Reassessing global change research priorities in Mediterranean terrestrial ecosystems: how far have we come and where do we go from here?

E. Doblas-Miranda1*, J. Martínez-Vilalta1,2, F. Lloret1,2, A. Álvarez1, A. Ávila1, F. J. Bonet1, L. Brotons1,2, J. Castro3, J. Curiel Yuste4, M. Díaz5, P. Ferrandis7, E. García-Hurtado5, J. M. Iriondo9, T. F. Keenan10, J. Latron11, J. Llusia1,12, L. Loepfe13, M. Mayol1, G. Moré1, D. Moya1, J. Peñuelas1,12, X. Pons2, R. Poyatos1, J. Sardans1,12, O. Sus1, V. R. Vallejo8, J. Vayreda1 and J. Retana1,2

1CREAF, Cerdanyola del Vallès 08193, Spain, 2Univ Autònoma de Barcelona, Cerdanyola del Vallès 08193, Spain, 3Univ Granada, iEcolab Lab Ecol, Instituto Interuniversitario Sistema Tierra, Granada 18006, Spain, 4CTFC (Forestry Technology Centre of Catalonia), St Llorenç de Morunys km 2, 25280 Solsona, Spain, 5Department of Ecology, University of Granada, E-18071 Granada, Spain, 6Department of Biogeography and Global Change, Museo Nacl Ciencias Nat, CSIC (BGC-MNCS-CSIC), E-28006 Madrid, Spain, 7Technical School of Agricultural and Forestry Engineering, University of Castilla-La Mancha, Campus Universitario s/n, 02071 Albacete, Spain, 8Fundación Centro de Estudios Ambientales del Mediterráneo (CEAM), Paterna, Valencia, Spain, 9Department of Biology and Geology, Area Biodiversidad y Conservación, University of Rey Juan Carlos, Móstoles, Madrid, Spain, 10Department of Biological Sciences, Macquarie University, North Ryde, NSW, Australia, 11CSIC, Instituto de Diagnosi Ambiental i Estudis de l’Aigua IDAEA, ES-08034 Barcelona, Spain, 12CSIC, Global Ecology Unit CREAT-CEAB-UAB, Cerdanyola del Vallès 08193, Spain, 13Grupo Interdisciplinar de Sistemas Complejos (GISC), Departamento de Matemáticas, Universidad Carlos III de Madrid, 28911 Leganés, Spain

ABSTRACT

Aim Mediterranean terrestrial ecosystems serve as reference laboratories for the investigation of global change because of their transitional climate, the high spatiotemporal variability of their environmental conditions, a rich and unique biodiversity and a wide range of socio-economic conditions. As scientific development and environmental pressures increase, it is increasingly necessary to evaluate recent progress and to challenge research priorities in the face of global change.

Location Mediterranean terrestrial ecosystems.

Methods This article revisits the research priorities proposed in a 1998 assessment.

Results A new set of research priorities is proposed: (1) to establish the role of the landscape mosaic on fire-spread; (2) to further research the combined effect of different drivers on pest expansion; (3) to address the interaction between drivers of global change and recent forest management practices; (4) to obtain more realistic information on the impacts of global change and ecosystem services; (5) to assess forest mortality events associated with climatic extremes; (6) to focus global change research on identifying and managing vulnerable areas; (7) to use the functional traits concept to study resilience after disturbance; (8) to study the relationship between genotypic and phenotypic diversity as a source of forest resilience; (9) to understand the balance between C storage and water resources; (10) to analyse the interplay between landscape-scale processes and biodiversity conservation; (11) to refine models by including interactions between drivers and socio-economic contexts; (12) to understand forest–atmosphere feedbacks; (13) to represent key mechanisms linking plant hydraulics with landscape hydrology.

Main conclusions (1) The interactive nature of different global change drivers remains poorly understood. (2) There is a critical need for the rapid development of regional- and global-scale models that are more tightly connected with large-scale experiments, data networks and management practice. (3) More attention should be directed to drought-related forest decline and the current relevance of historical land use.

Keywords Assessment, atmosphere–biosphere interaction, biodiversity, climate change, fire regime, forest management, factors interaction, land-use change, research gaps, water reserves.
INTRODUCTION

The earth system is changing, threatening the ecosystem services upon which we depend (Steffen et al., 2004). Greenhouse gas emissions are causing climate change, characterized by warmer temperatures and more frequent and intense droughts (Giorgi & Lionello, 2008), which, in turn, imply an increase in climatic fire risk (Pausas, 2004). Other anthropogenic changes include major changes in land use, increasing nitrogen deposition and the accumulation of tropospheric ozone (Steffen et al., 2004).

Mediterranean terrestrial ecosystems (MTEs), including forests, shrublands and pastures, serve as exemplary natural laboratories in which to study global change because they are highly sensitive to several drivers of such change and to the interactions among these drivers (Sala et al., 2000). The climate in MTEs shows a high sensitivity to global atmospheric changes due to the transitional nature between arid and temperate regions in these ecosystems (Giorgi, 2006). Increased aridity is expected in most existing MTEs (Sillmann et al., 2013). The combination of extreme climate events, a long history of land-use changes and the particular geology of these ecosystems has resulted in more frequent and intense fires, water scarcity and land degradation (soil and productivity loss), among other impacts (Conacher, 1998; Keeley et al., 2012). MTEs show high levels of heterogeneity at different scales due to these disturbances and large seasonal and inter-annual climatic variability (Rundel, 1998). This distinctive spatiotemporal variability of environmental factors has resulted in a singular and diverse biota, with elevated vulnerability to extinction induced by global change (Malcolm et al., 2006). Given that socio-economic trends are projected to have a greater effect than climatic drivers on land use (Schröter et al., 2005), it is important to be able to study global change in different social and economic contexts and across different policy regimes. Among the world’s MTEs, the Mediterranean Basin serves as a particularly valuable laboratory for studying global change because of its wide range of socio-economic conditions and government policies (Brauch, 2003).

A consistent evaluation of the principal research gaps within MTEs, with special consideration given to the Mediterranean Basin, has the potential to provide valuable information on how to advance in handling the future impacts of global change on a global scale. A previous study by the International Geosphere-Biosphere Programme (Lavorel et al., 1998; hereafter La98) provided the first roadmap for conducting global change research in Mediterranean Basin ecosystems and recommended that specific actions be carried out in the region. Now, after 15 years of increasing research efforts devoted to the impacts of global change, it is time to evaluate the current state of the art with regard to these targets and to propose a new set of priorities for the coming decades – including priorities relevant to the MTEs outside the Mediterranean Basin.

To do this we revisit the priorities recommended by La98, following their original order, and we provide an update of their current state and relevance. We then suggest a new set of priorities for the future. Our specific objectives are: (1) to evaluate the progress of the research carried out in MTEs; (2) to assess the accomplishment of previous priorities; and (3) to update the list of priorities with emerging topics and challenges.

EVALUATION OF THE ACCOMPLISHMENT OF THE LA98 RESEARCH PRIORITIES

To understand future fire regimes and their effects

Prediction of future fire regimes, involving interaction with global changes

Land-use change may modify the fire regime by altering fuel load and distribution or ignition patterns. In the MTEs of Europe, massive abandonment of agricultural land has increased landscape homogeneity and crown fire potential, which in turn facilitates the spread of fire (Lloret et al., 2002; Mitsopoulos & Dimitrakopoulos, 2007). In contrast, central Chile has experienced an overall trend of deforestation and loss of shrubland but no clear trend in burned area (Montenegro et al., 2004). In California, urban development is the major driver of land transformation, increasing ignitions in the wildland–urban interface (Syphard et al., 2007).

In the Mediterranean Basin, fire-suppression policies may reduce fire size in the short term but promote megafires in the longer term (Piñol et al., 2007; Brotons et al., 2013). In contrast, fuel reduction policies are regularly implemented with prescribed fires in several MTEs in order to reduce hazard in populated areas and to reproduce a fire regime that supports biodiversity in a fine-grain mosaic of vegetation (Price & Bradstock, 2010). Prescribed burning, however, remains controversial (Boer et al., 2009; Fernandes et al., 2011). Under extreme weather conditions, fuel quantity no longer serves as a control on fire regime and large fires may even occur with relatively low fuel loads (Keeley & Zedler, 2009; San-Miguel-Ayanz et al., 2013). Site idiosyncrasy is also important, affecting pre-fire patch grain and distribution (Syphard et al., 2007). Fire-induced landscape homogenization (by large or frequent fires) as opposed to heterogenization (by scattered fires through space and time) appears highly dependent on fire regime (Lloret et al., 2002).

Climate change is expected to increase dryness in MTEs due to warmer temperatures and reduced precipitation, particularly during the summer (Giorgi & Lionello, 2008; Sillmann et al., 2013). Overall, this tendency will lead to increasing climatic fire risk (Liu et al., 2010), as already apparent from historical records (Kraaij et al., 2013). However, this trend is also influenced by fuel availability, determined by both the quantity of fuel and climate-driven fuel moisture (Westerling et al., 2006; Battlori et al., 2013). Although lower air humidity and fuel water content are positively related to fire ignition and propagation, a drier climate eventually leads to a decrease in fuel load, due to lower productivity (Lenihan et al., 2003; Batllori et al., 2013).

$CO_2$ fertilization could affect fuel accumulation and thus fire regimes. Recent projections at the regional level reveal that the net effect of $CO_2$ fertilization combined with drought stress...
remains uncertain (Keenan et al., 2011). However, water appears to be more important than CO$_2$ as a driver of growth in water-limited MTEs (Fatichi et al., 2014). In addition, the combination of increased fire frequency and drought stress could enhance shrub encroachment (Pausas, 1999; Mouillot et al., 2002) and thus reduce carbon storage.

**Fire impacts**

On landscape patterns

The main aim behind the extensive development of spatially explicit landscape models for MTEs is to assess the vulnerability of forests to fire due to soil degradation or vegetation shifts (Franklin et al., 2005; Millington et al., 2009). Most of these models, therefore, include forest management and environmental factors within specific landscape configurations (Loepfe et al., 2011; Moreira et al., 2012). However, models are still incomplete, in the sense that anthropogenic factors are usually not included in the generation of landscape projections and thus the prediction of future fire impacts (Syphard et al., 2007; Le Page et al., 2010).

On vegetation

Simulation models of fire and vegetation dynamics, including the interaction between these variables, have been developed, considering different spatial scales, vegetation levels, successional approaches and explicit or implicit simulation of fire spread (Keane et al., 2004; Millington et al., 2009). Analysis of the regenerative traits of species and populations remains a key approach in the assessment of the sensitivity of plant species to predicted fire regimes and for modelling changes in species distribution and community composition (Lloret et al., 2005; Syphard & Franklin, 2010). Several studies have assessed the short-term responses of MTE vegetation (Keely et al., 2012; Moreira et al., 2012) but more attention should be paid to longer time frames.

Combined with other factors

The consequences of the combined effects of fire and drought in the form of a decline in the regeneration of plants and land degradation have been the object of intense study (e.g. Mouillot et al., 2002; Montenegro et al., 2004). More recently, the role of fire in facilitating the spread of biological invasions in MTEs has also attracted attention (Rouget et al., 2001; Pino et al., 2013) and research in this area is revealing the vulnerability associated with properties of the fire regime such as fire frequency (Keely & Brennan, 2012) and intensity (Franklin, 2010).

**Fire control and mitigation**

Prevention

Since La98, many studies have been conducted to characterize the relationship between different fire spread characteristics using diverse approaches. These include fire behaviour models coupling suppression policies and vegetation dynamics, forest inventories, wildfire databases and fire severity studies (e.g. Boer et al., 2009; Price & Bradstock, 2010). Such studies have provided quantitative information about the best way to manage forest fuels to obtain: (1) more favourable fire characteristics (behaviour, frequency, size) aiding future fire suppression (Crecenete-Campo et al., 2009) or unplanned fire extents (Boer et al., 2009), and (2) landscape configurations that are more efficient at reducing megafires (Millington et al., 2009; Loepfe et al., 2011). Several studies have also reported positive feedback between flammable vegetation types and fire frequency (Vilà et al., 2001; Grigulis et al., 2005).

Restoration

The last decade has seen substantial advances in key aspects of post-fire forest restoration, such as the analysis of vegetation recovery (Díaz-Delgado & Pons, 2001; Díaz-Delgado et al., 2002). A new field of study deals with the identification of previous land-use changes as drivers of post-fire regenration (Clavero et al., 2011; Puerta-Piñero et al., 2012). Additional breakthroughs have been made in the study of facilitative interactions and the use of shrubs as potential nurse plants (Gómez-Aparicio et al., 2004), underscoring the role of early and mid-successional shrubs for forest regeneration in burnt areas (Gómez-Aparicio et al., 2004; Siles et al., 2010). In addition, a novel focus has recently appeared in relation to the use of coarse woody debris to foster restoration success, as this debris may act as a nurse structure, improving microclimatic conditions for seedling establishment, increasing soil nutrient content and improving other physical and chemical properties of the soil (Castro et al., 2011; Marañón-Jiménez & Castro, 2013; Marzano et al., 2013). Burnt trees are also a biological legacy crucial for the recovery of communities and for the structure and function of regenerating mediterranean-type ecosystems by promoting plant-animal interactions and increasing plant and animal diversity (Castro et al., 2012; Lee et al., 2013; Marzano et al., 2013; Leverkus et al., 2014), reducing invasion by exotic species (Moreira et al., 2013), promoting soil microbial activity (Marañón-Jiménez & Castro, 2013) and carbon sequestration (Serrano-Ortiz et al., 2011).

To study the effects of land use on biosphere–atmosphere interactions

**Feedbacks of land-use changes on the climate system**

While a great deal of uncertainty persists concerning the impacts of land-use changes on regional climate models (Bonan, 2008), modelling results for the Mediterranean suggest that changes in land use significantly affect climate (Lionello et al., 2006). Changes in evapotranspiration rates and surface albedo due to deforestation in the Mediterranean Basin could provoke cooler and moister springs but warmer and drier summers (Heck et al., 2001) or instead cooling during summer (Zampieri & Lionello, 2011). In south-west Australia, deforestation may lead to long-term reductions in rainfall patterns (Pitman et al., 2004). In
summary, available models indicate that the climate of MTEs is sensitive to changes in vegetation cover, especially in summer. However, the induced climate anomalies can be associated with fine-grained, complex and non-local mechanisms and their relative weights in driving local effects are still uncertain (Seneviratne et al., 2010).

Feedbacks of ecosystem physiology on the climate system

Current evidence suggests that CO$_2$-driven feedbacks on temperature through physiological responses of vegetation are negligible (Keenan et al., 2011; Cheaib et al., 2012).

The effects of climate change on soil respiration and the emission of other biogenic gases are still a major concern. Increases in drought intensity in the Mediterranean Basin have been associated with episodes of tree mortality during recent decades (Martinez-Vilalta et al., 2012; Sánchez-Salgueiro et al., 2012). A recent study shows that although current tree mortality is not affecting the carbon balance of Mediterranean forests, increased warming and drought are likely to alter the capacity of these forests to absorb CO$_2$ and forest management may be a key factor determining the response of forest C balance to changing climate (Vayreda et al., 2012).

Some studies have reported an increase in soil organic carbon (SOC) and other nutrient fractions under drought due to rising quantities of litterfall and dead roots (Talmon et al., 2011) and to decreased soil decomposition and respiration (e.g., Curiel Yuste et al., 2007; Ryals & Silver, 2013). However, observational studies suggest that drought should decrease SOC in the long term by reducing plant cover, which implies a decrease in litterfall, soil protection and permeability (Boix-Fayos et al., 1998). Furthermore, in MTEs there is an overall reduction in biological activity in the soil due to a reduction in soil moisture (Brown et al., 1996), and this results in a decrease in soil nutrient availability and soil CO$_2$ emissions (Emmett et al., 2004; Sardans et al., 2008). An increasing body of research is also starting to reveal the key role of microbial communities in ecosystem processes under climate-change scenarios, particularly in soil carbon dynamics (Balser & Wixon, 2009; Asensio et al., 2012; Curiel Yuste et al., 2012).

Biogenic volatile organic compounds (BVOCs) were not previously considered but are also crucial for understanding both biological consequences and feedbacks on atmospheric chemistry and climate itself (Monson et al., 2007; Peñuelas et al., 2013). The emission rates of BVOCs increase with rising global temperature, but changes in species and community structure, land use and resource availability can also lead to major changes in Mediterranean regional BVOC fluxes (Peñuelas & Staudt, 2010).

Contribution of fire related emissions of carbon, nitrous oxides and other trace gases to the atmosphere and their potential effects on climate

Fire emissions cause significant perturbations of the chemical composition of the atmosphere and in the earth climate system, as several field campaigns as well as laboratory experiments and prescribed burnings in MTEs have shown (Ciccioli et al., 2001; Phuleria et al., 2005; Wain et al., 2008; García-Hurtado et al., 2013). The principal gases emitted include carbon dioxide (CO$_2$), carbon monoxide (CO) and methane (CH$_4$), but also nitrogen oxides (NO$_x$ and N$_2$O), ammonia (NH$_3$), sulphur dioxide (SO$_2$), light hydrocarbons, volatile and semi-volatile organic compounds, and particulate matter (10–2.5 μm), which could affect climate change and human health (Ciccioli et al., 2001; Bell & Adams, 2008).

Studies have been conducted to characterize biomarkers from woodstove combustions and wildfires (Muhle et al., 2007; Gonçalves et al., 2011), but the challenge of identifying the main tracer compounds emitted by forest fires in MTEs continues.

EMEP/CORINAIR emission inventories and satellite observations, including those using Moderate Resolution Imaging Spectroradiometer (MODIS) data, have been used to feed several emission and air quality models (Lazaridis et al., 2005; Paton-Walsh et al., 2012).

Coupled biosphere–atmosphere models for the Mediterranean Basin

Large-scale generalized simulations of the effects of climate and land-use changes on MTEs exist (Zaehle et al., 2007), but regional applications to key ecosystems (including cropland phenology and management to account for associated albedo feedbacks; Sus et al., 2010) are scarce. During the past decade, the development of non-fully-coupled models simulating Mediterranean terrestrial biosphere–atmosphere interactions has focused on the integration of information on ecosystem physiology and land-cover dynamics (e.g. Gritti et al., 2006). Only in recent years, however, have fire models begun to be incorporated into land-surface models (e.g. Prentice et al., 2011). Early efforts identified model deficiencies in reproducing the response of leaf gas exchange to drought events (Reichstein et al., 2003), leading to subsequent model development (Garbulsky et al., 2008; Keenan et al., 2010). Despite this, models continue to perform poorly in conditions of water stress (Vargas et al., 2013). Many ecosystem disturbances, processes and physiological responses remain poorly understood, and are not explicitly accounted for in models, such as, for example, competitive interactions, the depletion of carbohydrate reserves and stress-induced plant decline and mortality (e.g. Carnicer et al., 2011; Misson et al., 2011).

To study landscape effects on water availability and quality

Research at the patch scale

Leaf area index (LAI) and hydrological response

Land-use changes, hydroclimatic conditions and fires are the main drivers of changes in vegetation cover in MTEs and therefore exert great influence on the hydrological responses of these ecosystems. Fires, for instance, influence understorey regrowth
and hence may contribute to maintaining ecosystem evapotranspiration fluxes (Macfarlane et al., 2010). Land-use history also modulates the hydrological behaviour through changes in soil properties such as soil water repellency and infiltratability (Llovet et al., 2009).

Drought-induced episodes of vegetation dieback may result in different ecophysiological effects compared with canopy cover changes (Adams et al., 2012). For example, generalized drought-induced defoliation across southern European forests (Carnicer et al., 2011) may gradually reduce stand transpiration (e.g. Limousin et al., 2009). Drought severity and/or duration together with local factors such as soil water-holding capacity (Peterman et al., 2013) and species-specific drought-tolerance traits (Jacobsen et al., 2007; Matias et al., 2012) will ultimately determine plant survival and, hence, the impact of episodic drought on hydrological processes.

Temporal variability

In general, evapotranspiration in MTEs is strongly depressed during summer (Baldocchi et al., 2010; Raz-Yaseef et al., 2012). However, mediterranean plant species in MTEs show a variety of responses to cope with drought, from complete summer senescence observed in some grasslands (Baldocchi et al., 2004) to various degrees of stomatal control of transpiration (e.g. Quero et al., 2011). In general, increased atmospheric CO₂ concentrations will induce stomatal closure and improve plant water status, enhancing water-use efficiency and potentially reducing the effects of increases in evaporative demand. However, the impact of increased CO₂ on ecosystem water use will vary with vegetation type, species and stand development (Li et al., 2003). Regardless of all these functional responses to water deficits, water (and carbon) fluxes in MTEs are strongly reduced during extreme drought events (Granier et al., 2007).

Hydrological equilibrium and simulation models

In MTEs, maximum LAI is constrained by vegetation type, local climate and soil conditions, leading to the notion that there is an ‘equilibrium LAI’ that maximizes carbon assimilation (Hoff & Rambal, 2003). This hypothesis was framed by La98 within Eagleson’s (1982) broader concept of hydrological equilibrium, but the optimality hypotheses associated with Eagleson’s ecohydrological model have now been questioned in the context of water-limited environments (Kerkhoff et al., 2004).

Research at the landscape scale

Mapping and emergent properties

The availability of earth observational data for ecological studies has increased due to the launch of several multispectral high/medium spatial resolution platforms and it will increase further in the coming years with Landsat-8 and ESA’s Sentinel missions. These developments will give continuity to the wide use of remote sensing in previous MTE studies (Shoshany, 2000). Lidar technology is becoming an operative application for acquiring information about forest and shrubland structures in many regions (Estornell et al., 2010; García et al., 2010). In contrast, radar information, a promising data source in the past, has not provided the expected results (Lu, 2006). MTEs have been increasingly studied using remote sensing from different perspectives, including land-use/cover changes, drought, carbon budget and foliar biochemical concentration and canopy structure (e.g. Serrano et al., 2001; Bergerouglu & Akin, 2009). Unmanned aerial systems (UAV) provide another increasingly popular platform for ecological studies (Dunford et al., 2009; Hernández-Clemente et al., 2012). Another area of interest is the use of spectroradiometers as an augmentation to remote sensing for validating or training models (Xu & Baldocchi, 2004; Glenn et al., 2011).

Landscape change

Different studies at the operational catchment scale in several MTEs have evidenced decreasing trends in the flow records (e.g. Delgado et al., 2010; Zhao et al., 2010; see also Lespinas et al., 2010, for contrasting results) and modifications of the flow regime (e.g. López-Moreno et al., 2011; Morán-Tejeda et al., 2011), partly (but not exclusively) attributable to forest expansion. The effects of climate change on surface water quality and ecology are attracting growing attention in mediterranean areas (e.g. Munné & Prat, 2011; Otero et al., 2011). Investigations on post-fire flows of soil, water and nutrients, however, have not been so common, mainly because pre-fire data are frequently unavailable (Shakesby, 2011) and the effects of prescribed fires do not directly mimic natural wildfire influences (Seibert et al., 2010).

Simulation models

Numerous complex hydrological models (often spatially distributed, physically based) have been used to assess the effects of global change on water resources, soil erosion and vegetation productivity (e.g. D’Agostino et al., 2010; Senatore et al., 2011). However, there is growing concern about the current modelling approaches (Ewen et al., 2006; Beven, 2011) because of cumulative uncertainties in regional model projections, including uncertainties in downscaling procedures, land-use and landcover changes and choices of hydrological models.

To investigate the effects of climate change on ecological diversity

Genetic diversity

La98 suggested giving increased attention to studies linking genetic diversity with relevant ecosystem functions. However, there is still little knowledge of the adaptive variability present in the different MTEs. The technical difficulty of some measurements, the time-consuming nature of the relevant experiments and the large sample sizes required to determine heritability or
selection on functional traits have limited the implementation of reciprocal transplants and/or common garden studies, particularly for long-lived species (Ackerly, 2006). Exceptions include economically important species for which provenance trials have allowed the estimation of ecotypic variation in growth and functional traits (e.g. Ramírez-Valiente et al., 2009; Kurt et al., 2012).

Significant advances have been made in the last decade in understanding the range dynamics of mediterranean species in response to past climatic changes to validate predictions on ecological and evolutionary consequences of current climate change (e.g. Petit et al., 2005, 2008). In addition, there has been mounting evidence showing that maintaining genetic diversity within natural populations can maximize their potential to withstand and adapt to biotic and abiotic disturbances (Jump et al., 2008).

Species and functional diversity

Since La98 noted the effects of diversity on ecosystem functioning (DEF), those effects have continued to be intensely discussed in MTEs, although the relative importance of DEF in relation to global change still needs to be further assessed (Larsen et al., 2005; Dimitrakopoulos, 2010; Maestre et al., 2012). Further, the role of biodiversity in maintaining human-made systems that provide high-value ecosystem services is becoming a key issue in shaping environmental and land-use policies (Díaz et al., 2013).

In the Mediterranean Basin, higher diversity has been associated with more rapid recovery after fire (Lavorel, 1999). Fire effects also interact with species richness, increasing biomass production in rich communities (Dimitrakopoulos et al., 2006). In most MTEs, restoration of degraded environments due to human alteration could be facilitated by diversity of vegetation and associated soil microbes (García-Palacios et al., 2011; Viers et al., 2012). Recent work also emphasizes the role of diversity in the face of invasive species (Prieur-Richard & Lavorel, 2000; Selmans et al., 2012; see also Prieur-Richard et al., 2002, for contrasting results). Also, the effect on ecosystem functioning of invasion-induced species impoverishment is a contested issue (Vilà et al., 2006; Ruwanza et al., 2013).

Aboveground–belowground trophic interactions are of potential importance in the functioning of MTEs (e.g. Doblas-Miranda et al., 2009; Janion et al., 2011). Several experiments in mediterranean regions have related soil respiration and functioning to climate and land-use change (Eimett et al., 2004; Garnier et al., 2007; Lau & Lennon, 2012).

The expected increase in aridity in most MTEs may impact plant community dynamics and composition (Lloret et al., 2009; Matías et al., 2012). However, the heterogeneity of mediterranean landscapes and the variety of responses at different scales give rise to a variety of stabilizing mechanisms promoting community resilience (Lloret et al., 2012) and make predictions difficult (Maestre et al., 2005). Climate change could also affect the biodiversity of important and influential faunal communities (Botes et al., 2006; Gil-Tena et al., 2009). Another promising line of research is to disentangle the combined effects of different factors of change on species and functional diversity (Gil-Tena et al., 2009; Pasquini & Vourlitis, 2010).

Landscape diversity

The increasing availability of geospatial information at increasing spatial and temporal resolution has facilitated the study of landscape patterns. Projects in the Mediterranean Basin, in California’s mediterranean landscapes and in South Africa have boosted the development of studies addressing how drivers of global change might influence diversity and key ecosystem functions at broad spatial scales (e.g. Santos et al., 2006; Aparicio et al., 2008; García et al., 2011).

Current research is demonstrating that landscape structure modulates conservation efforts at local scales due to non-linear effects of landscape diversity on local diversity (Concepción et al., 2012). Conservation at local scales would be effective only at intermediate levels of landscape complexity, whereas landscape initiatives would be more effective in the simpler and more complex landscapes (Brotons et al., 2004; Concepción et al., 2008). Landscape-scale management is crucial for preserving both biodiversity and the ecosystem services the landscape provides (Díaz et al., 2013).

The effects of landscape heterogeneity also have a strong temporal dimension. Due to the long history of land-use changes in the Mediterranean Basin, there is increasing evidence of long-term impacts of past land uses on the current state of ecosystems (Puerta-Piñero et al., 2012; Navarro-González et al., 2013). In this way, several projects have aimed to disentangle the role of past land uses at different scales and in different ecosystems (Bonet et al., 2010; Ortega et al., 2010).

UPDATE OF PRIORITIES AND NEW CHALLENGES

Advancement of research effort in MTEs

In general, the study of global change in mediterranean ecosystems has increased since 1998. The proportion of global change studies on MTEs remains relatively low, but is now closer to the proportion of global change studies devoted to other ecosystems, which have diminished (boreal, tropical) or remained approximately constant (temperate) (Fig. 1). There has been an increase in studies in all four lines of research proposed by La98, especially from the mid 2000s, and particularly in the last few years (Fig. 2). This increase is quite similar for fire regimes, water availability and quality and ecological diversity, and somewhat lower for biosphere–atmosphere interactions. Studies about the effects of global change in mediterranean ecosystems have been mostly carried out in the Mediterranean Basin (88.4% of total studies), while studies within this region outside European countries (i.e. the southern rim of the Mediterranean Basin) constitute just a small fraction (7.8% of the Mediterranean Basin studies).
Figure 1 Trends in published research articles (excluding reviews and meeting abstracts) related to global change and Mediterranean forests in the scientific literature, for the years 1998–2012, based on ISI Web of Science search. The term forest, but not shrublands or pastures, has been used for comparative purposes. Plotted lines show the percentage of references retrieved using the topic words ‘(forest change) AND (fire or atmosphere* or ‘land use’ or water or diversity) NOT (marine sea)’ plus a regional definition (Mediterranean, boreal, tropical or temperate), relative to all references obtained without the regional specification.

Global change research in MTEs

Figure 2 Trends in published research articles (excluding reviews and meeting abstracts) related to global change and forests in the scientific literature, for the years 1998–2012, based on ISI Web of Science search. The term forest, but not shrublands or pastures, has been used for comparative purposes. Plotted lines show the total of references, after a one by one selective review to avoid articles not really related with the subject, using the following topic words.

For fire regimes: (Mediterranean forest fire change) AND (predict* OR model OR simulation OR impact OR effect OR consequence OR control OR prevention OR restoration) AND (‘land use’ OR ‘land cover’ OR landscape OR climate OR temperature OR humidity OR moisture OR atmosphere*) OR plant OR vegetation OR ‘ecosystem processes*) NOT (marine sea).

For biosphere–atmosphere interactions: (Mediterranean forest atmosphere* change) AND (feedback OR model OR soil OR physiology OR biogenic OR volatile OR emissions OR monitoring OR carbon OR ‘trace gases’ OR ‘nitro* oxides’ OR ammonia OR sulphur OR ozone OR transpiration OR eddy-covariance) AND (‘land use’ OR ‘land cover’ OR landscape OR climate OR temperature OR humidity OR water OR energy OR moisture OR fire OR plant OR tree OR vegetation OR ‘ecosystem processes’) NOT (marine sea).

For water availability and quality: (Mediterranean forest water change) AND (availability OR quality OR model OR simulation OR flow OR flux OR ‘patch scale’ OR ‘landscape scale’ OR ‘leaf area’ OR hydrological OR ‘temporal variability’ OR trend OR mapping OR ‘remote sensing’ OR catchment) AND (‘land use’ OR ‘land cover’ OR landscape OR climate OR temperature OR humidity OR moisture OR atmosphere* OR fire OR plant OR vegetation OR ‘ecosystem processes’) NOT (marine sea).

For ecological diversity: (Mediterranean forest diversity change) AND (bioindicator OR conservation OR restoration OR heterogeneity OR trait OR genotyp* OR phenotyp* OR model OR simulation OR impact OR effect OR trophic OR genetic OR species OR functional OR ecological OR biological) AND (‘land use’ OR ‘land cover’ OR landscape OR climate OR temperature OR humidity OR moisture OR fire OR invasi* OR atmosphere* OR soil OR ‘ecosystem processes’ OR ‘ecosystem function*’) NOT (marine sea).
New research priorities

Since 1998, great advances have been made in research techniques and knowledge. Most of the research priorities identified by La98 have been addressed (Table 1), but some remain and new MTE research topics and priorities have also emerged. Our evaluation has identified: (1) topics listed in La98 which have been only partially addressed, (2) new approaches to questions already suggested by La98, and (3) a new set of emerging issues (Table 2). We suggest a new classification of these priorities based on a framework describing how Mediterranean ecosystems will respond to human-induced global change, including ecosystem services derived from ecosystem functioning, and incorporating mechanisms of monitoring, studying and seeking to modify these responses (Fig. 3).

In our proposed scheme, the first step in organizing future research efforts on global change in MTEs (and other ecosystem types) is to understand the effect of the drivers of global change on ecosystem functioning. Second, these processes must be monitored, and data must be appropriately analysed to produce useful research outputs. Third, this information should be used to guide ecosystem management aimed at modifying the observed or expected effects. Fourth, the link between ecosystem functioning and ecosystem services should be made explicit, in order to fully realize the opportunities offered by ecosystem management in a global change context. Finally, all the previous steps will depend on spatial and temporal scales of functioning, observation and management, which should be analysed by means of ecosystem modelling approaches and well-designed critical experiments.

Effects of the interactions between the drivers of global change on ecosystem functioning

To establish the role of the landscape mosaic on fire-spread

A major challenge remains to establish how direct and indirect fire suppression policies influence fire regimes. These policies operate in spatially explicit landscapes that are determined by fuel load and continuity, which in turn determine fire regime. Specifically, we need to better understand the fraction and distribution of agricultural land needed to prevent the spread of megafires, and the role of the critical wildland–urban interface, as well as the associated modification of landscape structure, in preventing the massive crown fires that can cause megafires (Keeley et al., 2012; Loepfe et al., 2012). In addition, the disrup-
tion of the landscape–fire interaction by extreme climatic episodes should be included in these analyses, and increasing vulnerability to fires should be addressed in areas where climate is becoming similar to that of the existing Mediterranean regions.

To further research the combined effect of different drivers on biological invasions and pest expansion

Since La98 did not address the impact of fire in combination with factors other than climate change and land use, it did not include biological invasions. The effect of biological invasions in combination with different climatic events (e.g. droughts), disturbance (e.g. fires) and landscape structure (e.g. the wildland–urban interface) on biodiversity and ecosystem functioning stands as a priority for future research efforts. For example, the impact of the combination of fire and invading biota may be especially important in Mediterranean regions where the spread of invasive species is altering fire regimes. In addition, it is important to assess the influence of climate change combined with land-use change in the expansion of certain pest species (native or not) in previously non-accessible habitats like mountains. This new focus will complement the more classical, but still much needed, analyses on how responses of keystone species or communities to global change may ameliorate or amplify direct effects on forest structure and function (e.g. Valladares et al., 2013).

To address the interaction between drivers of global change and recent forest management practices

Human influences have shaped the current structure and composition of MTEs and their woodlands. In some regions these impacts have built up over the last decades as a result of changes in forest management and land-use practices. In the Mediterranean Basin, for instance, there is a widespread process of forest

Table 2 Proposed research priorities for Mediterranean terrestrial ecosystems in the face of global change.

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densification owing to widespread abandonment of intensive forest management. This process has critical implications in a global change context, as it affects fire spread and recovery after fire (e.g., Puerta-Piñero et al., 2012) and increases the competition for water and therefore the likelihood of drought-induced forest die-off (Martínez-Vilalta et al., 2012). Although the demographic implications of the interaction between changes in climate and competition are starting to be addressed (Vilà-Cabrera et al., 2011; Ruiz-Benito et al., 2013) there is an urgent need to expand these studies in order to disentangle the contribution of different drivers (and their interaction) to current stand dynamics and to translate this information into credible models of future forest dynamics. 

Monitoring and data assessment of ecosystem response to global change

To obtain more realistic information, at larger temporal and spatial scales, of global change impacts and ecosystem services to be used in models

La98 advised that, in order to disentangle the effects of landscape change on hydrological properties, research on larger spatial scales is necessary. In fact, other ecosystem services such as carbon storage are also better defined and studied at larger spatial scales and over longer time-scales (e.g. Vayreda et al., 2012). Similar reasoning can be applied to the factors that alter these services. For example, there is a need for reliable information on the efficiency of different fire and fuel management alternatives at reasonably large spatiotemporal scales. Long-term manipulative experiments show that ecosystem responses to disturbance frequently change over time (e.g. Barbeta et al., 2013). Thus, the data inputs for model calibration and validation should include, to the extent possible, long time series of observational data as well as long-term ecosystem manipulation experiments (Ecotron) focusing on key drivers (cf. Beier et al., 2012).

To assess forest mortality events associated with climatic extremes (particularly drought)

The drought-induced forest decline detected during recent decades remains insufficiently understood, as it is not yet known which biological mechanisms are involved and which factors other than drought have played causal roles. In MTEs, elevation, substrate, plant composition, stand structure and soil biota all appear to contribute to forest die-off (e.g. Martínez-Vilalta et al., 2012). Forest history and, particularly, management, appear to be key drivers, for instance by determining current forest structure and composition. Strategic actions include long-term monitoring at a regional scale, with implementation of common protocols, and rapid identification of new events (using for example remote sensing or UAVs), which would make it possible to study the process while it is happening. These actions would benefit critically from the involvement of forest owners and governmental agencies.

Managing ecosystems to enhance resilience

To focus global change research on identifying and managing vulnerable areas

Future research efforts should aim at identifying areas that might suffer from the combination of multiple drivers of climate change. For instance, mountains and sub-mediterranean zones may be particularly susceptible to the likely increase of climatic fire risk because these are landscapes that have not previously faced high fire risks and therefore may have low vegetation resilience (Lloret et al., 2005). Other susceptible areas include those where land-use transformation has led to a high fuel load and thus a high risk of massive crown fires. Similarly, the recent increase in temperature is likely to favour insect expansion, and unprecedented insect outbreaks can arise in areas with high tree density and landscape connectivity. The resulting management agenda should include the adaptation of MTEs to more arid conditions, for instance by species selection, or by management of stand and landscape structure and water use. Here, one major challenge is to determine how the suppression of wildfires and other management actions could eventually induce non-reversible state transitions of vegetation types and structure, resulting in service-impoverished states.

To use functional and life-history traits concepts to study resilience and community assembly after disturbance

Although the possibility of threshold-type responses in ecosystems is real and should be taken into account, the resilience of ecosystems to climate change is frequently substantial and deserves further study (cf. Lloret et al., 2012). Given the variability of species responses to different disturbance types (e.g. the responses of plants to fire regimes; Pérez et al., 2003; Rey Benayas et al., 2007) and the complexity of the factors shaping community dynamics there is an urgent need to find synthetic, yet powerful approaches to predict the ecosystem-level effects of environmental changes. In that respect, the functional trait concept has strong conceptual appeal (Lavorel & Garnier, 2002), although its empirical applicability remains to be properly established.

To promote cross-disciplinary research to study the relationship between genotypic and phenotypic diversity as a source of forest resilience

Given the complexities underlying evolutionary processes, there is a clear need to intensify cross-disciplinary research among different disciplines such as genetics, genomics, demography, functional ecophysiology and animal–plant interactions in order to investigate the effects of climate change on genetic diversity. Reciprocal transplants and common garden experiments, linked to next-generation sequencing approaches, have yet to be fully applied in mediterranean contexts. To understand how mediterranean species will respond to global change in the long term and what the genetic basis of this response will be, it
is essential to identify genes under natural selection, as well as to ascertain the relationship between naturally occurring genotypic and phenotypic diversity.

_Embracing the link between ecosystem functions and services_

To understand how forest management affects the balance between C storage and water resources at large spatial and temporal scales?

It has been recently suggested that management could increase the C storage capacity of forests (Vayreda _et al._, 2012), although the detailed mechanisms are yet to be properly characterized. Indeed, when assessing the C absorption capacity of MTE forests it is necessary to consider the importance of the water balance; tree density and species should be managed cautiously since high transpiration rates also imply high water losses in the system. The search for management practices favouring C storage should take into account the risk of forest decline due to scarcity of water.

To analyse the interplay between landscape-scale processes and biodiversity conservation along wide gradients of landscape complexity

Overall, large-scale collaborative efforts among teams in different regions should be promoted and prioritized in order to fully understand how and why landscape processes influence the responses of MTEs to global change. Biodiversity is likely to be crucial in modulating such responses, so effective conservation strategies over wide gradients of landscape complexity need to be designed and effectively implemented. In addition, research on the social and economic role of biodiversity in the maintenance of land-use systems is urgently needed (Campos _et al._, 2013) in order to establish how and why biodiversity is contributing to the ecological and economic sustainability of mediterranean low-intensity management systems of high natural value.

_Scaling ecosystem dynamics in space and time under different scenarios_

To refine predictive models by including interactions between drivers of global change and socio-economic contexts

More attention should be given to anthropogenic factors when generating landscape projections (Serra _et al._, 2008), to understand not only future fire impacts (Brotons _et al._, 2013) but also other components of global change such as biological invasions and land-use changes, taking into account interactions between these major drivers and the impacts on associated ecosystem services (Campos _et al._, 2013). Among these factors, further research needs to focus on the integration of the socio-economic scenarios that are already available into predictive models of land-use-driven climatic change (Verburg _et al._, 2010). The development of reference scenarios of land-use and forest change that can be used consistently together with available climate change scenarios remains a gap in current global change science. Furthermore, even if the present review is focused on forests, shrublands and pastures, the simulation of biosphere–atmosphere interactions in other key ecosystems such as croplands and urban environments should be considered.

To use manipulative, interdisciplinary and multiscale experiments to understand forest–atmosphere feedbacks

La98 were already conscious that manipulative experiments at large scales are needed to fully understand the feedbacks between terrestrial ecosystems and the atmosphere, in addition to a wider use of historical data. We have learned from a first generation of manipulative field experiments and we are now in a position to use new designs that are larger is scope and make full use of research networks working with standardized protocols (see the review by Beier _et al._, 2012, for precipitation manipulation experiments). Multifactorial (e.g. CO₂ × warming × drought) and interdisciplinary experiments combining different experimental approaches (field and microcosm experiments) with the use of innovative techniques (e.g. genome pyrosequencing, solid-state nuclear magnetic resonance) will facilitate the identification of key mechanisms and their integration into predictive models. Emerging issues, such as altered BVOC emissions, nutrient imbalances and soil microbial processes, deserve special attention.

To improve the representation of key mechanisms linking plant hydraulics with landscape hydrology

There is a need for improved representations of soil and plant hydraulics in process models of water and carbon fluxes, both in general and for mediterranean vegetation in particular (e.g. Hernández-Santana _et al._, 2009). Mechanisms leading to drought-induced vegetation die-off are poorly understood and their representation in models is frequently inadequate (McDowell _et al._, 2013), which limits our capacity to predict vegetation shifts and corresponding ecosystem-level implications (Anderegg _et al._, 2013). In addition, hydrological predictions are complicated by the difficulty in properly accounting for ‘natural’ successional dynamics and predicting stochastic events like insect outbreaks and the occurrence of fire.

_BROAD RECOMMENDATIONS_

From the full list of priorities offered in Table 2, three broad recommendations serve as a conclusion.

1. The interactive nature of different global change drivers remains poorly understood. Different global change factors and their interactions, as well as socio-economic constraints, must be included in the forecasts and modelling of future ecosystem changes.

2. There is a critical need for rapidly developing regional- and global-scale models. Better networking of research data, as well
as manipulative experiments, covering different abiotic and biotic factors and different temporal and spatial scales, is needed to calibrate and validate these ecological models.

3. More attention should be directed at emerging issues especially related to MTEs in the face of global change, including recent drought-related forest decline and the current consequences of historical land uses.

Although the MTEs are the focus on our evaluation and are the direct targets of our recommendations, we believe that these ecosystems serve as good reference laboratories for global change research more broadly and that our broad recommendations can be applied to other ecosystem types. Global change research in MTEs, and especially in the Mediterranean Basin, is mature enough to move a step forward and launch into an integrative phase. In this phase, research on global issues should become more inclusive and allow the development of joint projections on how ecosystems and the services they provide are expected to react to different scenarios of future change. This is the information that societies are likely to need in order to adapt to the new, uncertain changes to come.

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REFERENCES


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