



Invited review article

A review of the combination among global change factors in forests, shrublands and pastures of the Mediterranean Region: Beyond drought effects



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ABSTRACT

Climate change, alteration of atmospheric composition, land abandonment in some areas and land use intensification in others, wildfires and biological invasions threaten forests, shrublands and pastures all over the world. However, the impacts of the combinations between global change factors are not well understood despite its pressing importance. Here we posit that reviewing global change factors combination in an exemplary region can highlight the necessary aspects in order to better understand the challenges we face, warning about the consequences, and showing the challenges ahead of us. The forests, shrublands and pastures of the Mediterranean Basin are an ideal scenario for the study of these combinations due to its spatial and temporal heterogeneity, increasing and diverse human population and the historical legacy of land use transformations. The combination of multiple global change factors in the Basin shows different ecological effects. Some interactions alter the effects of a single factor, as drought enhances or decreases the effects of atmospheric components on plant ecophysiology. Several interactions generate new impacts: drought and land use changes, among others, alter water resources and lead to land degradation, vegetation regeneration decline, and expansion of forest diseases. Finally, different factors can occur alone or simultaneously leading to further increases in the risk of fires and biological invasions. The transitional nature of the Basin between temperate and arid climates involves a risk of irreversible ecosystem change towards more arid states. However, combinations between factors lead to unpredictable ecosystem alteration that goes beyond the particular consequences of drought. Complex global change scenarios should be studied in the Mediterranean and other regions of the world, including interregional studies. Here we show the inherent uncertainty of this complexity, which should be included in any management strategy.

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1. Introduction

The Earth system is subject to a wide range of new planetary-forces that are originated in human activities, ranging from the emission of greenhouse gases to the transformation of landscapes and the loss of biota. The magnitude and rates of human-induced changes to the global environment – a phenomenon known as global change – has accelerated since the second half of the last century (Steffen et al., 2004; Vitousek, 1994). There is general agreement about the factors of global environmental change and their ecological consequences on terrestrial ecosystems. They imply extreme climatic events, atmospheric chemical pollution, land use modifications, frequent fires and biological invasions, among others (Lindner et al., 2010; Sala et al., 2000). However, uncertainty prevails in our capacity to understand and predict the impact of their combination (Langley and Hungate, 2014; Scherber, 2015). Therefore, there is a growing interest in understanding not only the factors of global change and derived disturbances, but also the combinations among them (Moreira et al., 2011; Rosenblatt and Schmitz, 2014).

Having a good knowledge of the factors of global environmental change and their interactions is crucial to understand local to global implications, anticipate effects, prepare for changes and reduce the risks of decision-making in a changing environment (Sternberg and Yakir, 2015). This is especially certain in areas where many factors are involved and intermingled, as in the Mediterranean Basin (Mooney et al., 2001; Sala et al., 2000). The heterogeneity and transitional nature of the Mediterranean biogeography and the long history of human alterations result in a spatially-structured landscape mosaic (Blondel et al., 2010; Scarascia-Mugnozza et al., 2000; Woodward, 2009). All these aspects combined have contributed to sustain a rich biota, which make the Mediterranean Basin a global biodiversity hotspot (Myers et al., 2000), and to provide a scenario where historical legacies may have a greater effect on present ecological processes than current factors (Dambrine et al., 2007). However, future scenarios indicate that global change in the Mediterranean Basin will likely involve a great risk of biodiversity loss (Malcolm et al., 2006; Sala et al., 2000) and a decline of other ecosystem services, such as water and food resources, and carbon uptake (MEA, 2005; Schröter et al., 2005).

Numerous studies have examined the factors of global change on terrestrial ecosystems of the highly diverse Mediterranean Basin (as it could be appreciated in the following review), but a systematic revision of the effects of all factors of global change and their combination is lacking. Here we first review the current and future impacts of the main global change factors (drought and other climatic events, alteration of atmospheric composition, land use intensification and abandonment, wildfires and biological invasions) on forests, shrublands and pastures of the Mediterranean Basin (although the present work is focussed in

terrestrial ecosystems for practical reasons, we highly recommend Coll et al., 2010, as start point to a similar review in the Mediterranean Sea) to then provide an assessment of the main types of combinations among these factors. Our principal objectives are to show the impending challenges of global change in the Mediterranean Basin and to warn about the potential consequences of different combinations of global change factors.

2. Main global change factors in the Mediterranean Basin

2.1. Drought and other climatic events

Current aridity levels in the Mediterranean Basin appear to be unprecedented in the last 500 years (Nicault et al., 2008). Most climate models forecast substantial increases in temperature and declines in precipitation, which will increase heat stress and largely reduce water availability in the Basin (Gao and Giorgi, 2008; Hoerling et al., 2011). Models also predict increases in climatic variability, with more extreme temperature and precipitation events (Gao et al., 2006; Solomon et al., 2007).

Recent changes in precipitation have already been related to field data on tree growth decreases (Sarris et al., 2007), increased growth variability (Vieira et al., 2010) and crown defoliation on Mediterranean forests, in contrast to northern Europe (Carnicer et al., 2011). Modelling exercises also project important changes in forest growth, although they also highlight the complexity of the interactions involved (Fyllas et al., 2010; Sabaté et al., 2002). Several drought simulation experiments have shown that water (Limousin et al., 2009) and carbon fluxes (Matteucci et al., 2014; Misson et al., 2010) are highly sensitive to reductions in precipitation. At the same time, phenology (Klein et al., 2013; Morin et al., 2010), nutrient allocation and accumulation (Simoes et al., 2008) and key soil processes (e.g., Curiel-Yuste et al., 2011; Sherman et al., 2012) have been shown to be affected by rainfall and temperature manipulations. Described effects on plant communities should affect faunal communities, as in the case of seed feeders (e.g., Sánchez-Humanes and Espelta, 2011) and fauna affected by habitat loss (e.g., Scalercio, 2009). The effects of other climate extremes, such as cold temperatures, have been less studied, although they may also be important (Valladares et al., 2008).

Although evidence from both observational (e.g., Kazakis et al., 2007; Vennetier and Ripert, 2009) and experimental studies (e.g., De Dato et al., 2008; Matías et al., 2012) suggests that changes in species composition can occur, studying these changes is difficult because they require long-term monitoring. At the same time, some reports highlight the importance of intraspecific variability, phenotypic plasticity and local adaptation (Poirier et al., 2012; Ramírez-Valiente et al., 2010), among a plethora of stabilizing processes that may prevent

vegetation shifts from eventually occurring (cf. Lloret et al., 2012). Drought has also been shown to affect the composition of soil fauna (e.g., Legakis and Adamopoulou, 2005; Tsiapoulou et al., 2005) and butterfly communities (Parmesan et al., 1999).

2.2. Alteration of atmospheric composition

The orography of the Mediterranean Basin provokes that in summer a stagnant layer of air acts as a reservoir where most pollutants are transformed. Moreover, emissions in the Basin could be driven directly into the mid and upper troposphere, being transported toward the region (Moreno and Fellous, 1997). The impact of atmospheric composition changes in Mediterranean Basin forests has scarcely been studied, despite the fact that these forests are considered a significant carbon sink (Valentini et al., 2000).

Although short-term carbon dioxide (CO₂)-enrichment experiments in temperate forests show an increase in net primary production (Norby et al., 2005), several tree-ring studies have reported a general decrease in tree growth in the Mediterranean Basin (Nicault et al., 2008). The controversy may be due to the constraints imposed by water or nutrient scarcity on plant growth, affecting the overall impact of increased CO₂ effects (Leonardi et al., 2012; Zhao and Running, 2010). In addition, photosynthetic acclimation to high CO₂ cannot be ruled out (Peñuelas et al., 2011).

In the Western Mediterranean Basin, herbaria analysis shows a decrease in nitrogen (N) concentration in leaf tissues throughout the 20th century (Peñuelas and Estiarte, 1997). The increase in N deposition during recent decades in Europe (Galloway et al., 2008), can, at least partially, offset N limitation and sustain the growth promoted by the CO₂ fertilization (Milne and van Oijen, 2005). Nevertheless, other nutrients, such as phosphorus (P), will remain unaltered and immobilized in biomass and soils, limiting further plant growth and generating a significant imbalance in the N:P ratio (Peñuelas et al., 2012). Furthermore, N deposition causes changes in soil quality, plant physiology and community composition, and has been recognized as an important driver in biodiversity loss (Dias et al., 2011; Ochoa-Hueso et al., 2011). Total annual estimates of N deposition in the Mediterranean Basin are higher than those promoting adverse effects (Im et al., 2013).

Climatic conditions in the Mediterranean Basin favour Tropospheric ozone (O₃) formation and persistence (Cristofanelli and Bonasoni, 2009; Hodnebrog et al., 2012). Mediterranean woody vegetation seems to be in general tolerant to O₃ adverse effects due to its sclerophyllous leaf structure, low gas exchange rates, BVOCs emissions and active antioxidant defences (Paoletti, 2006). However, leaf senescence, increases in leaf mass per area and spongy parenchyma thickness, decreases in photochemical maximal efficiency and in the chlorophyll content, and biomass reduction caused by O₃ have been described in some Mediterranean forest species (Paoletti, 2006; Ribas et al., 2005). Interactive effects between CO₂ and O₃ are very variable as they depend on pollutant concentrations, species sensitivity and interactions with other stresses such as plant competition, drought and nutrient availability (Karnosky et al., 2007; Wittig et al., 2009).

The Mediterranean Basin is one of the hotspots of biogenic volatile organic compounds (BVOC) emissions in Europe (Steinbrecher et al., 2009). BVOCs can act as a chemical sink for O₃ at the leaf level, protecting vegetation from its negative effects (Fares et al., 2008; Loreto et al., 2004), or enhancing O₃ production in the atmosphere through photochemical reactions in the presence of N oxides (Peñuelas and Staudt, 2010). Increasing emissions of BVOCs have, in any case, ecological impacts on Mediterranean life, given their key role in plant defence and communication with other organisms (Peñuelas and Staudt, 2010). Rising temperatures increase BVOC emission rates by enhancing their synthesis and by facilitating vaporization (Peñuelas and Llusà, 2001), which likely results in an increasing feedback to warming. BVOC emission rates present a broad range among plant

species and therefore will be largely affected by changes in vegetation biomass, vegetation types and land uses.

2.3. Land use intensification and abandonment

In the Mediterranean Basin region, contrasting patterns of recent land use changes appear (Petit et al., 2001) with both abandonment and intensification co-occurring in the northern areas, while deforestation and intense use of forest resources is still dominant in the southern rim (Grove and Rackham, 2001) (Fig. 1).

In the southern part of the Mediterranean Basin, the increasing rates of deforestation threaten the scarce forest resources and ecological services of the region (Grove and Rackham, 2001). Even if the amount of deforestation in the southern Mediterranean in the 1990s was low compared to Latin America or Tropical Asia, the rate of increase compared to the '80s was four times higher (Hansen and DeFries, 2004). Consequences of deforestation in this region go beyond ecological effects, implying whole ecosystem change (Zaimeche, 1994).

In the northern Mediterranean Basin, metropolitan coastal landscapes are one of the most altered in the world (Hepcan et al., 2013; Myers et al., 2000). Simultaneously, forests around northern Mediterranean cities are suffering increasing ecological impact due to intense use for leisure and progressive forest fragmentation resulting from urban sprawl (Jomaa et al., 2008; Salvati et al., 2014). However, land use intensification of lowland regions is encompassed with afforestation of low productive uplands (Falcucci et al., 2007; Roura-Pascual et al., 2005) due to crop and pasture abandonment (Debussche et al., 1999; Tomaz et al., 2013), and also to deliberate reforestation (Hansen and DeFries, 2004). These changes are linked to profound socioeconomic shifts that led to a rural exodus and a decrease in many of the traditional uses of forests (Grove and Rackham, 2001; Hill et al., 2008). As a result, the northern Mediterranean forest landscapes have undergone large-scale changes, not only in their general extent, but also in terms of vegetation structure, composition and dynamics (Roura-Pascual et al., 2005). Novel forests composed of pioneer and introduced species, and with relatively unknown structural and functional attributes, have proliferated (Eldridge et al., 2011; Hobbs et al., 2006). These forests are becoming essential for the restoration of landscape corridors between what remains of the historical forests and for the recovery of forest species (Sirami et al., 2008). However, forest recovery could be heavily influenced by the long-term effects of past land uses, which might determine soil fertility, or by landscape impacts of current fire disturbance regimes (Puerta-Piñero et al., 2012). In fact, past land uses could be a key factor altering the effects of current global changes and thus differentiating the Basin from other Mediterranean regions of the world.

2.4. Wild fires

Wild fires of the Mediterranean Basin represent a dramatic hazard due to the dense human population of the region (Dwyer et al., 2000). Moreover, historical alteration of fire patterns in the Basin has modified vegetation resilience, differentiating it from the flora of other Mediterranean regions (Pausas, 1999). Although in recent decades there has been a steady increase in the resources invested in fire prevention and suppression, the number and extent of wildfires have increased over the same period (Carmo et al., 2011; Piñol et al., 2005). Climate has been the main driver of global biomass burning for the past two millennia (Marlon et al., 2009). In the Mediterranean region, predictions indicate a general rise in fire risk due to current warming (Moriondo et al., 2006).

Changes in the fire regime modify Mediterranean communities and their resilience to fire (Paula et al., 2009; Tessler et al., 2014) in two ways. First, non-resilient tree species dominant in sub-Mediterranean regions (Lloret et al., 2005) show very low regeneration after large wildfires and are replaced by oak forests, shrublands or grasslands



Fig. 1. Results for the Mediterranean Basin from time-series analysis of Landsat 7 ETM+ images in characterizing global forest extent and change from 2000 through 2012 (Hansen et al., 2013). Dark grey: forest cover in 2000; black: gain forest from 2000 to 2012; white: forest lost from 2000 to 2012. It is difficult to appreciate forest gain and losses due to the scattered nature of the process in the Region although lower scales could be accessed in the original webpage: <http://earthenginepartners.appspot.com/science-2013-global-forest>.

(Bendel et al., 2006; Retana et al., 2002). Second, the higher fire frequency and intensity in fire-prone areas might result in: (i) a decrease in the resprouting ability of plants and reduced resilience at the landscape level of forests dominated by resprouters (Díaz-Delgado et al., 2002; Marzano et al., 2012); (ii) a failure of obligate seeders regeneration when time intervals between fires are shorter than the time required for a sufficient seed bank to build up ('immaturity risk', *sensu* Zedler, 1995).

Additionally, wildfire events have major influences on the release of N and other air pollutants and on the water quality of burned catchments (Johnson et al., 2007). Moreover, increases in fire recurrence can affect ecosystem processes including long-term reductions in primary production (Delitti et al., 2005; Dury et al., 2011) and increases in erosion (Thornes, 2009) as a consequence of a slow recovery of the soil organic layers (Shakesby, 2011) and changes in microbial properties (Guénon et al., 2011). These changes frequently lead to changes in plant and animal communities favoured by open areas (e.g., Broza and Izhaki, 1997; Fattorini, 2010; Kiss et al., 2004).

2.5. Biological invasions

Patterns of recent invasions (i.e. neophytes) among habitat types seem to be quite consistent across Europe (Chytrý et al., 2008) and therefore across the Mediterranean Basin. The invasion patterns differ considerably amongst taxonomy groups, although they tend to mostly occupy anthropogenic habitats, while natural and semi-natural woody habitats are relatively resistant to invasions (Arianoutsou et al., 2010; DAISIE, 2009). As in other regions worldwide, the increase in the establishment of non-native species in the Mediterranean Basin will continue due to the expanding transport of goods and people. Currently, the information available on non-native species in the Basin is not complete and the number of non-native species across taxonomic groups is underestimated (DAISIE, 2009). Detailed information about their distribution and ecological impacts is necessary to determine exactly the current status of biological invasions in the Mediterranean region.

We are starting to identify the ecological and economic consequences of invasions in terrestrial ecosystems of the Mediterranean Basin. Non-native plants compete with native species, decreasing local diversity and changing community composition (Vilà et al., 2006). Changes in ecosystem functioning have been less explored, but they include alterations in decomposition rates (De Marco et al., 2013) and changes in soil C and N pools (Vilà et al., 2006). Even though the number of successful invaders seems to be higher in plants, the consequences caused by animal invasions are not of a lower magnitude. The presence of non-native vertebrates poses severe threats to native biodiversity through competition for resources, predation and hybridization with native species, as well as economic impacts (DAISIE, 2009). Most non-native terrestrial invertebrate species established in Europe are known

to be potential pests for agriculture and forestry products, while around 7% affect human and animal health (DAISIE, 2009). The ecological consequences of non-native invertebrates have received less attention. Certain ants, such as *Linepithema humile* or *Wasmannia auropunctata*, are known to have a dramatic effect on native invertebrate communities (Blight et al., 2014; Vonshak et al., 2010).

3. The combinations among factors alter the impacts of global change in the Mediterranean Basin

By addressing the principal global change factors affecting the Mediterranean Basin separately, we have already covered how different pollutants can interact and how their fluxes depend on forest cover, while current increases in fire frequency imply further atmospheric alterations. In order to disentangle the possible effects of global change combinations, we have crossed the different factors among them (Table 1), and different kinds of combinations have emerged (Fig. 2). In the following sections we review the potential combined effects of the various processes identified in the Region (following the numbering in Table 1), boosted in many cases by the effects of drought. First, one factor can alter the effect of another factor: for instance, the effects of atmospheric chemical compounds on plant ecophysiology can be enhanced or decreased by drought (Fig. 2a; Section 3.1). Second, several interactions among factors trigger new impacts, such as the alteration of water resources, land degradation, regeneration decline, and expansion of forest diseases (Fig. 2b; Sections 3.2, 3.3, 3.4, 3.5). Finally, different factors, alone or simultaneously, can enhance the risk of other factors, as in the case of wildfire or invasion risk (Fig. 2c; Sections 3.6, 3.7).

3.1. Modification of plant ecophysiology by interactions between atmospheric alteration and drought

Water availability is the main factor limiting biological activity in Mediterranean ecosystems and, thus, modulating the response to changes in atmospheric chemistry. The direct effects of higher atmospheric CO₂ include stomatal closure and enhancement of plant water-use efficiency (WUE). WUE can alleviate the effects of drought on plant physiology and slow down the depletion of soil water during drought progression (Morgan et al., 2004) (Fig. 2a). Observations of naturally grown Mediterranean forests show a clear increase in WUE during the 20th century, suggesting that the unobserved CO₂-fertilization benefits in growth have likely been counteracted by drought (Peñuelas et al., 2011) (Fig. 2a).

The reduction in plant growth caused by drought might be due to less N absorption. In this sense, foliar N concentration has been found to have a positive correlation with precipitation (Nahm et al., 2006). Also, drought affects soil microbial activity, leading to a reduction in N mineralization and thus in absorption of deposited N (Rutigliano

Table 1
Principal effects derived from the combinations between global change factors in the Mediterranean Basin region. Shaded cells correspond to repeated combinations and combinations of the same factor (including land-use intensification and land abandonment as the two opposite means of land-use change). As different pollutants could interact among them, these same factor interactions are explained in the first section of the manuscript together with other atmospheric chemical alterations. Numbered combinations are explained in the second section of the manuscript.

	Drought and other climatic events	Alteration of atmospheric composition	Land use intensification	Land abandonment	Wild fires
Alteration of atmospheric composition	Atmospheric alteration increase 1 Modification of plant ecophysiology	Interactions among pollutants			
Land use intensification	2 Alteration of water resources 3 Land degradation 4 Regeneration decline 5 Disease expansion 6 Increase of fire risk	Atmospheric alteration increase			
Land abandonment	2 Alteration of water resources 3 Land degradation	Atmospheric alteration increase			
Wild fires	3 Land degradation 4 Regeneration decline 6 Increase of fire risk	Atmospheric alteration increase	6 Increase of fire risk	6 Increase of fire risk	
Biological invasions	7 Increase of invasion risk	7 Increase of invasion risk	7 Increase of invasion risk	7 Increase of invasion risk	7 Increase of invasion risk

et al., 2009). All these factors can increase soil N accumulation in oxidized forms and result in greater N losses through leaching after torrential storms (Avila et al., 2010; MacDonald et al., 2002).

Depending on the level of stress, drought results in both decreases and increases in BVOC emission rates (Peñuelas and Staudt, 2010). Mild heat stress may increase BVOC emissions by making the isoprenoid synthesis pathway more competitive than carbon fixation (Niinemets, 2010). On the contrary, severe drought may greatly decrease emissions because of detrimental effects on protein levels and substrate supplies (Fortunati et al., 2008).

Drought stress protects plants against O₃ by inducing stomatal closure and pollutant uptake. Indeed, high summer O₃ levels in the Mediterranean Basin occur when the seasonal drought is more intense and plants are less physiologically active (Gerosa et al., 2009; Safieddine et al., 2014). However, the additive effects of drought and O₃ have been described mainly through an O₃-induced loss of stomatal regulation favouring drought stress (McLaughlin et al., 2007). Ambient O₃ concentrations can thus increase water use by forest trees, contributing to reduce water availability and thus amplifying the effects of climate change (Alonso et al., 2014).

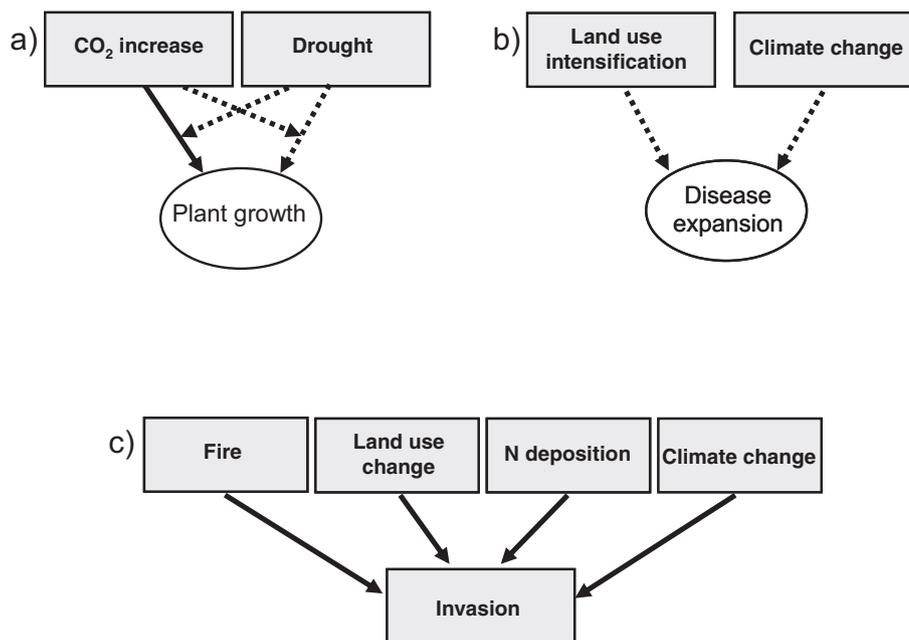


Fig. 2. Types of combination among global change factors. Solid arrows represent positive effects while shaded arrows represent negative effects. Some interactions alter the effects of a single factor (a), as for example CO₂ increase affects drought effects on plant growth through stomatal closure. New possible impacts can be caused by the interaction (b), such as the expansion of forest pests caused by the alteration of forest structure and climate warming. Finally, other combinations cause an increase in the risk of one of the factors implied (c) such as fire, land-use change, N deposition and climate change effects on invasion.

3.2. Alteration of water resources by interactions between land use change and climate change

Water resources are very important in the densely populated and water-limited Mediterranean Basin. The future of water resources in catchments must be assessed not only in view of climate-forcing predictions, but also considering land-cover changes (Bates et al., 2008), especially woody plant encroachment in mountain areas. A large set of catchment experiments demonstrates that changes in land cover from grassed to forested areas involve a reduction in runoff (i.e. Bosch and Hewlett, 1982; Brown et al., 2005). However, some debate exists concerning larger catchments, where the role of forest cover is not always clearly identifiable in the flow records (Andréassian, 2004; Oudin et al., 2008).

Historical records of large catchments studied in southern Europe show decreasing annual trends and changes in flow regimes (e.g. Dahmani and Meddi, 2009; Lespinas et al., 2010). These trends are attributed to climatic shifts, increasing water consumption and encroachment of forest cover due to land abandonment (García-Ruiz et al., 2011; Otero et al., 2011). There seems to be a forest expansion threshold over which the effect of forest cover on river discharges can be detected. In catchments with large and rapid forest expansion, the effects of forest encroachment in the reduction of river discharges are well documented (e.g., Gallart et al., 2011; Niedda et al., 2014). However, for other catchments, the effects of forest advance on runoff are not so clear, as for example in some mountain catchments in southern France or in catchments distributed from South to Central Italy (e.g. Lespinas et al., 2010; Preti et al., 2011).

Considering only climate predictions and water consumption scenarios, the frequency of floods is not expected to increase in Mediterranean Europe, except due to extreme climatic events (Lehner et al., 2006). However, the influence of land-cover changes on floods, even at the small catchment scale, is particularly difficult to assess in Mediterranean catchments (Wittenberg et al., 2007). Among other factors, less is known about the rainfall partitioning process in typical open woodlands, savannah-type ecosystems, isolated trees and shrub formations than in closed forests (Latron et al., 2009; Llorens and Domingo, 2007).

3.3. Land degradation favoured by interactions between either land use change or fire and climatic events

The loss of ecological and economical soil productivity is directly controlled by vegetation cover, but can be aggravated by dry and variable climates (Imeson and Emmer, 1995; Kosmas et al., 2002). Mediterranean ecosystems couple extreme climatic events with materials that are highly susceptible to erosion (Poesen and Hooke, 1997). Current predictions are that climate change, in combination with farmland abandonment, unsuitable plantations, deforestation, overgrazing and fire, can overload the resilience of natural ecosystem to erosion (Thornes, 2009).

While erosion is the initial process leading to soil and productivity losses, desertification is the irreversible positive feedback loop of over-exploitation favoured in certain dryland systems (Kéfi et al., 2007; Puigdefábregas, 1995). There is a threshold over which the effects of erosion are irreversible and the ecosystem cannot recover original biomass levels (Puigdefábregas and Mendizabal, 1998). Desertification can be intensified and extended by prolonged droughts (Kosmas et al., 2002), but also by potential human demographic explosions in south-eastern Mediterranean regions (Le Houérou, 1992; Naveh, 2007).

Among the aforementioned factors, farmland abandonment increases the risk of gully development when artificial systems are no longer maintained (Koulouri and Giourga, 2007; Lesschen et al., 2007). The reduction in forest cover by clear-felling or fire increases water runoff and sediment yields, especially when the organic layer is extensively affected (Imeson and Emmer, 1995; Thornes, 2009). Vegetation-cover

loss caused by overgrazing also results in soil compaction, gully development and ultimately erosion hotspots (Thornes, 2005). Overgrazing can result in greater impacts as climate become drier, combining both disturbances in a negative feedback cycle (Köchy et al., 2008).

Drought induces impacts on vegetation that may result in erosion intensification (Thornes and Brandt, 1994). The most direct effect of climate change may be increased rainfall erosivity in the Mediterranean Basin, where the total rainfall will decrease but rainfall intensity during certain events will increase (Nunes and Nearing, 2011). Aridity can also affect soil biota negatively and slow down soil decomposition processes, decreasing the content of organic matter (Curiel-Yuste et al., 2011; Imeson and Emmer, 1995). Appropriate vegetation recovery after abandonment, disturbance or management should prevent soil and nutrient loss (Duran Zuazo and Rodríguez Pleguezuelo, 2008; Fox et al., 2006).

3.4. Regeneration decline promoted by interactions between either land intensification or fire and drought

Forest resilience is based on both the forest capacity to recover the pre-disturbance state and the rate of plant growth. In this context, an increase in drought events might cause adverse impacts on plant regeneration. Recurrent droughts affect woody species performance differently, depending on species or functional type-specific sensitivity, leading to changes in species composition and structure (De Dato et al., 2008; Galiano et al., 2010).

Herbivory can inhibit or exacerbate plant responses to climate-change conditions (Post and Pedersen, 2008; Speed et al., 2010). In recent decades, the populations of wild ungulates have increased beyond carrying capacities in the Mediterranean Basin, particularly in protected areas and mountain regions (Noy-Meir et al., 1989). Where animals are selective consumers of saplings and resprouts (such as goats), overgrazing severely affects forest regeneration. This effect is aggravated in Mediterranean areas, where species such as *Pinus sylvestris* present low sapling growth rates in comparison with those of northern latitudes due to water limitation (Danell et al., 2003; Edenius et al., 1995). Furthermore, browsing on saplings and resprouts in the Mediterranean Basin is more severe in summer and dry years, when other food resources for ungulates are less abundant, diminishing the time for recovery from damage (Herrero et al., 2012; Hester et al., 2004).

Fragmentation can also lead to regeneration decline in combination with drought. Smaller patches not necessarily affect plant growth, which seems to be related to water stress, but definitely affect reproduction (Matesanz et al., 2009). Considering the functionality of the plant-soil-microbial system, small patches could even ameliorate the negative impacts of drought through increasing the capacity of the soil to retain water due to higher soil organic matter content than large patches. However, expected climatic changes in the already water-limited Mediterranean Basin will overcome these processes (Flores-Rentería et al., 2015).

Post-fire forest regeneration depends on the identity and the regeneration capabilities of dominant species (Buhk et al., 2007; Seligman and Henkin, 2000), which drives the regeneration pattern of the whole plant community (Montès et al., 2004). First, in forests dominated by seeders (such as several serotinous pine species, including *P. halepensis*, *P. pinaster* and *P. brutia*), post-fire regeneration can be affected by drought since seed germination requires imbibition of the embryo after the first autumn rains (Tsitsoni, 1997). Higher aridity may lead to a reduction in reproduction effort and diminished seed bank viability (Espelta et al., 2011; Keeley et al., 2005). Second, post-fire recovery of non-serotinous pines such as *P. sylvestris* and *P. nigra* depends mainly on seed dispersal from adjacent unburned patches. Therefore, frequent and intense fires might favour species shifts (Retana et al., 2002). Finally, the resprouting ability of broadleaved forests can also decrease due to long drought periods and low soil moisture (Castellari and Artale, 2010).

3.5. Disease expansions induced by interactions between land use change and climate change

There is common agreement that climate change will favour forest pest species, since survival of many arthropods depends on low temperature thresholds (Williams and Liebhold, 1995), while fungi or pathogens are also benefited by dry conditions (Ayres and Lombardero, 2000; Jactel et al., 2012). However, the role of forest structure and composition in disease expansion is more controversial (Fig. 2b).

A Mediterranean example of insect pest is the pine processionary moth (PPM) (*Thaumetopoea pityocampa/T. wilkinsoni* complex, Notodontidae), a well-known case due to its ecological, economic and medical importance (Erkan, 2011; Gatto et al., 2009; Vega et al., 2000). European cold-temperate species like the oak moth (*T. processionea*) and the summer pine processionary moth (*T. pinivora*) have increased the intensity of their outbreaks during the last two or three decades (Aimi et al., 2008; Groenen and Meurisse, 2012). Meanwhile, the PPM has expanded in altitude (Battisti et al., 2005; Hódar and Zamora, 2004) and latitude (Battisti et al., 2005; Kerdelhué et al., 2009). PPM is a paradigm case of sensitivity to global change for three reasons. First, due to its particular life cycle, with the larval development occurring during winter (instead of spring-summer as is usual in Lepidoptera), PPM is strongly dependent on minimum winter temperatures (Seixas Arnaldo et al., 2011). Second, PPM has also shown a high capacity for local adaptation, with some populations shifting to a summer cycle in cool areas and tolerating high temperatures at its southern limit of distribution (Pimentel et al., 2006; Santos et al., 2011). And third, extensive substitutions of broadleaved woodlands to pine plantations all over the Mediterranean have created a situation in which PPM can thrive (Jactel et al., 2009; Kerdelhué et al., 2009). Many other insect pests are showing similar dynamics and their importance is expected to increase in the coming years, although reliable estimates are still not available (Battisti, 2005).

The story is different for fungus pathogens, which will benefit from the physiological responses to temperature increase in combination with drought effects on plants. Cases such as charcoal disease (*Biscogniauxia mediterranea*; Desprez-Loustau et al., 2006), Dutch elm disease (*Ophiostoma ulmi*; Resco de Dios et al., 2007), chestnut blight (*Cryphonectria parasitica*; Waldboth and Oberhuber, 2009) or oak decline (*Phytophthora cinnamomi*; Brasier and Scott, 1994) are illustrative of the threats facing a large part of the Mediterranean woodlands. For example, the combination of longer drought periods and fire may extend the distribution of several diseases (such as *P. cinnamomi*) that affect forest stands in southern Europe (Bergot et al., 2004). However, the possible effects that host range expansion and forest connectivity increase have on pathogen dispersal have yet to be probed (Pautasso et al., 2010).

3.6. Increase of fire risk by the combination with drought and/or land-use change

There is increasing evidence to show that high temperatures and low air humidity conditions have become more common in recent decades and have been correlated with an increase in the total burned surface (Dimitrakopoulos et al., 2011). Models predict that these climatic conditions are going to become more frequent (Moriondo et al., 2006), determining changes in the fire regime (Mouillot et al., 2002). Wildfires are expected to be more frequent at higher altitudes and northern regions of the Mediterranean Basin, where they occurred only occasionally in the past (for the Southern Alps, Reinhard et al., 2005). This pattern will result in important consequences as dominant species of these areas often lack efficient post-fire regeneration mechanisms (Vacchiano et al., 2014; Vilà-Cabrera et al., 2012), but may also lead to more heterogeneous landscapes that have greater resilience to further disturbances.

The social and ecological impacts of wildfires are related to the implementation of large-scale, organized fire suppression strategies at the national level. These strategies decrease the area burned in the short term, but lead to contrasting results in the long term due to fuel accumulation (Piñol et al., 2005). In addition to climate, fuel is in fact the other main physical driver of fire. Extensive agricultural abandonment during the past century has led to extensive successional shrublands and forests mostly dominated by pines. The low investment in fuel reduction practices has favoured high fuel load and vertical continuity promoting high-intensity crown fires (Lloret et al., 2009; Mitsopoulos and Dimitrakopoulos, 2007). Crown fires have also affected large areas of managed pine woodlands, probably as a result of fuel continuity across the landscape and the mountainous nature of the territory. Also, in some areas, land use transformation to extensive grazing and human leisure activities can easily give rise to fires, while rural exodus prevents early fire extinction.

In summary, the conjunction of a trend towards a homogeneous landscape dominated by fuel-loaded vegetation (Loepfe et al., 2010) and a very active fire suppression policy is favouring fuel accumulation (Lloret et al., 2009). This state of affairs, together with the increasing climatic fire risk, is likely changing the fire regime to a set of large, frequent and intense wildfires, thus challenging the resilience of the Mediterranean vegetation (Moreira et al., 2011; Tsitsoni, 1997). To some extent, we may be contemplating wildfires as the catalyst for the adjustment of many Mediterranean Basin ecosystems to a new climate-driven status closer to semi-arid.

3.7. Increase of invasion risk by the combination with drought, land-use change, atmospheric alteration or fire

Climate change can enhance biological invasions through increasing survival, reproduction and spread of non-native species from warm climates (Walther et al., 2009). In the Mediterranean Basin terrestrial ecosystems, many non-native species from temperate and cold climates might only be able to shift their ranges northward or to expand in altitude. However, the empirical evidence that this is occurring is anecdotal. Non-native species whose native ranges are drier and warmer than their introduced ranges can be at an advantage due to physiological or reproductive adaptations (for insects, Bale and Hayward, 2010). Still, model simulations and experiments suggest that changes in temperature alone do not determine non-native plant distribution and fitness (Gritti et al., 2006; Ross et al., 2008). In fact, recent studies stress the important influence of land-cover change in accelerating invasions (Boulant et al., 2009; Polce et al., 2011).

Future projections of changes in land use highlight that the invasion levels of terrestrial ecosystems will increase regardless of the socioeconomic scenario (Chytrý et al., 2012). Open areas favoured by land-use changes frequently provide “windows of opportunity” for invasion as they increase propagule pressure and favour non-native species adapted to take advantage of resource release (Ross et al., 2008; Roura-Pascual et al., 2009). In the Mediterranean Basin, past crop uses explain the distribution and abundance of invasive species in recently recovered forests and shrublands after a process of land abandonment (Pretto et al., 2012). Moreover, certain land-use changes increase the fragmentation and isolation of forest landscapes, which are more invaded than large continuous forests (Malavasi et al., 2014). This landscape configuration enhances levels of invasion at forest edges with urbanized or agricultural areas (Carpintero et al., 2004).

The interaction of atmospheric N deposition and plant invasion has not yet been explored in the Mediterranean Basin, but it has been in other Mediterranean ecosystems (Padgett and Allen, 1999). Fertilization experiments in arid scrublands of California indicate that areas with high N deposition are more susceptible to non-native grass invasions, particularly in wet years (Rao and Allen, 2010).

Fire has been proven to increase the expansion of non-native perennial grasses in the Mediterranean Basin (Vilà et al., 2001; although see

Dimitrakopoulos et al., 2005 for contrasting results) which could feed back to increase the burnt area (Grigulis et al., 2005). Some non-native plants invade recently burnt forests but disappear later on as their persistence is constrained by the recovery of the native vegetation (Pino et al., 2013). On the other hand, little information is available on the increasing pool of plant species able to invade deeply shaded undisturbed forests (Martin et al., 2009). There are no similar studies for non-native fauna, but fires are expected to create new opportunities for the expansion of non-native animals already inhabiting the surroundings of the burned areas.

Combinations between environmental change and biological invasions are still largely unknown. However, as the interaction of different global change factors can alter historical succession patterns of native species (Keeley et al., 2005), similar interactions might lead to more frequent and resilient invasions, challenging the resistance of the Mediterranean terrestrial ecosystems.

3.8. Potential combinations between more than two factors of global change

Apart of the suggested combinations, more than two factors can interact generating even more complex effects. It has been already mentioned the complex feedbacks between climate, fire and atmospheric CO₂, the first increasing fire risk, which contributes to higher CO₂ concentration in the atmosphere, which can in turn increase global warming (Stavros et al., 2014). More specific are the studies of Dury et al. (2011) and Hodnebrog et al. (2012), where other interactions between changes in atmospheric composition, climate and fire are shown. Modelling the interaction between increasing levels of CO₂, drought and fire frequency shows dramatic effects on forest productivity and distribution (Dury et al., 2011). Also, the combined effects of fires, climate warming and different biogenic emissions affect atmospheric ozone levels (Hodnebrog et al., 2012). Gil-Tena et al. (2011) show how fire, land use changes and climate change can affect the distribution of bird species, while these effects that cannot be predicted by studying only one of these factors (Clavero et al., 2011). Similarly, Mairota et al. (2014) have modelled how the combined effects of climate change and fire on vegetation could be modified by land use changes.

Unfortunately, the few studies including three factors interaction mentioned in the previous paragraph are not selected examples but the only ones found after a meticulous search (lists of keywords related with each factor were included together and in all the potential different combinations of four and three factors by using different fields on the ISI Web of Science in the search of published research articles related to global change factors interaction in the Mediterranean region, from 1900 to 2015). Moreover, although interactions between more than three factors are also likely, we were not able to find any study considering this possibility in Mediterranean forests, shrublands or pastures.

4. Concluding remarks: global change combination in the Mediterranean Basin

Different global change factors combine and interact causing unprecedented ecological effects, which can be hardly predicted by the analysis of each factor in isolation. These combinations and interactions bring some inherent uncertainty, which should be considered in future research guidelines and when applying forest management strategies (Doblas-Miranda et al., 2015). Principal sources of uncertainty are the contrasting effects between atmospheric pollutants and drought, the role of forest cover in water availability, floods and pest expansion and the thresholds of irreversibility that lead the change from one ecosystem to another. In addition, much more complex interactions arise when combinations occur together. For example, through altering forest extension and density, reforestation can decrease erosion but may also reduce water availability, while drought can enhance erosion and decrease water reserves. Moreover, both reforestation and drought may

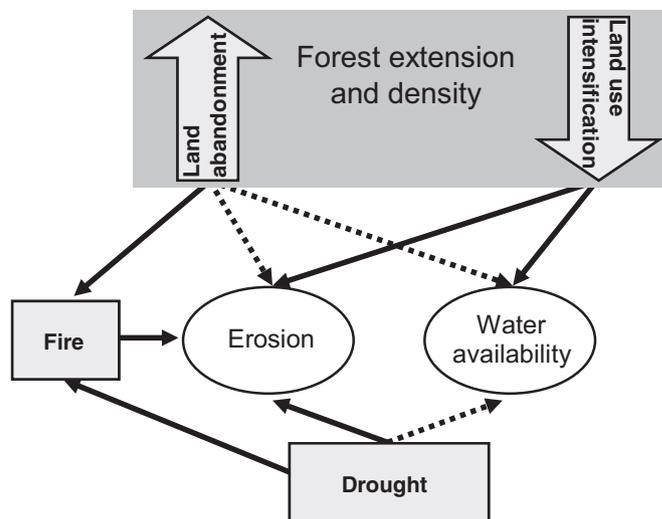


Fig. 3. Combined effects of land-use intensification and abandonment, fire and drought on soil erosion and water availability. Solid lines represent positive effects while dashed lines represent negative effects.

also indirectly contribute to erosion by increasing fire risk (Fig. 3). Uncertainty should be faced by developing balanced adaptive strategies that account for the most likely consequences of the major expected impacts and the inclusion of such information in any decision making process (McCarthy and Possingham, 2007).

Comparative studies across regions and ecosystems by multisite approaches are necessary to understand the impacts of global change. Particularly in the Mediterranean, previous evaluations of the effects of global change have been performed (Lavorel et al., 1998; MEA, 2005; Sala et al., 2000), but new considerations need to be addressed. Climate change, and especially drought, emerges as a crucial factor in most of the reviewed interactions and therefore it should be considered when it comes to designing and applying international management policies. For example, drought effects must be present when assessing critical levels of several pollutants or mitigation effects of carbon sequestration in forests. The ecological transitional nature of the Mediterranean Basin between temperate and arid regions supposes a delicate equilibrium for multiple ecosystems, where a combination of global change factors can balance their development to new arid states. Novel communities associated to new global change factors, such as land abandonment and new fire regimes, will be more prevalent, while our information about them remains scarce (Hobbs et al., 2006). The identification of transition states leading to novel systems and the understanding of the driving forces behind them remains a key priority for further research.

The information compiled in the present review highlights the potential relevance and impact of interactions among emerging global change factors in the Mediterranean Basin. Although global change is unavoidable in many cases, change does not necessarily mean catastrophe, but adaptation. The enormous challenge of conserving Mediterranean terrestrial ecosystems and the services they provide can only be met by means of a collective effort involving not only the scientific community, but also forest managers and owners, decision makers and the civic responsibility of society at large.

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