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Thermal niches are more conserved at cold than warm limits in arctic-alpine plant species

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ABSTRACT

Aim Understanding the stability of realized niches is crucial for predicting the responses of species to climate change. One approach is to evaluate the niche differences of populations of the same species that occupy regions that are geographically disconnected. Here, we assess niche conservatism along thermal gradients for 26 plant species with a disjunct distribution between the Alps and the Arctic.

Location European Alps and Norwegian Finnmark.

Methods We collected a comprehensive dataset of 26 arctic-alpine plant occurrences in two regions. We assessed niche conservatism through a multispecies comparison and analysed species rankings at cold and warm thermal limits along two distinct gradients corresponding to (1) air temperatures at 2 m above ground level and (2) elevation distances to the tree line (TLD) for the two regions. We assessed whether observed relationships were close to those predicted under thermal limit conservatism.

Results We found a weak similarity in species ranking at the warm thermal limits. The range of warm thermal limits for the 26 species was much larger in the Alps than in Finnmark. We found a stronger similarity in species ranking and correspondence at the cold thermal limit along the gradients of 2-m temperature and TLD. Yet along the 2-m temperature gradient the cold thermal limits of species in the Alps were lower on average than those in Finnmark.

Main conclusion We found low conservatism of the warm thermal limits but a stronger conservatism of the cold thermal limits. We suggest that biotic interactions at the warm thermal limit are likely to modulate species responses more strongly than at the cold limit. The differing biotic context between the two regions is probably responsible for the observed differences in realized niches.

Keywords

Air–soil temperature, biotic interactions, disjunct distribution, distance to tree line, European Alps, niche conservatism, Norwegian Finnmark, realized niche, species distribution models.

INTRODUCTION

Understanding the stability of a species' environmental niche – both fundamental (i.e. physiological) and realized (i.e. con-

strained by biotic interactions and dispersal) – is crucial for predicting a species' response to climate change (Pearman *et al.*, 2008; Lavergne *et al.*, 2010; Salamin *et al.*, 2010; Wiens *et al.*, 2010; Bellard *et al.*, 2012). It was notably suggested that the

fundamental niches of some species might evolve rapidly and this may attenuate the current effects of global change on ecosystems (Hoffmann & Willi, 2008; Hoffmann & Sgrò, 2011). Assessing the differences between populations of a species that occupy geographically disjunct regions or of populations of species that have recently colonized a new geographically separate region (e.g. invasive species) are thus promising ways of providing insight into the possible shifts of species niches (Wiens & Graham, 2005; Pearman *et al.*, 2008; Alexander & Edwards, 2010).

Both abiotic and biotic factors shape the ability of a species to occupy certain environmental conditions (Soberón, 2007). While these factors may change across regions and drive shifts in both fundamental (Hoffmann & Sgrò, 2011) and realized (Schweiger *et al.*, 2008) niches, only the realized niche is easily quantifiable, which limits ecological interpretation. Nonetheless, biotic drivers are thought to have differential effects across environmental gradients (Callaway *et al.*, 2002; Le Roux & McGeoch, 2010). According to the asymmetric abiotic stress limitation hypothesis (AASL), in general, fluctuations of the realized niche due to changing biotic interactions are expected at the warm, more productive end of environmental gradients (Normand *et al.*, 2009; Defossez *et al.*, 2011; Meier *et al.*, 2011). At the cold end, species distributions are primarily limited by physiological tolerance of environmental conditions that are less favourable to growth and reproduction (Pigott & Huntley, 1978; Normand *et al.*, 2009; Meier *et al.*, 2011). Investigating the realized niche of species that spans a wide range of environmental gradients, from warmer, productive conditions to colder, less productive ones, may provide insight into the prevalence of shifts in both fundamental and realized niches.

Climatic temporal variations affect the ranges of species and promote the differentiation of their realized niches among disjunct ranges (Hewitt, 2000; Davis & Shaw, 2001; Zimmermann *et al.*, 2009). During the last ice age, ice caps and glaciers covered most of northern Europe and its alpine areas, while most of central Europe comprised cold biomes (Frenzel *et al.*, 1992). With the end of these glaciations, cold-adapted species followed the retreat of the ice toward either higher latitudes or higher elevations, contributing to the current disjunct distribution of those species found both in the Alps and in the Arctic (whose members are referred to as arctic-alpine species; Schönswetter *et al.*, 2005; Espíndola *et al.*, 2012). The separation of species may have caused unequal distributions of the species genetic diversity (Després *et al.*, 2002) and genetic isolation (Espíndola *et al.*, 2012). In addition, cryptic refugia in the north may have contributed to the genetic difference in arctic and alpine species (Parducci *et al.*, 2012). This potentially provides the genetic basis for a shift of the fundamental niche (Ackerly, 2003).

Isolated populations without means to exchange genetic material may cause changes to the local fundamental niche and the emergence of ecotypes through adaptations to local environmental conditions (Comes & Kadereit, 1998; Ackerly, 2003; Wiens, 2004; Broennimann *et al.*, 2007; Jay *et al.*, 2012; Manel *et al.*, 2012). Differences existing in abiotic factors may differentially modulate the responses of species across environmental

gradients in the two regions. For instance, Billings (1973) suggested that the long separation between the arctic and alpine regions may have created distinct ecotypes. Individuals from alpine populations experience higher light saturation for photosynthesis, undergo maximum photosynthesis rates at higher temperatures and contain a lower chlorophyll content than their Arctic counterparts (Mooney & Johnson, 1965; Billings and Mooney 1968; Billings, 1973).

Geographically distant populations may also be part of regionally distinct species pools, such that biotic interactions may influence realized niches differently (Gallien *et al.*, 2010; Pellissier *et al.*, 2010). Plant species richness in the Alps is higher than in the Arctic (Lenoir *et al.*, 2010), potentially causing distinct competition regimes, which may result in different realized niches. Human pressure also differs: in the Alps, a long history of land use has reshaped the structures of lower alpine grasslands (Gehrig-Fasel *et al.*, 2007), while human impact has been lower in the Arctic. Therefore, one could expect to observe different realized niches for the same species between the Alps and the Arctic, but this has yet to be tested. Hence, a comparison of the Alps and Arctic regions represents a useful case study for considering niche conservatism along the thermal gradient.

For this research, we investigated whether single plant species occupy similar realized niches across the thermal gradients between the Arctic and the Alps. We first collected a comprehensive data set that comprised occurrences of 26 arctic-alpine plant species in the European Alps and in northern Norway. Across the two regions, we compared the rankings of the species when considering their colder and warmer thermal limits according to summer temperature and their distances in elevation from the tree limit. The tree line was shown to be physiologically controlled and conserved world-wide (Körner & Paulsen, 2004; but see Harsch *et al.*, 2009), it therefore constitutes a sound biogeographic reference for the comparison and ranking of non-tree species along thermal gradients (Randin *et al.*, in press).

MATERIALS AND METHODS

Study areas

The two study areas are the European Alps and Norway's northernmost counties (Troms and Finnmark, referred to as Finnmark; Fig. 1). These Norwegian counties form the northern frontier of the European continent and are bordered by the Barents Sea to the north and by birch forests and continuous taiga to the south. The western part of the region is characterized topographically by steep hills with peaks of approximately 800–1800 m a.s.l. that are often surrounded by glaciers, deep valleys, narrow fjords or open sea. In the eastern part of Finnmark, the mountain ranges gradually decrease in elevation towards the Barents Sea to plateaus of 300–500 m a.s.l., with the existence of abrupt cliffs interspersed with moderately sloped hills. The Alps represent the most distinct mountain range in central Europe, stretching from Austria and Slovenia in the east to France in the west. Rising up to 4800 m a.s.l., the Alps comprise cold climatic

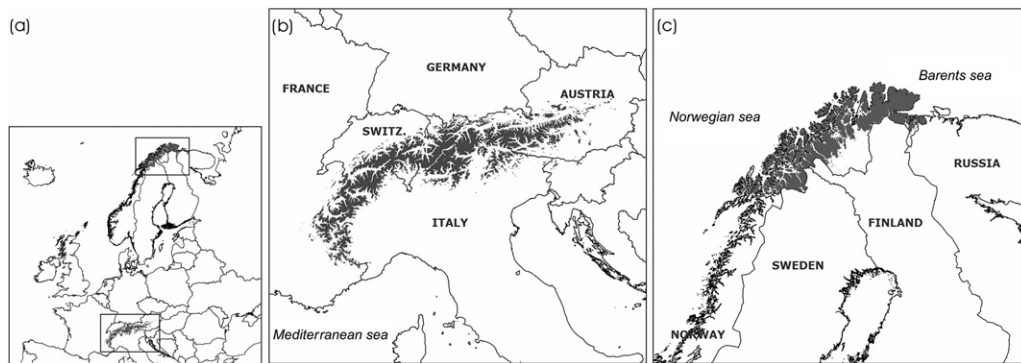


Figure 1 (a) Maps of the two regions of Europe examined in the present study. The dark colour indicates the area sampled, corresponding to the beginning of the subalpine belt of the Alps (b) and to the tundra of northern Norway's Finnmark (c), where the average temperature of the warmest month in both locations is less than 11 °C.

environments comparable to those of the Arctic, with short growing seasons and long snow cover during the winter. The present study focuses on the areas where the average temperature of the warmest month is less than 11 °C, corresponding to the regions of the subalpine belt and the subarctic tundra.

Species data

We selected 34 taxa that are relatively frequent both in the Alps and in Finnmark and that can also be identified in the field with limited risk of confusion. We sought a data set that was as close as possible to an equal-stratified sampling design (Hirzel & Guisan, 2002). Therefore, we stratified our study areas according to WorldClim's climate grids (Hijmans *et al.*, 2005) at a resolution of 30 arcsec (*c.* 1 km × 1 km). Three descriptors, representing summer (June–August) temperatures, humidity (June–August) and winter (December–February) precipitation were selected. Summer temperature represents the energy available during the growing season and winter precipitation represents the cover of snow. Each descriptor was divided into three equal classes. By combining these three layers with three classes each, we generated 24 realized climate combinations (strata) in the Alps and 25 in Finnmark, out of the 27 (= 3 × 3 × 3) possible classes. Species occurrences were collected for each stratum by using (1) existing observations and (2) a complementary sampling, which filled gaps in the existing data that originated from a non-stratified sampling.

For the previously existing data, we collected exhaustive vegetation inventories for both regions that contained at least one of the selected species. We randomly selected survey points in each climate class from the vegetation data to constitute these classes (with a maximum of 100 survey points). As the acquired data did not cover the entire available environment in the study areas, where the number of historical observation points was insufficient we set up a complementary sampling in Finnmark and in the Alps to achieve equal samples per climate class. To conduct this sampling, we randomly selected 750 m × 750 m plots (hereafter referred to as 750-m plots) in climatic strata with missing data. Each randomly selected plot was subsampled

by randomly selecting four 100 m × 100 m subplots (hereafter, 100-m subplots) that were separated from one another by at least 200 m. Within each 100-m subplot, we visited nine subplots of 2 m × 2 m (hereafter, 2-m subplots) and inventoried the species along a planned route. We first set a 2-m subplot at the centre of a 100-m subplot and recorded all of the target species present. We then moved 25 m to the north-east to sample the second 2-m subplot, moved another 25 m further to the north-east to sample the third 2-m subplot, and then returned to the central point. We performed similar sampling procedures for the other three directions (i.e. north-west, south-east and south-west). Additionally, we recorded whether the target species were present in the routes between the 2-m subplots. This nested design, with three plot levels of 750, 100 and 2 m, was chosen over a standard random sampling because accessibility to Finnmark's northern regions is limited and this procedure has proven to be the most cost efficient (Pellissier *et al.*, 2010).

Environmental data

We calculated the average summer temperature (hereafter referred to as the 2-m temperature) as the mean of the recorded temperatures for June, July and August. We considered average summer temperature only because: (1) it is physiologically more meaningful to alpine species than other temperature variables (Körner, 2003); (2) the altitude of the global tree line is also best explained by the average temperature of the summer growing season (Körner & Paulsen, 2004; Gehrig-Fasel *et al.*, 2008); and (3) other climatic variables that could have been derived from WorldClim, such as degree-days measured with the approach of Zimmermann & Kienast (1999), show anyway a high correlation to June–August average temperature ($R^2 = 0.9$ in the Alps and $R^2 = 0.7$ in Finnmark) and therefore were not expected to prove more informative than the summer average for our analyses.

We obtained the temperature layer from WorldClim (Hijmans *et al.*, 2005), which is based on 2-m air measurements from meteorological stations. To obtain more precise climatic

information at the sites, we downscaled WorldClim data from a 30-arcsec resolution to a 100-m resolution using a digital elevation model (for details see Engler *et al.*, 2011). While the temperature layer gives fairly robust results with this downscaling approach, the method is less reliable when applied to the precipitation layer (Gyalistras, 2003; Daly *et al.*, 2008; Randin *et al.*, in press). Consequently, we only analysed thermal niches in the present study. All other thermal variables from WorldClim or derived variables show a high correlation with the June–August average and we therefore did not consider them in the analyses.

We also estimated thermal differences in relation to the calculated distance to the potential local tree line (TLD), as tree lines are good biogeographic reference points for comparing and ranking non-tree species (Randin *et al.*, in press). For the two regions, we extracted data at a resolution of 100 m per pixel of forest-occupied areas of the land-cover layers of CORINE, for Europe, and GEOSTAT, for Switzerland. With this information, we calculated the elevations of the forest-occupied areas. After delineating a square window of 5 km × 5 km, we calculated the potential tree line of each 100-m pixel by computing the maximum of forest elevation within each window, following the procedure defined by Paulsen & Körner (2001) and Gehrig-Fasel *et al.* (2007). For each 100-m pixel, we subtracted the elevations of the pixel from the elevations of potential tree lines to obtain the distances in elevation to the potential tree line, one of the most relevant temperature proxies in cold environments.

Rankings of species across thermal gradients

We compared the warm and cold thermal limit values for the averaged 2-m temperature and calculated TLD in the Alps and in Finnmark. To investigate whether the rankings of species across temperature gradients are similar between the two regions, we considered the cold and warm thermal limits to be the 20th and 80th percentiles of the 2-m temperature and TLD gradients for both study regions. We preferred using the 20th and 80th percentiles rather than the absolute minima and maxima because they are less sensitive to outliers. We extracted the 2-m temperature and TLD at the locations where the species were recorded and calculated the 20th and 80th percentiles of the distribution of those values. Our analysis is thus based on presence only. We then tested for rank conservatism using Kendall's rank correlation of the 20th and 80th percentile values in the Alps and Finnmark. The formal null hypothesis for the conservatism of thermal limits in species is that the slope representing the relationship of two regions is equal to one while the intercept is zero. However, an alternative hypothesis can also be that, due to microclimatic differences between the two regions, the thermal niche limits are related but with a slope different from 1 and a non-zero intercept. We tested these alternative hypotheses using the *slope.test* function of the *smatr* R package using the standard major axis method, with and without the intercept fixed to the origin (Warton *et al.*, 2006).

RESULTS

Species sampling

In total, we obtained 6320 plots in the Alps and 2819 in Finnmark. Of the 34 species sampled, only 26 occurred with sufficient frequency in both regions to support further analyses (number of occurrences > 20; Table 1).

Warm thermal limit

The most interesting finding of this study is that the range of warm thermal limits demonstrated by the 26 species was much larger in the Alps than in Finnmark both when measured with 2-m temperature (4 °C in the Alps and 1 °C in Finnmark; Fig. 2) and with the TLD (350 m in the Alps and 180 m in Finnmark; Fig. 3). As a consequence, the relationships between the ranks of the warm thermal limits of the species in the two regions were weak (2-m temperature, $R^2 = 0.23$; Kendall tau = 0.3, $P = 0.04$; TLD, $R^2 = 0.31$, Kendall tau = 0.38, $P = 0.005$). The estimated slopes of those relationships differed from one with zero-forced intercept (TLD, slope = 2.16, confidence interval = 1.47–3.16) and with non-zero estimated intercept (2-m temperature, slope = 4.04, confidence interval = 2.81–5.79; TLD, slope = 1.84, confidence interval = 1.31–1.84), except along the 2-m gradient with zero-forced intercept (slope = 0.96, confidence interval = 0.9–1.02). This occurred because the points were equally distributed across both sides of (but not along) the 1 : 1 line (Fig. 2).

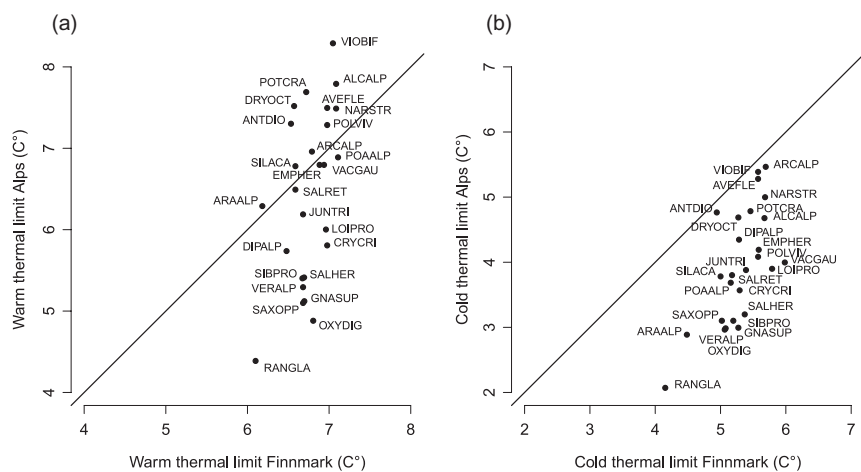
Cold thermal limit

We found a better correspondence of species limit in the Alps and Finnmark toward cold temperatures. We found a positive relationship between the ranks of cold thermal limits of the 26 species in the two regions measured with 2-m temperature ($R^2 = 0.41$, Kendall tau = 0.5, $P = 0.0005$). Yet, the slope of this relationship was unequal to one, being systematically biased, whether tested with zero-forced intercept (slope = 0.76, confidence interval = 0.71–0.82) or with non-zero estimated intercept (slope = 2.25, confidence interval = 1.64–3.07). The species with the coldest thermal limits tolerated colder 2-m temperatures in the Alps than in Finnmark, while species located in warmer conditions in the Alps and in Finnmark exhibited more equivalent cold thermal limits (Fig. 2). Except for one species (*Antennaria dioica*), along the TLD gradient the points were closer to the 1 : 1 relationship (Fig. 3). When excluding this outlying species, the correlation was high ($R^2 = 0.51$, Kendall tau = 0.48, $P = 0.0007$; when not excluded $R^2 = 0.28$, Kendall tau = 0.38, $P = 0.005$). The estimated slopes with zero-forced intercept (slope = 0.98, confidence interval = 0.88–1.08) were similar to one, and the lower bound of the confidence interval was close to one with non-estimated intercept (slope = 1.65, confidence interval = 1.15–2.39; Fig. 3).

Table 1 List of the arctic-alpine species sampled in the Alps (A) and in Finnmark (F), including the total number of occurrences (Pres.) obtained in each region. Nomenclature from Aeschmann *et al.* (2004).

Abbrev.	Species	Family	Growth form	Pres. (A)	Pres. (F)
ALALP	<i>Alchemilla alpina</i>	Rosaceae	Forb	95	178
ANDIO	<i>Antennaria dioica</i>	Asteraceae	Forb	278	81
ARALP	<i>Arabis alpina</i>	Brassicaceae	Forb	144	25
ARCAL	<i>Arctostaphylos alpina</i>	Ericaceae	Dwarf shrub	25	223
DEFLE	<i>Avenella flexuosa</i>	Poaceae	Graminoid	356	862
CALAC	<i>Carex lachenalii</i>	Cyperaceae	Graminoid	10	132
CHAAL	<i>Chamorchis alpina</i>	Orchidaceae	Forb	19	3
CRCRI	<i>Cryptogramma crispa</i>	Cryptogrammaceae	Spore plant	61	57
LYALP	<i>Diphysastrum alpinum</i>	Lycopodiaceae	Spore plant	52	141
DROCT	<i>Dryas octopetala</i>	Rosaceae	Dwarf shrub	228	133
EMHER	<i>Empetrum hermaphroditum</i>	Empetraceae	Dwarf shrub	119	1089
GENIV	<i>Gentiana nivalis</i>	Gentianaceae	Forb	83	8
GNSUP	<i>Gnaphalium supinum</i>	Asteraceae	Forb	308	194
JUTRI	<i>Juncus trifidus</i>	Jucaceae	Graminoid	241	673
LOPRO	<i>Loiseleuria procumbens</i>	Ericaceae	Dwarf shrub	176	404
NASTR	<i>Nardus stricta</i>	Poaceae	Graminoid	621	386
OXDIG	<i>Oxyria digyna</i>	Polygonaceae	Forb	115	118
POALP	<i>Poa alpina</i>	Poaceae	Graminoid	780	77
POVIV	<i>Polygonum viviparum</i>	Polygonaceae	Forb	777	428
POCRA	<i>Potentilla crantzii</i>	Rosaceae	Forb	231	30
RAGLA	<i>Ranunculus glacialis</i>	Renonculaceae	Forb	179	22
SEROS	<i>Rhodiola rosea</i>	Rosaceae	Forb	8	69
SALIN	<i>Sagina saginoides</i>	Caryophyllaceae	Forb	67	8
SAHER	<i>Salix herbacea</i>	Salicaceae	Dwarf shrub	364	721
SARET	<i>Salix reticulata</i>	Salicaceae	Dwarf shrub	161	62
SAUAL	<i>Saussurea alpina</i>	Asteraceae	Forb	9	155
SAOPP	<i>Saxifraga oppositifolia</i>	Saxifragaceae	Forb	206	41
SIPRO	<i>Sibbaldia procumbens</i>	Rosaceae	Forb	244	167
SIACA	<i>Silene acaulis</i>	Caryophyllaceae	Forb	256	125
THAAL	<i>Thalictrum alpinum</i>	Renonculaceae	Forb	14	174
VAGAU	<i>Vaccinium gaultherioides</i>	Ericaceae	Dwarf shrub	337	156
VEALP	<i>Veronica alpina</i>	Scrophulariaceae	Forb	317	104
VERFR	<i>Veronica fruticans</i>	Scrophulariaceae	Forb	129	6
VIBIF	<i>Viola biflora</i>	Violaceae	Forb	235	303

Figure 2 Relationship between (a) the warm (80th percentile) and (b) cold (20th percentile) thermal limits of species in the Alps and Finnmark for summer temperature. The straight line indicates the expected 1 : 1 relationship, which has a slope of one and passes through the origin. Abbreviations refer to Table 1.



DISCUSSION

At the warm thermal limits, the less climatically severe and more productive ends of the gradients for species, we found a low

conservatism of species limit rankings, with lower variation in thermal limits in Finnmark compared with the Alps. In contrast, we found higher correspondences in species rankings at the cold thermal limits across the two regions (especially along the TLD

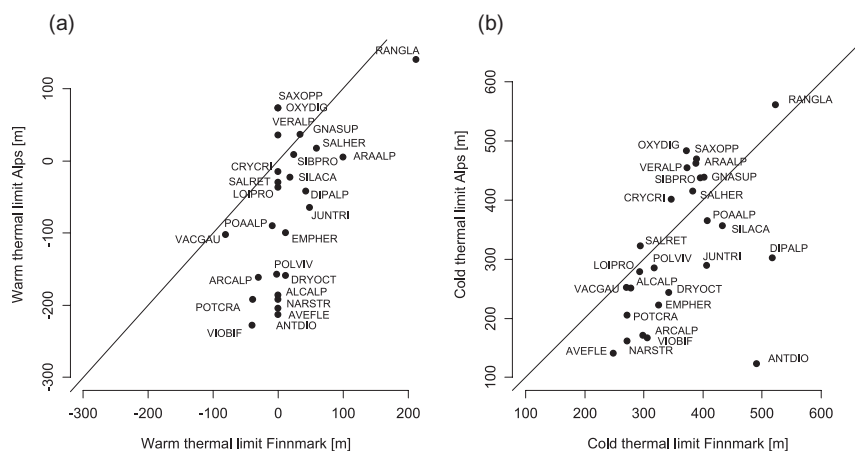


Figure 3 Relationship between (a) the warm (20th percentile) and (b) cold (80th percentile) thermal limits of species in the Alps and Finnmark as measured from the elevation difference to the potential tree line (TLD, unit in metres). The straight line indicates the expected 1 : 1 relationship, which has a slope of one and passes through the origin. Abbreviations refer to Table 1.

gradients). Our results thus conform with expectations raised by the asymmetric abiotic stress limitation hypothesis and indicate that the realized niches of species are more conserved in severe and physiologically limiting conditions, where the impacts of biotic interactions (such as competition) are weaker, than in the most productive parts of the same gradients. Under these latter conditions, the biotic interactions both within the same trophic level (Choler *et al.*, 2001) and between trophic levels are influential (Defossez *et al.*, 2011).

Warm thermal limits are different across arctic and alpine populations

We found little similarity between the Alps and Finnmark in the realized niches at the warm thermal limits. While species limits were distributed across the environmental gradients examined in the Alps and extended far below the potential tree line, the warm thermal limit of all species in Finnmark was narrower and was situated in closer proximity to the potential tree line than in the Alps (Fig. 3). Thus, temperature appears to be structuring species sequences at the warm thermal limit across environmental gradients in the Alps, but the same degree of structuring was not reached in Finnmark. In the latter, Müller (1952) suggested intense competitive effects from dwarf shrubs in the lower Arctic. Similarly, Pellissier *et al.* (2010) documented a large competitive effect of a dominant dwarf shrub in subarctic tundra. In comparison, because the land-use history of the Alps has been more intense, the heath vegetation is severely reduced or almost absent in the transitional zone (ecotone) between the subalpine and alpine vegetation belts (Gobet *et al.*, 2003). Human settlers have, since the Neolithic, freed low alpine grassland from shrubs and small trees (lowering the tree line as far as 300 m downslope), which created less gradual vegetation transitions than those found in Finnmark (Tinner & Theurillat, 2003). Many alpine species probably took the opportunity to extend their distribution in microniches in the subalpine belt after clearing. Furthermore, domesticated reindeer have been present for centuries in Finnmark (Muga, 1986), but only recently at high densities (Bråthen *et al.*, 2007). As a consequence, alpine plants with a low tolerance for competition may have been able to

colonize habitats towards much lower elevations than the potential tree line in the Alps, while the ecotone heath vegetation in Finnmark has probably limited the distribution of alpine plant species at their warm thermal limits. While this effect is mostly apparent at a local scale, it has been demonstrated that such effects can also have range-shaping influences, thus affecting the geographic distribution of species up to a large spatial extent (Meier *et al.*, 2012).

Realized niche conservatism at the cold thermal limit

Arctic and alpine plant populations occupy more similar rank positions in cold compared with warm thermal limits of their range, especially along TLD gradients where the distribution is relatively close to the 1 : 1 line. This is in accordance with the asymmetric abiotic stress limitation hypothesis, which states that the cold temperature end of a gradient should be less affected by biotic interactions (Callaway *et al.*, 2002) because it tends to be closer to the fundamental niche and its physiological limits (Normand *et al.*, 2009). Our results corroborate those of Wiens & Graham (2005), who also documented strong niche similarities for northern latitudes in invasive species between native and invaded ranges. Here we used the different distances in elevation from the tree line as a proxy for thermal difference. A clearer relationship may have been found if the units for these differences in elevation were transformed from metres to thermal units (K) using a local lapse rate (Randin *et al.*, in press). However, the lack of regional meteorological stations at high elevation in northern Norway does not allow for the calculation of accurate local lapse rates in Finnmark. Discrepancies in the niche at the more physiological cold limit may also arise from genetic differentiation of arctic and alpine populations, but finer quantification of the niche using for instance growing chambers is required to assess this hypothesis (Parducci *et al.*, 2012).

Discrepancies between analyses of distances to tree line and 2-m temperature

Our findings indicate a stronger similarity among realized niches at the cold than at the warm thermal limit in the Alps and

in Finnmark when considering distances in elevation from tree lines. Alpine populations seem to persist generally in colder temperatures than arctic populations, as inferred from interpolated 2-m air temperatures. However, this observation may be an artefact originating from considering air temperatures rather than soil temperatures during niche comparison. This bias may specifically occur when studying low-stature plants that are aerodynamically decoupled from atmospheric conditions, particularly in topographically complex terrains (Scherrer & Körner, 2011) and in regions with differential angles of solar radiation (Austin & Van Niel, 2011). In this case, solar radiation is more vertical in the Alps than in Finnmark. Vertical radiation is perpendicular to a larger proportion of the terrain, which provides a higher flux of heat to the soil surface and to low-stature plants. Radiation heat is unaccounted for in the 2-m air temperature interpolations, which may bias the level of tolerance for populations in the colder temperatures of the Alps than in the colder temperatures of Finnmark. We also showed that the bias increased for species with the coldest thermal limits. This finding suggests that soil temperature may be a more relevant variable for the distribution of high alpine species than for species located closer to the tree line. It could have serious implications for species distribution models that are calibrated across the entire ranges of species, as distal predictors (*sensu* Austin, 2002) lack the direct causal relationship to the ecophysiology of species that would be ideal for comparing distinct regions. For these reasons, the development of proximal temperature predictors that could fit mechanistic models (Austin & Van Niel, 2011) is necessary to improve our capacity to transfer models across regions (Randin *et al.*, 2006).

CONCLUSIONS

Our study provides evidence that the disjunct populations of arctic-alpine plant species retained more similar niche thermal limits at their cold than at their warm end of thermal tolerance. No clear similarity was observed at their warm thermal limits, where competition probably plays a dominant role in limiting the spatial and environmental opportunities of distinct species populations. This difference in the conservatism of warm thermal limits stresses the importance of including biotic interactions when modelling species distributions, as a way to improve their transferability (Wiszt *et al.*, 2013). Adding biotic interactions to models of species distribution may also shed light on realized niche differences observed for some invasive species between their native and adventive ranges (Petitpierre *et al.*, 2012). Still, niche differences were also observed at the cold limit. To unequivocally establish their cause, genetic comparison of arctic and alpine populations should also be performed. As a cautionary note, the differences in temperatures observed between regions might result from the use of 2-m air temperatures that are decoupled from the surface temperatures that plant species actually experience (Scherrer & Körner, 2011). Using more proximal surface temperatures would strengthen future research on climatic niche dynamics, particularly in regions with complex topography, and would particularly allow

us to assess more precisely whether genetic differences across regions may be associated with distinct tolerances to environmental conditions.

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