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MASTER'S THESIS

Intraspecific Functional Trait Variation in *Carex firma* Host and *Dryas octopetala* L. along an Elevation Gradient

Submitted by

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PREFACE

First of all, I would like to thank my supervisor, Manuela Winkler, and co-supervisor, Klaus Schmieder, for their support and guidance during the process of this thesis. Likewise, I would like to thank Patrick Saccone for his help and suggestions, especially regarding the statistical analysis of the data. I also want to thank him, Andrea Lamprecht, and my friends Marc and Daniel for accompanying me on Hochschwab and helping me with the conduction of the field work. I would like to thank Klaus Steinbauer for the provided research outcomes of his thesis such as the presence/absence data, as well as the functional trait data that I used for my analysis. Also, I would like to thank the Institute of Botany for financing my fieldwork and Dagmar Augustin for helping me in organisational matters. Finally, I would like to thank my family for their constant support.

This thesis will be submitted as a paper to the journal Diversity with Patrick Saccone, Klaus Steinbauer, Andrea Lamprecht and Manuela Winkler as co-authors.

ABSTRACT

Assessing intraspecific trait variation along an elevation gradient can give insights on possible future distributions and responses of plant species to the effects of climate change, such as increasing mean annual temperatures and the thus enabled upward movement of lower-elevation species. This study focussed on the intraspecific variation of *Carex firma* Host (*C. firma*) and *Dryas octopetala* L. (*D. octopetala*) in the Hochschwab mountain range (Styria, Austria). Sampling of the two species was carried out on 20 transects along an elevation gradient of 500 m to gather data of specific leaf area (SLA), leaf dry matter content (LDMC) and vegetative plant height (H). Slope, aspect and vegetation cover of the transects were considered as additional environmental factors to altitude. The data analysis revealed a large intraspecific variation of *C. firma* and *D. octopetala* leading to no consistent patterns of the response variables along the elevation gradient or any of the other environmental factors. However, similar patterns between the two species in similar aspects along elevation were observed. A comparison with interspecific trait values from the surveyed transects illustrated the positioning of both study species at the resource conservative ends of the overall range. Due to their constant range in traits at all altitudes, *C. firma* and *D. octopetala* are likely to keep their intraspecific variability on Hochschwab, even if lower ranges are lost to upward migrating species. Also, this large variability points to a diverse niche adaptation, which could help the persistence of both species in changing environments.

Key words: intraspecific variability, elevation gradient, alpine plant traits, Hochschwab, climate change

ABSTRACT IN GERMAN

Titel der Arbeit auf Deutsch:

Intraspezifische Merkmalsvariation von *Carex firma* und *Dryas octopetala* entlang eines Höhengradienten

Zusammenfassung:

Die intraspezifische Merkmalsvariation entlang eines Höhengradienten kann Aufschluss über zukünftige Veränderungen und Verbreitung von Pflanzen geben, die durch Klimawandeleinflüsse, wie etwa steigende Durchschnittstemperaturen und dadurch ermöglichtes Höherwandern von Pflanzen aus tieferliegenden Gebieten beeinflusst werden. Diese Studie befasst sich mit der intraspezifischen Merkmalsvariation von *Carex firma* Host (*C. firma*, Polstersegge) und *Dryas octopetala* L. (*D. octopetala*, Silberwurz) in der Hochschwabgruppe (Steiermark, Österreich). Mit der Probenentnahme der beiden Arten auf 20 Transektflächen entlang eines Höhengradienten von 500 m wurden Daten zur spezifischen Blattgröße (specific leaf area, SLA), Blatt-Trockensubstanzgehalt (leaf dry matter content, LDMC) und vegetativer Pflanzenhöhe (H) erhoben. Zusätzlich zu der Höhenlage wurden als Einflussfaktoren Hangneigung, Exposition und Vegetationsbedeckung zur Analyse der Daten berücksichtigt. Es wurde eine große intraspezifische Variation der Blattmerkmale von *C. firma* und *D. octopetala* ohne klare Trends entlang des Höhengradienten oder eines der anderen Faktoren festgestellt. Allerdings sind ähnliche Tendenzen zwischen beiden Arten in ähnlichen Expositionen entlang des Höhengradienten vorhanden. Ein Vergleich mit der Merkmalsausprägung aller in den untersuchten Plots vorkommenden Pflanzenarten verdeutlichte, dass beide Untersuchungsarten im interspezifischen Wertevergleich relativ niedrige SLA- und H-, sowie hohe LDMC-Werte aufweisen. Das entspricht einer Anpassung an geringe Nährstoffversorgung, Trockenheit und niedrige Temperaturen. Aufgrund ihrer in allen Höhenlagen gleichbleibenden Merkmalsvariationsbreite ist es wahrscheinlich, dass *C. firma* und *D. octopetala* ihre Merkmalsvielfalt auf dem Hochschwab beibehalten können, auch wenn Pflanzen aus tieferen Regionen aufsteigen. Die intraspezifische Ausprägung der Merkmale deutet außerdem auf eine Anpassung an viele Mikroklimata hin, welche sich positiv auf das Fortbestehen der beiden Arten in einer sich ändernden Umwelt auswirken kann.

Schlagwörter: Intraspezifische Merkmalsvariation, Höhengradient, Merkmale alpiner Pflanzen, Hochschwab, Klimawandel

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1. INTRODUCTION

Low temperatures are a characteristic of high mountain regions, leading to long periods of snow cover, short growing seasons and resource scarcity (Körner, 2003). These are characteristics that alpine plant species are adapted to (Körner & Larcher, 1988). Climate change effects in the European Alps cause, amongst other things, a faster rise of minimum temperatures than maximum temperatures (Beniston *et al.*, 1994) and a more accentuated rise of temperatures in the Alps compared to northern hemisphere means (Beniston *et al.*, 1997; Auer *et al.*, 2007). Hence, they result in shorter snow covers (Klein *et al.*, 2016), but also in more extreme weather events and natural hazard incidents (Gobiet *et al.*, 2014). These changing abiotic conditions generate pressure on species composition and alpine ecosystem functioning (Jump & Penuelas, 2005; Gottfried *et al.*, 2012; Steinbauer *et al.*, 2018; Steinbauer *et al.*, 2020). As this situation proceeds, it becomes more and more crucial to understand how plant communities and concrete species will react to these changes in the future (Verrall & Pickering, 2020). On this account, vegetation monitoring has been and is being conducted in the European Alps (Gottfried *et al.*, 2012; Steinbauer *et al.*, 2018; Steinbauer *et al.*, 2020) and in alpine regions around the globe (Pauli *et al.*, 2015). Changes in species composition and abundance in alpine environments were already detected (Gottfried *et al.*, 2012; Lamprecht *et al.*, 2018; Steinbauer *et al.*, 2020). While species richness in monitoring plots increases due to upslope shifts of species from lower regions (Lamprecht *et al.*, 2018; Steinbauer *et al.*, 2018), some cold adapted species are declining or even disappearing locally (Steinbauer *et al.*, 2020). These species either migrate towards the mountain tops or go extinct if regional conditions and dispersal ability do not allow for dispersion to new suitable sites. Due to longevity of most high-mountain species the process of extinction may be delayed, leading to an extinction debt (Dullinger *et al.*, 2012). Other studies suggest that micro-topography and its provision of refuges within short distances could extenuate the displacement of cold adapted species for regional warmings (Scherrer & Körner, 2011; Opedal *et al.*, 2015; Ohler *et al.*, 2020).

To understand the reaction of plant communities better, many studies focus on plant trait variation along environmental gradients (Albert, Thuiller, Yoccoz, Soudant *et al.*, 2010; Rosbakh *et al.*, 2015; Stanisci *et al.*, 2020). The functional approach explores the link between plant species composition, plant functional traits and ecosystem functioning (Lavorel & Garnier, 2002). Key aspects of plant functioning are captured with plant height (H), specific leaf area (SLA) and leaf dry matter content (LDMC) (Lavorel & Garnier, 2002; Pérez-Harguindeguy *et al.*, 2013). SLA and LDMC are indices for leaf-level carbon gain and resource conservation strategies, indicating a trade-off between growth rate of plants and longevity (Schläpfer & Ryser, 1996; Lavorel & Garnier, 2002; Wright *et al.*, 2004). SLA is a measure for the biomass allocation and resource conservation, indicating higher leaf longevity with lower SLA values, as well as reflecting photosynthetic capacity (Shipley *et al.*, 2005; Pérez-Harguindeguy *et al.*, 2013). LDMC shows a positive correlation with leaf life span and resistance to physical perils (Pérez-Harguindeguy *et al.*, 2013). H is related to competitive ability for light and to dispersal capacity of diaspores (Pérez-Harguindeguy *et al.*, 2013; Díaz *et al.*, 2016).

These relations explain the facilitation of fast growing species with reduced leaf longevity (high SLA, low LDMC) in nutrient rich and productive environments (Grime *et al.*, 1997). In contrast, slow growing species with efficient resource conservation and therefore longer leaf life-span (low SLA, high LDMC) have an advantage in nutrient poor environments (Woodward, 1983; Atkin *et al.*, 1996). Smaller plants are rather found at high elevations with low temperatures and low light competition than in competitive environments (Körner *et al.*, 1989; Körner, 2003; Halbritter *et al.*, 2018). Community structure and species abundance at a certain location is argued to be determined by several levels of environmental filters (Lavorel & Garnier, 2002; de Bello *et al.*, 2013). After the general species composition is determined by temperature, the abundance of each species and their intraspecific trait variation is determined by small scale, local influences like soil characteristics (Lavorel & Garnier, 2002; de Bello *et al.*, 2013).

A large part of the trait-based studies considers the average trait values, assuming a change in ecosystem functioning primarily associated to changes in species abundances and composition (Soudzilovskaia *et al.*, 2013; Bjorkman *et al.*, 2018; Delhaye *et al.*, 2020). However, other studies point out the importance of intraspecific trait variability (Albert, Thuiller, Yoccoz, Soudant *et al.*, 2010; Kichenin *et al.*, 2013; Wellstein *et al.*, 2013) on community processes to project the consequences of future conditions. In general, seen within habitats, a large intraspecific variability is assumed to reflect resilience of plant communities to climate change effects (Bellard *et al.*, 2012; Wellstein *et al.*, 2013; Des Roches *et al.*, 2018).

Due to the constant, negative relationship between free air temperature and elevation (on average 0.6 K decrease per 100 m altitude increase; Dillon *et al.*, 2006), many studies focussing on trait variation test variability along an elevation gradient (Rosbakh *et al.*, 2015; Midolo *et al.*, 2019). When combined with a space-for-time substitution (Fukami & Wardle, 2005) results might indicate upcoming changes caused by anthropogenic climate change: With increasing annual mean temperatures, characteristics of individuals and communities at lower altitudes might replace ones at higher altitudes. For intraspecific trait responses, a strong directional trend along an elevation gradient would suggest that the persistence of species in new environmental conditions is dependent on their migration or in contrast, their adaptive abilities (Thompson & Fronhofer, 2019). A weak response to elevation would indicate lower impacts of environmental changes, since changing conditions would not affect the trait response.

A study in the Berchtesgaden Alps found a strong positive correlation between SLA and temperature on a community-weighted mean (CWM) basis, where species traits are weighted according to species cover (abundance) (Rosbakh *et al.*, 2015). However, intraspecific SLA variation significantly correlated with temperature only in 14% of the tested species in the same study and the authors concluded that intraspecific variation of SLA was not driven by temperature (Rosbakh *et al.*, 2015). In contrast, a recent global review of intraspecific leaf trait patterns along elevation gradients concluded that intraspecific SLA values are significantly negatively correlated to elevation (Midolo *et al.*, 2019). In their intraspecific trait analysis of two distinct alpine slopes of the same valley, Wellstein *et al.* (2013) found significant differences among the sites. Within species, SLA and H were larger on the north facing slope than on the slope exposed to the south, for LDMC the opposite was detected. Also, LDMC values were less variable in their response than SLA (Wellstein *et al.*, 2013).

Other studies looking at trait variation along alpine elevation gradients found large intraspecific variability, with remarkable differences in the trait variation between species and between traits (Albert, Thuiller, Yoccoz, Soudant *et al.*, 2010; Kichenin *et al.*, 2013). Kichenin *et al.* (2013) found evidence in southern New Zealand that the influence of intraspecific relative contribution to trait mean values of alpine communities varied strongly depending on the trait. In general, variation between species had more influence on the trait mean response in plots over elevation than the intraspecific variation. Nevertheless, the variation within species of, in particular, SLA values had a similar effect on the trait mean on plot level as did the interspecific variation (Kichenin *et al.*, 2013). In a general meta-analysis, the same amount of trait variation of leaf mass per area ratio (1/SLA) within as among species in communities was found (Read *et al.*, 2014). Likewise, a study in the French Alps found that intraspecific variation made up 30 % of the interspecific variation in several functional traits (Albert, Thuiller, Yoccoz, Douzet *et al.*, 2010). This large intraspecific variability indirectly prompts the question if the use of trait means is suitable. The importance to consider intraspecific variation depends not only on the studied species and functional traits, but also on the aim of the study, e.g. for studies related to community structure the consideration of intraspecific variation will be valuable (Albert, Thuiller, Yoccoz, Douzet *et al.*, 2010). To gain more understanding of the role of within species variation, more quantification of functional trait variation is needed (Albert, Thuiller, Yoccoz, Douzet *et al.*, 2010). While in parts of the European Alps, studies on one or several functional traits were done and compared to the interspecific variation along environmental gradients (Albert, Thuiller, Yoccoz, Soudant *et al.*, 2010; Wellstein *et al.*, 2013; Rosbakh *et al.*, 2015), this is not the case for the easternmost part of the Alps, and every alpine species.

In this study, the aim was to explore the debated scenarios and further the knowledge of intraspecific variability by firstly, investigating the intraspecific variation of functional traits on two contrasted alpine species along an elevation gradient of 500 m on Hochschwab in the Northeastern Calcareous Alps (Austria), secondly, by determining the importance of elevation (as a surrogate for temperature) for the intraspecific variation of the two analysed species, and finally, by comparing their range of trait values to the interspecific variability in the surveyed transects. A directional trend of the functional traits along the elevation gradient was expected, with SLA and H decreasing and LDMC increasing with elevation increase.

2. MATERIALS AND METHODS

2.1 STUDY SITE

This study was conducted in the Hochschwab mountain range (Styria, Austria), located in the Northeastern Calcareous Alps. Hochschwab is a target region of the Global Observation Research Initiative in Alpine Environments (GLORIA, www.gloria.ac.at), which assesses climate change-related changes in plant species composition and abundance in a worldwide network. Reaching 2277 m a.s.l. with its highest peak (Figure 1), the mountain range belongs together with Schneeberg to the easternmost part of the Alps (Zückert, 1996). Limestone and dolomite are the predominant geological formation of Hochschwab, leading to karst formations and rendzina as the dominant soil type (Zückert, 1996). Although also siliceous soils are present on terraces and plateaus (Zückert, 1996), this study focussed on the dominant calcareous habitats. The region is characterized by mountain climate typical for alpine fringe areas, with a strong temperature gradient, more than 2000 mm annual precipitation in the summit areas and strong winds due to the exposed position of the mountain range (Zückert, 1996; Land Steiermark, 2021).

Figure 1: Hochschwab summit, 2277 m a.s.l., seen from west-southwest at around 2130 m a.s.l. underneath Ghacktkogel. (© Malena Steffens)

2.2 STUDY SPECIES

Two perennial, alpine plants of different growth forms that are abundant and widely distributed on Hochschwab (Elkington, 1971; Steinbauer, 2011), were chosen: *Carex firma* Host (Cyperaceae) and *Dryas octopetala* L. (Rosaceae). Due to their common occurrence in the

Alps (both) and a circumpolar distribution in the arctic and sub-arctic regions in the northern hemisphere (*D. octopetala*) (Elkington, 1971; Wagner & Reichegger, 1997), conclusions from this study might also be applicable to other regions. The graminoid *C. firma* (Figure 2 a) grows in tussocks on calcareous bedrock, adapted to wind exposure and scree (Wagner & Reichegger, 1997). While upper ranges of *C. firma* can reach 2900 m, the lower elevation range limit is at ca. 1700 m, and it has been recorded at least down to 1737 m a.s.l. on Hochschwab (Wagner & Reichegger, 1997; Steinbauer, 2011). The species reproduces asexually and sexually (Grabherr *et al.*, 1993; Wagner & Reichegger, 1997). *Carex firma* is the eponymous index species of the Caricetum firmae Rübel 1911, a plant association also present on Hochschwab (Dirnböck *et al.*, 1999; Steinbauer, 2011) in which *D. octopetala* is abundant as well (Grabherr *et al.*, 1993). Elkington (1971) described the dwarf shrub *D. octopetala* (Figure 2 b) with a distribution in Europe in the Alps from montane elevations up to 3115 m a.s.l., but also in other mountain regions, extending south into the Apennines and the Balkan. Its distribution is limited to sites with minimum rainfall exceeding 1000 mm/year and free drainage on calcareous rock (Elkington, 1971). Usually, *D. octopetala* reproduces through seeds, though vegetative reproduction is also possible (Elkington, 1971). *D. octopetala* is a sprawling prostrate dwarf-shrub, a pioneer of open sites (Elkington, 1971), contributing to soil formation with its dead leaves (Ellenberg, 1996) and acting as a nurse plant for seedlings of other plant species, especially under severe environmental conditions (Klanderud & Totland, 2004).

(a)

(b)

Figure 2: *Carex firma* (a) and *Dryas octopetala* (b) (© Malena Steffens)

2.3 SAMPLING DESIGN AND ENVIRONMENTAL VARIABLES

The sampling was carried out in August 2020 on transects along an elevation gradient from 1753 to 2262 m a.s.l.. In 2008, 24 transects were established by K. Steinbauer (Steinbauer, 2011). *C. firma* and *D. octopetala* were present in 22 and 23 transects respectively, of which the 20 most easily accessible with a high frequency of the study species were selected for this study. The 50x2m transects (original length 100 m) were arranged parallel to the contour lines. The distance between samples was at least 2 m to ensure collection from different individuals. Trait measurements of vegetative plant height (H), specific leaf area (SLA) and leaf dry matter content (LDMC) followed the procedures suggested by Pérez-Harguindeguy *et al.* (2013). Briefly, a branch or tussock with at least four fully grown, hardened leaves with no signs of disease of ten individuals per species and transect were collected for SLA and LDMC measurements. The samples were wrapped in a moist paper towel, placed in sealed plastic bags, transported in a cooling bag and then stored in a fridge as they rehydrated until being processed within 48 hours. Plant height was measured in 25 samples per species and transect. H was measured in mm perpendicular to the ground until the highest vegetative point of the undisturbed individual. In the laboratory, the four leaves of each sample were processed together. First, they were carefully dabbed dry with tissue paper, cut off the branch so as to include the petiole in the case of *D. octopetala* and weighed (fresh weight) on a 0.0001 g precision scale. Then the four leaves were scanned together at 600 dpi resolution. The resulting scans were corrected in Adobe Photoshop CS6 to eliminate slight shadows around the edges of the leaves and then processed in FIJI ImageJ (Schindelin *et al.*, 2012) to extract the leaf area (LA). Finally, the samples were oven-dried at 70°C for at least 72h, cooled down for two hours in a desiccator and weighed (dry weight). SLA and LDMC were calculated at the sample level per four leaves and expressed in mm^2 LA per mg of dry weight and mg of dry weight per g of fresh material, respectively.

Furthermore, elevation, aspect and slope were measured at a comparable point, i.e. at ten meters into the length of each transect, with a barometric altimeter and a compass. In order to be integrated in the statistical models as an explanatory variable, the aspect recorded in degree was transformed into radiant and then into eastness and northness by using

$$\text{eastness} = \sin(\alpha) \tag{1}$$

$$\text{northness} = \cos(\alpha), \tag{2}$$

thus, creating two linear variables from -1, representing west for eastness and south for northness, to 1, representing east for eastness and north for northness. Vegetation cover was classified in three categories by Steinbauer (2011): open (vegetation covers less than 25 %), semi-open (25-75 %) and closed (>75 %) for each ten-meter plot within the transects. Vegetation cover class was transformed to a numerical variable representing the mean for each transect by using the mid-point value of each class (i.e., 0.125, 0.5 and 0.875).

2.4 DATA ANALYSIS

All statistical analyses were carried out in R (R Core Team, 2019). First, the functional responses (SLA, LDMC and H) of the target species (*C. firma* and *D. octopetala*) to the environmental variables, i.e. elevation, aspect (eastness and northness), vegetation cover and slope, were examined. The vegan library (Oksanen, J., Blanchet, F.G. *et al.*, 2019) was used to visualize the dissimilarities and distribution of the individual functional responses using *metaMDS* function and to display the fixed effects onto a non-metric multidimensional scaling (NMDS) ordination with the *envfit* function. The effects of the environmental variables were evaluated by Permutational Multivariate Analyses of Variances Models (PERMANOVA) (Anderson, 2005) and their significance was assessed with 999 permutations using the *adonis* function. To analyse the effects of the environmental variables on SLA, LDMC and H separately, generalized linear mixed-effects models (GLMMs) were built using *glmmTMB* function of the glmmTMB package (Brooks *et al.*, 2017). Models were built with Gaussian link function and all possible combinations of environmental variables as fixed effects. Except for eastness:northness, which were always entered together in a model, no interactions were considered. Transect was included as a random intercept term to account for the spatial structure in the dataset. The best models were chosen by lowest corrected Akaike's information criterion (AIC_c). AIC_c and R^2 values were obtained with *AICC* and *r.squaredGLMM* of the MuMIn package (Barton, 2020). Fixed effects were tested for collinearity with variance inflation factors (VIF) by using *corvif* (Zuur *et al.*, 2009) and did only show moderate correlations (Suppl. Figure 10 & 11) with VIFs<2. The residual plots were inspected visually and did not reveal any strong deviations from normality or homoscedasticity (Suppl. Figure 9).

To get deeper insight on the interplay between elevation and aspect on plant traits, further analyses on pseudo-elevation gradients were conducted by pooling the transects of similar eastness (considered west for eastness between -1 and 0 and east for eastness between 0 and 1). To facilitate the pseudo-gradient comparison, the transects were pooled in elevation bands (<1850, 1850-1999, 2000-1999, 2100-2200, and > 2200 m a.s.l.). Then, the effect of species identity, eastness of the transects and elevation bands on plant traits were analysed using generalized linear mixed-effects models with transect identity as random intercept and an identity link function considering the Gaussian error structure. The significance of explanatory variables was assessed using the *anova* function in the car package (Fox & Weisberg, 2019). Finally, the similarities among the specific patterns along the pseudo-gradients were determined by pairwise comparison of GLMMs (with species' identity and eastness of the transects gathered in one categorical variable) with *emmeans* function in the emmeans package (Searle *et al.*, 1980; Lenth *et al.*, 2020) and *cld* function in the multcomp package (Hothorn *et al.*, 2008).

Additionally, the intraspecific trait variation of *C. firma* and *D. octopetala* was compared with the trait variation among species co-occurring in the surveyed transects. This comparison was done to investigate how much of the interspecific variation is covered by the intraspecific variation along the elevation gradient, and how much additional information the use of intraspecific variability conveys when compared to using only one mean trait value per species in trait-based studies. Species presence/absence data for the transects was taken from Steinbauer (2011) and combined with trait means taken from the TRY database (Kattge *et al.*, 2020) and Steinbauer *et al.* (unpublished) (Suppl. Table 4 & 5). On that account, data from measurements including and excluding petiole and rachis, and data that did not define if petiole and rachis were included was considered for SLA means in order to have as little NA values as possible. Only vegetative plant height (not generative plant height) was considered. Missing trait values were not estimated and therefore excluded from the analysis to avoid imputation errors (Johnson *et al.*, 2021). Frequency data of the occurring species was available in a coarse raster of presence/absence data for every 10 m plot within the original transects. Since true abundance data (species cover in every plot) were not available for the sites, the interspecific data was used without weighting, with species appearance reduced to one time per elevation category in case of multiple presences in transects. The same elevation categories as before were introduced for the interspecific and for the intraspecific data. Using the *density* function from base R, the density distribution of SLA, LDMC and H of *C. firma*, *D. octopetala* and species co-occurring in the transects was calculated and plotted for each elevation category. Plant height values exceeding 1 m were cut at 1 m. For the interspecific data, mean values were calculated for each trait in each elevation category and added as vertical lines into the graphs.

3. RESULTS

All traits (SLA, LDMC and H) in both species showed a similarly large intraspecific and intra-transect variation. The intraspecific variation of SLA and H in both species had almost or more than a difference of twice as much between minimum and maximum values. No clear pattern along elevation or other environmental factors could be detected (Figure 3, Suppl. Figure 5-8). In brief, SLA values ranged from 7.68 to 14.3 $mm^2\ mg^{-1}$ in *C. firma* and 6.06 to 13.76 $mm^2\ mg^{-1}$ in *D. octopetala*. LDMC values varied from 325.19 to 470.05 $mg\ g^{-1}$ in *C. firma* and 299.33 to 440.78 $mg\ g^{-1}$ in *D. octopetala*. Plant height ranged from 1.2 to 4.2 cm in *C. firma* and 1.2 to 4.0 cm in *D. octopetala*.

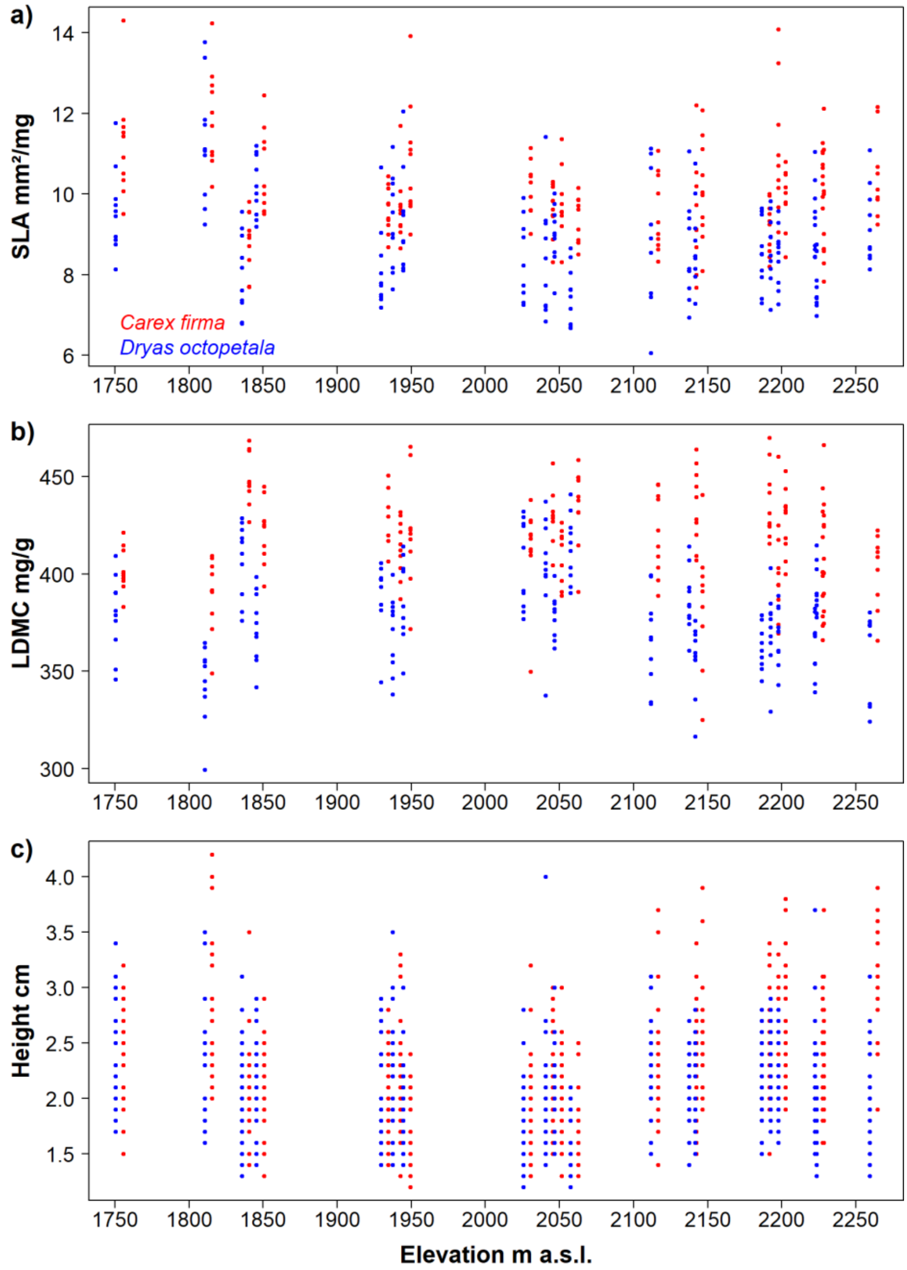

Figure 3: Functional trait variation in Carex firma (red) and Dryas octopetala (blue) along the elevation gradient of Hochschwab (Northeastern Calcareous Alps, Austria). a) SLA; b) LDMC; c) plant height. Values were jittered by species to avoid overlapping.

The multivariate trait space (NMDS biplots, Figure 4) captured large part of the functional variability within and among species (stress < 0.5) but did not show any clusters nor clear patterns along environmental gradients. The environmental factors showed significant, but weak correlations. For both species together, all environmental variables except cover and slope were significant, with the two aspect parameters having the highest explanatory value. All significant environmental variables together explained only 14 % of the variation in the data. In *C. firma*, arrows were similar with the main difference that eastness was not significant, whereas in *D. octopetala* only the two aspect parameters were significant. 17.9 % and 11,7 % of the variation in the data were explained by the significant environmental variables for *C. firma* and *D. octopetala* respectively.

Slope and the interaction of eastness and northness had a significant effect on multivariate trait space (Permanova, Table 1) in *C. firma*, but both showed only a weak correlation to the variation in the data (R^2=0.028 and 0.09). In *D. octopetala,* elevation, eastness, northness and their interaction term were significant. Though higher than in *C. firma*, the explanatory value was weak as well (together R^2=0.162). A large part of the variation was attributed to the random (spatial) effects, and therefore most of the variation was not captured by the model (residual R^2 86.2 % and 74 % for *C. firma* and *D. octopetala*, respectively).

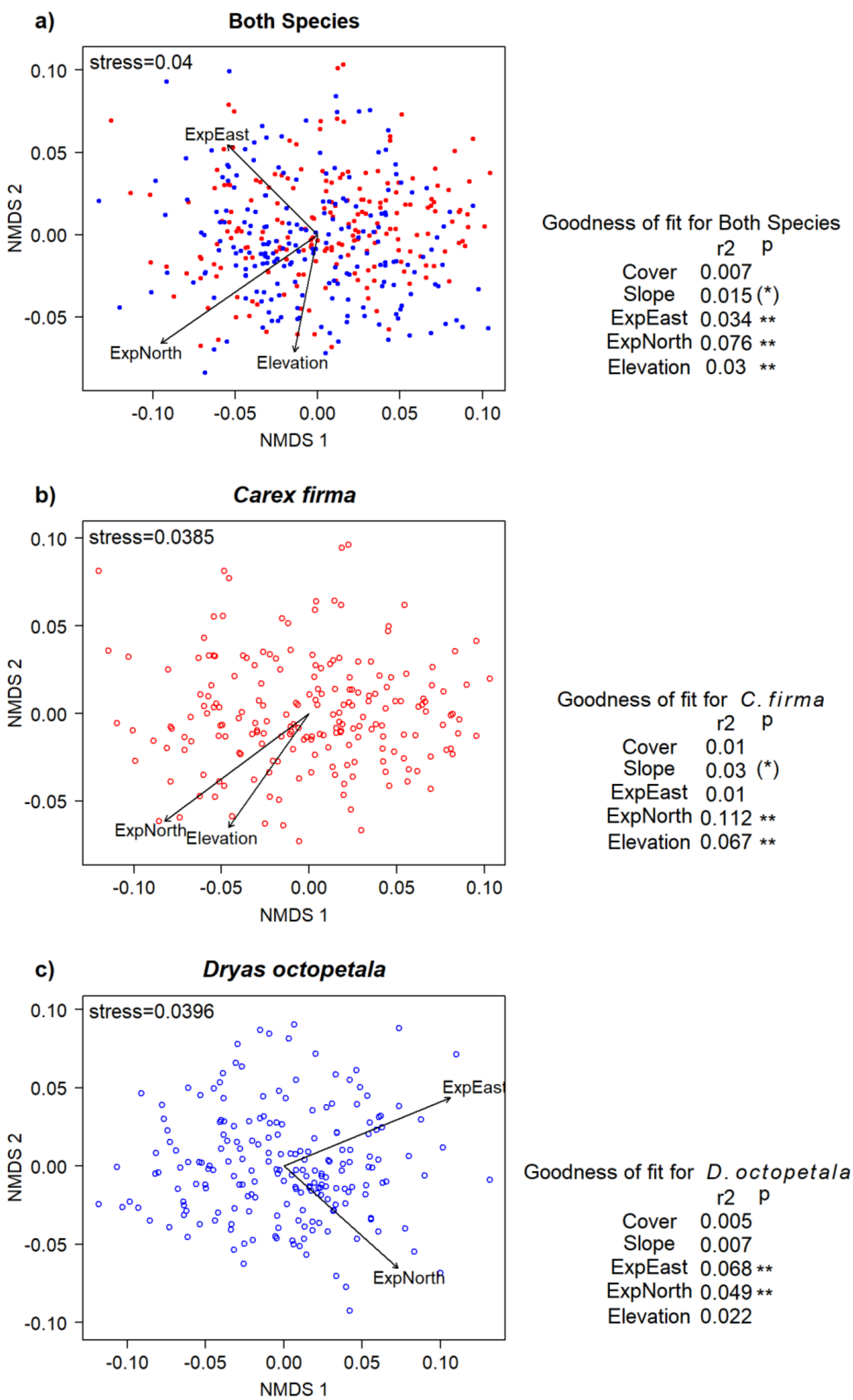

Figure 4: Non-metric multidimensional scaling (NMDS) biplots of SLA, LDMC and plant height of *Carex firma* and *Dryas octopetala* on Hochschwab (Northeastern Calcareous Alps, Austria). Overlaid are arrows of the environmental factors elevation, aspect (eastness and northness), vegetation cover and slope. The multivariate space was reduced to two dimensions: a) both species; b) *C. firma*; c) *D. octopetala*. Only significant variables ($p < 0.05$) are displayed. Cover: vegetation cover; ExpEast: aspect transformed into eastness; ExpNorth: aspect transformed into northness. Significance codes: (*) < 0.1, * < 0.05, ** < 0.01, *** < 0.001.

Table 1: Summary of Permanova for trait responses (SLA, LDMC, plant height) in a) *Carex firma* and b) *Dryas octopetala* along the elevation gradient of Hochschwab (Northeastern Calcareous Alps, Austria), predicted by environmental variables. Cover: vegetation cover; ExpEast: aspect transformed into eastness; ExpNorth: aspect transformed into northness

Terms	Df	SumsOfSqs	MeanSqs	F.Model	R^2	Pr(>F)
a) *C. firma*						
Elevation	1	468	467.5	0.782	0.003	0.384
Slope	1	3720	3720	6.223	0.028	0.006
ExpEast	1	1210	1209.7	2.024	0.009	0.157
ExpNorth	1	531	530.9	0.888	0.004	0.367
Cover	1	473	472.7	0.791	0.004	0.389
ExpEast:ExpNorth	1	12015	12015.4	20.100	0.090	0.001
Residuals	193	115373	597.8		0.862	
Total	199	133789			1	
b) *D. octopetala*						
Elevation	1	2136	2135.9	4.136	0.016	0.034
Slope	1	1799	1798.7	3.483	0.013	0.072
ExpEast	1	6429	6429.2	12.450	0.048	0.002
ExpNorth	1	4131	4131.3	8.000	0.031	0.005
Cover	1	786	786.2	1.522	0.006	0.229
ExpEast:ExpNorth	1	19666	19665.6	38.082	0.146	0.001
Residuals	193	99666	516.4		0.740	
Total	199	134613			1	

The marginal R^2 values for the best GLMMs (see selection procedure by lowest AIC_cs in Suppl. Table 1) ranged between 3 and 21 % (Table 2). The fixed effects of the best GLMM for SLA in *D. octopetala* explained 19.1 % and included the significant terms of elevation and the interaction of eastness and northness. For LDMC, the GLMM for *D. octopetala* had a marginal R^2 value of 21.6 % with significant effects of the interaction between eastness and northness. The best GLMM for H of *C. firma* explained 12.8 % of the data without random effects. Here, elevation and the interaction of eastness and northness were significant.

Summarizing the results of the three models above, the intraspecific trait variation could not be sufficiently explained by any of the models. Correspondingly, the permanova and NMDS that modelled all three traits as a response together could explain only little of the data. While elevation and the interaction term of eastness and northness were significant for most of the best GLMMs, the explanatory values were small. That conditional R^2 values were considerably higher than marginal R^2 values further emphasized the influence of the spatial structure on the variation.

Table 2: Summary of best GLMMs: Effect of environmental variables on trait variability in *Carex firma* and *Dryas octopetala* on Hochschwab (Northeastern Calcareous Alps, Austria) calculated with glmms with Gaussian link function. Shown are marginal (R^2m) and conditional (R^2c) R-square values and fixed effects of the linear mixed-effects model with the lowest AIC_cs, (a) SLA, (b) LDMC, and (c) plant height. ExpEast: exposition transformed into eastness; ExpNorth: exposition transformed into northness; Std. Error: standard error.

Species	R^2m	R^2c	Fixed effects	Estimate	Std. Error	z	Pr(>|z|)
a) SLA							
C. firma	0.033	0.299	(Intercept)	13.056	2.145	6.085	<0.001
			Elevation	-0.001	0.001	-1.409	0.159
D. octopetala	0.191	0.354	(Intercept)	13.028	1.952	6.673	<0.001
			Elevation	-0.002	0.001	-2.162	0.031
			ExpEast	0.253	0.193	1.309	0.190
			ExpNorth	-0.195	0.220	-0.883	0.377
			ExpEast:ExpNorth	1.086	0.409	2.655	0.008
b) LDMC							
C. firma	0.031	0.344	(Intercept)	403.801	10.751	37.560	<0.001
			Slope	0.595	0.463	1.290	0.198
D. octopetala	0.216	0.464	(Intercept)	381.012	3.222	118.260	<0.001
			ExpEast	-3.687	4.211	-0.870	0.382
			ExpNorth	-4.859	4.943	-0.980	0.326
			ExpEast:ExpNorth	-29.299	9.172	-3.190	0.001
c) Plant Height							
C. firma	0.128	0.281	(Intercept)	5.565	7.509	0.741	0.459
			Elevation	0.008	0.004	2.270	0.023
			ExpEast	0.251	0.745	0.337	0.736
			ExpNorth	1.180	0.849	1.391	0.164
			ExpEast:ExpNorth	3.750	1.579	2.375	0.018
D. octopetala	0.073	0.180	(Intercept)	20.416	0.405	50.460	<0.001
			ExpEast	0.989	0.529	1.870	0.061
			ExpNorth	0.951	0.621	1.530	0.126
			ExpEast:ExpNorth	1.814	1.152	1.580	0.115

The three traits' responses to elevation with transects pooled in similar expositions showed no linear trends (Figure 5, Table 3). However, similar response patterns along the elevation gradient between the species in the same exposition were visible, most dominantly in the response of plant height. The interaction between species and exposition was also not significant in all traits, emphasising that the response patterns were similar between the species in different expositions. The response of LDMC and H along elevation significantly differed between species, while this was not the case for SLA.

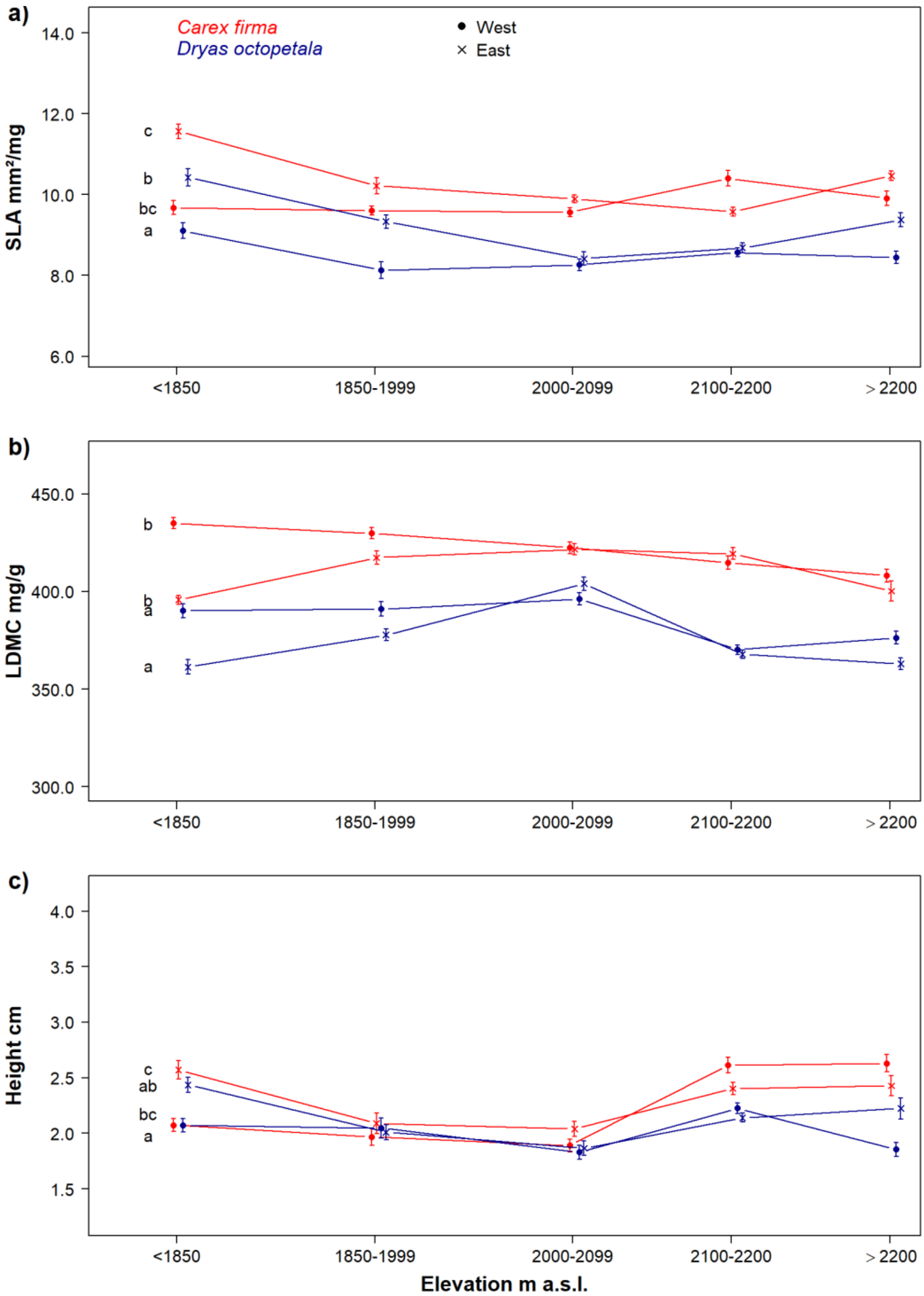

Figure 5: Pseudo-elevation gradients: Plant trait (mean ± SE) patterns a) SLA, b) LDMC, c) plant height) along easterly and westerly exposed pseudo-elevation gradients of *Carex firma* (red) and *Dryas octopetala* (blue) on Hochschwab (Northeastern Calcareous Alps, Austria). The transects were pooled by altitude bands and exposition (west for eastness between -1 and 0 and east for eastness between 0 and 1), X-axis values were jittered to avoid overlapping symbols. Different lower-case letters indicate significant difference of the patterns in pairwise comparison. The pairwise comparison was conducted with *emmeans* in the emmeans package (Searle *et al.*, 1980; Lenth *et al.*, 2020) and *cld* function in the multcomp package (Hothorn *et al.*, 2008).

For SLA, the pairwise comparison (lower-case letters Figure 5) indicated significant interspecific differences with an overlap between easterly exposed *D. octopetala* and westerly exposed *C. firma*, and in *D. octopetala* also intraspecific aspect differences. For LDMC a significant difference was found between species over elevation, whereas for H a significant difference could only be detected between *D. octopetala* in western and *C. firma* in eastern transects. All SLA response values, with the exception of the westerly exposed *C. firma* group, decreased with elevation and re-increased with elevation above 2099 m a.s.l.. The westerly exposed SLA response of *C. firma* showed a single increase for the elevation category of 2100-2200 m a.s.l. and otherwise no strong effect of elevation. Even though the pairwise comparison indicated a similarity between westerly exposed sites in *D. octopetala* and easterly exposed sites in *C. firma*, especially the easterly exposed transects of both species showed parallel patterns. Elevation had a positive effect on LDMC in easterly exposed sites up to the category of 2000-2099 m a.s.l. in both plant species, after which *D. octopetala* easterly response clearly decreased and *C. firma*'s response only marginally decreased. In the case of plant height, the aspect clearly prevailed on species identity at low altitude. After a decrease in H over elevation, the response increased again above 2000-2099 m a.s.l. for both plants in both aspects. In the last elevation category only the westerly exposed group of *C. firma* decreased. Table 3 shows the summary of the effects of species identity, eastness and elevation on plant traits.

Table 3: Effect of species identity, eastness and elevation on plant traits (SLA, LDMC, plant height) along the pseudo-elevation gradients of *Carex firma* and *Dryas octopetala* on Hochschwab (Northeastern Calcareous Alps, Austria), tested by generalized linear mixed-effects models with transect identity as random factor.

		SLA		**LDMC**		**Height**	
Source of deviation	df	Chisq	p	Chisq	p	Chisq	p
Species (sp)	1	130.81	<0.001	372.32	<0.001	57.86	<0.001
Exposition (ex)	1	5.93	0.015	3.56	0.059	2.22	0.137
Elevation (el)	4	15.39	0.004	10.06	0.040	36.48	<0.001
sp x ex	1	1.36	0.244	0.09	0.768	0.66	0.416
sp x el	4	3.24	0.519	23.91	<0.001	42.20	<0.001
ex x el	4	10.86	0.028	7.77	0.100	12.79	0.012
sp x ex x el	4	7.43	0.115	3.38	0.496	16.47	0.002

By comparison with the range of the community, *C. firma* and *D. octopetala* had a condensed (H) to large (LDMC) variability with strongly overlapping densities between the two species (Figure 6). The relative shares of the intraspecific trait values on the interspecific spectrum were highest in LDMC, where up to 32.5 and 29 % of the total interspecific value range was also presented by the values within *C. firma* and *D. octopetala,* respectively (Suppl. Table 6). Moreover, compared to the interspecific trait variation, intraspecific traits of both *C. firma* and *D. octopetala* were constantly below the interspecific SLA and H mean values, and above the interspecific LDMC mean value, respectively, in all elevation bands. The interspecific range of SLA values decreased with increasing altitude. The mean value decreased accordingly from 17.34 to 16.35 $mm^2\ mg^{-1}$ (mean values: Suppl. Table 5). Only between 2100-2200 m a.s.l. an increase of the mean value was noticeable. For the SLA response, *C. firma* and *D. octopetala* had a highly overlapping density distribution with the main peak around 10 $mm^2\ mg^{-1}$. *D. octopetala* occupied the lowest ranges of the overall interspecific SLA distribution at slightly lower SLA values than *C. firma*. The overall interspecific range of LDMC values stayed almost unchanged, with only a small decrease of the spectrum in the last elevation category from maximum 516 to 474 $mg\ g^{-1}$. The interspecific mean LDMC values increased from 268.96 to 281.39 $mg\ g^{-1}$ along elevation. Though having a large overlap in distribution range, the peak distributions of the study species differed from each other. *C. firma* had a clear peak just above and *D. octopetala* just below 400 $mg\ g^{-1}$ in all elevations, while *C. firma* had a higher density distribution around the peak value at lower and *D. octopetala* at higher elevations. The mean interspecific plant height decreased with elevation from 16.29 to 7.3 cm. *D. octopetala* and *C. firma* both had a very high density and overlapping distributions of plant height values, covering only 6.9 and 6.6 % of the overall interspecific trait range.

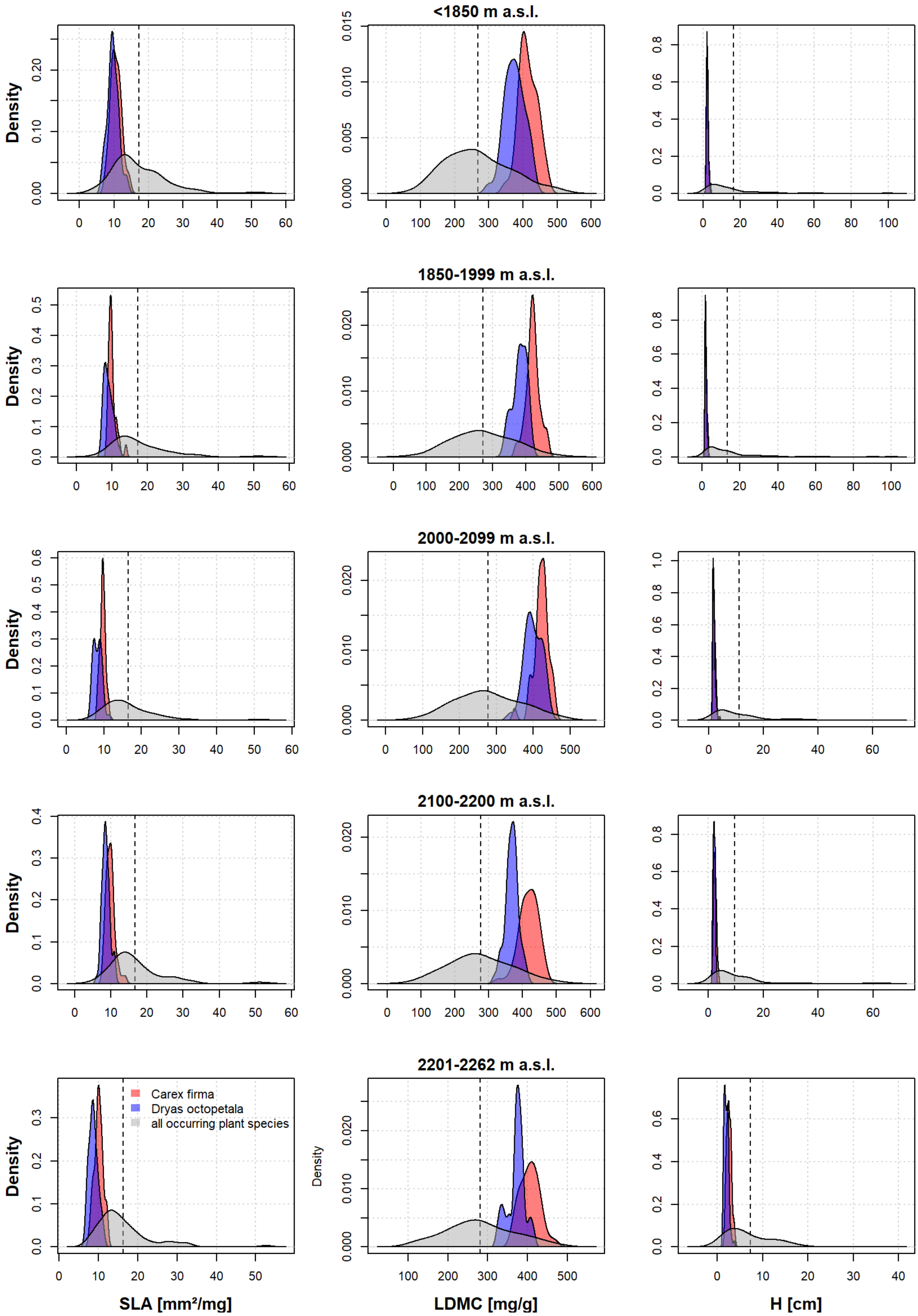

Figure 6: Density plots of plant functional trait distributions on Hochschwab (Northeastern Calcareous Alps, Austria): Within *Carex firma* (red) and *Dryas octopetala* (blue) and all (grey) occurring plant species of transects on Hochschwab, subdivided into five elevation categories. Species occurrence values taken from Steinbauer (2011), plant trait values taken from TRY database (Kattge *et al.*, 2020) and Steinbauer (unpublished) (Suppl. Table 3).

4. DISCUSSION

The presented results refute the hypothesis of a directional trend of the tested functional plant traits along the Hochschwab elevation gradient within species. The intraspecific variability was very large within the transects and overlapping between transects. Since neither elevation nor the other environmental factors could explain the data variation sufficiently, this study did not include the environmental factors that are responsible for most of the variation. The intraspecific variation of both plant species covered a considerable part (up to 14.3 % in SLA and 32,5 % in LDMC) of the interspecific variation of species co-occurring in the surveyed transects. Also, the interspecific comparison highlighted that *C. firma* and *D. octopetala* are comparably resource use efficient. Interspecific trait means changed only slightly with elevation. A reason for the weak interspecific trait response along the elevation gradient could be that the abundance of the species was not considered. The pseudo-elevation gradient trial showed a slight distinction between east and west exposed sites, while, more remarkably, both species showed similar patterns along the elevation gradient in similar aspects. A possible explanation for this behaviour could be their common occurrence in the same plant communities and therefore convergent adaptation strategies within different habitats.

4.1 COMPARISON TO OTHER STUDIES OF INTRASPECIFIC TRAIT VARIABILITY

The presented results are consistent with Rosbakh *et al*. (2015), who also found a large intraspecific variability for SLA values of *C. firma* and *D. octopetala* between sites, but consistent patterns regarding the SLA response only at community level. Another study found a large range of intraspecific values of LDMC values for *D. octopetala* too, and generally high within species variation for all traits and species measured along an elevation gradient (Albert, Thuiller, Yoccoz, Soudant *et al.*, 2010). Yet no general pattern along elevation was detectable within species as well. In their concluding remarks, they suggested the use of a range of values for traits or community-weighted means fitted to the habitats instead of trait means for studying relationships within habitats (Albert, Thuiller, Yoccoz, Soudant *et al.*, 2010). The meta-analysis of Midolo *et al.* (2019) found an overall negative response of SLA to increasing elevation differences. Not all data included in the study mirrored this response. Indeed, the larger the elevation difference the clearer became the negative response (Midolo *et al.*, 2019). A conclusion thereof could be that the detection of trait response patterns depends on the scale. When the focus is on a relatively small elevation gradient as in this study, a lot of noise instead of a clear pattern can be observed. On a larger scale (large elevation difference, global comparison) the pattern becomes clearer.

4.2 POSSIBLE INFLUENCE OF MICRO-CLIMATE

The tested environmental factors did not sufficiently explain the variation in *C. firma* and *D. octopetala*, which leads to the question what could have been the crucial factors. Other environmental variables such as wind, precipitation, soil temperature, length of snow cover periods, nutrient availability, soil composition and drainage ability, carbon dioxide concentrations were not in the scope of this study, but could have had an influence on the trait response (Körner, 2003; de Bello *et al.*, 2013; Ohler *et al.*, 2020). Even though air temperature decreases by a certain lapse rate (Dillon *et al.*, 2006), temperature in mountain slopes of different aspects differs (Winkler *et al.*, 2016), and wind speed and wind direction can have an influence (Wundram *et al.*, 2010). Also, topography and vegetation stature influence the temperature close to the soil (Scherrer & Körner, 2010). Therefore, temperatures can vary greatly within short distances (Scherrer & Körner, 2010) even adding up to a temperature discrepancy usually found 500 m in altitude apart (Ohler *et al.*, 2020). Hence, regional mean temperatures cannot give a good estimate for temperatures near the ground, especially if the goal is to analyse micro-climates (Scherrer & Körner, 2010). The availability of micro-climates implies that horizontal shifts, in contrast to upslope shifts, could be a possibility for plants to respond to climate warming, even though the most cold adapted species will likely be displaced in the process (Scherrer & Körner, 2011; Ohler *et al.*, 2020).

During the fieldwork, several aspects of microtopography and their influence on the studied species could be observed. *Carex firma* is the character species and *D. octopetala* a differential species of the Caricion firmae, they form low-growing swards on summits, at wind-exposed sites, ridges and ledges (Grabherr *et al.*, 1993). Correspondingly, *D. octopetala* was not and *C. firma* was less present in depressions that seemed to have a longer snow cover than the surrounding area, that were seemingly moister than the surrounding area. *C. firma* was always present in exposed sites, especially on rocks that were protruding from the surrounding meadow. On them and other dry sites they were smaller with tougher leaves. Contrastingly, in wind sheltered sites *C. firma* was noticeably larger than the observed medium within the transect. Also, *D. octopetala* seemed to grow higher and have bigger and softer leaves in places that were more sheltered from the wind, had relatively higher surrounding vegetation, possibly indicating light competition or higher nutrient availability, or both. In what ways and how much competition limited or even increased the growth of the two species could not be perceived. No known studies have analysed competitive behaviour of the two species to newly arriving species, yet. However, one experimental study found that competition from new species has a more severe impact on alpine species than solely annual mean temperature increase (Alexander *et al.*, 2015). Considering these results and due to their slow growth, it is likely that under fierce competition, *C. firma* and *D. octopetala* might not be “quick” enough to secure new suitable micro-habitats. However, they might still survive in small numbers in cold, and dry or nutrient poor niches that they already inhabit and that are too unfavourable for migrating species. Taking this into account, the persistence of *C. firma* and *D. octopetala* in lower regions of Hochschwab will likely depend on their biotic competitiveness and the availability of cold micro-climates.

4.3 INTERSPECIFIC COMPARISON

Even though very weak, the general directional trends in interspecific non-weighted mean trait values confirm the rule for the turnover of species to resource conservative, cold-adapted plants at higher elevations (lower SLA, smaller H, larger LDMC) (Atkin *et al.*, 1996; Körner, 2003). The comparison between intraspecific and interspecific variation within transects along elevation suggests that *C. firma* and *D. octopetala* are constantly below the average (SLA, H) and above the average (LDMC) of the trait spectrum. This means that they are both relatively slow-growing, long-lived and resource conserving (Woodward, 1983; Körner & Larcher, 1988; Atkin *et al.*, 1996; Ryser, 1996; Körner, 2003), and their range distribution might likely not be impacted by climate warming in the short term due to their high resistance to changing conditions (Cotto *et al.*, 2017). However, their abundance along the range distribution might decrease faster due to poor reproductive performance in changing conditions (Cotto *et al.*, 2017), which further confirms the conclusion of the previous paragraph. Though alpine ecosystems seem to have a natural buffer to changing conditions, effects of climate warming will put pressure on them if mean temperatures rise as quickly as predicted (Theurillat & Guisan, 2001).

The studied species covered up to ~ 30 % of the interspecific trait variation of LDMC at the sites. This is in alignment with findings of another study (Albert, Thuiller, Yoccoz, Douzet *et al.*, 2010). In contrast, the studied species did only cover approximately 6 % of the interspecific range of trait variation in H at the sites. From what can be said about this basic comparison, using intraspecific values instead of mean traits will not significantly influence the outcomes of studies addressing processes at larger scale, e.g. environmental relationships (Albert, Thuiller, Yoccoz, Douzet *et al.*, 2010; Cordlandwehr *et al.*, 2013). For small scale processes as to e.g. identify the micro-climate influence, intraspecific variation should be considered (Albert, Thuiller, Yoccoz, Douzet *et al.*, 2010; Cordlandwehr *et al.*, 2013). Also, large divergence between changes in non-weighted interspecific and abundance data were recorded in alpine monitoring plots, revealing the greater explanatory power of community-weighted means in detecting effects of climate changes (Steinbauer *et al.*, 2020). Furthermore, to assess the resistance of plant community composition to changing environmental factors, intraspecific variation and its relative influence on community-weighted means become important (Jung *et* *al.*, 2010). Seen in a larger context, as Lavorel & Garnier (2002) and de Bello *et al.* (2013) pointed out, the plant community composition is a result of a sequence of environmental filters. The occurrence of species can be determined by temperature and on that account also altitude, but the abundance and its intraspecific variation is rather dependent on small scale factors such as soil characteristics (Lavorel & Garnier, 2002; de Bello *et al.*, 2013).

4.4 IMPLICATIONS FOR THE STUDIED SPECIES

The findings of this study suggest that trait variation in *C. firma* and *D. octopetala* on Hochschwab might stay mostly intact despite climate warming, at least in the short term. Their range of trait variation might be maintained, even when the lower parts of their ranges are lost to upward migrating species. Also, their large variability in traits might be a sign of their adaptation to micro-climates. In case of no strong competition from migrating species, *C. firma* and *D. octopetala* might be able to shift horizontally to suitable micro-habitats of the study area, if given micro-topography is retained (Scherrer & Körner, 2011). With fierce competition, survival in lower regions might only be possible in resource scarce, cold niches that they already inhabit, or by adapting to the new conditions. Still, this highlights the importance of maintaining habitat diversity for nature conservation (Wellstein *et al.*, 2013; Opedal *et al.*, 2015).

4.5 DATA LIMITATIONS

Potential observer errors such as inconsistent measurement, or choice of individuals that were not in optimal conditions were minimised by several measures. Only one person conducted the field and lab work following a protocol for sampling and measurement. Collection and rehydration methods were tested and compared prior to the fieldwork to ensure their viability. Also, the fieldwork was finished within less than a month, therefore sampling the plants in similar phenology stages. In one of the transects (wek_ssw_09) plant height was only measured in 15 instead of 25 individuals, but since ten sample heights is the recommended minimum (Pérez-Harguindeguy *et al.*, 2013), this should not have caused any problems.

Among site variations due to different bedrock were restricted, measurements were only taken in the Hochschwab area, with sites situated on limestone. Still, other environmental conditions, such as soil fertility and the discussed microtopography are complex in mountain regions (de Bello *et al.*, 2013) and were not included in the models.

The influence of fauna on the transects were not considered. Since chamois and Alpine ibex are present on Hochschwab, trampling damage was possible, as well as local nutrient input through animal faeces. However, grazing damage on *C. firma* and *D. octopetala* is unlikely due to their tough leaves, no traces of grazing were noticed during fieldwork too. Interference of other humans on the transects was also restricted since all transects were far from the official hiking tracks.

Clearly, the trait data taken from the TRY database is from different studies and regions and it is not guaranteed that the used trait means are equivalent to the ones of the plants on Hochschwab mountain range. Additionally, for up to 24 % species per elevation category no trait values were available (Suppl. Table 2). Also, the interspecific variability shown in the density plots is not weighted by vegetation cover of the species (CWM), which means that the mean values are not to be read as true mean values of the community but rather as the interspecific mean of all occurring species. Nevertheless, it gives a rough estimate of the interspecific mean, the overall range of interspecific values and where to find *C. firma* and *D. octopetala* relative to it.

4.6 IMPLICATIONS FOR FUTURE RESEARCH

In their study Wellstein *et al*. (2013) suggested that in order to have the best resilience to climate change effects, intraspecific variation has to be large and therefore environmental diversity on small and large scale must be conserved. This is also in alignment with Des Roches *et al*. (2018) meta-analysis about the influence of intraspecific variation on community structure. This said, possible research in the future would be to assess, if the intraspecific variability of *C. firma* and *D. octopetala* on Hochschwab is indeed caused by micro-climate and what factors of it best describe the response of the functional traits.

To assess the micro-topography, as well as snow cover distribution, a digital surface model (DSM) and an orthophoto mosaic could be derived from high resolution images from drone imagery (Lucieer *et al.*, 2014; Harris & Baird, 2019), or drone borne LiDAR (Brubaker *et al.*, 2013). The corresponding small-scale temperature measurements could be done with high resolution infra-red (IR) imagery (Scherrer & Körner, 2010). Additionally, soil temperatures could be measured with small temperature loggers, buried within the topsoil in short horizontal distances (Scherrer & Körner, 2010). Since soil structure is influencing the amount of root penetration, aeration and water retention capacity (Amelung *et al.*, 2018), this could also have an influence on species distribution and assessing this should also be considered. Other possible variables to test on a finer scale could be windspeed, wind direction and precipitation.

Subsequently, the relative influence of the intraspecific variation of several dominant species on CWM could be tested to assess the resilience of the plant community to climate change effects and to understand their importance for community processes (Jung *et al.*, 2010;

Stanisci *et al.*, 2020). An intraspecific approach with other plant species in the same transects and the same species in another region could give insights if the parallel pattern between *C. firma* and *D. octopetala* was a coincidence or if they indeed adapted in the same way to niches.

Finally, more research towards biotic interaction in alpine ecosystems is needed to further the understanding of upcoming changes in community structures (Alexander *et al.*, 2015).

5. CONCLUSIONS

By analysing the intraspecific functional trait variation of two alpine species, this work showed the complexity of the relationship between environmental factors and trait responses. The presented outcomes add to the state of knowledge about functional trait variation within two alpine species. Intraspecific variability can be high within a short horizontal distance and give inconsistent patterns over an elevation gradient. The results showed the difficulty of modelling this response and that elevation is not the main driver for intraspecific trait variation. The most likely explanation for this outcome is the influence of micro-climate on functional responses. The two study species showed similar responses in similar aspects, possibly due to convergent adaptation strategies. Also, the analysis showed that the functional trait variation within species might be maintained *for C. firma* and *D. octopetala* on Hochschwab, even with rising annual mean temperatures. Unclear is if and to what extent the composition and abundance within the plant communities on Hochschwab will change due to climate change effects. For a better understanding of this process, the combination of intraspecific data and community-weighted means might be an option for future research. Furthermore, the species-specific ability to adapt to microtopography, the availability of micro-climates in different alpine ecosystems and the effect of new competitors should be considered for future research, in order to assess possible climate change effects in alpine ecosystems.

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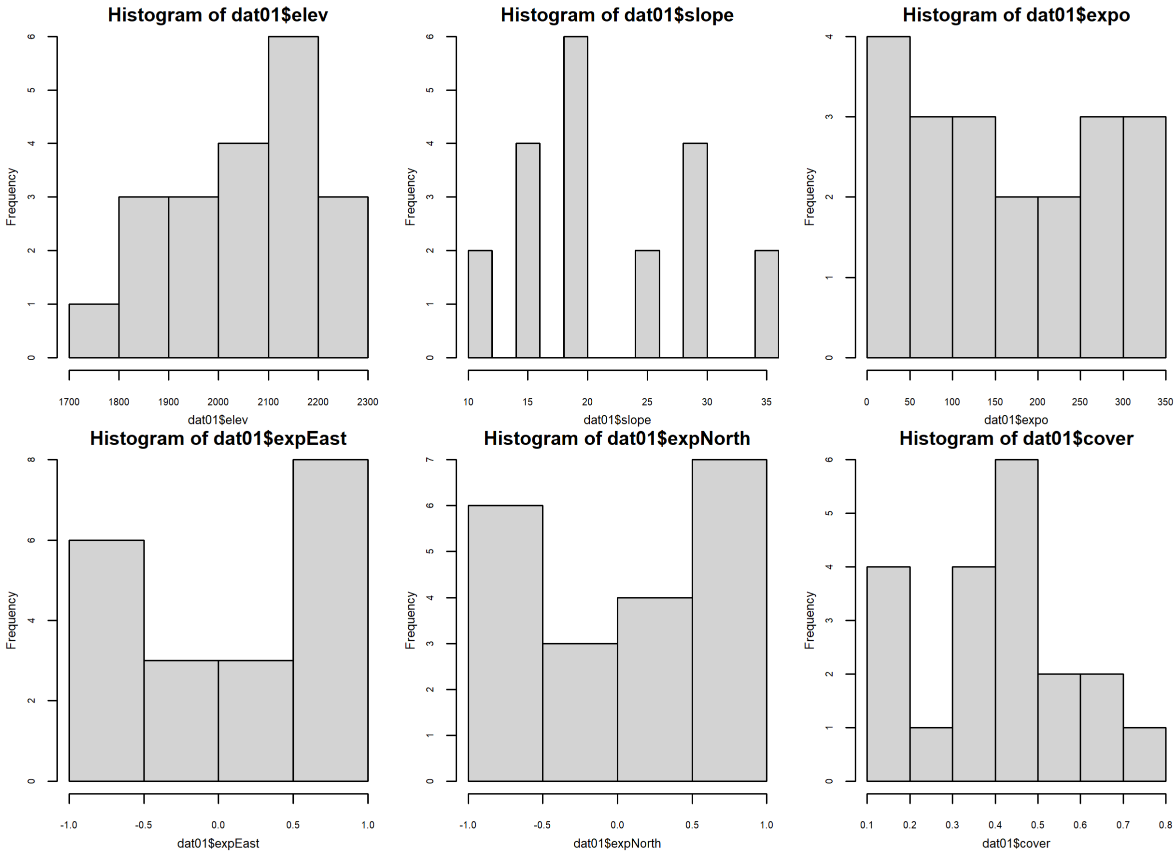
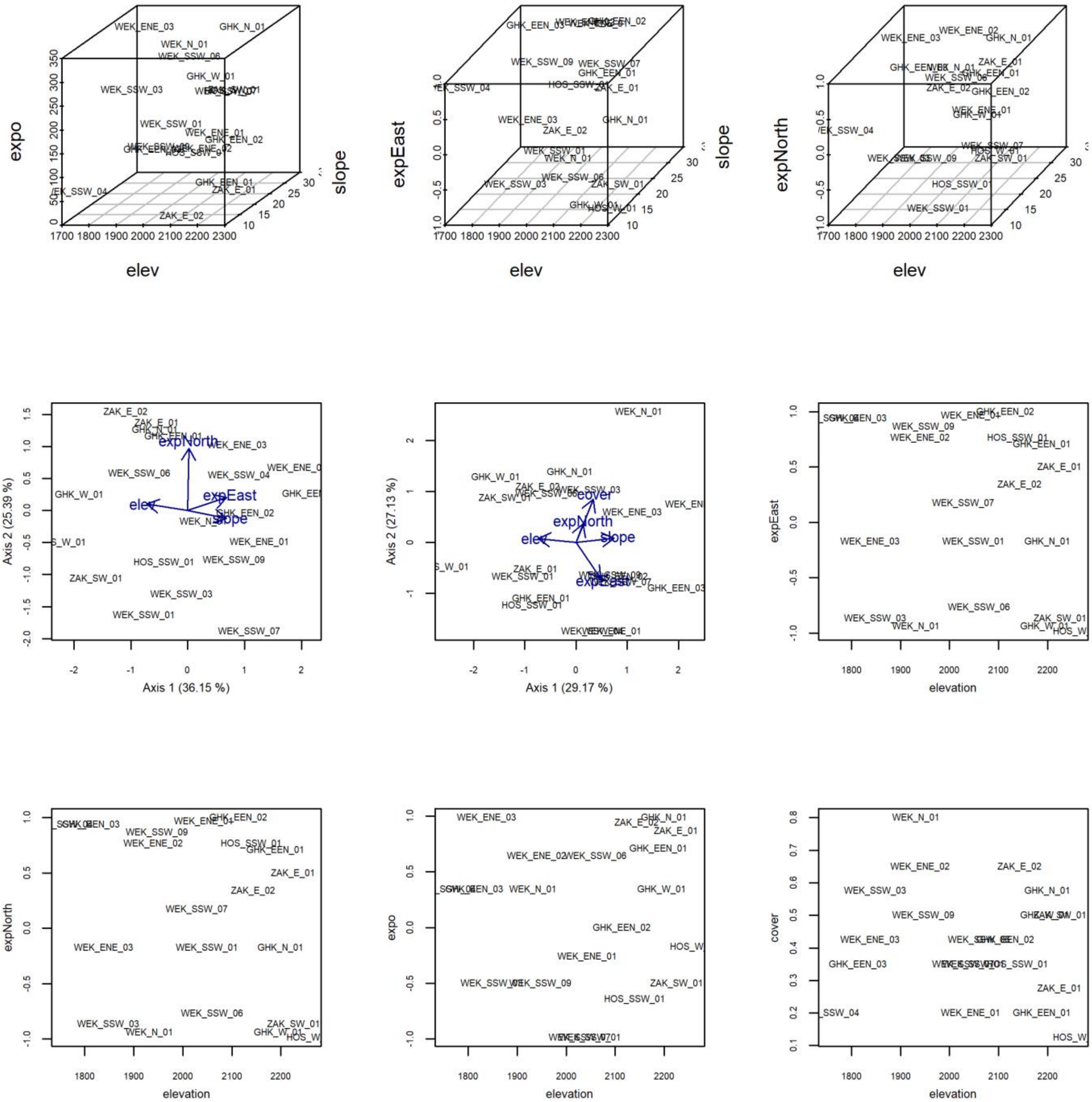
SUPPLEMENTARY INFORMATION

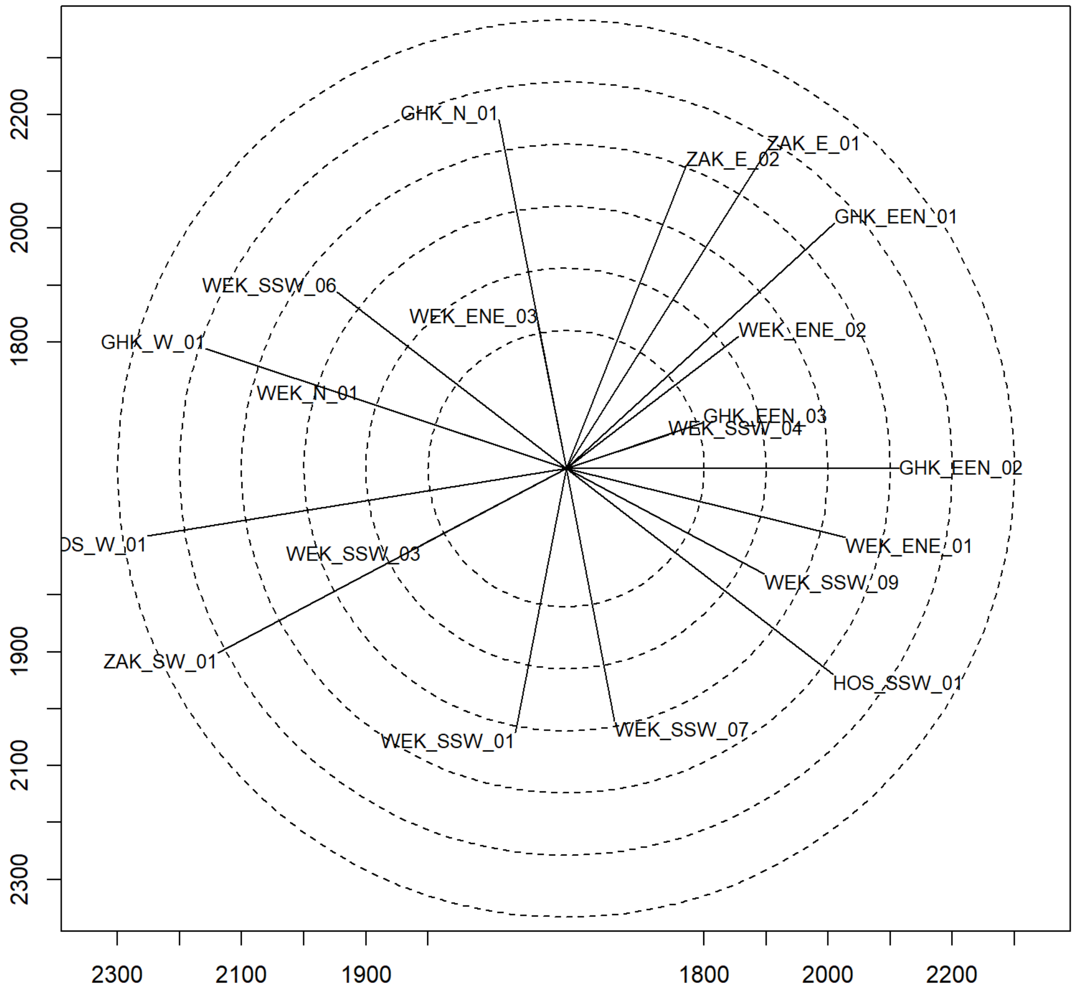
I. DATA EXPLORATION



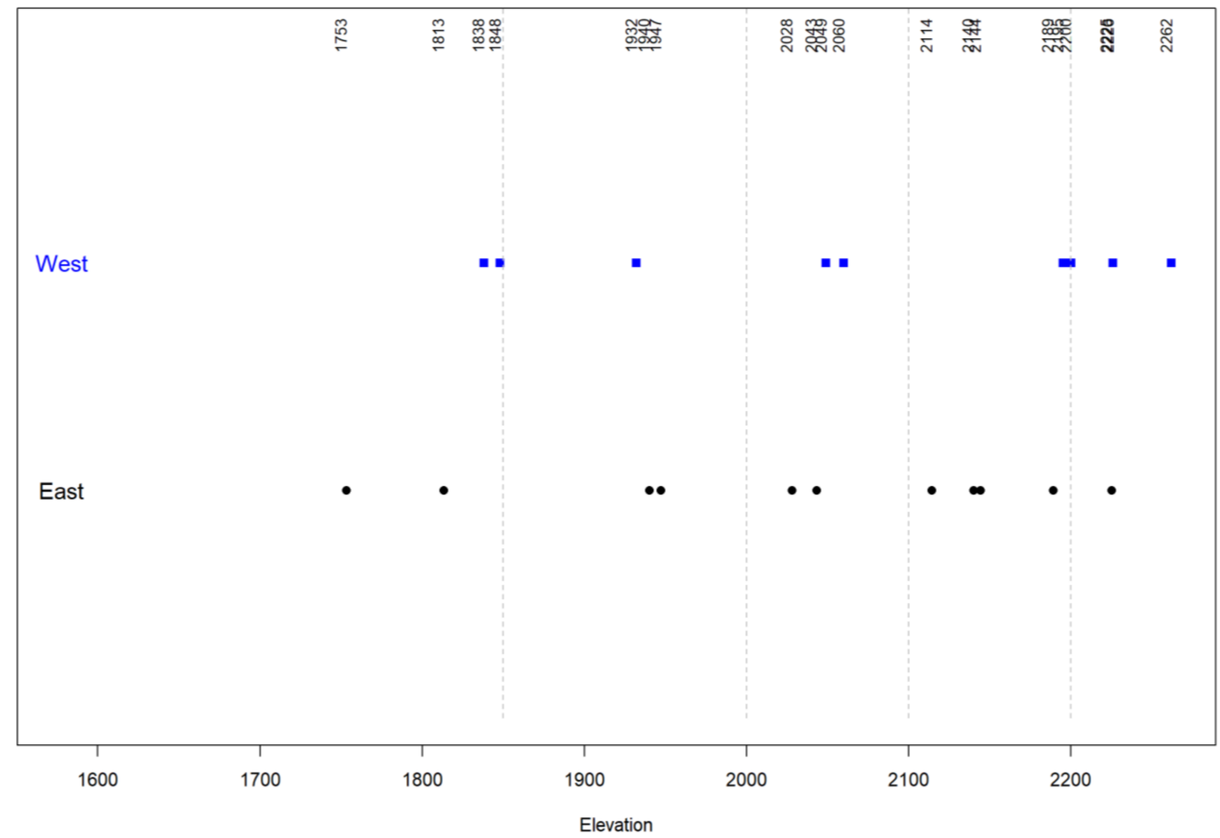
Suppl. Figure 1: Histograms of data distribution, data distribution of sampling design of 20 transects on Hochschwab, Austria. Measured environmental factors: elev, elevation [m a.s.l.]; slope [degree]; expo, aspect [degree]; expEast, aspect transformed into eastness; expNorth, aspect transformed into northness; cover, vegetation cover of transect from 0.15=open to 0.85=closed.



Suppl. Figure 2: PCA and 3D scatterplots of data distribution. Data distribution of sampling design of 20 transects on Hochschwab, Austria. Measured environmental factors: elev, elevation [m a.s.l.]; slope [degree]; expo, aspect [degree]; expEast, aspect transformed into eastness; expNorth, aspect transformed into northness; cover, vegetation cover of transect from 0.15=open to 0.85=closed.

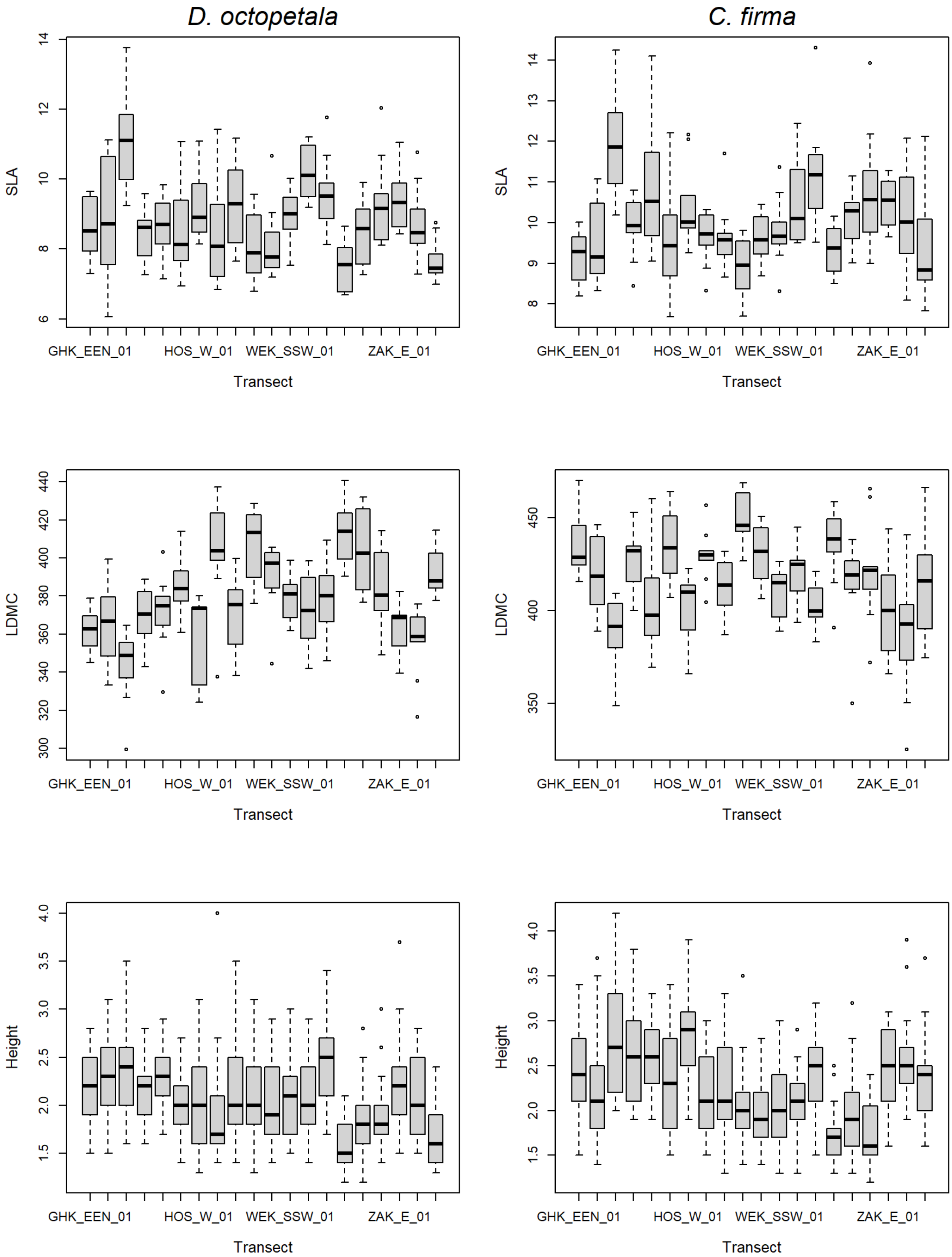


Suppl. Figure 3: Distribution of transects in aspects and elevation; sampling design of 20 transects on Hochschwab, Austria. Circles represent elevation [m a.s.l.]; position of transect on circle represents aspect [degree] comparable to compass directions.

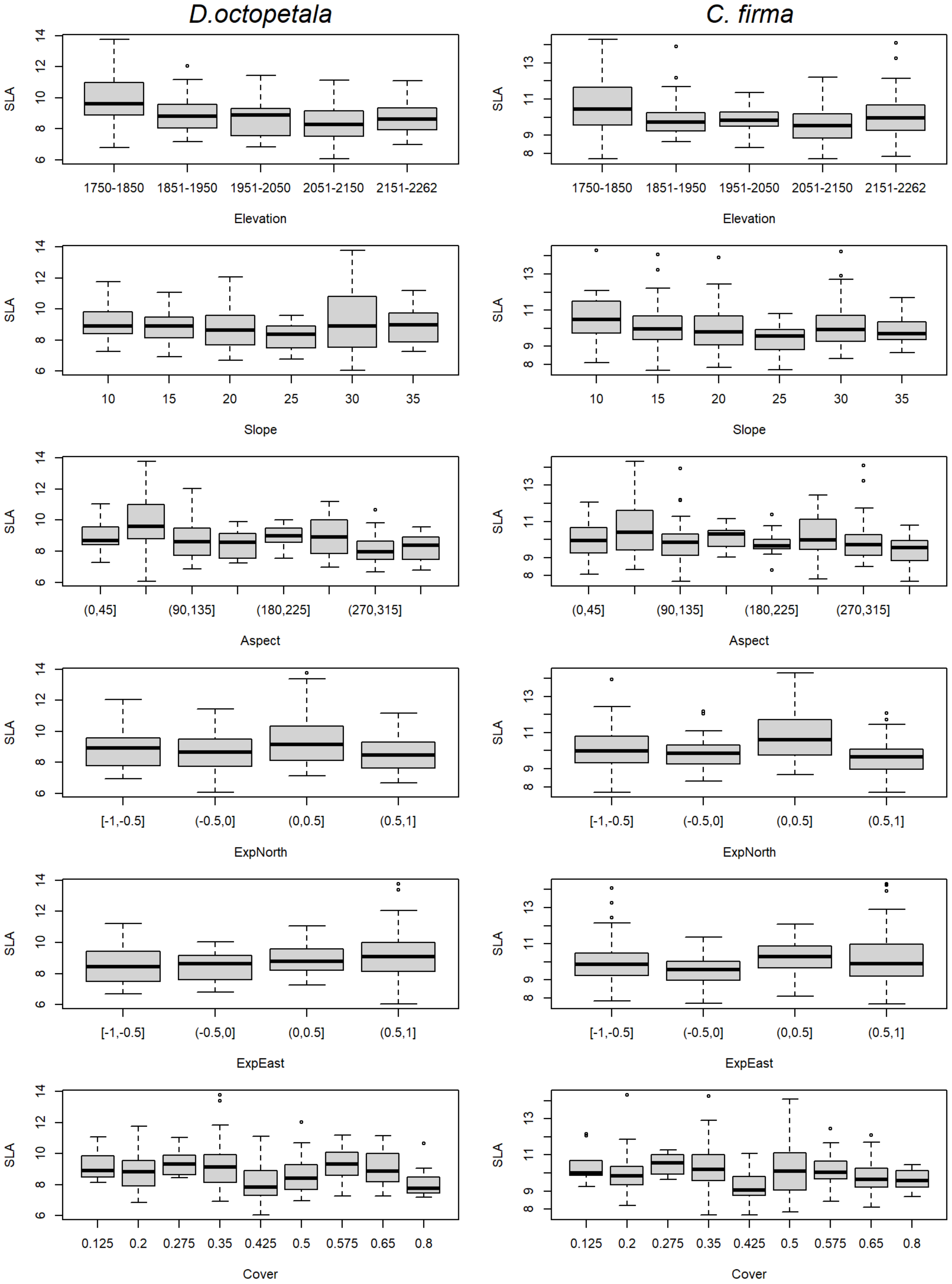


Suppl. Figure 4: Transects pooled into easterly and westerly exposed sites. Distribution of 20 transects on Hochschwab, Austria. West for eastness between -1 and 0 and east for eastness between 0 and 1. Elevation in m a.s.l.

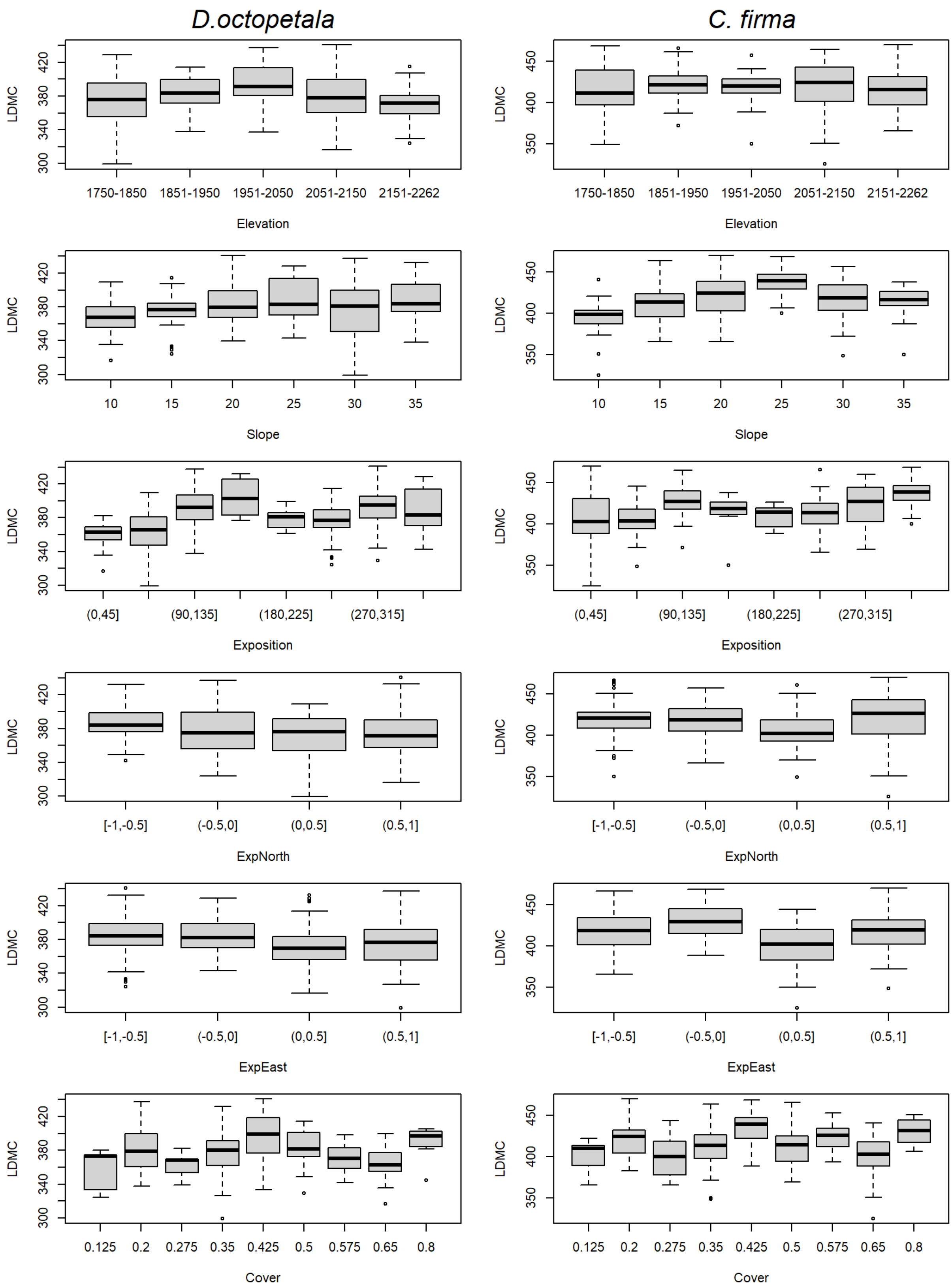
II. BOXPLOTS



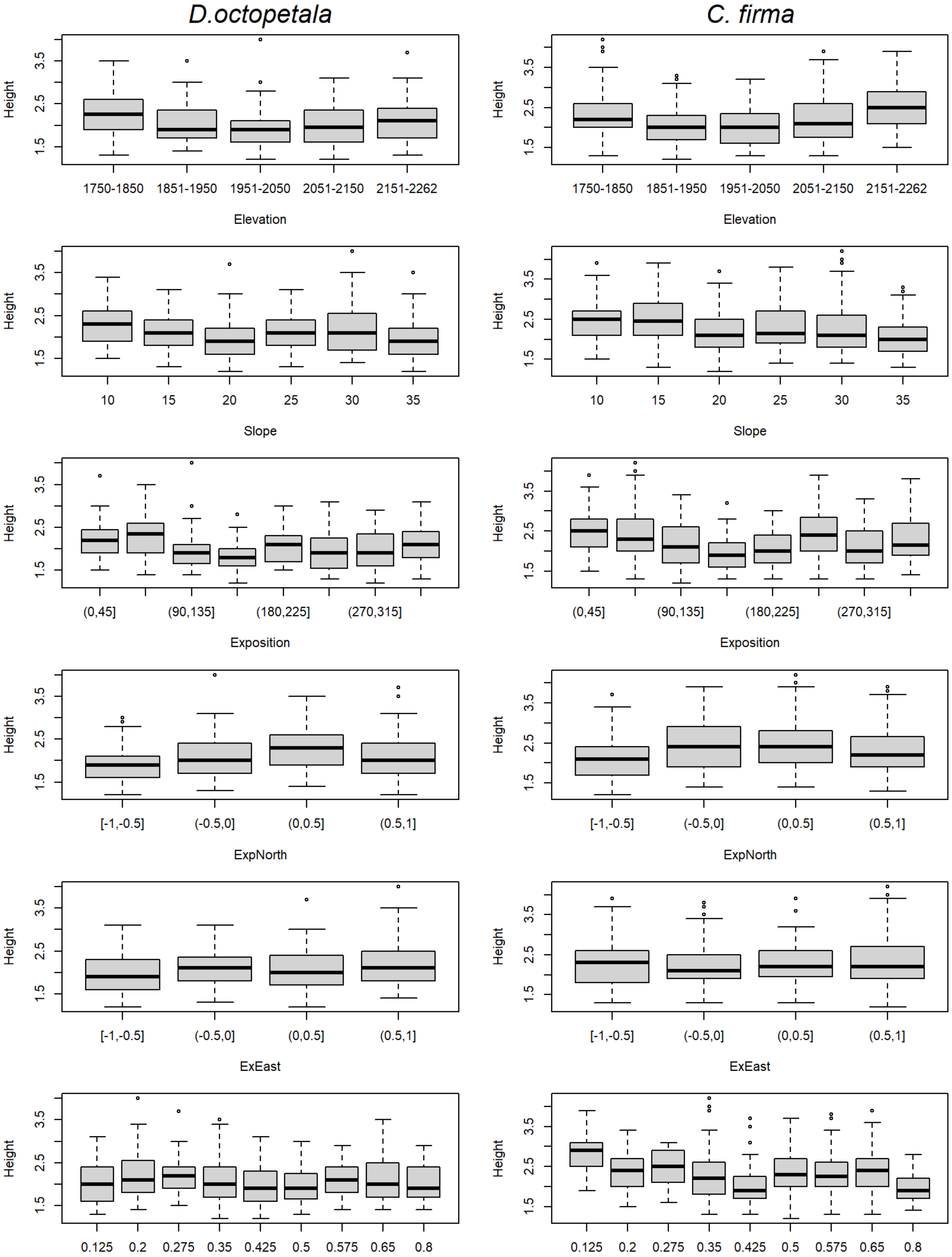
Suppl. Figure 5: Boxplots of trait response per transect per species. Trait response data from *Carex firma* (*C. firma*) and *Dryas octopetala* (*D. octopetala*) of 20 transects on Hochschwab, Austria. SLA, specific leaf area [mm² mg^{-1}]; LDMC, leaf dry matter content [mg g^{-1}]; Height, vegetative plant height [mm].



Suppl. Figure 6: Boxplots of SLA response to environmental factors per species. Trait response data from *Carex firma* (*C. firma*) and *Dryas octopetala* (*D. octopetala*) of 20 transects on Hochschwab, Austria. SLA, specific leaf area [mm^2 mg^{-1}]; elevation [m a.s.l.]; slope [degree]; expo, aspect [degree]; expEast, aspect transformed into eastness; expNorth, aspect transformed into northness; cover, vegetation cover of transect from 0.15=open to 0.85=closed.

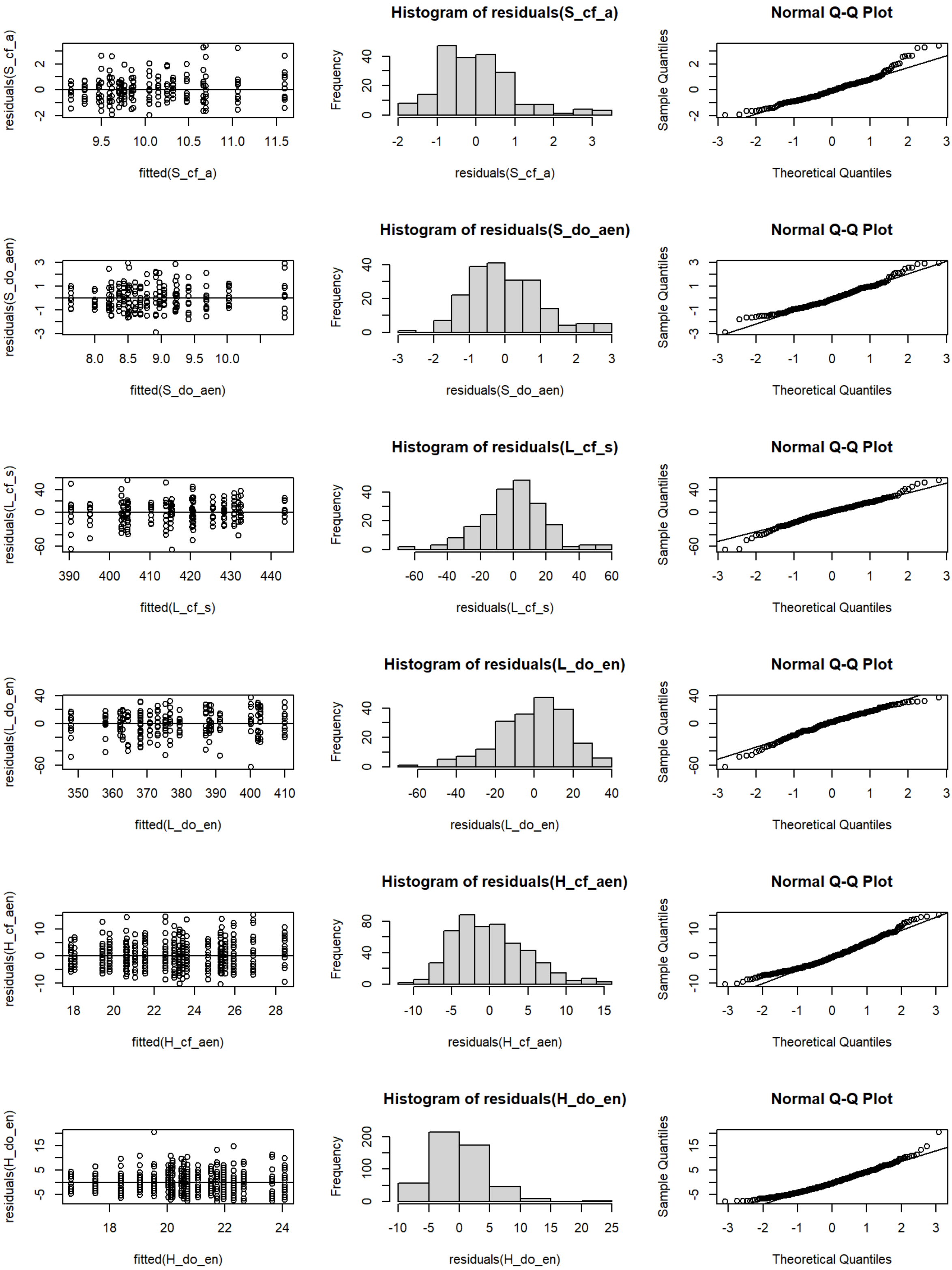


Suppl. Figure 7: Boxplots of LDMC response to environmental factors per species. Trait response data from *Carex firma* (*C. firma*) and *Dryas octopetala* (*D. octopetala*) of 20 transects on Hochschwab, Austria. LDMC, leaf dry matter content [mg g^{-1}]; elevation [m a.s.l.]; slope [degree]; expo, aspect [degree]; expEast, aspect transformed into eastness; expNorth, aspect transformed into northness; cover, vegetation cover of transect from 0.15=open to 0.85=closed.



Suppl. Figure 8: Boxplots of Height response to environmental factors per species. Trait response data from *Carex firma* (*C. firma*) and *Dryas octopetala* (*D. octopetala*) of 20 transects on Hochschwab, Austria. Height, vegetative plant height [mm]; elevation [m a.s.l.]; slope [degree]; expo, aspect [degree]; expEast, aspect transformed into eastness; expNorth, aspect transformed into northness; cover, vegetation cover of transect from 0.15=open to 0.85=closed.

III. RESIDUALS



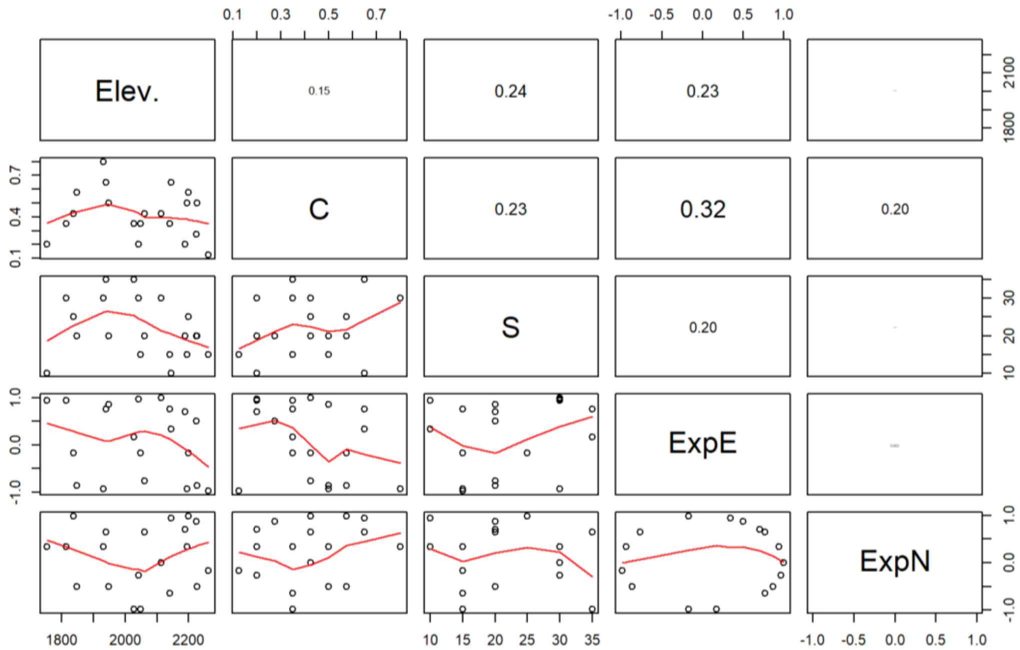
Suppl. Figure 9: Residual plots of best GLMMs. Effect of environmental variables on trait variability in *Carex firma* (cf) and *Dryas octopetala* (do) on Hochschwab, Austria, calculated with GLMMs with Gaussian link function. Shown are residual plots of the linear mixed-effects model with the lowest AIC_cs. Prefix of model name: S, specific leaf area; L, leaf dry matter content; H, vegetative plant height. Suffix of model name: a, altitude; en, interaction between eastness and northness; s, slope.

IV. LIST OF AKAIKE'S INFORMATION CRITERION

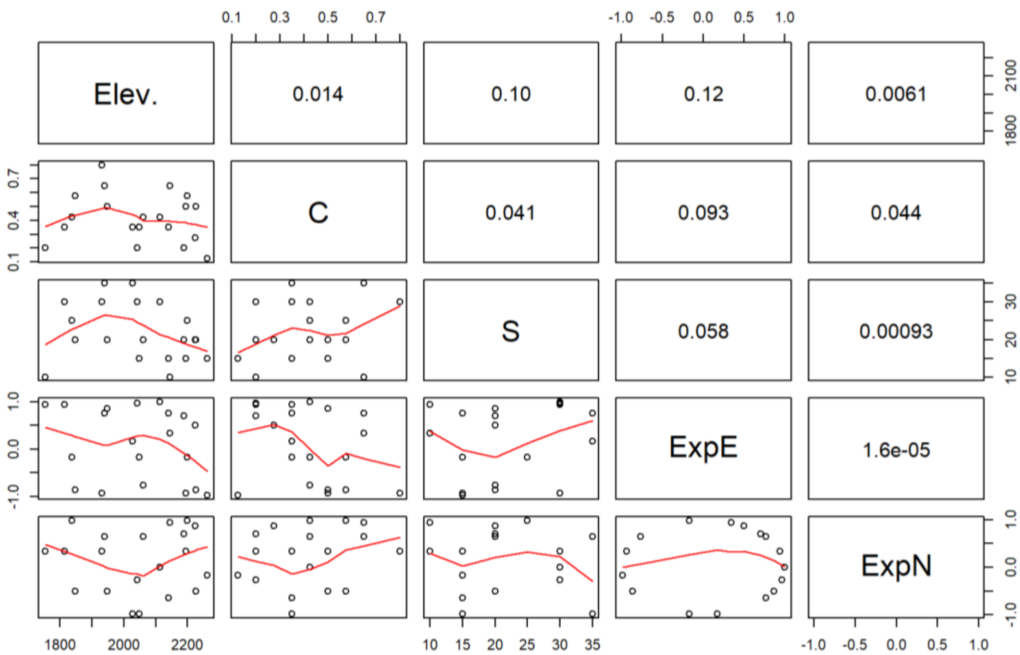
Suppl. Table 1: Akaike's Information Criterion (AIC_c) list of GLMMs for *Carex firma* (*C. firma*) and *Dryas octopetala* (*D. octopetala*) trait response to environmental factors. (a) SLA (specific leaf area), (b) LDMC (leaf dry matter content), (c) Plant Height. Suffix of model name indicates the factors included into model: a, altitude; s, slope; c, vegetation cover; en, interaction between eastness and northness. GLMMs built with transects as random intercept term and Gaussian link function. m R^2, marginal R^2; c R^2, conditional R^2.

Carex firma					***Dryas octopetala***				
(a) SLA									
model	df	AICc	m R²	c R²	model	df	AICc	m R²	c R²
S_cf_a	4	615.55	0.034	0.299	S_do_aen	7	626.91	0.191	0.354
S_cf_as	5	616.05	0.060	0.299	S_do_a	4	628.53	0.079	0.354
S_cf_s	4	616.73	0.013	0.299	S_do_aens	8	628.80	0.194	0.354
S_cf_ac	5	616.87	0.047	0.299	S_do_en	6	628.96	0.138	0.354
S_cf_c	4	617.05	0.007	0.299	S_do_aenc	8	628.99	0.192	0.354
S_cf_asc	6	617.71	0.067	0.299	S_do_ac	5	629.49	0.098	0.354
S_cf_cs	5	618.63	0.017	0.299	S_do_as	5	630.40	0.083	0.354
S_cf_en	6	620.26	0.025	0.299	S_do_aencs	9	630.97	0.194	0.354
S_cf_aen	7	620.79	0.052	0.299	S_do_enc	7	631.04	0.139	0.354
S_cf_aens	8	621.30	0.078	0.299	S_do_ens	7	631.10	0.138	0.354
S_cf_ens	7	621.51	0.040	0.299	S_do_asc	6	631.53	0.099	0.354
S_cf_enc	7	622.36	0.026	0.299	S_do_c	4	632.26	0.009	0.354
S_cf_aenc	8	622.59	0.058	0.299	S_do_s	4	632.68	<0.001	0.354
S_cf_aencs	9	623.41	0.079	0.299	S_do_encs	8	633.19	0.139	0.354
S_cf_encs	8	623.68	0.041	0.299	S_do_cs	5	634.33	0.009	0.354
(b) LDMC									
model	df	AICc	m R²	c R²	model	df	AICc	m R²	c R²
L_cf_s	4	1816.90	0.031	0.344	L_do_en	6	1784.55	0.216	0.464
L_cf_en	6	1816.96	0.103	0.344	L_do_aen	7	1784.95	0.242	0.465
L_cf_ens	7	1817.49	0.127	0.344	L_do_ens	7	1785.62	0.232	0.465
L_cf_a	4	1818.38	0.022	0.344	L_do_aens	8	1786.44	0.251	0.465
L_cf_c	4	1818.44	0.001	0.344	L_do_aenc	8	1786.55	0.249	0.465
L_cf_aen	7	1818.87	0.107	0.344	L_do_enc	7	1786.58	0.218	0.464
L_cf_cs	5	1819.00	0.032	0.344	L_do_encs	8	1787.26	0.239	0.465
L_cf_as	5	1819.00	0.031	0.344	L_do_aencs	9	1787.55	0.265	0.465
L_cf_enc	7	1819.06	0.104	0.344	L_do_s	4	1790.29	0.020	0.464
L_cf_encs	8	1819.20	0.133	0.344	L_do_a	4	1790.49	0.015	0.464
L_cf_aens	8	1819.60	0.128	0.344	L_do_c	4	1791.07	<0.001	0.464
L_cf_ac	5	1820.46	0.003	0.344	L_do_as	5	1792.05	0.029	0.464
L_cf_aenc	8	1820.90	0.109	0.344	L_do_cs	5	1792.39	0.021	0.464
L_cf_asc	6	1821.13	0.032	0.344	L_do_ac	5	1792.60	0.015	0.464
L_cf_aencs	9	1821.23	0.136	0.344	L_do_asc	6	1794.16	0.029	0.464
(c) Plant Height									
model	df	AICc	m R²	c R²	model	df	AICc	m R²	c R²
H_cf_aen	7	2969.97	0.128	0.281	H_do_en	6	2908.38	0.073	0.18
H_cf_aenc	8	2970.41	0.141	0.280	H_do_aen	7	2909.52	0.080	0.18
H_cf_aens	8	2971.46	0.134	0.282	H_do_ens	7	2909.95	0.076	0.18
H_cf_a	4	2971.52	0.046	0.283	H_do_enc	7	2910.39	0.073	0.18
H_cf_enc	7	2971.78	0.109	0.281	H_do_aens	8	2910.72	0.085	0.18
H_cf_aencs	9	2972.29	0.143	0.281	H_do_aenc	8	2911.35	0.081	0.18
H_cf_ac	5	2972.43	0.061	0.283	H_do_a	4	2911.43	0.013	0.18
H_cf_en	6	2972.49	0.082	0.282	H_do_encs	8	2912.02	0.076	0.18
H_cf_as	5	2972.92	0.055	0.283	H_do_c	4	2912.37	0.003	0.18
H_cf_c	4	2973.12	0.024	0.283	H_do_s	4	2912.53	0.002	0.18
H_cf_s	4	2973.38	0.019	0.283	H_do_aencs	9	2912.74	0.085	0.18
H_cf_ens	7	2973.39	0.096	0.283	H_do_ac	5	2912.88	0.019	0.18
H_cf_encs	8	2973.45	0.114	0.281	H_do_as	5	2912.97	0.018	0.18
H_cf_asc	6	2974.10	0.066	0.282	H_do_cs	5	2914.33	0.004	0.18
H_cf_cs	5	2974.33	0.036	0.283	H_do_asc	6	2914.60	0.022	0.18

V. PAIRPLOTS



Suppl. Figure 10: Pairplot of correlation coefficients between environmental factors used in GLMMs to model the trait response of *Carex firma* (*C. firma*) and *Dryas octopetala* (*D. octopetala*) of 20 transects on Hochschwab, Austria, tested on correlation. Elev., elevation [m a.s.l.]; C, vegetation cover of transect from 0.15=open to 0.85=closed; S, slope [degree]; ExpE, aspect transformed into eastness; ExpN, aspect transformed into northness. Smaller fonts indicate smaller correlation coefficients.



Suppl. Figure 11: Pairplot of R^2 values of the correlation between environmental factors used in GLMMs to model the trait response of *Carex firma* (*C. firma*) and *Dryas octopetala* (*D. octopetala*) of 20 transects on Hochschwab, Austria, tested on correlation. Elev., elevation [m a.s.l.]; C, vegetation cover of transect from 0.15=open to 0.85=closed; S, slope [degree]; ExpE, aspect transformed into eastness; ExpN, aspect transformed into northness. Smaller fonts indicate smaller explanatory value of the correlation.

VI. MISSING TRAIT VALUES

Suppl. Table 2: Absolute (and relative) amount of missing trait values of species trait list (Suppl. Table 4) per elevation category with species presence/absence data from Steinbauer (2011) on Hochschwab, Austria (each present plant species is only counted once per elevation category).

Elevation	absolute (relative) amount of NA values		
category	SLA	LDMC	Height
1800	39 (0.234)	39 (0.234)	16 (0.096)
1925	40 (0.242)	40 (0.242)	16 (0.097)
2050	32 (0.224)	32 (0.224)	15 (0.105)
2150	22 (0.182)	22 (0.182)	9 (0.074)
2250	13 (0.149)	14 (0.161)	6 (0.069)

VII. SPECIES TRAIT LIST, TRY REFERENCES

Suppl. Table 3: Species with traits taken from TRY database (Kattge *et al.*, 2020) (source label: TRY) and Steinbauer et al. unpublished (Source label: SB). Datasets from TRY Database cited with DatasetID, see Suppl Table 5.

Species name Flora Europaea	Species name TRY	Source	SLA	LDMC	Plant Height	DatasetID		
			[mm² mg⁻¹]	[mg g⁻¹]	[cm]	SLA	LDMC	Plant Height
Achillea atrata L. subsp. *atrata*	*Achillea atrata*	TRY	NA	NA	14.5			25;164
Achillea clavennae L.	*Achillea clavennae*	TRY	NA	NA	17			25;164
Achillea clusiana Tausch	*Achillea clusiana*	TRY	NA	NA	NA			
Acinos alpinus (L.) Moench subsp. *alpinus*	*Acinos alpinus*	TRY	14.9382061	326.71178	12.4375	161	161	25;161;164
Adenostyles alliariae (Gouan) A.Kern. subsp. *Alliariae*	*Adenostyles alliariae*	TRY	23.89320873	134.723869	90	25;228	25;228	25;164
Adenostyles alpina (L.) Bluff & Fingerh.	*Adenostyles alpina*	TRY	18.43500521	142.979518	39.30357143	228;416;421	228;416;421	164;421
Agrostis alpina Scop.	*Agrostis alpina*	SB	12.9	392	9			
Agrostis rupestris All.	*Agrostis rupestris*	SB	34.12	156	5			
Alyssum ovirense A.Kern.	*Alyssum ovirense*	TRY	NA	NA	6			164
Androsace chamaejasme Wulfen	*Androsace chamaejasme*	SB	19.57	216	1			
Anemone narcissifolia L. subsp. *narcissifolia*	*Anemone narcissiflora*	SB	12.96	267	10			
Antennaria carpatica (Wahlenb.) Bluff & Fingerh.	*Antennaria carpatica*	SB	12.58	284	3			
Anthoxanthum odoratum L. subsp. *alpinum* (Á.Löve & D.Löve) B.M.G.Jones & Melderis	*Anthoxanthum odoratum*	SB	19.86	335	9			
Anthyllis vulneraria subsp. *alpestris* (Hegetschw.) Asch. & Graebn.	*Anthyllis vulneraria*	TRY	15.99449987	176.055305	14.43709677	25;45;310;421	25;45;310;421	25;45;310;421
Arabis alpina L. subsp. *alpina*	*Arabis alpina*	SB	32.65	140	7			
Arabis caerulea (All.) Haenke	*Arabis caerulea*	TRY	19.65900733	171.611808	3.24516129	25;421	421	25;164;421
Arabis ciliata Clairv.	*Arabis ciliata*	TRY	NA	NA	13			25;164
Arabis pumila Jacq.	*Arabis pumila*	TRY	NA	NA	11.5			164
Arctostaphylos alpinus (L.) Spreng.	*Arctous alpina*	SB	11.66	366	5			
Arenaria ciliata L. subsp. *ciliata*	*Arenaria ciliata*	SB	16.26	298	6			
Armeria maritima subsp. *alpina* (Willd.) P.Silva	*Armeria maritima*	TRY	15.50888536	186.901	9.863636364	25;200	25	25;200
Asplenium trichomanes-ramosum L.	*Asplenium trichomanes-ramosum*	TRY	19.9	337	12.5	25	25	25
Aster bellidiastrum (L.) Scop.	*Bellidiastrum michelii*	TRY	NA	NA	NA			
Bartsia alpina L.	*Bartsia alpina*	SB	19.6	264	12			
Biscutella laevigata subsp. *austriaca* (Jord.) Mach.-Laur.	*Biscutella laevigata*	TRY	18.52543824	118.947232	22.5	228	228	25;164
Botrychium lunaria (L.) Sw.	*Botrychium lunaria*	TRY	20.61846577	192.659722	5.796875	25;227;421	25;227;421	25;164;310;421
Campanula alpina Jacq. subsp. *alpina*	*Campanula alpina*	SB	12.31	280	2			
Campanula cenisia L.	*Campanula cenisia*	TRY	15.37847002	219.817977	2.196428571	421	421	164;421

Species name Flora Europaea	Species name TRY	Source	SLA	LDMC	Plant Height	DatasetID		
			[mm^2 mg^{-1}]	[mg g^{-1}]	[cm]	SLA	LDMC	Plant Height
Campanula cochlearifolia Lam.	*Campanula cochlearifolia*	SB	20	261	7			
Campanula pulla L.	*Campanula pulla*	SB	27.26	235	5			
Campanula scheuchzeri VilL.	*Campanula scheuchzeri*	SB	21.94	258	8			
Carduus defloratus L. subsp. *defloratus*	*Carduus defloratus* subsp. *defloratus*	SB	15.19	171	58			
Carex atrata L. subsp. *atrata*	*Carex atrata*	SB	15.58	405	16			
Carex capillaris L.	*Carex capillaris*	SB	14.06	332	5			
Carex ferruginea Scop. subsp. *ferruginea*	*Carex ferruginea*	TRY	NA	374.666667	33.27777778		310	25;164;310
Carex firma Host	*Carex firma*	SB	8.71	474	3			
Carex fuliginosa Schkuhr	*Carex fuliginosa*	SB	13.26	435	11			
Carex mucronata AlL.	*Carex mucronata*	SB	6.05	406	7			
Carex ornithopoda subsp. *ornithopodioides* (Hausm.) Nyman	*Carex ornithopoda*	TRY	30.598	262.72	10	25	25	164
Carex parviflora Host	*Carex parviflora*	SB	12.95	380	13			
Carex sempervirens VilL.	*Carex sempervirens*	SB	8.48	397	14			
Cerastium arvense subsp. *strictum* Gaudin	*Cerastium arvense*	TRY	22.45001421	195.609476	9.531707317	25;45;227	25;45;227	25;45;164;383
Cerastium carinthiacum Vest	*Cerastium carinthiacum* subsp. *carinthiacum*	TRY	NA	NA	12.5			164
Cerastium holeostoides Fries subsp. *triviale* (Link) Möschl	*Cerastium fontanum* subsp. *Vulgare*	TRY	20.62553255	155.426781	28.125	45;228	228	45;164
Chaerophyllum hirsutum L.	*Chaerophyllum hirsutum*	TRY	31.11653673	192.658982	42.83125	25;45;228;310	25;45;228;310	25;45;164;310
Chamorchis alpina (L.) Rich.	*Chamorchis alpina*	TRY	NA	NA	7.25			25;164
Cirsium spinosissimum (L.) Scop.	*Cirsium spinosissimum*	TRY	15.94029366	120.182749	36.25	227	227	25;164
Coeloglossum viride (L.) Hartm.	*Coeloglossum viride* subsp. *viride*	TRY	NA	NA	NA			
Crepis aurea (L.) Cass. subsp. *aurea*	*Crepis aurea*	SB	27.75	151	8			
Crepis jacquinii Tausch subsp. *jacquinii*	*Crepis jacquinii*	TRY	NA	NA	12.5			25
Crepis terglouensis (Hacq.) A.Kern.	*Crepis terglouensis*	SB	12.82	176	4			
Cystopteris alpina (Lam.) Desv.	*Cystopteris alpina*	TRY	NA	NA	20.75			25;164
Daphne mezereum L.	*Daphne mezereum*	TRY	32.9758382	182.452221	85.20833333	25;227	25;227	25;68;164
Deschampsia cespitosa (L.) P.Beauv. subsp. *cespitosa*	*Deschampsia cespitosa*	TRY	14.13880887	333.898889	52.18022727	25;45	25;45;310	25;45;164;310
Deschampsia flexuosa (L.) Trin.	*Deschampsia flexuosa*	SB	10.26	362	20			
Dianthus alpinus L.	*Dianthus alpinus*	SB	12.78	284	2			

Species name Flora Europaea	Species name TRY	Source	SLA [mm^2 mg^{-1}]	LDMC [mg g^{-1}]	Plant Height [cm]	DatasetID SLA	DatasetID LDMC	DatasetID Plant Height
Doronicum glaciale (Wulfen) Nyman	*Doronicum glaciale*	SB	8.82	205	6			
Draba aizoides L.	*Draba aizoides*	SB	17.41	276	6			
Draba sauteri Hoppe	*Draba sauteri*	SB	14.16	283	2			
Draba stellata Jacq.	*Draba stellata*	SB	16.82	283	3			
Dryas octopetala L.	*Dryas octopetala*	SB	10.7	368	3			
Dryopteris villarii (Bellardi) Woyn. ex Schinz & ThelL.		NA	NA	NA	NA			
Empetrum nigrum L. subsp. *hermaphroditum* (Hagerup) Böcher	*Empetrum nigrum*	TRY	8.79755148	372.278182	31.82827586	25;45	25;45	25;45;68;164
Epilobium alsinifolium VilL.	*Epilobium alsinifolium*	TRY	23.38767732	NA	11.76923077	200		25;200
Erigeron glabratus Hoppe & Hornsch. ex Bluff & Fingerh.	*Erigeron glabratus* subsp. *candidus*	TRY	NA	NA	NA			
Erigeron uniflorus L.	*Erigeron uniflorus*	TRY	24.36643578	178.176592	6.75	25;227;228	227;228	25;164
Euphrasia minima Jacq. ex DC. subsp. *minima*		NA	NA	NA	NA			
Euphrasia rostkoviana agg.	*Euphrasia rostkoviana*	TRY	NA	NA	28.33333333			25;310
Euphrasia salisburgensis Funck	*Euphrasia salisburgensis*	SB	18.18	252	12			
Festuca alpina Suter	*Festuca alpina*	TRY	NA	NA	5			25
Festuca pulchella Schrad.	*Festuca pulchella*	TRY	NA	NA	28.75			25;164
Festuca quadriflora Honck.	*Festuca quadriflora*	SB	11.19	433	6			
Festuca rubra agg.	*Festuca rubra*	TRY	20.80767875	291.02387	38.31442754	25;45;228	25;45;228;310	25;45;164;310
Festuca rupicaprina (Hack.) A.Kern.	*Festuca rupicaprina*	SB	21.95	428	6			
Festuca versicolor subsp. *brachystachys* (Hack.) Markgr.-Dann.	*Festuca varia*	TRY	7.065486296	391.81599	35	227	227	164
Galium anisophyllon VilL.	*Galium anisophyllon*	SB	20.14	275	6			
Galium noricum Ehrend.	*Galium noricum*	SB	17.68	312	2			
Gentiana bavarica L.	*Gentiana bavarica*	SB	16.78	277.36	0			
Gentiana brachyphylla subsp. *favratii* (Rittener) Tutin	*Gentiana brachyphylla*	TRY	15.08361407	251.335495	3.5	228	228	164
Gentiana clusii E.P.Perrier & Songeon	*Gentiana clusii*	TRY	10.15337048	224.575093	6.75	228;416	228;416	25;164
Gentiana pannonica Scop.	*Gentiana pannonica*	TRY	NA	NA	38.75			25;164
Gentiana pumila Jacq. subsp. *pumila*	*Gentiana pumila*	SB	12.82	237	2			
Gentiana verna L. subsp. *verna*	*Gentiana verna* subsp. *verna*	SB	10.12	282	2			
Gentianella germanica (Willd.) E.F.Warb.	*Gentianella germanica*	TRY	23.87677277	146.784013	16	227	227	25;164

Species name Flora Europaea	Species name TRY	Source	SLA	LDMC	Plant Height	DatasetID		
			[mm^2 mg^{-1}]	[mg g^{-1}]	[cm]	SLA	LDMC	Plant Height
Geranium sylvaticum L. subsp. *sylvaticum*	*Geranium sylvaticum*	TRY	22.56640106	258.170667	28.61514286	25;45;310	25;45;310	25;45;164;310
Geum montanum L.	*Geum montanum*	SB	15.5	310	8			
Globularia cordifolia L.	*Globularia cordifolia*	SB	11.29	279	2			
Globularia nudicaulis L.	*Globularia nudicaulis*	TRY	11.19804284	251.29165	9.770833333	200;227;416	227;310;416	25;164;200;310
Gypsophila repens L.	*Gypsophila repens*	TRY	15.232	153.464	14.5	25	25	25;164
Hedysarum hedysaroides (L.) Schinz & ThelL. subsp. *hedysaroides*	*Hedysarum hedysaroides* subsp. *hedysaroides*	SB	13.44	346	12			
Helianthemum nummularium subsp. *glabrum* (W.D.J.Koch) Wilczek	*Helianthemum nummularium*	TRY	15.1049564	263.350943	15.62121212	25;45;161;378	25;45;161;310;378	25;45;68;161;310
Helianthemum nummularium subsp. *grandiflorum* (Scop.) Schinz & ThelL.	*Helianthemum nummularium* subsp. *grandiflorum*	TRY	13.022	261.3828	11.430625	45;310	45;310	45;310
Helianthemum oelandicum subsp. *alpestre* (Jacq.) Breistr.	*Helianthemum oelandicum*	TRY	10.5	NA	5.510714286	25		25;383
Heracleum austriacum L. subsp. *austriacum*	*Heracleum austriacum*	TRY	NA	NA	17.5			25
Heracleum sphondylium L. subsp. *montanum* (Schleich. ex Gaudin) Briq.	*Heracleum sphondylium*	TRY	21.89841458	208.306	98.48333333	25;45;310	25;45;310	25;45;310
Hieracium alpinum L.	*Hieracium alpinum*	TRY	21.85533333	174.09	9.86	25;45	25;45	25;45;164
Hieracium glaucum AlL.	*Hieracium glaucum*	TRY	NA	NA	30			25;164
Hieracium murorum agg.	*Hieracium murorum*	TRY	38.80333333	126.119167	24.25	25;378	25;378	25;164
Hieracium pilosum Schleich. ex FroeL.	*Hieracium pilosum*	TRY	NA	NA	15			25;164
Hieracium villosum Jacq.	*Hieracium villosum*	TRY	NA	NA	21.25			25;164
Hippocrepis comosa L.	*Hippocrepis comosa*	TRY	15.80777213	239.035403	18.09705882	25;228;310;416	25;228;310;416	25;68;164;310
Homogyne alpina (L.) Cass.	*Homogyne alpina*	TRY	11.76030172	230.642365	8.154615385	25;227;228	25;227;228;310	25;164;310
Homogyne discolor (Jacq.) Cass.	*Homogyne discolor*	SB	8.39	271	2			
Huperzia selago (L.) Bernh. ex Schrank & Mart. subsp. *selago*	*Huperzia selago*	TRY	14.102	343.148	11.68111111	25	25	25;45;164
Hypericum maculatum Crantz	*Hypericum maculatum*	TRY	28.33538462	333.097778	41.06470588	25;45	25;45;310	25;45;310
Juncus trifidus subsp. *monanthos* (Jacq.) Asch. & Graebn.	*Juncus trifidus*	TRY	10.99460436	402.758463	16.35333333	25;45;228	25;45;228	25;45;164
Juniperus communis L. subsp. *alpina* (Suter) Celak	*Juniperus communis* var. *saxatilis*	TRY	4.406555843	469.708779	38.05	227;421	227;421	68;421
Knautia drymeia subsp. *intermedia* (Pernh. & Wettst.) Ehrend.	*Knautia drymeia*	TRY	21.87391645	154.172807	52.5	228	228	25;164
Kobresia simpliciuscula (Wahlenb.) Mack.	*Kobresia simpliciuscula*	SB	12.37	457	10			
Larix decidua MilL.	*Larix decidua*	TRY	10.25622649	279.75	100	25	25	25;68;164
Leontodon hispidus L.	*Leontodon hispidus*	SB	16.41	192	3			
Leontodon montanus Lam. subsp. *montanus*	*Leontodon montanus*	TRY	NA	NA	6.5			164

Species name Flora Europaea	Species name TRY	Source	SLA	LDMC	Plant Height	DatasetID		
			[$mm^2\ mg^{-1}$]	[$mg\ g^{-1}$]	[cm]	SLA	LDMC	Plant Height
Leontodon pyrenaicus Gouan subsp. *helveticus* (Mérat) Finch & P.D.Sell	*Scorzoneroides helvetica*	TRY	17.03762213	250.505162	17.5	227;228	227;228	164
Leucanthemum atratum (Jacq.) DC. subsp. *atratum*	*Leucanthemum atratum* subsp. *atratum*	SB	14.42	174	10			
Ligusticum mutellina (L.) Crantz	*Ligusticum mutellina*	TRY	22.45511434	243.319579	26.7	25;227;228	25;227;228	25;164
Linaria alpina (L.) MilL.	*Linaria alpina*	TRY	21.40580597	170.545706	5.472222222	25;200;228;421	228;421	25;164;200;421
Linum perenne subsp. *alpinum (Jacq.)* Ockendon	*Linum perenne*	TRY	26.432	189.824	40.90909091	25	25	25
Loiseleuria procumbens (L.) Desv.	*Loiseleuria procumbens*	SB	3.68	516	2			
Lonicera caerulea L.	*Lonicera caerulea*	TRY	13.49527665	NA	100	25		25;68;164
Lotus corniculatus agg.	*Lotus corniculatus*	TRY	24.59007554	208.312428	24.62161364	25;45;228;310;378; 416	25;45;228;310;378; 416	25;45;164;310
Luzula glabrata (Hoppe) Desv.	*Luzula glabrata*	SB	15.93	333	18			
Luzula multiflora (Retz.) Lej.	*Luzula multiflora*	TRY	21.84005547	268.811772	19.69789474	25;45;227	25;45;227	25;45;164
Meum athamanticum Jacq.	*Meum athamanticum*	TRY	13.226	263.073875	32.64375	25	45;310	25;45;164;310
Minuartia cherlerioides (Hoppe) Bech. subsp. *cherlerioides*	*Minuartia cherlerioides*	SB	14.53	464	1			
Minuartia sedoides (L.) Hiern	*Minuartia sedoides*	TRY	17.18175592	283.163185	4.954545455	227	227	25;164
Minuartia verna (L.) Hiern subsp. *verna*	*Minuartia verna* subsp. *verna*	SB	16.06	310	2			
Moehringia ciliata (Scop.) Dalla Torre	*Moehringia ciliata*	TRY	NA	NA	11.25			25;164
Moehringia muscosa L.	*Moehringia muscosa*	TRY	NA	NA	11.25			25;164
Myosotis alpestris F.W.Schmidt	*Myosotis alpestris*	TRY	27.9172454	206.600527	8.931034483	200;227;228;421	227;228;421	25;164;200;310;421
Nardus stricta L.	*Nardus stricta*	TRY	10.19159887	382.139425	14.183125	25;45;227;310	25;45;227;310	25;45;164;310
Nigritella nigra (L.) Rchb.f.	*Gymnadenia nigra*	TRY	19.67738845	160.824421	NA	227	227	
Omalotheca Hoppeana (W.D.J.Koch) Sch.Bip. & F.W.Schultz	*Gnaphalium hoppeanum*	TRY	18.04829817	234.254524	5.151612903	421	421	25;164;421
Oreochloa disticha (Wulfen) Link	*Oreochloa disticha*	SB	6.39	393	8			
Oxytropis jacquinii Bunge	*Oxytropis jacquinii*	SB	16.08	237	3			
Papaver alpinum L.	*Papaver alpinum*	TRY	NA	NA	13.75			164
Parnassia palustris L.	*Parnassia palustris*	TRY	26.36716725	169.39166	14.09090909	25;228;416	25;228	25;164
Pedicularis portenschlagii Saut. ex Rchb.	*Pedicularis portenschlagii*	SB	11.78	273	4			
Pedicularis rosea Wulfen subsp. *rosea*	*Pedicularis rosea*	SB	10.44	334	4			
Pedicularis rostratocapitata Crantz subsp. *rostratocapitata*	*Pedicularis rostratocapitata*	SB	12.24	237	6			
Pedicularis verticillata L.	*Pedicularis verticillata*	SB	16.41	183	6			

Species name Flora Europaea	Species name TRY	Source	SLA	LDMC	Plant Height	DatasetID		
			[mm² mg^{-1}]	[mg g^{-1}]	[cm]	SLA	LDMC	Plant Height
Petrocallis pyrenaica (L.) R.Br.	*Petrocallis pyrenaica*	SB	14.71	330	1			
Peucedanum ostruthium (L.) W.D.J.Koch	*Peucedanum ostruthium*	TRY	23.19047268	254.838134	59.84090909	228;421	228;421	25;164;421
Phleum alpinum L. subsp. *rhaeticum* Humphries	*Phleum alpinum*	TRY	17.69449906	346.744577	14.55142857	25;45;227;228;310	25;45;227;228;310	25;45;164;310
Phleum hirsutum Honck.	*Phleum hirsutum*	TRY	15.22708175	NA	33.82758621	383		25;164;383
Phyteuma orbiculare L.	*Phyteuma orbiculare*	TRY	28.80824411	212.013018	29.17777778	416	310;416	25;164;310
Phyteuma spicatum L.	*Phyteuma spicatum*	TRY	45.90476612	137.33832	31.59642857	25;228	25;228;310	25;164;310
Picea abies (L.) H.Karst. subsp. *abies*	*Picea abies*	TRY	10.67402839	474.8	100	25;45	45	25;45;68;164
Pimpinella major (L.) Huds.	*Pimpinella major*	TRY	25.96025981	223.982857	55.08952381	25;45;200;310	25;45;310	25;45;164;200;310
Pimpinella saxifraga L.	*Pimpinella saxifraga*	TRY	15.3583431	304.016345	34.05367816	25;45;310;378	25;45;310;378	25;45;164;310
Pinguicula alpina L.	*Pinguicula alpina*	TRY	49.82	70.772	6	25	25	25;164
Pinus mugo Turra	*Pinus mugo*	SB	4.19	419	62			
Poa alpina L.	*Poa alpina*	SB	14.06	327	5			
Poa minor Gaudin	*Poa minor*	TRY	NA	NA	13.25			25;164
Polygonum viviparum L.	*Persicaria vivipara*	SB	14.36	249	6			
Polystichum lonchitis (L.) Roth	*Polystichum lonchitis*	TRY	11.77561973	301.516	24	25;200	25	25;164;200
Polytrichum juniperinum Hedw.	*Polytrichum juniperinum*	TRY	NA	NA	NA			
Potentilla aurea L. subsp. *aurea*	*Potentilla aurea*	SB	15.67	314	3			
Potentilla brauniana Hoppe	*Potentilla brauniana*	TRY	NA	NA	3.25			25;164
Potentilla clusiana Jacq.	*Potentilla clusiana*	SB	12.03	414	3			
Potentilla crantzii (Crantz) Beck ex Fritsch	*Potentilla crantzii*	SB	12.23	327	4			
Primula auricula L.	*Primula auricula*	TRY	20.65734746	120.387844	13.75	25;228	25;228	25;164
Primula clusiana Tausch	*Primula clusiana*	SB	11.53	207	3			
Primula elatior (L.) Hill	*Primula elatior*	TRY	34.64504365	141.289	10.83333333	25	25	25
Pritzelago alpina (L.) Kuntze subsp. *alpina*	*Pritzelago alpina*	SB	12.26	265	2			
Pseudorchis albida (L.) Á.Löve & D.Löve	*Pseudorchis albida*	TRY	21.672	127.512	16.75	25	25	25;164
Pulsatilla alpina (L.) Delarbre subsp. *alpina*	*Pulsatilla alpina* subsp. *alpina*	SB	13.38	248	40			
Ranunculus alpestris L. subsp. *alpestris*	*Ranunculus alpestris*	SB	11.68	219	4			
Ranunculus hybridus Biria	*Ranunculus hybridus*	TRY	NA	NA	7			25;164
Ranunculus montanus Willd.	*Ranunculus montanus*	SB	24.23	203	15			
Rhinanthus angustifolius C.C.GmeL.	*Rhinanthus serotinus*	TRY	20.29458922	273.3	28.36111111	25;200;378	378	25;200
Rhodiola rosea L.	*Rhodiola rosea* var. *rosea*	TRY	NA	NA	NA			
Rhododendron ferrugineum L.	*Rhododendron ferrugineum*	TRY	5.316293864	509.049312	43.63636364	421	421	25;68;164;421
Rhododendron hirsutum L.	*Rhododendron hirsutum*	TRY	NA	NA	64.375			25;68;164
Rhodothamnus chamaecistus (L.) Rchb.	*Rhodothamnus chamaecistus*	TRY	NA	NA	26.07142857			25;68;164
Rumex alpestris Jacq.	*Rumex alpestris*	TRY	35.71421289	127.268085	35.14	25;45;228	25;45;228;310	25;45;164;310

Species name Flora Europaea	Species name TRY	Source	SLA [$mm^2\ mg^{-1}$]	LDMC [$mg\ g^{-1}$]	Plant Height [cm]	DatasetID SLA	DatasetID LDMC	DatasetID Plant Height
Rumex scutatus L.	*Rumex scutatus*	TRY	35.98121935	96.806697	26.40909091	421	421	25;164;421
Salix alpina Scop.	*Salix alpina*	SB	12.19	396	4			
Salix reticulata L.	*Salix reticulata*	TRY	9.782604275	378.892857	15.052	25;45	25;45	25;45;68;164
Salix retusa L.	*Salix retusa*	SB	11	357	3			
Salix serpillifolia Scop.	*Salix serpyllifolia*	TRY	11.04467754	328.724726	5.1	227;421	227;421	25;164;421
Saussurea pygmaea (Jacq.) Spreng.	*Saussurea pygmaea*	SB	10.41	228	6			
Saxifraga aizoides L.	*Saxifraga aizoides*	TRY	12.90131398	192.021939	7.735294118	25;45;228	25;45;228	25;45;164
Saxifraga androsacea L.	*Saxifraga androsacea*	TRY	27.78218357	119.807545	3.612903226	421	421	25;164;421
Saxifraga caesia L.	*Saxifraga caesia*	SB	8.33	376	2			
Saxifraga exarata subsp. *moschata* (Wulfen) CaVilL.	*Saxifraga exarata* subsp. *moschata*	TRY	NA	NA	3.25			25;164
Saxifraga paniculata MilL.	*Saxifraga paniculata*	TRY	8.81	240.87	13.25	25	25	25;164
Saxifraga sedoides L. subsp. *sedoides*	*Saxifraga sedoides*	SB	31.56	133	3			
Saxifraga stellaris L.	*Saxifraga stellaris*	TRY	23.38888889	162.552222	10.8125	25;45	25;45	25;164
Scabiosa lucida VilL.	*Scabiosa lucida*	TRY	NA	NA	18.75			25;164
Sedum album L.	*Sedum album*	TRY	16.68029169	46.640471	11.03846154	25;228	25;45;228	25;45;164
Sedum atratum L.	*Sedum atratum*	TRY	8.1202014	93.4577	2.580645161	421	421	25;164;421
Selaginella selaginoides (L.) Link	*Selaginella selaginoides*	TRY	32.28501	286.084917	8.75	25;45;227	45;227	25;164
Senecio rivularis (Waldst. & Kit.) DC.	*Tephroseris crispa*	TRY	NA	NA	45			25
Sesleria albicans Kit. ex Schult.	*Sesleria albicans*	SB	14.48	344	14			
Sesleria ovata (Hoppe) A.Kern.	*Sesleria ovata*	SB	14.53	349	6			
Silene acaulis (L.) Jacq. subsp. *acaulis*	*Silene acaulis*	TRY	18.82791021	212.618142	2.101875	25;45;227;228;421	45;227;228;421	25;45;164;421
Silene alpestris Jacq.	*Silene alpestris*	SB	17.5	220	17			
Silene pusilla Waldst. & Kit.	*Silene pusilla*	TRY	NA	NA	12			25;164
Silene vulgaris (Moench*)* Garcke subsp. *vulgaris*	*Silene vulgaris*	TRY	22.0208225	148.589793	37.67692308	25;228	25;228;310	25;164;310
Soldanella alpina L.	*Soldanella alpina*	TRY	12.17728571	237.466	8.25	416	416	25;164
Soldanella austriaca Vierh.	*Soldanella austriaca*	TRY	NA	NA	NA			
Solidago virgaurea L. subsp. *minuta* (L.) Arcang.	*Solidago virgaurea* subsp. *minuta*	SB	24.48	269	29			
Stachys alopecuros (L.) Benth.	*Stachys alopecuros*	TRY	25.44408239	170.960908	28.75	228	228	25;164
Thamnolia vermicularis (Sw.) Schaer.	*Thamnolia vermicularis*	TRY	NA	NA	NA			
Thesium alpinum L.	*Thesium alpinum*	TRY	NA	NA	18.25			25;164
Thlaspi alpinum Crantz subsp. *alpinum*	*Thlaspi alpestre*	SB	12.98	269	2			
Thlaspi rotundifolium (L.) Gaudin, non Tineo subsp. *rotundifolium*	*Thlaspi rotundifolium*	TRY	NA	NA	10			164

Species name Flora Europaea	Species name TRY	Source	SLA [mm² mg^{-1}]	LDMC [mg g^{-1}]	Plant Height [cm]	DatasetID		
						SLA	LDMC	Plant Height
Thymus praecox Opiz subsp. *polytrichus* (A.Kern. ex Borb s) Jalas	*Thymus praecox* subsp. *polytrichus*	TRY	18.27172614	299.319648	4.95	45;227	45;227	45
Tofieldia calyculata (L.) Wahlenb.	*Tofieldia calyculata*	TRY	14.01237908	277.003636	14.25	25;228	25;228	25;164
Tofieldia pusilla (Michx.) Pers. subsp. *Pusilla*	*Tofieldia pusilla*	TRY	17.01785185	286.166923	4.64	25;45	25;45	25;45;164
Trifolium pratense L. subsp. *nivale* Arc.	*Trifolium pratense* var. *nivale*	SB	20.7	241	5			
Trisetum distichophyllum (VilL.) P.Beauv.	*Trisetum distichophyllum*	TRY	NA	NA	11.5			25;164
Trollius europaeus L.	*Trollius europaeus*	TRY	21.03323761	218.20367	30.21	25;228;310	25;228;310	25;164;310
Vaccinium myrtillus L.	*Vaccinium myrtillus*	TRY	24.00873083	392.529913	28.07447368	25;45;200;228	25;45;228;310	25;45;68;164;200;310
Vaccinium uliginosum L. subsp. *microphyllum* *Lange*	*Vaccinium uliginosum* subsp. *microphyllum*	TRY	NA	NA	15			68
Vaccinium vitis-idaea L. subsp. *vitis-idaea*	*Vaccinium vitis-idaea*	SB	5.98	476	5			
Valeriana celtica subsp. *norica* Vierh.	*Valeriana celtica*	TRY	NA	NA	NA			
Valeriana elongata Jacq.	*Valeriana elongata*	TRY	NA	NA	15			164
Valeriana montana L.	*Valeriana montana*	TRY	21.75942219	207.334816	19.29166667	200;416;421	416;421	25;164;200;421
Valeriana saxatilis L. subsp. *Saxatilis*	*Valeriana saxatilis*	TRY	NA	NA	12			25;164
Valeriana tripteris L.	*Valeriana tripteris*	TRY	42.70205541	123.104955	29.25	25;228	25;228	25;164
Veratrum album L.	*Veratrum album*	TRY	NA	209.49	87.3125		310	25;164;310
Veronica alpina L.	*Veronica alpina*	TRY	28.10593158	197.468209	6.924	25;45;228	25;45;228	25;45;164
Veronica aphylla L.	*Veronica aphylla*	SB	14.59	277	1			
Veronica fruticans Jacq.	*Veronica fruticans*	TRY	16.692	247.606	9.227272727	25	25	25;164
Viola alpina Jacq.	*Viola alpina*	TRY	NA	NA	NA			
Viola biflora L.	*Viola biflora*	TRY	52.50997131	132.28625	8.681818182	25;45;200	25;45	25;164;200

VIII. REFERENCES TRAIT MEANS

Suppl. Table 4: References of species traits from Suppl. Table 4, mean traits (SLA, LDMC, H) from these studies were taken to compile Figure 5.

DatasetID	Reference
25	Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J. M. van Groenendael, L. Klimes, J. Klimesova, S. Klotz, G. M. Rusch, Hermy, M. , D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J. G. Hodgson, A.-K. Jackel, I. Kühn, D. Kunzmann, W. A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B. Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96:1266-1274.
68	Wirth, C. and J. W. Lichstein. 2009. The Imprint of Species Turnover on Old-Growth Forest Carbon Balances - Insights From a Trait-Based Model of Forest Dynamics. Pages 81-113 in C. Wirth, G. Gleixner, and M. Heimann, editors. Old-Growth Forests: Function, Fate and Value. Springer, New York, Berlin, Heidelberg.
45	Garnier, E., S. Lavorel, P. Ansquer, H. Castro, P. Cruz, J. Dolezal, O. Eriksson, C. Fortunel, H. Freitas, C. Golodets, K. Grigulis, C. Jouany, E. Kazakou, J. Kigel, M. Kleyer, V. Lehsten, J. Leps, T. Meier, R. Pakeman, M. Papadimitriou, V. P. Papanastasis, H. Quested, F. Quetier, M. Robson, C. Roumet, G. Rusch, C. Skarpe, M. Sternberg, J.-P. Theau, A. Thebault, D. Vile, and M. P. Zarovali. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. Annals of Botany 99:967-985.
161	Campetella, G, Botta-Dukát, Z, Wellstein, C, Canullo, R, Gatto, S, Chelli, S, Mucina, L, Bartha, S (2011): Patterns of plant trait-environment relationships along a forest succession chronosequence. Agriculture, Ecosystems & Environment, 145(1), 38-48. doi:10.1016/j.agee.2011.06.025
164	Bragazza L (2009) Conservation priority of Italian alpine habitats: a floristic approach based on potential distribution of vascular plant species. Biodiversity and Conservation 18: 2823–2835.
200	Milla & Reich 2011 Annals of Botany 107: 455–465, 2011.
227	Pierce S., Ceriani R.M., De Andreis R., Luzzaro A. & Cerabolini B. 2007. The leaf economics spectrum of Poaceae reflects variation in survival strategies. Plant Biosystems 141(3): 337-343.
227	Pierce S., Luzzaro A., Caccianiga M., Ceriani R.M. & Cerabolini B. 2007. Disturbance is the principal ?-scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. Journal of Ecology 95: 698-706.

227 Pierce S., Brusa G., Vagge I., Cerabolini B.E.L. (2013) Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Functional Ecology, 27(4): 1002-1010

228 Cerabolini B.E.L., Brusa G., Ceriani R.M., De Andreis R., Luzzaro A. & Pierce S. 2010. Can CSR classification be generally applied outside Britain? Plant Ecology 210: 253-261

310 Gos P., Loucougaray G., Colace MP., Arnoldi C., Gaucherand S., Dumazel D., Girard L., Delorme S., Lavorel S. (2016) Oecologia 180:1001 doi:10.1007/s00442-016-3551-3

378 Lhotsky B., Anikó Csecserits, Bence Kovács, Zoltán Botta-Dukát: New plant trait records of the Hungarian flora

383 Giarrizzo E., Burrascano S., Chiti T., de Bello F., Leps J., Zavattero L., Blasi C. (2017) Re-visiting historical semi-natural grasslands in the Apennines to assess patterns of changes in plant species composition and functional traits. Applied Vegetation Science 20(2):247-258, doi: 10.1111/avsc.12288

416 Bucher, S.F., Auerswald, K., Tautenhahn, S., Geiger, A., Otto, J., Müller, A. and Römermann, C. (2016) Intra- and interspecific variation in stomatal pore area index along altitudinal gradients and its relation to leaf functional traits. Plant Ecology 217, 229-240

421 Thuiller W - Traits of European Alpine Flora - Wilfried Thuiller - OriginAlps Project - Centre National de la Recherche Scientifique

IX. INTERSPECIFIC MEAN TRAIT VALUES

Suppl. Table 5: Interspecific mean values of species trait list (Suppl. Table 4) calculated per elevation category with species presence/absence data from Steinbauer (2011) on Hochschwab, Austria (each present plant species is only counted once per elevation category).

Elevation	interspecific mean values		
category	SLA	LDMC	Height
1800	17.339	268.963	16.289
1925	17.261	271.102	13.400
2050	16.523	277.190	11.132
2150	16.745	275.906	9.526
2250	16.353	281.393	7.308

X. RELATIVE SHARE OF INTRASPECIFIC TRAIT VALUES

Suppl. Table 6: Relative share of intraspecific trait values of a) *Carex firma* and b) *Dryas octopetala* on the range of interspecific values (absolute difference between interspecific minimum to maximum values is equivalent to 100 %), calculated per elevation category. Interspecific trait values (Suppl. Table 4) combined with species presence/absence data from Steinbauer (2011) on Hochschwab, Austria to calculate range of values.

Elevation	relative range of intraspecific values		
category	SLA	LDMC	Height
a) *Carex firma*			
1800	0.135	0.269	0.029
1925	0.108	0.200	0.021
2050	0.066	0.268	0.030
2150	0.131	0.325	0.039
2250	0.095	0.283	0.066
b) *Dryas octopetala*			
1800	0.143	0.290	0.022
1925	0.100	0.162	0.021
2050	0.102	0.255	0.043
2150	0.104	0.219	0.026
2250	0.090	0.256	0.069

XI. R SCRIPT

```
####NMDS####
#---Packages and Libraries---------------------------------------------------
library(vegan) # for the Manova (adonis)
library(plotrix) # for addtable2plot()
library(stringi)
#---Functions-----------------------------------------------------------------
# To translate the p values in stars
stars <- function(p) {
  star<-ifelse(p<0.0001,"****",ifelse(
    p<0.001,"***",ifelse(
      p<0.01,"**",ifelse(
        p<0.05,"*",ifelse(
          p<0.1,"(*)",""))))) 
  star
}

# To extract character from a string from the end
substRight = function(x,n){
  substring(x,nchar(x)-n+1)
}
#---Script--------------------------------------------------------------------
dat00 <- read.csv('CFDO_Datacomplete_v7.csv', header=TRUE, sep=";")
head(dat00)
str(dat00)

# calculation of response metrics
dat00$SLA<- dat00$LA/(dat00$DW*1000) #in mm2.mg-1
dat00$LDMC <- (dat00$DW*1000)/dat00$FW #in mg/g

dat02<-dat00[dat00$IndNo<11,] ## only first 10 values for balanced design

##ordination
# Tables
bothSp<-as.data.frame(dat02[,c('Height','SLA','LDMC')],
  row.names=as.character(dat02$Individual))
envBothSP<-as.data.frame(dat02[,c('Cover','Slope','ExpEast',
  'ExpNorth','Elevation')],row.names=as.character(dat02$Individual))

cf_dat<-as.data.frame(dat02[dat02$Species=='CF',c('Height','SLA','LDMC')],
  row.names=as.character(dat02$Transect[dat02$Species=='CF']))
envCf<-as.data.frame(dat02[dat02$Species=='CF',c('Cover','Slope','ExpEast',
  'ExpNorth','Elevation')],
  row.names=as.character(dat02$Transect[dat02$Species=='CF']))

do_dat<-as.data.frame(dat02[dat02$Species=='DO',c('Height','SLA','LDMC')],
  row.names=as.character(dat02$Transect[dat02$Species=='DO']))
envDo<-as.data.frame(dat02[dat02$Species=='DO',c('Cover','Slope','ExpEast',
  'ExpNorth','Elevation')],
  row.names=as.character(dat02$Transect[dat02$Species=='DO']))

##NMDS
nmdsBothSp<-metaMDS(bothSp)
nmdsCf<-metaMDS(cf_dat)
nmdsDo<-metaMDS(do_dat)

##Fitting of environmental variables
ef<-envfit(nmdsBothSp,envBothSP) #both species
efTab<-cbind(round(ef$vectors[[2]],3),stars(ef$vectors[[4]])) #outcome table
colnames(efTab)<-c('r2','p')
```

```
efCf<-envfit(nmdsCf,envCf) #Carex
efCfTab<-cbind(round(efCf$vectors[[2]],3),stars(efCf$vectors[[4]]))
colnames(efCfTab)<-c('r2','p')

efDo<-envfit(nmdsDo,envDo) #Dryas
efDoTab<-cbind(round(efDo$vectors[[2]],3),stars(efDo$vectors[[4]]))
colnames(efDoTab)<-c('r2','p')

##the figures (and outcomes)
png('Traits_NMDS.png',width=21,height=29.7,units='cm',res=200)
par(mfrow=c(3,2))

#both species
fig<-ordiplot(nmdsBothSp,type='n', xlab='NMDS1',ylab='NMDS2',
  main='Both Species',pch='.')
cf<-fig$sites[stri_sub(rownames(fig$sites),-5,-4)=='CF',]
do<-fig$sites[stri_sub(rownames(fig$sites),-5,-4)=='DO',]
points(cf[,1],cf[,2],col='red',pch=20)
points(do[,1],do[,2],col='blue',pch=20)
plot(ef,p.max=0.05,col='black')
text(min(fig$site[,1])*0.7,min(fig$site[,2])*1.05,paste0('stress=',
  round(nmdsBothSp$stress,4)),adj=c(1,0))

plot(0,0,type='n',xaxt='n',yaxt='n',bty='n',xlab='',ylab='')
addtable2plot(-1,-1 ,efTab,bty="n",display.rownames=TRUE,title="Goodness of
  fit for Both Species") #to add R2 table

#Carex
figCf<-ordiplot(nmdsCf,type='n', xlab='NMDS1',ylab='NMDS2',
  main='Carex firma')
points(nmdsCf, display="sites", col="red")
plot(efCf,p.max=0.05,col='black')
text(min(figCf$site[,1])*0.6,min(figCf$site[,2])*1.1,paste0('stress=',
  round(nmdsCf$stress,4)),adj=c(1,0))

plot(0,0,type='n',xaxt='n',yaxt='n',bty='n',xlab='',ylab='')
addtable2plot(-1,-1 ,efCfTab,bty="n",display.rownames=TRUE,title="Goodness
  of fit for Carex firma")

#Dryas
figDo<-ordiplot(nmdsDo,type='n', xlab='NMDS1',ylab='NMDS2',
  main='Dryas octopetala')
points(nmdsDo, display="sites", col="blue")
plot(efDo,p.max=0.05,col='black')
text(min(figDo$site[,1])*0.55,min(figDo$site[,2])*1.1,paste0('stress=',
  round(nmdsDo$stress,4)),adj=c(1,0))

plot(0,0,type='n',xaxt='n',yaxt='n',bty='n',xlab='',ylab='')
addtable2plot(-1,-1 ,efDoTab,bty="n",display.rownames=TRUE,title="Goodness
  of fit for Dryas octopetala")

dev.off()
```

####PERMANOVA####

```
#---Packages and Libraries----------------------------------------------------
library(vegan)
#---Script--------------------------------------------------------------------
dat00 <- read.csv('CFDO_Datacomplete_v7.csv', header=TRUE, sep=";")
head(dat00)
str(dat00)
```

```
dat00$SLA<- dat00$LA/(dat00$DW*1000) #in mm2.mg-1
dat00$LDMC <- (dat00$DW*1000)/dat00$FW #in mg/g

dat02<-dat00[dat00$IndNo<11,] ## only first 10 values now for a balanced
  permanova

dat_cf<-dat02[dat02$Species=='CF',]
dat_do<-dat02[dat02$Species=='DO',]

adonis(dat_cf[,c(13,18,19)]~dat_cf$Elevation+dat_cf$Slope+dat_cf$ExpEast*
   dat_cf$ExpNorth+dat_cf$Cover, method="euclidian"))

adonis(dat_do[,c(13,18,19)]~dat_do$Elevation+dat_do$Slope+dat_do$ExpEast*
   dat_do$ExpNorth+dat_do$Cover,method='euclidian'))
```

##GLMMs##

```
#---Packages and Libraries---------------------------------------------------
library(glmmTMB)
library(MuMIn)
library(r2glmm)
#---Function-----------------------------------------------------------------
source("C:/Users/malen/Desktop/Masterarbeit/R/HighstatLibV10.R")
#---Script-------------------------------------------------------------------
dat<-read.table("CFDO_Datacomplete_v7.csv",header=TRUE, sep=";")
dat$SLA<- dat$LA/(dat$DW*1000) #in mm2/mg
dat$LDMC <- (dat$DW*1000)/dat$FW #in mg/g

datCF<-dat[dat$Species=="CF",]
datDO<-dat[dat$Species=="DO",]


####testing variance inflation factor####
Y <- cbind(datCF$Elevation, datCF$Slope, datCF$ExpEast,
 datCF$ExpNorth,datCF$Cover)
corvif(Y)

Z <- cbind(datDO$Elevation, datDO$Slope, datDO$ExpEast, datDO$ExpNorth,
 datDO$Cover)
corvif(Z)


####building GLMMs####
#S=SLA, L=LDMC, H=Plant height
#cf=Carex firma, do=Dryas octopetala
#a=altitude, en=eastness*northness, c=cover, s=slope

#SLA cf####
S_cf_a <- glmmTMB(SLA ~ Elevation + (1|Transect),family=gaussian, data=datCF)
S_cf_en <- glmmTMB(SLA ~ ExpEast*ExpNorth + (1|Transect),family=gaussian,
 data=datCF)
S_cf_c <- glmmTMB(SLA ~ Cover +  (1|Transect),family=gaussian, data=datCF)
S_cf_s <- glmmTMB(SLA ~ Slope +  (1|Transect),family=gaussian, data=datCF)
S_cf_aen<- glmmTMB(SLA ~ Elevation + ExpEast*ExpNorth + (1|Transect),
 family=gaussian, data=datCF)
S_cf_ac<- glmmTMB(SLA ~ Elevation + Cover + (1|Transect),family=gaussian,
 data=datCF)
S_cf_as<- glmmTMB(SLA ~ Elevation + Slope + (1|Transect),family=gaussian,
 data=datCF)
S_cf_enc<- glmmTMB(SLA ~ ExpEast*ExpNorth + Cover + (1|Transect),
```

```
 family=gaussian, data=datCF)
S_cf_ens<- glmmTMB(SLA ~ ExpEast*ExpNorth + Slope + (1|Transect),
 family=gaussian, data=datCF)
S_cf_cs <- glmmTMB(SLA ~ Cover + Slope +(1|Transect),family=gaussian,
 data=datCF)
S_cf_aenc<- glmmTMB(SLA ~ Elevation + ExpEast*ExpNorth + Cover +
  (1|Transect),family=gaussian, data=datCF)
S_cf_aens<- glmmTMB(SLA ~ Elevation + ExpEast*ExpNorth + Slope +
  (1|Transect),family=gaussian, data=datCF)
S_cf_asc<- glmmTMB(SLA ~ Elevation + Slope + Cover +
  (1|Transect),family=gaussian, data=datCF)
S_cf_encs<- glmmTMB(SLA ~ ExpEast*ExpNorth + Cover + Slope +
  (1|Transect),family=gaussian, data=datCF)
S_cf_aencs<- glmmTMB(SLA ~ Elevation + ExpEast*ExpNorth + Cover + Slope +
  (1|Transect),family=gaussian, data=datCF)


sink("AICcs_SLA_CF.txt")
print(AICc(S_cf_a , S_cf_en , S_cf_c , S_cf_s ,
     S_cf_aen, S_cf_ac, S_cf_as, S_cf_enc, S_cf_ens, S_cf_cs,
     S_cf_aenc, S_cf_aens, S_cf_asc, S_cf_encs,
     S_cf_aencs))
sink()


r.squaredGLMM(S_cf_a); r.squaredGLMM(S_cf_en); r.squaredGLMM(S_cf_c);
r.squaredGLMM(S_cf_s); r.squaredGLMM(S_cf_aen); r.squaredGLMM(S_cf_ac);
r.squaredGLMM(S_cf_as);r.squaredGLMM(S_cf_enc); r.squaredGLMM(S_cf_ens);
r.squaredGLMM(S_cf_cs);r.squaredGLMM(S_cf_aenc); r.squaredGLMM(S_cf_aens);
r.squaredGLMM(S_cf_asc); r.squaredGLMM(S_cf_encs); r.squaredGLMM(S_cf_aencs)


##repeat same steps for S_do; L_cf; L_do; H_cf; H_do
```

##PSEUDO GRADIENTS##

```
#---Packages and Libraries---------------------------------------------
library(glmmTMB)# for the GLMM
library(emmeans)
library(multcomp)# for the tukey comparisons
library(car)
#---Functions-----------------------------------------------------------
#Standard error calculation
se<- function(x, na.rm){
  sd(x, na.rm=na.rm)/sqrt(length(x))
}

#stars function
stars <- function(p) {
  star<-ifelse(p<0.0001,"****",ifelse(
    p<0.001,"***",ifelse(
      p<0.01,"**",ifelse(
        p<0.05,"*",ifelse(
          p<0.1,"(*)",""))))) 
  star
}

# To recode the variable
recodevar <- function(data, oldvalue, newvalue) {
  if (is.factor(data)){ data<- as.character(data)}
  newvec <- data
```

```
  for (i in unique(oldvalue)){newvec[data == i] <- newvalue[oldvalue == i]}
  newvec
}

#---Script---------------------------------------------------------------
dat00 <- read.csv('CFDO_Datacomplete_v7.csv', header=TRUE, sep=";")
head(dat00)
str(dat00)

# calculation of response metrics
dat00$SLA<- dat00$LA/(dat00$DW*1000) #in mm2/mg-1
dat00$LDMC <- (dat00$DW*1000)/dat00$FW #in mg/g


# data that we need for plots
dat03<-dat00

####Statistics####
#Outcome table
SummTable<-data.frame(source=c('Source of deviation','','Species (sp)',
      'Exposition (ex)','Elevation (el)','sp x ex','sp x el','ex x el',
      'sp x ex x el','','HSD tukey test'),
 sla1=c('','df',rep('',9)),sla2=rep('',11),sla3=c('SLA','Chisq',rep('',9)),
 sla4=c('','p',rep('',9)),
 ldmc1=rep('',11),ldmc2=rep('',11),ldmc3=c('LDMC','Chisq',rep('',9)),
 ldmc4=c('','p',rep('',9)),
height1=rep('',11),height2=rep('',11),height3=c('Height','Chisq',rep('',9),
 height4=c('','p',rep('',9)))

for (t in 1:3){
trait<-c('SLA','LDMC','Height')[t]
tab<-dat03[,c('Transect','Species','East_cat','Elev_cat',trait)]
colnames(tab)<-c('trans','sp','expo','elev','trait')
tab$elev<-as.factor(tab$elev)
tab$grp<-as.factor(paste(tab$sp,tab$expo,sep='_'))# groupe sp-expo (1 per
  curve on the graph)
mod1<-glmmTMB(trait~sp*expo*elev+(1|trans),family=gaussian,data=tab)# 3 way
  model
tab1<-Anova(mod1)
mod2<-glmmTMB(trait~grp*elev+(1|trans),family=gaussian,data=tab) # 2 Way
model for the pairwise comparison of curve patterns
mod2emm<-emmeans(mod2,spec='grp')
tab2<-cld(mod2emm) # for compact letter display
tab2$grp<-recodevar(tab2$grp,c('CF_East','CF_West','DO_East','DO_West'),
  c('C.f._ E','C.f._W', 'D.o._E','D.o._W'))
tukeys<-rep(NA,4)
for (i in 1:4){
groups<-strsplit(gsub(" ","",tab2$.group[i]),'')
groups2<-as.numeric(groups[[1]])
tukeys[i]<-paste0(letters[groups2],collapse='')
}
SummTable[11,(t-1)*4+3]<-paste(paste0(tab2$grp,': ',tukeys,collapse=', '))
if(t==1){SummTable[3:9,2]<-tab1$Df}
SummTable[3:9,(t-1)*4+4]<-round(tab1$Chisq,2)
SummTable[3:9,(t-1)*4+5]<-round(tab1$`Pr(>Chisq)`,4)

for (r in 3:9){
if(as.numeric(SummTable[r,(t-1)*4+5])<0.0001){SummTable[r,(t-1)*4+5]<-
  '<0.0001'}}
}

write.csv(SummTable,'Pseudo_gradients_GLMMSummary.csv',row.names = F)
```

```
####Plotting####
#Tables for plots
mTab<-aggregate(dat03[,c('SLA','LDMC','Height')],
  list(elev=dat03$Elev_cat,sp=dat03$Species,exp=dat03$East_cat),mean,
  na.rm=T)
sTab<-aggregate(dat03[,c('SLA','LDMC','Height')],
  list(elev=dat03$Elev_cat,sp=dat03$Species,exp=dat03$East_cat),se,na.rm=T)

# Pairwise comparisons table (from statistics)
tukTab<-data.frame(sp=c('CF','CF','DO','DO'),
  exp=c('West','East','West','East'),SLA=c('bc','c','a','b'),
  LDMC=c('b','b','a','a'),Height=c('bc','c','a','ab'))

####Plots###
png('Pseudo_gradients.png',width=21,height=29.7,units='cm',res=200)
par(mfrow=c(3,1),mar=c(5,5,2,1))
for (t in 1:3){
trait<-c('SLA','LDMC','Height')[t]
trait2<-c(expression(paste('SLA (',mm^2,'.',mg^-1,')',sep='')),
  expression(paste('LDMC (mg.',g^-1,')',sep='')), 'Height (cm)')[t]
plot(0,xlim=c(min(mTab$elev)*0.98,max(mTab$elev)),
  ylim=c(min(dat03[,trait],na.rm=T),max(dat03[,trait],na.rm=T)),
  type='n',ylab=trait2,xlab=paste0('Elevation (m a.s.l.)'), xaxt='n')
     # x-axis drawn separately to handle the representation of category
axis(1,at=unique(mTab$elev),labels=c('<1850', '1850-1999','2000-2099',
  '2100-2200',expression(''>2200)), cex=1.2)

for(s in 1:2){
sp<-unique(mTab$sp)[s]
colo<-c('red','darkblue')[s]
for(e in 1:2){
expo<-unique(mTab$exp)[e]
symb<-c(16,17)[e]
points(mTab[mTab$exp==expo & mTab$sp==sp,'elev']+(((s-1)*2+e)*3-5),
  mTab[mTab$exp==expo & mTab$sp==sp,t+3],
  col=colo,pch=symb,type='b') # +(s-1)* to jitter the points
arrows(mTab[mTab$exp==expo & mTab$sp==sp,'elev']+(((s-1)*2+e)*3-5),
  mTab[mTab$exp==expo & mTab$sp==sp,t+3]+sTab[sTab$exp==expo &
   sTab$sp==sp,t+3],
  mTab[mTab$exp==expo & mTab$sp==sp,'elev']+(((s-1)*2+e)*3-5),
  mTab[mTab$exp==expo & mTab$sp==sp,t+3]-sTab[sTab$exp==expo &
   sTab$sp==sp,t+3],
  length=0.02,angle=90,code=3,col=colo)
if(t==3){
 if(e==1){
  if(s==1){
text(min(mTab$elev)*0.99,mTab[mTab$exp==expo & mTab$sp==sp &
  mTab$elev==1800,t+3]*1.05,
  labels=tukTab[tukTab$sp==sp & tukTab$exp==expo,trait], cex=1.3)
}else{
text(min(mTab$elev)*0.99,mTab[mTab$exp==expo & mTab$sp==sp &
  mTab$elev==1800,t+3]*0.95,
  labels=tukTab[tukTab$sp==sp & tukTab$exp==expo,trait], cex=1.3)
}
}else{
text(min(mTab$elev)*0.99,mTab[mTab$exp==expo & mTab$sp==sp &
  mTab$elev==1800,t+3],
  labels=tukTab[tukTab$sp==sp & tukTab$exp==expo,trait], cex=1.3)
}
}else{
text(min(mTab$elev)*0.99,mTab[mTab$exp==expo & mTab$sp==sp &
  mTab$elev==1800,t+3],
```

```
  labels=tukTab[tukTab$sp==sp & tukTab$exp==expo,trait], cex=1.3)
}
}
}

if (t==1){
text(rep(min(mTab$elev,na.rm=T),2),c(0.99,0.95)*max(dat03[,trait],na.rm=T),
 labels=c('Carex firma', 'Dryas octopetala'),
 col=c('red','darkblue'),font=3,cex=1.3, adj=c(0,NA))

points(rep(min(mTab$elev,na.rm=T)*1.1,2),c(0.99,0.95)*max(dat03[,trait],
  na.rm=T),pch=c(16,17), cex=1.2)

text(rep(min(mTab$elev,na.rm=T)*1.105,2),c(0.99,0.95)*max(dat03[,trait],
  na.rm=T), labels=unique(mTab$exp)[1:2],cex=1.2,adj=c(0,NA))
}
}
dev.off()
```

##DENSITY PLOTS####

```
#---Script------------------------------------------------------------
#load intraspecific data
data_intraspec<-read.table("data_intraspec.csv",header=TRUE, sep=";")
#load interspecific data
data_interspec<-read.table("data_interspec_occurrenceonce.csv",header=TRUE,
sep=";")

#intraspecific data into species data sets
datCF<-data_intraspec[data_intraspec$Species=="CF",c("Transect","Species",
  "Elevation","SLA","LDMC","Height","Elev_cat")]
datDO<-data_intraspec[data_intraspec$Species=="DO",c("Transect","Species",
  "Elevation","SLA","LDMC","Height","Elev_cat")]

#calculate means of interspecific data per elevation category
elevcats<-sort(unique(data_interspec$Elev_cat))
df_means<-as.data.frame(matrix(data=NA,ncol=4,nrow=length(elevcats)))
colnames(df_means)<-c("Elev_cat","mean_SLA","mean_LDMC","mean_Height")
df_means[,1]<-elevcats

for (i in 1:length(elevcats)) {
df_means[i,2] <-
  mean(data_interspec$SLA[data_interspec$Elev_cat==elevcats[i]],
  na.rm=TRUE)
df_means[i,3] <-
  mean(data_interspec$LDMC[data_interspec$Elev_cat==elevcats[i]],
  na.rm=TRUE)
df_means[i,4] <-
  mean(data_interspec$Height[data_interspec$Elev_cat==elevcats[i]],
  na.rm=TRUE)
}


#densities
dens_SLA<-list()
dens_LDMC<-list()
dens_Height<-list()

for (i in 1:length(elevcats)) {
dens_SLA[[i]]<-list(density(datCF[datCF$Elev_cat==elevcats[i], "SLA"],
  na.rm=TRUE))
```

```
dens_SLA[[i+length(elevcats)]]<-
  list(density(datDO[datDO$Elev_cat==elevcats[i], "SLA"], na.rm=TRUE))
dens_SLA[[i+length(elevcats)*2]]<-
  list(density(data_interspec[data_interspec$Elev_cat==elevcats[i], "SLA"],
  na.rm=TRUE))

dens_LDMC[[i]]<-list(density(datCF[datCF$Elev_cat==elevcats[i], "LDMC"],
  na.rm=TRUE))
dens_LDMC[[i+length(elevcats)]]<-
  list(density(datDO[datDO$Elev_cat==elevcats[i], "LDMC"], na.rm=TRUE))
dens_LDMC[[i+length(elevcats)*2]]<-
  list(density(data_interspec[data_interspec$Elev_cat==elevcats[i],
  "LDMC"], na.rm=TRUE))

dens_Height[[i]]<-list(density(datCF[datCF$Elev_cat==elevcats[i],
  "Height"], na.rm=TRUE))
dens_Height[[i+length(elevcats)]]<-
  list(density(datDO[datDO$Elev_cat==elevcats[i], "Height"], na.rm=TRUE))
dens_Height[[i+length(elevcats)*2]]<-
  list(density(data_interspec[data_interspec$Elev_cat==elevcats[i],
  "Height"], na.rm=TRUE))
}

#plot
png('Density_plots_v10.png',width=21,height=29.7,units='cm',res=200)
par(mfrow=c(5,3),mar=c(4,4,2,1))

elevcats<-sort(unique(data_intraspec$Elev_cat))
cats<-c("<1850 m a.s.l.","1850-1999 m a.s.l.", "2000-2099 m a.s.l.",
  "2100-2200 m a.s.l.", "2201-2262 m a.s.l.")
col_cf<-rgb(1,0,0,0.5) #colour for CF
col_do<-rgb(0,0,1,0.5) #colour for DO
col_all<-rgb(169,169,169,125, maxColorValue = 255) #colour for all species

for (i in 1:length(elevcats)) {

##SLA
xlim<-range(dens_SLA[[i]][[1]]$x,
      dens_SLA[[i+length(elevcats)]][[1]]$x,
      dens_SLA[[i+length(elevcats)*2]][[1]]$x)
ylim<-range(dens_SLA[[i]][[1]]$y,
      dens_SLA[[i+length(elevcats)]][[1]]$y,
      dens_SLA[[i+length(elevcats)*2]][[1]]$y)

if (i < length(elevcats)){
plot(dens_SLA[[i]][[1]], xlim = xlim, ylim = ylim, xlab = " ", ylab= " ",
  main = " ",
  panel.first = grid())
abline(v=df_means[i, 2],lty=2)}

else{
plot(dens_SLA[[i]][[1]], xlim = xlim, ylim = ylim, xlab = " ", ylab="",
  main = " ",
  panel.first = grid())
mtext(side=1, line=3, "SLA [mm²/mg]", col="black", font=2, cex=0.9)
}
abline(v=df_means[i, 2],lty=2)

mtext(side=2, line=2.5, "Density", col="black", font=2, cex=0.9)
#add density plots
polygon(dens_SLA[[i]][[1]], density = -1, col = col_cf) #CF
polygon(dens_SLA[[i+length(elevcats)]][[1]], density = -1, col = col_do) #DO
```

```
polygon(dens_SLA[[i+length(elevcats)*2]][[1]], density = -1, col = col_all )
#all species

## add a legend
if (i == length(elevcats)){
legend('topright',c('Carex firma','Dryas octopetala',
  "all occurring plants"),
fill = c(col_cf,col_do, col_all), bty = 'n', border = NA)
}

  ##LDMC
xlim<-range(dens_LDMC[[i]][[1]]$x,
      dens_LDMC[[i+length(elevcats)]][[1]]$x,
      dens_LDMC[[i+length(elevcats)*2]][[1]]$x)
ylim<-range(dens_LDMC[[i]][[1]]$y,
      dens_LDMC[[i+length(elevcats)]][[1]]$y,
      dens_LDMC[[i+length(elevcats)*2]][[1]]$y)

if (i < length(elevcats)){
plot(dens_LDMC[[i]][[1]], xlim = xlim, ylim = ylim, xlab = " ",ylab= " ",
  main = cats[i], cex.main=1.3,
  panel.first = grid())}
else{
plot(dens_LDMC[[i]][[1]], xlim = xlim, ylim = ylim, xlab = "",
  main = cats[i], cex.main= 1.3,
  panel.first = grid())
mtext(side=1, line=3, "LDMC [mg/g]", col="black", font=2, cex=0.9)
}
abline(v=df_means[i, 3],lty=2)
#add density plots
polygon(dens_LDMC[[i]][[1]], density = -1, col = col_cf) #CF
polygon(dens_LDMC[[i+length(elevcats)]][[1]], density = -1, col = col_do) #DO
polygon(dens_LDMC[[i+length(elevcats)*2]][[1]],density= -1, col = col_all )
#all species

##plant height
xlim<-range(dens_Height[[i]][[1]]$x,
      dens_Height[[i+length(elevcats)]][[1]]$x,
      dens_Height[[i+length(elevcats)*2]][[1]]$x)
ylim<-range(dens_Height[[i]][[1]]$y,
      dens_Height[[i+length(elevcats)]][[1]]$y,
      dens_Height[[i+length(elevcats)*2]][[1]]$y)

if (i < length(elevcats)){
plot(dens_Height[[i]][[1]], xlim = xlim, ylim = ylim, xlab= " ", ylab= " ",
  main = " ",
  panel.first = grid())}
else {
plot(dens_Height[[i]][[1]], xlim = xlim, ylim = ylim, xlab = "", ylab="",
  main = " ",
  panel.first = grid())
mtext(side=1, line=3, "H [cm]", col="black", font=2, cex=0.9)
}
abline(v=df_means[i, 4],lty=2)
#add density plots
polygon(dens_Height[[i]][[1]], density = -1, col = col_cf)
polygon(dens_Height[[i+length(elevcats)]][[1]], density = -1, col = col_do)
polygon(dens_Height[[i+length(elevcats)*2]][[1]],density= -1, col = col_all)
}

dev.off()
```