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Testing the Abundant Centre Hypothesis for alpine species along environmental gradients

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Zusammenfassung

Die “Abundant Centre Hypothese” (ACH) geht von einer Normalverteilung der Artenpräsenz innerhalb des Vorkommens einer Art aus. Arten besitzen ihr Optimum im Zentrum ihrer ökologischen Nische und nehmen dann in ihrem Vorkommen graduell ab, je weiter man sich von dem Optimum entfernt. Des Weiteren verdichten sich die Anzeichen, dass es in den Alpen zu einer großflächigen Migrationsbewegung von Pflanzenarten kommt, da die steigenden Temperaturen für eine Verschiebung der ökologischen Nische in kühlere Bereiche sorgen. In der folgenden Arbeit wurde anhand von Vegetationsaufnahmen entlang des Höhenverlaufs des Schrankogels im Tiroler Alpenraum die Präsenz-Verteilung von 57 alpinen und nivalen Pflanzenarten ausgewertet und auf eine Normalverteilung entlang der Gradienten Seehöhe, durchschnittliche Jahrestemperatur und Dauer der Schneebedeckung überprüft. Außerdem wurde der Zusammenhang der Präsenzverteilung mit festgestellten Migrationsbewegungen alpiner Arten mittels linearer Regressionen überprüft. Im Vergleich zwischen den Gradienten ergab sich ein starker Unterschied bezüglich der Artenpräsenz. Im Gradienten der durchschnittlichen Jahrestemperatur wiesen 53% der Arten eine Normalverteilung aus, im Gradienten der Seehöhe weisen 18% der Arten und im Gradienten der Dauer der Schneebedeckung wiesen 2% der untersuchten Arten eine Normalverteilung der Präsenz auf. Im Vergleich zu den festgestellten Migrationsbewegungen von Pflanzenarten konnten bis auf die Beziehung zwischen der Bewegung des unteren Endes des Vorkommens der Arten („Rear edge“) und der kalkulierten Schiefe der Präsenzvorkommen im Gradienten der durchschnittlichen Jahrestemperatur, keine signifikanten Zusammenhängefestgestellt werden. Die starken Unterschiede zwischen den drei Gradienten bezüglich der Anzahl der normalverteilten Arten lässt darauf schließen, dass die ökologische Nische vor Allem durch die durchschnittliche Jahrestemperatur bestimmt wird und die Arten entlang dieser ihre Normalverteilung beibehalten. Für zukünftige Überprüfungen der ACH sollte daher vor Allem die Betrachtung der durchschnittlichen Jahrestemperatur eine wichtigere Rolle spielen, als die Konzentration auf den Höhengradienten.

Abstract

The ‚abundant centre hypothesis' (ACH) assumes a normally-distributed presence of species in a species' range. Species occur possess their optimum in the centre of their ecological niche and decrease in presence gradually the further away they are from their optimum. Furthermore, increasing observations detect a large-scale migration of plant species in alpine areas, as the rising temperatures lead to an upward shift of ecological niches towards cooler areas. In the following study, the distribution of presence of 57 alpine and nival plant species was checked, with the data deriving out of vegetation surveys along the mountain ridge of Mt. Schrankogel in the Tyrolean alps. The distribution of presence was checked against the gradients of elevation [m.a.s.l.], annual mean temperature [°C] and snow cover duration [d]. Additionally, the connection between the distribution of presence and determined migration movements of alpine species was checked using linear regressions. In comparison between the three gradients large differences in the presence distribution of species occurred. At the gradient of annual mean temperature 53% of the target species were normally distributed, at the gradient of elevation 18% and at the gradient of duration of snow cover 2% of the target species were normally distributed. The executed linear regressions could find almost no significant relation between the calculated skewness of species presence distribution and the determined migration movements, the only exception was the relation between rear edge movements of species and the calculated skewness at the gradient of annual mean temperature. The large differences regarding the distribution of presence between the three gradients, make the gradient of annual mean temperature seem to be the main predictor for species' ecological niches and that species maintain their normal-distribution along this gradient. For future studies regarding the ACH the annual mean temperature should play a more important role than the concentration on the gradient of elevation.

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Key Words

Abundant centre hypothesis, alpine plants, ecological gradients, ecological niche, presence distribution, species migration, Tyrolean Alps

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I Introduction

The 'abundant centre hypothesis' (ACH) assumes a general pattern of spatial distribution of a species´ abundance within its range (Brown 1984). Thereby, it projects the species´ ecological niche as defined by the combination of relevant abiotic and biotic factors into biogeographic space. The ecological optimum of a species´ is assumed to be in its range centre (Colwell and Rangel 2009). From there on, abiotic and biotic factors become less suitable in all directions and fade out towards the range edges. This decline in suitability is accompanied by decreases in the abundance and fitness of the species. This pattern predicted by the ACH has been confirmed only for a subset of investigated species. This mismatch between the theoretical predictions and the empirical data is often explained with the heterogeneity of microhabitats (Kulonen et al. 2018; Scherrer and Körner 2011), the phylogenetic history of a species (Pérez-Collazos et al. 2009; Pironon et al. 2015), or the anthropogenic-driven land-use change (Boakes et al. 2018; Hahn et al. 2012; Yang et al. 2021).

However, the ACH does not only apply along latitudinal or longitudinal gradients, but also to elevation gradients in mountain areas (Brown 1984), adding a third dimension. Thereby, the ecological optimum can then be expected at intermediate environmental gradients with populations upwards or downwards experiencing increasingly worse conditions and, consequently, a reduction in abundance and fitness. As geographic and climatic centres are not always concurring (Pironon et al. 2015) the testing of multiple gradients can be advantageous. The gradients of elevation and mean annual temperature are common when it comes to testing the assumptions of the ACH and are important drivers defining ecological niches (e.g. Abeli et al. 2014; Angert and Schemske 2005; Daco et al. 2021; Jump and Woodward 2003; Pironon et al. 2015; Sagarin et al. 2006). Additionally, the gradient of snow cover duration becomes an important factor for the development of plants especially in alpine environments and can create microhabitats like snow beds, hampering or fostering the development of plants and their distribution (Brown and Robinson 2011; Dullinger et al. 2011; Ladinig et al. 2013; Rammig et al. 2010). Measuring the local climate is important, because the small-scale climate is different than the climate projected on large scale simulations (Lenoir and Svenning 2015; Scherrer and Körner 2010). With this testing of multiple gradients, it can be detected if it would be better for future studies to focus on the distribution in the elevational gradient, climatic gradients or the combination of them.

Currently large migration movements have been shown in alpine environments worldwide (Auld et al. 2022; Freeman et al. 2018; Jiménez-García et al. 2021; Jump et al. 2012) and climate seems to be the main driver of plant community changes in temperate regions (Auffret and Svenning 2022). Over the last 30 years a mean increase of 2.5°C in spring and summer months could be observed (Marty and Meister 2012). Simulated snowmelt trends show a strong change towards earlier snowmelt dates. The growing season could be extended to almost a third by the end of the century (Vorkauf et al. 2021). With the warming, climate mountain environments get more suitable for species from lower elevations which are commonly more competitive (Bertness and Callaway 1994), including advancing treelines in alpine regions (Carlson et al. 2017; Frei et al. 2023; Hohensinner et al. 2021). This leads to an increase in species diversity (Cannone and Pignatti 2014; Rammig et al. 2010; Rogora et al. 2018; Rumpf et al. 2019a; Steinbauer et al. 2018; Walther et al. 2005) and, thus, to an altered competition regime potentially altering the abundance and fitness of resident plants, which might depart from a former possible abundant-centre distribution (Iseli et al. 2023; Staude et al. 2022). Furthermore, displacements of high-elevation plants which are well adapted to harsh abiotic conditions but less so to inter-specific competition (Gottfried et al. 2012; Kulonen et al. 2018; Rixen et al. 2022) and some degree of homogenization of mountain vegetation are likely consequences (Cannone and Pignatti 2014; Jump et al. 2012; Staude et al. 2022).

The vegetation at Mt. Schrankogel has been observed since 1994 for the GLORIA-Project (Global Observation Research Initiative in Alpine Environments; https://www.gloria.ac.at/home). Current trends at the observation area show first signs of a species redistribution and changes in environmental factors. On Mt. Schrankogel overall species richness increased by 10% between 1994 to 2004 (Pauli et al. 2007), but this trend is slowing down in the last decade as disappearance events start to increase (Lamprecht et al. 2018) and could become more often with rising temperatures (Wiens 2016). This general pattern hides opposing trends: Range expansions of alpine taxa are paralleled by range contractions of nival and subnival species, but no immigration events of lower-range species could be observed so far (Pauli et al. 2007). Range dynamics increase with lower elevations (Rumpf et al. 2018), indicating low-elevation alpine plant communities being the first that could experience strong vegetational changes. The species that increased their ranges the most were mostly nutriphilous and thermophilic (Rumpf et al. 2018), leading to the possibility of a change in the nutrient cycle. The environmental drivers of these migratory patterns are hardly known and seem to differ from site to site, from species to species and between leading and rear edges (Felde et al. 2012; Freeman et al. 2018; Rumpf et al. 2019b), but the tendency seems to be uniformly around Europe (Brown and Robinson 2011; Staude et al. 2022).

These recent changes add time as the fourth dimension. The concept of 'climatic niche conservatism' (i.e., the maintenance of species' climatic niches over time), can be used to classify species´ responses to climatic changes over time (Amano et al. 2014). Plants can respond to environmental changes (Brown and Robinson 2011; Marty and Meister 2012; Vorkauf et al. 2021) either by migration to keep track with the template of suitable conditions or adapting to be able to stay in place (Amano et al. 2014). Lenoir and Svenning (2015) labelled these two processes as 'movement' and 'persistence' and defined six broad categories of species range shifts under these two factors. Every species can have a high/low persistence rate and a high/low migration rate, the combination of these factors can lead to a special pattern of range shifts under changing environmental conditions.

1. High persistence rate and high movement rate (expand)
2. Low persistence rate and a low movement rate (retract) -> can lead to a crash and finally extinction
3. Low persistence rate but a high movement rate (march)
4. High persistence rate but a low movement rate (lean) (Lenoir and Svenning 2015)

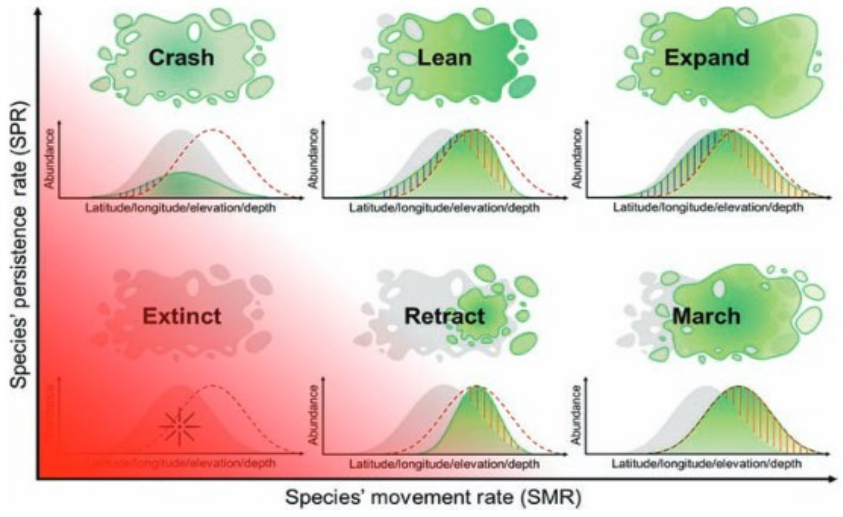

Figure I-1: Six broad categories of species range shifts and their positions in a bi-dimensional space of species persistence rate and movement rate (Lenoir and Svenning 2015, p. 24)

Taxa with high dispersal abilities (e.g. insects, birds) can evade changing environments faster than slower moving species like plants, making plants especially vulnerable to climate change (Lenoir and Svenning 2015; Maggini et al. 2011). The speed of population dynamics lags the warming climate, indicating that many species will grow in areas that already became climatically unsuitable to them and don't follow their climatic niches, creating an "extinction debt" (Dullinger et al. 2012b; Lenoir and Svenning 2015). The increase of species on mountainsides could hide this effect and lead to underestimation of range losses until tipping points will be reached and species must pay off their extinction debts (Rumpf et al. 2019a), especially species with leaning ranges are vulnerable (Lenoir and Svenning 2015). From the testing of the target species' distribution patterns, it can be derived if a species is still colonising its optimal range or if said extinction debt or even a colonization credit has formed. Species with high movement and persistence rates could be able to stay in their equilibrium and adapt towards the changing climate obtaining a normal-distributed occurrence, while species with lower dispersal and movement rates are more likely leaning upward and forming a credit or debt.

By the end of the century, it is expected that 50% of alpine species will reduce their range size, especially endemic plants face high risks (Dullinger et al. 2012b), as the endemism rates are generally rising with elevation (Steinbauer et al. 2016). Currently it is not known which species and under which conditions are 'migrators, 'adapters' or both. These patterns are strongly influenced by local microclimate and microhabitat structures (Maggini et al. 2011), suggesting an urgent need for data on presence and fitness patterns in alpine regions under climate change.

Right now, most studies concentrate on the upward movement of species in elevation but a possible migration of species to track climatic factors with the incorporating of microhabitats could also lead to migration patterns that current simulations do not project, like downwards or sidewards as some studies imply (Cannone and Pignatti 2014; Crimmins et al. 2011). The redistribution of species implies multiple future challenges in ecological, physiological, genetic and biogeographical perspectives, with unknown effects on the affected ecosystems (Bonebrake et al. 2018) and already established conservation management plans may not fit anymore (Shoo et al. 2006). Conservation science must develop new strategies for those rising challenges. Future range shifts can widely deviate from present scenarios when new biotic interactions arise with newly introduced plant communities (Alexander et al. 2015; Freeman et al. 2018). Long- and short-term monitoring of vegetation in combination with climate on the local scale is an important approach to study the effects of climate change and species migration (Rogora et al. 2018).

This study is based on monitoring data of the presence/absence of 57 species from 900 sites at a single mountain over three years to compare their empirical distribution patterns with predictions of the ACH and relate deviations to the migration ability of species. If the presences are distributed as it would be thought after the ACH a normal distributed curve would be expected. Hence, if the skewness of these curves was checked, possible shapes, like a 'leaning' uphill could be detected and therefore migratory patterns derived out of the data. The study of Rumpf et al. (2018) dealt already with the extent of migration in alpine species in Austria and provides sufficient data on species' migratory patterns in the last decades, this data can be compared to the data found on Mt. Schrankogel, to see if some migratory movements show a sufficient spread in multiple locations. In detail, we ask the following questions:

i) Does the distribution of species´ presence and absence along several environmental gradients match the predictions of the ACH at Mt. Schrankogel?

ii) Is the magnitude of dis-agreement between theoretical predictions (based on the ACH) and the empirical distribution (across the environmental gradients) related to the ability of species to adapt their ranges under climate change (i.e. to empirical migration rates)?

II Methods

1. Study site

The masterthesis is embedded in the project "MICROCLIM". A cooperation between the Österreichische Akademie der Wissenschaften (ÖAW), the Coordination of the GLORIA-Project, the University of Innsbruck and the University of Vienna. The goal of the project is to simulate the range dynamics of alpine plants all over the 21st century, so possible rescue effects of the alpine topographic-microclimate variability can be identified. Special conservation measures can potentually be set up afterwards to conserve the endangered alpine flora of Europe (Österreichische Akademie der Wissenschaften 2021). The project comprises three workpackages. The Masterthesis is associated with workpackage II – Task 7, which concentrates on the landscape scale, with a monitoring of the vital rates of selected vascular plant species on Mt. Schrankogel in Tyrol, Austria to be used to parameterize dynamic modelling of future vegetation changes at this mountain (Österreichische Akademie der Wissenschaften 2023).

Mt. Schrankogel is located in the Ötztal in Tyrol in the western Austrian Alps (47°02'39.1''N, 11°05'56.0''E). With a height of 3497 m.a.s.l. it is one of the highest mountains in the Tyrolian alps. The climate is temperate sub-continental, the annual average temperature is 2.5°C with an annual precipitation of 889mm (meteorological station Obergurgl, 1950 m.a.s.l., 20 km south of the study area). The slope of the mountain shows a continuous and uninterrupted change of vegetation types and is accessible throughout, which makes it well-suited to project changes in alpine vegetation. The lower elevations are dominated by pastures and nutrient-rich meadows as well as small trees and shrubs, while grasses and sedges dominate at intermediate elevations. At above 3100 m.a.s.l soil is largely lacking, large gravel and rock fields are the prevailing habitat. Only well-adapted nival and alpine species can survive under these conditions.

Figure II-1: Map of the Alps with the location of the study site in western Austria (red circle) (Veyret et al. 2024)

II-1 Data collection

During summer in 2021 and 2022 900 plots of 1m x 1m covering an elevational gradient from 1800m to 3450m have been established on Mt. Schrankogel, covering non-forest subalpine, alpine and nival habitats. The plot positions were selected with a stratified random sampling design, considering elevation, topography, solar radiation and the covered plant communities, creating a homogenous pattern that covers evenly all existing habitats around Mt. Schrankogel. At each plot a temperature

data logger was buried at 10 cm depth and recorded the temperatures at hourly intervals, from autumn 2021 to autumn 2023.

At every plot the cover of all vascular plants inside the 1m x 1m squares was estimated using a modified Braun-Blanquet scale and transformed to presence/absence data.

Within the MICROCLIM project a set of 57 abundant species was selected to be a representative sample of all growth form strategies in the area. This set was also used for the thesis. The nomenclature followed the "Exkursionsflora für Österreich, Liechtenstein und Südtirol" in the revised 3rd edition (Fischer et al. 2008).

II-2 Distribution patterns of species along three environmental gradients

For each target species we defined three environmental gradients according to their presence in the study plots: The data for the elevational gradient was derived out of a digital elevation model, based on airborne laser scanning performed in 2017 and delivered by the geoinformation division of Tyrol's federal government (Land Tirol - data.tirol.gv.at 2024). The mean annual temperature was calculated for the two years of observation. Additionally, the number of days each plot was covered with snow was also calculated, by a two-step procedure applying a Random Forest model to the meteorological data, trained by the observed snow cover via webcams and the climatic and topographic parameters at each site. Overall, 871 Plots were analysed from which species-specific subsets, based on presence/absence were created.

To check whether our study area covers the whole range of a species along a gradient, histograms for each species for each gradient were made. The bins of the histograms were defined by using equal intervals of 200m (elevation gradient), 1,5°C (annual mean temperature gradient) and 31 days (snow cover duration gradient). For *Ranunculus glacialis* and *Deschampsia cespitosa subsp. cespitosa* the distribution at the elevation gradient was truncated at the upper and the lower range margin covered by the study area, respectively (see Appendix).

As the results of our study depend heavily on the outcome of the tests for normal-distribution, the results have to be reliable and robust against data bias. To examine whether the distribution of study species along the environmental gradients match those predicted by the ACH, we performed Shapiro-Wilk (SW-test)- and D'Agostino-Pearson (AG-test) tests separately for each species along each gradient. If both tests indicated a normal-distributed curve, the distribution of presence for the tested species against the tested gradient was considered as 'normally-distributed'. The absolute number and the percentage of normally-distributed species under all species was calculated for each gradient, to see under which the assumption of an ACH pattern could be best proved.

II-3 Correlation of gradients

Histograms of species differing strongly between gradients, indicate non-monotonic correlations. To project the monotonic relation between the gradients, Pearson-Correlation-Tests were applied. First scatter plots were prepared, for a visual validation. In total three scatter plots were made: All three analysed gradients were tested 1:1. A value close to -1 indicates a strong negative monotonic correlation, meaning the lower the values of one gradient get, the higher become the values of the other gradient. A value close to +1 indicates a strong positive monotonic correlation, the higher a value of a gradient gets, the higher the value of the other gradient gets as well. A value close to 0 indicates no close correlation. Afterwards, p-values for each correlation value were calculated, to see if the 'cor.values' were significant.

II-4 Relation to migration data

The skewness v was calculated for each species along each gradient using the D'Agostino test. V indicates the 'leaning' of the distribution of a species along a gradient, ergo if there are more values left of the maximum, the right side or if the distribution is symmetric. With the v value we can deduce if a species' distribution has already shifted towards the upper edge (i.e. higher elevation, lower annual mean temperatures, longer snow cover duration) of its range (v<0), the lower edge (v>0) or it is in equilibrium with the environmental conditions (v ~ 0).

Linear regressions were performed using the 'lm' function of R, to check whether v depends on the empirical shift in elevation per decade at the leading and trailing edge of a species' distribution as well as at the zone of their optimal development as observed by Rumpf et al. (2018).

For all statistical analysis R Statistical Software Version 4.2.1 was used (R Core Team 2022).

III Results

III-1 Distribution pattern of species along three environmental gradients

In table III-1 the number of normally-distributed species is provided in absolute and relative numbers.

Table III-1: Total amount of normally-distributed presence distributions of the studies' target species

Gradient	Amount of normal-distributed species
Elevation (n=55)	10 (18.2%)
Annual mean temperature (n=55)	29 (52.7%)
Snow cover duration (n=55)	1 (1.8%)

Table III-2: Number of species that were normally-distributed at two or three gradients

Gradient	Amount of normal-distributed species
Elevation & Annual mean Temperature (n=55)	7 (12.7%)
Annual mean temperature & Snow Cover duration (n=55)	1 (1.8%)
Snow cover duration & Elevation (n=55)	1 (1.8%)

Seven species (12.7%) showed a normal-distributed pattern of presence at the gradients of elevation and annual mean temperature, namely: *Cerastium uniflorum*, *Juncus trifidus*, *Poa laxa*, *Primula glutinosa*, *Saxifraga bryoides*, *Saxifraga exarata* and *Sibbaldia procumbens*. One species, *Saxifraga exarata*, was normally-distributed in all three gradients. Following these results 3 species were only normally-distributed in the gradient of elevation, while 22 species were solely normally-distributed in the gradient of annual mean temperature.

Table III-3: Amount of normal distributed species sorted after growth forms and gradients

Growth forms	Elevation	Annual mean temperature	Snow cover duration
Cushion plants (n=5)	2 (40%)	4 (80%)	1 (20%)
Dwarf shrubs (n=6)	0 (0%)	4 (66.7%)	0 (0%)
Grasses (n=12)	2 (16.7%)	3 (25%)	0 (0%)
Perennial plants (n=26)	5 (19.2%)	16 (61.5%)	0 (0%)
Sedges & Rushes (n=6)	1 (16.7%)	2 (33.3%)	0 (0%)

Looking at growth forms of species, two (40%) of the cushion plants in our study were normally distributed regarding their presence in the elevation gradient, 4 (80%) in the gradient of annual mean temperature and 1 (20%) if plotted against the snow cover duration. None of the dwarf shrubs in our study were normally distributed in the elevation gradient nor the snow cover duration gradient, while 4 (66.7%) of them were normally distributed in the annual mean temperature gradient. From the 12 grass species in our study, 2 (16.7%) were normally distributed in their presence pattern in the elevation gradient, 3 (25%) were normally distributed in the gradient of annual mean temperature and none at the gradient of snow cover duration. Perennial plants were the largest group of growth forms in our study, 5 of them were normally distributed at the gradient of elevation (19.2%), 16 (61.5%) at the gradient of annual mean temperature and none in the gradient of snow cover duration. Finally, the sedges and rushes, of which one (16.7%) of them was normally distributed in the elevation gradient and two in the gradient of annual mean temperature (33.3%) none of them was normally distributed if looking at the gradient of snow cover duration.

III-2 Correlation of gradients

The results of the correlation between the three analysed gradients are listed in table III-4. In total, the climate data of 871 plots was analysed. The visualized scatter plots can be found in the Appendix.

*Table III-4: Listed results of the executed correlation tests. The results which are significant are marked by a *.*

Compared gradients	Used correlation test	coefficient (r)	p-value
Elevation – Annual mean temperature	Pearson	-0.732	<0.001*
Elevation – Snow cover duration	Pearson	0.523	<0.001*
Annual mean temperature – Snow cover duration	Pearson	-0.611	<0.001*

The relationship between the gradient of elevation and the annual mean temperature is monotonic negative (r = -0.732). The opposite relation occurs between the elevation and the snow cover duration, this relation is monotonic positive (r = 0.523). The influence on the snow cover duration is slightly larger from the annual mean temperature (r = -0.611), here the relation is monotonic negative. All executed correlation tests yield highly significant p-values (r = < 0.001).

III-3 Relation of skewness to migration rates

The overall results of the skewness of each species' histograms calculated by the D'Agostino-Test are listed in the Appendix.

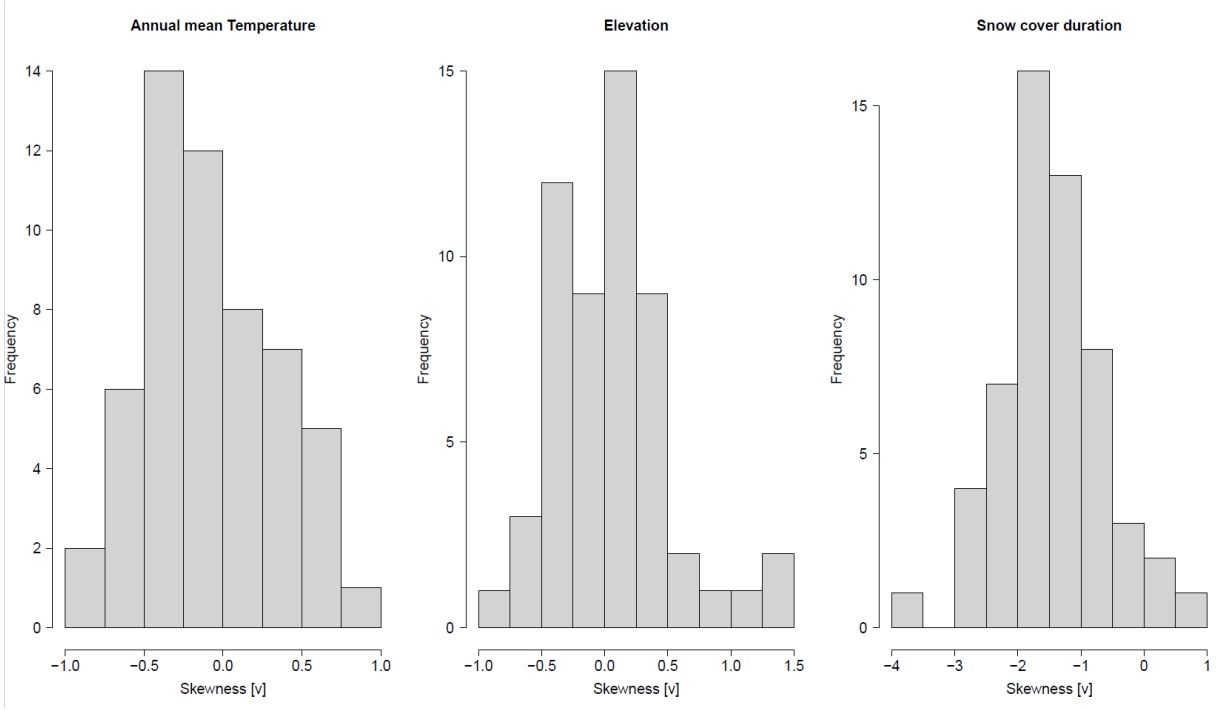

Figure III-1: Histograms of the distribution of the skewness value v at each gradient

Table III-5: Summary of calculated skewed distributions in the study data (n=55).

Gradient	Left-skewed species distributions (v<0)	Right-skewed species distributions (v>0)
Elevation	25 (~45%)	30 (~55%)
Annual mean temperature	34 (~62%)	21 (~38%)
Snow cover duration	52 (~95%)	3 (~5%)

Except for the gradient of the snow cover duration, no clear trend towards one direction of skewness could be found. Along the elevational gradient more (55%) species are skewed towards lower elevations. If plotted against the gradient of the annual mean temperature more species showed a left-skewed distribution (62%) than a right-skewed (38%). Regarding the gradient of snow cover duration almost all species (~95%) possess a left-skewed species distribution and are skewed towards higher amounts of snow cover duration.

In table III-6 the results of the conducted linear regressions are listed. The total number of analysed species that were present in both datasets was 27.

*Table III-6: Linear regressions relating elevational shifts of species at their rear and leading edge as well as the zone of optimal development as measured by Rumpf et al. (2018) to the skewness of species distribution along three gradients. Significant relations are indicated by a *.*

Edge	gradient	Estimate	Std. Error	t value	p-value
Rear edge shift	Elevation	< -0.01	< 0.01	-0.27	0.790
Leading edge shift	Elevation	< 0.01	< 0.01	0.29	0.772
Optimum shift	Elevation	< 0.01	< 0.01	0.78	0.443
Rear edge shift	Annual mean temperature	< -0.01	< 0.01	-2.11	0.045*
Leading edge shift	Annual mean temperature	< -0.01	< 0.01	-0.09	0.926
Optimum shift	Annual mean temperature	< 0.01	< 0.01	0.32	0.754
Rear edge shift	Snow cover duration	< 0.01	< 0.01	0.51	0.615
Leading edge shift	Snow cover duration	< 0.01	< 0.01	0.60	0.557
Optimum shift	Snow cover duration	< 0.01	< 0.01	0.37	0.714

The results show almost no significant linear relationship between skewness and migration rates. The only significant linear relation was calculated when analysing the rear edge shift of species in the provided data and its relation with the presence patterns of the analysed species in the gradient of annual mean temperature ($p = 0.045$).

IV Discussion

The results align with several previous studies that could find no sign of an abundant-centre distribution among species, strengthening the impression of the Abundant-Centre Hypothesis as an unproven hypothesis and not as a paradigm (but see e.g. Abeli et al. 2014; Csergő et al. 2017; Daco et al. 2021; Dallas et al. 2017; Pironon et al. 2017). Leading towards the assumption, that normal-distributed presence patterns are the exceptions under natural conditions and may originate more from local conditions than from a paradigm, which wants to set the rule. But even the few results that suggested an abundant-centre distribution in presence must be seen carefully as those mostly only occurred if plotted against the gradient of annual mean temperature, the gradient of elevation, after Brown (1984) the major cause for an Abundant-Centre distribution in mountain areas, showed even lesser signs of determining this distribution pattern. This seems rather unusual, as one would think that the relationship between snow cover duration, elevation and annual mean temperature would be linear.

Regarding the gradient of snow cover duration, most plots experience a snow cover duration in the middle range of the gradient of elevation, the linear relationship is only medium strong ($\rho = 0.523$, see table III-4). The linear relationship between the snow cover duration and the annual mean temperature is a bit stronger but also medium strong ($\rho = -0.611$, see table III-4). Almost all species showed left-skewed distributions and occurred more often in plots with a longer snow cover duration than at their centre of presence. The gradients of annual mean temperature and elevation have a stronger negative correlation ($\rho = -0.732$, see table III-4), meaning the higher you get the colder it gets. As the relationship between the three gradients is at least medium strong, one would expect different distributions of presence, but the differences are stronger than expected. Which makes the differences between the amount of normal-distributed presence patterns between these three gradients seem as there would be an underlying process defining the distribution of species, that is more complicated than these gradients could project. One of the influences that could determine the distribution patterns of species, weakening the meaningfulness of elevation and snow cover duration could be the mentioned heterogenous topography of alpine regions. The temperature lapse rate determines the mesoclimate which is modified by topography, exposition or elevation, leading to a strong variation in microclimates (Winkler et al. 2016). As we expect the target species adapting the range according to the niche requirements, it seems the influence of annual mean temperature on the migration of species is larger than the other two gradients. Plant species might follow the changing temperatures while adapting their ranges, making the distribution in the other gradients more skewed, as temperature refugia can occur in the same elevational belt, due to the mentioned microtopography of alpine areas. Microrefugia would be colder places, where the current temperature might fit better to the requirements of a species. In alpine areas those colder areas are often less exposed to the sun and are inside small valleys, like snow beds. Migrating species trying to evade rising temperatures could concentrate now in areas with those characteristics, in search for those colder places, following the centre of their ecological niche, which could create the leaning of species' presence patterns towards areas with higher snow cover duration as snow is staying longer in areas with more shadow and notched topography. The location of the temperature loggers could be another reason, for the high number of skewed distributions. Surface temperature and ground temperature daily amplitudes differ in alpine regions, but the data of our loggers might still be more precise than simulated data from lowland meteorological stations or satellite measures (Mountain Research Initiative EDW Working Group 2015; Scherrer and Körner 2010). Measuring the temperature directly at the surface might give the most reliable data but burying the loggers close to the surface, safe from animals and weathering is the most handy and reliable approach. The gradient of elevation is due to its easy applicability the

most common gradient for studies dealing with species distributions and range shifts (but see e.g. Abeli et al. 2014; Angert and Schemske 2005; Daco et al. 2021; Jump and Woodward 2003; Sagarin et al. 2006). On the large scale the gradient might be the most reliable one, elevational data is easier to obtain and topographic aspects play a minor role. But at local scale the annual mean temperature gradient might be the better indicator for projecting the climatic niches, especially in alpine regions (Lenoir and Svenning 2015; Pironon et al. 2017).

If looking at growth forms, dwarf shrubs, perennial plants and cushion plants seem to be able to follow their climatic niches the best and obtain a normal-distribution of presence with most analysed species (see table III-3). The dispersal traits might play an important role in this pattern. Dullinger et al. (2011) mention that wind dispersal, which mainly grasses, sedges and rushes rely on is not playing a crucial role in alpine areas, as most seeds only travel a few metres. More important regarding the long-distance dispersal is the dispersal by herbivores. The perennial plants, dwarf shrubs and cushion plants might be more favourable for herbivores, as they sometimes form fruits adapted to endozoochoric dispersal, like *Vaccinium spp.*. Such an enhanced ability for long-distance dispersal could help those species follow their climatic niches and obtaining their normal-distributed pattern of presence.

Multiple studies add the factor of precipitation as an effective determinant for species distribution and the migratory patterns of species as well. While a study which took place close to our study site could detect no effect of precipitation on community composition in alpine grasslands (Kaufmann et al. 2021), Felde et al. (2012) make the increased precipitation rates due to the alpine warming responsible for species' range shifts. Crimmins et al. (2011) observed increasing downhill shifts of species in Californian mountains, due to changes in precipitation. The species followed the higher availability of water downwards despite the warmer temperatures, which seems to make water availability more important than the annual mean temperature for species realising their climatic niches, this phenomenon was especially pronounced in species adapted to colder and wetter sites than to species being adapted to warmer and drier sites. The strength of the influence that precipitation can have on species' ranges is contradictory but if you looked at the water availability this gradient could explain partly the differences in the presence distributions between the gradients. The elevation could project the gradient of water availability worse than the gradient of annual mean temperature could, as the elevation is a uni-directional gradient, while the annual mean temperature gradient runs more multi-directional following topography, similar as water availability does which relies more on sediment and topography (Taheri et al. 2021). Furthermore, the humidity of soils influences the temperature as wetter soils are colder then dry soils, which could strengthen the importance of water availability for shaping ecological niches as well as the better suitability of the annual mean temperature gradient in projecting the water availability.

A classic discussion field in biogeographics is the definition of the centre of range. While Brown (1984) thought of the sheer geographical centre, nowadays the centre of the climatic niche is taken as the centre of a species range (Amano et al. 2014; Pironon et al. 2015) and in the last years the genetic diversity with the most diverse genes depicting the centre of the range became more important (Frei et al. 2014b; Hahn et al. 2012; Lira-Noriega and Manthey 2014). The advantage of the study design is the ability to project the geographical and the climatic centre of range, but the application of either of these gradients can't verify the ACH. Using the genetic variation of species under the ACH could lead to interesting new insights in species' range history and current situations that are not visible, with checking on abiotic and biotic gradients. Herrera and Bazaga (2008) found evidence for an abundant-centre distribution in within-population genetic diversity of *Lavandula angustifolia* in Spanish alpine grasslands. Furthermore, historical post-glacial species dynamics might be more important on plant performance than expected (MacLean and Beissinger 2017; Pironon et al. 2015). Pérez-Collazos et al. (2009) observed the highest genetic diversity in the former pre-glacial centre of range of the steppe

plant *Ferula loscosii*. The events of the Ice Age could possibly still affect species ranges, as species could still colonise suitable areas after their expulsion by the glaciation, and falsify the impression that species already found their optimum niches, especially in alpine regions a range filling process could still be ongoing (Dullinger et al. 2012a).

The historic and present-day land-use change are often mentioned as another possible influence on presence patterns of species. The extensive spreading of mountain pastures over the last centuries has overprinted the original mountain landscape, driving native mountain forest ranges downwards and help establish the nowadays extension of alpine grasslands, with its adapted species. Nowadays more and more pastures get abandoned as they are getting less profitable, than intensive livestock farming. The result is a succession of alpine grasslands by bushes and dwarf-shrubs, endangering the alpine grassland flora which has adapted to the grazing (Hahn et al. 2012). Anthropogenic infrastructure like ski resorts, streets or water reservoirs can disconnect habitats and create a barrier for the spreading of alpine species and destroy their former habitat (Boakes et al. 2018). Iseli et al. (2023) mention the higher occurrence of non-native invasive species in mountain environments along roads, where species from lower elevations travel with the tyre tracks. The natural heterogeneity of the mountain environment can also act as a barrier. Just like nival plants can benefit from this barrier (see below), species from lower elevations could be hindered colonising suitable habitats. These are dispersed like patches, disconnected by scree areas, valleys or landslide traces (Alexander et al. 2018). Even though the habitats on Mt. Schrankogel are quite homogeneously distributed, those patch-disconnections occur frequently, probably distorting the patterns in our histograms. The role of inter-specific competition is hard to detect but often mentioned as another reason why presence patterns seem to differ from site to site (Abeli et al. 2014; Alexander et al. 2018; Freeman et al. 2018; HilleRisLambers et al. 2013; Kulonen et al. 2018). In lower elevations less competitive species from higher elevations could be outperformed by more competitive species even if the climatic conditions might suite in their climatic niche (Alexander et al. 2018). Competition by surrounding plants can also alter the fitness of plants and therefore their reproductional success. Kulonen et al. (2018) found evidence that *Ranunculus glacialis* is decreasing in fitness parameters if the surrounding vegetation is higher. However, those factors could all have impacts on the distribution at our study site but couldn't be determined in the study and might have to be assessed in future studies.

Admittedly, there are difficulties in the understanding of Brown's hypothesis in its applicability to test for it or its scalability. Our study focused geographically on a very small-scale on a single mountain in the European Alps and used data from only one year, while the gradient of elevation in the study covers a large part of the alpine and nival zone. The gradient of elevation should therefore be properly projected, but only a few species showed a normal-distributed pattern of presence in that gradient. In his hypothesis Brown clarifies that his consideration should be applied on larger-scale species ranges, as environmental factors are often distributed patchy at the local scale (Brown 1984), but several studies dealt with species' occurrence on country- to continental wide scale and couldn't provide evidence for his thought (Sagarin et al. 2006; Santini et al. 2019). So, Brown's hypothesis should probably be more seen in a biogeographical context than in the elevational. The MICROCLIM-project is dealing with the question how to bring together the heterogeneity and microclimate of alpine regions with large scale species distribution models (Österreichische Akademie der Wissenschaften 2021). Showing the distribution of presence against different gradients is therefore an important factor, to see how they behave on a small scale, whether the ACH is designed for this approach is questionable. On local scale the local environmental factors seem to outcompete the large-scale environmental patterns. In the meta-analysis of Pironon et al. (2017) 248 empirical studies were analysed and no signs for large distributed ACH patterns could be found. The authors stress the importance of local factors as well, that seem to override those large-scale influences even on larger

spatial extents. In our study only data from one year was taken for the analysis, long-time approaches in combination with climate data to detect changes in the vegetation are still underrepresented after Rogora et al. (2018). But only with continuous data the mechanisms of species distribution could be detected and the fitting models be calculated. The extension of the MICROCLIM-approach should therefore be a desirable goal.

When it comes to the observed dis-agreement between the predictions based on the ACH and the empirical distributions of species and their relation to empirical migration rates, the overall picture is clear. All calculated linear regressions provided non-significant p-values (see table III-6). The calculated significant (p= 0.045*, see table III-6) linear relation between the annual mean temperature and the migration of species ranges at their rear end, could point towards a higher sensitivity of migration patterns to temperature at the rear edge of a species' distribution as Rumpf et al. (2019b) indicated in their paper, where they stated that the maximum temperature is a suitable indicator for rear edge shifts. Rumpf et al. (2018) only provided metre data in their paper the regression results have to be taken with care, but as almost all p-values were non-significant it can be assumed that all our observed distribution patterns do not correspond to their results. In the study of Rumpf et al. (2018), where our migration data is originating from, unexpected trends, were detected. Analysing rear edge, leading edge and optimum, more than half of the species shifted at least one range attribute downhill (Rumpf et al. 2018). In our analysis the same picture emerged, the ratio between left-skewed distributions and right-skewed distributions is almost equal, except for the gradient of the snow cover duration (see table III-5). As mentioned before, the skewness of elevation and annual mean temperature gradients has to be analysed opposed as a left-skewed distribution in the elevational gradient means that the plot curve is leaned towards higher altitudes and in the annual mean temperature gradient towards higher temperatures (ergo: lower altitudes). Remarkably the elevation gradient and the annual mean temperature show the same ration of left- and right-skewed distributions, which shows the same diverging picture as in the study by Rumpf et al. (2018), indicating that an uniformly upward migration pattern in species' presence can not be detected yet.

A more remarkable issue, that our study didn't cover is the amount of range or distribution losses within species which Rumpf et al. (2018) detected, which could be a more urgent problem. First signs of increasing disappearance events could already be reported for Mt.Schrankogel (Lamprecht et al. 2018). Cannone and Pignatti (2014) found similar effects in the Italian Alps, where especially the long-persisting species declined. The phenomenon of presence losses can be caused by maladaptations, as the effects of decreasing population sizes are happening faster than the contraction of ranges (Cotto et al. 2017), both processes happening simultaneously could be the sign of an already beginning "extinction vortex", in which the reduced populations decrease their ability to adapt evolutionary and are more vulnerable to random genetic drift, especially long-lived perennial plants (which most alpine-nival species are) can experience this vortex as they can adapt even slower than species from lower elevations (Cotto et al. 2017). If species migrate upwards but don't reduce in presence or range, the populations are not immediately endangered. The already detectable loss of range or presence is endangering plant populations right now. These losses are mostly caused by species deriving from the same elevational belt, that seem to outcompete some less adaptable species, causing the above-mentioned homogenization of plant communities (Cannone and Pignatti 2014; Pauli et al. 2007). Rumpf et al. (2018) and Auld et al. (2022) mention the increased competition regime on mountains, more competitive species could reduce the occupied area of alpine plants, creating the increasing competition as another factor of endangerment for alpine species. This is a more than disturbing statement, as the climate is going to change more drastically in the future, and alpine species are already experiencing those losses, meaning the future effects on plant populations could be severe (Wiens 2016).

A general weakness is the lack of data on range movement of nival species. Due to their endangerment by warming climate and their rarity, it is especially important to gain knowledge about possible range losses of them. The influence of the high alpine environment could be an underestimated factor projecting future species' movements. The topography of Mt.Schrankogel could be advantageous for nival species, persisting possible new competitors from lower ranges. At around 2800 m the characteristics of the soil change abruptly. Scree and rocks are the dominant subtrate, creating a natural barrier (Kulonen et al. 2018) These soils can barely absorb precipitation, experience extreme daily temperature fluctuations and additionally scree moves constantly, creating a physical harsh environment. Nival plants are adapted to the requirements these soils bring with them. Even if the climate conditions favour alpine plants from lower elevations, they could hardly colonise these soils. Also, if heat stress will increase, the migrating plants from lower elevations could be weakened in this new environment, as they depend on richer soil than nival plants, leading to less competition by them and increasing the persistence of nival species (Frei et al. 2014a). Graae et al. (2018) assume that alpine and nival species are well-adapted to small-scale migration, due to the patchy distribution of habitats in mountains, and may adapt partly to the changing climate. But with the accelerating warming it is questionable if alpine and nival species can adapt fast enough, making a stabilization of climate warming the only safe possibility for those species to maintain their current ranges (Cotto et al. 2017).

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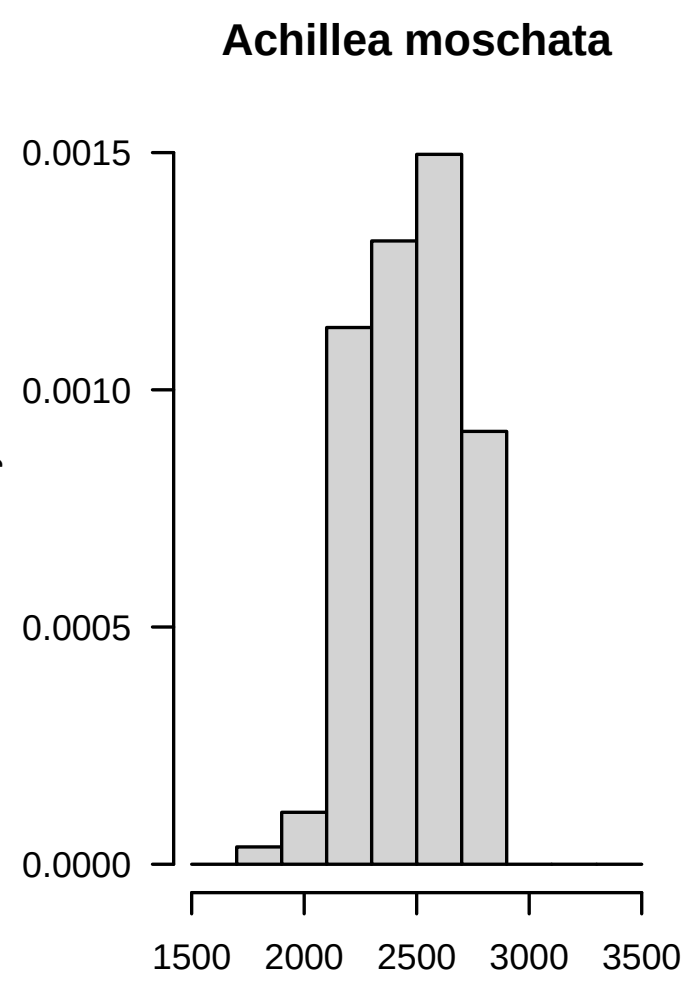
VI Appendix



Elevation [m.a.s.l.]

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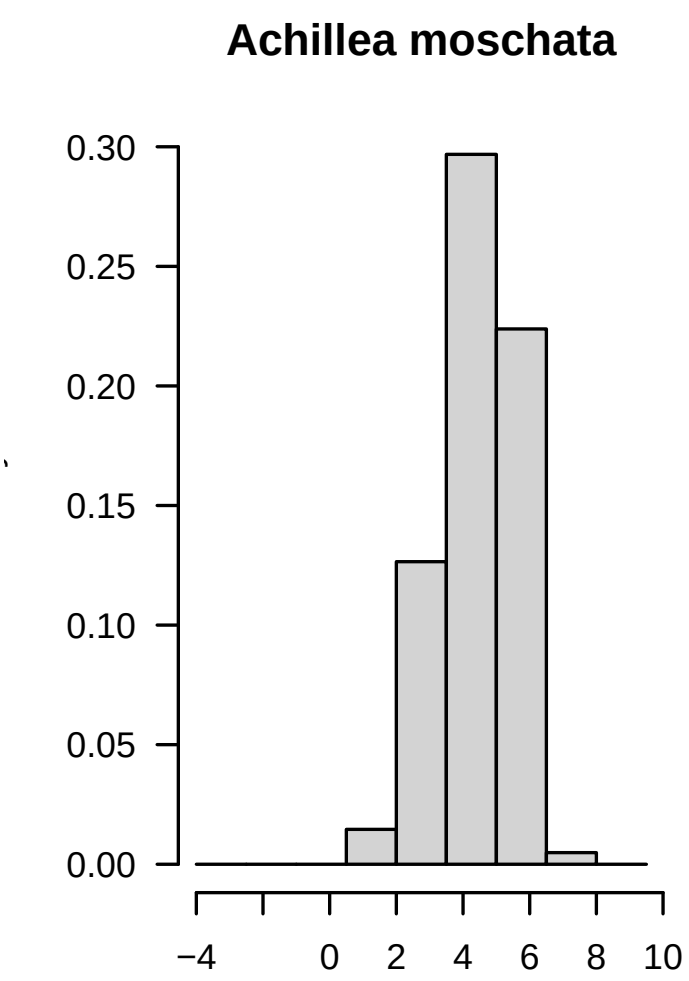

Annual mean temperature [°C]

p SW	p AG	skew
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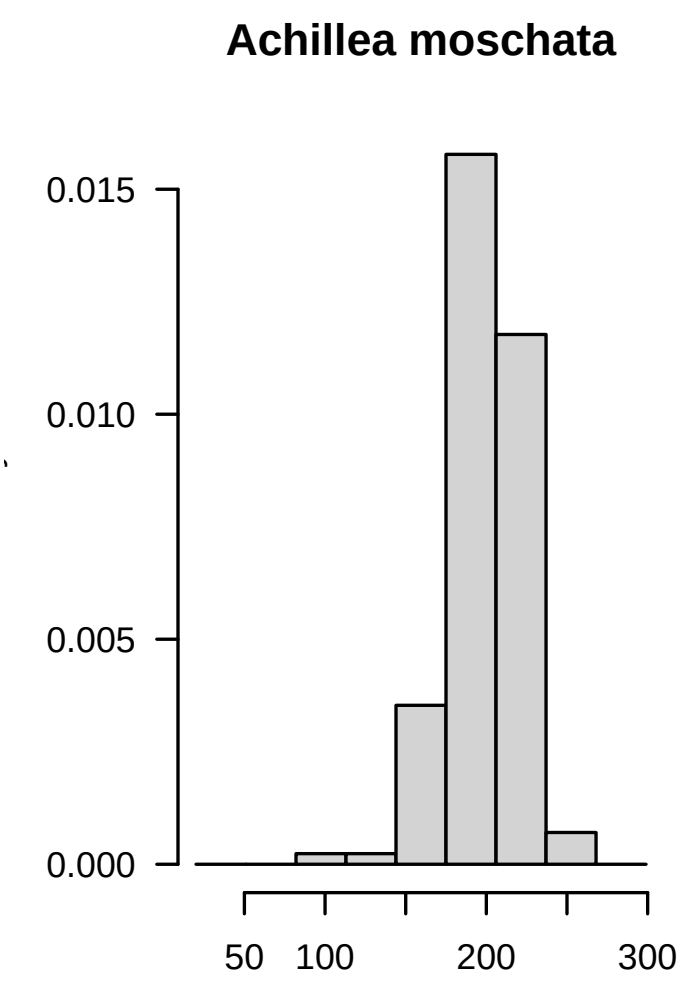

Snow cover duration [d]

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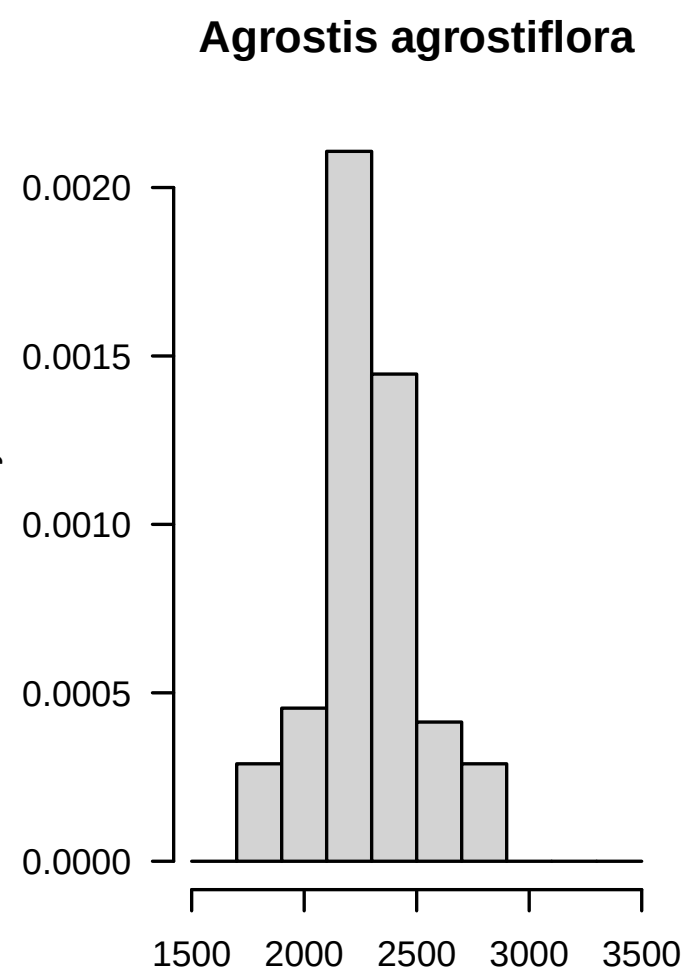

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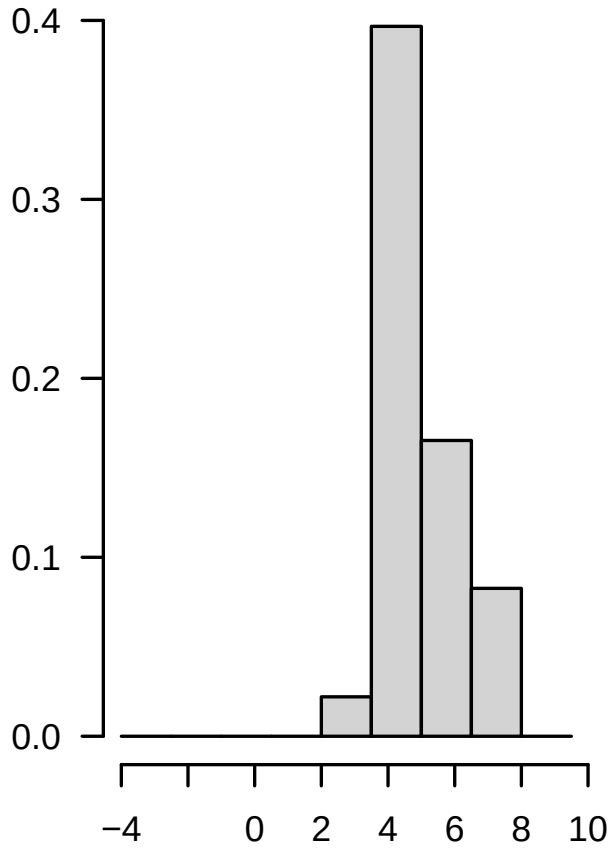

Annual mean temperature [°C]

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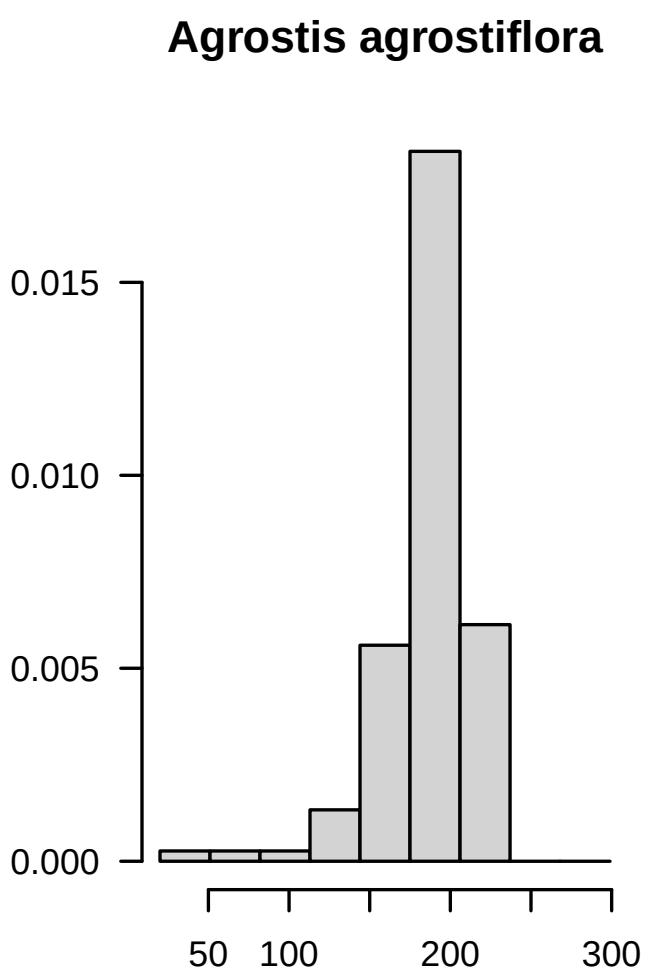

Snow cover duration [d]

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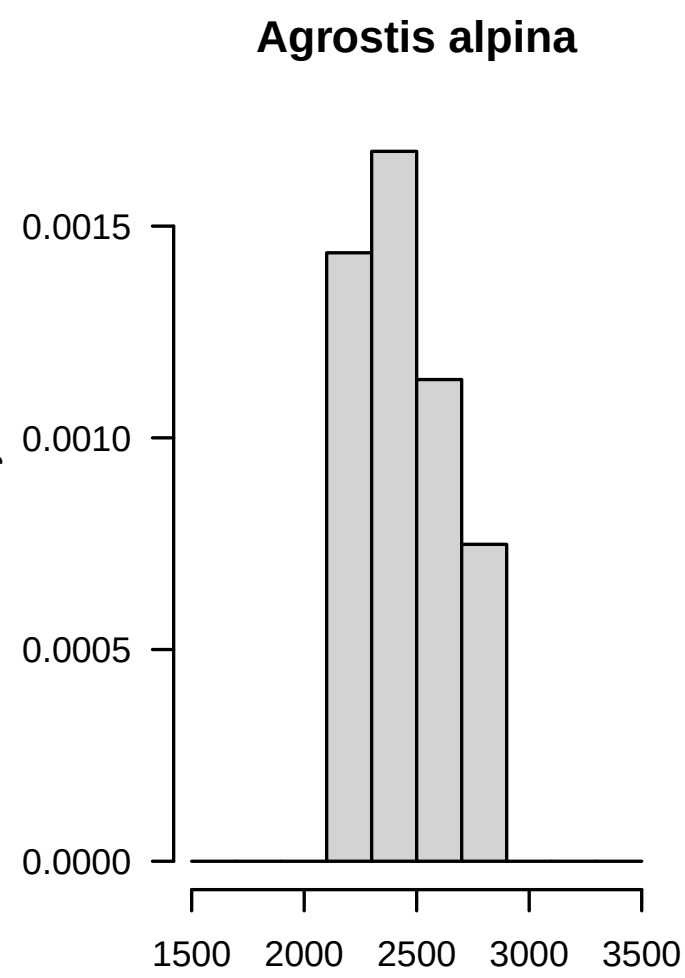

Elevation [m.a.s.l.]

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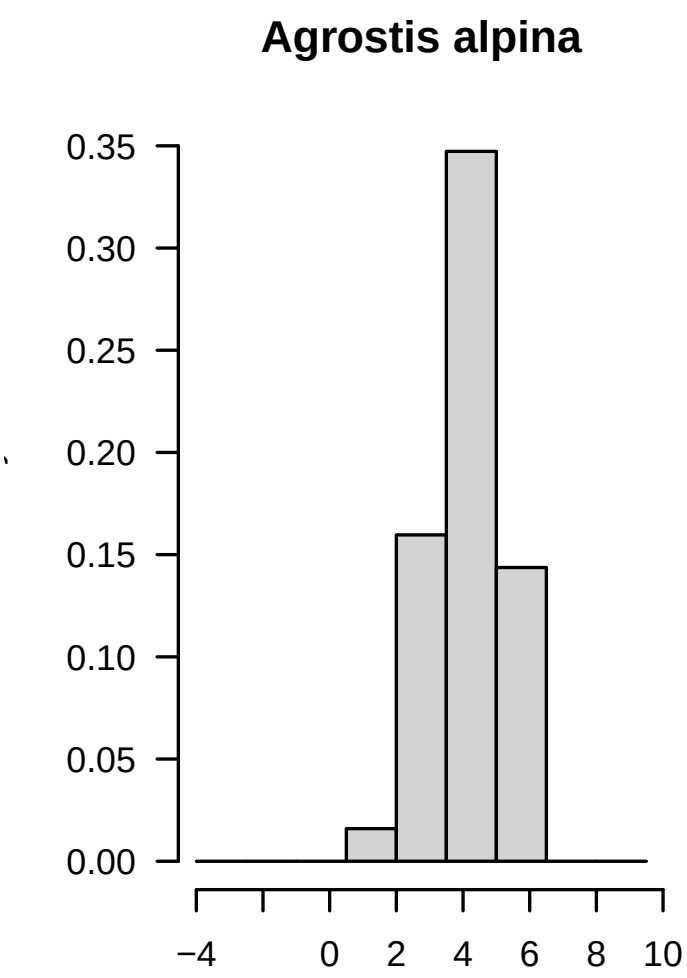

Annual mean temperature [°C]

p SW	p AG	skew
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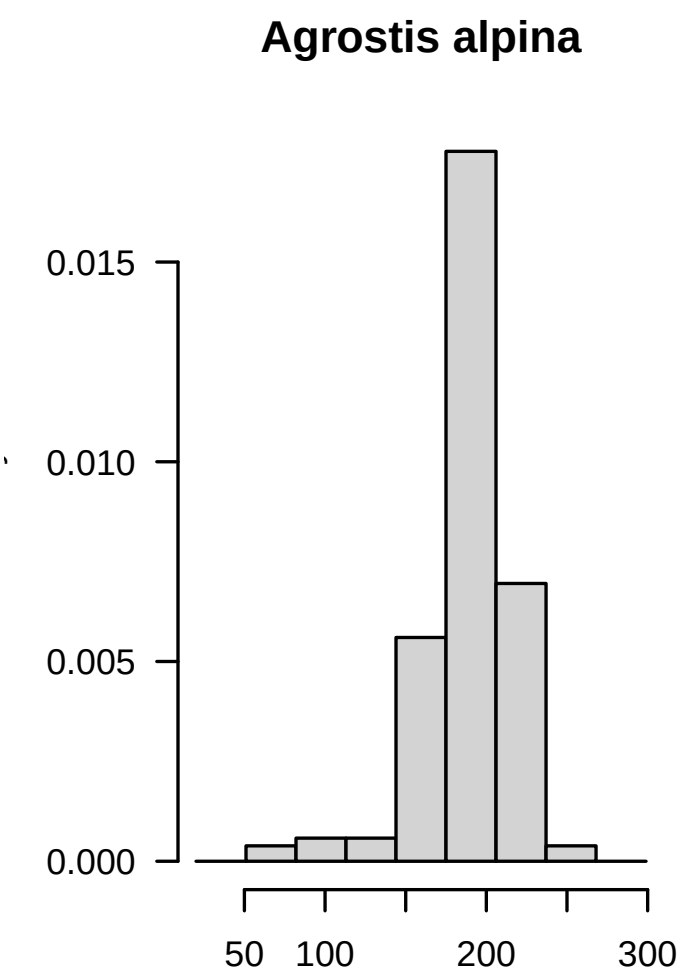

Snow cover duration [d]

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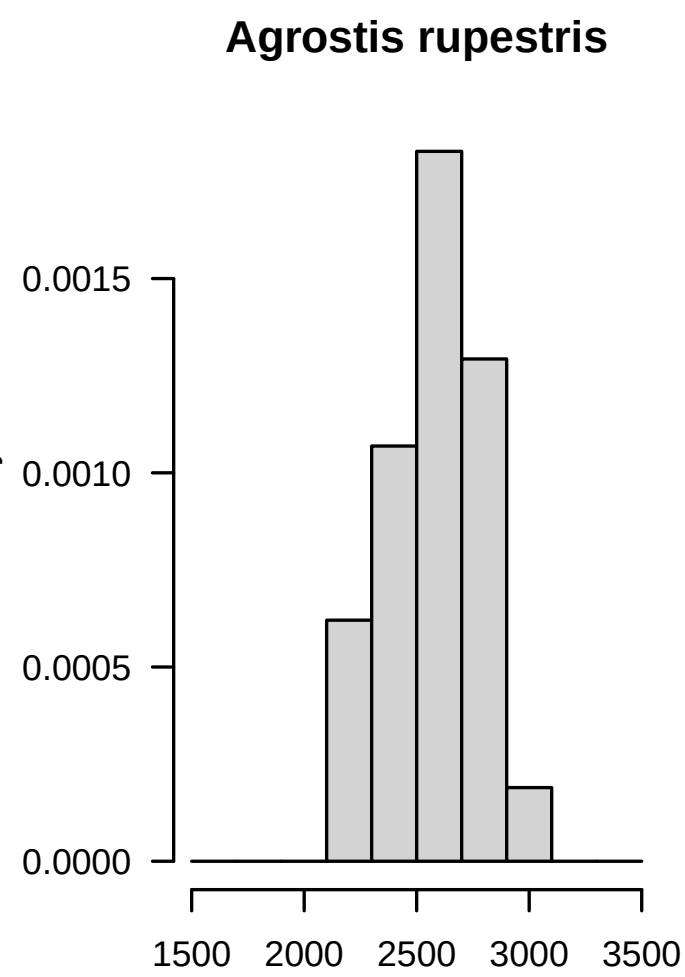

Elevation [m.a.s.l.]

p SW	p AG	skew
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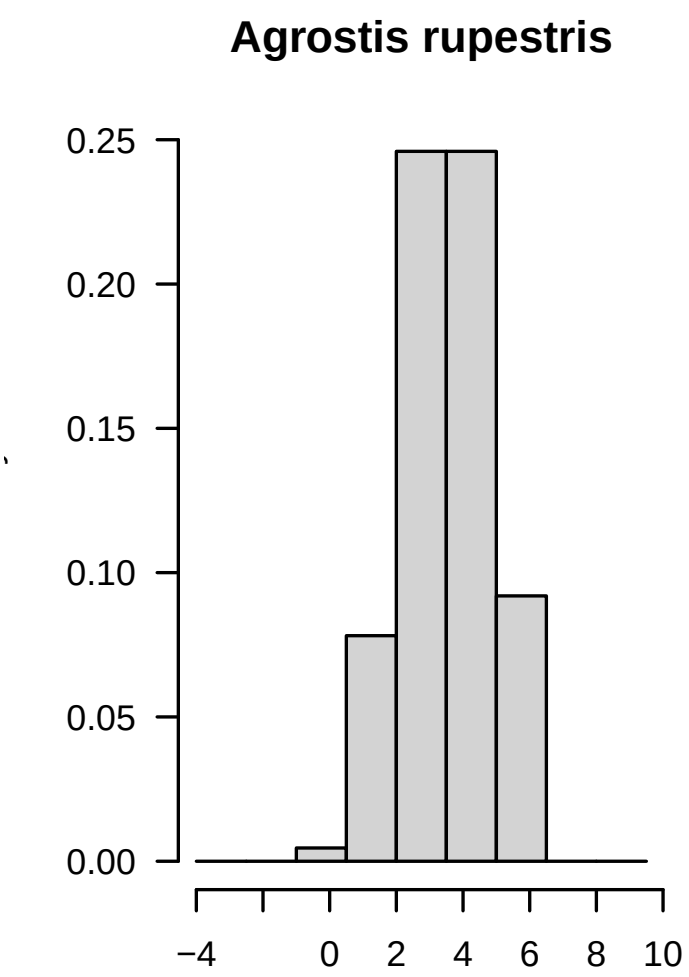
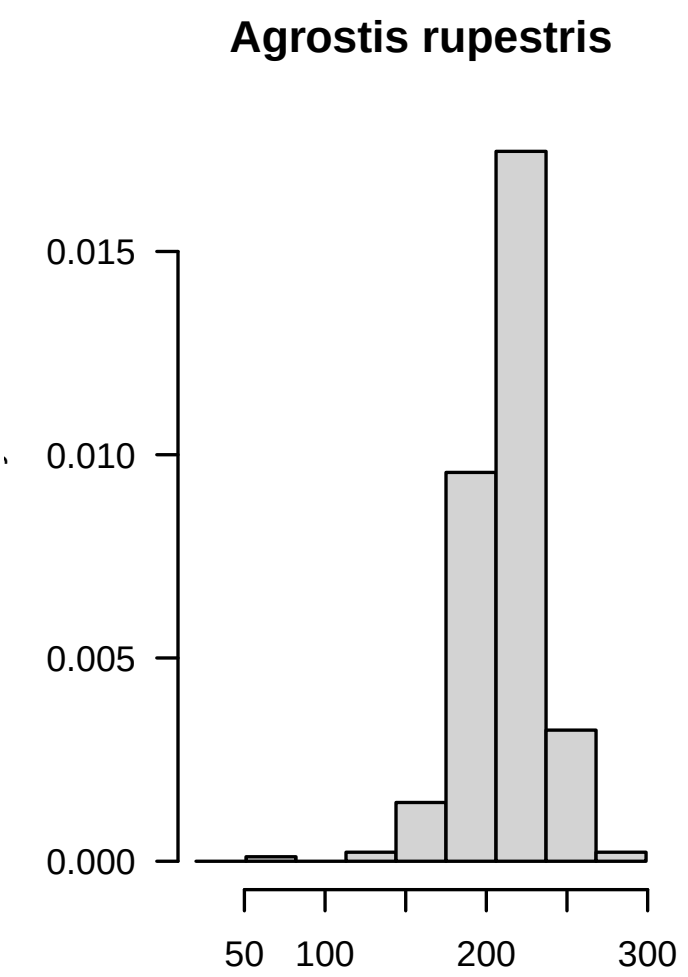


Annual mean temperature [°C]

p SW	p AG	skew
0.01	0.06	−0.27



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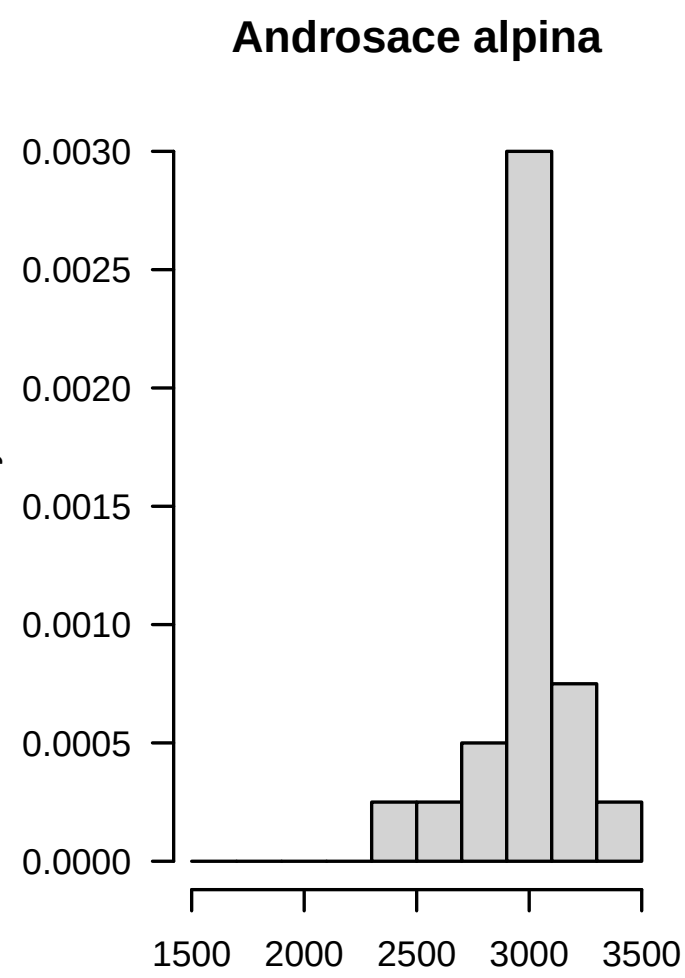

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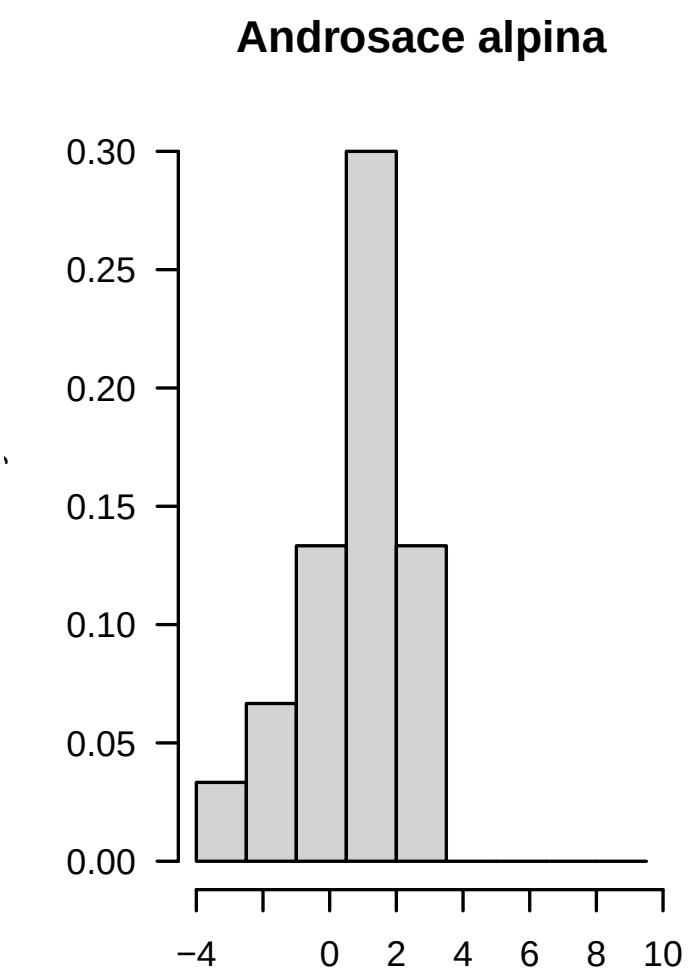
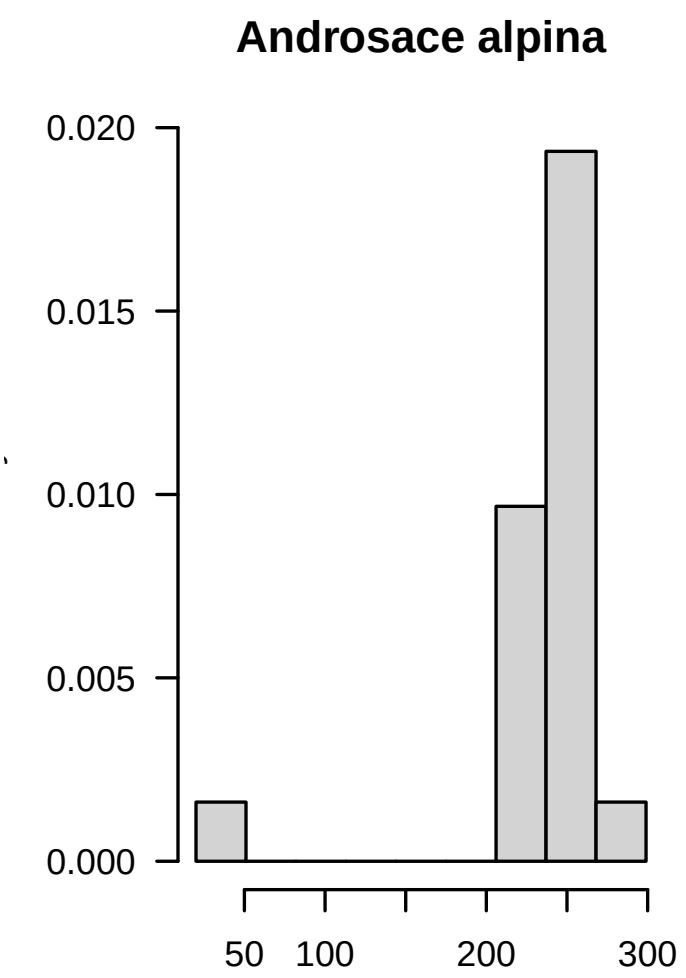


Annual mean temperature [°C]

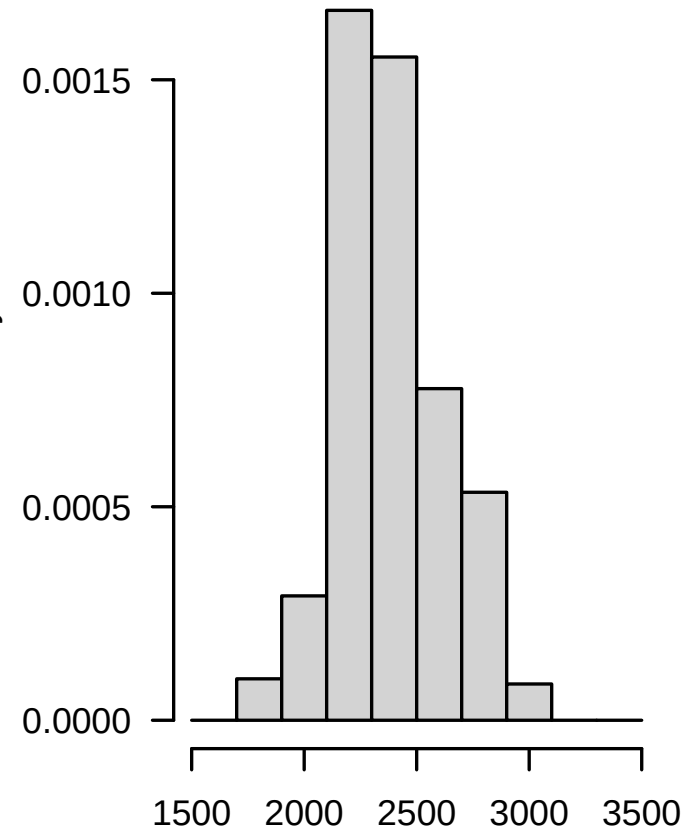
p SW	p AG	skew
0.3	0.05	−0.93



Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−3.67

Anthoxanthum alpinum



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p SW	p AG	skew
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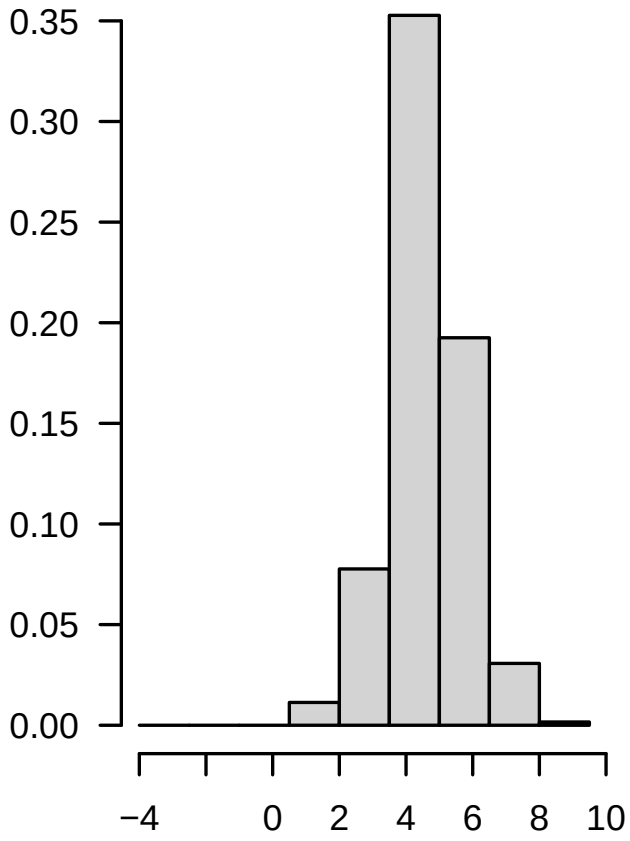

Annual mean temperature [°C]

p SW	p AG	skew
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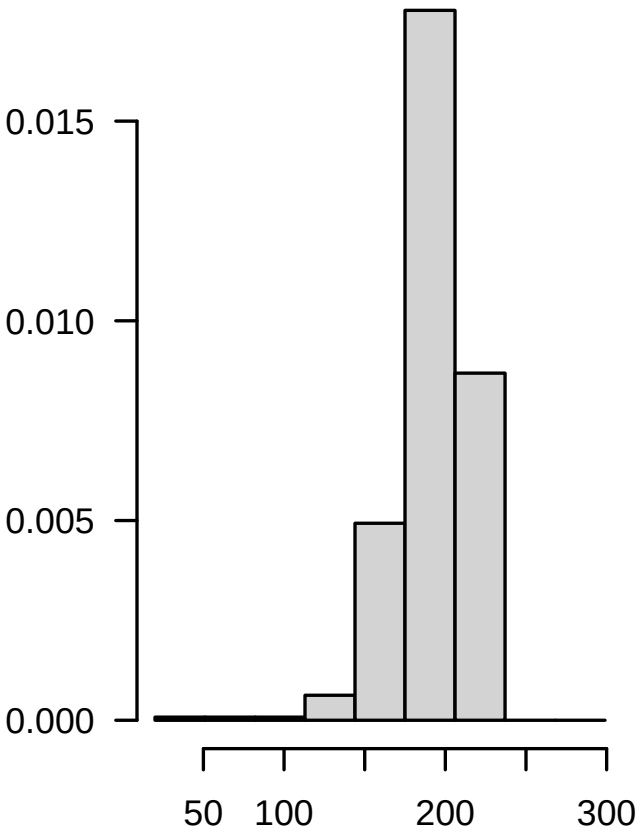
Anthoxanthum alpinum



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p SW	p AG	skew
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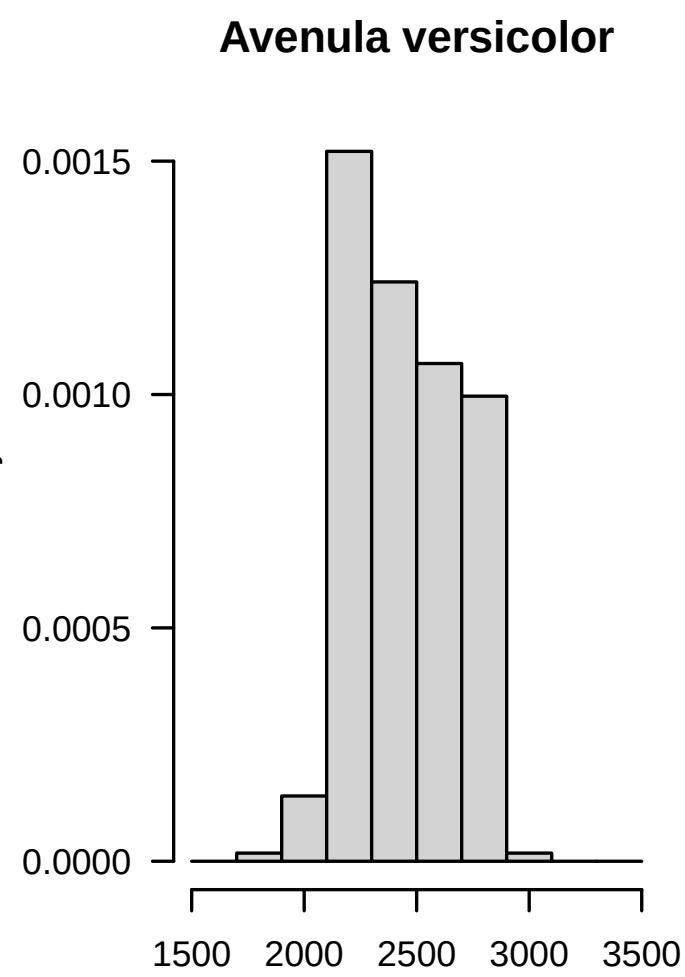

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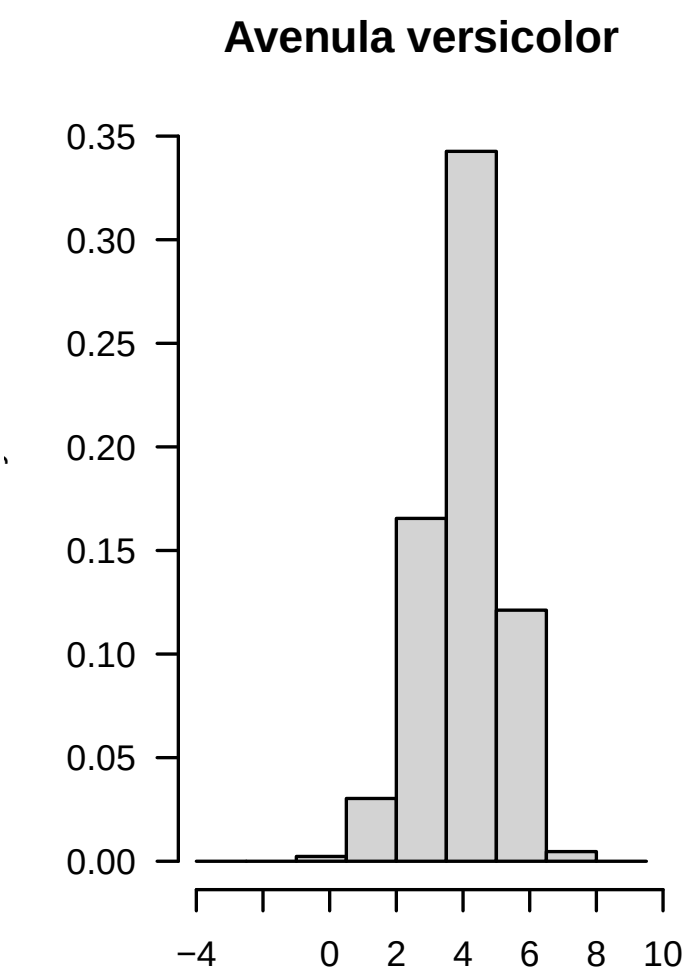
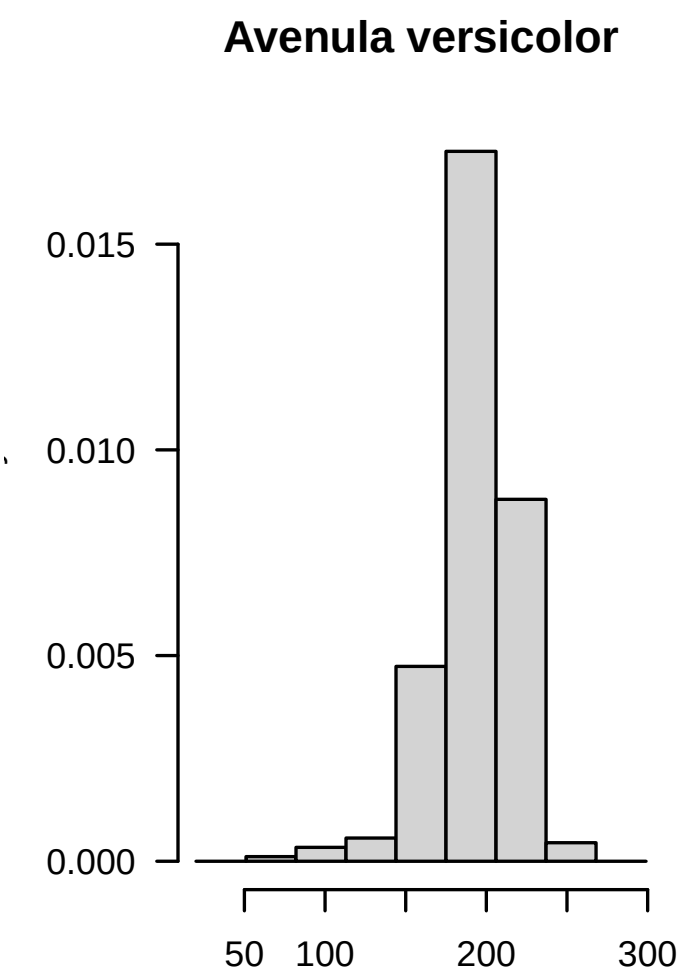


Annual mean temperature [°C]

p SW	p AG	skew
0.03	<0.01	−0.41



Snow cover duration [d]

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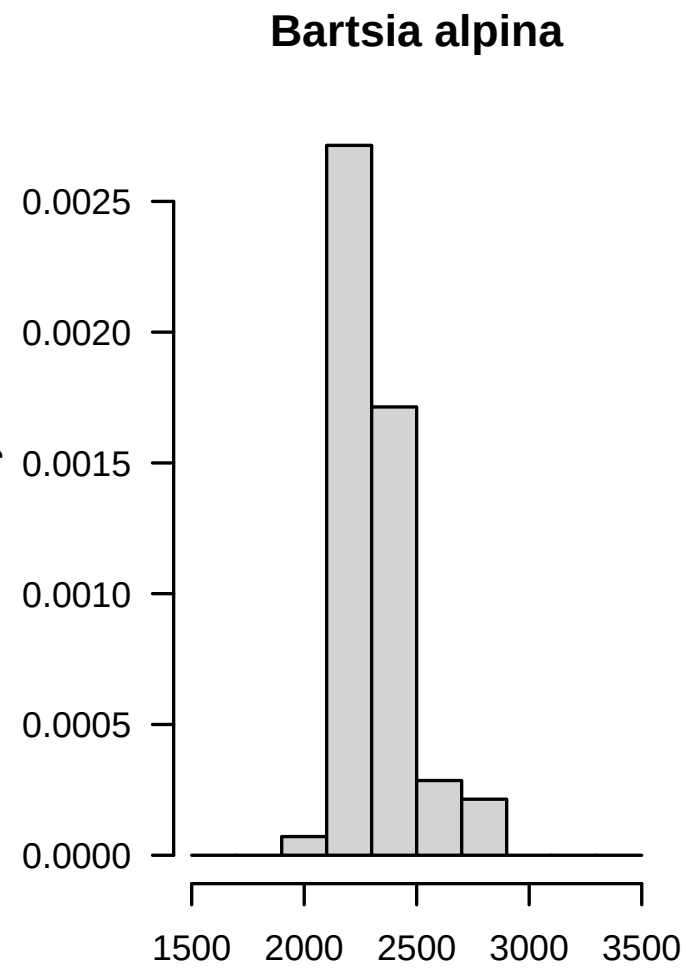

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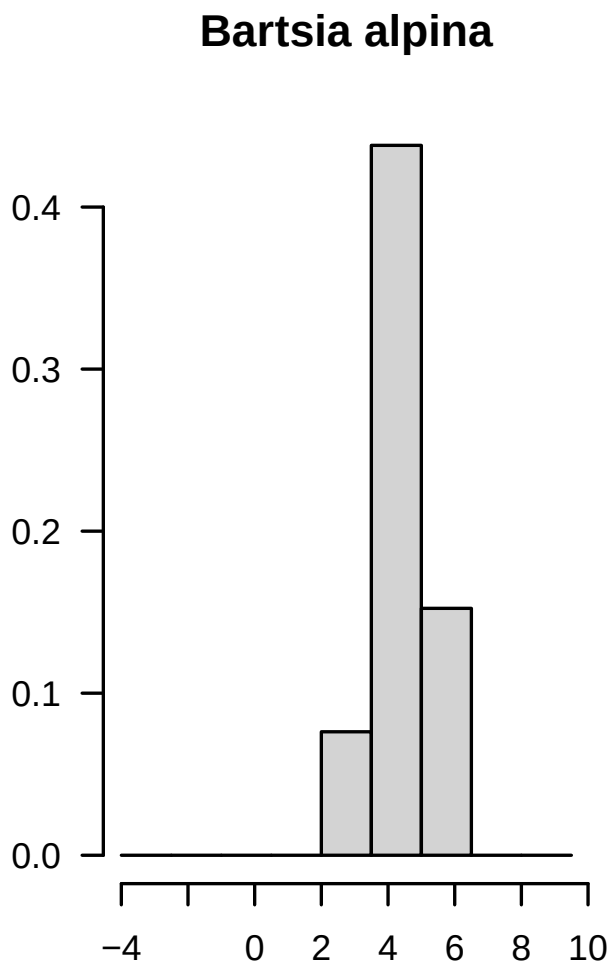

Annual mean temperature [°C]

p SW	p AG	skew
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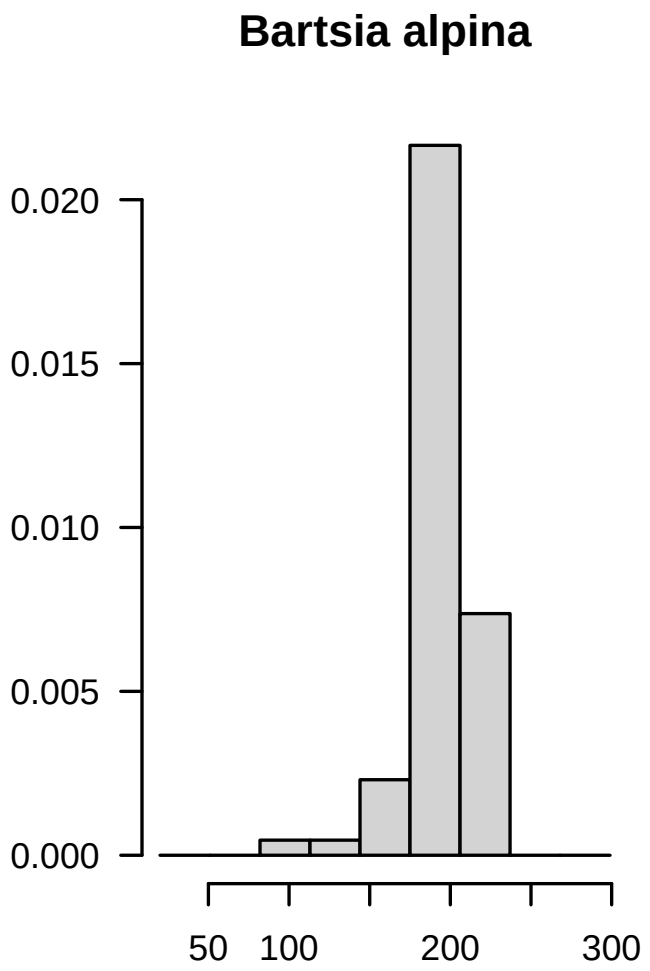

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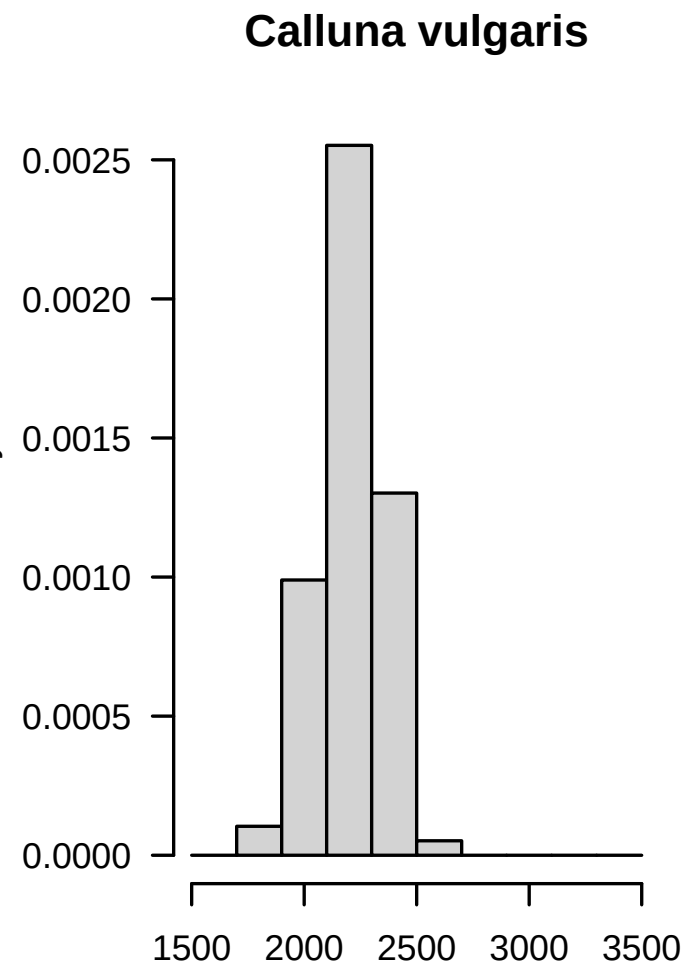

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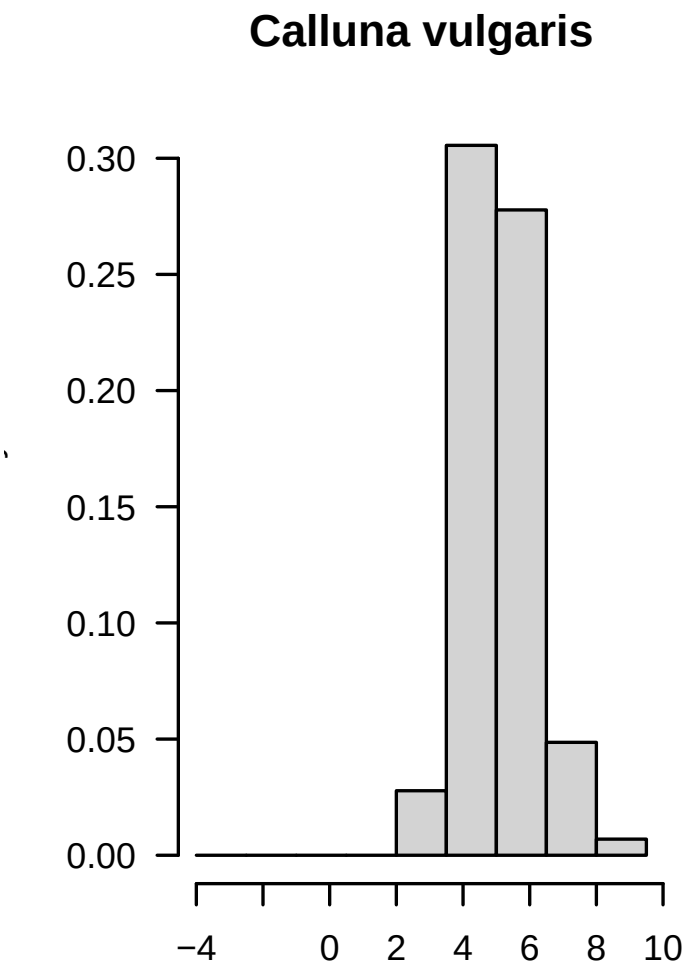

Annual mean temperature [°C]

p SW	p AG	skew
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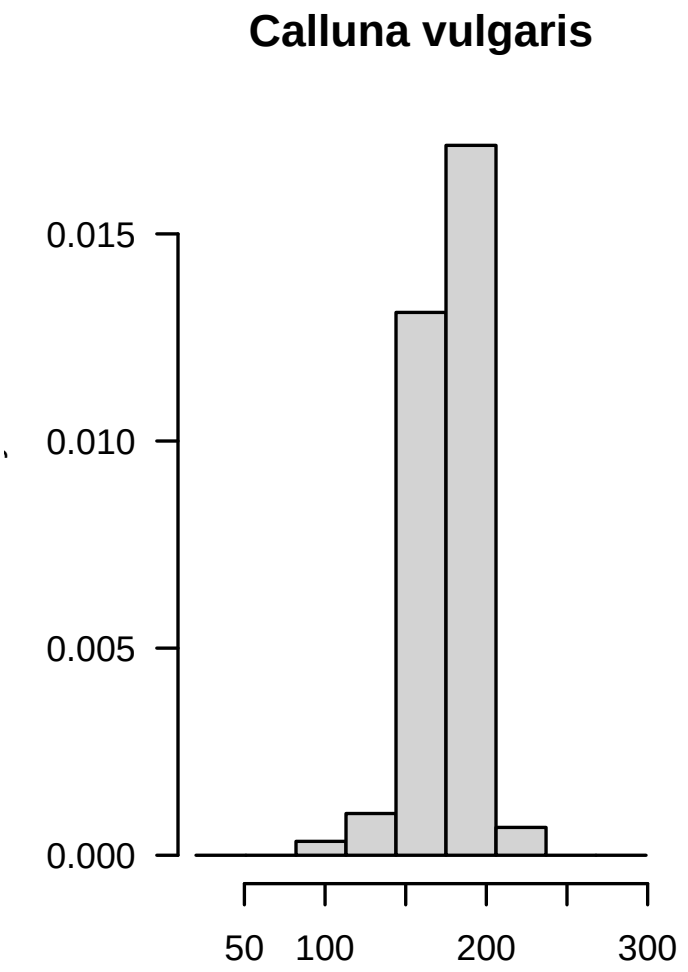

Snow cover duration [d]

p SW	p AG	skew
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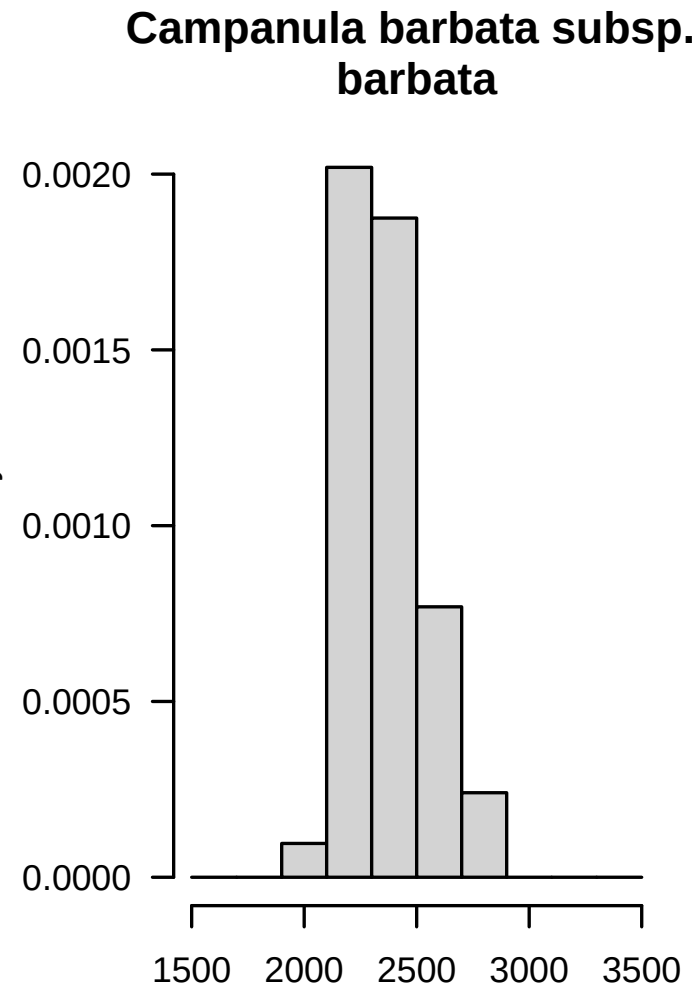

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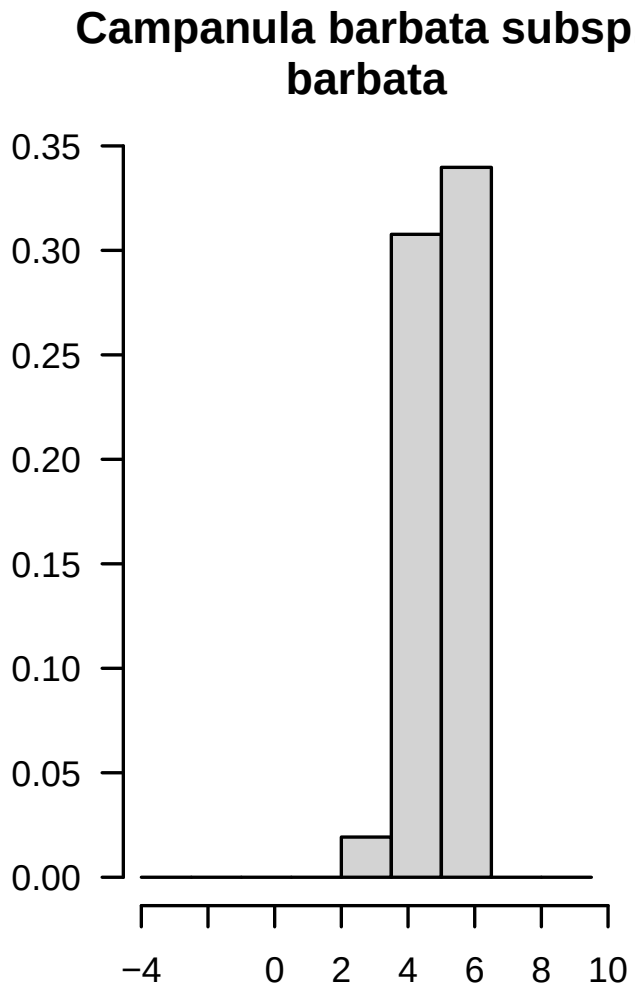
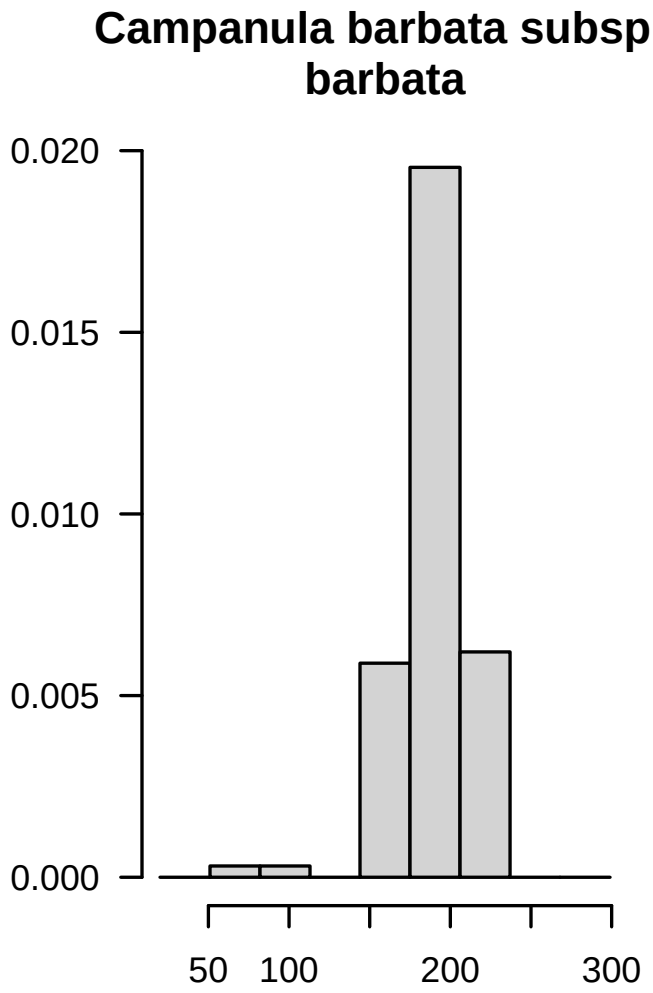


Annual mean temperature [°C]

p SW	p AG	skew
0.21	0.1	−0.39



Snow cover duration [d]

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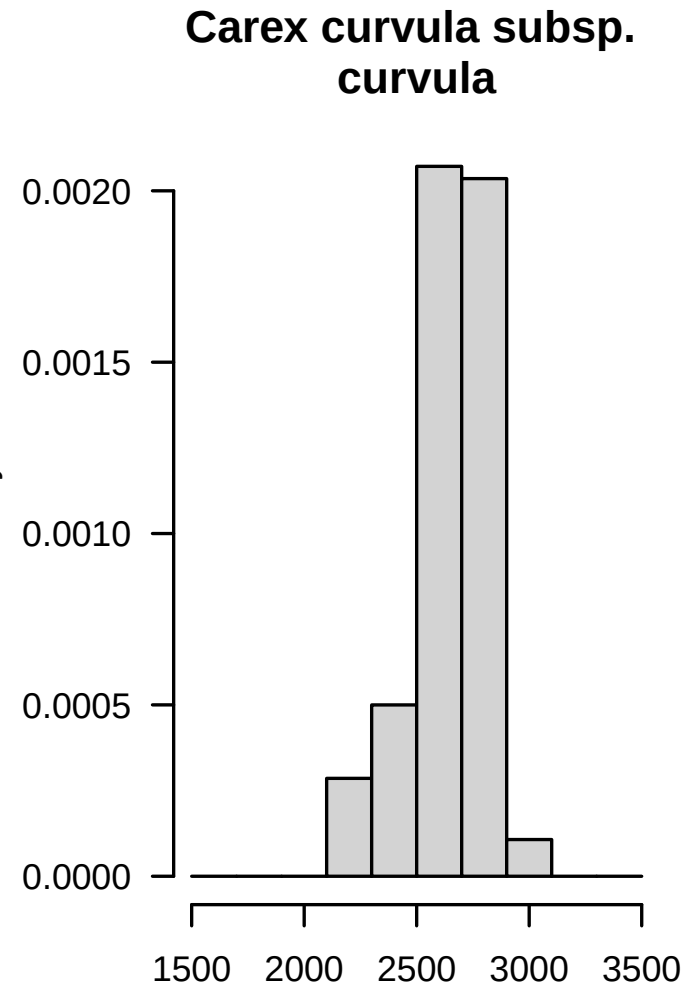

Elevation [m.a.s.l.]

p SW	p AG	skew
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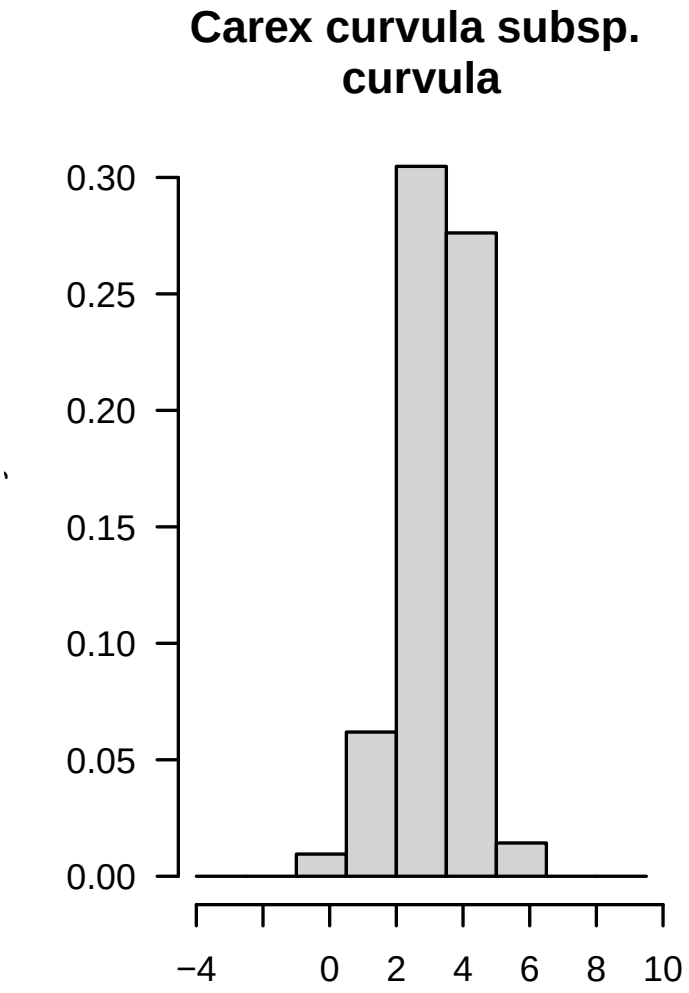
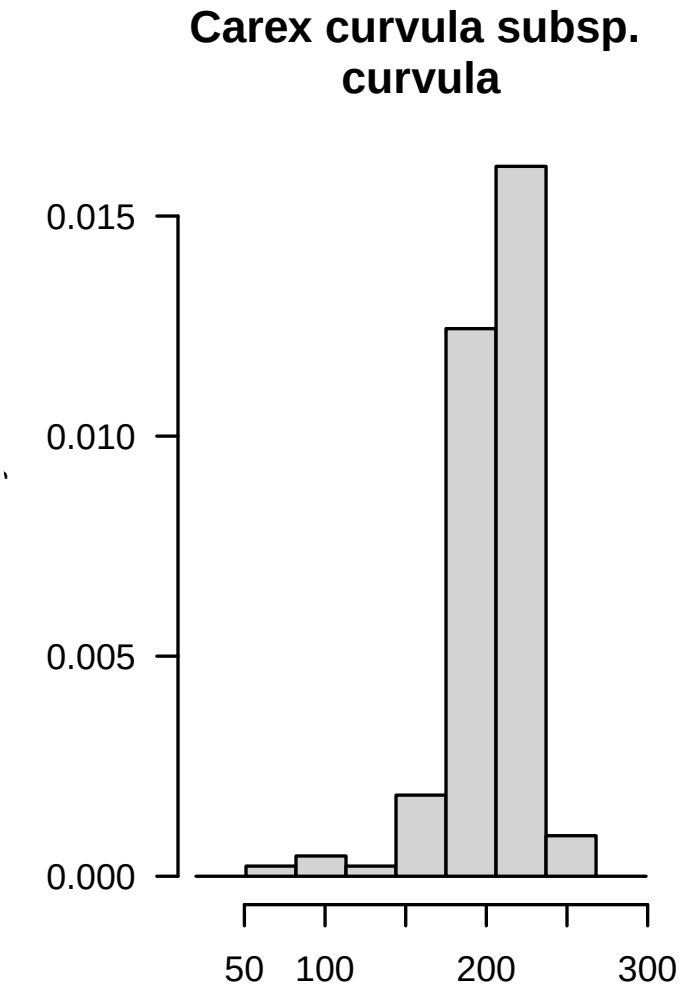


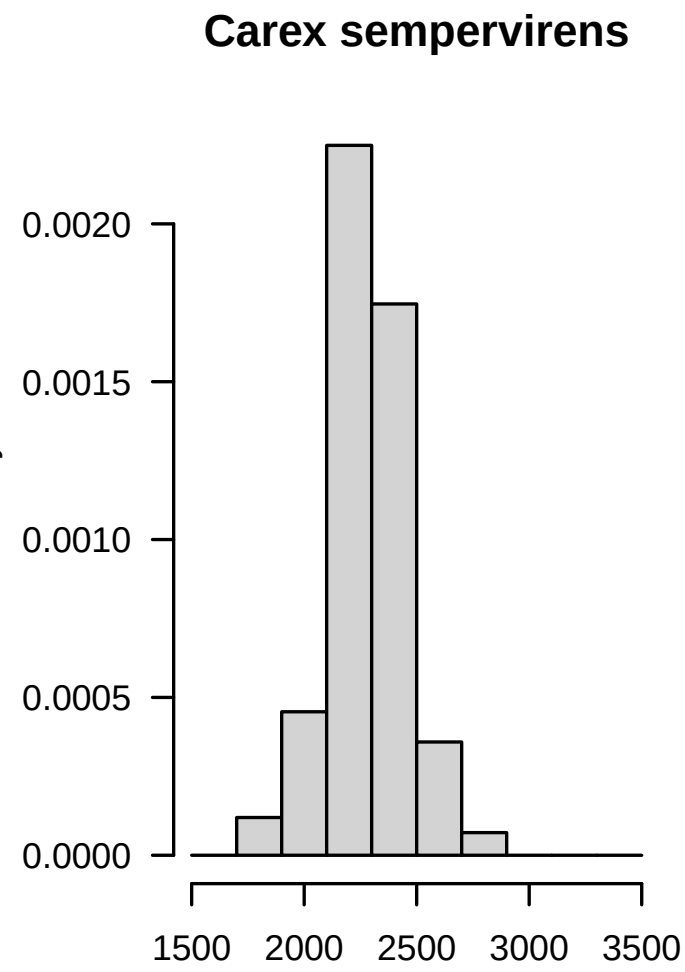
Annual mean temperature [°C]

p SW	p AG	skew
0.02	<0.01	−0.6



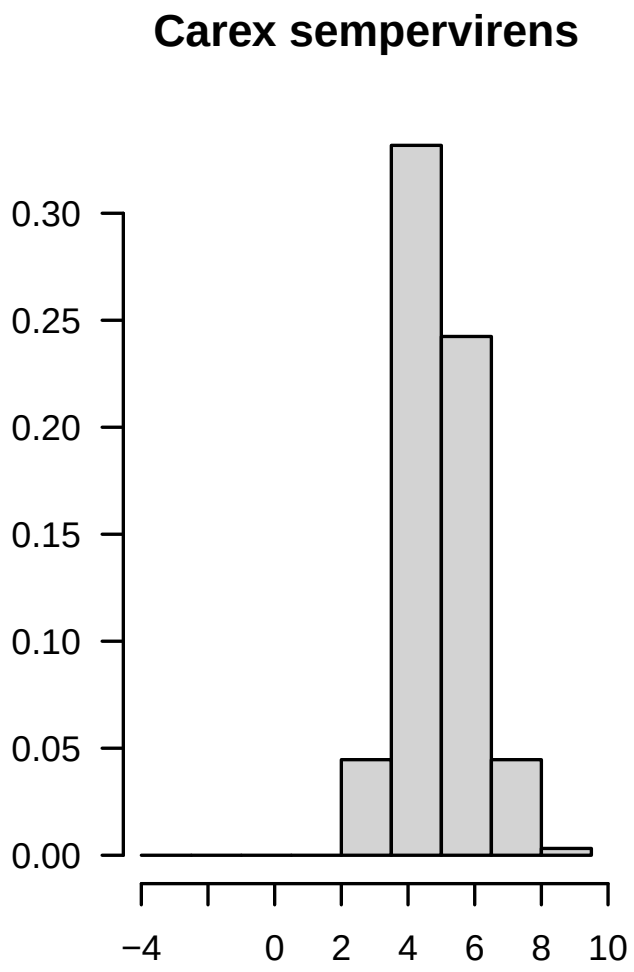
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.05



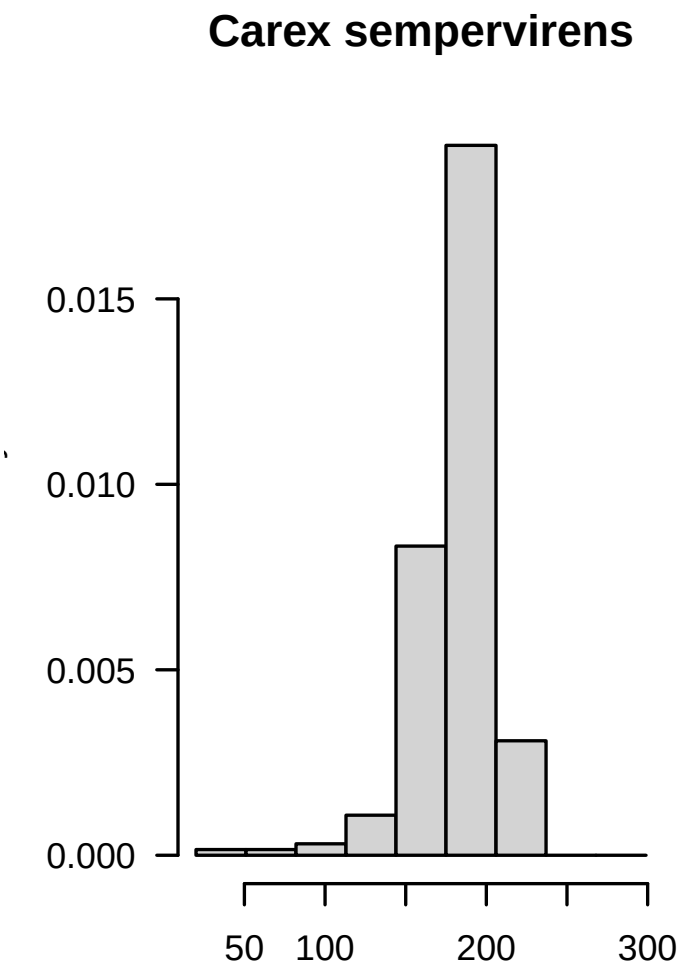
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.52	0.11



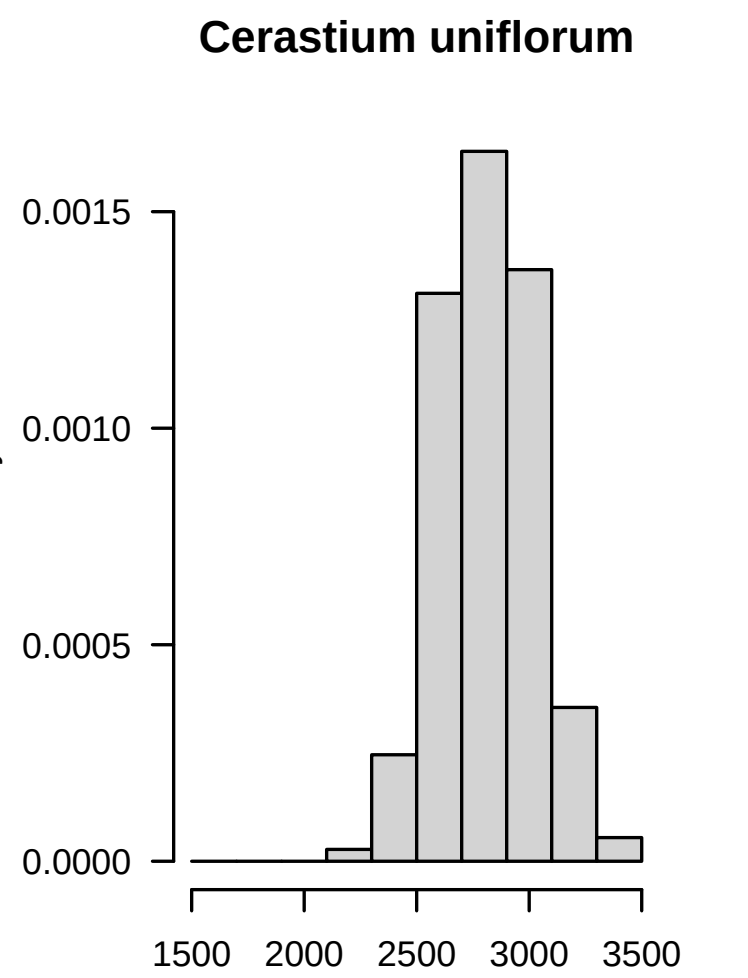
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	<0.01	0.45



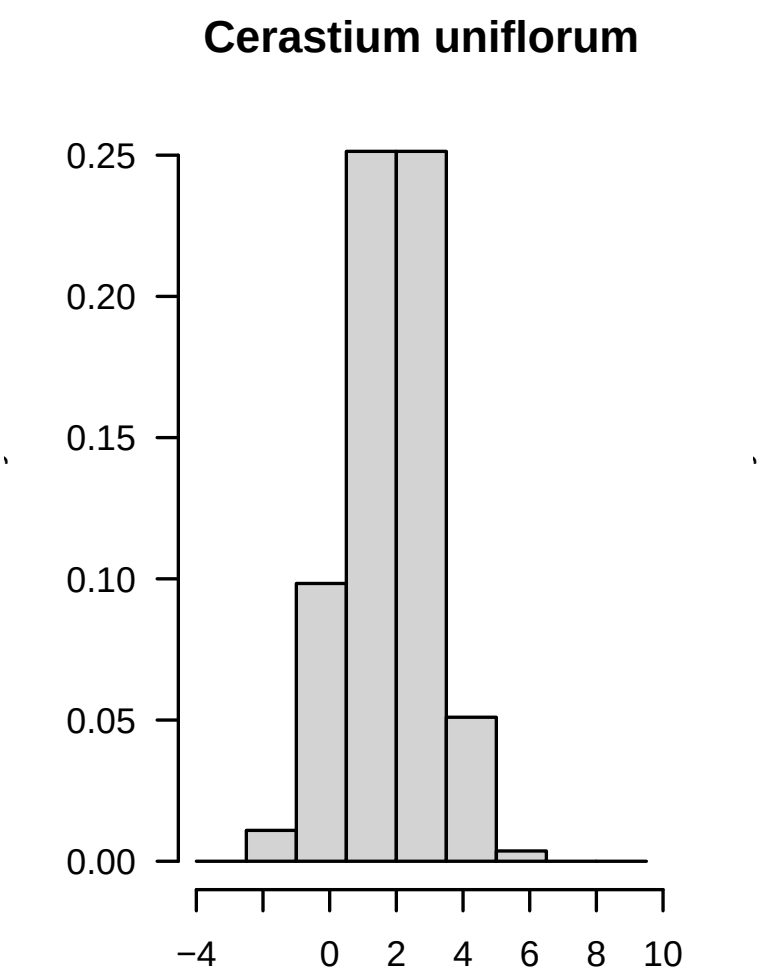
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.87



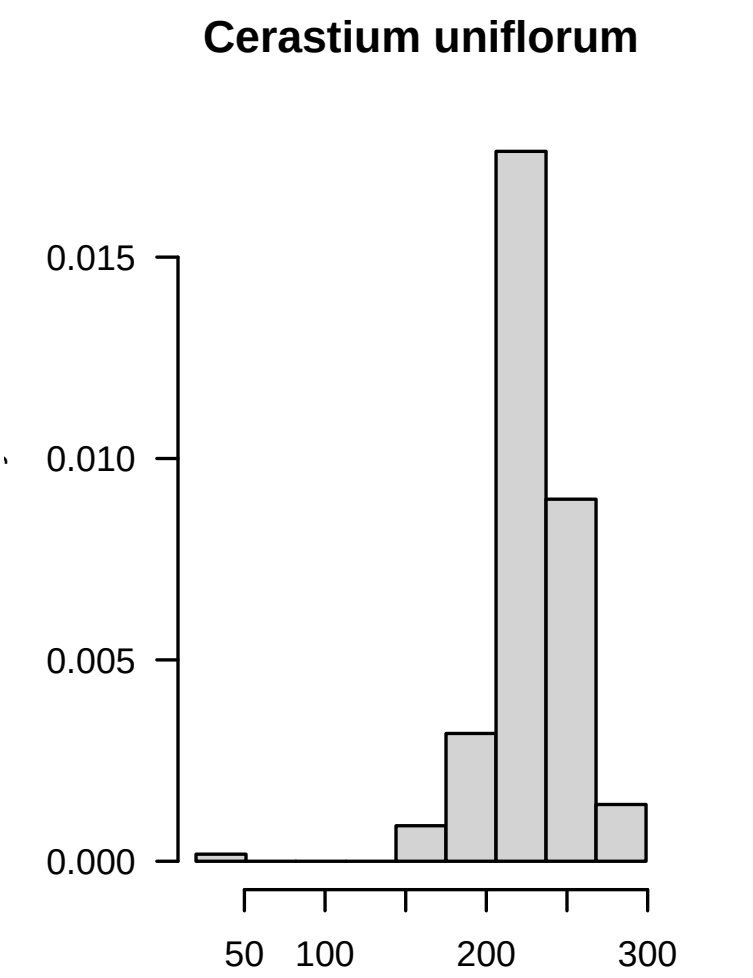
Elevation [m.a.s.l.]

p SW	p AG	skew
0.09	0.76	0.05



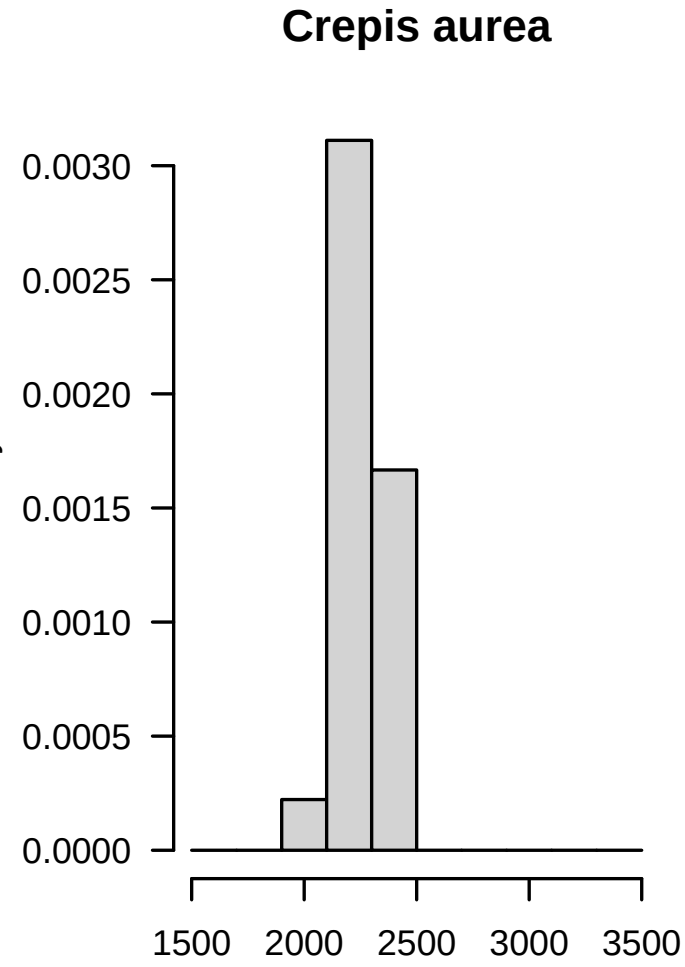
Annual mean temperature [°C]

p SW	p AG	skew
0.62	0.61	−0.09



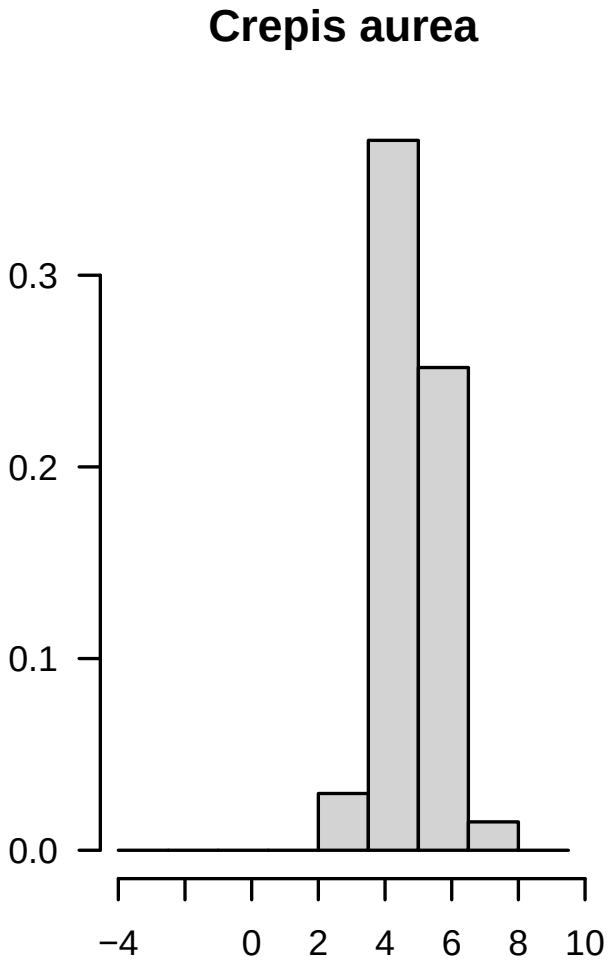
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.4



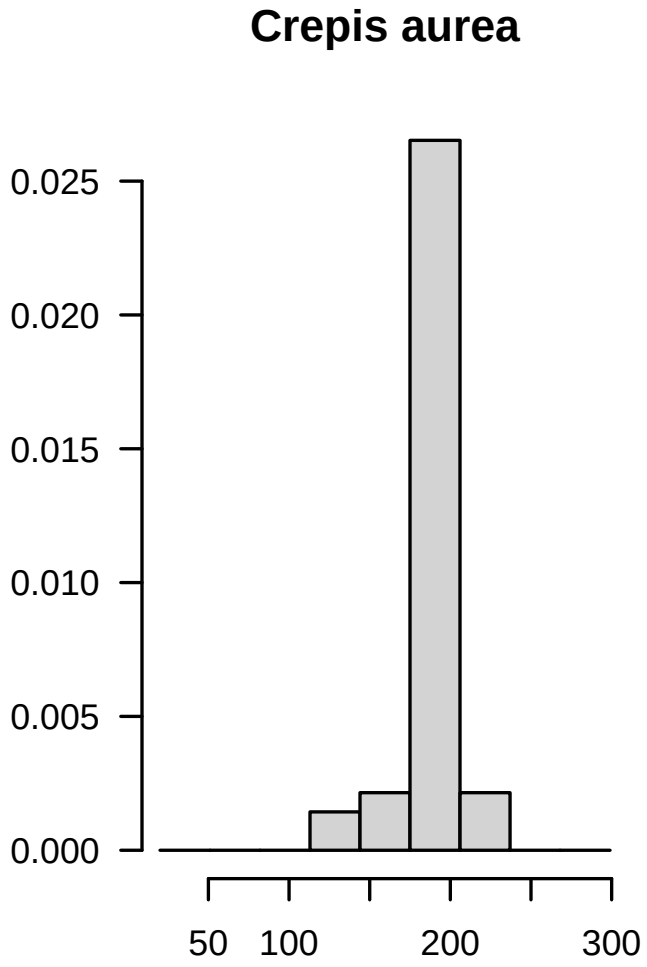
Elevation [m.a.s.l.]

p SW	p AG	skew
0.03	0.27	0.37



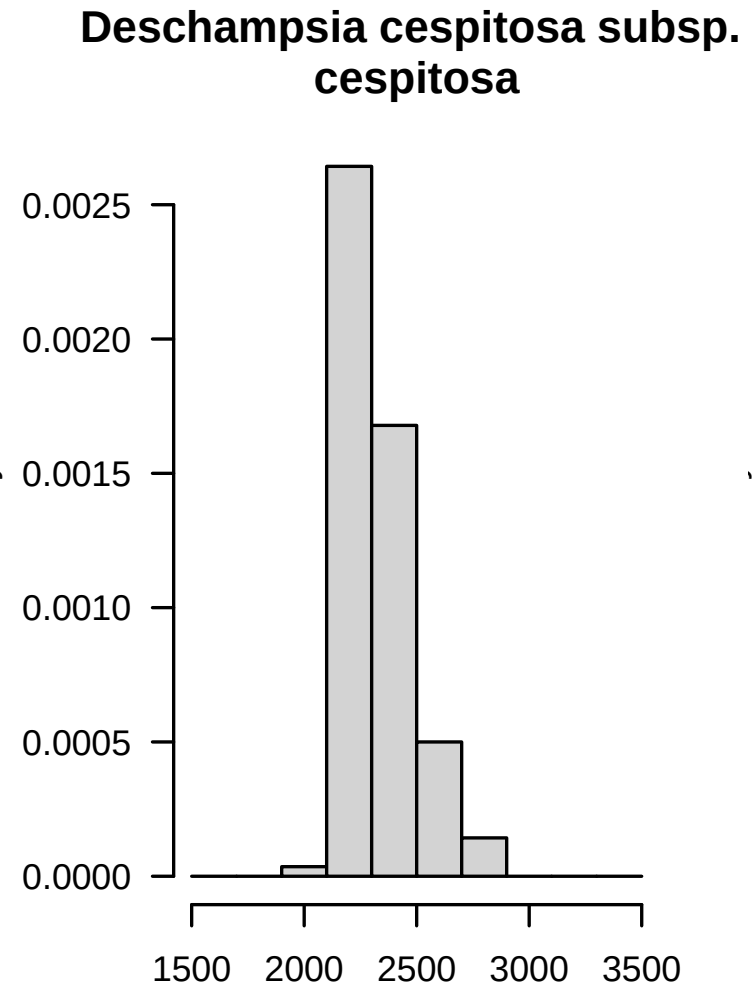
Annual mean temperature [°C]

p SW	p AG	skew
0.01	0.76	0.1



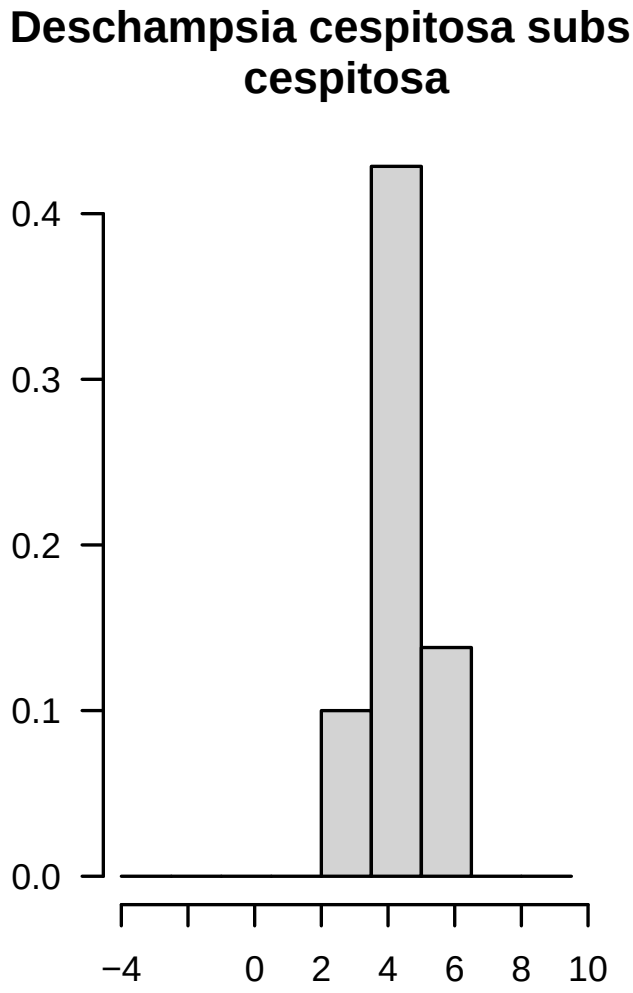
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.33



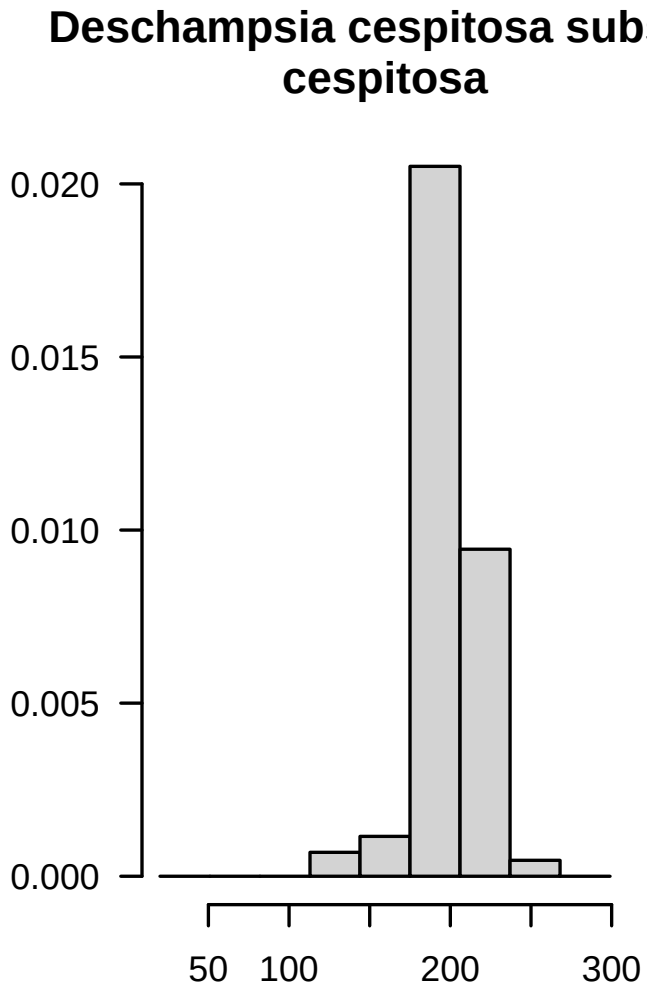
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	<0.01	0.86



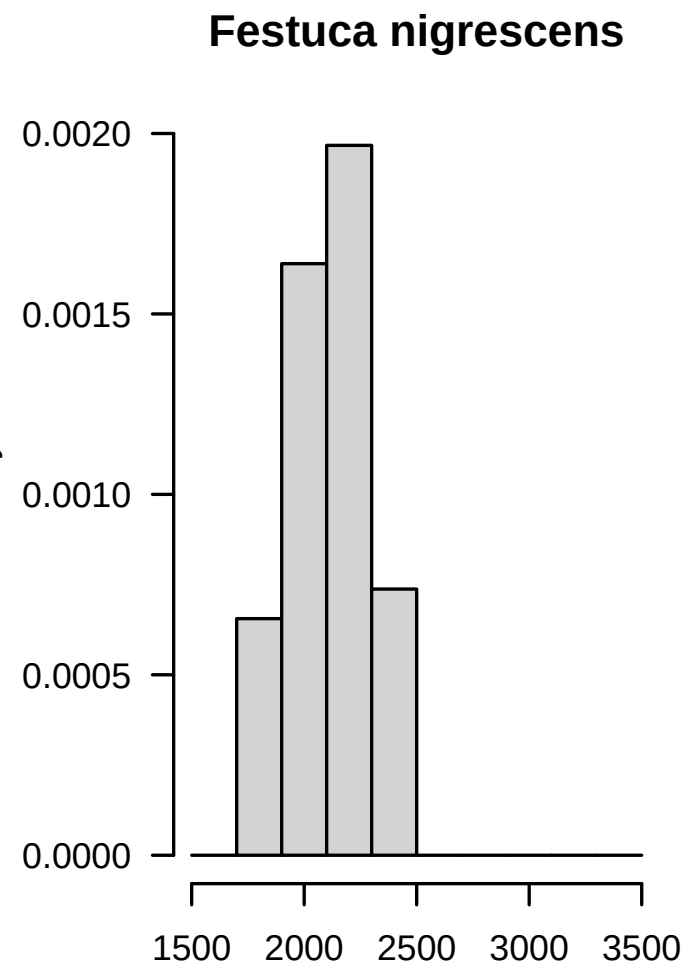
Annual mean temperature [°C]

p SW	p AG	skew
0.03	0.04	−0.42



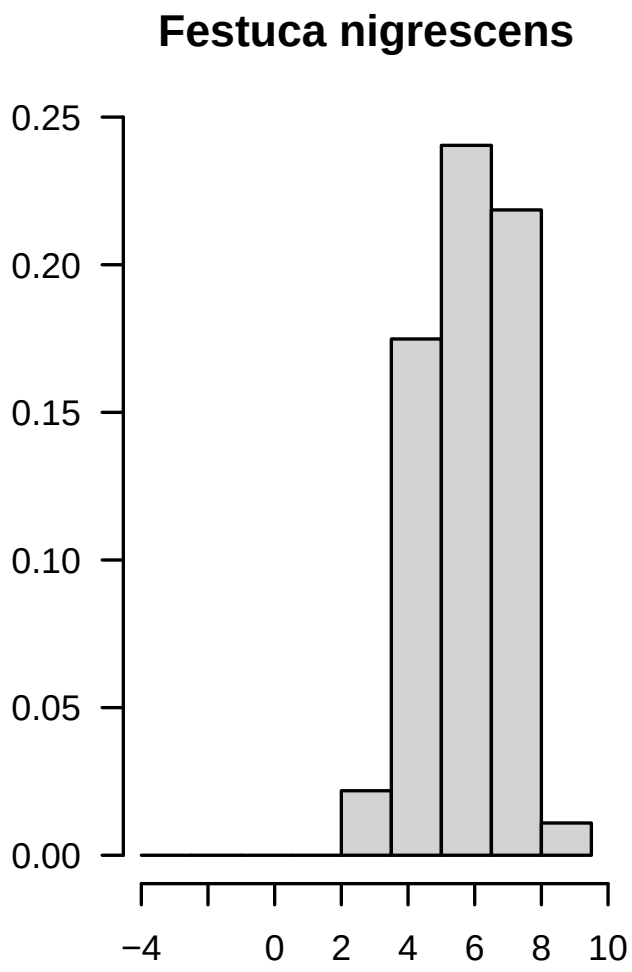
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−0.7



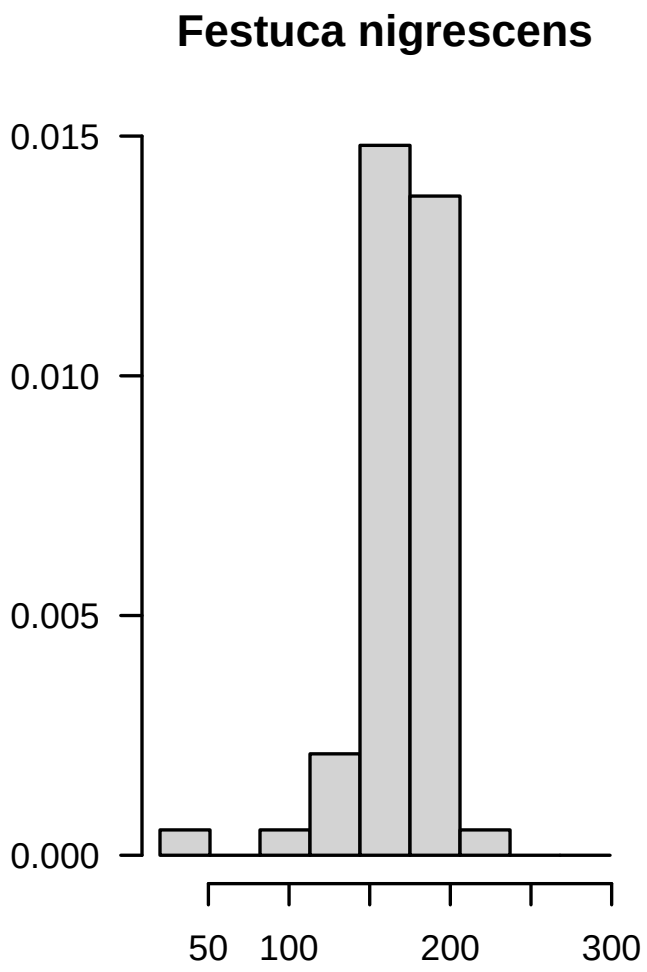
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.91	0.03



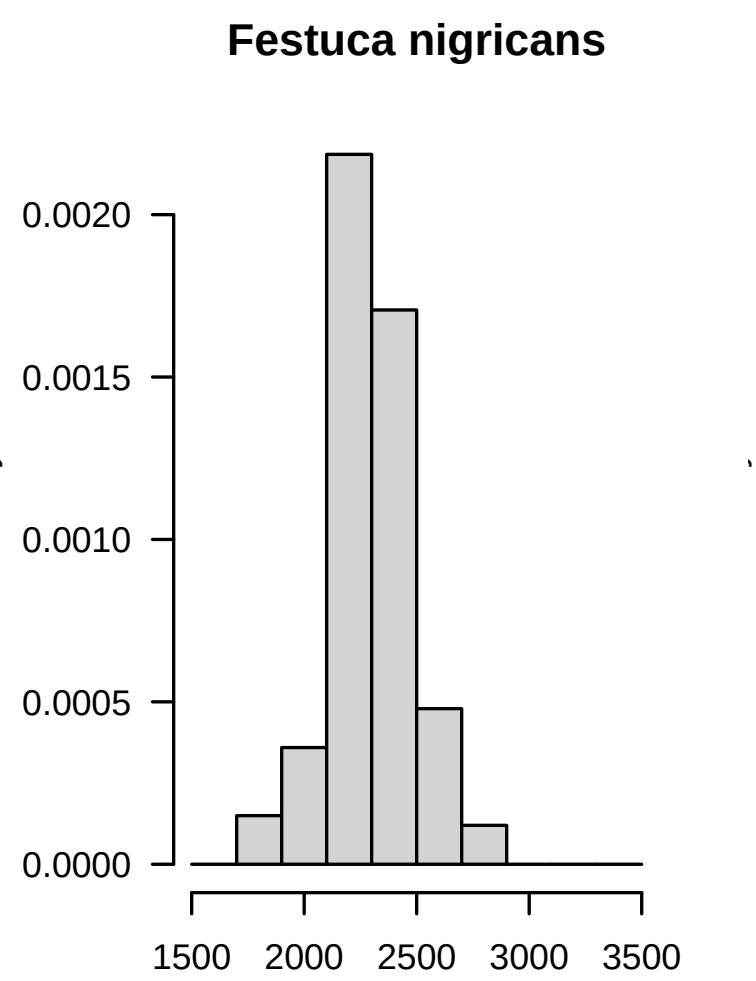
Annual mean temperature [°C]

p SW	p AG	skew
0.27	0.34	−0.28



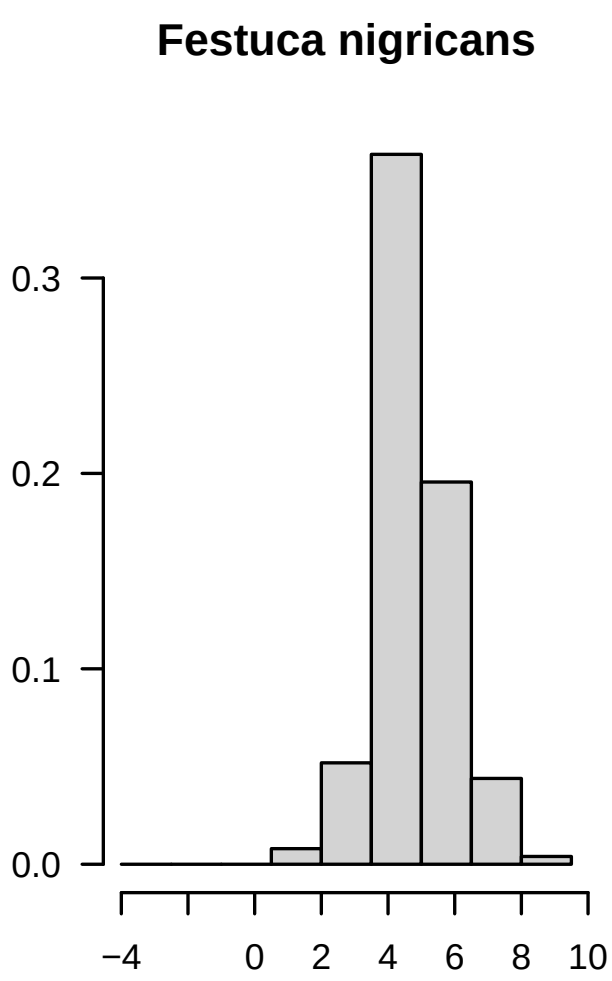
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.64



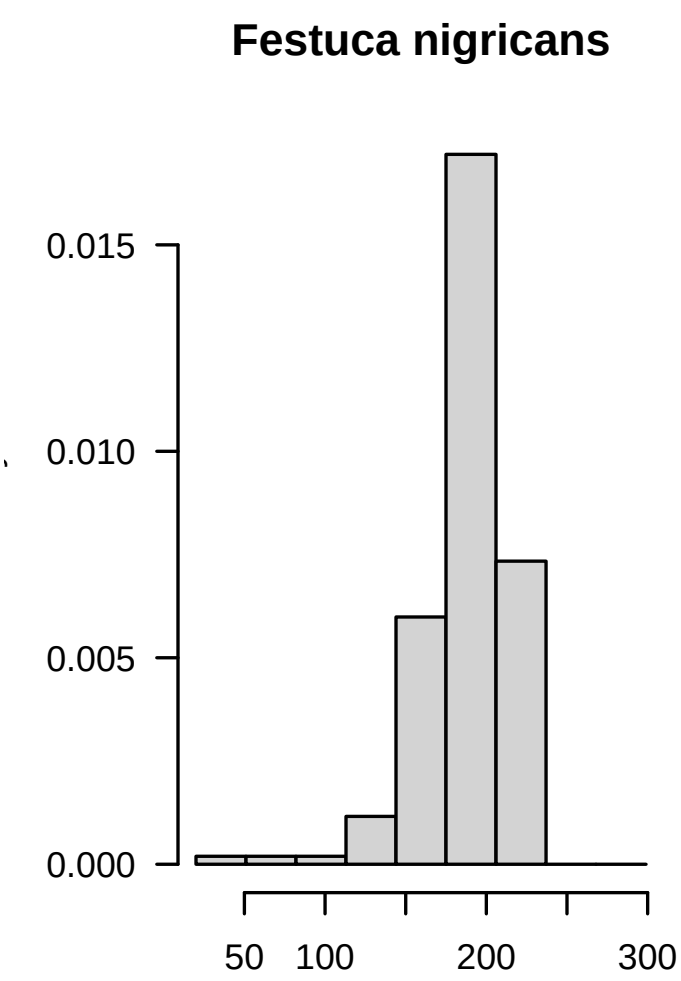
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.92	−0.02



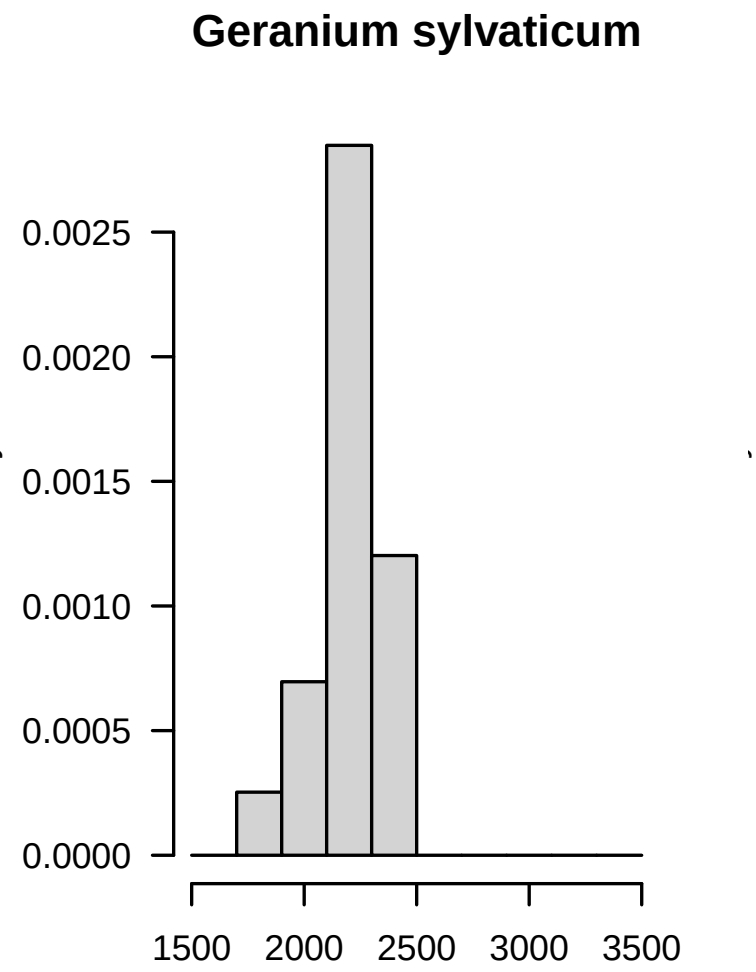
Annual mean temperature [°C]

p SW	p AG	skew
0.02	0.11	0.29



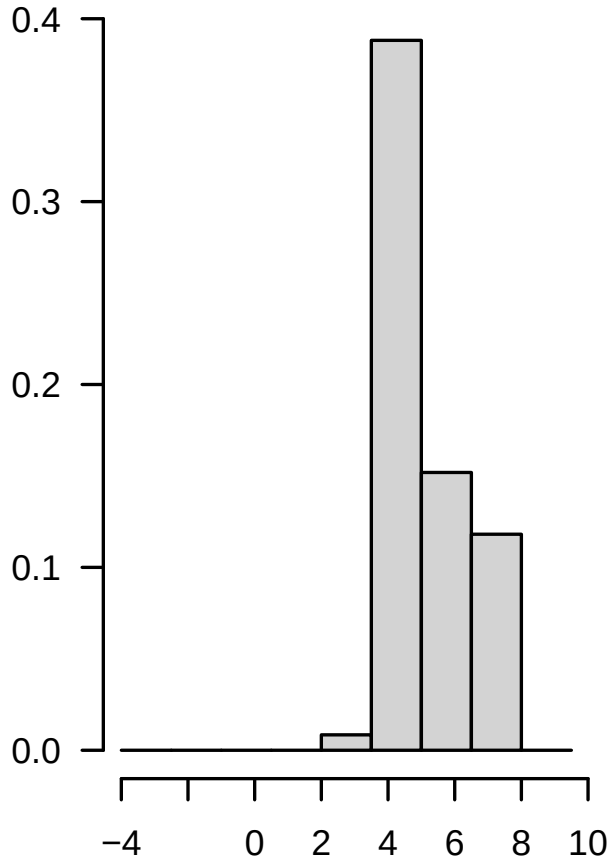
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.92



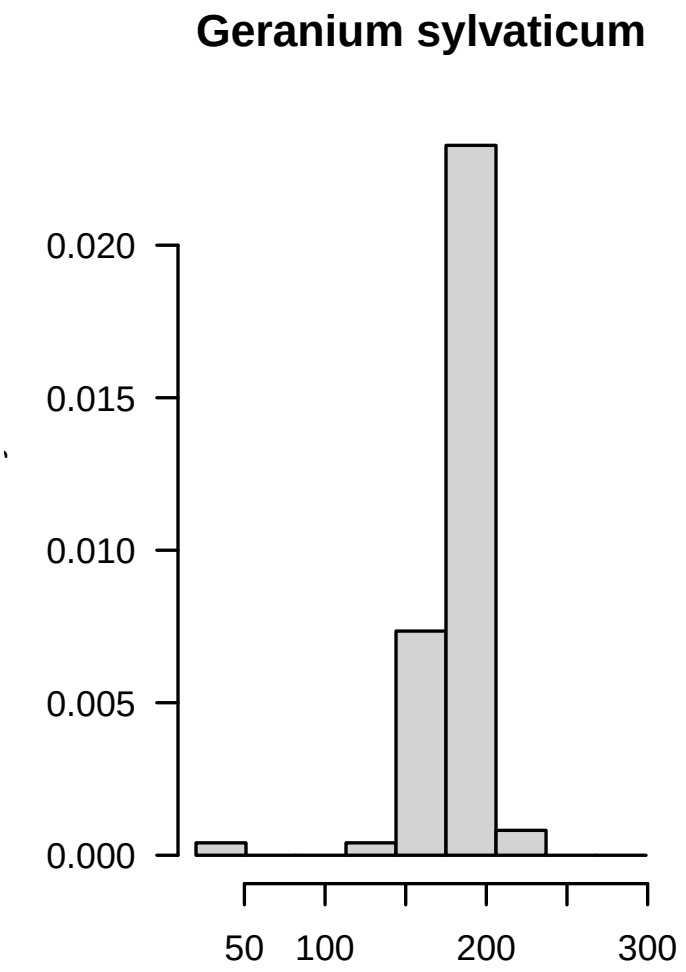
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.02	−0.66



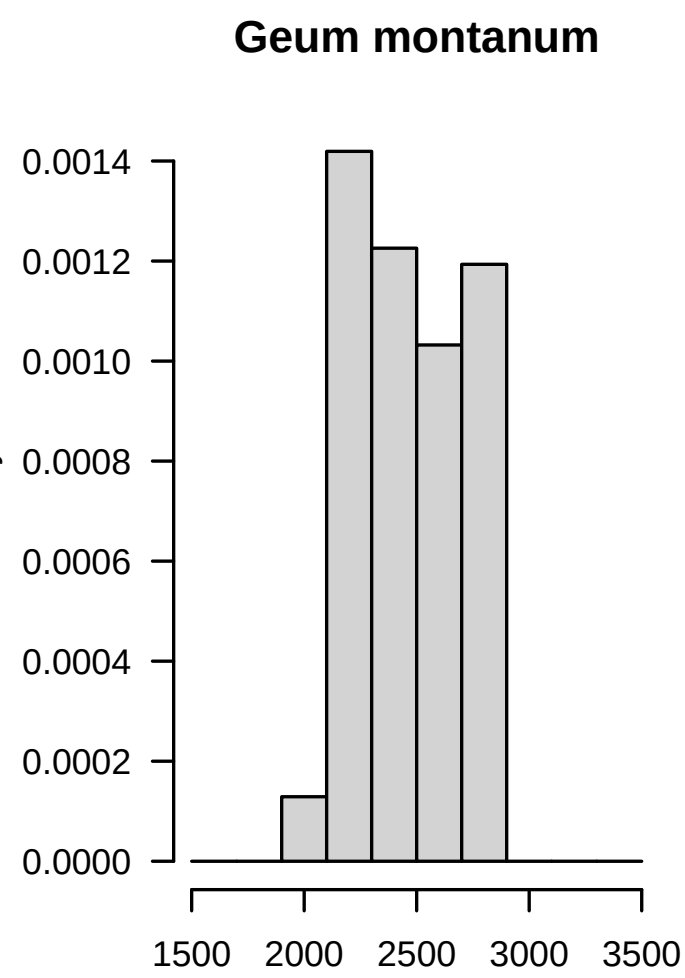
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	0.02	0.66



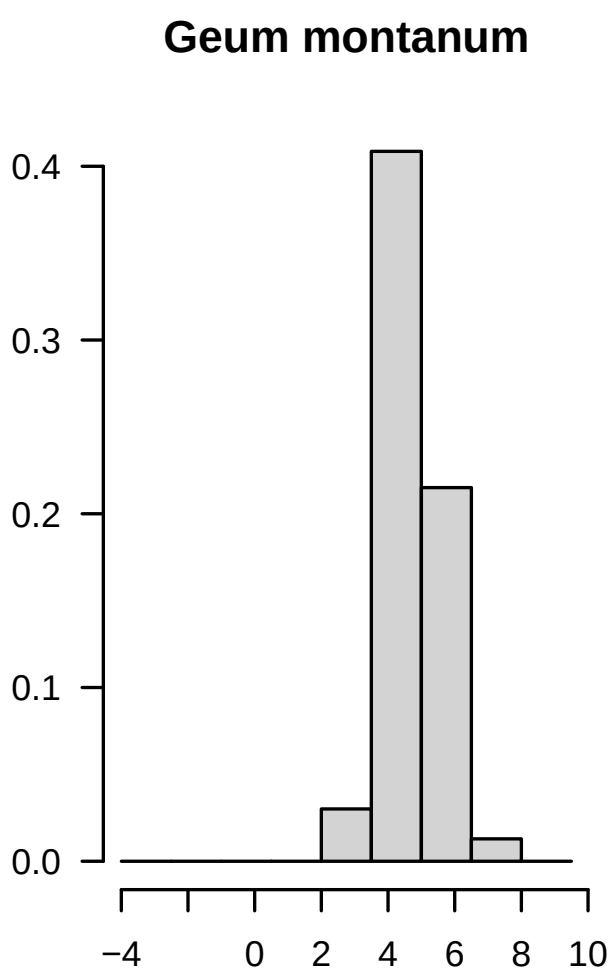
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.84



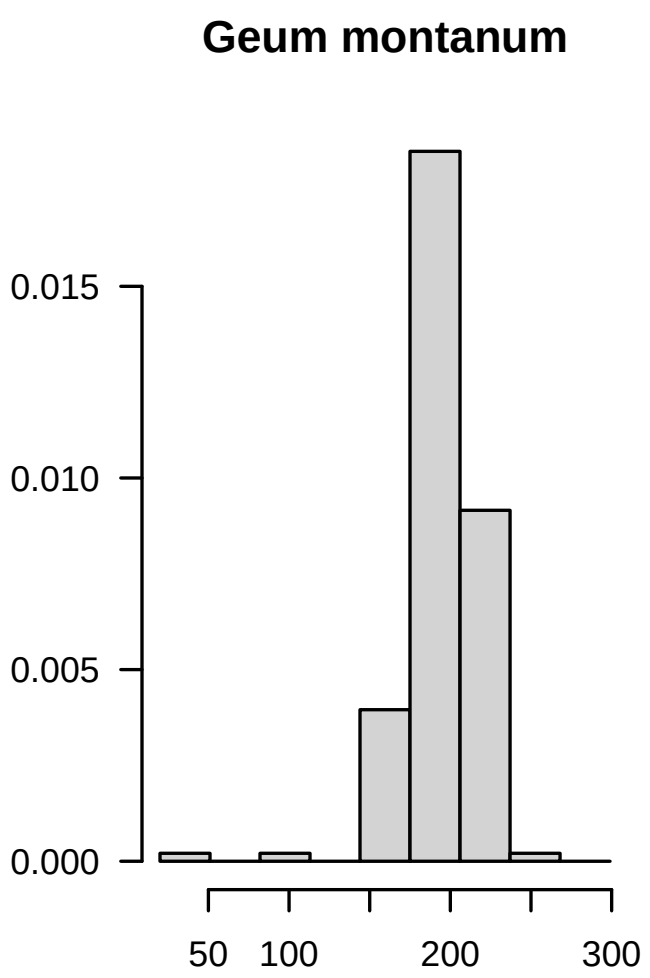
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.89	0.02



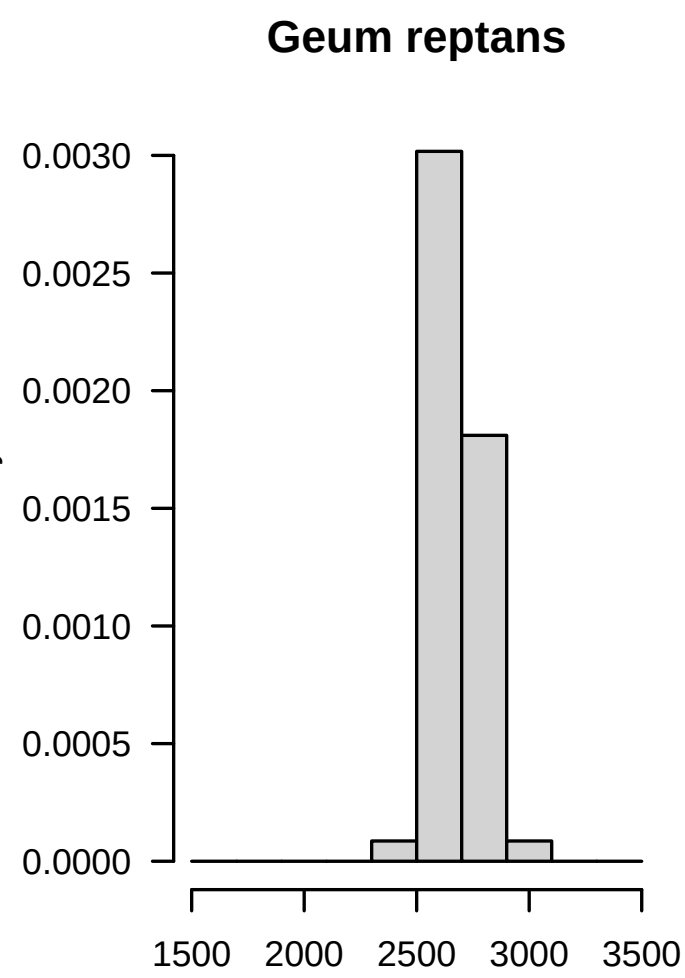
Annual mean temperature [°C]

p SW	p AG	skew
0.4	0.56	0.11



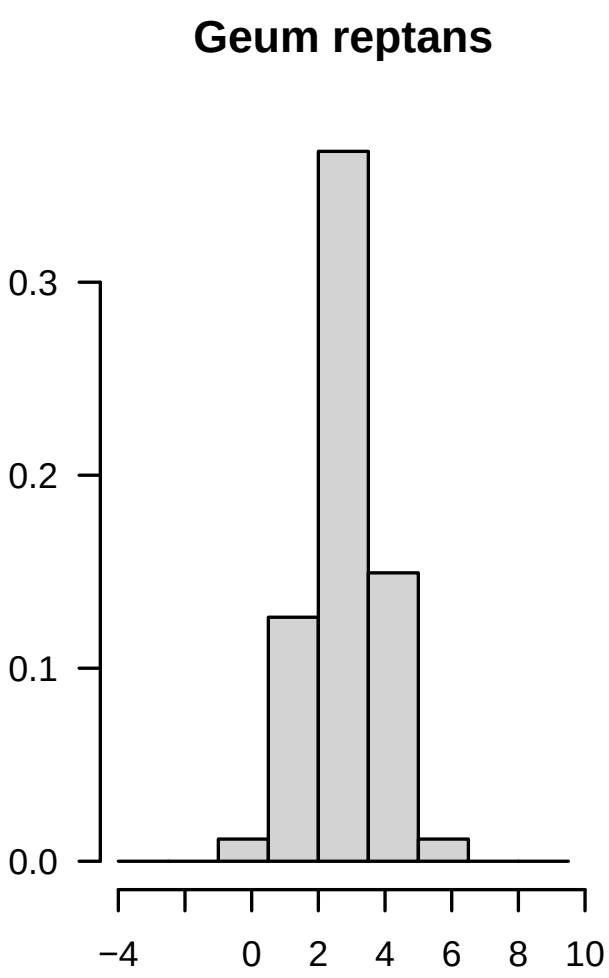
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.08



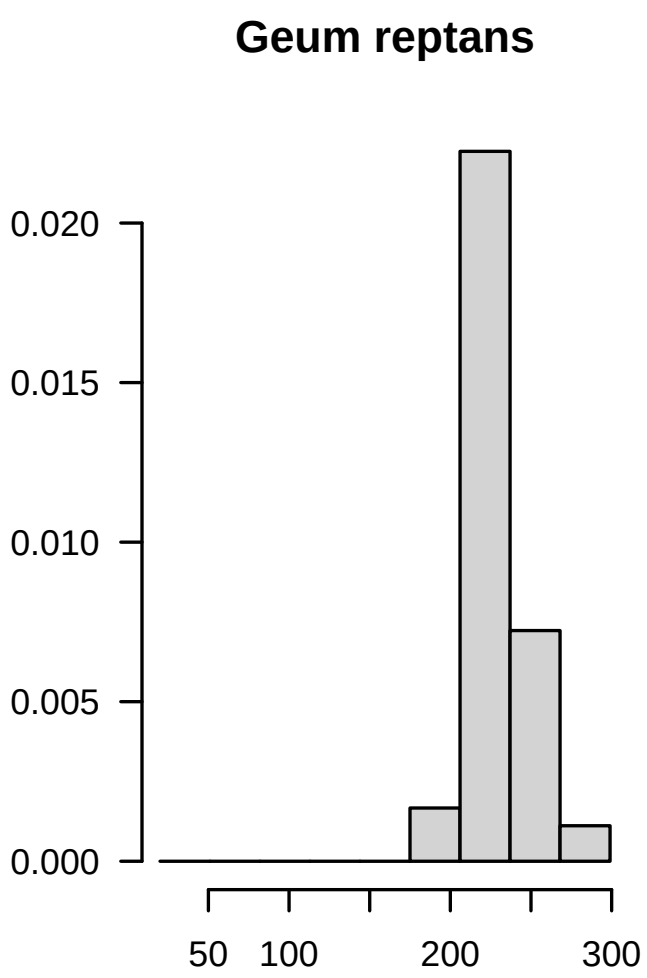
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.11	0.48



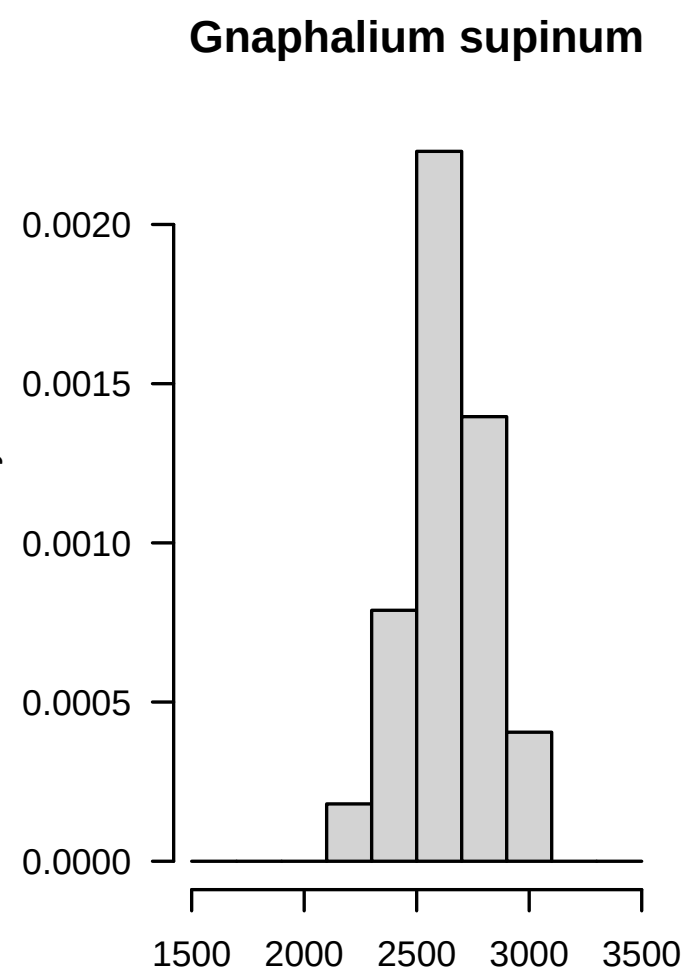
Annual mean temperature [°C]

p SW	p AG	skew
0.9	0.84	−0.06



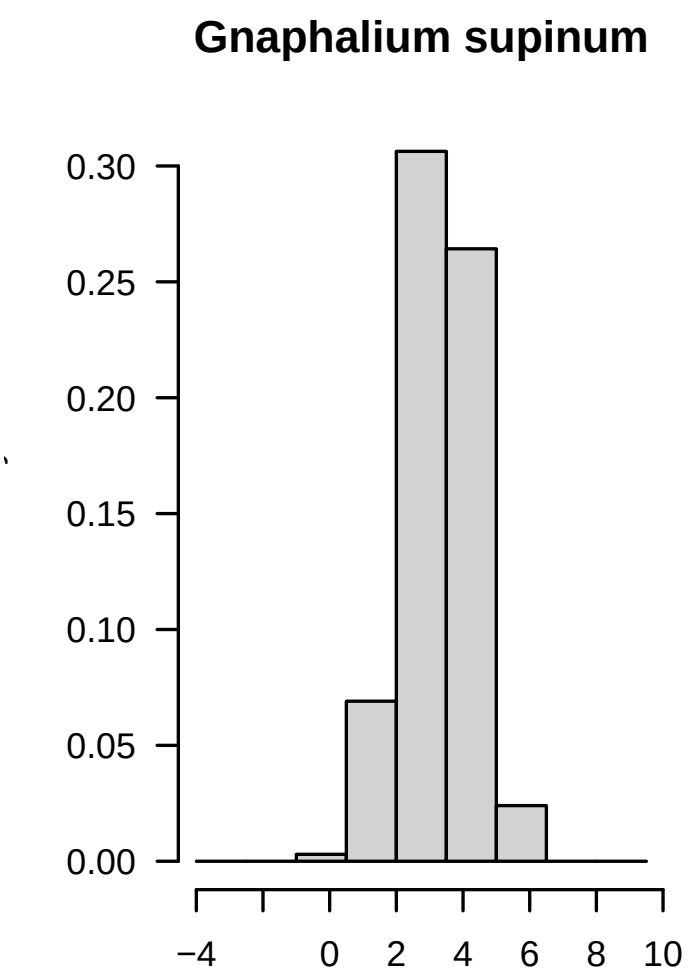
Snow cover duration [d]

p SW	p AG	skew
0.03	0.15	0.43



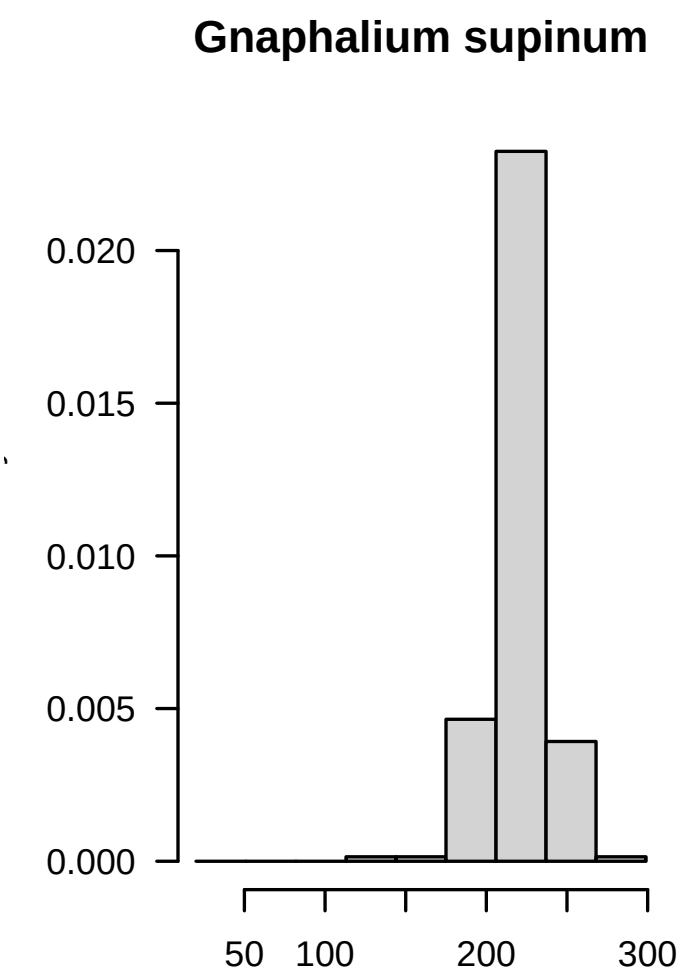
Elevation [m.a.s.l.]

p SW	p AG	skew
0.44	0.55	−0.1



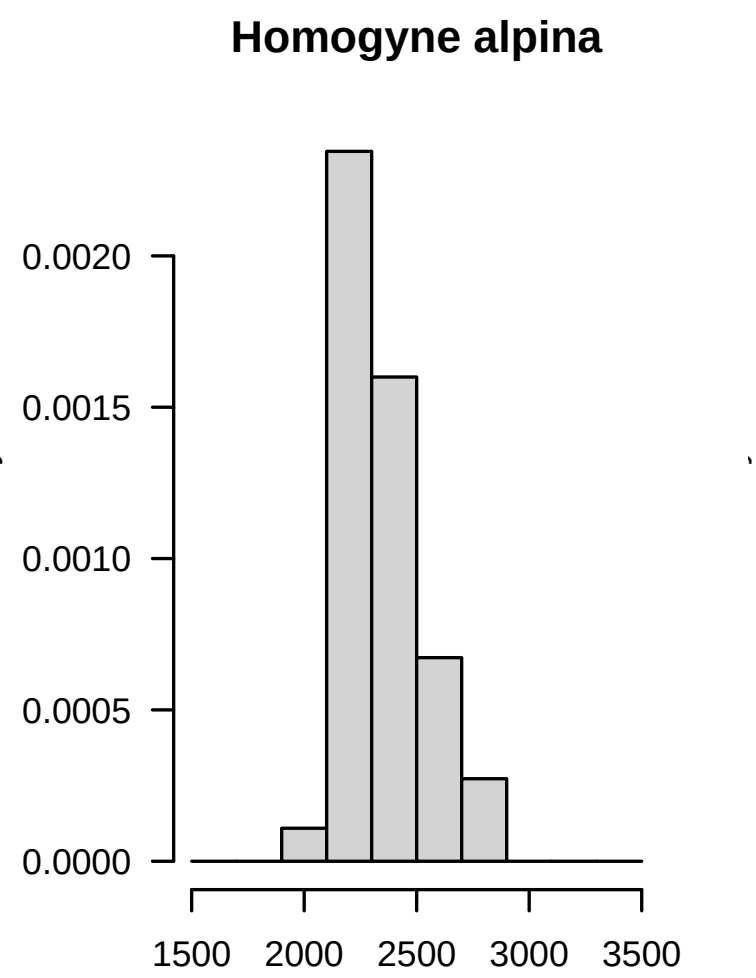
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	0.03	−0.36



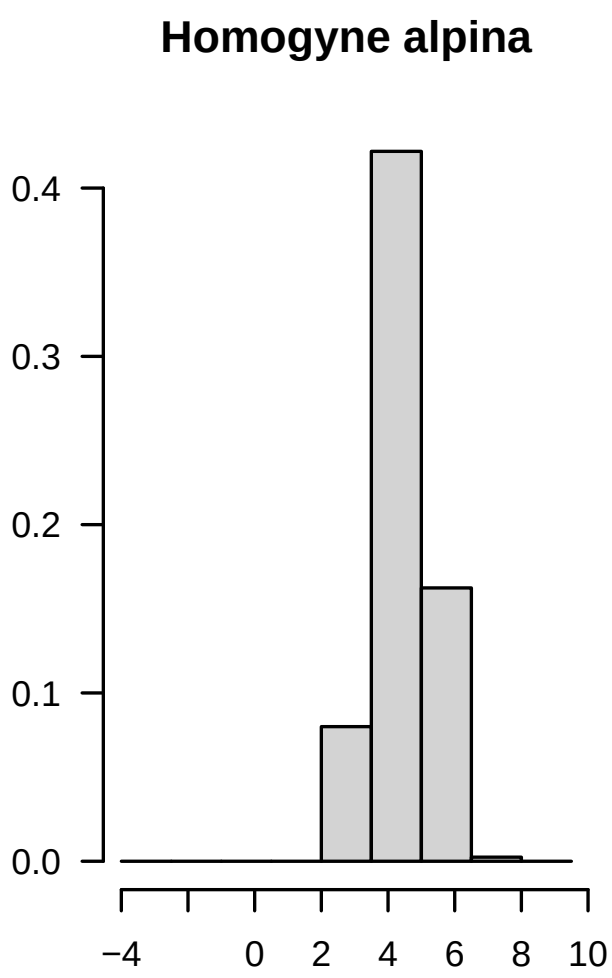
Snow cover duration [d]

p SW	p AG	skew
<0.01	0.06	−0.3



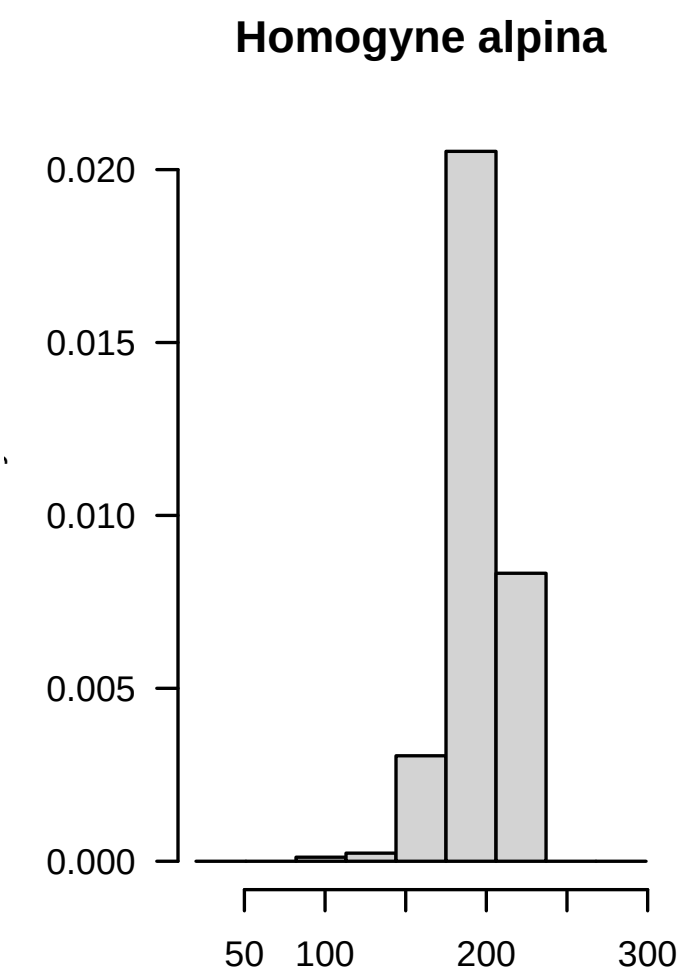
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	<0.01	0.71



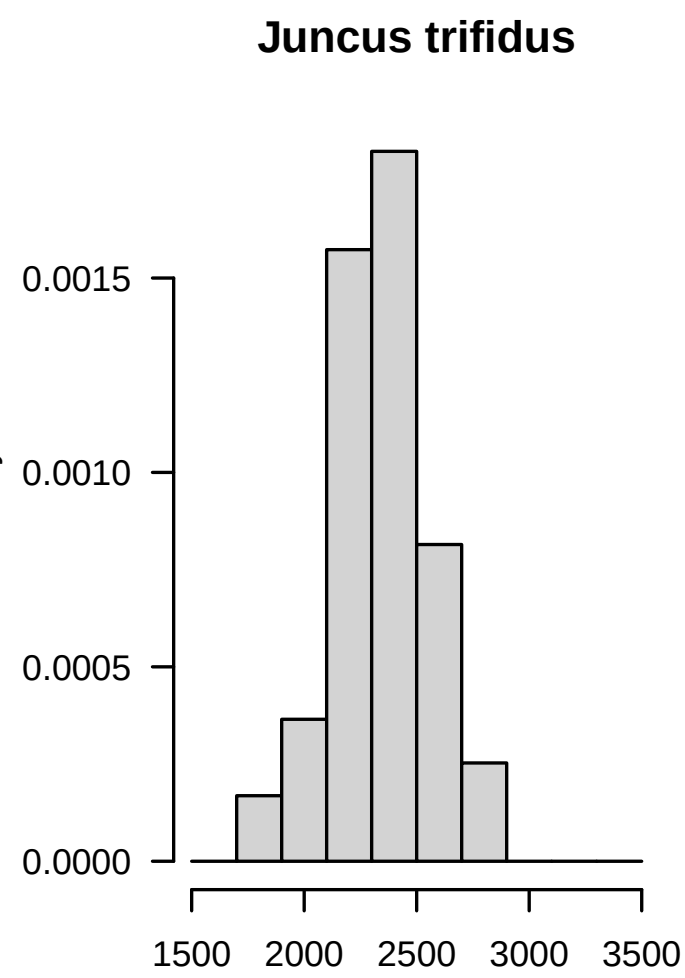
Annual mean temperature [°C]

p SW	p AG	skew
0.08	0.05	−0.29



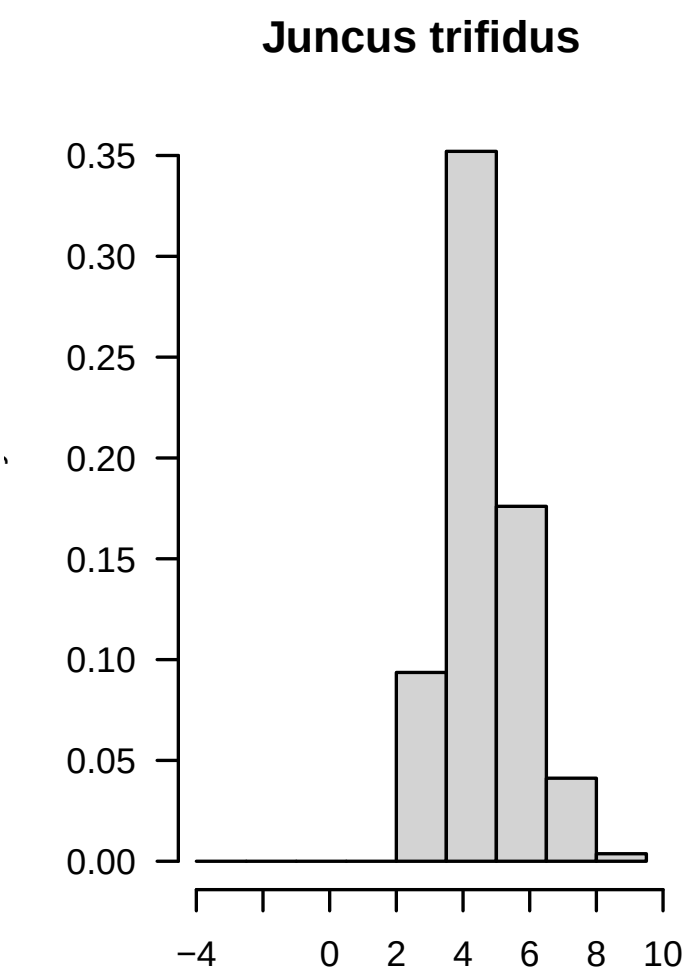
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−0.88



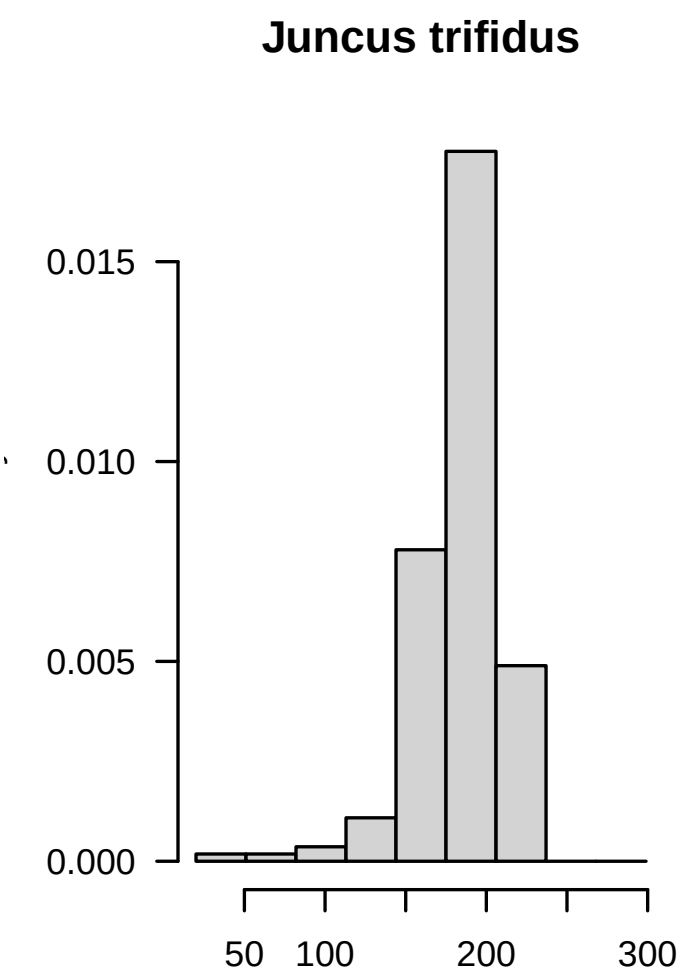
Elevation [m.a.s.l.]

p SW	p AG	skew
0.05	0.51	−0.12



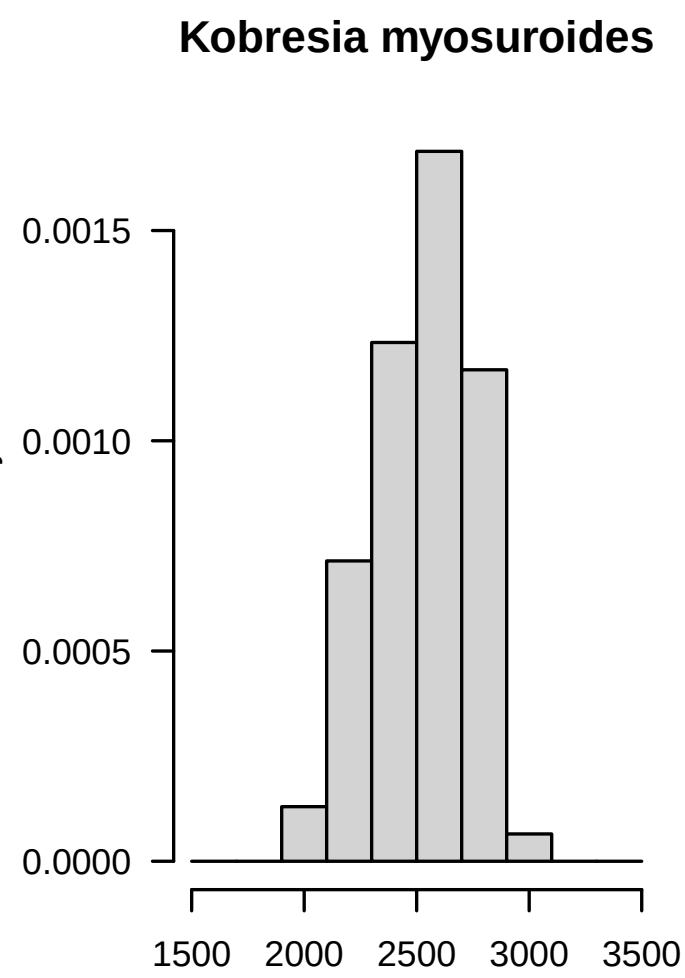
Annual mean temperature [°C]

p SW	p AG	skew
0.13	0.3	0.19



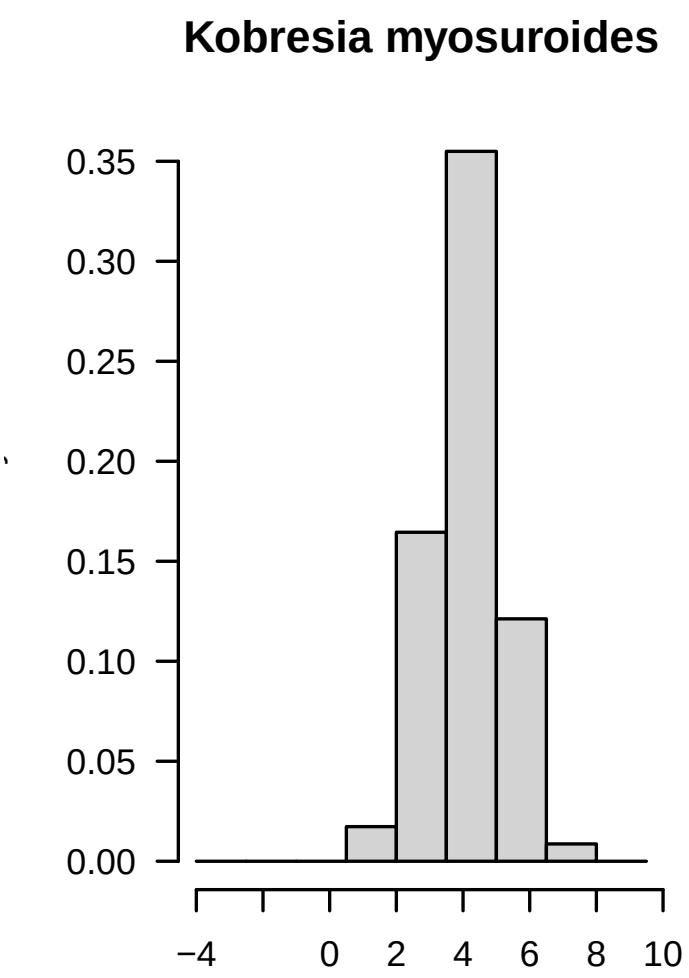
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.77



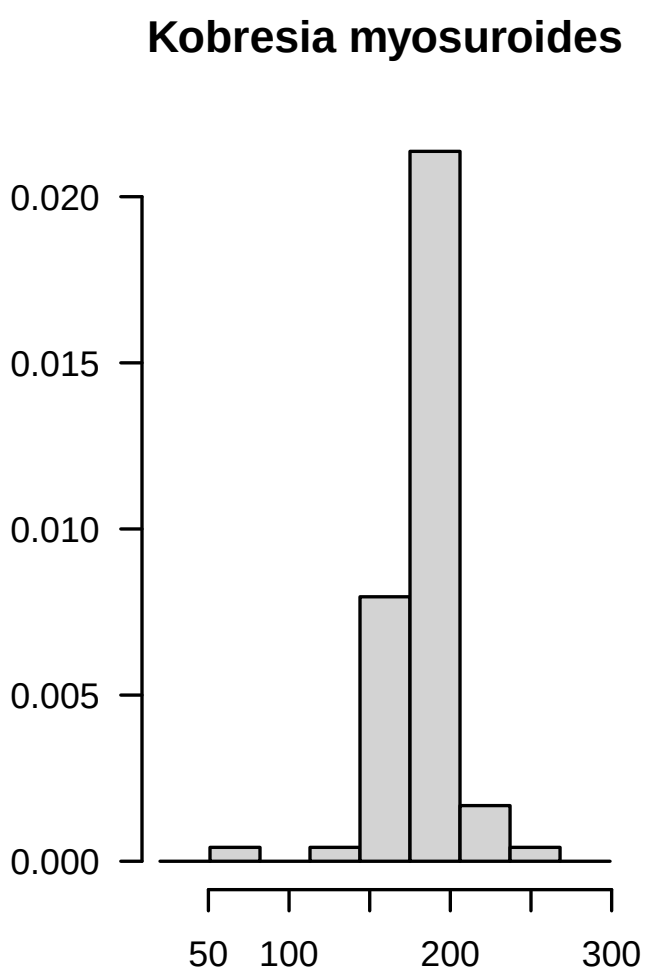
Elevation [m.a.s.l.]

p SW	p AG	skew
0.02	0.17	−0.37



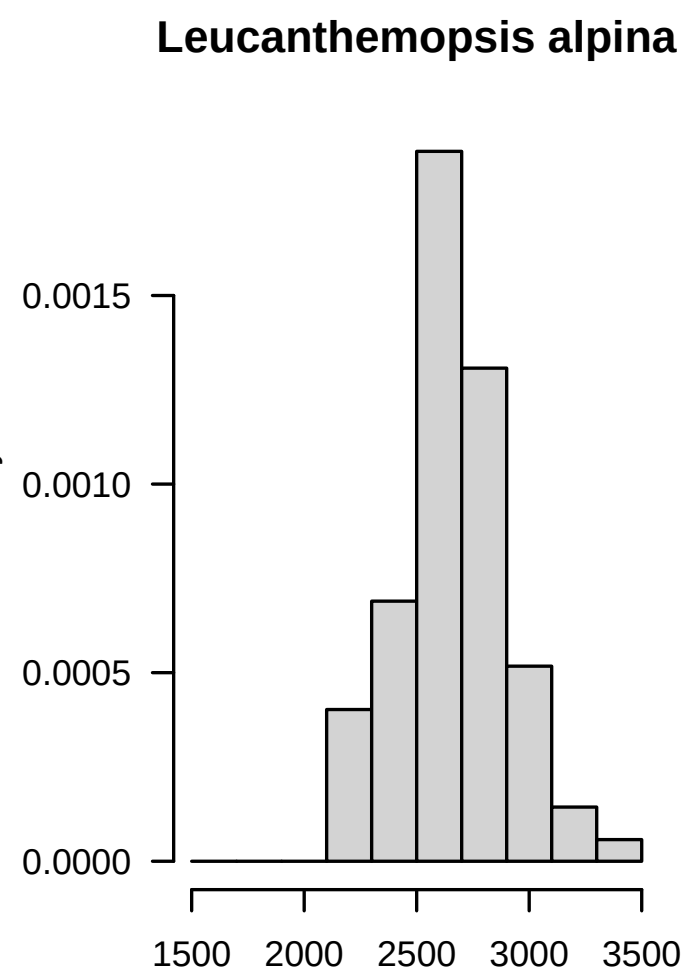
Annual mean temperature [°C]

p SW	p AG	skew
0.17	0.07	−0.48



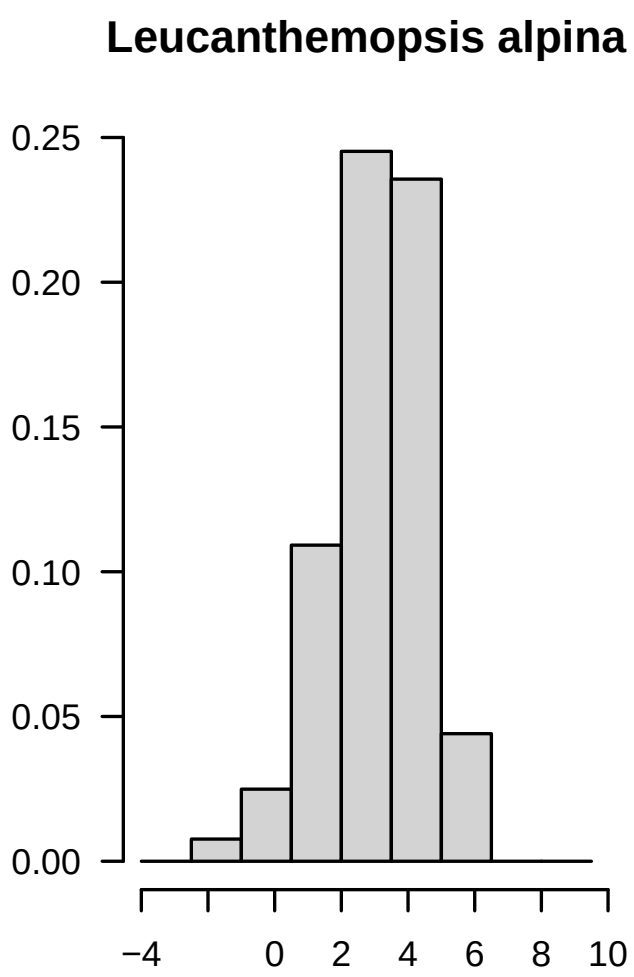
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.84



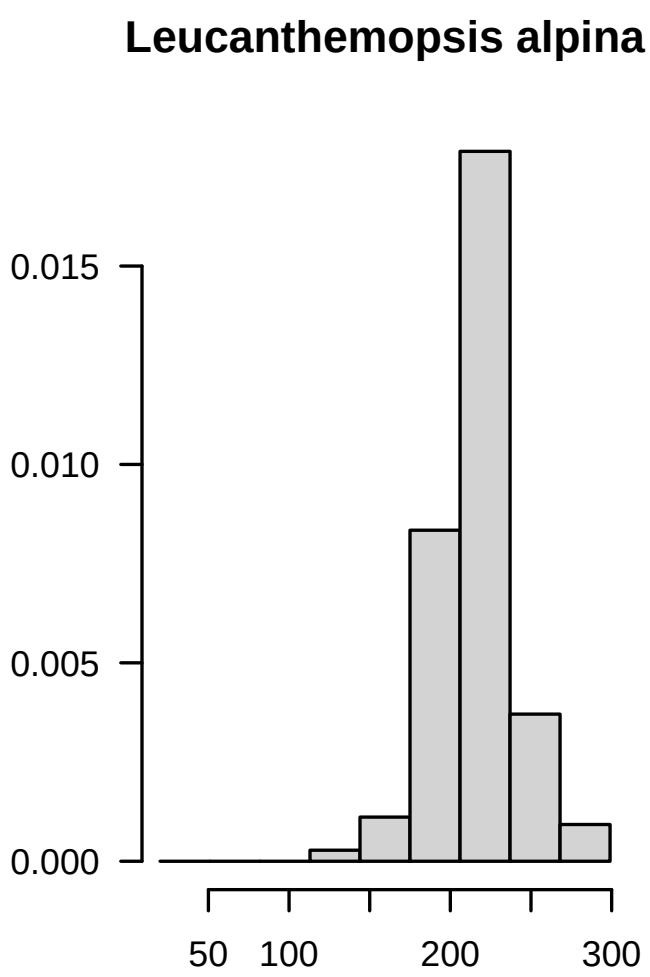
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.45	0.1



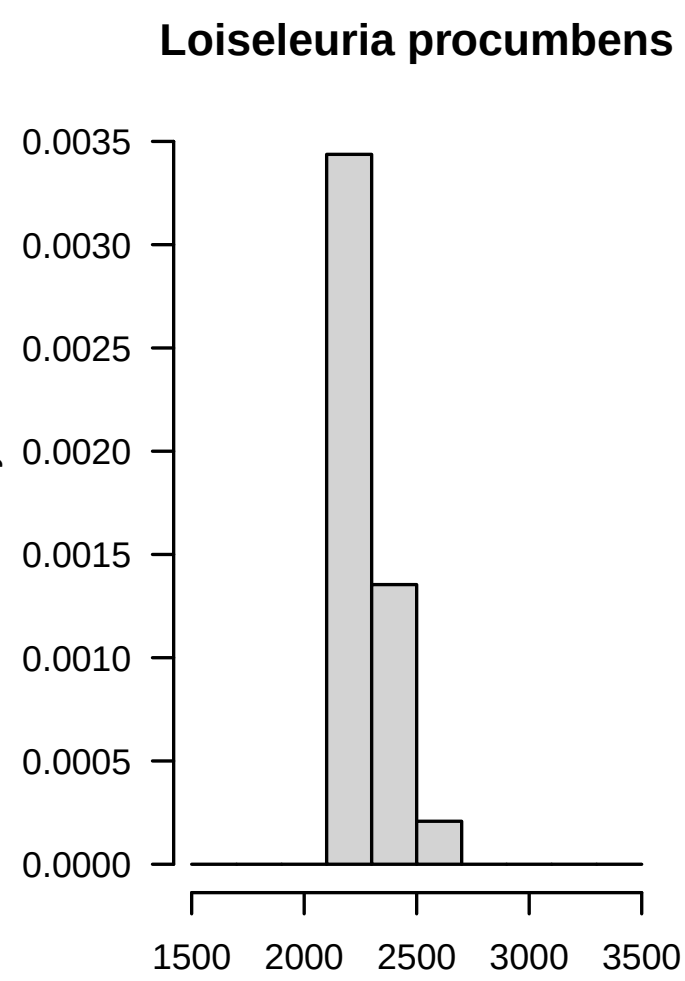
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	<0.01	−0.61



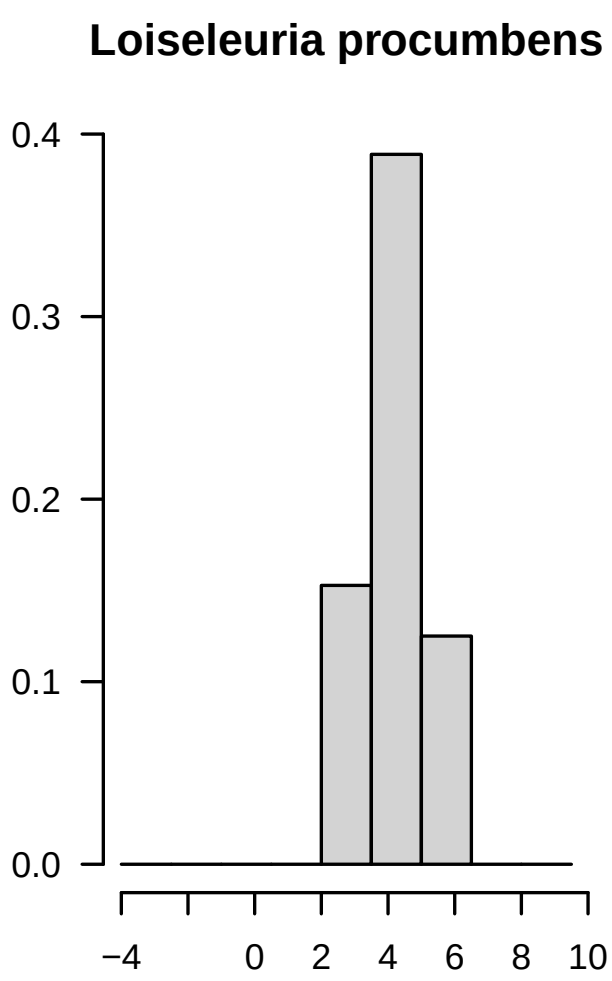
Snow cover duration [d]

p SW	p AG	skew
<0.01	0.98	0



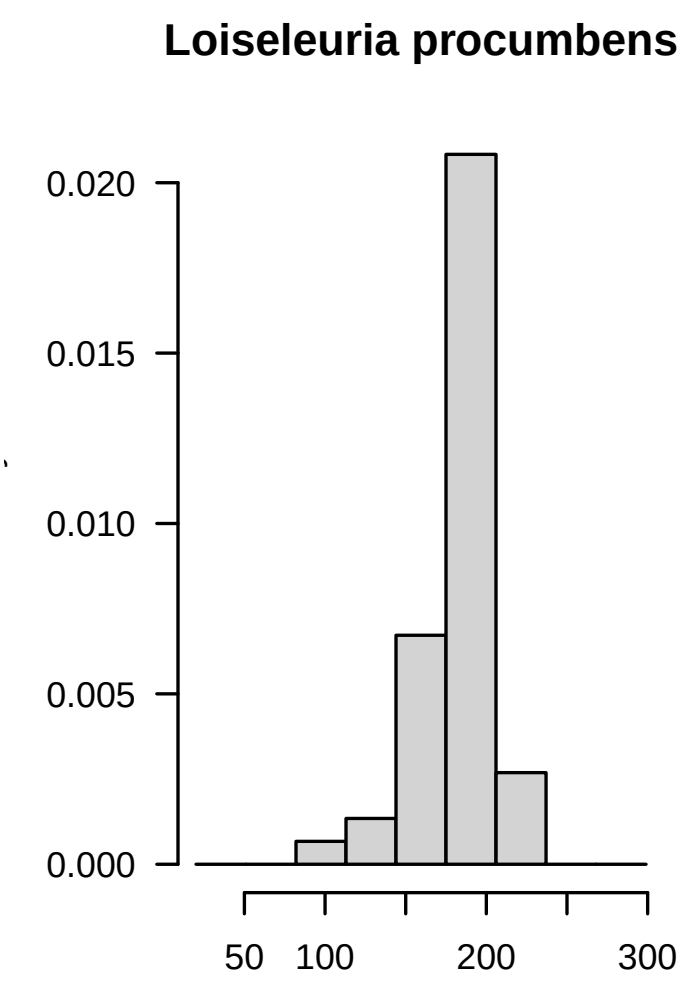
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	<0.01	1.45



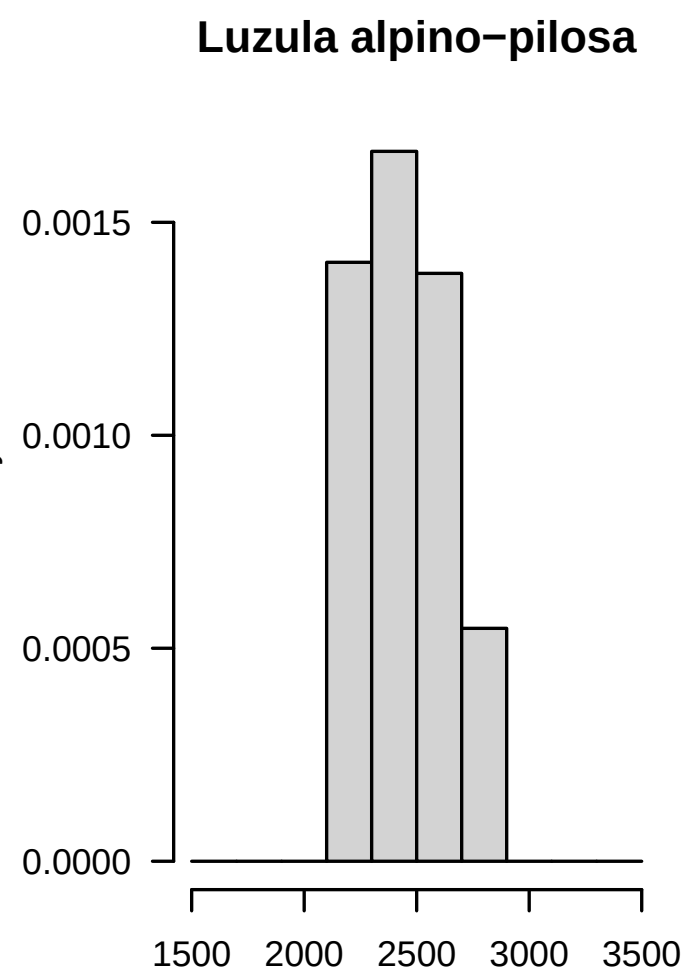
Annual mean temperature [°C]

p SW	p AG	skew
0.62	0.55	−0.19



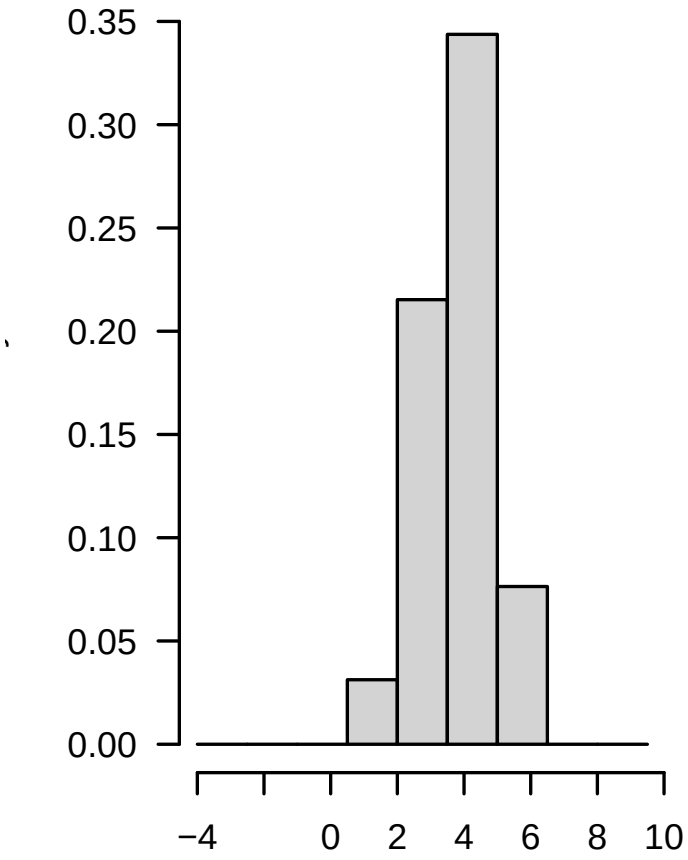
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.53



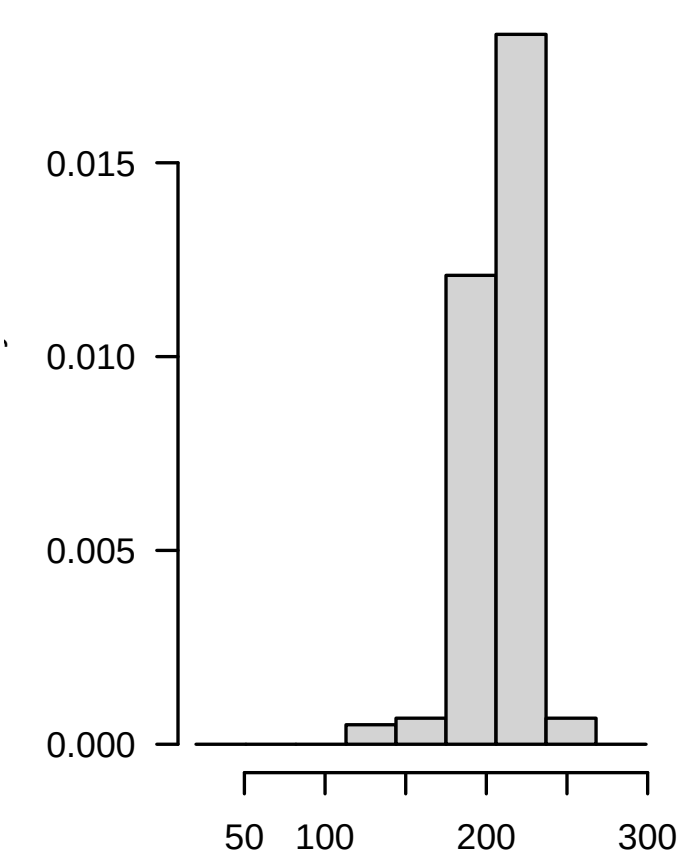
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.32	0.17



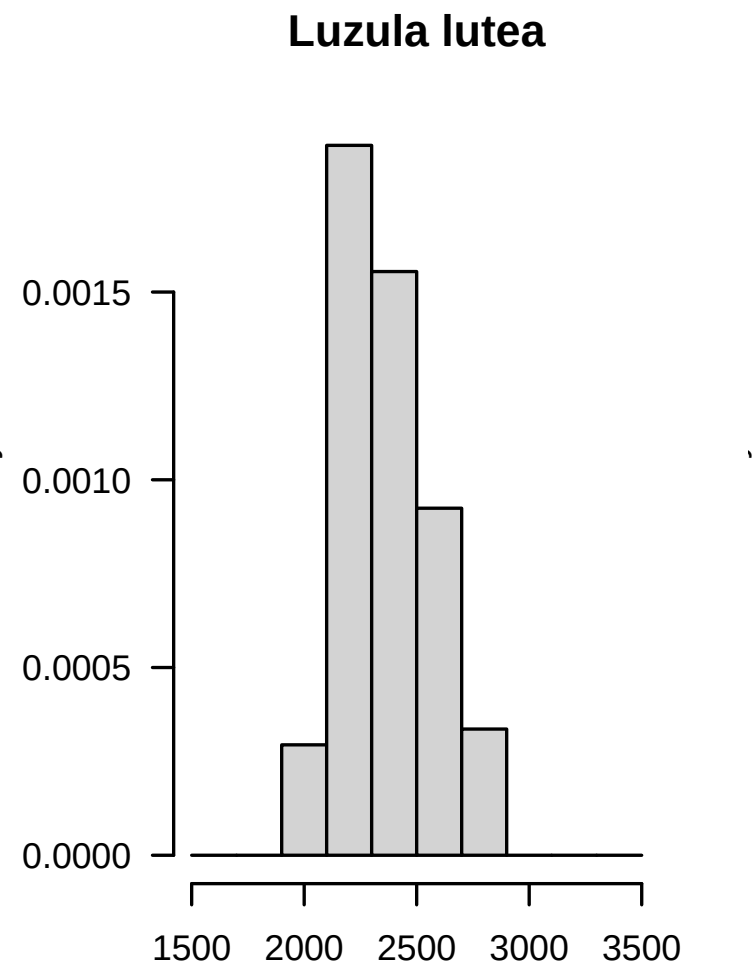
Annual mean temperature [°C]

p SW	p AG	skew
0.12	0.03	−0.38



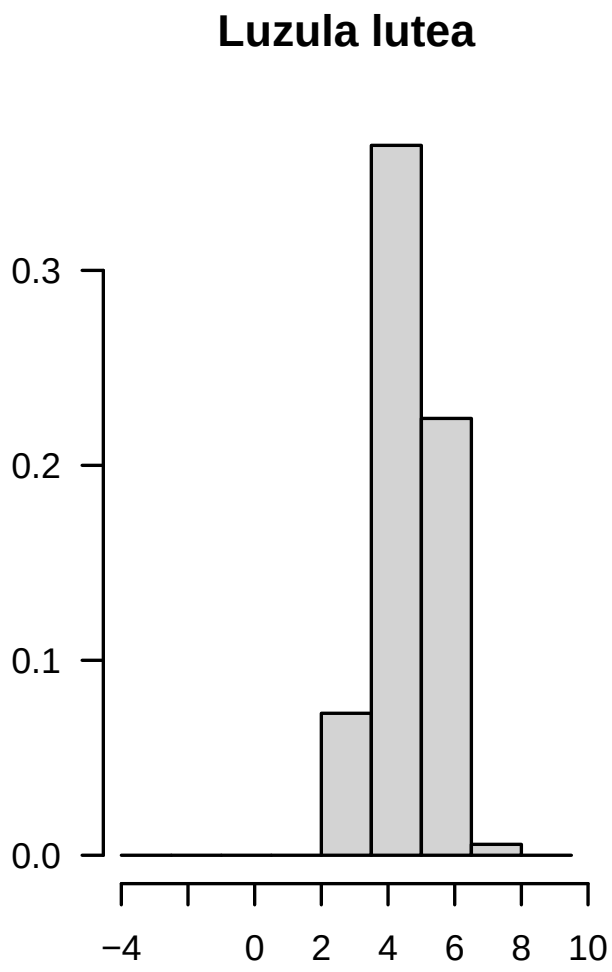
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−0.95



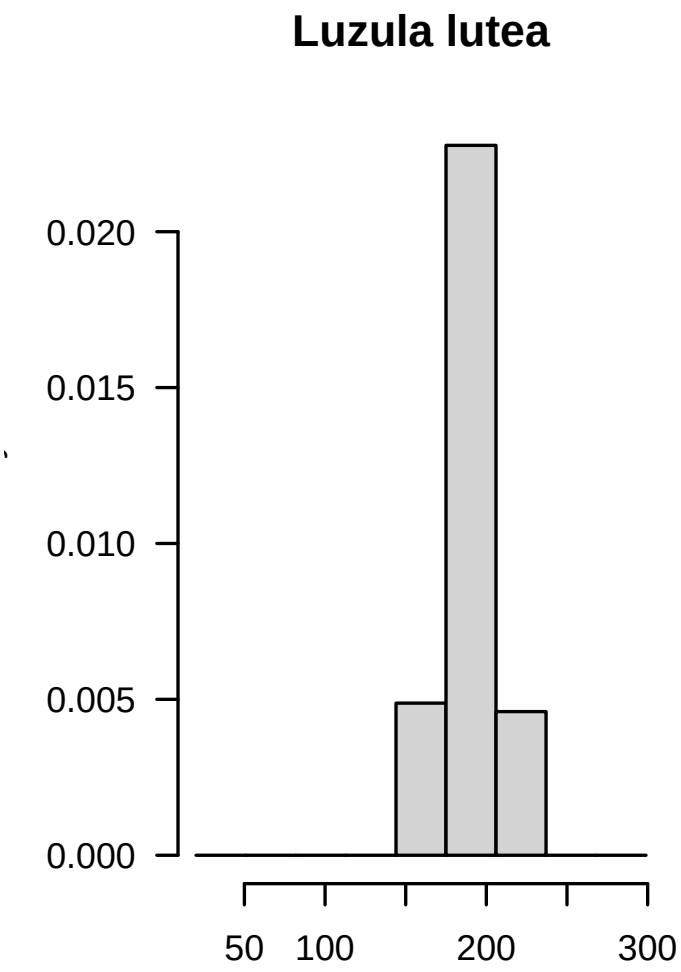
Elevation [m.a.s.l.]

p SW	p AG	skew
0.01	0.19	0.28



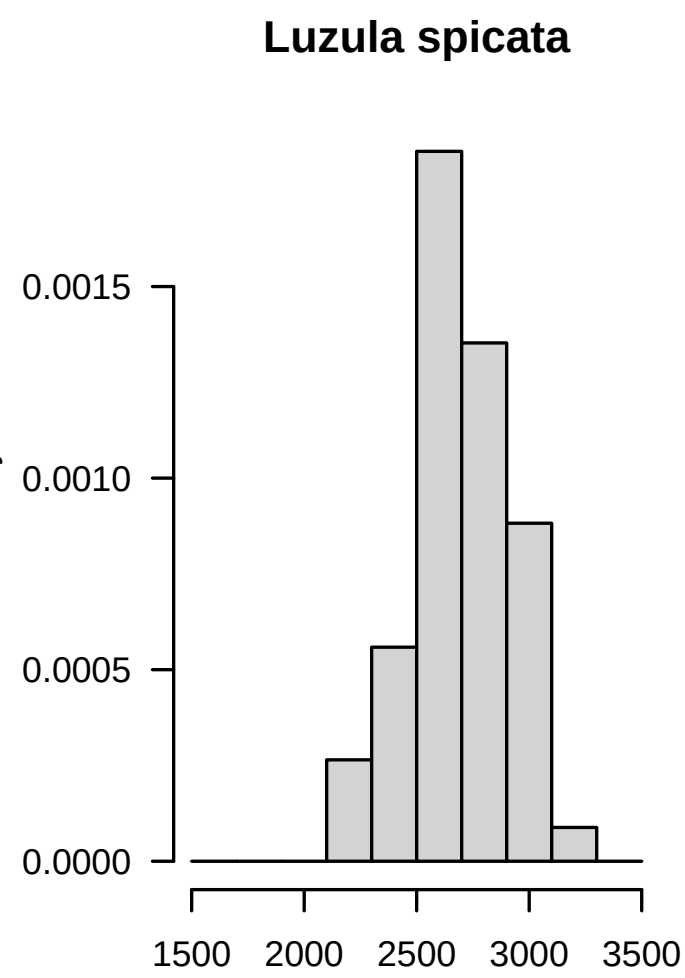
Annual mean temperature [°C]

p SW	p AG	skew
0.11	0.25	−0.25



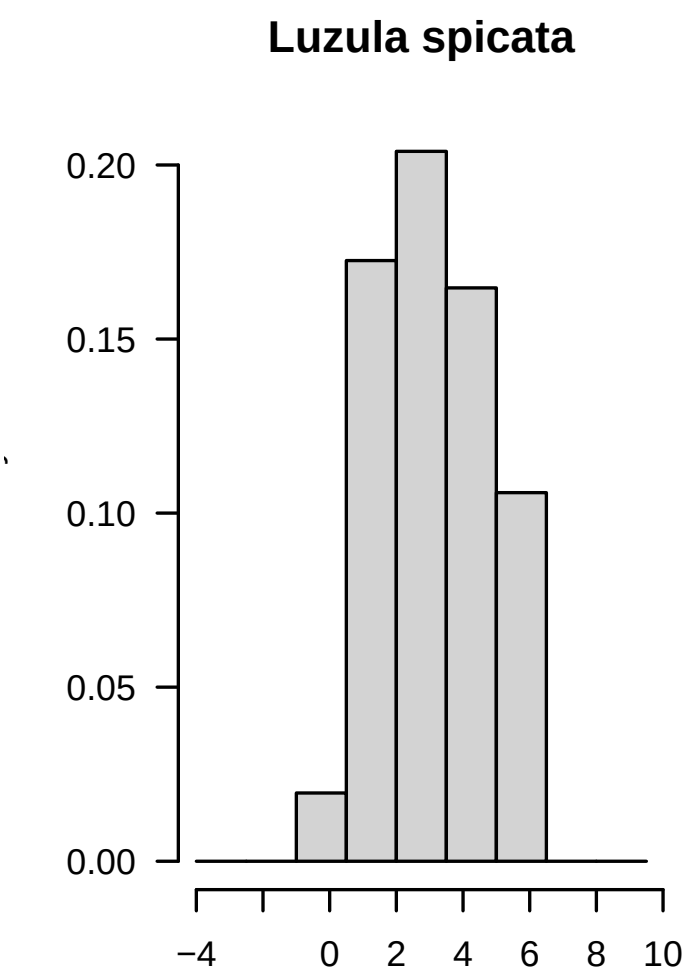
Snow cover duration [d]

p SW	p AG	skew
0.01	<0.01	−0.63



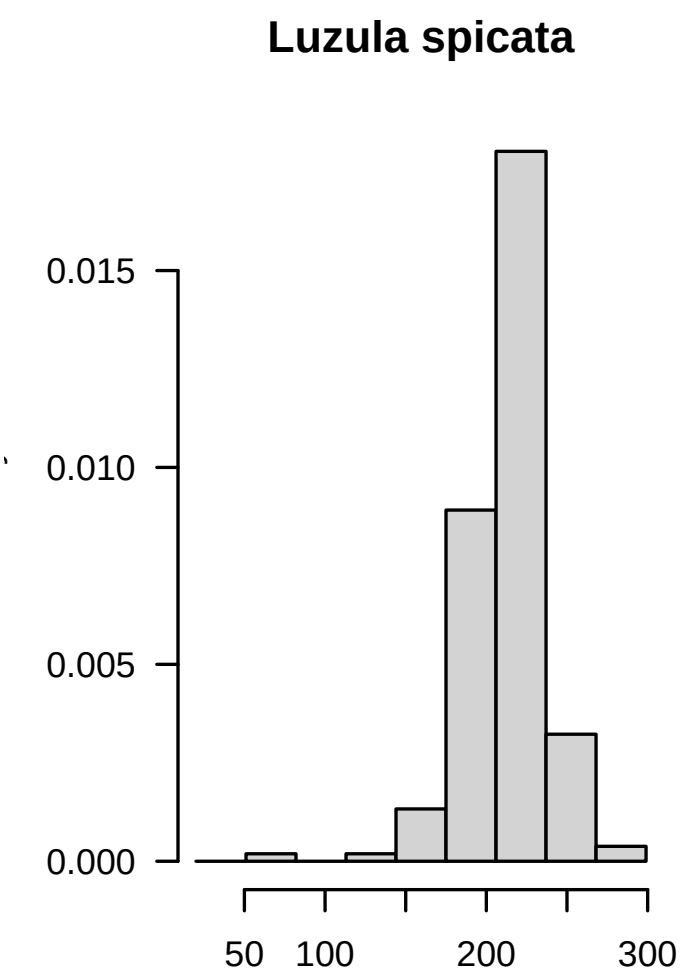
Elevation [m.a.s.l.]

p SW	p AG	skew
0.05	0.16	−0.26



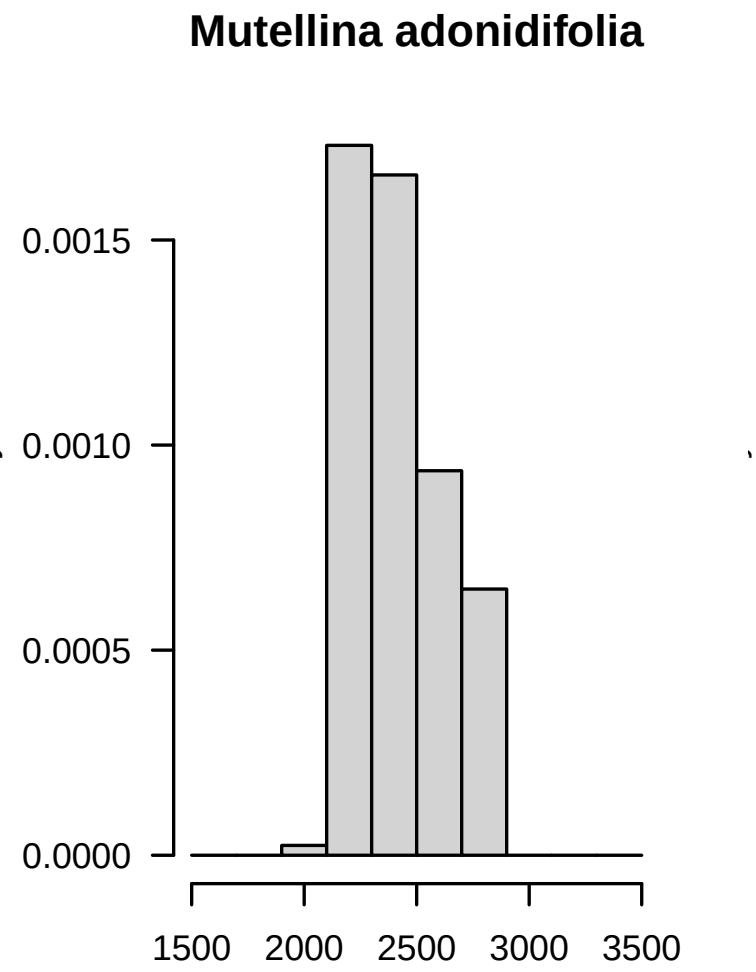
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	0.91	−0.02



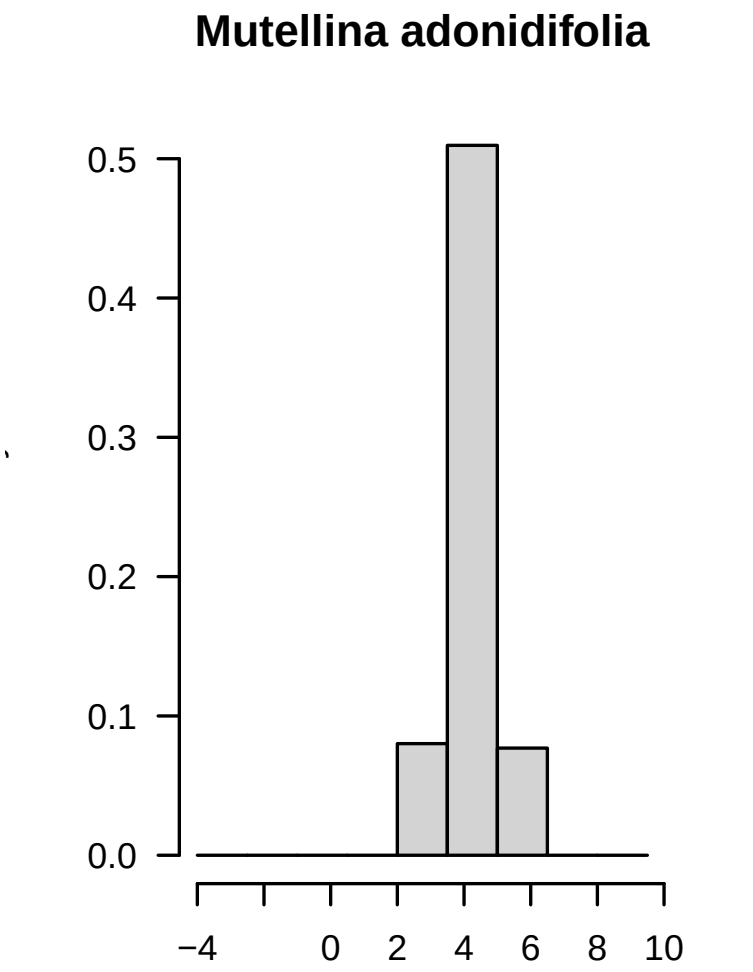
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.1



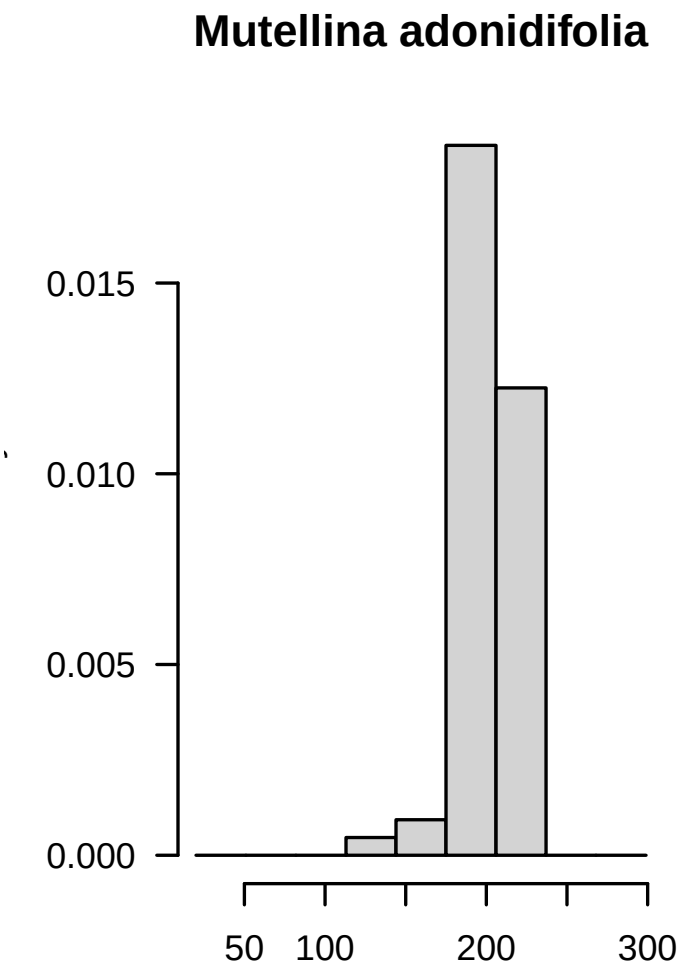
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	<0.01	0.46



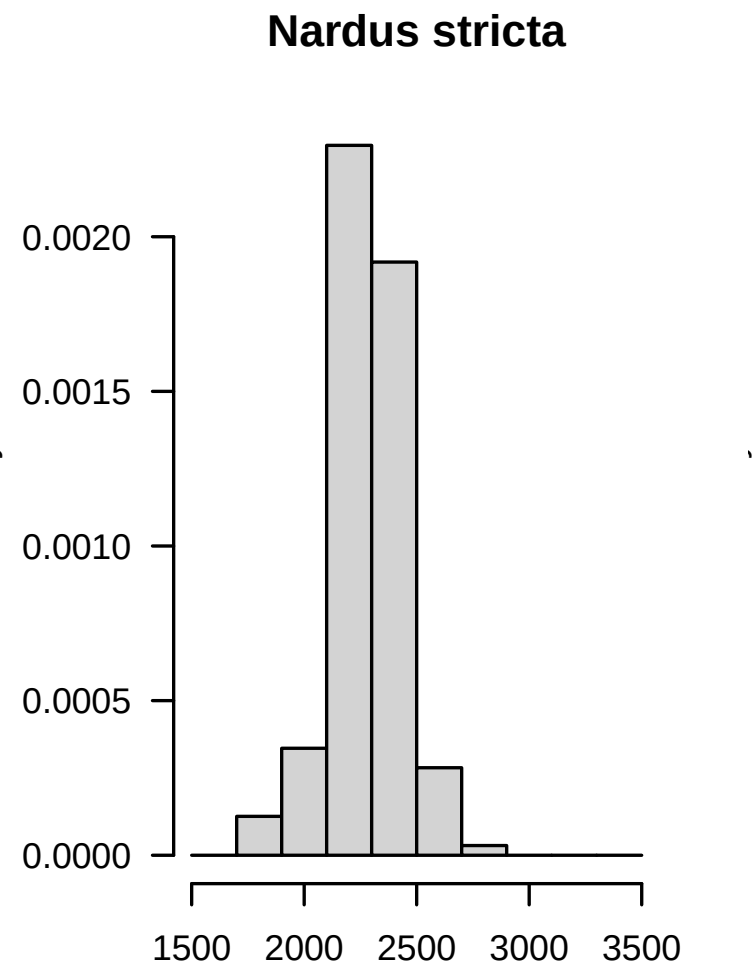
Annual mean temperature [°C]

p SW	p AG	skew
0.52	0.19	−0.22



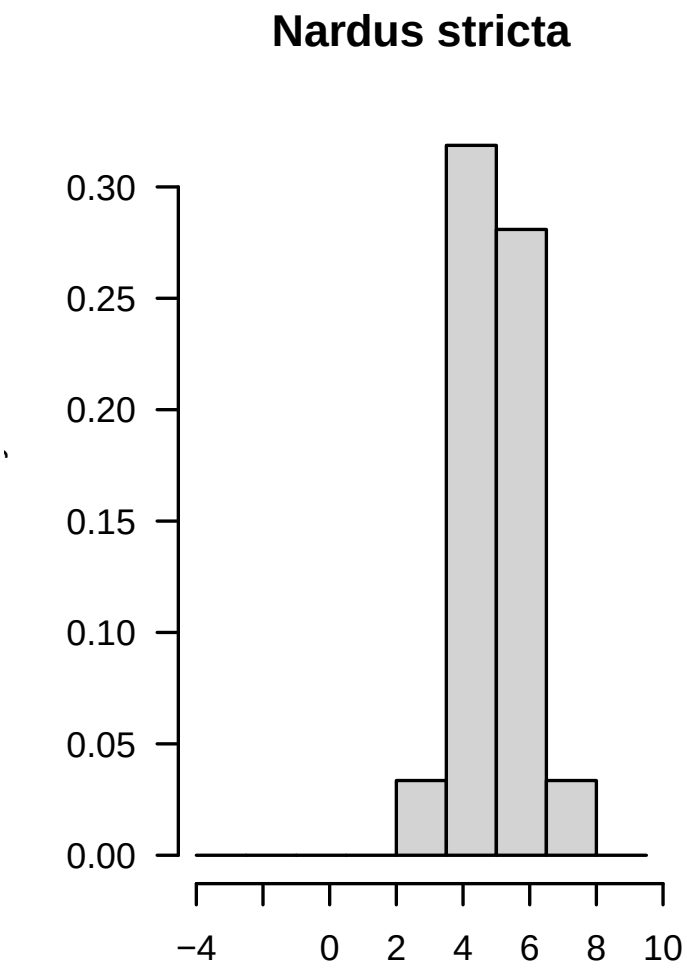
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.23



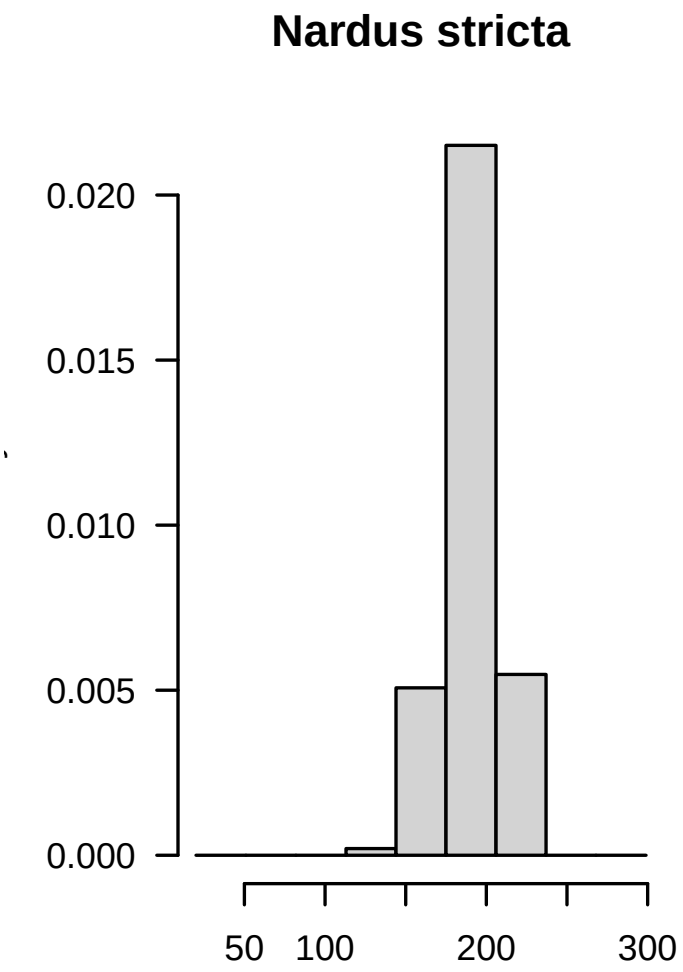
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.38	−0.16



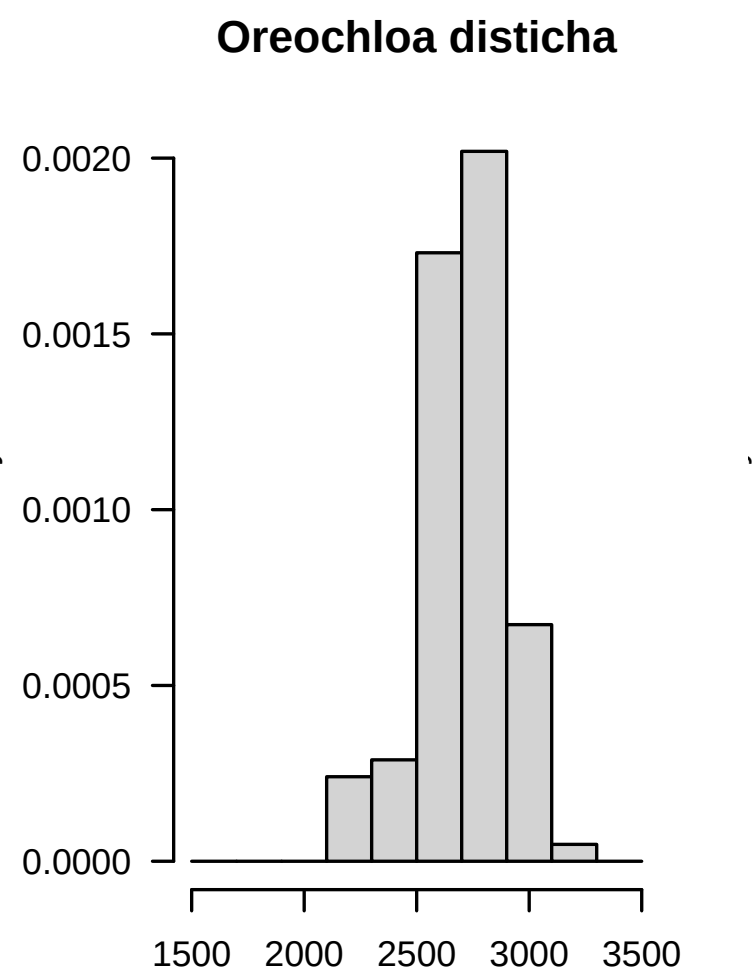
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	0.12	0.3



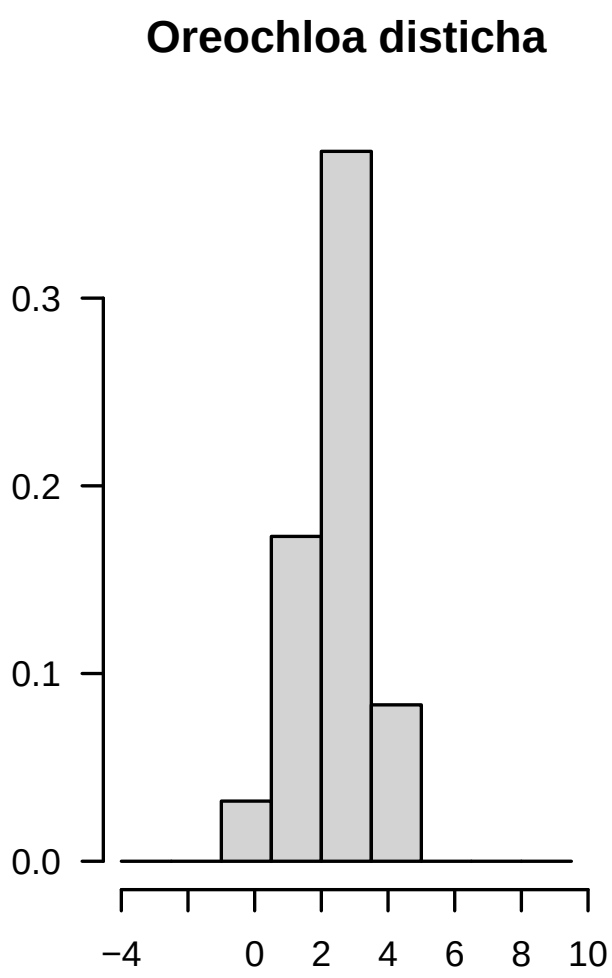
Snow cover duration [d]

p SW	p AG	skew
0.04	0.03	−0.43



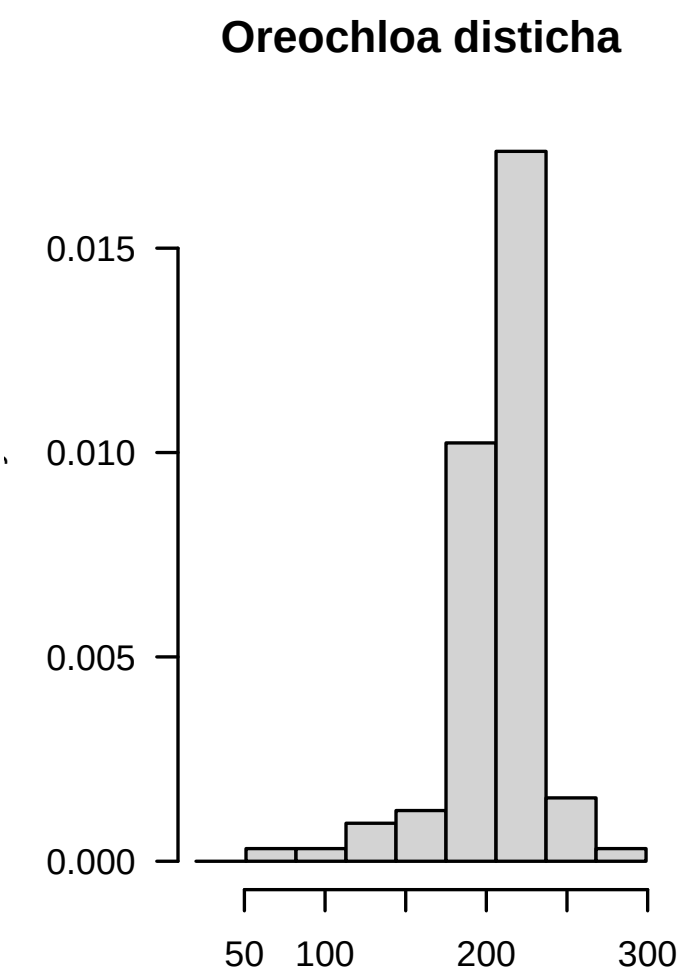
Elevation [m.a.s.l.]

p SW	p AG	skew
0.13	0.1	−0.39



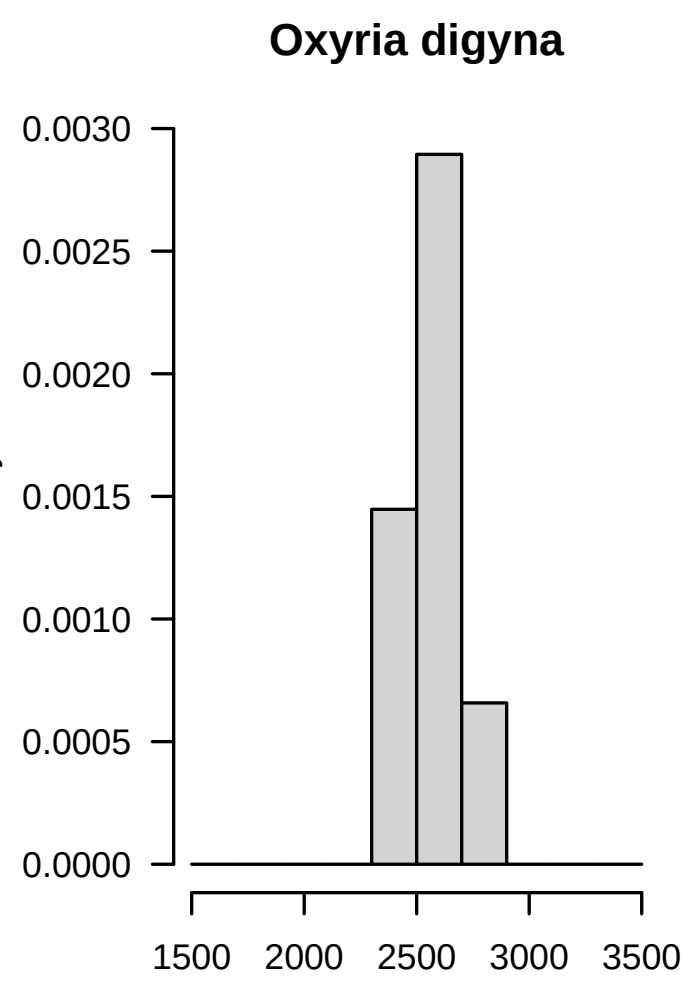
Annual mean temperature [°C]

p SW	p AG	skew
0.03	0.01	−0.59



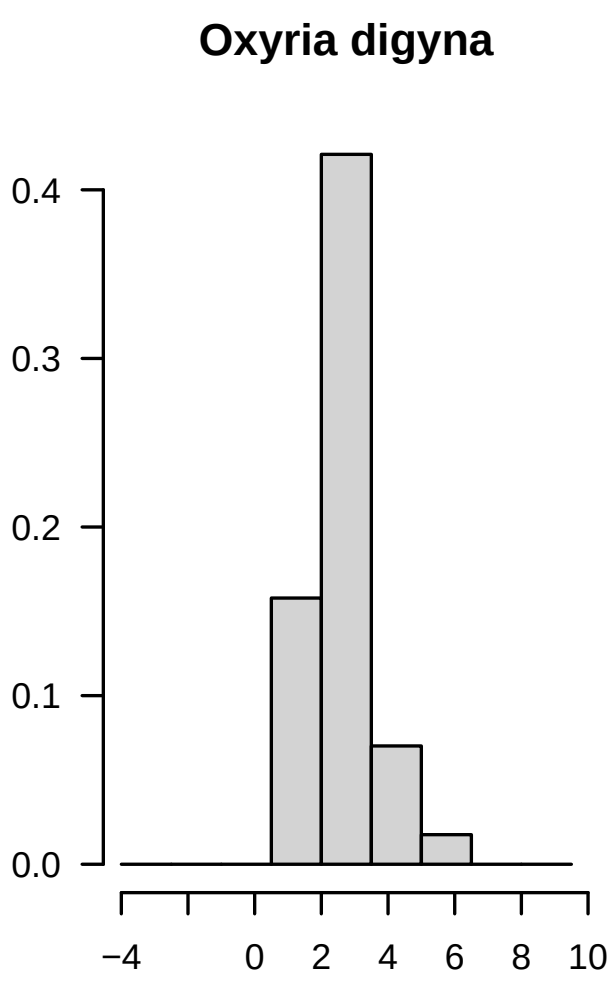
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.52



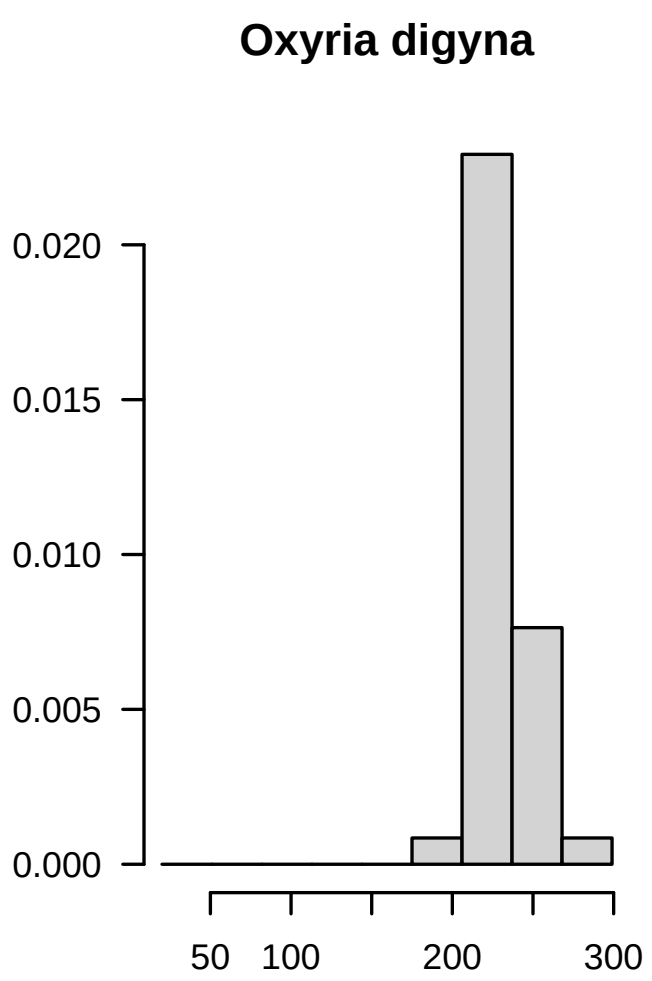
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	<0.01	1.3



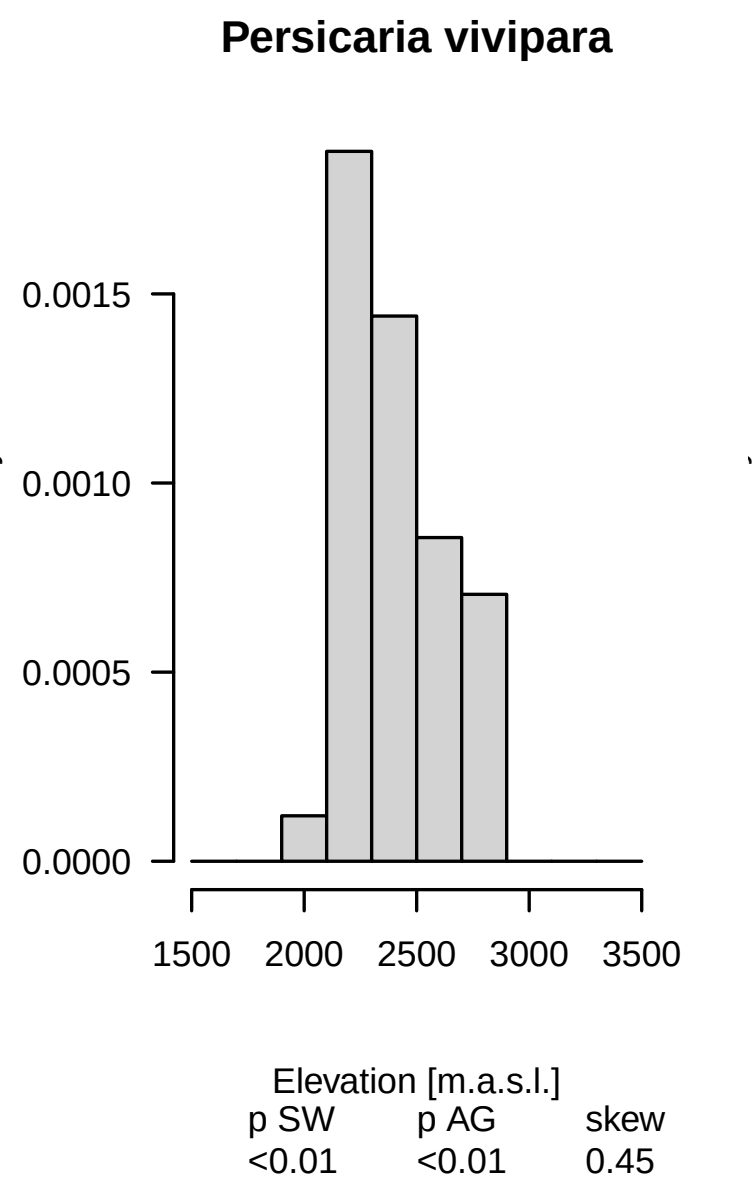
Annual mean temperature [°C]

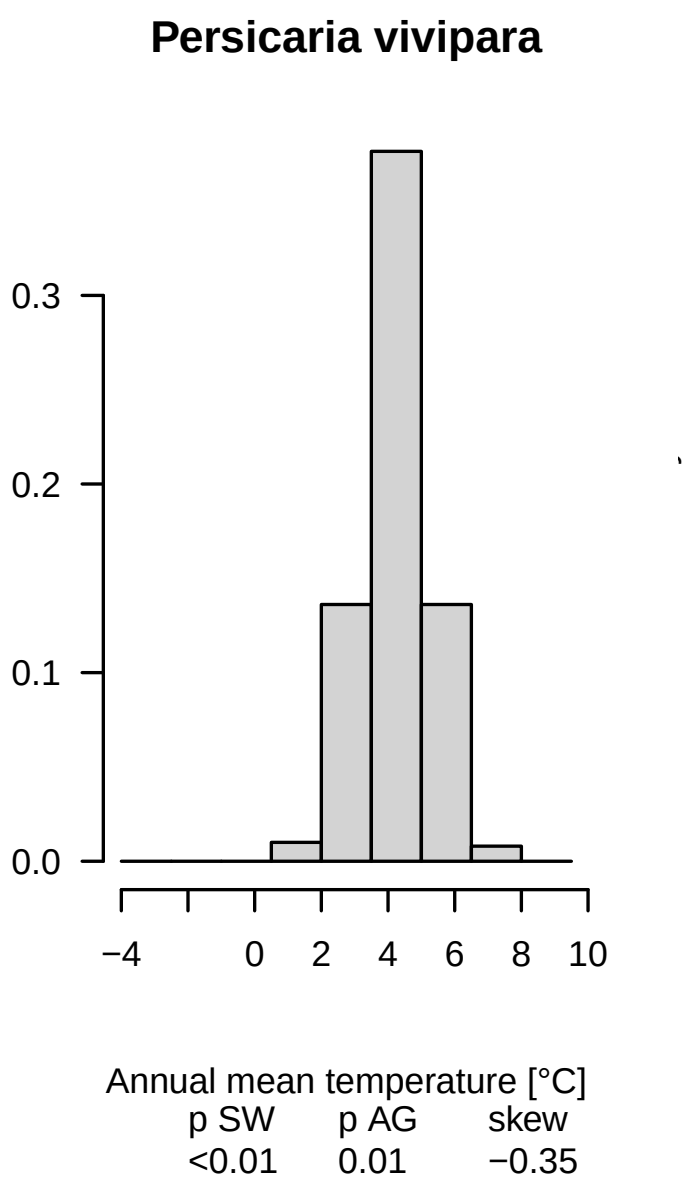
p SW	p AG	skew
0.34	0.06	0.69

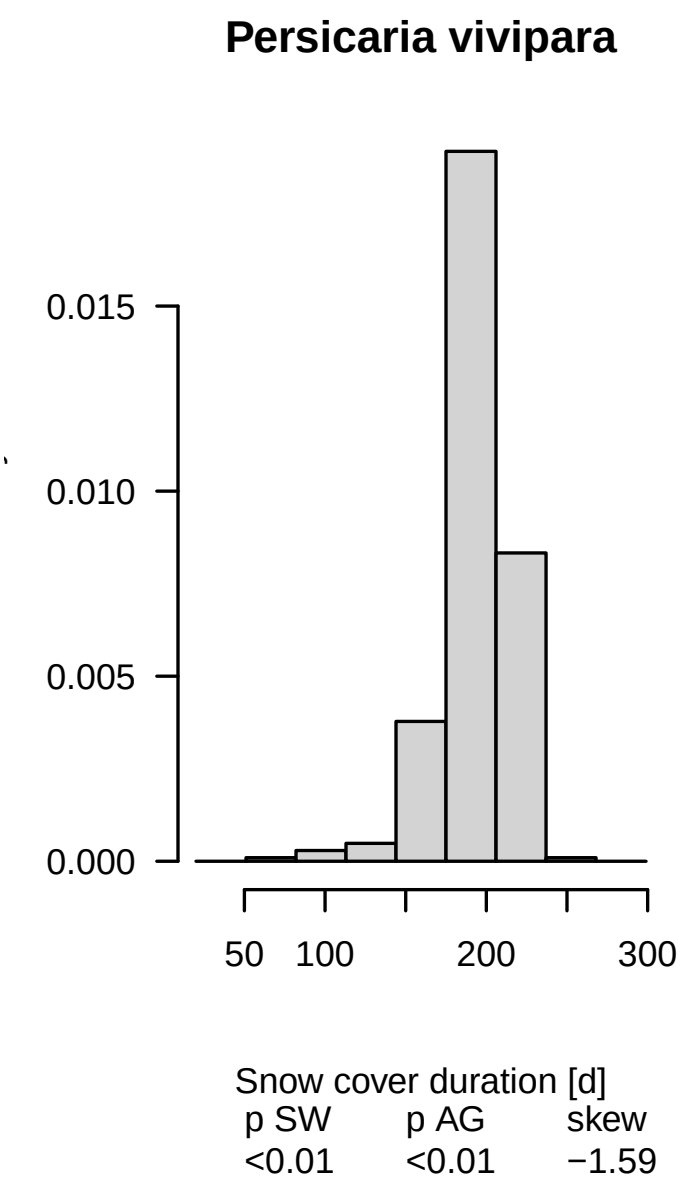


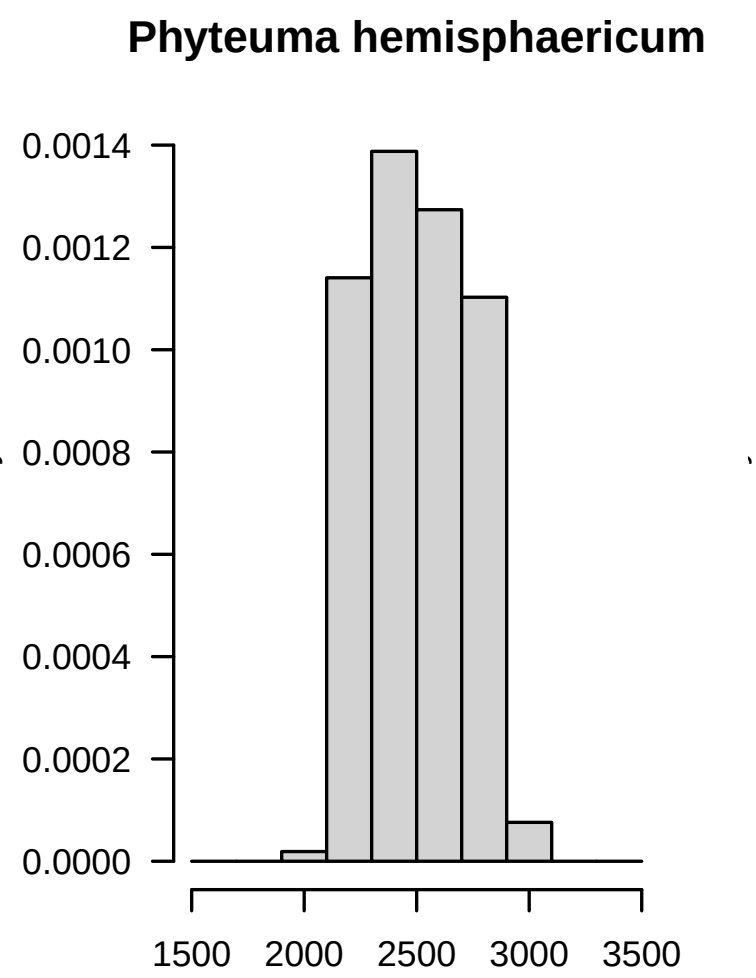
Snow cover duration [d]

p SW	p AG	skew
0.05	0.03	0.81


Persicaria vivipara
0.0015
0.0010
0.0005
0.0000
1500
2000
2500
3000
3500
Elevation [m.a.s.l.]
p SW
p AG
skew
<0.01
<0.01
0.45

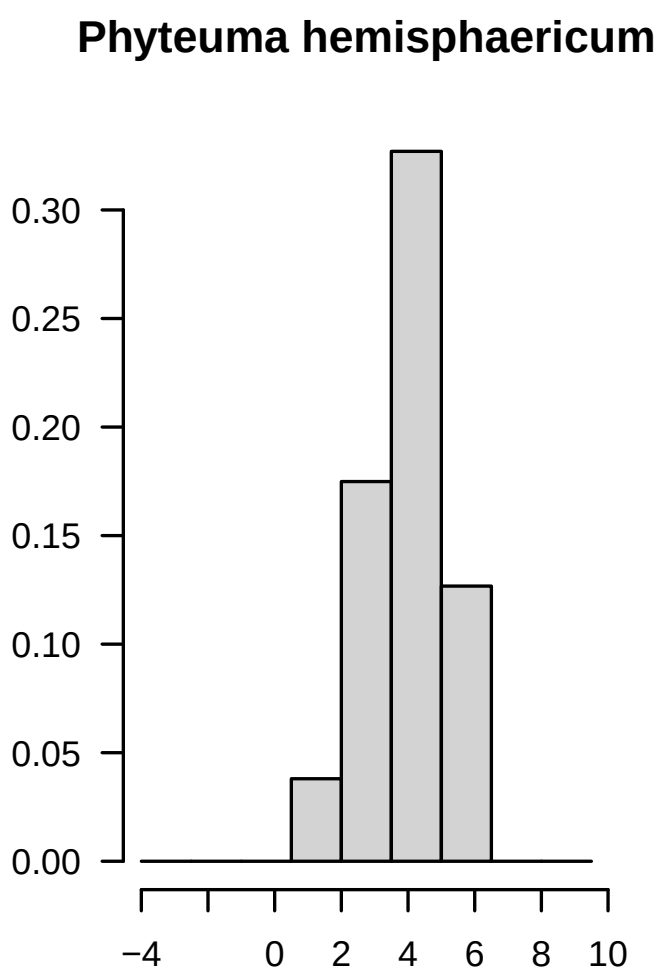

Persicaria vivipara
0.3
0.2
0.1
0.0
−4
0
2
4
6
8
10
Annual mean temperature [°C]
p SW
p AG
skew
<0.01
0.01
−0.35


Persicaria vivipara
0.015
0.010
0.005
0.000
50
100
200
300
Snow cover duration [d]
p SW
p AG
skew
<0.01
<0.01
−1.59



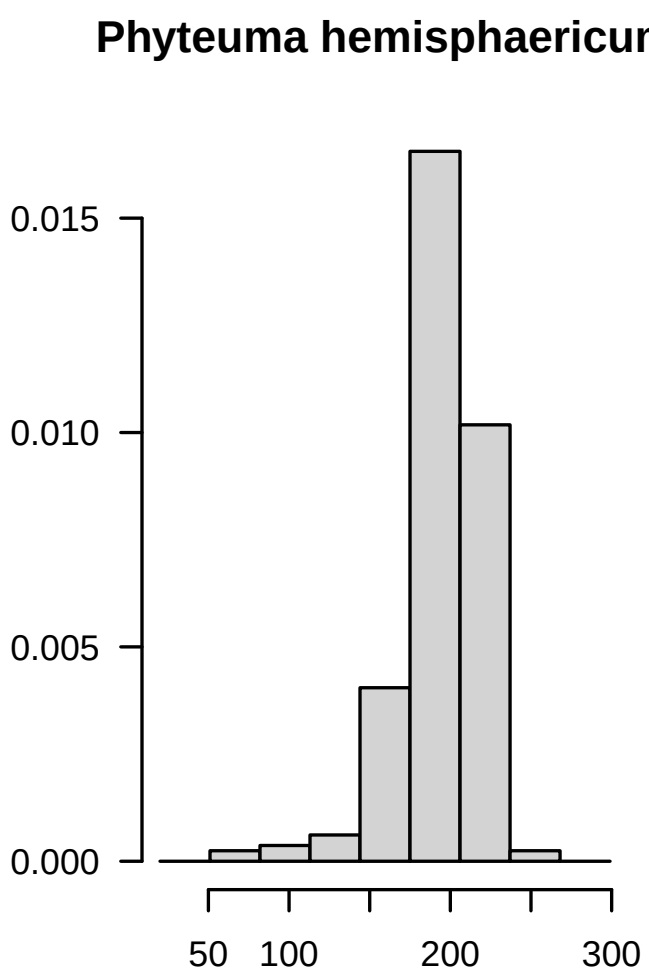
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.5	0.1



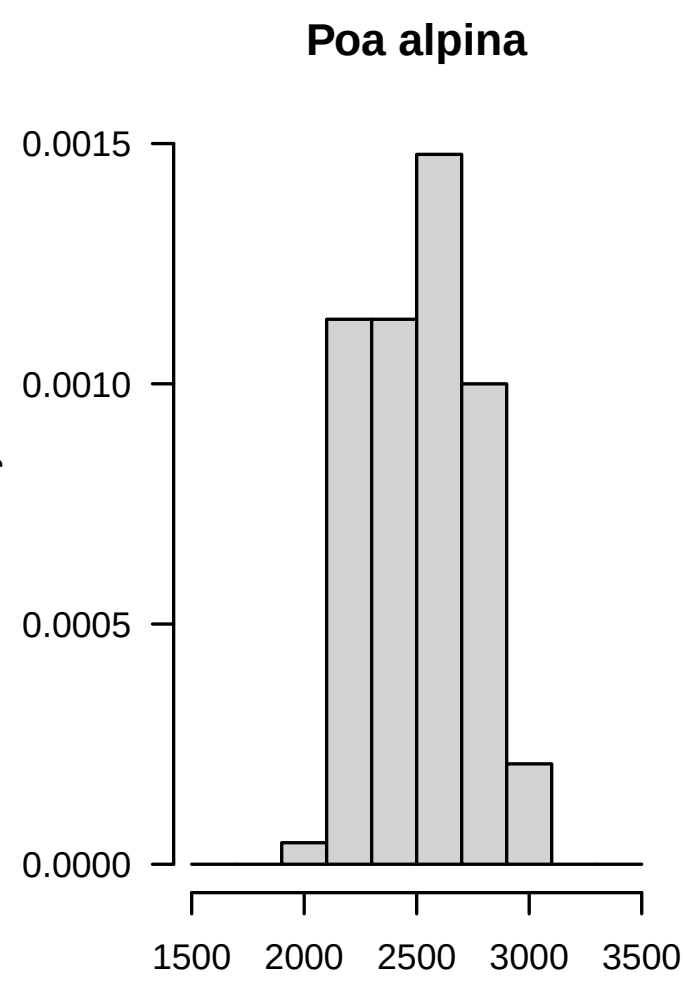
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	<0.01	−0.55



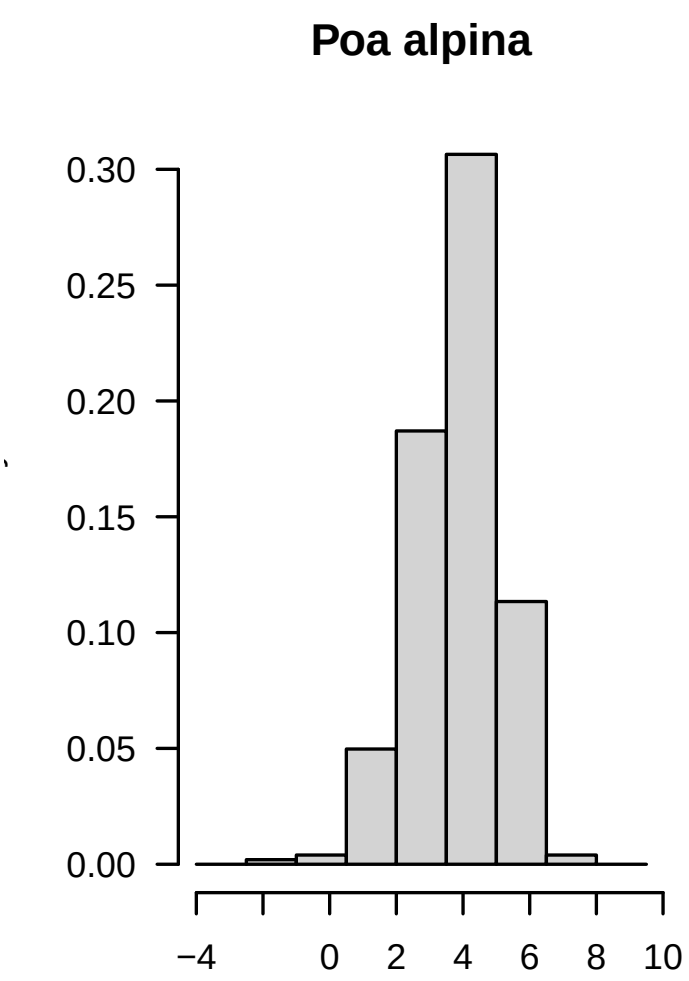
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.49



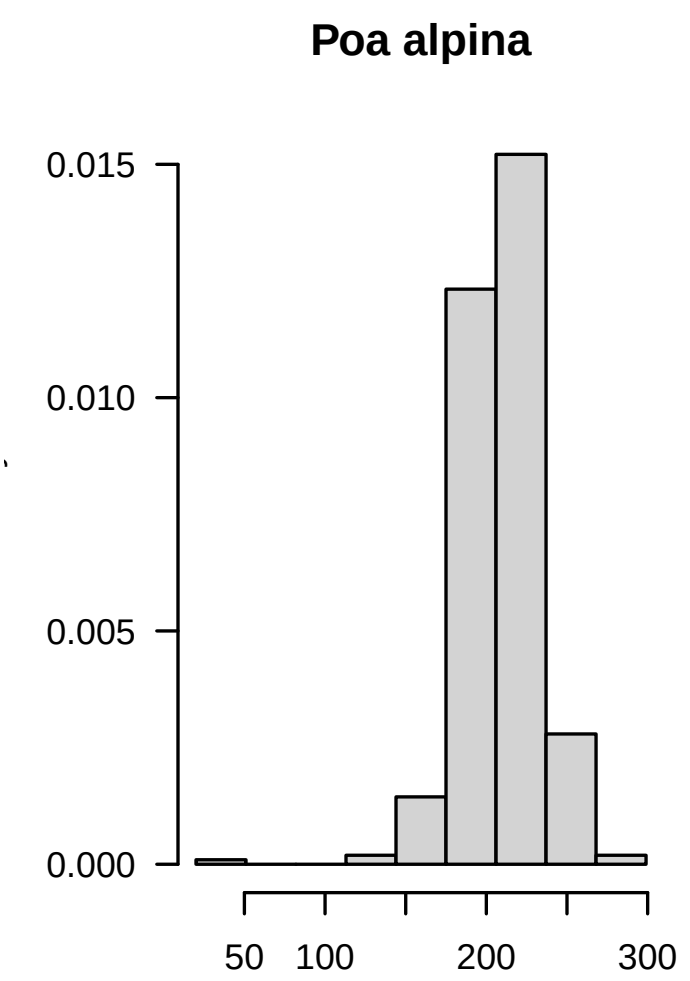
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.78	0.04



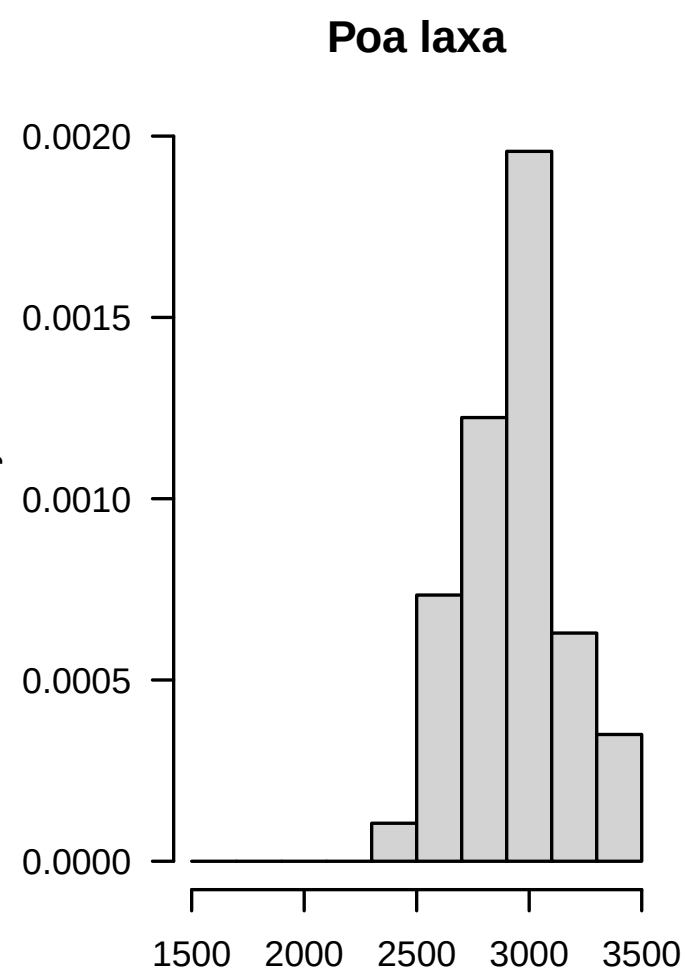
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	<0.01	−0.59



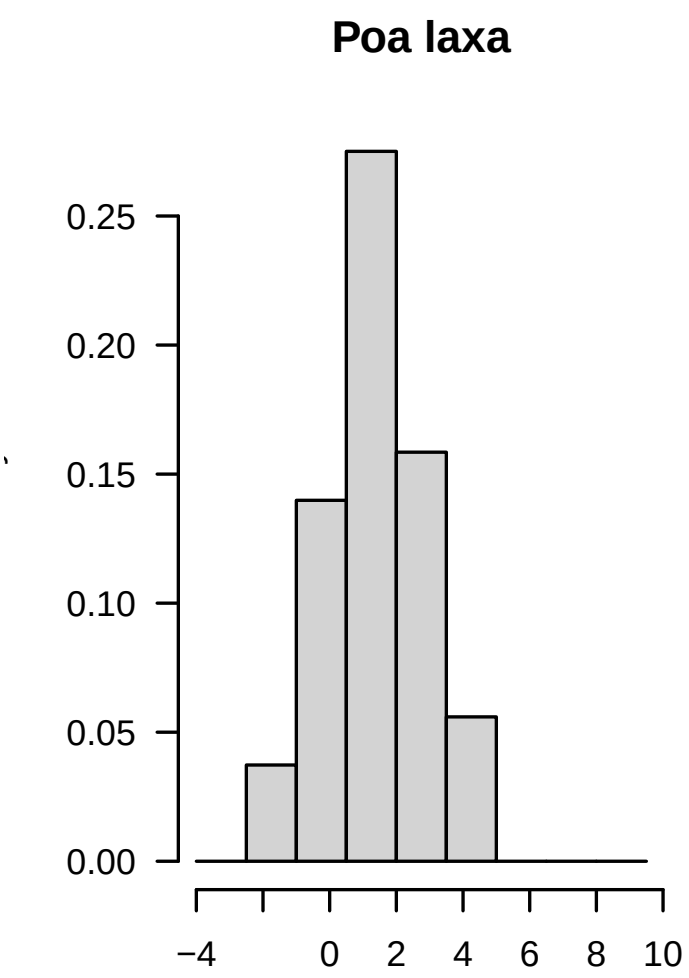
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.43



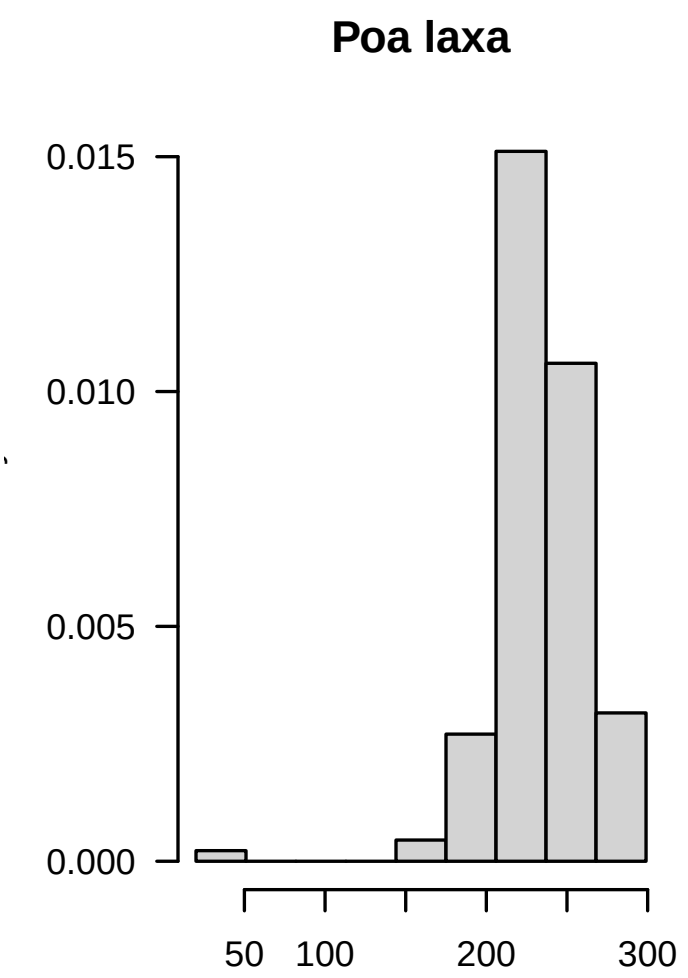
Elevation [m.a.s.l.]

p SW	p AG	skew
0.13	0.86	−0.03



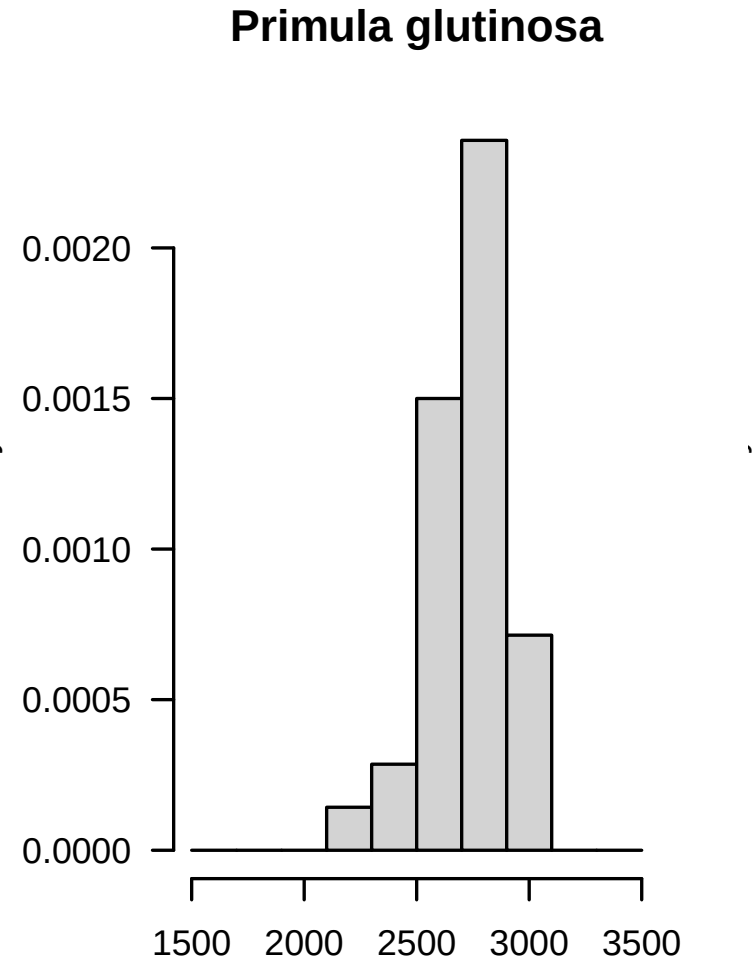
Annual mean temperature [°C]

p SW	p AG	skew
0.27	0.93	−0.02



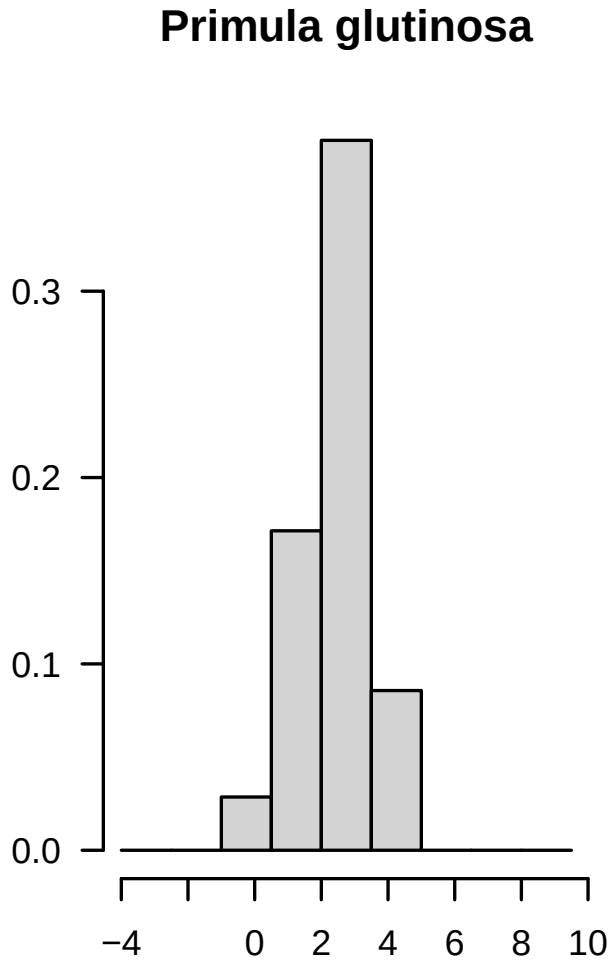
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.51



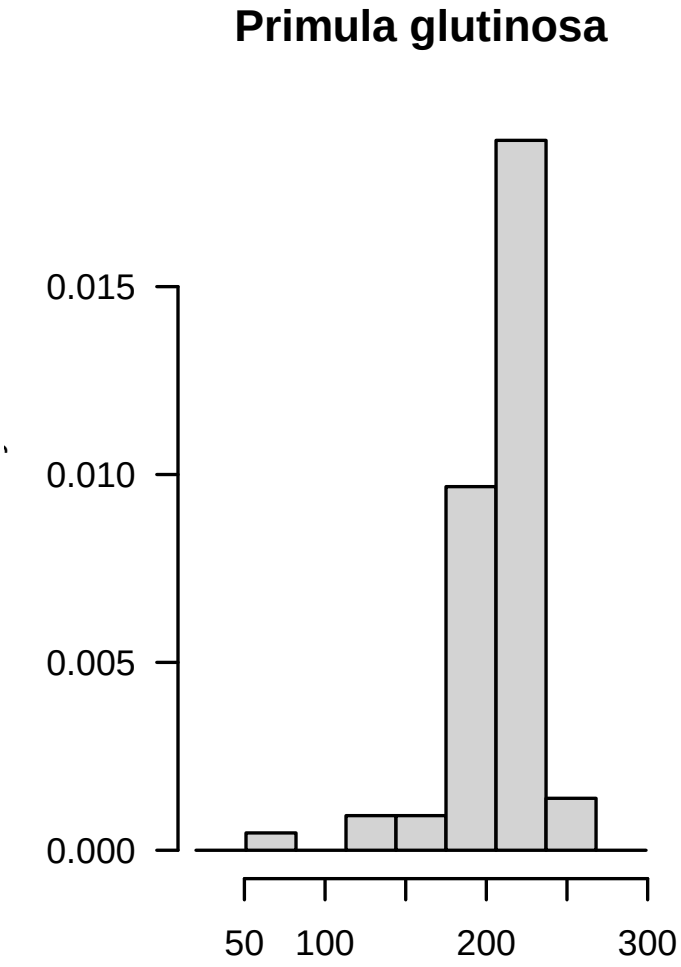
Elevation [m.a.s.l.]

p SW	p AG	skew
0.16	0.15	−0.4



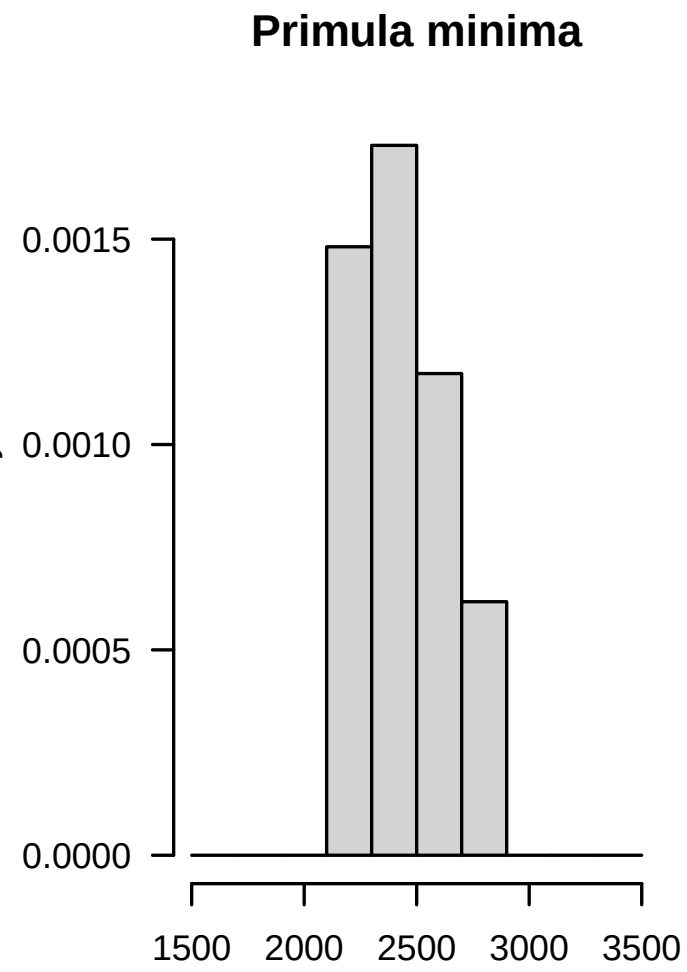
Annual mean temperature [°C]

p SW	p AG	skew
0.78	0.54	−0.17



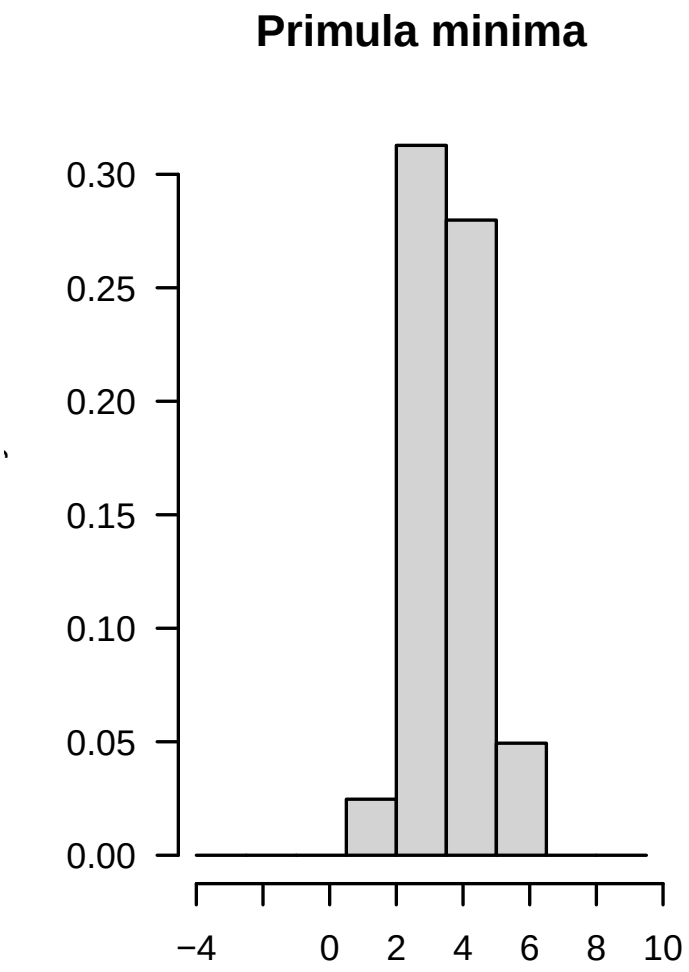
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.23



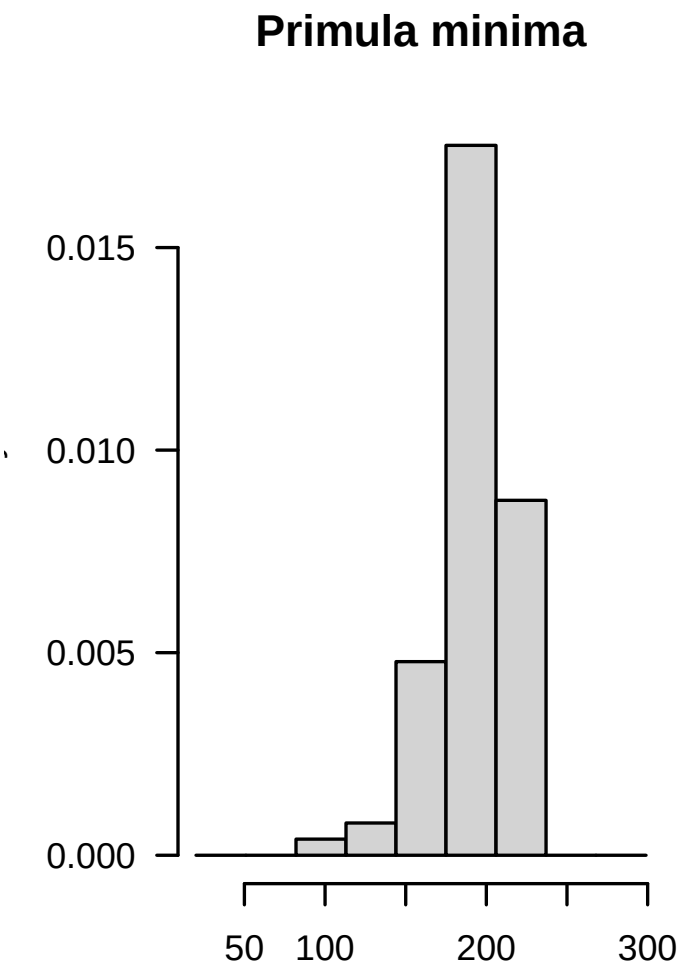
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.26	0.29



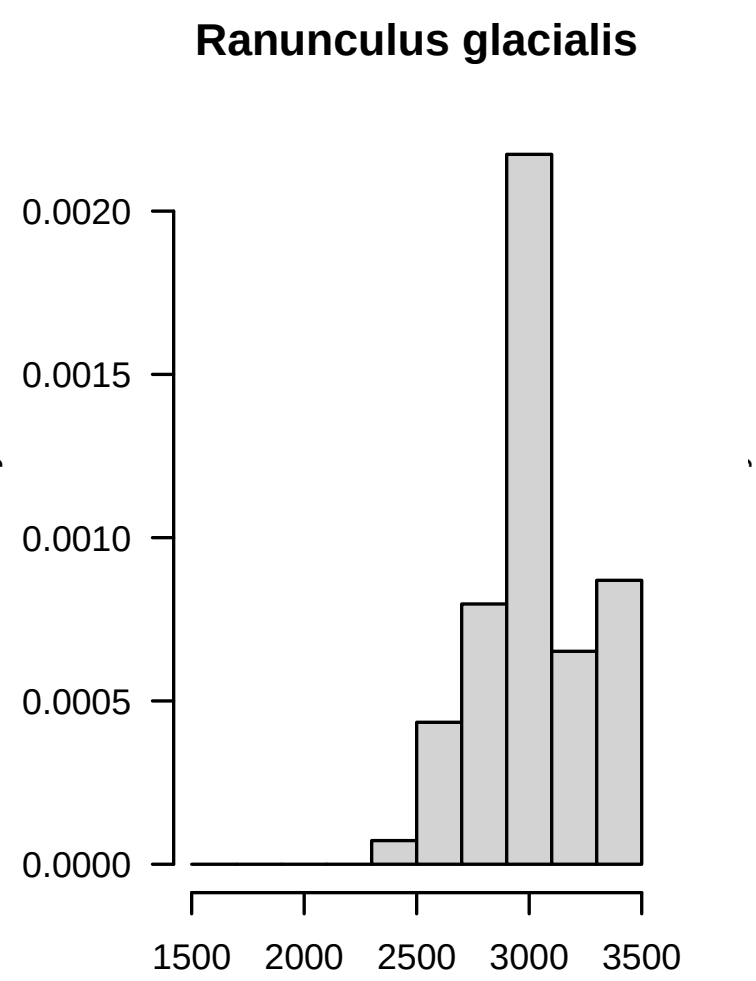
Annual mean temperature [°C]

p SW	p AG	skew
0.93	0.92	0.02



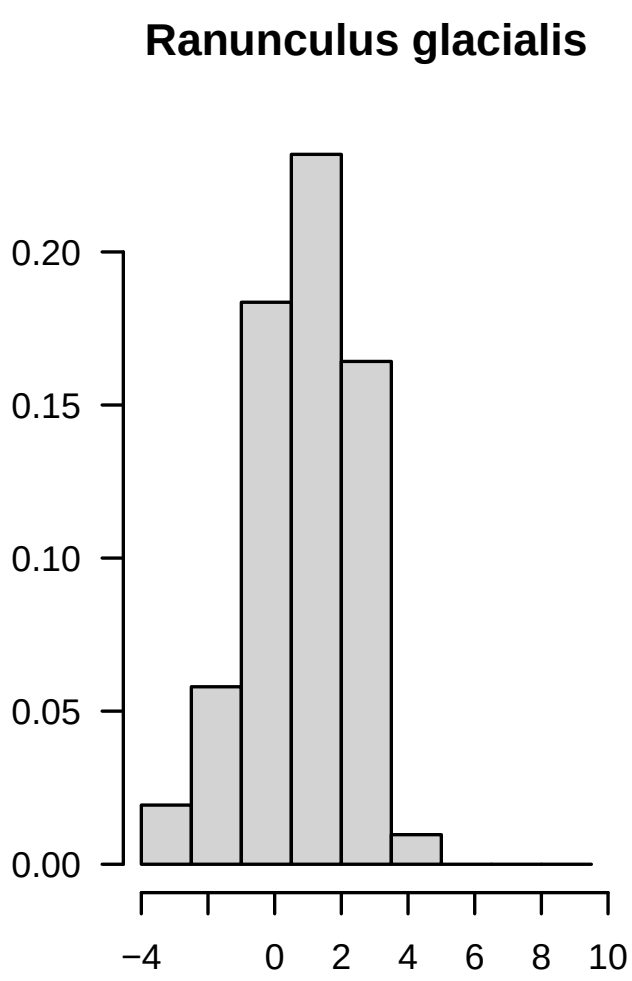
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.37



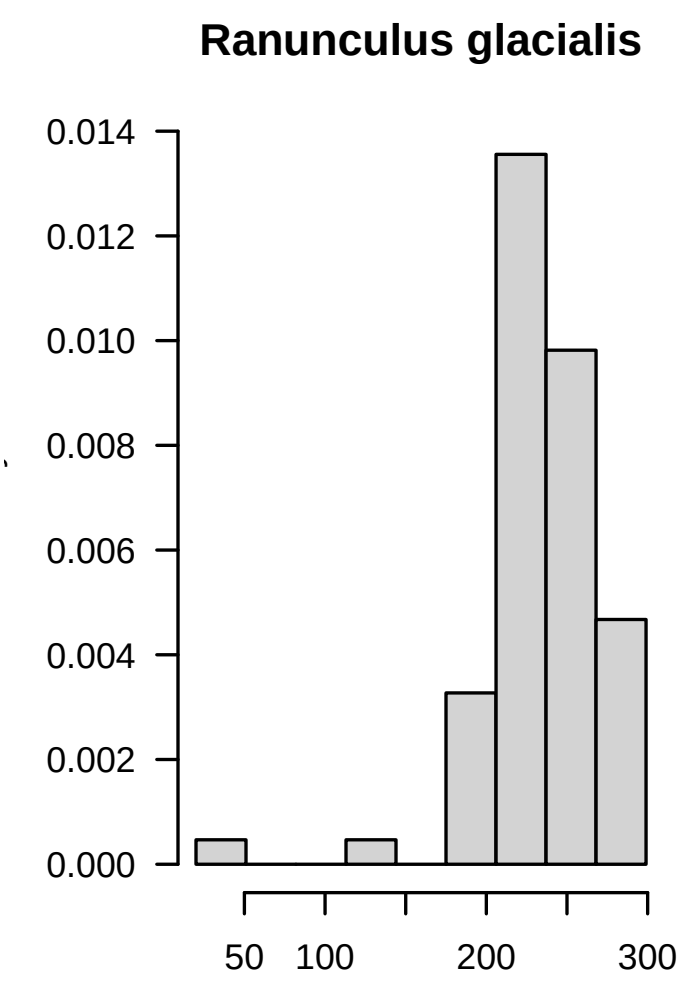
Elevation [m.a.s.l.]

p SW	p AG	skew
0.21	0.56	−0.16



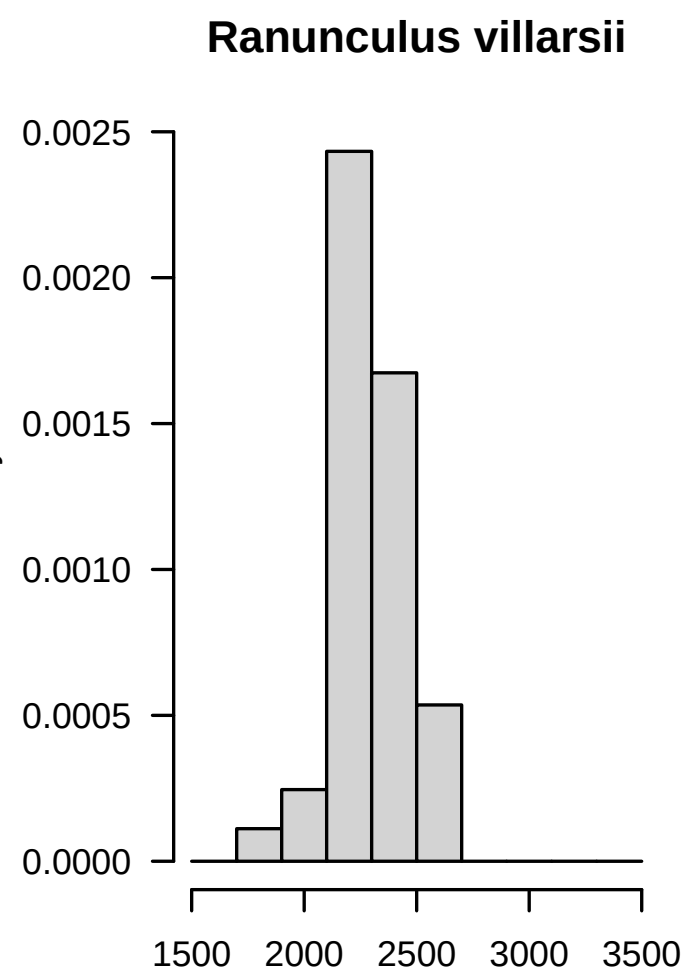
Annual mean temperature [°C]

p SW	p AG	skew
0.03	0.02	−0.69



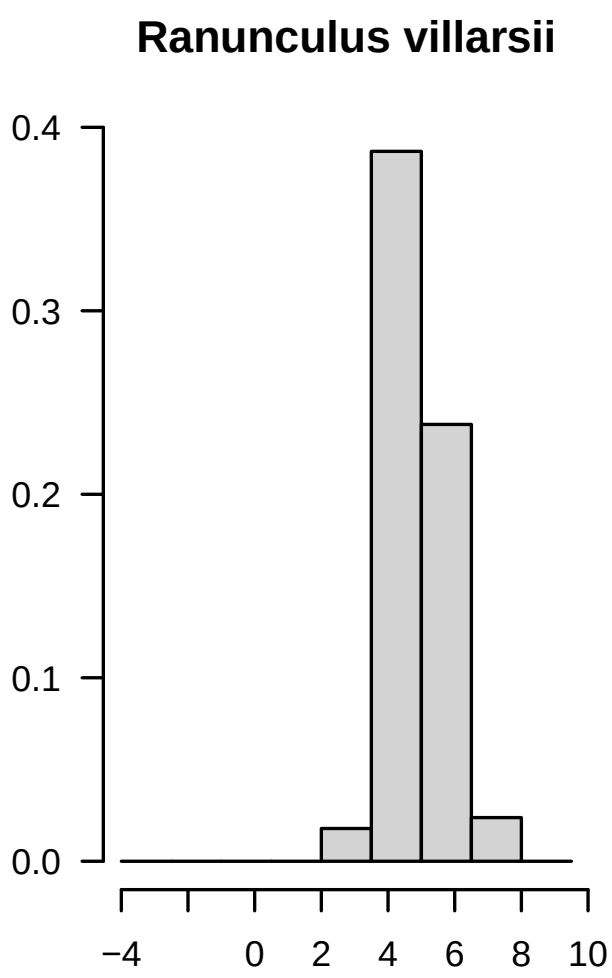
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.9



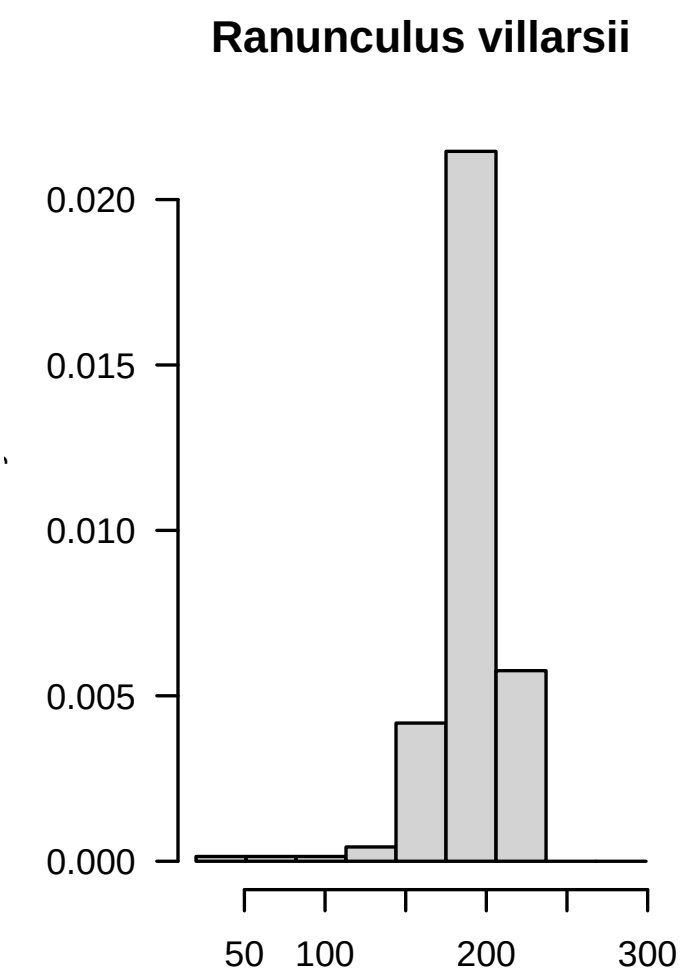
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.29	−0.17



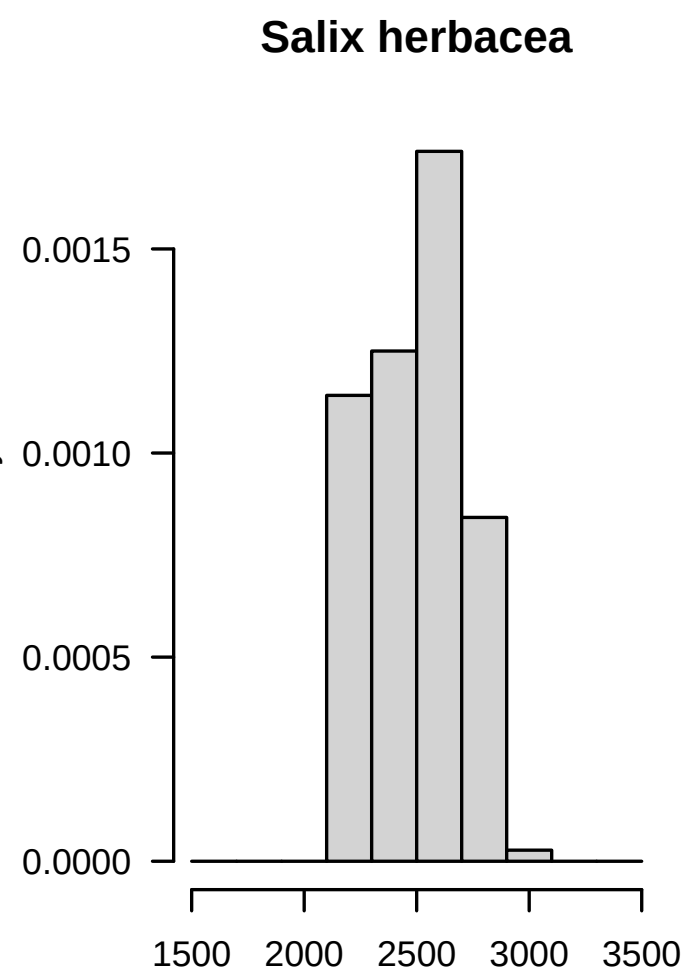
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	<0.01	0.44



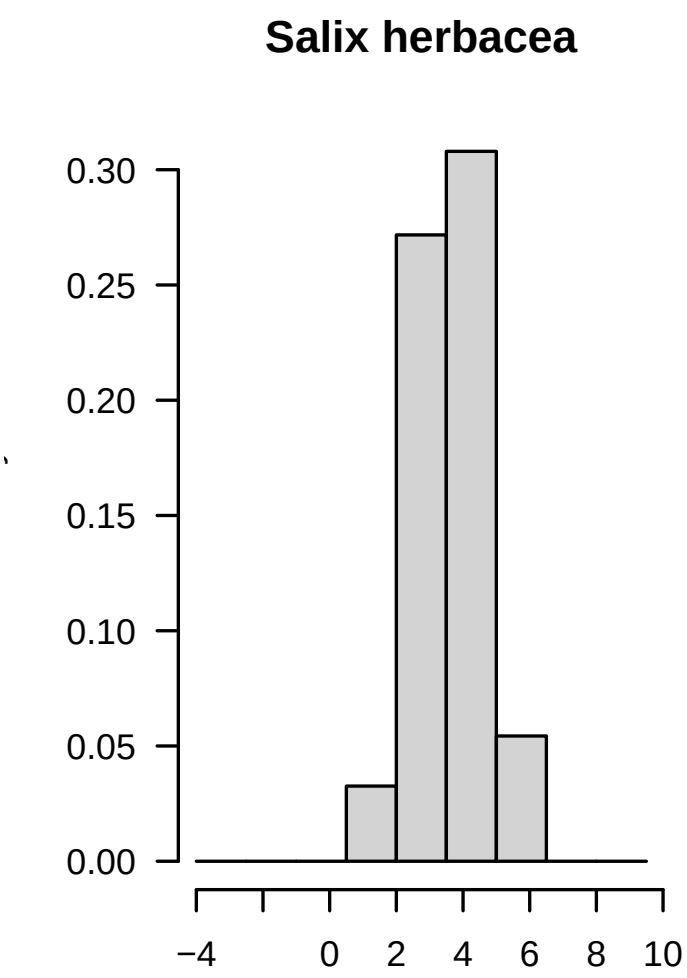
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.59



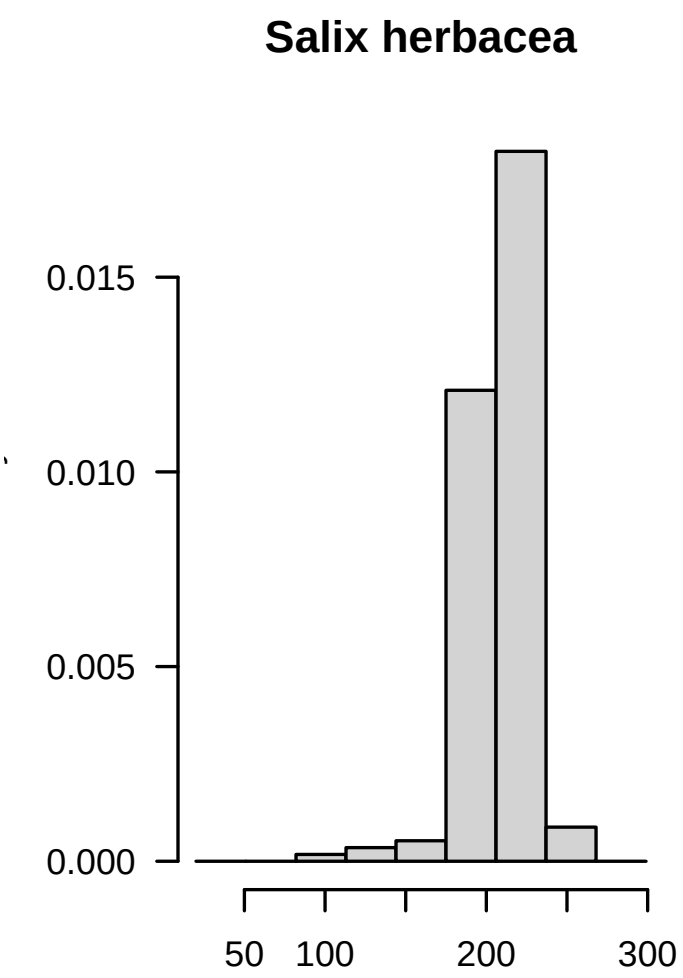
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.46	−0.13



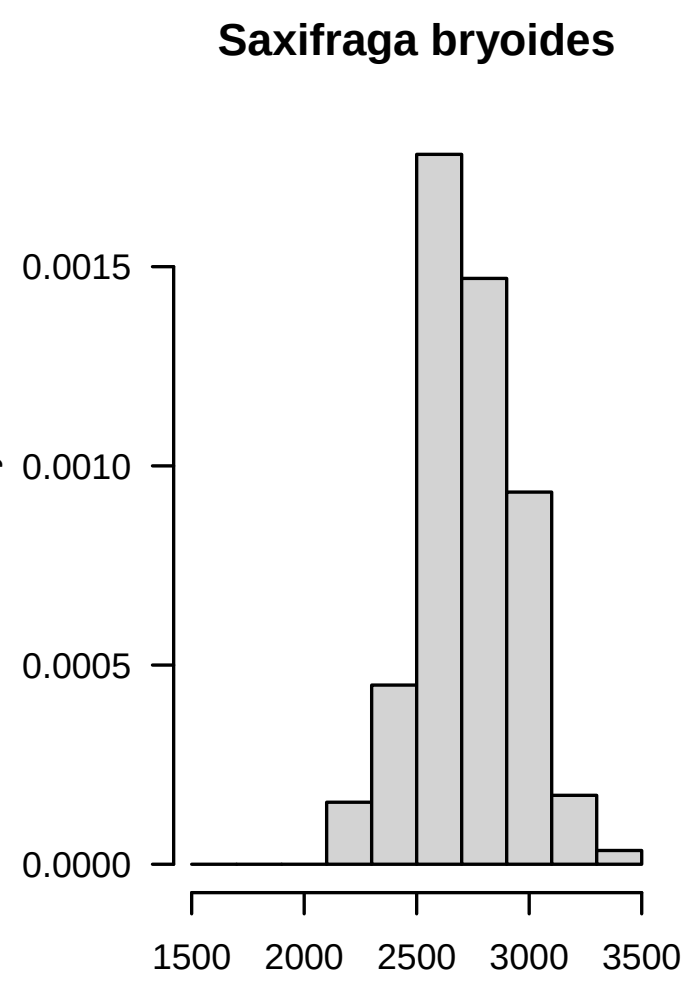
Annual mean temperature [°C]

p SW	p AG	skew
0.08	0.05	−0.35



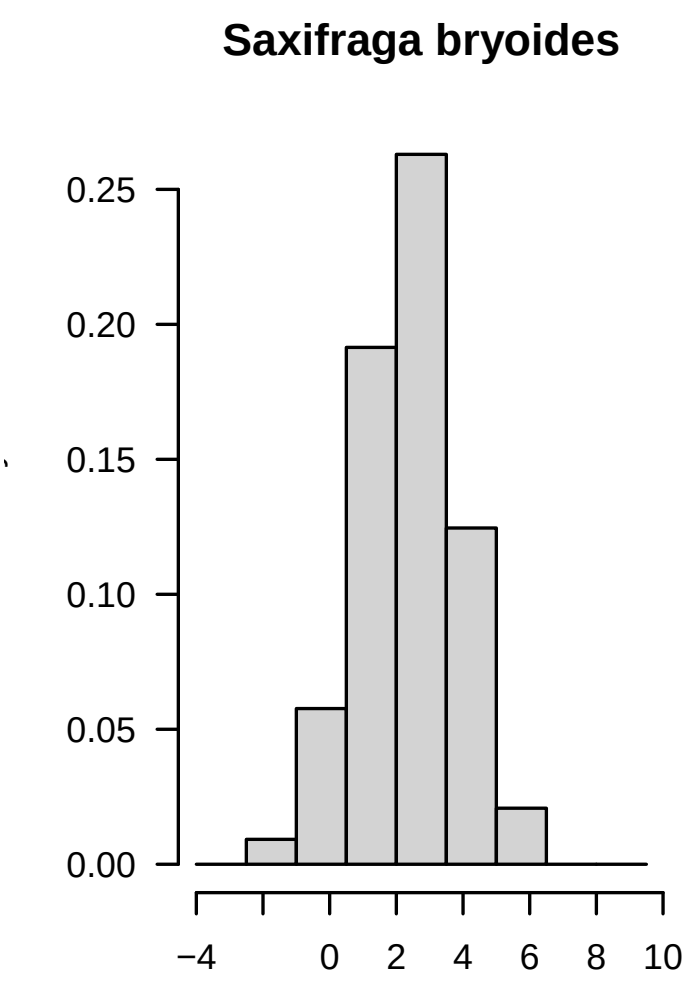
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.77



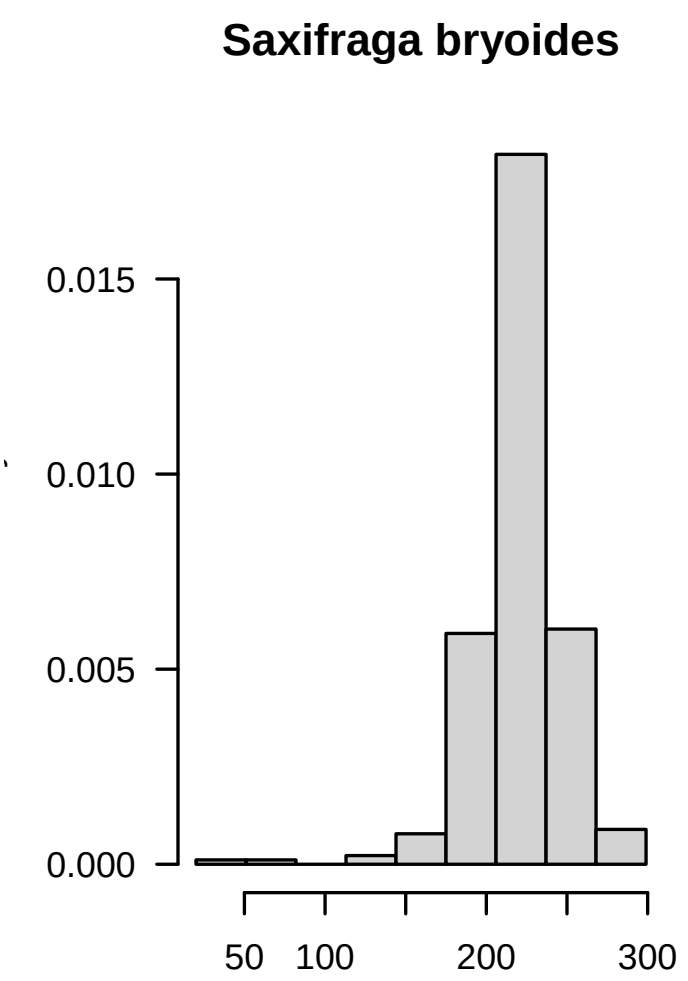
Elevation [m.a.s.l.]

p SW	p AG	skew
0.06	0.69	0.06



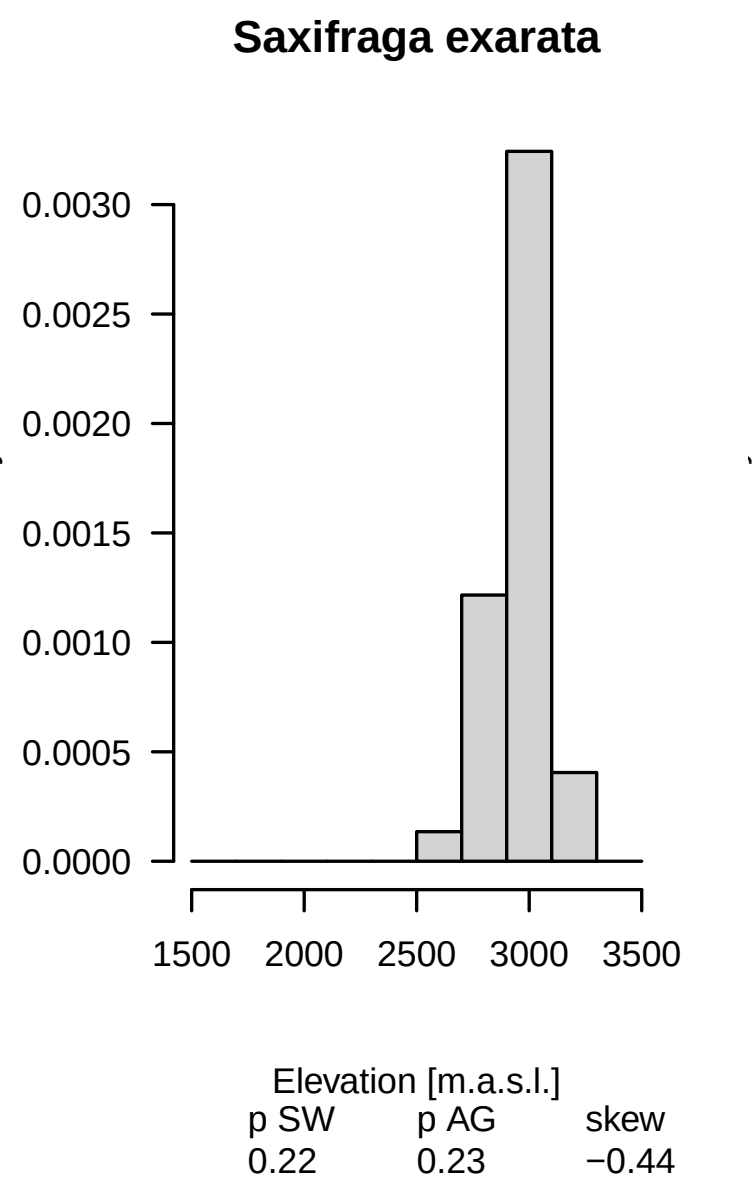
Annual mean temperature [°C]

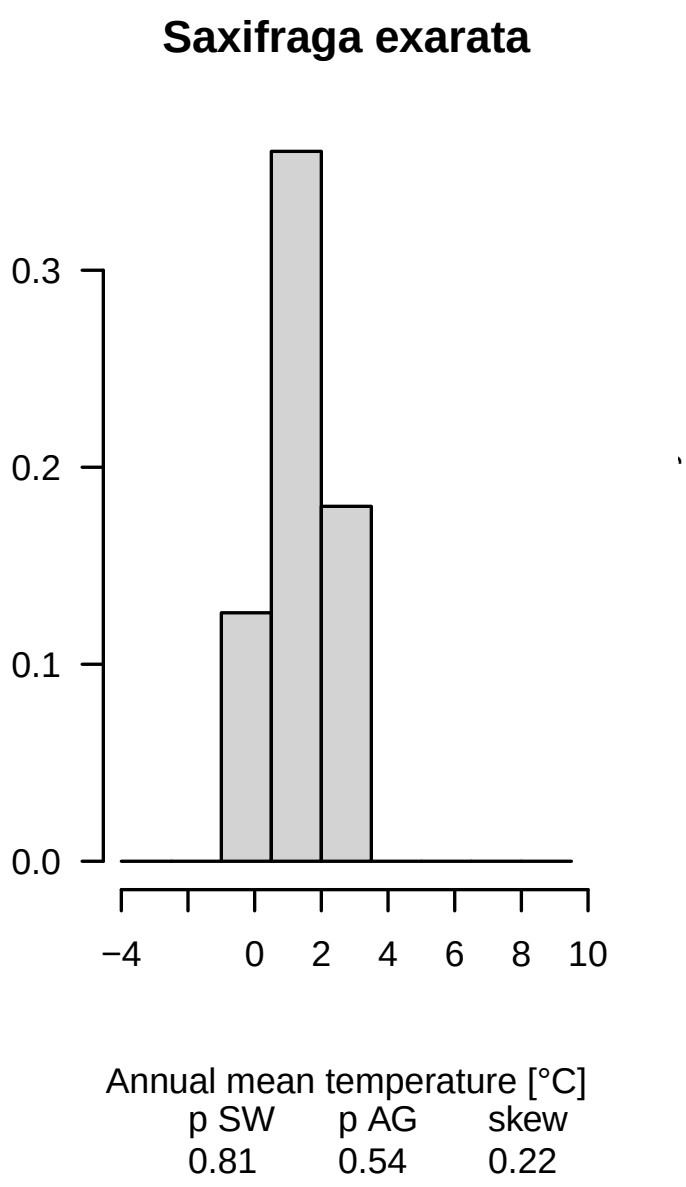
p SW	p AG	skew
0.37	0.2	−0.18

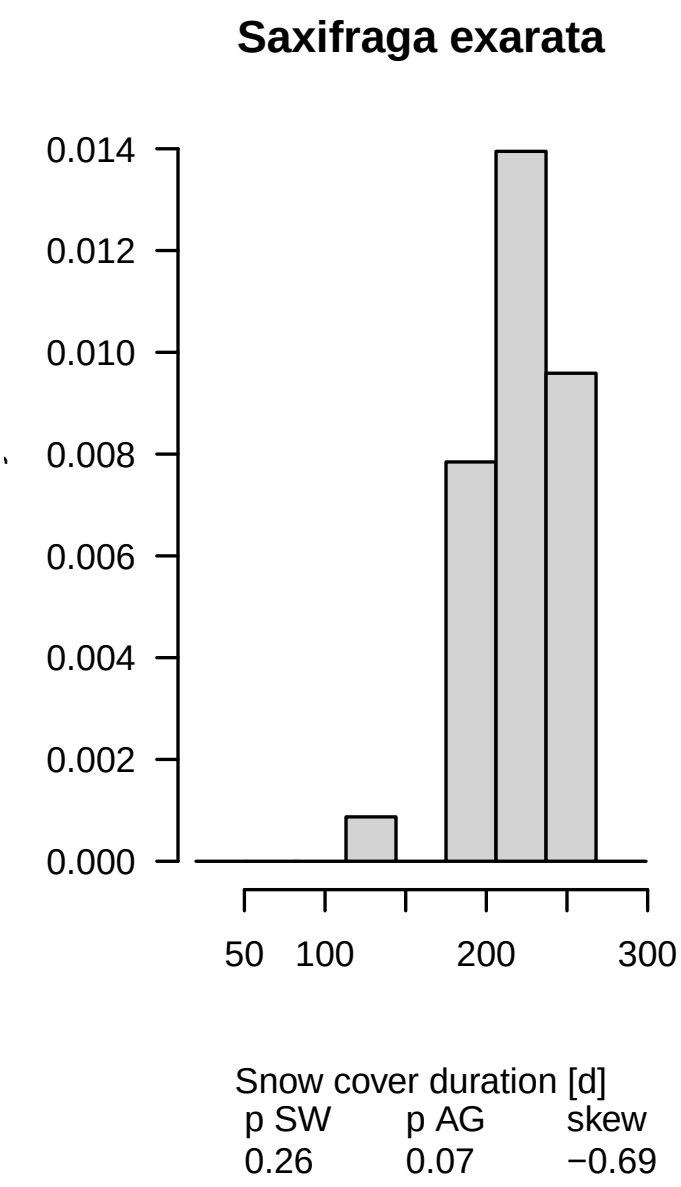


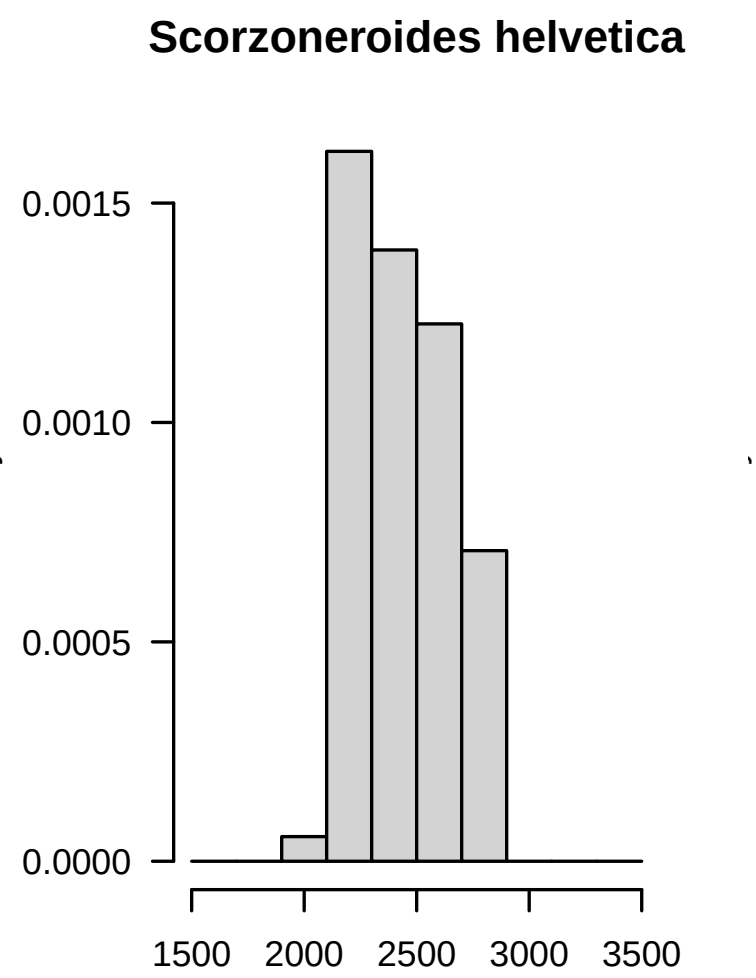
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.94


Saxifraga exarata
0.0030
0.0025
0.0020
0.0015
0.0010
0.0005
0.0000
1500
2000
2500
3000
3500
Elevation [m.a.s.l.]
p SW
p AG
skew
0.22
0.23
−0.44

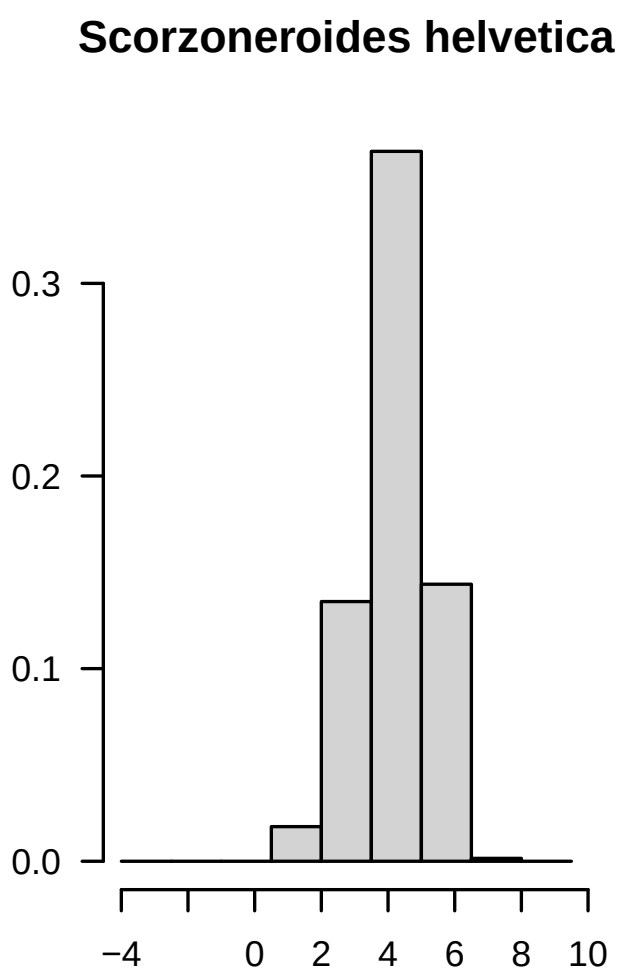

Saxifraga exarata
0.3
0.2
0.1
0.0
−4
0
2
4
6
8
10
Annual mean temperature [°C]
p SW
p AG
skew
0.81
0.54
0.22


Saxifraga exarata
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0.000
50
100
200
300
Snow cover duration [d]
p SW
p AG
skew
0.26
0.07
−0.69



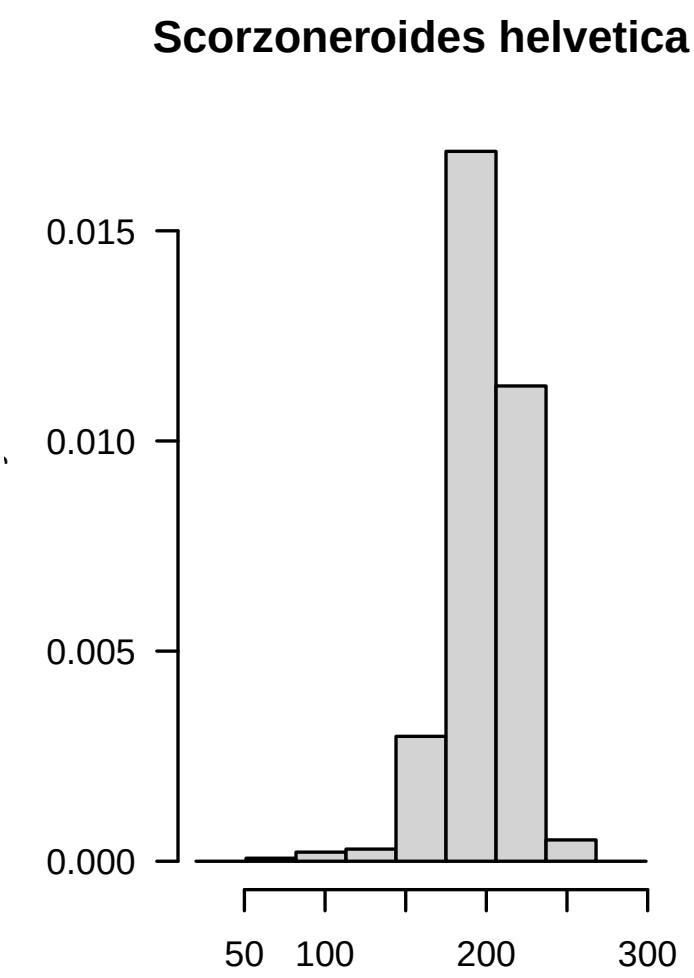
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.05	0.22



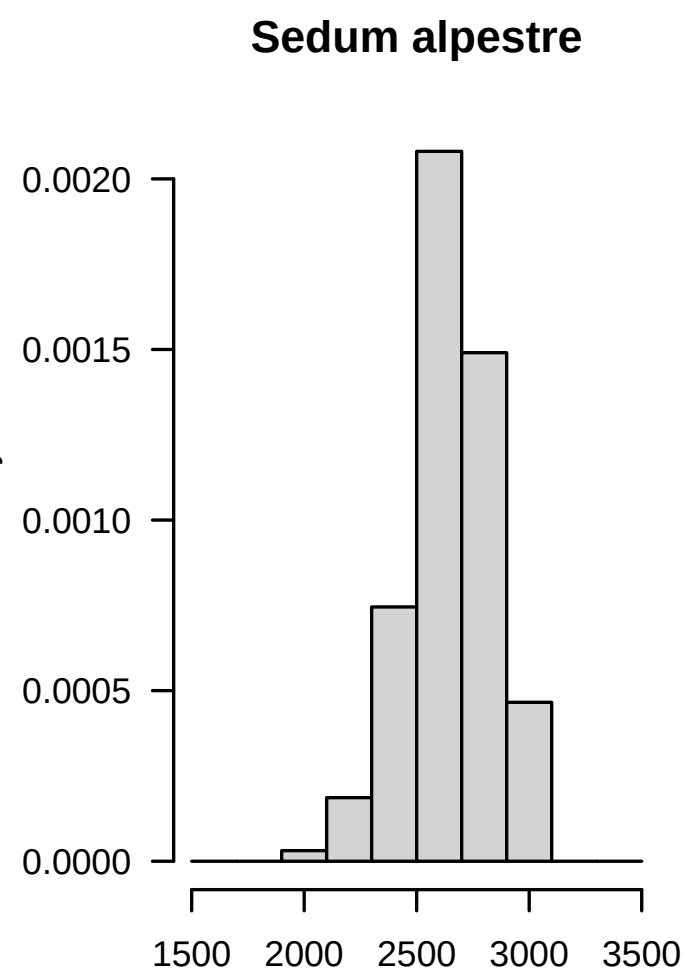
Annual mean temperature [°C]

p SW	p AG	skew
<0.01	<0.01	−0.58



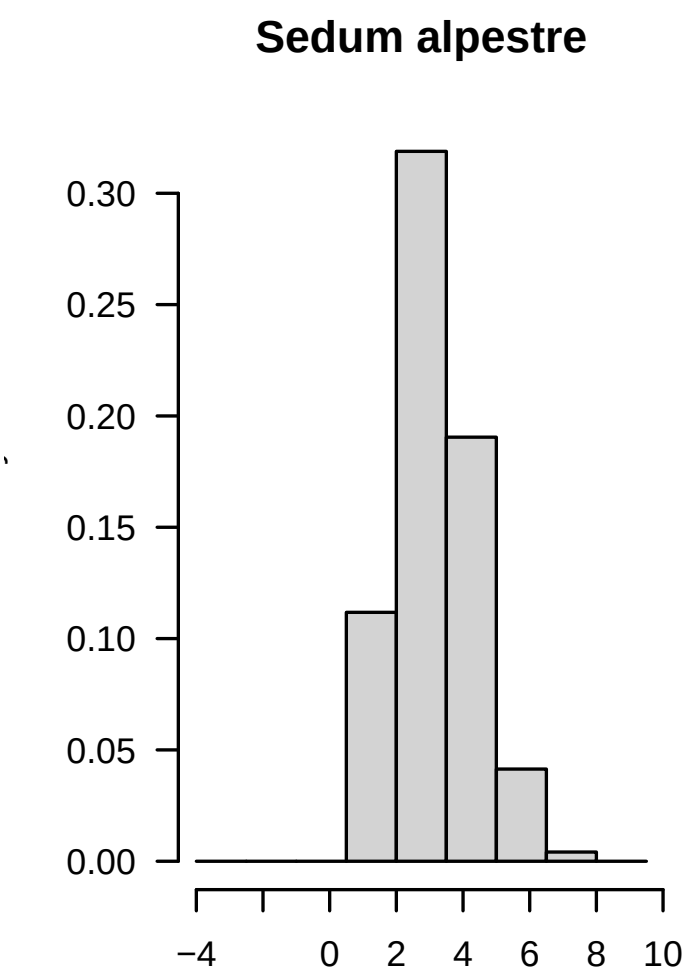
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.15



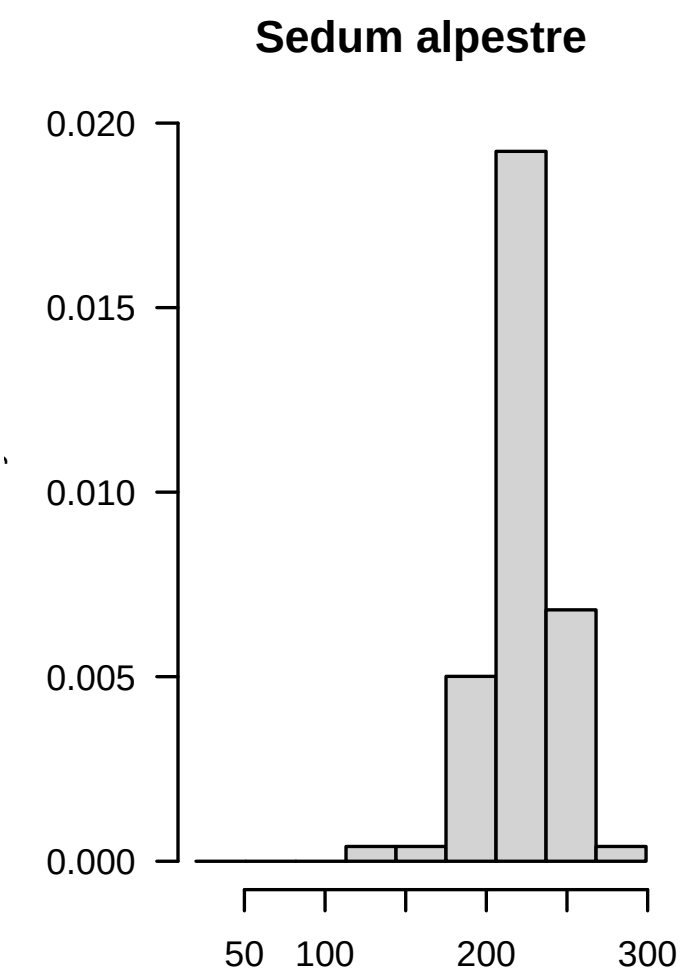
Elevation [m.a.s.l.]

p SW	p AG	skew
0.02	0.13	−0.29



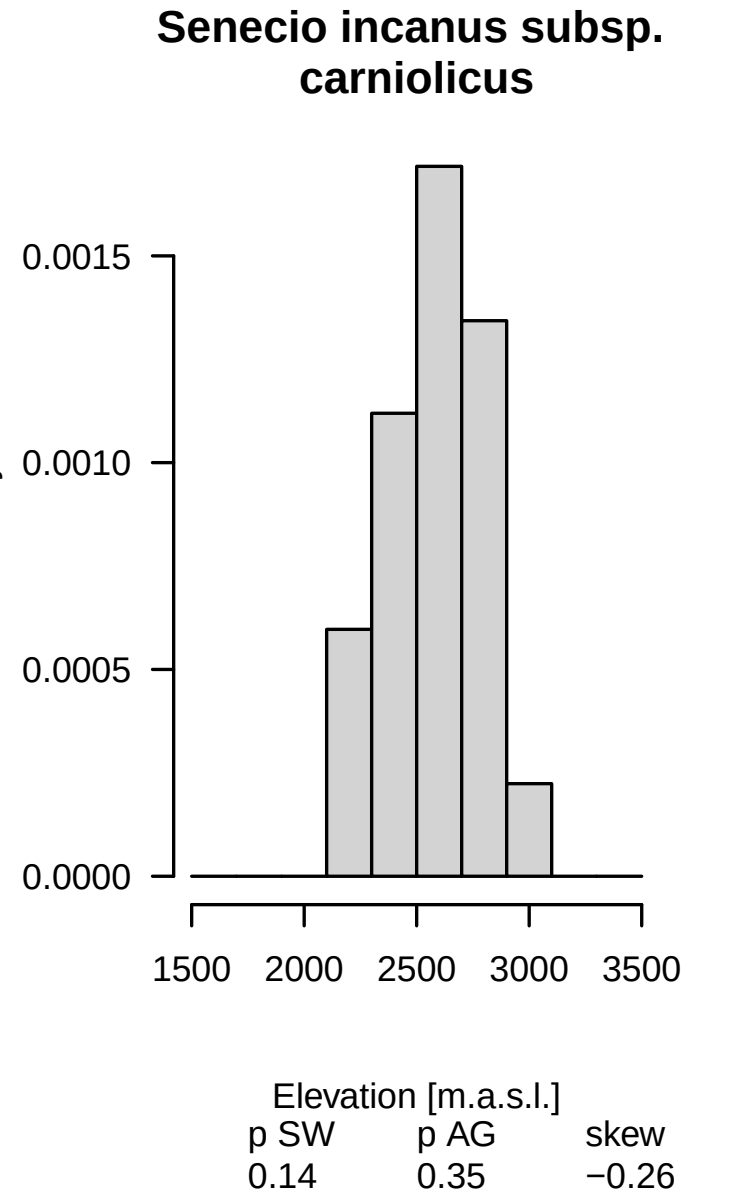
Annual mean temperature [°C]

p SW	p AG	skew
0.26	0.13	0.28



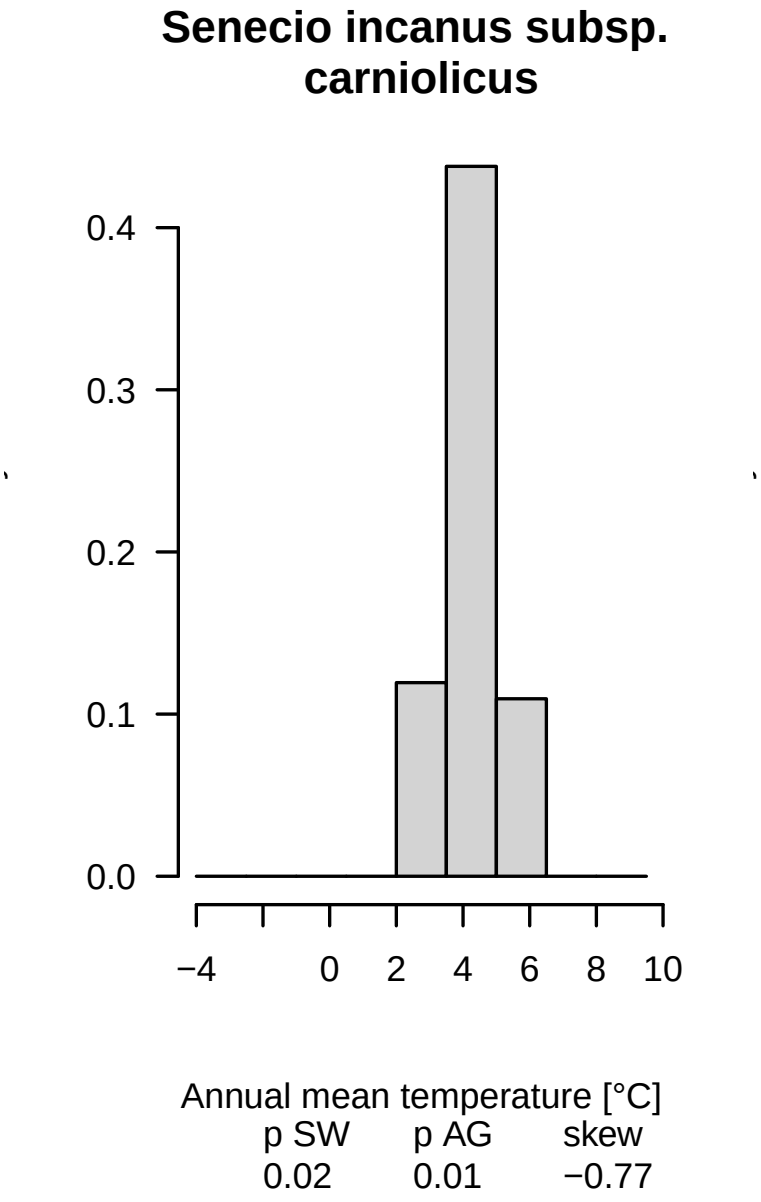
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.13



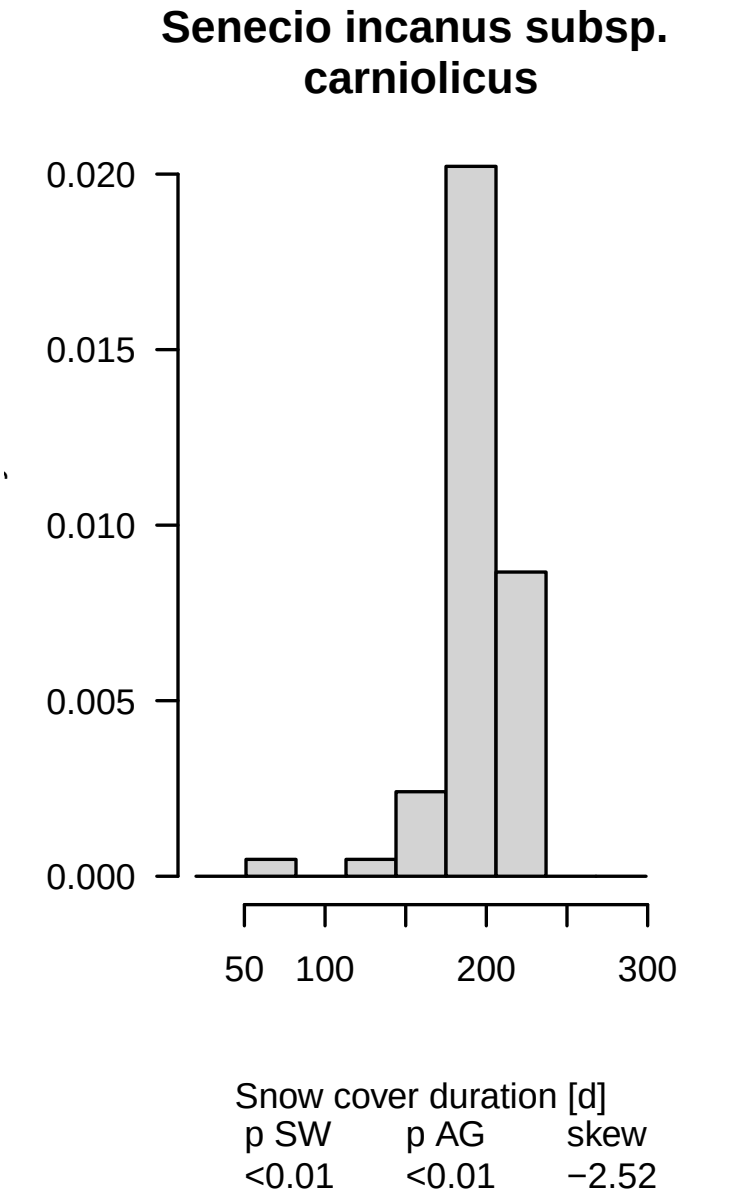
Elevation [m.a.s.l.]

p SW	p AG	skew
0.14	0.35	−0.26



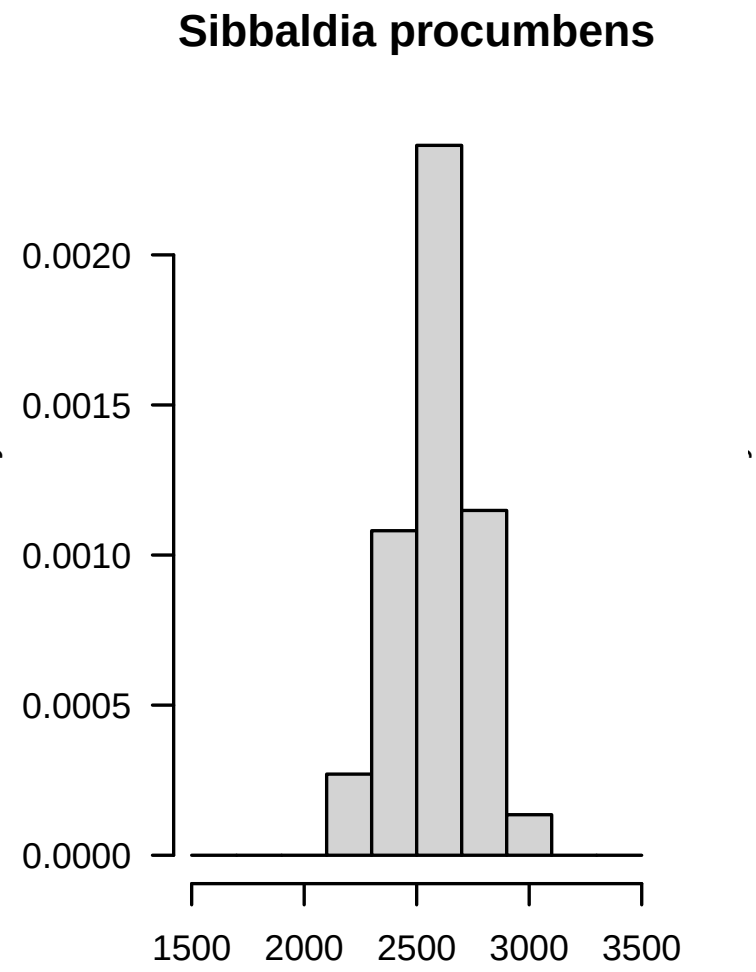
Annual mean temperature [°C]

p SW	p AG	skew
0.02	0.01	−0.77



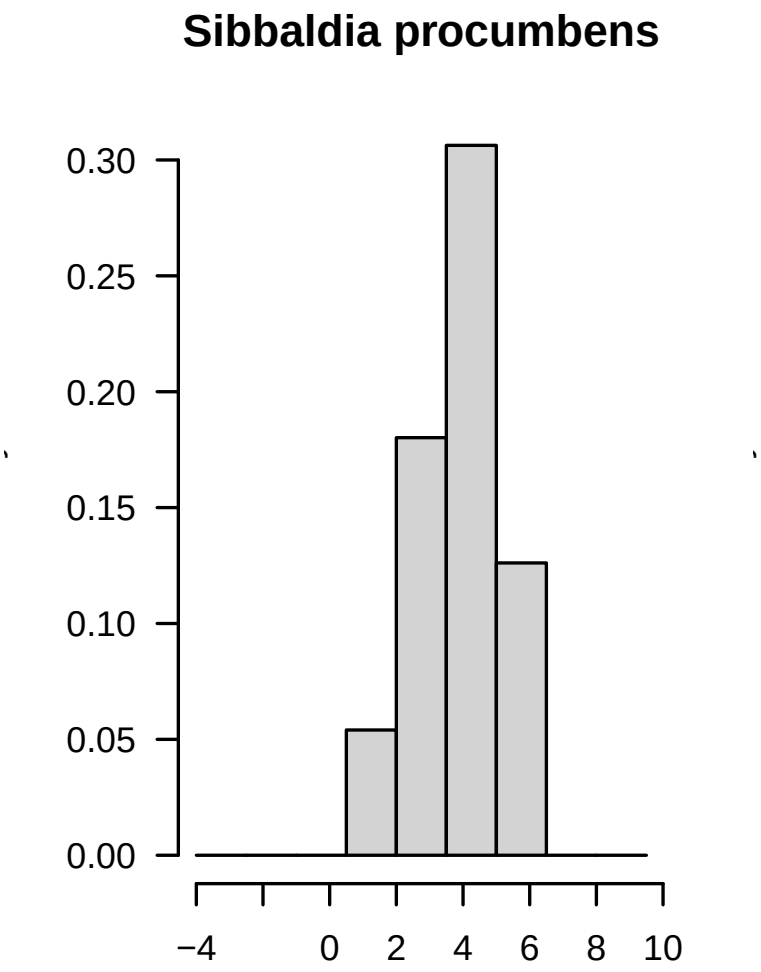
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−2.52



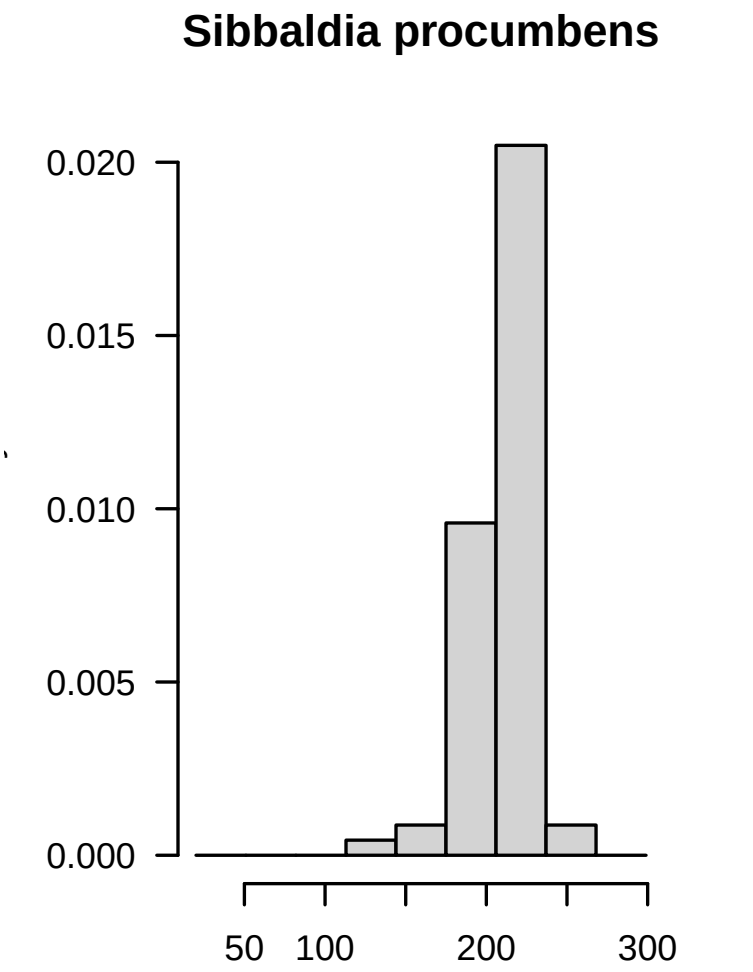
Elevation [m.a.s.l.]

p SW	p AG	skew
0.4	0.46	−0.19



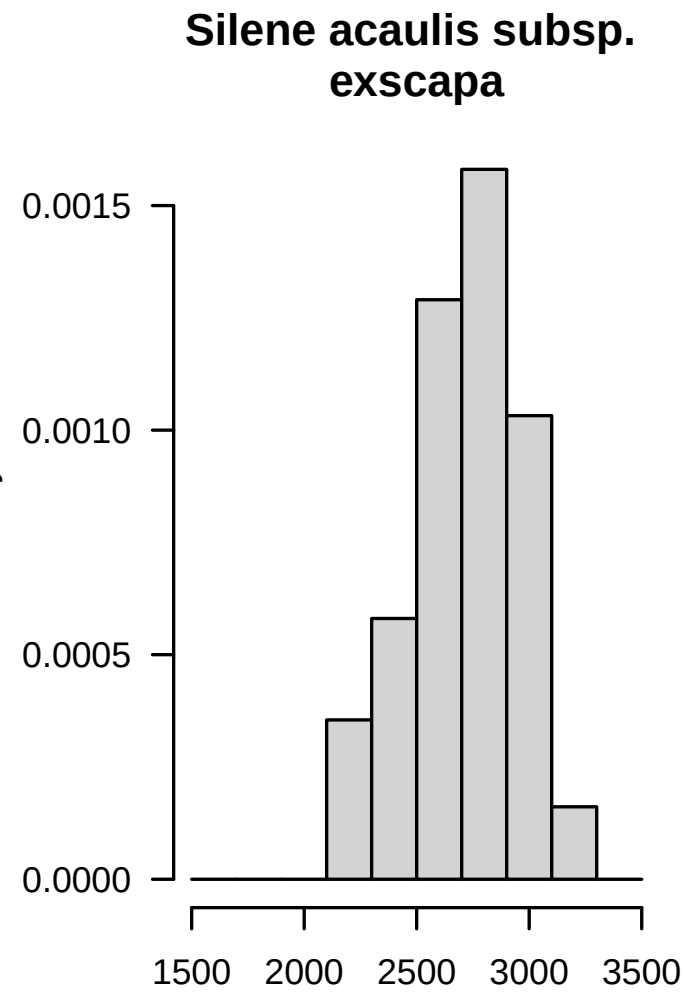
Annual mean temperature [°C]

p SW	p AG	skew
0.08	0.09	−0.47



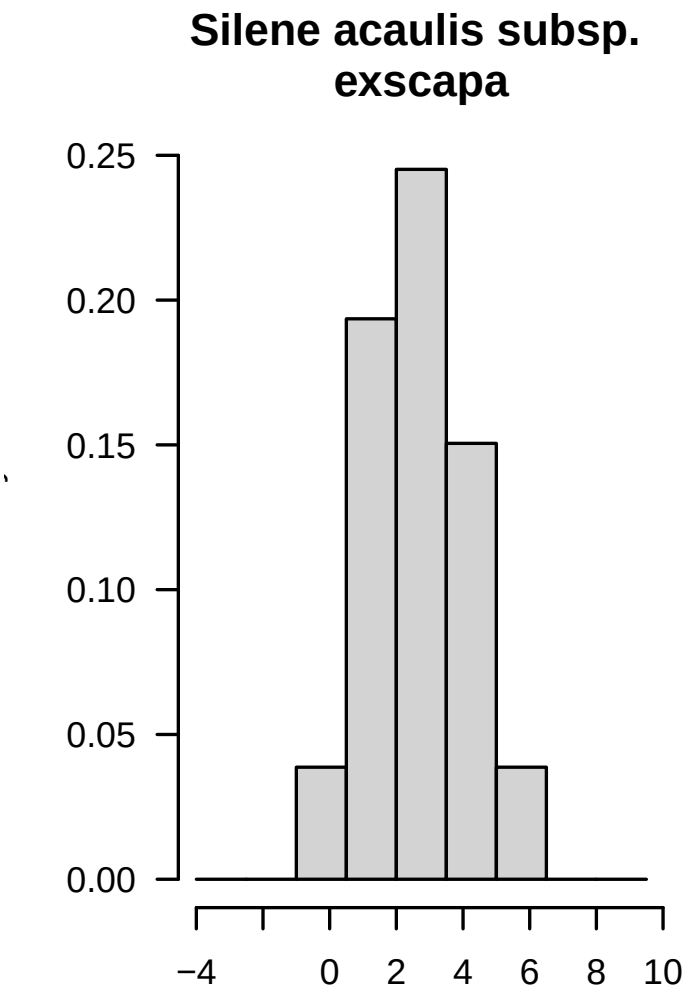
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.28



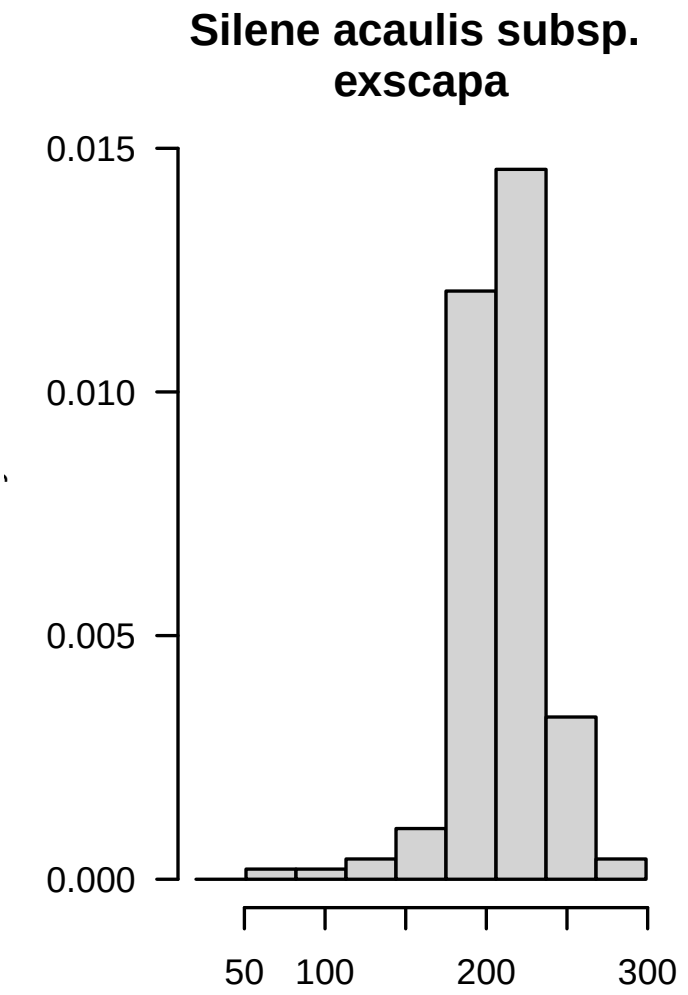
Elevation [m.a.s.l.]

p SW	p AG	skew
0.01	0.08	−0.34



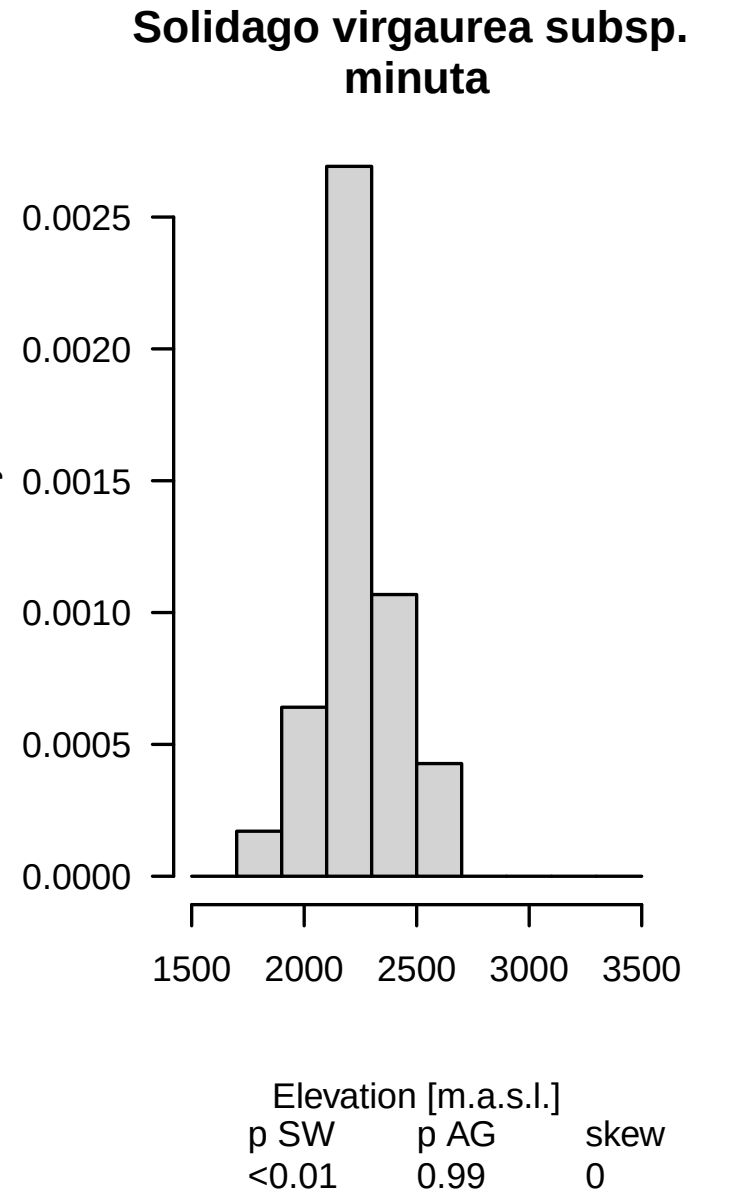
Annual mean temperature [°C]

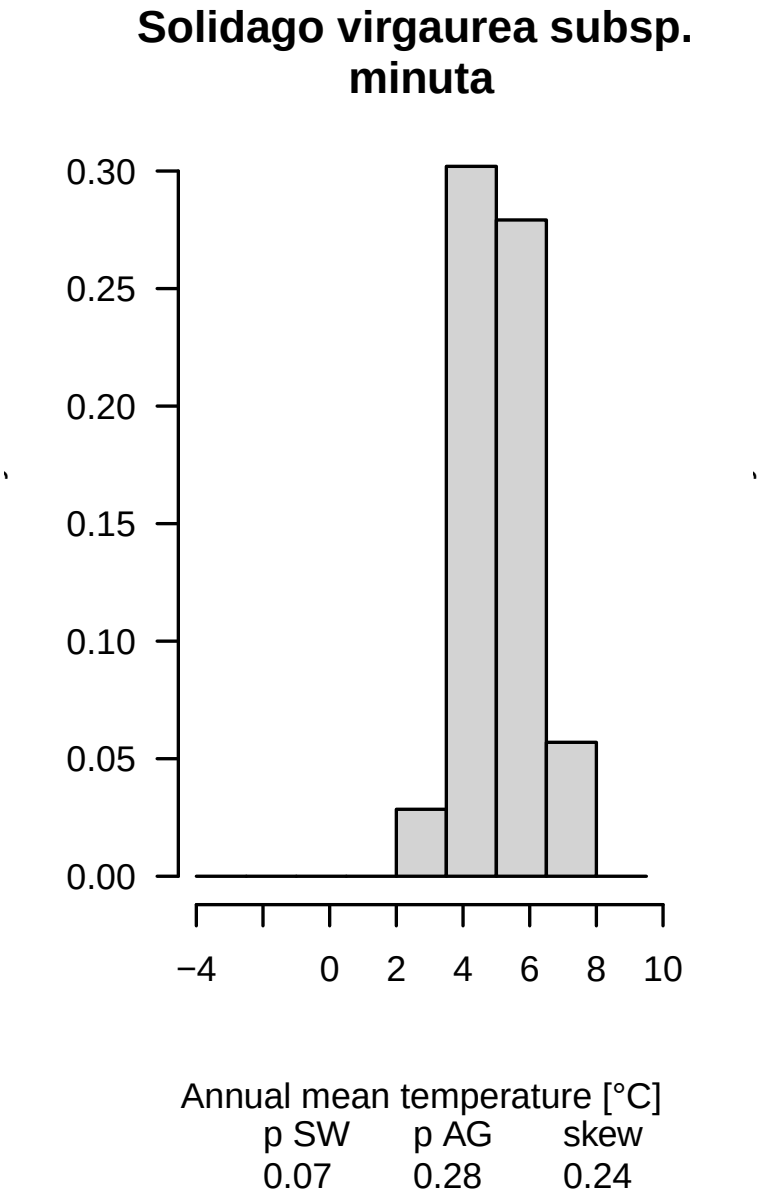
p SW	p AG	skew
0.57	0.8	0.05

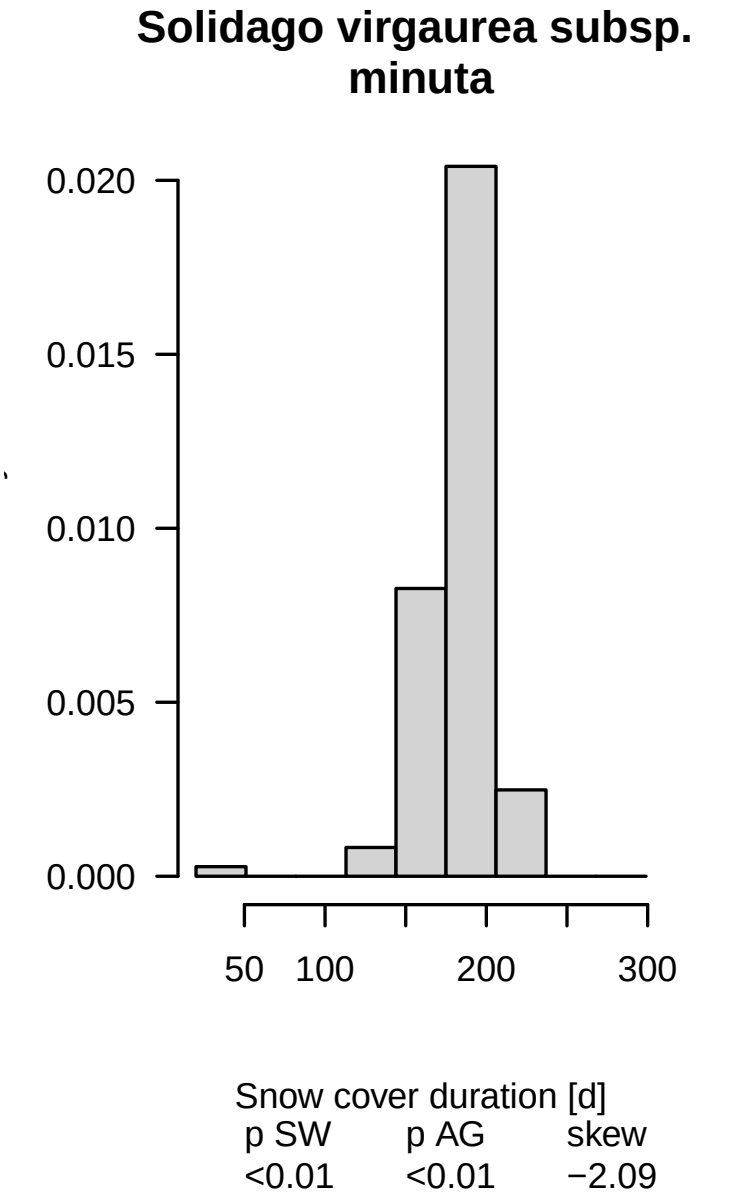


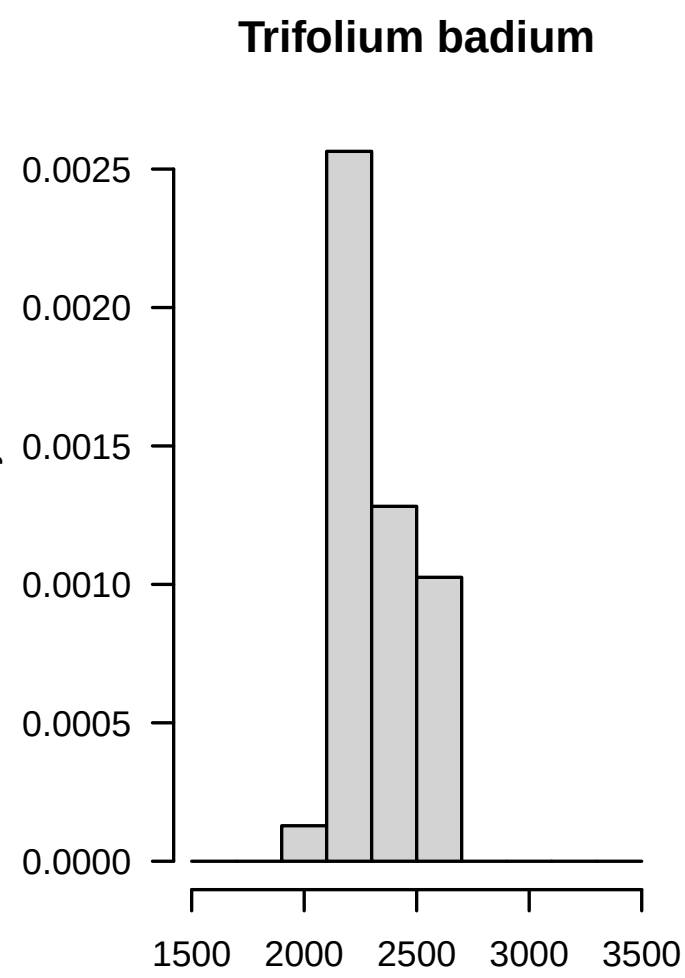
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.06


Solidago virgaurea subsp. minuta
0.0025
0.0020
0.0015
0.0010
0.0005
0.0000
1500
2000
2500
3000
3500
Elevation [m.a.s.l.]
p SW
p AG
skew
<0.01
0.99
0

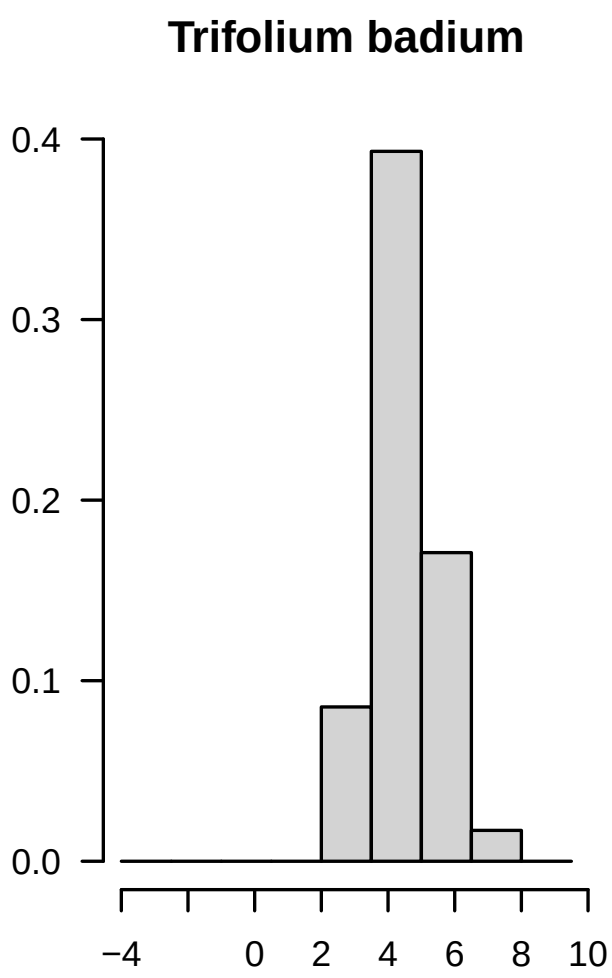

Solidago virgaurea subsp. minuta
0.30
0.25
0.20
0.15
0.10
0.05
0.00
−4
0
2
4
6
8
10
Annual mean temperature [°C]
p SW
p AG
skew
0.07
0.28
0.24


Solidago virgaurea subsp. minuta
0.020
0.015
0.010
0.005
0.000
50
100
200
300
Snow cover duration [d]
p SW
p AG
skew
<0.01
<0.01
−2.09



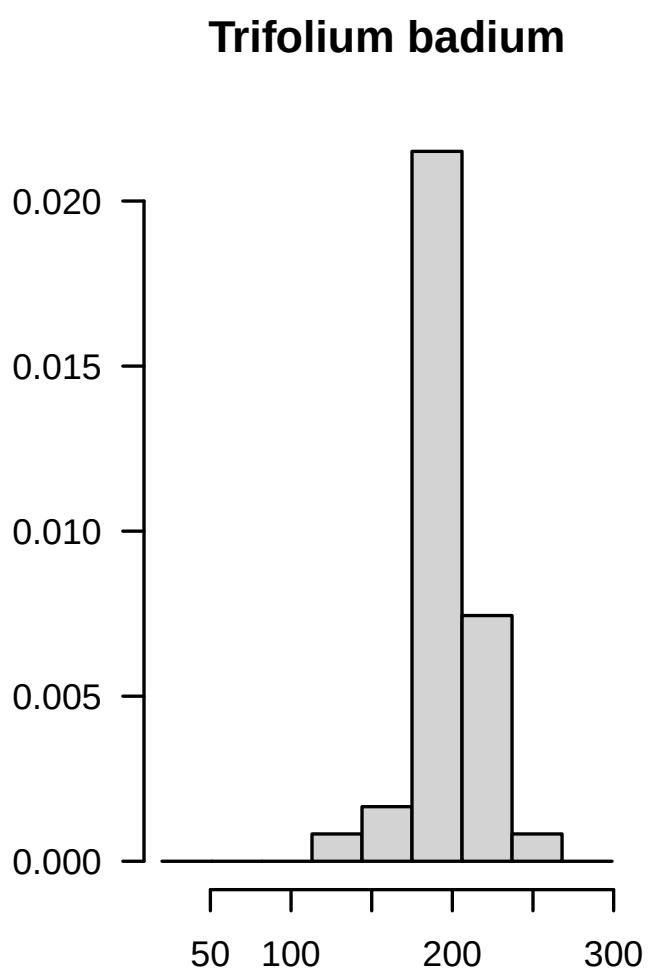
Elevation [m.a.s.l.]

p SW	p AG	skew
0.04	0.37	0.31



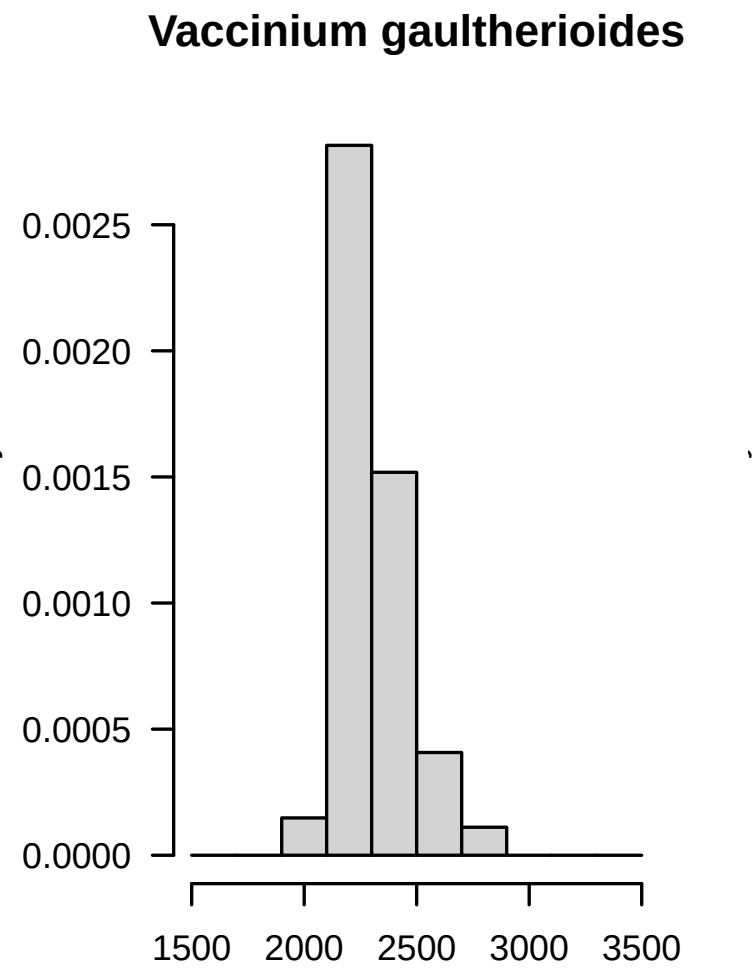
Annual mean temperature [°C]

p SW	p AG	skew
0.06	0.19	0.47



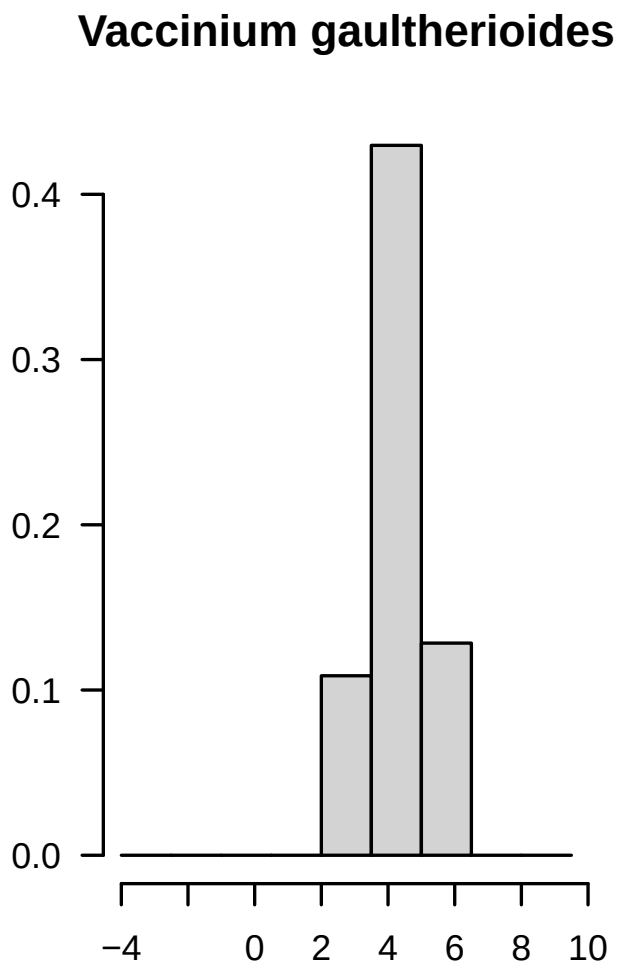
Snow cover duration [d]

p SW	p AG	skew
<0.01	0.01	−0.98



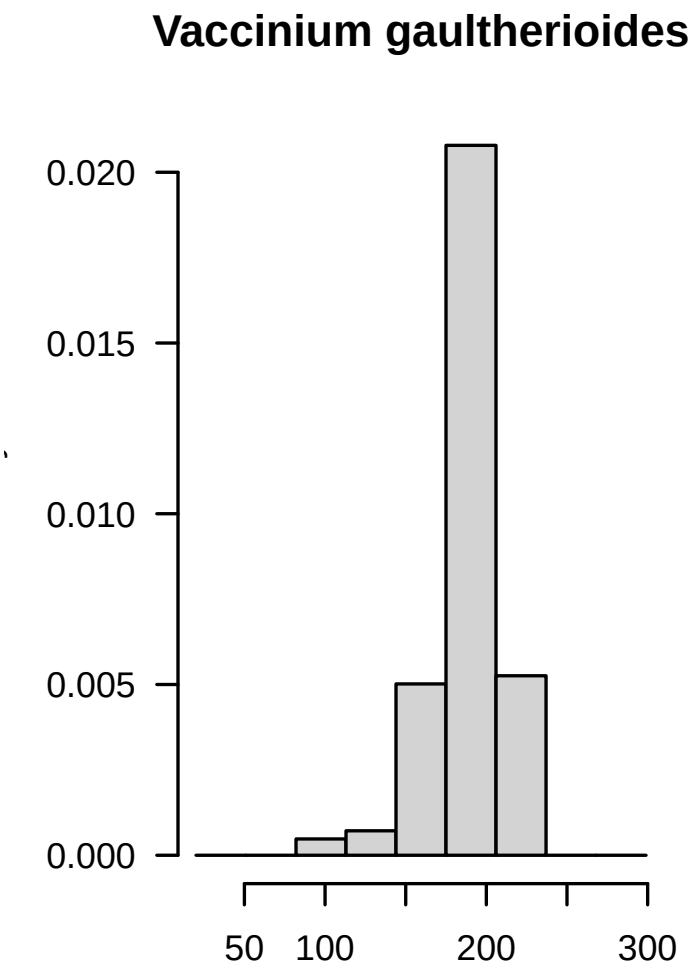
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	<0.01	0.91



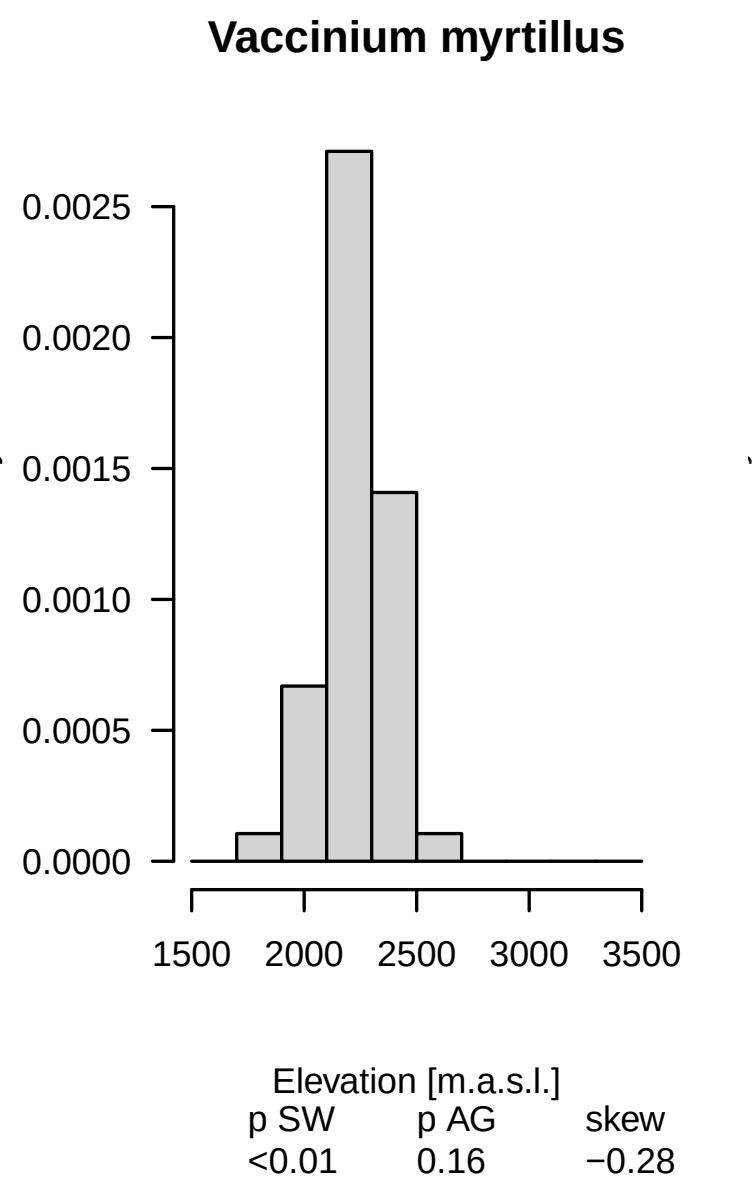
Annual mean temperature [°C]

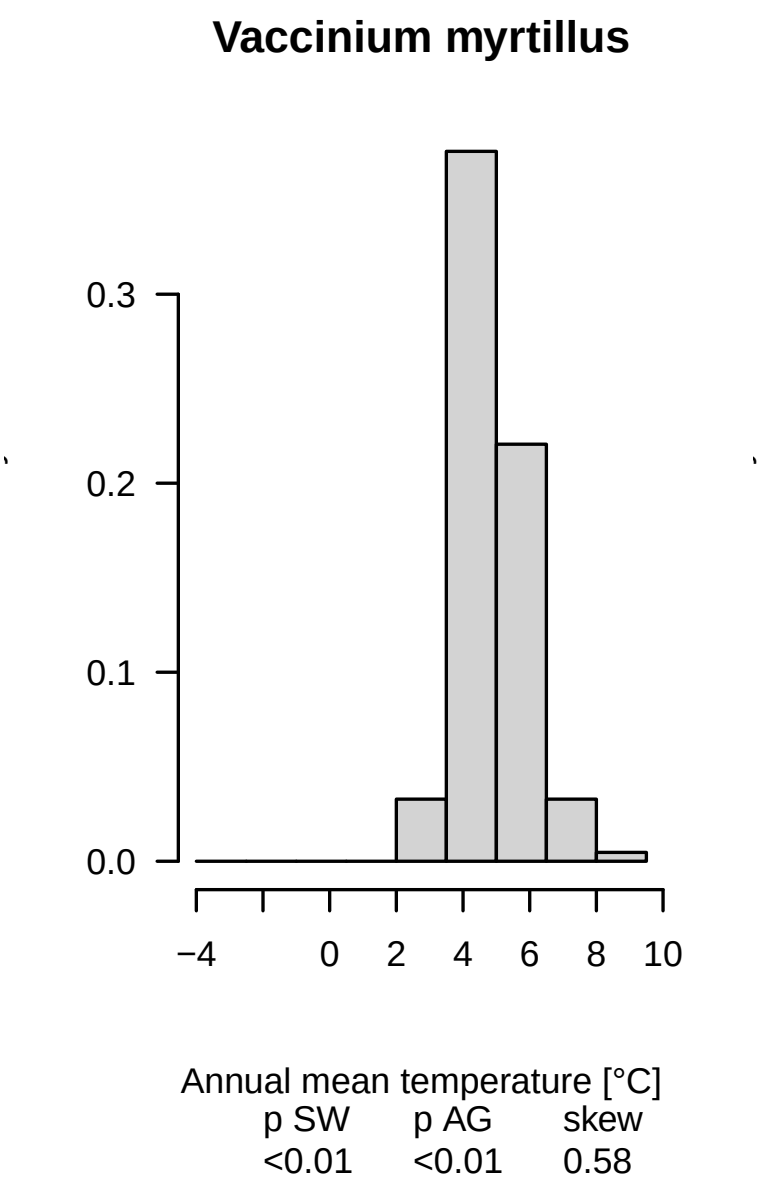
p SW	p AG	skew
0.63	0.56	−0.12

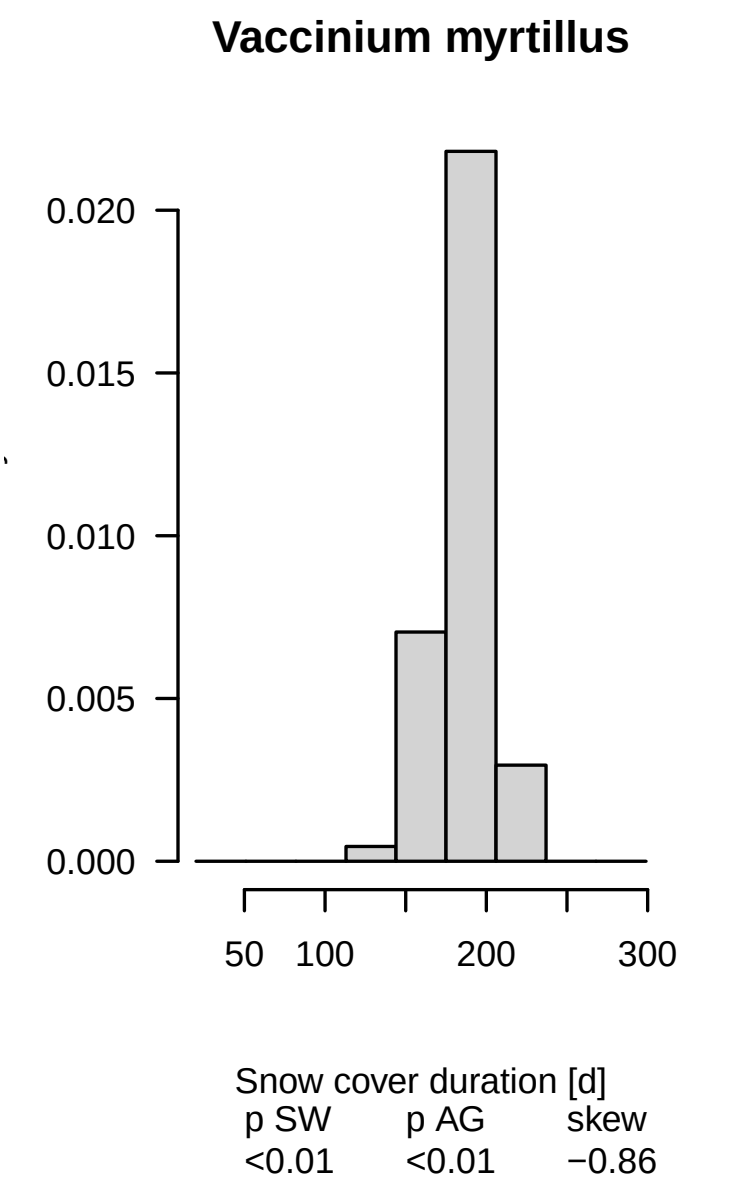


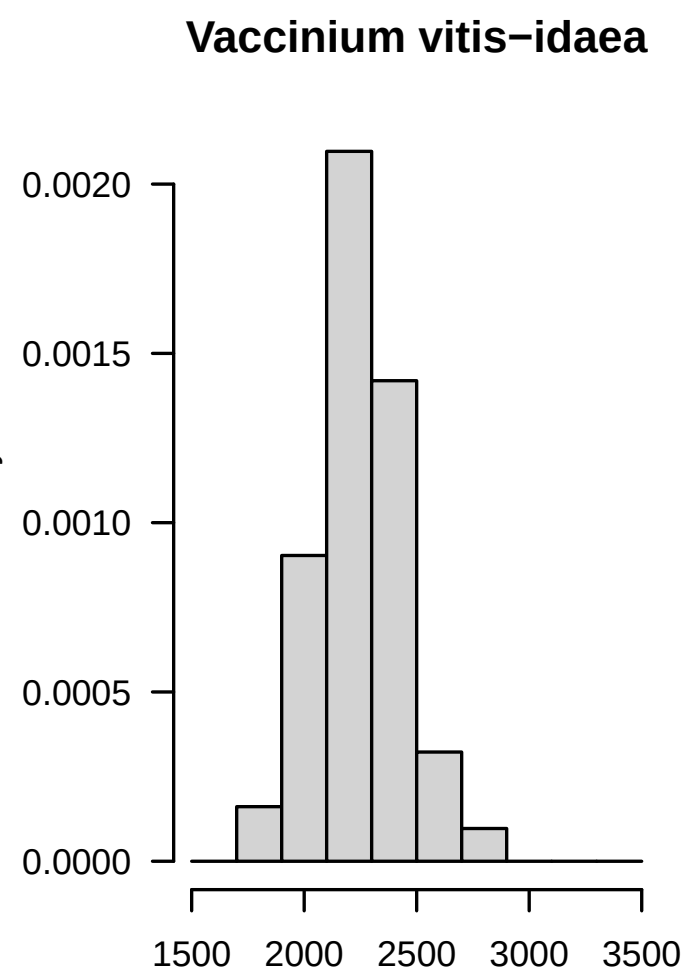
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.57


Vaccinium myrtillus
0.0025
0.0020
0.0015
0.0010
0.0005
0.0000
1500
2000
2500
3000
3500
Elevation [m.a.s.l.]
p SW
p AG
skew
<0.01
0.16
−0.28

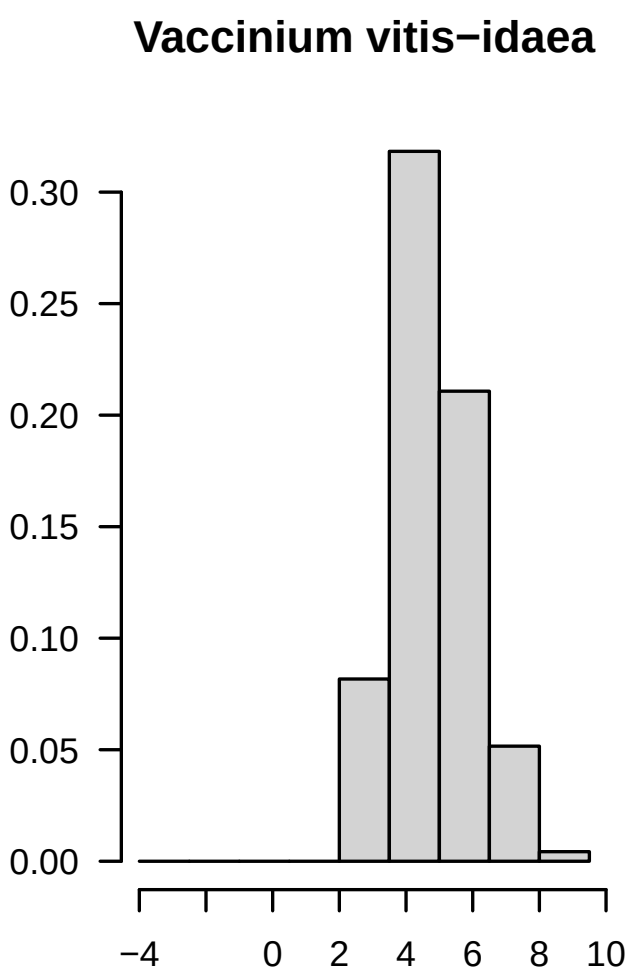

Vaccinium myrtillus
0.3
0.2
0.1
0.0
−4
0
2
4
6
8
10
Annual mean temperature [°C]
p SW
p AG
skew
<0.01
<0.01
0.58


Vaccinium myrtillus
0.020
0.015
0.010
0.005
0.000
50
100
200
300
Snow cover duration [d]
p SW
p AG
skew
<0.01
<0.01
−0.86



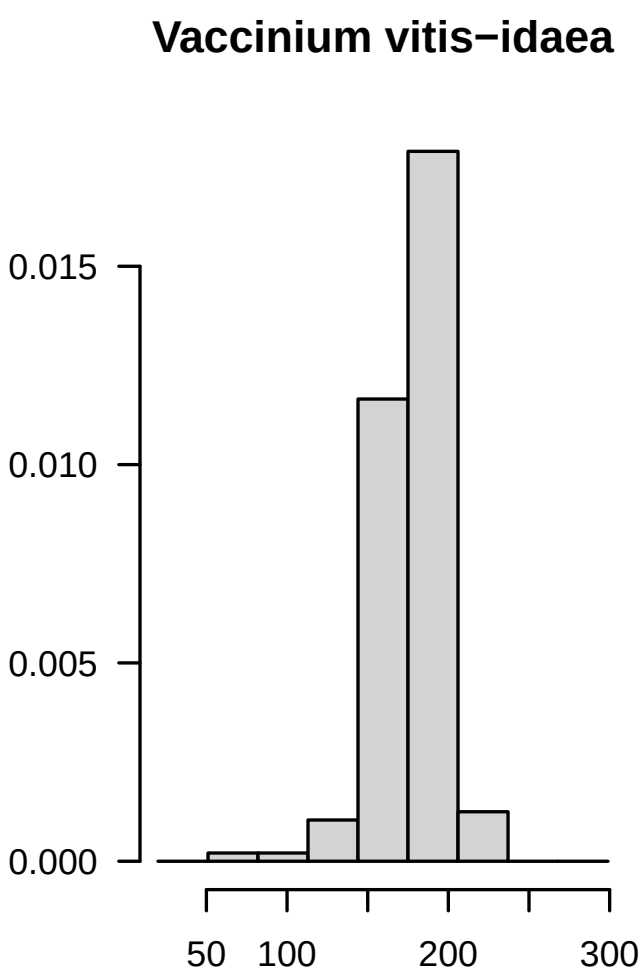
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.61	0.1



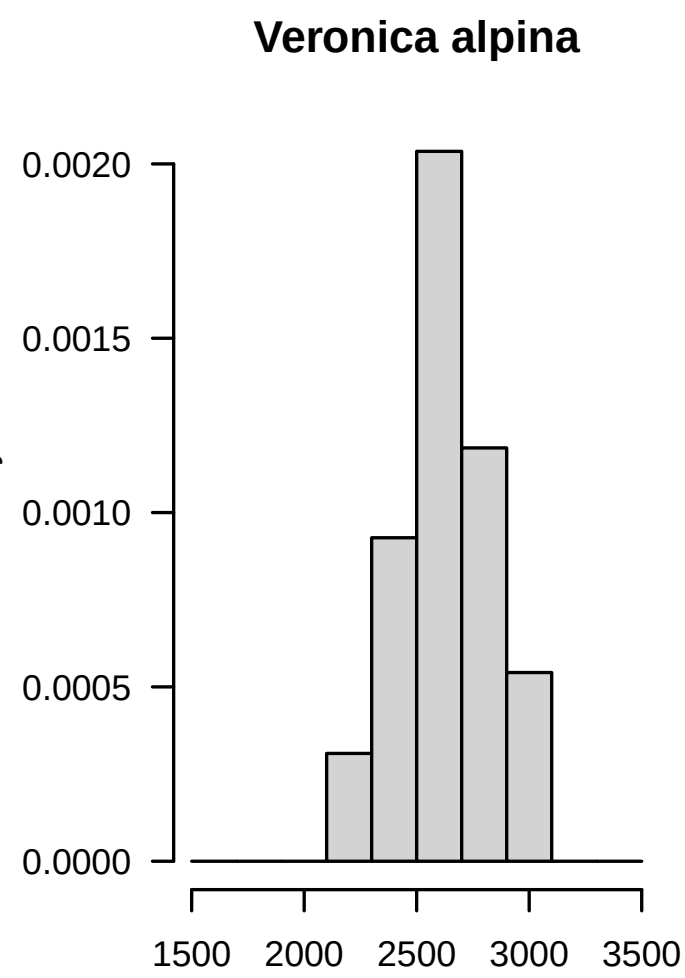
Annual mean temperature [°C]

p SW	p AG	skew
0.23	0.13	0.29



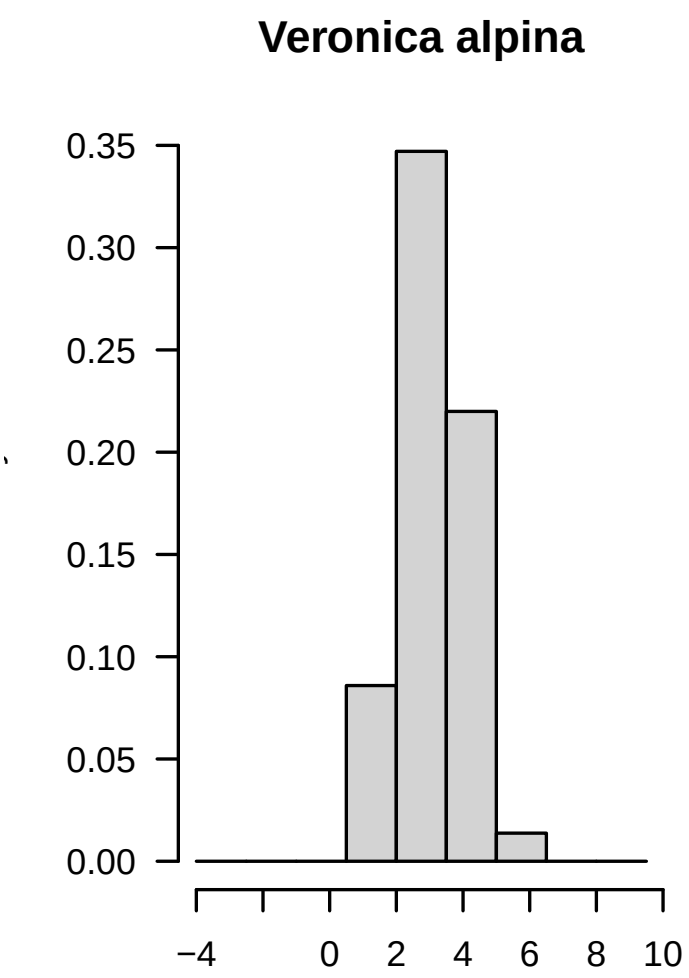
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.34



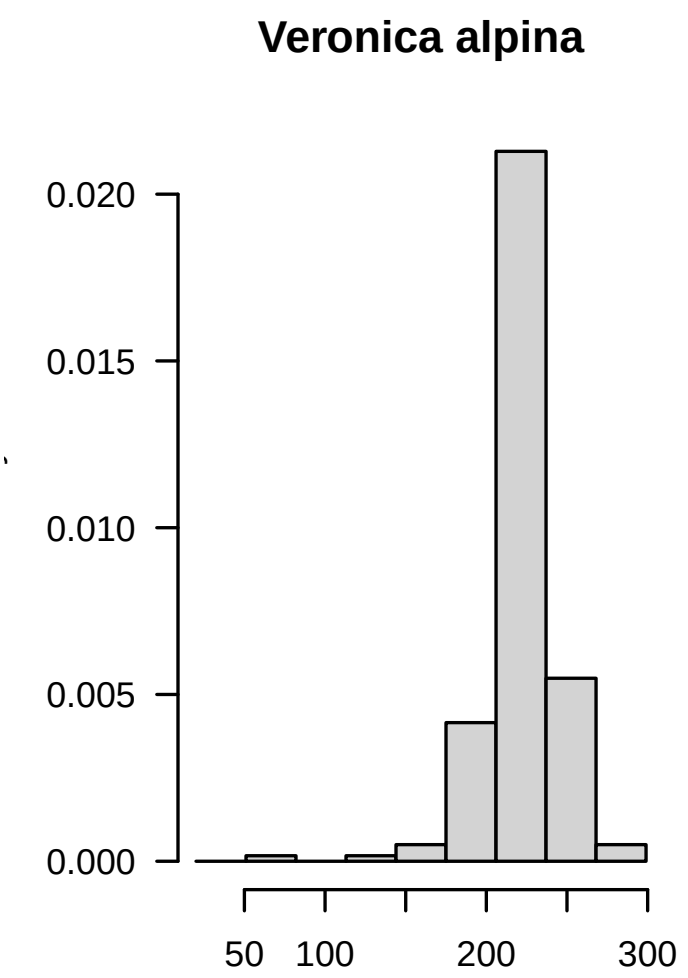
Elevation [m.a.s.l.]

p SW	p AG	skew
0.04	0.45	−0.13



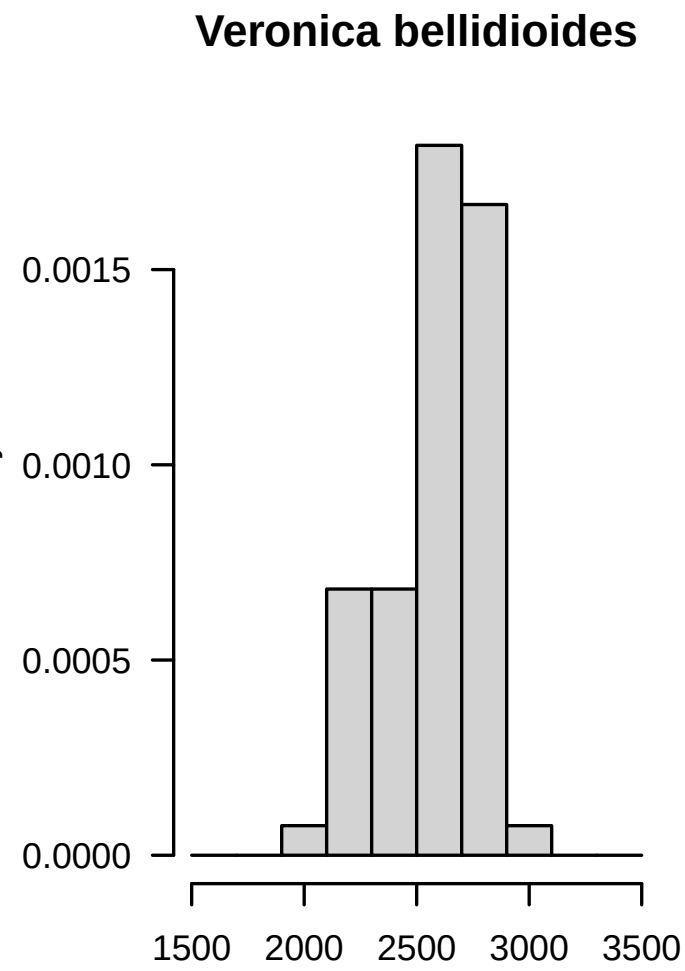
Annual mean temperature [°C]

p SW	p AG	skew
0.07	0.48	−0.12



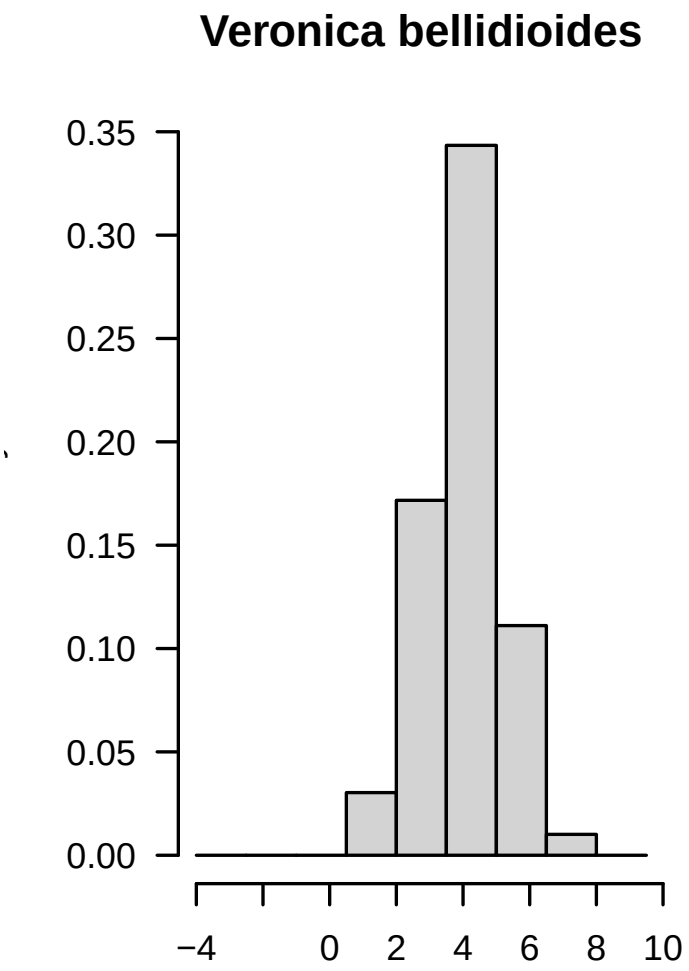
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.69



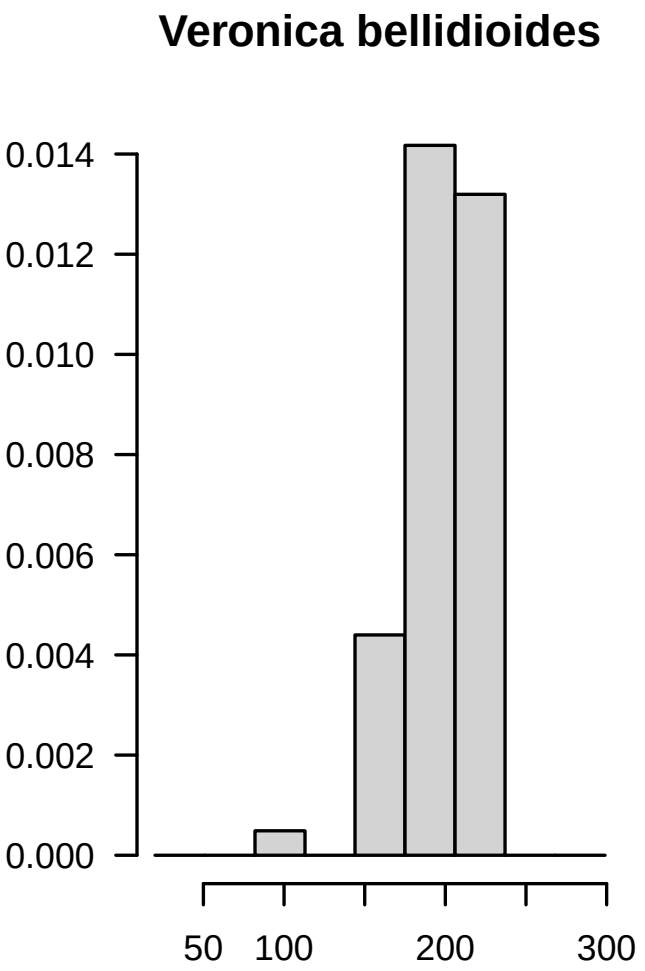
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.01	−0.73



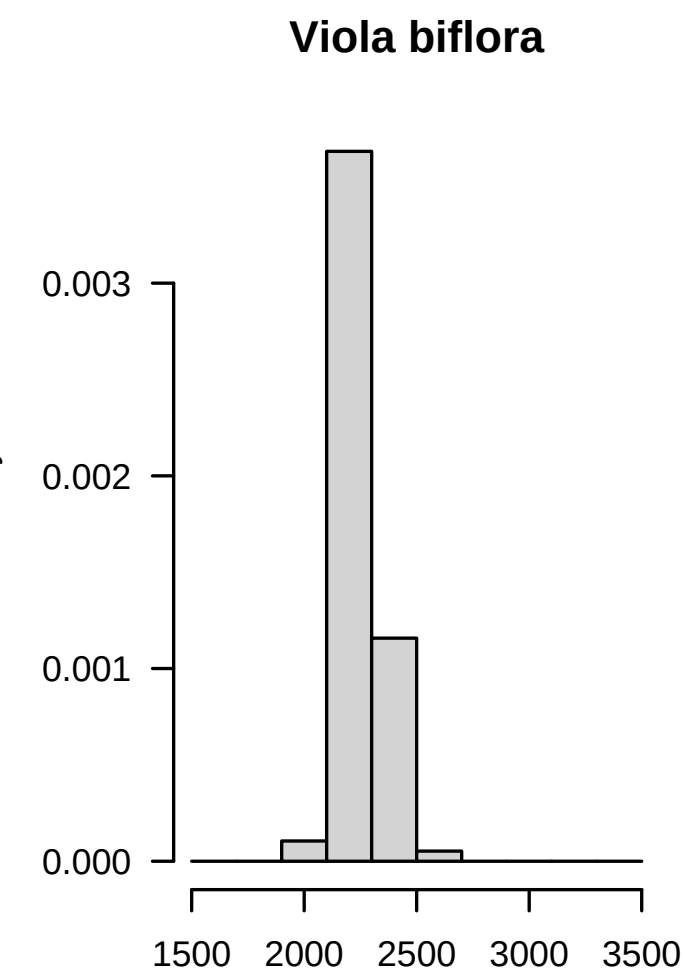
Annual mean temperature [°C]

p SW	p AG	skew
0.63	0.3	−0.29



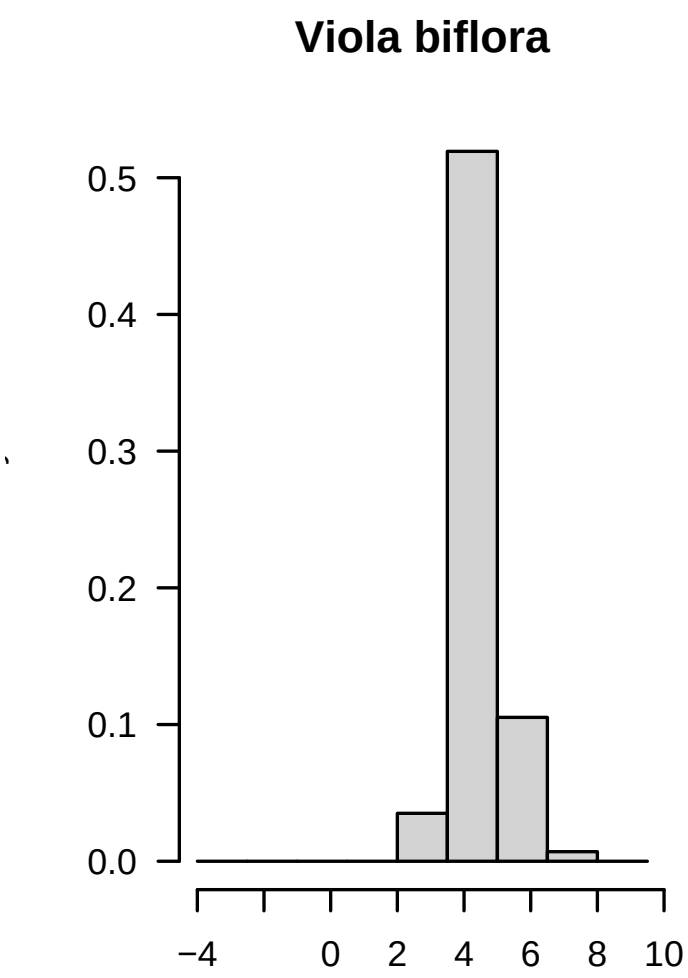
Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.16



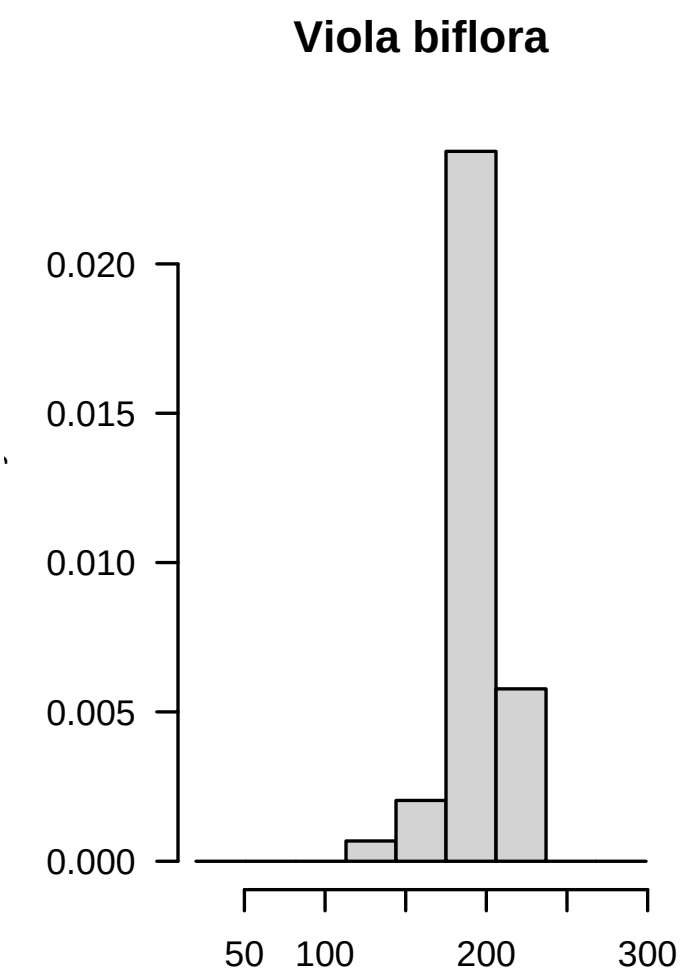
Elevation [m.a.s.l.]

p SW	p AG	skew
<0.01	0.3	0.25



Annual mean temperature [°C]

p SW	p AG	skew
0.01	<0.01	0.7



Snow cover duration [d]

p SW	p AG	skew
<0.01	<0.01	−1.7

Gradient	Taxon	SW.stat	SW.p	AG.stat	AG.p	Skewness	Kurtosis
Elevation	Achillea moschata	0.973229655	0.008453258	-1.265374028	0.205737281	-0.255959822	2.41042819
AnnualTemperature	Achillea moschata	0.979063069	0.033313099	-1.881125842	0.059954803	-0.386791626	3.044557826
SnowCover	Achillea moschata	0.975233542	0.013442405	-2.20961268	0.027132055	-0.459491143	4.605177372
Elevation	Agrostis agrostiflora	0.966870061	0.004469169	1.087870191	0.276652418	0.23228906	3.297248773
AnnualTemperature	Agrostis agrostiflora	0.938783106	3.30E-05	3.482236556	0.000497244	0.821705438	3.252031519
SnowCover	Agrostis agrostiflora	0.839306191	3.78E-10	-6.558781923	5.42E-11	-2.013942893	9.06196387
Elevation	Agrostis alpina	0.950229742	1.25E-05	1.628579585	0.103402049	0.302374482	1.932112098
AnnualTemperature	Agrostis alpina	0.9759542	0.005295257	-2.591126933	0.00956622	-0.495349476	3.214262943
SnowCover	Agrostis alpina	0.893759533	1.40E-09	-6.14635731	7.93E-10	-1.45418111	7.054414126
Elevation	Agrostis rupestris	0.976960997	0.00012708	-1.969798895	0.048861423	-0.281517898	2.417892239
AnnualTemperature	Agrostis rupestris	0.987063414	0.010568608	-1.896497833	0.057894246	-0.270693458	2.693000729
SnowCover	Agrostis rupestris	0.953641802	5.90E-08	-5.821400418	5.84E-09	-0.950021367	7.181061137
Elevation	Androsace alpina	0.903298857	0.047570119	-1.840346871	0.065717328	-0.875156091	3.925585023
AnnualTemperature	Androsace alpina	0.945482783	0.303666563	-1.932873623	0.053251768	-0.925406337	4.064539547
SnowCover	Androsace alpina	0.458391538	1.37E-07	-5.118010081	3.09E-07	-3.668139545	15.88118728
Elevation	Anthoxanthum alpinum	0.980957828	3.03E-05	2.35956278	0.018296485	0.28508399	2.721734263
AnnualTemperature	Anthoxanthum alpinum	0.982082826	5.54E-05	-0.900635277	0.367782272	-0.107110867	4.266393456
SnowCover	Anthoxanthum alpinum	0.914349888	1.56E-14	-9.744004486	0	-1.557826517	8.975474349
Elevation	Avenula versicolor	0.958596259	2.87E-07	0.703886285	0.481503593	0.099721018	1.969830763
AnnualTemperature	Avenula versicolor	0.98873361	0.025501668	-2.81148221	0.004931382	-0.412090195	3.27551699
SnowCover	Avenula versicolor	0.937588389	1.26E-09	-6.589769969	4.41E-11	-1.13019552	6.257743233
Elevation	Bartsia alpina	0.909430298	9.33E-05	3.580849466	0.000342479	1.140376385	4.816256835
AnnualTemperature	Bartsia alpina	0.984533483	0.54259803	0.086673196	0.930931283	0.023340094	2.833490428
SnowCover	Bartsia alpina	0.876252589	5.04E-06	-4.661571746	3.14E-06	-1.658151612	8.033855058
Elevation	Calluna vulgaris	0.941887866	0.000342203	-1.535510943	0.124658371	-0.369310849	2.363683438
AnnualTemperature	Calluna vulgaris	0.976690203	0.084751646	2.116716842	0.034283887	0.520992204	3.307300951
SnowCover	Calluna vulgaris	0.967718693	0.018106875	-2.5153658	0.011890894	-0.631568976	4.619500504
Elevation	Campanula barbata subsp. barbata	0.960542655	0.003482842	2.118352323	0.03414524	0.501768949	2.757356156
AnnualTemperature	Campanula barbata subsp. barbata	0.983257419	0.213985947	-1.658234933	0.097270056	-0.385822299	3.313264586
SnowCover	Campanula barbata subsp. barbata	0.87551884	7.49E-08	-5.774061713	7.74E-09	-1.810126857	10.75058818
Elevation	Carex curvula subsp. curvula	0.955997519	0.000188457	-3.000145449	0.002698507	-0.638473734	3.361248775
AnnualTemperature	Carex curvula subsp. curvula	0.977080338	0.018652931	-2.854229758	0.004314132	-0.603208131	3.419215829

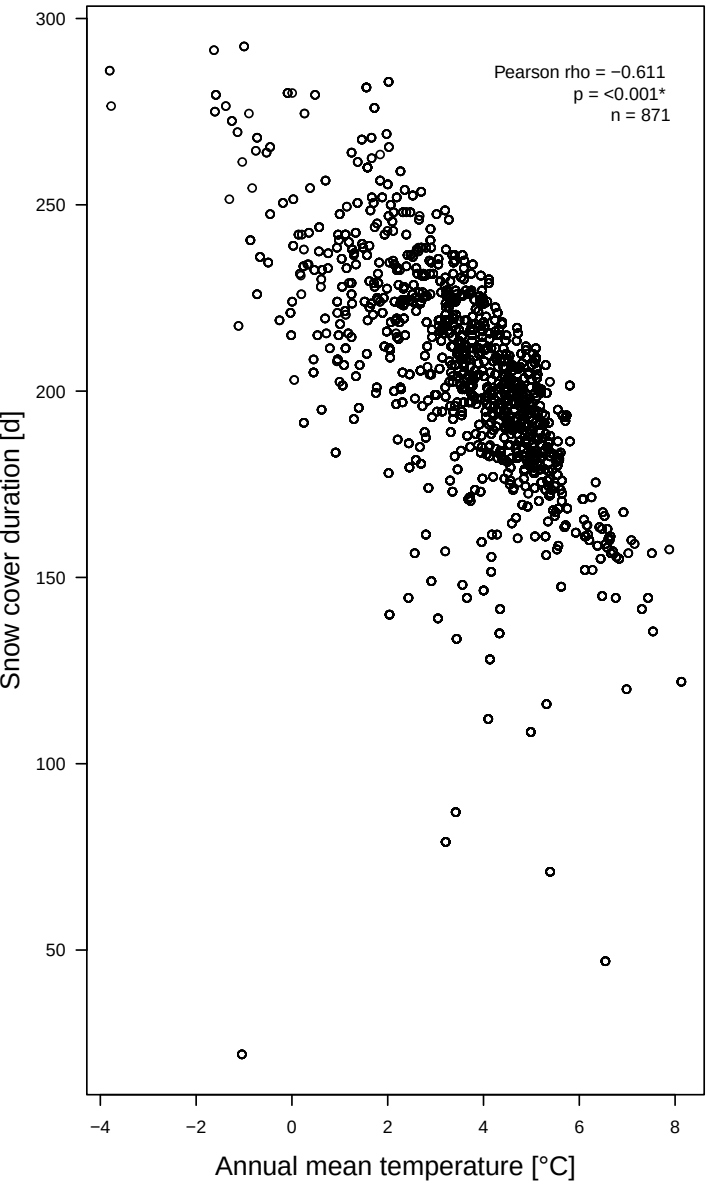
SnowCover	Carex curvula subsp. curvula	0.833968285	2.78E-11	-7.056909005	1.70E-12	-2.05330786	9.761280379
Elevation	Carex sempervirens	0.975250305	0.000965555	0.643631619	0.519814342	0.105819611	3.638977736
AnnualTemperature	Carex sempervirens	0.980034781	0.004590273	2.609694229	0.009062318	0.44587084	3.746147709
SnowCover	Carex sempervirens	0.875498256	4.37E-12	-7.956132552	1.78E-15	-1.866240299	9.706640344
Elevation	Cerastium uniflorum	0.986964953	0.089051025	0.303535658	0.761481677	0.053009423	2.298154002
AnnualTemperature	Cerastium uniflorum	0.993630155	0.615436869	-0.510693109	0.609565966	-0.089289186	3.050378218
SnowCover	Cerastium uniflorum	0.841057377	7.48E-13	-8.643129376	0	-2.395505185	19.33768075
Elevation	Crepis aurea	0.94263411	0.02689879	1.11332062	0.265570754	0.368994707	2.278882419
AnnualTemperature	Crepis aurea	0.932051117	0.011089703	0.309406036	0.757012679	0.100582788	5.458199475
SnowCover	Crepis aurea	0.756534342	2.99E-07	-4.910673286	9.08E-07	-2.332253246	9.376903169
Elevation	Deschampsia cespitosa subsp. cespitosa	0.917314662	3.17E-07	3.867506136	0.000109954	0.863542536	3.165382152
AnnualTemperature	Deschampsia cespitosa subsp. cespitosa	0.979562789	0.034117588	-2.060988481	0.039304139	-0.421845056	2.685583557
SnowCover	Deschampsia cespitosa subsp. cespitosa	0.936326014	5.66E-06	-3.257599725	0.001123588	-0.7023871	6.258124855
Elevation	Festuca nigrescens	0.933034397	0.00243041	0.10938377	0.912898106	0.031253054	1.683712516
AnnualTemperature	Festuca nigrescens	0.975829811	0.268462903	-0.951654447	0.341272259	-0.275477064	2.666799791
SnowCover	Festuca nigrescens	0.875753774	1.66E-05	-4.383378273	1.17E-05	-1.635354384	8.306694746
Elevation	Festuca nigricans	0.975957655	0.005300244	-0.095378367	0.924014298	-0.017372015	3.573836318
AnnualTemperature	Festuca nigricans	0.980814805	0.020619807	1.57633412	0.114948822	0.292319809	3.864681679
SnowCover	Festuca nigricans	0.863061984	3.48E-11	-7.318460351	2.51E-13	-1.917760852	9.186742445
Elevation	Geranium sylvaticum	0.939124566	0.000940673	-2.394854829	0.016626947	-0.656787148	2.906164471
AnnualTemperature	Geranium sylvaticum	0.918123359	8.59E-05	2.407331777	0.016069564	0.660692144	2.416332469
SnowCover	Geranium sylvaticum	0.773871559	1.10E-09	-6.682879478	2.34E-11	-2.839397858	16.68383807
Elevation	Geum montanum	0.947092812	1.39E-05	0.132144551	0.894869959	0.0249161	1.822185701
AnnualTemperature	Geum montanum	0.99063154	0.397536406	0.581545028	0.56087318	0.109923681	2.97752212
SnowCover	Geum montanum	0.872551712	3.05E-10	-7.431354914	1.07E-13	-2.081207591	14.07635056
Elevation	Geum reptans	0.943830637	0.009567872	1.57827733	0.114501912	0.478102845	2.151084324
AnnualTemperature	Geum reptans	0.989672735	0.903271395	-0.198313852	0.842799514	-0.057915416	3.041212586
SnowCover	Geum reptans	0.953732817	0.027072873	1.429825704	0.15276705	0.430271604	4.705589859
Elevation	Gnaphalium supinum	0.993444761	0.436793955	-0.594909409	0.551904028	-0.095023642	3.093319193
AnnualTemperature	Gnaphalium supinum	0.981879476	0.006021788	-2.176222158	0.029538653	-0.35643601	2.69965734
SnowCover	Gnaphalium supinum	0.970964397	0.000158273	-1.865206013	0.062152533	-0.303312561	5.599313304
Elevation	Homogyne alpina	0.946517235	1.82E-08	4.499007958	6.83E-06	0.712582965	3.075770904
AnnualTemperature	Homogyne alpina	0.990847842	0.083657003	-1.954104465	0.050688864	-0.286596794	3.160431301

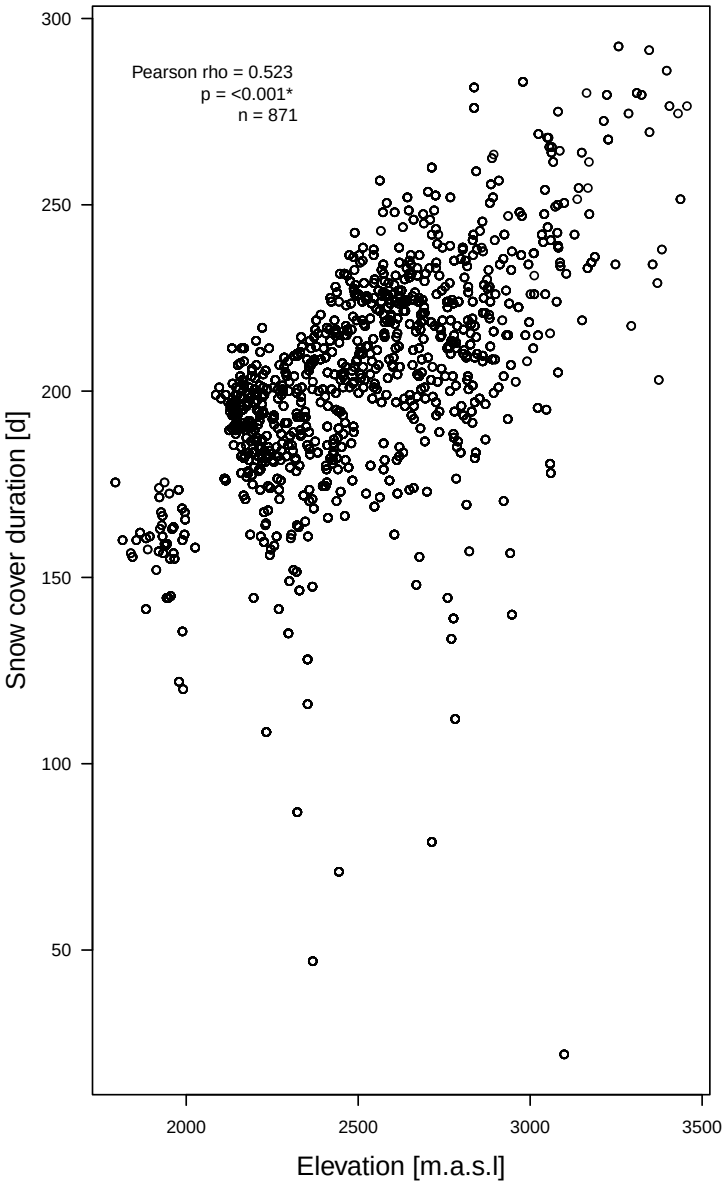
SnowCover	Homogyne alpina	0.960940218	9.08E-07	-5.363390139	8.17E-08	-0.883298414	5.368276415
Elevation	Juncus trifidus	0.985070755	0.054779515	-0.652018943	0.514388952	-0.115617082	2.94282001
AnnualTemperature	Juncus trifidus	0.987769822	0.126297846	1.04508826	0.295982179	0.186172742	3.251083128
SnowCover	Juncus trifidus	0.880406793	1.01E-10	-7.17583708	7.19E-13	-1.771834112	8.544478068
Elevation	Kobresia myosuroides	0.96281539	0.023840268	-1.386848663	0.165487915	-0.367122066	2.429948915
AnnualTemperature	Kobresia myosuroides	0.976768828	0.170618008	-1.78415427	0.074398601	-0.479853335	2.933569937
SnowCover	Kobresia myosuroides	0.86350937	7.06E-07	-5.166810083	2.38E-07	-1.838375462	10.74544712
Elevation	Leucanthemopsis alpina	0.986342499	0.002278738	0.75750113	0.448749689	0.097682514	3.168875493
AnnualTemperature	Leucanthemopsis alpina	0.975619913	1.30E-05	-4.381146361	1.18E-05	-0.606695741	3.354818875
SnowCover	Leucanthemopsis alpina	0.980063271	9.54E-05	0.029164352	0.976733512	0.00375249	4.252966233
Elevation	Loiseleuria procumbens	0.886965062	0.000244984	3.700748327	0.000214965	1.452573968	6.073651973
AnnualTemperature	Loiseleuria procumbens	0.980986369	0.620259157	-0.59133971	0.554292828	-0.18794754	2.624594721
SnowCover	Loiseleuria procumbens	0.880307449	0.000154321	-3.829879953	0.000128206	-1.525573905	6.459451042
Elevation	Luzula alpino-pilosa	0.968239697	0.000241136	0.986083316	0.32409223	0.169349209	2.173603897
AnnualTemperature	Luzula alpino-pilosa	0.988426327	0.120489701	-2.160385103	0.03074287	-0.379982471	3.089919111
SnowCover	Luzula alpino-pilosa	0.948619912	2.16E-06	-4.79506684	1.63E-06	-0.9463203	5.953866092
Elevation	Luzula lutea	0.97178603	0.013181287	1.296875815	0.194673919	0.280371943	2.505741659
AnnualTemperature	Luzula lutea	0.981943788	0.110982089	-1.157142525	0.247214135	-0.249356227	2.629213565
SnowCover	Luzula lutea	0.971752498	0.013091438	-2.752638246	0.005911718	-0.62867399	3.308230681
Elevation	Luzula spicata	0.983862362	0.04615695	-1.406630188	0.159537077	-0.25770142	2.819913699
AnnualTemperature	Luzula spicata	0.971771196	0.001541724	-0.116940189	0.90690745	-0.021124479	2.017100724
SnowCover	Luzula spicata	0.936382112	7.42E-07	-5.081860252	3.74E-07	-1.097997686	8.018661067
Elevation	Mutellina adonidifolia	0.94438273	3.58E-07	2.700826329	0.006916745	0.46389985	2.149568995
AnnualTemperature	Mutellina adonidifolia	0.993658555	0.519562928	-1.317343939	0.187723363	-0.21882357	2.968205362
SnowCover	Mutellina adonidifolia	0.929838953	1.98E-08	-6.058697028	1.37E-09	-1.233698615	7.103502891
Elevation	Nardus stricta	0.973879243	0.004126657	-0.873824226	0.382213985	-0.163753296	3.106165956
AnnualTemperature	Nardus stricta	0.960863018	0.000184742	1.565568839	0.11744959	0.297144501	4.486313297
SnowCover	Nardus stricta	0.981992593	0.036268147	-2.213682801	0.026850607	-0.42794492	3.295124464
Elevation	Oreochloa disticha	0.980542532	0.12992413	-1.65690772	0.097538133	-0.385495983	3.00597707
AnnualTemperature	Oreochloa disticha	0.972841384	0.030875253	-2.455612905	0.014064456	-0.59089833	3.292505306
SnowCover	Oreochloa disticha	0.874705577	6.93E-08	-5.158016299	2.50E-07	-1.518493459	7.878193991
Elevation	Oxyria digyna	0.871506102	0.000439294	3.149883044	0.001633358	1.303469139	4.242383693
AnnualTemperature	Oxyria digyna	0.968147833	0.344340947	1.86228965	0.062562274	0.689088686	3.874588221

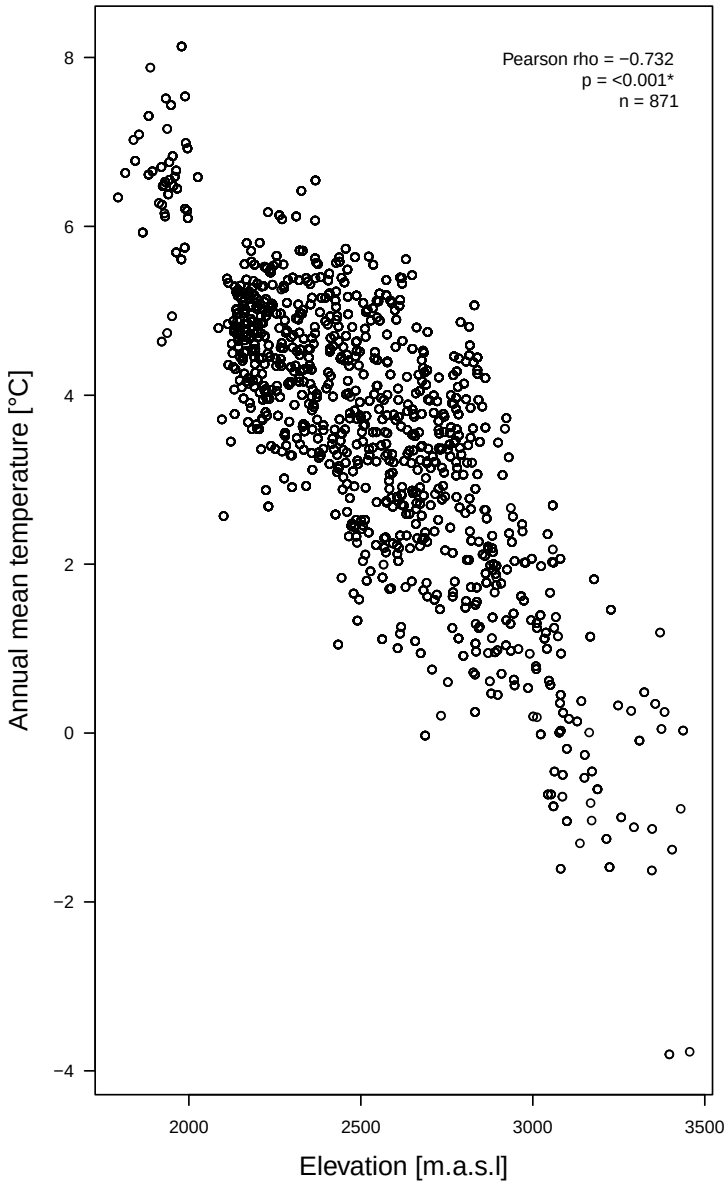
SnowCover	Oxyria digyna	0.941775022	0.047844015	2.1388649	0.032446611	0.807033221	3.79870782
Elevation	Persicaria vivipara	0.943340683	5.48E-10	3.284570781	0.001021378	0.450726778	2.222070864
AnnualTemperature	Persicaria vivipara	0.986996222	0.004363506	-2.568838804	0.010203991	-0.346671947	3.370530782
SnowCover	Persicaria vivipara	0.902313514	7.93E-14	-8.91164178	0	-1.585015261	8.207195328
Elevation	Phyteuma hemisphaericum	0.961570037	1.80E-06	0.675103732	0.499609863	0.099538155	1.870203562
AnnualTemperature	Phyteuma hemisphaericum	0.970294155	2.76E-05	-3.516466052	0.000437333	-0.549738526	2.858466666
SnowCover	Phyteuma hemisphaericum	0.904945064	7.65E-12	-7.682718649	1.55E-14	-1.492848041	7.430269732
Elevation	Poa alpina	0.978396607	6.31E-05	0.279817044	0.779617875	0.036679343	2.264563783
AnnualTemperature	Poa alpina	0.971740468	3.96E-06	-4.176115623	2.97E-05	-0.586431755	3.719590863
SnowCover	Poa alpina	0.918811669	1.73E-12	-8.355951483	0	-1.429296471	13.5092648
Elevation	Poa laxa	0.985306332	0.131290056	-0.170803655	0.864378155	-0.033427399	2.47827067
AnnualTemperature	Poa laxa	0.988282931	0.271459343	-0.085176838	0.932120804	-0.016666657	2.515464414
SnowCover	Poa laxa	0.833007047	1.84E-11	-7.955457839	1.78E-15	-2.505427402	19.55484362
Elevation	Primula glutinosa	0.974282537	0.158946327	-1.440647407	0.14968432	-0.398895005	2.908843994
AnnualTemperature	Primula glutinosa	0.988634293	0.781400379	-0.611844814	0.540640437	-0.165581701	2.659706289
SnowCover	Primula glutinosa	0.797075706	2.00E-08	-5.591365115	2.25E-08	-2.228212725	9.63876028
Elevation	Primula minima	0.948813249	0.002737997	1.12063082	0.26244504	0.287555324	1.959404856
AnnualTemperature	Primula minima	0.992632949	0.929585064	0.096081578	0.923455783	0.024278808	2.978086374
SnowCover	Primula minima	0.913116323	4.11E-05	-4.329222151	1.50E-05	-1.365455902	6.135069874
Elevation	Ranunculus glacialis	0.976131476	0.208825915	-0.586308881	0.557667964	-0.159602033	2.572826938
AnnualTemperature	Ranunculus glacialis	0.960457735	0.028236248	-2.363492439	0.018103596	-0.690310684	3.891328286
SnowCover	Ranunculus glacialis	0.755351086	2.22E-09	-6.423477528	1.33E-10	-2.899750972	17.90473098
Elevation	Ranunculus villarsii	0.977021643	0.001035902	-1.065188983	0.286790418	-0.170175791	2.993600135
AnnualTemperature	Ranunculus villarsii	0.977685967	0.001298279	2.65010166	0.008046755	0.437740593	3.571579737
SnowCover	Ranunculus villarsii	0.817047307	1.63E-15	-9.860208604	0	-2.591944646	15.59163061
Elevation	Salix herbacea	0.957981429	2.68E-05	-0.744396756	0.456636481	-0.130074515	1.951937714
AnnualTemperature	Salix herbacea	0.986645619	0.078788185	-1.934544538	0.053046212	-0.345336099	3.088769374
SnowCover	Salix herbacea	0.888262493	1.69E-10	-7.289526301	3.11E-13	-1.774689227	11.34786315
Elevation	Saxifraga bryoides	0.990578371	0.05996273	0.398098996	0.690557214	0.05603154	3.01689484
AnnualTemperature	Saxifraga bryoides	0.994424259	0.372239736	-1.272627115	0.203150392	-0.180321226	2.812395003
SnowCover	Saxifraga bryoides	0.874604465	1.27E-14	-9.433898493	0	-1.938431234	14.69994023
Elevation	Saxifraga exarata	0.960907088	0.215838703	-1.205747707	0.227914784	-0.435155481	2.504744886
AnnualTemperature	Saxifraga exarata	0.982422689	0.812701675	0.60944588	0.542228935	0.215659338	2.527942348

SnowCover	Saxifraga exarata	0.963706554	0.264120642	-1.840193371	0.065739853	-0.687640127	3.537374568
Elevation	Scorzoneroides helvetica	0.957125597	4.37E-10	1.932485025	0.053299669	0.223384861	1.952429638
AnnualTemperature	Scorzoneroides helvetica	0.977205468	1.92E-06	-4.729971561	2.25E-06	-0.578814981	3.326757853
SnowCover	Scorzoneroides helvetica	0.938917929	1.51E-12	-8.199117421	2.22E-16	-1.145109448	7.38627514
Elevation	Sedum alpestre	0.980475749	0.022460475	-1.517568322	0.129123258	-0.286003606	3.540130651
AnnualTemperature	Sedum alpestre	0.989275193	0.260375087	1.501689342	0.133177358	0.282909879	2.838126213
SnowCover	Sedum alpestre	0.934548707	9.78E-07	-5.055417403	4.29E-07	-1.126774172	6.799564188
Elevation	Senecio incanus subsp. carniolicus	0.972364836	0.141114539	-0.929728326	0.352511764	-0.258193491	2.429970934
AnnualTemperature	Senecio incanus subsp. carniolicus	0.954721675	0.015922883	-2.568122042	0.010225115	-0.771021203	3.426885016
SnowCover	Senecio incanus subsp. carniolicus	0.811500766	8.02E-08	-5.893945233	3.77E-09	-2.518252623	13.95968189
Elevation	Sibbaldia procumbens	0.982566203	0.400324043	-0.73068436	0.464971971	-0.193400209	2.774177622
AnnualTemperature	Sibbaldia procumbens	0.970236689	0.077903868	-1.706823702	0.087854826	-0.465923192	2.848525389
SnowCover	Sibbaldia procumbens	0.919633762	0.000167749	-3.995032869	6.47E-05	-1.283476926	5.682045614
Elevation	Silene acaulis subsp. exscapa	0.977328622	0.011704828	-1.777089606	0.075553498	-0.343274482	2.478110236
AnnualTemperature	Silene acaulis subsp. exscapa	0.992270753	0.570268314	0.25888267	0.79572577	0.048831525	2.54216377
SnowCover	Silene acaulis subsp. exscapa	0.933814706	1.30E-06	-4.75656562	1.97E-06	-1.062163261	7.013808644
Elevation	Solidago virgaurea subsp. minuta	0.968606786	0.007639773	0.017817757	0.985784239	0.003820583	2.759029141
AnnualTemperature	Solidago virgaurea subsp. minuta	0.979341751	0.068191077	1.084892855	0.277969113	0.235263387	3.561643965
SnowCover	Solidago virgaurea subsp. minuta	0.862553246	5.04E-09	-6.614961594	3.72E-11	-2.09340685	13.7246565
Elevation	Trifolium badium	0.942052146	0.044511611	0.899542399	0.368363823	0.314043396	2.16110296
AnnualTemperature	Trifolium badium	0.946110248	0.060809034	1.312689826	0.189287487	0.465806705	3.553197114
SnowCover	Trifolium badium	0.902143544	0.00254309	-2.538238768	0.011141194	-0.978157032	6.936425132
Elevation	Vaccinium gaultherioides	0.944741689	3.27E-05	3.971402068	7.15E-05	0.910760648	4.497720759
AnnualTemperature	Vaccinium gaultherioides	0.991837446	0.625192418	-0.582058205	0.560527476	-0.117274537	2.699732679
SnowCover	Vaccinium gaultherioides	0.895922309	2.98E-08	-5.878880913	4.13E-09	-1.565509314	7.175714955
Elevation	Vaccinium myrtillus	0.973106296	0.00670314	-1.421937159	0.155044495	-0.283814311	3.072209828
AnnualTemperature	Vaccinium myrtillus	0.97412294	0.008523802	2.753397656	0.005898021	0.575068328	4.018774248
SnowCover	Vaccinium myrtillus	0.951078931	6.53E-05	-3.892412743	9.93E-05	-0.863653271	3.898101631
Elevation	Vaccinium vitis-idaea	0.96961294	0.001684633	0.512757887	0.608120692	0.096865153	2.769385834
AnnualTemperature	Vaccinium vitis-idaea	0.988416731	0.229149162	1.503026066	0.132832323	0.288338811	2.791660653
SnowCover	Vaccinium vitis-idaea	0.920871051	1.65E-07	-5.638317917	1.72E-08	-1.344408045	6.962079877
Elevation	Veronica alpina	0.985478816	0.043168083	-0.757672689	0.448646953	-0.129153782	2.919467824
AnnualTemperature	Veronica alpina	0.98677924	0.066869931	-0.702733825	0.482221644	-0.119726953	2.580929758

SnowCover	Veronica alpina	0.888344617	7.71E-11	-7.246970195	4.26E-13	-1.692115365	12.42733938
Elevation	Veronica bellidioides	0.933560657	0.001592789	-2.437910869	0.014772416	-0.730776193	2.873441623
AnnualTemperature	Veronica bellidioides	0.985328864	0.627146969	-1.028813431	0.303567354	-0.288374905	3.274079531
SnowCover	Veronica bellidioides	0.929976182	0.001095199	-3.541392356	0.000398021	-1.159150702	5.405702849
Elevation	Viola biflora	0.952893304	0.00180675	1.046936058	0.29512907	0.249527409	3.986343837
AnnualTemperature	Viola biflora	0.965367445	0.012888008	2.72464235	0.006437117	0.695840853	4.369074419
SnowCover	Viola biflora	0.869053142	1.16E-07	-5.344273691	9.08E-08	-1.697957407	7.168095237


Pearson rho = −0.611
p = <0.001*
n = 871
Snow cover duration [d]
Annual mean temperature [°C]


Pearson rho = 0.523
p = <0.001*
n = 871
Snow cover duration [d]
Elevation [m.a.s.l]


Pearson rho = −0.732
p = <0.001*
n = 871
Annual mean temperature [°C]
Elevation [m.a.s.l]