Ain't no mountain high enough: plant invasions reaching new elevations

Aníbal Pauchard[1*], Christoph Kueffer[2], Hansjörg Dietz[3], Curtis C Daehler[2], Jake Alexander[3], Peter J Edwards[3], José Ramón Arévalo[4], Lohengrin A Cavieres[1], Antoine Guisan[5], Sylvia Haider[6], Gabi Jakobs[2], Keith McDougall[7], Constance I Millar[8], Bridgett J Naylor[9], Catherine G Parks[9], Lisa J Rew[10], and Tim Seipel[10]

Most studies of invasive species have been in highly modified, lowland environments, with comparatively little attention directed to less disturbed, high-elevation environments. However, increasing evidence indicates that plant invasions do occur in these environments, which often have high conservation value and provide important ecosystem services. Over a thousand non-native species have become established in natural areas at high elevations worldwide, and although many of these are not invasive, some may pose a considerable threat to native mountain ecosystems. Here, we discuss four main drivers that shape plant invasions into high-elevation habitats: (1) the (pre-)adaptation of non-native species to abiotic conditions, (2) natural and anthropogenic disturbances, (3) biotic resistance of the established communities, and (4) propagule pressure. We propose a comprehensive research agenda for tackling the problem of plant invasions into mountain ecosystems, including documentation of mountain invasion patterns at multiple scales, experimental studies, and an assessment of the impacts of non-native species in these systems. The threat posed to high-elevation biodiversity by invasive plant species is likely to increase because of globalization and climate change. However, the higher mountains harbor ecosystems where invasion by non-native species has scarcely begun, and where science and management have the opportunity to respond in time.

Front Ecol Environ 2009; 7(9): 479–486, doi:10.1890/080072

Biological invasions are recognized as a major driver of biodiversity decline and altered ecosystem services worldwide. In the lowlands, where most studies have been conducted, large-scale invasions have been facilitated by human-mediated propagule dispersal and disturbance (Dietz and Edwards 2006). In contrast, high-elevation environments appear to be less affected by invasions – because of the harsher climatic conditions and comparatively low human population densities – and it has been assumed that this situation will not change substantially in the future (MA 2003; Panel 1).

In this article, we question the assumption that mountain environments are not at risk from invasive plants (MA 2003). We present evidence that many non-native plant species have colonized high-elevation environments across wide climatic and latitudinal ranges, and that some invading species have already had a major impact on mountain ecosystems. These developments are a matter for concern, because mountains provide valuable ecosystem services for lowland human settlements (eg water supply, recreation; Körner 2004), as well as supporting rare and fragile ecosystems. Indeed, most of the world's protected areas are situated in mountainous regions (Scott *et al.* 2001; Spehn *et al.* 2002; Kollmair *et al.* 2005). Furthermore, because of climate change and the rapidly growing use of mountain areas for tourism and other purposes (Price 2006), plant invasions into mountain areas are likely to increase, affecting biodiversity and disrupting important ecosystem services. The consequences of such invasions may not only affect mountain habitats, but also adjacent lowland areas (eg downstream water availability; Mark and Dickinson 2008). From a practical viewpoint, research into high-elevation plant invasions is important for developing appropriate management policies, and is also important scientifically, helping us to understand the factors that influence the

In a nutshell:

- Most studies of invasive species have concentrated on lower elevations, with little attention being directed to the most pristine, high-elevation environments, where most of the world's protected areas are located
- Relative isolation and harsh climatic conditions may have allowed mountain ecosystems to experience lower levels of species invasions than have other areas
- The constraining factors for invasion are now changing due to globalization and climate change, increasing the chances of plant invasions into high-elevation environments
- A conceptual research framework focused on gradients will improve our understanding of the causes and effects of invasions of mountain environments, as well as in other ecosystems, especially those that are currently less invaded
- Researchers need to address the patterns and effects of invasions in mountain ecosystems, to provide a useful set of guidelines for managers who are in charge of conserving alpine biodiversity and ecosystem services

---

[1]*Universidad de Concepción, Concepción, Chile, and Institute of Ecology and Biodiversity, Santiago, Chile* [*]*(pauchard@udec.cl);* [2]*Botany Department, University of Hawaii at Manoa, Honolulu, HI;* *(continued on p486)*

Panel 1. Differentiating zones of elevation

Low elevations: areas from sea level to the bottom of mountain ranges.

Mid-elevations: areas in the montane belt up to the treeline.

High elevation: areas above the treeline.

spread of plant species along steep environmental gradients (Körner 2007).

Here, we review evidence that plant invasions are increasing in mountain systems and discuss the relevant drivers that have led to the current situation, and those that may increase invasion risk in the near future. We propose a research agenda to assess both the current state and potential future threat of plant invasions into mountainous regions, as well as the applied and theoretical implications. Finally, we emphasize the need and opportunity for understanding plant invasions in mountain ecosystems, in order to reduce their future impacts.

■ Trends in plant invasions in mountain ecosystems

Over a thousand non-native plant species have been reported as being naturalized in high-elevation ecosystems worldwide (MIREN unpublished). Non-native plants are consistently present in most mountain ecosystems, from the Arctic to the Tropics (eg Japan [Tachibana 1968], Borneo [Beaman and Anderson 1998], Rocky Mountains [Weaver *et al.* 2001], Argentina [Petryna *et al.* 2002], South Africa [Carbutt and Edwards 2003], Switzerland [Becker *et al.* 2005], Hawaii [Daehler 2005], Australia [McDougall *et al.* 2005], Réunion Island [Baret *et al.* 2006], Himalayas [Khuroo *et al.* 2007]; Figure 1).

For temperate mountain systems, a continuous decrease in non-native plant species richness with elevation has been reported (Pauchard and Alaback 2004; Becker *et al.* 2005; McDougall *et al.* 2005; Figure 2). In contrast, on subtropical oceanic islands, non-native species richness is generally highest at mid-elevation (Tassin and Riviere 2003; Arévalo *et al.* 2005; Jakobs and Kueffer unpublished; Figure 2). In all the mountain systems studied so far, non-native species richness is lowest in the highest subalpine or alpine zones, which may indicate that these ecosystems are resistant to invasion. However, because land area decreases with elevation, as does overall species richness (Rahbek 1995; Romdal and Grytnes 2007), non-native species diversity along elevational gradients should be analyzed in relation to corresponding patterns of native species diversity (Körner 2007).

There are few reliable datasets showing changes in species distributions over time, but there is some indication that non-native species are expanding their range upwards. Becker *et al.* (2005) have shown that the highest elevation attained by non-native species in the Swiss Alps is positively correlated with time since first introduction. The diversity and abundance of alien plants in the Australian Alps have also increased dramatically in recent years (Johnston and Pickering 2001).

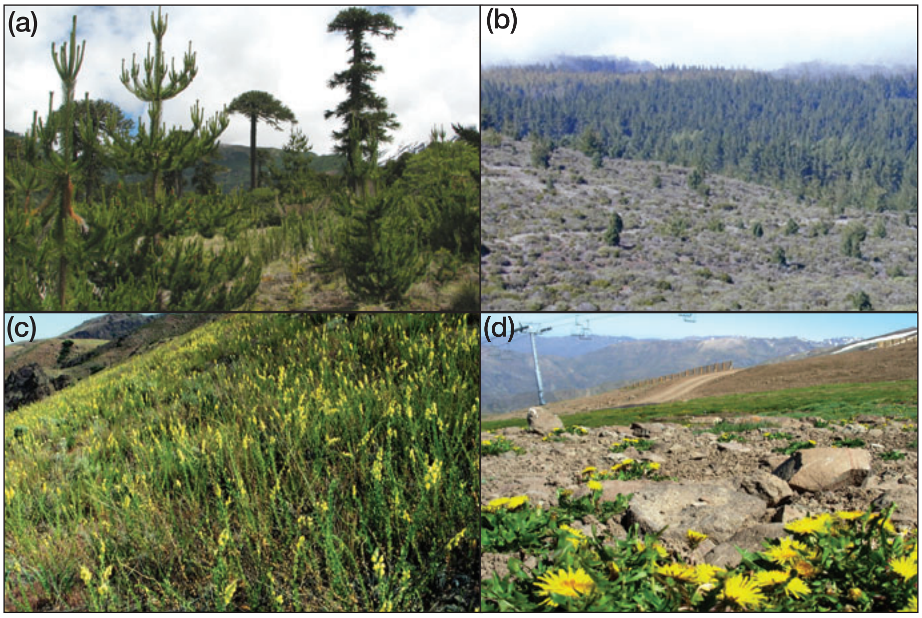

Figure 1. *Examples of non-native plants that have invaded mountain environments, reaching high density and modifying ecosystem functioning. (a) Invasive* Pinus contorta *in* Araucaria araucana *forests of southern Chile, (b)* Pinus radiata *invading high-elevation native shrubland, Hawaii, (c)* Linaria dalmatica *in the Blue Mountains of Oregon, and (d)* Taraxacum officinale *in the Andes of central Chile.*

F and K Starr

While many non-native species do not reach high densities in mountain ecosystems, some may become sufficiently abundant to affect normal biodiversity and ecosystem functions (Figure 1). From the limited evidence available, invasive species are most likely to become problematic in open sites at higher elevations. At Haleakala National Park, on the Hawaiian island of Maui, for example, introduced pines are invading high-elevation sophora shrublands (*Sophora chrysophylla*, a shrub species endemic to Hawaii), transforming these communities into tall forest. Although not studied in detail, it seems probable that such a major structural change in vegetation will eventually lead to the complete replacement of the present native biota by other species. In Chile, *Pinus contorta* is invading the timberline ecotone, where native *Nothofagus* spp and *Araucaria araucana* are less tolerant than non-native conifers to above-timberline climate (Peña *et al.* 2008). Similar transformations in vegetation composition have occurred in South Africa, as a result of invasions by pines, as well as by *Hakea* spp (Richardson *et al.* 1990). In high-elevation grasslands, invasive species such as *Linaria dalmatica* can replace native grasses, changing ecosystem structure and functioning (Weaver *et al.* 2001). Invasive species can also have cascade effects, such as those reported for non-native European forbs disrupting food resources for grizzly bears in North America (Reinhart *et al.* 2001), or *Taraxacum officinale* (European dandelion) competing with native species for pollinators in the high-elevation environments of Chile (Muñoz and Cavieres 2008).

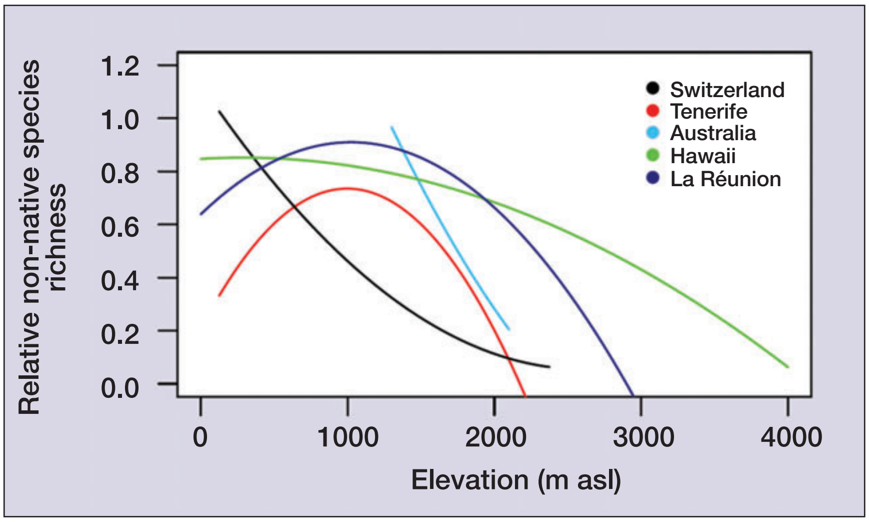

Figure 2. *Changes in non-native plant species richness with altitude (asl = above sea level) from a range of climatic zones, continental areas, and islands. Data have been scaled relative to the maximum richness recorded in each study. Altitudinal richness patterns vary across regions, but the highest elevation areas show consistently low levels of invasion. (Sources – Switzerland: Becker* et al. *[2005]; Tenerife: Arévalo [2005]; Australia: McDougall [2005]; Hawaii: Jakobs and Kueffer [unpublished]; La Réunion: Tassin and Riviere [2003]).*

Factors determining invasions into mountain ecosystems

Four main drivers that promote plant invasions are recognized by biologists: (1) (pre-)adaptation of non-native species to abiotic conditions (eg Daehler 2003), (2) disturbances (especially anthropogenic disturbances; eg Davis *et al.* 2000), (3) low biotic resistance of native communities (eg Levine *et al.* 2004), and (4) high propagule pressure (eg Colautti *et al.* 2006). We suggest that these four main factors and their interactions are also relevant for understanding the current and future risks of plant invasions into mountain ecosystems; however, the relative importance of these factors is likely to change across elevational gradients (Figure 3).

Abiotic resistance of mountain ecosystems to invasions: permanent or transient?

Mountains are characterized by strong environmental gradients (Körner 2000). Thus, increasing elevation is associated with lower temperatures and harsher conditions for plant growth, such as a decrease in the length of the growing season, coupled with increased duration of snow cover, frequency of frost, and ultraviolet-B exposure (Körner 2003). Soil development is also often lower at high elevations, limiting successful plant establishment. Environmental stress is considered an important barrier for plant invasions (Alpert *et al.* 2000), and abiotic factors probably constrain upper-range expansion in most invasive species (Figure 3), which may explain the negative relationship between the number of alien species and elevation (Figure 2). Alexander (2008) found that invasive Asteraceae forbs reach the same altitudinal limit in climatically similar parts of their native and introduced ranges, suggesting that species responses to altitudinal gradients are conserved between ranges.

The degree of pre-adaptation to abiotic conditions in mountainous areas is probably important in determining whether a particular species can spread. Stress-tolerant species (ie S-strategists, sensu Grime 1977) seem to be poorly represented among invaders, which might partly explain the apparent resistance to invasion of many high-altitude areas. However, the pool of species that is adapted to high-elevation environments is considerably smaller than the pool of species adapted to lowland environments (eg area effects; see Körner 2000); therefore, what appears to be resistance to invasion could simply be a result of species non-availability. In addition, because many species are initially introduced into lowland habitats, there may be selection against genotypes adapted to higher elevations (Becker *et al.* 2005).

The importance of this "lowland filter" could diminish if the intensity of trade and transport into mountainous regions increases. In the past few decades, for instance, many non-native species have been deliberately introduced to mountain ski resorts in Australia for the purposes of revegetation and amenity plantings (Johnston and Pickering 2001; Figure 4). Unlike the earlier naturalization of lowland agricultural species, most "ski resort" plants were selected for their cold-hardiness (McDougall *et al.* 2005). For example, the invasive species currently causing most concern in the Australian Alps, *Hieracium aurantiacum* (orange hawkweed), is thought to have originated from a ski-resort garden (Williams *et al.* 2008). Deliberate introductions of cold-adapted species for rangeland improvement have also been, and may continue to be, a source of invasions in mountain ecosystems (eg Hawaii; Daehler 2005). The transport of non-native plants that evolved in mountain areas may be rapidly increasing due to globalization (see conceptual framework in Meyerson and Mooney 2007), reducing the role

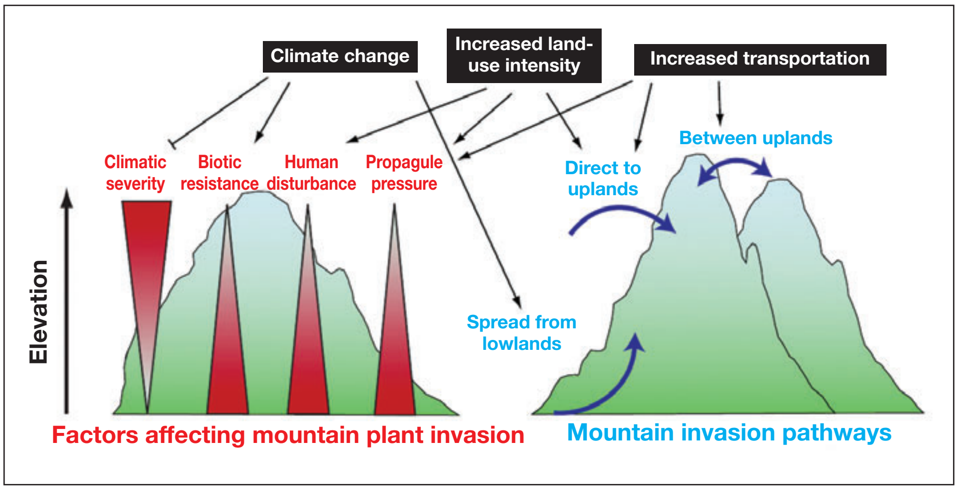

Figure 3. *Factors affecting mountain plant invasions change in importance along altitudinal gradients (in triangles; wider bases and dark shading represent higher importance). The current low levels of invasion observed globally at high altitudes might be explained by increasing climatic severity (negative effect on invasion) and decreasing human disturbance and propagule pressure with increasing altitude. Natural disturbances also increase with altitude, but so far seem to have a neutral effect on mountain invasion (see text). Aspects of global change (black boxes) are likely to directly affect these factors (black arrows for increasing effect, bar for decreasing effect), leading to potentially increased invasion of mountains in the near future. Global change will also affect invasion pathways (blue arrows) through increased commerce/agriculture and the introduction of non-native species directly to high-altitude areas (eg via agriculture, tourist infrastructure, ornamental species). Furthermore, by reducing climatic barriers at higher elevations, climate change could increase the chances of an upward movement of lowland invasive plants.*

of the harsh abiotic conditions characteristic of high elevations as a barrier against plant invasions.

Despite the importance of pre-adaptation, alien species may, at times, be able to extend their altitudinal range beyond that which they occupy in their native environment (Broennimann *et al.* 2007). Alexander (2008) found evidence that *Lactuca serriola* reached a higher altitude in the northwestern US, where it was introduced, than in its native range in the Swiss Alps, and suggested that multiple introductions and intraspecific hybridization could have favored rapid, adaptive evolution. Thus, the scarcity of non-native plants in some high-elevation habitats may, at least partly, reflect the long lag time needed for introduced populations to adapt to harsher environmental conditions (Dietz and Edwards 2006).

Global warming will probably weaken the abiotic resistance of most mountain ecosystems to plant invasions, but the interactions with other factors (eg native biota response) may complicate the forecasting of future scenarios for plant invasions. Generally, increases in temperature and the length of the growing season, and corresponding decreases in the frequency and duration of frost and snow cover, are predicted for mountains around the world (Cannone *et al.* 2007; Nogues-Bravo *et al.* 2007). These warmer conditions could facilitate the invasion of lowland species into higher elevations (Theurillat and Guisan 2001), with plant invasions becoming more frequent and severe in the future (Loope and Giambelluca 1998; Walther *et al.* 2002).

Increased anthropogenic disturbance may open new opportunities for invasive plants

Both natural and anthropogenic disturbance have been shown to promote plant invasions, particularly when coupled with pulses of additional resource availability (Davis *et al.* 2000). High levels of natural disturbance – for example, landslides, rock falls, volcanic activity, and soil fluction – are a characteristic of alpine systems, especially at higher altitudes (Figure 3). In many areas, such disturbances are forecast to increase in frequency and scale as a result of global warming and the associated melting of glaciers and permafrost. However, in contrast to those that occur in lowland areas, these disturbances are not linked to high nutrient levels, as soils at high elevations are generally poorly developed. Under these conditions, early successional native species, adapted to exploiting disturbances under harsh and infertile conditions, may still outcompete non-native species. However, because of increasing nutrient inputs into mountainous regions through agriculture and air pollution (MA 2003; Price 2006), nutrient levels in alpine soils may increase rapidly, which could change the competitive outcome between native and non-native species in the wake of natural disturbance.

In contrast to natural disturbances, anthropogenic disturbances are generally correlated with high nutrient levels and high propagule pressure from non-native species, caused by human transportation. In the past, human disturbance intensity, frequency, and density tended to decrease strongly at higher elevations (Figure 3). This may have prevented the expansion of disturbance-adapted invaders. However, as human activity in mountains increases – for example, through the increasing recreational use of mountain areas, including the construction of ski resorts and vacation retreats in industrialized nations, or expanding agriculture in poorer countries (Price 2006) – opportunities for invasion are likely to increase (Figure 4). Anthropogenic disturbances may be particularly problematic in mountains because of the slow growth and long life cycles of native plants, and therefore the slow rate of recolonization of disturbed areas.

While little is known about the role of anthropogenic or natural physical disturbances for plant invasions into mountain ecosystems, the importance of grazing as an anthropogenic disturbance factor facilitating plant invasions in high-elevation habitats has been well documented (Keeley *et al.* 2003; Vavra *et al.* 2007; but see Stohlgren *et al.* 1999), especially on oceanic islands (Daehler 2005; Baret *et al.* 2006). In Hawaii, for instance, large grazed areas are completely dominated by Eurasian grasses (Daehler 2005). *Ulex europaeus* is another species that typically profits from overgrazing at high elevation (Daehler 2005; Baret *et al.* 2006).

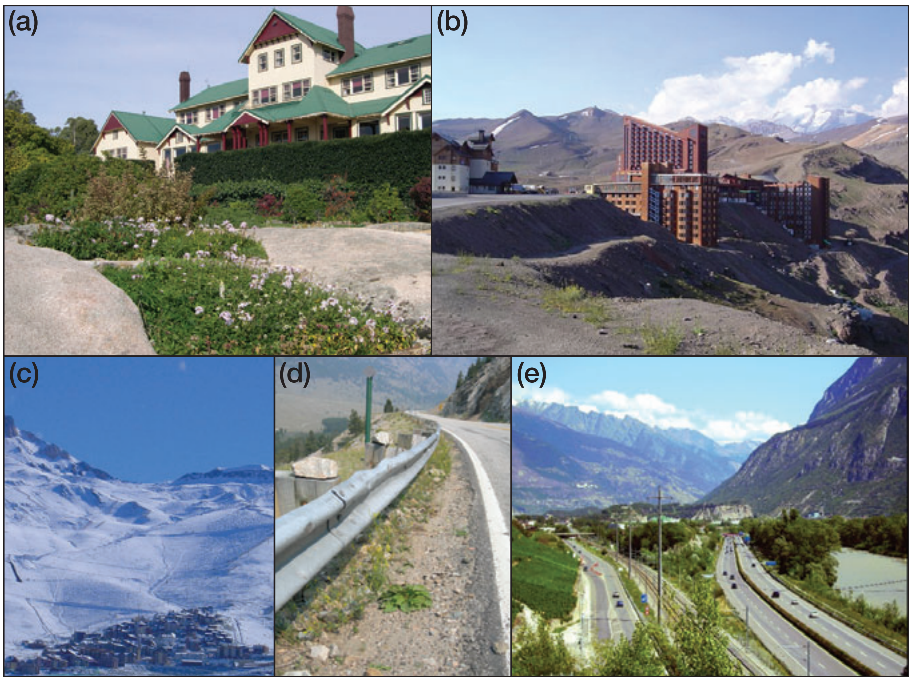

Figure 4. *Human development of mountain areas is increasing the risk of non-native plant invasions at high-elevation ecosystems. (a) Pre-adapted plants are introduced to alpine gardens (Mt Buffalo Chalet in the Australian Alps); (b) tourism resorts are increasingly built at higher elevations and in untouched areas, creating anthropogenic disturbances and bringing non-native plant propagules (Colorado resort in the Andes of Central Chile, located at 3000 m asl); (c) urbanization is accelerating in mountains, with similar effects (La Parva urbanization in the Andes of Central Chile); (d) high-elevation roads are major pathways for invasive plants in protected areas (non-native plant establishment along a road in Yellowstone National Park, WY); (e) increased transportation and traffic do not halt at the bottom of mountains, increasing propagule pressure even into historically undisturbed environments (highways in the valley of Valais, Switzerland).*

Biotic interactions: competition and facilitation affect invasibility

The paucity of non-native species at high elevations cannot be explained by biotic resistance, because most alpine plant communities have low species diversity and low biomass (Körner 2003). On the other hand, facilitation is often found to increase with elevation, whereas competition decreases (Callaway *et al.* 2002), and, therefore, the presence of native plants at higher elevations could even increase the risk of invasion. In the Chilean Andes, native cushion plants have been shown to facilitate the establishment and growth of the alien *Taraxacum officinale* (Cavieres *et al.* 2005, 2008), with the facilitative effects being stronger at higher elevations (Badano *et al.* 2007).

Facilitative effects may be particularly important for lowland-adapted plants invading higher elevations, because facilitation often lowers the barrier created by harsh abiotic conditions (eg microclimate, snow cover duration, soil fertility), increasing the potential for range expansion (Bruno *et al.* 2003). Thus, the role of biotic interactions may change along altitudinal gradients: competitive interactions and biotic resistance will play an important role at lower elevations, while facilitative interactions – and not biotic resistance – may prevail at higher elevations. Indeed, facilitative effects at high elevations could enhance the risk of "invasional meltdown" (Simberloff and Von Holle 1999), leading to major changes in ecosystem functioning. Nonetheless, facilitation in stressful environments operates at fine scales (eg plant–plant interaction), whereas disturbance increases limiting resources or reduces barriers to establishment at a coarser scale. Facilitation may become increasingly frequent at high elevations, but anthropogenic disturbances, including new microhabitats created by dwellings and roads, remain as a major factor in helping invaders to become established.

Propagule pressure: isolation constrains invasions

The abundance of propagules introduced to a site can be the predominant factor shaping invasions (Lockwood *et al.* 2005; Colautti *et al.* 2006). Thus, the number of visitors to, or the extent of road systems throughout, natural areas are often effective predictors of the presence of non-native species in an area (Lonsdale 1999). Correspondingly, the diversity and number of non-native species in mountains are generally higher along roads than in adjacent habitats (Pauchard and Alaback 2004; Rew *et al.* 2005).

Because of improved infrastructure, many mountain areas are becoming more accessible (Figure 4), and the naturally high isolation and low connectivity of mountain environments, which formerly restricted the natural dispersal of non-native species, are being reduced. While most human habitation is at lower elevations, some mountainous regions attract large numbers of tourists, either seasonally or throughout the year, and in some countries more people are settling in mountain areas (Hansen *et al.* 2005). The increased use of mountains may promote the dispersal of non-native species at a local scale (eg between roadsides and adjacent habitat), at a regional scale (eg between urban and natural areas or dif-

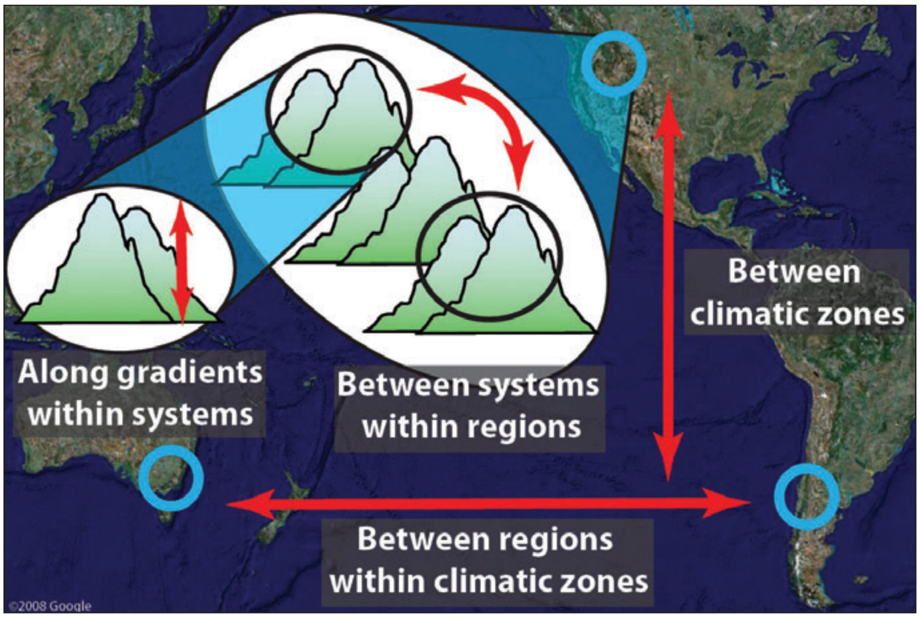

Figure 5. *A hierarchical approach to studying patterns of non-native plant invasions into mountains at multiple spatial scales. Local, regional, and global scales can be used to study plant invasions. Local scales provide detailed insight into particular invasion processes. At the regional scale, comparisons are made in climatically similar regions. At the global scale, studies can find broader generalities by including elevational gradients in multiple biomes.*

ferent mountain systems), and at a global scale (ie between different mountain areas). Thus, as anthropogenic influences in mountain areas increase, propagule pressure from non-native species can be expected to rise (Price 2006), resulting in a sharp increase in accidental and deliberate introductions.

A research agenda for tackling the problem of plant invasions into mountain regions

Although an increasing number of studies on plant invasions are being conducted in mountain areas, much remains to be learned. We therefore propose a comprehensive research agenda for understanding plant invasions into mountain environments, involving three main approaches: (1) detection and analysis of invasion patterns at multiple scales, (2) experimental studies of invasion drivers, and (3) assessment of the impacts caused by non-native species and their conservation implications. We have initiated a research network called the Mountain Invasion Research Network (MIREN) that uses these different approaches in a multiregional, standardized research program, aimed at improving our understanding of mountain invasions (Dietz *et al.* 2006).

The first approach – documentation of patterns – must recognize the multiscale nature of plant invasions (Pauchard and Shea 2006). Surveys of distributions of non-native plants should differentiate at least three scales for testing hypotheses: local, regional, and global (Figure 5). Local scales could provide insights into the specific factors determining the patterns of non-native species distribution associated with steep elevational gradients. Regional scales include one or more mountain ranges within the same climatic/latitudinal region (see Pauchard *et al.* 2004), which could help to test whether local drivers of plant invasions are consistent at larger scales. Finally, a global scale is the sum of multiple mountain ranges across several climatic and geographic regions (latitudinal gradients), allowing for large-scale generalizations that may apply to other invasion processes. These scales are nested in a hierarchical structure, promoting the integration of results across scales (Figure 5).

The second approach seeks to understand the mechanisms behind the patterns of invasion, through studies at the local scale, of the four sets of drivers proposed in this article (ie abiotic range limits, disturbances, biotic resistance, and propagule pressure). Experiments should be designed to take advantage of the multiple environmental and anthropogenic gradients associated with mountains. Common experimental protocols across regions could better serve to identify generalities and allow for scaling up of results obtained at the local scale.

The third approach – assessment of the impacts of non-native species and the implications for conservation – should identify and quantify current impacts of non-native species on natural and social systems in mountains, and predict future impacts. Furthermore, to develop best-practice management strategies that are tailored to the specific circumstances of mountain regions, researchers should communicate with managers at an early stage. Special considerations are required to avoid the accidental introduction and dispersal of non-native species during the research process. Therefore, a clear protocol to assess and limit the risk of such accidental introductions should be developed and followed by scientists and managers.

Conclusions: understanding mountain plant invasions to prevent biodiversity losses

The rather low level of invasions at high elevations by alien plants should not lead us to conclude that they are per se more resistant to plant invasions than other ecosystems. Rather, invasion theory suggests that species-poor ecosystems that are frequently disturbed through large-scale events, such as landslides, should be vulnerable to invasions. It seems likely that three factors – the paucity of non-native species that are pre-adapted to the harsh abiotic conditions of mountains, low non-native propagule pressure, and low human disturbances – have so far limited plant invasions in many mountain areas.

However, several of the factors that have, up to now, restricted plant invasion into mountainous areas are changing rapidly. Increased use of mountain-adapted plants is exacerbating the risk that pre-adapted, non-native species will be introduced to other mountain regions. Climate change and nutrient inputs are likely to diminish the abiotic resistance of habitats. Rapidly increasing mobility and development in mountain areas will increase propagule pressure at local and regional scales, as will the frequency and scale of anthropogenic disturbances. These changes will often occur concurrently, and may further weaken the resistance of alpine ecosystems to plant invasions through synergistic interactions (Didham *et al.* 2007).

Current evidence on invasive plants at high elevations and biological invasion theory indicate that plant invasions may become a more serious threat to mountain biodiversity in the near future. Adopting the precautionary principle, managers and scientists should respond to this potential emergent threat immediately. This is not a matter of a tradeoff between directing research and resources to lowland versus highland plant invasions. On the contrary, a broad view of plant invasions across elevational gradients could deepen our understanding of these phenomena, and help us to better control the threats to mountain biodiversity and ecosystem services. At present, limited data are available for predicting how invasions may be affected by different aspects of global change, and much more research will be needed. However, mountains are among the few areas where invasion by non-native species has scarcely begun, and where science and management, for once, have the opportunity to respond in time.

Acknowledgements

AP and LAC were supported by ICM 05-002, Conicyt-Chile PFB-23, and Fondecyt 1070488. AG benefited from support provided by the Swiss SNF-NCCR "Plant Survival". JRA was funded by "Consejería de Educación, Cultura y Deportes, Gobierno de Canarias" through the project PI042004/096. CK was funded by USDA CSREES grant # 2006-35320-17360 to CCD. JA was funded by CCES through the "BioChange" project (0-21214-07). SH was funded by a graduate scholarship from Universität Bayern eV. The Mountain Invasion Research Network received funding from the Swiss Academy of Sciences and the Ruebel Foundation. Thanks to R Mack and P Bocaz for editing.

References

Alexander J, Naylor B, Poll M, *et al.* 2008. Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges. *Ecography*. **32**: 334–44.

Alpert P, Bone E, and Holzapfel C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol* **3**: 52–66.

Arévalo JR, Delgado JD, Otto R, *et al.* 2005. Distribution of alien vs native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspect Plant Ecol* **7**: 185–202.

Badano EI, Villarroel E, Bustamante RO, *et al.* 2007. Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *J Ecol* **95**: 682–88.

Baret S, Rouget M, Richardson DM, *et al.* 2006. Current distribution and potential extent of the most invasive alien plant species on La Réunion (Indian Ocean, Mascarene Islands). *Austral Ecol* **31**: 747–58.

Beaman JH and Anderson C. 1998. The plants of Mount Kinabalu, vol 3–5. Kota Kinabalu, Malaysia and Kew, UK: Natural History Publications (Borneo) and The Royal Botanic Gardens Kew.

Becker T, Dietz H, Billeter R, *et al.* 2005. Altitudinal distribution of alien plant species in the Swiss Alps. *Perspect Plant Ecol* **7**: 173–83.

Broennimann O, Treier UA, Müller-Schärer H, *et al.* 2007. Evidence of climatic niche shift during biological invasion. *Ecol Lett* **10**: 701–09.

Bruno JF, Stachowicz JJ, and Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol Evol* **18**: 119–25.

Callaway RM, Brooker RW, Choler P, *et al.* 2002. Positive interactions among alpine plants increase with stress. *Nature* **417**: 844–48.

Cannone N, Sgorbati S, and Guglielmin M. 2007. Unexpected impacts of climate change on alpine vegetation. *Front Ecol Environ* **5**: 360–64.

Carbutt C and Edwards TJ. 2003. The flora of the Drakensberg alpine centre. *Edinburgh J Bot* **60**: 581–607.

Cavieres LA, Quiroz CL, and Molina-Montenegro MA. 2008. Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high-Andes of central Chile: are there differences between nurses? *Funct Ecol* **22**: 148–56.

Cavieres LA, Quiroz CL, Molina-Montenegro MA, *et al.* 2005. Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspect Plant Ecol* **7**: 217–26.

Colautti R, Grigorovich I, and MacIsaac H. 2006. Propagule pressure: a null model for biological invasions. *Biol Invasions* **8**: 1023–37.

Daehler CC. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annu Rev Ecol Syst* **34**: 183–211.

Daehler CC. 2005. Upper-montane plant invasions in the Hawaiian Islands: patterns and opportunities. *Perspect Plant Ecol* **7**: 203–16.

Davis MA, Grime JP, and Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* **88**: 528–34.

Didham RK, Tylianakis JM, Gemmell NJ, *et al.* 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol Evol* **22**: 489–96.

Dietz H and Edwards PJ. 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology* **87**: 1359–67.

Dietz H, Kueffer C, and Parks CG. 2006. MIREN: a new research network concerned with plant invasion into mountain areas. *Mt Res Dev* **26**: 80–81.

Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* **111**: 1169–95.

Hansen AJ, Knight RL, Marzluff JM, *et al.* 2005. Effects of exurban development on biodiversity patterns, mechanisms, and research needs. *Ecol Appl* **15**: 1895–1905.

Johnston FM and Pickering CM. 2001. Alien plants in the Australian Alps. *Mt Res Dev* **21**: 284–91.

Keeley JE, Lubin D, and Fotheringham CJ. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol Appl* **13**: 1355–74.

Khuroo AA, Rashid I, Reshi Z, *et al.* 2007. The alien flora of Kashmir Himalaya. *Biol Invasions* **9**: 269–92.

Kollmair M, Gurung-Ghana S, Hurni K, and Maselli D. 2005. Mountains: special places to be protected? An analysis of worldwide nature conservation efforts in mountains. *Int J Biodiv Sci Manage* **1**: 181–89.

Körner C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. *Trends Ecol Evol* **15**: 513–14.

Körner C. 2003. Alpine plant life. Functional plant ecology of high mountain ecosystems, 2nd edn. Berlin, Germany: Springer.

Körner C. 2004. Mountain biodiversity, its causes and function. *Ambio* **13**: 11–17.

Körner C. 2007. The use of "altitude" in ecological research. *Trends Ecol Evol* **22**: 569–74.

Levine JM, Adler PB, and Yelenik SG. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol Lett* **7**: 975–89.

Lockwood JL, Cassey P, and Blackburn T. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol Evol* **20**: 223–28.

Lonsdale WM. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**: 1522–36.

Loope LL and Giambelluca TW. 1998. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. *Climatic Change* **39**: 503–17.

MA (Millennium Ecosystem Assessment). 2003. Ecosystems and human well-being: a framework for assessment. Washington, DC: Island Press.

Mark AF and Dickinson KJ. 2008. Maximizing water yield with indigenous non-forest vegetation: a New Zealand perspective. *Front Ecol Environ* **6**: 25–34.

McDougall KL, Morgan JW, Walsh NG, and Williams RJ. 2005. Plant invasions in treeless vegetation of the Australian Alps. *Perspect Plant Ecol* **7**: 159–71.

Meyerson LA and Mooney HA. 2007. Invasive alien species in an era of globalization. *Front Ecol Environ* **5**: 199–208.

Muñoz AA and Cavieres LA. 2008. The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *J Ecol*. **96**: 459–67.

Nogues-Bravo D, Araujo MB, Errea MP, and Martinez-Rica JP. 2007. Exposure of global mountain systems to climate warming during the 21st century. *Global Environ Chang* **17**: 420–28.

Pauchard A and Alaback PB. 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south–central Chile. *Conserv Biol* **18**: 238–48.

Pauchard A and Shea K. 2006. Integrating the study of non-native plant invasions across spatial scales. *Biol Invasions* **8**: 399–413.

Pauchard A, Cavieres LA, and Bustamante RO. 2004. Comparing alien plant invasions among regions with similar climates: where to from here? *Divers Distrib* **10**: 371–75.

Peña E, Hidalgo M, Langdon B, and Pauchard A. 2008. Patterns of spread of *Pinus contorta* Dougl ex Loud invasion in a natural reserve in southern South America. *Forest Ecol Manag* **256**: 1049–54.

Petryna L, Moora M, Nuñes CO, *et al.* 2002 Are invaders disturbance-limited? Conservation of mountain grasslands in Central Argentina. *Appl Veg Sci* **5**: 195–202.

Price ME. 2006. Global change in mountain regions. Duncow, UK: Sapiens Publishing.

Rahbek C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* **18**: 200–05.

Reinhart DP, Haroldson MA, Mattson DJ, and Gunther KA. 2001. Effects of exotic species on Yellowstone's grizzly bears. *West N Am Nat* **61**: 277–88.

Rew LJ, Maxwell BD, and Aspinall R. 2005. Predicting the occurrence of nonindigenous species using environmental and remotely sensed data. *Weed Sci* **53**: 236–41.

Richardson DM, Cowling RM, and LeMaitre DC. 1990. Assessing the risk of invasive success in *Pinus* and *Banksia* in South African mountain fynbos. *J Veg Sci* **1**: 629–42.

Romdal TS and Grytnes JA. 2007. An indirect area effect on elevational species richness patterns. *Ecography* **30**: 440–48.

Scott JM, Frank W, Davis R, *et al.* 2001. Nature reserves: do they capture the full range of America's biological diversity? *Ecol Appl* **11**: 999–1007.

Simberloff D and Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol Invasions* **1**: 21–32.

Spehn EM, Messerli B, and Körner C. 2002. A global assessment of mountain biodiversity: synthesis. In: Körner C and Spehn EM (Eds). Mountain biodiversity: a global assessment. London, UK: The Parthenon Publishing Group.

Stohlgren TJ, Schell LD, and Heuvel BV. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecol Appl* **9**: 45–64.

Tachibana H. 1968. Weed invasion upon the mountain areas in Mt Hakkoda. *Ecol Rev* **17**: 95–101.

Tassin J and Riviere JN. 2003. Species richness altitudinal gradient of invasive plants on Reunion Island (Mascareigne Archipelago, Indian Ocean). *Rev Ecol-Terre Vie* **58**: 257–70.

Theurillat JP and Guisan A. 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change* **50**: 77–109.

Vavra M, Parks CG, and Wisdom MJ. 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecol Manag* **246**: 66–72.

Walther G-R, Post E, Convey P, *et al.* 2002. Ecological responses to recent climate change. *Nature* **416**: 389–95.

Weaver T, Gustafson D, and Lichthardt J. 2001. Exotic plants in early and late seral vegetation of fifteen northern Rocky environments. *West N Am Nat* **61**: 417–27.

Williams NSG, Hahs AK, and Morgan JW. 2008. A dispersal-constrained habitat suitability model for predicting invasion of alpine vegetation. *Ecol Appl.* **18**: 347–59.

---

[3]*Swiss Federal Institute of Technology (ETH Zurich), Zurich, Switzerland;* [4]*Departamento de Ecología, Facultad de Biología, Universidad de La Laguna, Tenerife, Spain;* [5]*Département d'Ecologie et Evolution, Faculté de Biologie et Médecine, Université de Lausanne, Lausanne, Switzerland;* [6]*Technische Universität München, Munich, Germany;* [7]*Department of Environment and Climate Change, Queanbeyan, NSW, Australia;* [8]*Pacific Southwest Research Station, USDA Forest Service, Berkeley, CA;* [9]*Pacific Northwest Research Station, USDA Forest Service, LaGrande, OR;* [10]*Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT*