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A MECHANISTIC VIEW OF THE CAPACITY OF FORESTS TO COPE WITH CLIMATE CHANGE

1. INTRODUCTION

From an evolutionary point of view, trees have at least one intriguing feature: they tend to have high levels of genetic diversity, but at the same time, they are known for their low evolutionary rates. Thus, trees are characterized by a counterintuitive combination of rapid micro-evolutionary change and a low macro-evolutionary change (Petit & Hampe, 2006). Trees experience highly heterogeneous environmental conditions and are exposed to extreme climatic events within their lifetime, which could contribute to the maintenance of their typically high genetic diversity (Gutschick & BassiriRad, 2003; Petit & Hampe, 2006). Trees are not only highly diverse but also highly fecund over their extended lifetime, allowing them to respond to high selection intensity and to adapt quickly to local conditions (Petit & Hampe, 2006). Mean antiquity of tree species is one order of magnitude higher than for herbs, which implies low rates of extinction to compensate for their low rates of speciation. However, forest species are more vulnerable to environmental change than this combination of evolutionary features may suggest (Jump & Peñuelas, 2005). Recent studies of Spanish populations of beech (*Fagus sylvatica*) are showing that the fragmentation of the forests that took place several centuries ago has led to a high genetic divergence of the populations and a reduced genetic diversity despite the fact that the species is wind-pollinated and the fragments are very near to each other (Jump & Peñuelas, 2006). These studies show the negative genetic impact of forest fragmentation, demonstrating that trees are not at reduced risk from environmental change (Fig. 1). This rather unexpected sensitivity of trees to forest management is particularly important under the current climate change since it can exacerbate the impact of human activities on forest dynamics and natural regeneration (Castro *et al.*, 2004a).

The capacity of forests to cope with climate change has been considered to be relatively ample, and many physiological, genetic and evolutionary aspects have been suggested to contribute to the persistence of key forest trees and plants in a changing climate. However, the fast rate of current environmental change is imposing severe limitations to the capacity of trees to adapt to new climatic conditions (Alcamo *et al.*, 2007). For example, levels of heritable variation for date of budburst, a crucial plant trait involved in the responses to global warming, were considerable but inadequate to track forecast changes in climate in two *Betula* species (Billington & Pelham, 1991), and similar results were obtained for variation of bud set and frost hardiness in *Pinus sylvestris* (Savolainen *et al.*, 2004). It must be taken into account that adaptation to future climates may require the simultaneous evolution of a number of different traits, which is constrained by correlations between them as discussed by Jump and Peñuelas (2005). Besides, climate change is only one environmental challenge directly or indirectly imposed to natural ecosystems by human activities, while it is the combined effect of climate change with loss and fragmentation of habitats, loss of soil, pollution and introduction of exotic species that is significantly reducing the regeneration and long term survival of many forest species (Valladares, 2004b). And forests are far more complex than just the sum of a given number of individual trees. Biotic interactions among

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co-occurring plants, animals and microorganisms are considered crucial for ecosystem functioning but our understanding of them and of their sensitivity to global change is very limited (Bascompte *et al.*, 2006; Peñuelas & Filella, 2001). The simple fact that not all species are equally sensitive to global change leads to the realization that global change can have greater and more complex effects on communities than on individual species.

A look into human history reveals that human induced deforestation and environmental degradation coupled with climate change has led to the collapse of civilizations as developed and rich as Maya and Anazasi (Diamond, 2005). Our current civilization shares many circumstances with old civilizations that disappeared due to overexploitation of natural resources under unfavourable climatic conditions, but has a number of unique features that could prevent its collapse, namely a sophisticated technology, a rapid transfer of information and a global view of environmental problems. Understanding the limits of natural systems to cope with multifactor environmental changes can potentially improve our capacity to preserve them and to manage them in a sustainable way. I wrote this chapter with this hope in mind.

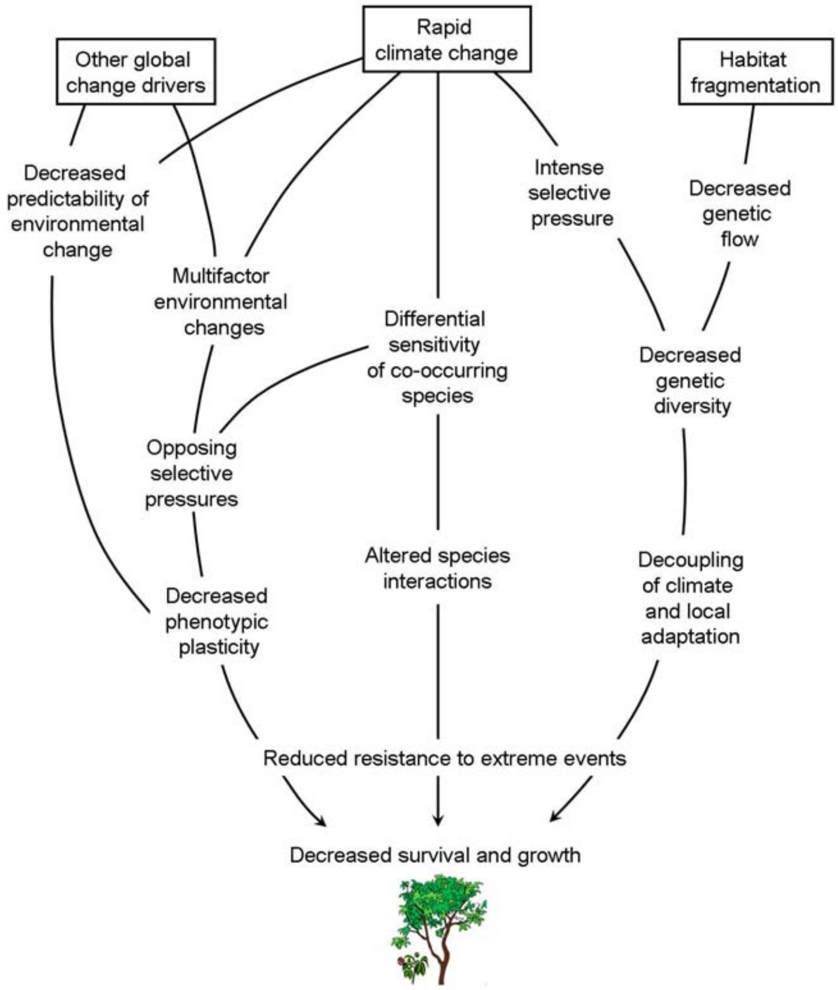

Figure 1. Interactive effects of global change drivers on plant survival and growth. Rapid climate change is at the centre of a whole suite of environmental changes that is imposing complex and opposing selective pressures to forest species; this in turn limits the extent and ecological benefits of phenotypic plasticity, modifies species interactions, and decouples climate and local adaptation, leading to an increased vulnerability to extreme climatic events and to a higher risk of mortality under the new climatic scenarios. The ideas of habitat fragmentation and climate change effects on genetic diversity and local adaptation are taken from Jump and Peñuelas (2005)

2. THE COMPLEXITY OF CLIMATE CHANGE AND OF ITS EFFECTS

2.1. The Many Sides of Climate Change

Climate is changing rapidly and in various and complex ways since anthropogenic climate change is much more than global warming. It is not only mean air temperatures that are rising but also the frequency of extreme climatic events (Meehl *et al.*, 2007). Unusual heat waves and frosts are becoming more frequent together with severe droughts in arid and Mediterranean regions and floodings in many temperate and subtropical zones (Castro *et al.*, 2004b; Christensen *et al.*, 2007; Inouye, 2000)}. The intensity of the radiation reaching the ecosystems is also changing. After studies reporting a global dimming (i.e. a global reduction in the radiation reaching the ecosystems due to reductions in the transmittance of the atmosphere, Stanhill & Cohen, 2001) during the second half of the XX century, recent revisions report a widespread brightening, showing a reversal from dimming to global brightening during the 1990s in agreement with changes in cloudiness and atmospheric transmission (Pinker *et al.*, 2005; Wild *et al.*, 2005). Irradiance is, thus, globally changing, with contrasting trends towards dimming or brightening depending on the particular region of the world (Matesanz *et al.*, 2007; Wild *et al*., 2005), and with a relative increase in diffuse over direct radiation due to increasing cloudiness and density of atmospheric particles (Roderick *et al.*, 2001; Stanhill & Cohen, 2001). All these climatic changes associated with global warming are leading to significant changes in the energy and mass balances in ecosystems all over the Earth. Obviously, underlying most of these climatic alterations is the rising of the concentration of greenhouse gases, particularly of carbon dioxide. And carbon dioxide is relevant not only because it is the key greenhouse gas but also because it is the very substrate of photosynthesis so plant productivity and vegetation dynamics are directly and indirectly influenced by atmospheric concentrations of CO_2 (Fig. 2). Thus, climate change is in reality a complex mix of changes in frequency and intensity of a wide range of factors. The different components of the current climate change affect differently each hierarchical level of the ecosystem, leading to cascade effects and complex feedbacks when responses are analyzed in processes ranging from the molecule to the whole ecosystem (Fig. 2).

2.2. The Many Sides (and Scales) of Ecosystem Responses to Climate Change

Terrestrial ecosystems exposed to the many aspects of climate change are already showing effects and responding (Buchmann, 2002; Camarero & Gutiérrez, 2004; Dullinger *et al.*, 2004; Richardson *et al.*, 2006; Saxe *et al.*, 2001, Menzel *et al.* 2006). Perhaps one of the most evident and general ecosystem effects of climate change is an altered energy and mass flux, and, in particular, a modified rate of evapotranspiration. Counterintuitively, evaporative demand from atmosphere (i.e. pantranspiration, which is correlated with potential evapotranspiration) is globally declining despite the rise of temperatures. The trend for decreasing evaporative demand has been reported throughout the Northern Hemisphere terrestrial surface and it seems to be also widespread in the Southern Hemisphere, as part of a greenhouse-related phenomenon (Michael L. Roderick & Farquhar, 2005). Cloudiness and decreased wind are the main reasons argued to explain this global pattern, but the real causes of this unexpected trend are far from established. Global warming is expected to increase evapotranspiration, but experimental studies of plant communities rendered a more complex picture (Zavaleta *et al.*, 2003). Another surprising trend in terrestrial ecosystems exposed to climate change is the increase in continental runoff through the twentieth century despite the more intensive human water consumption (Gedney *et al.*, 2006). Climate change and variability, deforestation, changes in irradiance and direct atmospheric CO_2 effects on plant transpiration have been suggested as possible reasons for this globally increased runoff. Using a mechanistic landsurface model and optimal fingerprinting statistical techniques to attribute observational runoff changes to these factors, it was concluded that twentieth-century climate alone is insufficient to explain the runoff trends. The trends were consistent with a suppression of plant transpiration due to CO_2-induced stomatal closure, representing the detection of a key direct CO_2 effect on the functioning of the terrestrial biosphere (Gedney *et al.*, 2006).

All this illustrates well that ecosystem responses to climate change are different at different spatial and temporal scales. There is a globally decreased evapotranspiration and increased runoff at a very large spatial scale, with important heterogeneities at intermediate scales, such as in arid and Mediterranean regions that tend to exhibit the reverse pattern. These heterogeneities can be magnified at the local or micro spatial scale, so evapotranspiration can decrease in a region of increasing aridity by counterintuitive responses of the vegetation. And the same applies to temporal scales, so results have to be interpreted differently if responses are explored within decades (e.g. Martínez-Alonso *et al.*, 2007), between decades (e.g. Matesanz *et al.,* 2007), over centuries (e.g. Woodward, 1987) or over longer periods of time. It must be noted that the notion of what is long for a period of time is logically dependent on the ecosystem process or property of interest (for a thorough discussion and interesting examples see Greenland *et al.*, 2003).

2.3. The Complexities Underlying Basic Responses to Climate Change

Climate has a strong control on plant survival, growth and reproduction. And vegetation is not only responding to warming and changes in water availability but also to changes in the diffuse fraction of irradiance, so its productivity and structure is strongly influenced by changing clouds and atmospheric particles. Thus, changes in irradiance are both cause and consequence of climate change, and direct effects on vegetation and feedbacks are complex but significant. As an evidence of this, the decline in atmospheric CO_2 concentration observed following the mount Pinatubo eruption was in part caused by the increased vegetation CO_2 uptake induced by the enhanced diffuse fraction due to volcanic aerosols (Roderick *et al.*, 2001). Quantity and quality of the irradiance in the understory of a forest or within its canopy is crucial to many aspects determining ecosystem functioning including not only productivity but also species interactions and dynamics (Valladares, 2003; 2004a).

A changing climate is leading to a changing distribution range of plants and animals (Alcamo et al., 2007; Kullman, 2002; Parmesan, 1996; Sturm *et al.*, 2001). Climate change-induced changes in forest growth and distribution are the subject of intense investigation because of their impacts on the terrestrial carbon sink (Saxe et al., 2001). And climate change is leading not only to distribution shifts but also to phenological shifts, with significant advances in the timing of leafing and delays in the timing of leaf shedding, combined with changing reproductive and productivity peaks in many plant species (Peñuelas & Filella, 2001; Richardson *et al.*, 2006; Menzel *et al.* 2006; Alcamo *et al.,* 2007). Seasonal cycles will be differentially affected by climate change since species not only differ in their sensitivity to environmental changes but also in the cue that triggers their response. For instance, budburst is triggered by either warm temperatures, longer days or both depending on the species, and since only temperature but not daylength is changing only some species will anticipate budburst as climate change progresses (Sanz-Perez *et al.*, 2008). These altered phenologies coupled with differential tolerances of co-occurring species to distorted temperatures and water availabilities are leading to quick changes in the competitive abilities of species (Ogaya & Peñuelas, 2003; Peñuelas & Filella, 2001). But the overall result in terms of forest regeneration and dynamics is unknown. The few experimental and realistic results on climate change effects on community composition revealed that warm temperatures and drought resembling extreme climatic scenarios make the new assemblage of plant communities unpredictable, with composition and abundance changes affecting both common and rare species (Lloret *et al.*, 2004).

Despite the capacity of individual species to modify their phenology and to respond to climate change by acclimation and phenotypic plasticity, the overall performance of forest species seems to be, in general, negatively affected by climate change (Alcamo *et al.*, 2007). For instance, and contrary to expectations, ecosystem water-use efficiency of photosynthetic carbon uptake decreased during an exceptional drought in three Mediterranean forests dominated by Holm oak (Reichstein *et al.*, 2002). Populations of beech at their lower and southern most ranges are growing less (e.g. beech forests in Montseny, Spain, annual secondary growth is 49% less now than 50 years ago when mean temperature was 1.65 ºC lower, and the associated evapotranspiration was significantly lower as well, Jump *et al.*, 2006). Tertiary relict populations of *Frangula alnus*, *Rhododendron ponticum*, and *Prunus lusitanica*, among other species, are having difficulties in rendering viable seeds and juveniles in Mediterranean habitats of increasing aridity (Hampe, 2005; Mejías *et al.*, 2002; Pulido *et al.*, 2007).

2.4. Many Approaches to One Elusive Goal: a Mechanistic Understanding of the Responses

There is a globally increasing interest in monitoring and understanding the responses of Earth ecosystems to climate change (Alonso & Valladares, 2007), and there are many approaches to the study of forest responses to this complex environmental threat (Nabuurs *et al.*, 2007; Valladares, 2004b). Many important efforts of national and international research programs have focused on basic ecophysiological studies of forests aimed at monitoring and understanding their net gas exchange (e.g.Morales *et al.*, 2005). These research programs have rapidly scaled up in technological sophistication and ambition but they have remained surprisingly similar to the classical plant ecophysiology studies of the 70’s (Buchmann, 2002). Even though this research is essential for carbon balance modelling and for calculating the complex mass and energy balances at the biosphere level, I argue that they are insufficient not only to accurately estimate forest growth under future climatic scenarios but also to fully account for the already observed responses of forests to global change. As I will develop in the following, there are both important ecophysiological uncertainties that can alter the calculations of whole ecosystem carbon and water balances, and poorly understood ecological and evolutionary aspects that can significantly affect the response of forest ecosystems to global change.

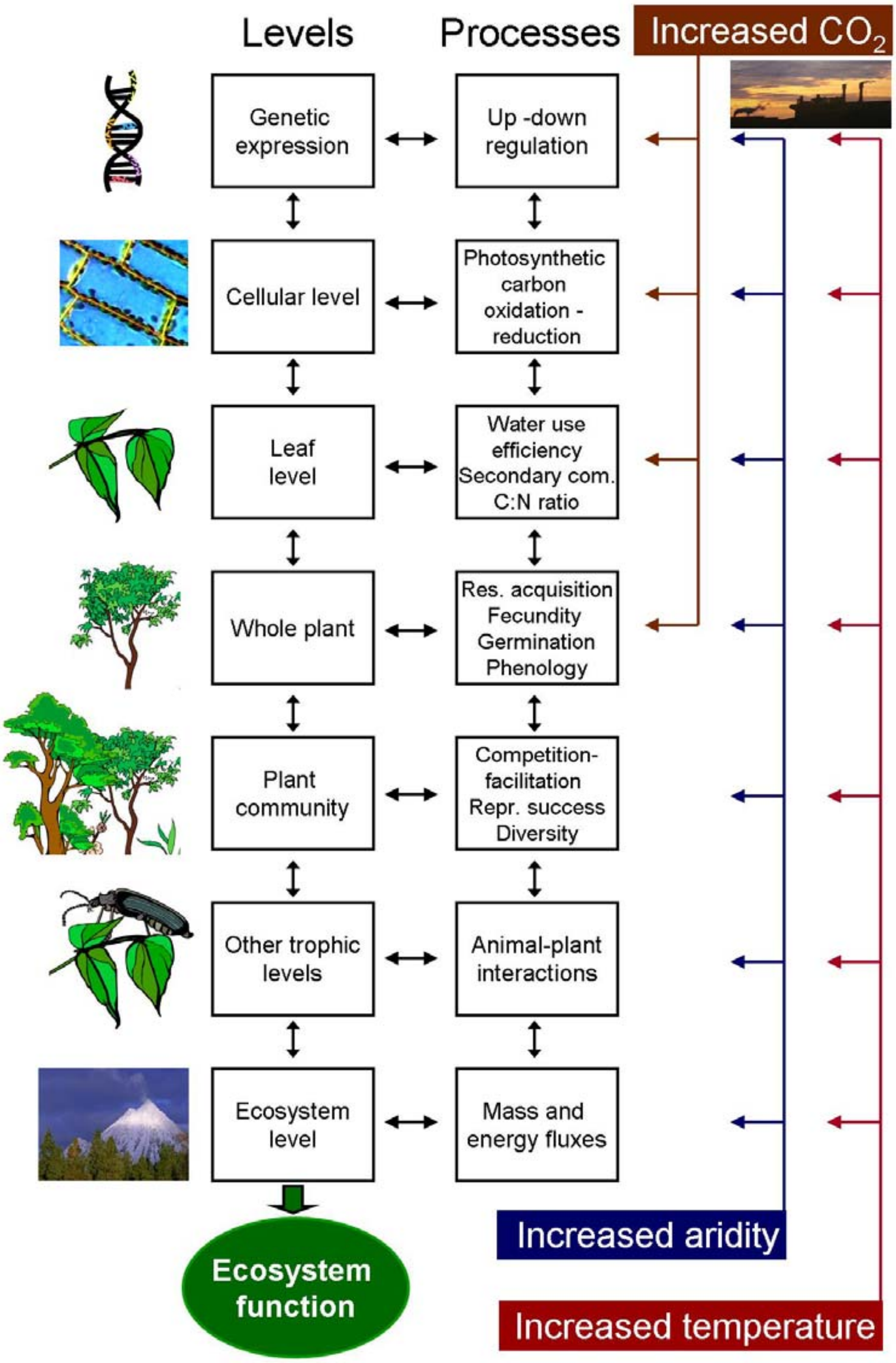

Figure 2. Impacts of rising atmospheric CO_2 concentrations and the associated increases in temperature and aridity for different organizational levels from the molecule to the ecosystem. Main processes being affected at each level are indicated. Inspired on ideas by Ziska and Bunce (2006) on plant responses to rising CO_2.

3. CLIMATE CHANGE AND TREE PHYSIOLOGY

3.1. Carbon Dioxide, at the Origin of the Problem and at the Core of Mitigation Plans

Climate change is primarily induced by increased greenhouse concentration in the atmosphere, with CO_2 as the most important one. But as mentioned before, CO_2 has itself an effect on plant performance since it is the basis for photosynthesis and growth and it has a significant influence in stomatal opening (Fig. 2, Gedney *et a*l., 2006; Fig. 2, Lambers *et al.*, 1998). It has been assumed that because increases in atmospheric CO_2 concentration usually enhance water use efficiency per unit leaf area, there will be a tendency for plants to show greater drought tolerance as well as increased biomass in the future. But critical examinations of plant responses to elevated CO_2 show that this assumption is seldom correct (Beerling *et al.*, 1996; Körner, 2003a).The progressive increase in the concentration of atmospheric CO_2 over the past centuries might have accentuated differences in drought sensitivity between co-occurring tree species but does not seem to have led to a generally increased water use efficiency and growth (Beerling *et al.*, 1996). General revisions of available information reveal that plant growth does not seem to be limited by carbon supply in a range of contrasting habitats, suggesting that little if any leeway exists for further CO_2 fertilization effects on growth (Körner, 2003a).

Forest ecophysiology has gained increased recognition due to the potential insights for understanding and managing terrestrial carbon sinks (Grace, 2004). Carbon sinks develop in ecosystems that have high carbon storage, such as mature forests, when these systems increase productivity, so that carbon gains by photosynthesis run ahead of carbon losses by respiration, and the stocks of carbon therefore increase (Grace & Zhang, 2006). The required stimulation may occur through elevated CO_2 concentration, nitrogen deposition or by climate change. Sinks also occur during the 'building' phase of high carbon ecosystems and there is agreement on the fact that carbon sinks are important in tropical, temperate and boreal forests, although their effect on a global scale is largely offset by deforestation in the tropics (Grace, 2004). Unfortunately, although the Kyoto Protocol provides incentives for the establishment of sinks, it does not provide incentives to protect existing mature ecosystems which constitute both stocks of carbon and carbon sinks (Grace, 2004).

Since respiration rates scale more rapidly with temperature than photosynthetic rates, understanding the effect of temperature on plant respiration is fundamental to predicting the impact of global change on the biosphere (Atkin & Tjoelker, 2003; Zaragoza-Castells *et al.*, 2007b). But respiration is not as well understood as photosynthesis (Cannell & Thornley, 2000; Grace & Zhang, 2006). Although respiration has been shown to be very sensitive to short-term changes in temperature (i.e. exponential rise with temperature with a Q_{10} of 2), the impact of long-term temperature changes depends on the degree of respiratory acclimation, which is not accounted for in most models (i.e. Q_{10} is not constant Atkin *et al.*, 2006; Atkin & Tjoelker, 2003). Respiration, which is an important component of carbon exchange in most terrestrial ecosystems and can release more than half of the total carbon fixed by photosynthesis, becomes particularly relevant in low-productivity ecosystems such as Mediterranean and boreal evergreen forests, since minor changes in respiratory rates may change the very sign of the overall carbon balance of plants living under limiting conditions and, in turn, of the whole ecosystem (Zaragoza-Castells *et al.*, 2007a). In these ecosystems, the reduced photosynthesis and increased respiration associated with climate change might increase the frequency and length of periods of negative carbon balance as suggested by studies in Mediterranean Holm oak forests (Joffre *et al.*, 2001; Rambal *et al.*, 2004; Zaragoza-Castells et al., 2007a).

During the last decade of the 20th century, deforestation in the tropics and forest regrowth in the temperate zone and parts of the boreal zone were the major factors responsible for CO_2 emissions and removals, respectively (Barker *et al.*, 2007). However, the extent to which the loss of carbon due to tropical deforestation is offset by expanding forest areas and accumulating woody biomass in the boreal and temperate zones is an area of contention since actual land observations and estimates using top-down models do not match. The growing understanding of the complexity of the effects of land-surface change on the climate system shows the importance of considering the role of surface albedo, the fluxes of sensible and latent heat, evaporation and other factors in formulating policy for climate change mitigation in the forest sector. Complex modelling tools are still to be developed to fully consider the climatic effect of changing land surface and to manage carbon stocks in the biosphere. The potential effect of projected climate change on the net carbon balance in forests, thus, remains uncertain (Barker *et al*., 2007).

3.2. Warming Temperatures and the Short Term Dimension of our Ecophysiological Knowledge

One of the main problems of understanding the effects of climate change on plant performance derives from the short-term nature of most ecophysiological studies. While most ecophysiological processes exhibit a dramatic response to a sudden increase in temperature, many regulatory and feedback mechanisms, and the capacity of plant to acclimate, significantly reduce the extent of such a response over the long run. This is exemplified by Körner (2006) with two paradoxes: i) the high contrast in the productivity of ecosystems operating at contrasting temperatures vanishes when the productivity is divided by the number of months available for growth, although the case is valid only for native vegetation with no severe water limitations; ii) while soil metabolism is very sensitive to temperature, respiratory fluxes during the growing season is quite similar from the Arctic to the tropics, being substrate driven and not temperature driven. The take home message from these two paradoxes is that temperature differences more than five times larger than those expected in the worse climate change scenario can have almost no effect on key ecosystem processes provided that there is time enough for the ecosystems to adapt to the new conditions. From a mechanistic point of view, the main challenge of current climate change for forest ecosystems is thus not the magnitude of the temperature rise but the speed of the rising together with the co-occurrence of many other environmental changes.

The time dimension of the study and of the plant responses to changing conditions have an important bearing on the choice of the response variable. While many ecophysiological efforts have gone into the characterization of photosynthetic responses, which are intrinsically short-termed, much less research has focused on plant growth, an essential ingredient to understand whole plant performance that is long-term. And the available studies show a remarkable uncoupling between growth and photosynthesis due to the important influence on growth of tissue density and duration and whole plant allometry (Körner, 2006). The scarcity of sound studies determining growth rates in a range of conditions should move more research in this direction if we are to understand plant responses to climate change since growth data are more informative than photosynthesis data: actual photosynthetic carbon gain is much less sensitive to temperature than growth, and growth is more strongly related to plant life than photosynthesis (Körner, 2006).

3.3. Climate Change as a Source of Stress

Ecophysiologists have been always attracted by the study of plant tolerance and responses to stress (see for example Larcher, 1995). And climate change is bringing a whole suite of abiotic stresses such as extreme temperatures, excessive irradiance and increased aridity, which are classic targets of ecophysiological studies. We now know that changing extreme temperature events are more relevant for plant survival than changing mean temperatures, with low-temperature extremes being particularly important. The climate is getting warmer but the chances for late or early season frosts are also increasing (Christensen *et al.,* 2007; Meehl *et a*l., 2007). The dangerous periods for plants are not the coldest or the hottest moments of the year, but the transitions, when the extreme event hits plants that are either dehardened or not fully hardened (Taschler & Neuner, 2004). And these transitional periods are getting less predictable and more variable. There is a common misconception that plants from cold habitats are cold stressed while they are in fact stressed when temperatures rise (Körner, 2003b). Global warming is favouring the invasion of cold habitats by frost sensitive species, which are outcompeting native, cold-adapted plants. But unusual frost events are then killing these invaders and the net result is a loss of species and a malfunctioning of the whole ecosystem. Climate change is thus challenging the very concept of stress and it is opening new avenues for research on stress physiology.

3.4. Our Limited Understanding of Co-Occurring and Interacting Stresses

Plants under natural conditions are simultaneously exposed to many limiting factors, and climate change is making this combination far more complex and intense. Although increasing attention is being paid to responses to multiple stresses, most of our knowledge comes from studies on responses to single stresses (see discussions in Mooney *et al.*, 1991; Valladares & Pearcy, 1997). Recent research has shown that the response of plants to a combination of several abiotic stresses is unique and cannot be directly estimated from plant responses to each of the different stresses applied individually (Mittler, 2006). Thus, the main ecophysiological challenge now relies in understanding plant responses to complex stresses (e.g. late frost, where timing and duration is even more important than temperature), to several interactive stresses (e.g. high light and drought or high light and freezing temperatures) and to relatively new combinations of stresses (e.g. low light and drought, Fig. 3), without overlooking biotic stresses (e.g. those induced by competing neighbours, herbivores, pathogens etc.; Figs. 3 and 4). This is not only a more attractive research arena but also an approach more likely to give a realistic view of ecosystem responses to global change, a truly multifactor phenomenon.

The effects that below-freezing temperature (frost) can have at times of year when it is unusual are an interesting ecological phenomenon that has received little attention (Inouye, 2000). The degree to which plants will suffer from frost damage in the future will depend on the interactions between temperature and precipitation, both of which are predicted to change, and also on the timing of cold snaps. According to some models, alder, birch and poplar trees will be affected and in general early- flowering trees will suffer greater frost damage in the future (Cannell *et al.*, 1989; Howe *et al.*, 2003; Inouye, 2000). The potential for climate change to influence the frequency and distribution of frost events is not fully understood yet but it is clear that will be very different for different regions, becoming more frequent in some areas and less frequent in others (Christensen *et al.*, 2007). Since the impact of frost events are also very dependent on the microclimatic and microtopographic circumstances of each site, and also on the frequency and duration of the events, they are a good example of a complex climate-change related phenomenon resulting from the interplay of different temporal and spatial scales.

A canopy imposes some light limitations to understory plants but it provides some protection against excessive irradiance, particularly harmful when photosynthesis is impaired by temperature or lack of water (Valladares *et al.*, 2005a), and it also protects against radiation frost (Ball *et al.*, 1991). Thus, the shade represents a fairly balanced situation of positive and negative aspects, with the outcome depending on the ecological and physiological features of each species occurring in the understory (Fig. 3). I argue that this balance is affected by climate change by making the negative aspects relatively more important than the beneficial ones, at least for plants from ecosystems characterized by a short growing season such as Mediterranean and arid ones.

Plant ecophysiology in the shade is particularly important for a mechanistic approach to the response of forest to climate change because on the one hand most of the individuals and species that will make up the forest of the future get established in the shade, and, on the other hand, several potentially limiting or stressful factors affected by climate change co-occur in the shade (Gómez-Aparicio *et al.*, 2006). Low light interacts with altered water and nutrient availabilities, temperature and herbivore pressure among other factors (Fig. 3). Shade is in itself a stress for most plants (Valladares & Niinemets, 2008), and it has been shown that shade tolerance is decreased under dry conditions, with significantly different responses among species to the interaction between low light and limited water availability (Sánchez-Gómez *et al.*, 2006a; 2006b).

Nocturnal temperatures in the shade are relatively warmer than in the open due to decreased radiative and convective heat losses; nocturnal air temperature in the shade can be up to 2.5 ^{o}C higher than in the open as has been found in continental Mediterranean forests (Valladares *et al.*, 2007b). The impacts of these warmer nights, expected to become even warmer, on the carbon balance of understory plants requires attention, particularly in low productivity forests where minor changes in respiration rates can affect the net balance of carbon. Temperature response of photosynthesis interacts with light availability, so the lower the light, the lower the temperature sensitivity of photosynthesis (Körner, 2006). Photosynthesis can be said to be largely driven by light with temperature playing only a marginal role. But this is not the case of respiration, so the warmer nocturnal temperatures experienced in the shade can have an important negative impact on the carbon balance of understory plants due to an enhanced respiratory carbon release in plants that are already carbon-limited for being in the shade (Fig. 3). However, not always the consideration of additional factors brings in more complexity: a recent study reveals that predictive carbon cycle models can assume that growth irradiance and photosynthesis do not significantly affect the temperature sensitivity of respiration of long-lived evergreen leaves (Zaragoza-Castells *et al.*, 2007b).

Our understanding of plants coping with stress is further limited by two facts: i) stress tolerance changes over the ontogeny of the plant (Niinemets, 2006), which is of great importance for long-living species such as trees, and ii) stress tolerance is not achieved by a single combination of traits or trait values, so evolutionary processes and individual responses to ecological conditions do not necessarily match as has been shown for tolerance to drought (Valladares & Sánchez-Gómez, 2006). The natural occurrence of simultaneous gradients of multiple abiotic factors (light, temperature, water and fertility) makes polytolerance, i.e. the capacity to withstand two or more uncorrelated stress factors, highly adaptive. However, the empirical evidence and a recent revision of stress tolerance of Northern Hemisphere trees and shrubs suggest that it is hard to achieve if possible at all (Niinemets & Valladares, 2006).

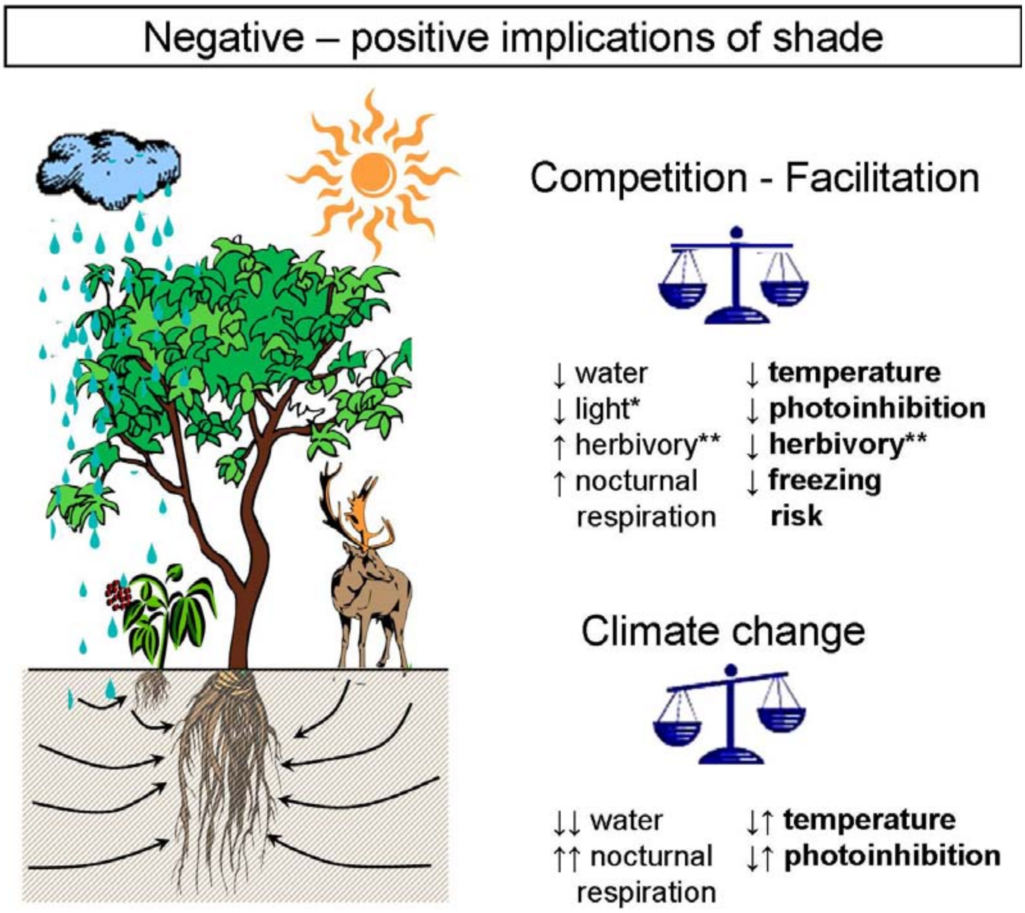

Figure 3. Many forest plants get established in the shade due to either higher density of propagules or better environmental conditions than in open microsites. However, not all effects of established plants (i.e. those casting the shade) are beneficial for understory plants. There is a balance of negative and positive implications of being in the shade. Understory plants compete with established plants for water and light and the latter affect herbivory and nocturnal respiration (warmer overnight temperatures) of the former. Understory plants may obtain some benefits by alleviated photoinhibition and extreme temperatures, although light availability might be too low in the shade. Even though transpiration is reduced in the shade, the overstory reduces the amount of precipitation reaching the ground and the roots of the established plants might deplete

*most of the water in the soil, leading to a rather dry shade. Climate change is expected to increase the negative effects of the shadein dryland ecosystems by further reducing water availability and by increasing nocturnal respiration of understory plants. Climate change is likely to decrease the magnitude of the positive effects of the shade in a number of ecological situations. * the negative impact of low light on carbon gain and growth depends on the shade tolerance of the understory plant (protégée);** herbivory has been shown to be higher in the shade since many animals spend more time feeding in the shade and plants tend to be less protected against herbivory when growing in the shade, but some nurse plants can bring special protection against herbivores, so the balance between the positive and negative impacts of shade on herbivory damage depends not only on the pressure and ecology of the herbivores but also on nurse plant identity.*

4. CLIMATE CHANGE, PHENOTYPIC PLASTICITY AND RAPID EVOLUTION

All organisms exhibit a certain degree of 'phenotypic plasticity', which is the ability of individuals to modify their behaviour, morphology or physiology in response to altered environmental conditions. And it has been suggested many times that plasticity is an effective way to cope with environmental change in general and with climate change in particular (see references in Valladares *et al.*, 2006). Plasticity *sensu lato* includes all sort of phenotypic responses to the environment that take place at different time scales, that might or might be not reversible, and that might or might be not adaptive (Piersma & Drent, 2003). In a rapidly changing environment, narrowly adapted populations with low plasticity in important characters might involve high probability of extinction. However, little is known about the plasticity of many key plants, particularly of those of great longevity such as trees (Rehfeldt *et al.*, 2001; Valladares *et al*., 2005a).

Various studies argue that global change should in principle favor high levels of phenotypic plasticity in plants (e.g. Rehfeldt *et al.,* 2001; Parmesan 2006). But more often than not, global change involves simultaneous changes in two or more abiotic and biotic factors, which can be expected to impose restrictions on plastic responses to the environment. Different pieces of evidence suggest that there is not a universal plasticity level that enhances fitness under multifactor changes. The complexity emerging from the simultaneous effects of several species and factors together with the interactions among them can explain the coexistence of species with contrasting plasticities and questions the notion that plastic phenotypic responses to global change are always adaptive (Valladares *et al.,* 2005b). Global change might alter phenotypic integration as suggested by the uncoupling of growth, foliage dynamics and cone production induced by mid-term climatic variability in a Scots pine population at its southern range (Martínez-Alonso et al., 2007). Thus, global change may both induce differential plastic responses in co-occurring species and influence features such as phenotypic integration that may in turn influence plasticity for certain traits (Valladares *et al.*, 2007a).

As argued for the tolerance to multiple stresses, plasticity in response to one factor (e.g. light) can be affected by another factor (e.g. water availability or herbivory pressure), so there are many ecological limits to phenotypic plasticity in plants (Valladares *et al*., 2007a). And examples relevant for understanding plant responses to climate change come from the acclimation to light. The light environment of the plant has been shown to affect the sensitivity of respiration to short- and long-term changes in temperature under controlled conditions and also in the field where other abiotics factors also varied (Zaragoza-Castells et al., 2007a; 2007b). Sun and shade leaves of the Mediterranean evergreen oak *Quercus ilex* were capable of approaching full acclimation to changes in the growth temperature. Seasonal changes in the thermal sensitivity (Q_{10}) of respiration were observed in this tree, with higher values in winter than in summer. However, while irradiance affected photosynthesis, it had no effect on the Q_{10} of leaf respiration although the latter rates were lower in shade-grown leaves than in their high-light grown counterparts (Zaragoza-Castells *et al*., 2007b). Nevertheless, *Quercus ilex* plants under shade showed respiratory thermal acclimation. Dynamics shifts of temperature response curves of respiration through the year were observed in the field under both sun and shade providing further evidence that these plants can acclimate (Zaragoza-Castells *et al.,* 2007a). What this kind of studies reveal is that acclimation must be taken into account in order to establish accurate leaf gas exchange models in systems like these Mediterranean oak forests with very low carbon inputs.

In addition to ad-hoc plastic changes over the life of an individual, there is another type of change at the level the genes that is being caused by rapid climate change. Many studies are showing that phenotypic plasticity is not the only way species has to cope with climate change, and perhaps for some plants not even the most important one. It has been repeatedly reported over the past several decades that rapid climate change has led to heritable, genetic changes in plant populations (Billington & Pelham, 1991; Etterson, 2004), so small plants with short life cycles and large population sizes will probably adapt to altered growing seasons and be able to persist (Franks *et al.*, 2007).

Since plasticity of most tree species seems not able to compensate for the current rate of environmental change, the option would be to take advantage of the capacity of trees for microevolutionary change (Fig. 1) (Jackson, 2006). But even this microevolution and local adaptation is not enough to compensate for the rate of change so many species are either going extinct locally or moving upward or northward at rapid rates: 6.1 m and 6.1 km per decade respectively (Jump & Peñuelas, 2005; Parmesan, 2006). This poleward range shift has important implications (Parmesan, 2006). The response of species to changing environments is likely to be determined largely by population responses at range margins (Hampe & Petit, 2005). In contrast to the expanding edge, the low-latitude limit of species ranges remains understudied, and the critical importance of rear edge populations as long-term stores of species genetic diversity and foci of speciation is becoming to be more and more appreciated (Hampe, 2005; Jump *et al.*, 2006). In fact low-latitude populations are often disproportionately important for the survival and evolution of forest species, and their ecological features, dynamics and conservation requirements differ from those of populations in other parts of the range.

5. SCALING UP TO THE COMMUNITY: SPECIES INTERACTIONS

All plants are killed by temperatures somewhere 46 and 56^{o}C, temperatures that are only found in nature near an unshaded soil in arid habitats (Körner, 2006). This fact drastically affect plant establishment in high irradiance environments and is the main reason for the initial requirement of some shading by the already established vegetation. This process by which some plants improves the conditions for other plants is named facilitation and it has been argued to be common among plants in stressful habitats (Bertness & Callaway, 1994). However, its generality in arid zones is far from absolute since plant-plant interactions dynamically switch from competition to facilitation and vice versa under still not well understood environmental conditions (Flores & Jurado, 2003; Maestre *et al.*, 2006). Climate change is affecting the net balance of plant-plant interactions, shifting competition to facilitation and viceversa depending on local conditions (Maestre & Cortina, 2004; Maestre *et al.*, 2005). Whether plants facilitate each other or compete against each other have profound implications in ecosystem functioning and it is a good prove of the importance of considering species interactions under climate change scenarios. Plant-plant interactions are known to play a key role in mediating the impacts of atmospheric nitrogen deposition, increased atmospheric carbon dioxide concentrations and climate change (Brooker, 2006).

Plant-plant interactions determine the regeneration of the forest. Many important tree species require other species to get established, specially at the southern or lower latitudinal or altitudinal range of their distribution. This is the case of Scots Pine (*Pinus sylvestris*), which requires facilitation by shrubs to get established in dry areas of the Iberian Peninsula (Castro et al., 2004a). But facilitation translates into competition depending on the particular conditions of each year (Tielborger & Kadmon, 2000; Valladares & Pearcy, 2002; Valladares *et al.*, 2007b) and there is no consensus on whether the shade cast by a potential nurse is always beneficial (Fig. 3, see discussions in Maestre et al., 2005, 2006). One way of solving the empirical discrepancies on the beneficial aspects of the shade is to consider the age of the protégé (i.e. the target plant). It is frequently the case that facilitation does take place in the very initial stages of plant germination and establishment, but as the protégé, there is a shift to competition (e.g. seedlings of *Pinus sylvestris* are initially facilitated by shrubs but then they compete with established trees Castro *et al.*, 2004a), which has been named the ontogenetic shift (Fig. 4, Miriti, 2006). I suggest that climate change will have a relatively higher impact on the initial stages of plant-plant interaction, making facilitation more transient and of a lower magnitude and, thus, decreasing the possibilities for forests to regenerate (Fig. 4). All this applies primarily to relatively dry ecosystems that are expected to become drier in the future. Interestingly, it has been recently shown in Mediterranean-type ecosystems that the ancestry of the lineage significantly determines the type of plant-plant interactions, with Tertiary species being facilitated by Quaternary species, the latter better adapted to the current levels of aridity (Valiente-Banuet *et al.*, 2006).

But plant-plant interaction is just one case of the more general situation of multiple species interactions, which includes those involved in predation, herbivory, pollination and dispersal. In fact, the differential effect of climate change on each of these interacting species might have more profound impacts on ecosystem functioning than expected from single species studies (Peñuelas & Filella, 2001; Parmesan, 2006). Butterflies might move uphill to escape the increasing heat, but their host plant might not ,so butterflies cannot feed and plants do not get pollinated (Wilson *et al.*, 2005), and the same applies to many other plant-animal systems that climate change may uncouple (Fig. 1).

In a changing world, a complex network of interacting species is more likely to survive than a simple one with just a few interactions (Bascompte *et al.*, 2006). And co-evolution becomes the key for understanding the chances of such a network to cope with environmental change. It is not only the trees that evolve, but all the co-occurring species and even the established interactions that evolve. Trees and their pathogens and herbivores are always changing, but antagonistic organisms usually have shorter generation times than the host trees, so they are more likely to outcompete trees in a long term evolutionary race. In support of this, it seems quite a general phenomenon that climate change is exacerbating the impact of pathogens with Dutch elm disease and chestnut blight as good forest examples (Harvell *et al.*, 2002). Trees have, though, many ways to compensate for this asymmetric rate of evolution and, interestingly, their longevity leads to the formation of mutualisms, opening a totally new front against pathogens and herbivores (Petit & Hampe, 2006). The fact that we are only beginning to understand the complexity of coevolutionary biodiversity networks should not deter us from considering them in realistic analyses of the capacities of tree to cope with environmental change.

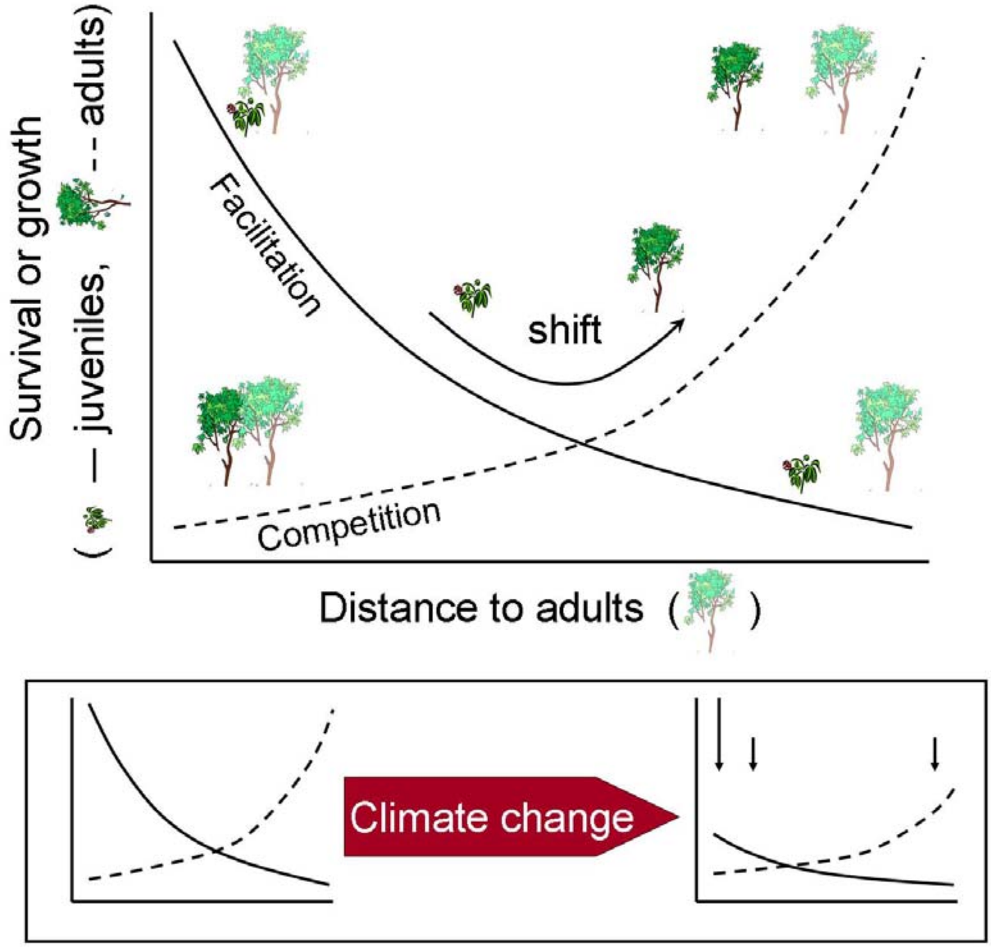

Figure 4. Performance of juvenile plants (expressed by any surrogate of fitness like survival or growth) versus distance to adult, established plants in the field. The initial facilitation of juveniles by adult plants shifts into competition at a certain ontogenetic stage (indicated by the arrow in the upper graph), so an increasing distance to adults becomes progressively more beneficial as the target plant grows. This ontogenetic shift may help to reconcile contrasting results on facilitation vs. competition outcomes on plant-plant interaction in dry ecosystems. It must be noted that the distance to the adult plant required for the shift from facilitation to competition is relative to the size of the adult plant; in the case of shrubs, the transition can be difficult to detect since nurse and protégé compete at early stages and short distances so the balance of the interaction may fluctuate more over time and over ranges of environmental conditions than in the case of trees; however, competition between understory plants and trees is highly asymmetrical so positive interactions might be less frequent. Plant performance will be in general negatively affected by climate change, and facilitation of juveniles by established adults is expected to be particularly reduced due to earlier and more pronounced competition for water. The idea of the ontogenetic shift in the facilitation by neighbour plants is taken from Miriti (2006)

6. THE CHALLENGE OF MODELLING DISTRIBUTION RESPONSES TO CLIMATE CHANGE

Climate change is a major threat for the maintenance of biological diversity worldwide, and modelling is a crucial tool for evaluating its overall impact and for accurate simulation of climatic scenarios and species potential ranges. The well-established relationships between temperature, precipitation and plant distribution included in global vegetation models allowed for direct predictions of the consequences of climate change on species distribution (Parmesan, 1996; 2006). And many of the predictions have been confirmed: the movement of forest species to higher elevations and latitudes as the climate to which they are adapted is displaced has been reported for numerous regions of the world (Camarero & Gutiérrez, 2004; Kullman, 2002; Lloyd & Fastie, 2003; Peñuelas & Boada, 2003; Sturm et al., 2001; Walther *et al.*, 2002). Some general rules, such as the 6^{o}C threshold temperature for plant development that establishes the treeline worldwide (Körner & Paulsen, 2004), seems to work well and can be easily incorporated in modelling exercises of plant distribution under new climate scenarios. However, there are many important uncertainties, such as the capacity and speed of acclimation and plasticity, which need, first, to be better understood and, second, explicitly accounted for in the models.

Mechanistic, and not only phenomenological, models are needed to advance our predictive capacity, but they must incorporate feedbacks due to the response of the organisms to the environmental change and not only the physiology underlying these responses. For instance, global warming is expected to increase evapotranspiration, causing soil moisture declines that can be more important than changes in precipitation in arid systems. But the models that predict this drying do not incorporate direct biotic responses to warming. Interestingly, the interactions between warming and the dominant biota in a grassland ecosystem produced the reverse effect on soil moisture, suggesting that declines in plant transpiration mediated by changes in phenology can offset direct increases in evaporative water losses under global warming (Zavaleta *et al.*, 2003). The importance of phenotypic plasticity as a buffer against extinction has not been widely appreciated. In fact, the extent of species losses may have been overestimated in many simulations of distribution shifts induced by global change because the plasticity of species is not considered (Thuiller *et al.*, 2005). Araujo and Guisan (2006) have revised the new challenges for modelling species distribution, suggesting the revision of the niche concept and the improvement of model parameterization among the five most important ones. However, they did not explicitly mention mechanisms, although they were somehow included under the niche concept, which is in turn highly contested (Gravel *et al.*, 2006). I argue that not only mechanisms must be incorporated into the modelling of the changes of species distributions but also that mechanisms must not be limited to ecophysiological ones: they should at least include the most essential ingredients of evolutionary biology (e.g. genetic diversity, rate of evolution, phenotypic plasticity) and community ecology (e.g. species interactions). The most immediate challenge, though, would be to learn how to incorporate them into the models.

Our knowledge on genetic diversity, phenotypic plasticity, and ecophysiological performance of fragmented populations of trees in a changing climate is still very limited. Bioclimate envelope models can serve as a first approximation, but future management and conservation strategies require models that incorporate more detail and attain greater biological realism (Hampe, 2004; Hampe & Petit, 2005).

7. THE CASE OF MEDITERRANEAN FORESTS

Most of our knowledge on forest ecology comes from temperate and tropical forests, but dryland forests such as those in Mediterranean-type regions have received much less attention. And this is not only a gap in scientific knowledge but also a serious limitation in our capacity to anticipate and mitigate the effect of climate change on forests because climate change is expected to affect these forests more dramatically than most temperate and tropical forests (Barker *et al.*, 2007; Christensen *et al.*, 2007). Mediterranean forests in a changing climate are exposed to at least two distinct features: a) the unpredictability of the timing and intensity of drought, the most limiting factor, and, b) the combination of several limiting abiotic factors, which involves functional trade-offs and imposes conflictive selective pressures. Given the magnitude of forecasted climatic trends, there are great concerns for the particularly rich biodiversity found in the region (Alcamo *et al.*, 2007). These features, which can be shared to same extent by a number of forests worldwide, make Mediterranean forests a fitting study case of the challenges entailed by a changing climate. Besides, Mediterranean woody flora is represented by taxa originated under very different climatic conditions (Petit *et al.*, 2005; Suc, 1984). Interestingly, the high biodiversity of the Mediterranean basin is due at least in part to the effects of previous climate changes since the region has in fact acted as a glacial refuge for many groups of species (Carrión *et al.*, 2003). The present-day tree flora of the Mediterranean Basin is made up of both very resilient taxa that have already experienced many abrupt and intense climate changes in the past (Benito-Garzon *et al.*, 2007; Petit *et al.*, 2005), and of very vulnerable taxa that are climatically isolated and geographically restricted to places where local, more humid conditions allow them to survive (Hampe, 2005). The latter are interesting not only from a conservation point of view but also as early warning systems of climate change. Relict tree populations in the Mediterranean Basin represent an evolutionary heritage of disproportionate significance for the conservation of European plant biodiversity.

Though a considerably resilience in the face of abrupt climatic changes in the continent is a necessary common feature for relict species of tropical origin to persist (Petit *et al.*, 2005), the functional attributes and the extent of phenotypic plasticity, local adaptation and genetic variability involved in their persistence are still poorly understood (Balaguer *et al.*, 2001; Hampe, 2005; Hampe & Petit, 2005; Valladares *et al.*, 2002). Mediterranean marginal populations of relict tree species usually concentrate in river belts, presumably because of down-slope habitat displacement from mountain slopes as the characteristic summer drought of these environments became more pronounced (Mejías et al., 2002). Despite the extremely low range filling in this drought-prone region, shift towards riparian habitats provides a likely explanation for the long term stability of peripheral populations. It is suggested that for these pre-Mediterranean species buffered range modification through habitat shift could be a widespread phenomenon, whose importance is likely to increase under the predicted decrease in precipitation (Pulido *et al*., 2007). For natural regeneration of many Mediterranean forest trees and shrubs, the shade cast by the established vegetation has been crucial. But climate change is making this shade too dry so the final balance of pros and cons of the Mediterranean shade might become more negative (Fig. 3), which may significantly change dynamics and long term stability of present day Mediterranean forests.

8. CONCLUDING REMARKS

Forests have been frequently exposed to important environmental changes over ample geological and historical periods of times, but the speed and the complex nature of the current global change impose a novel challenge that seems particularly hard to overcome. The intrinsically slow evolutionary rates of trees and the limits to their phenotypic plasticity imposed by complex environmental changes suggest a reduced capacity of forests to successfully cope with a rapid climate change coupled with many other simultaneous changes in the environment. Recent studies suggest that species with a long life cycle might not be able to cope with the rapid pace of climate change (Savolainen *et al*., 2004; Franks *et al.,* 2007; for a review see Parmesan, 2006). However, our knowledge is clearly insufficient. We do not have a clear picture of the real drivers of climate and atmospheric changes and of all relevant climatic aspects that are changing beyond the global rise of temperatures. We are beginning to understand forest responses to changes in individual environmental factors, but many factors are simultaneously changing and they act in concert, and many species, which differ in their sensitivity and responsiveness to environmental change, co-occur and interact with each other leading to a complex network of responses. It is only after we fill some of these basic gaps that we will be able to understand forest trends in a changing world and to interpret their capacity to cope with the plethora of phenomena and processes involved in the notion of climate change. However, scientific understanding of forest sector mitigation options is sufficient for a prompt start and immediate implementation of the forestry mitigation activities implemented under the Kyoto Protocol (Nabuurs *et al*., 2007). As argued for the case of ecological restoration of degraded ecosystems (F Valladares & Gianoli, 2007), we do not have to wait till all scientific uncertainties on patterns and processes of changing ecosystems are understood to mitigate and to adapt to the increasingly important ecological and socio-economical threats imposed by climate change.

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