

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.

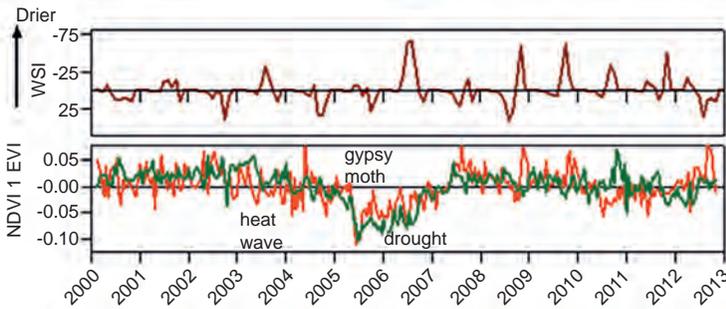


Figure 1.

Time series of anomalies of MODIS 8 day composite NDVI and EVI over the evergreen broadleaf ecosystem surrounding the Puéchabon study site. The green line represents the NDVI and brown line the EVI. The time course of the Water Stress Integral anomaly expressed in MPa. day showing the recurrence of dry years in 2003, 2006, 2009 and 2010 is also plotted.

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 (Luysaert 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 *Quercus 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 m² and each treatment is replicated three times (for a more detailed description of the TEE, see Limousin et al. 2009).

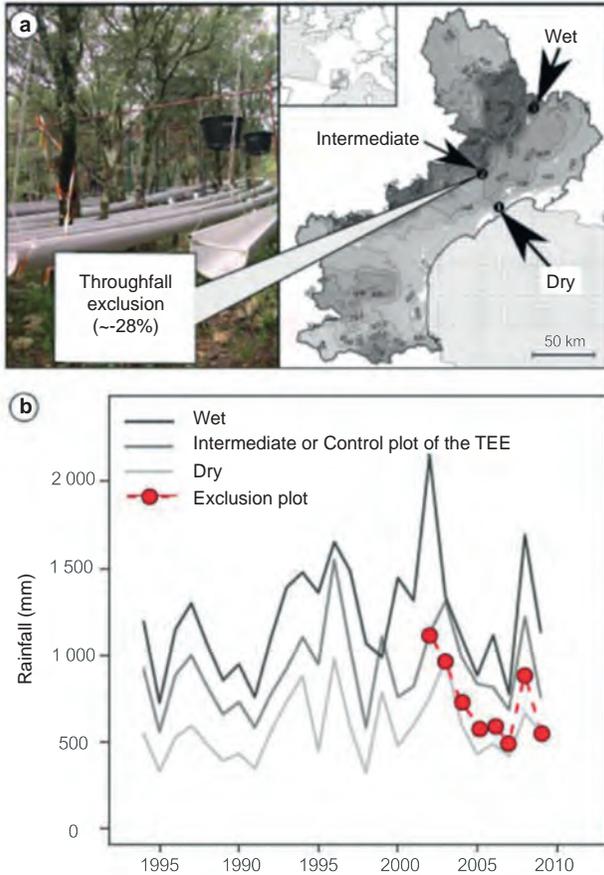


Figure 2
 Location of the partial rain exclusion experiment in the Puéchabon TEE in southern France (top right panel). a) PVC gutters intercept 27% of rainfall under the tree canopy in TEE (top left panel). b) Regional rainfall gradient (annual rainfall at the wet study site, TEE and dry study sites are presented for the period 1983-2009).

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,

length and intensity (Martin-St Paul et al. 2013). As automated dendrometers capturing the seasonal trend of tree growth showed that drought onset, kept constant in TEE, was the main driver of inter-annual tree growth and not the -14% reduction in the carbon budget (Lempereur et al. 2015), we did not observe any change in tree growth despite reduced precipitation.

The second major impact observed in the TEE in the dry treatment was a +8% increase in tree mortality over time from the beginning of the experiment (figure 3). This was attributed to hydraulic failure after repeated prolonged droughts, and in accordance with the recent observed trend in the Mediterranean basin (Carnicer et al. 2011).

Table 1
Functional responses of a Quercus ilex ecosystem
to a 27% reduction in rainfall between 2003 and 2015

Tree mortality	↗	+8%	Unp. data
Tree growth	=		Rodriguez-Calcerrada et al. 2011
Leaf area	↘	-22%	Limousin et al. 2009
Litter fall	↘	-21%	Limousin et al. 2009
Acorn production	↘	-32%	Perez Ramos et al. 2010
Transpiration	↘	-23%	Limousin et al. 2009
Photosynthesis	↘	-14%	Misson et al. 2010
Tree respiration	↘	-14%	Rodriguez-Calcerrada et al. 2011
Soil respiration	↘	-11%	Misson et al. 2010

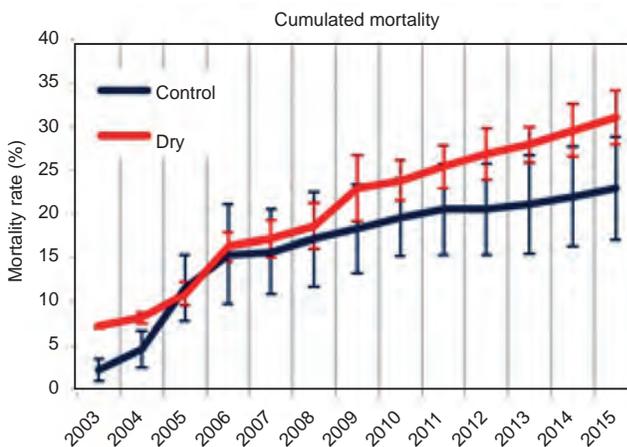


Figure 3
Cumulated annual tree mortality (in %) in TEE under the control (dark blue) and dry (red) treatment since the beginning of the experiment in 2003.

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 et al. 2016).

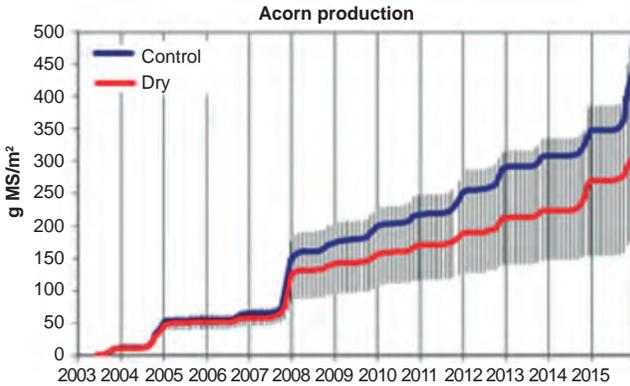


Figure 4
Cumulated annual acorn production in TEE under the control (blue) and dry (red) treatments since the beginning of the experiment in 2003.

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 ilex* in 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 *Quercus ilex* study site are needed in multispecies stands to better capture potentially contrasted strategies 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 *maquis* shrubland composed of *Arbutus unedo*, *Phyllirea latifolia*, *Cistus monspeliensis*, *Erica arborea*, *Pistacia lentiscus* and *Calicotome villosa* in northern Tunisia (36°36'18"N, 8°33'58"E), at the southern limit of the Mediterranean biome (see details in Longepierre et al. 2014). Interannual variability in species functioning and their response to increasing drought were assessed under a rainfall interception experiment. Weekly predawn plant water potentials were measured in the six species over the course of the experiment, along with plant moisture content, growth and leaf dynamic. We observed contrasted strategies among the species to cope with summer drought: deep rooted evergreen species (*Phyllirea latifolia*, *Pistacia lentiscus*) were able to maintain a water potential higher than -3MPa, while more shallow rooted species (*Erica arborea*) experienced severe water stress with water potential lower than -7MPa under the driest conditions (*Erica arborea*). Twig elongation was highly constrained in all the species below a water potential threshold of -1.2 MPa, but we identified different short term leaf area adjustment strategies, from fully evergreen for *P. lentiscus* and *P. latifolia*, to partially drought deciduous for *E. arborea* and summer deciduous for *C. villosa* as soon as water potential reached -1.2 MPa. We also observed that the species with the lowest predawn water potential (*E. arborea* and *C. villosa*) started growth early so that twig elongation was not affected by the early drought in 2012, while in less water-constrained species (*P. lentiscus* and *P. latifolia*) twig elongation was seriously affected (figure 5). These results illustrate different strategies ranging from drought avoidance to drought tolerance, depending on root exploration, leaf life span and leaf phenology, indicating high ecosystem-level resilience independent of the particular drought feature occurring in a given year. They also extend our first result on the high resilience of MTEs to increasing drought. However, like in *Quercus ilex*, in most of these species, seed germination was shown to be affected by soil water deficit, but enhanced by fire cues, a peculiar feature of these highly flammable species (Chamorro et al. 2016).

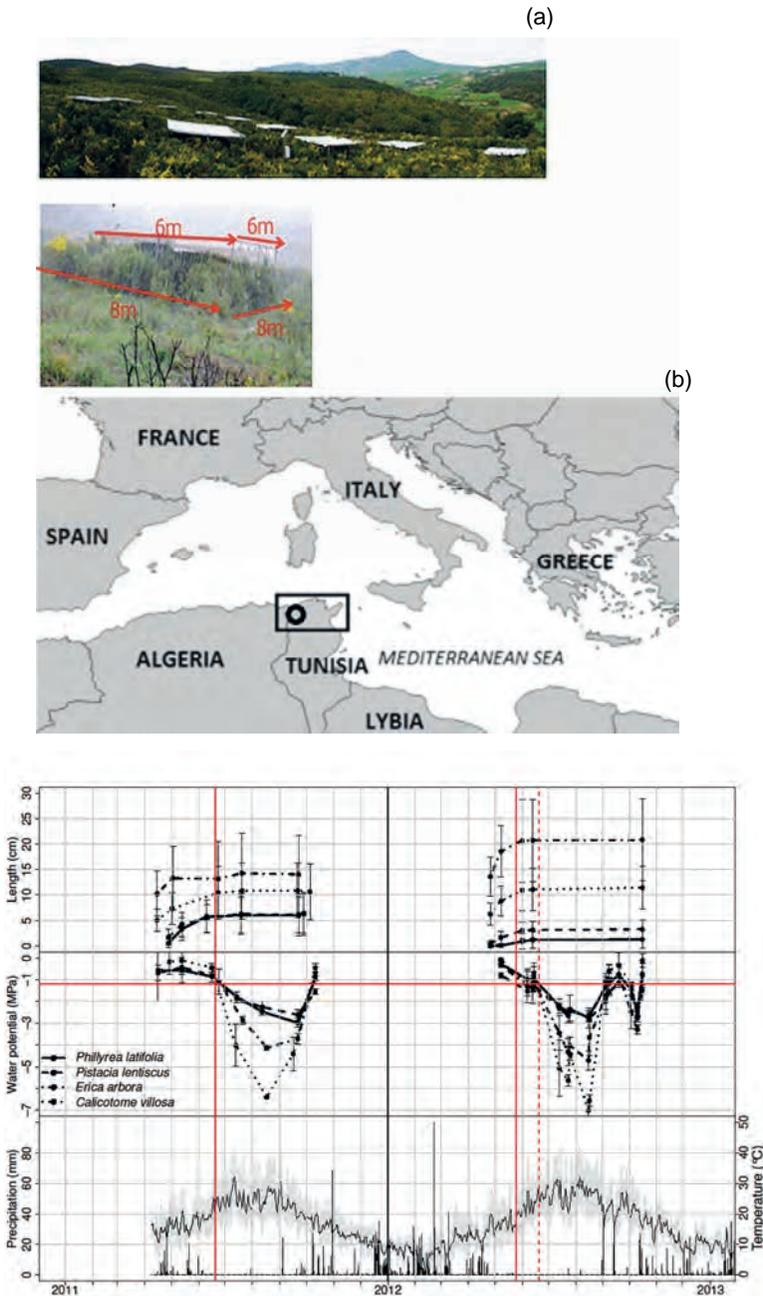


Figure 5

Rainfall interception experiment in a mixed Mediterranean shrubland in Tunisia (a). Map showing the location of the experiment (b). The graphs show seasonal variations in temperature and rainfall in the period 2011-2012, predawn leaf water potentials (MPa) for *Phillyrea latifolia*, *Pistacia lentiscus*, *Erica arborea* and *Calicotome villosa*, and the yearly cumulated apical twig elongation in the same species (c). The horizontal red line represents the -1.2MPa threshold, and the vertical red line identifies the day of the year when this threshold was reached and twig elongation stopped.

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 (Rodríguez-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.

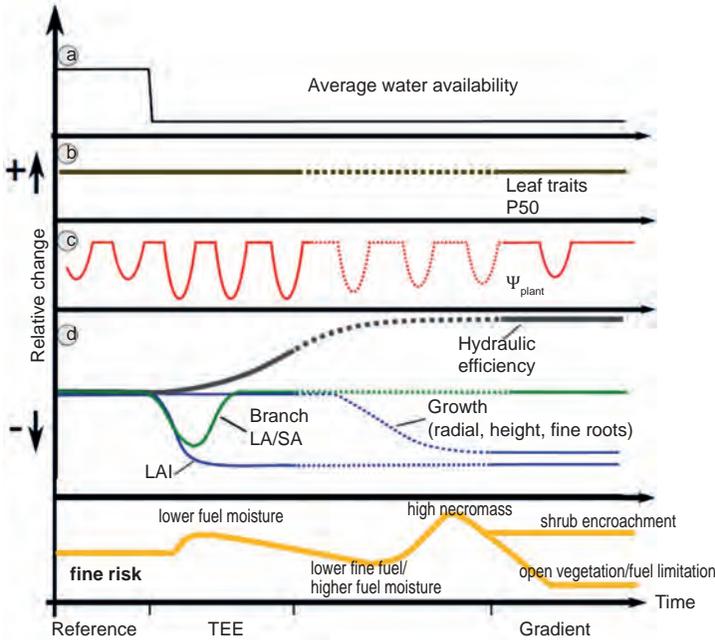


Figure 6

Temporal dynamics of the responses of *Quercus ilex* to decreasing precipitation.

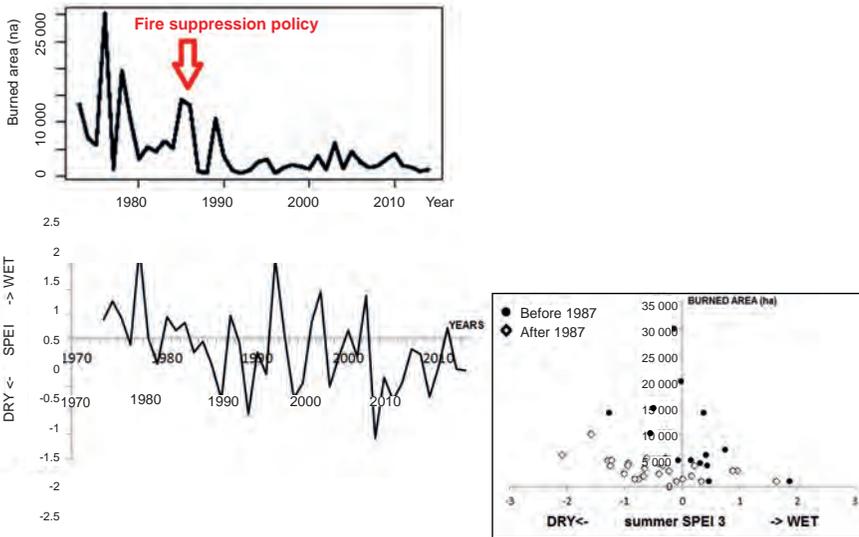
The y axis represents the relative changes from the reference value (intermediate site) when average water availability was reduced for a suite of traits. The x axis represents the time after the reduction of precipitation caused either by the TEE or the precipitation gradient.

Panel (a) shows the level of water availability. Panel (b) shows changes in leaf traits and P50 (the water potential causing 50% loss of conductivity). Panel (c) shows the change in Ψ_{plant} (plant water potential). Panel (d) shows the changes in shoot LA/SA (the ratio of apical shoot leaf area to sapwood area), LAI (the leaf area index); growth and hydraulic efficiency (i.e. the ability to transport and extract water). The dotted lines denote the interpolation between responses observed in the TEE and in the gradient. Implications for fire risk are shown as a combination of biomass moisture and changes in the amount of fine fuel.

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 strategies a community exploits to withstand high variability (prolonged, earlier, later, more intense, bimodal) drought features. The latter experiment reinforced our results concerning the high resilience of MTEs with respect to diverse functional traits at the ecosystem level. In the future, it will be important to

Languedoc Roussillon Region, southern France
(*Quercus ilex* dominated)



Tunisia

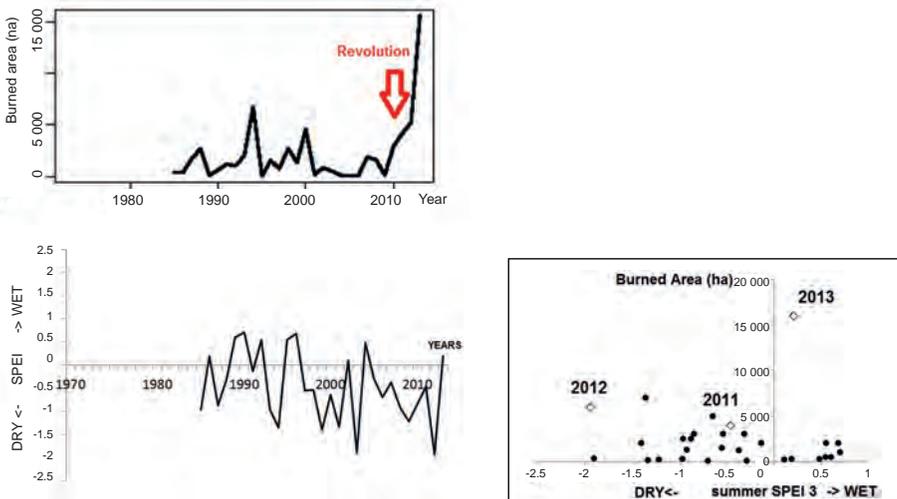


Figure 7

Annual burnt area (in ha) in southern France (*Quercus ilex* dominated Languedoc Roussillon Region) (source www.promethee.com) and Tunisia (Source General Directorate for Forests, Direction générale des forêts Tunis, and Landsat images for the period 2000-2013) for the period 1973-2013. Red arrows identify the timing of abrupt socio-political changes such as the introduction of a new fire suppression policy in France in 1987 and the revolution in Tunisia in 2011. Temporal trends in the standard precipitation evaporation index SPEI and the relation between burnt area and the summer SPEI3 are also shown for both sites. Languedoc Roussillon Region, southern France (*Quercus ilex* dominated) Tunisia.

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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The Mediterranean Region under Climate Change

A Scientific Update

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IRD ÉDITIONS
INSTITUT DE RECHERCHE POUR LE DÉVELOPPEMENT

Marseille, 2016

Revision and translation

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With the collaboration of:

Desk

Gris Souris

Layout

Desk

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Cover illustrations

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ISBN : 978-2-7099-2219-7

This book, coordinated by AllEnvi, is published on the occasion of the 22nd Conference of the Parties to the United Nations Framework Convention on Climate Change (COP22, Marrakech, 2016)

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AllEnvi, the French National Alliance for Environmental Research, is tasked with making the great environmental transitions work, coordinating French research into major societal issues such as food, water, climate and territories. AllEnvi i) sets policy guidelines and research priorities for advance planning before approaching funding agencies, ii) supports the emergence and structuring of research organizations, iii) coordinates innovation and technology transfer policies between public research operators, businesses and industries, and iv) contributes to the European research environment and international programme development.

Alliance nationale de recherche pour l'environnement, AllEnvi coordonne la recherche française sur les enjeux des grands défis sociétaux que sont l'alimentation, l'eau, le climat et les territoires pour réussir les grandes transitions environnementales. AllEnvi i) définit les orientations et priorités de recherche pour la programmation à l'amont des agences de financement, ii) soutient l'émergence et la structuration d'infrastructures de recherche, iii) coordonne les politiques d'innovation et valorisation entre opérateurs publics de la recherche, entreprises et industries, et iv) participe à l'Europe de la recherche et favorise l'émergence de programmes internationaux.

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