

REVIEW ARTICLE

How does climate change affect regeneration of Mediterranean high-mountain plants? An integration and synthesis of current knowledge

L. Giménez-Benavides¹ , A. Escudero¹, R. García-Camacho¹, A. García-Fernández¹, J. M. Iriondo¹ , C. Lara-Romero² & J. Morente-López¹

¹ Department Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos-ESCET, C/Tulipán, Móstoles, Madrid, Spain

² Global Change Research Department, Mediterranean Institute of Advanced Studies (CSIC-UIB), Esporles, Mallorca, Balearic Islands, Spain

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Correspondence

L. Giménez-Benavides, Department Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos-ESCET, C/Tulipán, s/n. 28933-Móstoles, Madrid, Spain.
E-mail: luis.gimenez@urjc.es

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ABSTRACT

Mediterranean mountains are extraordinarily diverse and hold a high proportion of endemic plants, but they are particularly vulnerable to climate change, and most species distribution models project drastic changes in community composition. Retrospective studies and long-term monitoring also highlight that Mediterranean high-mountain plants are suffering severe range contractions. The aim of this work is to review the current knowledge of climate change impacts on the process of plant regeneration by seed in Mediterranean high-mountain plants, by combining available information from observational and experimental studies. We also discuss some processes that may provide resilience against changing environmental conditions and suggest some research priorities for the future. With some exceptions, there is still little evidence of the direct effects of climate change on pollination and reproductive success of Mediterranean high-mountain plants, and most works are observational and/or centred only in the post-dispersal stages (germination and establishment). The great majority of studies agree that the characteristic summer drought and the extreme heatwaves, which are projected to be more intense in the future, are the most limiting factors for the regeneration process. However, there is an urgent need for studies combining elevational gradient approaches with experimental manipulations of temperature and drought to confirm the magnitude and variability of species' responses. There is also limited knowledge about the ability of Mediterranean high-mountain plants to cope with climate change through phenotypic plasticity and local adaptation processes. This could be achieved by performing common garden and reciprocal translocation experiments with species differing in life history traits.

INTRODUCTION

High mountains are biologically relevant because they are home to island-like ecosystems and many narrow endemics (Nagy & Grabherr 2009). Their long past of tectonic uplifts and climate fluctuations have shaped multiple evolutionary processes that lead to a high level of taxon richness and rarity (Körner 2003). High-mountain zones are also ideal places to assess the ecological effects of current climate change, because they provide steep ecological gradients and a lower effect of human disturbance than lowlands (Grabherr *et al.* 1994; Dullinger *et al.* 2007; Körner 2007). For these reasons, high-mountain ecosystems have largely inspired scientists and naturalists around the globe. Most research in plant ecology has been centred in the temperate regions of Europe and North America, and more recently in the temperate regions of Asia and the Southern Hemisphere. Comparatively, some mountainous regions are underrepresented in the ecological literature of plant ecology, especially the tropics, subtropics and arid/semi-arid zones (Körner & Spehn 2002; Körner 2003). This is also

the case of mountains located in regions with a Mediterranean climate (characterised by the existence of a drought period during the summer; Aschmann 1973), although some efforts have recently been made (Escudero *et al.* 2012; Barrio *et al.* 2013; Gavilán *et al.* 2013; Doblas-Miranda *et al.* 2015).

Mountain ecosystems located in Mediterranean-type climates usually harbour remarkable levels of taxonomic diversity and singularity (Pauli *et al.* 2003; Väre *et al.* 2003; Stanisci *et al.* 2016). In a recent standardised sampling study through major European mountain ranges (GLORIA initiative), the percentage of plant endemism found on some Mediterranean sites was outstanding (Stanisci *et al.* 2005; Kazakis *et al.* 2007; Fernández-Calzado *et al.* 2012). Moreover, many arctic and alpine species in Europe find their southern limits in the Mediterranean region (Pauli *et al.* 2003; Kazakis *et al.* 2007; Stanisci *et al.* 2011; Van Gils *et al.* 2012; Gutiérrez-Girón & Gavilán 2013; Gentili *et al.* 2015). These marginal populations located at the eroding edge of the species' ranges are clearly distinguishable from a phylogeographic point of view (Médail & Diadema 2009; Feliner 2014), and usually survive in 'cold'

refuges next to their limits of environmental tolerance, so current climate warming may limit their viability dramatically (Médail & Diadema 2009; Hampe & Jump 2011; Abeli *et al.* 2014; Gentili *et al.* 2015). The magnitude of projected climate warming in Mediterranean mountains is similar in magnitude to those reported for other temperate mountain ranges (Nogués-Bravo *et al.* 2007). However, a characteristic trend of Mediterranean mountains is that warming is generally coupled with a reduction in precipitation mainly in spring and summer (Nogués-Bravo *et al.* 2007, 2008; Giorgi & Lionello 2008; Sillmann *et al.* 2013), declines in spring snowpack (Mote *et al.* 2005) and an increasing frequency of extreme events (Baldi *et al.* 2006; Della-Marta *et al.* 2007). This makes Mediterranean mountain ranges particularly sensitive to climate change (Giorgi 2006; Ballester *et al.* 2010; Zamora *et al.* 2016).

The present work briefly reviews the current state of plant regeneration ecology in Mediterranean high-mountain ecosystems (*i.e.* communities occurring above the tree line), with special reference to the risks associated with the sequential stages of plant reproduction and seedling establishment in the context of climate change (Fig. 1). We also provide evidence of diverse alleviating processes at individual, population and community scales that may counteract the negative outcomes of climate change. To provide an integrative view, our work is not geographically restricted to the Mediterranean Basin but covers other high mountains with a Mediterranean-type climate around the globe (McNeill 2002). Hereafter, we will collectively refer to them as ‘Mediterranean high mountains’. We try to synthesise recent progress, main gaps and further directions for research.

MODELLED ASSESSMENTS AND EMPIRICAL EVIDENCE OF EFFECTS OF CLIMATE CHANGE ON MEDITERRANEAN HIGH-MOUNTAIN FLORA

In the last decades, most projections of species distribution models (SDMs) based on climate change scenarios show that mountain plants are highly vulnerable to global warming (Theurillat & Guisan 2001; IPCC 2007; Mariotti *et al.* 2008). However, high-resolution analyses reveal different levels of risk of habitat loss across regions. Mountain ranges with narrow elevation gradients and limited extent above the tree line are the most susceptible to species extinctions because local flora has less space for upward migration than in larger mountain ranges (Marris 2007; Engler *et al.* 2011). This is the case of most Mediterranean mountains, with isolated peaks and limited surface of the highest bioclimatic belts (Gavilán *et al.* 2013; Jiménez-Alfaro *et al.* 2014). Unfortunately, the information derived from SDMs is more limited for Mediterranean mountains compared to other alpine habitats due to the lack of fine-grain plant distribution data in these mountains (but see Keenan *et al.* 2011; Benito *et al.* 2011; Ruiz-Labourdette *et al.* 2012). In any case, SDMs may under- or overestimate the effects of climate change on species’ distribution, because they do not consider the phenotypic plasticity, adaptive potential, dispersal efficiency or species interactions (Theurillat & Guisan 2001; Thuiller *et al.* 2008; Lavergne *et al.* 2010; Wisz *et al.* 2013; but see Cotto *et al.* 2017), so observational and experimental studies are also welcome to improve these projections (Valdareo *et al.* 2014; Ehrlén & Morris 2015). Also SDMs do not commonly take into account the fine-scale environmental

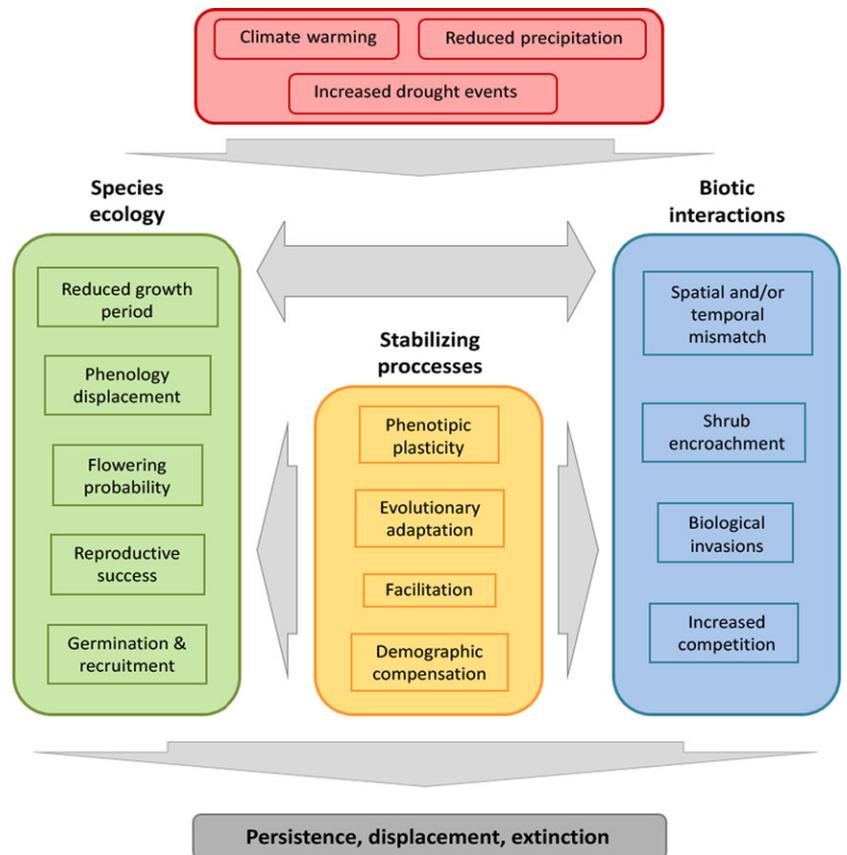


Fig. 1. Conceptual framework showing the potential effects of climate change on Mediterranean high-mountain plants based on the literature. Left-hand panel shows direct consequences of climate change on the sequential processes of regeneration by seed. Right-hand panel shows processes mediated by biotic interactions. Central panel highlights some processes that may provide resilience against changes.

conditions created by the topographic variability of steep mountain slopes, nor the plant–plant interactions such as facilitation, which may drive the composition and structure of alpine plant communities by ameliorating the harsh micro-environmental conditions that constrain plant performance and survival (Sutherst *et al.* 2007; Cavieres & Sierra-Almeida 2012; Michalet *et al.* 2014; McCullough *et al.* 2016).

Most studies dealing with the effects of climate warming on arctic and alpine plants worldwide have been performed by either experimental manipulation (direct responses to warming and reduction of snow cover and snowmelt timing, (e.g. Henry & Molau 1997; Dunne *et al.* 2003; Blankinship *et al.* 2014), or mainly through observational studies along climatic gradients as indirect support. Monitoring networks, like the GLORIA initiative (Gottfried *et al.* 2012) and other long-term ecosystem research (LTER) stations, have been implemented in Mediterranean high-mountain sites in the last decades (e.g. LTER Sierra Nevada; Pérez-Luque *et al.* 2016; Zamora *et al.* 2016). At European scale, the GLORIA consortium recognised two tendencies in plant species composition and abundance in the short term (7 years), with a rapid increase in richness in the northern European mountains, and a significant decrease in the Mediterranean summits (Fernández-Calzado *et al.* 2012; Gottfried *et al.* 2012; Gutiérrez-Girón & Gavilán 2013; Stanisci *et al.* 2016). Retrospective studies have also provided clear evidence of rapid vegetation changes in Mediterranean high mountains, both by re-visiting surveys (Petriccione 2005; Kelly & Goulden 2008; Jiménez-Alfaro *et al.* 2014; Evangelista *et al.* 2016) and analysis of historical aerial images (Peñuelas & Boada 2003; Sanz-Elorza *et al.* 2003; García-Romero *et al.* 2010) and palynological records (Dull 1999; Jiménez-Moreno & Anderson 2012). These surveys therefore confirm an upward shift of drought-tolerant lowland plants coupled to a decline in the frequency and number of highland specialists (Sobrino *et al.* 2001; Jiménez-Alfaro *et al.* 2014). Although the ‘escalator effect’ (Marris 2007) seems to be a general trend, the great challenge is to discern which factors are the main drivers: direct effects of climate warming, changes in land use (like reductions in livestock density) or a combination of these factors. Moreover, altitudinal shifts of species’ distribution may be more complex in Mediterranean-type regions where water availability increases in spite of warming. In California, Crimmins *et al.* (2011) found a significant downward shift in the optimum elevation of many species, likely as a result of a local increase in precipitation that has resulted in a net decrease in the climatic water deficit.

IMPACTS OF CLIMATE CHANGE ON REPRODUCTION AND REGENERATION OF MEDITERRANEAN HIGH-MOUNTAIN PLANTS: FROM FLOWER TO SEEDLING AND BEYOND

Effects of climate change on plant phenology and reproductive success

Flowering phenology in alpine ecosystems worldwide is mostly constrained by cold, so research efforts on the impacts of climate warming have focused frequently on the onset and success of reproductive phases (Körner 2003). In a warming scenario, with snow beginning later and melting earlier,

alpine plants would respond by flowering earlier and should be theoretically favoured by longer growing seasons (Molau 1993; Alatalo & Totland 1997; Molau *et al.* 2005). However, it is also important to take into account the specific reproductive risks associated with different phenological strategies. Some authors suggest that the early-flowering plants in alpine environments are especially vulnerable to pollinator limitation (Molau 1993; Totland 1997; Totland & Alatalo 2002; Kudo & Hirao 2006; Ladinig *et al.* 2013) and flower bud mortality from late spring frosts (Inouye 2008), whereas late-flowering plants are more susceptible to damage from frost events at the end of the growing season (Molau 1993; Galen & Stanton 1995). Nonetheless, the results of experimental warming studies on flower production and seed output with early- and late-flowering species are inconsistent, with either positive (Alatalo & Totland 1997; Arft *et al.* 1999; Kudo & Suzuki 2003; Aerts *et al.* 2004; Kudo & Hirao 2006), neutral (Totland & Alatalo 2002; Kudo & Suzuki 2003; Hovenden *et al.* 2008) or negative effects (Saavedra *et al.* 2003; Bokhorst *et al.* 2008). Therefore, the positive effect of a longer growing season on alpine plant phenology and performance has been challenged because other climate-driven processes can counteract it, such as shifts in species interactions from facilitation to competition (Klanderud & Totland 2005; Baptist *et al.* 2010; Wipf & Rixen 2010).

In the specific case of Mediterranean high mountains, the global warming trend runs in parallel to higher intensity of summer droughts, so the growing season of plants may not be extended (Fig. 2; Giménez-Benavides *et al.* 2011a). Observational studies along altitude gradients and in climatically contrasting years have shown extreme summer heatwaves may have negative effects on the reproductive performance of mountain species (Giménez-Benavides *et al.* 2007a; Abeli *et al.* 2012a,b; Table 1). However, responses may be variable (Orsenigo *et al.* 2014) and the degree of vulnerability of each species to increasingly stressful conditions may depend on their phenological strategy. For instance, the late-flowering *Silene ciliata* experienced strong reproductive failure at its lower range limit, especially in extreme hot and dry years (Giménez-Benavides *et al.* 2007a). In contrast, the reproductive performance of the early-flowering *Armeria caespitosa* was more stable along its altitude range and between years (García-Camacho & Escudero 2009; García-Camacho *et al.* 2010). This suggests that the opportunistic early-flowering species, and those able to colonise more stable microhabitats, may better endure the warmer and drier conditions, but the late-flowering species controlled by photoperiod cues will face longer summer droughts (Giménez-Benavides *et al.* 2011a). Unfortunately, to our knowledge, there are no other comparative studies between early- and late-flowering high-mountain Mediterranean plants to support this hypothesis. The most realistic experimental setup for Mediterranean high-mountain plants would be a combination of early snowmelt, warming and increased summer drought. Several studies of imposed drought and warming in Mediterranean lowland forests and shrublands have documented the prevalence of negative effects on flower and fruit production (Llorens & Peñuelas 2005; Ogaya & Peñuelas 2007; Prieto *et al.* 2008; Matesanz *et al.* 2009; Pérez-Ramos *et al.* 2010), but unfortunately such experimental studies have not been performed to date in the high mountains.

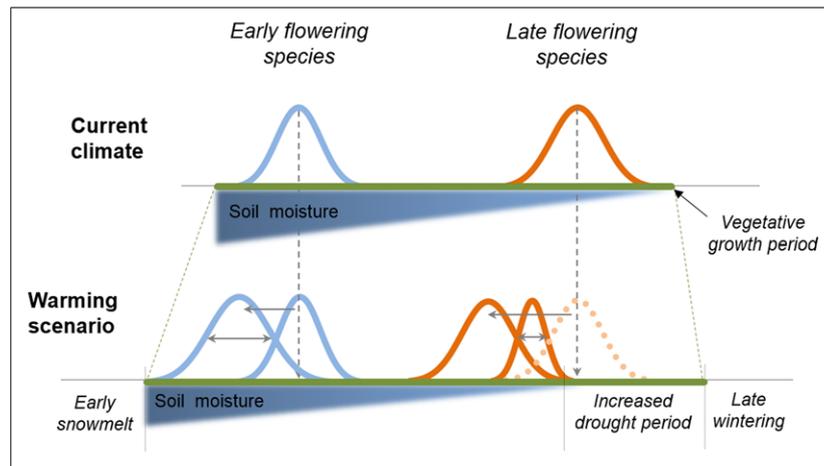


Fig. 2. Diagram depicting the contrasting risk of early and late flowering plants in a climate-warming scenario as projected for Mediterranean high mountains. With rising temperatures and reduced precipitations in spring and summer the main source of soil moisture is the snowmelt water, and this becomes limiting earlier in the season. Facultative early-flowering species have the chance to maintain or anticipate their flowering peak, even increasing the reproductive period. However, late-flowering species are forced to shift the flowering peak and/or reduce the length of reproductive period to avoid the driest end of the season (adapted from Giménez-Benavides *et al.* 2011a).

Effects of climate change on plant–pollinator interactions

Current climate change may also affect the performance of high-mountain plants through their effects on plant–pollinator interactions. In high-mountain ecosystems the pollinator richness, diversity, activity and pollinator services are limited by the harsh environmental conditions (Inouye & Pyke 1988; Kearns & Inouye 1994; Dupont *et al.* 2003), such as the low temperatures, short snow-free growing season and strong winds that affect insects directly (*e.g.* Arroyo *et al.* 1985; Totland 1994; Bingham & Orthner 1998; Muñoz & Cavieres 2008). For these reasons, many authors have suggested in the past that pollen limitation might be very frequent in arctic and high-mountain habitats (Arroyo *et al.* 1982, 1985; McCall & Primack 1992; Totland 1994). However, some reviews highlight that pollen limitation might not be especially higher in alpine habitats compared to lowlands (García-Camacho & Totland 2009; Wagner *et al.* 2016). To our knowledge, most of the Mediterranean high-mountain plants surveyed have been limited by quantity and/or quality of pollination (Muñoz & Arroyo 2006; Alonso 2005; Muñoz & Cavieres 2008; Gómez *et al.* 2010; Amat *et al.* 2011; Torres-Díaz *et al.* 2011; Fernández *et al.* 2012; Alonso *et al.* 2013; but see Gómez & Zamora 1996), but the lack of direct comparisons with lowland relatives does not allow us to extract general conclusions.

There is also growing interest on how the interrelated drivers of global change such as climate warming and habitat fragmentation can affect plant–pollinator mutualisms around the globe (Memmott *et al.* 2007; Potts *et al.* 2010; Winfree *et al.* 2011). According to the review of Hegland *et al.* (2009), global change may alter the abundance and distribution of pollinators, cause phenological mismatches among plants and pollinators, and promote vegetation shifts and invasion processes affecting plant–pollinator interactions (Fig. 1). The information from Mediterranean high mountains is still limited, but we will attempt to synthesise it in the following paragraphs.

Climate trends may alter the abundance and distribution of pollinators and cause phenological mismatches

Most studies of abundance change in Mediterranean high-mountain sites are related to butterflies and bumblebees, two of the most important pollinator groups of Mediterranean high-mountain plants (Santamaría *et al.* 2011; Lara-Romero *et al.* 2016). Several studies in the Spanish Central Range have reported elevation shifts in butterflies with a significant reduction of habitat area in the last century (Wilson *et al.* 2007; Nieto-Sánchez *et al.* 2015). The effect of climate change combined with changes in land use is also producing population declines and changes in community composition of butterflies in the Sierra Nevada Mountains of northern California (Forister *et al.* 2010) and in other montane Mediterranean areas of Spain (Catalonia) (Stefanescu *et al.* 2011a,b). These patterns especially affect high-elevation and grasslands specialists and produce a faunistic homogenisation, with communities progressively dominated by common species (Wilson *et al.* 2007). Butterflies have been globally identified as good indicators for other terrestrial insects for which little information is available (Thomas 2005), because they are very sensitive to climate change and habitat transformation (Parmesan *et al.* 1999; Stefanescu *et al.* 2003; Thomas *et al.* 2004). Evidence of elevation changes at species and community levels has also been reported for bumblebees (*e.g.* in the Cantabrian mountain range, a transition zone between the Euro-Siberian and Mediterranean regions; Ploquin *et al.* 2013). This agrees with a cross-continental trend across Europe and North America in range losses of widespread bumblebee species at their southern range limits, and shifts to higher elevations among species restricted to southern geographic ranges (Kerr *et al.* 2015).

The reproduction of high-mountain plant species can also be affected by plant–pollinator phenological mismatches driven by climate warming (Sherry *et al.* 2007; Hegland *et al.* 2009; Donoso *et al.* 2016). The influence of plant phenology has been assessed as one important factor structuring plant–pollinator

Table 1. List of studies examining different stages of the regeneration process from the ovule to the seedling stage in Mediterranean high-mountain plants.

locality	country	latitude	longitude	process	reference
Snowy Mountains	Australia	36N	148W	POL	Inouye & Pyke 1988
Andes of central Chile	Chile	33N	70W	POL	Muñoz & Cavieres 2008
Guadarrama Range	Spain	40N	3W	POL	Wilson <i>et al.</i> 2007
Guadarrama Range	Spain	40N	3W	POL	Nieto-Sánchez <i>et al.</i> 2015
Catalonia and Andorra	Spain & Andorra	na	na	POL	Stefanescu <i>et al.</i> 2003
Catalonia and Andorra	Spain & Andorra	na	na	POL	Stefanescu <i>et al.</i> 2011a,b
Guadarrama Range	Spain	40N	3W	POL	Lara-Romero <i>et al.</i> 2016
Puig Major Mountain	Spain	39N	2W	POL	Tur <i>et al.</i> 2015
Andes of central Chile	Chile	33N	70W	FLL, POL	Arroyo <i>et al.</i> 1981, 1982, 1985, 2006, 2013; Torres-Díaz <i>et al.</i> 2011
Sierra Nevada Mountains	Spain	37N	3W	POL	Valverde <i>et al.</i> 2016
Guadarrama Range	Spain	40N	3W	FLO, POL	Giménez-Benavides <i>et al.</i> 2007a
Guadarrama Range	Spain	40N	3W	FLO, POL	García-Camacho & Escudero 2009
Guadarrama Range	Spain	40N	3W	FLO, POL, GER, REC	Giménez-Benavides <i>et al.</i> 2008
Baetic System	Spain	37N	3W	REC	Castro <i>et al.</i> 2004
Australian Alps	Australia	37S	146E	REC	Venn <i>et al.</i> 2013
Baetic System	Spain	37N	3W	REC	Herrero & Zamora 2014
Pyrenees	France	42N	1W-1E	REC	Gonzalo-Turpin & Hazard 2009
Guadarrama Range	Spain	40N	3W	REC	Pescador <i>et al.</i> 2016
Guadarrama Range	Spain	40N	3W	REC	Lara-Romero <i>et al.</i> 2014a
Córdoba Mountains	Argentina	31S	64W	GER, REC	Marcora <i>et al.</i> 2008
Andes of central Chile	Chile	33S	70W	GER	Cavieres & Arroyo 2000; Cavieres <i>et al.</i> 2006, 2007; Cavieres and Sierra-Almeida 2012
Guadarrama Range	Spain	40N	3W	GER	Giménez-Benavides <i>et al.</i> 2005
Northeast Spain	Spain	na	na	GER	Montesinos-Navarro <i>et al.</i> 2012
South France	France	43N	3W	GER	Wagmann <i>et al.</i> 2012
Australian Alps	Australia	36S	148E	GER	Hoyle <i>et al.</i> 2013
Cantabrian Mountains	Spain	43N	6W	GER	Fernández-Pascual <i>et al.</i> 2013
Gredos Mountains	Spain	40N	5W	GER	Amat <i>et al.</i> 2014
Italian Rhaetian Alps	Italy	46N	10E	GER	Bernareggi <i>et al.</i> 2016
Lombardy Alps	Italy	46N	10E	GER	Mondoni <i>et al.</i> 2012
Gennargentu massif, Sardinia	Italy	40N	9E	GER	Mattana <i>et al.</i> 2012
Baetic System	Spain	37N	3W	GER, REC	Castro <i>et al.</i> 2005
Guadarrama Range	Spain	40N	3W	GER	García-Fernández <i>et al.</i> 2015
Albany, Southwest Australia	Australia	35S	118W	GER	Cochrane <i>et al.</i> 2015
Guadarrama Range	Spain	40N	3W	GER, REC	Giménez-Benavides <i>et al.</i> 2007b
Guadarrama Range	Spain	40N	3W	GER, REC	García-Camacho <i>et al.</i> 2010
Córdoba Mountains	Argentina	31S	65E	GER, REC	Marcora <i>et al.</i> 2008

FLO, Flowering probability; FLL, Flower longevity; POL, Pollination; GER, Germination; REC, Recruitment/establishment.

*Study took place only partially in Mediterranean-type climate.

interactions in Mediterranean high mountains (Petanidou *et al.* 2014; Martín González *et al.* 2012; Tur *et al.* 2015; Valverde *et al.* 2016). Shifts in phenology have been reported as a potential cause of mismatches between plants and pollinators and so alter ecological interactions in Mediterranean areas (Petanidou *et al.* 2014). However, the potential uncoupling of the activity periods of plants and pollinators forced by climate change and its direct consequences in the reproductive success of Mediterranean high-mountain plants has not been assessed.

Climate trends may promote vegetation shifts and invasion processes affecting plant–pollinator interactions

As mentioned above, several studies have revealed a significant change in the structure and composition of Mediterranean high-mountain vegetation in the last decades. However, climate warming is not the only driver of this trend. Changes in

land use, including abandonment, represent another force for global change and may have significant effects on the reproduction of high-mountain plant specialists. Mountain tree lines and pastures have been maintained historically by traditional human activities such as livestock grazing and managed fires (Ninot *et al.* 2008; Engler *et al.* 2011). The slow abandonment of these uses also contributes to the upward shift of tree lines and encroachment of subalpine shrub communities in the Mediterranean Basin and California (Taylor 1995; Sanz-Elorza *et al.* 2003; Millar *et al.* 2004; Batllori & Gutiérrez 2008; Améztegui *et al.* 2010; García-Romero *et al.* 2010; Jiménez-Alfaro *et al.* 2014). The upward encroachment of oro-mediterranean trees and shrubs may cause serious threats to the specialised high-mountain flora, that can be eventually overgrown by advancing shrub patches, thus reducing the availability of open spaces for germination and growth (Sanz-Elorza *et al.* 2003;

Giménez-Benavides *et al.* 2011b; Amat *et al.* 2013). However, there may be other sources of risk such as the disruption of mutualistic interactions. In central Spain, Lara-Romero *et al.* (2016) found that the intrusion of oro-mediterranean shrubs with massive flowering displays in the cryoro-mediterranean grasslands affects flower visitation patterns of forb species, increasing flower visitor diversity and plant–plant competition for shared pollinators, although the effect of these changes on the reproductive success of each plant species requires further investigation.

The presence of invasive plant species with attractive flower displays is other key process with potential impacts on the pollination of native flora (Bjerknes *et al.* 2007). Although harsh abiotic conditions are considered an important filter for plant invasions, worldwide assessments have reported more than a thousand non-native plant species naturalised in mountain ecosystems (Pauchard *et al.* 2009). Global warming, combined with anthropogenic disturbance and rupture of dispersal barriers due to globalisation, facilitates the upward invasion of lowland plant species. However, to date there are limited data on the impacts of current invasions for reproduction of high-mountain plants (Pauchard *et al.* 2009). In the Mediterranean Chilean Andes, native cushion plants facilitate the invasion of the non-native *Taraxacum officinale* at high altitudes (Cavieres *et al.* 2005, 2008), and this species alters the pollinator visitation and seed output of several native species, although the negative effects vary with the density of the invasive species (Muñoz & Cavieres 2008).

In summary, changes in the structure and composition of plant communities may largely affect plant–pollinator interactions. Due to the low abundance and diversity of pollinators in high-mountain environments, the intrusion of lowland and alien plants with attractive floral display may have important implications. The presence of the alien plant species may improve pollinator visitation to native plants, but high densities of these species could disrupt plant–pollinator interactions of the native flora (Muñoz & Cavieres 2008).

Effects of climate change on post-pollination processes

High-mountain plant recruitment depends ultimately on the production of viable seeds as well as on the availability of suitable microsites for seed germination and seedling survival. Research efforts on the impact of warming on post-pollination stages such as seed germination and establishment are more frequent in the literature of Mediterranean high-mountain plants (Table 1). Temperature and water supply are the main drivers for seed dormancy, germination and establishment, so climate change may severely alter sexual plant regeneration through seed persistence in soil banks, phenology of germination and seedling success (Walck *et al.* 2012; Hoyle *et al.* 2013; Bernareggi *et al.* 2016). Giménez-Benavides *et al.* (2008) aimed at identifying the most critical stages in the ovule-to-seedling regeneration process of *Silene ciliata*, a high-mountain plant, along its altitude range in Central Spain for two climatically contrasting years. One of the most limiting steps found in this case was seedling emergence and survival (also flowering probability and seed set) because they were highly dependent on summer drought conditions, and were especially restrictive at the lower altitudinal margin of the species. These constraints in the early stages of the plant's life cycle may affect global

viability of the populations, with implications that may scale up to the community level. Many other studies have consistently found that recruitment in Mediterranean high mountains is mainly constrained by low seed production and low seedling survival in the post-dispersal stage, due to drought stress in summer (Castro *et al.* 2004; Marcora *et al.* 2008; García-Camacho *et al.* 2010; Lara-Romero *et al.* 2014b). In a recent study, experimental soil warming had strong impacts on regeneration by seed, significantly slowing seedling emergence and reducing total seedling emergence and performance in a set of species collected in Mediterranean-type mountains in Australia (Cochrane *et al.* 2015).

The timing of germination is critical for subsequent seedling survival in alpine environments (Baskin & Baskin 1998; Shimono & Kudo 2003). Snow precipitation and snowmelt are among the most important triggers for seed germination (Amen 1966; Shimono & Kudo 2005; Walck *et al.* 2012). Seed dormancy prevents precocious seedling emergence and avoids frost damage in late spring or late summer (Amen 1966; Billings & Mooney 1968; Shimono & Kudo 2005; Walck *et al.* 2012). In Mediterranean mountains, where topsoil desiccation dramatically increases during the growing season, summer drought may be more restrictive for plant recruitment than freezing events (Giménez-Benavides *et al.* 2007b). As in other alpine environments, Mediterranean mountains harbour many plant species with relative dormancy that is naturally broken after exposure to a cold stratification treatment simulating the snow cover period (Cavieres & Arroyo 2000; Giménez-Benavides *et al.* 2005; Fernández-Pascual *et al.* 2013; Giménez-Benavides & Milla 2013; Amat *et al.* 2014). However, in the Mediterranean mountains a high proportion of species seem to be physiologically prepared for rapid germination or have a lower requirement for a cold stratification period (Giménez-Benavides *et al.* 2005; García-Fernández *et al.* 2015). This may be adaptive under climate change (Bernareggi *et al.* 2016) because the snow cover duration is reducing due to declining precipitation and increasing mean minimum temperatures in winter.

Lower snow precipitation and early snowmelt could also shift the timing of seed germination in many species (Mattana *et al.* 2012; Mondoni *et al.* 2012; Walck *et al.* 2012). In this vein, a recent study performed on the endemic Mediterranean high-mountain species *Centaureum somedanum*, has shown that seed dormancy has the capacity to adjust to the weather during seed maturation, especially through sensitivity to dormancy-breaking factors (Fernández-Pascual *et al.* 2013). This highlights the great potential of physiological dormancy to evolve in the relatively near future because of climate change (Montesinos-Navarro *et al.* 2012; Wagmann *et al.* 2012; Fernández-Pascual *et al.* 2013). Observations in other cold environments suggest that when the timings of snowmelt and seed emergence shift earlier, the frequency of seedling damage by occasional freezing events in spring may increase (*e.g.* Schaerberg *et al.* 2008; Hennon *et al.* 2012). Nonetheless, the limited empirical evidence suggests that freezing temperatures soon after snowmelt in spring are not especially damaging to Mediterranean high-mountain species (Venn *et al.* 2013; Pescador *et al.* 2016). A close correlation between some plant traits and adaptive responses to water deficit and frost would help to explain this outcome. For example, the osmotic adjustment of cells through synthesis of low-molecular osmolytes and

hydrophilic proteins such as dehydrins are responses induced both by drought and cold stress (Beck *et al.* 2007). Also, leaves with high dry matter content can maintain turgor at lower water potential, enhancing drought tolerance in parallel to freezing resistance (Pescador *et al.* 2016). Another source of risk in regeneration from seed induced by climate change may be due to seedling emergence in seasons that the species are not adapted to experience (Walck *et al.* 2012). An experimental study that assessed the effect of climate warming on the timing of seed germination found that autumn warming increased germination in all but two alpine plants (Mondoni *et al.* 2012). Although the appearance of this pattern in Mediterranean high mountains has not been assessed, this may be particularly critical because emergence in late summer will have major implications, as small emerging seedlings may succumb to cold winter (Mondoni *et al.* 2012; Walck *et al.* 2012).

Effects of climate change on plant population dynamics

As we have seen above, the effect of climate change on population dynamics is usually deduced from effects on individual components of the plant life cycle, such as pollination, fecundity, germination or seedling survival. Nonetheless, individual stages of the regeneration cycle of plants must not be used to infer the final performance and demographic behaviour of populations (Gómez 2005; Giménez-Benavides *et al.* 2008). Despite its vital importance, as far as we know, very few demographic studies have been conducted in Mediterranean high mountains to study the potential impact of climate change, and all of them are observational along elevation gradients. In *S. ciliata*, the pressure of extreme summer droughts especially affected the longevity of individuals in the lowland populations and resulted in declining growth rates, while the summit populations persist through higher longevity coupled with occasional recruitment episodes (Giménez-Benavides *et al.* 2011b). In contrast, García-Camacho *et al.* (2012) found a rather stable situation in *A. caespitosa* along its elevation range maintained by demographic compensation among populations, with higher growth rates and fecundity of the small-sized individuals at the low-elevation edge compared to the longer life span and much higher fecundity of the largest individuals at the high-elevation edge. This example confirms the idea that plant populations may respond to environmental constraints, adopting alternative demographic strategies to persist in the long term (García & Zamora 2003; Morris *et al.* 2008; Doak & Morris 2010; Benavides *et al.* 2015).

POTENTIAL STABILISING PROCESSES CONFERRING RESILIENCE TO CLIMATE CHANGE

Mediterranean mountain species have undergone several past climate changes, exhibiting capacities to survive, adapt and evolve under changing conditions (Vargas 2003). Most species can endure moderate variability in climate through phenotypic plasticity, but beyond the tolerance limit, adaptive evolution is essential for their persistence (Jump & Penuelas 2005). There is great concern regarding whether current climate change may be fast enough to make species' responses non-viable (Davis & Shaw 2001; Jump & Penuelas 2005), so the magnitude of phenotypic plasticity and local adaptation along the species' range is essential for understanding their ability to face changing

climate conditions (Matesanz & Valladares 2014). Plant–plant interactions may also play an essential role in mitigating the potential consequences of climate change in plant communities, especially facilitation, which is very frequent in harsh environments such as that of alpine regions (Brooker 2006; Anthelme *et al.* 2014; Michalet *et al.* 2014). All these processes can complement each other, providing tolerance and/or resilience against climate changes (Lloret *et al.* 2012; Fig. 1). However, these have rarely been studied and thus are largely ignored in most predictive models of species distribution under climate change (Theurillat & Guisan 2001; Sutherst *et al.* 2007; Thuiller *et al.* 2008; Lavergne *et al.* 2010; Wisz *et al.* 2013). In this section, we briefly focus on some areas of research regarding the role of phenotypic plasticity, local adaptation and plant–plant facilitation as potential alleviating processes against climate change, with a special focus on the processes of regeneration by seed in Mediterranean high-mountain plants.

Phenotypic plasticity and adaptive potential

Since the degree of phenotypic plasticity and adaptive potential may vary across functional traits and through plant ontogeny, it is important to consider multiple traits throughout the regenerative process (Münzbergová *et al.* 2017). For instance, the above-mentioned limitation of pollinators in alpine ecosystems might be compensated by increased flower longevity (Bingham & Orthner 1998; Lundemo & Totland 2007; Trunschke & Stöcklin 2016). The existence of this potential compensatory strategy has been confirmed in some Mediterranean high-mountain plants (Arroyo *et al.* 1981, 1985, 2006, 2013; Bliionis & Vokou 2001; Bliionis *et al.* 2001; Makrodimos *et al.* 2008; Torres-Díaz *et al.* 2011). However, the longer period of sexual receptivity of non-pollinated flowers could be an adaptive trait under selection, or merely a consequence of slower flower development in the cold conditions of mountain zones (Arroyo *et al.* 1981; Steinacher & Wagner 2010). An interesting study in the high Andes of Mediterranean Chile explored the effect of experimentally increased temperature on flower longevity of *Oxalis compacta* (Arroyo *et al.* 2013). Using open-top chambers (hereafter OTCs), these authors highlight that phenotypic plasticity of flower longevity in response to ambient temperature could play a stabilising role in the reproductive success of Mediterranean high-mountain plants under climate warming. Extended flower longevity in cold microsites or seasons may help plants to compensate for low pollinator visitation rates, whereas reduced flower longevity under warmer conditions may be offset by increased pollinator activity (Arroyo *et al.* 2013).

Seed and seedling traits could also evolve relatively quickly to keep pace with climate change (Walck *et al.* 2012). One of the most common experimental methods to assess local adaptation is the use of reciprocal sowings or reciprocal transplants along altitudinal gradients (Etterson 2004; Kim & Donohue 2013; Scheepens & Stocklin 2013). In the altitudinal range of *Silene ciliata* in the Spanish Central Range, the existence of local adaptation process conferring drought tolerance has been found on seedling emergence and survival (Giménez-Benavides *et al.* 2007b; García-Fernández *et al.* 2015) and in adult plants (García-Fernández *et al.* 2013). Such adaptive processes may help to counteract the projected contraction of the distribution range of this species under climate change (Giménez-Benavides

et al. 2011b). However, other studies have showed that these adaptive responses are not widespread. Several irrigation experiments have found species-specific differences in resistance and resilience to drought stress at the early developmental stages (Castro *et al.* 2005; Herrero & Zamora 2014; Cochrane *et al.* 2015). Life-history traits of species, microhabitat conditions or genetic constraints may explain these differences in the responses, or even failure to adopt some of these responses or simple association of the effect–response could be unrealistic. Finally, some studies suggest that longevity and vegetative propagation may provide alternative ways to ensure population persistence when regeneration by seed is constrained by temperature or drought, especially in peripheral populations (García *et al.* 1999; García & Zamora 2003; Giménez-Benavides *et al.* 2011b). In fact, many relict and endemic plants in the Mediterranean area are perennial long-lived species inhabiting mountain and rocky habitats and showing lower investment in sexual regeneration than their widespread congeners (Lavergne *et al.* 2004), so persistence might be a successful strategy conferring resilience against past environmental changes for many species. These species-specific differences, with winners and losers, could trigger changes in vegetation structure and composition, promoting the emergence of novel communities (Walther *et al.* 2002; Walther 2003; Herrero & Zamora 2014). Therefore, the adaptive potential of Mediterranean alpine plants to cope with rapid ongoing climate change must be confirmed in a case-by-case analysis in a wide range of taxa and environments.

Plant–plant interactions

Most studies on the effects of climate change in mountain plants have focused on the direct effects of abiotic stress on plant performance or indirectly through interactions with herbivores and pollinators (see above). However, the indirect effects of climate change through changes in plant–plant interactions have received little attention (Klanderud 2005; Brooker 2006), especially the plant–plant facilitative interactions (Anthelme *et al.* 2014). This is particularly relevant in high mountains because the stress gradient hypothesis (Bertness & Callaway 1994) predicts that facilitative interactions will increase as conditions become harsher (Choler *et al.* 2001; Callaway *et al.* 2002). In Mediterranean high-mountain environments, many nurse plants, especially cushion-like ones, act as facilitators, improving soil conditions and providing protection against environmental stress for species growing inside, with positive consequences for their reproduction and seedling establishment (Cavieres *et al.* 2002, 2006, 2007; Escudero *et al.* 2004; Badano *et al.* 2006; Mihoč *et al.* 2016).

Since amelioration of extreme temperatures is one of the principal mechanisms of facilitation, one interesting hypothesis explored by some authors is that the net outcome of plant–plant interactions may shift from facilitation to competition if climate change makes high mountains warmer and therefore less severe (Olsen *et al.* 2016). A recent review found that warming imposed by OTCs in arctic and alpine sites decreased the magnitude of facilitation in more than half of the studies (Anthelme *et al.* 2014). However, in this review there was only one case study from Mediterranean-type climates, which found that positive effects did not disappear under warmer conditions. In the Central Andes of Chile, Cavieres & Sierra-Almeida

(2012) used *Azorella madreporica* as nurse model species and found that facilitative effects on the seedling establishment of *Hordeum comosum* prevailed even under experimental warming. This example highlights that causal relationships between warming and reduced facilitation cannot be generalised because the alleviation of extremely low temperatures is not the unique positive effect provided by benefactor species. Soils beneath cushions are more fertile and retain water for longer periods than the surrounding bare ground (Escudero *et al.* 2004; Mihoč *et al.* 2016), and this is extremely important in Mediterranean climates where early snowmelt can be considered as an additional stress (Fig. 2). Therefore, facilitative interactions can mitigate the potential consequences of climate change and might play a central role in the resilience of high-mountain communities.

FUTURE PERSPECTIVES

In general, we have made substantial advances in the last decades in understanding the singularities of climate change projections in Mediterranean areas, and the associated risks for high-mountain plants. Retrospective studies and long-term monitoring sites and networks in Mediterranean high mountains are still scarce, but they have gathered mounting evidence that climate change is involved in recent range contractions and changes in community composition of plants and pollinators. However, there is still little information of the direct effects of climate change on the phenology and reproductive success of Mediterranean high-mountain plants and on their interactions with pollinators and herbivores. Due to these limitations, most expectations of climate change impacts on the reproduction of Mediterranean mountain plants have been inferred from arctic and alpine environments, but these cold habitats may not be ecologically comparable. We expect that summer droughts that are going to become more intense in the future may impose regeneration bottlenecks in Mediterranean high-mountain plants, but there is an urgent need to gain more information at larger temporal and spatial scales. Comparative studies of Mediterranean high-mountain plants with sister taxa inhabiting boreo-alpine regions, or comparing central populations of alpine species with Mediterranean peripheral populations may help to assess the specific risks associated with the reproduction of Mediterranean high-mountain plants (see Abeli *et al.* 2014; Benavides *et al.* 2015; Pironon *et al.* 2015). Long-term studies integrating elevational gradient approaches with experimental manipulations could also provide powerful information to improve predictions of climate change impacts (*e.g.* Dunne *et al.* 2003; Sundqvist *et al.* 2013), especially when combined with different levels of temperature and water supply (Llorens & Peñuelas 2005; Ogaya & Peñuelas 2007; Prieto *et al.* 2008; Matesanz *et al.* 2009). With some exceptions, there is also little knowledge about the adaptive potential of Mediterranean high-mountain plants under current climate change (see Matesanz & Valladares 2014). There is a clear need to perform common garden and reciprocal translocation studies to determine the plasticity, heritability and adaptive value of key functional traits throughout the plant regeneration process (*e.g.* Richter *et al.* 2012; Lara-Romero *et al.* 2014a; Doblas-Miranda *et al.* 2015; Münzbergová *et al.* 2017). In this sense, long-term demographic studies across the geographic ranges of different species with contrasting life-history traits may help to detect

demographic compensation processes (e.g. Doak & Morris 2010) and to ascertain all the attributes conferring resilience to changing environmental conditions at population and community scales (Lloret *et al.* 2012). Finally, plant–animal and plant–plant interactions, such as facilitation and competition, can

speed up or slow down the responses of plants to changing environmental conditions (Anthelme *et al.* 2014), but their consequences for population viability and species range shifts in Mediterranean high-mountain plants remain quite unexplored.

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