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

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Abstract

Aim: Mediterranean terrestrial ecosystems serve as reference laboratories for investigating 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 global change drivers and recent forest management practices; 4) To obtain more realistic information of global change impacts 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 rapidly developing regional and global scale models

to be more tightly connected with large-scale experiments, data networks and management practice; (3) more attention should be directed at drought-related forest decline and the current relevance of historical land use.

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 tropospheric ozone accumulation (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). Climate in MTEs shows 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 have 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 global change-induced extinction (Malcolm *et al.*, 2006). Given that socioeconomic 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 global change laboratory because of its wide range of socio-economic conditions and government policies (Brauch, 2003).

A consistent evaluation of 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 global change impacts, 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 of the Mediterranean Basin.

To do so, 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 upcoming years. 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 LA98 RESEARCH PRIORITIES

1. To understand future fire regimes and their effects.

1.1. Prediction of future fire regimes, involving interaction with global changes

Land use change may modify fire regime by altering fuel load and distribution or ignition patterns. In MTEs of Europe, massive abandonment of agricultural land has increased landscape homogeneity and crown fire potential, which in turn facilitates fire spread (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 at larger temporal scales (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 occur even 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 heterogeneization (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 temperature and reduced precipitation, particularly during summers (Giorgi & Lionello, 2008; Sillman *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 fuel quantity and climate-driven fuel moisture (Westerling *et al.*, 2006; Batllori *et al.*, 2013). Although lower air humidity and fuel water content are positively related to fire ignition and propagation, drier climate eventually leads to a decrease of 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.*, 2013). In addition, the combination of increased fire frequency and drought stress could enhance shrub encroachment (Mouillot *et al.*, 2002; Pausas, 1999) and thus reduce carbon storage.

1.2 Fire impacts

On landscape patterns. One main goal of extensively develop spatially explicit landscape models for MTEs is to assess forest vulnerability 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 to generate landscape projections and thus to predict future fire impacts (Syphard *et al.*, 2007; LePage *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 species and population regenerative traits remains a key approach to assess sensitivity of plant species to predicted fire regimes and to model changes in species distribution and community composition (Lloret *et al.*, 2005; Syphard & Franklin, 2010). Several studies have assessed short-term responses of MTEs vegetation (Keeley *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 plant-regeneration decline 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 MTE has also attracted attention (Rouget *et al.*, 2001; Pino *et al.*, 2013) and research in this area is revealing the vulnerability associated with fire regime properties such as fire frequency (Keeley & Brennan, 2012) and intensity (Franklin, 2010).

1.3 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 (Crecente-Campo *et al.*, 2009) or unplanned fire extent (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 regeneration (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, 2009), 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 soil properties (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 increasing plant and animal diversity (Castro *et al.*, 2012; Lee *et al.*, 2013; Marzano *et al.*, 2013), 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).

2. To study the effects of land use on biosphere-atmosphere interactions

2.1. 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 Southwest Australia, deforestation may lead to long term reductions in rain fall patterns (Pitman *et al.*, 2004). In summary, available models indicate that the climate of the 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).

2.2 Ecosystem physiology feedbacks on the climate system

CO_2-driven feedbacks on temperature through physiological responses of vegetation are negligible, as current evidence suggests (Keenan *et al.*, 2011; Cheaib *et al.*, 2012).

Climate change effects on soil respiration and the emission of other biogenic gases are still a major concern. Increases of drought intensity in the Mediterranean Basin have been associated to tree mortality episodes during recent decades (Martínez-Vilalta *et al.*, 2012; Sánchez-Salguero *et al.*, 2012). A recent study shows that, although current tree mortality is not affecting the carbon balance of Mediterranean forests, (1) increased warming and drought are likely to alter the capacity of these forests to absorb CO_2 and (2) 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 soil biological activity due to soil moisture reduction (Brown *et al.*, 1996), and this results in a decrease in soil nutrient availability and soil CO_2 emissions (Sardans *et al.*, 2008; Emmett *et al.*, 2004). 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 were not previously considered but are also crucial to 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).

2.3 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; Garcia-Hurtado *et al.*, 2013). These gases include principally carbon dioxide (CO_2), carbon monoxide (CO) and methane (CH_4), but also nitrogen oxides (NO_x and N_2O), ammonia (NH_3), sulfur dioxide (SO_2), light hydrocarbons, volatile and semi-volatile organic compounds, and particulate matter (10 to 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), have been used to feed several emission and air quality models (Lazaridis *et al.*, 2005; Paton-Walsh *et al.*, 2012).

2.4 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, 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, carbohydrate reserve depletion and stress-induced plant decline and mortality (e.g., Carnicer *et al.*, 2011; Misson *et al.*, 2011).

3. To study landscape effects on water availability and quality

3.1 Research at the patch scale

Leaf area index (LAI) & hydrological response. Land use changes, hydro-climatic conditions and fires are the main drivers of vegetation cover changes in MTEs and, therefore, exert great influence on these ecosystems' hydrological responses. Fires, for instance, influence understory 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 infiltrability (Llovet *et al.*, 2009).

Drought-induced vegetation dieback episodes may result in different ecohydrological effects compared to canopy cover changes (Adams *et al.*, 2012). For example, generalised 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*. 2012) and species-specific drought-tolerance traits (Jacobsen *et al.*, 2007; Matías *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 CO_2 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 CO_2 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 maximises 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).

3.2 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; Berberoglu & 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. Climate change effects 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 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 global change effects on water resources, soil erosion and vegetation productivity (e.g., D'Agostino *et al.*, 2010; Senatore *et al.*, 2011). However, there is a 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 land-cover changes, and hydrological model choices.

4. To investigate the effects of climate change on ecological diversity

4.1 Genetic diversity

La98 suggested increasing 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; Petit *et al.*, 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).

4.2 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 man-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 vegetation and soil microbial functional diversity (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; Selmants *et al.*, 2012; see also Prieur-Richard *et al.*, 2002 for contrasting results). Also, the effect of invasion-induced species impoverishment on ecosystem functioning is a contested issue (Vilà *et al.*, 2006; Ruwanza *et al.*, 2013).

Above-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 the Mediterranean region have related soil respiration and functioning to climate and land-use change (Emmett *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).

4.3 Landscape diversity

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 South Africa boost the development of studies addressing how global change drivers 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 to preserve both biodiversity and the ecosystem services it provides (Díaz *et al.*, 2013).

Landscape heterogeneity effects 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 aim 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

1. 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 the total studies), while studies within this region outside European countries (i.e., the Basin's southern rim) constitute just a small fraction (7.8% of the Mediterranean Basin studies).

2. 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 (i) topics listed in La98 which have been only partially addressed, (ii) new approaches to questions already suggested by La98, and (iii) 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 (Figure 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 global change drivers 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 aiming 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 analyzed by means of ecosystem modelling approaches and well-designed, critical experiments.

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

1) 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 (Loepfe *et al.*, 2012; Keeley et al. 2012). In addition, the disruption 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.

2) 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 wild-land and 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).

3) To address the interaction between global change drivers 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 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.

2.2. Monitoring and data assessment of ecosystem response to global change

4) To obtain more realistic information, at larger temporal and spatial scales, of global change impacts and ecosystem services to be used in models. La98 already 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 and longer temporal 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).

5) 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 the 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 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.

2.3. Managing ecosystems to enhance resilience

6) 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 climate change drivers. 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 they therefore may have low vegetation resilience (Lloret *et al.*, 2005). Other susceptible areas include those where land use transformation has led to high fuel load and, thus, 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.

7) To use the 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, ecosystem resilience 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., plant responses 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.

8) 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.

2.4. Embracing the link between ecosystem functions and services

9) 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 water scarcity.

10) 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 prioritised in order to fully understand how and why landscape processes influence the responses of MTEs to global change. Biodiversity will likely 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.

2.5. Scaling ecosystem dynamics in space and time under different scenarios

11) To refine predictive models by including interactions between global change drivers 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 already available socioeconomic scenarios into predictive models of land-use driven climatic change (Verburg *et al.*, 2010; Li *et al.*, 2011). 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 focussed on forests, shrublands and pastures, to simulate biosphere-atmosphere interactions in other key ecosystems such as croplands and urban environments should be considered.

12) To use manipulative, interdisciplinary and multi-scale 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 standardised protocols (e.g., see the review by Beier *et al.*, 2012, for precipitation manipulation experiments). Multifactorial (e.g., CO_2 x Warming x 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.

13) 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 fire occurrence.

3. 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 they 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 a 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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BIOSKETCH

E D-M is the research coordinator of the MONTES-Consolider project (http://www.creaf.uab.es/MONTES/), which aims to examine the relationship of Mediterranean woodlands with the components of global change, and to identify opportunities to modify these components through appropriate woodland management. The present paper synthesizes most of the work carried out preparing the background of that project and analysing its outputs. E D-M, J R, J M-V and P L conceived the ideas and principal scheme of the manuscript. E D-M led the writing, with all authors contributing their different areas of expertise.

Table 1. Overview of the degree of accomplishment of La98 priorities by the scientific community. It should be noted that, while practical for abstracting purposes, categorical "yes" or "no" are never applied to science. We recommend therefore consider "yes" as "great effort invested in this particular subject" and "no" as "although some attempts have been made to study the subject, it still needs further development".

<table>
<tr><th colspan="3">Previous priorities</th><th>Accomplishment quick view</th></tr>
<tr><td rowspan="9">1. Understand future fire regimes</td><td rowspan="3">1.1 Prediction</td><td>Effects of land use</td><td>Partially</td></tr>
<tr><td>Effects of climate</td><td>Yes</td></tr>
<tr><td>Effects of atmospheric composition</td><td>No</td></tr>
<tr><td rowspan="4">1.2 Impacts</td><td>On landscape</td><td>Yes</td></tr>
<tr><td>On vegetation</td><td>Partially</td></tr>
<tr><td>Combined with climate change</td><td>Yes</td></tr>
<tr><td>On ecosystem processes</td><td>Partially</td></tr>
<tr><td rowspan="2">1.3 Control</td><td>Prevention</td><td>Yes</td></tr>
<tr><td>Restoration</td><td>Partially</td></tr>
<tr><td rowspan="5">2. Study biosphere-atmosphere interactions</td><td colspan="2">2.1 Land use and climate</td><td>Partially</td></tr>
<tr><td rowspan="2">2.2 Physiology and climate</td><td>CO_2 & temperature</td><td>Partially</td></tr>
<tr><td>Temperature & biogenic emissions</td><td>Partially</td></tr>
<tr><td colspan="2">2.3 Fire emissions</td><td>Yes</td></tr>
<tr><td colspan="2">2.4 Coupled models</td><td>Partially</td></tr>
<tr><td rowspan="8">3. Landscape effects on water</td><td rowspan="4">3.1 Patch scale</td><td>LAI & hydrological response</td><td>Yes</td></tr>
<tr><td>Hydrological equilibrium</td><td>Partially</td></tr>
<tr><td>Temporal variability</td><td>Partially</td></tr>
<tr><td>Simulation models</td><td>No</td></tr>
<tr><td rowspan="4">3.2 Landscape scale</td><td>Mapping</td><td>Yes</td></tr>
<tr><td>Scales and emergent properties</td><td>Yes</td></tr>
<tr><td>Landscape change</td><td>Yes</td></tr>
<tr><td>Simulation models</td><td>Partially</td></tr>
<tr><td rowspan="3">4. Changes in ecological diversity</td><td colspan="2">4.1 Genetic</td><td>Partially</td></tr>
<tr><td colspan="2">4.2 Species and functional</td><td>Partially</td></tr>
<tr><td colspan="2">4.3 Landscape</td><td>Partially</td></tr>
</table>

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

New Priorities
Effects of the interactions between global change drivers on ecosystem functioning
1 To establish the role of the landscape mosaic on fire-spread
2 To further research the combined effect of different drivers on biological invasions and pest expansion
3 To address the interaction between global change drivers and recent forest management practices
Monitoring and data assessment of ecosystem response to global change
4 To obtain more realistic information, at larger temporal and spatial scales, of global change impacts and ecosystem services to be used in models
5 To assess forest mortality events associated with climatic extremes (particularly drought)
Managing ecosystems to enhance resilience
6 To focus global change research on identifying and managing vulnerable areas
7 To use the functional and life-history traits concepts to study resilience and community assembly after disturbance
8 To promote cross-disciplinary research to study the relationship between genotypic and phenotypic diversity as a source of forest resilience
Embracing the link between ecosystem functions and services
9 To understand how forest management affects the balance between C storage and water resources at large spatial and temporal scales
10 To analyse the interplay between landscape-scale processes and biodiversity conservation along wide gradients of landscape complexity
Scaling ecosystem dynamics in space and time under different scenarios
11 To refine predictive models by including interactions between global change drivers and socio-economic contexts
12 To use manipulative, interdisciplinary and multi-scale experiments to understand forest-atmosphere feedbacks
13 To improve the representation of key mechanisms linking plant hydraulics with landscape hydrology

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 atmospher* 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.

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 atmospher* OR plant OR vegetation OR "ecosystem processes") NOT (marine sea)*

For biosphere-atmosphere interactions: *(Mediterranean forest atmospher* 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 atmospher* 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 atmospher* OR soil OR "ecosystem processes" OR "ecosystem function*") NOT (marine sea)*

Figure 3. Framework for global change research priorities in Mediterranean terrestrial ecosystems. The framework is structured according to different causal and observational pathways, as follows: 1) Effects of the interactions between global change drivers on ecosystem functioning. 2) Monitoring and data assessment of ecosystem response to global change. 3) Managing ecosystems to enhance resilience. 4) Embracing the link between ecosystem functions and services. 5) Scaling ecosystem dynamics in space and time under different scenarios.

Figure 1

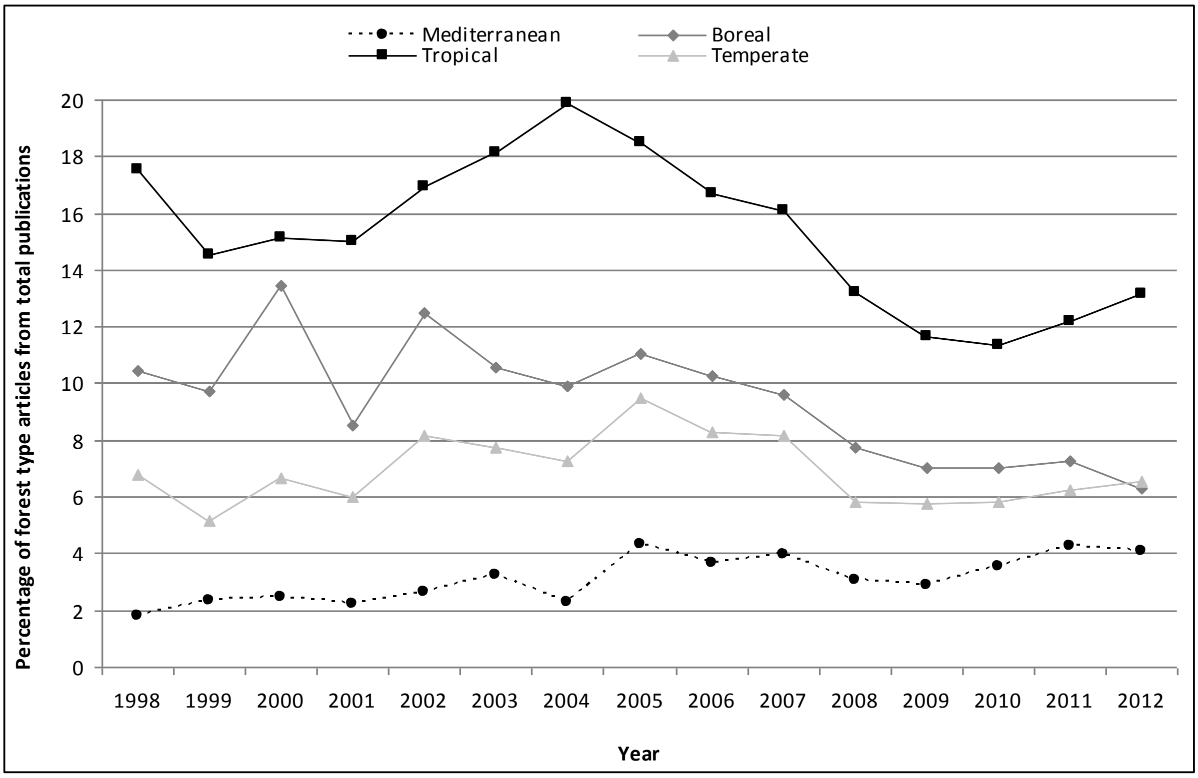
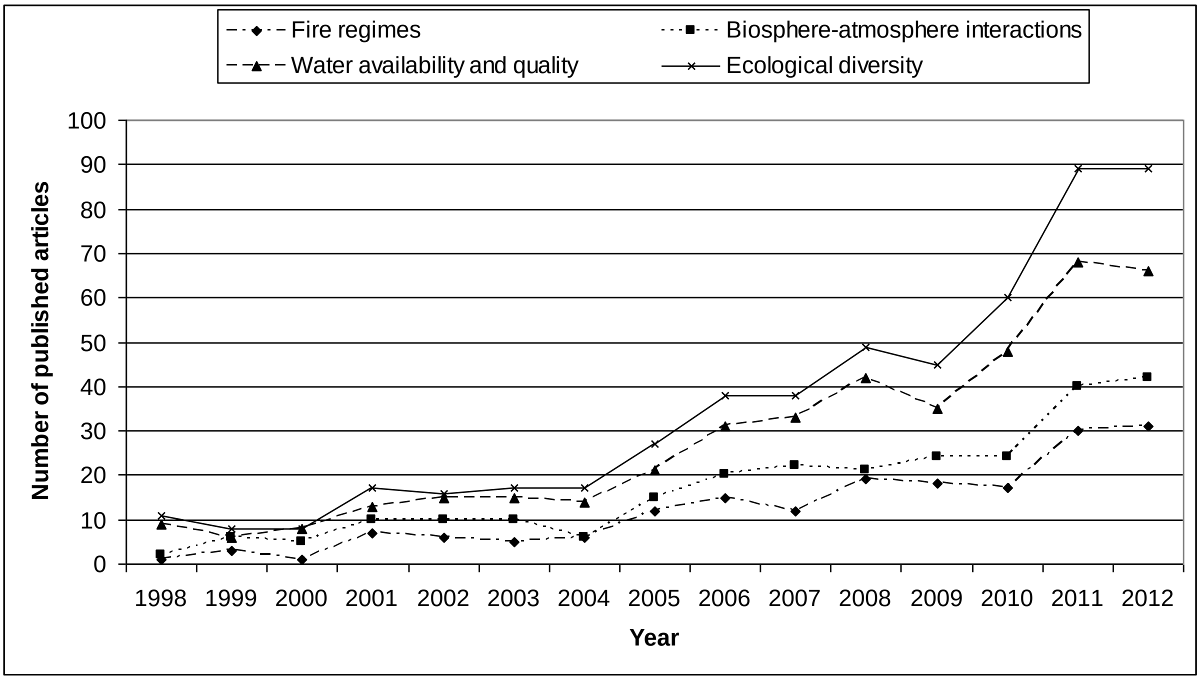
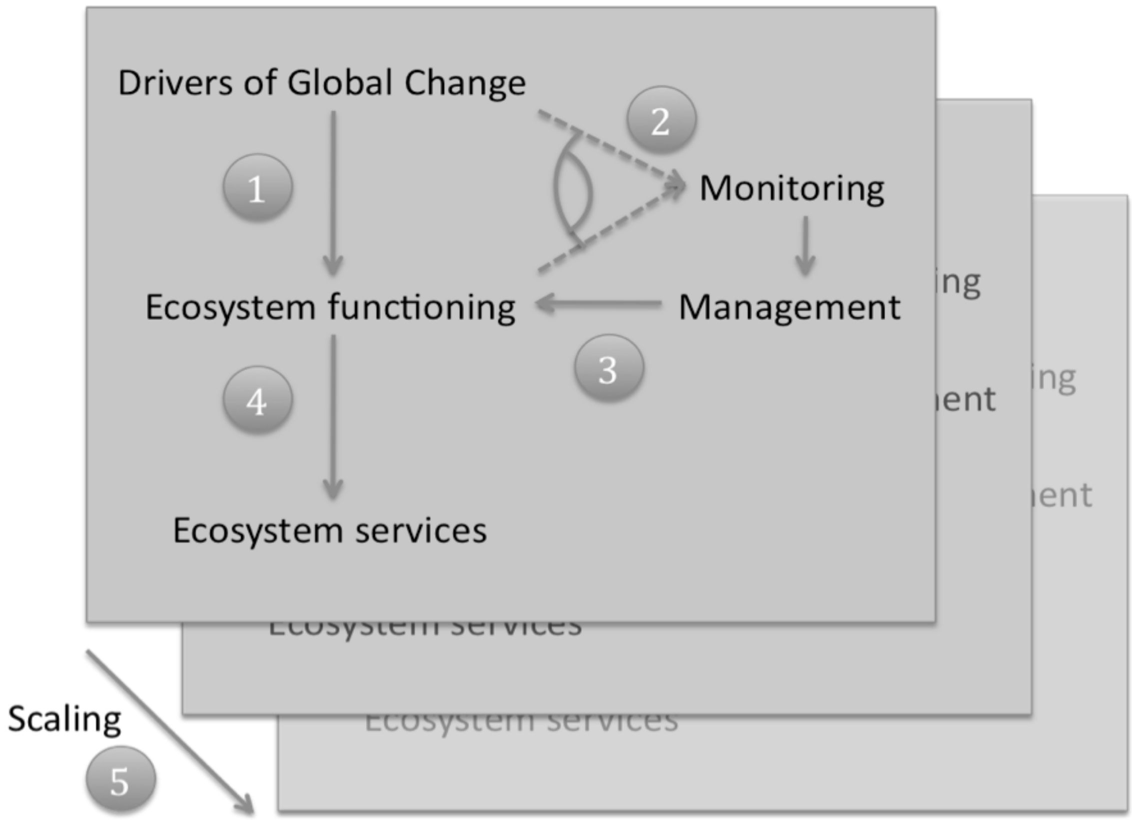

Mediterranean
Boreal
Tropical
Temperate
Percentage of forest type articles from total publications
0
2
4
6
8
10
12
14
16
18
20
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
Year

Figure 2



Fire regimes
Biosphere-atmosphere interactions
Water availability and quality
Ecological diversity
Number of published articles
100
90
80
70
60
50
40
30
20
10
0
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
Year

Figure 3



Drivers of Global Change
1
2
Monitoring
Ecosystem functioning
Management
3
4
Ecosystem services
Scaling
5