Ecological and evolutionary responses of Mediterranean plants to global change

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Abstract

Global change poses new challenges for plant species, including novel and complex combinations of environmental conditions to which plants should adjust and adapt. Mediterranean ecosystems are recognized biodiversity hotspots but are also global change hotspots due to the concerted action of multiple environmental drivers. In the face of these changes, Mediterranean plants can migrate to more suitable habitats, adapt through natural selection, adjust via phenotypic plasticity or go extinct. In this paper, we review responses of Mediterranean plants to global change, specifically focusing on plastic and microevolutionary responses to climate change, and common factors that affect and limit such responses, such as habitat fragmentation.

The available evidence suggests that Mediterranean species can respond plastically to environmental change, but plasticity differs not only among species and populations but also among traits and environmental factors to which the plants are responding. Dry Mediterranean climates could limit the expression of plasticity in still uncertain ways. Although there is evidence for significant within-population evolutionary potential for functionally important traits in several Mediterranean species, little is known about whether this variation drives measurable evolutionary change. Habitat fragmentation exacerbates the negative impacts of climate change because it limits both the expression of plasticity and the evolutionary potential of plants. Invasive species, typically initiated as small populations in novel environments, provide important ecological and evolutionary insights on responses to global change that can foster specific research on Mediterranean plants. Our revision revealed that knowledge for Mediterranean plants is particularly scant on the constraints to plasticity, its adaptive value and its transgenerational potential, as well as on the fine-tuning of genetic change to environmental change.

Keywords: Mediterranean; evolutionary potential; local adaptation, environmental stress; global change; fragmentation; phenotypic plasticity; rapid evolution; fitness

1. Global challenges for Mediterranean plants

Mediterranean regions occur between 30° to 40° north and south latitude on the western or south-western coasts of continents, and are characterized by mild winters and the co-occurrence of high temperatures and low precipitation during the summer. Due to their high biological diversity, Mediterranean ecosystems have been recognized as biodiversity hotspots and a prime target for conservation efforts (Cowling et al., 1996; Lavorel et al., 1998; Myers et al., 2000). Mediterranean ecosystems are defined and configured by the climate, which is rapidly changing. Climate change in these ecosystems encompasses not only increased mean temperatures and lower precipitation but also increased variability and a higher frequency of extreme climatic events such as heat waves and droughts (Gao et al., 2006; Gao and Giorgi, 2008; Hoerling et al., 2011; IPCC, 2012; Lloret et al., 2012). But Mediterranean ecosystems are not only exposed to a changing climate. They have been profoundly transformed by human activities for centuries, and many of these activities are also changing resulting in increased habitat fragmentation, deforestation and land abandonment (Alados et al., 2004; Blondel et al., 2010; Fig.1). Because of the prevalence of multiple global change drivers in these regions and the uncertainties of the impacts of the many interactions among them, global change is expected to notably affect Mediterranean ecosystems at very different levels (Lavorel et al., 1998; Sala et al., 2000; Mooney et al., 2001; Matesanz et al., 2009; Matias et al., 2011; Gimeno et al., 2012; Doblas-Miranda et al., 2013).

Given current and future global change scenarios, the ability to tolerate and withstand novel and changing environmental conditions is critical for Mediterranean plants. Plants in Mediterranean environments possess distinctive trait syndromes and adaptations that can help them to cope with environmental stress and, presumably, also with environmental change (see section 2). When faced with global change, organisms can exhibit three main non mutually-exclusive responses. First, they can migrate to track more favorable environmental conditions (Hampe and Petit, 2005; Jump and Peñuelas, 2005; Parmesan, 2006; Lenoir and Svenning, 2013). Second, they can accommodate the novel environmental conditions via phenotypic plasticity (see Glossary, section 3), and, third, they can evolve through natural selection (Parmesan, 2006; Ghalambor et al., 2007; Jump et al., 2008; Visser, 2008; Hoffmann and Sgrò, 2011) (section 4; Fig. 1). The relative importance of these different responses for each species will depend on a variety of factors such as intensity and direction of the environmental change, life-history traits, standing genetic variation and interactions among coexisting species (Jump et al., 2009; Matesanz et al., 2010; Nicotra et al., 2010; Fig. 2).

Numerous observational and manipulative studies have illustrated some of these responses and have shown the effects of global change on Mediterranean vegetation (see Thuiller et al., 2005; Jump et al., 2006; Sarris et al., 2007; Matesanz et al., 2009; Gimeno et al., 2012). Although several studies have documented distribution shifts in Mediterranean species (see Peñuelas and Boada, 2003; Penuelas et al., 2007; Lenoir et al., 2008), little is yet known about the adaptive value of plasticity in functionally-important traits in Mediterranean plants (Valladares, 2008). Similarly, information on the evolutionary potential of Mediterranean plants and the ability to evolve adaptive plasticity is scarce, despite their implications for species’ persistence under global change (Crispo et al., 2010; Nicotra et al., 2010; Hoffmann and Sgrò, 2011; Hansen et al., 2012; Shaw and Etterson, 2012).

In this paper, we review documented responses of Mediterranean plants to global change, focusing specifically on plastic and microevolutionary responses and on the interacting factors that may favor or limit such responses. We first review studies showing plasticity of Mediterranean plants as a response to global change scenarios, particularly focusing in those where plasticity was shown to be adaptive, and the evidence for rapid evolution of Mediterranean plants in response to global change. Further and to gain insight into the evolutionary potential of plant populations, we highlight studies that show within- and among-population genetic variation in functional traits and plasticity, and discuss the role of habitat fragmentation in mediating ecological and evolutionary plant responses to the environment. We combine the revision with a short overview on key studies of invasive plants because they represent promising model systems to rapid responses in novel environments. We finally discuss the implications of our findings for predicting future responses of Mediterranean plants to global change.

2. Trait syndromes and adaptations of Mediterranean taxa

Extant flora of the Mediterranean is a complex mixture of taxa of various biogeographical origins and evolutionary histories, including more than 48000 species of flowering plants – about 20% of all known species– of which approximately 50% are endemic (Cowling et al., 1996; Blondel et al., 2010). Low rates of competitive exclusion resulting from the harsh environmental conditions in these resource-poor ecosystems, together with low growth rates, different strategies to cope with stress and a high frequency of disturbance events like fire and grazing are some of the determinants of the high plant species diversity of Mediterranean ecosystems (Cowling et al., 1996; Gratani and Varone, 2004; Maestre, 2004; Blondel et al. 2010; Bradshaw et al., 2011; Nurfadilah et al., 2013). Although very diverse, Mediterranean plant communities are dominated by stress-tolerant evergreen trees and shrubs, semi-deciduous shrubs, geophytes and winter annual herbs that often share morphological, anatomical and phenological traits, which have been commonly explained by an evolutionary convergence driven by the Mediterranean climate (Cowling et al., 1996; Davis et al., 1996). The reasons for such convergence are, however, controversial (see Cody and Mooney, 1978; Herrera, 1992; Verdú et al., 2003; Joffre et al., 2007; Ackerly, 2009; Blondel et al., 2010 for discussion on alternative or complementary explanations for the functional similarities among Mediterranean taxa).

Among the most ubiquitous and best-studied traits of Mediterranean plants are sclerophylly and evergreenness, leaf traits that have been associated with drought tolerance and low resource availability (Salleo et al., 1997; Salleo and Nardini, 2000; Valladares et al., 2000; Mooney et al., 2001). In Mediterranean environments, plants are exposed to a combination of abiotic stress conditions, especially during the summer when low water availability is overlaid with high light intensity and high mid-day temperatures (Tenhunen et al., 1990; Davis et al., 1996; Martinez-Ferri et al., 2000; Valladares et al., 2000). The hard and thick sclerophyllous leaves allow plants to control transpiration and minimize water loss during water stress, something crucial for coping with summer drought (di Castri, 1981; Cowling et al., 1996; Blondel et al., 2010).

Tolerance of the multiple stresses imposed by the Mediterranean climate is also expressed in the form of complex physiological, anatomical and morphological adjustments and adaptations. For instance, when compared with plant species from other biomes, Mediterranean plants generally show higher water use efficiency under drought conditions (Gulías et al., 2003; Medrano et al., 2009). Increased water use efficiency (WUE) is achieved through a complex interplay of mechanisms leading to reduced water loss per unit of carbon gain. As soil water potential falls, stomata close to minimize water loss, reducing the risk of hydraulic failure. Stomatal closure necessarily impairs photosynthesis, but the relative decrease in net assimilation with respect to stomatal conductance is small, leading to increased iWUE as a result of partial stomata closure. This has been observed with measurements of iWUE in both controlled and field conditions (see e.g. Medrano et al., 2002; Gimeno et al., 2008; Medrano et al., 2009; Pias et al., 2010; Sánchez-Gómez et al., 2011; Gimeno et al. 2012; Klein et al., 2013). Analyses of carbon isotopic composition, delta-13C, in leaves and wood –a good proxy of intrinsic WUE at the time of tissue formation– confirm these observations (e.g. Damesin et al., 1998; Martinez-Vilalta and Pinol, 2002; Ferrio et al., 2003; Valladares et al., 2008; Aranda et al., 2010; Linares and Camarero 2012; Granda et al. 2013). Besides decreased stomatal conductance, increased WUE in response to drought is partly due to decreased mesophyll conductance, i.e. the resistance to the movement of CO_2 from the sub-stomatal cavities to the chloroplastic stroma, which is often attributed to modified membrane proteins such as aquaporins (Flexas et al., 2003; Gulías et al., 2003; Flexas et al., 2006; Galmés et al., 2007; Cano et al., 2013). Mediterranean plants also present other strategies to cope with summer drought, such as osmotic adjustments to maintain positive cell turgor through the accumulation of solutes, complex antioxidant and photoprotective defense systems that minimize drought-induced cell damage and the ability to grow deep roots (Gulias et al. 2002; Gratani and Varone, 2004; Hernandez et al., 2004; Padilla and Pugnaire, 2007; Warren et al., 2007).

Regardless of their evolutionary origin, the most common suite of morphological, physiological and life-history traits and adaptations present in Mediterranean plants enhances survival and viability under summer drought (Salleo et al., 1997; Valladares et al., 2000; Joffre et al., 2007; Medrano et al. 2009; Blondel et al., 2010; Grivet et al. 2013).

Furthermore, the high plant diversity in the Mediterranean likely reflects the different adaptive strategies of these taxa to cope with abiotic stress, which in turn can partly explain species' abundance and distribution in the Mediterranean region (Gulias et al. 2002; Gratani and Varone 2004).

3. Phenotypic plasticity of Mediterranean plants as an immediate, individual response to global change

Phenotypic plasticity is the capacity of a genotype to produce functionally different phenotypes in different environments (Sultan, 1995; Pigliucci, 2001). Phenotypic responses to different environments may include highly specific developmental, morphological and physiological adjustments that can enhance survival and persistence in those novel environments, and therefore, phenotypic plasticity is a major mode of adaptation in plants (Sultan 1995; Sultan, 2000; Pigliucci, 2001; Sultan, 2003; Valladares et al., 2006; Ghalambor et al. 2007). At the individual level, plasticity can buffer environmental change throughout the plant's lifetime, increasing further its tolerance to stress (e.g. short-term acclimation to light and water conditions). At the population –and ultimately species– level, plasticity can allow colonization and establishment in diverse habitats and therefore influence a species' ecological breadth (Pigliucci, 2001; Sultan, 2003; Gimeno et al., 2008). Furthermore, plasticity can provide an initial rapid response to environmental change that can later promote subsequent genetic adaptation (Ghalambor et al., 2007; Hansen et al., 2012) as well as influence patterns of evolutionary diversification by shielding genotypes from selection (Sultan 2000).

For these reasons, there is increasing interest in understanding the prevalence and importance of plasticity for plants under global change scenarios (Visser, 2008; Matesanz et al., 2010; Nicotra et al., 2010). Various studies argue that global change may favor high levels of adaptive phenotypic plasticity in plants (Parmesan, 2006; Nicotra et al., 2010; Hoffmann and Sgrò, 2011), although others suggest that plastic responses to global change may be less important than local adaptation leading to canalized phenotypes or range shifts due to costs and limits to plasticity (Jump and Peñuelas, 2005; Visser, 2008; Valladares et al 2007)(Fig. 1).

Long-lived organisms such as many Mediterranean shrubs and trees are exposed to large seasonal and interannual variability in environmental conditions throughout their life cycles compared to annuals or short-lived perennials (Cowling et al., 1996; Bolle, 2003; Blondel et al., 2010). Therefore, plasticity may be of greater benefit to woody plants compared to short-lived taxa under global change conditions (Willson, 1983; Santos-del-Blanco et al., 2013). However, the particular characteristics of the Mediterranean climate can impose restrictions on the expression of adaptive plasticity. First, Mediterranean climate can be highly unpredictable, which can limit plasticity if the environmental cues that elicit the plastic response are not reliable or there are costs to maintaining an induced phenotype when conditions change (DeWitt et al., 1998; Kawecki, 2000; Pigliucci, 2001; Valladares et al., 2002, 2007; Ghalambor et al., 2007; Sánchez-Gómez et al., 2008; Visser, 2008). Second, Mediterranean environments are characterized by the occurrence of simultaneous stresses or limiting abiotic factors that can involve functional trade-offs and impose conflicting selection pressures (Valladares et al., 2007, 2008 Gianoli et al., 2009). In fact, several studies have shown that certain Mediterranean plants growing under adverse conditions show a conservative strategy, with low plasticity and high phenotypic canalization of physiological and morphological traits (e.g. Valladares et al. 2000, 2002, 2005; Sack et al., 2003; Aranda et al., 2008; Quero et al., 2008; Sánchez-Gómez et al., 2008).

Despite the constraints observed and discussed in the expression of plasticity, numerous studies have provided evidence of the capacity of Mediterranean plants to adjust their morphology, physiology, phenology and reproduction as a response to varying temperature (Gratani et al., 2003; Cavender-Bares et al., 2005; Gimeno et al., 2008; Andivia et al., 2012; Kreyling et al., 2012; Klein et al., 2013), nutrients (Sardans et al., 2006; Andivia et al., 2012), light (Balaguer et al., 2001; Quero et al., 2008; Rubio de Casas et al., 2011; Zavala et al., 2011; Letts et al., 2012) and water availability (Chambel et al., 2007; Padilla et al., 2007; Baquedano et al., 2008; Gimeno et al., 2008; Ramirez-Valiente et al., 2010; de Luis et al., 2011; Sánchez-Gómez et al., 2011; Zavala et al., 2011; Kreyling et al., 2012; Limousin et al., 2012; Klein et al., 2013). These plastic responses have been observed in a number of Mediterranean trees, shrubs and herbs, and span over morphological and allocation traits such as specific leaf area or shoot: root ratio, phenological traits such as flowering and date of leaf senescence or size at reproduction, and physiological traits such as stomatal control and water use efficiency. For example, to functionally accommodate the high light conditions typical of Mediterranean sites, plants may express developmental modifications that minimize light stress, by decreasing specific leaf area and increasing leaf angle, producing thicker leaves and reducing the amount of chlorophyll content during the summer to alleviate overexcitation and enhance the photoprotective action of carotenoids (Kyparissis et al., 2000; Valladares et al., 2000; Mendes et al., 2001; Valladares et al., 2005; Valladares et al., 2008; Rubio de Casas et al., 2011). Likewise, to produce phenotypes that are functionally appropriate in moisture-limited conditions, Mediterranean plants may respond by allocating more biomass to roots and by increasing water use efficiency (Fernández et al., 2006; Padilla et al., 2007; Gimeno et al., 2008; Gianoli et al., 2009; Aranda et al., 2010; Sánchez-Gómez et al., 2011).

However, not all observed plastic responses are adaptive, i.e. enhance the plant's success in the environment that elicited the response (Sultan, 2000), but can also be neutral (non-adaptive; Ghalambor et al., 2007) or have a negative effect on fitness (Van Kleunen and Fischer, 2005; Crispo, 2007; Valladares et al., 2007; see response 1-3 in Fig. 2). In fact, examples of maladaptive plasticity do exist in Mediterranean plants (Valladares et al., 2002; Sánchez-Gómez et al., 2006; Baythavong and Stanton, 2010; Godoy et al., 2012). Formal tests of the adaptive value of plasticity in Mediterranean plants are not widespread, probably due in part to the interpretive limitations of the statistical approaches used to test for adaptation (Mitchellolds and Shaw, 1987; Sultan, 2000; Matesanz et al., 2012) and most studies assess whether a plastic response is adaptive based on ecophysiological and theoretical predictions. For example, Padilla et al. (2007) found that faster root elongation and greater absorptive root surface was correlated to enhanced relative growth rate under reduced moisture conditions in *Genista umbellata* and *Lycium intricatum*, two drought-tolerant Mediterranean shrubs. Ramírez-Valiente et al. (2010) explored key functional traits in 13 populations of *Quercus suber,* and found that plants with lower SLA presented larger aboveground growth in a dry year (but not in a wet year), agreeing with the observed pattern of plasticity of this trait, and suggesting that plasticity was adaptive. In a field transplant experiment, Santos-del-Blanco et al. (2013) found plasticity of size at reproduction in *Pinus halepensis* to be adaptive as a response to stressful conditions (see Gratani et al., 2003; Nahum et al., 2008 for other studies of Mediterranean species where plasticity is interpreted to be adaptive).

If phenotypic plasticity is indeed adaptive and leads to functionally appropriate phenotypes in contrasting environments, the same genotypes may be successful in varying temporal and spatial conditions, and therefore adaptive differentiation and selection for canalized phenotypes may be obviated (Sultan and Spencer, 2002). This can lead to the maintenance of genetic –and epigenetic– variation both at the within- and among-population level (Sultan and Bazzaz, 1993; Sultan and Spencer, 2002; Byers, 2005; Bossdorf et al. 2008), which can in turn have profound implications for subsequent adaptation to global change, since genetic variation is the substrate for natural selection (Jump et al., 2009; see next section). For Mediterranean species, several studies have shown that plasticity can indeed blur ecotypic differentiation (Baquedano et al., 2008; Mutke et al., 2010). For instance, Gimeno et al. (2008) found that *Quercus ilex* seedlings from contrasting natural habitats could similarly acclimate to heat waves and cold snaps, and Mutke et al. (2010) found high phenological plasticity in 34 accessions of *Pinus pinea* covering its natural range. In both studies, plasticity was sufficient to cope with the environmental heterogeneity experienced by these species, which prevented ecotypic differentiation. Interestingly, genetic assimilation, i.e. the process by which traits that were originally environmentally induced become genetically determined and canalized by directional selection (Pigliucci et al 2006; Ghalambor et al. 2007) can incorporate phenotypic novelties induced by environmental changes and thus accelerate evolution. Should genetic assimilation play an important role in adaptation to global change, species exhibiting high phenotypic plasticity could be less threatened by intense and rapid environmental change than presented in Fig. 2. However, this issue has not deserved attention in studies with Mediterranean species.

Another important –yet largely unexplored in Mediterranean plants– aspect of plasticity is transgenerational plasticity, i.e. the ability of parent individuals to alter specific developmental traits in their progeny (Galloway, 2005; Galloway and Etterson, 2007; Herman and Sultan, 2011). These non-genetically inherited paternal environmental effects can enhance offspring success when subject to similar stresses as those of the parental environment, and therefore these effects can improve plant performance under global change. Estimations of transgenerational plasticity require complex, usually large experiments where replicate parental plants are grown in contrasting conditions, and the offspring of these parents are subsequently raised in the same environments to evaluate functionally adaptive adjustments (Herman and Sultan, 2011). To date, we have not found studies properly documenting transgenerational plasticity in Mediterranean plants, probably due to the long life cycles of many of these species, which drastically limits the possibility of rearing multiple generations of the same species in controlled environments.

Epigenetic processes, i.e. heritable changes in gene expression and function that do not result from changes in DNA sequence (Richards, 2006; Bird, 2007), are thought to be related not only to phenotypic plasticity (see e.g. Herrera and Bazaga, 2013), including the transmission of environmental effects across generations such as the above-mentioned transgenerational plasticity, but also to the regulation of gene function induced by the environment within an individual's life cycle (Bossdorf et al., 2008; Richards et al., 2010; Braeutigam et al., 2013). Epigenetic mechanisms include DNA methylation –so far the best-studied mechanism–, post-translational modifications of histone proteins and regulatory processes mediated by RNA molecules (Bossdorf et al., 2008; Herman and Sultan, 2011; Braeutigam et al., 2013). Importantly, epigenetic variation can rapidly regulate plant responses to current and novel environmental stresses, which can be especially important for long-lived organisms such as trees species (Braeutigam et al., 2013). For example, Correia et al. (2013) studied DNA methylation and histone post-translational modifications in relation to heat tolerance in cork oak (*Quercus suber)* and found that these epigenetic mechanisms could play a critical role in the acclimation and survival of the species under high temperatures. Also, Herrera and Bazaga (2013) studying the spinescence of Holly (*Ilex aquifolium*) found a three-way link between the stress induced by herbivory, phenotypic plasticity and epigenetic changes, contributing to the notion that epigenetic variation can complement genetic variation as a source of phenotypic variation in natural populations, which is important in itself and also with regards to the evolutionary capacity of organisms exposed to new environments. Furthermore, epigenetic processes can increase the evolutionary potential of plant populations under global change scenarios (see next section) and contribute to their adaptive divergence (Bossdorf et al., 2008; Richards et al., 2010; Braeutigam et al., 2013; see Herrera and Bazaga, 2010 for an example).

Taken together, the available evidence suggests that Mediterranean species show some capacity to respond plastically to environmental change, but plasticity is likely to differ not only among species and populations (see section 3.3) but also among the traits involved in the response and the environmental factors to which the plants are responding. Furthermore, the particular idiosyncrasy of the Mediterranean climate may limit the expression of plasticity in still uncertain ways. Further studies should aim at increasing our understanding of limits to plasticity limits in Mediterranean plants, especially focusing on the determination of the adaptive value of plasticity in this type of ecosystems.

4. Evolutionary potential of Mediterranean plants in global change scenarios

4.1 Within-population evolutionary potential

Several studies have shown that evolutionary change can be rapid in a number of taxa (Jump and Peñuelas, 2005; Parmesan, 2006; Hendry et al., 2008; Hansen et al., 2012), including invasive species colonizing new areas and native species responding to rapidly changing conditions (Franks et al., 2007; Matesanz et al., 2010; Shaw and Etterson, 2012; Sultan et al., 2012). This indicates that evolutionary adaptation can be an important way for natural populations to cope with global change (Reusch and Wood, 2007; Hoffmann and Sgrò, 2011; Fig.1; see response 4 in Fig. 2), which can in turn affect predictions of colonization patterns as well as changes in species distributions (Benito Garzón et al., 2011).

Global change drivers, particularly climate change, can impose novel and strong selection pressures on plants (Davis et al., 2005; Jump and Peñuelas, 2005; Reusch and Wood, 2007; Hansen et al., 2012). For natural populations to adapt to these new conditions, sufficient genetic variance for relevant functional traits involved in adaptation needs to be present in the population, since heritable variation reflects evolutionary potential (Fisher, 1958; Falconer and Mackay, 1996; Jump et al., 2009). The evolutionary potential of a population can be investigated in a common garden with a known family structure. Significant differences among families (or clones) in the target trait signify its potential for evolution (Blows and Hoffmann, 2005; Hoffmann and Sgrò, 2011).

Mediterranean species, particularly long-lived ones, are believed to harbor large amounts of genetic variation due to survival in glacial refugia and high gene flow among populations (Petit and Hampe, 2006; Aitken et al., 2008; Robledo-Arnuncio, 2011). Several studies have estimated within-population genetic variation in several traits related to adaptation to drought. De Miguel et al. (2012) detected significant differences in water use efficiency, specific leaf area and stomatal conductance between clones of the same family in *Pinus pinaster* and moderate to high (broad-sense) heritabilities under drought conditions. Also for this species, Aranda et al. (2010) reported significant differences among families in biomass traits and isotopic discrimination, as well as significant (narrow-sense) trait heritabilities. Similarly, Fernández et al. (2006) found interfamily differences in growth, nutrient content and water use efficiency, and Santos-del-Blanco et al. (2010) showed variation in reproductive allocation in families within populations from contrasting sites. These studies suggest that *P. pinaster* has the potential to improve both physiological and overall performance as a response to the predicted increases in aridity.

A similar pattern of significant inter-clonal differences in key functional traits related to performance in dry conditions (e.g. specific leaf area, leaf area ratio, photosynthetic rate, stomatal conductance and intrinsic water use efficiency) was found by Sánchez-Gómez et al. (2011) for stone pine (*Pinus pinea*). These authors interpreted this pattern of intraspecific variation as potential for adaptation to short-term water deficit in this species. Further examples of the evolutionary potential of Mediterranean plant populations have been reported for *Pinus brutia* (Kandemir et al., 2010), *Quercus suber* (Ramírez-Valiente et al., 2011), *Pinus halepensis* (Santos-del-Blanco et al., 2010), *Hordeum spontaneum* (wild barley) and *Avena sterilis* (Volis, 2007). These studies show significant within-population genetic variation and/or significant heritabilities for a diverse array of reproductive, life-history, morphological, phenological and physiological traits such as reproductive allocation, seed size, specific leaf area, chlorophyll content, onset of flowering and cold hardiness. Since many of these studies used long-lived plants for which parental effects cannot easily be controlled, it is worth mentioning that part of the variation found may not be genetic but rather due to parental effects.

Interestingly, within-population variation can vary not only for different traits but also for different populations. In a detailed study with cork oak (*Quercus suber)*, Ramírez-Valiente et al. (2011) found that heritabilities and additive genetic variance greatly varied among populations. These results suggest that populations of the same species may differ in their adaptive evolutionary potential, with important implications for adaptation to novel environments, for future species distributions, and for the maintenance and distribution of genetic variation (Merilä and Crnokrak, 2001; Jump et al., 2009).

The presence of global change-related genetic variation in natural populations does not necessarily imply that there will be adaptation to the new conditions. Genetic correlations –or covariance– among traits can constrain the adaptive response to selection if two traits that are positively correlated are selected for in opposing directions (Etterson and Shaw, 2001; Walsh and Blows, 2009; Hoffmann and Sgrò, 2011). In a comprehensive study in a population of recombinant inbred lines of *Avena barbata*, Maherali et al. (2008) investigated whether there was genetic variation and covariation for leaf blade hydraulic conductivity, photosynthetic rate, stomatal conductance and time to flowering, to understand the potential for adaptive evolution of coordination between xylem and photosynthetic functions. They found a positive genetic covariation between photosynthetic rate and leaf hydraulic conductivity, suggesting that natural selection for increased photosynthetic capacity in arid environments would also cause indirect natural selection to increase xylem water transport capacity. This coordinated evolutionary change could reduce hydraulic limitations on gas exchange as well as increase nitrogen delivery to leaves, therefore influencing the evolution of mechanisms of drought adaptation in this species (see Ramírez-Valiente et al., 2011 for other studies where genetic correlations among traits are investigated as potential constraints for evolution in a Mediterranean oak). Furthermore, the rate at which environmental conditions change can also constrain adaptive evolution if species are not able to track predicted changes, despite the presence of genetic variation (Jump and Peñuelas, 2005; Reusch and Wood, 2007; Valladares, 2008; Shaw and Etterson, 2012).

Only a few studies have experimentally tested whether rapid evolution as a response to simulated global change is possible in Mediterranean species. Taking a novel molecular approach that can detect the signature of selection, Jump et al. (2008) provided evidence of rapid evolution as a response to drought and warming in the Mediterranean shrub *Fumana thymifolia*. These authors established replicated drought, warming and control (no manipulation) plots in a natural population of the shrub, and monitored seedling establishment for 7 years, after which leaf tissue was collected and used in a genome scan. When compared against control samples, high divergence had occurred in the drought and warming treatment samples, and several candidate loci (marking regions of the genome subject to natural selection) were detected, demonstrating rapid evolution in this species. In a conceptually similar study, van Dijk and Hautekeete (2007) studied the potential for evolutionary change in flowering time in the sea beet *Beta vulgaris* subsp. *maritime* using artificial selection. After only nine generations, the authors found that the necessary day length for flowering induction could be considerably reduced, which is considered an adaptive response under global warming conditions. Shaw and Etterson (2012) discuss other examples of within-population genetic variation and responses to simulated changes in non-Mediterranean species.

Collectively, these studies show that, although there is evidence for significant within-population evolutionary potential for functionally important traits in several Mediterranean species, little is known about whether this variation can drive a measurable evolutionary change. Further studies should focus not only on assessing genetic variation (distinguishing between parental environmental effects and genetic variation) and the genetic basis of adaptive variation (see e.g. Grivet et al. 2013) but also on studying potential constraints to the adaptive response, including genetic correlations among traits as well as the ability of populations to genetically track environmental changes that may be quite rapid (i.e. fine-tuning between the rate of environmental change, genetic variation and microevolution). Studies assessing evolutionary response to experimental simulations of global change scenarios –using novel molecular tools or classical artificial selection approaches– in long-lived species are particularly needed. Hansen et al. (2012) and Shaw and Etterson (2012) provide comprehensive description of methods to monitor adaptive genetic responses to environmental change.

4.2 Local adaptation as a source of preadapted genotypes

Responses to the novel selection pressures exerted by global change can also occur at the population as well as at the within-population level. Local adaptation –including clinal variation (see e.g. Grivet et al., 2011)– of populations of a species to contrasting climatic conditions can be taken as evidence for the existence of the underlying genetic variation necessary for a response to selection, and hence represents a species' evolutionary potential (Jump and Peñuelas, 2005; Reusch and Wood, 2007; Jump et al., 2009). For instance, populations adapted to contrasting regimes of water availability can produce genotypes well-adapted to drought that could persist and even expand under climate change.

Therefore, divergence among populations in traits related to adaptation to global change may represent an inherent source for stress-tolerant ecotypes (Hamrick, 2004; Reusch and Wood, 2007; Rose et al., 2009; Hoffmann and Sgrò, 2011; Camarero et al., 2012).

We reviewed the existent literature on local adaptation on Mediterranean species, and found 12 studies where there was evidence of local adaptation (Table 1). These studies span a wide variety of taxa such as evergreen oaks and conifers, annual and perennial herbs and shrubs and an aquatic plant. Local adaptation was evaluated in common gardens or via field reciprocal transplants or sowings, and in most cases, population divergence was found to have occurred as a response to local temperature and precipitation. For example, in a study with the high mountain plant *Silene ciliata*, Giménez-Benavides et al. (2007) found evidence of local adaptation in populations along an altitudinal gradient that underlies a drought stress gradient. Seedling performance (emergence, survival and growth) was higher for home seeds than for foreign seeds. Local adaptation at the rear edge of the species range can help counteract the loss of habitat expected due to global warming. Similarly, using a comparison between differentiation in neutral markers and quantitative traits that can have the potential to reveal the effects of natural selection, Badri et al. (2007) found that several quantitative traits of two coexisting herbs were significantly associated with eco-geographical factors such as rainfall and soil properties, a pattern consistent with selection for local adaptation. In a study with *Quercus ilex*, Camarero et al. (2012) found that plants from a xeric site, when grown in a common garden, had significantly higher leaf reflectance and trichomes than plants from mesic and continental populations. These morphological traits can play a key role in photoprotection by reducing the amount of solar radiation absorbed by the leaf, which can be critical both in summer and winter Mediterranean conditions. The higher photoprotection of the xeric ecotype may confer such genotypes with higher resistance to face the warmer and drier conditions expected for Mediterranean forests.

The presence of stress-adapted genetic variants in a species can be promising for its adaptation to global change. However, if environmental change involves the occurrence of truly novel environments (e.g. novel combinations of environmental factors), or environmental variation surpasses the range experienced by the species in the past (Crispo et al., 2010), current stress-tolerant ecotypes may still fail to provide a successful response for plants under global change (see response 5 in Fig. 2). Knowledge of future environments and selection pressures will help elucidate the role that preadapted, stress-tolerant ecotypes can play in future adaptation.

4.3. Evolutionary potential of phenotypic plasticity

Phenotypic plasticity is a property of the genotype and can have effects on fitness and, therefore, is in itself a trait subject to evolution by natural selection or other evolutionary mechanisms such as genetic drift (Schlichting, 1986; Scheiner, 1993; Pigliucci, 2001; Ghalambor et al., 2007). If there is genetic variation for plasticity in natural populations (genotype × environment interaction), and a positive correlation between fitness and the plastic response (i.e. plasticity is adaptive), phenotypic plasticity can evolve by natural selection (Via and Lande, 1985; Scheiner, 1993; Matesanz et al., 2010; Shaw and Etterson, 2012; Sultan et al., 2012; Fig. 1). In a recent meta-analysis, Crispo et al. (2010) calculated evolutionary rates for plasticity in response to anthropogenic disturbance. The study revealed that plasticity has evolved in several cases, including both increases and decreases in plasticity following disturbances such as increased ozone concentration or changes in the light environment, although the evolution of plasticity greatly depended on the focal trait as well as the study taxon.

Several studies have estimated within-population genetic variation for plasticity (i.e. its evolutionary potential) in Mediterranean species (Sánchez-Gómez et al., 2011; Sixto et al., 2011; de la Mata et al., 2012; de Miguel et al., 2012), although in most cases it has been quantified for crops or forage plants (e.g. Voltas et al., 1999; Gunasekera et al., 2006; Aslam et al., 2009). At the population level, divergence in plasticity patterns (population × environment interactions) represents evolutionary potential for a species, if a population expresses a more adaptive norm of reaction as a response to a particular environment compared to another population. Furthermore, population differentiation in plasticity suggests the potential for plasticity to mediate further population divergence as the environment changes. For example, if two populations converge in trait values in one environment (e.g. moist conditions) but diverge in a different environment that resembles future conditions (e.g. drought conditions), it can be expected that population differentiation will increase with time, with important implications for future adaptation and speciation (Thompson, 1999; Pfennig et al., 2010 and references therein).

We found 13 studies where population divergence in plasticity patterns has been assessed in common conditions for 12 Mediterranean species, including trees, shrubs, herbs and grasses (Table 2). While these studies generally showed significant plastic responses of all populations to the test environments, we found no clear pattern as to whether phenotypic plasticity differs among populations in Mediterranean plants, as only half of the studies showed evidence of divergence among populations in patterns of plasticity (population × environment interaction). As for other quantitative traits, lack of genetic variation for plasticity may be due to costs of plasticity, genetic correlations and past selection (DeWitt et al., 1998; Agrawal, 2001; Relyea, 2002). Moreover, population divergence in plasticity depended on the study traits and sampled populations as well as the environmental factors to which the plants were subjected. For example, Santos-del-Blanco (2013) reported high population variation for plasticity for growth traits but no variation for reproductive traits in *Pinus halepensis*, and Volis (2002) found that population divergence in plasticity varied among reproductive, fitness and resource allocation traits in *Hordeum spontaneum* (Table 2). Similarly, the same species may show population variation for plasticity as a response to one environmental factor –or in a specific portion of the environmental gradient– and no variation in response to a different factor. For instance, Gimeno et al. (2008) found similar plasticity patterns in populations of *Quercus ilex* as a response to drought and cold, but Gratani (2003) found high population divergence in plasticity as a response to seasonal changes in temperature in the same species.

The studies outlined above demonstrate that population differentiation in plasticity as a response to environmental change does exist in several Mediterranean species. However, little is known about whether this is a general rule and how populations differ in patterns of plasticity for different traits and environmental factors. Future research should focus on these aspects as well as on understanding whether the existing reaction norms will still be adaptive under future conditions (Visser, 2008).

5. The interactive influence of habitat fragmentation on plant responses

Land use change, including habitat loss and fragmentation, is one of the most severe drivers of biodiversity, particularly in Mediterranean systems that have been transformed for centuries (Sala et al., 2000; Millennium Ecosystem Assessment, 2005; Lindenmayer and Fischer, 2006). Habitat fragmentation reduces the sizes of populations and increases their isolation. These changes, in turn, have important ecological and genetic effects on plant populations, such as disruptions in plant-animal interactions, increased genetic drift and inbreeding, lower gene flow and reduced genetic variation (Young et al., 1996; Honnay and Jacquemyn, 2007; Leimu et al., 2010).

The consequences of habitat fragmentation for Mediterranean plants are many. First, fragmentation can reduce individual plant fitness and increase a population's extinction risk due to environmental and demographic stochasticity (see e.g. Lazaro and Traveset, 2006; Matesanz et al., 2009; Rabasa et al., 2009; Gonzalez-Varo et al., 2010; Pias et al., 2010). Second, fragmentation can prevent plant migration if suitable habitat patches are not sufficiently connected to allow gene flow via pollen and seeds (Jump and Peñuelas, 2005; Albaladejo et al., 2009; reviewed in Leimu et al., 2010; Fig. 1), especially for species with specific requirements for particular habitat characteristics such as narrow soil endemics (Matesanz et al., 2009).

But more important are the interactive and indirect effects that habitat fragmentation can have on the adaptive potential of plants to other global change drivers such as climate change. Reduced genetic variation associated to fragmentation can limit the evolutionary potential response to global change of plant populations (Young et al., 1996; Leimu et al., 2010; section 3.1). For example, López-Pujol et al. (2003) found extremely low levels of genetic variation in Iberian populations of the threatened coastal sand dune plant *Stachys marítima* due to severe, human-mediated fragmentation, and Ortego et al. (2010) reported reduced genetic variability and increased genetic differentiation in holm oak from fragmented populations. Interestingly, the effects of habitat fragmentation can be species-specific, with important implications for long-term community composition and dynamics. For example, Aparicio et al. (2012) compared the genetic diversity and structure of four co-occurring woody species with contrasting life histories from a highly fragmented forest in south-western Spain, and evaluated the effects of fragment size, historical and current connectivity, and stability. They found that, although the genetic diversity of three out of four species was affected by fragmentation, each species responded differently to the set of fragment features considered.

In addition to reducing genetic variation for fitness-related traits, habitat fragmentation can also reduce genetic variation for plasticity. However, to our knowledge, this hypothesis has not yet been tested in Mediterranean plants. A few studies have tested whether populations from small and isolated fragments are less plastic than those from large and connected fragments in non-Mediterranean species, with mixed and sometimes contradictory results (see Kery et al., 2000; Berg et al., 2005; Paschke et al., 2005). Future studies should focus on the evaluation of the amount of genetic variation for quantitative traits and plasticity along fragmentation gradients in co-occurring species and how such variation can influence the evolution of Mediterranean plants in response to global change.

6. Lessons from invasive species

Nearly all regions of the Earth are subject to biological invasions, and the Mediterranean region, due partly to its long history of trade with distant parts of the world, is no exception (Lloret et al., 2005; Gritti et al., 2006; Gaertner et al., 2009). Numerous studies have focused on the various factors that can determine plant invasiveness in the Mediterranean, including key traits –or trait values– that promote survival and spread in a novel range, phenotypic plasticity and the ability to rapidly evolve (see e.g. Lloret et al., 2005; Cano et al., 2008; Godoy et al., 2011; Godoy et al., 2012).

Invasive species represent unequalled opportunities to study plant acclimation and adaptation to novel environments. When they are introduced into different biogeographical regions, non-indigenous species are often subject to new environmental conditions to which these species respond and potentially adapt (Mooney and Cleland, 2001; Sakai et al., 2001; Novak, 2007; Prentis et al., 2008). A remarkable feature documented in plant species invading the Mediterranean is their different phenology when compared to coexisting natives (Lloret et al., 2005; Godoy et al., 2009a; Godoy et al., 2009b). Godoy et al. (2009a) compared the flowering phenology of Spanish invasive species in their native and introduced range, and to that of coexisting native species. They found that invasive species did not shift their flowering phenology in the introduced range: tropical and temperate invasives flowered in summer, which contrasts with the spring flowering of native and invasive species of Mediterranean origin. The exploitation of empty temporal niches provides invasive species with a benefit from reduced competition with natives for abiotic and biotic resources (Godoy et al., 2009a; Godoy et al., 2009b). Accordingly, shifting physiological, phenological and reproductive temporal patterns can offer a stress-avoidance alternative to cope with changing conditions for Mediterranean native species, a possibility that is supported by observational studies (e.g. Peñuelas et al. 2002) but that has been little studied evolutionarily and mechanistically (e.g. Sánz-Pérez et al 2009).

Another relevant aspect of invasive species is their potential to rapidly evolve in the introduced range as a response to novel selection pressures (Lee, 2002; Buswell et al., 2011; Dormontt et al., 2011). Several studies have documented rapid evolution of mating systems (Barrett et al., 2008), phenological and life-history traits (Blair and Wolfe, 2004; Maron et al., 2004; Dlugosch and Parker, 2008), and reproductive traits (Lavergne and Molofsky, 2007; see Bossdorf et al., 2005; Matesanz et al., 2010 for further references on evolutionary changes between native and introduced plant populations). These evolved changes can lead not only to increased performance in the introduced range but also to the ability to expand the array of climatic conditions where invasives can establish (i.e. niche evolution, see e.g. Broennimann et al., 2007). For example, Cano et al. (2008) reported higher survival, relative growth rate, reproductive performance and plasticity in Spanish populations of *Senecio pterophorus*, an invasive shrub from South Africa, and pointed to post-introduction evolution as a potential mechanism involved in the observed differences.

Not only Mediterranean plants that are invading other ecosystems but also exotic plants invading Mediterranean habitats are excellent model systems to gain insights into mechanisms and constraints to plant adaptation to global change. Thus, the expanding research area of biological invasions can provide crucial empirical information to estimate future impacts of global change on Mediterranean plants.

7. Concluding remarks

Mediterranean plants are able to tolerate stressful abiotic conditions, and thus they can tolerate warming and increased drought to a certain extent. However, only species with significant phenotypic plasticity and particularly those capable of rapid evolutionary change both in their functional traits and in their plasticity will persist in the rapidly changing environmental conditions induced by global change. The available information reveals potential for some plant species for significant plasticity and rapid evolutionary change, even in long-living ones. However, this information is fragmentary and is pointing to large differences among species, with some of them being quite vulnerable to fast rates of environmental change. More research is needed to unveil whether the limits that Mediterranean ecosystems are observed to impose on the expression of plasticity indicate a limited adaptive value of plasticity or a constraint that could render beneficial to overcome. The field of transgenerational plasticity, for instance, remains largely unexplored in Mediterranean plants despite promising results with plants from other temperate ecosystems. The potential importance of genetic assimilation to incorporate phenotypic innovations and accelerate evolution is controversial (e.g. Pigliucci et al 2006) but deserves particular attention in a global change framework, a research attention that, to our knowledge, has not yet been given. The influence of fragmentation on the capacity of plants to evolve in response to climate change requires particular attention due to the ubiquity of the interaction between these two global change drivers in Mediterranean regions. Global change in Mediterranean ecosystems involves challenges both to natural plant populations to cope with this rapid environmental change and to scientists to understand the complex interactions among simultaneous drivers and to provide management guidance that could be no only fitting but available on time.

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Glossary

Acclimation: increased tolerance to stress and/or improved performance of a given organism as a result of structural and physiological adjustment to specific environmental conditions.

Adaptation: a trait or trait value that increases the ability of an individual to survive or reproduce compared to individuals without the trait or with a different trait value. Adaptation occurs over generations and not over the lifetime of an individual.

Ecotype: a genetically specialized population that has evolved specific adaptations to cope with a particular set of (often narrow) environmental conditions.

Evolutionary potential: the amount of heritable variation within a population that is available to be selected.

Fitness: the extent to which an individual contributes genes to future generations, or an individual's measure of performance expected to correlate with genetic contribution to future generations (such as reproductive fitness).

Global change: Anthropogenic environmental changes that alter the ecosystems, including local changes that have global effects. Global change drivers include climate change, land use changes, biological invasions and pollution.

Heritability: The proportion of phenotypic variance within a population that is attributable to differences among genotypes, i.e. a measure of how fast a trait can respond to selection.

Local adaptation: Adaptation of populations of a species to their specific home environments relative to other populations. To prove local adaptation, local genotypes in a population should have on average higher relative fitness in their local habitat than genotypes originating from other habitats.

Microevolution: Change in allele frequencies within a population.

Norm of reaction: A function that relates the environments to which a particular genotype is exposed and the phenotypes produced by that genotype.

Phenotypic plasticity: The property of a given genotype (population or species) to produce different phenotypes in response to distinct environmental conditions. When plasticity improves plant survival and reproduction, it is considered **adaptive plasticity**.

Rapid evolution: Evolutionary change that occurs in a scale of years to a few decades.

Stress: Reduced organismal performance due to adverse environmental circumstances. Typically applied to an abiotic factor such as extreme temperatures or drought.

Tolerance: capacity to maintain a given function (e.g. growth, survival, reproduction) under stress.

Trait syndrome: nonrandom pattern of covariation of morphological, life-history, and/or reproductive traits across taxa.

Table 1. Evidence of local adaptation in Mediterranean plants. Species name, growth form, type of experiment, number of populations/experimental units, traits measured, environmental factors to which populations are locally adapted and the main findings are given for each study. Only studies where local adaptation was detected are included.

Species	**Growth form**	**Type of experiment**	**Number of populations/ experimental units**	**Traits measured**	**Environmental factor(s)**	**Main findings**	**Reference**
Buxus balearica	Evergreen shrub	Field experiment	3 populations	Seed mass	Varying selection pressures (e.g. seed predation)	Observed seed mass matched predicted optimal seed mass in two of the three examined populations, suggesting local adaptive responses to the spatial mosaic of selective pressures	Lázaro and Traveset, 2009
Crepis sancta	Annual herb	Reciprocal transplants	Three populations from recently abandoned old fields	Growth and reproductive traits	Precipitation, soil conditions and community composition	Plants tended to have higher survival in their native sites	Imbert et al., 1999
Medicago trunculata and M. laciniata	Annual herbs	Comparison of neutral markers and quantitative traits	Four sympatric populations	19 quantitative traits and 20 microsatellites	Eco-geographical factors	Several quantitative traits were significantly associated with eco-geographical factors, consistent with selection for local adaptation. Correlations were more moderate for *M. laciniata* than for *M. truncatula*	Badri et al., 2007
Pinus brutia	Evergreen conifer tree	Long-term common garden	Six populations along altitudinal gradients	Growth traits	Clinal variation in environmental factors such as precipitation and temperature	Local adaptation to environmental gradients related to altitude	Kurt et al., 2012
Pinus nigra	Evergreen conifer tree	Common garden	Eight provenances throughout Europe	Cold hardiness	Factorial combinations of drought and warming	Provenances from colder origins reached superior cold hardiness	Kreyling et al., 2012
Pinus pinaster	Evergreen conifer tree	Common garden	23 populations sampled across the species range	Male and female reproduction and growth	Temperature and precipitation	Several female reproductive traits were correlated with a gradient of growth conditions, with populations from more unfavorable sites tending to commence female reproduction at a lower individual size	Santos-del-Blanco et al., 2012

Potamogeton pectinatus	Aquatic plant	Reciprocal transplants at three experimental sites across a latitudinal cline	54 genets, collected from 14 populations from four climatic regions	Growth and performance traits	Mean air temperature, mean water temperatures, and daily irradiance	Marginal populations showed changes in life-history traits that allowed them to perform better locally	Santamaria et al., 2003
Quercus ilex	Evergreen oak	Field experiment and common garden	3 field sites	Morphological and physiological parameters related to photoprotection	Precipitation regime, temperature	Morphological traits (e.g. trichome density and leaf reflectance) were higher in plants from the xeric site	Camarero et al., 2012
Quercus suber	Evergreen oak	Common garden	13 populations spanning a wide range of climates	Growth and key functional traits (leaf size, specific leaf area, carbon isotope discrimination and leaf nitrogen content)	2 years of contrasting precipitation	Inter-population differences in leaf size, SLA and Δ13C associated with rainfall and temperature at the sites of origin	Ramirez-Valiente et al., 2010
Silene ciliata	Perennial herb	Reciprocal sowings	3 populations along an altitudinal gradient	Seedling emergence, survival and size	Drought stress	Local adaptation in seedling survival and growth along the gradient	Giménez-Benavides et al., 2007
Thymus vulgaris	Perennial herb	Reciprocal transplants	Chemical forms from different climatic environments.	Survival and growth	Annual and summer precipitation, monthly maxima of warmest month monthly minima of coldest month	Evidence for local adaptation to either summer drought or severe early-winter freezing	Thompson et al., 2007

Table 2. Population variation for plasticity in Mediterranean species as a measure of potential evolution of plasticity at the species level. Species name, growth form, number of populations, experimental treatments where plasticity was quantified, traits measured and the main findings are given for each study.

Species	**Growth form**	**Number of populations**	**Experimental treatments**	**Traits measured**	**Evidence of population variation for plasticity**	**Reference**
Arrhenatherum elatius	Perennial grass	Three populations from woodland and three from open habitats for both diploids and tetraploids	Two light intensity levels	Morphological, phenological and fitness-related traits	No differences in phenotypic plasticity were observed between or within the ploidy levels	Petit and Thompson, 1997
Cistus albidus	Perennial shrub	Three populations that are exposed to differing temperature and precipitation	Factorial experiment with two irrigation treatments	Branch growth and leaf dimensions	Populations differed both in their manner of allocating resources and their response to availability of water.	Grant et al., 2005
Chaetanthera moenchioides	Annual herb	Seven populations from a strong latitudinal aridity gradient in Mediterranean Chile	Four watering treatments	Flowering-time, plant longevity and size of capitulum	Population divergence in plasticity only for time of senescence	Bull-Herenu and Arroyo, 2009
Hordeum spontaneum	Annual grass	Four populations along a stress gradient	Four treatments: no stress (optimum water and nutrients), water, nutrient and both water and nutrient stress	Reproductive, fitness and resource allocation traits	Plants from the four populations (or ecotypes) exhibited different patterns of plasticity in response to the different stresses (water and nutrients) and in different trait categories (reproductive, fitness and resource allocation)	Volis et al., 2002
Olea europaea	Evergreen tree	Six populations	Two exposures (fully exposed upper canopy and inner canopy leaves)	Eight morphological and physiological characters	Differences in plasticity between populations were only clearly significant for morphological traits in the field and for chlorophyll content in the common garden	Rubio de Casas et al., 2011
Pinus canariensis	Evergreen conifer tree	Natural populations, selected to cover a wide range of environments	Two contrasting watering treatments	Height, stem diameter and root, stem and leaves dry weight	Low phenotypic plasticity and no population divergence	Chambel et al., 2007

Pinus halepensis	Evergreen conifer tree	52 range-wide populations	Two environmentally contrasting sites	Vegetative growth, threshold size for female reproduction, Reproductive-Vegetative size relationships and reproductive efficiency	Genetic variation for plasticity was high for vegetative growth whereas it was non-significant for reproduction	Santos-del-Blanco et al., 2013
Pinus halepensis	Evergreen conifer tree	Natural populations, selected to cover a wide range of environments	Two contrasting watering treatments	Height, stem diameter and root, stem and leaves dry weight	High population divergence for phenotypic changes	Chambel et al., 2007
Pinus pinaster	Evergreen conifer tree	Ten populations that cover the distribution range of *P. pinaster*	Two contrasting watering treatments	Biomass allocation, growth and morphological traits	Drought tolerance and phenotypic plasticity to water availability did not differ among populations	Sánchez-Gómez et al., 2010
Pinus pinaster	Evergreen conifer tree	Natural populations, selected to cover a wide range of environments	Two contrasting watering treatments	Height, stem diameter and root, stem and leaves dry weight	High population divergence for phenotypic changes	Chambel et al., 2007
Pinus pinaster	Evergreen conifer tree	Four populations covering a latitudinal cline (France, Central and Southern Spain, and Morocco)	Two watering regimes	Different biomass partitioning variables, pre-dawn water potential, and isotopic discrimination of ^{13}C in needles (Δ) as surrogate of long-term water use efficiency	Absence of treatment by population interaction (except for Δ), i.e., lack of differences in plasticity between provenances	Aranda et al., 2010
Pinus pinea	Evergreen conifer tree	Natural populations, selected to cover a wide range of environments	Two contrasting watering treatments	Height, stem diameter and root, stem and leaves dry weight	The species showed marked allocational shifts and no population divergence in traits or plasticity	Chambel et al., 2007
Quercus coccifera	Evergreen oak	Three natural populations growing in contrasting environments on the Iberian Peninsula	Common garden at 100% and 20% full sunlight	Photochemical efficiency, xanthophyll pool, nutrient allocation, growth, crown architecture and light absorption	Populations diverged in their plastic response to the light environment, with the population from the most homogeneous light environments showing less phenotypic plasticity	Balaguer et al., 2001
Quercus ilex	Evergreen oak	Six selected populations from climatically contrasting localities	3 treatments (control, drought and cold treatment)	Maximum photosynthetic rate (Amax), instantaneous water use efficiency (iWUE), and thermal tolerance to freeze and heat	The observed plastic responses were similar for the six populations	Gimeno et al., 2008

Quercus ilex	Evergreen oak	Three different localities along a gradient from the north to the south of Italy	Common garden with seasonal changes in air temperature and precipitation	Morphological and anatomical leaf traits	Higher plasticity in the population from the most favorable environment	Gratani et al., 2003
Quercus suber	Evergreen oak	13 populations spanning a wide range of climates	2 years of contrasting precipitation	Growth and key functional traits (leaf size, specific leaf area, carbon isotope discrimination and leaf nitrogen content)	Population × environment interaction was very weak for all traits, suggesting low population divergence in plasticity	Ramirez-Valiente et al., 2010

Figure 1. Effects of global change on Mediterranean plants and potential responses. Inward arrows to the plant represent global change drivers affecting Mediterranean plants. Outward arrows from the plant denote potential responses to cope with global change. Dashed arrows represent constraints to plant responses. Plant drawing: Dr. E. Granda.

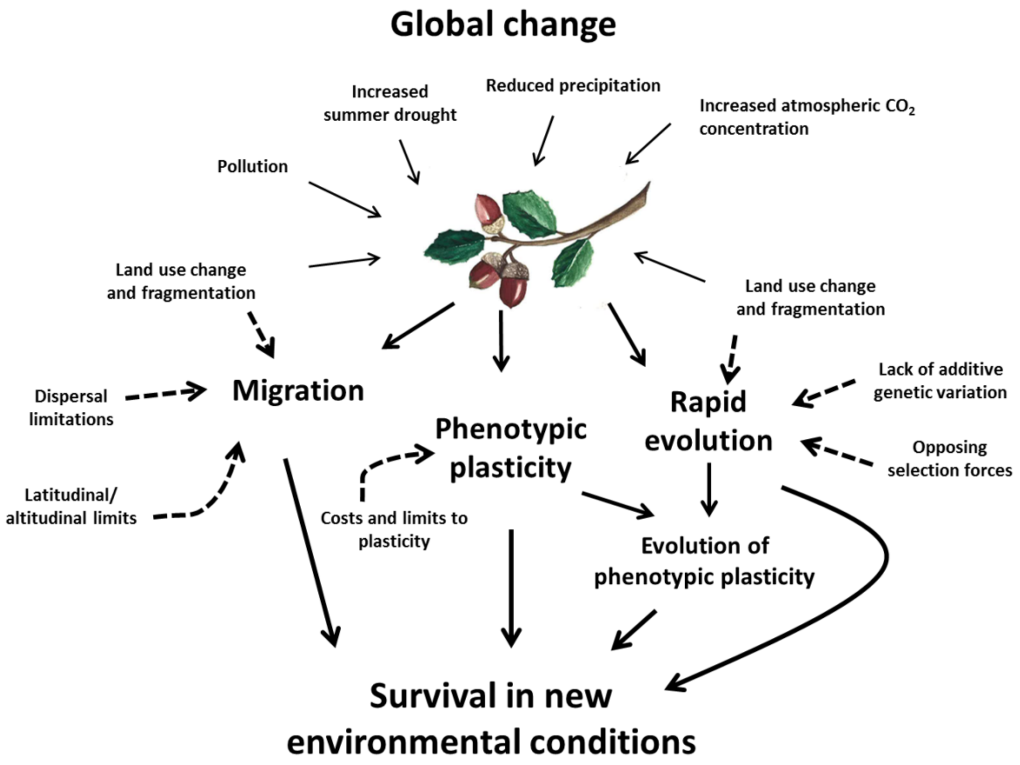

Figure 2. Theoretical framework representing the effect of the intensity of environmental change on the fate of species with contrasting stress tolerances and response abilities. When the intensity of the environmental change is low, species with different tolerances and response capacities coexist (left). As the intensity of the environmental change increases, the abundance of species that are not able to respond or whose response is not adaptive decreases. When the intensity of the environmental change is maximal, only species able to rapidly evolve (either adaptive traits, plasticity for these traits or both) will remain in the community. Pie charts represent the relative abundance of each species type. Relative size of the pie chart represent total number of individuals of all the species present in each case. Many species may exhibit intermediate or mixed strategies, which is not considered here for the sake of simplicity.