



# Alien flora of mountains: global comparisons for the development of local preventive measures against plant invasions

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## ABSTRACT

**Aim** We use data from 13 mountain regions and surrounding lowland areas to identify (1) the origins, traits and cultural uses of alien plant species that establish in mountains, (2) the alien species that are most likely to be a threat and (3) how managers might use this information to prevent further invasions.

**Location** Australia, Canada, Chile, India, New Zealand, South Africa, Spain, Switzerland, USA.

**Methods** Lists of alien species were compiled for mountains and their surrounding or nearby lowlands. Principal co-ordinates analysis was performed on a matrix of similarities created using presence/absence data for alien species. The significance of differences between means for (1) similarity metrics of lowland and mountain groups and (2) species traits of lowland and mountain alien floras was determined using *t*-tests. In seven of the 13 mountain regions, lists of alien species undergoing management were compiled. The significance of differences between proportions of traits for species requiring and not requiring management input was determined with chi-square tests.

**Results** We found that the proximal lowland alien flora is the main determinant of a mountain region's alien species composition. The highest similarities between mountain floras were in the Americas/Pacific Region. The majority of alien species commonly found in mountains have agricultural origins and are of little concern to land managers. Woody species and those used for ornamental purposes will often pose the greatest threat.

**Main conclusions** Given the documented potential threat of alien species invading mountains, we advise natural resource managers to take preventive measures against the risk of alien plant invasion in mountains. A strategy for prevention should extend to the surrounding lowland areas and in particular regulate the introduction of species that are already of management concern in other mountains as well as climatically pre-adapted alien mountain plants. These may well become more problematic than the majority of alien plants currently in mountains.

## Keywords

Altitude, biological invasions, invasion pathways, land use history, mountain ecosystems, non-native plant invasion.

## INTRODUCTION

Mountains are of great significance to people and biodiversity (Messerli & Ives, 1997). The orographic influence of mountains traps rain, providing water that is essential for downstream

agriculture and the persistence of major urban and industrial centres (Viviroli *et al.*, 2007). The complexity of mountain habitats typically leads to diverse ecosystems of plants and animals and a high degree of endemism (Körner, 2003; Nagy & Grabherr, 2009). For these and historic, aesthetic and economic

reasons, many mountain systems world-wide have been designated as national parks and reserves for the protection of their biodiversity and natural resources (Spehn *et al.*, 2002).

Mountain biota, however, face increasing pressures, especially from tourism and climate change (Price, 2006; Nagy & Grabherr, 2009). An expansion of tourism (or a shift from winter- to summer-based activities) will lead to increased disturbance through the provision of new infrastructure (e.g. roads, walking tracks and accommodation) and increased utilization. Climate change may have direct impacts on vegetation by affecting productivity, phenology and competition (e.g. Theurillat & Guisan, 2001) but may have a greater indirect impact through changes to hydrology, fire frequency and herbivore abundance (e.g. Beniston *et al.*, 1997; Price, 2006; Spehn *et al.*, 2006; McDougall & Broome, 2007; Nagy & Grabherr, 2009).

High mountains are often considered to be at low risk of plant invasions (Humphries *et al.*, 1991; Millennium Ecosystem Assessment, 2003). However, evidence shows that plant invasions do occur, and even though the risk may be lower than in some other ecosystems, it is not insignificant (e.g. Rouget *et al.*, 2003; Baret *et al.*, 2006; Pauchard *et al.*, 2009). The currently observed low number of alien species in mountains may be more related to a time-lag effect or less intensive human activities at higher elevations than an inherent resistance of mountain ecosystems to plant invasions (Seabloom *et al.*, 2006; Pauchard *et al.*, 2009). The invasion of new alien plant species may be facilitated by increases in tourism, through anthropogenic disturbance, and climate change, the creation of favourable environments at higher elevations for species currently limited to low to mid elevations (e.g. Simberloff, 2000; Pauchard *et al.*, 2009). Mountains, because of their high levels of endemism, have much to lose from disruptive plant invasions.

It is widely accepted that prevention of invasion is far more cost-effective than eradication or control once an invasion has

occurred (e.g. Wittenberg & Cook, 2001; Leung *et al.*, 2002; Lodge *et al.*, 2006). Because mountains are generally not as badly affected by alien plant invasions as some other ecosystems, invasive species researchers and managers have the opportunity to respond in time to the threat by preventing invasions. However, effective management will rely on information about the species likely to become problematic. In this paper, we use data from 13 mountain regions and surrounding lowland areas from all continents (except Antarctica) and several oceanic islands to identify (1) the origins, traits and cultural uses of species that typically establish in mountains, (2) the species that are most likely to be a threat and (3) how managers might use this information to prevent further invasions.

## METHODS

### Data

Lists of alien species were compiled for mountains and their surrounding or nearby lowlands in 13 regions: Australia (Alps), Canada (British Columbia), Chile (Mediterranean central zone, temperate south-central zone), India (Kashmir), New Zealand (South Island), South Africa (Drakensberg area), Spain (Canary Islands), Switzerland (Alps), USA (Alaska, Hawaii, New Mexico, northern Rocky Mountains) (Fig. 1).

Mountains were defined as areas possessing steep topography that culminates in a treeless alpine or nival zone. Lowlands were below the altitudes of the mountains. Altitudinal limits of mountains and lowlands for each region and source citations are provided in Appendix S1.

In most cases, no distinction was made in the lists between casual, naturalized and invasive species (in the sense of Pyšek *et al.*, 2004), and we refer to all species from these lists as alien. In seven of the 13 mountain regions [Australia, Canada, New Zealand, USA (Alaska, Hawaii, New Mexico, northern Rocky

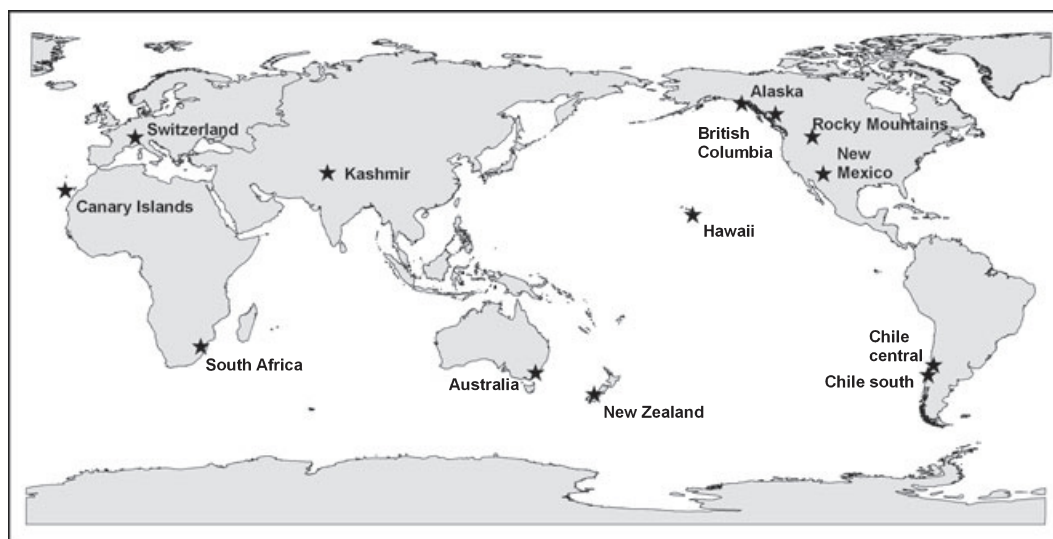


Figure 1 Location of the 13 mountain regions included in the study.

Mountains)], we were able to assemble lists of alien species undergoing management from management plans, monitoring reports and personal knowledge (Appendix S1); these species may be considered invasive in a broad sense. In most cases, these species were undergoing management because of their disruptive invasiveness but in a few cases, management was directed at removing new incursions before they became disruptive. The lists cannot be interpreted as comprehensive assessments of invasiveness in a region because they may reflect regional priorities and the resources available for dealing with invasions.

For each alien species, accepted name, origin and utility data were compiled from the Germplasm Resources Information Network (GRIN) online database (URL: <http://www.ars-grin.gov/cgi-bin/npgs/html/taxgenform.pl>) and species traits were compiled from the USDA Plants database (URL: <http://plants.usda.gov/index.html>). Synonymy was checked and standardized. Taxa below species level were aggregated. For species not listed in GRIN, other sources were checked (e.g. local floras). Life-form and longevity were grouped as annual forb, annual grass, perennial forb, perennial grass and woody plants (including trees, shrubs, woody vines and succulents). Origin was classified as *Europe* (including northern Africa, the Fertile Crescent of Western Asia and Russia west of the Ural Mountains and the Caspian Sea), *Asia* (south, central, south-east and east), *Australasia/Oceania* (Australia and islands of the south-west Pacific), *southern Africa* (south of the Sahara, including Madagascar), *North America* and *South/Central America* (south of central Mexico) or *unknown*. Where a species occurred in an area near the boundary of two regions, it was attributed to both.

### Data analysis

A matrix of similarities between lowland and mountain regional alien floras was created with Primer v.5 (Clarke & Gorley, 2001) using the Bray–Curtis metric on presence/absence data. Principal co-ordinates analysis (PCO) was performed on the matrix with R using the vegan package (Oksanen *et al.*, 2009; R Development Core Team, 2009). The significance of differences between means for (1) Bray–Curtis similarity metrics of lowland and mountain groups and (2) species traits of lowland and mountain alien floras were determined using *t*-tests. For tests of difference in mean percentage, means were arcsine transformed prior to analysis. Back-transformed means and 95% confidence limits were calculated following analysis. The significance of differences between proportions was determined with Pearson's chi-square tests (Rosner, 2006).

## RESULTS

### Mountain alien flora

In the 13 mountain areas, 972 alien species from 483 genera and 103 families were recorded. The number of alien species recorded per mountain area ranged from 64 for the Canary

Islands to 272 for South Africa (mean =  $147 \pm 19$ , median = 117). The families Asteraceae and Poaceae accounted for about one-third (31%) of species. More than two-thirds (68%) of species were forbs, almost 40% were annuals and only 13% were woody. The majority of species originated in Europe (64%) and/or Asia (45%). Of species with a documented use, most (57%) were ornamentals.

About 60% of species were recorded from a single mountain area, and less than 5% occurred in more than half of the mountain areas. The most frequently occurring species were *Capsella bursa-pastoris* (11 regions), *Plantago lanceolata* (11), *Plantago major* (10), *Poa annua* (10), *Polygonum aviculare* (10), *Rumex acetosella* (11), *Stellaria media* (12), *Taraxacum officinale* sens. lat. (11) and *Trifolium repens* (11). In their native European range, all of these species are widespread and, in most cases, regarded as ruderals. None is restricted to mountain habitats (Tutin *et al.*, 1964–1980).

### Comparison of mountain and lowland alien floras

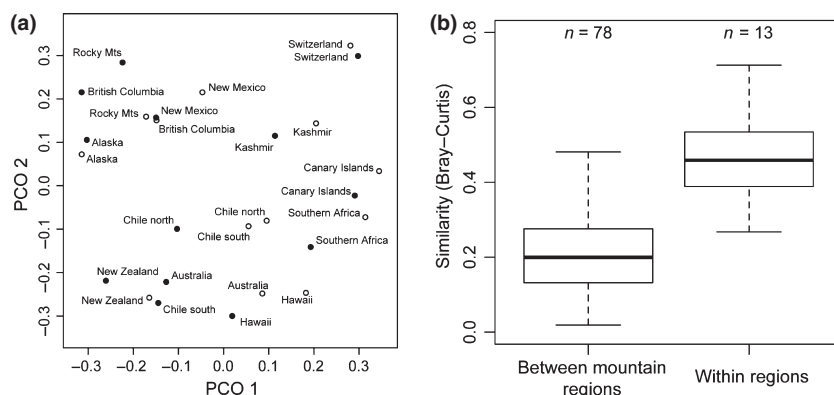
A total of 1993 species were recorded as alien in the 13 regions; 1840 (92%) of these were recorded in lowlands, and 972 (49%) were recorded in mountains. The five families with the highest number of species per family were the same in mountain and lowland areas, and there was no difference in the mean percentage of species in these families between mountains and lowlands (Table 1). There were a significantly higher mean percentage of perennial grasses and a significantly lower percentage of woody species in mountains compared with lowland areas. Mountain areas had significantly more species from Europe and Asia and fewer species from South and Central America, Australasia/Oceania and southern Africa than lowland areas. The mean percentage of ornamentals was lower in mountains than in lowland areas. About half the species had no documented use in lowlands and mountains.

### Similarity among alien floras

The PCO (Fig. 2a) shows that mountain and lowland alien floras are generally more similar to each other than to floras of other regions. The first two axes of the PCO explain 27% of the variability in the data. The first axis is negatively correlated with overall similarity ( $R^2 = 0.58$ ,  $P < 0.01$ ). In all but two cases, mountain areas have a lower value on axis 1 than adjoining lowland areas indicating a convergence of the floristic composition of mountain areas (i.e. overall, mountain areas are more similar to each other than lowlands are to other lowlands). Of the mountain areas, those with greatest similarity (lowest values on axis 1) are from the Americas [Alaska, British Columbia, northern Rocky Mountains (USA), and New Mexico], the Pacific Region (Hawaii, Australia, and New Zealand) and South America (Chile). The mountain floras of Switzerland, Canary Islands and South Africa are highly dissimilar to other mountain floras and to each other. Of the mountain areas with the highest similarity, areas group largely by latitude with most northern hemisphere regions having high

**Table 1** Mean percentage of species in the five most species-rich families, and by life-form, origin (where known) and utility attributes (where identified) for the 13 mountain ( $n = 972$ ) and lowland regions ( $n = 1\,840$ ), and proportion of species requiring management action ( $n = 102$ ) or not identified for management action ( $n = 466$ ) for seven mountain regions. The significance of differences between means was determined by a *t*-test (d.f. = 12). Percentages were arcsine transformed prior to analysis. Back-transformed means and 95% confidence limits are presented. The significance of differences between proportions was determined with Pearson's chi-square tests (d.f. = 1). Significant differences ( $P < 0.05$ ) are indicated in bold.

	Mountain regions (mean % of species)	Lowland regions (mean % of species)	<i>t</i>	<i>P</i>	Species requiring management (% of species)	Species not identified for management (% of species)	$\chi^2$	<i>P</i>
<b>Families</b>								
Asteraceae	16.6 ± 1.8	14.4 ± 1.3	2.013	0.067	28.4	12.9	15.325	< <b>0.001</b>
Brassicaceae	6.9 ± 2.1	6.2 ± 1.9	1.064	0.308	3.9	8.8	2.728	0.099
Fabaceae	7.3 ± 2.1	8.3 ± 1.2	1.438	0.176	7.8	4.9	1.371	0.242
Poaceae	18.1 ± 2.7	16.2 ± 2.8	1.546	0.148	12.7	19.5	2.574	0.109
Rosaceae	2.9 ± 2.3	2.9 ± 1.4	0.090	0.930	7.8	4.5	1.923	0.166
<b>Life-form</b>								
Annual forb	35.0 ± 1.6	34.0 ± 2.5	0.547	0.594	15.7	35.6	17.322	< <b>0.001</b>
Annual grass	7.2 ± 1.4	7.3 ± 2.2	0.125	0.902	2.0	8.3	4.678	<b>0.031</b>
Perennial forb	34.8 ± 2.4	31.8 ± 1.8	1.948	0.075	49.0	33.2	7.897	<b>0.005</b>
Perennial grass	12.5 ± 3.0	9.2 ± 3.0	2.729	<b>0.018</b>	11.8	14.4	0.406	0.524
Woody	8.7 ± 2.7	14.5 ± 4.3	3.328	<b>0.006</b>	21.6	8.5	15.209	< <b>0.001</b>
<b>Origin</b>								
Europe	73.6 ± 6.0	63.6 ± 7.2	3.038	<b>0.010</b>	78.4	69.7	3.088	0.079
Asia	51.1 ± 4.6	45.6 ± 4.5	3.000	<b>0.011</b>	58.8	48.3	3.719	0.054
North America	14.7 ± 3.8	13.3 ± 3.3	0.980	0.347	13.7	16.1	0.355	0.551
South & Central America	7.5 ± 4.7	12.5 ± 5.1	3.861	<b>0.002</b>	2.9	9.4	4.660	<b>0.031</b>
Australasia/Oceania	2.3 ± 2.9	3.7 ± 2.5	2.595	<b>0.023</b>	2.9	4.9	0.762	0.383
Southern Africa	4.4 ± 2.2	7.6 ± 3.3	2.958	<b>0.012</b>	3.9	6.7	1.079	0.299
<b>Utility</b>								
Ornamental	26.1 ± 2.2	31.4 ± 2.4	2.732	<b>0.018</b>	40.2	24.0	11.106	<b>0.001</b>
Food, timber or tannin	15.6 ± 2.7	14.5 ± 2.2	1.570	0.143	17.7	12.4	6.016	<b>0.014</b>
Fodder, pasture or erosion control	11.6 ± 1.8	13.4 ± 2.7	1.048	0.315	14.7	12.4	0.381	0.537
No documented use	54.2 ± 1.4	49.1 ± 2.5	2.146	0.053	43.1	56.7	6.158	<b>0.013</b>



**Figure 2** Principal co-ordinates analysis (PCO) (a) of the floristic similarity (Bray–Curtis metric) of the 13 mountain regions (closed points) and adjoining lowland (open points) alien floras. Note that the mountain alien flora of each region tends to cluster close to the corresponding lowland flora. Accordingly, the similarity between mountain/lowland data sets within a region (b) is greater than the pairwise similarities among mountain regions.

values on axis 2, and all southern hemisphere regions having low values on axis 2. An exception is Hawaii, which is most similar to the southern hemisphere regions.

The mean Bray–Curtis similarity between mountain and adjacent lowland alien floras ( $0.47 \pm 0.03$ ) was significantly greater than between nearest mountain alien floras in terms of

linear distance ( $0.31 \pm 0.05$ ;  $t = 5.6$ , d.f. = 12,  $P = 0.0001$ ), latitudinal difference ( $0.23 \pm 0.03$ ;  $t = 2.9$ , d.f. = 12,  $P = 0.01$ ) and all pairwise similarities among mountain regions ( $0.21 \pm 0.01$ ;  $t = 7.7$ , d.f. = 89,  $P < 0.0001$ ; Fig. 2b).

### Alien species requiring management in mountains

Of the 568 alien species occurring in the seven mountain areas for which data were available, 102 species (18%) were deemed to require management in at least one region. There was a significantly greater proportion of Asteraceae, perennial forbs, woody plants and species used as ornamentals, food, tannin or timber, and a significantly smaller proportion of annual forbs and species originating in South and Central America and species with no documented use compared with species that were not identified as requiring management (Table 1). A disproportionately high number of ornamentals were perennial forbs ( $\chi^2 = 5.486$ ;  $P = 0.019$ ) and woody plants ( $\chi^2 = 51.749$ ;  $P < 0.001$ ), and a disproportionately high number of food/timber/tannin species were woody ( $\chi^2 = 52.111$ ;  $P < 0.001$ ). As with the general population of alien species in mountains, the majority of species requiring management originated in Europe and Asia.

The following species were identified for management in three or more mountain areas: *Carduus nutans*, *Centaurea stoebe*, *Cirsium arvense*, *Cirsium vulgare*, *Cytisus scoparius*, *Hieracium aurantiacum*, *Lepidium draba*, *Leucanthemum vulgare*, *Linaria dalmatica*, *Linaria vulgaris*, *Potentilla recta*, *Verbascum thapsus*. Of these species, only *Hieracium aurantiacum* is regarded as a predominantly mountain species in its native range (Tutin *et al.*, 1964–1980). At least half of the species of the genera *Pinus*, *Salix*, *Hieracium*, *Carduus*, and *Centaurea* required management (Fig. 3).

### DISCUSSION

This study represents, to our knowledge, the first global survey of alien plants in mountains. In the mountains of 13 regions from all continents (except Antarctica) and from temperate to tropical climates, we found that close to 1000 alien species from over 100 families have naturalized with between 64 and 272 species per region. The fact that about half of the species recorded in the adjoining lowlands were also present in mountains indicates that high-elevation ecosystems may not be especially resistant to alien plant invasions. The high proportion of species occurring in only one region suggests that many more alien species are present in other mountain regions not included in this study.

The magnitude of naturalization in mountains globally is currently difficult to determine because comprehensive published data are apparently unavailable for most mountain areas, especially in Africa and Asia. The biased representation of geographic areas is a well-known limitation of invasion biology (Pyšek *et al.*, 2008). For predicting future invasion risks in mountain ecosystems, it will be important to include data from other biogeographic and socio-economic contexts

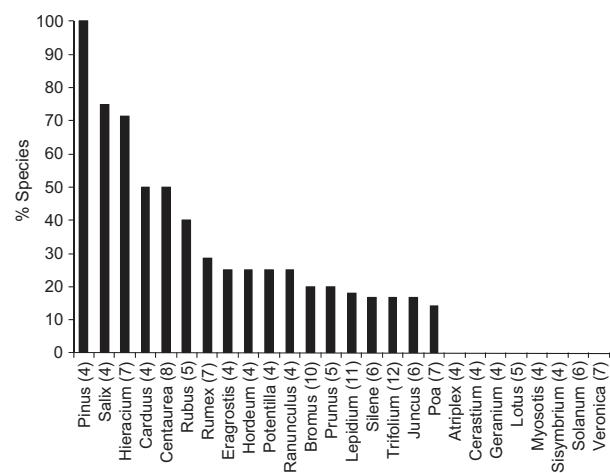


Figure 3 Percentage of species in genera requiring management action. A genus was plotted if it contained four or more species. The number of species in a genus is shown in parentheses.

(cf. Kueffer, 2010). We hope that our study will encourage the publication of comprehensive alien floras from more mountain regions.

### Characteristics of mountain alien floras

According to our data, mountain alien floras are characterized by three main features. First, they are typically composed of herbaceous species with an almost equal proportion of annual and perennial species. Although native mountain floras are also dominated by herbaceous species (Körner, 2003), these are mostly perennial. Second, a majority of species originated in Europe and/or Asia. Third, alien plants in mountains are mainly climatically broad lowland species rather than mountain specialists in their native range (Tutin *et al.*, 1964–1980). These climatically broad species also occurred in the lowlands of the 13 regions, leading to a high similarity between lowland and mountain areas within regions. Characteristic mountain genera such as *Primula* or *Gentiana*, which are often cultivated in gardens, were absent from both lowland and mountain alien floras.

The first two observations are in line with the characteristics of lowland alien floras. Herbaceous and annual species make up an important proportion of lowland alien weed floras of anthropogenic areas (Daehler, 1998; Sutherland, 2004), and most observations of alien species in mountains come also from anthropogenic areas such as roadsides or pastures. However, it is important to note that the few alien woody species were disproportionately of more concern to mountain managers. Indeed, in some mountain areas, woody species are the primary focus of management [e.g. the fynbos region of South Africa; Roura-Pascual *et al.*, 2009]. Woody species are also over-represented in lowland floras among natural area invaders in contrast to weeds of anthropogenic areas (Daehler, 1998; Sutherland, 2004; Kueffer *et al.*, 2010). The predominance of European and Asian species in the mountain and



lowland alien floras is also typical of alien floras world-wide (e.g. Rejmánek, 1996; Goodwin *et al.*, 1999; Prinzing *et al.*, 2002; Sutherland, 2004).

In contrast, the third observation was not expected because pre-adaptation of a species in its native range to the climate of the invaded range (climate matching) is often considered an important predictor of problematic invasive plants (e.g. Parker *et al.*, 2003; Pauchard *et al.*, 2004; Thuiller *et al.*, 2005; Kueffer *et al.*, 2010). One may rather have expected that the harsh climate in mountains would favour species that are pre-adapted to mountain environments in their native range, and consequently that alien species in mountains would be mainly mountain specialists, leading to a convergence of floristic similarity among different mountains, rather than between lowland and mountain floras.

### The influence of introduction pathways on mountain alien floras

Recent research in invasion biology has highlighted the importance of introduction pathways and events in shaping plant invasions (Kowarik & von der Lippe, 2007; Hulme, 2009; Wilson *et al.*, 2009). Past introduction pathways are also likely to have been important in the development of mountain alien floras.

First, the higher frequency of perennial grasses and lower proportion of ornamental plants compared to lowland alien floras and the predominance of European and Asian species may in our view mainly be explained by the history of land use in mountains. Mack & Lonsdale (2001) describe three phases of invasion by alien plants into the New World which seem to fit well for most of the mountain regions for which we obtained data: the accidental phase (where alien species were inadvertently dispersed as Europeans colonized the New World, e.g. species associated with pastoralism), the utilitarian phase (where new plants were introduced for direct use by the new colonists, e.g. food species) and the aesthetic phase (where ornamental species were introduced once new colonies became self-reliant). The alien species that were most commonly recorded in mountains are likely to represent invaders of the accidental and utilitarian phases. About three-quarters of the species recorded in mountains had no documented use or may have been used for fodder, pasture, erosion control, food, timber or tannin. However, the high proportion of ornamental species requiring management in mountain areas may represent the growing importance of the aesthetic phase, resulting from the replacement of livestock grazing by tourism in many mountain areas.

Second, the predominance of species in mountain areas that also occur in adjoining lowlands may be explained by a lowland introduction pathway. Because there are few direct transport links between mountain regions, the majority of alien species found in mountains are likely to have arrived from adjoining lowland areas along roads and rail links. Such a lowland introduction pathway will also explain why mountain alien plants are mostly climatically broad species rather than

mountain specialists, i.e. they need to be able to establish under a lowland climate before they can spread into high elevations (Becker *et al.*, 2005; Haider *et al.*, 2010).

### Alien plants of management concern in mountains

At present, alien mountain floras in the regions covered by our analysis are dominated by agrestal and accidentally introduced ruderal alien species that are not specialists of mountain climates. Accidentally, introduced ruderal species tend to be less problematic in natural areas than deliberately introduced alien plants (Daehler, 1998; Kueffer *et al.*, 2010) and the same seems to be the case for species that are not specifically pre-adapted to a particular climate (e.g. Parker *et al.*, 2003; Pauchard *et al.*, 2004; Kueffer *et al.*, 2010). This may explain why many long-established alien plant species have not posed major problems in mountains. In Australia, for instance, agrestal species that naturalized more than 100 years ago (e.g. *Lolium perenne*, *Phleum pratense*, *Trifolium repens*) are infrequent in native vegetation, where they have low cover and never dominate (McDougall & Walsh, 2007).

However, more recently, ornamental species have been deliberately introduced to mountain areas, including species from new source areas such as temperate China (National Academies of Sciences, 2002; Mack, 2005). In Australia, a shift from pastoral use to tourism in mountains has led to the introduction of climatically pre-adapted alien plants for horticulture (McDougall *et al.*, 2005). Our analyses show that species of ornamental use are more likely to be of management concern, so this trend should be of concern to natural resource managers.

Based on our findings, at least 100 alien species recorded in mountains are currently managed for nature conservation purposes. Unless locally native, *Leucanthemum vulgare*, *Potentilla recta*, *Verbascum thapsus*, herbaceous plants in the genera *Carduus*, *Centaurea*, *Cirsium*, *Hieracium*, and *Linaria*, and woody plants such as *Acacia* spp., *Cytisus scoparius*, *Pinus* spp. and *Salix* spp. will often be a threat in mountains.

Impacts from these species and genera in mountains have already been reported. For instance, in 1989, *Hieracium* species (mostly *H. lepidulum* and *H. pilosella*) in montane grasslands in New Zealand were estimated to be costing the pastoral industry between \$1.1 and 4.4 million annually in lost production (Grundy, 1989). In the last two decades, *H. aurantiacum* and *H. praealtum* have been discovered in mountain protected areas in Australia. Their rapid spread, competitive nature and capacity to invade undisturbed vegetation have alarmed nature conservation managers (e.g. McDougall *et al.*, 2005; Williams & Holland, 2007) and necessitated very costly containment and eradication programs. *Centaurea maculosa* is highly invasive in many mountains in western North America. In Montana, it threatens the endangered mountain endemic herb *Arabis fecunda* through direct competition (Lesica & Shelly, 1996). It is also believed to be having an impact on the reproductive success of chipping sparrows (*Spizella passerina*) in Montana by reducing food availability (Ortega *et al.*, 2006). In Kashmir,

invasive *C. iberica* is affecting species composition in montane grasslands and reducing the abundance of palatable species used by the threatened Kashmir Stag (*Cervus elaphus hanglu*) (Reshi *et al.*, 2008). *Pinus* species introduced for forestry operations have escaped in many mountain regions (Peña *et al.*, 2008; Pauchard *et al.*, 2009; Simberloff *et al.*, 2010). As well as direct impacts associated with competition for resources with native species, *Pinus* species may alter mountain fire regimes (Richardson & van Wilgen, 2004; Daehler, 2005). South African fynbos ecosystems have been heavily invaded by species of the genera *Acacia*, *Hakea* and *Pinus* (Roura-Pascual *et al.*, 2009), which have greatly reduced water production from watersheds (Le Maitre *et al.*, 2000).

### Management implications

Contrary to earlier non-quantitative assessments (Humphries *et al.*, 1991; Millennium Ecosystem Assessment, 2003), our study indicates that the potential threat of alien species invading mountains may have been underestimated. It is widely accepted that prevention of invasion is far more cost-effective than eradication or control once invasion has occurred (e.g. Wittenberg & Cook, 2001; Leung *et al.*, 2002; Lodge *et al.*, 2006), and our study provides a baseline for preventive measures. Because the proximal lowland alien flora is the main determinant of a mountain region's alien species composition, we suggest that preventive measures for mountain areas must encompass the surrounding lowlands. We also argue that past introduction pathways may have limited the risk of plant invasions in mountain but that this may change, e.g. as a response to a shift from winter to summer tourism and associated increase in the introduction of mountain specialist plants for horticulture (McDougall *et al.*, 2005). A priority preventive measure should thus be to regulate the introduction of climatically pre-adapted alien mountain plants because they may well become more problematic than the majority of alien plants currently in mountains. This measure should commence at national borders through quarantine legislation.

The known invasive behaviour from other regions is one of the best predictors in weed risk assessment systems (e.g. Daehler *et al.*, 2004). We found that several species were invasive and of management concern in multiple regions indicating that such information could be especially important to mountain managers for prioritizing prevention and containment measures. Unfortunately, these data were difficult to obtain and apparently unavailable for most regions, so there is an urgent need to gather and publish data on plant invasiveness in mountains. The Mountain Invasion Research Network (MIREN, <http://www.miren.ethz.ch>) has prepared an online database of alien plants in mountains that should help with the global assessment of plant invasion risks in mountains by centralizing data from published and unpublished sources.

Given the lack of data and the expected change in alien and invasive plant floras in mountains because of novel introduction pathways and climate change, early detection surveys are

recommended to identify new incursions of alien plant species when eradication is still possible. The removal of existing alien ornamental plantings in mountain areas is also likely to be a beneficial preventive measure. Future amenity plantings should utilize locally native species.

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## BIOSKETCH

The authors are part of the Mountain Invasion Research Network (<http://www.miren.ethz.ch>), a group of scientists and managers who undertake collaborative, global research on mountain plant invasions. MIREN aims to compile information about alien species distribution in mountains, understand the mechanisms of invasion and provide information to managers to facilitate prevention and control of problem species.

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