How much of their thermal fundamental niche do high-elevation species occupy? A test with botanical garden records

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First step project

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Abstract

Since the apparition of the environmental niche concept, fundamental and realized niches have been a key subject of studies in ecology and evolution, and a useful conceptual tool for biologists. In particular, the realized niche being the part of the fundamental niche actually occupied in the field, as constrained by biotic interactions and dispersal, is commonly used by ecologists to predict species distributions. However, due to the challenge that represent the quantification of the fundamental niche, which requires constraining experiments, still little is known about the proportion of their fundamental niche that species occupy. In recent years, the use of botanical garden records has been a way to understand the relationship between species' fundamental and realized niches, but no formal quantification of this relation has yet been achieved. Here, using a large survey of botanical garden records, we quantified the difference between the realized and fundamental thermal niches of 27 alpine and subalpine species. In a second step, we showed that competitive species tend to occupy a larger part of their thermal niche than stress-tolerant species, indicating that competition is actually critical involved in the relationship between realized and fundamental niches.

Keywords

fundamental, realized, niche, alpine, subalpine, plant species, botanical garden, competition

Introduction

The concept of niche, first coined by Grinnell in 1917 and then formalized by Hutchinson in 1957, has been studied by ecologists for decades. The Hutchinson's population ecological niche is defined as a *n*-dimensional hyper volume in which the axes are the environmental variables or resources (nutriments, [N], temperature, UV's etc.)(Hutchinson, 1957). In his studies, Hutchinson noted the difference between the fundamental and realized niche.

The fundamental niche can be defined as the physiological limits for the distributions of a species. This physiological limits can be the need of a given concentration of nutriments, or a lethal minimal temperature etc. (Araujo et al., 2013; Kearney & Porter, 2004; Pulliam, 2000)

The realized niche is the part of the fundamental niche that is actually occupied by a species. The species can be excluded from their fundamental niche by numerous factors, including not being able to reach those locations due to an insufficient dispersal or because the biologic interaction in that place are not allowing the organism to survive (competition or lack of commensalism).

The concept of realized niche is the basement for Species Distributions Models (SDM)(Guisan, Thuiller, & Zimmermann, 2017). Thanks to the rise of new powerful statistical and GIS techniques at the beginning of the 21th century (Guisan & Zimmermann, 2000), we have those last decades witnessed an increasing use of SDM in ecology studies (Guisan & Thuiller, 2005). They allow us to predict the habitats and therefore potential presence of different species. One common point of the SDM is the assumption that species' realized niches are not changing overtime (Pearman et al., 2008). However, it has been shown that those niches are not static over time, and can see drastic fluctuation of their realized niche inside the fundamental one (Araujo et al., 2013; Nogues-Bravo, 2009; Pearman et al., 2008). Therefore, understanding clearly how the limits of species distribution works is a critical step in producing accurate predictive models. In a context where our environment is seeing critical changes, it is crucial to understand what drives species distribution, what excludes species from an habitat, and by extension to have good predictive models to serve conservation.

The realized niche, by its nature, is quite easy to understand: simple observation of a species on a big scale is sufficient to have a good approximation of its niche. However, this is not the

case for the fundamental niche. By definition, the latter cannot be observed in nature. This means that experiments are needed to quantify its boundaries. Most commonly used techniques are transplantation (Cunningham, Rissler, & Apodaca, 2009; Lee-Yaw et al., 2016) or growth rooms (Colwell & Fuentes, 1975). But such solution can be quite hard to implement in the conditions of a short scientific study.

A novel approach is to resort to botanical gardens. By definition, in a botanical garden plants grow without any negative biotic interaction, thereby making them a huge source of data for the study of fundamental niches. However, due to the fact that plants are sometimes watered or given nutriments, such data should be treated with care, or reducing the study to only one dimension such as temperature.

Using botanical garden records, it has already been shown that four *rhododendron* species exceed their realized thermal niche in the field when in *ex-situ* conditions (Vetaas, 2002). In addition, this study showed that the most competitive *rhododendron* species occupies in the field a range nearly similar to the one observed in *ex-situ* conditions. In the field, this species likely excludes the other species from a part of their fundamental niche through competition. However, this study did not quantify the precise differences between the realized and fundamental niches. In 2018, Cardenas showed in her unpublished master thesis, using simple percentile analyses, that when considering the warm limit of their niche, alpine and subalpine plant all have a higher tolerance *ex-situ,* than what is observed *in-situ,* but she did not use more quantitative approaches to the comparison of realized and fundamental niches. Furthermore, to our knowledge, there is no other evidence that a significant number of species do not occupy all their fundamental thermal niche, nor quantitative evidence that competitive species occupy a larger proportion of their fundamental niche.

Here, we attempt filling this gap by analyzing the fundamental and realized niches of 27 alpines and sub-alpines species from botanical garden records and observed data from the GBIF database.

In a first step, we assessed whether those species occupy all or part of their fundamental thermal niche, and in what proportion. In a second time, we investigated whether competitive species occupy a larger part of their fundamental niche than other plants, based on the Grime CSR strategies (J. Grime, 1974).

Material and Methods

Species data

For this study, a set of 27 emblematic alpine vegetal species was selected. This selection is based on the work of Cardenas 2018. The emblematic status of those species ensure a good representation of the selection in botanical gardens around the word.

The data for the fundamental niche comes from the dataset provided by D. Cardenas (unpublished Master Thesis). This is a survey of 130 botanical garden around the world (figure 1). Each species is marked as "absent", "present", "present with watering", "present in interior" or "present in interior with watering", with the coordinates of the botanical garden. Since we are interested in the thermal niche, it has been decided that we exclude plants that are reported as being in interior, but keep those with watering.

We had only few botanical garden at extremely high latitude and/or altitude, we can expect a bias in the cold limit of the niche, due to low or no data at those temperatures.

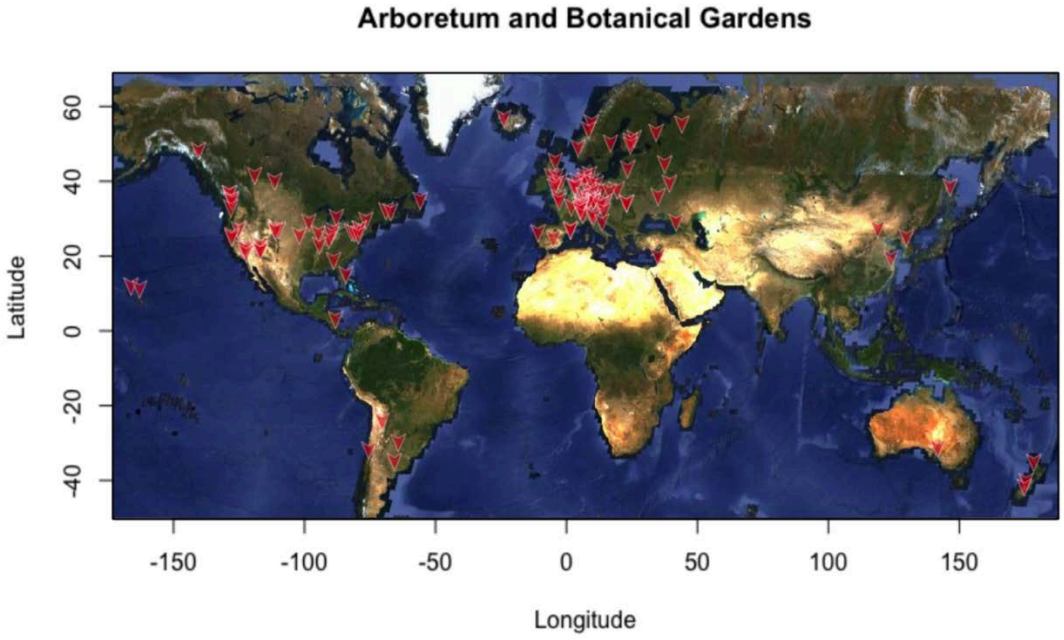

Figure 1 :Location of the 130 botanical gardens used for this study. Cardenas 2018.

The realized niche for the same species was obtained by using the Global Biodiversity Information Facility (GBIF) database (www.gbif.org). We extracted the latitude and longitude of every observation of each species using the RGBIF package (version 1.1.0, Scott Chamberlain et al, 2018). The extraction was followed by a disaggregation, performed in R thanks to the ecospat package (version 3.0, Broennimann et al, 2018), with a minimal distance of one observation for each 5 km^2 square. This disaggregation aims to reduce the spatial bias due to uneven sampling in the GBIF database. We obtained variable numbers of observations for different species, from 76 to 30279 (maps in annexes 1).

The CSR strategies for our 27 plants are taken from Flora Indicativa (J. P. Grime, 1979; Landolt et al., 2010). Each dominant strategy was used for each plant if they had one, leaving 3 classes: Competitive (C), Stress resistant (S), no specific known strategy (CSR). There were no strict Ruderal (R) plants in our set.

Environmental variables

The environmental data come from the Chelsa website. We decided to use such a database, which is a downscale of a Global Circulation Model (GCM), instead of a usual statistical interpolation such as the worldclim data. The Chelsa data is considered as fitting the reality better than other climatic models (Karger et al., 2017). For this study, 3 variables have been used: the monthly mean of daily mean temperature, the monthly mean of daily max temperature and the monthly mean of daily min temperature. The data was based on a 30 years time period (1980-2010). Since we wanted only one value for each observation, each variable has been extracted for each GBIF's and botanical garden presence location in order to build the realized and fundamental thermal niches of each species.

Niche comparison

All statistical analysis was performed in R (Version 3.3.1).

First, for visual representation, a Kernel density plot was used for each species and each environmental variable in order to produce graphs for both niches. Since it was only used for display representation and not for quantitative analysis, the adjustment of the degree of smoothing was only done visually. However, due to a high bias in the botanical gardens location, the fundamental niche resulting was not overlapping the realized one. The fact that the realized niche is smaller than the fundamental makes sense in regard of our hypothesis, but there is no biological way to explain the fact that the realized is bigger than the fundamental one as highlighted in figure 2. In our dataset, this is almost all the time the case for the cold temperature limit. It makes no sense that a plant could grow at a given temperature in the wild but not in a botanical garden. This can by explain by the fact that we have a big bias in the temperature distribution of the botanical gardens. There are not much of them in the cold extreme of the spectrum, which explain the fact that realized niche is bigger than the fundamental one on this side of the spectrum. We overcame this problem by using the 0.05 quantile of the thermal distribution of the botanical gardens (for the 3 variables) and excluding all the data below that temperature limit. This means that all further analysis will be performed only the part of the gradient where enough data is available to accurately quantify both realized and fundamental niches, i.e. on the warmer part of the temperature gradient.

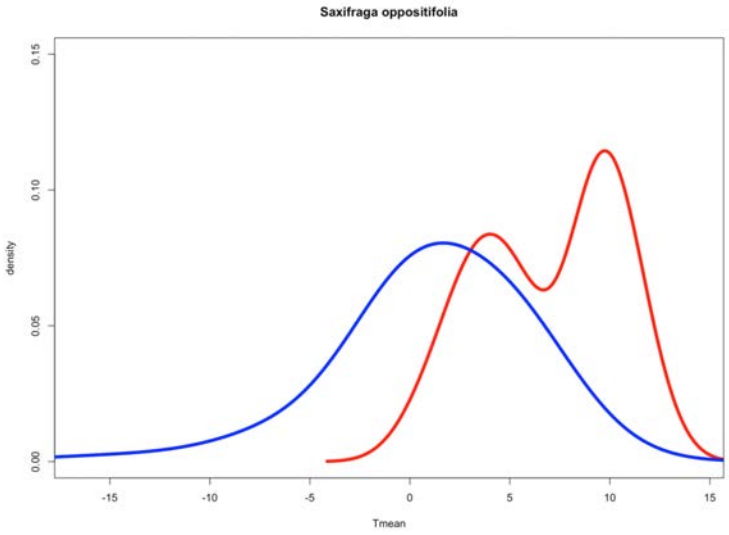

Figure 2 : Kernel density plot for the fundamental (red) and realized (blue) thermal niches for Saxifraga oppositifolia. In the cold part of the spectrum, the fundamental niche is small than the realized niche, indicating a bias in the location of the botanical gardens.

Then, an asymmetric Kolmogorov-Smirnov test on the resultant cumulative curve of the distribution was used to compare the fundamental and realized niche of each specie for each temperature variable. The Kolmogorov-Sminov test is often used to check normality of a

142 distribution (Lilliefors, 2012), but it can also be used to compare two density functions. Here,
143 we used it to compare the fundamental and the realized thermal niche functions, transformed
144 into cumulative distribution functions. Since we want to test whether the fundamental
145 thermal niche is larger than the realized thermal niche, and only on the warm side, we used a
146 one-sided test with adjusted p-values. This test gives the proportional difference in area
147 between the two niches, and thus provides a metric of the proportion of the fundamental
148 niche being occupied in the field. Since we had multiple test (81 in total) the p-values were
149 adjusted with a Bonferroni correction.

150 This difference was, in a second step, used to assess if different CSR strategies have an effect
151 on the proportion of the fundamental niche occupied. A three factors ANOVA was performed
152 to see if the three classes (competitive, stress resistant, no specific strategy; we had no strict
153 R plants in our data) differed regarding a niche difference. This was followed by a TuckeyHSD
154 test, which additionally provides the specific effect of each strategies compared to each other.
155 For representing the proportion of the fundamental niche occupied, two variables were
156 plotted and a factorial maps with representation of point classes was performed in the "ade4"
157 package (Dray et al., 2018)

Results

Species do not occupy all their fundamental thermal niche

For almost all 27 species and all 3 environmental variables (81 Kolmogorov-Smirnov tests in total), there is a significant difference between the two niches (Kolmogorov-Smirnov test, pval<0.05, all *d*-val and *p*-val in annexes 2). Only 6 p-values were not significant (all for the Tmax variable) and we can add that two of them were borderline (between 0.05 and 0.065). In the regard to all the test that have been performed, added to the fact that we used a Bonferonni correction which is known to be stringent (Sibuya, 1991), we can state that this is not sufficient to reject our hypothesis. This means that our species do not occupy all their fundamental thermal niche for the 3 environmental variables. The D-Values are quite variable for each species, meaning that the proportion of the fundamental thermal niche occupied by the plants is not always the same.

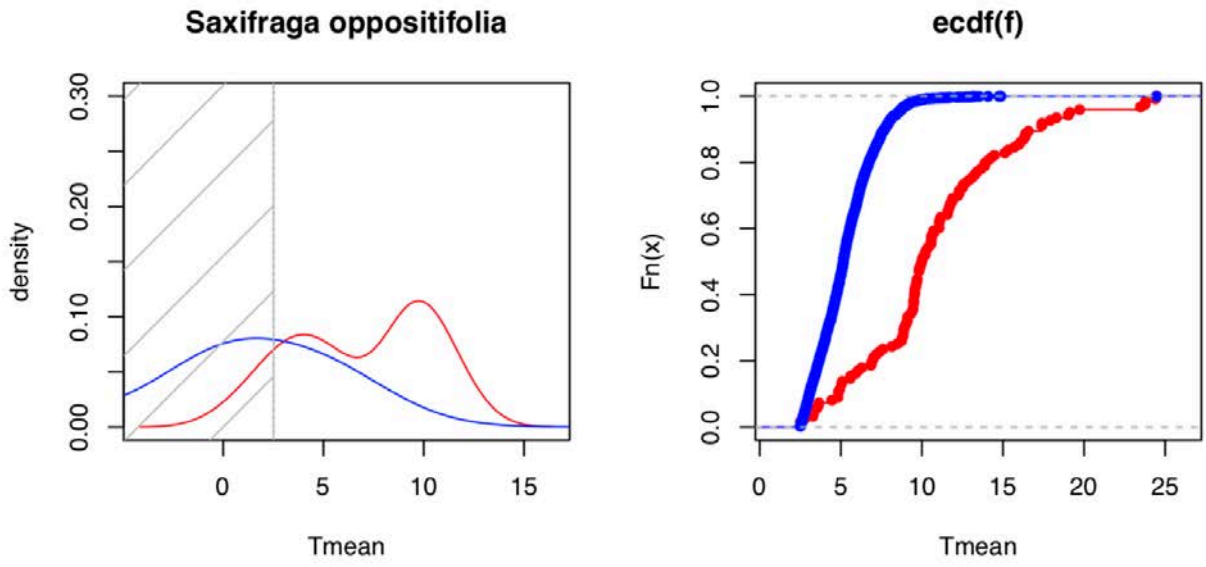

Figure 3 : On the left: Kernel density plot for the fundamental (red) and realized (blue) thermal niches. The hatched portion represent the data that was removed. On the right: the additive curves (same color code). On the warm boundary of the niches, the realized thermal niche is smaller than the fundamental thermal niche. This indicates that species don't occupy all of their fundamental niche.

Proportion of occupied fundamental niche is linked to the plant's CSR strategy

With the Kolmogorov-Smirnov test, we obtained the percentage of fundamental niche not occupied by the species. On that basis, we wanted to check whether the adaptive strategy of plants have an effect on the proportion of their fundamental thermal niche occupied. Results show that for 2 out of the 3 environmental variables (Tmax and Tmean), different CSR (Competitive, Stress resistant, Ruderal) strategies occupy a significantly different proportion of their Fundamental thermal niche (anova, Tmax: DF=2, fval= 12.108, *p*-val<0.01; Tmean: DF=2, *f*-val=5,2989, *p*-val<0.05). However, no significant difference was found for the Tmin variable. In addition, we observed that for the variable Tmax, species in the stress resistant group (S) are occupying a significantly smaller part of their fundamental thermal niches than the C and CSR groups (TuckeyHSD, respectively diff=0.337, *p*-val<0.01, diff=0.299, *p*-val<0.01). However, no significant difference was found between the C and CSR groups. For Tmean, the only difference between groups was the S group that is occupying a significantly smaller part of the fundamental thermal niche compared to the C group (TuckeyHSD, diff=0.08, *p*-val<0.05).

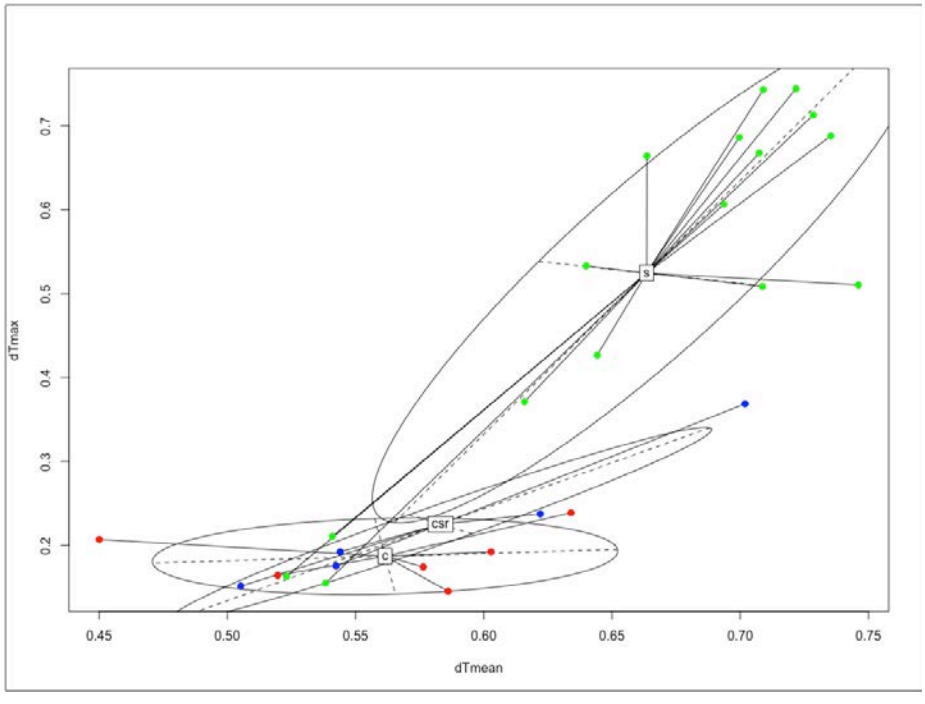

Figure 4 : Factorial map with point classes for the CSR strategies (C=competitive, S= stress resistant, CSR= no specific strategy), plotted for the difference between the fundamental and realized niches for the environmental variables Tmean and Tmax. The C species are clustered down left in the graph, showing that they occupy a large part of their fundamental thermal niche. S species tend to occupy a smaller part of their fundamental thermal niches.

Discussion

First of all, we can note that the fact that we were not able to analyze the data from the cold limit of the temperature gradient should not have any effect on the impact of our finding. One can realistically expect the limits of the fundamental and realized niche at the cold end of the temperature gradient should be equivalent in the case of alpine species (Pellissier et al., 2013). There is not much competition at those extremes that can excludes the plants from their fundamental niche, making this limit a strict physiological boundary. However, this would still have to be formally tested in a distinct study, but the lack of botanical gardens at extreme cold temperatures makes any such study difficult.

In addition, our novel technique used to compare fundamental and realized niche has given consistent results. To our knowledge, there is no reported use of cumulative distribution function coupled to a Kolmogorov-Smirnorv to compare fundamental and realized niches. Not only results are congruent with the literature, but we also have been able to quantify the difference between fundamental and realized niche.

Alpine species are excluded by competition from their fundamental niche.

The fact that almost all species do not occupy all their fundamental niche is in adequacy with the results of Vetaas (2002). He has shown that 3 out of 4 species of *Rhododendron* have botanical records overpassing the warm limit of their realized niche. This is probably because more competitive species are excluding them in the more productive part of the thermal gradient. This was supported by the fact that the most competitive *Rhododendron* had almost no observation out of its realized range, meaning that it was occupying most of its fundamental range. Our study has shown that this is likely the case for most alpine species. In addition, our results also confirm those from Cardenas (2018) that show that for the same botanical garden records, the warm limit of the fundamental niche exceed that of the realized niche. It has already been shown that alpine species have a high conservatism of their cold thermal limit around the world, but low conservatism when the warm limit is considered (Pellissier et al., 2013).

Our study provides quantitative support to the hypothesis the that even if the cold limit of the niche probably come from physiological constrains *in-situ*, the warm limit is likely to be driven

by biotic interactions (Normand et al., 2009). The fact that warmer temperature usually means less constrains for the species (e.g. no adaptation) allows the more competitive species to exclude the less competitive species (e.g. constrained by penalizing adaptations) at lower temperatures (Colwell & Fuentes, 1975). However, when the biotic interaction part of the equation is removed, as it is the case in a botanical garden, alpine and subalpine plants can survive at higher temperature that at which they are found *in-situ.*

However, it is important to note that this study was only about thermal niches. All the others dimensions were neglected. This is due to the fact that botanical garden, even if handy, can pretty much only give us information about the thermal niche. Further analysis could try to investigate whether our conclusions are applicable to other dimensions of the fundamental and realized niches(Vetaas, 2002, Cardenas, 2018).

Competitive species occupy a larger part of their fundamental niche.

The fact that we found that competitive plant occupies a larger part of their fundamental niche is congruent with the conclusions of Vetaas (2002). He showed that, unlike others species of its genus studied, the most competitive *Rhododendron* species had almost no individuals out of its realized range. This would mean that the competitiveness of the plants could be critical to determine the relationship between their fundamental and realized thermal niches.

However, the results for this part our study were not as striking as they were for the niche comparison. The CSR strategy is significantly related to the ratio of the realized to fundamental niche for 2 out of 3 environmental variables (Tmax, Tmin and Tmean). The way C-S-R strategies are attributed to species is not very clear and sometimes criticized by experts. Further studies that aim to resolve the effect of the specie's competiveness on the proportion of the fundamental niche being occupied could use the same design as we did, but selecting a larger range of species for which the competition strategies are clearly known.

Our results show the importance of the competition on the species distribution. Therefore, this is a critical parameter to take in count when assessing predictive models. Despite the impact of the biotic interactions on the realized niche concept, this point is too often overlooked (Meineri, Skarpaas, & Vandvik, 2012). Our results also support the conclusion of

Pearman (2008) that state that niches are not stable in time. We can hypothesize that the apparition of new competitor for examples could shift drastically the realized niche inside the fundamental range. If were to be proven, this would be a challenge for SDM that until now assumes a static niche over time (Pearman et al., 2008).

Overall, in the context of SDM, questioning the niche concept in general could help building more accurate predictive models (Araujo & Guisan, 2006).

Importance of the botanical gardens for research

This work is a good illustration of the role that botanical gardens can play in fundamental research. Until recently, most of the studies about comparison between the fundamental and the realized niches were performed using either transplantation or growth rooms (Cunningham et al., 2009; Lee-Yaw et al., 2016). The use of botanical gardens data has a few advantages over these methods: It is relatively fast and less costly. But it also has obvious drawback. First of all, the absence of a species in a botanical garden does not necessarily mean that the species is not able to grow there, but that it might not have been planted. Secondly, as we have seen in this study, botanical gardens are usually not placed in extreme environments, e.g. at very high altitudes. This means that properly fitting the fundamental niche in extreme cold temperatures can be difficult, and often will simply mean that this boundary cannot be analyzed, just as it was the case for our cold niche boundary. Finally, as assessed before, it is hard to analyze other fundamental dimensions than the thermal one. This comes to the fact that in botanical gardens plants are usually watered of provided with nutriments. For analysis of other gradients, transplantations or growth rooms would still be the only possible approach, thanks to the control they can offer on all the other environmental variables. Nevertheless, botanical gardens remain a considerable and valuable source of data for the type of study as performed here.

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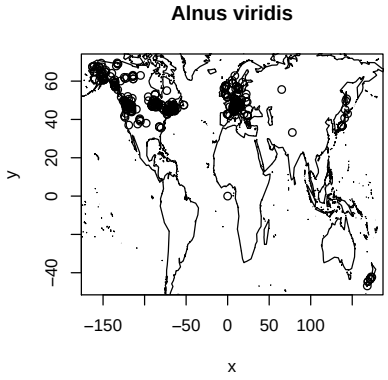
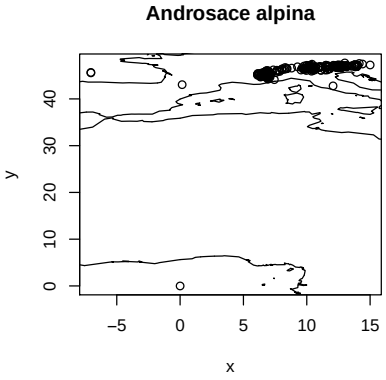
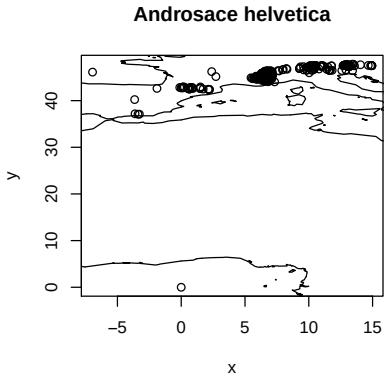
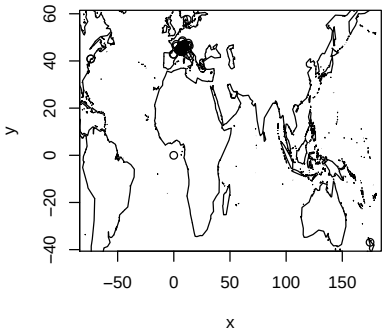
Annexes

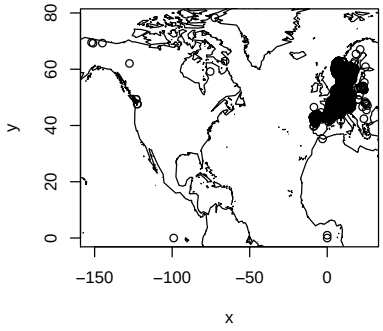
Annexes 1: Maps for Gbif observations

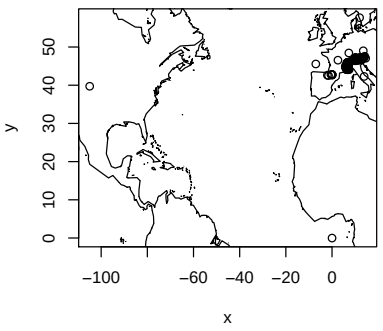


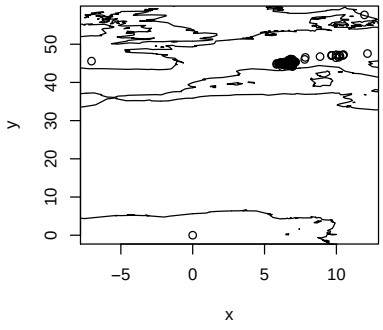


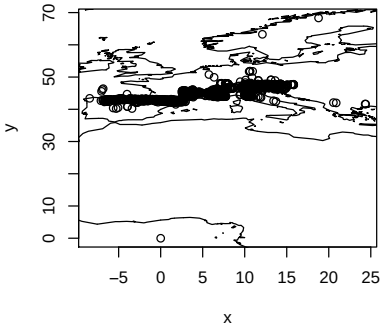


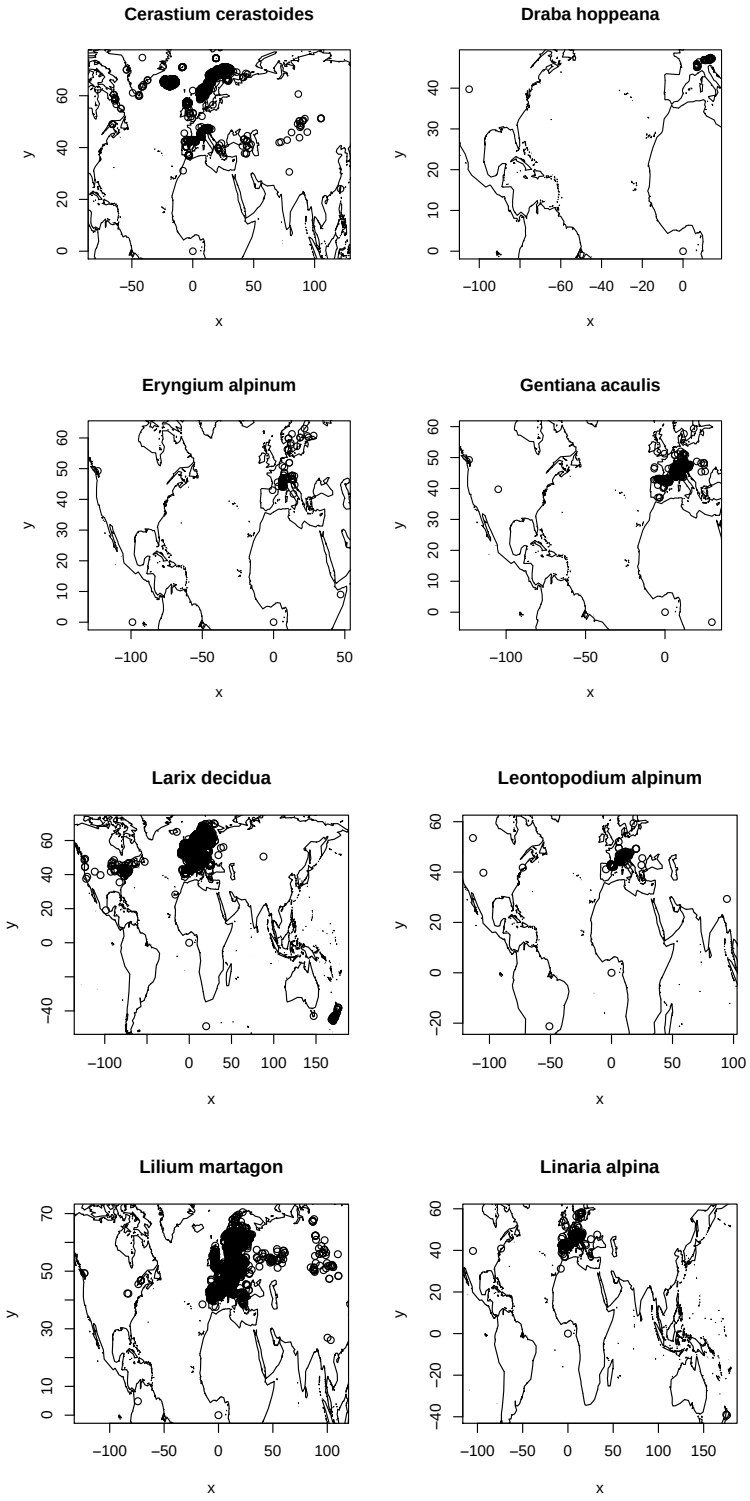


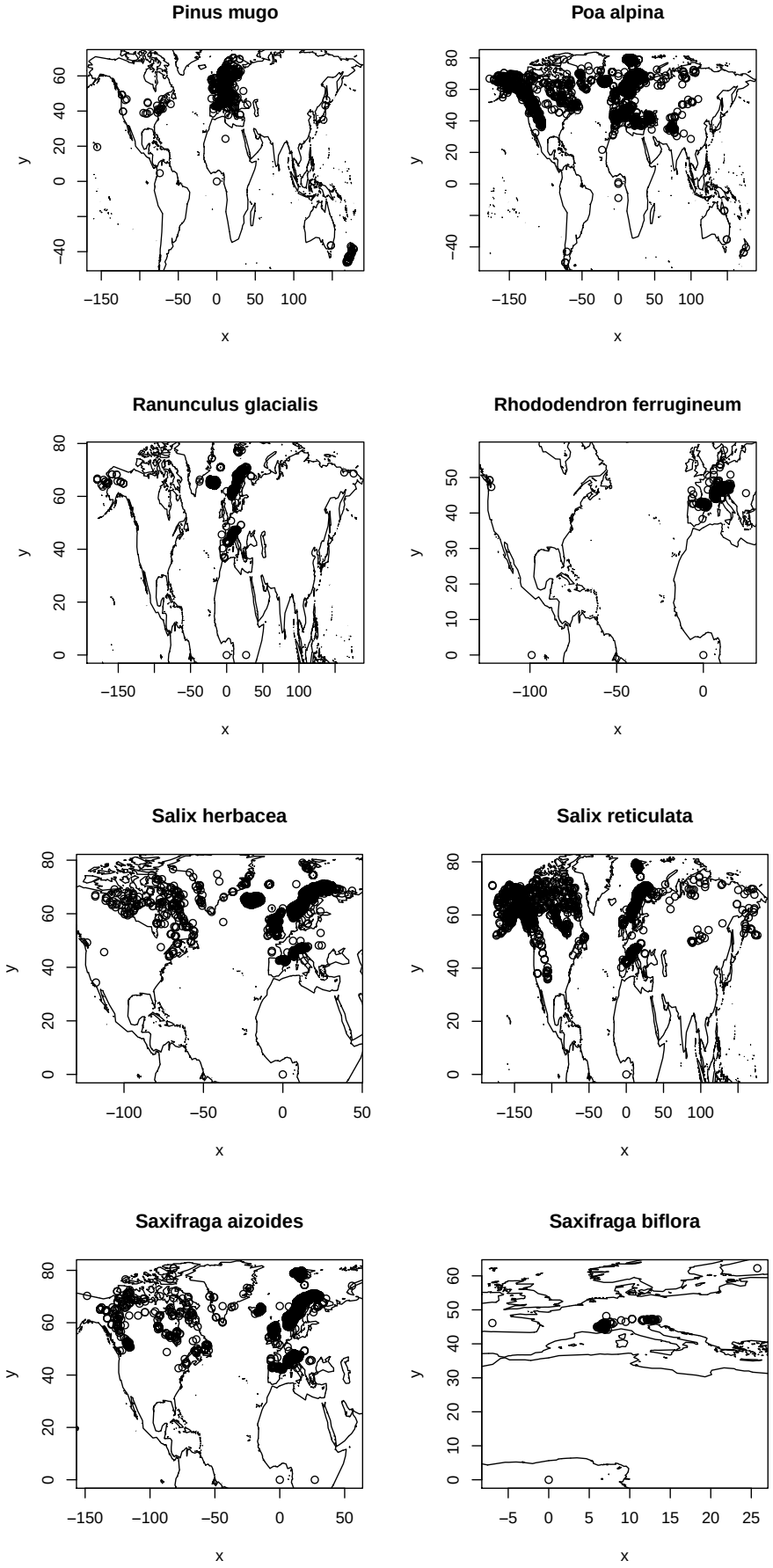


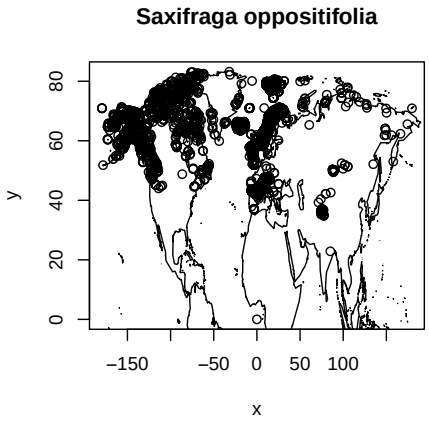


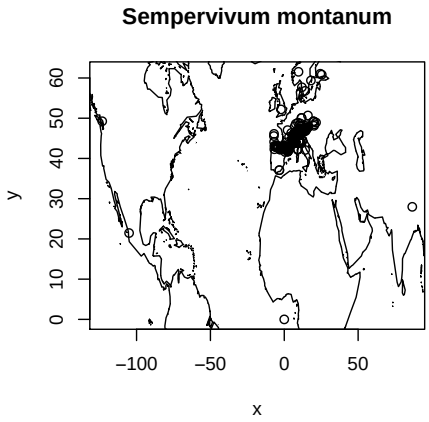


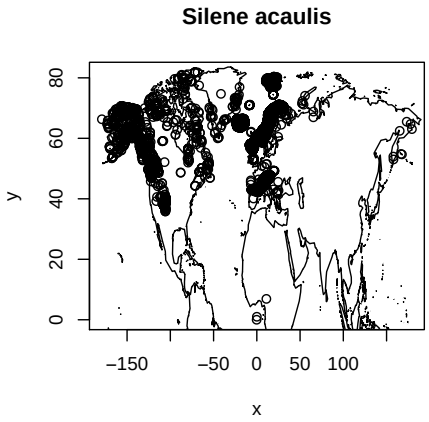



Cerastium cerastoides
Draba hoppeana
Eryngium alpinum
Gentiana acaulis
Larix decidua
Leontopodium alpinum
Lilium martagon
Linaria alpina
x
y


Pinus mugo
Poa alpina
Ranunculus glacialis
Rhododendron ferrugineum
Salix herbacea
Salix reticulata
Saxifraga aizoides
Saxifraga biflora
x
y


Saxifraga oppositifolia
y
x
0
20
40
60
80
−150
−50
0
50
100


Sempervivum montanum
y
x
0
10
20
30
40
50
60
−100
−50
0
50


Silene acaulis
y
x
0
20
40
60
80
−150
−50
0
50
100

Annexes 2: Species' list with CSR strategies

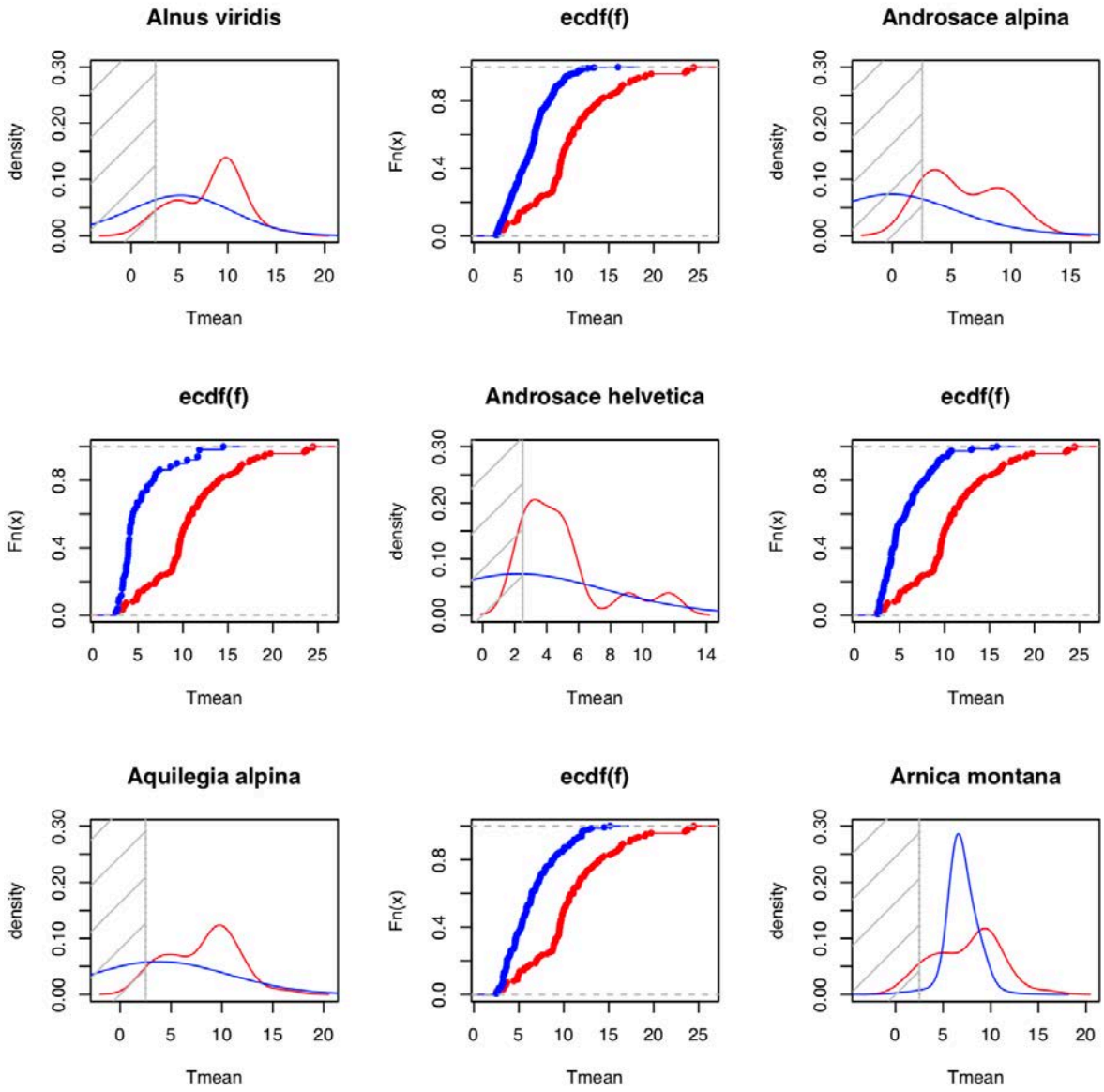
NO_ISFS2	Complete_name	Species_name	Flora_Indicativa	FI_simp
25400	*Alnus viridis (Chaix) DC.*	*Alnus viridis*	ccs	c
31300	*Androsace alpina (L.) Lam.*	*Androsace alpina*	rss	s
32100	*Androsace helvetica (L.) All.*	*Androsace helvetica*	css	s
38800	*Aquilegia alpina L.*	*Aquilegia alpina*	crs	csr
45700	*Arnica montana L.*	*Arnica montana*	crs	csr
47000	*Artemisia genipi Weber*	*Artemisia genipi*	rss	s
75000	*Campanula cenisia L.*	*Campanula cenisia*	css	s
77200	*Campanula scheuchzeri Vill.*	*Campanula scheuchzeri*	crs	csr
103400	*Cerastium cerastoides (L.) Britton*	*Cerastium cerastoides*	css	s
140900	*Draba hoppeana Rchb.*	*Draba hoppeana*	css	s
157200	*Eryngium alpinum L.*	*Eryngium alpinum*	ccs	c
182200	*Gentiana acaulis L.*	*Gentiana acaulis*	css	s
227200	*Larix decidua Mill.*	*Larix decidua*	ccc	c
234600	*Leontopodium alpinum Cass.*	*Leontopodium alpinum*	ccs	c
238500	*Lilium martagon L.*	*Lilium martagon*	crs	csr
238800	*Linaria alpina (L.) Mill. s.l.*	*Linaria alpina*	rss	s
305495	*Pinus mugo Turra s.l.*	*Pinus mugo*	ccc	c
309000	*Poa alpina L.*	*Poa alpina*	crs	csr
338700	*Ranunculus glacialis L.*	*Ranunculus glacialis*	css	s
345300	*Rhododendron ferrugineum L.*	*Rhododendron ferrugineum*	ccs	c
364800	*Salix herbacea L.*	*Salix herbacea*	css	s
366100	*Salix reticulata L.*	*Salix reticulata*	css	s
371600	*Saxifraga aizoides L.*	*Saxifraga aizoides*	css	s
372050	*Saxifraga biflora All. s.l.*	*Saxifraga biflora*	css	s

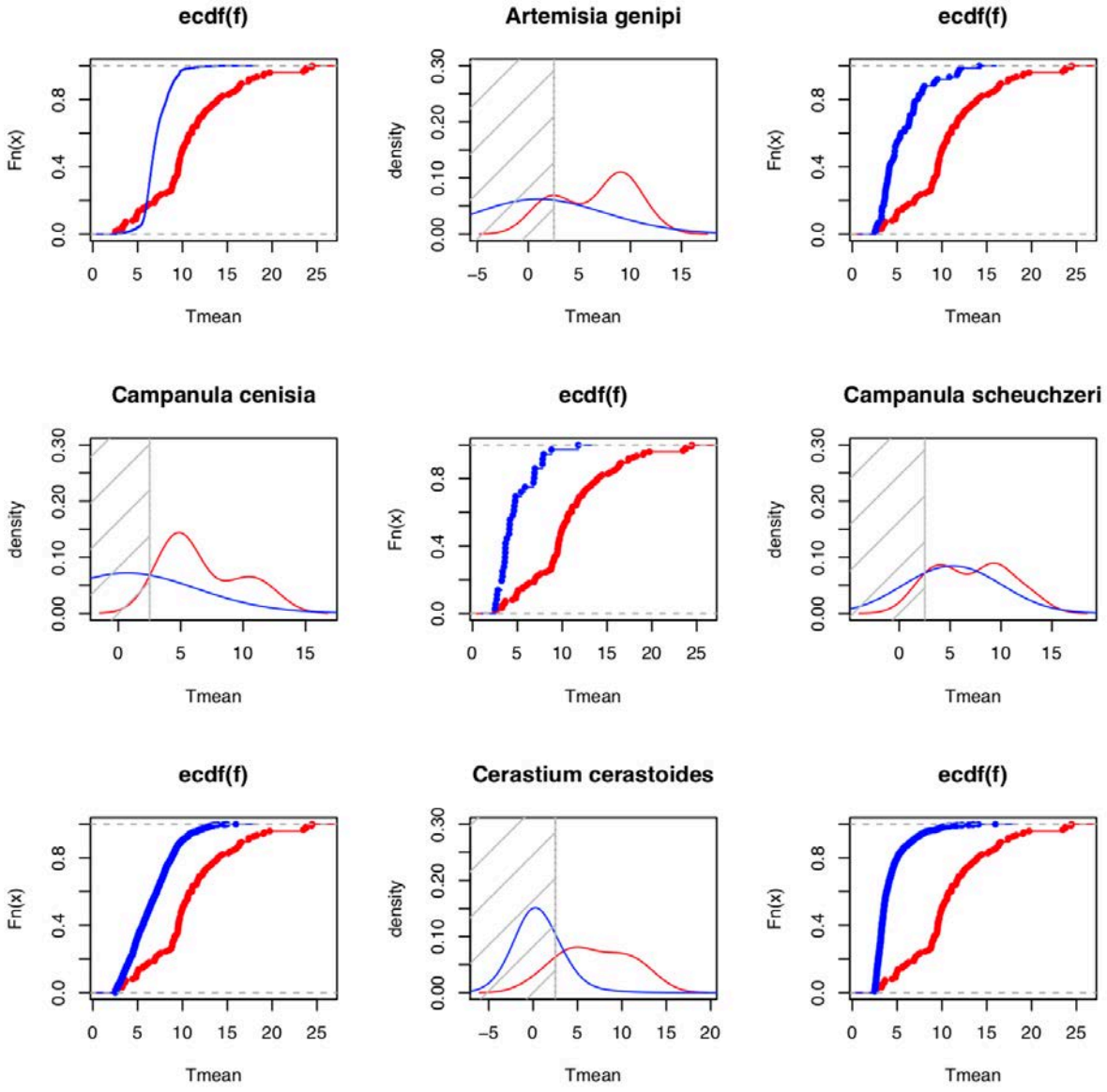
374500	*Saxifraga oppositifolia L. s.str.*	*Saxifraga oppositifolia*	css	s
387000	*Sempervivum montanum L.*	*Sempervivum montanum*	sss	s
394300	*Silene acaulis (L.) Jacq.*	*Silene acaulis*	css	s

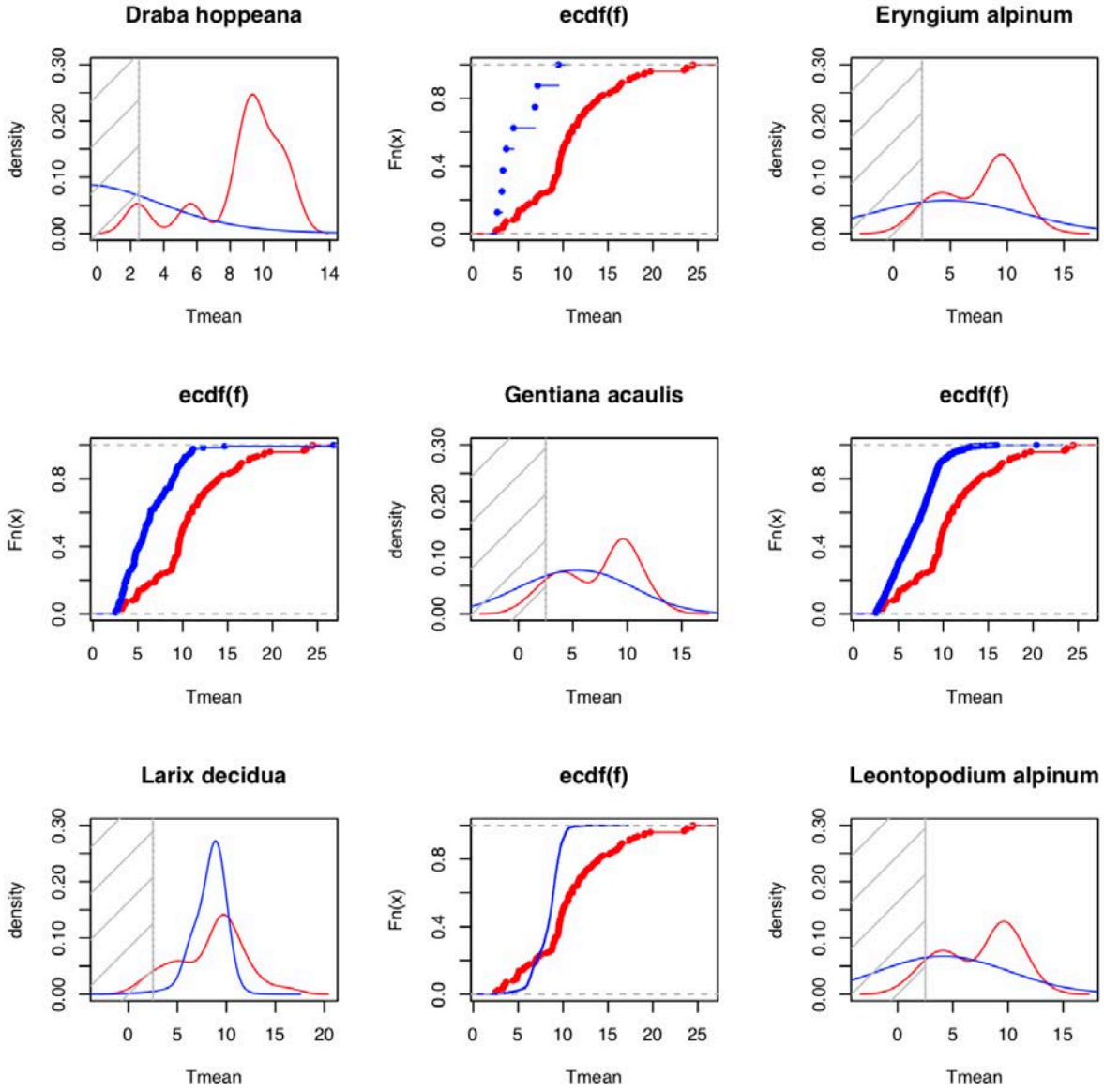
Annexes 3: D-values and P-values for the Kolmogorov-Smirnov test

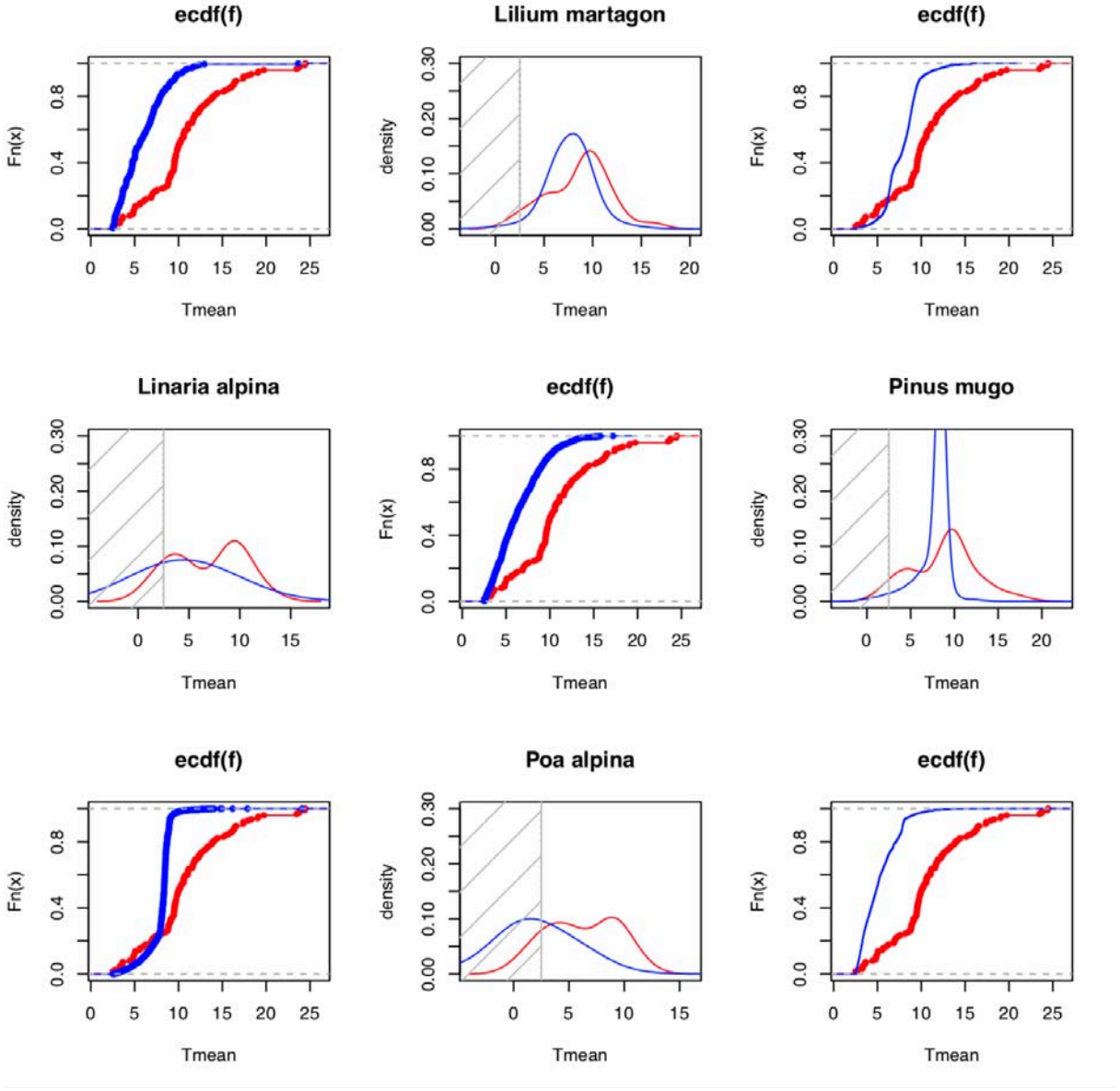
sp.names	compTmean_dval	ad_compTmean_pval	compTmin_dval	ad_compTmin_pval	compTmax_dval	ad_compTmax_pval
Alnus viridis	0.5860822337731 57	1.3225415558897 e-28	0.4229921476787 44	2.18495742501014e -14	0.1455430327868 85	0.3516067418106968
Androsace alpina	0.6398852223816 36	4.0709554316828 7e-12	0.6550905953408 11	9.46555524483547e -17	0.5329169919333 85	1.387281626504e-17
Androsace helvetica	0.6158920079766 84	3.8183047001251 9e-22	0.5802858343841 95	9.48385627680493e -23	0.3714549788393 25	4.96961148961008e -10
Aquilegia alpina	0.5440201112537 44	9.0080737067195 7e-17	0.5007232401157 18	6.39112237142021e -16	0.1926229508196 72	0.0645908667557559
Arnica montana	0.6220331813556 22	1.8975806639177 3e-40	0.3597363797173 3	5.99994917462306e -13	0.2376708115806 69	2.96206701681589e -05
Artemisia genipi	0.6442276422764 23	4.3232946738163 2e-16	0.5822765233529 23	5.3457490758295e-16	0.4268852459016 39	2.73642822339246e -11
Campanula cenisia	0.7086720867208 67	1.9189577893925 4e-11	0.6742150597388 16	5.36714602389549e -15	0.5086243763364 22	1.34689035158241e -12
Campanula scheuchzeri	0.5424087072370 43	1.2277761300671 6e-28	0.3743802922836 79	2.64260176674068e -13	0.1757741347905 28	0.0213619544492629
Cerastium cerastoides	0.7285034353760 39	3.7543986262238 9e-51	0.5279767620999 62	4.16319048116194e -28	0.7128515566256 56	8.29521731239206e -52
Draba hoppeana	0.6636178861788 62	0.0361499810630 367	0.7622950819672 13	1.23745092197127e -05	0.6640782283577 8	3.55045426883974e -14
Eryngium alpinum	0.5196210229818 83	5.9889578752414 6e-14	0.4163274287604	2.15161179932496e -09	0.1644194393248 62	0.5856888719217298
Gentiana acaulis	0.5230390553729 11	3.4555444506317 1e-26	0.4177177148064 49	1.53274230154554e -16	0.1631980362935 04	0.0605216099848028
Larix decidua	0.4500613344817 24	7.5810894528901 2e-21	0.2254670593357 51	0.000116481684089 152	0.2073147253837 32	0.0007857566694883 43
Leontopodium alpinum	0.6028061893522 16	3.0231071564891 9e-25	0.5021333932180 55	3.85850930034998e -18	0.1925995316159 25	0.0328511952054935
Lilium martagon	0.5052119285933 42	2.5557032846742 8e-26	0.3411231252179 98	1.61970727803023e -11	0.1517376199228 67	0.1029853197739178
Linaria alpina	0.5383026316623 26	1.5193889756733 3e-27	0.3780206046985 43	2.43385669837274e -13	0.1551320814031 97	0.11100135521173
Pinus mugo	0.6340246525045 9	1.4303254352160 9e-41	0.3363667710817 35	4.21119100963991e -11	0.2390215696705 91	2.94057712395583e -05
Poa alpina	0.7018746445413 8	3.2599884158967 9e-51	0.4594875924728 1	1.71944376090641e -21	0.3688307528750 99	1.31420961938602e -13
Ranunculus glacialis	0.7090129183500 42	2.7368893093063 7e-38	0.6079218493543 47	8.97634138145316e -36	0.7431539500516 43	4.52790331925903e -55
Rhododendron ferrugineum	0.5763857102377 99	2.8388424582043 7e-31	0.4895334174022 7	1.07926035300337e -22	0.1745256953398 42	0.0270443132686373
Salix herbacea	0.7217357278499 79	1.9896318567700 9e-53	0.3955567584287 04	1.09583707957878e -15	0.7442582192837 66	2.304998070086e-57
Salix reticulata	0.7353071487118 14	1.3586995536243 7e-52	0.5670979877089 72	2.23918193836848e -32	0.6878282638019 66	1.54114992307134e -48
Saxifraga aizoides	0.6936635476875 49	4.8779860428805 8e-50	0.2640184041823 39	1.28602667997577e -06	0.6063916203285 69	5.78254046069874e -38
Saxifraga biflora	0.7460545193687 23	3.5778239905228 7e-12	0.6770204199022 15	9.21718643283004e -15	0.5104624816739 97	3.70584598161338e -13
Saxifraga oppositifolia	0.7073872690030 65	1.2095803406083 9e-51	0.3068880261341 86	3.73852861528789e -09	0.6674141813919 66	6.02910518883733e -46
Sempervivum montanum	0.5409434500999 35	9.1199370010736 4e-25	0.4387462768013 46	9.65712052424125e -17	0.2107341242959 72	0.0020794070337044 7
Silene acaulis	0.6996583009308 35	2.4897490728285 3e-50	0.3424223806412 39	1.42824529945062e -11	0.6862313645412 59	1.30911477366218e -48

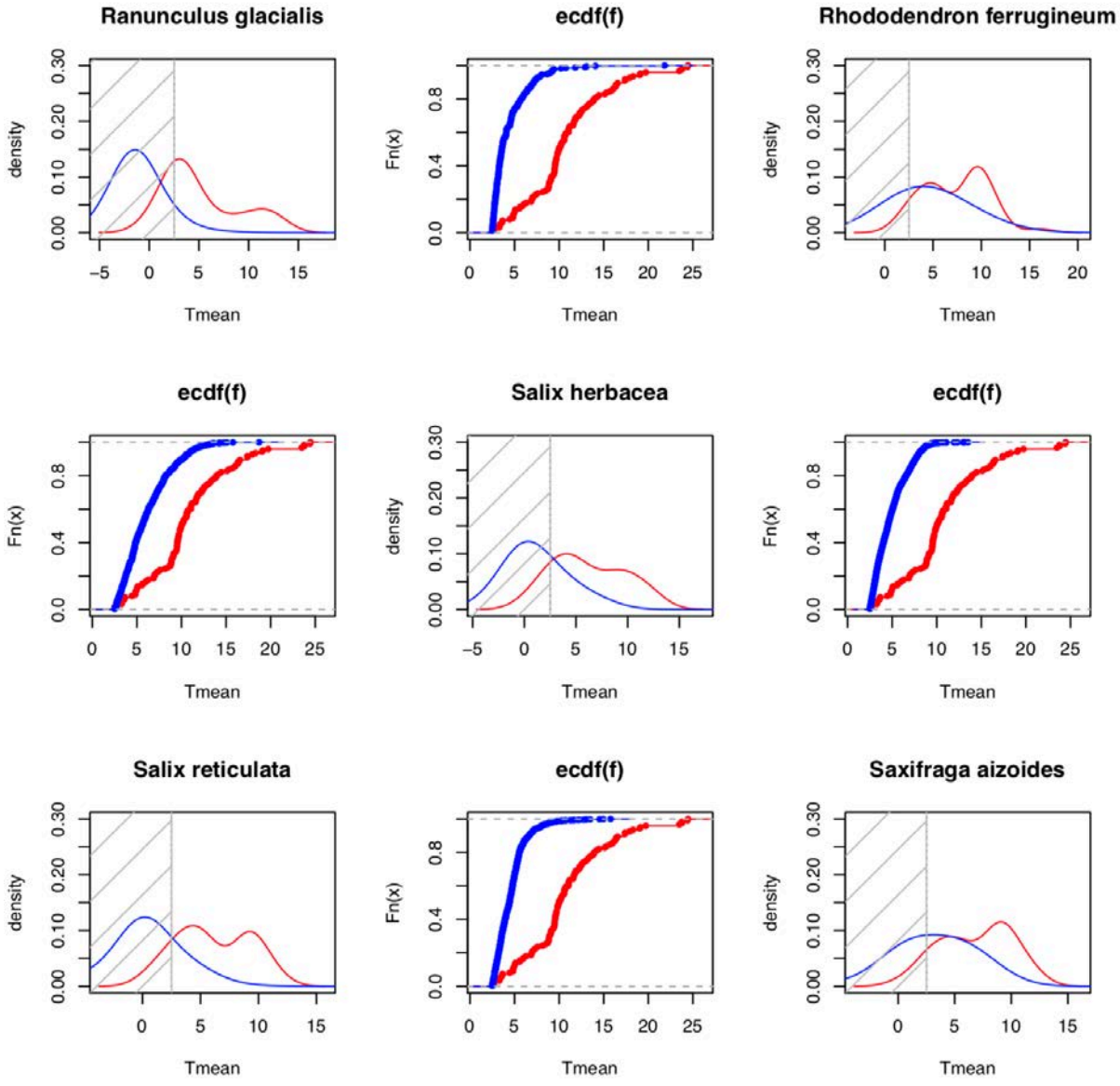
Annexes 4: Kernel density plot and cumulative functions for Tmean variable

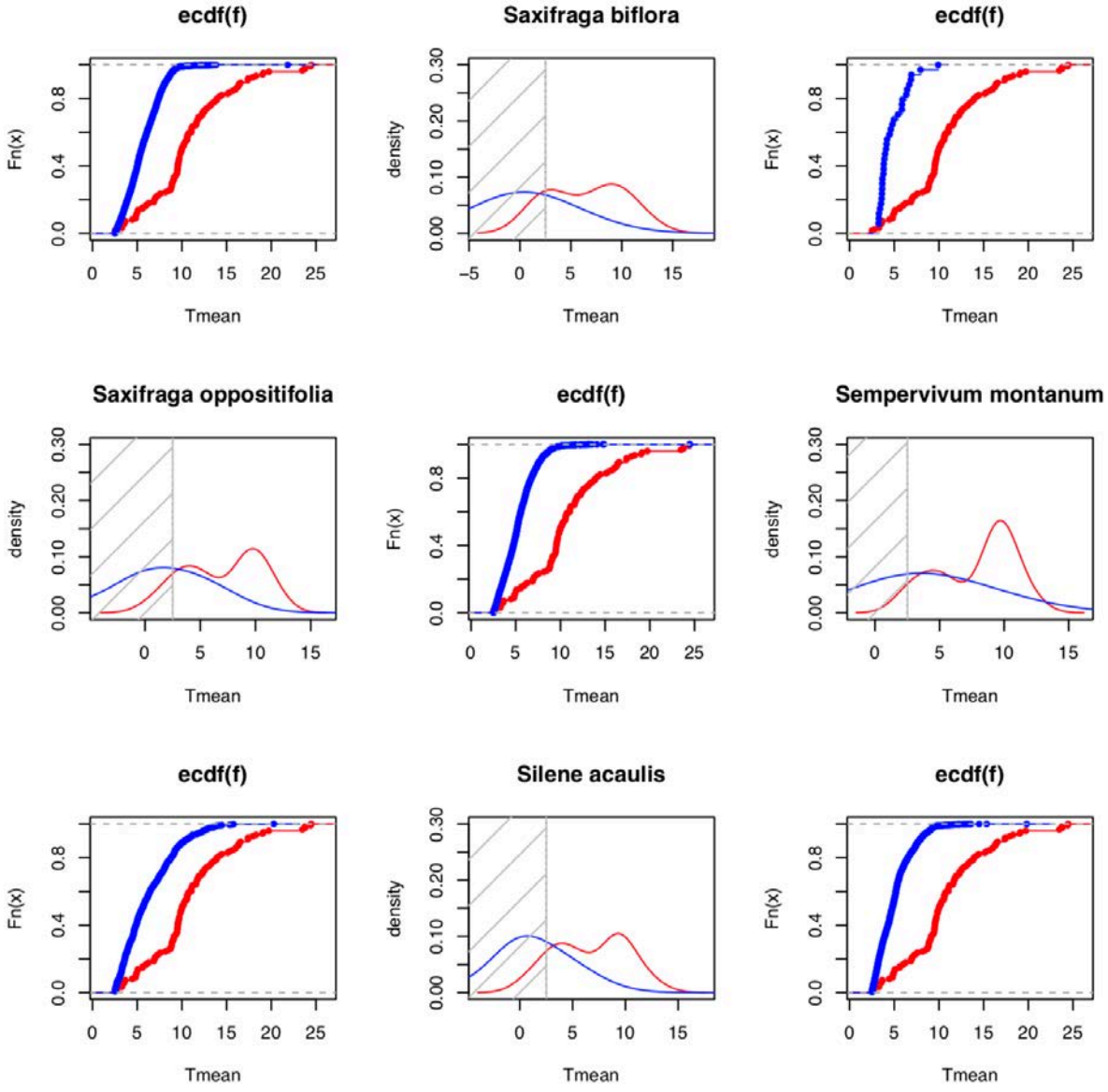



ecdf(f)
Fn(x)
Tmean
Artemisia genipi
density
Tmean
ecdf(f)
Fn(x)
Tmean
Campanula cenisia
density
Tmean
ecdf(f)
Fn(x)
Tmean
Campanula scheuchzeri
density
Tmean
ecdf(f)
Fn(x)
Tmean
Cerastium cerastoides
density
Tmean
ecdf(f)
Fn(x)
Tmean

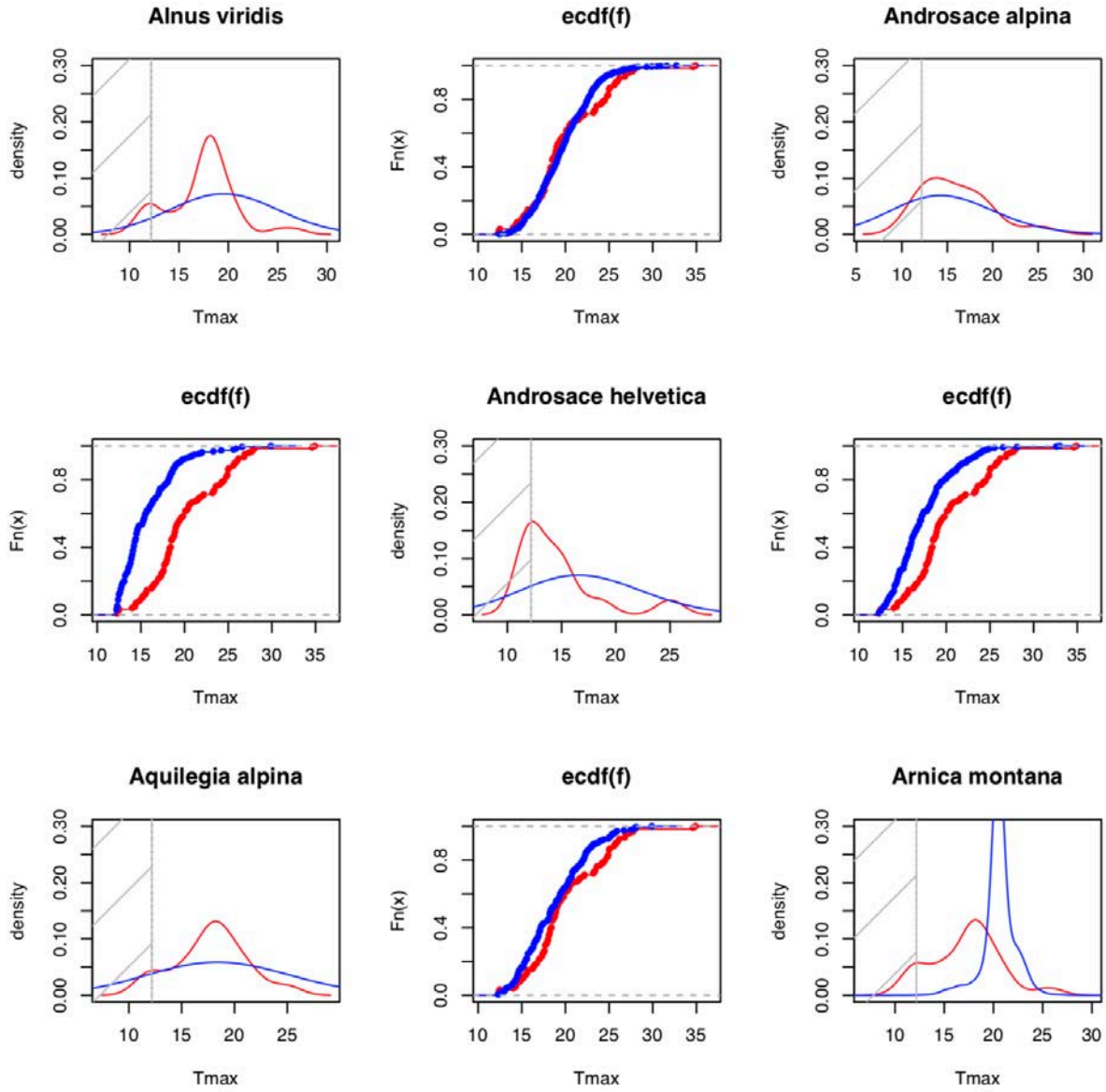

Draba hoppeana
density
Tmean
ecdf(f)
Fn(x)
Tmean
Eryngium alpinum
density
Tmean
ecdf(f)
Fn(x)
Tmean
Gentiana acaulis
density
Tmean
ecdf(f)
Fn(x)
Tmean
Larix decidua
density
Tmean
ecdf(f)
Fn(x)
Tmean
Leontopodium alpinum
density
Tmean

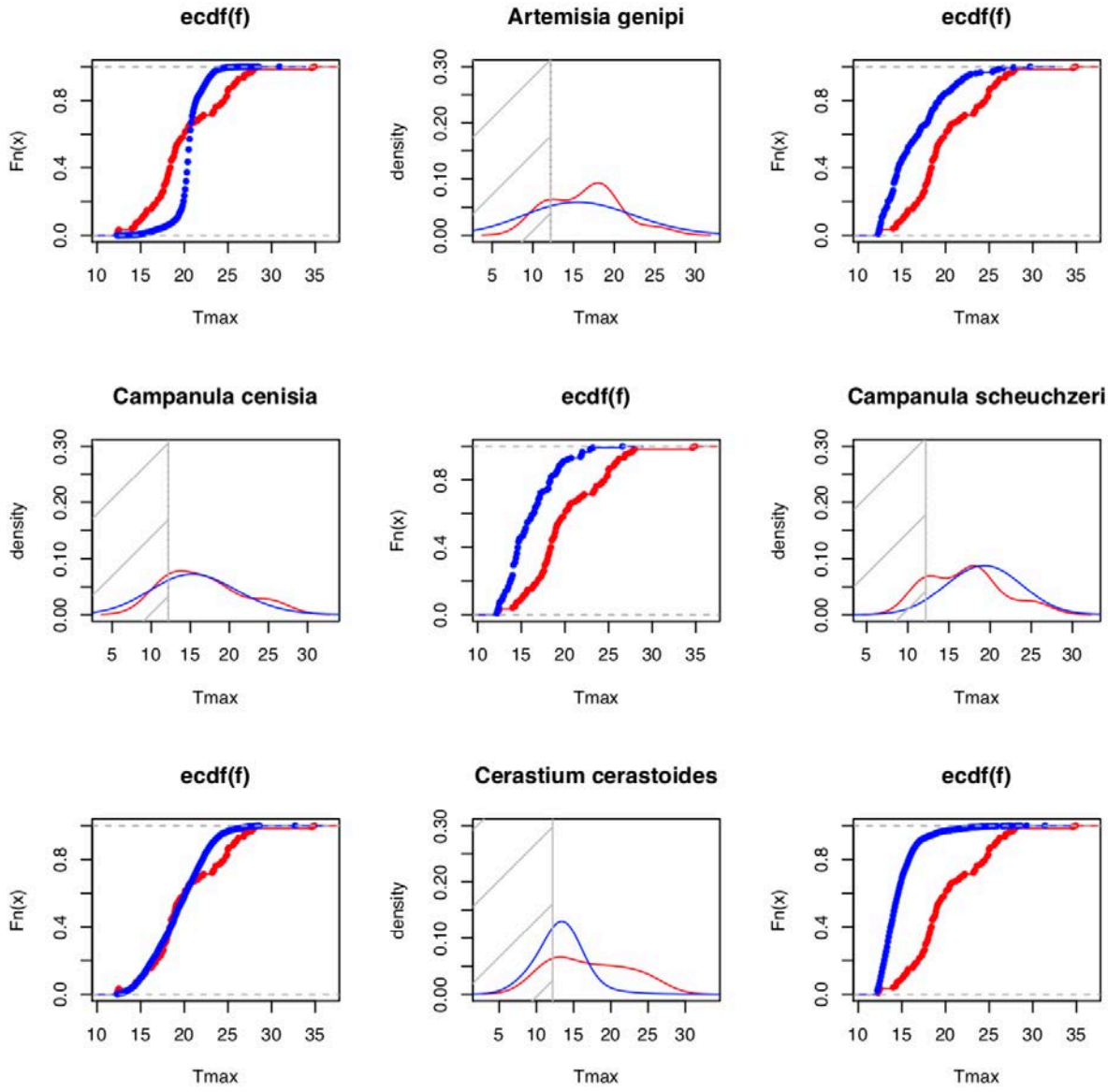

ecdf(f)
Fn(x)
Tmean
Lilium martagon
density
Tmean
ecdf(f)
Fn(x)
Tmean
Linaria alpina
density
Tmean
ecdf(f)
Fn(x)
Tmean
Pinus mugo
density
Tmean
ecdf(f)
Fn(x)
Tmean
Poa alpina
density
Tmean
ecdf(f)
Fn(x)
Tmean

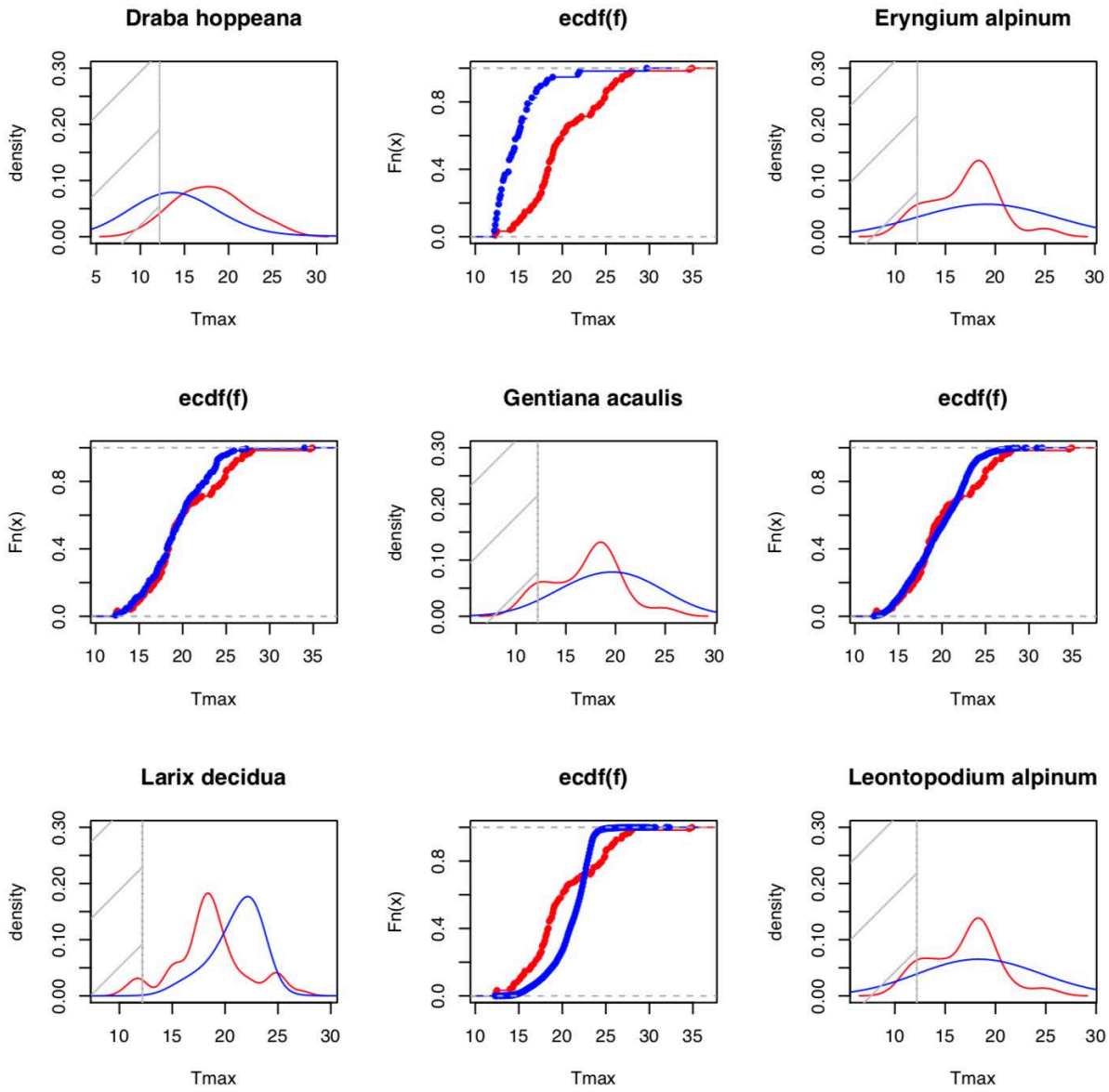

Ranunculus glacialis
density
Tmean
ecdf(f)
Fn(x)
Tmean
Rhododendron ferrugineum
density
Tmean
ecdf(f)
Fn(x)
Tmean
Salix herbacea
density
Tmean
ecdf(f)
Fn(x)
Tmean
Salix reticulata
density
Tmean
ecdf(f)
Fn(x)
Tmean
Saxifraga aizoides
density
Tmean

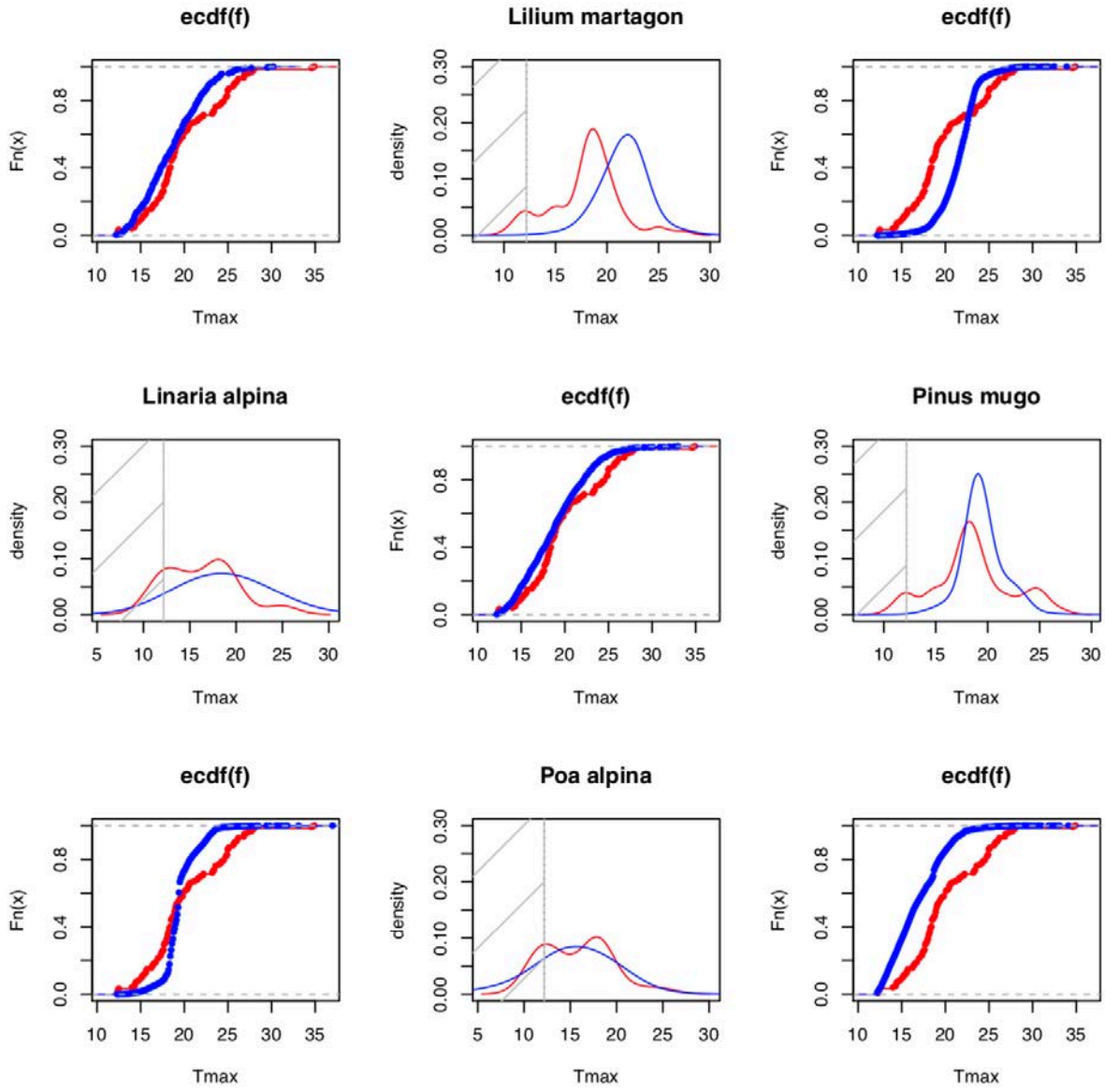

ecdf(f)
Fn(x)
Tmean
Saxifraga biflora
density
Tmean
ecdf(f)
Fn(x)
Tmean
Saxifraga oppositifolia
density
Tmean
ecdf(f)
Fn(x)
Tmean
Sempervivum montanum
density
Tmean
ecdf(f)
Fn(x)
Tmean
Silene acaulis
density
Tmean
ecdf(f)
Fn(x)
Tmean

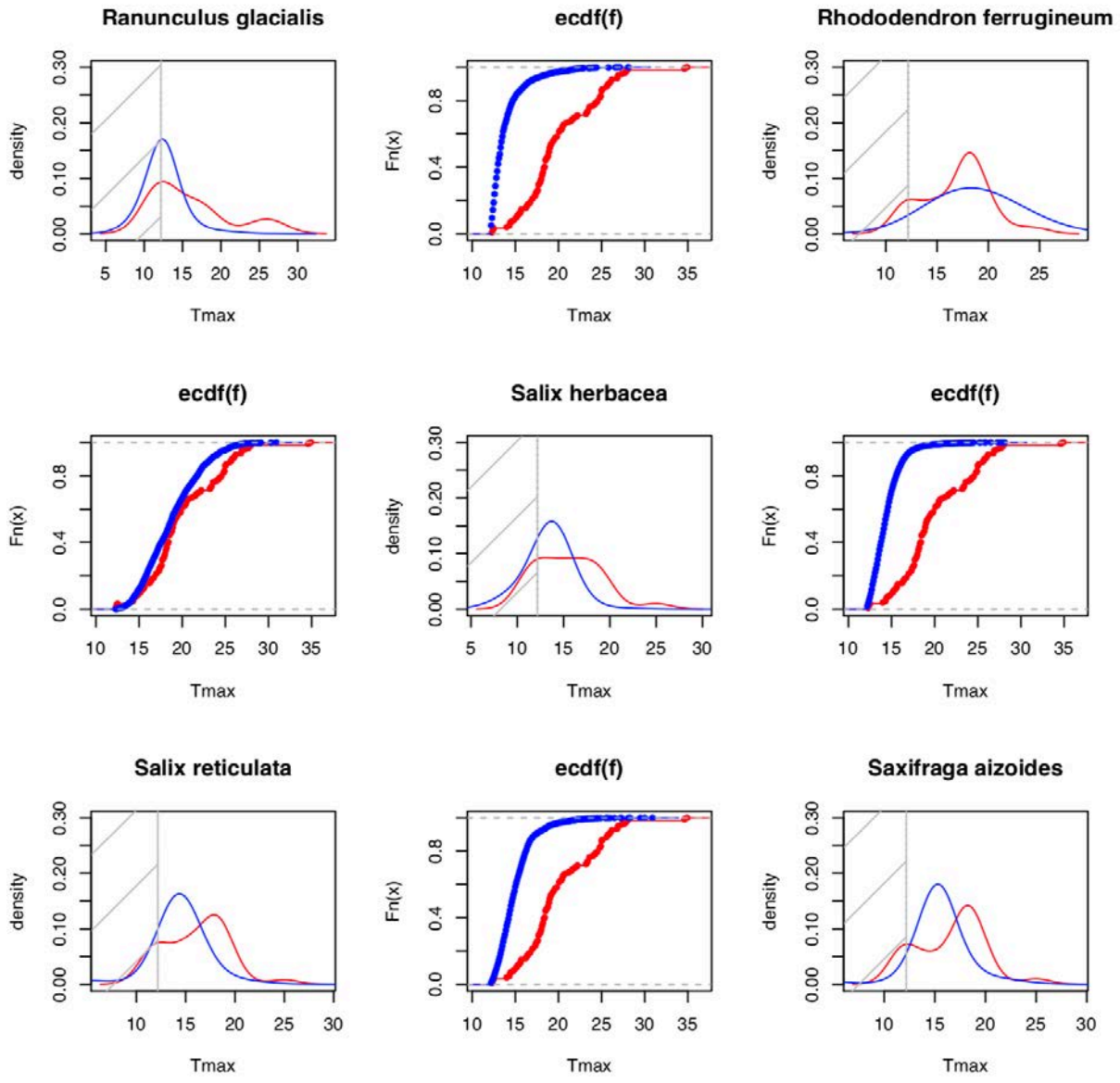
Annexes 5: Kernel density plot and cumulative functions for Tmax variable

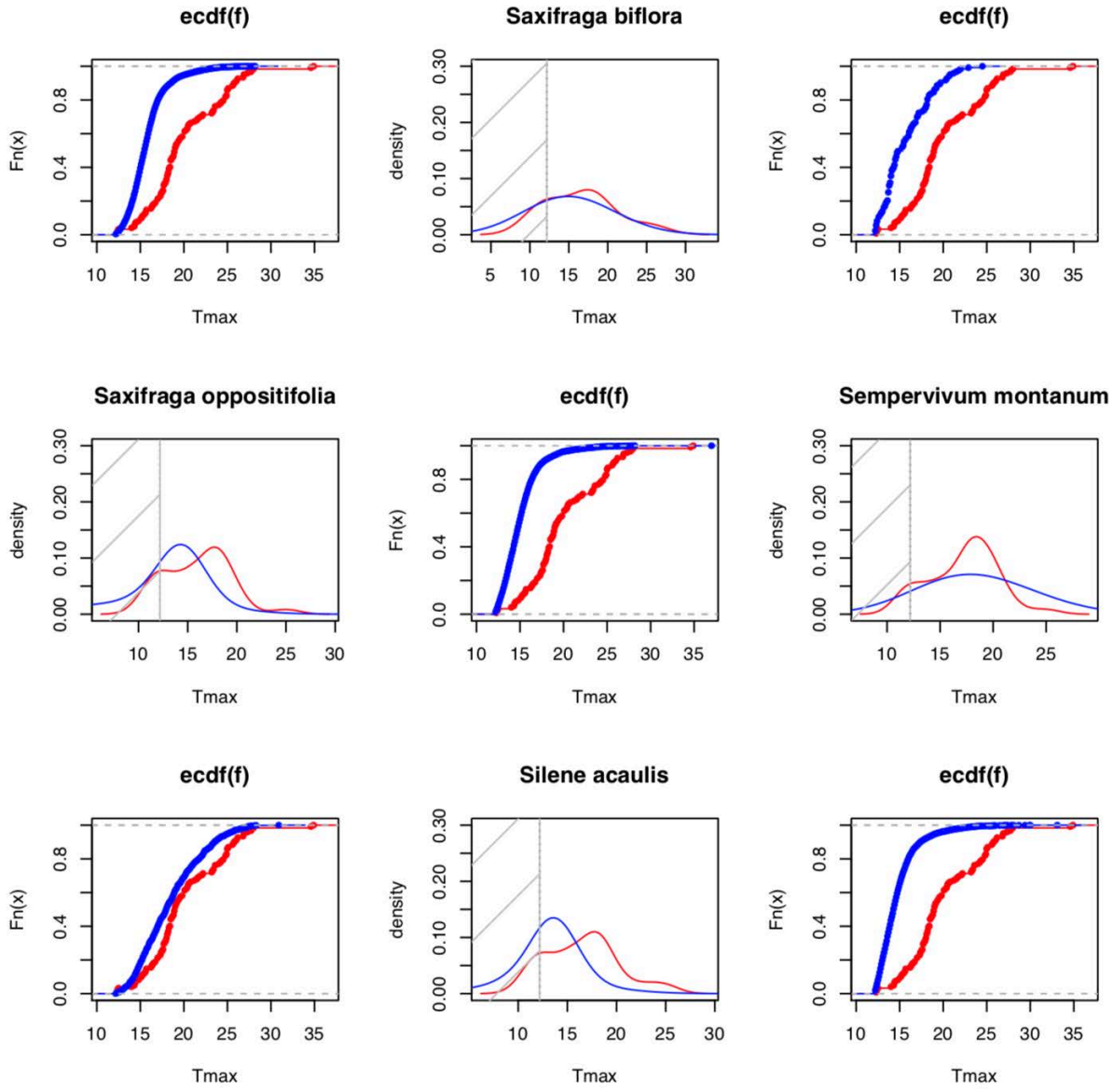



ecdf(f)
Fn(x)
Tmax
Artemisia genipi
density
Tmax
ecdf(f)
Fn(x)
Tmax
Campanula cenisia
density
Tmax
ecdf(f)
Fn(x)
Tmax
Campanula scheuchzeri
density
Tmax
ecdf(f)
Fn(x)
Tmax
Cerastium cerastoides
density
Tmax
ecdf(f)
Fn(x)
Tmax

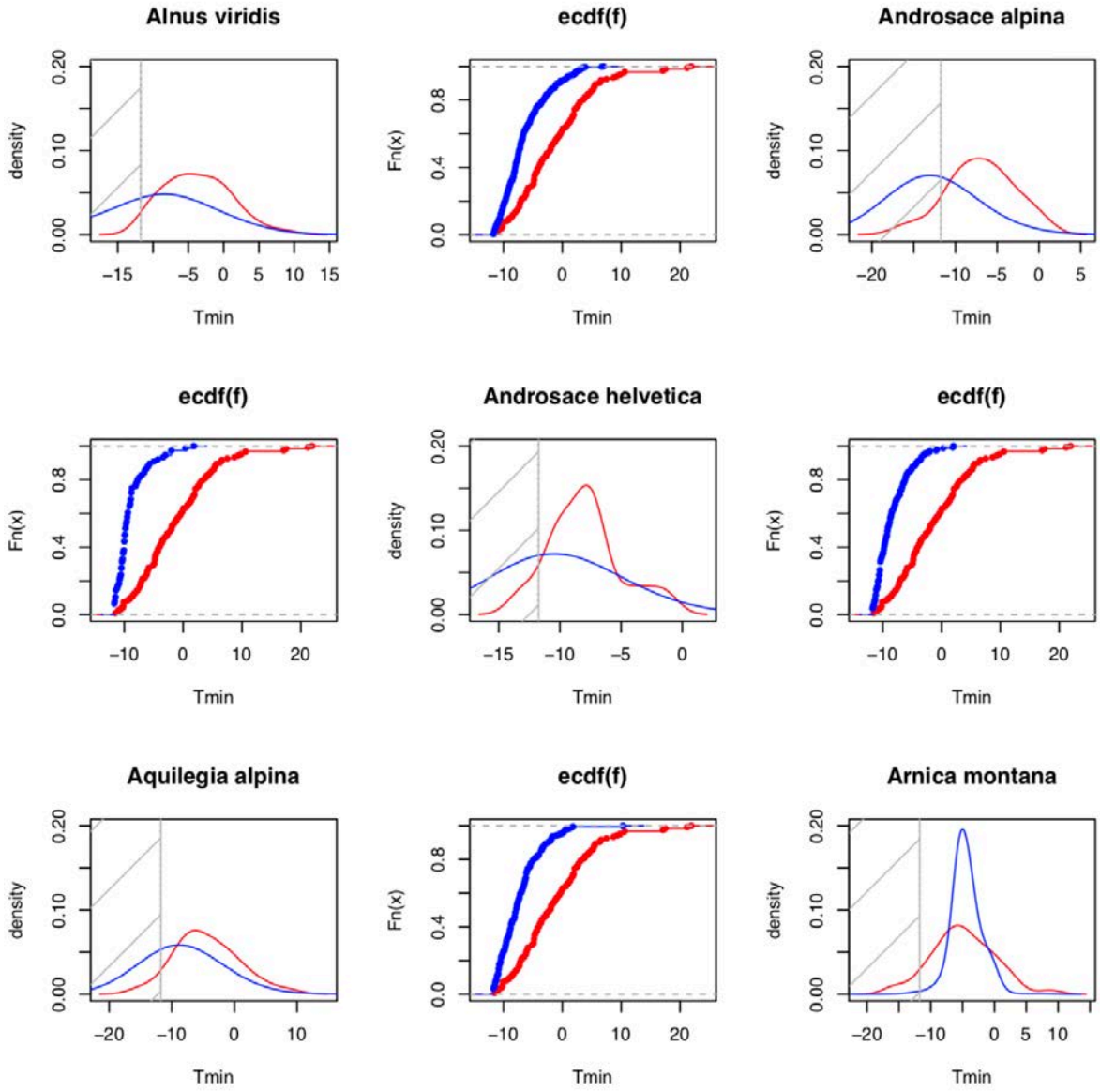

Draba hoppeana
density
Tmax
ecdf(f)
Fn(x)
Tmax
Eryngium alpinum
density
Tmax
ecdf(f)
Fn(x)
Tmax
Gentiana acaulis
density
Tmax
ecdf(f)
Fn(x)
Tmax
Larix decidua
density
Tmax
ecdf(f)
Fn(x)
Tmax
Leontopodium alpinum
density
Tmax

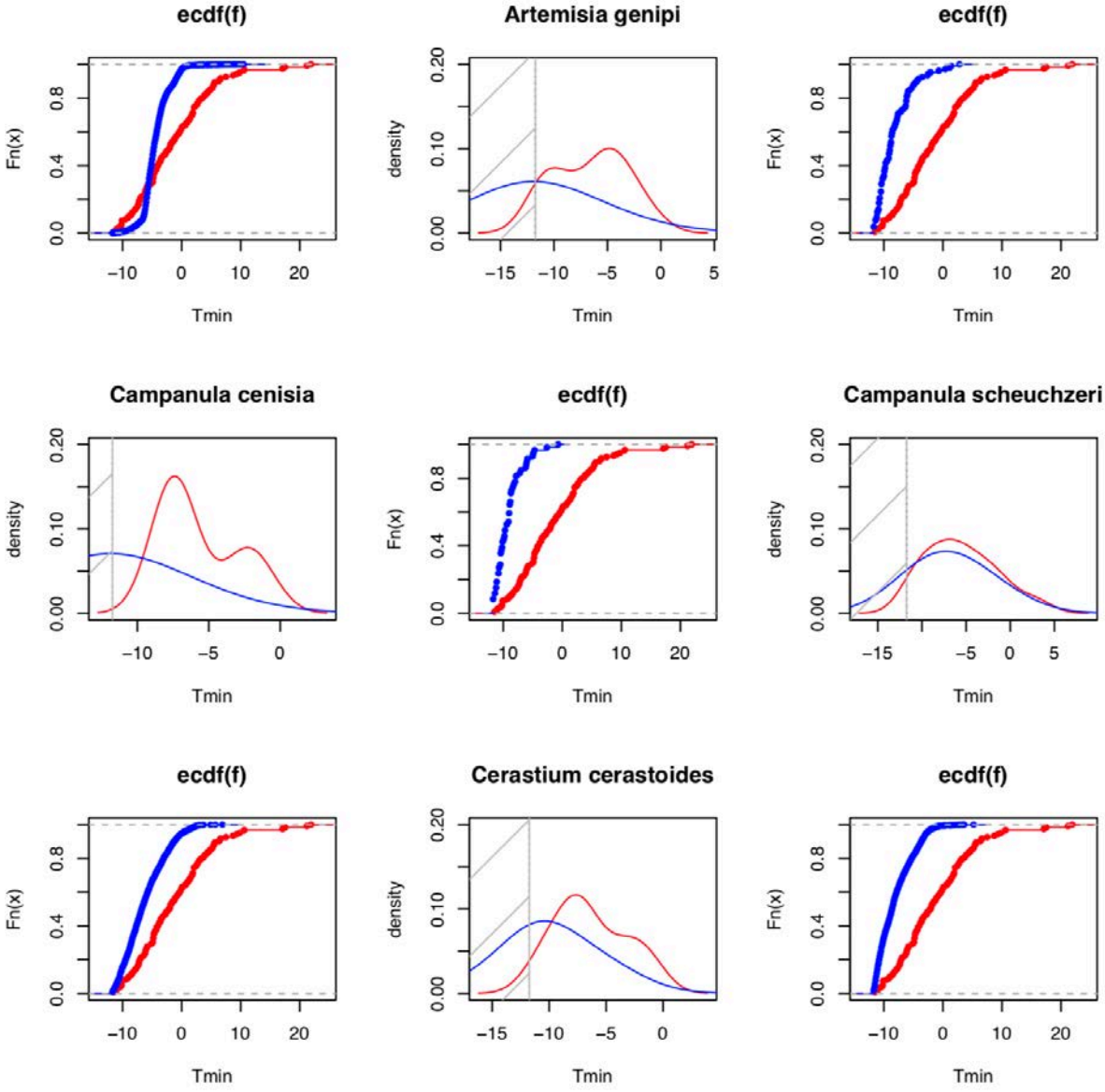

ecdf(f)
Fn(x)
Tmax
Lilium martagon
density
Tmax
ecdf(f)
Fn(x)
Tmax
Linaria alpina
density
Tmax
ecdf(f)
Fn(x)
Tmax
Pinus mugo
density
Tmax
ecdf(f)
Fn(x)
Tmax
Poa alpina
density
Tmax
ecdf(f)
Fn(x)
Tmax

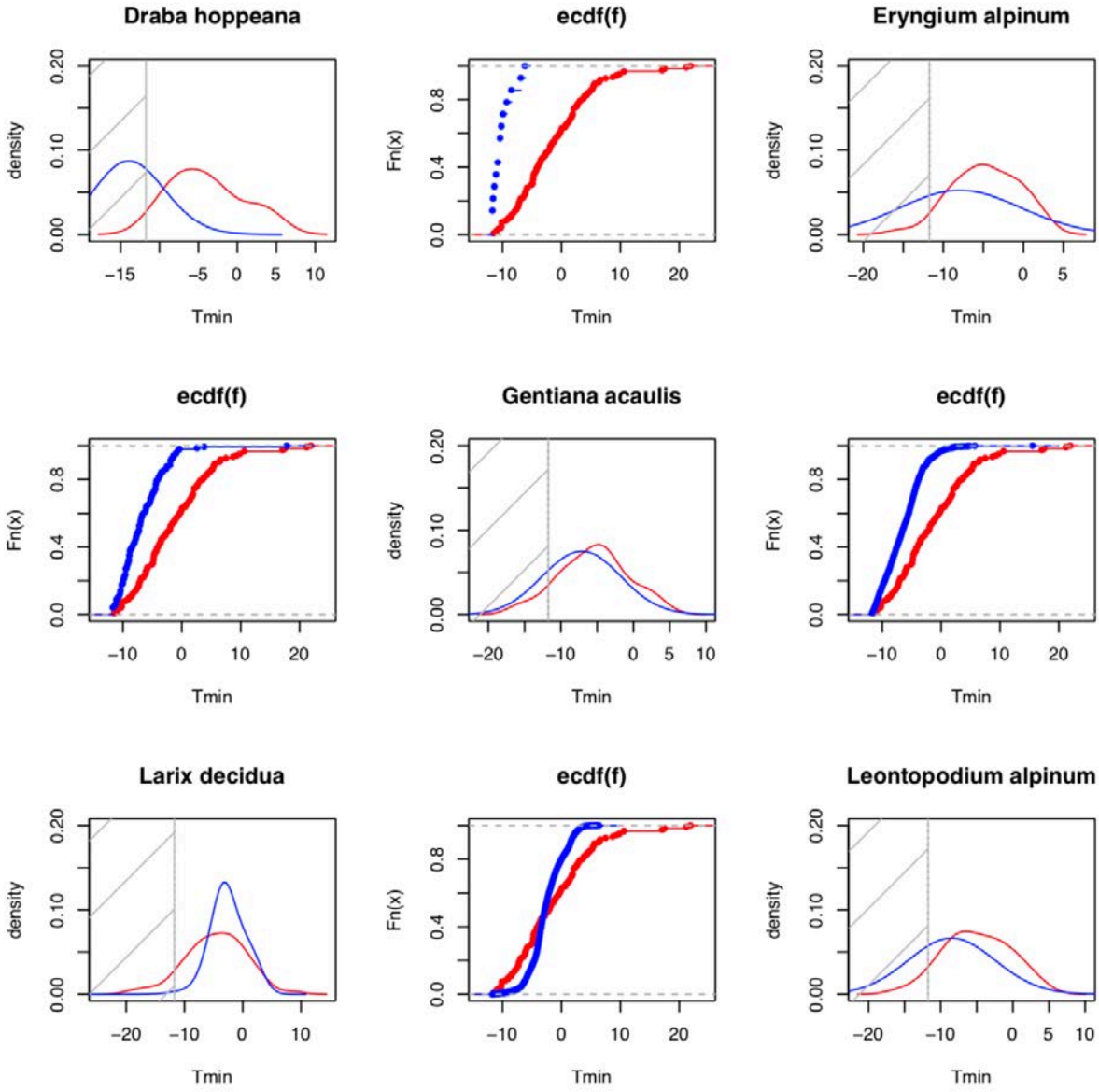

Ranunculus glacialis
density
Tmax
ecdf(f)
Fn(x)
Tmax
Rhododendron ferrugineum
density
Tmax
ecdf(f)
Fn(x)
Tmax
Salix herbacea
density
Tmax
ecdf(f)
Fn(x)
Tmax
Salix reticulata
density
Tmax
ecdf(f)
Fn(x)
Tmax
Saxifraga aizoides
density
Tmax

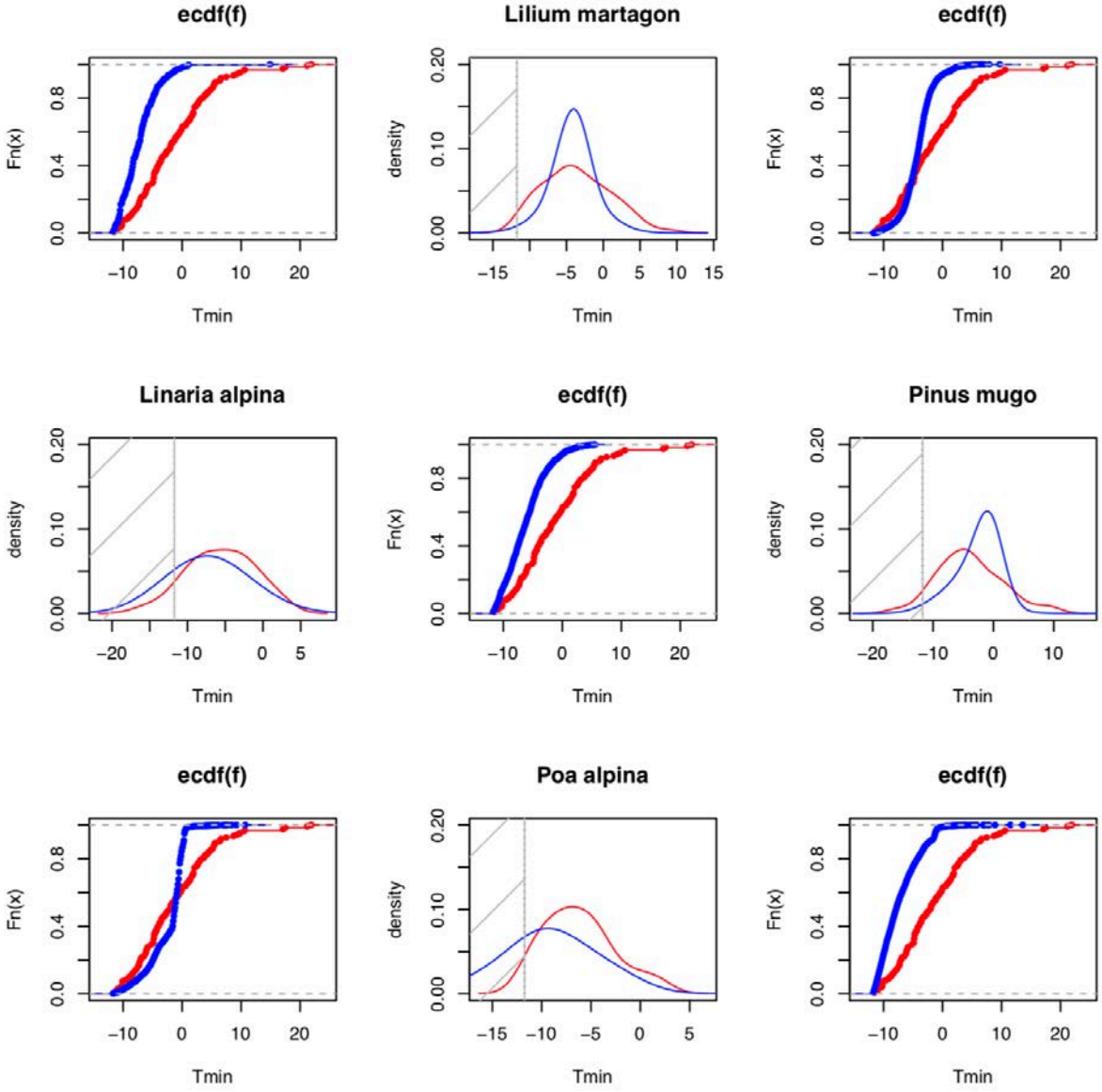

ecdf(f)
Fn(x)
Tmax
Saxifraga biflora
density
Tmax
ecdf(f)
Fn(x)
Tmax
Saxifraga oppositifolia
density
Tmax
ecdf(f)
Fn(x)
Tmax
Sempervivum montanum
density
Tmax
ecdf(f)
Fn(x)
Tmax
Silene acaulis
density
Tmax
ecdf(f)
Fn(x)
Tmax

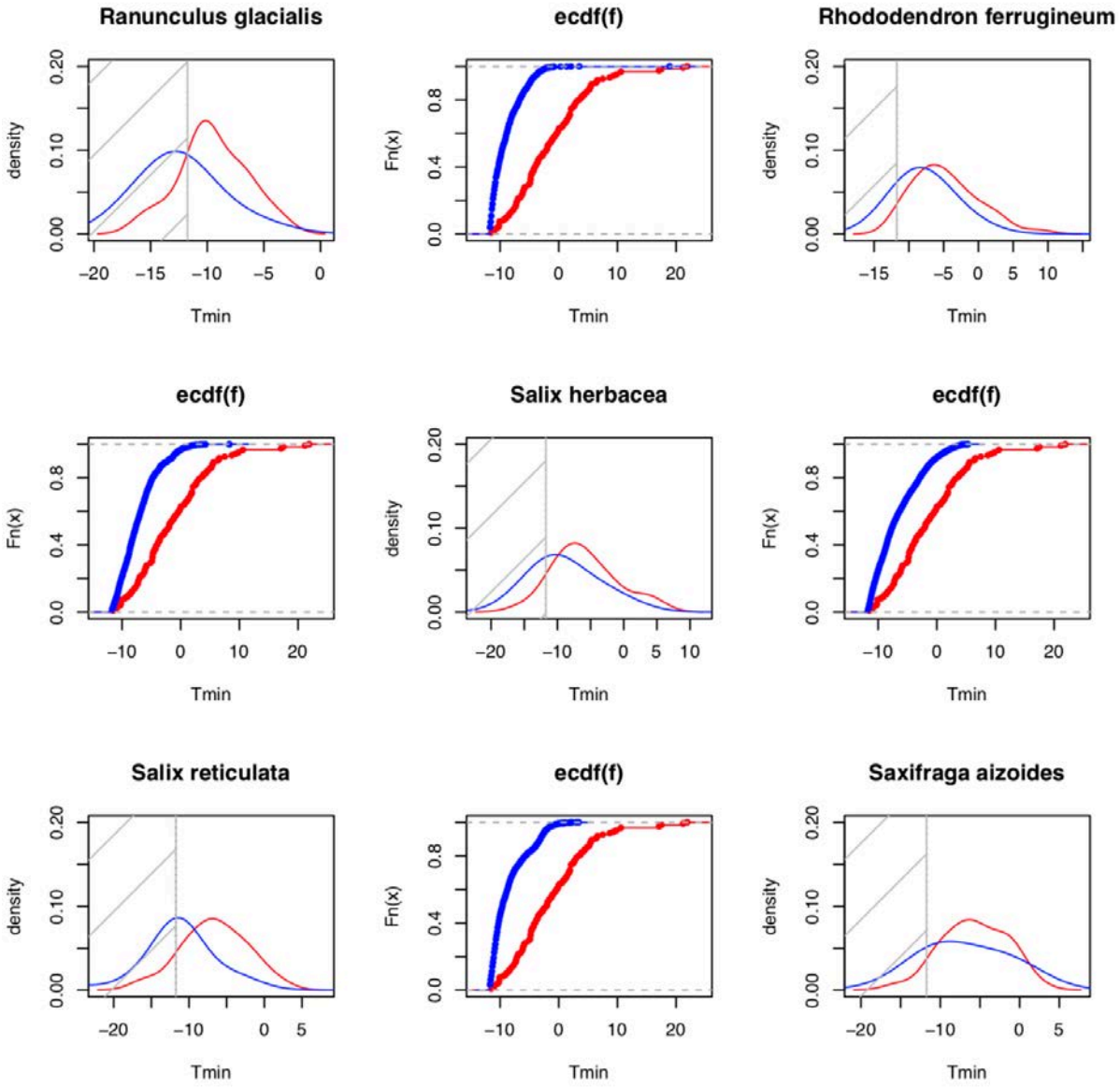
Annexes 6: Kernel density plot and cumulative functions for Tmin variable

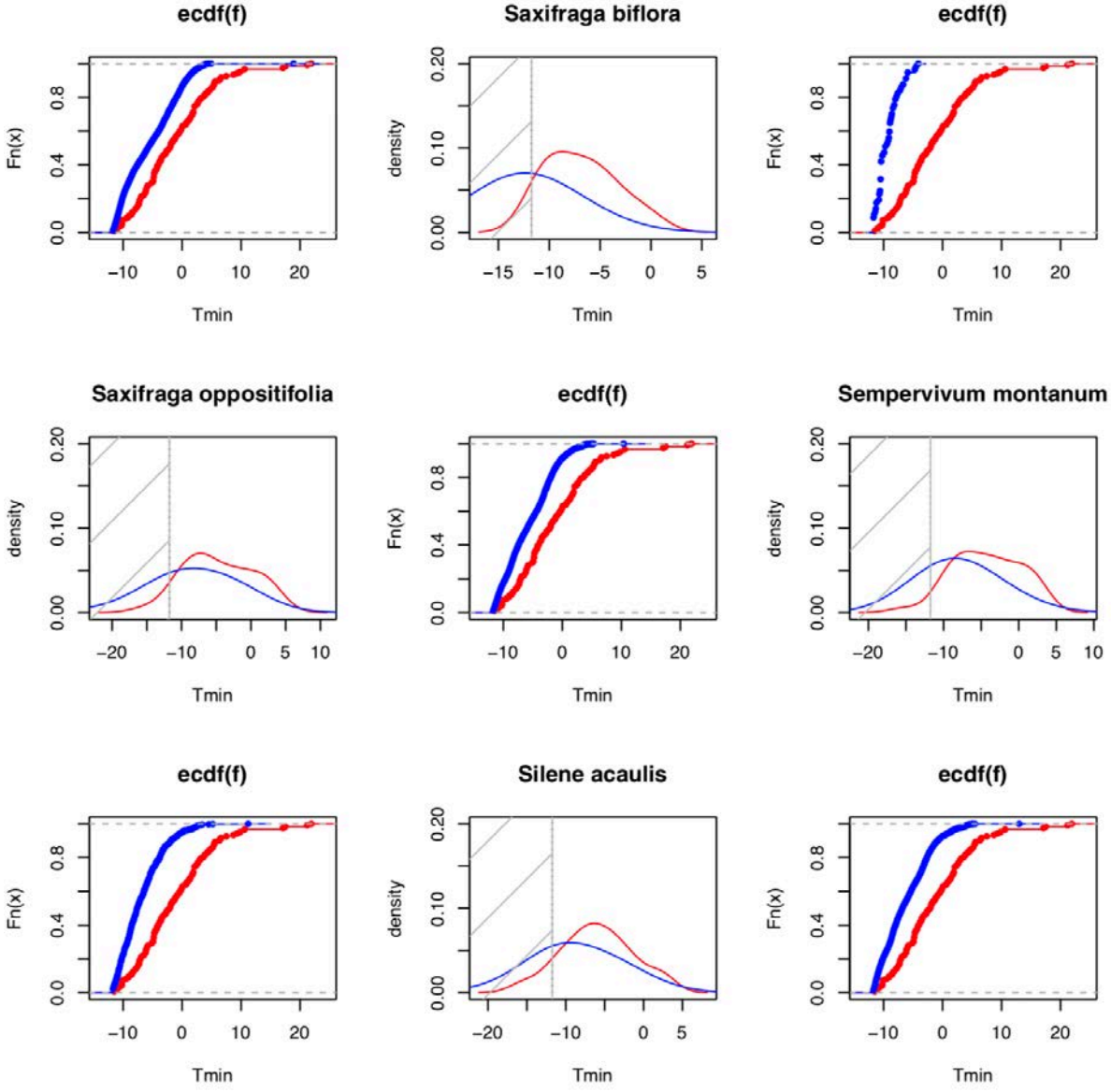



ecdf(f)
Fn(x)
Tmin
Artemisia genipi
density
Tmin
ecdf(f)
Fn(x)
Tmin
Campanula cenisia
density
Tmin
ecdf(f)
Fn(x)
Tmin
Campanula scheuchzeri
density
Tmin
ecdf(f)
Fn(x)
Tmin
Cerastium cerastoides
density
Tmin
ecdf(f)
Fn(x)
Tmin

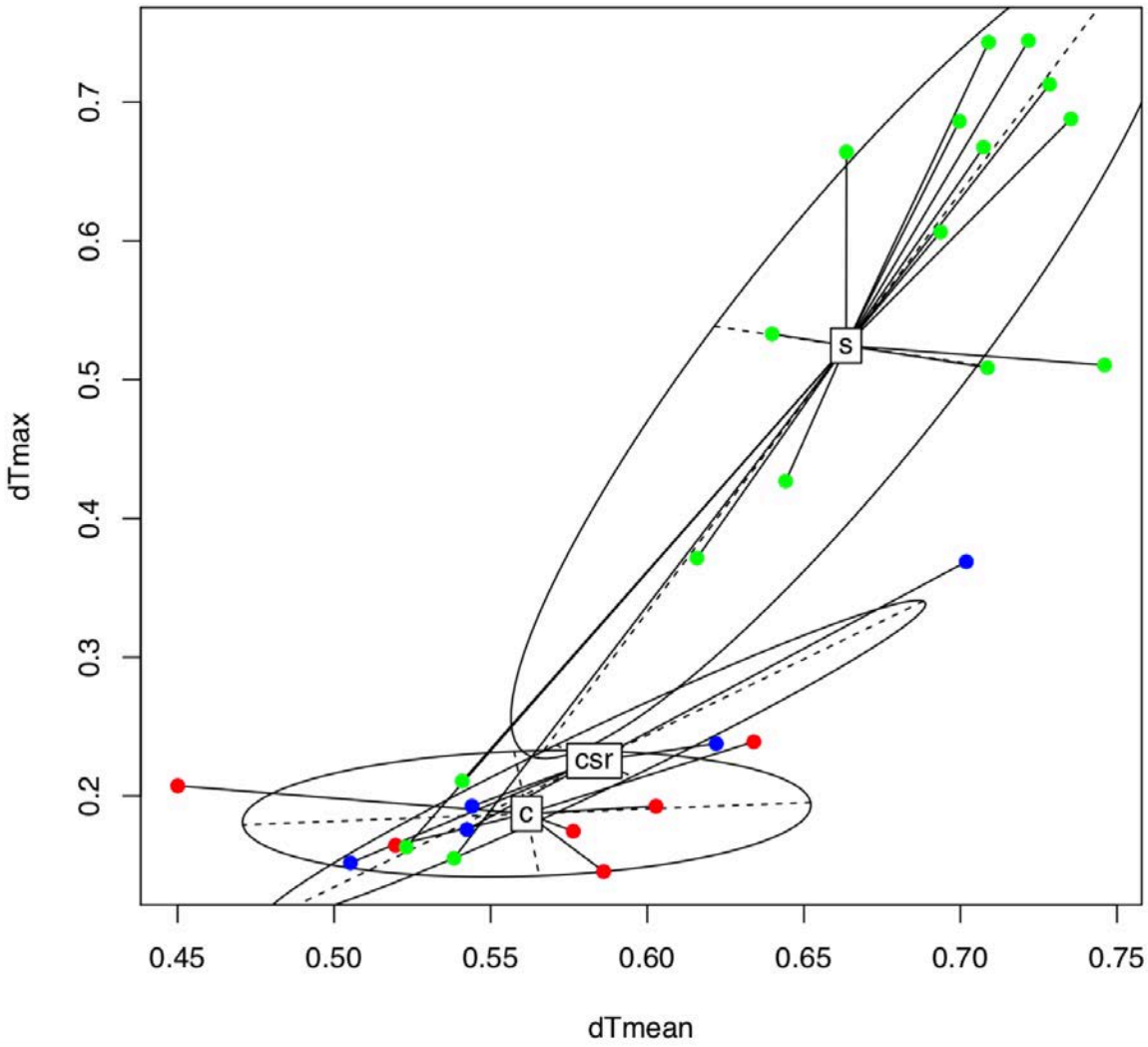

Draba hoppeana
density
Tmin
ecdf(f)
Fn(x)
Tmin
Eryngium alpinum
density
Tmin
ecdf(f)
Fn(x)
Tmin
Gentiana acaulis
density
Tmin
ecdf(f)
Fn(x)
Tmin
Larix decidua
density
Tmin
ecdf(f)
Fn(x)
Tmin
Leontopodium alpinum
density
Tmin

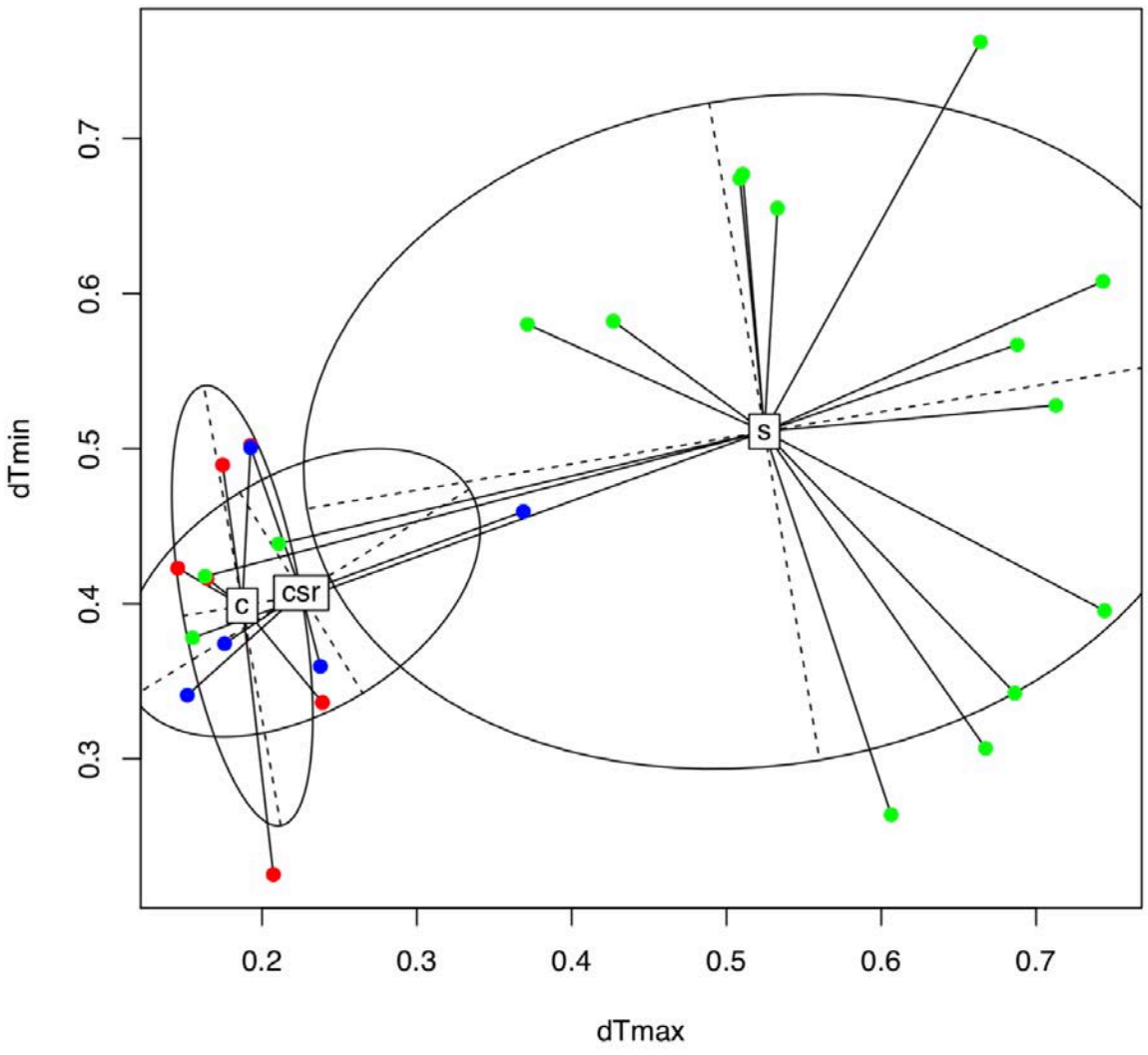

ecdf(f)
Fn(x)
Tmin
Lilium martagon
density
Tmin
ecdf(f)
Fn(x)
Tmin
Linaria alpina
density
Tmin
ecdf(f)
Fn(x)
Tmin
Pinus mugo
density
Tmin
ecdf(f)
Fn(x)
Tmin
Poa alpina
density
Tmin
ecdf(f)
Fn(x)
Tmin

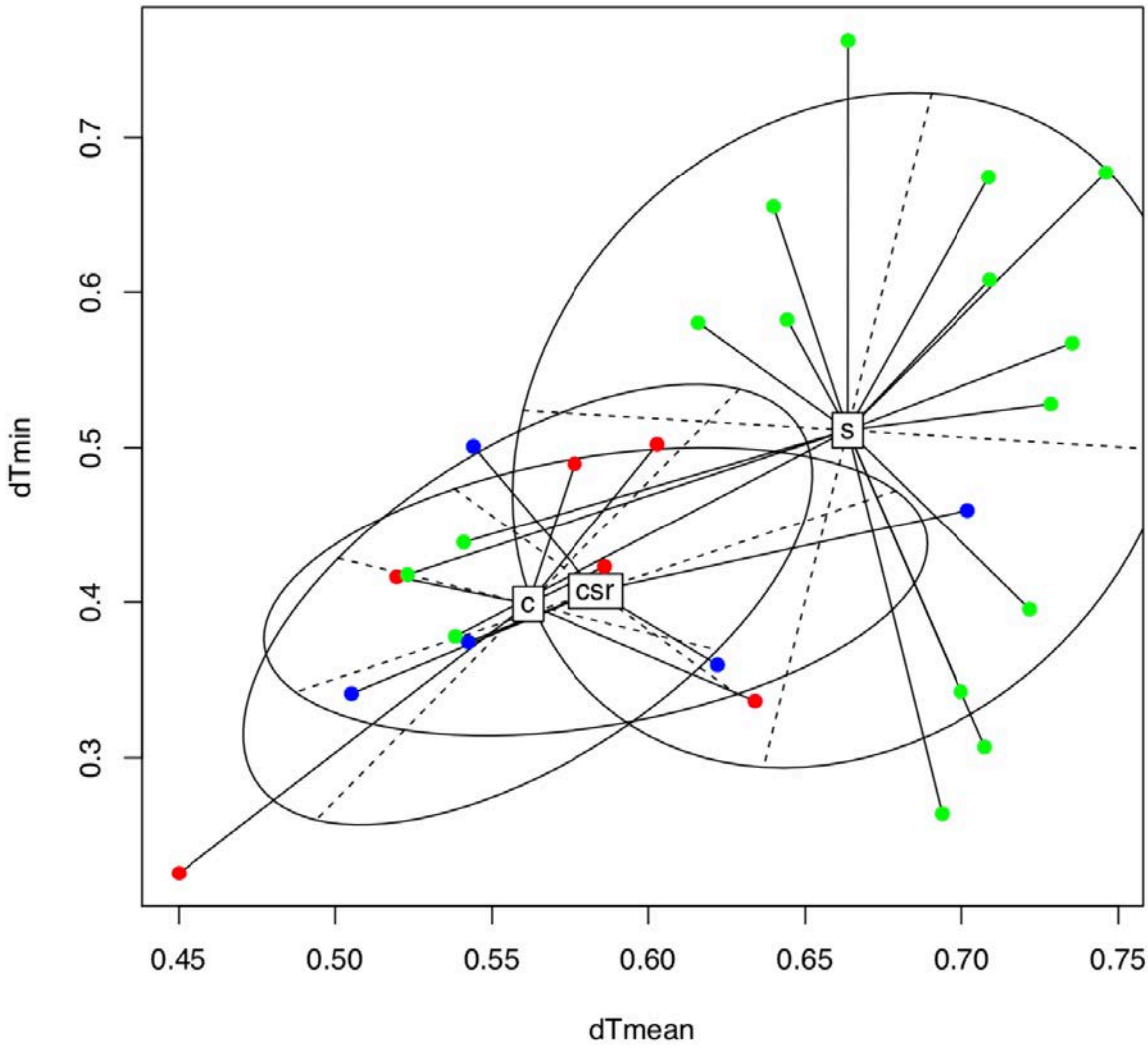

Ranunculus glacialis
density
Tmin
ecdf(f)
Fn(x)
Tmin
Rhododendron ferrugineum
density
Tmin
ecdf(f)
Fn(x)
Tmin
Salix herbacea
density
Tmin
ecdf(f)
Fn(x)
Tmin
Salix reticulata
density
Tmin
ecdf(f)
Fn(x)
Tmin
Saxifraga aizoides
density
Tmin


ecdf(f)
Fn(x)
Tmin
Saxifraga biflora
density
Tmin
ecdf(f)
Fn(x)
Tmin
Saxifraga oppositifolia
density
Tmin
ecdf(f)
Fn(x)
Tmin
Sempervivum montanum
density
Tmin
ecdf(f)
Fn(x)
Tmin
Silene acaulis
density
Tmin
ecdf(f)
Fn(x)
Tmin

Annexe 7: S-class plots for CSR strategies




dTmin
0.3
0.4
0.5
0.6
0.7
dTmax
0.2
0.3
0.4
0.5
0.6
0.7
C
CSR
S


dTmin
0.3
0.4
0.5
0.6
0.7
0.45
0.50
0.55
0.60
0.65
0.70
0.75
dTmean
s
csr
c