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Plant invasions into mountains and alpine ecosystems: current status and future challenges

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Abstract Recent years have seen a surge of interest in understanding patterns and processes of plant invasions into mountains. Here, we synthesise current knowledge about the spread of non-native plants along elevation gradients, emphasising the current status and impacts that these species have in alpine ecosystems. Globally, invasions along elevation gradients are influenced by propagule availability, environmental constraints on population growth, evolutionary change and biotic interactions. The highest elevations are so far relatively free from non-native plants. Nonetheless, in total nearly 200 non-native plant species have been recorded from alpine environments around the world. However, we identified only three

species as specifically cold-adapted, with the overwhelming majority having their centres of distribution under warmer environments, and few have substantial impacts on native communities. A combination of low propagule availability and low invasibility likely explain why alpine environments host few non-native plants relative to lowland ecosystems. However, experiences in some areas demonstrate that alpine ecosystems are not inherently resistant to invasions. Furthermore, they will face increasing pressure from the introduction of pre-adapted species, climate change, and the range expansion of native species, which are already causing concern in some areas. Nonetheless, because they are still relatively free from non-native plants, preventative action could be an effective way to limit future impacts of invasions in alpine environments.

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Introduction

Understanding the spread of non-native species underpins our ability to protect native species and habitats vulnerable to invasion. In recent years, there has been an explosion of studies of plant invasions into mountain areas (e.g. Marini et al. 2009; Paiaro et al. 2011; Pauchard et al. 2016; Seipel et al. 2012), motivated in part by concern about the possible impacts of non-native plants in mountain ecosystems. Whilst providing a global view of the status of plant invasions in mountains, these studies also emphasise the value of steep environmental gradients for understanding the processes limiting non-native species' spread more generally.

Studies of plant invasions in mountains have mostly focused on patterns of non-native species richness and the dynamics of spread along elevation gradients. However, often these gradient studies do not reach the highest areas, and therefore, much less is known about the status of non-native plants in alpine areas. Alpine areas are generally considered to be relatively free from non-native plants (Pauchard et al. 2009; Zefferman et al. 2015). Whether this means that alpine environments are inherently resistant to invasion is, however, still unclear (Kueffer et al. 2013; Pauchard et al. 2009). Increasing recreational or agricultural demands on alpine ecosystems, combined with climate and other environmental changes, might increasingly expose alpine areas to invasion. To foresee and forestall these changes, it is important to understand current patterns of non-native plants in alpine areas.

Our aim in this article is to provide an overview of the current status of plant invasions in mountain—and especially alpine—ecosystems worldwide. We first review the patterns and processes of plant invasions along elevation gradients in mountains that have emerged from the recent literature. We then compile a checklist of non-native species recorded specifically from alpine environments, including published records and previously unpublished data, and analyse patterns in this global alpine non-native flora. We review evidence for impacts that these species have in alpine ecosystems, and consider hypotheses for why alpine areas have until now received few non-native species relative to lowland ecosystems. Finally, we discuss possible future challenges that alpine ecosystems will face from plant invasions, and suggest priority areas for future and on-going research.

Non-native plant invasions along elevation gradients

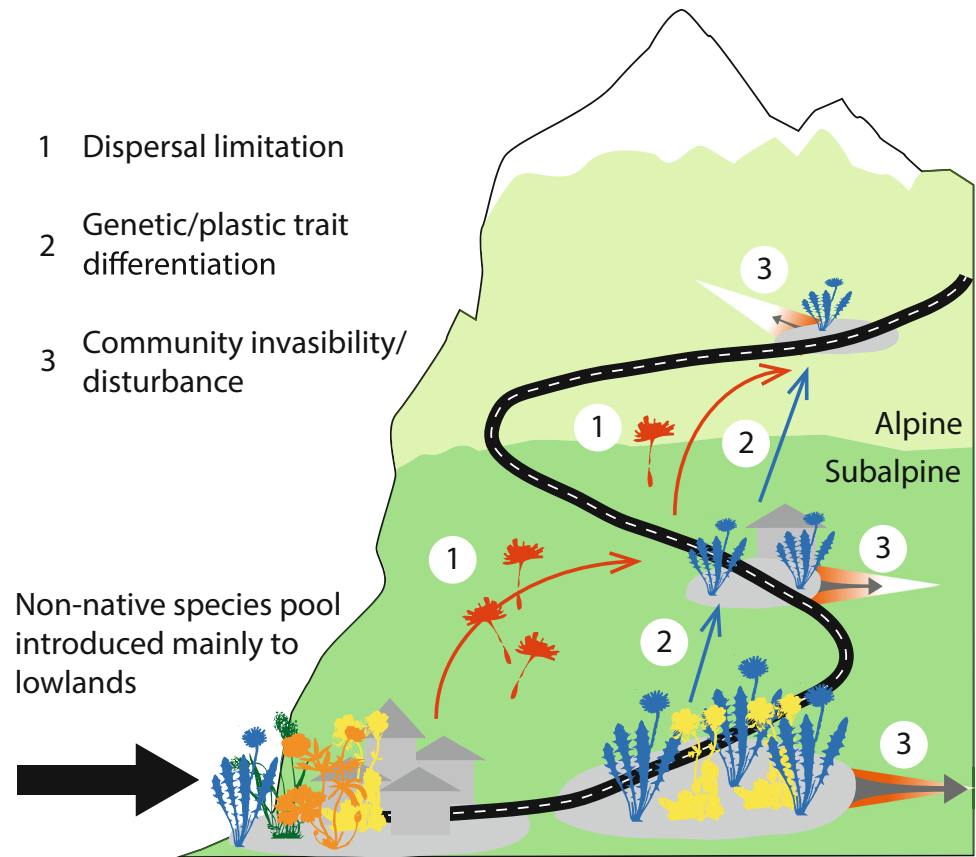
To understand the origin and diversity of non-native plants currently found in alpine areas, it is necessary to first consider patterns and processes of invasions along complete elevation gradients. We start by reviewing the dominant patterns of non-native species richness in mountains, and the processes influencing non-native species spread (Fig. 1). Some of these processes will also affect spread in alpine ecosystems, but such areas have received much less direct empirical attention.

Patterns of non-native species richness along elevation gradients

Until recently, patterns of non-native plants in mountains had received little attention because most experts thought that non-native species were rare in upper montane to alpine ecosystems (Pauchard et al. 2009). Most research does indicate that non-natives are less frequent when compared to the lowest elevations regionally, but upper elevations (montane to alpine areas) are not free of non-native species (Alexander et al. 2011; Marini et al. 2013). Studies from around the world support a consistent pattern of declining non-native plant richness from a maximum at the lowest elevation, or within the lower third of the elevation gradient, irrespective of the broad bioclimatic region. This pattern has been observed in all biomes of the world in global (Alexander et al. 2011; Seipel et al. 2012) and regional studies from cold arctic systems (Lembrechts et al. 2014), temperate mountains in North America (Andersen et al. 2015; Pollnac et al. 2012), Europe (Becker et al. 2005; Marini et al. 2013; Medvecká et al. 2014; Pyšek et al. 2011), New Zealand (Tomasetto et al. 2013), South America (Pauchard and Alaback 2004) and China (Zhang et al. 2015), Mediterranean mountains (Barros and Pickering 2014; Haider et al. 2010) and subtropical and tropical mountains (Jakobs et al. 2010; Khuroo et al. 2011; Paiaro et al. 2011).

Patterns of non-native plant invasion along elevation gradients are driven by a combination of climatic constraints and human influences. Declining non-native species richness with elevation has been explained by the introduction of non-native species predominantly to low elevations, coupled with environmental filtering as species spread towards higher elevation (Alexander et al. 2011). Consistent with this explanation, most non-native species found at high elevation have broad ecological ranges and are also present at low elevation (Alexander et al. 2011; Haider et al. 2010; McDougall et al. 2011a). However, other studies suggest that richness of non-native species along elevation gradients

Fig. 1 Processes known to influence the invasion of non-native plants along elevation gradients and into mountain ecosystems. Until now, most non-native species have been introduced to low elevations, and species with broad climatic tolerances spread towards higher elevation. This can be influenced by (1) dispersal rates to suitable sites and the availability of seed sources, (2) evolutionary and plastic changes in life-history traits (here plant size) and (3) levels of anthropogenic disturbance and the resistance of native communities to invasion. Non-native plants are currently scarce in alpine ecosystems, due likely to a combination of low propagule availability, an absence of species adapted to environmental conditions, low anthropogenic disturbance and low invasibility of natural communities



at higher elevations is limited more by propagule pressure and availability of novel niches created by human activities (i.e. disturbances) than by climatic filtering (Marini et al. 2012). Indeed, in most regions, the lowest elevations encompass the highest densities of human population and disturbances associated with agriculture, roads and urban development (Dainese et al. 2014; Jauni et al. 2015). This can provide opportunities for non-native species establishment and conduits for dispersal (Becker et al. 2005); roads and trails are recognized as major pathways for invasion into mountains (Fuentes et al. 2010; Lembrechts et al. 2016; Pauchard and Alaback 2004). In sum, declining non-native species richness towards higher elevation is explained by a combination of climatic constraints on species' distributions and fewer anthropogenic disturbances.

Processes influencing spread along elevation gradients

A number of different factors can influence the spread and establishment of non-native species along elevation gradients. Here we briefly review recent research into the main drivers (Kueffer et al. 2013; Pauchard et al. 2009): dispersal, rapid evolution and phenotypic plasticity, and community invasibility and disturbance.

Dispersal

The transportation network plays a key role in the introduction of species to mountain systems, with roadways and associated vehicle transport a main driver of non-native plant introductions (Lembrechts et al. 2016). The rate of spread along roads can be rapid (Kalwij et al. 2015; Vacchiano et al. 2013). For instance, a spread rate of 24.5 and 9.7 m in elevation per year was observed for annuals and perennials, respectively, over a 7 year period along a mountain road in southern Africa (Kalwij et al. 2015). Nonetheless, the availability of seed sources can limit spread rates. For example, Kalwij et al. (2015) found that non-native occurrences were clustered around four points of potential seed introduction along the road. This pattern corresponds with results from vehicle seed dispersal studies, where most seeds fall off within short distances, but others remain on the vehicle for long distances (Taylor et al. 2012). Consequently, propagule pressure decreases with increasing distance from seed sources, such as upwards along a mountain road. Thus, even if some non-native species are able to rapidly reach high elevations along transport networks, their distribution will tend to be dispersal limited at local scales (Seipel et al. 2016).

Rapid evolution and phenotypic plasticity

The ability of non-native plants to adjust their phenotype to the changing conditions they encounter along elevation gradients can be important to support population persistence and continued spread. Responses can involve both phenotypic plasticity and genetically based trait differentiation, and evidence for both mechanisms has been reported, although not specifically from alpine areas. For instance, the success of *Verbascum thapsus* in numerous mountain systems worldwide can be attributed to its broad ecological tolerance and its plastic response to varying environmental conditions (Ansari and Daehler 2010; Seipel et al. 2015). Further examples are plastic responses along elevation gradients in growth of *Pinus strobus* in the Czech Republic (Münzbergová et al. 2013), in photosynthetic ability in the perennial vine *Mikania micrantha* in southern India (Prabu et al. 2014), and in reproductive traits of *Ageratina adenophora* in the Yunnan Province of China (Zhao et al. 2013).

Populations along elevation gradients can also become genetically differentiated with respect to ecologically important traits. Monty and Mahy (2009) and Haider et al. (2012) found genetically based differentiation in growth traits (plant height and above-ground biomass) between populations of different elevations. Adaptation to drought has allowed *Taraxacum officinale* to colonise high elevation environments in the Andes (Quiroz et al. 2009). Although these patterns are consistent with local adaptation, fewer studies have tested for this directly with reciprocal transplant experiments along elevation gradients. For example, Leger et al. (2009) found evidence that genetic differentiation in traits related to germination and seedling survival resulted in local adaptation of *Bromus tectorum* at low elevation, but not at high elevation. However, the presence of genetic variation in traits related to survival suggests the potential for adaptation in high elevation populations.

Not all non-native species found at higher elevations show differentiation in quantitative traits or possess high levels of phenotypic plasticity (Compagnoni and Adler 2014; Poll et al. 2009; Trtikova et al. 2010). Nonetheless, the capacity for genetic and plastic trait differentiation appears to be a common feature of species that are successful invaders across broad elevation ranges.

Community invasibility and disturbance

Interactions with native mountain plant communities can shape non-native species' spread and abundance at landscape and local scales (Poll et al. 2009; Pollnac et al. 2012, 2014; Pollnac and Rew 2014). Partly this is suggested

by the observation that the richness and probability of occurrence of non-native plants is much lower in semi-natural mountain vegetation than along disturbed roadsides, especially at higher elevation and in protected areas (Seipel et al. 2012). Direct evidence from more detailed studies of non-native populations in mountains is scarcer. Although the distribution of *Linaria dalmatica* along mountain roadsides in the Intermountain West, USA, is correlated strongly with climate, its abundance once established is reduced by the total cover and richness of native species (Pollnac and Rew 2014), indicating negative interactions with the native vegetation. Effects of native vegetation on population growth rates were less clear, although the highest growth rate was observed where the cover of vegetation and litter was low and cover of bare ground was high (Pollnac et al. 2014). Similarly, vegetation structure and species composition influenced non-native species establishment in undisturbed vegetation in the northern Scandes of Sweden (Milbau et al. 2013).

Disturbance can promote the establishment of non-native species by reducing competition from native species and by releasing additional resources (Davis et al. 2000). Milbau et al. (2013) found that, on average, three times as many seedlings established in vegetation gaps compared with undisturbed vegetation in a seed addition experiment along a gradient ranging from subarctic birch forest to the alpine zone in northern Sweden. Disturbance was also found to promote the spread of non-native species from lower elevations in montane forests in California (Stevens and Latimer 2015). Petryna et al. (2002) found that the establishment of six non-native plants, including *Cirsium vulgare*, depended on local disturbances in mountain grasslands in Central Argentina. However, disturbance doesn't always promote non-native species establishment: in similar nearby natural grasslands in Argentina, Paiaro et al. (2007) found that disturbance reduced recruitment of the non-native *C. vulgare* and *Melilotus albus* along an elevation gradient from 1200 to 2000 m a.s.l., but improved recruitment of *C. vulgare* from 2000 to 2200 m a.s.l. These findings could potentially be explained by a higher degree of desiccation and increased light intensity in the disturbed patches (Paiaro et al. 2007). Similarly, disturbance and biotic resistance had little influence on the abundance of *Taraxacum officinale* colonizing high elevation areas in the Chilean Andes (Quiroz et al. 2011).

It is expected that with increasing elevation, there will be a shift from negative plant-plant interactions (competition) to positive interactions (facilitation; Cavieres et al. 2005), suggesting that the effect of disturbance on invader establishment will change along elevation gradients. For instance, Cavieres et al. (2007) demonstrated that cushions of the native plants *Laretia acaulis* and *Azorella monantha*

facilitated the non-native species *Cerastium arvense* at 2800 and 3600 m a.s.l. in the Andes of central Chile. Also the non-native *T. officinale* was facilitated by cushion species in the high Andes of central Chile (Cavieres et al. 2008), but here it was shown that the facilitative effects were dependent on the nurse species. Recently, it was even shown that nurse plants can modulate diversity-invasibility relationships in harsh environments, with increasing invader abundance if native plant diversity within cushion patches increases (Badano et al. 2015).

Overall, this body of work reveals that resident mountain plant communities can strongly resist invasion of non-native species, especially in arctic-alpine environments. Disturbance that disrupts the native community tends, therefore, to promote invasion into mountain ecosystems, but depends on the environmental context (e.g. whether the dominant stresses are caused by coldness vs. drought vs. photoinhibition). Indeed, native alpine vegetation can also facilitate non-native species establishment, although this seems more likely in arid than humid alpine areas.

Non-native plant invasions in alpine areas

As the previous sections show, a diverse body of research has investigated patterns and processes of plant invasions along elevation gradients. Yet we lack an overview of the current status of plant invasions at the highest elevations. In this section, we establish which non-native species are present in alpine habitats worldwide, describe attributes of this non-native alpine flora, review impacts that the species have in native alpine communities and consider hypotheses to explain these patterns.

Which non-native species are present in alpine environments?

We searched the literature for records of non-native plant species from alpine areas worldwide. Data were extracted from several sources: (1) records from surveys conducted by the Mountain Invasion Research Network (MIREN; <http://www.mountaininvasions.org/>) and partners; (2) unpublished data and personal observations known to the authors; (3) other published papers. To identify suitable papers, we performed an ISI Web of Science search on 22.1.2016 using the terms: TOPIC = ((invasiv* OR non*native OR introduced) NEAR plant) AND (alpine OR “high elevation” OR “high-altitude”), which retrieved 407 papers. We combined this with a further 124 papers that cite Pauchard et al. (2009) and Alexander et al. (2011) and additional literature identified from the bibliographies of these papers. From these sources we only extracted records of species defined by the

authors as non-native and from alpine environments. Alpine environments can be defined as those occurring above the physiological potential treeline in mountains (Körner et al. 2011). Whilst the treeline corresponds to the alpine ecotone in some, especially temperate regions, this is not the case in regions where tree growth is limited by factors other than low temperature (e.g. drought) or where treeline has been modified by human activity. Because the non-native plant records we obtained were rarely georeferenced, we did not apply a strict bioclimatic definition of “alpine”. Instead, we retained only records from elevations defined by the authors of a study to be from the alpine zone. Information about the origin and ecological attributes (ecological strategies, temperature affinity, growth form and life-history) of the species were obtained from various databases (Landolt et al. 2010; BioFlor, Klotz et al. 2002; USDA Plants database, <http://plants.usda.gov>; U.S. National Germplasm System, npgsweb.ars-grin.gov). All were accessed between 20/02/2016 and 10/03/2016). Taxonomy was verified and standardized with the R-package “taxonstand” (Cayuela et al. 2012).

Altogether we obtained data from 36 sources for 15 different mountain ranges (Table 1), including 372 records of in total 183 distinct species (excluding one unidentified fern from Hawaii; Online Resource 1), with nine regions containing more than ten different species. Of these, only 49 species were found in more than 1 region, and 21 in three or more regions (Table 2). This alpine non-native flora is a small subset of total regional non-native floras. For example, the 28 species recorded from alpine areas in five mountain regions during the MIREN survey in 2012 (Lembrechts et al. 2016; MIREN unpublished; Table 1) accounted for only 6 % of the total number of non-native species recorded from across the complete elevation gradients in these regions. Our literature search probably did not capture all non-native species present in alpine regions globally (for example, we were not able to include information available in floras). Nonetheless, based on the large number of sources included and species records retrieved, we expect this data synthesis to be representative.

Most non-native species were in the families Poaceae, Asteraceae, Caryophyllaceae, Fabaceae and Brassicaceae (Fig. 2a). They originated primarily from Europe and temperate Asia (63.9 and 39.9 %, respectively, 68.9 % combined) and to a lesser degree from the Americas (Fig. 2b), consistent with the over-representation of northern hemisphere species in the global non-native flora (van Kleunen et al. 2015). Half (51.6 %) of the non-native species were perennial, and 46.7 % were annual. 69.9 % of species were forbs and 24.6 % graminoids, and only 5 vines, 6 shrubs, and 1 tree species (*Prunus persica*, recorded as a seedling from South Africa/Lesotho; J. Kalwij, pers. com.; Kalwij et al. 2015) were recorded, and these patterns were

Table 1 List of regions and data sources included in the review of alpine non-native floras, including the number of non-native species (“Spp.”) for each country and the threshold taken for the lowest elevation of the alpine zone (m a.s.l.)

Region	Abb.	Country	Spp.	Elevation (m)	Reference
Andes, central	AnC	Argentina	16	2500	Barros and Pickering (2014)
Andes, central	AnC	Bolivia	3	4100	Fernández-Murillo et al. (2015)
Andes, central	AnC	Chile	21	2890	Lembrechts et al. (2016); Seipel et al. (2012)
Andes, central	AnC	Chile	3	1600	A. Pauchard, pers. comm.
Andes, northern	AnN	Ecuador	36	3500	Sandoya (unpublished)
Andes, northern	AnN	Venezuela	4	3500	Herrera and Goncalves (unpublished)
Australian Alps	AuA	Australia	25	1850–1875	Lembrechts et al. (2016); Seipel et al. (2012), J. Morgan pers. comm., K. McDougall pers. comm.
Drakensberg Mountains	Dra	Lesotho	25	2800	Kalwij et al. (2015)
East African Mountains	EAM	Kenya	4	3600–3900	Hedberg (1970); Hemp (2008)
European Alps	EuA	Switzerland	7	2000	Becker et al. (2005); Irl et al. (2013), Seipel et al. (in review)
Hawaii	Haw	USA	45	2900–3000	Daehler (2005); Jakobs et al. (2010); Juvik et al. (2011); Seipel et al. (2012), MIREN unpublished
Iceland	Ice	Iceland	16	400	Wasowicz (2016)
La Reunion	LRe	La Reunion	7	2600	Tassin and Rivière (2003)
New Zealand Alps	NZA	New Zealand	3	1250	(Burrows 1986; Steer and Norton 2013)
Qinghai-Tibet	QTi	China	32	3580	Xu (2015); Zhang (2011)
Rocky Mountains	RoM	USA	12	2900	Lembrechts et al. (2016); Seipel et al. (2012); Weaver et al. (2001)
Scandes	Sca	Norway	4	560–1000	(Lembrechts et al. 2016); Rydgren et al. (2015)
Tenerife	Ten	Spain	16	1900	Dickson et al. (1987); Seipel et al. (2012)
White Mountains	WhM	USA	6	3500	Rundel et al. (2008)

very consistent across the different regions (Fig. 3a). Overall, 7.5 % of species were nitrogen-fixers.

A striking pattern was observed in the ecological affinity of the species. For the species for which data were available (80 %), we recorded their temperature indicator value according to Landolt (Landolt et al. 2010) (where 1 = alpine species and 5 = warm adapted temperate species of Central Europe) and CSR strategy according to Grime (Grime 1977) (C, competitive strategy; R, ruderal strategy; S, stress-tolerating strategy). Only three species (2.1 %) have a Landolt temperature indicator (T) ≤ 2, indicative of alpine or mountain plants (Fig. 3b). These species were *Alnus alnobetula* ssp. *sinuata* (syn. *A. viridis*; CCS, T = 2), *Papaver nudicaule* (syn. *P. croceum*; CSS, T = 2) and *Phleum alpinum* (CSR, T = 2). No species were recorded as being stress-tolerators (S), although five are listed as CSS or SSR (Fig. 2c). The vast majority of species have broad temperature tolerances, or are more typical of lower elevations, and have a ruderal or competitive life-history strategy (Figs. 3b, 2c). Among the species for which Landolt temperature indicator data were not available, Wasowicz (2016) identified three species in Iceland that reach alpine environments in their native North America (*Lupinus nootkatensis*, *Deschampsia cespitosa* subsp.

beringensis and *Salix alaxensis*), although none are exclusively alpine species.

Do non-native plants invade alpine communities, and what impacts do they have?

Non-native species in alpine areas, as elsewhere, are most frequently encountered in disturbed sites (Seipel et al. 2012), and most records compiled here come from surveys conducted along road corridors. For instance, in surveys conducted in alpine areas in five different mountain regions (data from Lembrechts et al. 2016; MIREN unpublished; Table 1), we recorded in total 28 non-native species occurring in plots at roadsides and 50–100 m away from roads. Of these, only 10 were recorded in plots 50–100 m from the disturbed road corridor, together accounting for only 18 % of the total number of non-native occurrences in the alpine zone.

Although many of the non-native species found along alpine roads have been introduced accidentally (McDougall et al. 2011a), some non-native species have been deliberately introduced to alpine areas away from roads. For example, *Lupinus nootkatensis* was initially introduced to Iceland for soil stabilization, where it is now considered an

Table 2 The 21 non-native plant species recorded from three or more regions

Species name	Family	Growth form	Regions present
<i>Achillea millefolium</i>	Asteraceae	Forb	AnC, AuA, Haw
<i>Anthoxanthum odoratum</i>	Poaceae	Graminoid	AnN, AuA, Haw
<i>Capsella bursa-pastoris</i>	Brassicaceae	Forb	Dra, EAM, Ten, WhM
<i>Cerastium fontanum</i> ssp. <i>vulgare</i>	Caryophyllaceae	Forb	AnN, AuA, Haw
<i>Dactylis glomerata</i>	Poaceae	Graminoid	AuA, Haw, Ten
<i>Erodium cicutarium</i>	Geraniaceae	Forb	AnC, AnN, Haw
<i>Festuca rubra</i>	Poaceae	Graminoid	AuA, Haw, Sca
<i>Holcus lanatus</i>	Poaceae	Graminoid	AnC, AnN, Haw, LRe
<i>Hypochaeris radicata</i>	Asteraceae	Forb	AnC, AuA, Dra, Haw, LRe
<i>Lolium perenne</i>	Poaceae	Graminoid	Dra, Ice, QTl
<i>Phleum pratense</i>	Poaceae	Graminoid	AuA, Ice, RoM, Sca
<i>Plantago lanceolata</i>	Plantaginaceae	Forb	AnC, AnN, Haw
<i>Poa annua</i>	Poaceae	Graminoid	AnC, AnN, AuA, Dra, EAM
<i>Poa pratensis</i>	Poaceae	Graminoid	AnC, Haw, RoM, Ten
<i>Polygonum aviculare</i>	Polygonaceae	Forb	AnC, Dra, RoM
<i>Rumex acetosella</i>	Polygonaceae	Forb	AnC, AnN, AuA, Dra, Haw, NZA
<i>Rumex crispus</i>	Polygonaceae	Forb	AnC, Dra, LRe
<i>Sonchus asper</i>	Asteraceae	Forb	AnC, AnN, Haw
<i>Stellaria media</i>	Caryophyllaceae	Forb	Dra, Haw, Ten, WhM
<i>Taraxacum officinale</i>	Asteraceae	Forb	AnC, AnN, AuA, Dra, Haw, Him, RoM
<i>Trifolium repens</i>	Fabaceae	Forb	AnC, AnN, AuA, Haw, RoM, QTl

For region abbreviations see Table 1, and for a complete species list see Online Resource 1

invasive species, competing strongly with native species and altering soil properties through nitrogen fixation (Magnússon et al. 2004; Wasowicz 2016). The construction of ski pistes sometimes relies on non-native grassland species for re-vegetation of disturbed sites, albeit not necessarily above tree line (e.g. Titus et al. 2003). Seeded species can be highly persistent (e.g. more than 50 years; McDougall 2013) and inhibit re-colonisation by native species (Isselin-Nondedeu and Bédécarrats 2009). Nonetheless, climate and competition barriers to establishment and spread can be substantial for new species arriving in the alpine, with high mortality of seedlings and slow growth rates (Mallen-Cooper 1990). Even for species deliberately introduced to alpine areas, some will not persist (e.g. *Lolium perenne* in Australia, McDougall 2001; *Schedonorus pratensis* and *Phleum pratense* in Norway, Rydgren et al. 2015) or spread beyond the restoration area (e.g. Brown et al. 2003; Rydgren et al. 2015).

The presence of a non-native species does not mean that it will have an important impact. In the Australian Alps, the non-native forb *Rumex acetosella* has been present for more than 100 years and common in the alpine zone for at least 60 years (Mallen 1986). Despite this, there is no evidence that this species affects native plant richness (McDougall & Walsh, unpublished data). In the alpine zone of the Andes of central Chile, native species richness did not differ among

plots with or without *T. officinale* (Cavieres et al. 2005; Quiroz et al. 2011), although the abundance of some native forb species (e.g. *Chaetanthera lycopodioides*, *Montiopsis potentilloides*, *Oxalis compacta*, *Phacelia secunda* and *Viola philippi*) was significantly lower in plots dominated by *T. officinale* (Cavieres et al. 2005). Nonetheless, at high densities *T. officinale* can draw pollinators away from native species, decreasing their reproductive output (Muñoz and Cavieres 2008).

Of the 10 species recorded in MIREN surveys away from roads, three (*Agrostis capillaris*, *Hypochaeris radicata*, *Poa annua*) have been tested in glasshouse experiments for competitive abilities against native species that occur in cold environments. In conditions simulating cold Antarctic islands, the presence of *P. annua* caused a reduction in biomass of two native species it was grown with, while maintaining its own biomass (Molina-Montenegro et al. 2012). Mallen-Cooper (1990) demonstrated higher above- and below-ground productivity in pot trials for a range of non-native herbaceous species in comparison to selected Australian native alpine species, and at a range of nutrient levels. The non-native species tested are common and have a long residence time in disturbed Australian alpine and subalpine environments but are only occasionally found in natural vegetation, indicating that their rapid growth does not confer dominance over native species in the absence of clear

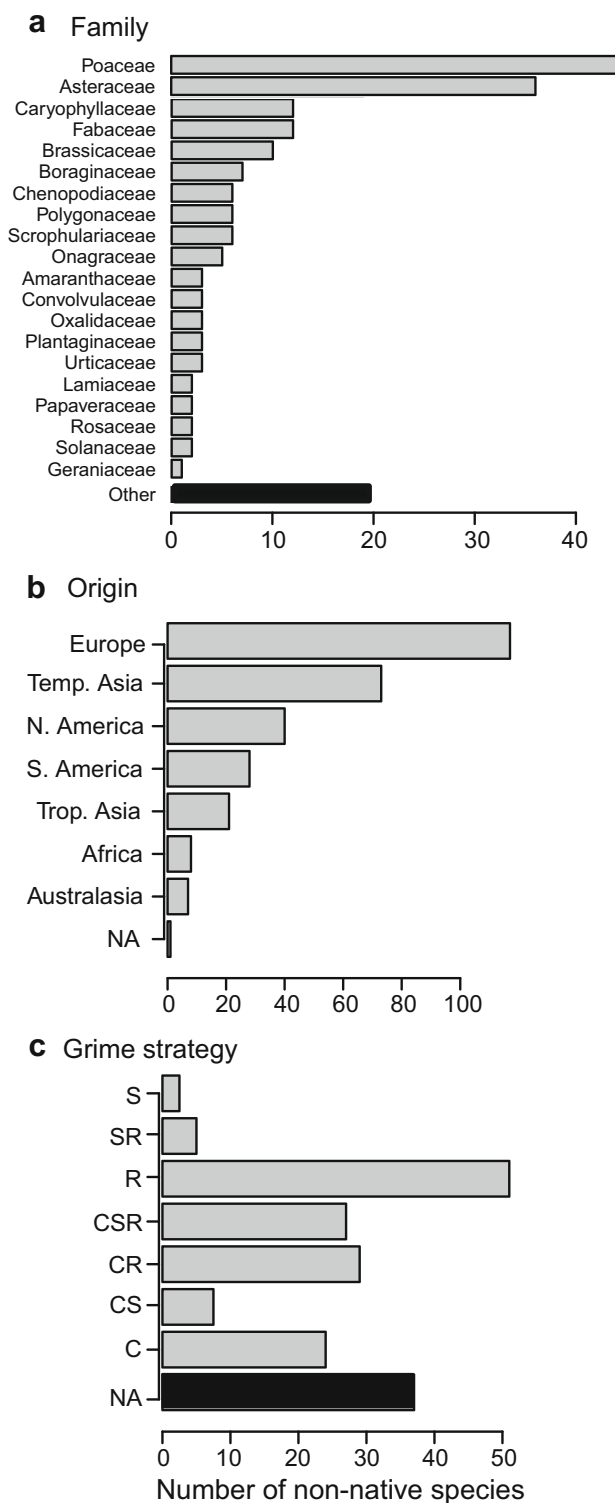


Fig. 2 Global numbers of non-native species in the alpine zone broken down by **a** family, **b** origin and **c** ecological strategy according to Grime (*CSR*, with *C* = competitive, *S* = stress-tolerant and *R* = ruderal). In **a**, families with fewer than three species are grouped as ‘other’. In **b**, origin was classified according to the TDWG continental scheme (see van Kleunen et al. 2015) as Europe, Temperate Asia (Russia, China, Eastern Asia and the Middle East), Tropical Asia (India and South-East Asia, including the islands of Indonesia) Australasia (Australia and New Zealand), Africa (here, only species south of the Sahara), North America and South America (south of Mexico). Species assigned to >1 origin were counted once for each origin. In **c**, species with intermediate Grime strategies (e.g. *CCR*) were counted as contributing 0.5 species to each category (e.g. *C* and *CR*)

lepidulum on species richness, evenness, diversity and composition after 6 years, regardless of *Hieracium* abundance (Meffin et al. 2010). The authors concluded that *H. lepidulum* co-exists with native species in these environments.

At least some non-native species are causing concern in alpine areas. *Pilosella officinarum* (syn. *Hieracium pilosella*) was discovered in the alpine zone of Kosciuszko National Park (KNP) in Australia in 2015. Much of the site was sparsely vegetated because of a past grazing disturbance, but *P. officinarum* dominated vegetation cover where it occurred, up to 150 m² in area (Caldwell et al. 2015). Although the pre-invasion vegetation was not documented, the monocultural nature of *P. officinarum* in KNP is consistent with its known biology. Studies in New Zealand indicate that some native montane species are poor competitors with *P. officinarum* (Moen and Meurk 2001). Nevertheless, it seems likely that disturbance facilitated invasion and subsequent dominance by *P. officinarum* in the alpine zone at KNP. Overall, we see that even for species currently introduced deliberately to alpine areas, impacts on native communities have so far been slight. However, there are exceptions, warranting greater efforts to understand the conditions under which impacts do arise.

Why is the alpine relatively free from non-native species?

Similar to alpine ecosystems, other “harsh” environments, for example those characterized by very low soil nutrient concentrations or soil toxicity, tend to be little invaded (Zefferman et al. 2015). Zefferman et al. (2015) proposed two non-mutually exclusive explanations for these patterns: low propagule availability, or an inherent resistance of these environments to invasion. Here we consider the evidence for these hypotheses.

Low propagule availability

The low number of non-native species present in alpine areas globally might be explained by limited opportunities

disturbance. At a small scale then, especially in the vicinity of disturbance and in less stressful environments, increased vigour of non-native species may lead to a reduction in cover of proximal native species. However, an empirical study in montane forest and subalpine grassland in New Zealand found no significant effect of non-native *Hieracium*

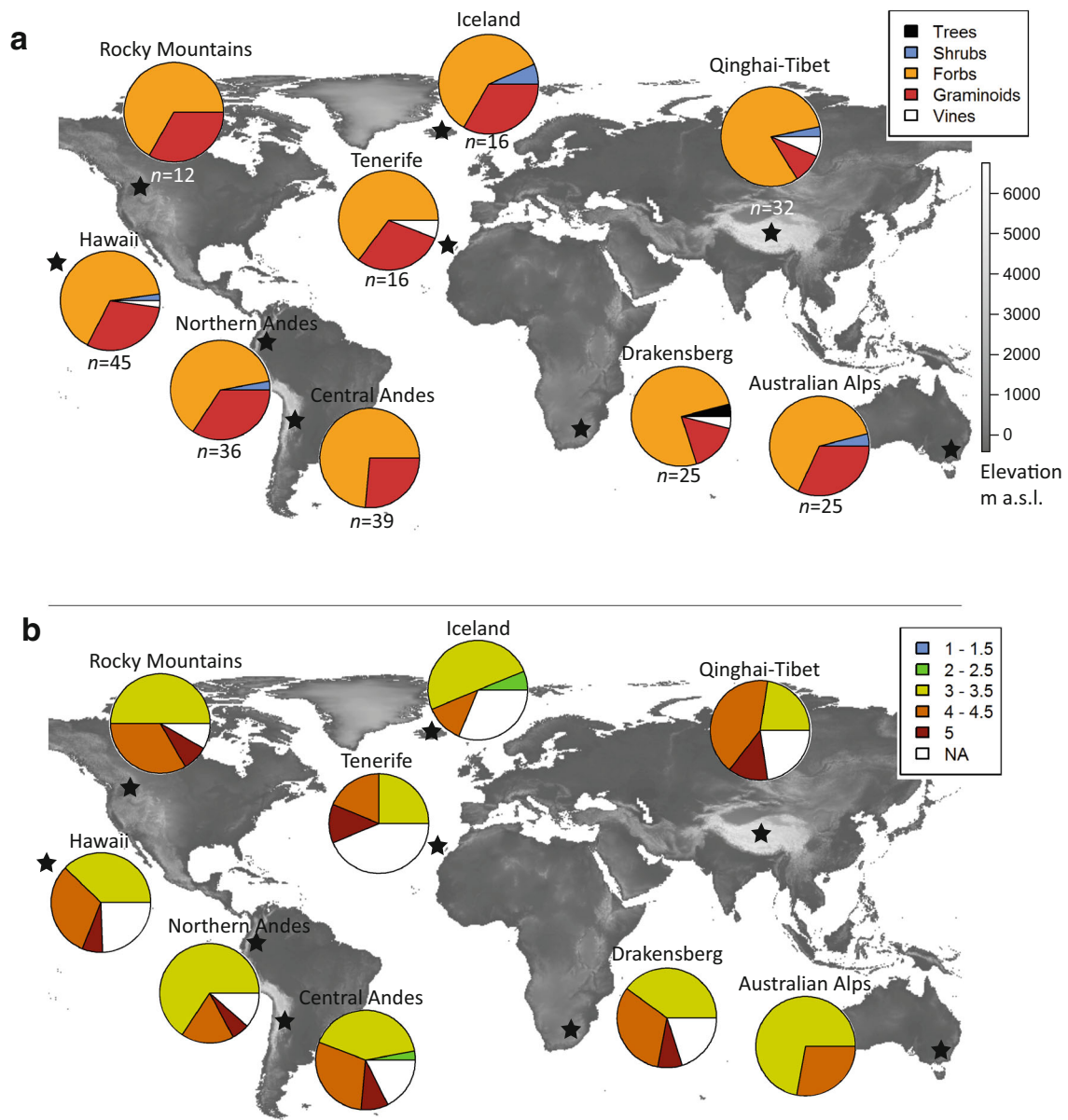


Fig. 3 Proportions of species with **a** different growth forms and **b** Landolt indicator values for temperature affinity (where 1 = alpine species and 5 = warm adapted temperate species of Central Europe)

for the 9 mountain regions (stars) with at least 10 non-native species recorded from the alpine zone (regional n shown in Fig. 1a)

for introduction and establishment. First, because alpine areas constitute a small fraction of global land surface (Körner 2003), and human activities there are limited, we would expect relatively few opportunities for alpine species to be transported to new parts of the world. Secondly, even when they are transported to a new region, alpine species might have limited opportunities for establishment. Studies along elevation gradients support this idea, because they suggest that most non-native species are introduced at low elevation and from there spread upwards (Alexander et al. 2011). The preponderance of ruderal species typical of warmer climates among the non-native species recorded

from alpine areas is in agreement with this hypothesis (Fig. 2, 3). Furthermore, whilst these species might be able to persist in favourable, disturbed sites at the edges of their climate niches, their ability to spread in closed vegetation appears to be constrained (Marini et al. 2009). As our review shows, specialized alpine species appear to have been only very rarely introduced directly to alpine ecosystems. The invasion of *L. nootkatensis* in Iceland indicates that some cold-adapted species are able to spread in alpine vegetation, once introduced (Wasowicz 2016). Therefore, low propagule availability of species pre-adapted to alpine ecosystems could explain why these ecosystems have so far been so little

impacted by invasions, or in other words, the separation of harsh environments from sites of species introduction through steep environmental gradients shields them from invasions. Similarly, alpine areas within a region are “islands” isolated by unfavourable lowland environments, limiting opportunities for spread to other alpine areas. Nonetheless, we cannot fully exclude the possibility that species adapted to harsh alpine environments are frequently introduced but fail to establish.

Resistance of alpine environments to invasion

Even given sufficient propagule availability, low temperatures, short seasons and drought conditions might directly limit rates of growth and population spread (Pollnac et al. 2014), making alpine areas inherently less susceptible to invasion (but see Lembrechts et al. 2014). This could explain the limited success of species sown for restoration purposes at high elevation (Brown et al. 2003; Rydgren et al. 2015).

Alpine environmental conditions might also indirectly limit invasion by reducing the ability of non-native species to competitively displace natives. This would also explain why most non-native species are restricted to disturbed sites in the alpine zone. According to this hypothesis, we would expect non-native species to occur in alpine vegetation subject to disturbances that reduce competition with natives. Although alpine vegetation is exposed to many different natural disturbances to which native species are adapted (e.g. from burrowing mammals, avalanches, rock falls, solifluction and freeze–thaw dynamics), anthropogenic disturbances, which are most strongly associated with invasions in lowland ecosystems (Jauni et al. 2015), are generally few. An exception is the alpine pasture of the Qinghai-Tibetan plateau, where anthropogenic activities have promoted the expansion of some vigorous native plants (Shang et al. 2014). The dominance of these native alpine species, which are considered problematic weeds, remarkably increased following pasture degradation caused by the alteration of grazing regimes (e.g., *Aconitum pendulum*, *Axyris prostrata*, *Lepidium capitatum*, *Ligularia virgaurea*, *Ligularia sagitta*, *Oxytropis ochrocephala*, *Pedicularis kansuensis*, *Plantago depressa*, and *Stellera chamaejasme*) (Hou 2011; Xie et al. 2014). These species are poisonous to livestock, and usually exert strong allelopathic effects, accelerating the degradation of alpine grasslands (Hou 2011). Although it concerns native species, this example illustrates that even in alpine ecosystems, disturbances associated with human activities can lead to dramatic increases in some species, and cautions against the interpretation that alpine environments are inherently resistant to invasion.

Future alpine invasions

As shown above, a combination of factors explains why alpine ecosystems currently host so few non-native species. Partly this reflects limited propagule availability, with species specialized to growing in alpine environments being very rarely introduced to high elevations, and partly because undisturbed native alpine vegetation likely poses a strong barrier to invasion. These limitations could be relaxed in the future, due to increasing anthropogenic pressures and climate change. Climate change will also bring new challenges in the form of native species expanding their ranges to higher elevations.

Continued introductions of non-native species

Current plant invasions in mountains still represent a subsample of the species that were first introduced, for example, by settlers and agriculture in the New World (Seipel et al. 2012), and only a few of those have been able to reach alpine environments. Other non-native species may still be in a lag phase in the lowlands adapting to mountain conditions or increasing their propagule pressure. Therefore, a large “invasion debt” (Essl et al. 2011) may be accumulating with unpredictable outcomes for the future. In addition, new species are being brought not only to lowland environments, but also increasingly to higher elevations as cultivars and ornamentals or accidentally through increasing tourism (Pickering et al. 2011), and some of these species might be specialized for growth in alpine environments (Kueffer et al. 2013; McDougall et al. 2011b).

Effects of climate change on non-native invasions

Climate change is likely to increase the susceptibility of alpine areas to invasion in two ways. Firstly, climate warming will ease the climate filters that currently restrict many abundant non-native species in mountains to lower elevations. Nonetheless, substantial warming could be required before alpine areas are strongly affected. For example in the Swiss Alps, invasive species are expected to shift their ranges into montane and subalpine, but not alpine, areas following climate change during this century (Petitpierre et al. 2015). These patterns will, however, be region-specific, depending on how changes in temperature and precipitation interact, with upward shifts being less pronounced in the Australian Alps than in Switzerland (Petitpierre et al. 2015).

The second way in which climate change could promote invasions is by reducing the ability of native alpine vegetation to resist the establishment of non-native species (Diez et al. 2012; Sorte et al. 2012). On the one hand, climate

change could increase resource availability (e.g. enhancing mineralization of organic matter in alpine soils) or disturbances (e.g. due to extreme events; Diez et al. 2012) upon which invading species could capitalize (Sorte et al. 2012). On the other hand, declines in the abundance or competitive performance of native species under warming could provide opportunities for invading species to establish (Hampe and Petit 2005). For example, a warming experiment in Tibet indicates that increased temperature could cause significant and rapid native species loss of the alpine grasslands on the Qinghai-Tibet plateau (Klein et al. 2004).

Native range-expanding species

In addition to concerns about impacts of non-native species, the spread of native species into higher elevations in response to climate change, and perhaps human-facilitated dispersal, poses new questions about impacts (Pauchard et al. 2016). Homogenisation of vegetation in alpine summits in Switzerland caused by the uphill movement of natives has already been observed (Jurasinski and Kreyling 2007). Some range expanding species will lead to dramatic community changes, particularly for shrubs and trees invading alpine grasslands (Dullinger et al. 2003). But herbaceous species from lower elevations can also have large impacts. In the Changbai Mountains of China, the native grass *Deyeuxia angustifolia* has invaded alpine tundra from the birch forest zone and displaces native species (Zong et al. 2016). In Japan, the dwarf bamboo *Sasa kurilensis* has recently expanded into alpine snow meadows, probably driven by climate change, where it decreases species richness by 75 % (Kudo et al. 2011). Lowland competitors reduce the performance of focal alpine plants in the Swiss Alps under warmer climate to a greater extent than their current alpine competitors (Alexander et al. 2015). Altogether, these examples suggest that in some areas the arrival of new native competitors from lower elevations could drive the extirpation of alpine species after climate change.

Conclusions and research needs

Our review has shown that non-native species are widespread at lower and mid-elevations in mountains, and with increasing climate change and human development many of them could spread and become abundant at higher elevations. Although we found nearly 200 non-native species recorded from alpine areas worldwide, our review reveals that alpine ecosystems remain relatively little affected by plant invasions. However, information on the distribution of non-native species and their impacts in alpine ecosystems is sparse, and we lack a clear understanding of how resistant

alpine communities currently are to the establishment and spread of non-natives. We therefore suggest three areas where research is particularly needed:

1. *Invasion resistance and species pools*: the low number of non-native species in alpine areas does not necessarily imply that these ecosystems are inherently resistant to invasion, but might simply reflect an absence of suitably adapted species. To assess the risk of invasions, one approach could be to screen the establishment success of specialist alpine and climatically generalist species in alpine vegetation under controlled conditions using propagule addition experiments, under a range of anthropogenic and natural disturbances. Also, risk assessment protocols and biosecurity measurements at national levels should explicitly include cold mountain environments.
2. *Impacts*: Although documented impacts of non-native plants are currently few, some species are causing concern in some areas (e.g. *L. nootkatensis* in Iceland and *P. officinarum* in Australia). Comparative studies to better document these impacts, also in regions where these species are present but not yet abundant, could help to understand and predict the circumstances under which non-native plants do negatively affect alpine communities.
3. *Climate change and other synergies*: To test whether climate change makes alpine communities more susceptible to invasion, addition experiments like those just described could be crossed with climate manipulations. By adding both non-native and native “range expanding” species, it would be possible to further test for any differences in their impacts on subsequent community development. In addition, more comprehensive studies looking at multiple drivers of global change (e.g. climate change, land use change, nutrient additions) and how they interact to promote plant invasions in mountains should be pursued.

These research efforts will be an important part of a wider research agenda to understand the magnitude and pace of alpine community alteration with global change (Pauchard et al. 2016). In this context, native range-expanding species might be of greater concern to managers than non-native species. Whether native range expansions are regarded as deleterious and worthy of mitigation, or inevitable and beneficial responses to global change, will largely depend on local land use requirements and perceptions, as well as jurisdictional policies. However, alpine areas are largely untested ground for non-natives so it is better to minimize the risk of impact by preventing invasion altogether. As alpine areas are effectively islands within a lowland landscape with well-defined corridors of access, this is likely to be achievable with careful vigilance and rapid response to incursions.

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