Mediterranean ecosystems facing global change

Resilient or close to tipping point?

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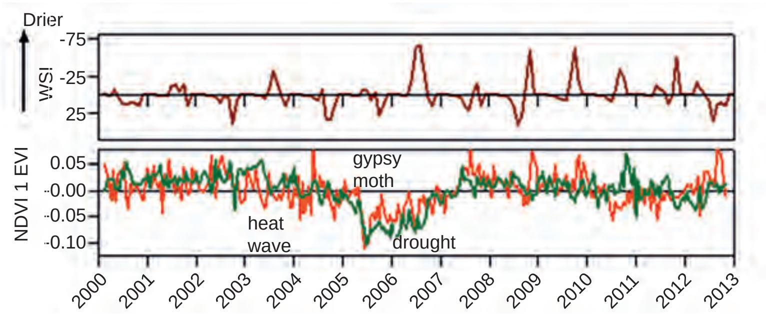
Introduction

Mediterranean-type ecosystems (MTEs) cover a small fraction of the terrestrial component of the Earth, and their functioning is driven by a recurrent summer drought concomitant with the hottest temperatures. Climate projections by general circulation models (GCM) under RCP 6.0 and 8.5 scenarios collectively forecast substantial drying and warming in regions surrounding the Mediterranean Sea, especially in summer (Schleussner et al 2016). MTEs are expected to be highly responsive to global climate change (Giorgi 2006) as a result of a change in large-scale circulation conditions (Kjellström et al. 2013), together leading to 1) increasing temperatures and decreasing rainfall (Hoerling et al. 2012), 2) the persistence of heat wave anomalies (Jaeger and Seneviratne 2011) and 3) longer, more intense and earlier drought periods (Ruffault et al. 2014). In this context, the fate of MTEs depends on their ability to withstand, adapt or recover from different disturbing forces, particularly drought. In addition, human impacts, an intrinsic aspect of MTE functioning, can increase, accelerate, or mitigate direct climate impacts, through forest management, setting fires or extinguishing fires, a significant process in MTEs. We assessed the short and long term resilience of MTEs to increasing drought as affected by direct climate forcings, and explored how similar drought trends driving fire risk, the major disturbance in MTEs, can lead to contrasted extents of burned area depending on local socio-economic features.

Theoretical framework for ecosystem stability assessment under climate change: resilience vs. tipping point?

Reyer et al. (2015a) reviewed different approaches used to study the response of forests systems to anthropogenic global changes, to understand their capacity to recover from disturbances. These authors' underlying hypothesis is based on resilience theory, suggesting that forests might be able to tolerate disturbances and maintain their functioning and structure only up to a critical threshold. A slow rate of an ecosystem's recovery from a disturbance might be an early signal that its status is close to tipping point, a set of conditions under which a minor change leads to a major change in the state of the system. Among the most pertinent environmental drivers that predispose water-limited ecosystems like MTEs to tipping points are a reduction in rainfall amounts, especially in the dry season, an increase in temperatures, an increase in the frequency of extreme events, intensifying fire regimes, emerging invasions, pathogens and pests (Laurance et al. 2011). Using resilience theory, we assessed the current (in)-stability of an evergreen broadleaf forest (Quercus ilex), an ecosystem covering 6 Mha in the Mediterranean basin. The remotely-sensed MODIS normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI), two indicators of green canopy functioning, were used to test the recovery of the ecosystem from successive disturbances between 2000 and 2013, including the peculiar 2003 heat wave, a pest attack in 2005 (gypsy moth defoliation), and a severe drought in 2006. Both the NDVI and EVI were affected in 2005 and 2006, but a quick recovery was observed after 2007 followed by a stable trajectory even during the dry years 2009 and 2010, supporting the hypothesis of a high stability of this ecosystem. We further analyzed local ecosystem functioning to disentangle the mechanisms enabling such high resilience.



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We used the approaches proposed by Rustad (2008) to assess MTE resilience to increasing drought across the Mediterranean basin:

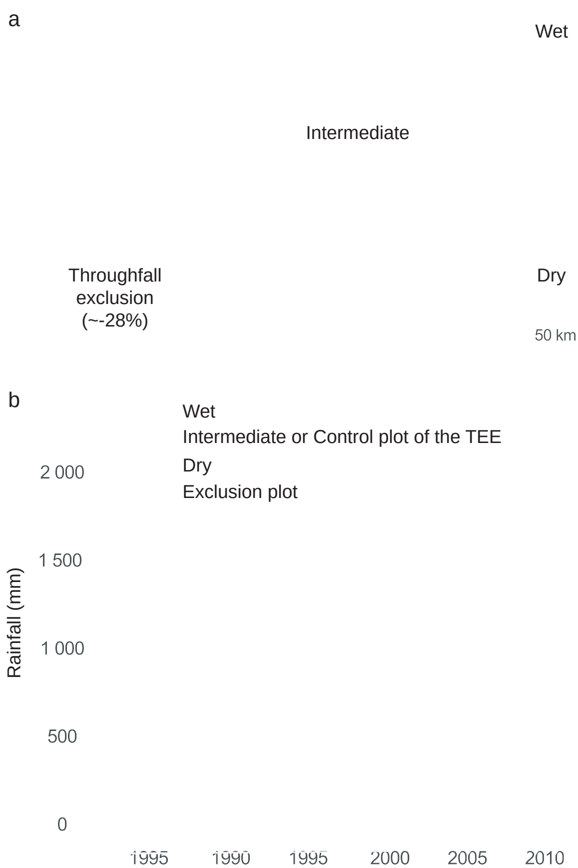
i) Long term observations in space and over time can be made at a single site, using networks of sites, and more recently, using global networks of sites such as Fluxnet (Luyssaert et al. 2009). Long term monitoring provides both deep insights and background information on ecosystem responses to short term “pulses” in weather and long term changes in climate (called a “press” constraint).

ii) Climate gradient studies are performed across geographical gradients and can exploit “space-for-time” substitutions for long term studies.

iii) Experimental manipulations (on climate drivers, and management strategies that affect the whole ecosystem) make it possible to study some cause and effect relationships and provide a mechanistic understanding of short term responses of ecosystems to one or more drivers of climate change and/or disturbance regime.

Comparative resilience analysis from a throughfall exclusion experiment (TEE) and climate gradient on a 1UERCUS ILEX monospecific coppice

The Puéchabon study site (43°44’30”N, 3°35’40”E, elevation 270 m, France), an intermediate dry site on the drought gradient of the Quercus ilex distribution (figure 2), offers a spectrum of ecosystem scale measurements and manipulative experiments that includes water, energy and carbon fluxes since 1998 and a throughfall exclusion experiment (TEE) monitored continuously since 2003. In the TEE, the control treatment receives ambient precipitation and the dry treatment is subjected to partial throughfall exclusion (-27% precipitation by means of PVC gutters suspended under the canopy). Each treatment plot covers 100 m^2 and each treatment is replicated three times (for a more detailed description of the TEE, see Limousin et al. 2009).



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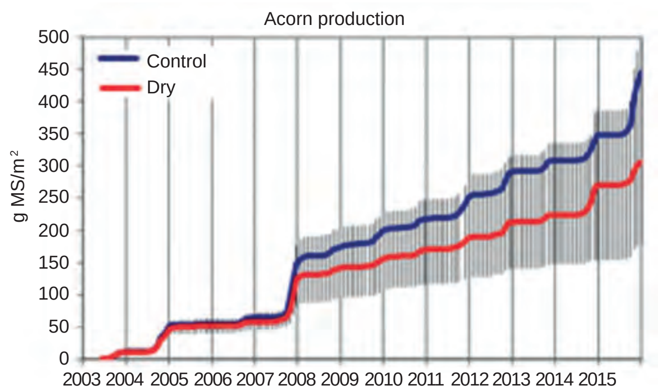
The main results of the TEE after 13 years of experiment are presented in table 1. Increasing drought primarily led to a rapid loss of leaf area (-22%), which in turn reduced photosynthesis (-14%), litter fall (-21%) and carbon loss through autotrophic (-14%) and heterotrophic respiration (-11%). The loss of leaf area had a negative impact on tree and ecosystem carbon balance but, by concomitantly limiting transpiration by -23%, maintained the soil water content at a level similar to that in the control plot, and subsequently similar drought timing,

The increased mortality was not offset by enhanced regeneration, a key mechanism of forest resilience (Reyer et al. 2016b), as we observed a 32% decrease in acorn production (figure 4), and significant effects on seed maturation, seedling emergence and survival, and, to a lesser extent, on post-dispersal seed survival as a result of desiccation of winter acorns (Joet al. 2016).



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Our study indicates rapid acclimation of the ecosystem to the reduced water supply, by saving carbon through a decrease in leaf and stem respiration, and saving water through a reduction in transpiring leaf area. This Mediterranean forest appears to be able to develop functional strategies to withstand increasing drought stress, but these strategies lead to tree self-thinning and increased tree mortality, together leading to forest opening and potentially toward open woodland or shrublands, two widely observed alternative systems in MTEs.

We compared the responses of leaf level physiological traits, branch level hydraulic traits, and stand level allocation traits to drought in the evergreen Quercus ilexin the TEE to a regional precipitation gradient (long term changes) with the driest extreme reaching the annual rainfall in TEE. At the leaf scale, gas exchange, mass per unit area and nitrogen concentration showed no response to drought as they did not change in either experiment (figure 6). A similar absence of response has been observed for xylem vulnerability to cavitation at the branch level (Martin St Paul et al. 2013). In contrast, the ratio of leaf area (LA) to sapwood area (SA) of young branches exhibited a transient response to drought because it decreased in TEE only in the four first years of treatment, but did not differ among the sites of the gradient. However, at the stand level, the leaf area index (LAI) decreased, and the ratios of stem sapwood area to LAI and of fine root area to LAI both increased in TEE and from the wettest to the driest site of the gradient. Taken together (figure 6) these results suggest a trajectory of tree acclimation to recurrent drought that shifts progressively from low (branch) to high (stand) organizational levels, and acts to maintain the leaf water potential within the range of xylem hydraulic function and leaf photosynthetic assimilation.

Diversity of water use strategies in mixed Mediterranean shrublands enhance ecosystem resilience to variable drought features

The acclimation of perennial changes to changing precipitation regime is likely species-specific, so that additional studies using similar designs to the one we used at our uQuerlus ilexustudy site are needed in multispecies to better ucapture potentially contrastedgies to cope with increasing drought. We therefore investigated how co-occurring Mediterranean species respond differently and compete under water limited conditions. From 2011 to 2013, we studied a typical maquisushrubland composed of uArbutus unedo, uPhyllirea
latifolia,uCistus monspeliensis, Erica arborea, uPistacia lentislus anduCalicotome
uin northern Tunisia (36°36'18''N, 8°33'58''E), at the southern limit of
anean biome (see details in Longepierre et al. 2014). Interannual
species functioning and their response to increasing drought were
r a rainfall interception experiment. Weekly predawn plant water
re measured in the six species over the course of the experiment,
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s among the to cope with summer drought: deep
een species (u) were able to
water potential higher than -3MPa, while more shallow rooted

MPa under the driest conditions (uErica arborea
constrained in all the species below a water potential threshold of
we identified different short term leaf area adjustmentgies,
vergreen for uP. lentislus anduP. latifolia
. arborea and summer deciduous for uC. villosa uas soon as
eached -1.2 MPa. We also observed that the species with the
ater potential (anduC. villosa) started growth
ngation was not affected by the early drought in 2012,
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affected (figure 5). These results illustrate different
ught avoidance to drought tolerance, depending on
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d our first result on the high resilience of MTEs
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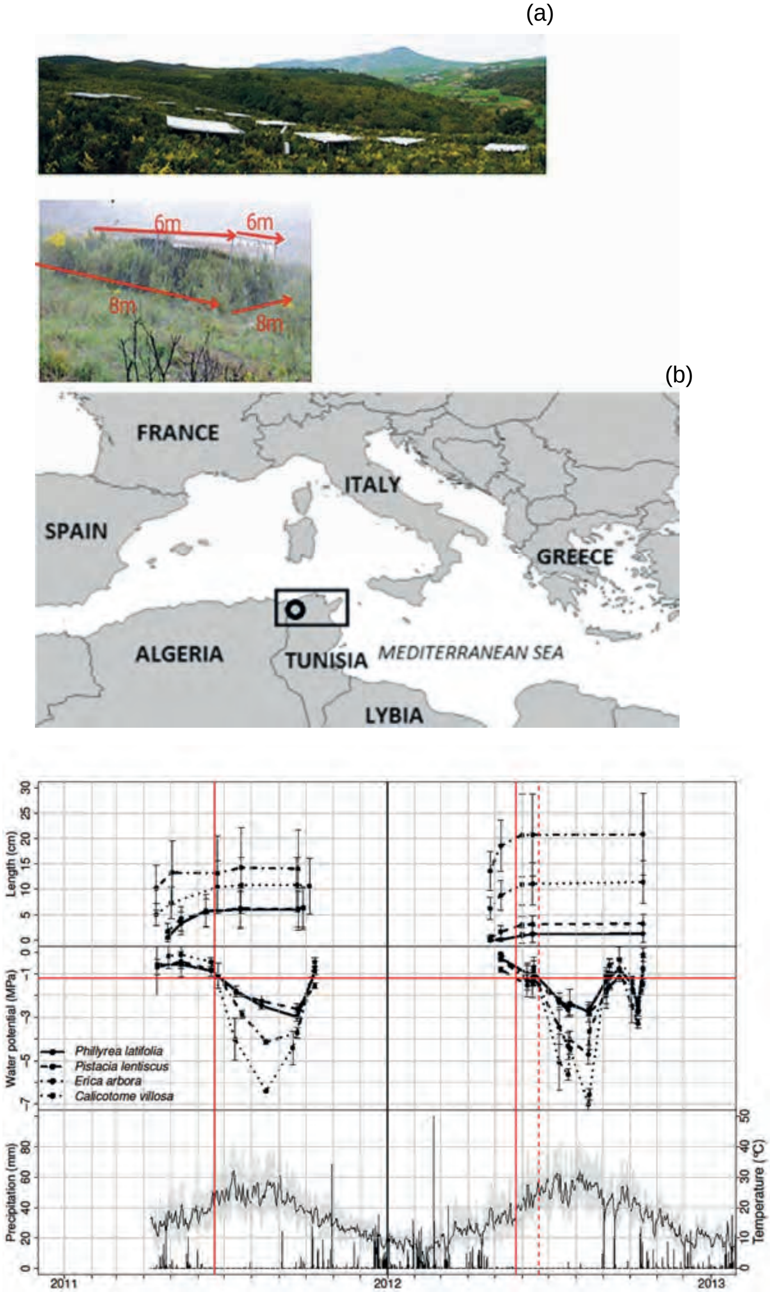
to be affected by soil water deficit, but enhanced
ure of these highly flammable species (Chamorro



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F OR *Phyllirea latifolia* *Pistacia lentiscus* *Erica arborea* A N D *Calicotome villosa* AND THE YEARLY
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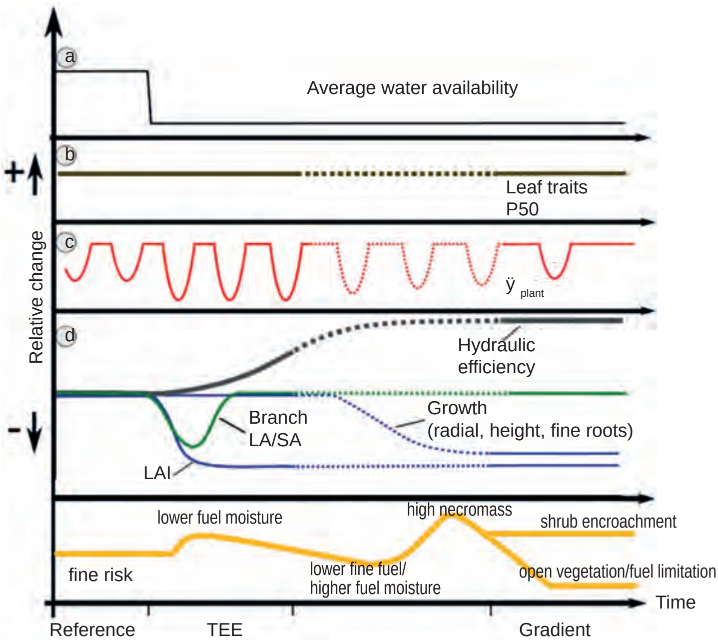
Fire disturbances affecting MTEs: a process affected by climate change in a varying socio-economic context

From our experiments, we concluded that plant adjustments to drought lead to functional responses that affect the plant water budget and hence the leaf moisture content on one hand, and the biomass of leaves and twigs, two major components driving biomass combustibility, on the other hand. Adjusting leaf area to limit water loss and fine fuel would then decrease fire risk in the short term, so that the temporal trend of fire risk as a response to increasing drought is not the widely assumed linear trend (figure 6). The development of understory shrubs in tree gaps (Rodriguez-Calcerrada et al. 2013) and the dead plant material that accumulates as a result of increased tree mortality might actually contribute to a drastic increase in fire risk in the medium term. After the decomposition of wood necromass (a significant aspect of global biogeochemical cycles not covered in our experiment, but see Cornwell et al. 2009), fire risk would be driven either toward higher levels in the case of shrub encroachment, or to lower levels in the case of open shrublands, depending on drought intensity. Fire is actually the main disturbance affecting MTEs, and may abruptly affect the smooth trend in plant acclimation to increasing drought, and subsequently modify plant composition and ecosystem functioning in the long term.

Fires are to some extent controlled by human factors, both as a source of ignition and prevention and suppression. In southern France, despite the increase in drought intensity and in summer temperatures in recent decades (Ruffault et al. 2013), increasing expenditures for firefighting led to an abrupt decrease in burned area after the 1990s (figure 7), even during extreme years (2003, 2006) (Ruffault and Mouillot 2015). Figure 7 illustrates the differential relationship between annual burned area / summer drought index (SPEI3) for the pre- and post-fire suppression period, summer SPEI3 being the 3-month standard precipitation evaporation index for June-July-August obtained from the global gridded SPEI database (Begueria et al. 2010). Human factors are the most important drivers of global change in fire risk nowadays (see Turco et al. 2016 for a review of trends in recent burned areas in southern Europe), so that contrasted socio-economic status affecting expenditure for firefighting can significantly modify fire hazard and the subsequent ecosystem dynamics. Figure 7 also presents the temporal pattern in burned area in a contrasted socio-ecological system in Tunisia, where the ‘Arab spring’ revolution led to political instability, local riots and loss of government control over rural populations. We observed a 3-fold increase in burned area since 2011. The relationship between annual burned area and the summer SPEI3 drought index shows that 2011 and 2012 remain within the usual range of variability in burned area according to drought, only 2013 was out of the range of the historical record. This non-climatic trend can be attributed to social change, most of this additional burned area being related to military interventions in the southern pine forests (Chaambi national park), a key –but hardly predictable- aspect of ecosystems response to global and regional changes.



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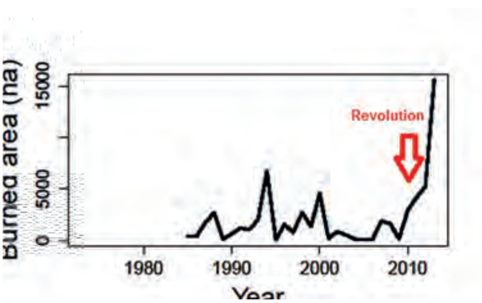
Conclusion

Our combined multi temporal/multi scale approach including experimental throughfall interception and gradient analysis revealed the hierarchical adjustments of MTEs in the face of increasing drought, in the case of the evergreen Quercus ilex, leading to overall high resilience to this aspect of climate change. The multispecies approach in a maquis shrubland also revealed the multifaceted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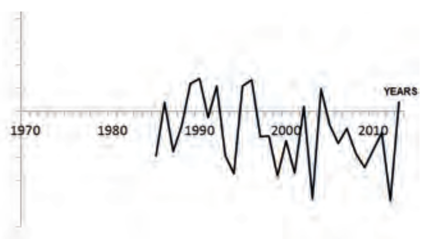
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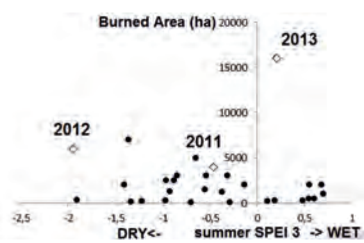
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assess the contribution of ecotypic differences in the acclimation processes, which could be achieved by incorporating common garden experiments in the design we used. However, fire disturbances remain a critical process, a partial understanding of which can be captured from vegetation functioning, but which are widely overlooked and difficult to predict when socio-economic and political issues are taken into consideration (Moritz et al. 2014).

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The Mediterranean Region under Climate Change

A Scientific Update

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Marseille, 2016

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