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Range limits and population dynamics of non-native plants spreading along elevation gradients

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ABSTRACT

Monitoring the elevation limits of non-native species is a potentially sensitive means of detecting effects of environmental change on invasion dynamics and species ranges. The aim of this study was to investigate temporal changes in the distribution of non-native plant species along elevation gradients in the Swiss Alps by repeating, in 2009, a regional survey from 2003 of 230 sites ranging in elevation from 200 to 2400 m a.s.l. We also studied the fine-scale spatiotemporal population structure of two of the non-native species – *Erigeron annuus* and *Solidago canadensis* – along an elevation gradient in a heterogeneous landscape.

Most non-native species in the Swiss Alps rapidly decline in probability of occurrence as elevation increases. We found little change in the elevation ranges limits of species in time, suggesting that most species are not rapidly expanding at their high elevation range limits. For most species, populations were more dynamic (colonizations and extinctions) at the upper range limit where occurrence rapidly declined. Population turnover was negatively correlated with probability of occurrence at the regional and local scale. At low elevations, where probability of occurrence was higher, the number of individuals in a population was also greater. At the local and regional scales, *E. annuus* and *S. canadensis* had similar range limits. At the local scale, propagule production of both *E. annuus* and *S. canadensis* was greater in the core of their distributions at lower elevations, and distance to nearest neighbor increased as occurrence decreased.

Our data demonstrate that range limits of non-native species at high elevation are associated with high population turnover, which results in a transition zone characterized by source-sink dynamics. Populations within this zone exhibit reduced probability of occurrence, and smaller patches. This result has important implications for the monitoring of spreading species along environmental gradients. To understand these limits and predict range expansion, multi-year monitoring and demography data that includes information on colonization and extinction events will be needed.
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1. Introduction

There is a great need to understand and monitor changes in species richness and individual species distributions in the face of global change (Gottfried et al., 2012; Hellmann et al., 2008; Stohlgren et al., 2000). An increasing proportion of species are expanding their ranges beyond historical distributions because of environmental change, including non-native species, and some of these species can threaten biodiversity and ecosystem functioning (Caplat et al., 2013; Carey et al., 2012; Pyšek et al., 2012). Shifts in distribution of plants to higher elevations have been demonstrated for many native species in the European Alps (Grabherr et al., 1994; Lenoir et al., 2008; Pauli et al., 2012), apparently in response to warmer conditions, but species in other parts of the world have also shifted in response to water availability (Crimmins et al., 2011). It is expected that climate change will also trigger rapid expansion of non-native plants into mountain ecosystems, which may become an important threat to species-rich and unique mountain floras (Diez et al., 2012; Kueffer et al., 2013; Pauchard et al., 2009; UNEP, 2009). Monitoring species distributions to detect changes in species' range distributions is therefore an important

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component of a proactive management strategy to protect these least invaded habitats at high elevations from future invasions of upwards moving species (McDougall et al., 2011b).

Species distribution modeling has been an important tool for understanding the current and potential distributions of species (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Thuiller et al., 2008), and is therefore used to make assessments of potential changes in a species distribution in time and in relation to different environmental controlling factors; including of elevational distributions of non-native species (Petitpierre et al., 2016). Monitoring changes in populations has been an important tool for detecting changes in species occupancy regionally and locally. While species distribution models are often fit with coarse data covering a large area, population monitoring is more usually performed at a fine scale and small extent. Yet, despite the obvious importance of combining these scales if we are to understand shifts in distributions, there have been few attempts to integrate studies conducted at regional and local scales. The integration of locally scaled monitoring of populations across a regional scale will help to understand how range limits form (Schurr et al., 2012).

Species range limits are ultimately caused by varying birth, death, and dispersal rates across space and time (Holt and Keitt, 2000; Oborny et al., 2009). Examining the turnover of populations (i.e. colonization and extinctions) can provide information about the dynamics of range margins because there should be an approximate balance between extinction and colonization if the range limit is stable, whereas colonization should exceed extinctions if ranges are expanding (Anderson et al., 2009; MacArthur, 1972; Travis, 2004). Also possible are variable ratios of colonization to extinction that affect probability of occurrence and abundance within the current range. Colonization is affected by the ability of populations to disperse to suitable habitat and extinction rates affected by habitat quality, hence population turnover gives general insight into range dynamics (Brown and Kodric-Brown, 1977; Holt and Keitt, 2000; Holt et al., 2005; Kawecki, 2008; Lennon et al., 1997; Schurr et al., 2012; Sorte, 2013).

Many non-native invasive plant species occupy disturbed habitats (Alpert et al., 2000; Seipel et al., 2012), and spread of these species depends upon the capacity of their propagules to disperse from one suitable habitat patch to the next. However, because these habitat patches tend to be temporary, local populations are often short-lived and the persistence of a species depends upon its ability to colonize new sites. Under favorable conditions, a high density of individuals may develop in a suitable patch, making it likely that some of the seeds produced will disperse to unoccupied patches nearby. Under these conditions, we would expect most suitable sites in the region to be occupied (Hanski, 1997). However, under less favorable conditions – for example, towards the margin of a species' fundamental or Hutchinsonian niche – local seed production may be much lower, reducing the probability that seeds will reach unoccupied patches nearby. For this reason, we would expect to observe a marked decline in the occupancy of sites towards the edge of a species niche; indeed the potential range margin, where growth and reproduction are still possible, may be unoccupied simply because too few seeds reach these patches (Brown and Kodric-Brown, 1977; Hanski, 1997). Therefore an interaction of population dynamics and fundamental niche gives rise to the range limit of species (Pulliam, 2000; Schurr et al., 2012).

In this study we use non-native plant species spreading along elevation gradients in mountains to understand the relationships between distribution limits and population-level processes that form species' ranges. In most mountainous regions, non-native plant species richness peaks in the lower third of the elevation gradient and declines rapidly as elevation increases (Becker et al., 2005; McDougall et al., 2011a; Seipel et al., 2012). A global analysis suggests that high elevation sites are rarely invaded because non-native species are normally introduced to lowland areas from which they may subsequently spread to higher elevations (Alexander et al., 2011; McDougall et al., 2011b; Seipel et al., 2012). This makes the distribution of non-native species along elevation gradients an excellent model system for studying the dynamics of species distributions in response to global change, because the spread and environmental gradient is unidirectional from low to high elevations and are the result of contemporary environmental factors and biotic interactions. There is some evidence that longer established non-native species reach higher elevations (Becker et al., 2005; Haider et al., 2010), which has been interpreted as the result of long-term expansion possibly involving local adaptation (Haider et al., 2012). On the other hand, non-native species often show similar distributional limits to those in their native range (Alexander and Edwards, 2010; Alexander et al., 2009), suggesting that they have reached the limits of their climatic niche and thus elevation range limits may be stable as long as the climate does not change.

The aim of this study was to investigate the distribution and population turnover of non-native plant species along elevation gradients in the Swiss Alps. To do this we utilize two datasets to analyze elevation distributions of non-native species, and their associated population dynamics. At the scale of the complete Swiss Alps we repeated a survey performed six years earlier of 230 ruderal sites ranging in elevation from 200 m to 2400 m a.s.l. (Becker et al., 2005). At a local scale we monitored population dynamics of two model species – *Erigeron annuus* and *Solidago canadensis* – in the upper Rhine river drainage in the Swiss Alps over three years. By combining these two datasets we can examine both population dynamics regionally at disturbed sites (i.e. Swiss Alps), and locally within a heterogeneous landscape (i.e. varying habitat and land use). Our specific research questions were:

1 How stable are the upper elevation range limits of non-native species?
2 Do population dynamics differ along the elevation range a species occupies?
3 How are elevation range limits and population-level processes interrelated?

2. Materials and methods

2.1. Species richness and population turnover at a regional scale

In 2003, Becker et al. (2005) investigated the elevation distribution of non-native plant species in Switzerland using a sample of 230 sites of 0.5-1.0 km^2 in size located at roadsides or at railway stations that ranged in elevation between 200 and 2400 m above sea level. We resurveyed these sites in 2009, visiting them at the same time of year (individual sites were recorded between July and September) and following exactly the same procedures. Most species recorded in 2003 were recorded in 2009; for newly recorded species, origin (native vs. non-native) was determined using *Flora Helvetica* (Lauber and Wagner, 2001). At each site, two trained botanists searched the surveyed area for 30 min and estimated the abundance of all non-native species using a four point scale: 0 (absent), 1 (1–10 individuals), 2 (10–100 individuals) and 3 (greater than 100 individuals). The records of the two botanists were then combined to yield one list for each site, and the abundance was estimated based on consensus between the botanists. To estimate the error in recording species, we revisited three sites at low, middle and high elevations and made a detailed study of the species present (Supplementary material Appendix A Fig. A1).

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