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Long-term experimental drought combined with natural extremes accelerate vegetation shift in a Mediterranean holm oak forest

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ABSTRACT

Increasing drought combined with natural extremes are expected to accelerate forest die-off and shifts in vegetation in the Mediterranean Basin. However, fewer studies have explored these climate-driven changes in forest ecosystems.

A long-term (17-year) experimental drought (−30% precipitation) was established in a Mediterranean holm oak forest with high (H) and low (L) canopies to determine the changes in stem mortality, recruitment and composition shifts.

Experimental drought increased annual stem mortality rate at the community level for both H- and L-canopies. Natural drought amplified the effects of experimental drought on stem mortality at the community level and of *Q. ilex* for H- and L-canopies. The timescales of natural drought, however, varied substantially with canopy types and species, with shorter timescales in L- than H-canopy and for *Q. ilex* than *P. latifolia*. Furthermore, experimental drought combined with natural extremes amplified the increases in stem mortality and decreases in growth for L-canopy. Contrasting responses between *Q. ilex* and *P. latifolia* for the relative in abundance and growth were observed in L-canopy and drought treatment reinforced the vegetation shift favoring *P. latifolia*.

These findings suggest continuous drought regimes accelerated a vegetation shift, implying potential consequences for the functions and services for water-limited forest ecosystems.

1. Introduction

Anthropogenic climate change with increasing temperatures and shifting precipitation regimes has contributed to severe water deficits, causing ecological consequences for the Earth's vegetation ecosystems (Allen et al., 2010, 2015). Water deficits have become common disturbances affecting forest ecosystems globally, and leading to large-scale tree mortality (Phillips et al., 2010; Anderegg et al., 2013; Greenwood et al., 2017), forest canopy die-off or defoliation (Breshears et al., 2005, Allen et al., 2010, 2015) and shifts in composition (Allen and Breshears, 1998; McIntyre et al., 2015). Mediterranean regions are particularly suffering water deficits due to the unprecedented rate of warming and more frequent extreme events (e.g. heat waves and droughts) (Myers et al., 2000; Dai, 2013; BAIC, 2015). Annual mean temperature in Western Mediterranean regions has increased by 0.23 °C per decade while annual mean precipitation has decreased by 1.5% per decade between 1950 and 2015, with the changes being more notable in summer (0.36 °C and −4.5% per decade, respectively) (BAIC, 2015). These climatic trends have been associated with episodes of widespread tree mortality (peñuelas et al., 2000, 2001; Lloret et al., 2004a; Carnicer et al., 2011), changes in the composition and dominance of forest species (Peñuelas and Boada, 2003; Peñuelas et al., 2007; Coll et al., 2013; Saura-Mas et al., 2015) and reversed trajectories of succession (e.g. forests toward open woodlands or shrublands) (Doblas-Miranda et al., 2015; Franklin et al., 2016; Natalini et al., 2016). General circulation models have projected an increase in the intensity and duration of droughts for the coming decades (IPCC, 2014), which would further threaten the conservation of forest biodiversity, carbon budgets and climatic feedbacks (Myers et al., 2000; Peñuelas et al., 2013; Doblas-Miranda et al., 2015, 2017).

Vegetation shifts represent gradual, nonlinear and sometimes abrupt changes in relative abundance or dominance caused by differential mortality rates and recruitment failure between coexisting species (Lloret et al., 2012; Zeppel et al., 2015; Pausas et al., 2016). Martínez-Vilalta and Lloret (2016) recently reported that vegetation shifts in response to drought have clearly occurred in about a quarter of

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all study cases across terrestrial ecosystems. The scarcity of vegetation shifts has been primarily attributed to the processes of regeneration (e.g. increased survival, enhanced recruitment and regrowth) of dominant species that reinforce their resilience and recovery after droughts (Lloret et al., 2012; Zeppel et al., 2015; Martínez-Vilalta and Lloret, 2016; Pausas et al., 2016). Frequent and intense droughts, however, would weaken these regeneration processes, via more negative effects on seed maturation, seedling survival and growth (Allen and Breshears, 1998; Kéfi et al., 2007; Allen et al., 2015; Reyer et al., 2015). Increased drought would in fact induce differential rates of recruitment among the coexisting species, particularly favoring the re-establishment of drought-resistant species and thus promoting vegetation shifts (Mueller et al., 2005; Suarez and Kitzberger, 2008, 2010; Fauset et al., 2012; Lloret et al., 2012). For example, declines in large trees and increases in seedling establishment of drought-resistant species in Californian forests have been associated with a progressive increase in water deficit (McIntyre et al., 2015). Most field surveys unfortunately cannot deliver the long timescales and precision of field data required for properly tracking changes in forest structure and composition in response to climate change. Forest dynamics (e.g. changes in stem mortality, recruitment and structure) are also complicated by other confounding factors associated with land-use changes, wild fires and insect pests, leading to large uncertainties in the prediction of the effects of future climate change on forest dynamics (Doblas-Miranda et al., 2015, 2017; Franklin et al., 2016; Martínez-Vilalta and Lloret, 2016).

Long-term drought experiment is a practical method for examining the impacts of increasing drought on forest dynamics and can provide unique insights into physiological and demographic processes and their underlying mechanisms (Jentsch et al., 2007; Smith et al., 2009; Martin-Stpaul et al., 2013; Liu et al., 2015; Franklin et al., 2016). Manipulative field experiments in recent decades have identified relevant effects of drought on forests, such as limitations in carbon assimilation (Ogaya and Peñuelas, 2003; Misson et al., 2010; Ogaya et al., 2014), decreases in canopy leaf area (Limousin et al., 2009; Martin-Stpaul et al., 2013) and reductions in biomass accumulation (Ogaya et al., 2003; Ogaya and Peñuelas, 2007a; Barbeta et al., 2013; Liu et al., 2015). These effects may lead to more severe consequences associated with population dynamics and compositional changes by long-term processes (Smith et al., 2009; Martin-Stpaul et al., 2013; Peñuelas et al., 2013). Abrupt changes such as vegetation shifts are thus likely to emerge after long-term drought manipulation, probably in association with the accumulated or legacy effects (Smith et al., 2009; Luo et al., 2011; Allen et al., 2015). In particular, extreme natural droughts could also intensify the forest dynamics that trigger synergistic effects on the changes in forest structure and composition by substantial tree mortality (Lloret et al., 2012). Long-term drought experiments have been relatively rare, especially in forests, leading to a lack of understanding of forest dynamics and vegetation shifts in response to the increasing frequency and severity of droughts (Leuzinger et al., 2011; Luo et al., 2011; Knapp et al., 2015, 2017).

Holm oak (*Quercus ilex* L.) forests are the dominant vegetation type between the temperate forests and shrublands (e.g. maquia) in the Mediterranean Basin (Peñuelas et al., 2000; Lloret et al., 2004a; Ogaya and Peñuelas, 2007a). *Q. ilex* has the typical features of Mediterranean species, with sclerophyllous leaves, high belowground biomass and bimodal growth patterns, but it has been affecting by the increasing length and intensity of droughts with high rates of evapotranspiration and low precipitation (uelas et al., 1998, 2000; ; Lloret et al., 2004a; Galiano et al., 2012; Barbeta and Peñuelas, 2016). Numerous studies have reported substantial changes in community structure and composition in holm oak forests in response to drought, which were especially severe on hillslopes with shallow soils (Peñuelas et al., 2000; Lloret et al., 2004a; Galiano et al., 2012; Saura-Mas et al., 2015). Recent extreme droughts have triggered large-scale tree mortality and canopy die-off in these forests Peñuelas et al., 2000, 2001; Carnicer et al., 2011; Saura-Mas et al., 2015). Extreme natural droughts have also reduced the resistance and resilience of holm oak forests; resprouting capacity from above- and belowground buds has decreased (Lloret et al., 2004a; Galiano et al., 2012; Saura-Mas et al., 2015). Some affected forests have therefore degraded into low-canopy type forests due to a greater loss of larger stems that were less resistant to increased drought (Lloret et al., 2004a; Carnicer et al., 2011; Bennett et al., 2015; Natalini et al., 2016). Recruitment in these low-canopy forests would be enhanced once competition decreases after drought induced higher mortality, and the forests would be more favorable for drought-resistant seedlings (Lloret et al., 2004b, 2012; Martínez-Vilalta and Lloret, 2016).

The presence of drought-resistant species (*Phillyrea latifolia* L.) may promote vegetation shifts in the holm oak forests since they are favored under drought. Holm oak forests usually contain the tall shrub *P. latifolia*, which is more drought-resistant than *Q. ilex*. *P. latifolia* develops physiological plasticity (Peñuelas et al., 1998; Ogaya and Peñuelas, 2003; Ogaya et al., 2014), adjusts phenologically and morphologically (Serrano et al., 2005; Liu et al., 2015) and acclimates its water-use efficiency (Peñuelas et al., 2000; Lloret et al., 2004b; Ogaya and Peñuelas, 2008) in response to drought differently than *Q. ilex*. Experimental drought and/or severe natural droughts that trigger abrupt and nonlinear increases in stem mortality and decreases in aboveground growth in *Q. ilex*, it is expected to affect less *P. latifolia* (Ogaya et al., 2003; Ogaya and Peñuelas, 2007a; Barbeta et al., 2013, 2015; Liu et al., 2015). Field surveys have demonstrated that *P. latifolia* tended to increase in abundance in some cases, indicating potential shifts in forest structure and composition (Lloret et al., 2004b; Saura-Mas et al., 2015). The claims supporting vegetation shifts, however, are mainly assumptions from the contrasting physiological, phenological and morphological responses to drought between *Q. ilex* and *P. latifolia*, which are insufficiently reliable for predicting long-term shifts in forest composition (Barbeta et al., 2013; Barbeta and Peñuelas, 2016). The absence of supporting data of tree mortality, recruitment and compositional change for *Q. ilex* and *P. latifolia* in response to drought may generate inaccurate assessments of the responses of vegetation shifts to future climate change (Lloret et al., 2012; Martínez-Vilalta and Lloret, 2016).

This study was conducted as part of a long-term drought experiment (−30% precipitation) established in 1999 in a Mediterranean holm oak forest with high (H) and low (L) canopies. H-canopy distributes in the deep soils (30–50 cm) of the study sites, whereas L-canopy distributes in shallow soils (10–30 cm) (more details in Methods). We hypothesized that long-term experimental drought (1999–2015) and natural droughts would imposed severe water deficits, and would trigger differential stem mortality and growth rates for the two canopy types and thus a vegetation shift (*Q. ilex* replaced by *P. latifolia*) in L-canopy. More specifically, we (1) evaluated the combined effects of a long-term (17-year) experimental drought and natural droughts on the changes in stem mortality, new recruitment, density and growth (basal area) for the two canopy types at the community and species levels, (2) assessed the synergistic effects of experimental drought on stem mortality and growth rates during extreme dry years for the two canopy types at the community and species levels and (3) analyzed the net-changes in relative abundance (stem density) and growth for the two species (*Q. ilex* and *P. latifolia*) for the two canopy types.

2. Materials and methods

2.1. Experimental site

The experiment was carried out in the Prades holm oak forest in Catalonia, northeastern Iberian Peninsula (41°21′N, 1°2′E). The vegetation is dominated by the evergreen tree *Q. ilex* and the tall shrub *P. latifolia*, accompanied by other Mediterranean shrub species (e.g. *Arbutus unedo* L., *Erica arborea* L. and *Juniperus oxycedrus* L). The formation and structure of the forest are naturally variable due to the heterogeneity of soil depth and bedrock type. Holm oak forests at sites