Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation

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Abstract

Cold environments at high elevation and high latitude are often viewed as resistant to biological invasions. However, climate warming, land use change and associated increased connectivity all increase the risk of biological invasions in these environments. Here we present a summary of the key discussions of the workshop 'Biosecurity in Mountains and Northern Ecosystems: Current Status and Future Challenges' (Flen, Sweden, 1-3 June 2015). The aims of the workshop were to (i) increase awareness about the growing importance of species expansion – both non-native and native – at high elevation and high latitude with climate change, (ii) review existing knowledge about invasion risks in these areas, and (iii) encourage more research on how species will move and interact in cold environments, the consequences for biodiversity, and animal and human health and wellbeing. The diversity of potential and actual invaders reported at the workshop and the likely interactions between them create major challenges for managers of cold environments. However, since these cold environments have experienced fewer invasions when compared with many warmer, more populated environments, prevention has a real chance of success, especially if it is coupled with prioritisation schemes for targeting invaders likely to have greatest impact. Communication and co-operation between cold environment regions will facilitate rapid response, and maximise the use of limited research and management resources.

Keywords: alien species, arctic, exotic species, biosecurity, migration, range expansion, risk, sub-polar.

Introduction

Cold environments at high elevation and high latitude are characterised by unique biodiversity and provide crucial ecosystem services to local and global human wellbeing, including provisioning of food and water, and carbon storage (Crawford 2014, Kueffer 2015). These cold regions are often viewed as resistant to biological invasions (Ruiz & Hewitt 2009, Bennet et al. 2015, Zefferman et al. 2015). Due to an extreme climate and limited accessibility, these areas have until recently been characterised by low human population density and relatively little direct human modification. However, climate warming, land use change (e.g. expansion of tourism and resource extraction), and associated increased global connectivity all increase the risk of biological invasions in these cold environments (Pauchard et al. 2009; Convey 2011, Petitpierre et al. 2015). These changes facilitate the introduction and establishment of new species that may alter the composition and dominance patterns of existing communities of microorganisms, plants and animals (cf. thermophilization, northern greening; Gottfried et al. 2012; Duque et al. 2015). Species movements into colder environments can be viewed as a double edged sword with both positive and negative consequences on biodiversity: having desired species track climate change would be positive for biodiversity conservation and reduce the risk of extinctions; conversely, some of the new invasions and potential interactions may pose a new threat to the communities they invade. Beyond classical invasions of non-native species arriving from other biogeographic areas, native species moving into new habitat types or climate zones along elevation or latitudinal climate gradients (Lenoir & Svenning 2015) will pose a new type of invasion issue. Therefore, biological invasions are rapidly becoming an important threat to the unique biodiversity and important ecosystem services of cold environments, as well as to the human populations' health and wellbeing in these regions.

Here we present a summary of the key concepts discussed during the first international workshop on biosecurity in cold environments, entitled 'Biosecurity in Mountains and Northern Ecosystems: Current Status and Future Challenges' (Flen, Sweden, 1-3 June 2015). The workshop was organized by the Mountain Invasion Research Network (MIREN), a global network aimed at understanding the effects of global change on plant invasions and biodiversity in mountainous areas (Kueffer et al. 2014). The aims of the workshop were to (i) increase awareness about the growing importance of species expansion – both non-native and native – at high elevation and high latitude with climate change, (ii) review existing knowledge about invasion risks in these areas, and (iii) encourage more research on how species will move and interact in cold environments, and the consequences for biodiversity, and animal and human health and wellbeing.

The workshop brought together 22 scientists with expertise covering most major organism groups (plants, animals, fungi and pathogenic microorganisms) and geographic regions (Africa, the Americas, Asia, Australia, Europe and the Arctic). Based on case studies presented during the workshop, we focused on three main questions: (i) how will changing conditions affect invasion risks in cold environments, (ii) how can we understand and deal with novel multi-species interactions that might emerge in these environments, and (iii) what are the immediate threats posed by emerging invasive species, including diseases and pathogens? In this report we summarize some of the presented case studies and synthesise first insights gained at the workshop to answer our three guiding questions. We specifically focus our discussion on alpine, arctic and subantarctic ecosystems world-wide. We did not consider Antarctica as this cold continent represents a very unique set of conditions, which have been discussed elsewhere in the literature (e.g. Kevin et al. 2015).

Changing conditions causing invasions: Climate, connectivity and migration

While there is a clearly documented trend of species migration towards colder places (Lenoir et al. 2015), there are still several knowledge gaps in the literature. There are also important biases in research efforts, with the tropics and the coldest places on Earth far less studied than temperate biomes, and many more published case studies reporting range shifts towards higher latitudes for animals than for plants (Lenoir & Svenning 2015). Methodological shortfalls are also present with a strong bias towards reporting unidimensional and unidirectional range shifts, while multi-facetted assessments of species range shifts are strongly needed (Lenoir & Svenning 2015, Petitpierre et al. 2015). For instance, terrestrial native organisms are not only shifting their ranges towards higher latitudes or elevations as is usually reported, but they are also shifting ranges in unexpected directions (e.g. toward the equator or downward; e.g. Lenoir et al. 2010). These other types of range shifts involve regional or local anomalies in climate change velocity as well as interactions of climate, environment (including land use modification) and species traits.

Non-native plant invasions at high elevation have so far been limited by reduced human activity at high elevation coupled with a climatic filter (Alexander et al. 2011, Petitpierre et al. 2015). Roads and other anthropogenic environments have been the main corridors for species spread into mountain habitats.

MIREN is using multiple methods to detect how species are moving in mountain environments (www.mountaininvasions.org; Kueffer et al. 2014). Among the main findings of MIREN are that most non-native species at high elevations are lowland generalists that have been able to pass the climatic filter, and that many of these species are common across continents (Alexander et al. 2011; McDougall et al. 2010). However, a new wave of invasions of specialists may be underway due to increasing tourism and transcontinental movement (Pauchard et al. 2009), and the rate of such invasions is likely to increase as the human population continues to increase and become more mobile. A methodological framework such as MIREN's could be applied to study species movement in arctic regions, thereby combining multiple factors of global change. For example, the on-going Swedish Research Links Project "Plant invasions at high altitudes and latitudes: What drives them and how to manage them?" is currently testing how other factors besides temperature (e.g. disturbance, fertilization and increasing propagule pressure) influence the future spread of non-native plants into high elevation and high latitude ecosystems (Milbau et al. unpublished, Figure 1). Preliminary results suggest that even in cold places disturbance, fertilization and propagule pressure facilitate the invasion process.

The response of other less studied taxa to changes in cold ecosystems is even more uncertain. Non-vascular plants such as bryophytes play key ecosystem roles in cold environments and therefore changes in their distribution and abundance may trigger important ecosystem changes (Rozzi et al. 2008). Until recently, non-native bryophytes have received little attention. However, it has become clear that these silent invaders have the potential to spread into cool and humid environments (Essl et al. 2013) such as northern and high-altitude environments. Given their high dispersal capacity, they may rapidly track climate change (Lenoir et al. 2012; Essl et al. 2013). There are first indications that non-native bryophytes forming dense mats (e.g. *Campylopus introflexus*) can have important environmental effects including changes in microclimate, seedling establishment, and habitat quality for arthropods (Essl et al. 2014). The spread of non-native bryophytes may be a greater threat to biodiversity in cold environments, e.g. in open vegetation types such as alpine swards, than in more productive ecosystems in warmer climates.

Human-driven connectivity has continued to increase throughout the Anthropocene between and within all regions of the world, via the main transportation vectors (land, sea and air). However, natural connectivity has decreased due to habitat fragmentation and the creation of dispersal barriers. Such opposing trends have ambiguous effects on biodiversity, which is for instance evident for freshwater

Figure 1. Changes in biotic interactions in cold environments. Upper left, reindeer herding and migration may increase the rate of new pathogen introductions especially under warmer conditions. Upper right, mycorrhizal mutualism is needed for *Pinus contorta* to invade above treeline in Southern Argentina (inset: pine root colonized by ectomycorrhizal fungi). Lower panel, comparative research across hemispheres may help to understand how cold environments and their species will respond to new conditions. A standardized seeding experiment is conducted in Sweden (subartic, lower left) and Chile (subantartic, lower right) to test which factors determine the successful establishment of non-native plant species in cold regions.

fishes. The spread of warm-adapted fish species upstream and to northern latitudes often results in local extinctions of cold-adapted salmonid species (Hein et al. 2014). Barriers such as waterfalls, dams and weirs can limit the upstream spread of such novel colonizers, thereby creating refuges for threatened native species. However, the same barriers simultaneously restrict the capacity of native species to track climate change. Therefore, an important challenge for managers is how to restore natural connectivity letting native species move freely so they can adapt to the changing climate, but also limiting the movement of invasive species to protect native species and local genetic pools. How non-native species take advantage of connectivity in the landscape remains uncertain and should be taken into account when designing biological corridors aimed to facilitate the movement of native species with climate change (Fausch et al. 2009). Another conservation conundrum is the potential for genetic dilution from intentional introduction and supplementation of populations for conservation purposes (e.g. alpine marmots, Kruckenhauser & Pinsker 2008). Such introduction programs could cause loss of fitness or species integrity through gene exchange (hybidization and introgression) with closely related species (IUCN 2013).

New multi-species and multi-trophic interactions

Differences in how species and populations respond to climate change can lead to asynchrony in the rate at which species track climate change, decoupling current species associations (Alexander et al. 2015), causing possible ecosystem disruption. Studies have shown that plants and animals seem to track suitable abiotic conditions under climate change (Chen et al. 2011, Bertrand et al. 2011) and because of differential migration rates, shifts in interactions across trophic levels are expected (Rasmann et al. 2014). For instance, given higher dispersal capacities, insect herbivores will react more rapidly than plants to climate change and migrate faster to higher elevations (Rasmann et al. 2014). As a result, herbivore pressure might increase at higher elevation, which could promote plant community turnover. In high elevation areas, the lower resistance of plants to herbivores will likely exacerbate this turnover (Pellissier et al. 2012, 2014). This is being assessed by artificially increasing the abundance of grasshoppers in an on-going field study (Descombes & Pellissier Unpublished). Initial results show that herbivore impact on alpine plants is highly species-specific. Insect herbivore movement into the alpine zone is thus expected to strongly modulate plant species abundance and migration into higher elevations. For example, native, thermophilous plants spreading to higher altitudes have traits that make them particularly vulnerable to generalist herbivores: thus, generalist herbivores can retard changes to plant communities due to warming. However, this may not be the case for human-dispersed non-native species, which can possess different traits to thermophilous species, possibly making them less susceptible to generalist herbivores (Alexander et al. 2015).

More generally, little is known about emerging species interactions because the migration of many ecologically important species is poorly understood. There is, for instance, growing evidence showing that climate change will influence the distributions of non-native ants (Roura-Pascual et al. 2011; Bertelsmeier et al. 2013). While it is unlikely that any of the most prevalent or most ecologically damaging invasive ant species will spread to the coldest environments, there is some evidence that climate change has the potential to lead to shifts in the distribution and abundance of both native and invasive ant species. Warren and Chick (2013) showed how changing climates influenced the distribution of native ant species along an elevation gradient in southern United States, with consequences for seed dispersal mutualisms. In addition, several studies in low elevation forest sites have demonstrated how the Asian needle ant (*Brachyponera chinensis*) alters native ant communities and seed-dispersal mutualisms (e.g., Rodriguez-Cabal et al. 2012) and models suggest that this invasive ant is likely to move upward in both latitude and elevation (Bertelsmeier et al. 2013).

Mutualistic interactions may also be modified by species migration. For example, some mycorrhizal species, especially ectomycorrhizae, which tend to be highly host specific and the main type of mycorrhizal association for trees in cold environments, might already be a limiting factor for plant movement into higher elevations and northern latitudes (Nuñez et al. 2009, Figure 1). Plants and their associated fungi disperse independently; therefore dispersal limitations for mycorrhizae (e.g. lack of dispersal vector such as large herbivores, Nuñez et al. 2013) may hamper the rate of plant movement. This may have implications for conservation management: reducing fungi dispersal may help to reduce the rate of plant invasions.

Emerging diseases and pathogens

Many interconnected factors are responsible for the continuing and growing importance of infectious human diseases in the Arctic and mountain environments. In the late 19th and early 20th centuries, infectious diseases were the major causes of mortality in Arctic communities. Although the health of indigenous peoples of the circumpolar region has improved over the last 50 years, the rates of many human infectious diseases are still higher in Arctic indigenous communities than in non-indigenous populations in the area (Parkinson et al. 2015). More recently, the emergence of climate-sensitive infectious diseases in the Arctic region presents a new threat to those living there (Evengard & McMichael 2011). A particular challenge will be to understand and address interactions between animals, disease agents and humans under new climatic conditions. Climate change has already caused an increased burden of tularemia in northern Sweden, due to increasing mosquito outbreaks in the boreal forest region (Ryden et al. 2012). Haemorrhagic fever puumula virus is another example of a climate sensitive infection, with an unexpected and large outbreak in northern Sweden in 2008 (Pettersson et al. 2008).

Climate warming can facilitate the rapid dispersal of infectious disease vectors and pathogens, which will not only affect humans but also their associated animals. For example, semi-domesticated reindeer in Scandinavia and the Arctic are adapted to harsh environments but immunologically naïve to new diseases (Figure 1). In this situation, West Nile fever is the emerging vector borne disease. Fenced reindeer in more southern locations have already been severely affected by infections of West Nile fever (Palmer et al. 2004), suggesting more northerly reindeer populations could be severely impacted if the disease continues to spread. Because it is a zoonotic infection it may also cause diseases in humans (Montgomery & Murray 2015). Rapid detection of newly emerging diseases may be difficult and slow, particularly for free-ranging species such as reindeer. The movement of ticks northward is already noticeable in Sweden, posing similar threats to animal and human health (Jaenson and Lindgren 2011). Warming climates can also indirectly increase disease risks. For instance, freeze-thaw conditions might limit wild foraging of reindeer in winter, thereby increasing the need for supplementary feeding, which requires fencing and thus causes crowding, stress and increased potential for disease transmission (e.g. zoonotic diseases) between reindeer but also with the surrounding human population.

While warming may stress certain species, it can ameliorate harsh conditions or provide additional habitats for other species living at their climatic limits. For example, native amphibians residing at high elevations are likely to colonize additional habitat made available by climate warming (Seimon et al. 2007). However, the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*, Bd), a lethal pathogen responsible for amphibian declines worldwide, readily colonizes habitats alongside its amphibian hosts (Seimon et al. 2007). Bd is routinely found at high elevations from the Rocky Mountains (Pilliod et al 2010), to the Sierra Nevadas (Vredenburg et al. 2010), the Andes (Seimon et al. 2007) and at high latitudes (e.g., Northwest Territory, Canada, Schrock et al. 2009). Some research from high elevation locations indicates that cold environments do not necessarily limit this pathogen (e.g., Knapp et al.

2011), although other studies indicate that cold temperature limits Bd (Muths et al. 2008, Pilliod et al. 2010). Certainly, Bd and significant amphibian declines have been reported at high altitudes but the relationship between the two is not straight-forward (Fisher et al. 2009) and will likely to be further complicated by a changing climate.

Tracking species movement with climate change is challenging, particularly for cryptic species. For example, *Phytophthora cinnamomi,* one of the most devastating plant pathogens in temperate regions worldwide (Cahill et al. 2008), has recently been recorded in diverse subalpine ecosystems previously considered unsuitable for its survival. It is not yet clear if it has established there because climatic conditions are changing or, because of adaptation to cold climates. In any case, disease expression is likely to increase with climate warming (Cahill et al. 2008).

Conclusions

The diversity of potential and actual invaders reported at the workshop and the likely interactions between them create major challenges for managers of cold environments: but, there are also opportunities. Historically, cold environments have experienced fewer invasions when compared with warmer, more populated environments. Many native and non-native species are migrating along with the changing climate, which could generate positive and negative conservation outcomes depending on the species and the receiving community. The source and nature of many of the likely invaders are already known because for high altitudes they will often come from surrounding lowlands, and for high latitudes they will often come from adjoining lower latitudes. Furthermore, the human-mediated vectors of invasion in these cold environments are relatively few and well-identified. However, as globalization increases, there will not only be an intensification of invasion vectors and their agents, but the incidence of new invaders pre-adapted to cold environments may rise. In this scenario, prevention has a real chance of success, especially if it is coupled with prioritisation schemes for targeting invaders likely to have greatest impact. Communication and co-operation between cold environment regions (e.g. the Arctic Council; http://www.arctic-council.org) will facilitate rapid response and maximise the use of limited research and control resources for managing native and non-native invaders in high-latitude and high-altitude areas.

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