

CHAPTER THREE

Global change and Mediterranean forests: current impacts and potential responses

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3.1 Global change exacerbating Mediterranean stresses

Mediterranean forests have always had to cope with challenging environmental conditions that change across different temporal and spatial scales. However, the rapidity of current environmental change, driven by greater-than-ever human influences on natural processes, is unprecedented and has triggered renewed research endeavour into the impacts on Mediterranean ecosystems (Valladares 2008). The climate of Mediterranean areas is expected to become drier and warmer, with decreasing water availability for plants and increasing evapotranspiration (IPCC 2007). This will result in more acute physiological stress, increased importance of species-specific tolerances, plasticity and thresholds, phenological change and recruitment effects (Montserrat-Martín *et al.* 2009; Morin *et al.* 2010; Peñuelas *et al.* 2004). Several studies have demonstrated how the conditions currently experienced by seedlings and saplings are quite different to those when current adults recruited (Lloret & Siscart 1995; Montoya 1995). The anticipated impacts of such changes have led to a renewed interest in classic ecophysiological research into drought stress and tolerance (Wikelskia & Cooke 2006), as well as population-level studies on phenotypic plasticity and the evolution of tolerance in certain key tree species, such as Holm (*Quercus ilex*) and cork oaks (*Q. suber*) (Gimeno *et al.* 2009; Ramírez-Valiente *et al.* 2010).

Niche modelling techniques are used to forecast changes to species distributions under future climate scenarios, and the results predict abrupt shifts of dominant tree species in the next decades. Forest diebacks, species migration and displacement, and altitudinal shifts of forest types have already been recorded (Peñuelas & Boada 2003; Allen *et al.* 2010). For example, in northeast Spain *Fagus sylvatica* and *Calluna vulgaris* are being replaced by *Quercus ilex* at high elevations (Peñuelas & Boada 2003).

However, the expected changes do not always match with observations: vegetation stability after extreme climatic events points to a suite of mechanisms – beyond individual physiological stress tolerance – that we are only beginning to understand (Lloret *et al.* 2012). A forest community is characterised by a large number of mutualistic and antagonistic ecological interactions, and the net result of changes to these will determine eventual outcomes of environmental change on forest distribution and dynamics.

In this chapter we review a range of concepts and processes relevant for Mediterranean forests coping with accelerated environmental change. We take the Mediterranean Basin as our focus, but draw in examples and lessons from other Mediterranean climate zones. Rather than concentrating on climate *per se*, we discuss two inter-related drivers of change which are also important in Mediterranean systems: land-use and fire. We then explore the significance of the complex network of biotic interactions for interpreting how forests will respond to global change. We conclude that, whilst in the short term these species interactions will result in significantly less change than could be expected, the simultaneous action of climate, land-use, fire and other global change drivers may lead to threshold situations over which mechanisms underlying this resilience of Mediterranean forests could collapse. Finally, we consider how forest management philosophy and strategy itself needs to adapt to global change, through measures anticipating the most likely impacts to these ecosystems, but also the high degree of uncertainty in how they will play out.

3.2 Land-use change

3.2.1 Land-use trends in the Mediterranean Basin

Land-use change is one of the most severe drivers of biodiversity loss (Sala *et al.* 2000), and its impact is especially relevant in Mediterranean ecosystems where the richness of the biota has been linked throughout history to traditional land-use practices (Blondel *et al.* 2010). Mediterranean forests have long been subjected to intense exploitation, which is rapidly changing because of urbanisation, industrialisation and pressure from tourism (Valladares 2004). Understanding the response of species to land-use changes has become a major concern in recent ecological research. Some of the most common changes in land-use in the Mediterranean Basin include:

- *Conversion of natural vegetation into cultivated and urban areas.* Native habitat removal to expand agricultural land and pastures has been the most common land-use conversion during the last centuries. In particular, Mediterranean forests have widely disappeared because of exploitation and substitution by agricultural landscapes and, more recently, by urban development around cities and in coastal areas (Blondel *et al.* 2010). These changes in land-use cause irreversible degradation of soil and vegetation, contributing to processes of desertification which will probably worsen because of climate change.
- *Land abandonment.* The abandonment of traditional practices because of socio-economic changes and rural exodus is an ongoing process occurring throughout Europe, and especially in Mediterranean areas with generally low soil nutrient levels. Negative impacts of land abandonment on ecosystems include loss of biodiversity and vulnerable species, altered ecosystem services, and increased size and intensity of wildfires (see Section 3.3 below). Alternatively, land abandonment can lead to an increase in species diversity, favouring the natural regeneration of woodland (Gimeno 2011; Pausas *et al.* 2006; Ramírez & Díaz 2008).
- *Differences in management intensity within the same land-use.* Differences in management intensity have typically not been considered in recent research, because of the lack of knowledge on possible interactions with climate change. For instance, some studies have shown changes in diversity and richness of species due to different management regimes for livestock grazing (Celaya *et al.* 2010; Jauregui *et al.* 2008).

Of all the processes related to land-use changes, habitat fragmentation has been recognised as one of the most significant impacts on biodiversity in Europe (Fahrig 2003). Its relevance for Mediterranean ecosystems is being recognised in a growing number of studies (Gimeno *et al.* 2012a and references therein). We discuss this process in more detail below.

3.2.2 Fragmentation, an increasingly important driver in Mediterranean ecosystems

Mediterranean ecosystems have historically suffered from strong human impacts which have led to significant levels of fragmentation. Effects of habitat fragmentation on the populations of forest organisms are widely known. It results in habitats of reduced area, increased isolation and altered physical environment, with important implications for population genetics and species ecology. In small habitat fragments there is an increased influence of genetic drift, homozygosity, accumulation of deleterious mutations and inbreeding within populations (Ellstrand & Elam 1993; Young, Boyle & Brown 1996), processes that reduce the performance of populations. The probability

of extinction in small fragments also increases as a consequence of the strengthened effects of stochastic demographic processes on small populations (Lande 1988). Moreover, isolation between fragments favours the increase of genetic differentiation between populations and outbreeding depression, as well as preventing demographic rescue by immigration from individuals coming from adjacent fragments (Templeton 1986; Fischer & Matthies 1997). Evidence of the effects of fragmentation in Mediterranean ecosystems is available for a range of different organisms including birds (e.g. Santos, Tellería & Carbonell 2002), butterflies (e.g. Rabasa, Gutiérrez & Escudero 2007; Stefanescu, Herrando & Páramo 2004) and plants (e.g. García & Chacoff 2007; Jump & Peñuelas 2005). In addition to effects on individual species, habitat fragmentation can also lead to the disruption of biotic interactions such as pollination, seed dispersal and herbivory (see González-Varo, Arroyo & Aparicio 2009; Santos & Tellería 1994). Pollination services may be reduced in small and isolated populations owing to decreased attractiveness and increased distances among fragments (e.g. Cunningham 2000; Duncan *et al.* 2004). Larger fragments attract more predators than smaller ones, but herbivores with limited mobility may have problems in reaching more isolated fragments (Duncan *et al.* 2004; Kéry, Matthies & Fischer 2001). The importance of biotic interactions in the context of global change is explored further in Section 3.4.

The two main options for species coping with climate change (acclimate/adapt or migrate to more favourable areas) are affected by fragmentation. The ability of populations to adapt to changing conditions is decreased because of reduced genetic variation, while dispersal or movement ('range shift') to habitats with optimal conditions is also compromised. Fragmented populations are therefore expected to be more vulnerable to environmental drivers such as climate change than if they were not fragmented (Opdam & Wascher 2004). *Fagus sylvatica* populations in northeast Spain provide an example of a species meeting such challenges (Jump & Peñuelas 2005, 2006; Figure 3.1). In this case, the fragmentation of these forests, which took place several centuries ago, has led to a reduced genetic diversity. The recent rapid climate change can exacerbate the impact of human activities on the dynamics of *F. sylvatica* forests in these fragmented landscapes because of their reduced capacity for adaptation. Habitat fragmentation is also expected to decrease the ability to resist and recover from environmental disturbances such as extreme climatic events, which are expected to increase as a result of climate change (Opdam & Wascher 2004; Travis 2003). Temperature increases are expected to cause shifts to the high-latitude margins of species distributions, but habitat fragmentation could act as a barrier to such colonisation for most species, as has been shown in butterflies (Wilson, Davies & Thomas 2010). It is expected that the combined effects of habitat fragmentation and climate

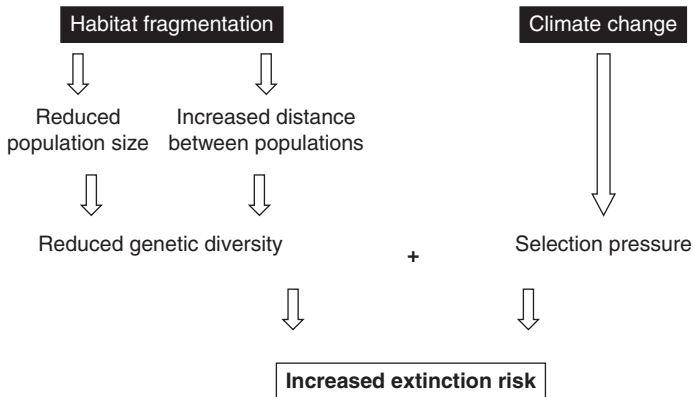


Figure 3.1 The synergistic interaction of climate change and habitat fragmentation within *Fagus sylvatica* populations leading to a range-wide increase in extinction risk. Conceptual model elaborated from Jump and Peñuelas (2005).

change will be even more pronounced for species that are less mobile (e.g. plants) and at the species' range limits (Opdam & Wascher 2004), which is the case for many of the species in Mediterranean areas. In such cases, species survival will depend on their environmental tolerance. Good colonisers, however, might benefit from climate change and expand their distributions polewards (Hill *et al.* 2001; Warren *et al.* 2001).

Hence, it is clear that the susceptibility of species to climate change is modified by habitat fragmentation, but the way in which individual species respond will depend on many factors, including their dispersal capability, ecological niche, climate sensitivity, life cycles and interactions with other species. Synergy among multiple drivers of change occurs when the net impact of two drivers is significantly higher than the sum of the two operating independently (Sala *et al.* 2000). The interplay between the two important drivers of fragmentation and climate change is not completely understood, and they might generate non-additive effects that cannot be predicted from single-factor studies.

3.3 Fire, a characteristic Mediterranean disturbance interacting with global change

3.3.1 Mediterranean wildfires and their causes

Wildfires have always been a feature of terrestrial ecosystems; they help explain their biodiversity and distribution (Bond, Woodward & Midgley 2005; Pausas & Keeley 2009). This is especially evident in the Mediterranean Basin, which suffered environmental drying and an increased prevalence of fire in the Quaternary (and probably during the end of the Tertiary; Keeley *et al.* 2012). These fires have shaped Mediterranean plant traits, communities and landscapes (Pausas & Verdú 2005; Verdú & Pausas 2007), and have

played a key role in determining this area as a biodiversity hotspot. However, during the past few decades, social, land-use and climatic changes have all influenced fire regimes (Pausas 2004; Pausas & Fernández-Muñoz 2012), sometimes to unsustainable limits, and have generated high social and economic costs (Bowman *et al.* 2009; Viegas 2004).

The main factors determining current fire regimes are debated (Whitlock *et al.* 2010); they result from a complex climate–vegetation relationship, and their role under future climatic conditions is still poorly understood. Both dry conditions (climate) and fuels (vegetation) are needed for fire. Vegetation development depends on plant growth, and so fire activity is tightly related to ecosystem productivity (Bowman *et al.* 2009; Krawchuk & Moritz 2011; Pausas & Bradstock 2007; Pausas & Paula 2012; Pausas & Ribeiro 2013). Drying conditions convert vegetation into available fuel for fire, and this occurs in many regions of the world, although with different frequencies ranging from annual (e.g. savannas; Archibald *et al.* 2010) to centennial (e.g. tropical rain forest; Cochrane 2003) cycles. The fire regime of Mediterranean ecosystems is attributed to their seasonal climate: springtime mild temperatures and abundant rainfall promoting biomass production, followed by summertime warm and dry conditions resulting in severe water deficit (Pausas 2004; Piñol, Terradas & Lloret 1998; Viegas & Viegas 1994). Large fires that occurred in the Mediterranean Basin in the past decade have been related not only to heat waves (Founda & Giannakopoulos 2009; Pereira *et al.* 2005), but also to positive anomalies in the previous wet season that promoted plant growth and fuel build-up (Trigo *et al.* 2006).

3.3.2 Fire and climate change

In the past decade, a lot of effort has gone into predicting the potential impacts of climate change on ecosystem dynamics (Sala *et al.* 2000; Thomas *et al.* 2004). Fire is increasingly included in such models, owing to its tight relationship with climate and its relevant role in terrestrial ecosystem functioning (Cramer *et al.* 2001; Scholze *et al.* 2006). Changes in fire activity are expected to occur in most ecosystems worldwide (Flannigan *et al.* 2009; Krawchuk *et al.* 2009; Scholze *et al.* 2006). For a large proportion of the Mediterranean area, a general rise in fire risk is predicted because of an increase in both the length of the fire seasons and the frequency of extreme heatwaves. The strongest changes are expected in mountainous areas (e.g. the Alps, Pyrenees and mountains of the Balkan region; Carvalho *et al.* 2010; Giannakopoulos *et al.* 2009; Moriondo *et al.* 2006). On the other hand, in more arid ecosystems, increasing temperature might reduce productivity and thus fuel amount and continuity, with a consequent reduction of fire activity.

Fire responds to climate, and therefore climate change, in complex ways. It initiates and spreads only when dry and warm weather conditions make

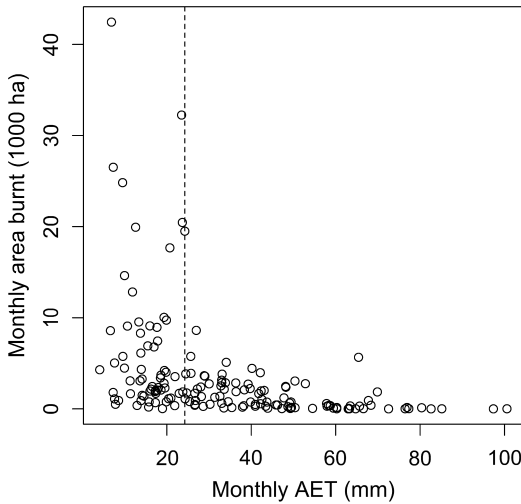


Figure 3.2 Relationship between monthly actual evapotranspiration (AET) and monthly area burnt for the 1968–2007 period in central Spain. Vertical dashed line indicates the AET threshold from which area burnt increases abruptly. Modified from Pausas and Paula (2012).

vegetation flammable. The fire–climate relationship is not straightforward, however, as the two variables are related in a threshold fashion, with fire probability increasing sharply when certain climatic states are reached (Flannigan & Harrington 1988; Pausas & Paula 2012; Westerling & Bryant 2008; Figure 3.2) and decreasing sharply in dry conditions when a discontinuity threshold in cover is reached (Pausas & Bradstock 2007). Even small changes in climate can therefore cause shifts between non-flammable and flammable conditions. Consequently, future fire regimes may change abruptly, with their impacts on ecosystems possibly overwhelming any direct effects of climate change. For example, vegetation changes in mountainous Mediterranean forests are predicted to relate more to changes in fire regime than to the increased drought due to climate change (Fyllas & Troumbis 2009). Besides, increased fire-induced emissions will have a feedback effect on climate change (Bowman *et al.* 2009), thus amplifying impacts on ecosystems.

3.3.3 Fire and land-use

Land-use has an important role in mediating the effect of climate change on fire regimes. When simulations of future fire scenarios take into account how vegetation will track climate change (Cramer *et al.* 2001), predicted changes in fire activity become greater (Krawchuk *et al.* 2009), thus highlighting the key role of fuels. In turn, the build-up of fuels is heavily influenced by land-use change, as confirmed by historical reconstructions of fire occurrence. For instance, global reduction in fire activity during the nineteenth and mid-twentieth centuries is attributed to a decrease in fuel loads due to the expansion of intensive grazing and agriculture, whereas the increased fire activity in the past decades is explained by fuel accumulation resulting from fire

suppression policies and land abandonment (Marlon *et al.* 2008; Pausas 2004; Pechony & Shindell 2010).

In the Mediterranean Basin, there was a clear shift in the fire regime in the second half of the twentieth century when fires began to increase in frequency and, especially, in size (Dimitrakopoulos *et al.* 2011; Moreira, Rego & Ferreira 2001; Pausas & Fernández-Muñoz 2012). In another Mediterranean climate region, California, there is no evidence of similar changes in fire regime during the same time period (Keeley & Zedler 2009). The fire regime change detected in the Mediterranean Basin was not gradual but sudden (Figure 3.3), and cannot be explained by the progressive changes in climate observed in this region (Pausas 2004). Instead, changes in fuel conditions need to be considered (Pausas & Fernández-Muñoz 2012), and the turning point seems to be related to a critical threshold in landscape connectivity. As we have seen, one of the main current landscape-scale ecological processes at work in the Mediterranean Basin is the expansion of shrublands and woodlands (Bonet & Pausas 2007). This is driven by the abandonment of agriculture and livestock, and the use of new domestic energy sources (instead of wood). Land abandonment promotes the build-up of large and continuous fuel beds, composed of highly flammable species characteristic of early successional communities (Baeza *et al.* 2011). Concomitant to this land abandonment was the trend of afforesting old fields with conifers and eucalypts and the increasing efforts in fire suppression (Badia *et al.* 2002; Moreira, Rego & Ferreira 2001; Pausas *et al.* 2008). All these factors augmented the biomass and connectivity of landscapes, allowing fires to spread further and thus increase in size. In addition, the increase in human populations and a developing wildland-urban interface led to more frequent fire ignitions (e.g. Keeley, Fotheringham & Morais 1999).

3.3.4 Overall impacts of fire on changing Mediterranean ecosystems

Although Mediterranean plant communities show exceptional resilience to recurrent fires, very high fire frequencies reduce their regeneration ability. Fire return intervals shorter than the time period required to recover seed banks (for seeders) and carbohydrate reserves (for resprouters) reduce post-fire recovery (e.g. Lloret, Pausas & Vilà 2003; Moreira *et al.* 2012). In addition, post-fire regeneration in species that neither resprout nor recruit after fire is low when the area burnt is large, given that their recovery relies on colonisation from neighbouring unburned populations (e.g. Ordóñez, Molowny-Horas & Retana 2006). Furthermore, future wildfires are expected to increase in intensity/severity, owing to warmer and drier conditions (Moriondo *et al.* 2006) as well as the higher fuel accumulation resulting from land-use changes. Higher temperatures and/or longer exposure to fire

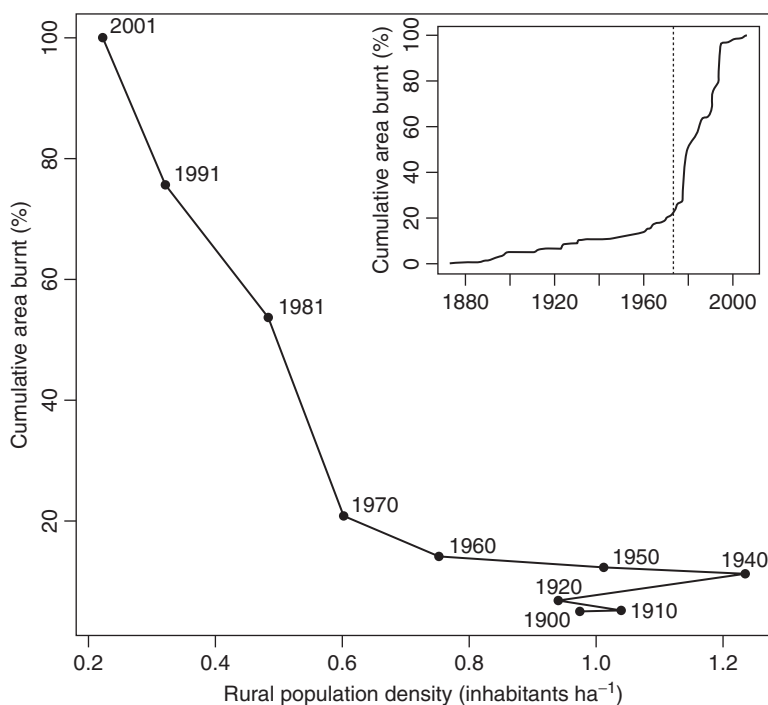


Figure 3.3 Relationship between the rural population density (inhabitants per ha) and the cumulative area burnt (%) during the twentieth century in the Eastern Iberian Peninsula (from Pausas & Fernández-Muñoz 2012). The inset figure shows the cumulative area burnt (%) for the studied period; vertical dotted line (in 1972/73) indicates an abrupt shift in area burnt coinciding with the rural exodus to the cities.

diminish post-fire regeneration, either by resprouting or seeding (Lloret & López-Soria 1993; Pausas *et al.* 2003; Paula & Pausas 2008). Fuel accumulation can even shift surface fires into more severe crown fires. Such changes are already detected in montane forests, for example threatening the survival of *Pinus nigra*, a species which is able to withstand surface fires but not large and intense crown fires (Fulé *et al.* 2008; Rodrigo, Retana & Picó 2004; Trabaud & Campant 1991).

3.4 Biotic interactions

3.4.1 Asymmetric responses to abiotic stress and negative species interactions

Species respond in an individualistic fashion to the changing abiotic environment owing to differences in basic life-history traits (e.g. Thuiller *et al.* 2011). However, species are also integrated in complex webs of negative and positive interspecific interactions that are themselves subject to environmental change (Pascual & Dunne 2006). Ecophysiological stress and pathogen attack

may be synergistically affecting overall vulnerability and stability of forest ecosystems, especially for species (including many in the Mediterranean Basin) that are at their distributional limits (Fujimori 2001; Resco de Dios *et al.* 2007). Warmer temperatures can act indirectly on trees by accelerating pathogen life cycles. Some studies have predicted more active attacks of Dutch-elm disease (*Ceratocystis ulmi*) and Hypoxylon canker (*Hypoxylum mediterraneum*) (Tainer & Baker 1996) in southern Europe, and an increasing incidence of Phytophthora root rot (*Phytophthora cinnamomi*) on Spanish *Quercus ilex* and *Q. suber* stands (Tuset & Sánchez 2004).

New interactions between any one species and its antagonists (competitors, herbivores or pests) are expected to arise when the spatial distribution or local performance of the latter is affected by global change, perhaps as a result of the breakdown of climate-driven dispersal barriers (Gilman *et al.* 2010). In one documented case, the processionary moth caterpillar (*Thaumetopoea pityocampa*) expanded its range towards higher elevations in the Sierra Nevada, establishing new contacts with populations of a relict, endemic subspecies of *Pinus sylvestris* (Hódar *et al.* 2003). In general, shifts in distributional range in response to climate change will be fast for small ectothermal organisms with high fecundity and dispersal ability such as most insect pests and pathogens (Helmuth *et al.* 2005), whereas tree responses will be slow owing to low dispersal ability and long generation time, especially for large-seeded species with restricted dispersal in an increasingly fragmented landscape (Jump & Peñuelas 2006).

Many Mediterranean plants are likely to be disadvantaged by asymmetric species responses to abiotic stress and pathogen attack. For example, the capacity of certain Mediterranean tree species to cope with drought is negatively affected by competition with other coexisting species that are less affected, or even benefited, by ongoing climate change (Gimeno *et al.* 2012a, 2012b; Granda *et al.* 2012). In other cases, Mediterranean plants may actually benefit from asymmetric species responses, for example induced by a mismatch between phenologies. This can happen when antagonistic interactions of plants and their natural enemies are broken down. For example, Rabasa, Gutiérrez and Escudero (2009) found that climatic variation between years causes differences in the effect of isolation on the fitness of the Mediterranean shrub *Colutea hispanica*. Contrary to expectations, plant fitness, measured as the production of fruits and viable seeds, increased in isolated patches in years in which a low seed predation coincided with extreme weather conditions (Figure 3.4). The explanation lay in how climatic change affected the temporal and spatial dynamics of the two main seed predators of *C. hispanica* (the lycaenid species *Iolana iolas* and *Lampides boeticus*), which opened a reproductive window for the shrub in isolated patches.

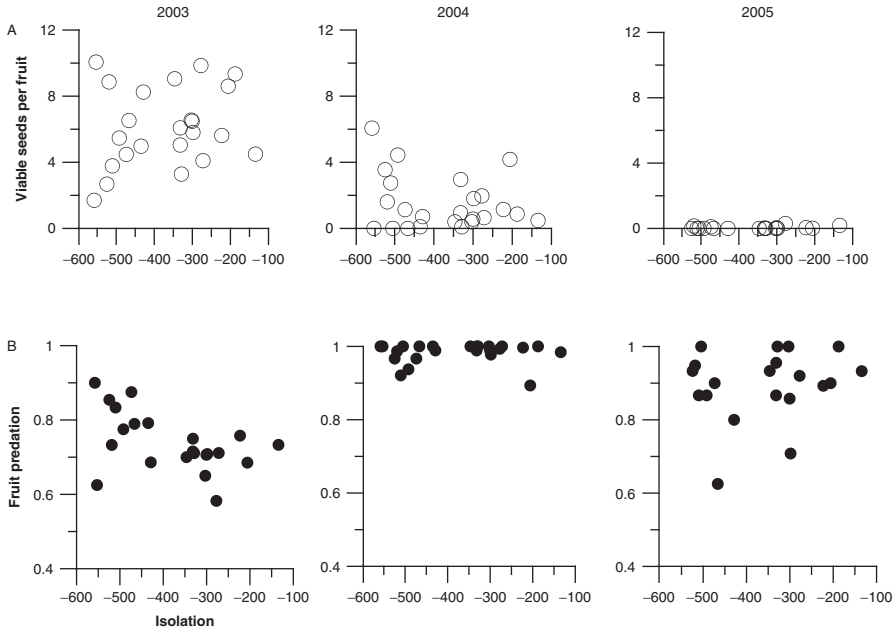


Figure 3.4 Relationship between the average number of viable seeds per fruit of *Colutea hispanica* (A) and proportion of fruit predation (B) with isolation in three consecutive years with contrasting climate conditions. Isolation index according to Hanski, Kuussaari and Nieminen (1994); less negative values indicate greater isolation. The year 2003 was particularly hot and dry, whereas 2005 was more favourable for plant growth and reproduction. Data elaborated from Rabasa, Gutiérrez and Escudero (2009).

3.4.2 Do positive species interactions help reduce global change impacts?

Positive biotic interactions can ameliorate the effects of global change (Brooker 2006; Valladares 2008). In all five Mediterranean regions, facilitation by drought-tolerant plant lineages that evolved during the Holocene has been key for the survival of plant lineages that evolved during the humid Tertiary (Valiente-Banuet *et al.* 2006). However, Brooker (2006) noted that there is less evidence for facilitative plant interactions than for competitive ones in mediating the impacts of environmental change. Indirect interactions and third-party effects on plant–environment interactions can involve threshold situations in which spatial decoupling of the plant and its key positive interactor amplify, rather than ameliorate, changes in abiotic stress (Gilman *et al.* 2010). Facilitation can be transient and it has been shown to be less ubiquitous in Mediterranean ecosystems than previously thought (Granda *et al.* 2012; Valladares *et al.* 2008).

3.4.3 The case of plant-plant interactions

Many studies have investigated plant-plant interactions along gradients of environmental severity, supporting the stress-gradient hypothesis (SGH). SGH proposes net positive interactions (facilitation) among plants prevailing in stressful sites, and negative interactions (competition) prevailing under less stressful conditions (Bertness & Callaway 1994). Net positive relationships are frequent in the Mediterranean (Figure 3.5). Facilitation is thus expected to become more and more relevant in Mediterranean ecosystems owing to the nature of the climate change scenarios expected for this region (Christensen *et al.* 2007).

The most frequent case of positive plant-plant interaction studied in Mediterranean areas is the relationship between shrubs (acting as nurse or benefactor) and seedlings of woody species (the *protégé* or beneficiary). Shrubs ameliorate stressful conditions, particularly during summer, reducing irradiance and temperature under their canopies, and consequently attenuating photoinhibition and water stress of seedlings (Castro, Zamora & Hódar 2006; Cuesta *et al.* 2010; Gómez-Aparicio *et al.* 2004; Soliveres *et al.* 2010), as well as providing physical protection against storms or grazing animals (Gómez-Aparicio *et al.* 2004; Smit, den Ouden & Díaz 2008). Similar phenomena have been detected in Mediterranean grasslands, where the scattered trees protect the annual pasture during hard droughts, increasing their growth and yield and delaying their withering (Joffre & Rambal 1993; Cubera & Moreno 2007).

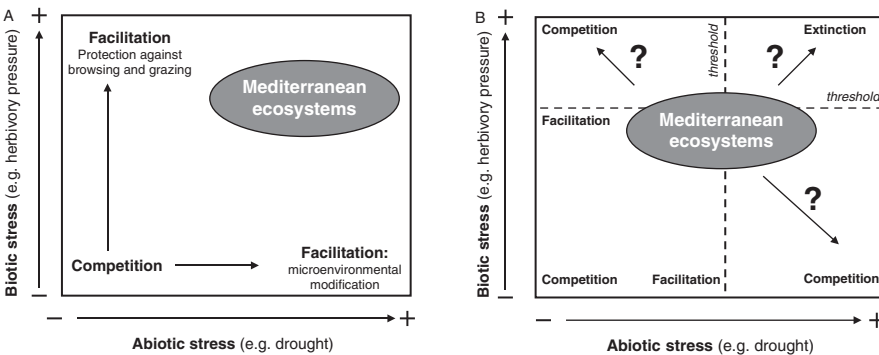


Figure 3.5 A: plant-plant interactions according to biotic and abiotic stress levels. In Mediterranean areas, both herbivory and drought stress factors co-occur, stimulating facilitation (after Zamora *et al.* 2004, based on Bertness & Callaway 1994). B: positive interactions in severe environments have thresholds after which benefits provided by the benefactor plants do not overcome negative effects. This leads to a change from net facilitative to net competitive interactions, which can lead to extinction under increased levels of both stresses.

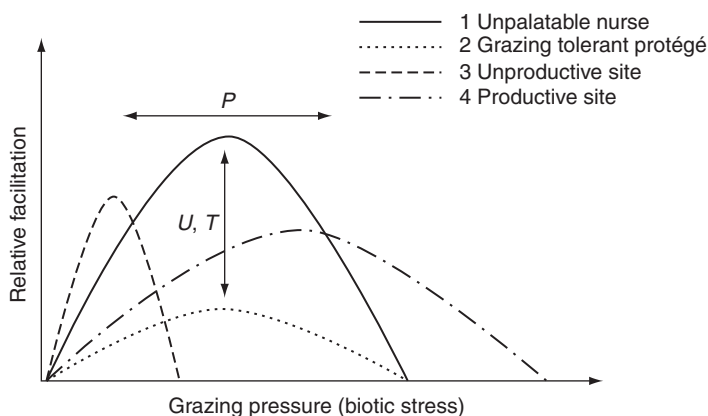


Figure 3.6 Conceptual model of relative facilitation along gradients of biotic stress (grazing pressure). Competition between nurse and protégé at low grazing levels leads to low relative facilitation. Herbivore damage to nurses at high grazing levels also decreases relative facilitation. Relative facilitation thus peaks at intermediate grazing pressure. The peaks shift horizontally as a function of site productivity (P) if the latter determines relative grazing pressure on nurses and protégés, and shift vertically as a function of the unpalatability of nurse plants (U) or grazing tolerance of the associated protégés (T). Adapted from Smit *et al.* (2007).

The importance and intensity of plant–plant interactions vary temporally and spatially, sometimes in complex ways (Granda *et al.* 2012). As a result, the SGH is not always supported; some studies show a decrease in the intensity of facilitative interactions at the very extreme end of stress gradients. This casts doubts on facilitation being able to help plants to cope with the increased abiotic stress of climate change under Mediterranean conditions (Figure 3.6). Maestre and Cortina (2004) showed that the protection by the tussock grass *Stipa tenacissima* for the seedlings of *Pistacia lentiscus* disappeared under high abiotic stress. Smit *et al.* (2007) similarly demonstrated a bell-shaped relationship between a biotic stress (herbivory) and facilitation in the case of the protection against livestock browsing afforded by thorny shrubs to tree seedlings. In this case the protection became ineffective after a certain threshold livestock density was passed (Figure 3.6). Malkinson and Tielbörger (2010) explained exceptions to the SGH in terms of the non-linear response of plant physiological processes to environmental changes, leading to the asymmetrical change of competition and facilitation along stress gradients, especially when several factors are involved. Together with the multiplicative nature of both facilitation and competition on individual fitness, more complex predictions than those resulting from the original SGH are inevitable (Freckleton, Watkinson & Rees 2009) (Figure 3.6).

3.4.4 The case of animal dispersal

Plant–animal interactions may also counteract expected effects of abiotic stress on plant populations under climate change scenarios. Directed dispersal, i.e. the non-random movement of seeds to suitable microsites for plant establishment (Wenny & Levey 1998), may overcome dispersal limitations of dominant, large-seeded forest trees. Recent work has shown how seed dispersal by animals could determine population trends (Montoya *et al.* 2008), recruitment (Pulido & Díaz 2005), regional distribution (Purves *et al.* 2006), community structure (Pausas *et al.* 2006; Svenning & Skov 2007; Zamora *et al.* 2010) and genetic structure and gene flow (Jordano *et al.* 2007) of Mediterranean forest trees facing global change.

Animal responses to fragmentation are usually non-linear, and relationships between presence in patches and patch size are best modelled by sigmoidal/logistic functions including two thresholds: the minimum patch size below which the species is never found, and the patch size above which all patches are occupied (Fahrig 2003). In patches smaller than the minimum threshold for keystone pollinators or dispersers, plant populations will be thus locally decoupled from essential animal interactors, even when this is not predicted by regional-scale models. A further complexity is related to spatial variation in the parameters of incidence functions, with larger minimum sizes for patch occupation towards the borders of distribution areas. This has been shown to be the case for forest birds in Mediterranean regions. Keystone seed dispersers of Eurosiberian affinities, such as jays *Garrulus glandarius* or thrushes *Turdus* spp., show increasing minimum forest sizes towards the southern, warmer borders of their distribution areas, whereas for species of Mediterranean origin such as small *Sylvia* warblers, minimum forest sizes increase northwards (Díaz *et al.* 1998; Santos *et al.* 2006). Local decoupling of plants and seed dispersers due to forest fragmentation will thus be more severe in climate change scenarios for plants depending on birds of northern distribution, such as large-seeded oaks *Quercus* spp. and jays.

Effectiveness of the interaction in patches of intermediate size (i.e. above minimum size but below the fragment size over which all fragments are occupied) will depend on the foraging behaviour of seed dispersers, which is also sensitive to fragmentation (Damschen *et al.* 2008). Differential use of fragments according to size for foraging and resting may lead to a collapse in recruitment in small patches if visitation rates are too low to result in efficient seed dispersal (e.g. Santos & Tellería 1994). Fragment size could also influence the outcome of conditional mutualisms between scatter-hoarding animals and large-seeded plants such as oaks (Forget *et al.* 2005). In this way, scatter-hoarding mice act as keystone acorn dispersers for holm oaks *Quercus ilex* in large forest tracts (Gómez *et al.* 2008) but become a net seed predator hampering oak recruitment in small fragments (Santos & Tellería 1997).

3.4.5 The challenge of prediction: modelling plant-animal interactions

Species-specific niche envelope models are currently being developed for both plant and animal species (Thuiller *et al.* 2011). Modelling the effects of global change on the distribution, abundance and foraging behaviour of seed dispersers or herbivores, and coupling these models to predictive models of plant distribution, can significantly improve our understanding of how plant populations will respond to future changes. However, uncoupled, or ‘parallel’, modelling approaches are still all too common (Figure 3.7). Animal models usually include plant data only through the well-known effects of vegetation-related land-uses on animal distributions (e.g. Vallecillo *et al.* 2009), whereas plant models either ignore animal effects on plants altogether, or include coarse surrogates for them (e.g. dispersal mode; Thuiller *et al.* 2008). This parallel approach may eventually predict new negative interactions

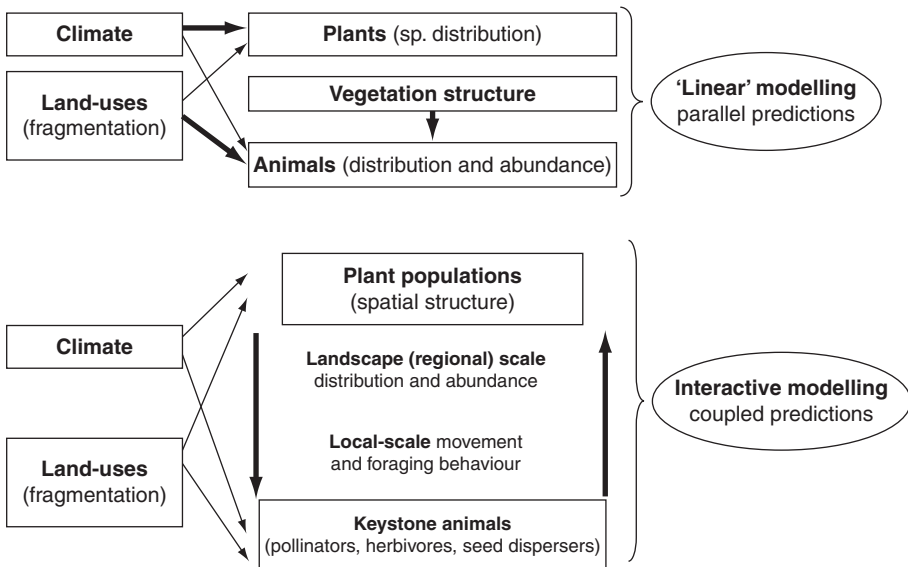


Figure 3.7 Conceptual modelling approaches to predict plant and animal responses to the two main global change drivers in Mediterranean forests: climate and land-use changes (including forest fragmentation). The upper scheme indicates the current approach, based on parallel niche envelope models for either plant or animal species. Arrow width indicates the relative importance of variables related to drivers in models. The lower scheme outlines basic ideas for developing coupled models for interactive plant-animal systems. Common variables should be used for niche envelope modelling of both animal and plants, as indicated by the arrow width. Sub-models for plants should explicitly include the spatial structure of plant populations, and coupled animal and plant models should consider both regional-scale and local-scale effects.

resulting from new range overlaps, as for instance in the case of the processionary moth and Scots pine mentioned earlier. However, this approach fails to estimate the influence of the interaction on the distribution of each species under new climates. Moreover, the spatial decoupling of specialist positive interactions involving plants and their pollinators or seed dispersers will be missed.

Coupled models for interactive plant–animal systems would overcome these limitations. They have four requirements. First, the same variables for measuring climate and land-use changes are needed for niche envelope modelling of both animal and plant species. Second, sub-models for plants should explicitly include the spatial structure of plant populations, as this trait is usually key to the modelling of animal distributions under fragmentation and land-use change scenarios (Concepción *et al.* 2008). Third, coupled models should consider both regional-scale effects of plants on the distribution and abundance of keystone animal species (pollinators, herbivores and seed dispersers) and local-scale effects of plant distributions on the movement and foraging behaviour of these same animals (e.g. Damschen *et al.* 2008). Finally, the consequences of animal behaviour on plant performance should be considered (i.e. dispersal behaviour and seed dispersal effectiveness, or herbivore behaviour and plant reproduction and survival; Schupp *et al.* 2010).

In conclusion, plant–plant and plant–animal interactions can positively influence forest responses to climate change by improving local abiotic and biotic conditions (facilitation) and the ability of large-seeded plants to track environmental changes (directed dispersal). Antagonistic interactions (e.g. herbivory) may also be broken down, leading to net gains for some species. On the negative side of the balance sheet, amelioration of global change impacts is not an inevitable result of existing positive interactions. Non-linear facilitation–competition balances along stress gradients, and the effects of fragmentation on the distribution and behaviour of dispersers, could lead to threshold situations across which positive interactions could vanish or even shift to negative interactions. Mediterranean areas represent an important model system for testing these predictions, owing to their heterogeneity and contrasting levels of fragmentation at a wide range of spatial scales.

3.5 Implications for practice

3.5.1 Characteristics of Mediterranean forests from a forest management perspective

There are a number of characteristics of Mediterranean forests relevant to management approaches, especially in the context of global change. We have introduced a number of them in the course of our discussion.

- They have a low productivity of wood products and pastures, and – together with the small size of holdings – this leads to low profitability. The Mediterranean climate with summer drought conditions constrains plant growth when temperature is optimum for vegetation development.
- They are highly multifunctional, with a high diversity of non-wood products such as game, cork, honey and mushrooms, as well as a provision of vital ecosystem services such as carbon sequestration and regulation of water resources (Balmford *et al.* 2002; Campos *et al.* 2013; Daily *et al.* 2000).
- They are extremely diverse in species and the interactions between them. Climatic evolution, high interannual variability, topographic diversity and long history of anthropogenic influence have combined to create some of the planet's most significant biodiversity hotspots (Myers *et al.* 2000).

Management of Mediterranean forests has evolved to take account of these particular characteristics, but in the future it needs to adapt to the changes taking place in these systems. The forests are currently subject to rapid socio-economic changes, such as rural depopulation and abandonment of traditional forestry taking place in the European Mediterranean countries since the 1950s (Pausas & Fernández-Muñoz 2012). Such changes have serious repercussions in terms of landscape heterogeneity and biodiversity (Atauri & de Lucio 2001). Employment generation, population stabilisation and increasing the profitability of unproductive areas are new challenges relevant to forestry management. At the same time, actively managed forests are an important component of any strategy to preserve heterogeneous landscape mosaics and their biodiversity (Díaz *et al.* 2013). We have also noted how global change drivers will modify species interactions (Lindner *et al.* 1997; Maestre *et al.* 2009; Soliveres *et al.* 2010) and disturbance regimes (Gillett *et al.* 2004; McKenzie *et al.* 2004; Pausas & Fernández-Muñoz 2012) in Mediterranean environments. By triggering changes in forest composition and structure, these changes again have important implications for forest management. Moreover, prolonged droughts and heat waves aggravate forest fire risks and subsequent soil erosion (Certini 2005), accelerating the desertification of dry areas. Consequences include a decline in wood production (Bravo *et al.* 2008; Loustau *et al.* 2005), decreased timber values in burned areas, and effects on non-wood products (e.g. mushrooms; Martínez de Aragón *et al.* 2007) and services (e.g. biodiversity and carbon sequestration; Bravo *et al.* 2008).

3.5.2 Guiding principles for Mediterranean forest under environmental change

Sustainable Mediterranean forest management and planning is more important than ever in the face of challenges imposed by global change (Lindner

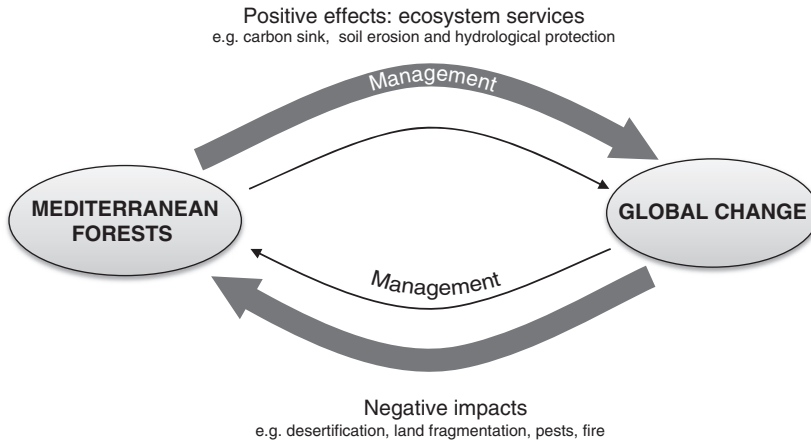


Figure 3.8 The relationships between global change and forests can be modulated by proper management. The negative impacts of global change on Mediterranean ecosystems, such as desertification, land fragmentation, increased fire or higher impacts of pests, can be reduced by management. Moreover, properly managed forests may help reduce the rate of environmental change, e.g. increasing the carbon sink or protecting soil from erosion and desertification.

2000). Whilst mitigating for such effects, an additional objective of management is to help combat global change itself (Figure 3.8). Mediterranean forest management regimes obviously require tailoring to the specificity of local sites, taking into account main limiting factors (water availability, soil nutrients), species composition and structure, and the products and services required (protection against anomalous fires, carbon sequestration, biodiversity, endangered species). However, some overall guidelines for silvicultural strategies in Mediterranean areas can be suggested to mitigate the effects of global change.

- **Flexible thinning schedules** according to stand age and state. Given uncertainties in how the climate will evolve, high densities of saplings (Aitken 2003), both natural or planted, are recommended to increase the selection opportunities of best-adapted individuals. However, in sites particularly prone to drought, low adult tree densities may be important in maintaining vigour and adaptive ability (Bravo *et al.* 2008), reducing tree competition and favouring good individual mycorrhisation and tree health.
- **Extension of rotations and regeneration cuttings.** Changes in phenology may lead to less than optimal conditions for reproduction and compromise the success of regeneration cuttings and long-term

persistence of stands. Extending the regeneration period, and reinforcing natural recruitment, can mitigate such impacts. Alternatively, the use of shrubs as nurse plants for seedlings can be used in reforestation protocols.

- **Reduction of tree densities in traditional coppiced forests** (Bravo *et al.* 2008). Over centuries, many stands of principally *Quercus* species were managed to obtain fire wood, favouring forest regeneration from sprouts or root suckers of cut trees. Acorns were also used to feed livestock. Abandonment of these stands has led to many-stemmed individual trees, reduced growth rates, lack of vigour in seed production and high mortality rates under extreme events. Selecting the most vigorous stems per individual in thinning operations has the potential to improve water availability, carbon sequestration (Tello *et al.* 1994) and recruitment from seedlings.
- **Less intense management** in timber production stands to reduce vulnerability to disturbances or pest breakouts and to maintain their hydrological protection role. Clear-felling should be replaced by selected cutting of single trees or groups, or else by shelterwood systems with longer rotations, weak thinning and natural regeneration whenever possible.
- **Mixed forests, diversity of stand types and uneven-aged stands** should be favoured as they are more resilient to changing environmental conditions. They provide different products and services to owners, and help mitigate the proliferation of forest fires and pathogen infestations. This should be a priority for forests with specific roles, such as hydrologic or soil protection, biodiversity conservation and landscape enhancement. Selective removal of individuals will favour continuous natural regeneration, avoiding excessive densities that hinder recruitment and stand rejuvenation and increase vulnerability to pest breakouts or fires.
- **Sustainable strategies for dealing with forest fire** are essential. It is not a reasonable objective to eliminate forest fires from Mediterranean ecosystems, and fire suppression policies can generate more destructive fires in the long term. Mediterranean landscape management should instead be aimed towards a sustainable coexistence with forest fires in terms of both human security and ecological processes/biodiversity (Pausas & Vallejo 2008).

In summary, management of Mediterranean forests should avoid forest senescence and high tree densities, and instead favour natural regeneration in mixed and uneven-aged stands. The conservation of biological diversity should be of paramount importance in forest management strategies (CBD,

2001), with measures to preserve the pool of native species, increase genetic variability of trees and reduce habitat fragmentation by creating ecological corridors and restoring degraded lands.

3.5.3 Uncertainty, adaptive management and modelling approaches

The uncertainty of global change evolution and the difficulty in predicting the direction and rate of change requires heightened efforts to gather empirical data, develop better knowledge and understanding of ecological processes and mechanisms, and make appropriate management decisions (Zavala *et al.* 2004).

Key to this success are adaptive management approaches (Nyberg 1998; Stephens *et al.* 2010) in which every silvicultural activity is treated as part of a real-world experiment, and systematic learning is developed for future management. Such adaptive approaches are yet to become widely practised in Mediterranean forest management planning. Simulation modelling is another important tool to anticipate species responses. Innovative progress has been made on this front owing to technological and statistical advances, for example in niche-based modelling. Many studies are now benefiting from these to assess future distribution responses to global change (Benito-Garzón *et al.* 2008; Keenan *et al.* 2010). There has been also significant progress in process-based models that incorporate eco-physiological processes from empirical relationships and mechanistic descriptions based on physical laws. Such models include GOTILWA+ (Gracia *et al.* 1999), which has been widely tested in Mediterranean areas. GOTILWA+ is a forest growth model that can assess responses to water availability (Sabaté *et al.* 2002) in changing environmental conditions, because of either climate or management drivers.

In conclusion, silvicultural management of Mediterranean forests should recognise the importance of non-linear, interrelated causes and feedback loops at different hierarchical levels of organisation, spatial and temporal scale (Puettmann *et al.* 2008). Modern ecological understanding of forests as complex adaptive systems must be the new cornerstone (Puettmann *et al.* 2008) of efforts to achieve sustainable management under global change scenarios.

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