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Interspecific Soil Water Partitioning as a Driver of Increased Productivity in a Diverse Mixed Mediterranean Forest

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Key Points:

- A mixed Mediterranean forest is more productive than forests of individual tree species
- Fundamental differences in niche-partitioning of soil water resources among five co-occurring tree species enhanced forest productivity
- Forests in semi-arid regions act as a significant carbon sink, and mixed forests in this region can further enhance this carbon sink

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract It has been assumed that mixing of species with high physiological diversity reduces competition over water and light resources, compared to single-species forests. Although several mechanisms to explain this observation have been proposed, quantification of these effects is lacking. Here we studied water-use dynamics for five tree species in a mature, mixed, evergreen, and Mediterranean forest. We use empirical measurements of key tree structural attributes including root distribution, through DNA barcoding and soil cores, tree height and biomass along with measurements of species-specific water use for two years. These measurements at the tree-scale were used to parameterize an ecosystem model of coupled water, carbon and energy fluxes (Regional Hydro Ecologic Simulation System, RHESSys). Site-scale empirical measurements showed contrasting diurnal and seasonal transpiration and sap flow curves across tree species, with year-round activity in angiosperms, and mostly wet season-activity in gymnosperms. Water-use patterns matched the rooting depth patterns, with the deep- and shallow-rooted *Ceratonia* and *Cupressus*, showing year-round and seasonal behaviors, respectively. RHESSys estimates of species-specific and stand-scale transpiration, biomass and productivity across 20 years of climate variation showed substantial differences between mixed and monoculture scenarios. Stand-scale annual net primary productivity and transpiration increased by 20–70 g C m^{-1} yr^{-1} and 40–80 mm yr^{-1}, respectively, for mixed stands relative to average fluxes aggregated across monocultures. Model results, collaborated by field data provide evidence for niche partitioning of the soil water resource among co-habiting tree species, and demonstrate that this mechanism can facilitate higher productivity and an enhanced forest carbon sink especially in semi-arid regions.

Plain Language Summary Tree species diversity has been shown to enhance forest productivity in different forest types. While several studies proposed mechanisms to explain this observation, empiric evidence is lacking. Our measurement setup revealed fundamental differences in water-use patterns and niche-partitioning of soil water resources among the phylogenetic groups of trees co-occurring in widespread forests around the Mediterranean. Our model simulations show that this partitioning has an important role in the higher productivity of the mixed forest compared to monoculture forests.

1. Introduction

The effect of tree diversity on forest productivity and resilience has been the subject of numerous research programs in the past decade. Large research projects like the BEF-China experiment, and networks like TreeDivNet and EuMIXFOR are evidence for the large investments into deciphering diversity-productivity relationships (DPR) in mixed forests around the globe (Zhang et al., 2012). For example, EuMIXFOR established a network of hundreds of research plots with a triplet design of a mixed *Fagus sylvatica* - *Pinus sylvestris* stands compared to pure stands of the two species (Ruiz-Peinado et al., 2018). A global meta-analysis showed that forest productivity increases with species richness and trait variation (Zhang et al., 2012). Mixed forests are, on average, 24% more productive than monoculture forests, with large variability among studies. Indeed, cases where mixtures are less productive than monocultures also exist (Forrester, 2014). In the BEF-China tree diversity experiment in a subtropical forest, tree growth increased with neighborhood species richness, leading to a positive DPR at the community scale (Fichtner et al., 2018). In a tropical seasonal forest, mixed reforestations of 13 native tree species grew better than pure plots, but not as fast as a fast-growing exotic species (Piotto et al., 2004). In contrast to these examples, most of what we know on mixed forest function comes from temperate forests in Europe, and less from other forest regions and types (TreeDivNet). Overall, DPR studies are notably under-represented in water-limited environments such as semi-arid and Mediterranean forests.

What is the mechanism behind the overall positive DPR? Processes like competition reduction and facilitation are involved, but how these processes interact and change with climate and other conditions is not well understood (Ammer, 2019). Complementarity in eco-physiological traits is also a relevant process, which tends to increase in sites where stress is the norm (Forrester, 2014). However, the underlying mechanisms behind these processes are not fully understood (Ammer, 2019). In the global meta-analysis, heterogeneity of shade tolerance was found to be the second most affecting factor on forest productivity (Zhang et al., 2012). In mixed temperate forests across France, with *Quercus robur*, *F. sylvatica*, *P. sylvestris*, and *Abies alba*, covariation between tree size and shade tolerance determined productivity, such that stands with taller, shade-intolerant, species, dominating lower, shade-tolerant, species, are more productive than others (Cordonnier et al., 2018). In mixtures of broadleaf species of *Carpinus*, *Fagus*, *Tilia*, *Fraxinus*, and *Acer*, without accompanying conifers, increased complementarity in canopy space filling among species did not an affect productivity (Seidel et al., 2013). In these examples, reduced competition for light is the major underlying mechanism. Indeed, competition for light is such a fundamental mechanism in forests, that it governs tree growth even in the most light-abundant, water-limited, forests (Tsamir et al., 2019). In a mixed temperate forest in Switzerland, competition for light means that the lower-stature *Carpinus betulus* flushes earlier in spring than the canopy dominant species of *Quercus* and *Fagus*, an adjustment that costs in carbon allocation to stem growth (Klein, Vitasse, & Hoch, 2016). There is some evidence that diversity-driven over-yielding is related to stand structure (Williams et al., 2017). Interspecific growth distribution modifies the canopy structure, and thereby the stand conditions, which, in turn, enhance the interspecific growth distribution (Pretzsch, 2017). Thus, there is a positive feedback, where greater productivity in a mixed stand leads to greater biomass. For example, diversity-driven over yielding increased with time in a temperate forest in Japan, resulting in 64% greater biomass in mixed versus pure stands after 31 years (Tatsumi, 2020). In that study, early succession species were enhanced whereas late-succession species were suppressed. Additionally, divergent diel hydrodynamics among trees with different canopy architecture was suggested as an alternative mechanism (Pappas et al., 2018). Tree species diversity enhances ecosystem functions while not necessarily improving forest resistance to drought (Grossiord et al., 2014).

While photosynthetic light interception is a major driver of tree growth, a major predictor of forest canopy height across the globe is water availability (Klein et al., 2015). Therefore, niche partitioning in soil water-use is being recognized as a mechanism for reduced interspecific competition (Ammer, 2019; Hildebrandt, 2020). Mixing of tree species typically increases throughfall and water storage in soil, while differences in rooting depth and water-use strategies, along with facilitation through hydraulic redistribution are the major underlying mechanisms (Ammer, 2019). Importantly, belowground connections between neighboring trees have also been shown (Klein, Siegwolf, & Körner, 2016), for example, through mycorrhizal networks (Rog et al., 2020). In a study of belowground competition in a temperate mixed forest of species of *Carpinus*, *Quercus*, *Fagus*, and *Tilia*, there was a broad overlap of the root systems of neighboring trees, with higher competitive ability of *Fagus*, and lower in *Quercus* (Rewald & Leuschner, 2009). Under imposed drought, shallow-rooted *Fagus* reduced water-use while deep-rooted *Quercus* was sustained, and ^{18}O water labeling showed interspecific partitioning in soil water-use (Zapater et al., 2011). Partitioning of soil water by *Fagus*, *Tilia*, and *Fraxinus* according to rooting depth, determined by ^{2}H water labeling showed that tree species' rooting depths in the mixed forest were similar with the monocultures, albeit the deep-rooted *Fraxinus* competed also at the shallow layer (Meißner et al., 2012). In a temperate mixed forest in France, a *Fagus*-*Acer* mixture did not show niche partitioning when using the same shallow soil water, in spite of deeper fine root distribution, detected with ^{2}H (Fruleux et al., 2020).

Although empiric evidences for interspecific soil water partitioning are emerging in recent years, those are limited in the number of studied tree species, and moreover, they miss the important link to forest productivity. Further it is unclear how the partitioning of soil and light interact as canopy structures develop over time to influence productivity. Particularly in semi-arid regions, seasonal and inter-annual variation in precipitation adds additional complexity in the timing and magnitude of soil water partitioning and its links with growth. Recognizing the complexity of these interactions suggests an opportunity to use mechanistic ecosystem models to quantify the impacts of light and soil water partitioning on productivity given seasonal and year to year variation in water inputs and the development of canopy structures over time. To do this, models must account for differences between species and their interactions in the use of light and water. Models must also account for feedbacks between productivity and growth and ideally be scalable to stands and watersheds in order to predict implications for longer term productivity and water use.

Many forest dynamic vegetation growth or ecosystem process models account different species as plant functional type (PFT; Koven et al., 2020; Powell et al., 2018; Sakschewski et al., 2016; Xu et al., 2016). For regional to global scale dynamic vegetation models, partitioning and competition for light between plant functional types is based on representing stands as cohorts of plant function types, with different heights and canopy cover that allow between-PFT shading to occur (e.g., Fisher et al., 2010; Medvigy et al., 2009). Recent work has shown that accounting for plant trait diversity within these PFTs can alter estimates of vegetation water and carbon fluxes (Pavlick et al., 2013; Pappas et al., 2016). The high sensitivity, but limited availability, of species-specific parameters for these models, often presents a barrier for their usage in exploring more complex questions around niche partitioning and productivity (Huber et al., 2018). In semi-arid regions, where water limitation is a key control on forest productivity, additional uncertainty is introduced related to subsurface parameters that influence spatial heterogeneity in plant available water, including plant rooting depths and soil water retention properties (Fan et al., 2017; Fatichi et al., 2014). Model-data fusion, that relies on local species specific measurements, is a promising approach, particularly for assessing within regional patterns of competition in semi-arid environments where species adaptation to water-limitations may have substantial impacts on forest productivity (Fatichi et al., 2016; Ren et al., 2018).

Here we studied tree water-use dynamics in five key tree species in a mature, evergreen, and diverse mixed Mediterranean forest (Klein et al., 2013; Lapidot et al., 2019).

Our model-data fusion approach is designed to take advantage of a well-studied field station settings where measurements campaigns are focused on specific mechanisms or eco-physiological dynamics, in this case species differences in water use. Modeling is used to extend these field-based measurements and offer insight into implications of alternative scenarios (fully mixed vs. uniform species) for stand scale water use and growth. Our approach integrates several data types, including both site based measurements and information from regional synthesis. We use a moderate complexity vegetation growth model account for both light and water partitioning and competition. Specifically we use an ecohydrologic model Regional Hydro Ecologic Simulation System (RHESSys) to (a) assess species differences in canopy structure and water use, (b) develop model scenarios to estimate the impact of this mixture of species on productivity, and (c) investigate the underlying mechanisms that explain any differences between mixed and monoculture stands. Field measurements include sap flow, leaf water potential, and transpiration, measured at a seasonal resolution along three years. Root distribution in the soil layer was measured with DNA barcoding and soil cores and upscaled based on allometric relationships. We combined these local field measurements with literature review of observed canopy-structural information for each of the five species in order to derive species-specific ecophysiological parameter sets for RHESSYs. Parameter selection used a calibration approach that retained information about parameter uncertainty. Using these parameter sets, we estimated stand structure development for mixed and monoculture plots (e.g., stand biomass and biomass for each species) and associated species and stand scale productivity and water use for a range of meteorological forcing conditions. We use this model-data fusion approach to test the following hypotheses: (a) species differ in their water-use strategies, both spatially (rooting patterns) and temporally (phenological activity); In turn this, in combination with structure related difference in light availability, produce niche partitioning that leads to (b) higher productivity of the mixed forest compared to monocultures of each of its species.

2. Materials & Methods

2.1. Site and Study Trees

Field measurements of mature trees were conducted in a forest research plot in Yishi forest (formerly Harel forest), at the Judean foothills, Israel (Klein et al., 2013; Lapidot et al., 2019). Yishi forest is located 4 km

Table 1
Summary of Tree Size Characteristics and Carbon Allocation (kg) Patterns of the Five Studied Species at Yishi Forest (Means ± SE)

Species	Family	Clade	Height (m)	Stem diameter (cm)	Foliage	Stem and branches	Roots	Source for allometric equation
Ceratonia Siliqua	Fabaceae	Angiosperm	7.0 ± 0.3	15.8 ± 1.0	89.2 ± 3.8	257.2 ± 11.0	95.3 ± 4.1	Ruiz-Peinado et al. (2012)
Quercus calliprinos	Fagaceae	Angiosperm	4.4 ± 0.4	7.9 ± 1.0	13.7 ± 1.2	44.9 ± 4.1[a]	25.4 ± 2.3[a]	Schiller et al. (2003) Ruiz-Peinado et al. (201)2
Cupressus sempervirens	Cupressaceae	Gymnosperm	11.9 ± 0.8	19.6 ± 2.5	N.A.	88.5 ± 5.9	11.4 ± 0.8	Tabacchi et al. (2011)
Pinus halepensis	Pinaceae	Gymnosperm	18.9 ± 1.6	30.5 ± 1.3	17.4 ± 1.5	235.3 ± 19.9	30.4 ± 2.6	Grünzweig et al. (2007)
Pistacia lentiscus	Anacardiaceae	Angiosperm	1.9 ± 0.2	<2	2.3 ± 0.2	7.2 ± 0.8	22.0 ± 2.3	Har-Adom and Grunzweig (2013) (unpublished[b])

Note. Carbon allocation patterns are based on the measured tree size parameters and allometric equations (means ± SE). These data were used for the modeling of each species in RHESSys. N.A., data not available.
[a] These values were estimated from *Quercus suber*. [b] This is the only available source for allometric equations for *Pistacia lentiscus*.

south-west of Beit Shemesh, Israel (31° 43′N 34° 57′E, 320 m elevation). Climate is hot Mediterranean, with annual precipitation of 510 mm, falling between September and May, and mean diurnal temperatures of 16.0°C and 25.3°C in February and August, respectively. The predominant soil type in the study area was terra rossa with neutral acidity (pH 6.9–7.2), consisting of an A horizon of soil, and then C horizon which consists of soil that penetrates the cracks between the weathered limestone bedrock. Soil depth (A horizon) is 20.6 ± 0.7 cm, with minimum and maximum depths of 16 and 25 cm, respectively. Stoniness was estimated at 4.8%. The vegetation is dominated by the planted gymnosperm tree species *Pinus halepensis* and *Cupressus sempervirens,* and the local Mediterranean angiosperm woody species *Quercus calliprinos*, *Ceratonia siliqua*, and *Pistacia lentiscus*, accompanied by a variety of annual plants that thrive from winter to spring. For brevity, we hereby refer to each of the five species by its genus name, that is, *Pinus, Cupressus, Quercus*, *Ceratonia* and *Pistacia*. In Yishi forest, conifers were planted 51 years ago, while broadleaf species populated the afforestation soon after conifer planting. The forest canopy is dominated by the relatively tall conifers, and especially the *Pinus*, with lower stature *Quercus* and *Ceratonia*, and *Pistacia* forming a forest understory (Table 1). Within the 1 ha forest research plot, there were 242, 146, 109, 31, and 9 individual trees of various growth stages, from young saplings of 1 m height up to 30 m, 50 years-old trees of *Pistacia*, *Cupressus*, *Quercus*, *Pinus*, and *Ceratonia*, respectively (Using a GPS instrument eTrex30x [Garmin]). Among these 537 individuals, accounting only for the mature individuals, stand density was 134 trees ha^{-1}, that is, on average, 74.5 m^2 tree^{-1}. We selected 4–5 representative trees (evenly distributed across size and age classes) of each of the five studied species. All measurements were performed repeatedly along three years on these individuals. Environmental conditions and their monitoring are included in the Supporting Information.

2.2. Adjacent Single-Species (Monoculture) Forest Plots

To test whether species-specific tree eco-physiology is retained across mixed and single-species plots, monocultures of each of the five species were located in proximity to the mixed forest sites (Table S1; Figure S1). These plots were either planted as single-species (*Pinus*, *Cupressus*, and *Ceratonia*) or developed naturally as nearly single-species (*Pistacia* and *Quercus*). Trees in the *Pinus*, *Cupressus*, and *Ceratonia* plots were 54, 31, and 62 years-old. Notably, monoculture *Cupressus* reached the same size as mixed *Cupressus* in a shorter period (31 vs. 51 years). Monoculture plots were only 1–9 km away from our main study plot, and were similar in terms of climate, bedrock, soil, and tree age. At the plot scale, we noticed the following patterns: (a) stand density was lower at the monocultures than at the mixed forest; (b) the conifer monocultures were moderately denser than the broadleaf monocultures. Stand density in the *Pinus* monoculture has decreased with time due to drought-induced tree mortality 3–4 years ago (Klein et al., 2019); (c) gaps between trees were occupied by local grass species. At the species level, species-specific DBH and height of each tree species was equivalent with that measured in the mixed plot (Table 1), with the exception of *Pinus*, where monoculture trees were 13% smaller in stem diameter and 27% shorter in height. Interestingly, *Ceratonia* trees in the monoculture were overall similar in biomass, however 40% shorter in height and 56% larger in stem diameter. *Quercus* trees in the monoculture were similar in height, but 81% larger in diameter.

2.3. Root Identification and Species-Specific Root Distribution

In order to ensure the identification of the species, root samples were taken for DNA identification based on the rRNA second internal transcribed spacer 2 (ITS2) sequence (Cheng et al., 2016). In order to study tree rooting patterns in Yishi forest, while minimizing disturbance to the rhizosphere, we integrated four complementary approaches: (1) sampling of forest soil cores around each of the study trees and measurement of lateral root biomass in each core (below); (2) identification of excavated roots (5–20 cm depth) around each of the study trees, based on DNA barcodes (above); (3) upscaling the measurements in (1) and (2) to the entire soil layer based on stand density information and allometric relationships for each of the species, based on stem diameter and height and applying asymptotic equations for the distribution of root biomass in depth (Jackson et al., 1996); and (4) estimation of root biomass in the rock layer, based on the difference between the soil root biomass calculated in (3) and the total root biomass, calculated by species-specific allometric equations. For the complete procedure please see the Methods in the Supporting Information.

2.4. Leaf Gas Exchange and Water Potential

Leaf transpiration and stomatal conductance rates were measured, every two weeks, on leaves of the same trees measured for sap flux density and top soil root growth. These measurements were performed using a portable photosynthesis, infra-red gas analyzer system (IRGA; Walz). A standard leaf chamber (Walz 3010-S) with top LED light source (Walz 3040-L) was set to the ambient light intensity for each round of measurements (morning, noon, after noon). The CO_2 level was set to provide a stable concentration of 400 ppm; flow rate was set to 750 μmol s^{-1}; and the impeller to speed 7; temperature was set as ambient with offset of 1°C. In each measurement, a single intact mature leaf from the *broadleaves*, or a needle cohort of 10 adult needles from the *Pinus* or ~8 cm^2 of scale-like leaf of *Cupressus*, was randomly sampled. The projected leaf area relative to the chamber size was calculated and corrected for each tree species. All measurements were taken (average of 5 s) after the IRGA values were stable based on the *Ci* parameter, and flow rate was similar in the cuvette and reference analyzers. Leaf water potential was measured, every two weeks, on leaves from the same trees, using a pressure chamber (PMS Instrument Company).

2.5. Sap Flow

Continuous sap flux density measurements were taken 2–3 days in each season (every two months) between September 2017 and September 2019, using heat balance sensors (EMS, Brno, Czech Republic; Čermak et al., 1973; Cermak, 1976) on the two conifers (*Pinus* and *Cupressus*) and two broadleaves (*Ceratonia* and *Quercus*) (n = 4–5, not all sensors produced high quality measurements in all dates). No sap flux was measured in *Pistacia* because of the small stem diameter. The sensors were installed at breast-height of the conifers and in the largest diameter area of the broadleaves stem (usually at 0.2–0.5 m height), and 2 cm into the sapwood. The coniferous and diffuse-porous sapwood depth was estimated in an earlier study, showing that the 2 cm sensors measured directly 68%–71% of the flux (Cohen et al., 2008). In multi-stem trees (*Ceratonia* and *Quercus*), only the largest stem was measured. Sap flow sensors were connected to the permanent part of the sensors (metal plates) that were kept on the trees throughout the two measurements years. Plates were checked before each campaign by visual detection of scar formation and resin secretion and by electric detection of heat conductance and were replaced *ad hoc*. Stem growth rates were low and hence did not affect sensor location. Sensors measured during 2–3 days in each campaign, logged every 10 min, and calculated sap flow for the sapwood area (2 cm of the outer part ignoring the bark).

2.6. Statistical Analysis

Statistical analysis was done using R (R Core Team, 2013) and the interface R Studio (R Core Team, 2018). We used repeated-measures ANOVA to test the sensitivity transpiration rate to differences among tree species (5 species, 4 replicates of each), years (water year 2018 and water year 2019), calendar months (averaging the bi-monthly values) and time of diurnal measurement (morning, noon, and after-noon), and the interactions between them (Package *afex* [version 0.27–2] and *car* [version 3.0]) (Fox & Weisberg, 2019; Singmann et al., 2020). Reciprocal transformation ($1/x$) was applied to the transpiration rate. For testing the significant effect between water year and tree species we used Tukey-HSD test (Using *stats* package).

2.7. Eco-Hydrologic Model

Mechanistic models complement and extend field-based approaches. For this study we use RHESSys—a spatially distributed model of ecosystem carbon and nutrient cycling and hydrology to estimate vegetation productivity, growth and water use. RHESSys code is open-source and available online at https://zenodo.org/record/5159825#.YQq3eo4zaUk; (version 7.2 was used for this paper). In this study, we use field and literature data on study site species to parameterize the model and then use the model to develop comparisons between mixed and monoculture stands implementations and show how each species contributes to stand scale fluxes in each scenario. Monoculture stands were simulated by replacing all trees in the mixed stand by trees of a single species. The model also allows us to extend flux estimates to a longer time period and assess the impact of climate variation on monoculture and mixed stand differences.

Coupled ecohydrology models like RHESSys estimate energy, water, carbon and nutrient cycling using semi-mechanistic submodels that have been previously evaluated by comparison with observations in multiple settings. Examples of RHESSys evaluation include recent studies in an Aleppo Pine forest 50 km south from this site (Tsamir et al., 2019) and other studies in semi-arid regions, for example, evaluation of model estimates of mortality (Tague & Peng, 2013), productivity (Tague & Grant, 2009; Vicente-Serrano et al., 2015), water use and streamflow (Bart et al., 2016; Garcia & Tague, 2014) and fire regimes (Kennedy et al., 2017). In RHESSys, differences in species are represented by ecophysiological parameters such as maximum stomatal conductance (see Table S2 for a full list of parameters). A key assumption in this study is that ranges for these parameters are species-specific but do not substantially change when species are grown in relatively similar climatic and soil conditions. Thus we assume that parameter ranges are similar for monoculture and mixed conditions but species difference do translate into site (and climate forcing) driven differences and short-term responses to water and energy availability and these, in turn, influence longer term growth responses. We emphasize that we do not rely on a unique species-specific parameter set but rather utilize multiple parameter sets for each species that allow for some within-species parameter variation. All estimates account for the uncertainty associated with sampling across this within-species parameter variation.

RHESSys forest canopy distinguishes between overstory and understory vegetation, sunlit and shaded canopy components and, in this most recent version (RHESSys 7.2), shading and exchanges of water between clumps of trees. While RHESSys does not explicitly resolve individual trees it does account for how small stands, comprised of several individuals within 10–30 m^2 patches (or clumps), are influenced by neighbors, through shading and the exchange of subsurface moisture. Within a uniform species clump, the model lumps overstory and understory leaf, stem and root carbon stores to provide a mean height, rooting depth and leaf area index that evolves through time with growth; this approach is intermediate in complexity between a lumped canopy model and an individual tree model, similar to approaches used in other global dynamic vegetation growth models (Fisher et al., 2010; Medvigy et al., 2009). Importantly for the application to a semi-arid, water limited study site, a full canopy, litter and soil moisture model is maintained for each clump and the model also explicitly represents the sharing of subsurface moisture between tree clumps, accounting for variation in rooting depth and uncertainty in lateral root distributions via a sharing coefficient as well as local soil water holding capacity parameters (additional details on lateral moisture moisture fluxes and shading within and between tree clumps is provided in supporting information). The intermediate complexity of RHESSys reduces the need for specific tree locations, which may be highly uncertain, while still approximating potential neighbor scale interactions. The intermediate complexity approach also facilitates computationally efficient sensitivity analysis and scaling to larger hillslopes and watersheds. In this study, we assume that clumps of different species are evenly distributed throughout the total modeled stand.

A full description of RHESSys carbon, water and nutrient submodels can be found in previous papers (Tague & Grant, 2009; Vicente-Serrano et al., 2015) and open source model code on Zenodo (https://zenodo.org/record/5159825#.YQq3eo4zaUk). Here, we provide an overview of key sub-models relevant to this paper.

Gross photosynthesis is computed daily for overstory/understory canopies within each tree clump. Gross photosynthesis is allocated first to fulfill respiration requirements and second to carbohydrate storage. Depending on allocation parameters, this storage is then allocated to grow of stem, leaf and root carbon stores. Turnover of these plant component occurs seasonally and also varies with species-specific parameters. Species-specific parameters further translate root and stem carbon stores into rooting depth and vegetation height, respectively. Gross photosynthesis is coupled with root zone water availability by reducing stomatal conductance as a function of rooting zone soil water potential, again incorporating species-specific parameters that alter stomatal sensitivity to moisture deficits. Evaporation of canopy, litter and soil water and transpiration are computed using a Penman or Penman-Monteith type approaches (Monteith, 1965). A Jarvis-type sub-model of stomatal regulation includes responses to vapor pressure deficit, soil water potential, air temperature and photosynthetically active radiation (Jarvis, 1976). The canopy model accounts for diffuse and direct radiation and the attenuation of radiation, wind and moisture through the forest canopy as a function of leaf area index. Canopy throughfall and open area rainfall is directed to litter moisture storage and then any excess infiltrates into shallow and ultimately deeper subsurface moisture stores.

We develop estimates for species-specific ecohydrologic parameters sets using a two-step calibration process. First, we undertake a global sensitivity analysis of model estimates of tree structural variables including canopy height, root depth, biomass and allometric relationships (e.g., leaf to stem carbon ratios) across ecophysiological parameters. We use Latin Hypercube Sensitivity analysis to select parameter sets from a priori distributions, using the PSE package in R (Chalom & Prado, 2014). Table S2 and Figure S8 provide the parameter ranges used for sensitivity analysis and resulting partial regression coefficients for biomass and leaf to stem carbon responses for each parameter set. Soil parameters for the site were based on values for loamy soil. Additional details on parameter ranges were previously reported (Garcia et al., 2016; Tague & Band, 2004; Tague & Peng, 2013).

For each parameter set, we complete a 30 year spin-up run to initialize carbon-nitrogen stores, and followed this with 2-year simulations over field observation period (2017–2019). We do this both for a mixed scenario, where forest clumps with different parameters interact with each other and monoculture scenarios where forest clumps all contain the same species. For all scenarios, forest clumps are initialized as even age, single size cohorts. Meteorological forcing for model spinup and for multi-year comparisons of mature monoculture and mixed stands was based on WFDEI reanalysis meteorological data downscaled to Yishi (Weedon et al., 2014). For short-term comparisons with field observations we used data from Yishi forest for 2017–2018 (see supporting information for additional details on meteorology data and downscaling approach). All simulations were done at a daily time step. Simulations for the global sensitivity analysis included 11,000 replicates of a 30 year spinup (1980–2010) followed by simulation of 2018 water year using local meteorology for analysis. We repeat the global sensitivity analysis for a model implementation of mixed and for monoculture stands. We then select possible parameter sets for each species where estimates for both monoculture and mixed stands fall within literature ranges of canopy structural variables for each species. We retain all parameters the give canopy structural estimates within literature ranges for each species. Second, we further refine parameter set selection to develop locally adapted parameter sets by selecting, separately for each species, only the parameters that give correlations of greater than 0.5 with observed stomatal conductance measurements for that mixed stand model scenario. This second parameter refinement is designed to select parameters that reflect species adaptions to local soil and climate conditions. However, we repeat analysis for the full range of possible species parameters and find that our conclusions are robust across this larger range of parameter uncertainty (see supporting information), To further support our assumption that ecophysiological parameters derived from the mixed forest were transferrable to monoculture stands we used limited observations from monoculture plots located 1–9 km away from our mixed forest sites. Overall, species-specific size parameters of each species were equivalent with that measured in the mixed plot (Table S1), although stand density was consistently lower (Figure S1). Species-specific differences in midday leaf water potential at the end of the dry season (representing the annual minimum) were also retained across mixed and single-species plots, although *Cupressus* was less

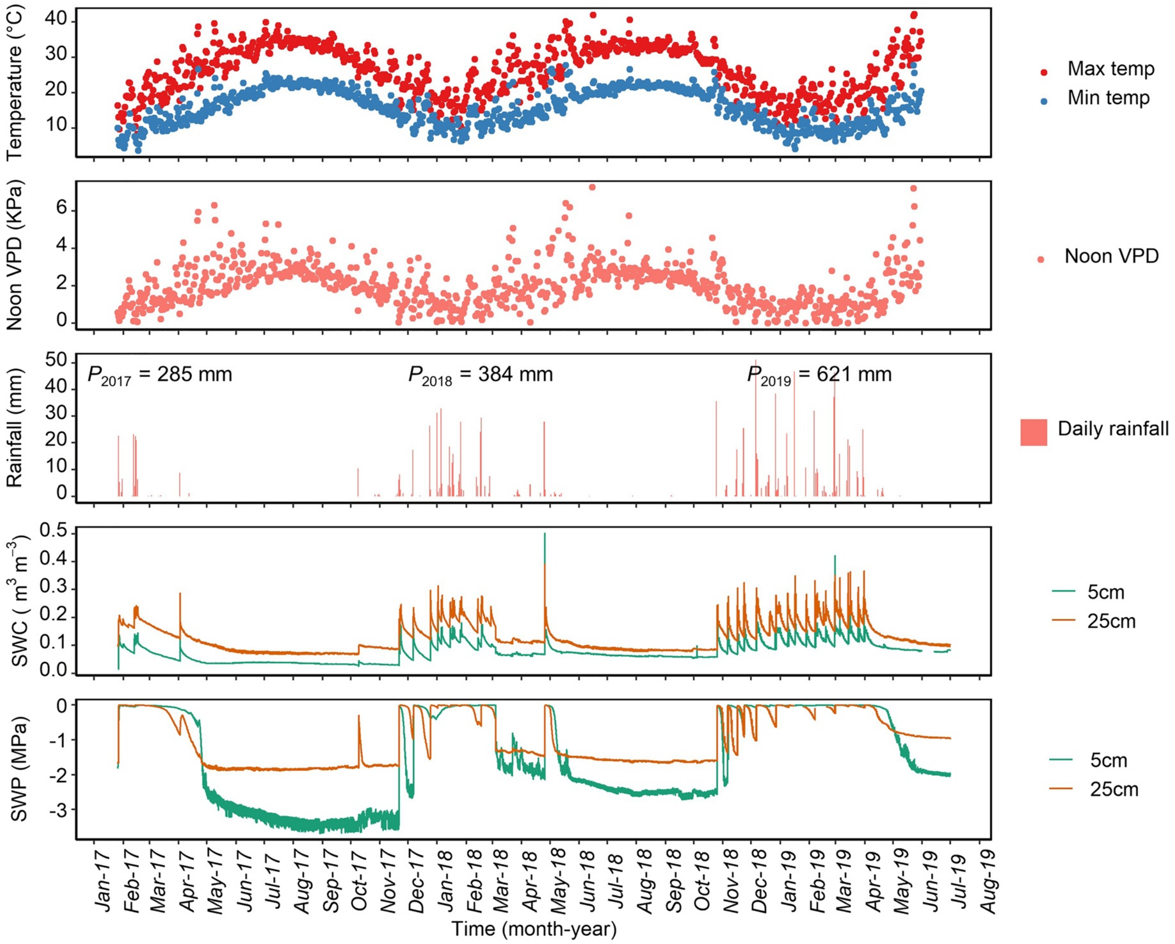

Figure 1. Environmental conditions in Yishi forest in 2017–2019. Diurnal maximum and minimum temperatures; noontime vapor pressure deficit (VPD); precipitation; soil water content (SWC) and soil water potential (SWP) at two soil depths. Meteorological data are from Beit Jimal meteorological station (750 m East of the study stand), whereby VPD was calculated according to Sadler and Evans (1989). Soil water parameters were monitored continuously on site, with SWP corrected for temperature bias (Walthert & Schleppi, 2018).

water-stressed in the single-species plot (Figure S7). Our parameter selection approach assumes that ecophysiological parameters (such as maximum stomatal conductance or optimal temperature for growth) will be similar for species growth in mixed and in monocultures at this site. We emphasize however that we retain substantial parameter uncertainty, and thus, results should be robust across small variations in any parameter. We use 200 samples from these species-specific parameter sets for multi-year simulations to compare transpiration and carbon sequestration for mixed and monoculture stands. We consider our five species as potential or hypothetical species where the model explicitly implements functional differences (reflected by ecophysiological parameters), that are similar to those observed in the Yishi forest, rather than an exact replication of actual species and their distribution.

Further details on eco-hydrologic model parameterization and species-specific parameter sets are included in the Supporting Information (Table S2).

3. Results

3.1. Atmospheric and Soil Conditions

Atmospheric conditions over the mixed forest showed the typical warm climate for the site, with winter rains and large inter-annual fluctuations, and heatwaves during autumn and spring (Figure 1). The diurnal minimum temperature was never below freezing, and up to 25°C in mid-summer, while the diurnal maximum

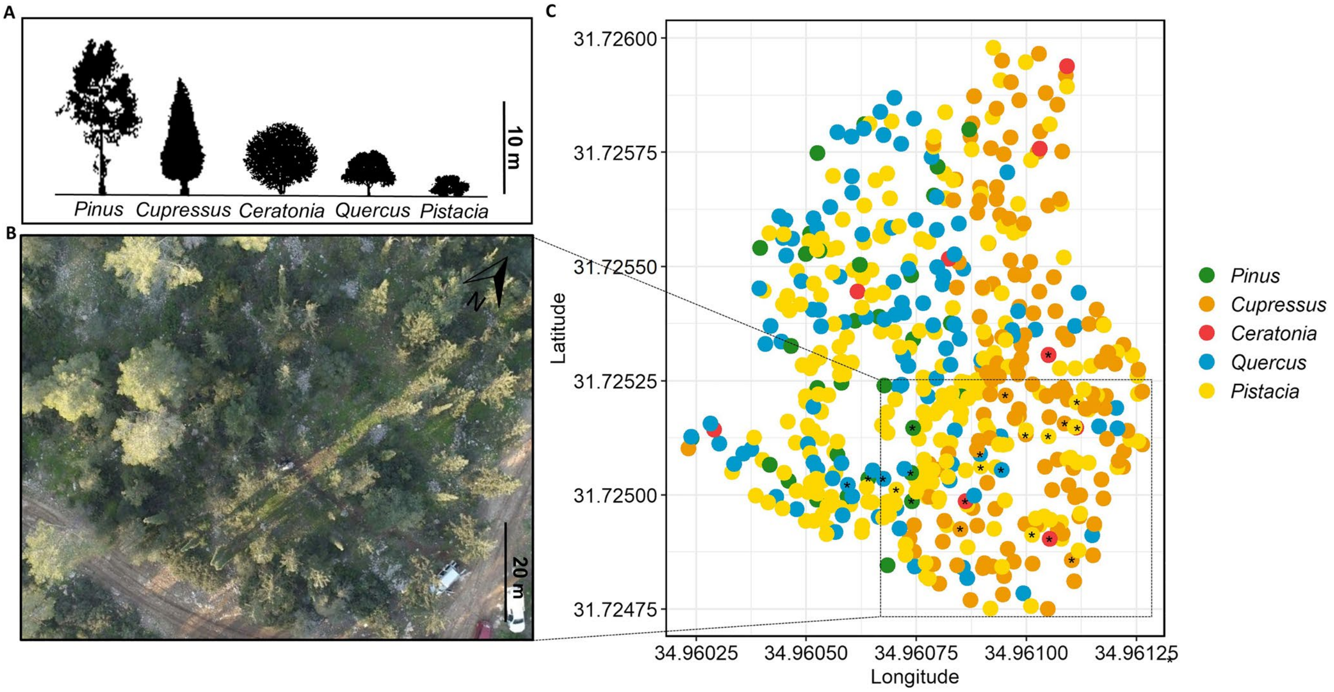

Figure 2. Aboveground tree growth in Yishi forest. (a) The five study tree species and their relative heights: *Pinus halepensis, Cupressus sempervirens, Ceratonia Siliqua, Quercus calliprinos*, and *Pistacia lentiscus*. (b) An aerial photo of the mixed forest stand. (c) Actual distribution of the tree species (all individuals > 1 m height) within the stand.

temperature was peaking at 40°C during summer and spring heatwaves. In such episodes, VPD increased to 5–6 kPa, and even 7 kPa during two heatwave events. Annual rainfall amounts in 2017 (285 mm), 2018 (384 mm), and 2019 (621 mm) roughly matched the minimum, mean, and maximum precipitation typical for the site. Increasing annual rainfall result from both an increasing number of rainfall events, and an increase in the size of these events. The wet season was usually confined to October–April, rendering May–September as a prolonged dry season. Exceptions to this rule were March 2017 and March 2018, which were dry, and May 2018, which was wet. Soil moisture patterns mirrored the precipitation dynamics, with ~8% water by volume during summer, reaching ~30% and over during winter rains (Figure 1). In winter, dry-down cycles in between two consecutive events decreased soil moisture from ~30% to ~15%. Interestingly, soil moisture at 5 cm depth was usually ~7% (v/v) lower than moisture at 25 cm depth. Accordingly, soil water potential (SWP) was usually higher in the deeper layer, reflecting differences in water retention properties between the layers. Seasonal variations in SWP were low at 25 cm soil depth, fluctuating between 0 and −2 MPa in winter and summer, respectively. At 5 cm depth, seasonal variations were higher, especially in the long summer of 2017, when SWP reached a minimum of −4 MPa.

3.2. Tree Sizes and Aboveground Growth

The studied tree species diverged in diameter and height, ranging from the small and low-stature *Pistacia*, to the wide and tall *Pinus* (Table 1; Figure 2a). These size differences translated into yet larger biomass differences. Applying allometric equations from the literature on these measured size parameters, the aboveground woody biomass of *Pistacia* had <10 kg C, whereas that of *Quercus* and *Cupressus* was just below 50 and 100 kg C, respectively, and that of *Ceratonia* and *Pinus* ~250 kg C (Table 1). The species diverged also in their C allocation, with relatively low C allocation to foliage and roots in *Pinus*, higher C allocation to roots in *Quercus*, and more so in *Pistacia*, and higher C allocation to both foliage and roots in *Ceratonia* (Table 1). At the stand level, trees of each of the five species were well mixed, with the exception of the conifers: *Pinus* and *Cupressus* merely overlapped, reflecting the planting scheme at the time of afforestation (Figures 2b and 2c). The spatial arrangement of tree species within the plot is far from that representing an ideal mixing, nor is it random. However, to satisfy our simplified approach, we note that local species

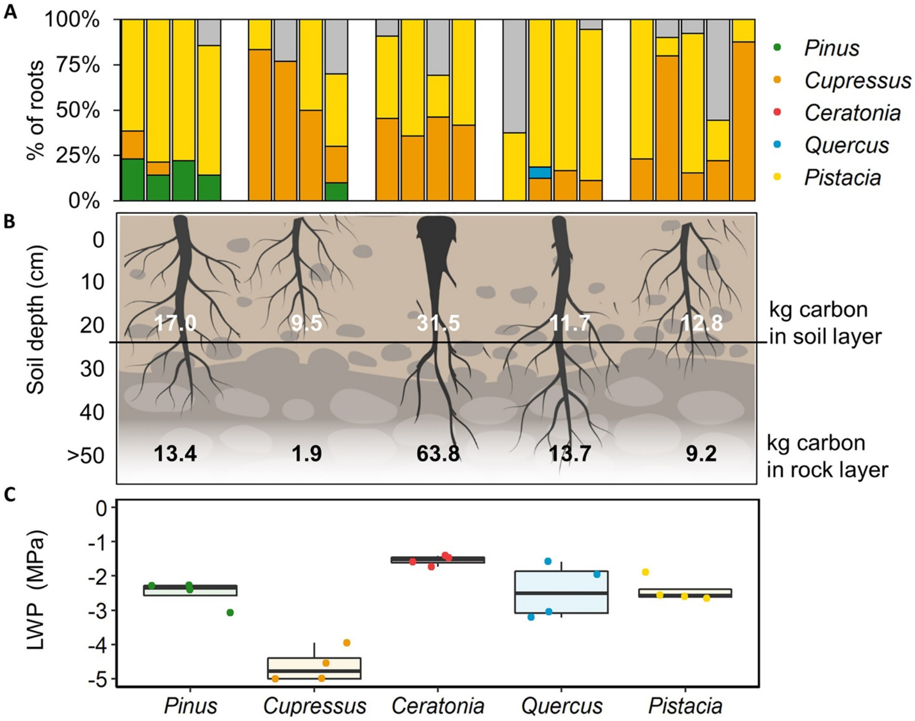

Figure 3. Belowground tree growth in Yishi forest. (a) Percentages of DNA-identified fine roots around stems of the five study tree species (10–20 cm soil depth; $N = 4$–5 trees per species). (b) Root biomass (g carbon) distribution in the soil and rock fractions. (c) Predawn leaf water potential (LWP) at the end of the dry season (September 2019, $N = 4$ trees per species).

combinations within the plot are inclusive of at least one situation whereby each of the five species is within a 3 m distance from each of the other species.

3.3. Tree Rooting Patterns

DNA-based root identification showed that, regardless of the proximity to any tree species, the 20 cm soil layer was dominated by only two of the species, namely *Pistacia* and *Cupressus* (Figure 3a). *Pinus* roots accounted for 14%–23% of the roots growing around *Pinus* trees, whereas *Quercus* roots accounted for only 6% of roots around one of the *Quercus* individuals (*Quercus* roots were not found around the other individuals). We were unable to identify any *Ceratonia* root in soil. This unexpected observation meant that root growth was mostly horizontal in *Pistacia* and *Cupressus*, mostly vertical in *Ceratonia* and *Quercus*, and mixed in *Pinus*. Species-specific allometric ratios and root depth distribution equations from the literature, were used to provide estimates for species-specific root partitioning between the soil and rock layers (see Methods). Overall, *Ceratonia*, *Pinus*, and *Pistacia* had a large root biomass in the soil layer (Figure 3b), however in contrasting ways: while *Pistacia* had mostly lateral roots, *Ceratonia* had only a tap root sinking through the soil and into the deeper rock layer, where it had a massive root biomass (Figure S2). *Pinus* and *Pistacia* had roots in both the soil and rock layers, with higher partitioning to the soil. *Quercus* had a smaller root system in terms of biomass than *Ceratonia*, but partitioned to the rock layer in a rather similar ratio. Last, *Cupressus* had only few roots in the rock layer, as also confirmed by visual observations (Figure S2). Predawn leaf water potential measured at the end of the dry season confirmed the contrasting rooting patterns, with *Ceratonia* having a very mild value (Figure 3c), evidencing access to deep water sources below the soil layer and beyond our sensors (Figure 1). Next, *Quercus, Pistacia,* and *Pinus* had more negative water potentials around −2.5 MPa, while the shallow-rooted *Cupressus* showed the expected negative values approaching −5 MPa. The annual minimum diurnal water potentials were −3.0 in *Ceratonia* and *Pistacia*, −4.0 in *Pinus*, −4.5 in *Quercus*, and −5.0 in *Cupressus* (Figure S3). These species differences also translated into differences in leaf activity, whereby in peak activity season (March-April) all trees operated at about −2.0 MPa, but stomatal

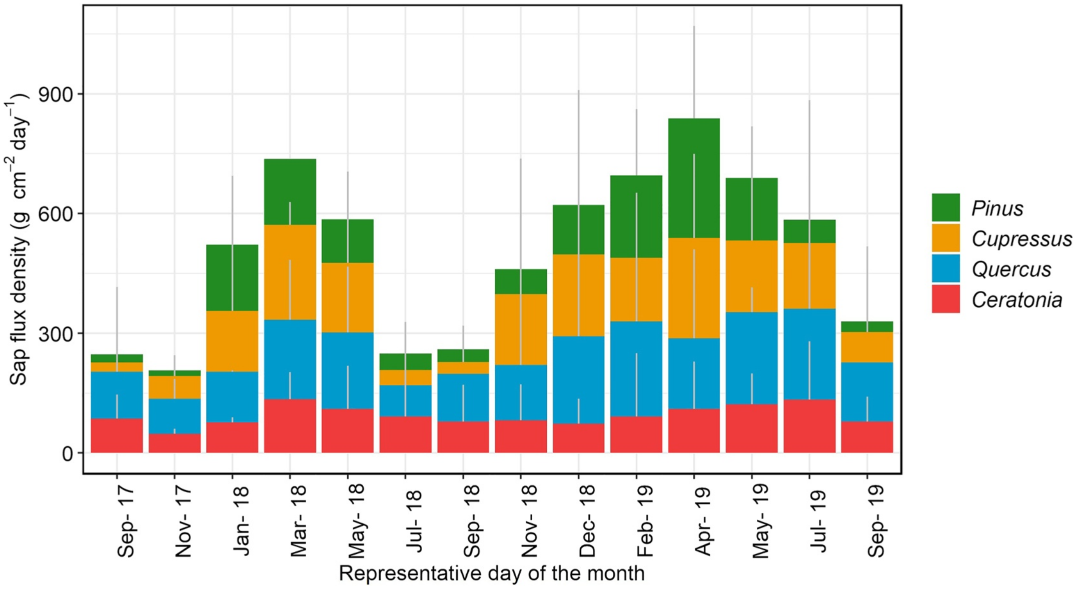

Figure 4. Tree water-use in Yishi forest. Water amounts are normalized per stem basal area, assuming equal spatial representation of the tree species within the stand ($N = 3$–4 trees per species; *Pistacia* stems were too narrow for this measurement).

conductance was higher than 0.1 mol m^{-2} s^{-1} in *Ceratonia*, at 0.1 in *Quercus* and *Pinus*, and lower than 0.1 in *Cupressus* (Figure S4). Along with height and allometric measurements, we used these measurements to develop RHESSys species-specific parameters such that the most active roots of *Cupressus* and *Pistacia* were less than 0.5 m deep, *Pinus* between 0.5 and 1.5 m, and *Quercus* and *Ceratonia* greater than 2 m.

3.4. Measured Tree Water-Use Dynamics and Soil Water Partitioning

Fourteen sap flow campaigns revealed contrasting seasonal patterns among the tree species in the mixed forest, with year-round activity among angiosperms, and mostly winter-activity among gymnosperms (Figure 4; *Pistacia* stems were too narrow for this sap flow instrumented measurement). Representing the two extremes, *Pinus* was almost dormant during the end of the dry season (September, November), while *Ceratonia* had almost the same diurnal curve in any given month (Figure S5), with a minimum at the end of the prolonged dry season in 2017 (Figure 4). Diurnal dynamics were also different among the species, with a solar-shape curve in *Ceratonia*, small diurnal declines in the conifers, and a larger declining pattern during the day in *Quercus*. Sap flow rates peaked at 10, 25, and 30 g H_2O cm^{-2} hr^{-1} in *Ceratonia*, the conifers, and *Quercus*, respectively (Figure S5). Transpiration measurement at the leaf scale added more detail to these observations (Figure S6). The interaction between tree species and month of measurement produced a significant effect on transpiration (Table S3, ANOVA, $F_{44,176} = 4.88$, $p < 0.001$). Per leaf area, transpiration rates were highest in *Ceratonia* and *Pistacia*, reaching a median of 2 mmol m^{-2} s^{-1} at the end of the wet season, and maintained at these high levels throughout summer in the deep-rooted *Ceratonia* following the rich wet season of 2019. In contrast, median transpiration rates rarely surpassed 1 mmol m^{-2} s^{-1} in *Quercus* and *Cupressus*, and were close to zero during summer in the latter, as well as in *Pinus* (Figure S6). Sap flow amounts (Figure S5) were further integrated over the diurnal scale to produce species-specific water-use amounts. In turn, these amounts were summed for the four species, and presented as totals for the stand scale (assuming equal spatial representation of the tree species within the stand) (Figure 4). In terms of partitioning of the water resource among the tree species, angiosperms and gymnosperms shares were ca. 60% versus 40%, respectively (calculated based on Figure 4). This pattern was in agreement with the higher access of the angiosperms to deep water, and in spite of the taller stature of the gymnosperms. Yet, there were large seasonal fluctuations, and while angiosperms used >80% of the water in September 2017, they decreased to 35% in April 2019. Among the two angiosperms, the share of *Quercus* was more stable, around 30%. Among gymnosperms, the share of *Cupressus* was mostly higher than that of the *Pinus*. The

Table 2

Correlation Coefficients Between Regional Hydro Ecologic Simulation System Estimates and Field Observations for Water Year 2018 (November 2017–October 2018) for Transpiration (E), Stomatal Conductance (gs) and Assimilation (A), by Species

	gs			E			A		
Species	Median	Low	High	Median	Low	High	Median	Low	High
Ceratonia Siliqua	0.87	0.65	0.89	0.51	−0.41	0.62	0.84	0.62	0.85
Quercus calliprinos	0.81	0.66	0.84	0.30	−0.51	0.54	0.85	0.64	0.86
Cupressus sempervirens	0.31	0.17	0.36	0.70	0.67	0.72	0.44	0.25	0.57
Pinus halepensis	0.58	0.51	0.66	0.45	0.35	0.54	0.32	0.12	0.55
Pistacia lentiscus	0.50	0.13	0.63	0.66	0.58	0.70	0.75	0.60	0.79

Note. Values are given as Median, and ±1 standard deviation (Low and High), of correlations computed for different parameter sets as sampled across ecophysiological parameter uncertainty.

latter, in spite of dominating the forest canopy, used only 20% of its water source. In terms of total water-use amounts, values in 2019 were higher than in 2018 (Figure 4; Table S4, ANOVA, species:year, $F_{4,16} = 4.56$, $p = 0.01$, Tukey, $p < 0.05$). However, in both years, *Ceratonia* had the most stable, and modest, water-use; *Pinus* had the second modest water-use (which was negligible in summer and peaked in spring); and *Quercus* and *Cupressus* had higher values, decreasing in the dry season.

3.5. Measured and Modeled Stomatal Behavior of the Five Tree Species

Table 2 shows correlations between observed values and RHESSys estimates of stomatal conductance, transpiration and assimilation. Model estimates here reflect estimates for the mixed stand scenario across all ecophysiological parameters that produced height, root and leaf to stem biomass estimates within literature reported ranges for each species. Ranges in the Table reflect parameter uncertainty. Median correlation estimates are above 0.3 for all species, although all species show a wide range of correlations across parameter variation. We note that some differences between model and observations are expected given that we do not represent the explicit spatial structure of the Yishi forest but rather assume that species are evenly distributed throughout the stand. Shifts in the timing of decrease in gas exchange parameters in the transition to dry season can explain the few negative correlations. Uncertainty in soil and rooting depth parameters are also likely to be a substantial source of error, especially considering that root biomass was not measured directly. Figure 5 shows observed and RHESSys estimates of stomatal conductance of 2018 water year (November 2017–October 2018) for those parameter sets where correlations with stomatal conductance were above 0.5. For the observed g_s, species and seasonal differences were overall significant ($P = 0.014$ and $P < 0.001$ respectively; Table S3), with significant species differences in January-February (Figure 5a). Model estimates show similar seasonal behavior to observations, with peak conductance occurring in early spring transitioning to low late summer conductance While considerable variation due to parameter uncertainty remains, results demonstrate a reasonable correspondence between observed and measured g_s for the mixed stand. Moreover, here we use RHESSys to explore hypothesis about the potential for species-specific difference in key ecophysiological parameters (including parameters that influence height, rooting depth, carbon allocation and stomatal function), to lead to difference in mixed versus monoculture forest dynamics.

3.6. Tree Water-Use Dynamics in Mixed Versus Monoculture Scenarios

Figure 6 shows RHESSys estimates of monthly transpiration for both mixed and monoculture scenarios. The most substantial difference in transpiration occurred during mid-summer, when soil water limitations occur. Three species (*Pinus*, *Ceratonia*, and *Quercus*) showed substantial increases in June–August for mixed stands, while *Cupressus* and *Pistacia* showed little change. There were small changes during the winter, where transpiration was sometimes higher in the monoculture stands but differences were small. Figure 7 shows monthly additional water gained in the mixed case by transfer of rooting zone water from neighboring clumps. The plot shows only transfers in and out of clump rooting zone water storage. Thus,

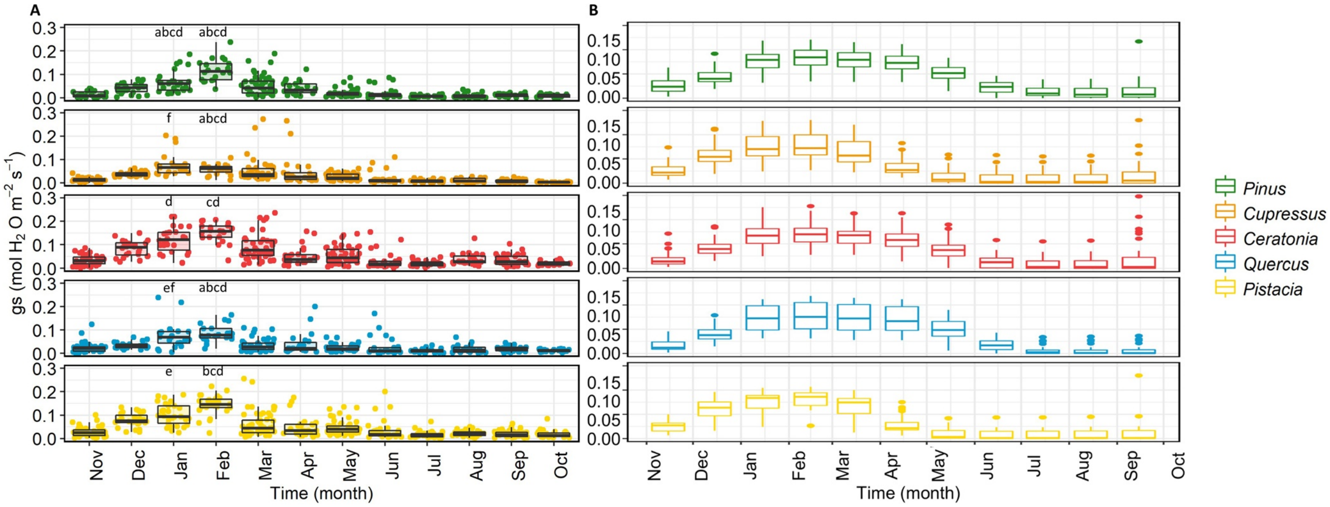

Figure 5. Measured and modeled stomatal conductance (*gs*) seasonal dynamics in Yishi forest. (a) Measured *gs* during November 2017–October 2018 ($N = 4$ trees per species, bi-monthly). Different letters denote significant differences among species in January and February, according to a Tukey-HSD test. (b) RHESSys gs estimates for water year 2018. Box plots show the impact of ecophysiological parameter uncertainty. Results are shown for the mixed stand scenario.

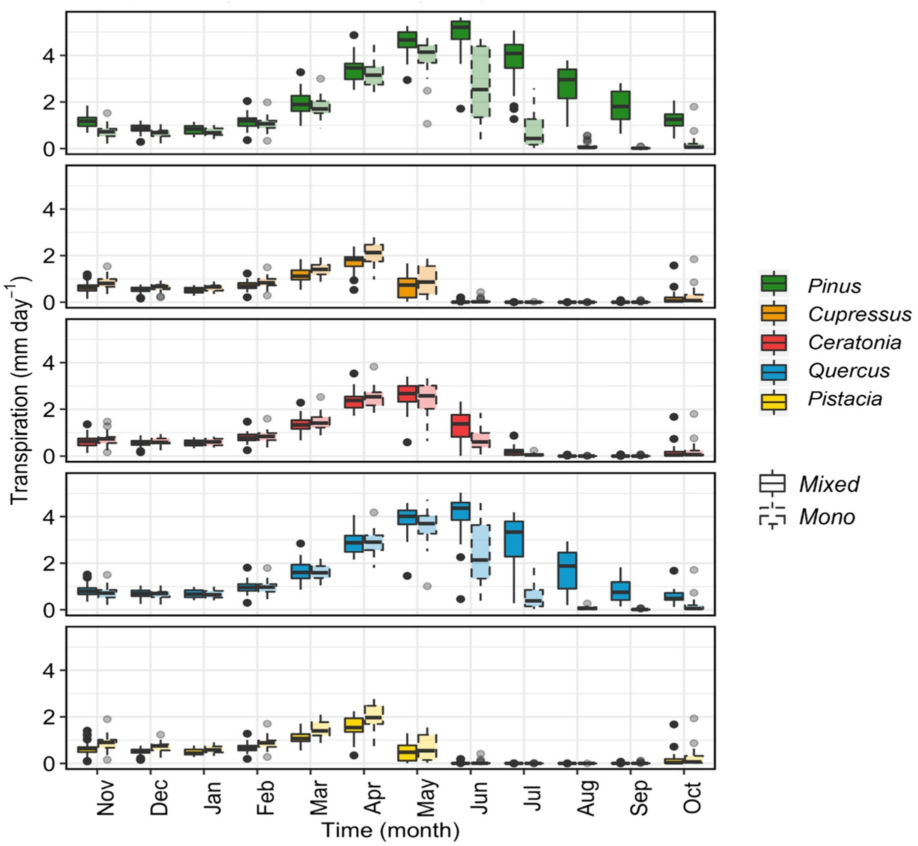

Figure 6. Regional Hydro Ecologic Simulation System estimates of transpiration seasonal dynamics in Yishi forest for monoculture (light) and mixed (dark) scenarios. Boxplots show inter-annual variation across 30 years (1983–2018). Estimates are averaged across parameter uncertainty.

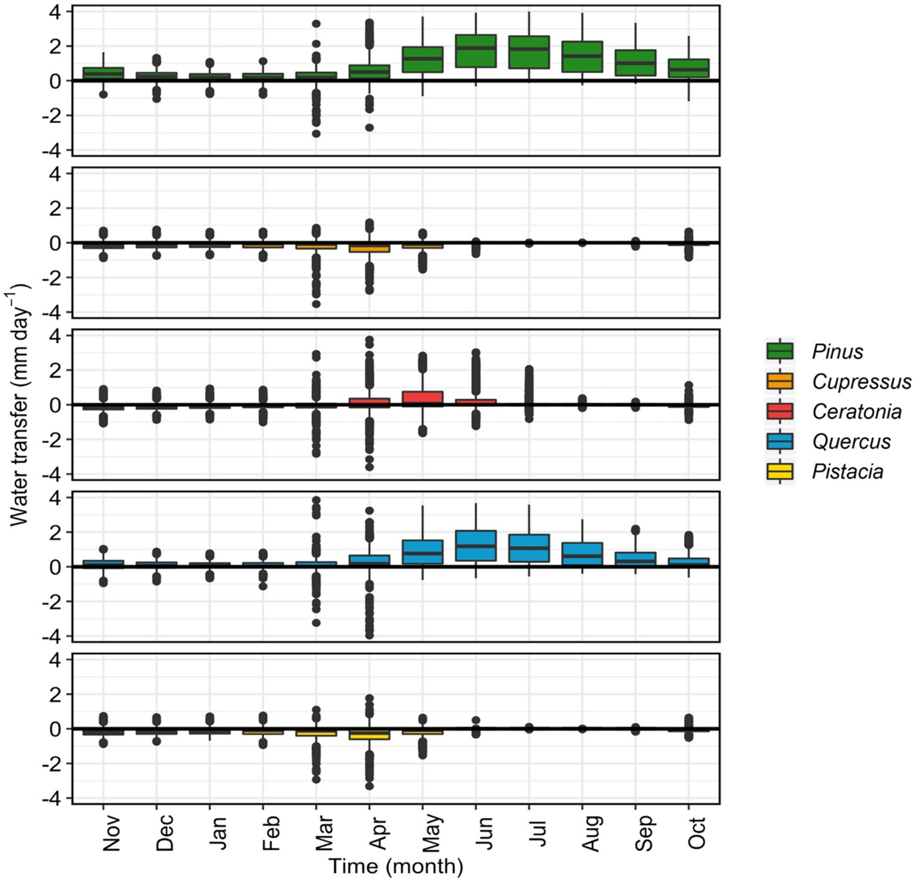

Figure 7. Regional Hydro Ecologic Simulation System estimates of root zone water transfer seasonal dynamics in Yishi forest. Results are shown for the mixed stand scenario. Boxplots show inter-annual variation across 30 years (1983–2018). Estimates are averaged across parameter uncertainty. Note that only transfers from rooting zone of each species are shown and do not include losses or gains from below the rooting zone.

some of the gains in water in deeper root species (*Pinus*, *Quercus*, *Ceratonia*) reflect water extracted from below the rooting zone of more shallow root species (and is therefore not shown as a loss of rooting zone water for those species). Note that water transfer between species-specific clumps is zero in the monoculture case. While climate variation and parameter uncertainty have substantial effects on water transfer estimates, several consistent general patterns emerged: (a) Deeper rooted species (*Pinus*, *Quercus*, and to lesser extent, *Ceratonia*) gained additional water particularly during the spring and early summer; (b) Some losses occurred for shallow rooted species (*Pistacia* and *Cupressus*) but these were more modest, and occurred earlier in the year; (c) Thus, losses occurred in the wet period when water is not limiting and gains occurred during drier period when a given species becomes water limited. This temporal shift between gains in water relative to losses helps to explain why the mixed scenario shows greater overall water use. It is also notable that *Pinus* shows gains in water use later in the season relative to *Ceratonia* and to a lesser extent *Quercus*–these differences in temporal pattern help to support overall stand scale effective water use. Differences in transpiration are also related to inter-species shading for mixed versus monoculture scenarios, across species. Taller species such as *Pinus* showed moderate increases in PAR, while shorter stature species such as *Pistacia* showed decreases (Table 3). These differences in height largely impact early season transpiration when water is less limiting and small differences in PAR between mixed and homogeneous scenarios matter most. For example, *Pinus* shows greater May transpiration in the mixed stand relative to monoculture scenarios; while *Pistacia* shows slightly greater transpiration in the monoculture scenario (Figure 6). Later in the season, however, water limitations dominate and shading differences become less important.

Table 3

Regional Hydro Ecologic Simulation System Estimates of Heights (m) for Monoculture and Mixed Stands by Species and Percent Change in Absorbed Photosynthetically Active Radiation Due to Mixing (Delta PAR) (Mixed-Mono)/Mono (Percent Change)

	Monoculture height			Mixed forest height			Delta PAR		
Species	Median	Low	High	Median	Low	High	Median	Low	High
Ceratonia Siliqua	8.7	7.3	10.1	9.0	7.7	10.3	−7.9	−12.4	−3.4
Quercus calliprinos	7.7	6.5	8.9	10.7	8.8	12.6	2.7	−0.5	5.9
Cupressus sempervirens	8.4	7.1	9.7	6.2	5.0	7.4	−18.2	−22.5	−13.9
Pinus halepensis	12.1	10.6	13.6	18.8	16.7	21.0	11.5	9.2	13.8
Pistacia lentiscus	3.4	2.5	4.4	2.9	2.1	3.6	−23.8	−27.8	−19.7

Note. Values are given as Median, and ±1 standard deviation (Low and High), of correlations computed for different parameter sets as sampled across ecophysiological parameter uncertainty. Shifts in the timing of decrease in gas exchange parameters in the transition to dry season can explain the few negative correlations equations.

3.7. Stand Scale Water Use and Productivity in Mixed Versus Monoculture Settings

Changes in water availability and PAR led to differences in species-specific growth, which translated into difference in estimated stand structure and species biomass. Total plant carbon increased for 2 of the 5 species (Figure 8; Table S5). For *Ceratonia* there was no significant change and for *Pistacia* and *Cupressus* there was a loss of plant carbon. Variation across parameters was high but results were significant for all species except *Ceratonia*. While there was some loss of carbon in *Pistacia* and *Cupressus*, overall carbon storage increased in the mixed scenarios. Comparing stand scale estimates of water use and carbon flux between monoculture and mixed stands, illustrates the aggregate impact of species-specific changes in water use and stand structure. Figure 9 summarizes the mean change in hydrologic and carbon fluxes and leaf area averaged over the stand area, and over the 30 years of meteorological forcing. Histograms show ranges across parameter uncertainty for both local and regional parameter sets. The mixed stand shows consistently greater transpiration and gross photosynthesis, and slightly lower groundwater recharge (Although because groundwater recharge is small and zero in many years, these declines are essentially negligible). Evaporation is also greater in the mixed stand for most but not all years and parameters and changes are smaller than for transpiration. The mixed stand also generally supports greater overall leaf area, reflecting a more complete utilization of incoming radiation and precipitation. The greater productivity and water-use of the mixed stand is robust across parameter uncertainty, although the magnitude of gains varies. Differences between the mixed and monoculture stands vary with precipitation such that gains in transpiration with mixed scenario tend to increase with precipitation up to a threshold annual precipitation of 500 mm (Figure 10a). Gross primary production (GPP) and net primary productivity (NPP) increases with mixed scenario also increase with annual precipitation although less dramatically (slope with precipitation is 0.16 and is significant) (Figures 10b and 10c).

4. Discussion

We provided empiric evidence for interspecific soil water partitioning and model-data fusion results indicating higher productivity of mixed than monoculture forests. Doing so, we confirmed both our hypotheses, namely of soil water partitioning in mixed stands, and of higher productivity of the mixed forest compared to monocultures. In our study we were able to: (a) provide field-based analysis of soil water-use partitioning as an underlying mechanisms for over-yielding; (b) simulate each of five divergent tree species in a mixed forest using a mechanistic model that explicitly represents soil water partitioning and inter-species shading, and use this model to quantify increase in productivity associated with mixed versus monoculture stands, across climate variation; and (c) expand the study of DPR and their mechanisms beyond temperate and tropical forests (Ruiz-Peinado et al., 2018; Fichtner et al., 2018, respectively) and into the water-limited forests of the mid-latitudes. In this respect, our work continues previous key studies of the mixed Mediterranean forest, such as del Castillo et al. (2016).

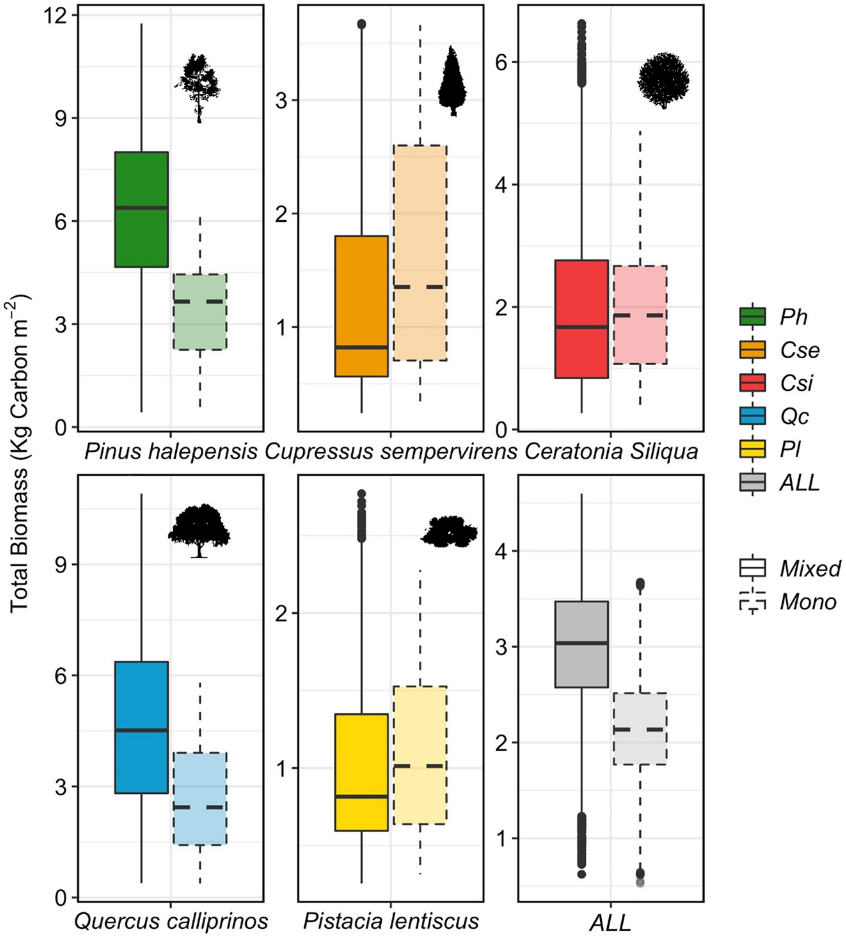

Figure 8. Regional Hydro Ecologic Simulation System estimates of tree clump total biomass in Yishi forest for monoculture (light) and mixed (dark) scenarios. Boxplots show inter-annual variation across 30 years (1983–2018). Estimates are averaged across parameter uncertainty. All denotes average plant carbon for the stand (including all species).

4.1. Diversity-Productivity Relationships

How are the DPR in our mixed Mediterranean forest compare with those in other mixed forest ecosystems? The global average over-yielding associated with mixed forests versus monocultures was reported as 24% (Zhang et al., 2012). Here we report an average over-yielding of 7%–32% in gross photosynthesis which is expressed as an increase of ~130 g C m^{-2} year^{-1} (Figure 9), and a higher increase in NPP, of ~170 g C m^{-2} year^{-1}, depending on precipitation amounts (Figure 10). Not all the five species benefitted from the mixing: while *Pinus* and *Quercus* showed a substantial biomass increase in the mixed forest versus their respective monocultures, *Cupressus* showed a very small (negative) effect, and the low-stature *Pistacia* seemed to grow better in the monoculture (Figure 8). These findings are in line with previous observations from a diversity of forest ecosystems that find that: (a) cases where mixtures are less productive than monocultures, as the case of *Pistacia* here, are not uncommon (Forrester, 2014); (b) in sites where stress is the norm, such as in our water-limited forest complementarity in eco-physiological traits tends to increase (Forrester, 2014); (c) Our results are also consistent with studies that find overyielding in the mixing of conifers with broadleaf tree species (Seidel et al., 2013); (d) moreover, in our case, the taller conifers were combined with lower stature shade-tolerant broadleaf species, a canopy structure inducing over-yielding (Cordonnier et al., 2018; Zhang et al., 2012); (e) specifically, *Pinus-Quercus* combinations have been shown to partition soil water-use in the most efficient way (Bello et al., 2019), whereby *Quercus* uses water from a deeper layer than the more shallow-rooted *Pinus*, enabling higher activity during the long dry season in

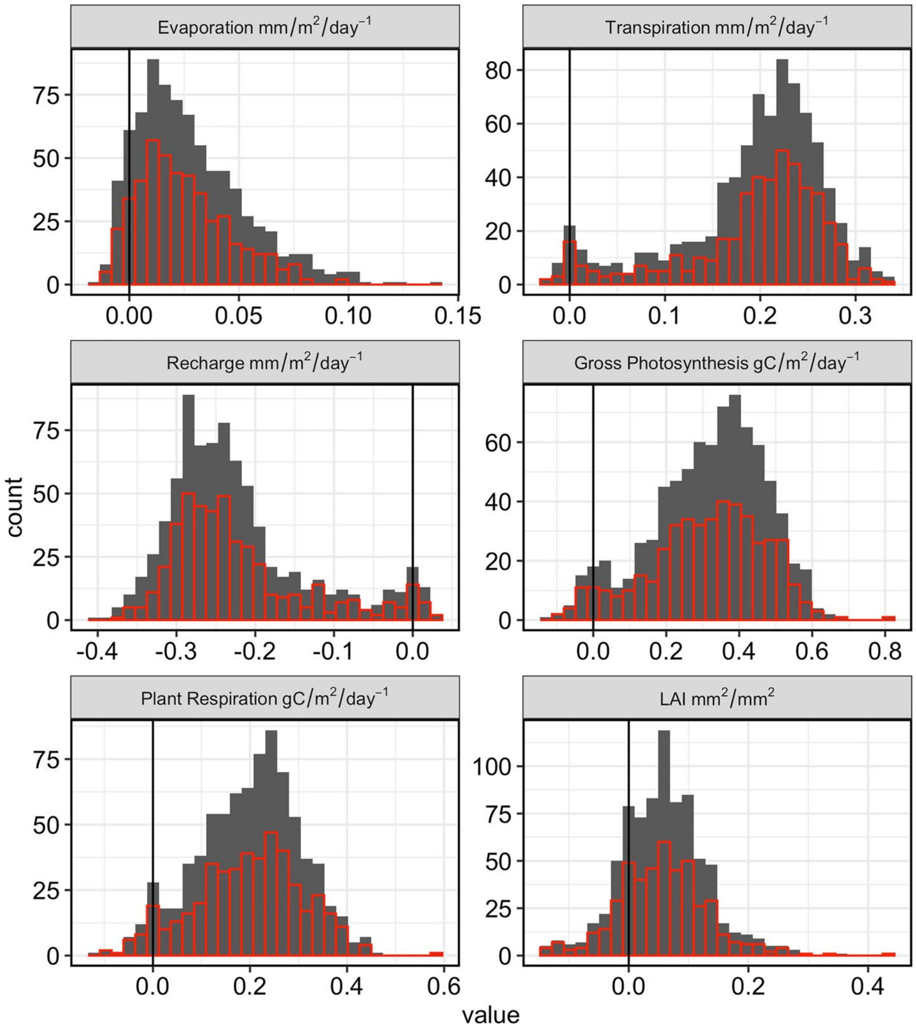

Figure 9. Histograms of Regional Hydro Ecologic Simulation System estimates of the difference in ecohydrologic estimate between mixed and monoculture scenarios in Yishi forest. Panels show difference in daily values (Mixed-Monoculture), averaged over the entire 30 years (1983–2018), and aggregated over all species. Variation in estimates shown by the histograms reflect the impact of ecophysiological parameter uncertainty. We show parameter uncertainty for two sampling strategies, one that includes all parameters that fit broad regional species canopy structural attributes (black) and a second where only parameters that also give good correlations with measured stomatal conductance for mixed stands are used (red).

the Mediterranean (del Castillo et al., 2016). Here we linked this *Quercus-Pinus* divergence in rooting depth (Figure 3) and water-use patterns (Figure 4) to the higher productivity compared to pure *Quercus* and *Pinus* stands.

The composition of forest ecosystems in the Eastern Mediterranean is also supportive of our observations. Among the five studied species, *Q. calliprinos* has been the dominant tree species across the Mediterranean vegetation zone in Israel along the past ten millennia (Liphschitz & Biger, 1990; Zohary, 1960). Notably, *Q. calliprinos* has rarely been growing without accompanying woody species (Table S1). In northern Israel, it is mostly accompanied by *Pistacia palaestina* (Liphschitz & Biger, 1990). It establishes better in the presence of another woody species than in the open field or under mature *Quercus* trees (Alon & Kadmon, 1996). Afforestation activities in the past 100 years increased the prevalence of the conifers *P. halepensis*, and, to lesser extent, *C. sempervirens* (Klein et al., 2019). In time, pine-oak forests have been forming (Sheffer, 2012), reflecting both oak establishment in planted pine forest (Sheffer et al., 2014), as in our case, and pine invasion into the oak maquis, forming a new overstory (Sheffer et al., 2013). In contrast with this spontaneous

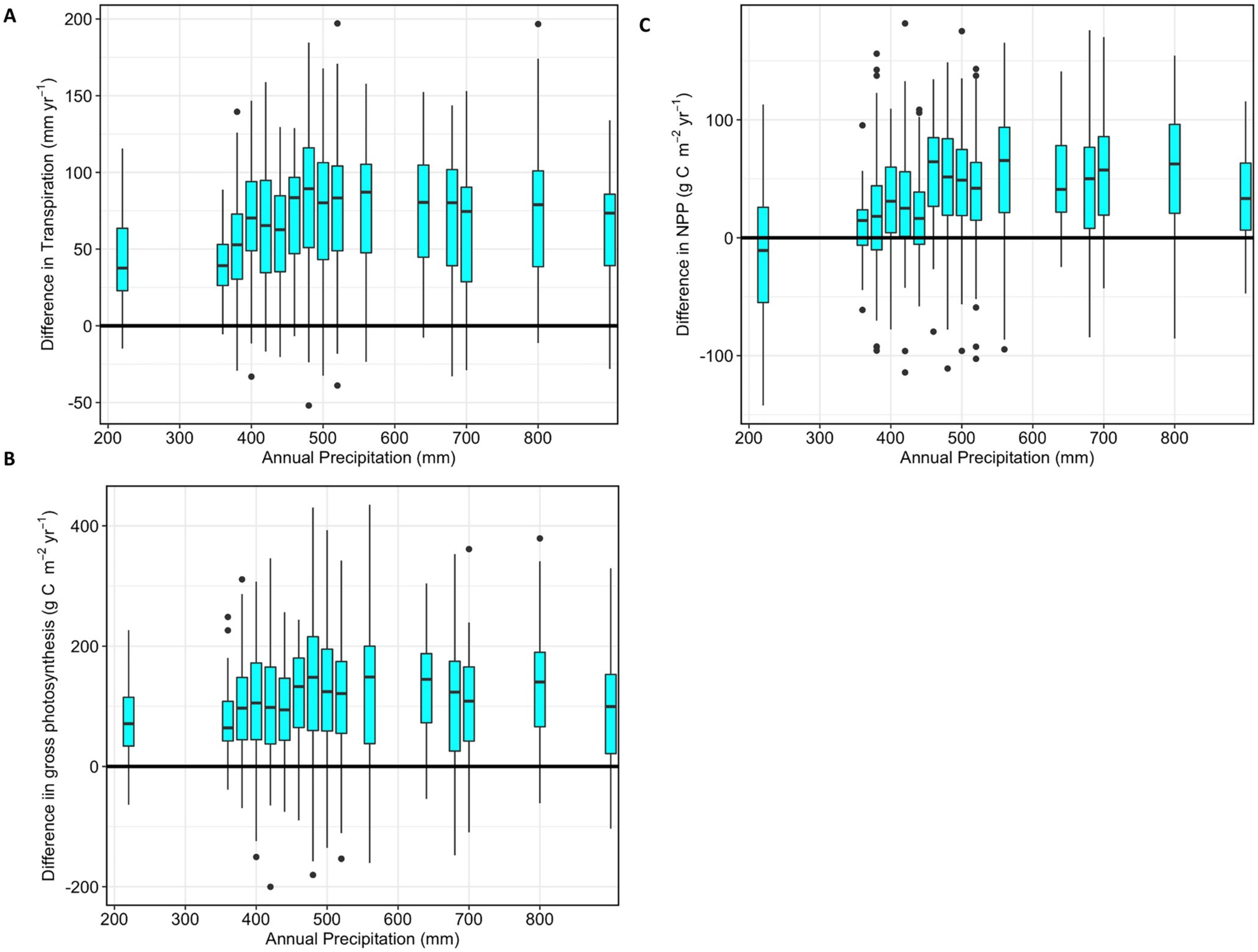

Figure 10. Regional Hydro Ecologic Simulation System estimates of the difference in water-use and productivity between mixed and monoculture scenarios in Yishi forest across the annual precipitation range. Boxplots show the impact of ecophysiological parameter uncertainty.

mixed forest formation, the dominant plant community in the Judean foothills has been that of *P. lentiscus* and *C. siliqua* (Danin, 1988; Zohary, 1962). This community is characterized by the high coverage of *P. lentiscus* accompanied by a low density of the taller *Ceratonia* trees. It is hence possible that the exception of *P. lentiscus* in our study, showing a negative DPR (Figure 8), relates to its actual occurrence in a near-monoculture maquis. Finally, our field observations indicate higher density (and hence, more biomass) in the mixed versus monoculture forests (Figure S1) which is consistent with greater overall biomass for mixed versus monoculture forests by RHESSys. Notably monoculture benefit to water status was found only for *Cupressus* in monoculture observations, again consistent with our model results where *Cupressus* was more productive in the monoculture scenario (Figure S7 confirming the model result in Figure 8).

4.2. Soil Water Partitioning, Shading and Interspecific Competition

Our results bring new evidence supporting the hypothesis that soil water niche partitioning is a mechanism to decrease interspecific competition (Ammer, 2019; Hildebrandt, 2020). Both field observations and model estimates demonstrate divergent tree water-use strategies among the different species in our study site and others (Chitra-Tarak et al., 2018). Mixing of the tree species (and hence, decreasing the competition over soil water) allowed for higher transpiration in the deeply rooted species in the first half of the dry season (Figure 6). To what extent do contrasting rooting depth patterns drive these divergent tree water-use strategies? In these water-limited environments, spatial differences in root zone water access can cause temporal differences in water use, and in particular how long plant water-use can continue into the summer period. However, root depth differences cannot fully explain differences in water-use strategies found in this study, for example, between the conifers and the broadleaf species. These seasonal differences also reflect differences in stomatal behavior, shading and canopy structure (height, leaf area), in addition to rooting depth. We show that the species-specific differences between mixed and monoculture stands reflected the combined impacts of shading and root zone water transfer in the mixed case (Figures 5 and 6). For example, *P. halepensis* decreases its water-use in the dry season by up to 95% in a monoculture (Klein, Cohen, et al., 2016), as well as in our mixed forest (Figure 4), whereas *Q. calliprinos* maintains its water-use longer into the summer in an oak-dominated maquis (Schiller et al., 2003), as well as in our mixed forest (Figure 4). Further differences in height and total biomass for each species in mixed versus monoculture suggest that niche partitioning of water use and light translate into longer term differences in canopy structure (total carbon or biomass store and height; Figures 7–9). Thus, these structural changes (e.g., greater leaf area, biomass and height) to some extent reinforced shading and water transfer changes, a positive feedback loop previously shown in temperate forests (Pretzsch, 2017; Tatsumi, 2020).

Changes related to shading and root zone typically suggest trade-offs—winners (taller, deeply rooted species) versus losers (shorter, shallow rooted species). However, in our case, the taller species were not always the more deeply rooted species, and vice versa, and hence the competition was somehow more balanced. Aggregate NPP, GPP, carbon sequestration and transpiration were all higher for mixed scenario—Thus the stand as a whole showed a net sum gain. The differences in flux estimates for *Q. calliprinos* in mixed and monoculture scenarios, provide an illustration of why this occurs. Additional shading led to a 10% loss in PAR for this species (Table 3) but an overall gain in GPP of 27% and a 16% increase in plant carbon. Thus, in this case, the increased shading reduced overall demand for water, and thereby increasing its GPP, and supporting greater overall plant carbon. Inter-annual variations are discussed in the supporting information.

4.3. Implications to Forests in the 21st Century

Forests in semi-arid regions have been shown to act as a major and relatively stable carbon sink, far beyond previously estimated (e.g., a net ecosystem exchange of 2.3 ton C ha^{-1} $year^{-1}$; Poulter et al., 2014; Rotenberg & Yakir, 2010). That assessment was based on carbon sequestration and productivity measurements in a pine forest (Grünzweig et al., 2007). Based on our analyses, it is possible that mixed forests in this region can further enhance this carbon sink. Considering the warming climate and the related increase in VPD, we found that this over-yielding might become smaller and less stable with time. However, excess carbon uptake and growth in wetter years can still make a big difference. Another important perturbation, which is constantly growing, is the level of atmospheric CO_2. Due to competition over light, water, and nutrients, this change is not expected to facilitate faster tree growth. However, broadleaf tree species are expected to reduce stomatal conductance, and thus, water-use, whereas conifers are unlikely to respond (Klein & Ramon, 2019). As a consequence, conifers sharing their water source with broadleaf species, such as *Cupressus-Pistacia* and *Pinus-Quercus* in our site, might benefit from these water savings. Increased conifer growth might, in turn, enhance canopy closure and shading over the shorter broadleaf trees. However, we expect that such changes will be counter-balanced by other processes like intraspecific competition.

Our combination of observations and mechanistic modeling demonstrate that the secret to the success of the studied forest lies in its high functional diversity, which is expressed in high complementarity in multiple traits. Functional diversity is being increasingly recognized as a key aspect of biodiversity, alongside species diversity, and both are responsible for higher ecosystem productivity and stability (Guo et al., 2020). Therefore, mixed forests should be recognized as higher priority for conservation. An implication of our study is that species mixing based on a high trait diversity could be beneficial to forest productivity. *Pinus-Quercus* combinations have been known to offer benefits for both species in temperate forests (Bello et al., 2019), as well as in Mediterranean forests (del Castillo et al., 2016; Sheffer, 2012), and specifically at this site (Klein et al., 2013). Yet, combinations with other species, such as *Ceratonia* and *Cupressus*, representing the extremes in water-use patterns in our site, might become even more productive. To permit this, the forestry management must take on the challenges of creating the mixed forests of the future.

Conflict of Interest

The authors declare no conflict of interest in the preparation of this manuscript.

Data Availability Statement

All empiric data from the field used in this paper, and RHESSys model code are available via https://zenodo.org/record/5159825#.YQq3eo4zaUk (DOI: 10.5281/zenodo.4966654).

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