

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

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ABSTRACT

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 CO₂ 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; Lübke 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 (LAI_{stand}). 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 LAI_{stand} 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

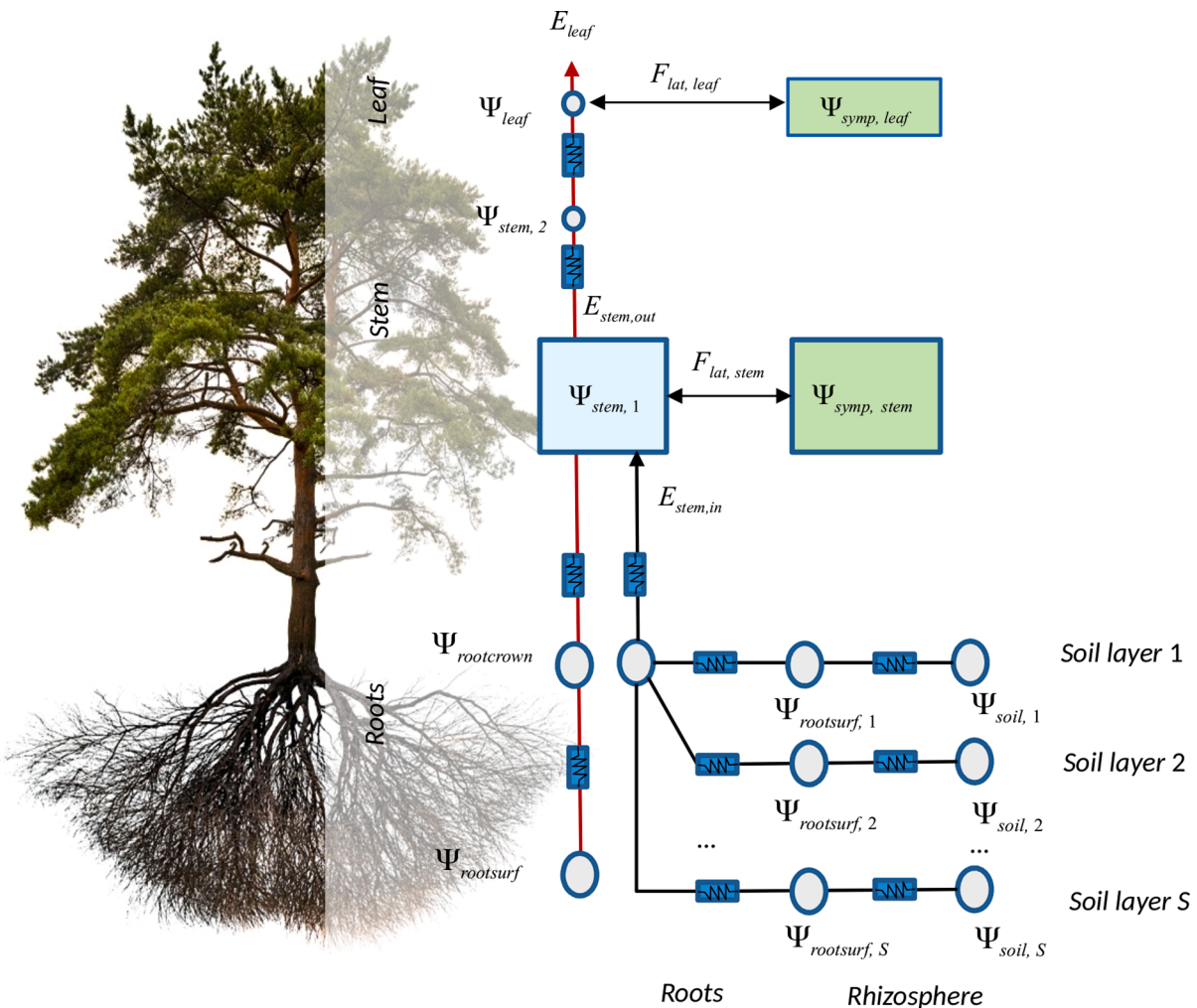


Fig. 1. Schematic representation of the hydraulic submodel in MEDFATE. Black arrows represent the soil-to-plant hydraulic pathway and the red arrow represents the plant-to-atmosphere pathway. Notation for water potentials in nodes (circles) and water compartments (boxes), transpiration flows and lateral flows (double-headed 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 (Ogaya 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 co-dominated 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 (V_{max298} and J_{max298} , respectively), maximum leaf hydraulic conductance ($k_{leaf,max}$), maximum stem xylem hydraulic conductivity ($K_{stem,max}$), maximum leaf conductance to water vapour ($G_{w,max}$) 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_v) 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 LAI_{stands} , 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 ($k_{root,max}$, $k_{stem,max}$ 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

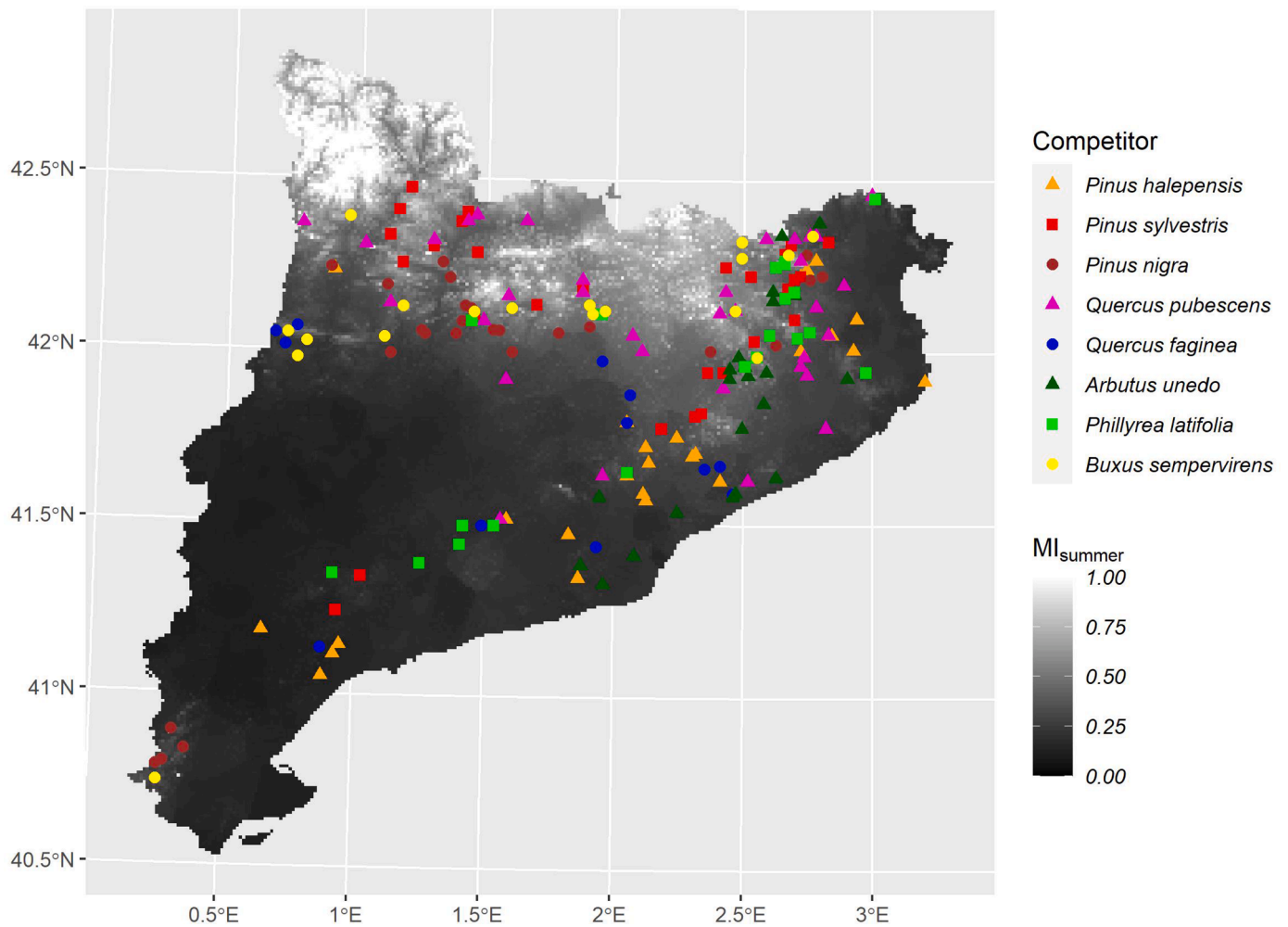


Fig. 2. Distribution of selected forest inventory (SFI3) plots within Catalonia (NE Spain) for each of the eight competitor species. The summer moisture index (MI_{summer}), calculated as the ratio of mean summer precipitation over mean summer potential evapotranspiration for 1 km grid cells, is indicated 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 ± 0.058 in relative extractable water). The ability of the model to predict transpiration rates from sapflow data was also acceptable (MAE $0.178 \pm 0.083 \text{ l}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), but model predictions of water status were less satisfying when compared to measured leaf water potentials (MAE $0.805 \pm 0.178 \text{ MPa}$), 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} 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 Z_{50} and Z_{95} , 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, $k_{plant,max}$ 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_y . 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 LAI_{stand} 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 LAI_{stand} and MI_{summer} 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 (MI_{summer}) and stand structure (LAI_{stand}). 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, MI_{summer} , LAI_{stand} , and the $LAI_{stand} / MI_{summer}$ ratio representing their interaction. We partitioned R^2 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 E and 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. 3c-d). 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 (W_{leaf} and W_{stem}) 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

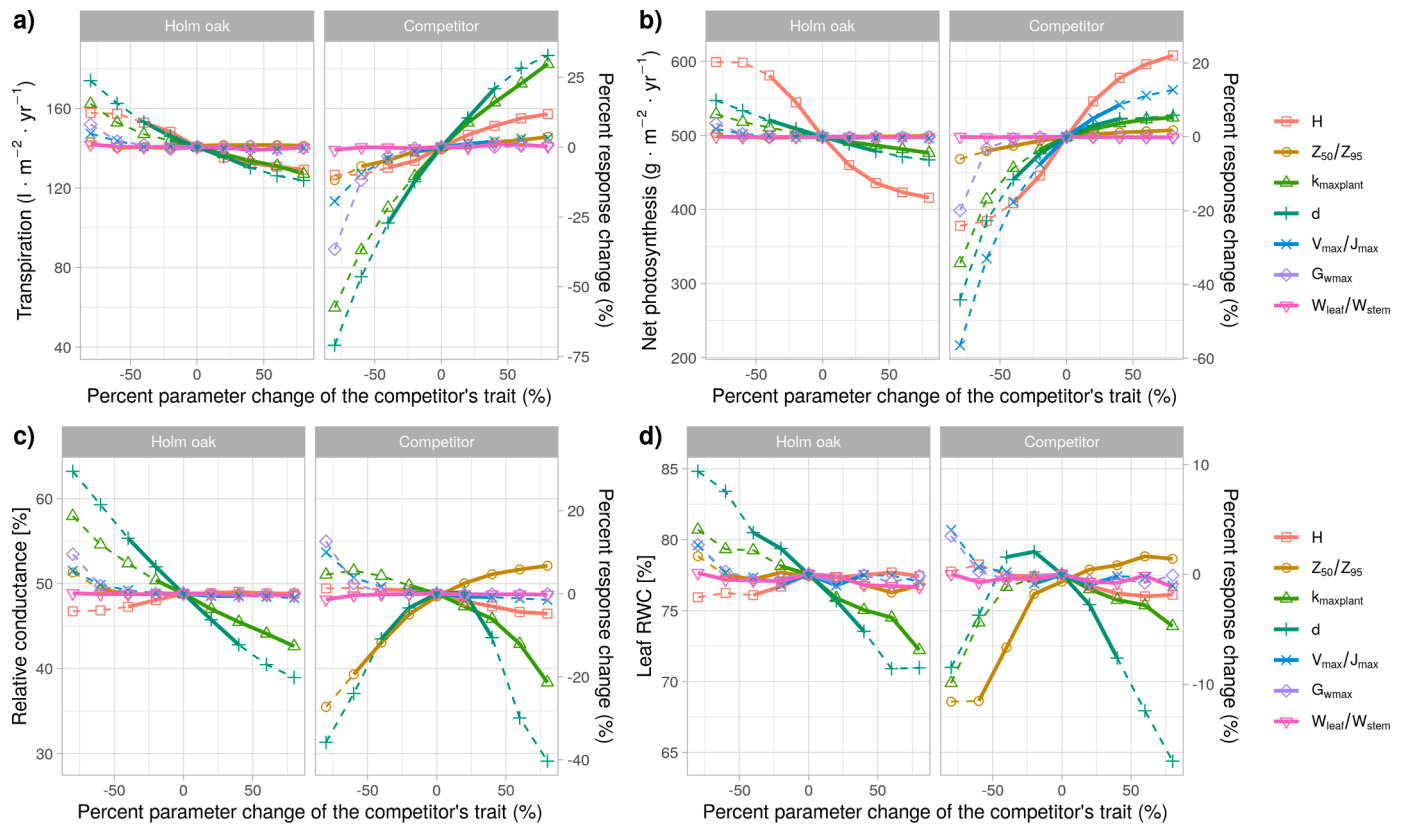


Fig. 3. Variation of *Quercus ilex* (QI) and competitor's annual transpiration per unit leaf area (E), net photosynthesis per unit leaf area (A_n), relative whole-plant conductance ($k_{plant,rel}$) and leaf relative water content (RWC_{leaf}) with respect to changes in competitor's individual plant 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 ($V_{max,298}$ and $J_{max,298}$) 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 RWC_{leaf} 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 $+4.8 \text{ mm}\cdot\text{yr}^{-1}$ (+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). Stand-level 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 R^2 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 species-level, 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 stand-level (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

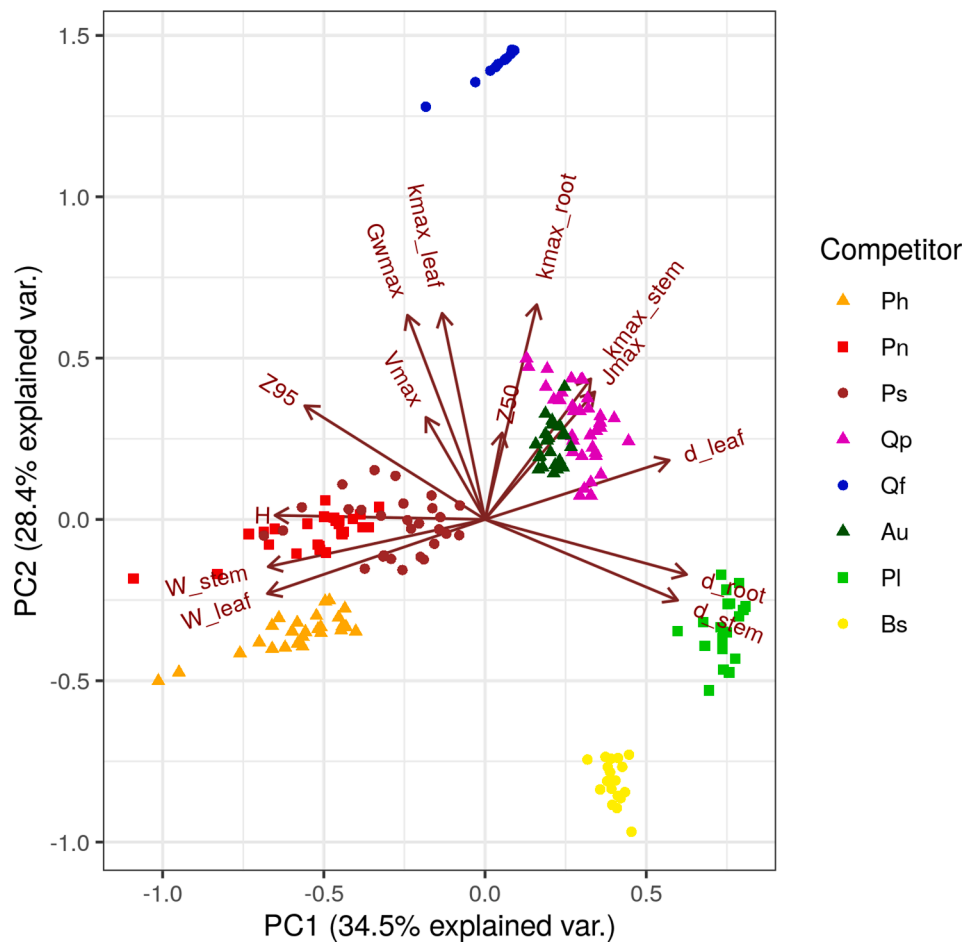


Fig. 4. Principal component analysis biplot of trait value differences between QI and its competitor on each SFI3 plot (mean differences are included in Table S4.2). Trait difference loadings are represented by arrows and SFI3 are represented by points. Au - *Arbutus unedo*; Bs - *Buxus sempervirens*; 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 ($1.4 \text{ l}\cdot\text{m}^{-2}$) 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

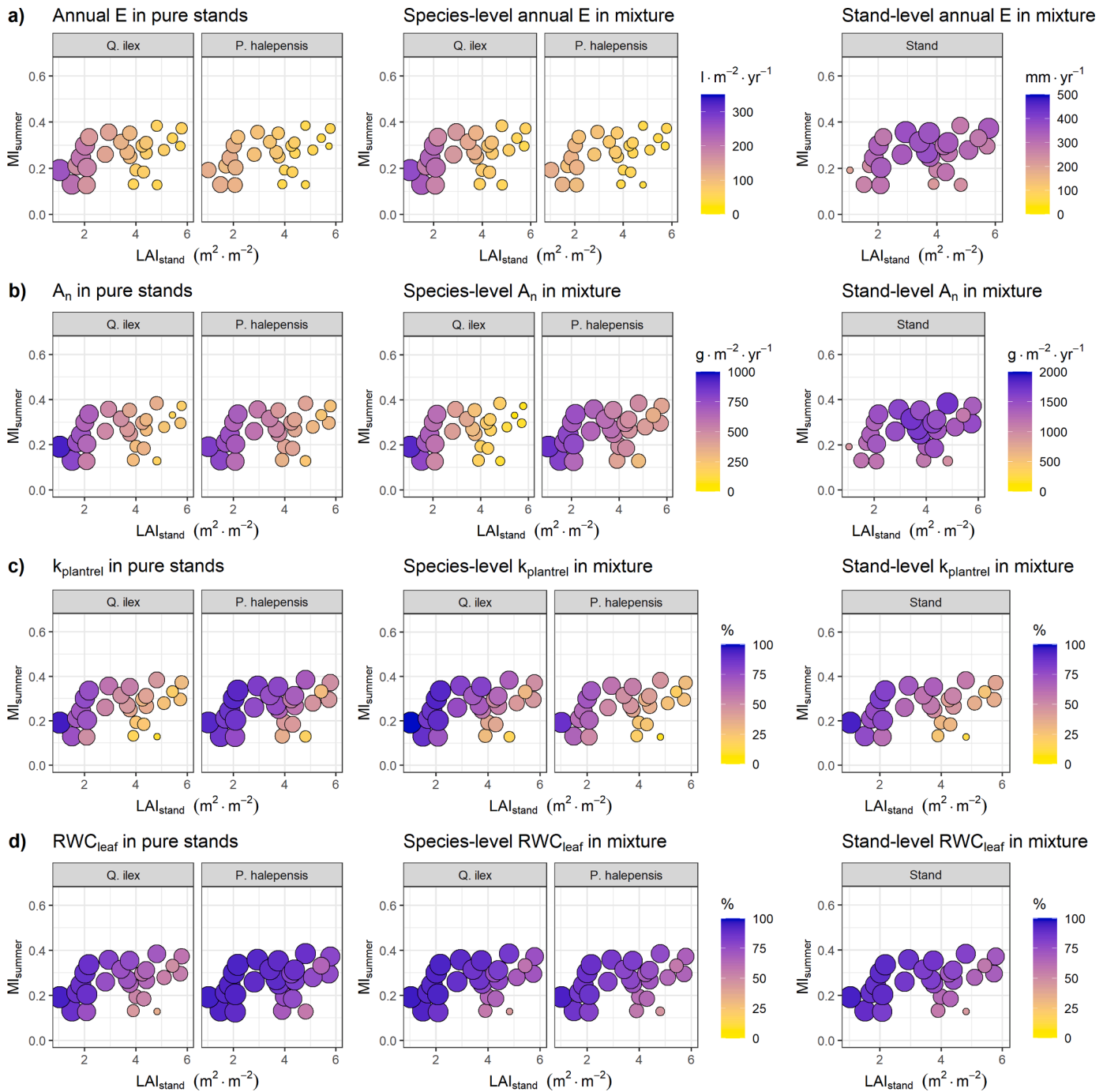


Fig. 5. Simulated species- and stand-level water use, photosynthesis, and summer drought stress in pure and mixed (50–50% LAI) stands of QI and *Pinus halepensis*: (a) annual transpiration (E), (b) annual net photosynthesis (A_n), (c) relative whole-plant conductance ($k_{plant,rel}$) and (d) leaf relative water content (RWC_{leaf}). 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. 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

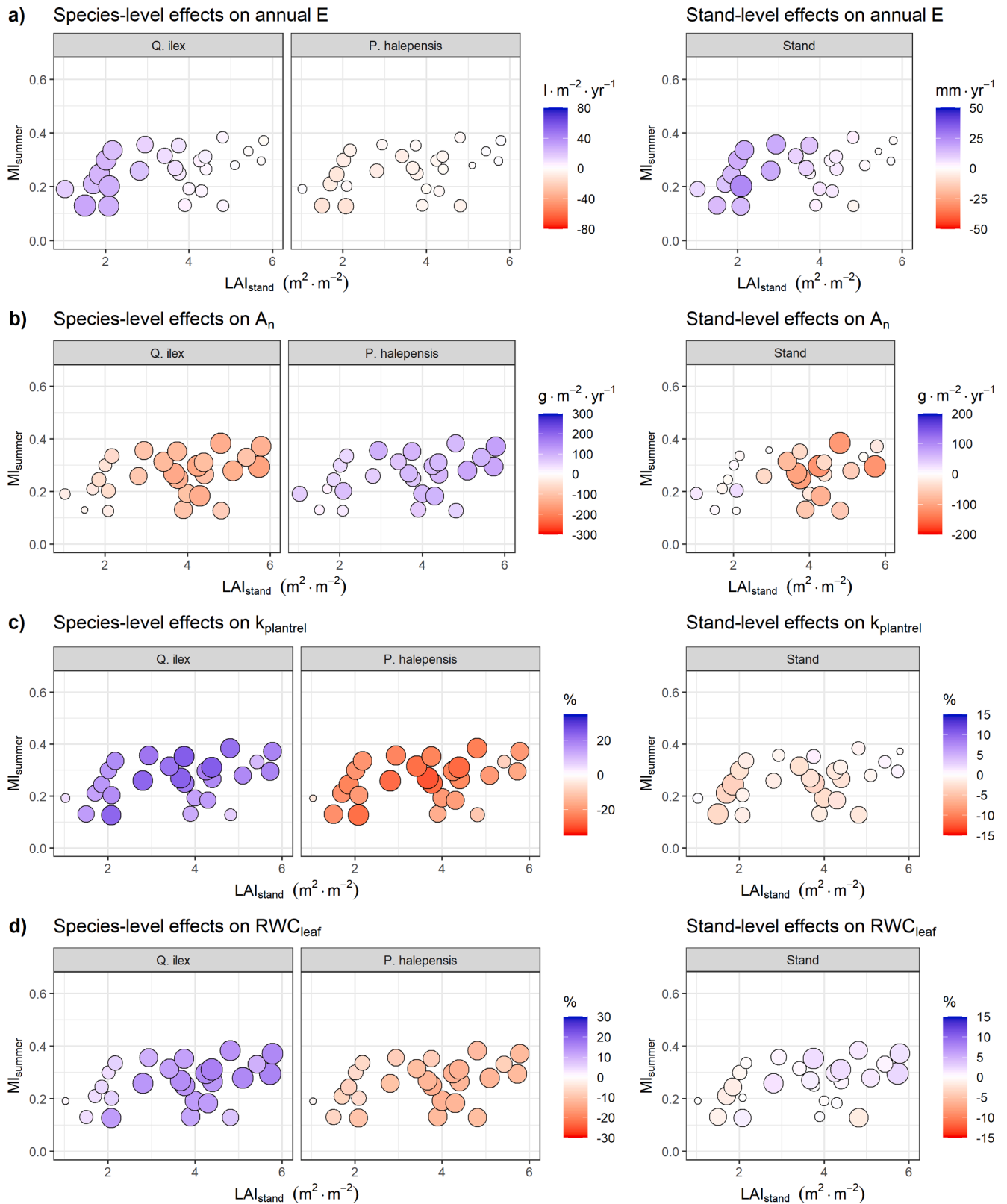


Fig. 6. Species- and stand-level effects of mixing QI with *Pinus halepensis* on (a) annual transpiration (E), (b) annual net photosynthesis (A_n), (c) relative whole-plant conductance ($k_{plant,rel}$) and (d) leaf relative water content (RWC_{leaf}). Species-level E and A_n values are calculated per 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. .

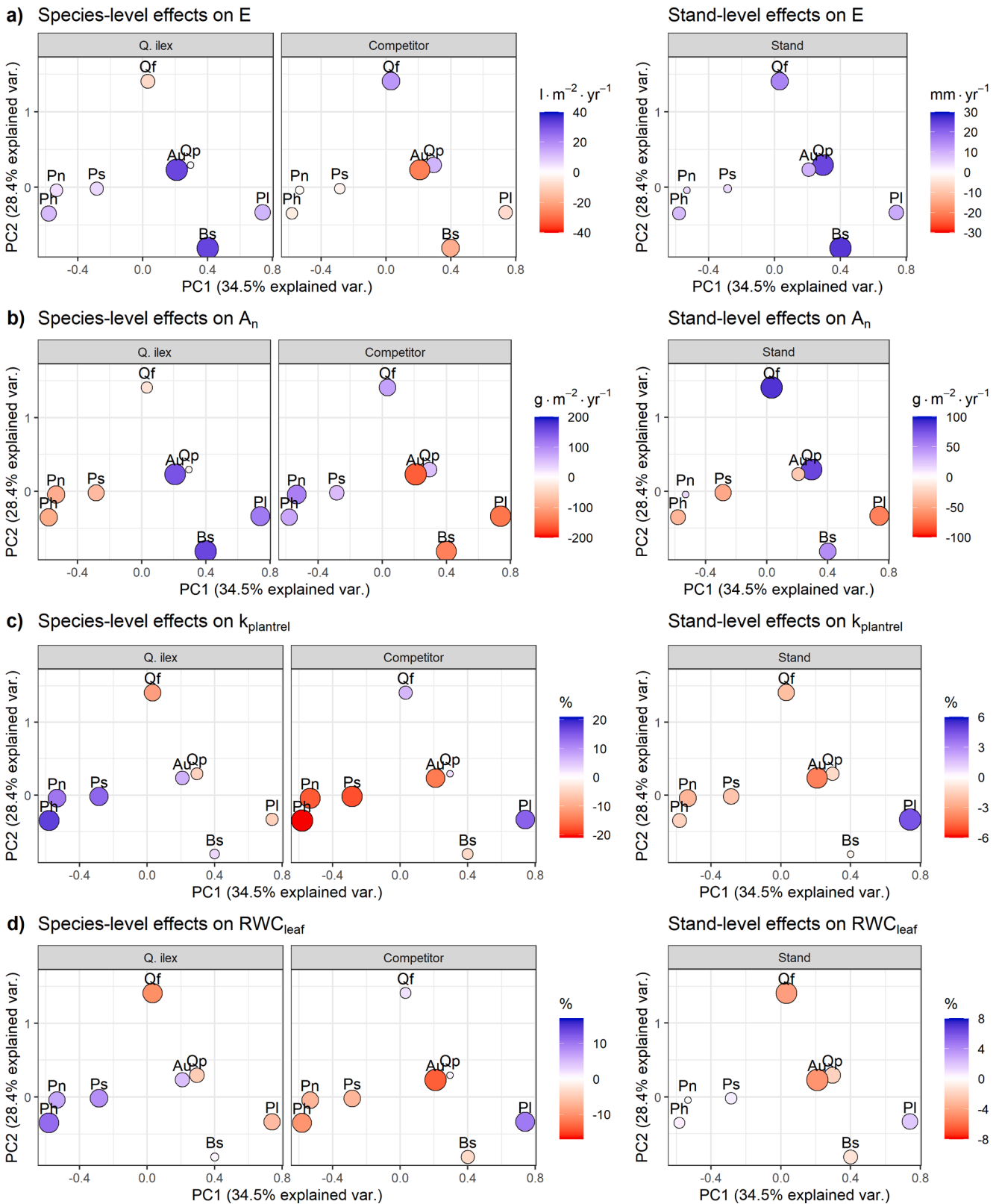


Fig. 7. Average species- and stand-level mixing effects on (a) annual transpiration (E), (b) annual net photosynthesis (A_n), (c) relative whole-plant conductance ($k_{plant,rel}$) and (d) leaf relative water content (RWC_{leaf}), depending on the species identity of the competitor (Au - *Arbutus unedo*; 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 as indicated in the text. In both cases, values shown are means calculated across SFI plots (see Figs. S5.1–16).

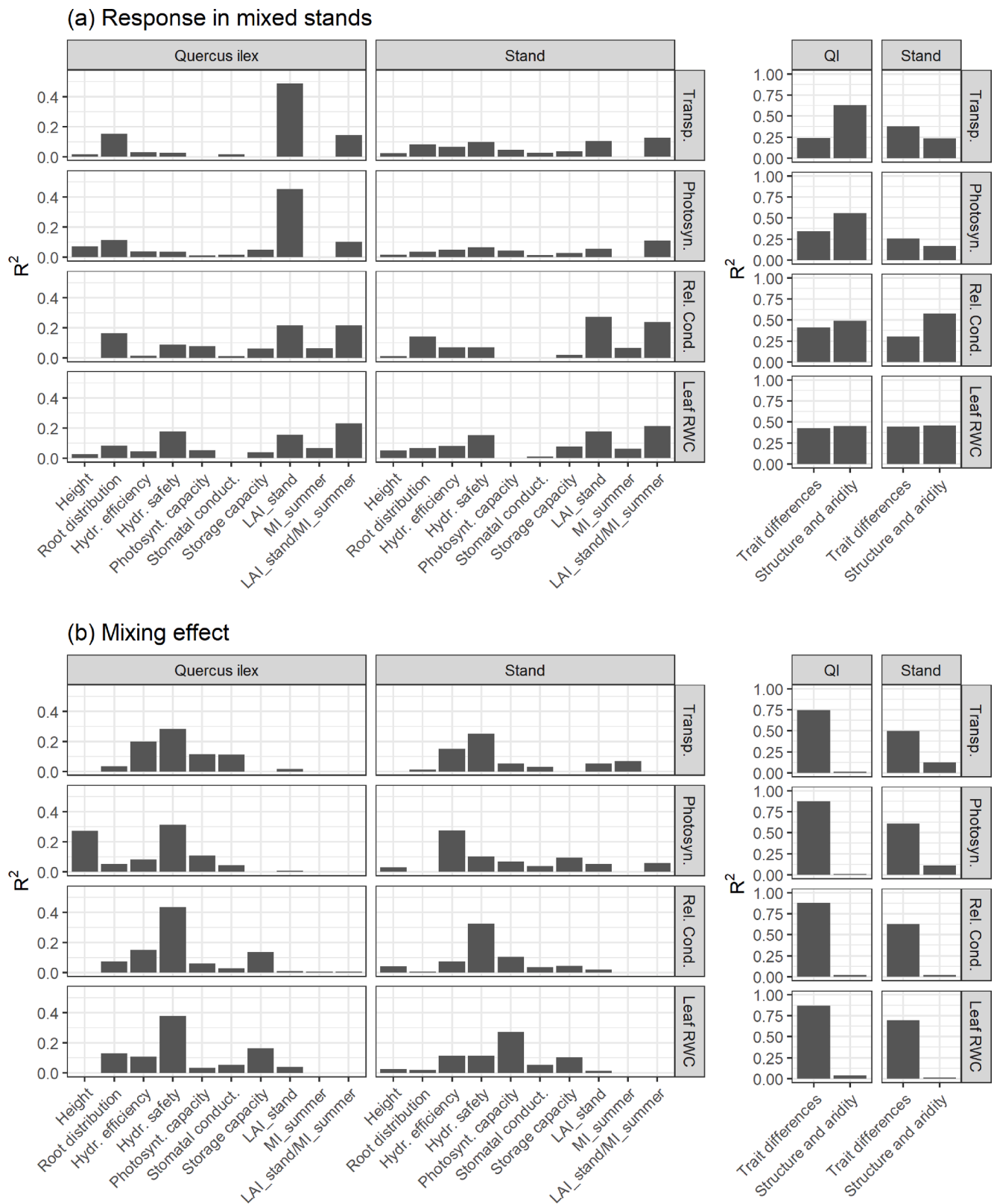


Fig. 8. (a) Percentage of variation (R^2) of species-level (QI) and stand-level performance in mixed stands – in terms of transpiration, photosynthesis, whole-plant relative conductance and leaf relative water content – explained by differences in traits, stand structure (LAI_{stand}) and climatic aridity (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; Barbata 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 Peñuelas, 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 LAI_{stand} . 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 LAI_{stand} 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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