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REVIEW PAPER

The silent extinction: climate change and the potential hybridization-mediated extinction of endemic high-mountain plants

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Abstract Most global-warming models predict an altitudinal movement of plants. This upward migration of lowland species will surely result in contact with related species inhabiting high-mountain ecosystems. We propose that an overlooked consequence of this upland movement is the possibility for interspecific hybridization between narrowly endemic alpine plants and widely distributed lowland plants. Genetic swamping due to introgressive hybridization might even lead to the genetic extinction of the endemic species, without any apparent detrimental demographic effect. Unfortunately, this phenomenon has long been ignored in the ecological literature, probably because is widely assumed that the ecological effects of climate change are more detrimental than its genetic effects. We tested our idea by searching for human-induced hybridization in a worldwide hotspot biodiversity, the high-mountains of the Sierra Nevada (south-eastern Spain). About 25 % of the endemic flora is already hybridizing in these mountains, mostly with widespread lowland congeners. Some species are even already threatened due to genetic swamping. It is thereby urgent including in future conservation agendas a protocol for

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detecting and monitoring positive and negative effects of genetic swamping mediated by climate change in high mountains and other sensitive ecosystems.

Human-mediated plant hybridization

Hybridization is a widespread phenomenon in plants (Rieseberg and Wendel 1993; Arnold 2006), occurring in up to 40 % of the plant families and 16 % of the plant genera (Whitney et al. 2010). The consequence of this frequent hybridization for plant ecology and evolution is still an unresolved question. Hybridization clearly has positive consequences (Rieseberg and Wendel 1993). It may increase the genetic diversity of the hybridizing species, may transfer adaptations from one species to another, may prompt new adaptations, and may give rise to new taxa by means of hybrid speciation (Mallet 2007; Soltis and Soltis 2009). In contrast to its creative role, hybridization also has detrimental effects for a given species. Hybridization may pose a threat pushing plant populations to the brink of extinction as a consequence of gene swamping, genetic assimilation and outbreeding depression (Levin et al. 1996; Hails and Morley 2005). In some extreme situations, hybridization may cause the entire assimilation of the genome of one species, triggering its genetic extinction (Allendorf et al. 2001; Hails and Morley 2005).

Table 1 Types of isolation barriers between plant species, based on Coyne and Orr (2004) and Arnold (2006)

Type of barrier		Hybridization hindered in plants by
Prezygotic		
Spatial isolation	Extrinsic	Differences in geographic range
Temporal isolation	Extrinsic	Differences in flowering time
Ecological isolation	Extrinsic	Differences in habitat selection
Ethological isolation	Extrinsic/intrinsic	Differences in pollinator fauna
Mechanical isolation	Intrinsic	No transfer of pollen due to mismatching
Mating isolation	Intrinsic	Self-pollination
Gamete competition	Extrinsic/intrinsic	Better performance of conspecific pollen
Gametic incompatibility	Intrinsic	No ovule fertilization
Postzygotic		
Zygotic mortality	Intrinsic	Inviability of embryo
Hybrid inviability	Intrinsic	Inviability of F1 hybrids
Hybrid fertility	Intrinsic	Sterility of F1 hybrid
Hybrid fitness	Extrinsic/intrinsic	Lower fitness of hybrids
Hybrid breakdown	Intrinsic	Sterility and inviability of F2 and back-crossed hybrids

Following Coyne and Orr (2004), intrinsic refers to genetically based barriers and extrinsic refers to environmentally based barriers

Many, non-exclusive isolating barriers prevent interspecific hybridization (Table 1). Some of those barriers are intrinsic and determined by well-established genetic differences between species (Coyne and Orr 2004). Many species cannot hybridize because of reproductive barriers to fertilization and embryo development. In contrast, other isolating barriers are extrinsic, mediated by the action of environmental factors (Coyne and Orr 2004). Thus, many other species do not hybridize in the wild because they occupy geographically separated areas, are pollinated by different animals, or live in contrasting habitats. When isolation is due to extrinsic barriers, changes in the environment favouring the contact between species may enhance the possibility of interspecific hybridization.

Human activity is favouring secondary contact throughout the world between potentially hybridizing species that have been geographically separated (Vilá et al. 2000). Two human activities are widely acknowledged to increase rates of hybridization: introductions of alien species and habitat modification (Crispo et al. 2011). The massive movement of plant and animals mediated directly or indirectly by humans is causing the meeting of closely related species that have been geographically separated for a long period (Vilá et al. 2000; Allendorf et al. 2001; Ellstrand et al. 2013). Anthropogenic hybridization between introduced species and their native congeners occurs frequently and can create serious conservation concerns (Ellstrand and Schierenbeck 2000). Similarly, habitat alterations may cause the eventual contact of related species that have remained separated by inhospitable habitats (Hengstum et al. 2012).

Climate change is another important consequence of human activity. Recent anthropogenic global warming is altering species physiology, phenology, biotic interactions and distribution (Walther et al. 2002; Chown and Gaston 2008). As the climate warms, it is expected that species will shift their latitudinal and altitudinal distributions (Theurillat and Guisans 2001; Thomas et al. 2006; Fitzpatrick et al. 2008; Thuiller et al. 2008; González-Megías et al. 2008; Engler et al. 2011). Most empirical evidence and theoretical approaches suggest that altitudinal migration will be much faster than latitudinal movements (Jump et al. 2009). Due to the high speed in altitudinal movements, many migrating plant species could make contact with evolutionarily related species living at high altitudes. When the isolating barriers between these species are mostly extrinsic (Table 1), this contact would result in interspecific hybridization (Crispo et al. 2011). As mountain ecosystems are rich in narrowly endemic species (Cox and Moore 2010), the consequences of this hybridization would have both positive (i.e., increasing genetic diversity and leading new adaptations) and negative effects (i.e., genetic swamping) for the high-altitude species. In this article, we propose that hybridization mediated by climate change has been largely overlooked and consequently the possible negative and positive outcomes must be monitored in the conservation programs of endangered high-altitude plant species. We test this idea evaluating how human-mediated hybridization could affect a worldwide biodiversity hotspot such as Sierra Nevada (SE Spain), specifically its endemic high-mountain flora.

Evidence of climate change-induced hybridization

It is striking that, despite the greatly acknowledged consequences of climate change for the conservation and persistence of many species, virtually no information is available concerning its potential effects on interspecific hybridization (Franks and Hoffmann 2012). This scarcity of studies in plants is noticeable, particularly because these organisms seem to show a higher frequency of hybridization than animals (Arnold 2006; Whitney et al. 2010). There are, however, very few examples of hybridization induced by climate change

in plants. Gérard et al. (2006) suggested that climate change favours the hybridization of *Fraxinus angustifolia* with *F. excelsior*, a process enabling the northward expansion of this latter species. Tauer et al. (2012) found that hybridization between shortleaf pine (*Pinus echinata*), a narrow distributed species, and loblolly pine (*P. taeda*), a widespread species, is causing the loss of genetic integrity in shortleaf pine that it is also declining due to land-use changes such us fire suppression. Natural hybridization has increased from 3 % in the 1950s to 45 % for present-day regeneration. Because shortleaf pine is more fire and drought tolerant than loblolly pine, loss of genetic integrity of shortleaf pine may reduce the resiliency and adaptability of these conifer forests to climate change. Also, *Saxifraga spathularis* and *S. hirsuta* form a recognised hybrid *S. x polita*. Beatty et al. (2015) have recently reported the occurrence of introgression of the abundant *S. spathularis* into the rarer *S. hirsuta*. Introgression would represent a threat to the genetic integrity of this latter species, a phenomenon that can be aggravated due to the ongoing climatic change that is favouring the widespread *S. spathularis*.

Hybridization induced by climate change has been also reported in several animal species (Scriber 2011). Garroway et al. (2010) found that the southern flying squirrel (*Glaucomys volans*) is expanding its northern range limit and consequently is making contact with the northern flying squirrel (*Glaucomys sabrinus*). As a consequence, extensive hybridization is occurring between the two squirrel species in sympatry. Similarly, Morgan et al. (2011) have reported hybridization between two species of black-tip sharks (*Carcharhinus tilstoni* and *C. limbatus*). These authors attributed this phenomenon to changing distribution as a response to climate change. Maybe the most renowned example is that of the polar bear (*Ursus maritimus*) hybridizing with grizzly bears (*Ursus arctos horribilis*) after the latter expanded northward into the Arctic (Crispo et al. 2011).

Climatic change and the potential for hybridization in high-mountain plants

Copious empirical evidence shows that climate change affects the elevation ranges of many plant species (Wardle and Coleman 1992; Grabherr et al. 1994; Kullman 2002; Lenoir et al. 2008; Benito et al. 2011; Engler et al. 2011). Since altitudinal ecological gradients are sharper than latitudinal gradients, the distance necessary to travel in order to change between ecosystems is much smaller along the altitudinal than the latitudinal axis. Moreover, the possibility of migrating between different mountain ranges is very low, because mountain ecosystems are surrounded by habitats inhospitable to most mountain species (La Sorte and Jetz 2010). For most montane species, upward movement will be the only response to climate change (Jump et al. 2009). As plants move uphill, species distributions will contract and, therefore, the number of populations and individuals per population will dwindle (Theurillat and Guisan 2001; Dullinger et al. 2012; Vegas-Vilarúbia et al . 2012). In many cases, the loss of range will be also associated with loss of genetic diversity (Franks and Hoffmann 2012). Under these circumstances, stochastic demographic and genetic processes may provoke first the extirpation of the smallest populations and, in the long term, the extinction of the whole species (Franks and Hoffmann 2012). However, speed of upward migration of lower-altitude species will probably lead to contact with high-altitude species before the latter go extinct (Jump et al. 2009). In fact, high-altitude species have fewer possibilities of moving upward, because the area of available habitat diminishes, the topography becomes more hostile

Fig. 1 Potential consequences of the contact between lowland (*species A*) and high-mountain (*species B*) plant species. **a** *No hybridization* occurs when two species with strong intrinsic reproductive barriers contact. The outcome is the demographic decline of the less competitive species. **b** *Speciation reversal* occurs after the primary contact between an incipient species and the widespread species. The result is a single, genetically homogeneous, species. **c** *Non-introgressive hybridization* occurs when two species contact and hybridize without between-species transfer of genes. The outcome is a hybrid zone in the contact area. **d** *Introgressive hybridization* occurs when two species contact and there is a net transfer of genes from one species to the other. When the two species in contact differ markedly in their abundance, the rarer may be completely replaced by hybrids
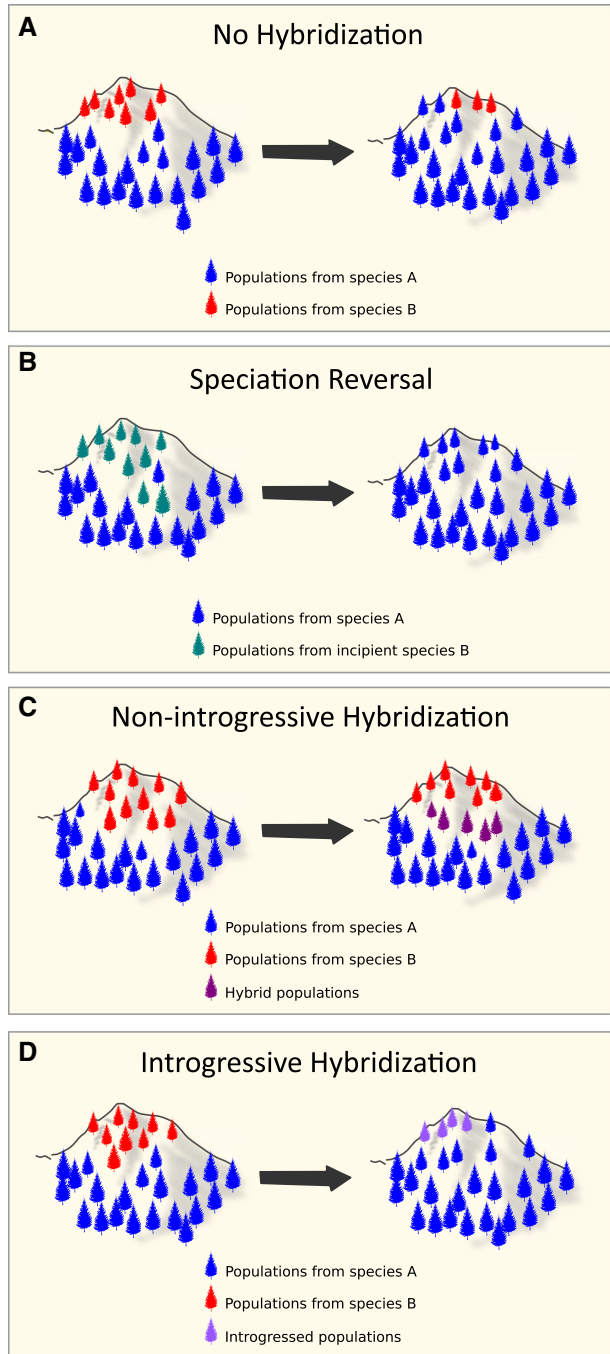
(higher slopes), and the soil loses its ability to sustain plants, especially shrubs and trees (Benito et al. 2011; Dirnböck et al. 2011). By remaining at the same altitudinal belt, they will eventually contact low-altitude species moving upward.

Potential outcomes of hybridization for high-mountain plants

We envision several possible scenarios when two taxa come into contact due to climate-change upward movement (Fig. 1).

No hybridization

A situation occurs when two species come into contact but there is no possibility of hybridization. In this case, one outcome could be the demographic decline of one species due to interspecific competition with the other species (Fig. 1a). Lowland plants would probably overcome high-altitude plants because tend to be strong competitors (Roux et al. 2012). A less explored potential effect is related to the expected increase in local species richness on the summit of mountains as a consequence of the massive upward migration by lowland species (Pauli et al. 2012). This accumulation of species at the top of the mountains would exacerbate the intensity of interspecific competition (Roux et al. 2012).

Speciation reversal

A contrasting situation occurs when populations of two incipient species, with a still low evolutionary divergence, make contact because the barriers promoting speciation are broken (Fig. 1b). Under these circumstances, factors promoting the primary contact between incipient species or between locally adapted populations, without strong genetic differentiation, may cause genetic homogenization and arrest the speciation process (Seehausen 2006). Incipient species evolving by adapting to alpine environments may disappear before becoming a true species after re-contacting with their lowland ancestral species (Fig. 1b).

Non-introgressive hybridization

When the contacting populations, although capable of hybridizing, have developed intrinsic isolation barriers during the process of evolutionary divergence, hybridization usually occurs without any transfer of genes from one species to another (Fig. 1c). In these cases, hybrids tend to be uncommon and ephemeral or restricted to specific ecological conditions where they can survive forming a hybrid zone (Arnold 2006). The fitness of the hybrids tends to be lower than the fitness of any of the two parental species due to outbreeding depression (Ellstrand and Elam 1993; Rhymer and Simberloff 1996). The consequence for the parental species is wasted reproductive effort rather than genetic mixing (Allendorf et al. 2001). Another potential outcome of non-introgressive hybridization is allopolyploid speciation, a process occurring when there is somatic chromosome doubling in a diploid hybrid, followed by selfing to produce a tetraploid (Mallet 2007).

Introgressive hybridization

Finally, when the populations in contact belong to species that have not yet developed strong isolation barriers, hybridization may entail the net long-term transfer of genes from one species to another (Fig. 1d). The outcome of this introgression may depend on the differences in abundance between the species, both in terms of number and size of

populations (Levin et al. 1996). A first outcome called widespread introgression occurs when the two species in contact are similar in abundance. In this case, pure populations of the two species coexist with hybrid populations (Allendorf et al. 2001). Alternatively, a second outcome called complete admixture may occur when the two species in contact differ markedly in their abundance, and one species (usually the rarer) is completely replaced by hybrids via genetic assimilation (Levin et al. 1996). Complete admixture can occur even if the hybrids have lower fitness, simply due to numbers of individuals and the probability of an individual of a rare species mating with a hybrid or the other species versus its own species. Under these circumstances, no pure population remains, and hybrid swamping becomes widespread (Allendorf et al. 2001).

Introgressive hybridization is especially detrimental for rare endemic species if they come into contact with widespread congeners because there is a high probability of complete admixture (Levin et al. 1996; Wolf et al. 2001; Thompson et al. 2009). Rare endemic species are more likely to show higher levels of introgression with their widespread congeners than the opposite (Levin et al. 1996; Thompson et al. 2009). This effect is exacerbated when endemic species live in small populations already at risk from biotic or abiotic stress (Ellstrand and Elam 1993). Furthermore, populations on the periphery of a species' range are often small and spatially isolated, exhibit lower genetic diversity and subsist in marginal conditions and, in the absence of local adaptation, tend to be maladapted to the conditions in which the entire species evolved (Eckert et al. 2008). When two hybridizing species come into a contact, the populations of the lower edge of the upland species, that is usually less adapted to the novel conditions, are thereby more likely to be introgressed when they hybridize (Thompson et al. 2009). The consequences would be detrimental for rare species even under non-introgressive hybridization because the reproductive waste due to hybridization will disproportionally affect the less common species (Ellstrand and Elam 1993).

In conclusion, under the current scenario of climate change, high-mountain plants will no doubt face severe ecological threats that will probably drive many of them to extinction in the near future (Pauli et al. 2012). The question is what fraction of this high-mountain biodiversity is threatened as a consequence of hybridization induced by climate change.

An example: Climate change and hybridization in the Sierra Nevada (SE Spain)

The Mediterranean Basin is one of the most diverse biological areas in the world, containing over 24,000 vascular plant species (10 % of the world's total) (Myers et al. 2000). One main feature of the Mediterranean flora is its high rate of diversification, with most of the current diversity in this region having evolved very recently as the consequence of the segregation of widespread taxa into populations isolated on the many mountaintops that form the complex Mediterranean landscape (Valente et al. 2010). Most Mediterranean high-mountain plants therefore belong to young lineages with related species inhabiting the surrounding lowlands, a feature that may enhance the probability of hybridization after secondary contact.

The Sierra Nevada, a mountain range in the SE Iberian Peninsula, is the most important hotspot of plant diversity in the western Mediterranean (Blanca et al. 2002). It hosts 7 % of the 24,000 Mediterranean vascular plants, despite covering just 0.01 % of its area (Blanca et al. 2002). Another characteristic of the Sierra Nevada is the great singularity of its flora. About 20 % of the plants are endemic (Blanca et al. 2002). There are about 500 plant taxa

living above the treeline, 106 of them endemic to the high mountains of the Sierra Nevada and surrounding areas (77 species and 29 subspecies, Appendix S1). These endemic taxa belong to 31 families, particularly Asteraceae (16 endemic taxa), Poaceae (15) and Brassicaceae (10). Furthermore, about 70 % of the endemic taxa of the Spanish Sierra Nevada are endangered (Blanca et al. 2002).

Climate change is predicted to be especially severe in Mediterranean mountains (Nogués-Bravo et al. 2007), where warming is causing a decline in the average annual rainfall, resulting in longer summer droughts (IPCC 2007). Moreover, many studies have already shown that Mediterranean plants are migrating upward (Peñuelas and Boada 2003; Benito et al. 2011). Climatic models predict the upslope movement of Sierra Nevada plants within the current century at a rate as high as 12 m/year (Benito et al. 2011), a prediction that has recently been confirmed with empirical evidence not just for the Spanish Sierra Nevada but also for many other European mountains (Lenoir et al. 2008; Pauli et al. 2012). Under these circumstances, contact between many lowland and highland plants is expected.

According to Blanca et al. (2002), about 25 % of the endemic taxa in the Sierra Nevada are relict, belonging to Arctic-Alpine or Euro-Siberian lineages, whereas the remaining 75 % seem to have evolved from Mediterranean lineages by adapting to high-mountain conditions (Fig. 2, Appendix S1). Most Arctic-Alpine or Euro-Siberian plants inhabiting
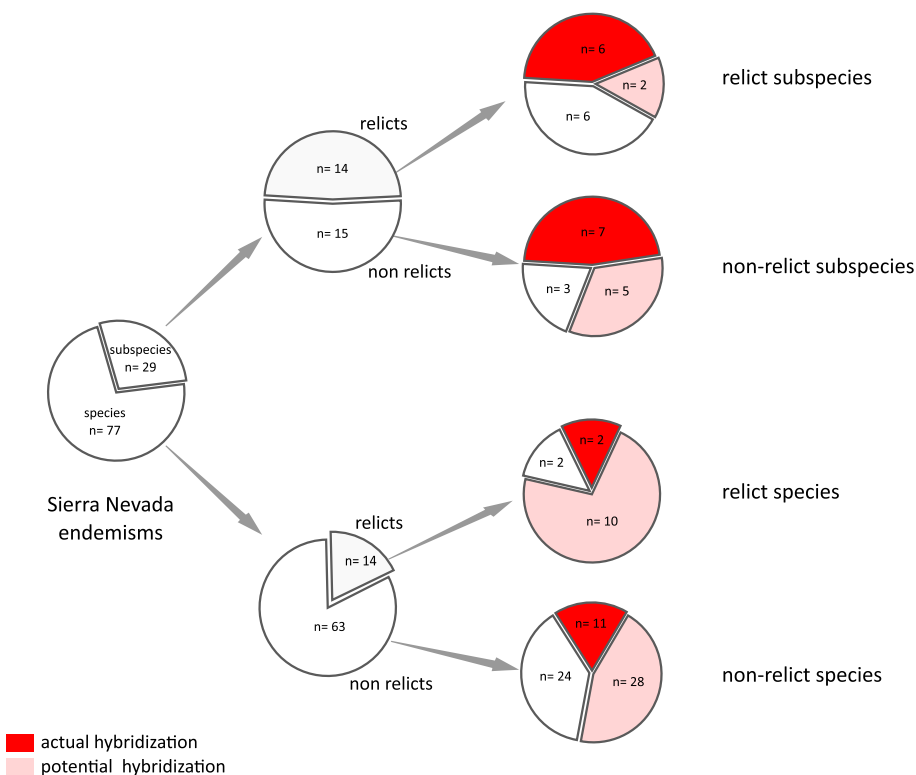

Fig. 2 Sierra Nevada endemic taxa (n = 106) at species and subspecies levels were separately grouped as relict or non-relict taxa. Pie charts at the third column depict the proportion of these groups affected by actual hybridization (i.e., already reported in the literature) or by potential hybridization (i.e., reported only for related species). See supporting literature in Appendix S1

Table 2 Hybridizing endemic taxa in Sierra Nevada (SE Spain)

Endemic taxa			Hybridizing with		
Name	Altitudinal distribution	Relict	Name	Geographical distribution	Altitudinal distribution in Sierra Nevada
Agrostis canina subsp. *granatensis*	2000–2900	No	*Agrostis canina s.l.*	Eurasia	600–2200
Agrostis nevadensis	2000–3300	No	*Agrostis canina s.l.*	Eurasia	600–2200
Anthyllis vulneraria subsp. *pseudoarundana*	2200–3200	No	*Anthyllis vulneraria s.l.*	Eurasia	50–2000
Armeria filicaulis subsp. *nevadensis*	2300–3000	Yes	Hybrid species		
Armeria filicaulis subsp.*trevenqueana**	1700–2000	Yes	*Armeria villosa* subsp. *bernisii*	Baetic mountains	900–2200
Armeria splendens	2400–3000	Yes	*Armeria filicaulis*	Baetic mountains	900–1900
Artemisia granatensis	2500–2700	Yes	*Artemisia umbelliformis*	Alpine mountains	2800–3000
Centaurea bombycina subsp. *xeranthemoides*	1000–1500	No	*Centaurea bombycina s.l.*	Baetic mountains	200–1600
*Centaurea gadorensis**	1300–1700	No	*Centaurea pulvinata*	Sierra Nevada	1200–2000
Centaurea pulvinata	1500–1900	No	*Centaurea gadorensis*	Penibaetic mountains	1100–1900
Cerastium alpinum subsp. *aquaticum**	2500–3300	Yes	*Cerastium alpinum* subsp. *nevadense*	Sierra Nevada	2700–3300
Cerastium alpinum subsp. *nevadense**	2700–3300	Yes	*Cerastium alpinum* subsp. *aquaticum*	Sierra Nevada	2500–3300
Dactylis glomerata subsp. *juncinella*	2000–3300	No	*Dactylis glomerata s.l.*	Eurasia	600–1500
Draba hispanica subsp. *laderoi*	2500–3200	Yes	*Draba hispanica* subsp. *hispanica*	Western Mediterranean	1000–2200
Erigeron frigidus	3000–3400	No	*Erigeron major*	Baetic mountains	1800–3000
Eryngium glaciale	2400–3400	No	*Eryngium bourgatii*	Western Mediterranean	1500–3000
Erysimum baeticum	1600–2600	No	*Erysimum mediohispanicum*	Iberian Peninsula	700–1900
Erysimum nevadense	2000–2800	No	*Erysimum mediohispanicum*	Iberian Peninsula	700–1900
Helianthemum apenninum subsp. *estevei*	1300–1800	No	*Helianthemum apenninum s.l.*	Baetic mountains	0–1800
Nepeta boissieri	1700–2200	No	Hybrid species		
Pinus sylvestris subsp. *nevadensis*	1700–2200	Yes	*Pinus sylvestris s.l.*	Eurasia	700–1900
Santolina elegans	1700–2000	No	*Santolina rosmarinifolia*	Western Mediterranean	300–2100

Table 2 continued

Endemic taxa			Hybridizing with		
Name	Altitudinal distribution	Relict	Name	Geographical distribution	Altitudinal distribution in Sierra Nevada
Saxifraga trabutiana	1600–2400	No	*Saxifraga granulata*	Eurasia	200–2800
Sideritis arborescens subsp. *luteola*	1000–1600	No	*Sideritis arborescens s.l.*	Western Mediterranean	500–1000
Sideritis glacialis	2000–3000	No	Sideritis hirsuta	Western Mediterranean	50–2000
Thymus serpylloides subsp. *serpylloides*	2000–3000	No	*Thymus serpylloides* subsp. *gadorensis*	Iberian Peninsula	1500–2200

Information on altitudinal distribution is from Blanca et al. (2002). Information on actual hybridization has been taken from the literature (see Appendix 1 for the sources). The endemic taxa were always located above the altitudinal distribution of the widespread non-endemic taxa except for those marked with *asterisks*

the Sierra Nevada's high mountains are not endemic but have a wider distribution across other European mountains (Pauli et al. 2003). According to Kropf et al. (2006), fragmentation of a once broad and continuous distribution area during the Holocene cold period into small areas resembling the original climate and acting as glacial refugia (vicariance) was a key mechanism for the origin of many of those cold-adapted relict taxa. Whereas about half of the relict endemic plants are subspecies of species widely distributed in other European mountains, most non-relict Sierra Nevada endemic plants have been described as species (Fig. 2).

Natural hybridization has been already reported for 26 of the 106 endemic taxa in the Sierra Nevada (Table 2; Appendix S1). That is, about 25 % of the endemic flora is currently hybridizing and, in most cases, with taxa from lowland areas (Table 2). The intensity of hybridization currently occurring in Sierra Nevada might even increase in the near future if we take into account that: 1) most theoretical models on climate change predict an overall uphill movement of the Mediterranean plants in this mountain range (Benito et al. 2011); and 2) two-thirds of the endemic taxa belong to lineages where hybridization has been demonstrated in at least one of its members (Fig. 2; see Appendix S1).

We would expect hybridization to be more frequent in non-relict than in relict taxa, because the former usually belong to lineages having taxa in the surrounding lowland areas of the Sierra Nevada. However, we found that the percentage of hybridizing taxa was similar in both (29 % of non-relict vs. 22 % of relict taxa). Nevertheless, most hybridizing relict taxa were subspecies, which interbreed with other subspecies of the same species (Table 2). By contrast, few endemic relict species are currently hybridizing in Sierra Nevada (Fig. 2). We presume that, rather than promoting hybridization, climate change will threaten relict species mostly by contracting the area of suitable habitat, causing the appearance of novel antagonistic interactions and/or triggering interspecific competition with uphill-moving Mediterranean species. For example, herbivorous insects will move uphill in the Sierra Nevada as climate warms, feeding on relict plants (Hódar et al. 2003).

The impact of hybridization is still difficult to predict, mostly because no genetic or demographic studies have yet been performed. Nevertheless, we can envisage some

potential outcomes depending on the taxonomic status, geographic distribution, and abundance of the hybridizing taxa. A clear scenario can be forecast when the hybridizing taxa are endemic non-relict subspecies. If we consider that these taxa are currently in a dynamic divergence process that could eventually lead over the long term to new species, their ongoing hybridization with other subspecies of the same species will surely collapse this speciation process. We conclude that the consequence of hybridization will, in this case, be speciation reversal (Fig. 1).

It is harder to infer whether the hybridization involving the endemic species of Sierra Nevada is introgressive or non-introgressive. Nevertheless, we have found that most hybridizing species are non-relict, and are interbreeding with phylogenetically related species (Table 2). As a consequence of the rapid diversification rate undergone by many Mediterranean plant lineages, many allopatric endemic species with weak reproductive isolation exist (Valente et al. 2010; Gutiérrez-Larena et al. 2002). Under these circumstances, we presume that the observed hybridization will lead to introgression.

Introgressive hybridization can produce complete admixture or widespread introgression (Fig. 1). Some evidence suggests that complete admixture is frequent for Sierra Nevada endemic taxa. Hybridization is mostly occurring with lowland taxa that have wider distributions (Table 2). In addition, the population size of endemic taxa that are currently hybridizing is lower than the population size of non-hybridizing endemic taxa (16,110 ± 72,118 vs. 85,824 ± 33,997 individuals; see Appendix S1). Complete admixture would have negative outcomes because it can trigger the extinction of rare, endemic taxa (Levin et al. 1996). Widespread introgression may also happen among Sierra Nevada endangered taxa. In this study, we have focused exclusively on endemic taxa. But hybridization has already been reported for populations of endangered taxa inhabiting not only Sierra Nevada but also other mountain ranges. For example, the only known Sierra Nevada population of *Artemisia umbelliformis*, an alpine species inhabiting many European mountains, is threatened by hybridization with other *Artemisia* species (Blanca et al. 2002).

Finally, we should remark that hybridization, besides having the aforementioned negative effects, may also increase the diversity of the Sierra Nevada flora by giving rise to new species (Soltis and Soltis 2009). In fact, it seems that two endemic taxa in Sierra Nevada have a hybrid origin (Table 2). Gutiérrez-Larena et al. (2002) have suggested that altitudinal migrations within a contraction–expansion model have resulted in the formation of a new hybrid taxon (*Armeria filicaulis* subsp. *nevadensis*) as a consequence of the hybridization of *A. splendens* and *A. filicaulis* subsp. *filicaulis*. Similarly, Blanca et al. (2002) have indicated that *Nepeta boissieri* originated from the hybridization between *N. granatensis* and *N. amethystina* subsp. *laciniata*.

It seems that hybridization, together with other ecological consequences of global warming, will have an impact on the Sierra Nevada endemic flora in the near future. It is urgent to determine how important hybridization will be for the loss of plant diversity in Sierra Nevada, as well as in other endangered ecosystems (McClanahan et al. 2008). Unfortunately, this question as yet has no precise answer. Nevertheless, we presume that hybridization may be more important than previously believed. For example, 8 % of the 2223 populations belonging to the 600 endangered plant taxa in Spain are already threatened by hybridization (Bañares et al. 2003). As Boyd et al. (2008) pointed out, conservation problems usually overpass the extent of a single site constituting a large landscape-scale issue, so the solution or mitigation must be also at large scale.

Conclusion

We have postulated in this article that, under some circumstances, climate change could cause genetic swamping of endemic high-mountain plants. This phenomenon has been frequently overlooked, probably because most conservationists and policy-makers have paid more attention to the ecological effects of global warming to high-mountain plants, because its possible genetic effects could go unnoticed by most people.

Some management actions could be done when widespread lowland species and rare endemic high-altitude species come into contact. The specific actions will obviously depend on the consequences of the contact. When no hybridization is taking place, or when hybridization is not introgressive, the only concern for the high-altitude taxa is over competition and decrease in reproductive output. In this scenario, traditional conservation strategies are probably adequate in some situations (Pauchard et al. 2009). Introgressive hybridization between lowland and high-altitude species imposes a challenge to conservation management. While the traditional management plans tend to propose the removal of the hybridizing species, there is now a tendency to promote the so-called assisted migration (Lazarus and McGill 2014). We presume that assisted migration will favour hybridization events between species that were once geographically separated. It is also crucial to determine whether hybridization is natural or anthropogenic, a task that is most of the time difficult to achieve (Allendorf et al. 2001). In case of anthropogenic hybridization, some decisions need to be taken before developing any conservation plan. Allendorf et al. (2001) suggest that is necessary to decide which proportion of genetic admixture is acceptable before introgressed taxa will no longer be protected. This is a difficult decision, since hybrid plant populations deserve protection in many cases (Cozzolino et al. 2006; López-Pujol et al. 2012), mostly when they represent a source of novel diversity (Thompson et al. 2009) and facilitate the survival of endemic species under current climate change (Becker et al. 2013). In the case of high-altitude plants, with already impoverished populations due to global warming, hybridization might represent in some cases the only way to circumvent demographic extinction. Under these circumstances, protecting the hybrids would contribute to preserve part of the genetic diversity of those endemic high-altitude species that are vanishing.

Nevertheless, we need to be cautious. We have to improve our knowledge about how human-induced hybridization threats high-altitude plants before taking any decision. We think that, prior to developing any conservation strategy, it is urgent to gather more information about the extension and long term consequences of hybridization in high altitude environments. These actions may go from removing lowland species that hybridize (in order to preserve the genetic diversity of upland species) to promote hybridization via assisted migration (in order to rescue some genetic diversity of the upland species that will disappear), depending on the identity of hybridizing species and the conservation targets. Time has come to include in future conservation agendas a protocol for the surveillance and monitoring of potential genetic swamping in endemic high-mountain plants. This will provide precious knowledge that will help to preserve these unique environments.

Conflict of interest The authors declare that they have no conflict of interest.

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