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Forum

Stay or go – how topographic complexity influences alpine plant population and community responses to climate change

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ABSTRACT

In the face of climate change, populations have two survival options − they can remain *in situ* and tolerate the new climatic conditions ("stay"), or they can move to track their climatic niches ("go"). For sessile and small-stature organisms like alpine plants, staying requires broad climatic tolerances, realized niche shifts due to changing biotic interactions, acclimation through plasticity, or rapid genetic adaptation. Going, in contrast, requires good dispersal and colonization capacities. Neither the magnitude of climate change experienced locally nor the capacities required for staying/going in response to climate change are constant across landscapes, and both aspects may be strongly affected by local microclimatic variation associated with topographic complexity. We combine ideas from population and community ecology to discuss the effects of topographic complexity in the landscape on the immediate "stay" or "go" opportunities of local populations and communities, and on the selective pressures that may have shaped the stay or go capacities of the species occupying contrasting landscapes. We demonstrate, using example landscapes of different topographical complexity, how speciesö thermal niches could be distributed across these landscapes, and how these, in turn, may affect many population and community ecological processes that are related to adaptation or dispersal. Focusing on treeless alpine or Arctic landscapes, where temperature is expected to be a strong determinant, our theorethical framework leads to the hypothesis that populations and communities of topographically complex (rough and patchy) landscapes should be both more resistant and more resilient to climate change than those of topographically simple (flat and

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homogeneous) landscapes. Our theorethical framework further points to how meta-community dynamics such as mass effects in topographically complex landscapes and extinction lags in simple landscapes, may mask and delay the long-term outcomes of these landscape differences under rapidly changing climates.

1. Introduction

Our understanding of the magnitude and ecological implications of climatic variation in space and time has greatly developed over the past decades. Studies focusing on the capacity for species to track their climatic niches over large spatial extents, including palaeoecological reconstructions (reviewed in Feurdean et al., 2013) and climate envelope models (Pearson and Dawson, 2003; Sykes et al., 1996), typically suggest high migration rates in response to rapid redistribution of climates at the global scale (Clark et al., 1998; Loarie et al., 2009). For plants, these findings have been challenged by more recent molecular (Westergaard et al., 2010, 2011), palaeoecological (Birks and Willis, 2008; Cheddadi et al., 2014) and meso- to micro-scale climate envelope modelling (Franklin et al., 2013; Lenoir et al., 2017; Randin et al., 2009; Trivedi et al., 2008;), all suggesting occasional species persistance within refugia or through short-distance escapes (Hampe and Jump 2011). Here, we discuss how the propensity for species to “stay”, through adaptation processes, or “go”, through dispersal processes, so as to survive in the face of climate change, depends not only on the magnitude of climate-change exposure and the climate-change sensitivity of the constituent species and communities (Dickinson et al., 2014; Bertrand et al., 2016), but also on the spatial structure of the landscapes in which the species occur (Körner, 2004; Slavich et al., 2014).

Topography is a key determinant of climatic variation across spatial scales ranging from regions, covering hundreds of square kilometres, to microsites of less than a square metre, especially in treeless areas like the high Arctic and alpine regions (see Box 1). Across these spatial scales, we can find regions, landscapes, patches, and microsites that are relatively topographically uniform, as well as others that are topographically complex, with associated differences in climatic heterogeneity. For example, there are clear differences in topographic complexity between mountainous *vs*. flat landscapes in high-latitude regions (Lenoir et al., 2013), flat areas *vs*. ridge-snowbed gradients in alpine landscapes (Graae et al., 2011; Körner, 2003), and flat *vs*. microtopographically complex patches within grassland and tundra vegetation (Armbruster et al., 2007; Moeslund et al., 2013; Opedal et al., 2015). The topographic complexity at scales of a few tens of metres can give rise to microclimatic variation in e.g., mean temperatures that often matches what is expected under future climate change scenarios (2–6 °C; Armbruster et al., 2007; Dobrowski et al., 2013; Graae et al., 2012; Lenoir et al., 2013; Opedal et al., 2015; Scherrer and Körner, 2010; Scherrer and Körner, 2011).

It is important to focus on high-latitude and high-elevation landscapes beyond treeline, not only because the complex topography there provides more spatial heterogeneity in temperature, but especially because temperature itself is expected to be the main determinant of plant distribution in these landscapes (Körner, 2003; Raunkiaer 1934). Indeed, temperature has both direct effects on alpine plant life through setting limits to species’ fundamental niches, as well as indirect effects through determining, for instance, decomposition and nutrient cycling, access to water, as well as the abundance of herbivores, pathogens,

Box 1
The thermal niche of alpine plants.

The thermal niche of plants is often described in a highly simplified manner with a strong focus on synoptic or ambient air temperature characterizing macroclimate. For small-stature and slow-growing alpine and Arctic plants there is a major difference and decoupling between the temperature that the plants experience near the ground and the temperature conditions obtained from weather stations measuring synoptic temperature at 2 m height (Graae et al., 2012; Lenoir et al., 2013; Körner, 2003; Scherrer and Körner, 2010, 2011). During summer, the difference and decoupling between temperature conditions near the ground and synoptic temperature is to a high degree controlled by topography, vegetation structure, proximity to ground and, in the soil, also the moisture level. During winter, difference and decoupling is also caused by topography, vegetation structure and proximity to ground, but this is mostly due to its effect on snow cover and depth that determines the microclimate (temperature and moisture) and light conditions to the plants. Körner (2003) as well as Wipf and Rixen (2010) describes in detail how snow cover and duration matters for alpine and Arctic vegetation.

In addition to these scale effects, it is well established that the multifaceted nature of temperature (maximum, minimum, mean, growing season length, etc.) affects different life cycle and phenological stages to various extent. For instance, extreme temperatures are mostly associated with mortality events and the timing of these extreme events is crucial, whereas mean temperatures are chiefly associated with growth processes. Körner et al. (2016) describe how the many different components of climate affect tree distribution, and this complexity of niche limiting factors and interactions is expected to be even greater for small-stature plants occurring near the ground. Understanding the ecophysiological and ecological mechanisms underlying plant species distribution needs to take such microclimatic considerations into account. Accounting for all these limiting factors to model alpine plant species distribution is rarely done in the scientific literature. The more simplified concept of thermal niche has, however, shown useful because plant species distribution, especially trees for which most studies are done, correlate well with macroclimatic variables such as mean summer and winter temperatures. However, for mechanistic understanding of what is driving these correlations we need to go beyond mean temperatures (Körner et al., 2016) and assess the importance of this topographically-driven heterogeneity in temperature conditions near the ground and its consequences for alpine plant distribution and redistribution under climate change.

Legend: Diagram showing the many factors shaping the microclimatic niche in alpine plant communities. The growing season macroclimate is filtered into microclimate by factors listed in the red arrow and winter macroclimate is filtered into microclimate by factors listed in the blue arrow. The resulting summer microclimatic niche in green for survival, growth and reproduction of plants are determined by temperature extremes (max. and min. temperatures mostly for survival), season length and growing degree hours (GDH) that gives the accumulated temperature for growth and reproduction. Also the winter microclimatic niche in blue is determined by the temperature extremes for survival while season length, that also to a high extent is driven by snow cover, determines important winter processes, for instance respiration and dormancy break.