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# 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.



## 1. Global challenges for Mediterranean plants

Mediterranean regions occur between 30° and 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., 2012a,b; 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

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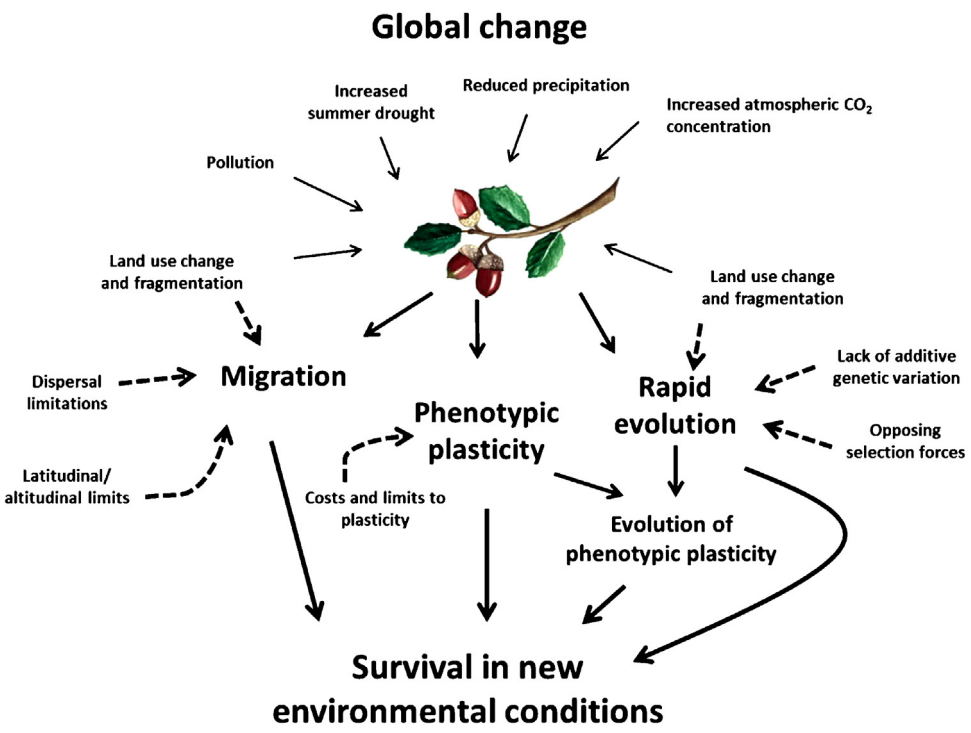


**Fig. 1.** Effects of global change on Mediterranean plants and potential responses. Inward arrows to the plant represent global change drivers affecting Mediterranean plants. Outward arrows from the plant denote potential responses to cope with global change. Dashed arrows represent constraints to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

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., 2012a,b). Although several studies have documented distribution shifts in Mediterranean species (see Peñuelas and Boada, 2003; Peñuelas 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 48,000 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).