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Nonlinear plant–plant interactions modulate impact of extreme drought and recovery on a Mediterranean ecosystem

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Summary

- Interaction effects of different stressors, such as extreme drought and plant invasion, can have detrimental effects on ecosystem functioning and recovery after drought. With ongoing climate change and increasing plant invasion, there is an urgent need to predict the short- and long-term interaction impacts of these stressors on ecosystems.
- We established a combined precipitation exclusion and shrub invasion (*Cistus ladanifer*) experiment in a Mediterranean cork oak (*Quercus suber*) ecosystem with four treatments: (1) *Q. suber* control; (2) *Q. suber* with rain exclusion; (3) *Q. suber* invaded by shrubs; and (4) *Q. suber* with rain exclusion and shrub invasion. As key parameter, we continuously measured ecosystem water fluxes.
- In an average precipitation year, the interaction effects of both stressors were neutral. However, the combination of imposed drought and shrub invasion led to amplifying interaction effects during an extreme drought by strongly reducing tree transpiration. Contrarily, the imposed drought reduced the competitiveness of the shrubs in the following recovery period, which buffered the negative effects of shrub invasion on *Q. suber*.
- Our results demonstrate the highly dynamic and nonlinear effects of interacting stressors on ecosystems and urges for further investigations on biotic interactions in a context of climate change pressures.

Introduction

Over the past decades, environmental stresses caused by extreme drought and plant invasion have increased in frequency and intensity in many terrestrial ecosystems, with strong detrimental impacts on ecosystem functioning, stability and resilience (Bradley *et al.*, 2012; Diez *et al.*, 2012; Doblas Miranda *et al.*, 2017). Both stressors have been studied extensively, demonstrating their profound and often detrimental impact on terrestrial ecosystems (for reviews, see Gaertner *et al.*, 2009; Vilà *et al.*, 2011; Diez *et al.*, 2012; Allen *et al.*, 2015). Nevertheless, still little is known about the interaction of these stressors and results are hard to generalize (Sorte *et al.*, 2013; Côté *et al.*, 2016). Prediction of the impact of interacting stressors is difficult and complex, as interaction effects can be amplifying, neutral or even buffering. For the interaction of drought and plant invasion, amplifying as well as buffering effects have been observed recently. Esch *et al.* (2019) detected amplifying effects in a Mediterranean ecosystem, dominated by the shrubs *Salvia mellifera* and *Artemisia californica*, where drought and invasive annuals mutually altered the shrubs phenological sensitivity and ecosystem productivity. On the other hand, Fahey *et al.* (2018) observed buffering effects of drought and the non-native grass *Imperata cylindrical* in a *Pinus palustris* ecosystem, where the invader ameliorated the impact of experimental drought on the ecosystem by increasing soil moisture. Similar to those examples, interacting drought and plant invasion or competition have been shown to alter ecosystem transpiration and the resilience of native species (Rascher *et al.*, 2011; Caldeira *et al.*, 2015), change N-composition in the soil (Castro *et al.*, 2020), impact biodiversity (Vetter *et al.*, 2020), facilitate the invasion of other competitive plants (White *et al.*, 2001; Scott *et al.*, 2010; Manea *et al.*, 2016), decrease tree growth and increase mortality rates (Gleason *et al.*, 2017; Young *et al.*, 2017), or even provoke permanent ecosystem state changes when tipping points are reached (Klose *et al.*, 2019).

It might be assumed that the direction of an interaction effect between stressors should be consistent over time (e.g. buffering, neutral or amplifying). However, there is evidence that interactions often induce highly diverse, surprising and counterintuitive processes (Côté *et al.*, 2016), which change the direction of interaction effects over time or in dependence on environmental conditions. Thus, such a change in the direction of an interaction, which cannot be predicted from the effects of the single stressors, can be considered as nonlinear. For example, Alba *et al.* (2019) demonstrated that the interaction effect of drought and the

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invasive grass *I. cylindrical* shifted unexpectedly from facilitation to competition over time. Similar changes in the direction of interaction effects in ecosystems can be provoked by different levels of environmental stress (Armas & Pugnaire, 2005; Brooker *et al.*, 2005; Brooker, 2006), plant age (Miriti, 2006), species composition (Maestre *et al.*, 2009; Grant *et al.*, 2014) or tree diversity (Grossiord, 2019). Without exact knowledge of the underlying processes, mechanisms and directions of interaction effects, the short- and long-term impact on terrestrial ecosystems is difficult to predict. Potentially, the stress gradient hypothesis (SGH) (Bertness & Callaway, 1994; Callaway & Walker, 1997; Maestre *et al.*, 2009) can provide a valuable framework to shed light onto the complex plant–plant interactions under varying drought conditions. The SGH predicts the prevalence of competitive or facilitative plant–plant interactions along a stress gradient (Maestre *et al.*, 2009). In ecosystems where water resources are limiting, competition is expected to dominate plant–plant interactions under low and high water stress conditions, whereas facilitation is expected to occur under moderate drought stress (Maestre *et al.*, 2009). Yet, studies of interacting drought and plant invasion provide the opportunity to investigate the response of a plant species to different drought stress levels with and without plant–plant interactions.

Extreme drought and plant invasion have been increasing problems in the Mediterranean basin in recent years (Hoerling *et al.*, 2011; Seneviratne *et al.*, 2012; Doblas Miranda *et al.*, 2017). Mediterranean ecosystems are biodiversity (Médail & Quézel, 1999; Sala *et al.*, 2000) and climate change hotspots (Giorgi, 2006; Guiot & Cramer, 2016), rendering these systems particularly worth preserving. To study interacting stressors under field conditions, we used a man-made, savannah-type cork oak (*Quercus suber* L.) ecosystem. *Q. suber* is a species with a strong control of transpiration water loss during dry seasons and well-adapted to natural drought (David *et al.*, 2007; Kurz-Besson *et al.*, 2014). However, these ecosystems have been progressively invaded by successional pioneer species, such as gum rockrose (*Cistus ladanifer* L.) (Acácio *et al.*, 2009; Costa *et al.*, 2009; Bugalho *et al.*, 2011). A rapid range expansion in monospecific stands (Acácio *et al.*, 2009; Costa *et al.*, 2009) following climate change-induced alterations, such as higher temperatures and extended drought, and human disturbances, such as soil and land degradation (Acácio & Holmgren, 2014), argue for *C. ladanifer* as a native invasive species (cf. Simberloff, 2011; Carey *et al.*, 2012). Furthermore, shrubs express high growth rates, transpiration and phenotypic plasticity, reacting strongly to changes in environmental conditions (Correia *et al.*, 1987; Correia & Ascensao, 2016; Haberstroh *et al.*, 2018), which further illustrate the invasive characteristics of this species (cf. Leishman *et al.*, 2007; Cavaleri & Sack, 2010; Funk, 2013; Sorte *et al.*, 2013). A first study of interacting effects of drought and shrub invasion pointed towards detrimental amplifying effects on *Q. suber* ecosystems (Caldeira *et al.*, 2015), in which tree transpiration was strongly reduced during and after a severe drought, potentially driving tree mortality (Caldeira *et al.*, 2015).

The main objectives of this study are to investigate the impact of extreme drought, plant invasion and their interaction in a Mediterranean *Q. suber* ecosystem (1) in the natural drought periods in summer and (2) in the recovery periods after autumn and winter rains, to capture the direction and dynamic of the interaction effects over time and seasons. To this end, we established a rain exclusion (RE) and shrub removal experiment in a *Q. suber* ecosystem invaded by *C. ladanifer*. We hypothesize that both experimental stressors reduce tree transpiration and lead to highly dynamic interaction effects in the natural summer drought and the recovery period in winter with potentially detrimental effects on the ecosystems' functioning and persistence.

Materials and Methods

Experimental site

The investigated *Quercus suber* L. ecosystem is part of the Tapada Real in Vila Viçosa, Portugal (marked by a red star in Fig. 1a). The site has a Mediterranean climate (Cs; Kottek *et al.*, 2006), with dry summers and wet winters. Soils on site were classified as haplic Leptosols with a high gravel content of the dominant bedrock schist (Caldeira *et al.*, 2014). The shallow, poorly

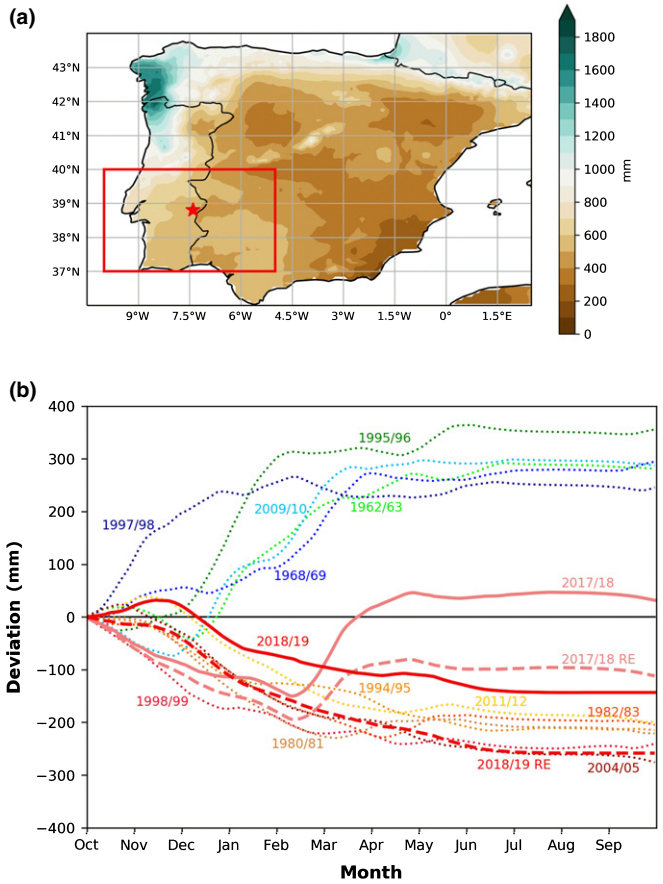


Fig. 1 Climatology of annual precipitation (mm) for 1981–2010 over the Iberian Peninsula. The red star marks the study site in Vila Viçosa (a). Temporal evolution of accumulated precipitation anomalies (relative to climatology 1981–2010) along the hydrological year (1 October–30 September) for the red box (10°W–5°W, 37°N–40°N) in (a). Depicted are the five driest/wettest years since 1950 and the years of the measurement with/without rain exclusion (RE) (b).

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developed soils seldom exceed a depth of 0.4 m (Haberstroh *et al.*, 2018). All investigated plots were invaded by *Cistus ladanifer* L. before 2011, when the shrubs were cut on half of the plots, allowing a sparse grass layer to repopulate the understorey (Caldeira *et al.*, 2015). In November 2017, an RE experiment was implemented by mounting nontransparent half-pipe-PVC-tubes of 12.5 cm diameter 10–40 cm aboveground to assure water run-off and minimize the influence on the soil surface. Plots were situated at flat positions in the landscape with a negligible slope. At the start of the experiment, the RE coverage was 30% of the plot area, which was increased to 45% in April 2019. For measurements under ambient precipitation conditions, we also established respective control plots, which resulted in four different treatments: Control with *Q. suber* trees; RE with *Q. suber* trees (RE); *Q. suber* trees invaded by *C. ladanifer* shrubs (Invasion); and a RE invaded by *C. ladanifer* shrubs (Invasion + RE). As we were investigating different periods of the hydrological year, including recovery phases, we use the term reduced water availability for the RE treatments. In each treatment, three trees and three shrubs (in invaded plots) were chosen randomly for long-term monitoring. For replication, we applied a randomized block design, with each treatment being randomly assigned in each of three separate blocks, giving 12 experimental plots with a total of 36 trees and 18 shrubs. The plot size of 180 m^2 was sufficient as the measured trees and shrubs were positioned in the middle of the respective plots with a buffer zone at the edges. The lateral root system with sinkers of *Q. suber* was found to be within the tree crown (David *et al.*, 2013), which had an average size of 29.6 ± 1.5 m^2 for the investigated trees. Shrub density was set to 11 000 individuals ha^{-1} at the start of the experiment in March 2018 in all invaded plots by cutting surplus shrubs. Measurements were conducted in the hydrological years 2018 (October 2017–September 2018), 2019 (October 2018–September 2019) and in the first half of the hydrological year 2020 (October 2019–March 2020). Further information about the experimental design, field site and experiments are available in the Supporting Information (Figs S1, S2) and previous studies (Caldeira *et al.*, 2015; Haberstroh *et al.*, 2018, 2019; Dubbert *et al.*, 2019).

Local meteorological conditions and volumetric soil water content

Meteorological parameters were monitored on each block. Precipitation was measured with rain gauges (ARG100, Campbell Scientific, Logan, UT, USA; RG1, Delta-T Devices Ltd, Cambridge, UK) and stored half-hourly on data loggers (CR300/CR800, Campbell Scientific). The meteorological stations included an air temperature and relative humidity sensor (RHT2, AT2, Delta-T Devices Ltd; S-THB-M002, Onset, MA, USA). Data were stored every 30 min on independent data loggers (HOBO USB Micro Station Data Logger, Onset; ECH2O Em50, METER Group Inc., Pullman, WA, USA). Volumetric soil water content (VWC) was measured at three depths (0.05, 0.20, 0.40 m) with ECH2O 5TM probes (METER Group). Per plot, we installed two profiles to preclude sensor failure. Sensors were calibrated individually in the laboratory before installation in the field. The laboratory calibration was complemented by frequent soil coring under field conditions to verify the sensor calibration. As a consequence of the high level of volumetric soil skeleton with ≤ 0.61 g skeleton cm^{-3} soil at 0.40 m depth, a correction factor was introduced for some sensors. Data gaps caused by logger or sensor failure were gap filled with linear regressions.

Sap flux density and transpiration

Trees were equipped with Granier-type sap flow sensors (SFS2, Type M-M12; UP GmbH, Ibbenbüren, Germany) at *c.* 1 m height. The sensor probes with a 20-mm heating zone were inserted 30 mm into conducting sapwood. Sapwood coring revealed that the functional sapwood area of *Q. suber* was always > 30 mm (Caldeira *et al.*, 2015). Sap flow calculations (see Haberstroh *et al.*, 2020) followed the standard procedure suggested by Granier (1985) and Granier & Gross (1987). To determine the maximum temperature difference between the needles, which is required for the sap flow calculation, an average moving window of three days was applied (Haberstroh *et al.*, 2020). Shrub sap flow was measured with custom-made sap flow gauges, comparable to the SGA13 (Dynamax Inc., Houston, TX, USA), following the stem heat balance method (Sakuratani, 1984). All sensors were recorded as half-hourly average on data loggers (CR300/CR800/CR1000 and AM16/32 multiplexer; Campbell Scientific). Missing data resulting from sensor or data logger failure were gap-filled with linear regressions before and after the malfunctioning period for trees and shrubs. Shrub sap flow was corrected with an allometric equation for the increment of the functional sapwood area. For a better comparison of tree and shrub sap flow, sap flow per sapwood area was computed (sap flux density). We are aware that the use of two different sap flow measurement systems can hamper the upscaling to transpiration rates, which should thus be interpreted with care. Nevertheless, these sap flow methods have been applied successfully in the past (Caldeira *et al.*, 2015; Haberstroh *et al.*, 2018) and there is evidence that they are comparable (Tournebize & Boistard, 1998). The determination of sapwood area and the shrub increment correction are presented in Methods S1, S2, Table S1 and Fig. S3.

Daily transpiration was calculated as sap flux density (m^3 m^{-2}) and the sapwood area per ground area (m^2) for both species. The exact values and procedures for the determination of sapwood per ground area can be retrieved from Methods S3 and Table S2. The transpiration was summed up for each hydrological year to calculate the ecosystem water balance. In addition, the study period was separated into three winter and two summer periods according to the development of the sap flux density. The summer periods were defined as the interval where sap flux was decreasing continuously up to the first increase after the autumn precipitation. For all periods, average transpiration rates per day were calculated to account for the varying lengths of the different periods. Subsequently, we calculated the drought legacy effects for the different treatments in the winter periods, as the difference between actual tree transpiration in each treatment and expected transpiration without stressor (Control) as following with Eqn 1:

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$$\text{Legacy effect}\,(\%) = \frac{E_{\text{treatment}} - E_{\text{control}}}{E_{\text{control}}} \times 100 \qquad \text{Eqn 1}$$

($E_{\text{treatment}}$, tree transpiration in one of the three applied treatments (Invasion, RE, Invasion + RE); E_{control}, transpiration of trees in the Control treatment). This equation was adapted from Sala *et al.* (2012) to be consistent with the terminology used in arid and semi-arid ecosystems. To account for the absolute difference between the winter periods, results were standardized with the expected transpiration (E_{control}).

Definition of interaction effects

For the assessment of interaction effects on tree transpiration, we defined interaction effects stronger than the exposure to the single stressors as amplifying and interaction effects weaker than the exposure to the single stressors as buffering. Interaction effects, which did not differ substantially from the single stressors (± 10%) were deemed neutral. The terms amplifying and buffering are sometimes used as synonym for synergy and antagonism (e.g. Cannon *et al.*, 2017). However, for the determination of synergies or antagonisms, an additive or multiplicative null-model usually is defined (Piggott *et al.*, 2015; Côté *et al.*, 2016), which could lead to unrealistically low transpiration rates for our ecosystem. Hence, we base our argumentation on the comparison between the interaction effect and the effect of the stronger single stressor (cf. Holmstrup *et al.*, 2010).

Leaf water potential, leaf area index and trunk increment

Leaf water potential was measured at pre-dawn (Ψ_{PD}) with a Scholander-type pressure chamber (PMS 1000; PMS Instruments, Corvalis, OR, USA) between 02:00 and 06:00 h. For each tree and shrub, we measured two leaves (trees) or small branches (shrubs). Leaf area index (LAI) was measured at dusk and dawn with the LAI-2000 plant canopy analyser (Li-Cor Inc., Lincoln, NE, USA). For trees, one measurement was taken in an open space; subsequently 10 measurements were taken under the canopy with the same orientation. Afterwards, we removed the 68° ring from the measurement with the software FV2200 (Li-Cor), as this outer ring was most likely measuring clear sky (Li-Cor, 1992). For shrubs, we measured 15 points along each transect ($n = 3$) of 10 m per plot. For all measurements, we used the 45° view cap to avoid any influence of the operator or tree trunks (Li-Cor, 1992). LAI measurements were conducted each spring after the growing period in late June and each autumn after the natural summer drought in October. In March 2018, all trees were equipped with dendrometers (DB20 manual band dendrometer; EMS, Brno, Czech Republic) at breast height and read manually at least every month to calculate the tree trunk increment.

Meteorological and climatic conditions

We evaluated the temperature and precipitation conditions for the two measurement years based on the observational dataset E-OBS (Haylock *et al.*, 2008) and put these in context of the regional climate. E-OBS is issued by the European Climate Assessment & Dataset project (ECA&D) and provides regularly updated gridded temperature and precipitation fields for European land areas. The current ensemble version V20e (Cornes *et al.*, 2018) has a regular 0.1° × 0.1° grid. The long-term climatology of annual temperature and precipitation was estimated for 1981–2010 (reference period) focussing on hydrological years (1 October to 30 September). Statistics were derived for the nearest E-OBS grid point to the site location, the nine surrounding points, and for Southwestern (SW) Iberia (red box in Fig. 1a). The information is summarized in Table S3, together with the meteorological site measurements for 2017/2018 and 2018/2019. Anomalies relative to the mean annual precipitation were computed to identify wet (exceedances) and dry periods (deficits). Finally, the temporal development of cumulative precipitation anomalies along the individual hydrological years was analyzed for SW Iberia, allowing a direct comparison of the site measurements with the wettest/driest years on record since 1950.

Data analysis

We applied linear mixed effect models (package NLME) in R (R core team, 2020) to account for the randomized block design. Differences in VWC were assessed by comparing the four different treatments, the three depths (0.05, 0.20, 0.40 m) and their interaction in the same model. Tree and shrub sap flux density were analyzed separately with treatment as fixed factor. For Ψ_{PD}, trunk increment, LAI, transpiration and legacy effect in tree transpiration, treatment and measurement periods were treated as fixed effects and their interaction considered. For all linear mixed effect models, we handled block and tree/shrub identity, if applicable, as random effects. For a species comparison of sap flux densities and transpiration rates, we applied additional linear mixed effect models and handled the experimental treatment as supplementary random factor. Model assumptions (normal distribution of residuals and variance homogeneity) were checked visually and supported by the Shapiro–Wilk and Levene tests in R (R Core Team, 2020). In the case of violations, data were square-root- or log-transformed. Subsequently, differences between treatments and measurement periods were assessed by a pairwise Tukey-adjusted comparison of the means. The exact packages and commands can be found in Table S4. In this publication, we will try not to base our argumentation and conclusions solely on *P*-values, but rather use them to support our argumentation (Wasserstein *et al.*, 2019).

Results

Abiotic conditions: meteorology and volumetric soil water content

In terms of mean air temperature, both hydrological years were comparable with 15.9°C in 2018 and 16.4°C in 2019 at the site, which were similar to the long-term average of 16.7–16.8°C for E-OBS (Table S3). The comparison with precipitation records since 1950 revealed that the hydrological year of 2018 corresponded to an average year for SW Iberia. When looking at

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seasonal trends (Fig. 1b), 2018 was characterized by a precipitation deficit in winter, which was compensated by rainfall starting in early spring. Under the RE, 2018 was a moderately dry year. 2019 was a moderately dry year under ambient conditions (–112 mm by the end of September; Fig. 1b), with below-normal precipitation in all months except November and December. With the RE, 2019 became an extremely dry year (–258 mm; Fig. 1b), similar to the driest year on record since 1950, namely 2004/05 (–276 mm; García-Herrera *et al.*, 2007). Overall, the site measurements are largely consistent with the E-OBS data, with exception of a strong deviation in precipitation in 2018 (713 mm vs 518 mm; Table S3). This large deviation is associated with the occurrence of localized convective precipitation events (thunderstorms) in late February and March 2018. Given the nature of this type of rainfall events, which produce very heterogeneous spatial precipitation patterns, these large precipitation amounts were not captured by the (area averaged) E-OBS data (Fig. S4).

The VWC developed according to the precipitation occurrence (Fig. 2). Soils were wet from November 2017 until June 2018, followed by the summer dry-down period from July to mid October 2018. Frequent precipitation occurrence until April 2019 was superseded by an extended drought period from April to the end of October 2019, which was reflected in low VWC during this period. Overall, there were strong differences between treatments, depths and their interaction (all $P < 0.001$). Integrating over the complete soil profile, strong variations could be observed between ambient precipitation (Control and Invasion) and RE treatments (Fig. 2; all $P < 0.001$). At 0.20 m depth all treatments differed in their VWC ($P < 0.001$): in the summer drying periods, the Invasion and Invasion + RE (Fig. 2b) treatments showed a stronger dry-down in the soil profile. Overall, on the one hand, the VWC at 0.20 m depth (Fig. 2b) for Invasion + RE (0.11 ± 0.04 m^3 m^{-3}) was reduced by 18% on average during the summer periods in comparison to the Control (0.13 ± 0.06 m^3 m^{-3}). On the other, in the winter periods when soil water resources recharged, both RE treatments with and without Invasion received less precipitation (Fig. 2). In these periods, trees and shrubs in the Invasion + RE treatment (0.18 ± 0.06 m^3 m^{-3}) received 24% less water on average at 0.20 m depth (Fig. 2b) than the Control treatment (0.24 ± 0.08 m^3 m^{-3}).

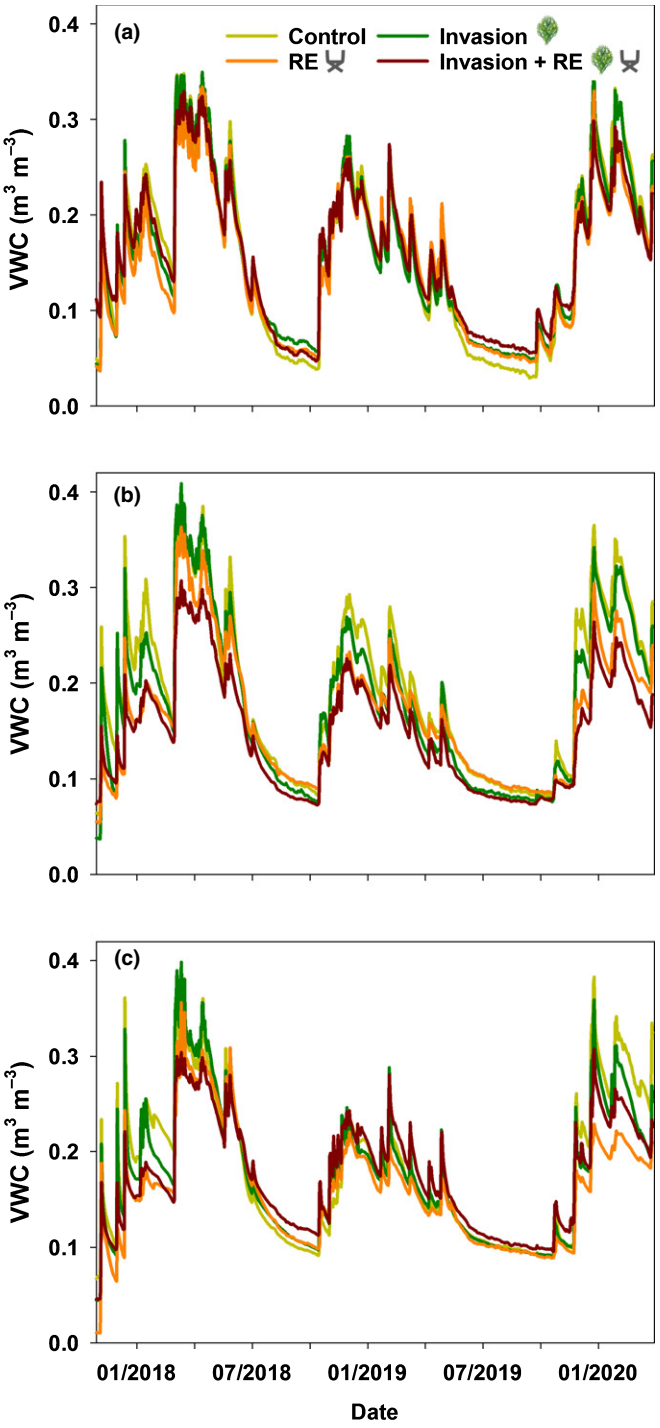


Fig. 2 Volumetric water content in m^3 m^{-3} for Control, Invasion, rain exclusion (RE) and Invasion + RE treatments at 0.05 (a), 0.20 (b) and 0.40 m (c) depth ($n = 6$ per treatment and depth).

Plant water status

The patterns observed in precipitation and VWC (Fig. 2) were reflected in tree and shrub water status, which led to different patterns of sap flux density and leaf water potential during the two hydrological years (Fig. 3). Although mean tree sap flux densities varied only marginally between treatments ($P = 0.11$), differences emerged after dividing the study period into several seasons (Fig. 3a). During summer 2018, all experimentally stressed trees reached similar sap flux densities, and only Control trees had slightly higher values. In 2019, maximum sap flux densities were lower compared to 2018 for all trees, yet to a different extent. In particular, trees with Invasion + RE reached a lower maximum and their sap flux densities decreased earlier with the onset of summer drought (Fig. 3a). Similar sap flux densities were observed in trees under Invasion and trees under RE, which were distinctly lower than Control trees. In general, shrub sap flux densities were higher than those of trees ($P < 0.001$). In 2018, they were approximately four-fold higher (max. 8.66 ± 0.83 m^3 m^{-2} d^{-1}) but only two-fold higher in 2019 (max. 4.69 ± 0.31 m^3 m^{-2} d^{-1}) compared to Control trees,

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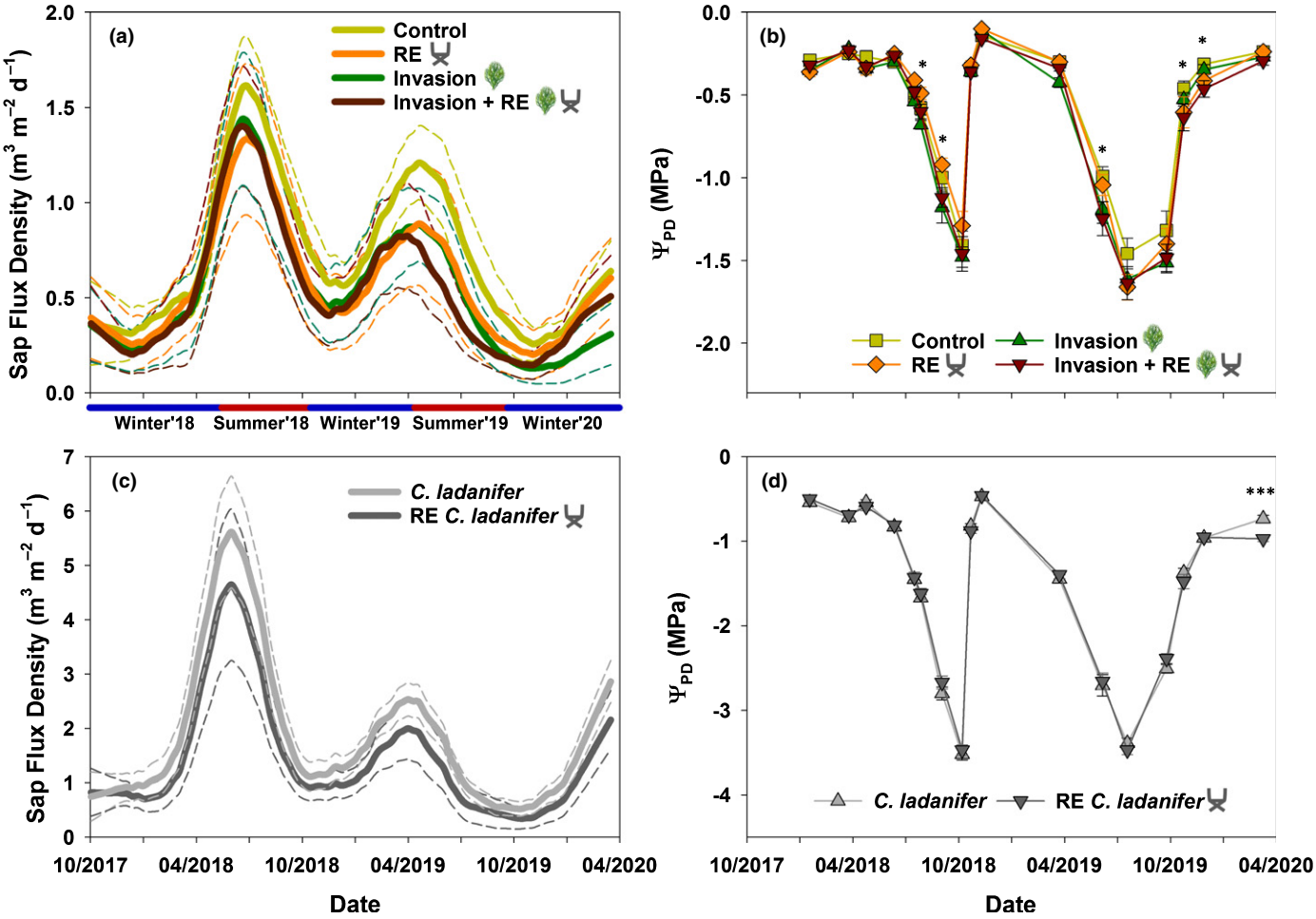


Fig. 3 Daily sap flux density for *Quercus suber* (n = 9 per treatment) (a) and *Cistus ladanifer* (n = 9 per treatment) (c) in m^3 m^{-2} d^{-1} with 95% confidence interval and pre-dawn leaf water potential for *Q. suber* (n = 9 per treatment) (b) and *C. ladanifer* (n = 9 per treatment) (d) in MPa with standard error (1 SE). Sap flux density was smoothed for plotting purposes (negative exponential). Asterisks indicate significance level (pairwise Tukey-adjusted comparison of the means): *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Note the different scales between species. RE, rain exclusion.

indicating a strong reduction from 2018 to 2019 (Fig. 3c). The RE reduced the overall sap flux densities of the shrubs substantially ($P < 0.001$). Also, for Ψ_{PD}, the different drying patterns of the two years were evident (Fig. 3b,d). In 2019, Ψ_{PD} of all trees and shrubs decreased earlier in the year and the recovery after the autumn rainfalls was slower compared to 2018. Treatment differences between trees with Invasion and trees with the RE were moderate, but became distinct in September 2018 ($P < 0.05$; Fig. 3b). Moreover, Ψ_{PD} of Control trees was higher (–1.46 ± 0.09 MPa) compared to trees under Invasion +RE (–1.64 ± 0.10 MPa) during the summer drying period in July 2019 ($P <$ 0.05), which reflected sap flux density measurements (Fig. 3a).

Differences between leaf water potentials of Control (–0.46 ± 0.05 MPa) and trees under Invasion + RE (–0.64 ± 0.08 MPa) ($P < 0.05$) persisted during the winter period in late October and early December 2019 (Fig. 3b). Likewise, differences were evident for shrub leaf water potentials with –0.60 ± 0.04 MPa in the Invasion treatment and –0.85 ± 0.03 MPa under the RE treatment ($P < 0.001$) in March 2020 (Fig. 3d). In the winter recovery periods of 2018 and 2019, no clear differences were detected in shrubs Ψ_{PD}. However, the daily sap flux densities revealed interesting patterns (Fig. 3a,c). In 2018, all trees and shrubs had similar sap flux densities, and in the following recovery period in winter 2019, Control trees had higher sap flux densities compared to all other treatments. However, in winter 2020, an interesting pattern emerged when comparing the trees under shrub Invasion with and without RE: trees under Invasion + RE did recover with only slightly lower sap flux densities (max. 0.85 ± 0.12 m^3 m^{-2} d^{-1}) than Control trees (max. 1.02 ± 0.21 m^3 m^{-2} d^{-1}). Surprisingly, sap flux densities of trees under Invasion under ambient rainfall did not recover to the same extent (max. 0.45 ± 0.11 m^3 m^{-2} d^{-1}) (Fig. 3a). Shrubs in the same treatment, however, showed a strong recovery in sap flux densities (max. 3.80 ± 0.30 m^3 m^{-2} d^{-1}), almost reaching the maximum rates of the previous year 2019 (4.69 ± 0.31 m^3 m^{-2} d^{-1}) (Fig. 3c). By contrast, sap flux densities of shrubs under RE recovered more slowly (max. 2.88 ± 0.32 m^3 m^{-2} d^{-1}) (Fig. 3c).

Ecosystem transpiration

Figure 4 illustrates the cumulative transpiration rates for all treatments, species and hydrological years. Although the Control trees

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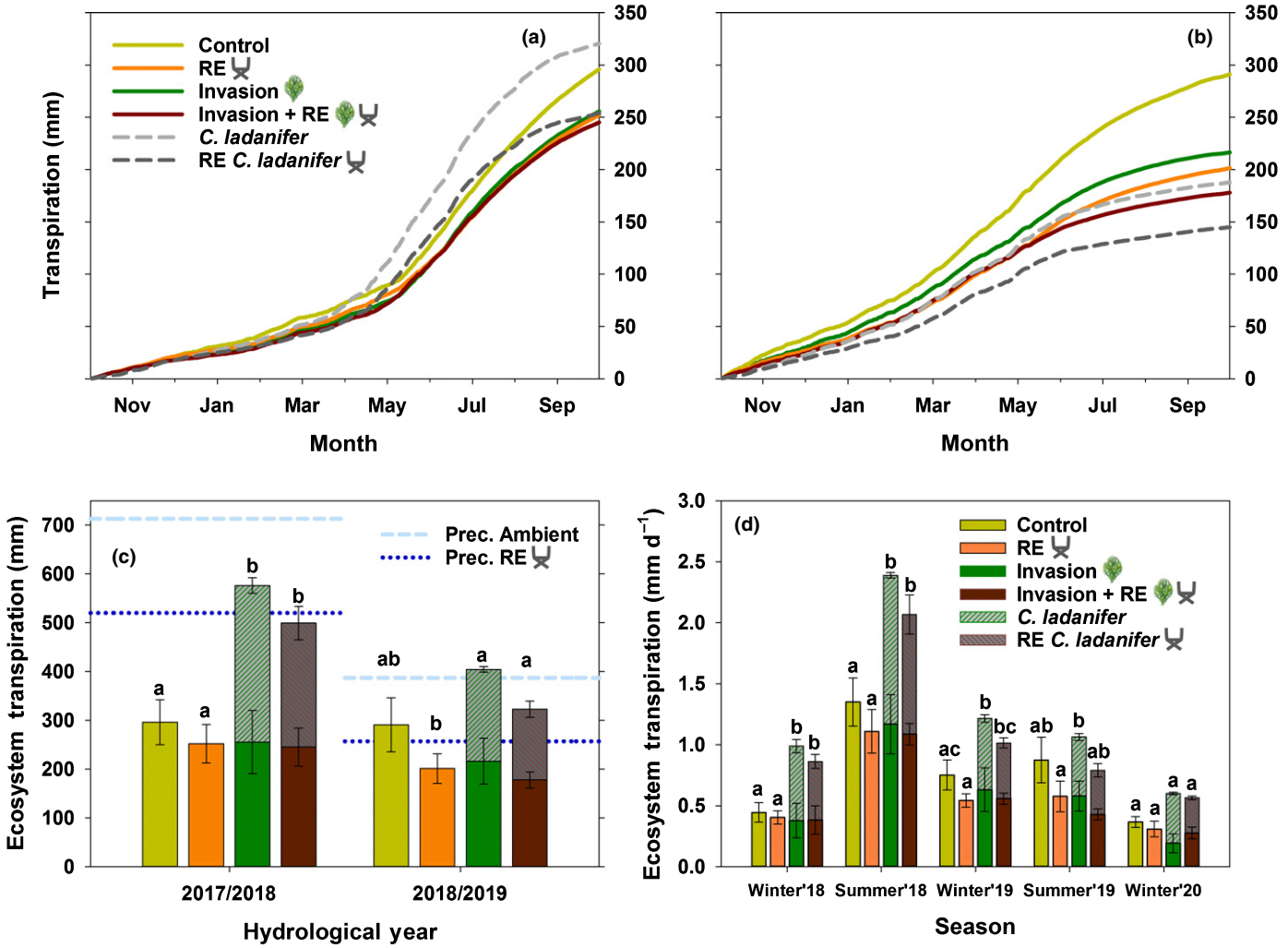


Fig. 4 Transpiration for the hydrological year 2017/2018 (a) and 2018/2019 (b) for all tree (n = 9 per treatment) and shrub (n = 9 per treatment) treatments in mm. Ecosystem transpiration for the hydrological year 2017/2018 and 2018/2019 with standard error (1 SE) (c) for all ecosystems (n = 9 per species and treatment) in mm and daily average ecosystem transpiration in mm d^{-1} (n = 9 per species and treatment) for winter and summer phases throughout the study period with 1 SE (d). For winter and summer phases see Figure 3. Different letters indicate a P-value < 0.05 (pairwise Tukey-adjusted comparison of the means) for each hydrological year/season separately. RE, rain exclusion.

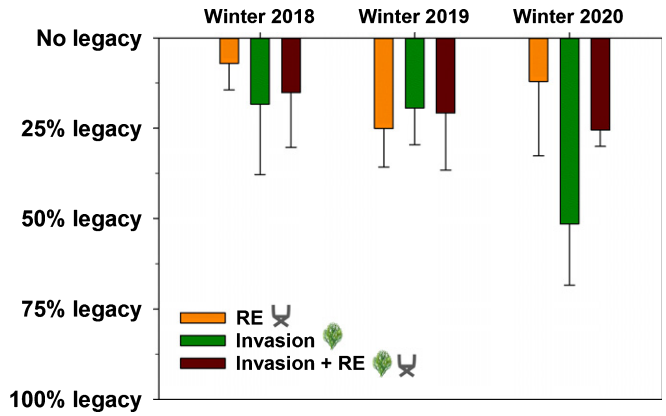


Fig. 5 Transpiration legacy for *Quercus suber* trees (n = 3) in % in comparison to the Control treatment with standard error (1 SE) for the winter periods 2018, 2019 and 2020. For calculations see Eqn 1. RE, rain exclusion.

reduced their maximum sap flux densities in 2019 compared to 2018 (Fig. 3a), overall cumulative rates remained stable at around 300 mm between years (Fig. 4a–c, 2018: 296 ± 46 mm; 2019: 291 ± 55 mm). For all other treatments, cumulative transpiration was reduced in 2019 (Fig. 4b,c). This effect was most pronounced for shrub transpiration, which declined by 41% (Invasion, $P < 0.01$) and 43% (RE, $P < 0.001$). Tree transpiration was reduced by 14% for trees under Invasion, 16% for trees under RE and 23% for trees under Invasion + RE relative to 2018, respectively (all $P > 0.05$) (Fig. 4a–c). Ecosystem transpiration (Fig. 4c) dropped by 30% (Invasion) and 34% (Invasion + RE) (both $P < 0.01$) from 2018 to 2019. In 2019, the transpiration of the invaded ecosystem with and without RE were close to or surpassed the precipitation input without taking into account evaporation losses (Fig. 4c). These results should be handled with care, as uncertainties during transpiration upscaling cannot be excluded. However, *Q. suber* trees do mainly use deep

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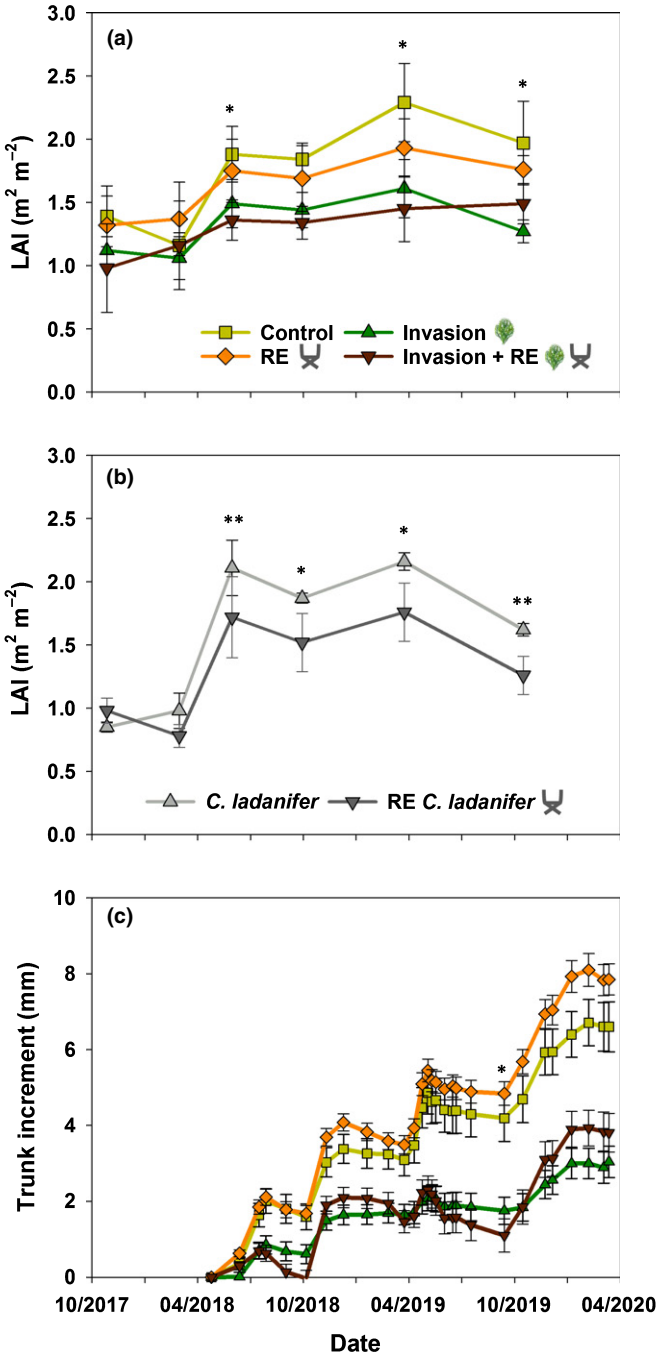


Fig. 6 Leaf area index for *Quercus suber* ($n = 9$ per treatment) (a) and *Cistus ladanifer* ($n = 9$ per treatment) (b) in m^2 m^{-2} with standard error (1 SE) and trunk increment in mm for *Q. suber* ($n = 7$–9 per treatment) with 1 SE (c). Asterisks indicate significance level (pairwise Tukey-adjusted comparison of the means): *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. RE, rain exclusion.

groundwater for transpiration in the summer periods (e.g. Kurz-Besson *et al.*, 2014).

Dividing the study period into summer and winter periods (Fig. 3a) revealed different seasonal patterns of ecosystem transpiration between treatments (Fig. 4d). In general, the ecosystem under Invasion had the highest transpiration rates in all seasons, followed by the ecosystem with Invasion + RE, Control and RE. The overall highest transpiration rates were observed during the summer of the normal precipitation year 2018 ($P < 0.001$), where the invaded treatments with and without RE had a clearly higher ecosystem transpiration compared to Control and RE without shrubs ($P < 0.001$). The situation changed during summer drought in the following year 2019, where Control trees transpired slightly more water on average than shrubs and trees combined under the RE. This was mostly the consequence of a substantial reduction in tree transpiration (–47% vs Control trees), especially compared to the effect of the single stressors in this period (Fig. 4d). An extensive comparison of the reductions in tree transpiration is given in the Table S5.

Winter transpiration was slightly higher in 2019 compared to 2018, but lowest in 2020 ($P < 0.05$) after the severe summer drought. Although there was a clear differentiation between non-invaded and invaded treatments in the winter period 2018 ($P < 0.05$), differences started to vanish in the 2019 recovery period (Fig. 4d). In winter 2020, Control and trees under RE reached slightly lower, but similar transpiration levels as in winter 2018. The ecosystem transpiration in Invasion and Invasion + RE, however, did not reach comparable levels (Fig. 4d). For the ecosystem under Invasion, the majority of this reduction was attributable to a decline in tree transpiration, which showed a legacy of 51% compared to the Control ecosystem (Fig. 5). Yet, in the ecosystem with Invasion + RE, shrubs and trees contributed equally to ecosystem transpiration (Fig. 4d). Trees only expressed a legacy of 25% compared to the Control tree transpiration (Fig. 5). Such patterns were not evident in the winter periods before 2020, when trees in all three experimental treatments showed a similar legacy (Fig. 5).

Growth indicators

After 2017, which was a dry year, the LAI increased for trees and shrubs (Fig. 6a,b). For *Q. suber* this pattern continued in 2019 (Fig. 6a), whereas shrubs reduced their leaf area (Fig. 6b). Shrubs under the RE had a clearly lower LAI after April 2018 ($P < 0.05$). Invaded trees, independent of the RE, had a lower LAI than the ones in the Control or RE treatment (Fig. 6a). In April 2018 and 2019, Control trees differed clearly from trees with Invasion + RE ($P < 0.05$). However, in spring 2020 the strongest variation was found between Control and Invaded trees (Fig. 6a; $P < 0.05$). Dendrometer readings of the trunk increment supported the LAI measurements (Fig. 6c). Control and trees under RE had higher trunk increments than invaded trees with or without RE over time.

Discussion

Reduced water availability and shrub invasion both pose strong threats to the functioning and recovery of *Quercus suber* ecosystems in the Mediterranean basin. With this study, we investigated both stressors and their interaction in the natural drought and recovery periods to determine the effect dynamics. Interestingly, there was an amplifying interaction of reduced water availability and shrub invasion during the severe summer drought in 2019, which shifted

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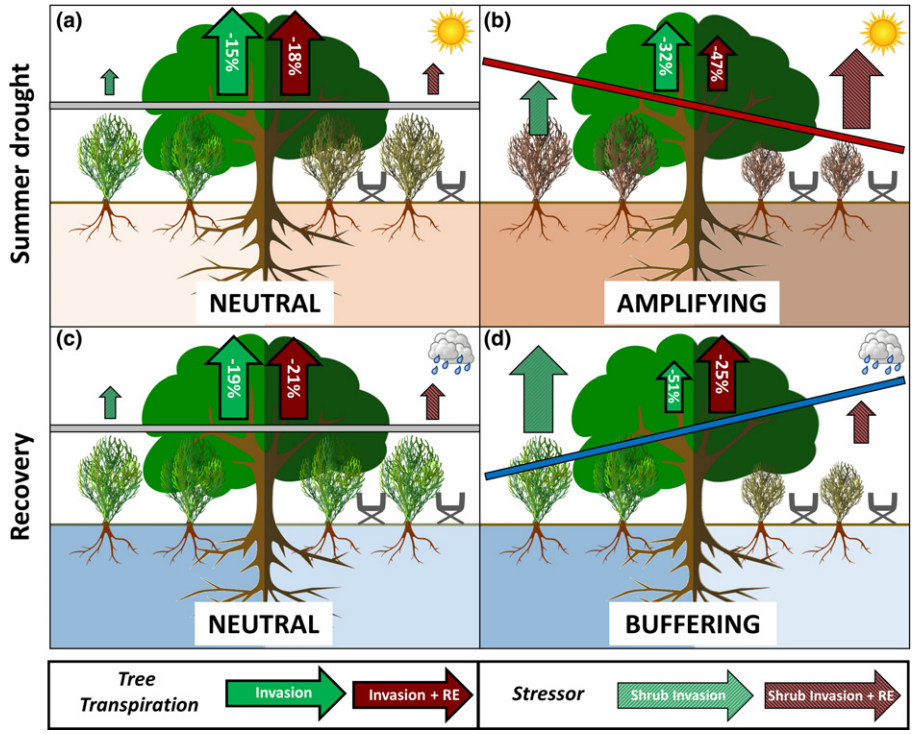


Fig. 7 Conceptual illustration of the interaction effects of shrub invasion and extreme drought for the summer drought period 2018 (a) and 2019 (b) and the recovery periods 2018/2019 (c) and 2019/2020 (d) for *Quercus suber* trees growing under invaded (left side) and invaded and RE conditions (right side). The size of the arrows above the trees is proportional to the absolute tree transpiration. The numbers in the arrows show the reduction in tree transpiration compared to Control trees. The size of the arrows above the shrubs (and RE) illustrates the impact of the stressors shrub invasion and RE. The bars indicate the interaction direction of extreme drought and plant invasion. Grey = neutral; red = amplifying; blue = buffering. RE, rain exclusion.

to a buffering effect in the following recovery period (Fig. 7). This demonstrates the highly dynamic nature of these interaction effects, which will be discussed in detail in the following.

Reduced water availability and shrub invasion act amplifying during extreme drought

During the investigated summer periods, reduced water availability and shrub invasion acted either neutral (2018) or strongly amplifying (2019) on the tree transpiration (Fig. 7a,b). In 2019, where we imposed the second driest year on record since 1950 a strong competition for water resources between trees and shrubs was triggered in the combined treatment (Fig. 7b), which was reinforced by the high water use strategy of *Cistus ladanifer*. This supports the prediction of the stress gradient hypothesis (SGH) that competitive effects occur under extremely low water availability (Armas & Pugnaire, 2005; Maestre *et al.*, 2009; Michalet *et al.*, 2014; O'Brien *et al.*, 2016). The strong reduction in tree transpiration by 47% can severely limit C uptake, induce xylem embolism and lead to a chronical decline of *Q. suber* trees (Camilo-Alves *et al.*, 2017), potentially with detrimental drought legacy effects on the whole ecosystem (Caldeira *et al.*, 2015; Seneviratne & Ciais, 2017). Thus, the results for 2019 confirm our hypothesis that the interaction of shrub invasion and drought has detrimental effects on the ecosystems' functioning in the summer drought period in extremely dry years.

However, trees under the RE without shrubs were affected only mildly by the RE. The slight reduction in transpiration might be a result of diminished winter and spring precipitation, as our experiment continuously excluded 30–45% of water from the ecosystem. Lower transpiration rates also have been demonstrated for experimentally drought stressed holm oak (*Quercus ilex*) trees all year round, even under well-watered conditions (Limousin *et al.*, 2009). Winter and spring precipitation is critical for plants in semi-arid ecosystems to withstand summer drought (Piayda *et al.*, 2014; Caldeira *et al.*, 2015; Forner *et al.*, 2018).

Large spring rainfalls in 2018 also reduced the competitive effects of shrubs on trees in the Invasion + RE treatment (Fig. 7a). Leaf water potentials indicated a higher water availability for *Q. suber* than in dry years (Kurz-Besson *et al.*, 2014; Haberstroh *et al.*, 2018) and in dry years under invasion (Caldeira *et al.*, 2015). Net facilitation, as predicted by the SGH (Maestre *et al.*, 2009), did not occur. This implies that shrubs did not strongly increase nor decrease the overall water availability for trees, but rather used different soil water resources, which resulted in neutral interaction effects (Fig. 7a). This fits the concept of hydrological niche segregation (Araya *et al.*, 2011), where co-existing plants occupy different temporal and spatial niches under moderate drought conditions and do not necessarily compete strongly for water resources so long as water reserves are sufficient (Rodríguez-Robles *et al.*, 2020).

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Buffering interaction effects in the recovery after a severe drought

By contrast with all other assessed periods (Fig. 7), the interaction of reduced water availability and shrub invasion resulted in a buffering effect in the recovery after the dry year 2019 (Fig. 7d), which contradicts our hypothesis, that detrimental interaction effects occur in the winter recovery periods. Instead, transpiration of invaded trees under ambient precipitation was reduced by >50%, whereas tree transpiration in the combined treatment was diminished only by 25%. These contrasting tree responses are best explained by investigating the response of the invader: shrubs under RE showed a drought legacy as a consequence of the summer drought 2019. This supports the hypothesis that under certain conditions the competitive strength of invaders declines in a low-resource environment (Brooker *et al.*, 2005), even after stress relief. Our RE experiment induced a stress effect on shrubs beyond a critical threshold, where their recovery was strongly diminished (Fig. 7d), resulting in lower sap flux densities, transpiration and leaf area index (LAI). By contrast, shrubs under ambient precipitation were not stressed as strongly during the summer drought 2019 (Fig. 7b) and, therefore capable of profiting from the increased water availability in the following winter (Fig. 7d). Shrubs thus were strong competitors under wet conditions, confirming results obtained in other ecosystems (Callaway & Walker, 1997; Ploughe *et al.*, 2019). Hence, the recovery of tree transpiration was determined by the drought legacy effects on shrubs. This response of the shrubs potentially is related to a precipitation threshold, determining their competitiveness in the following recovery period. There is evidence that the shrubs are still highly competitive at an annual precipitation of *c.* 400 mm (Caldeira *et al.*, 2015), which precisely matched our measurements for the shrubs under ambient precipitation in the hydrological year 2019.

Stress interactions are highly dynamic and nonlinear

This study highlights that invasive shrubs modulated the transpiration response of *Q. suber* trees in a highly dynamic way. The direction of interaction was strongly dependent on the predominant meteorological conditions and ranged from neutral to amplifying to buffering responses (Fig. 7). This implies that the interaction of shrub invasion and drought did not reduce the tree transpiration in a linear way. This deduction is based on the fact that the competitive impact of the shrubs cannot increase linearly with increasing drought stress, as shrubs are, at some point, also negatively affected by reduced water availability. Physiological responses of plants to environmental stressors often are nonlinear (e.g. Malkinson & Tielbörger, 2010; Holmgren *et al.*, 2012), which further supports the notion that nonlinear responses of ecosystem processes to interacting stressors might actually be a common effect (Côté *et al.*, 2016). For example, Sheffer *et al.*, (2020) observed negative effects of *Pinus halepensis* on *Quercus calliprinos* water status during summer drought, which shifted to a neutral or buffering effect in the wet winter periods. Wright *et al.* (2015) even demonstrated that plant interactions involving *Quercus macrocarpa* can switch on a daily basis from competition to facilitation, depending on the predominant environmental conditions. It also has been pointed out that tree diversity *per se* does not systematically increase drought resistance in forests, as changing environmental conditions lead to complex interactions between tree species with both, negative and positive impacts on ecosystems (Grossiord, 2019).

In future decades, meteorological conditions similar to our RE experiment might become more prevalent, given that the frequency, intensity and duration of drought are projected to increase under changing climate conditions for large parts of the Mediterranean including the Iberian Peninsula (Seneviratne *et al.*, 2012; Kirtman *et al.*, 2013; Touma *et al.*, 2015; Seager *et al.*, 2019; Spinoni *et al.*, 2020). Based on the new Climate Model Intercomparison Project – Phase 6 ensemble (CMIP6; Eyring *et al.*, 2016), Ukkola *et al.* (2020) detected enhanced and more consistent drought changes during the 21st Century compared to CMIP5 (Taylor *et al.*, 2012). In particular, Cook *et al.* (2020) identified an increasing intensity and incidence of drought in our study region for a wide range of scenarios. Cook *et al.* (2020) argued that soil moisture and runoff reduction apparently play a more crucial role than the changes in precipitation itself, indicating the importance of temperature-sensitive drought processes such as evapotranspiration. Given this marked impact of reduced water availability and shrub invasion during drought and recovery periods, the persistence of valuable *Q. suber* ecosystems and similar invaded systems is uncertain and strongly threatened by ongoing climate change. Thus, management strategies, such as reducing the density of shrubs or removing them completely from the ecosystem are highly recommended to increase the resilience of ecosystems to extreme drought. Such positive effects resulting from thinning have been demonstrated in a Mediterranean *Q. ilex* forest (Gavinet *et al.*, 2019) and provide evidence that management strategies can have a stronger impact on ecosystem functioning than simulated climate change in the form of precipitation manipulation. Nevertheless, further studies are required to determine the implications of drought for *Q. suber* and comparable Mediterranean ecosystems, as progressing drought and plant invasion might trigger detrimental nonlinear responses in the future, potentially contributing to the global tree mortality patterns observed already (Allen *et al.*, 2015).

Conclusion

Our study demonstrates that noninvaded *Q. suber* ecosystems seem to be well-adapted to withstand regular drought impacts. However, (additional) shrub invasion strongly enhanced transpiration losses, which could lead to a long-term groundwater depletion (Acharya *et al.*, 2018). Yet, as *Q. suber* relies on groundwater in the summer periods (David *et al.*, 2013; Dubbert *et al.*, 2019), this might be critical for survival (Mendes *et al.*, 2016) and overall ecosystem functioning (Peñuelas *et al.*, 2017). Other measures such as lower LAI and trunk increments of invaded trees point towards a persistent lower tree C assimilation, which in the long term may lead to C legacies (Anderegg *et al.*, 2015) with trees unable to fully recover their ability for C assimilation after stress

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relief. Such processes could further jeopardize the persistence of *Q. suber* ecosystems. Thus, it will be of high importance to investigate if the invaded ecosystem might change in favour of the invasive species (cf. Prieto *et al.*, 2009; Caldeira *et al.*, 2015; Lloret *et al.*, 2016; Ogaya & Peñuelas, 2020) or if drought legacy effects on shrubs will result in a decline of the invader.

In conclusion, this study clearly demonstrates that the interaction of drought and shrub invasion is highly dynamic and nonlinear, ranging from amplifying to neutral to buffering effects. These effects change in dependence of the predominant environmental conditions, as well as during drying and recovery periods. In this regard, further experimental evidence and combined modelling efforts could help to improve our understanding of these nonlinear interaction effects and help preserve valuable ecosystems around the globe.

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Author contributions

CW and MCC conceived and designed the experiment; SH performed the experimental fieldwork, collected the data and maintained the measuring system with RL-d-V, JIM and MCC; SH analyzed the data; JM and JGP analyzed the climatic/meteorological data; and SH wrote the manuscript with input from CW and MCC. All co-authors contributed significantly and discussed the manuscript.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request. All data used in the meteorological and climatological modelling is freely available at http://www.uerra.eu and https://www.ecad.eu.

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Fig. S1 Experimental design with the four treatments in Vila Viçosa, Portugal.

Fig. S2 Experimental plots in Vila Viçosa, Portugal.

Fig. S3 Shrub sapwood increment correction over time.

Fig. S4 Time series of daily precipitation sums derived from the measurement sites and E-OBS.

Methods S1 Determination of functional sapwood area for trees and shrubs.

Methods S2 Shrub sapwood area increment correction.

Methods S3 Determination of sapwood per ground area.

Table S1 Allometric equation for the determination of functional sapwood for *Q. suber* and *C. ladanifer*.

Table S2 Sapwood per ground area and tree/shrub density.

Table S3 Meteorological data for the field site and the E-OBS dataset.

Table S4 R commands used for the statistical analysis.

Table S5 Reduction of daily average transpiration fluxes in all investigated periods and classification of interaction effects.

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