthus* and *Juniperus oxycedrus*, which together compose a sparse shrubby layer with percentage cover of <25% (Limousin et al., 2010). The soil has silty clay loam texture and is extremely rocky, formed on a limestone of Jurassic origin, with an average volumetric fractional content of stones of 75% for the top 0-50 cm and 90% below (Rambal et al., 2003).
- 3. The FontBlanche experimental site is mixed Mediterranean forest located in the south-eastern of France at 10 km from Marseille. An upper vegetation layer is dominated by Pinus halepensis whereas a lower tree strata is dominated by Quercus ilex. The understory is composed different woody species: Phillyrea latifolia, Quercus pubescens, Quercus coccifera, Arbutus unedo, Pistacia terebinthus. The rocky substrate is formed by a Cretaceous rudist-bearing limestone with an average rock volumetric fraction of 0.5 in the first 70 cm and

about 0.9 below. Texture in the topsoil (within 0–50 cm) is a homogeneous silty clay loam (Simioni et al. 2016).

- 4. *Can Balasc* experimental site is located in the coastal massif of Collserola (NE Spain). Soils are predominantly developed above lithological strata of shales and granite and have sandy-loam texture. The study plot is dominated by QI, accompanied by downy oak (*Q. pubescens* Mill.) and strawberry tree (*Arbutus unedo* L.), with some scattered Aleppo pines (*P. halepensis* Mill.) above the main canopy. The understory is a dense stratum mainly consisting of *Pistacia lentiscus*, *Erica arborea* L., *Phillyrea latifolia* L., *Rhamnus alaternus* and other less abundant species (Sánchez-Costa et al., 2015).
- Armallones plot contains a sparse forest located at the Alto Tajo Natural Park, Guadalajara (central Spain). Soils are shallow, calcisols from Cretaceous and Jurassic limestone. The plot is co-dominated by *Quercus faginea* Lam., *Pinus nigra* ssp. *salzmannii* J.F. Arnold and *Quercus ilex* ssp. *ballota* (Desf.) Samp. (Forner et al., 2018).

All experimental are dominated by QI in terms of leaf area index (LAI), but secondary species vary from stand to stand. Among those, we selected for each experimental site those species for which there was enough trait data and validation data (i.e. sapflow data) to conduct a model evaluation (see Table S3.1).

Table S3.1: Main characteristics of the five experimental plots, including their location, topography, climate, leaf area index (*LAI*_{stand}), species composition, soil properties and period used for model evaluation.

	Prades	Puéchabon	Fontblanche	Can Balasc	Armallones	
Longitude (°)	1.02	3.60	5.68	2.07	-2.33	
Latitude (°)	41.33	43.74	43.24	41.43	40.78	
Elevation (m)	1018	270	420	270	1079	
Slope (°)	35	0	0	0.86	26	
Aspect (°)	8.53	0	0	90	270	
MAP (mm)	664	916	722	585	490	
MAT (°C)	11.3	13.2	13.5	17.0	10.3	
LAI $(m^2 \cdot m^{-2})$	3.2	2.3	2.5-2.7	3.3	1.1	
Species selected for model evaluation	Quercus ilex, Pinus sylvestris	Quercus ilex, Buxus sempervirens	Quercus ilex, Phillyrea latifolia, Pinus halepensis	Quercus ilex, Arbutus unedo, Quercus pubescens, Pinus halepensis	Quercus ilex, Quercus faginea, Pinus nigra	
Parent material	Schist	Limestone	Limestone	Shales and granite	Limestone	
Soil texture class (USDA)	Loam	Clay loam	Clay loam	Sandy loam	Loam	
Coarse fragments (% vol) per layer (0-30;30- 100;100-200;200-450)	45/70/80/80	75/75/84/88	50/65/85/95	20/30/85/90	45/60/70/80	
Extractable water (mm; 0- 4.5 m; -4 MPa)	195	140	141	185	218	
Year validation	2011	2004-2006	2014	2011	2011-2013	
References	(Aguadé et al., 2015)	(Limousin et al., 2010)	(Simioni et al., 2016)	(Sánchez-Costa et al., 2015)	(Forner et al., 2018)	

S3.2 Model parametrization

For all forest plots we considered four soil layers down to a total depth of 4.5 m: 0-30 cm; 30-100 cm; 100-200 cm; 200-450 cm (Table S3.1). Soil parameters were defined from in situ soil profile measurements in the case of Prades, Puéchabon and Can Balasc. Soil properties at Armallones were obtained from a query to the SoilGrids world database (Hengl et al., 2017). Soil texture and bulk density at FontBlanche were assumed equal to those at Puéchabon. While the proportion of coarse fragments were measured in the two topmost layers, coarse fragments were manually tuned for two bottom ones (100-200 cm and 200-450 cm), in order to achieve a known or expected amount of extractable water from field capacity to -4MPa according to observed transpiration data. Plant trait

parameters were defined as explained in Appendix S2. While species-specific values are reported in Table S2.1 of Appendix, in Table S3.2 below we report the plot- and species-specific parameters for the experimental plots. Fig. S3.1 shows vertical profiles of leaf area density and percentage of fine roots as well as vulnerability curves of each species in each experimental plot.

Table S3.2: Plot- and species-specific parameters in the five experimental plots (other species parameters can be found in Table S2.1). Parameter definition and units are given in Table S1.1.

	Prades		Puéchabon		FontBlanche				Can B	alasc	Armallones			
Param.	Quercus ilex	Pinus sylvestris	Quercus ilex	Buxus semper.	Quercus ilex	Phill. latif.	Pinus halep.	Quercus ilex	Arbutus unedo	Pinus halep.	Quercus pubesc.	Quercus ilex	Quercus faginea	Pinus nigra
Н	500	1424	530	200	496	323	1196	1020	810	1710	960	882	779	1144
LAI	2.69	0.58	1.9	0.27	1.75	0.25	0.78	2.50	0.10	0.30	0.30	0.25	0.61	0.22
CR	0.56	0.53	0.63	0.89	0.55	0.50	0.58	0.55	0.50	0.50	0.57	0.64	0.64	0.47
Z_{50}	72	49	45	25	80	46	58	30	30	24	30	38	38	28
Z_{95}	400	278	196	91	400	102	333	104	95	76	78	138	138	94
Al2As	1311	791	1541	4255	1541	1699	631	1009	1297	631	1488	1541	1488	1272
SLA	5.87	6.289	4.55	5.19	5.87	9.27	4.34	5.87	6.69	4.34	10.4	5.87	7.91	4.35
k _{stem,max}	4.54	5.09	3.81	1.90	3.87	5.33	2.41	5.03	6.64	2.23	5.32	3.384	5.957	3.177
k _{root,max}	2.50	3.36	2.33	1.74	2.35	2.88	2.25	2.59	3.74	2.15	3.87	2.22	4.48	2.66
W_{leaf}	0.13	0.12	0.17	0.15	0.13	0.08	0.18	0.13	0.12	0.18	0.07	0.13	0.10	0.18
Wstem	1.59	12.09	1.43	0.21	1.34	0.96	12.15	4.20	2.92	17.37	2.83	2.43	2.27	6.21
$k_{plant,max}$	0.999	1.344	0.933	0.698	0.939	1.152	0.901	1.036	1.498	0.859	1.547	0.888	1.794	1.062
R_{leaf} (%)	38.0%	33.6%	35.5%	23.3%	35.7%	38.4%	22.5%	39.4%	37.4%	21.5%	30.9%	33.8%	29.9%	26.6%
R _{stem} (%)	22.0%	26.4%	24.5%	36.7%	24.3%	21.6%	37.5%	20.6%	22.6%	38.5%	29.1%	26.2%	30.1%	33.4%
R _{root} (%)	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%	40.0%

Fig. S3.1. Species above-ground leaf area density, belowground fine root distribution and segment vulnerability curves for each forest stand.



a) Distribution of leaf area density (upper row) and fine roots (lower row)

b) Vulnerability curves of leaves (upper row), stems (middle row) and roots (lower row)



S3.3 Model evaluation

We conducted model evaluation exercises focusing on MEDFATE's ability to reproduce topsoil moisture, plant transpiration and water status dynamics. Daily weather, soil moisture at 25-30 cm and sap flow data for all sites, except Fontblanche, were accessed from the SAPFLUXNET data base (Poyatos et al., 2016). Soil water content was compared in terms of relative extractable water (REW), defined as a proportion of soil moisture at field capacity, which in the case of observed data was set to the 90% percentile of data. Tree sap flux density per sapwood area was scaled to daily transpiration per unit leaf area using tree-specific H_v measurements and then averaged across trees of the same species. Sapflow data in Armallones was available as flux density per tree. Since leaf area of instrumentalized trees was missing we could not scale values to daily flow per unit area. Predawn/midday leaf water potential (Mpa) measurements were available for some species and days in all plots except at Can Balasc. For each variable (REW, transpiration per unit area and pre-dawn/midday water potentials) we calculated the Nash-Sutcliffe efficiency coefficient as well as the mean absolute error and the mean bias.

Model evaluation statistics are shown in Table S3.3, whereas graphical comparisons for each plot and variable are given in Figs. S3.2-6. Predictive capacity for moisture dynamics was good at Prades, Puéchabon and FontBlanche (Figs. S3.2a, S3.3a and S3.4a, respectively). Simulated moisture dynamics was reasonably good at Can Balasc (Fig. S3.5a) excepting during winter periods. A similar mismatch is also observed for Armallones (Fig. S3.6a), in addition to observed soil moisture being lower during the summer drought compared to the model. The ability of the model to predict daily transpiration rates per unit leaf area was acceptable, in general. However, an overestimation of transpiration was often observed for *Quercus ilex* in summer days for several experimental plots (e.g., Figs. S3.2-4b), also observed for other oaks (Figs. S3.5b). Transpiration rates of pine trees were reasonably modelled, except for overestimations in the case of *Pinus halepensis* at FontBlanche (Fig. S3.4b). Note that only curve shapes should be compared in the case of Armallones, since the sapflow

data could not be propertly scaled to transpiration per unit leaf area. Model predictions were generally not satisfying in terms of leaf water potentials, including substantial (~1MPa) biases for some species in some stands. Underestimation of summer leaf water potentials (i.e. more negative than observed) occurred specially in the case of pines (Figs. S3.2c and S3.3c), but also for *Quercus ilex* and *Q*. *faginea* in FontBlanche and Armallones (Figs. S3.4c and S3.6c). This indicates overestimation of summer drought stress for these species.

Table S3.2. Results of the evaluation of predictive capacity of MEDFATE on the five experimental plots. Predicted daily series for soil water content, transpiration per leaf area, leaf predawn water potential and leaf midday water potential are compared to observations (n – number of observations; NSE⁻Nash-Sutcliffe efficiency coefficient; MAE – Mean absolute error; Bias – Mean bias).

Soil water content (% REW)				$\begin{array}{c} Transpiration \ per \ leaf \ area \\ (l \cdot m^{-2} \cdot d^{-1}) \end{array}$				Predawn leaf water potential (MPa)				Midday leaf water potential (MPa)				
Plot	n	NSE	MAE	Bias	Species	n	NSE	MAE	Bias	n	NSE	MAE	Bias	NSE	MAE	Bias
Prades	363	0.754	0.109	0.045	Pinus sylvestris	362	0.759	0.086	0.008	4	-4.76	0.916	-0.859	-31.8	1.241	-1.220
					Quercus ilex	253	0.148	0.111	0.094	4	0.582	0.768	-0.449	0.609	0.697	-0.658
Puéchabon	1012	0.722	0.081	0.043	Quercus ilex	1087	0.056	0.153	0.072	28	0.688	0.493	0.010	0.043	0.600	0.341
Fontblanche	364	0.707	0.106	0.076	Quercus ilex	309	-0.392	0.161	0.127	3	-3.65	0.924	-0.924	-4.19	0.785	-0.786
					Pinus halepensis	300	-0.013	0.086	0.047	3	-1.80	0.586	-0.413	-14.0	0.714	-0.593
Can Balasc	339	0.159	0.152	-0.031	Arbutus unedo	315	0.102	0.152	-0.149							
					Pinus halepensis	282	0.271	0.120	-0.093							
					Quercus pubesc.	315	-0.031	0.197	0.109							
					Quercus ilex	315	-0.462	0.189	-0.007							
Armallones	1013	0.280	0.269	0.225	Pinus nigra	927	0.462	0.230	-0.059	6	-2.09	0.831	-0.296	-8.85	0.765	-0.665
					Quercus faginea	805	0.380	0.359	-0.095	6	-5.88	0.943	-0.726	-8.89	0.941	-0.316
					Quercus ilex	945	0.376	0.294	0.040	6	-0.225	0.768	-0.505	-2.60	0.910	-0.910

Fig. S3.2: Prades

a) Soil water content









c) Predawn and midday leaf water potentials

Fig. S3.3: Puéchabon





b) Transpiration per leaf area



c) Predawn and midday leaf water potentials



Fig. S3.4: Fontblanche

a) Soil water content









c) Predawn and midday leaf water potentials

Fig. S3.5: Can Balasc





b) Transpiration per leaf area



Fig. S3.6: Armallones

a) Soil water content



b) Transpiration per leaf area





c) Predawn and midday leaf water potentials

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Appendix S4. Supplementary tables

Table S4.1: Modified competitor's trait (parameter) values in model sensitivity analyses. Values of the central (0%) column are those of the QI cohort. Columns 'Min. obs.' and 'Max. obs.' indicate the minimum and maximum parameter values among species in experimental plots. Shaded cells correspond to modified trait values outside the observed range. Parameter definitions and units can be found in Table S1.1.

Parameter Group	Parameter	-80%	-60%	-40%	-20%	0%	+20%	+40%	+60%	+80%	Min. obs.	Max. obs.
Plant height	Н	106.0	212.1	318.1	424.2	530.2	636.3	742.3	848.4	954.4	323	1710
Fine root	Z_{50}	9.0	18.0	27.1	36.1	45.1	54.1	63.2	72.2	81.2	24	80
distribution	Z95	39.2	78.3	117.5	156.7	195.8	235.0	274.1	313.3	352.5	76	400
Hydraulic	$k_{leaf,max}$	0.5	1.1	1.6	2.1	2.6	3.2	3.7	4.2	4.7	2.6	5
efficiency (<i>k</i> _{plant,max})	k _{stem,max}	0.8	1.5	2.3	3.0	3.8	4.6	5.3	6.1	6.9	1.9	6.6
	k _{root,max}	0.5	0.9	1.4	1.9	2.3	2.8	3.3	3.7	4.2	1.7	4.5
	$k_{plant,max}$	0.2	0.4	0.6	0.7	0.9	1.1	1.3	1.5	1.7	0.7	1.8
Vulnerability to	d _{leaf}	-1.3	-1.7	-2.5	-3.3	-4.2	-5.0	-5.9	-6.7	-7.5	-1.8	-4.8
embolism (<i>d</i>)	<i>d</i> _{stem}	-2.3	-3.1	-4.6	-6.2	-7.7	-9.3	-10.8	-12.4	-13.9	-3.2	-9.7
	d _{root}	-0.6	-0.9	-1.3	-1.7	-2.1	-2.6	-3.0	-3.4	-3.8	-1.2	-6.2
Photosynthetic	V _{max298}	13.2	26.5	39.7	53.0	66.2	79.4	92.7	105.9	119.2	60	93
capacity (V_{max}/J_{max})	J_{max298}	26.0	52.0	78.0	104.0	130.0	156.0	182.0	208.0	234.0	115	157
Stomatal cond.	$G_{w,max}$	0.04	0.08	0.13	0.17	0.21	0.25	0.29	0.34	0.39	0.17	0.26
Storage capacity	W _{leaf}	0.03	0.07	0.10	0.14	0.17	0.21	0.24	0.27	0.31	0.07	0.18
	W _{stem}	0.28	0.57	0.86	1.14	1.43	1.72	2.00	2.29	2.57	0.21	17.4

Table S4.2: Trait (parameter) value differences between each competitor species and QI, averaged across SFI3 plots. Parameter definitions and units can be found in Table S1.1.

Parameter	H	Z ₅₀	Z_{95}	k _{root,max}	k _{stem,max}	$k_{leaf,max}$	d _{root}	<i>d</i> _{stem}	d _{leaf}	V_{max298}	J_{max298}	G _{w,max}	W _{stem}	W _{leaf}
Pinus halepensis	679	-73	-258	-0.08	-1.45	1.37	0.89	2.43	2.21	-4	-1	-0.02	10.72	0.05
Pinus nigra	473	-54	-130	0.38	-0.61	1.37	-0.07	4.35	2.21	27	-15	0.01	3.57	0.05
Pinus sylvestris	405	-85	-621	1.00	1.04	1.37	0.89	4.52	2.21	-6	-12	0.01	6.37	-0.01
Quercus pubescens	208	-52	-785	1.26	-0.08	2.37	-1.55	2.74	0.76	0	20	-0.01	-0.10	-0.06
Quercus faginea	222	0	0	2.14	2.15	3.37	-1.49	2.75	0.98	34	34	0.39	0.87	-0.03
Arbutus unedo	-195	-56	-607	1.28	2.22	1.37	0.52	-0.33	2.32	0	57	-0.04	-1.01	-0.02
Phillyrea latifolia	-344	-86	-1899	0.60	1.75	0.37	-3.96	-2.01	0.84	-2	6	-0.13	-0.84	-0.05
Buxus sempervirens	-290	-58	-1024	-0.62	-2.01	0.37	-4.12	-1.14	1.52	5	-7	-0.16	-1.14	-0.02

Appendix S5. Supplementary figures

Fig. S5.1: Simulated species- and stand-level water use, photosynthesis and summer drought stress in pure and mixed (50-50% LAI) stands of QI and *Pinus halepensis*: (a) annual transpiration (*E*), (b) annual net photosynthesis (A_n), (c) relative whole-plant conductance ($k_{plant,rel}$) and (d) leaf relative water content (RWC_{leaf}). Species-level *E* and A_n values are calculated per unit leaf area, whereas stand-level values are presented per unit soil area. Plot axes are the leaf area index of the stand (LAI_{stand}) and summer moisture index (MI_{summer}). Point size and color indicate the magnitude of the response. The corresponding mixing effects are shown in Fig. S5.2.



Fig. S5.2: Species and stand-level effects of mixing QI with *Pinus halepensis* on (a) annual transpiration (*E*), (b) annual net photosynthesis (A_n), (c) relative whole-plant conductance ($k_{plant,rel}$) and (d) leaf relative water content (RWC_{leaf}). Plot axes are the leaf area index of the stand (LAI_{stand}) and summer moisture index (MI_{summer}). Point size and color indicate the magnitude and sign of the mixing effect. Species-level mixing effects are estimated as the difference between the response in the 50-50% mixed stand and a pure stand of the same species (Fig. S5.1). Stand-level mixing effects are estimated as indicated in the manuscript.



Fig. S5.3: Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50-50% LAI) stands of QI and *Pinus nigra* (see caption for Fig. S5.1).The corresponding mixing effects are shown in Fig. S5.4.



Fig. S5.4: Species and stand-level effects of mixing QI with *Pinus nigra* (see caption for Fig. S5.2). The corresponding responses in pure and mixed stands are shown in Fig. S5.3.



Fig. S5.5: Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50-50% LAI) stands of QI and *Pinus sylvestris* (see caption for Fig. S5.1). The corresponding mixing effects are shown in Fig. S5.6.



Fig. S5.6: Species and stand-level effects of mixing QI with *Pinus sylvestris* (see caption for Fig. S5.2). The corresponding responses in pure and mixed stands are shown in Fig. S5.5.



Fig. S5.7: Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50-50% LAI) stands of QI and *Quercus pubescens* (see caption for Fig. S5.1). The corresponding mixing effects are shown in Fig. S5.8.



Fig. S5.8: Species and stand-level effects of mixing QI with *Quercus pubescens* (see caption for Fig. S5.2). The corresponding responses in pure and mixed stands are shown in Fig. S5.7.



Fig. S5.9: Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50-50% LAI) stands of QI and *Quercus faginea* (see caption for Fig. S5.1). The corresponding mixing effects are shown in Fig. S5.10.



Fig. S5.10: Species and stand-level effects of mixing QI with *Quercus faginea* (see caption for Fig. S5.2). The corresponding responses in pure and mixed stands are shown in Fig. S5.9.


Fig. S5.11: Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50-50% LAI) stands of QI and *Arbutus unedo* (see caption for Fig. S5.1). The corresponding mixing effects are shown in Fig. S5.12.



Fig. S5.12: Species and stand-level effects of mixing QI with *Arbutus unedo* (see caption for Fig. S5.2). The corresponding responses in pure and mixed stands are shown in Fig. S5.11.



Fig. S5.13: Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50-50% LAI) stands with QI and *Phillyrea latifolia* (see caption for Fig. S5.1). The corresponding mixing effects are shown in Fig. S5.14.



Fig. S5.14: Species and stand-level effects of mixing QI with *Phillyrea latifolia* (see caption for Fig. S5.2). The corresponding responses in pure and mixed stands are shown in Fig. S5.13.



Fig. S5.15: Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50-50% LAI) stands of QI and *Buxus sempervirens* (see caption for Fig. S5.1). The corresponding mixing effects are shown in Fig. S5.16.



Fig. S5.16: Species and stand-level effects of mixing QI with *Buxus sempervirens* (see caption for Fig. S5.2). The corresponding responses in pure and mixed stands are shown in Fig. S5.15.

