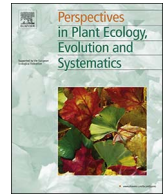




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Research article

Winter soil temperature dependence of alpine plant distribution: Implications for anticipating vegetation changes under a warming climate

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ABSTRACT

The topographical heterogeneity of mountain landscapes and the associated species turnover over short distances should prompt us to examine the relationships between climate and mountain plant distribution at a much finer scale than is commonly done. Here, I focused on the root zone temperature experienced by low-stature perennial-dominated plant communities of temperate mountains, which are seasonally covered by snow. Based on the analysis of multi-annual recordings of ground temperatures across a broad spectrum of plant communities, I propose a habitat template using Growing Degree Days (GDD) and Freezing Degree Days (FDD). These two indices summarize soil thermal conditions experienced during the favorable and the unfavorable period for growth. This heuristic framework allows refining our working hypotheses on the range shifts of mountain plants in response to recent and future climate change. Regional trends in climate variables controlling GDD and FDD indicate that the combination of earlier snow melt-out and higher summer temperatures have led to an overall increase in GDD over the last decades. However the persistence of cold episodes in spring and in fall along with the shorter snow coverage suggest that the positive effect of an extended growing season might be counteracted by the detrimental effects of increasing FDD. I thus hypothesize (i) a local-scale, downward shift of plant species along mesotopographical gradients, with marked species infilling in sparsely vegetated, long-lasting snow patches that contain vacant niches and (ii) a watershed-scale upward shift of subalpine species inhabiting south-exposed grasslands and able to cope with moderate FDD. This perspective challenges the simplistic view of an overall range shift of mountain plants along elevational gradients and calls for the improvement of models of snow cover dynamics and root zone temperature to draw up realistic scenarios of mountain vegetation changes under a warmer climate.

1. Introduction

In arctic and temperate mountain ecosystems, snow cover dynamics not only determine the length of the favorable period for growth but also tightly control the duration and intensity of freezing temperatures that belowground, perennial tissues have to cope with during the unfavorable period. Shallow or inconsistent winter snowpack causes soil frosts that can persist over weeks or months in cold contexts and this has a long-term ecological significance for the distribution of overwintering organisms (Callaghan et al., 2011; Sutinen et al., 1999). A seasonal reduction of snow cover duration may expose tissues to damaging frosts in spring or in fall and several studies emphasized the impact of this climatic hazard on the performance of organisms (Abeli et al., 2012; Inouye, 2000; Kreyling, 2010; Pauli et al., 2013; Wipf et al., 2009). The legacy of wintertime temperature regime on nutrient availability for plant growth during the following summer is also a key

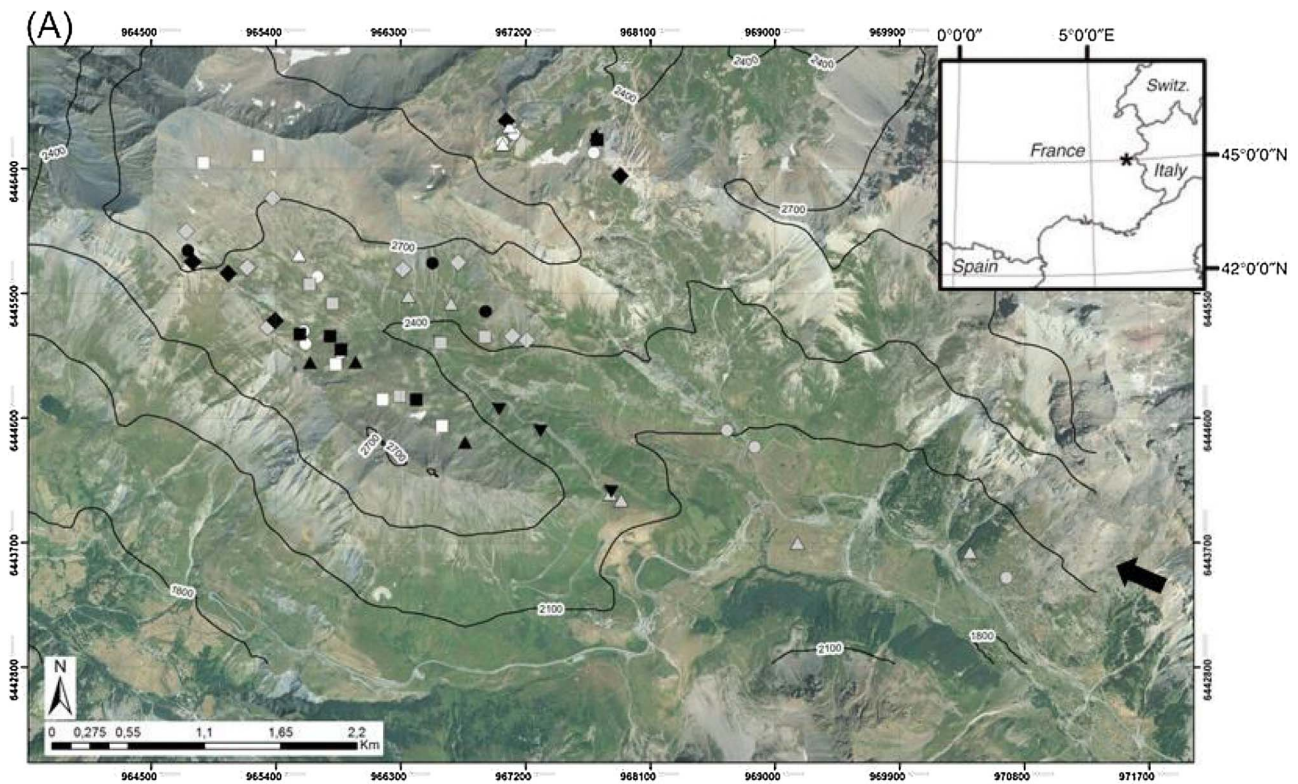
aspect of the functioning and the vegetation dynamics of snow-covered arctic and alpine ecosystems (Kreyling, 2010; Sturm et al., 2005). For example, increased microbial activity and higher N retention are observed in soils that benefit from the insulating effect of the snow (Baptist et al., 2010; Edwards et al., 2007) whereas freezing temperatures may favor the physical degradation of soil organic matter and the amount of inorganic nitrogen (Freppaz et al., 2008).

In mountain landscapes, thermal differentiations among nearby sites are related to the high topographical heterogeneity (Billings, 1973; Scherrer and Körner, 2010; Walker et al., 1993). During winter, these differences might be exacerbated by wind snow redistribution between sheltered sites where snow accumulates and exposed, wind-blown sites where it is eroded (Essery and Pomeroy, 2004). As a result, highly contrasting soil temperature regimes are reported over mesotopographical gradients, i.e. ridge-to-snow bed gradients which typically represent a distance of a few meters (Baptist and Choler, 2008;

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(B)



Fig. 1. Location of plots in the study area (A) and overview of the Roche Noire watershed (B). The arrow on the map indicates the position of the photographic shooting. The inset map shows the location of the study area in the French Alps. Symbols for plant communities follow [Table 1](#).

[Wundram et al., 2010](#)). Consistent patterns of functional and taxonomic beta diversity and for different trophic levels have been documented along these gradients ([Heegaard, 2002](#); [Kudo et al., 1999](#); [Zinger et al., 2009](#)). Consequently, the response of alpine plants to ongoing climatic change cannot be properly assessed if this patchiness of the thermal landscape is not properly understood ([Graae et al., 2012](#)). In line with

this reasoning, a recent study pointed out that the magnitude of predicted change in temperature is relatively weak compared to what plants would experience given a very short-distance range shift ([Scherrer and Korner, 2011](#)).

Current models that aim to project the distribution of high elevation species under a warmer climate suffer from the insufficient

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