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Are alpine plants constrained by biotic interactions at their warm niche limits? A test with field data and botanical garden records.

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ABSTRACT

Due to habitat destruction and rapid global environmental changes, launching initiatives to guarantee the maintenance of species and biodiversity in the long-term is crucial. However, this needs an adequate knowledge of species ecological requirements, so that it can be used to improve their conservation. Along with this line, accurate predictions of species distribution models are essential to anticipate conservation efforts. Botanical gardens and arboreta represent a significant source of knowledge for plant conservation efforts from all around the world. These collections of living specimens can be considered as ex-situ laboratories for plants. They provide the possibility to assess the suitable conditions that species require for existence. More particularly, this information allows the quantification of the fundamental climatic requirements of species by removing the effect of competition from other species. Using this approach, we found that the large majority (24) of 27 alpine and subalpine plants investigated here show a higher physiological tolerance (i.e. fundamental) than observed (i.e. realized) on the warm side of the temperature gradient. This result is consistent with theory supporting, e.g. the Asymmetric Abiotic Stress Limitation hypothesis. We discuss the importance of these findings and their implications for future projections of climate change impact on plant distributions.

RESUME

Dû à l'accélération de la destruction des habitats et aux changements environnementaux globaux, il est urgent de mettre en place des initiatives visant à garantir le maintien des espèces et de la biodiversité sur le long terme. Néanmoins, ceci nécessite une certaine connaissance de l'écologie des plantes. Conformément à cela, des prédictions de distributions futures des espèces, obtenues à l'aide de modèles de distribution, permettent de cibler les efforts nécessaires à leur conservation. Les jardins botaniques et arboretums représentent d'importantes sources de connaissance pour la conservation des espèces végétales dans le monde entier. Ces collections de spécimens vivants peuvent être considérées comme laboratoires ex-situ pour les plantes. Ces jardins offrent la possibilité d'identifier les conditions abiotiques nécessaire au bon développement de chaque espèce. Plus particulièrement, ces informations permettent de quantifier les besoins climatiques fondamentaux de chaque espèce, en retirant toute compétition des autres espèces, qui modifierait les réponses observées en

milieu sauvage (niche réalisée). Grace à cette approche, nous avons démontré que la majorité (24) des 27 plantes alpines et subalpines inclues dans cette étude ont une tolérance physiologique (c.à.d. fondamentale) plus élevée qu'observée (c.à.d. réalisée) dans la partie supérieur du gradient de température. Ces conclusions se trouvent être en accord avec l'hypothèse prédite par l'AASL (Asymmetric Abiotic Stress Limitation). Nous débattons de l'importance de ces résultats, ainsi que leurs implications pour les futures prédictions de l'impact du changement climatique sur la distribution des plantes.

Keywords: Fundamental, realized, niche, physiological warm tolerance, alpine, subalpine, plant species, botanical gardens, AASL hypothesis.

INTRODUCTION

Due to habitat destruction and rapid global warming, it is crucial to provide information on the biological responses of species under global change (Sexton et al., 2017). Accurate predictions of the future response of species distributions, for instance, based on species distribution models (SDMs also called ecological niche models or other terms; see: Guisan et al., 2017), are essential to anticipate conservation efforts (Broennimann et al., 2007; Guisan et al., 2013; Sánchez-Fernández et al., 2016). SDM quantify the environmental requirement of species by positioning the observed populations in environmental space (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005) and allow predicting the occurrence and abundance of species in time and space based on the quantification of environmental suitability. A marked characteristic of SDMs is that they are based on the central concept in ecology and evolution of the environmental niche. First proposed by Grinnell (1917) and further developed by Hutchinson (1957), the environmental niche is defined as a set of biotic and abiotic conditions in which a species can persist indefinitely and can be represented by an N-dimensional hypervolume of suitable conditions. Hutchinson also introduced the distinction between the fundamental niche and the realized (or ecological) niche.

The fundamental niche summaries the full range of abiotic conditions in which a species can persist (i.e. its physiological requirements), while the realized niche is the portion of the fundamental niche that species can access by dispersal and where they can withstand biotic interactions with other species (i.e. competitors and predators) (Futuyma & Moreno, 1988; Pulliam, 2000; Silvertown, 2004; Wiens & Graham, 2005; Soberón, 2007). In this regard, each species has a unique ecological niche and range determined by its limiting conditions along environmental variables (Hargreaves et al., 2014). Despite this, there appear to be general patterns in the range boundaries. Some authors have suggested that species' range limits are associated with constraints in the realized niche. Furthermore, this hypothesis has been tested based on transplant experiments (Gaston, 2003; Hargreaves et al., 2014; Lee-Yaw et al., 2016). In this regard, describing and quantifying these patterns holds the promise of a better understanding of processes and mechanisms involved in the maintenance of the boundaries of species geographic ranges (Brown et al., 1996; Gaston, 2009) and a better ability to make predictions for the future.

Observations have shown that biotic interactions (e.g. competition, facilitation) will tend to limit the distribution and the abundance of species towards milder climates (e.g. lower latitudes and altitudes with warmer conditions). Whereas abiotic stress (i.e. physiological constraints) is more likely to be limiting at upper-latitudinal and upper-altitudinal (colder conditions) range boundaries (Brown et al., 1996). The AASL hypothesis (the asymmetric abiotic stress limitation) has been used to support this prediction mainly focussing on temperature-related factors (Normand et al., 2009; Soberon & Arroyo-Peña, 2017).

In the vast majority of cases, SDMs are based on the observed distribution of species. This implicitly considers biotic interactions and thus represents the realized niche. Alternatively, the fundamental niche might be approached in SDMs based on ex-situ (e.g. experimental or cultivated) data (Guisan & Thuiller, 2005). SDMs can generate predictions about suitable habitat across the landscape, yielding values that are probabilities or presence or suitability index.

Vetaas (2002) performed climatic analyses of Rhododendron tree species to measure their realized and fundamental niches using respectively field data and ex-situ observations from botanical gardens because in the latter plants are expected to occupy most of their fundamental niche due to removed biotic interactions. He showed that ex-situ plants growing outside their natural range could also be outside their realized climate niche. He also identified on which end of the temperature gradient, i.e. cold or warm limits, the fundamental limit overpassed the realized limit. A remarkable result of this study is the trend that many species exhibited ex-situ observations (i.e. in botanical gardens) beyond the warm end of their realized thermal range, which was interpreted as the result of biotic exclusion. On the contrary, the most dominant species had less discrepancy between in- and ex-situ observations, suggesting the congruence of realized and fundamental niches. This hypothesis was assumed as well in other climatic analyses (Huntley et al., 1995; Sykes et al., 1996; Pearman et al., 2008) but, except for Vetaas (2002) on four species and Li et al. (2016) on one species, was not often tested. If proven officially, these results on the strength of temperature as a limiting factor imply that observations outside the realized niche could provide information on the fundamental niche, and paves the way towards a better understanding of which margins of the realized niche boundaries can be overpassed by the fundamental niche. The fundamental niche is of high relevance to understanding the range dynamics of a particular species. Thus, it is a significant challenge to map the fundamental niche in geographical space (and possibly in time, but not

assessed here), because it corresponds to a physiological feature of the species (Soberon & Arroyo-Peña, 2017).

However, more studies are required to elucidate the potential boundaries of fundamental niches and the relationship between species and temperature (Vetaas, 2000; Sax et al., 2013). Fundamental niches have rarely been explored and are mostly unknown for the majorities of the plants, except for some species of agricultural or medical interest (i.e. Booth, 2016).

Owing to the increase in temperatures on the gradients in the mountain regions, alpine environments represent an important model for examining the effects realized and fundamental limits under climate change. Previous studies have shown that the Alps have been enduring pronounced warming during the last decades, and this trend is expected to enhance in the future (Rebetez, 2002; Rebetez & Reinhard, 2008). High-altitude ecosystems should thus be particularly affected by the continuing warming (Nogue-Bravo et al., 2007; Ceppi et al., 2012; Zubler et al., 2014; Pepin et al., 2015). We thus propose to use the observed distribution in the wild (i.e. empirical field observations) and ex-situ data based on botanical gardens and arboreta records of a set of emblematic alpine plants, to assess the potential boundaries of their realized and fundamental niches. For this purpose, Soberon & Arroyo-Peña (2017) recommend calculating both niches along one dimension, because available information is lacking for multiple dimensions of the fundamental niche. Instead, observations are substantially more accessible for the realized niche (field observations), which permits establishing a direct relationship between species observations and many environmental (e.g. climatic) variables (Soberon & Arroyo-Peña, 2017). In our case, we aim to test the physiological limit of the species tolerance along the temperature gradient only, as it is the most easily quantifiable dimension of the fundamental niche.

Since botanical gardens are less likely to be beyond the cold limits of alpine plants (i.e. they cannot be located at very high altitude), the aim here is more specifically to evaluate the potential limits of the fundamental niche on the warm side of the thermal gradient. We further discuss implications of related findings on species geographic predictions under global warming.

In more detail, we aim to:

1- For each species, compare the warm thermal boundaries of the realized niche (R niche, in-situ observation) and the fundamental niche (F niche, ex-situ botanical garden data).

2- Identity if the boundaries of the F niche are similar or expand beyond the R niche.

3- Evaluate if the magnitude of the F versus R discrepancy is related to specific biotic constraints and species traits.

Hypothesis:

- For dominant species, a congruency of the F and R limits is expected on the warm side of the thermal gradient.
- For subordinate species, the F limit is expanded beyond the boundaries of the R limit on the warm thermal gradient.

METHODS

Species and data source

We composed a dataset of twenty-seven cold-adapted target species from alpine and sub-alpine regions. To assess the potential fundamental niche, we collected ex-situ data from surveys (appendix 1) sent out to the network of Botanic Gardens Conservation International (BGCI; www.bgci.org). We obtained binary data (presence/absence) from 129 herbariums and arboretums (Fig. 1). Their geographic locations are shown in Appendix 2. To represent the realized niche, we extracted distributional records for the species from the databases of the global biodiversity information facility (assuming random sampling) (GBIF; www.gbif.org, accessed May. 2017) which can be reported as data representing the true realized niche. Due to the strong spatial bias in specimen distribution data found in the GBIF database (Beck et al., 2014), we restricted the input data as follows. To cover the best representation of the range of species and to get an unbiased assessment, we kept an accuracy finer or equal to 10 km for valleys (flat areas; areas with focal standard deviation with a 10 km moving window <100 m) and 1 km of uncertainty in mountain areas (rugged areas; focal standard deviation >100 m). We excluded data with false locality coordinate (e.g. urban areas, bare areas, water bodies, permanent snow and ice) and duplicate data. The validation was made according to the mosaics and land cover from the descriptor of GlobalCover Land Maps (Bicheron et al., 2008).

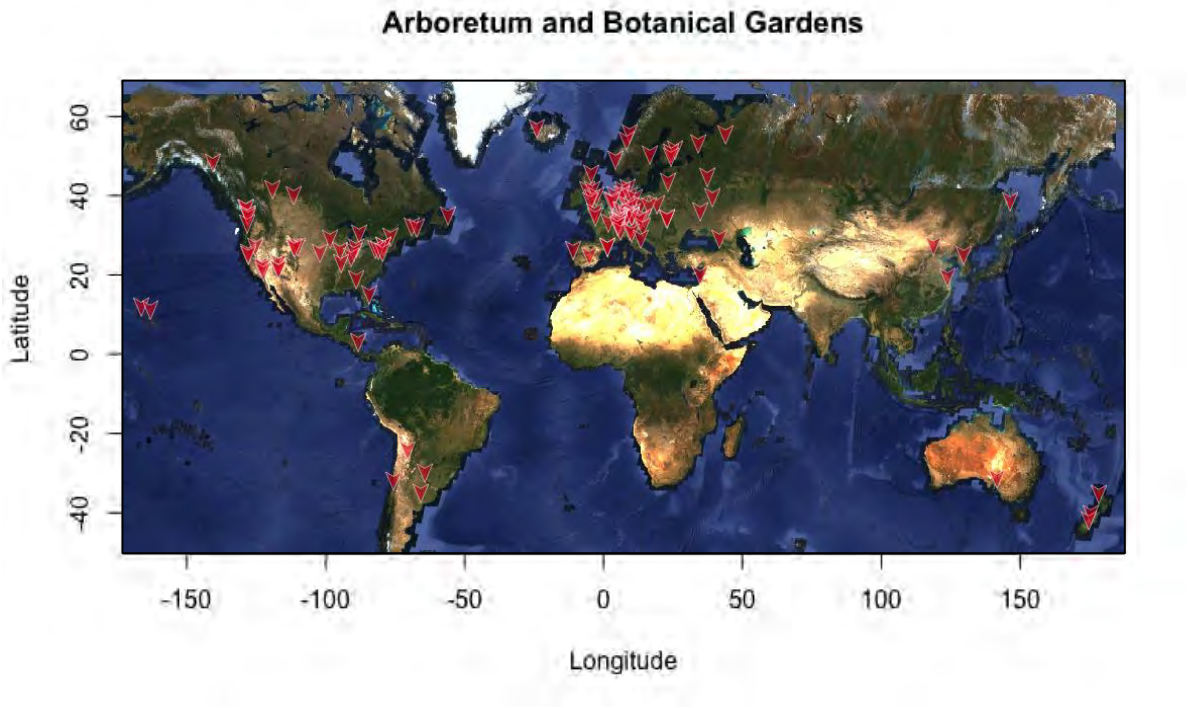

Figure 1. Map showing the location of the botanical gardens and arboreta (∇). Coordinates are in degrees' longitude (X-axis) and latitude (Y-axis).

Environmental variables

To reconstruct the realized R niche and fundamental F niche, we relied on global temperature maps. These were shown to be among the dominant factors determining the distribution patterns of the major vegetation types (Woodward, 1987). Considering that species most likely respond to the interactive influences of several climatic factors (Körner et al., 2016), we accounted for extremes temperatures, freezing (chilling signals for the plant to recognise whether it is autumn or spring) and mean temperature (thermal forcing). To represent these, we choose the following six bioclimatic descriptors from www.worldclim.org under the period 1970-2000 (accessed June. 2017): "Annual Mean Temperature (MAT)", "Minimum Temperature of the Coldest Month (MTCM)", "Maximum Temperature of the Warmest Month (MTWM)", "Coldest Temperature of the Growing Season (CTGS)", "Warmest Temperature of the Growing Season (WTGS)" and "Mean Temperature of the Growing Season (MTGS)", in a spatial resolution of a 2.5-arc-minute (Fick & Hijmans, 2017). The growing season was estimated based on the four warmest months (summer season). We extracted attributes of these bioclimatic variables for each species observation, both in- and ex-situ, to estimate the two types of niche limits (i.e. R versus F niches respectively).

Niche comparison

All the analyses were performed in R version 3.3.2 (Team, 2015). To provide an overall estimate of the thermal breadth, we quantified the interval between minimum and maximum temperature for each species for the climatic factors. For each climatic variable, due to a bias in the location of botanical gardens (very few or none at high elevation), the realized cold limit was in most cases artificially larger than the fundamental cold limit. We truncated the field data on the cold edge limit (i.e. realized niche) that went beyond the ex-situ data. The idea behind this was to standardise data to ensure a fair comparison of the potential warm limit (mainly if using mean or median values) by removing the bias on the cold side. We subset the data dividing the range observation into contiguous intervals using the quantiles (Q) 100%, 99% and 95% to remove potential outliers. To compare the warm limit along each climatic gradient, we measure the Maximum (Max.) for each the quantiles.

Furthermore, to test the discrepancy between the realized thermal niche (hereafter called R) and the fundamental thermal niche (hereafter called F), we calculated the absolute difference (F-R) and the ratio between their R and F limits (F/R). To assess whether species were dominant or subordinate, we considered the plant functional strategy scheme from the CSR theory (Competitor, Stress-tolerator, Ruderal; Grime, 2001). We determined a "C" species as dominant and "S" and "R" species as subordinate.

As a null hypothesis, we expected for dominant species the congruency between F and R at the warm thermal limit, with a relationship of F = R represented by slope equals one with an intercept of zero (Slope= 1 correspond to R=F). We defined as the alternative hypothesis the discrepancy between F and R, described by a slope differing from one and with a non-zero intercept, using the slope.test function (Warton et al., 2015) and applying the Standard Major Axis Regression (Warton et al., 2006). Finally, we compared the slope of the observations among climatic variables.

It is important to remind here that the botanical garden data were less or not likely to be beyond the cold limit of the field observation data while at the same time the quality of the field data is likely better than that of the botanical gardens, which were likely not representing the whole climatic gradients. In this regard, we thus only describe the results for those variables that presented species data well distributed along the climatic gradients, resulting in three variables:

MAT, MTCM, and CTGS which also occurred with sufficient ecological meaning to support further analysis.

RESULTS

In total, following our survey, we obtained 129 responses from the botanical gardens, providing data for 27 alpine and sub-alpine species (with a number of occurrences >6; Appendix 1). In a broad perspective, the tendency of most species to present F>R across the temperature variables were generally confirmed (MTCS; number of species with F>R with Q.99=18, Q.95=25, CTGS; Q.99=24, CTGS Q.95=25, MAT; Q.99=23, Q.95=26) (Table 1). Deviations from the F=R assumption can be visualized species by species in Figure 2 by points below the diagonal (i.e. slope = one). We didn`t found a correspondence (R=F) for CTGS and MAT at the species boundaries towards the warm limit. Here the slope of this relationship was reported as different than one (CTGS; Q.99%, slope=0.19, confidence interval=0.12-0.28, Q.95%, slope= (-)0.61, confidence interval= (-)0.41-(-)0.91, MAT; Q.99% slope=0.54, confidence interval=0.36-0.80, Q.95%, slope=0.41, confidence interval=0.28-0.61) (Table 2). On the opposite, for MTCM the slope is not different than one (MTCM; Q.99% slope=0.9, confidence interval=0.61-1.33, Q.95%, slope=0.83, confidence interval=0.58-1.21).

The variable MTCM presented the highest difference between the quantile 99% and quantile 95% (Fig. 2). 66% of species presented F>R when using the quantile 99%, against 93% of species when using the quantile 95% (Table 1). However, we identified R>F at the quantile 99% for the species: Gentiana acaulis, Campanula scheuchzeri, Sempervivum montanum, Androsace alpina, Linaria alpina, Artemisia genipi, Androsace helvetica, Cerastium cerastoides and Ranunculus glacialis (Table 3). Conversely, at the quantile 95%, R>F was only observed for A. genipi and C. scheuchzeri (Table 3). Still for MTCM, from the Table 2, we noted a significant F/R ratio for the species Leontopodium alpinum (F/R = 30.15), Silene acaulis (F/R = 13.85) and Draba hoppeana (F/R = 11.13), all at quantile 95% (Table 3). For the variable CTGS, two species presented the conditions R<F, showing a congruency between the quantiles 99% and 95%. This was observed for the species G. acaulis [F/R = 1.46 (quantile 99%), F/R = 1.1 (quantile 95%)] and A. genipi [F/R = 1.18 (quantile 99%), F/R = 1.41 (quantile 95%)] (Table 3). Interestingly, for this variable, one species Rhododendron ferrugineum L showed a congruency F=R (Table 1). Finally, the variable MAT revealed an R>F for the species A. genipi G. acaulis A. alpina, and S. montanum.

Regarding the "CSR" strategy of Grime (2001), twenty-three species presented a "C" strategy and were accordingly categorised as dominant, whereas only four species presented an "R/S" strategy and were accordingly categorized as subordinate (Table 3).

Table 1. The total number of the species that presented the conditions F>R, R>F or F=R for the climatic variables at the quantiles 99% and 95%.

	F > R	R > F	F=R	F > R	R > F	F=R
Climatic variables		Q.99 %			Q.95 %	
MTCM	18	9	0	25	2	0
CTGS	24	2	1	25	2	0
MAT	23	4	0	26	1	0

Table 2. Results of the statistic test validating the prediction of the alternative hypothesis showing that the slopes are differing from one in each climatic variable and the values of the estimates slopes for the observation at each climatic variable, except for MTCM.

Climatic variables	Estimated slope	r^2	p-value	CI-upper	CI-lower
MTCM $^{Q.99\%}$	0.90	0.32	0.60 ^{NS}	0.61	1.33
MTCM $^{Q.95\%}$	0.83	0.44	0.33 ^{NS}	0.58	1.21
CTGM $^{Q.99\%}$	0.19	0.97	1.39E-12***	0.12	0.28
CTGM $^{Q.95\%}$	-0.61	0.68	0.016**	-0.41	-0.91
MAT $^{Q.99\%}$	0.54	0.75	2.53E-03***	0.36	0.80
MAT $^{Q.95\%}$	0.41	0.84	3.07E-05***	0.28	0.61

**significant at p<0.01; ***significant at p <0.001; NS= not significant

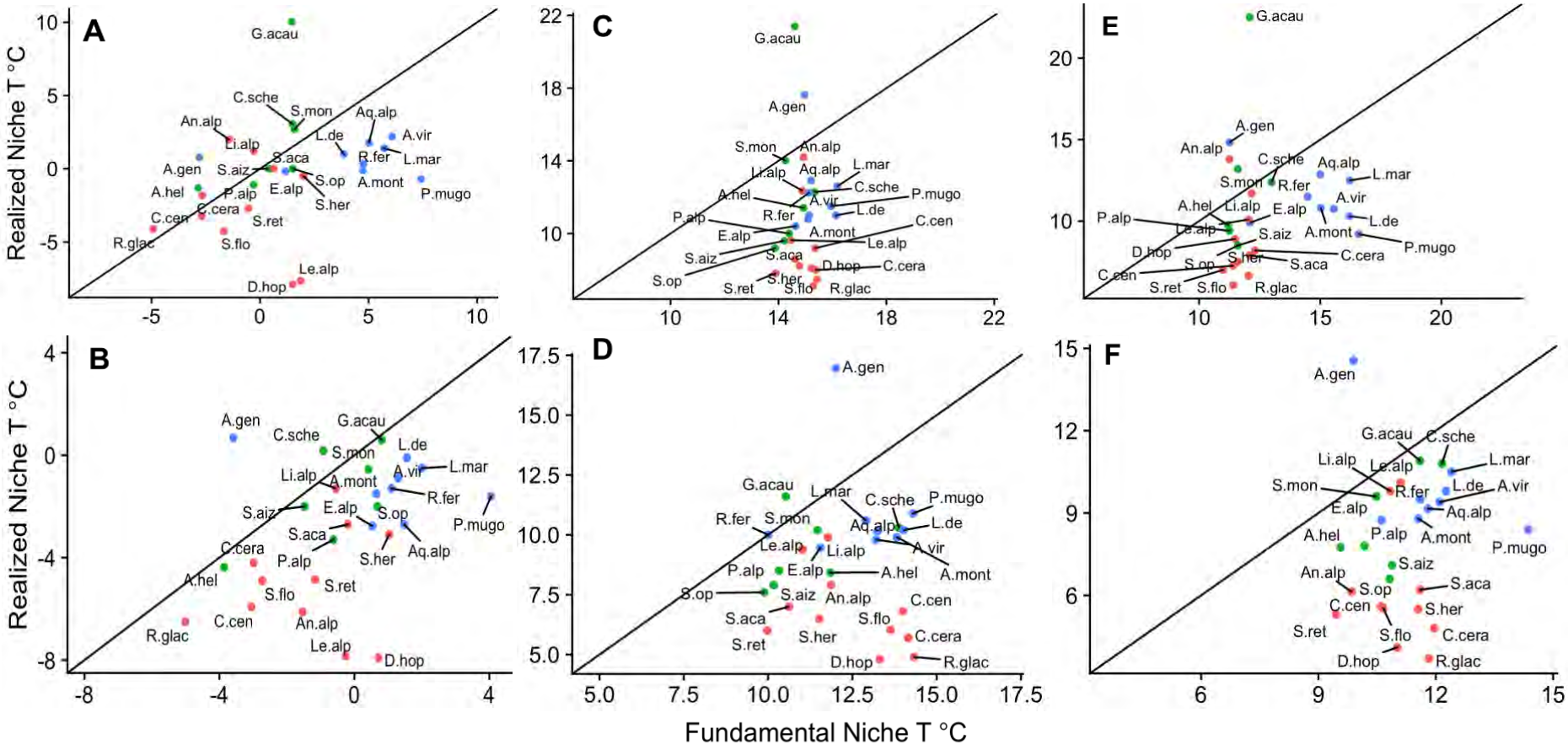

Figure 2. The thermal relationship (T°C) between F and R at the warm limit across the climatic variables; Minimum Temperature of the Coldest Month (MTCM); (A) Q.99% and (B) Q.95%, Minimum Temperature of the Growing Season (CTGS); (C) Q.99% and (D) Q.95% and Annual Mean Temperature (MAT); (E) Q.99% and (F) Q.95%. The straight line represents the slope one intercepted in zero; equivalent to the relation 1:1 (R = F). Here species are aggregated by their altitudinal gradient (Red=Alpine, Green= Alpine-Subalpine, Blue= Subalpine). The abbreviations of each species are referred in table 3 as "code".

Table 3. Results of the F and R comparison at the maximum thermal limit (Max.) for each climatic variable (MTCM, CTGS and MAT). Values represent the difference between F – R temperatures (°C) and F / R ratios for the 27 alpine and sub-alpine species calculated at the Quantile 99% and Quantile 95%. The negative values (-) represent the condition of R > F, positive values represent F > R and (+/-) represent congruency between F and R (F = R). SN: species name, LD: Life strategies sensu Grime, AD: altitudinal distribution.

Climate Variables				Warm Thermal Limit											
				MTCM				CTGS				MAT			
Code	SN	LS	AD	F-R (T°C)	F/R	F-R (T°C)	F/R	F-R (T°C)	F/R	F-R (T°C)	F/R	F-R (T°C)	F/R	F-R (T°C)	F/R
				Q.99		Q.95		Q.99		Q.95		Q.99		Q.95	
A.vir	*A. viridis*	ccs	Subalpine	3.88	0.36	2.2	0.69	4.14	0.73	3.4	0.74	4.81	0.69	2.7	0.78
An.alp	*A. alpina*	rss	Alpine	(-)3.426	1.4	4.58	3.99	0.73	0.95	3.96	0.67	(-)2.551	1.23	3.72	0.62
A.hel	*A. helvetica*	css	Alp-subalpine	(-)1.553	0.46	0.51	1.13	3.52	0.76	3.43	0.71	1.43	0.87	1.82	0.81
Aq.alp	*A. alpina l.*	crs	Subalpine	3.25	0.35	4.18	1.83	2.29	0.85	3.09	0.77	2.14	0.86	2.64	0.78
A.mont	*A. montana L.*	crs	Subalpine	4.84	0.02	2.15	2.31	4.3	0.72	3.92	0.72	4.22	0.72	2.76	0.76
A.gen	*A. genipi*	rss	Subalpine	(-)3.574	0.28	(-)4.27	0.19	(-)2.667	1.18	(-)4.935	1.41	(-)3.573	1.32	(-)4.665	1.47
C.cen	*C. cenisia*	css	Alpine	0.54	1.2	2.88	1.94	6.16	0.6	7.19	0.49	4.14	0.64	5	0.53
C.sche	*C. scheuchzeri*	crs	Alp-subalpine	(-)1.554	2.04	(-)1.1	0.2	3.05	0.8	3.58	0.74	0.61	0.95	1.36	0.89
C.cera	*C.cerastoides*	css	Alpine	(-)0.844	0.68	1.22	1.41	7.39	0.52	8.46	0.4	4.11	0.67	7.16	0.4
D.hop	*D. hoppeana*	css	Alpine	9.4	5.26	8.62	11.13	7.14	0.53	8.52	0.36	2.58	0.78	6.92	0.37
E.alp	*E. alpinum*	ccs	Subalpine	1.35	0.15	3.29	5.21	4.23	0.71	2.09	0.82	2.2	0.82	1.87	0.82

G.acau	*G. acaulis*	css	Alp-subalpine	(-)8.57	6.85	0.22	0.74	(-)6.792	1.46	(-)1.075	1.1	(-)10.432	1.86	0.7	0.94
L.de	*L.decidua*	ccc	Subalpine	2.86	0.26	1.66	0.06	5.13	0.68	3.82	0.73	5.91	0.64	2.46	0.8
Le.alp	*L. alpinum*	ccs	Alpine	9.52	4.09	7.58	30.15	4.83	0.67	1.64	0.85	1.95	0.84	1	0.91
L.mar	*L. martagon*	crs	Subalpine	4.32	0.24	2.5	0.25	3.58	0.78	2.3	0.82	3.72	0.77	1.9	0.85
Li.alp	*L. alpina*	rss	Alpine	(-)1.487	4.18	0.76	2.39	2.54	0.83	1.88	0.84	0.46	0.96	1.04	0.9
P.mugo	*P. mugo*	ccc	Subalpine	8.12	0.09	5.65	0.4	4.45	0.72	3.4	0.76	7.39	0.55	5.97	0.58
P.alp	*P. alpina*	crs	Alp-subalpine	0.8	3.67	2.68	5.28	4.4	0.69	1.83	0.82	1.85	0.84	2.38	0.77
R.glac	*R. glacialis*	css	Alpine	(-)0.822	0.83	1.49	1.3	7.96	0.48	9.43	0.34	5.4	0.55	8.13	0.31
R.fer	*R. ferrugineum*	ccs	Subalpine	4.41	0.07	2.4	1.18	2.89	0.81	(+/-)0	1	2.98	0.79	2.1	0.82
S.her	*S. herbacea*	css	Alpine	2.49	0.25	4.13	3.01	6.56	0.56	5.02	0.56	4.1	0.65	6.06	0.48
S.ret	*S. reticulata*	css	Alpine	2.17	5.06	3.69	4.18	6.09	0.56	3.98	0.6	3.99	0.64	4.15	0.56
S.aiz	*S. aizoides*	css	Alp-subalpine	0.4	0	0.52	1.35	4.62	0.68	2.26	0.78	3.1	0.73	3.78	0.65
S.flo	*S. biflora*	css	Alpine	2.61	2.56	2.17	1.79	8.18	0.46	7.6	0.44	5.34	0.53	5.12	0.52
S.op	*S. oppositifolia*	css	Alp-subalpine	1.51	0	2.68	2.94	4.68	0.66	2.28	0.77	3.1	0.73	4.22	0.61
S.mon	*S. montanum*	sss	Alp-subalpine	(-)1.117	1.7	0.97	1.31	0.24	0.98	1.26	0.89	(-)1.6	1.14	0.88	0.92
S.aca	*S. acaulis*	css	Alpine	0.63	0	2.51	13.85	6.01	0.59	3.62	0.66	4.19	0.65	5.4	0.53

DISCUSSION

The most interesting finding in this study is that, for most species (24) of 27, the limit of the fundamental niche (F; i.e. derived from ex-situ observations) exceeds the one of the realized niche (R; derived from field observations) on the warm side of the temperature gradient (Fig. 2). The variable MTCM presented an estimated slope of 0.9; this can be explained because some points are in the upper areas of the graph, and this force the estimated slope near to one. Also, we don't observe any species presenting points in congruency with R = F (Fig. 2.a, 2.b). However, most of the species across the climatic variables are in the lower region of the slope, predominantly interpreted as F > R.

Our results are in agreement with Sexton et al. (2017), who hypothesized that the R niche is considerably smaller than the F niche, and thus already contribute to a better understanding of the physiological versus ecological (i.e. including biotic interactions) tolerances of species. Typically, the warm thermal limit (i.e. the lower one along elevation) is characterised by a less severe climate and more productive conditions for species (Pellissier et al., 2013). When one removes the effect of competition from other species (as done in botanical gardens), it becomes possible for alpine and subalpine species to establish and persist. In other words, the physiological tolerance of species goes beyond the one realized in the field (F>R). As a matter of fact, the majorities of the species are thus not strictly adapted to high elevations, but their observed restriction to the upper elevations seems mostly due to their exclusion (by more competitive species) from the lower elevations. In this regards, the results show consistency with the prediction of the asymmetric abiotic stress-limit (AASL) hypothesis. According to the latter, purely abiotic (here temperature–related) stress tend to be the primary determinant of species' upper altitudinal range limit, while biotic factors such as competition determine their lower range limit (Normand et al., 2009). Therefore, biotic exclusion (usually competition) is expected to have an active role in modulating species' range boundaries. Moreover, F>R is also in agreement with Pellissier et al. (2013) in suggesting that competition plays a dominant role in limiting the spatial and environmental opportunities of species at their warm thermal limit.

Besides, it exists a common consensus that plant-plant interactions are an essential part of the response of vegetation to the effects of climate change. The long-term effects of global warming are still uncertain, and unfortunately, the cost of future competition that defines the

R niche is a crucial component of the impact of global warming. In this perspective, previous studies have revealed that several mountain species have already shifted their upper distribution limit towards higher elevations, resulting in upward range shifts for many species and ultimately in some spectacular increases in species richness on mountain tops (Pauli et al., 2007, 2012; Leonelli et al., 2011; Stöckli et al., 2011; Matteodo et al., 2013; Dvorský et al., 2016), with climate warming being the primary driver (Pauli et al., 2007; Vittoz et al., 2008; Leonelli et al., 2011). This trend in upward shifts of species ranges may, in turn, cause dramatic declines of alpine and subalpine species (Klanderud & Birks, 2003; Pauli et al., 2007; Dullinger et al., 2012), especially if the lower limit of their R niche is due to low resistance to competitive exclusion.

We didn't report much species with significant R>F results, only Artemisia genipi and Gentiana acaulis, that showed the contrary to the general F>R tendency. The condition R>F might be cause for the following reason; the database was containing poor estimates of the range, biased due to geo-referencing errors and/or result from a collector's bias (or taxonomy mistake). The later could particularly affect these few R>F species, recognised by collectors without considering the possibility that they may be cultivated specimens: G. acaulis is well-known to be grown as an ornamental plant, while A. genepi is popular in Alpine regions for its use as a traditional herbal liquor. Low elevation field observations for these species, beyond the F limit, could thus relatively easily be individuals escaped from private or public gardens. For instance, specimen considered as representing the realized niche might represent the fundamental niche in this case. And thus they might simply not be cultivated in the lowest botanical gardens, although they might potentially be.

Regarding the hypothesis that dominant species under natural condition should have less discrepancy between F and R (Vetaas, 2002), we expected F=R for the vast majority of the species identified as dominant in our sample. In total, 23 species were categorised as dominant by having a "C" (table 2) in their CSR strategy (Grime 2001), meaning that species were at least shown to be competitive in their R habitat (but not necessarily against lower elevation competitors; see below). Specifically, for this purpose, we additionally included Pinus mugo and Larix decidua, as competitive tree species (compared to high elevation herbaceous alpine plants) to test this idea. According to expectations, surprisingly we only found R=F for Rhododendron ferrugineum, which might indicate that this species is a successful competitor which, in the field, occupies most of its F niche (Gauch & Whittaker, 1972). Additionally, this

can give a glimpse of what is observed for "C" species where they grow without competition (i.e. when F>R), but more evidence is needed to confirm this statement.

Essentially, our results substantially highlight the importance of botanical gardens and arboreta records as a source for science to elucidate physiological requirements - and particularly the effects of climate - on plants. Various approaches had been proposed to examine the processes beyond species' range boundaries (Gaston, 2009), but until now the use of ex-situ botanical garden records had only been applied by Vetaas, (2002) and Li et al., (2016), and since now in the present study. Although surprisingly rarely used, the latter approach has one advantage in particular over the transplant experiments that have been commonly applied before for testing niche constraints on range limits (e.g. Lee-Yaw et al., 2016), which is to potentially assess the whole F niche breadth across both environmental (i.e. here climatic) and spatial gradients. For this reason, as future perspective, we propose to apply this approach to a larger number of species, including those of lower elevations than considered here (i.e. collinean and montane), and to try to find ex-situ conditions at higher elevations. Thereby testing the physiological tolerance limits along a broader temperature gradient and testing not only warm but also cold (i.e. which was not considered here) thermal limits.

However, there are also some limitations to this approach, which should be better taken into consideration in future studies, such as the sampling bias that be might be highly influential in such approach. The herbarium and arboreta specimens are not randomly distributed, however, the plants in these collections where cultivated independently of the current research question. For instance, most of the Botanical gardens and arboretums are located in the North Hemisphere (Fig.1). Another limitation is that precipitation variables, which is an essential variable to predict plant response to climate change (Austin, 1992) could not be included because individuals in botanical gardens are being watered regularly, and thus water is never a limiting factor for plants. Finally, as such available data for the F niche remain scarce (Vetaas, 2002; Li et al., 2016; Soberon & Arroyo-Peña, 2017), it also represents an important obstacle to make consistent predictions and comparisons of species distributions under future climate.

To summarise, our results bring new insights into the warm thermal requirements of alpine and subalpine plants, and in this represent a valuable contribution to better understand the F niche. Most of the alpine and subalpine species studied here presented a greater physiological (i.e. F) than ecological (i.e. R) tolerance on the warm side of the thermal gradient. These findings

support the AASL hypothesis prediction in showing that biotic exclusion is a strong determinant of the warm thermal limit of species observed at high altitude (Normand et al. 2009), and can be observed across large areas. Surprisingly, for most of the species having a competitive strategy, we didn't found the F=R congruency, except for R. ferrugineum. Our results, therefore, suggest that future studies will need to take the F niche breadth (ideally both cold and warm limits) into account to develop more comprehensive theory and improve prediction of species responses to climate change. Botanical gardens and arboreta present an excellent potential for this for scientists involved in climate change (Vetaas, 2002). Alpine habitats could be particularly sensitive to ecosystem change mostly under warming climate change due to an increase in biotic exclusion at high elevations. Here we report for most of the species an F thermal tolerance higher than R. This condition suggests that exist areas in the world with the suitable temperatures that may fulfil this requirement. SDMs can be used to detect suitable habitat that meets these criteria across time, which can be used as an index of suitability. Finally, combining the effort from empirical and experimental research programs to assess the full F niche breadth could further contribute to improving our understanding and quantification of the role of non-climatic factors (such as biotic interactions but also dispersal factors) (Lee et al., 2009), in explaining and modelling species distributions.

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APPENDIX

Appendix 1. Alpine botanical Survey.

Alpine botanical survey
University of Lausanne, Switzerland

1. What is the name and location of the garden/arboretum?
2. Please select the options when applying

Answer Options	**Species present in your garden/arboretum**	**Plants growing in greenhouse**	**Plants that are being watered**
Androsace alpina	17	0	2
Androsace helvetica	12	2	3
Alnus viridis	43	2	5
Aquilegia alpina	40	1	12
Artemisia genipi	13	1	3
Arnica montana	48	0	10
Campanula cenisia	6	0	0
Campanula scheuchzeri	29	0	4
Cerastium cerastoides	14	0	3
Draba hoppeana	10	0	3
Eryngium alpinum	42	0	6
Gentiana acaulis	45	2	14
Larix decidua	68	0	8
Leontopodium alpinum	50	3	11
Lilium martagon	69	4	18
Linaria alpina	31	0	5
Pinus mugo	84	0	21
Ranunculus glacialis	12	0	2
Rhododendron ferrugineum L.	46	2	9
Poa alpina	26	0	6
Saxifraga oppositifolia	35	0	6
Saxifraga biflora	8	0	1
Saxifraga aizoides	30	0	4
Sempervivum montanum	37	1	4
Silene acaulis	43	1	10
Salix herbacea	24	0	4
Salix reticulata	36	0	5

3. During which months are the plants flowering? Write the months in the blank space next to the species.
4. Which soil did you use to grow the plant?
5. Do you have any other comments, questions, or concerns?
6. Your name and e-mail contact.

Appendix 2. Ex-situ locations; latitude, longitude (negative values indicate western- and southern-hemispheres).

Latitude	Longitude	Country	Garden/Arboretum
-38.720006	-62.245736	Argentina	Jardín Botánico Bahía Blanca
-26.585478	-66.949429	Argentina	Parque Botánico Andino Paul Günther Lorentz
-33.028076	-60.890721	Argentina	Parque José Félix Villarino
-34.916943	138.610797	Australia	Botanic Gardens of South Australia
47.081573	15.456834	Austria	Botanical Garden Graz
47.267661	11.378792	Austria	Botanischer Garten Innsbruck Und Alpengarten Patscherkofel
47.267673	11.378989	Austria	Botanischer Garten Und Alpengarten Patscherkofel
46.629192	14.293539	Austria	Landesmuseum Für Kärnten Kärntner Botanikzentrum
50.954769	4.6269	Belgium	Arboretum Wespelaar
50.805917	4.492964	Belgium	Geographical Arboretum of Tervuren
51.035717	3.72225	Belgium	Ghent University Botanical Garden
44.740669	-65.513957	Canada	Annapolis Royal Historic Gardens Annapolis Royal
37.469826	-122.308463	Canada	Filoli Botanic Garden
44.642807	-63.582124	Canada	Halifax Public Gardens
47.571667	-52.758641	Canada	Memorial University of New found land Botanical Garden
52.128349	-106.620277	Canada	Patterson Garden Arboretum Saskatoon
49.251528	-123.247377	Canada	Botanical Garden University of British Columbia
53.407516	-113.759749	Canada	University of Alberta Botanic Garden
49.238513	-123.128939	Canada	Vandusen Botanical Garden,
-35.405853	-71.630357	Chile	Universidad de Talca Jardín Botánico
39.999404	116.209504	China	Beijing Botanical Garden
31.148484	121.440096	China	Shanghai Botanical Garden
9.982832	-84.080635	Costa Rica	Hotel Bougainvillea Botanic Garden
44.810919	14.971051	Croatia	Velebit Botanical Garden
49.586262	17.249566	Czech Republic	Palacký University Botanical Garden
50.124428	14.420374	Czech Republic	Prague Botanical Garden
59.4714	24.88072	Estonia	Tallinn Botanic Garden
60.730237	26.423868	Finland	Arboretum Mustila
60.174657	24.945595	Finland	Kaisaniemi Botanic Garden
45.036173	6.400029	France	Jardin Botanique Alpin Col Du Lautaret
48.114029	-1.669815	France	Jardin Botanique De La Ville De Rennes
47.219378	-1.542604	France	Jardin Botanique De Nantes
45.800201	3.123057	France	Jardin Botanique De La Charme
48.749955	7.340107	France	Saverne Botanical Garden
45.035404	6.400798	France	Jardin Botanique Alpin Du Lautaret, Station Alpine Joseph Fourier
48.583382	7.76695	France	Strasbourg University Botanical Garden
41.694463	41.707482	Georgia	Batumi Botanical Garden
47.491694	11.095496	Germany	Alpengarten Auf Dem Schachen

53.561713	9.861773	Germany	Botanical Garden of Hamburg University
52.281221	8.028457	Germany	Botanical Garden of Osnabrueck University
49.765808	9.933193	Germany	Botanical Garden University Wuerzburg
53.147488	8.197948	Germany	Botanischer Garten der Carl von Ossietzky Universität
49.599228	11.006755	Germany	Botanischer Garten der Friedrich-Alexander
51.329079	12.391999	Germany	Botanischer Garten Leipzig - Universität Leipzig
51.963685	7.60911	Germany	Botanischer Garten Der WWU - Universität Münster
48.162697	11.500361	Germany	Botanischer Garten München-Nymphenburg
51.798455	10.617608	Germany	Brockengarden In the Nationalpark Harz
47.420799	11.112478	Germany	Schachen Alpine Garden
47.691941	9.17928	Germany	Universität Konstanz Botanischer Garten
64.140313	-21.869975	Iceland	Reykjavík Botanic Garden Iceland
31.767632	35.199918	Israel	Jerulasem Botanical Garden
43.784605	7.554124	Italy	Giardini Botanici Hanbury
41.844977	14.27676	Italy	Giardino Della Flora Appenninica
45.674361	6.880893	Italy	La Chanousia Col Du Petit Saint Bernard
43.313697	11.330243	Italy	Museo Botanico Orto Botanico - University of Siena
43.719307	10.396073	Italy	L'Orto Botanico Dell'università Di Pisa
54.84188	24.044073	Lithuania	Dubrava Arboretum
52.08875	5.171977	Netherlands	Utrecht Botanic Gardens
-45.856604	170.518169	New Zealand	Dunedin Botanic Garden
-39.200301	173.980421	New Zealand	Pukeiti
-44.410297	171.253969	New Zealand	Timaru Botanic Gardens
62.303004	9.60866	Norway	Kongsvoll Alpine Garden
63.448267	10.45262	Norway	Ringve Botanical Garden Ntnu University Museum
58.939372	5.702579	Norway	Stavanger Botanic Garden
50.062987	19.957964	Poland	Botanical Garden Jagiellonian University
38.706244	-9.200529	Portugal	Parque Botánico Da Tapada Da Ajuda L
46.762507	23.58847	Romania	Alexandru Borza Botanical Garden Babeș-Bolyai University
46.762053	23.588432	Romania	Notulae Botanicae Horti Agrobotanici Cluj-Napoca
61.842567	34.381879	Russia	Botanic Garden of Petrozavodsk State University
51.711611	39.208885	Russia	Botanical Garden Bm. Kozo-Polyansky Voronezh State University
55.705074	37.527847	Russia	Botanical Garden of Moscow Palace of Pioneers
63.222717	44.076338	Russia	Dendrological Garden of The Northern Research Institute of Forestry
50.690989	142.949927	Russia	Sakhalin Botanical Garden
56.335983	-2.806429	Scotland	St Andrews Botanic Garden
46.398754	13.745516	Slovenia	Alpine Botanical Garden Juliana
37.542406	126.996285	South Korea	Seoul Botanic Park
39.764313	2.709373	Spain	Jardín Botánico De Sóller
37.084743	-3.469637	Spain	Jardín Botánico De La Cortijuela
39.764687	2.709638	Spain	Soller Botanic Garden
59.862627	17.634866	Sweden	Uppsala Linnaean Gardens

47.283486	9.485117	Switzerland	Alpengarten Hoher Kasten
46.431773	6.982902	Switzerland	Alpine Garden La Rambertia Rochers-De-Naye
46.952954	7.444783	Switzerland	Botanischer Garten Bern
47.439868	9.407538	Switzerland	Botanischer Garten St.Gallen
46.252055	7.109974	Switzerland	Jardin Alpin La Thomasia Pont De Nant
46.227198	6.081841	Switzerland	Jardin Botanique Alpin Meyrin
46.032912	7.112912	Switzerland	Jardin Botanique Alpin Flore-Alpe Champex-Lac
46.792387	7.15691	Switzerland	Jardin Botanique De l'Université De Fribourg
46.514376	6.624019	Switzerland	Jardin Botanique De Lausanne
53.121305	-4.129442	UK	Fossilplants
53.200834	-2.301807	UK	Lovell Quinta Arboretum
50.685827	-3.248639	UK	Plant Heritage National Collection of Artemisia
51.477768	-2.625948	UK	University of Bristol Botanic Garden
51.75168	-1.08806	UK	Waterperry Gardens
48.43602	35.042763	Ukraine	Botanic Garden of Oles Gonchar Dnepropetrovsk National University
33.425853	-111.931106	USA	Arizona State University Arboretum
36.993233	-86.517054	USA	Baker Arboretum
39.639652	-106.365461	USA	Betty Ford Alpine Gardens
41.662478	-93.988429	USA	Brenton Arboretum
43.023983	-83.673579	USA	Charles Stewart Mott Estate
39.731918	-104.960915	USA	Denver Botanic Gardens
34.200876	-118.211946	USA	Descanso Gardens
33.460615	-111.94776	USA	Desert Botanical Garden in Phoenix Arizona
38.130022	-97.4333	USA	Dyck Arboretum of The Plains Hesston
47.727611	-122.363225	USA	E.B. Dunn Historic Garden Trust
30.544992	-84.593951	USA	Gardens of The Big Bend
40.009397	-75.307117	USA	Haverford College Arboretum
58.481663	-134.786421	USA	Jensen-Olson Arboretum
45.474581	-122.535544	USA	Leach Botanical Garden Portland
20.892713	-156.486258	USA	Maui Nui Botanical Gardens
38.612662	-90.259316	USA	Missouri Botanical Garden
39.488044	-106.068379	USA	Mountain View Experimental Gardens Breckenridge
21.907616	-159.510474	USA	National Tropical Botanical Garden Kalaheo
39.063003	-78.063922	USA	Orland E. White Arboretum
25.670075	-80.285065	USA	Pinecrest Gardens Pinecrest
47.336825	-122.32748	USA	Powellswood Garden
38.346338	-75.606299	USA	Salisbury University
32.735318	-117.149051	USA	San Diego Zoo
35.160665	-111.734641	USA	The Arboretum at Flagstaff
39.997426	-75.241522	USA	The Barnes Foundation Arboretum Merion
47.710008	-122.544683	USA	The Bloedel Reserve
42.318386	-72.639735	USA	The Botanic Garden of Smith College
39.377561	-84.5639	USA	The Conservatory, Miami University Hamilton

35.106563	-89.91718	USA	The Dixon Gallery and Garden
38.887985	-77.012942	USA	U.S. Botanic Garden
33.97027	-117.319301	USA	Uc Riverside Botanic Gardens Riverside
37.873927	-122.238486	USA	University of California Botanical Garden
39.545954	-119.825204	USA	Wilbur D. May Arboretum and Botanical Garden
38.338033	-85.46306	USA	Yew Dell Botanical Gardens

Appendix 3. Acronyms and abbreviation.

F	Fundamental niche, ex-situ botanical garden and arboreta data
R	Realized niche, in-situ observation
MAT	Annual Mean
MTCM	Minimum Temperature of the Coldest Month
MTWM	Maximum Temperature of the Warmest Month
WTGS	Warmest Temperature of the Growing Season
CTGS	Coldest Temperature of the Growing Season
MTGS	Mean Temperature of the Growing Season
SDM	Species Distribution Models
GBIF	Global Biodiversity Information Facility
BGCI	Botanic Gardens Conservation International
Q	Quantile
Max.	Maximum temperature (°C)
AASL	Asymmetric Abiotic Stress Limitation Hypothesis
A.vir	Alnus viridis
An.alp	Androsace alpina
A.hel	Androsace helvetica
Aq.alp	Aquilegia alpina l.
A.mont	Arnica montana L.
A.gen	Artemisia genipi
C.cen	Campanula cenisia
C.sche	Campanula scheuchzeri
C.cera	Cerastium cerastoides
D.hop	Draba hoppeana
E.alp	Eryngium alpinum
G.acau	Gentiana acaulis
L.de	Larix decidua
Le.alp	Leontopodium alpinum
L.mar	Lilium martagon
Li.alp	Linaria alpina
P.mugo	Pinus mugo
P.alp	Poa alpina
R.glac	Ranunculus glacialis
R.fer	Rhododendron ferrugineum L.
S.her	Salix herbacea
S.ret	Salix reticulata
S.aiz	Saxifraga aizoides
S.flo	Saxifraga biflora
S.op	Saxifraga oppositifolia
S.mon	Sempervivum montanum
S.aca	Silene acaulis

Appendix 4. Maximum thermal values (Max.) T (°C) founded for the investigated alpine and subalpine species across the climatic variables for the quantiles Q.100, Q.99 and Q.95.

Climate Variables	*Warm Limit Annual Mean Temperature*							*Warm Limit Minimum Temperature Coldest Month*							*Warm Limit Minimum Temperature of the Growing season*						
	100%		*Q.99%*		*Q.95%*			*100%*		*Q.99%*		*Q.95%*			*100%*		*Q.99%*		*Q.95%*		
Species name	*F*	*R*	*F*	*R*	*F*	*R*	*p.value*	*F*	*R*	*F*	*R*	*F*	*R*	*p.value*	*F*	*R*	*F*	*R*	*F*	*R*	*p.value*
Alnus viridis	11.6	13.8	11.25	13.80	9.85	6.13	3E-05	-1.40	2.00	-1.43	2.00	-1.53	-6.11	1E-03	15.7	14.2	14.93	14.20	11.87	7.91	6E-05
Androsace alpina	11.6	14.3	15.56	10.75	12.10	9.40	1E-04	-2.60	1.50	6.08	2.20	1.30	-0.90	4E-01	15.7	14.3	15.14	11.00	13.20	9.80	5E-07
Androsace helvetica	16.4	13.6	11.19	9.77	9.57	7.75	2E-01	6.80	4.30	-2.85	-1.30	-3.87	-4.38	4E-01	15.7	13.6	14.93	11.41	11.85	8.43	3E-01
Aquilegia alpina l.	16.4	13.8	15.00	12.86	11.80	9.16	4E-06	6.80	2.00	5.01	1.77	1.48	-2.70	7E-02	15.7	14.2	15.21	12.92	13.25	10.16	1E-06
Arnica montana L.	11.6	14.9	15.02	10.80	11.56	8.80	7E-01	-2.60	0.80	4.74	-0.10	0.65	-1.50	2E-02	15.7	17.8	15.10	10.80	13.82	9.90	6E-02
Artemisia genipi	16.4	15.4	11.26	14.83	9.90	14.56	7E-01	6.80	7.30	-2.80	0.78	-3.59	0.68	5E-02	15.7	14.4	14.96	17.63	12.02	16.95	7E-01
Campanula cenisia	11.6	9.6	11.40	7.26	10.60	5.60	3E-04	-2.60	-2.70	-2.69	-3.23	-3.05	-5.93	3E-01	15.7	10.6	15.36	9.20	14.00	6.81	2E-03
Campanula scheuchzeri	13.2	13.7	12.99	12.38	12.16	10.80	1E-01	2.20	5.30	1.50	3.05	-0.92	0.18	3E-01	15.7	14.4	15.34	12.28	13.88	10.30	3E-03
Cerastium cerastoides	12.4	14	12.31	8.20	11.96	4.80	2E-06	-2.60	3.20	-2.68	-1.83	-2.99	-4.20	8E-03	15.7	15.3	15.39	8.00	14.16	5.70	7E-06
Draba hoppeana	11.6	10.1	11.48	8.90	11.02	4.10	5E-05	1.70	-7.90	1.50	-7.90	0.71	-7.91	7E-01	15.7	8.9	15.22	8.08	13.32	4.80	3E-05
Eryngium alpinum	12.4	9.9	12.10	9.90	10.61	8.74	1E-04	1.40	0.10	1.17	-0.18	0.53	-2.76	3E-02	15.7	10.5	14.64	10.41	11.55	9.46	1E-05
Gentiana acaulis	12.4	25.1	12.09	22.52	11.60	10.90	3E-01	1.70	17.10	1.47	10.04	0.81	0.60	2E-01	15.7	22.5	14.61	21.40	10.53	11.60	2E-02
Larix decidua	16.4	13.7	16.21	10.30	12.26	9.80	4E-01	6.80	5.30	3.86	1.00	1.56	-0.10	6E-05	16.9	14.3	16.13	11.00	14.02	10.20	9E-02
Leontopodium alpinum	12.4	10.1	12.05	10.10	11.10	10.10	5E-02	2.00	-7.60	1.87	-7.65	-0.26	-7.84	6E-03	15.7	9.7	14.47	9.64	11.02	9.38	8E-02
Lilium martagon	16.4	15.5	16.22	12.50	12.40	10.50	2E-02	6.80	6.30	5.72	1.40	2.00	-0.50	9E-01	16.9	16.9	16.18	12.60	12.90	10.60	5E-06
Linaria alpina	12.4	15.1	12.17	11.71	10.84	9.80	2E-01	-0.20	3.20	-0.29	1.20	-0.55	-1.30	9E-01	15.7	14.9	14.89	12.35	11.78	9.90	3E-03
Pinus mugo	11.6	15.8	16.59	9.20	14.37	8.40	2E-04	-0.20	5.10	7.42	-0.70	4.05	-1.60	1E-03	15.7	15.6	15.95	11.50	14.30	10.90	3E-02
Poa alpina	12.1	14	11.25	9.40	10.18	7.80	7E-07	-4.90	3.20	-0.30	-1.10	-0.63	-3.30	8E-03	15.7	15.3	14.40	10.00	10.33	8.50	3E-07
Ranunculus glacialis	16.4	18.1	12.05	6.64	11.83	3.70	3E-06	6.80	5.80	-4.92	-4.10	-5.01	-6.50	1E-02	15.7	17.4	15.43	7.47	14.33	4.90	3E-04

Rhododendron ferrugineum L.	*11.6*	*14.8*	*14.48*	*11.50*	*11.60*	*9.50*	*2E-03*	*1.70*	*4.50*	*4.76*	*0.35*	*1.10*	*-1.30*	*6E-01*	*15.7*	*16.1*	*15.14*	*12.25*	*10.00*	*10.00*	*4E-05*
Salix herbacea	*11.6*	*13.1*	*11.60*	*7.50*	*11.56*	*5.50*	*3E-10*	*2.20*	*2.70*	*1.99*	*-0.50*	*1.03*	*-3.10*	*2E-05*	*15.7*	*12.4*	*14.78*	*8.23*	*11.52*	*6.50*	*2E-09*
Salix reticulata	*11.6*	*12.5*	*10.99*	*7.00*	*9.45*	*5.30*	*1E-15*	*-0.50*	*1.60*	*-0.53*	*-2.70*	*-1.16*	*-4.85*	*2E-08*	*15.7*	*14.4*	*13.90*	*7.81*	*9.98*	*6.00*	*2E-13*
Saxifraga aizoides	*11.6*	*13.8*	*11.60*	*8.50*	*10.88*	*7.10*	*9E-09*	*1.10*	*2.70*	*0.40*	*0.00*	*-1.48*	*-2.00*	*2E-03*	*15.7*	*14.4*	*14.22*	*9.60*	*10.16*	*7.90*	*4E-09*
Saxifraga biflora	*11.6*	*6.6*	*11.41*	*6.07*	*10.66*	*5.54*	*1E-02*	*-1.40*	*-4.20*	*-1.67*	*-4.27*	*-2.73*	*-4.90*	*3E-01*	*15.7*	*8.2*	*15.29*	*7.11*	*13.64*	*6.04*	*2E-03*
Saxifraga oppositifolia	*11.6*	*23.1*	*11.60*	*8.50*	*10.82*	*6.60*	*5E-12*	*2.20*	*12.50*	*1.51*	*0.00*	*0.68*	*-2.00*	*3E-06*	*15.7*	*15.2*	*13.88*	*9.20*	*9.88*	*7.60*	*1E-11*
Sempervivum montanum	*12.4*	*13.8*	*11.60*	*13.20*	*10.48*	*9.60*	*2E-06*	*1.10*	*2.00*	*1.59*	*2.71*	*0.42*	*-0.55*	*9E-02*	*15.7*	*14.2*	*14.26*	*14.02*	*11.46*	*10.20*	*2E-07*
Silene acaulis	*17.3*	*13.2*	*12.09*	*7.90*	*11.60*	*6.20*	*2E-14*	*7.50*	*2.20*	*0.63*	*0.00*	*-0.20*	*-2.70*	*2E-05*	*16.9*	*14.3*	*14.61*	*8.60*	*10.62*	*7.00*	*1E-13*