

Divergent adaptive strategies in vascular and bryophyte species: Intraspecific trait variation in cold scree slope microrefugia versus adjacent forests

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Abstract

Microrefugia provide unique habitats where species can persist despite unfavourable regional conditions. Cold scree slope microrefugia, typically found in the montane and subalpine forest belts in the Alps, host mixed communities of cold-specialised and generalist species, reflecting long term adjustment of biotic interactions following abiotic forcing. The patterns and extent of intraspecific trait variation, underpinning how generalist species from surrounding forests may modify their traits to persist in these harsh conditions, remain poorly understood, especially for non-vascular plants.

In this study, we analysed intraspecific variability in functional traits (height, SLA, LDMC, leaf N content, leaf C/N ratio, and leaf pH) for eight generalist species (five bryophytes and three vascular plants) across four cold scree slopes microrefugia and adjacent montane forests in the French Alps. All species exhibited intraspecific variability, but the magnitude and traits involved differed markedly between them. *Maianthemum bifolium* and *Hylocomium splendens* exhibited significantly lower SLA and higher LDMC on cold scree slopes. In contrast, *Pleurozium schreberi* showed a much lower leaf C/N ratio, while *Ptilium crista-castrensis* displayed a much higher ratio. Additionally, our observations for *Rhododendron ferrugineum* and *Vaccinium myrtillus* diverged from those reported in a previous study conducted in other alpine microrefugia.

These findings demonstrate how phenotypic plasticity allows widespread generalist species to persist in harsh marginal environments such as cold scree slope microrefugia, through species-specific trait adjustments. Furthermore, we underscore the impact of distinct environmental conditions of each microrefugia, which coupled with its cold microclimate, shape biotic interactions and contrasting species adaptations.

1. Introduction

Microrefugia are small-scale habitats where populations can survive outside their main distribution range due to local abiotic conditions that are sufficiently unique to protect them from unfavourable regional environmental conditions (Rull, 2009). One essential property of microrefugia is that, following a change in environmental conditions, they provide habitats where certain species can persist and potentially disperse (Keppel et al., 2012). Mountain ranges, with their complex topography and geomorphology offering a mosaic of contrasting abiotic conditions at fine scales, promote the formation of small ecosystem islands embedded within much larger ecosystems, which can act as microrefugia (Gentili et al., 2015; Keppel et al., 2015). Microrefugia are thus of particular interest in conservation biology, as they may harbour populations of species that would otherwise be unable to survive due to climate warming in the medium to long term (Hannah et al., 2014; Morelli et al., 2020).

Cold scree slopes are a striking example of cold microrefugia. These are porous formations found in the Alps, ranging from the lower montane to the subalpine zone (typically between 1000 and 1800 meters above sea level, e.g., Uxa et al., 2019). They are characterized by a complex reversible internal ventilation system, known as *the chimney effect*, which depends on the temperature differences between the core

of the scree and the atmospheric air according to the seasons (see Delaloye et al., 2003, for a detailed description). Consequently, the soil temperature in the upper part of cold scree slopes is significantly milder in winter, while the lower zone is continuously and strongly cooled throughout the year, with soil temperatures 10 to 15°C lower than those of the surrounding environments during summer. Ultimately, the soil temperature and light resource availability due to the openness of the environment are comparable to those of the alpine treeline (Körner and Hoch, 2006). However, humidity is also very high due to the condensation of external air in contact with cold air outlets, as frequently encountered in the boreo-arctic environments. This unique abiotic context leads to the formation of extra-zonal ecological islands in areas continuously cooled by the ventilation system, which serve as cold microrefugia for many species. These small islands, ranging from a few tens of square meters to a few hectares, stand out from the surrounding environments due to the presence of dwarf trees, boreo-arctic communities dominated by bryophytes, ericaceous shrubs, and terrestrial lichens (Bertinelli et al., 1993). Additionally, the abundant primary production of bryophytes due to high light availability and humidity can lead to atypical soils reaching remarkable accumulation of raw organic matter (Gobat et al., 2004; Meynier and Brun, 2018).

However, the small size of cold scree slopes limits their species pool compared to the strongly contrasting adjacent environments. The species they can harbour are therefore those that can both develop in the harsh abiotic conditions that characterize them and have a biogeographical history compatible with the local species pool, of which the microrefugia may have been an integral part since the last glaciations (Růžicka et al., 2012). Consequently, cold scree slopes host mixed communities, including cryophilic species specialized in the cold conditions they provide, for which they can effectively act as microrefugia, and widespread generalist species with broad ecological amplitudes originating from the surrounding ecosystems, which are often dominant in the cooled zone of the scree (Meynier & Loucugaray, in prep.).

Climatic relics such as cold microrefugia are natural laboratories for studying ecosystem adjustments to climate change, particularly because they also allow for the analysis of the long-term results of biotic interactions following climatic forcing (Keppel et al., 2012; Woolbright et al., 2014). In this context, analysing the ability of generalist species from surrounding environments to modulate physiological traits in response to these highly constraining conditions appears particularly relevant. Warmer conditions in cold environments are expected to favour individuals or species adopting a resource-acquisitive strategy, relative to the more conservative traits observed under pre-warming conditions: an overall increase in Specific Leaf Area (SLA), leaf nitrogen content (N), vegetative height, and a decrease in Leaf Dry Matter Content (LDMC) (Bjorkman et al., 2018). A study highlighting the significant but contrasting intraspecific variability of four vascular species has already been conducted between populations from microrefugia similar to cold scree slopes and populations from higher altitudes in Italy (Tonin et al., 2020). However, bryophytes play a fundamental role in a wide range of cold ecosystems and are understudied compared to vascular flora (St. Martin and Mallik, 2017). In this regard, the few studies that have attempted to assess intraspecific variation in bryophytes in response to warming in

cold environments have reported inconsistent observations at the community level (Roos et al., 2019; van Zuijlen et al., 2022).

In this study, we analysed the intraspecific variability of traits related to competition and resource acquisition in eight generalist plant species, including five bryophytes, able to develop both in mid-altitude cold scree slopes microrefugia (1200–1450 m a.s.l.) and in the adjacent montane forests at similar elevations.

2. Materials and Methods

Study sites

Table 1

Location and main characteristics of the study sites. For temperature, the number in brackets is the year of measurement.

Site	Pellafol	3 Ruisseaux	La Croix 1	La Croix 3
Site Abbreviation	PEL	3R	LC1	LC3
Latitude	44.7635	45.1825	45.3957	45.3971
Longitude	5.8728	5.9245	6.7066	6.7034
Altitude (m a.s.l.)	1250	1220	1400	1450
Bedrock	Limestone	Gneiss	Quartzite	Quartzite
Dominant Tree Species in Surrounding Forest	Abies alba, Picea abies	Picea abies	Picea abies	Picea abies
Exposure	N	NW	NE	N
Mean Summer Temperature in Scree Core (°C)	1.47 (2016)	5.58 (2018)	2.04 (2018)	3.39 (2018)
Mean Summer Temperature in Control Zone (°C)	15.09 (2016)	12.31 (2018)	10.51 (2018)	

Our study focuses on four cold scree slopes in the French Alps (Table 1). In the immediate vicinity of each site (between 100 and 500 meters away), we selected a "control" zone in the surrounding forest, located approximately at the same altitude and exposure. These control zones are on non-ventilated scree slopes and share the same bedrock as the associated cold scree. The La Croix 1 and La Croix 3 sites are two independent cold scree slopes with markedly different floristic compositions (Meynier and Loucugaray, in prep.). But being only a few hundred meters apart from each other, only one control zone was set for these two sites in their nearby environment. We recorded summer soil surface temperatures during the summer period (June 1 to August 31) with a data logger in the soil of the cooled zone and the control zone (Thermo-button, Progresplus) at approximately 20 cm depth. Note that these

measurements, based on a single data logger per site and conducted in different years, are likely influenced by microtopography. They were only used to demonstrate the presence of overcooling on the different sites and should not be used to assess the temperature difference between them.

Species selection

During previous work, we conducted an exhaustive inventory of the vascular and non-vascular plants present in seven cold scree slopes in the French Alps (Meynier & Loucougaray, in prep.). In this study, we focused on all vascular and non-vascular plant species that were locally dominant (cover > 60% in at least one 10*10 cm plot previously recorded) in the cold scree slopes and also present in the neighbouring forest. In total, eight species were selected, including five bryophytes, two ericaceous shrubs, and one herb (Table 2). Even when occurring in several cold scree slopes, each species was only inventoried at one site and in the control zone associated with that site.

Table 2
Species selected in our study.

Species	Abbreviation	Growth Form	Sampling Site
<i>Hylocomium splendens</i>	Hyl spl	Moss	LC3
<i>Maienthemum bifolium</i>	Mai bif	Herb	LC3
<i>Pleurozium schreberi</i>	Ple sch	Moss	PEL
<i>Ptilium crista-castrensis</i>	Pti cri	Moss	3R
<i>Rhododendron ferrugineum</i>	Rho fer	Shrub	LC3
<i>Rhytidiadelphus loreus</i>	Rhy lor	Moss	3R
<i>Rhytidiadelphus triquetrus</i>	Rhy tri	Moss	LC3
<i>Vaccinium myrtillus</i>	Vac myr	Shrub	3R

Measurement of functional traits

For each species, we analysed 10 individuals in the cold scree slope and 10 from the control zone. We first measured the vegetative height *in situ*. For bryophytes, this measurement corresponds to the vertical height of the green part. These measured individuals were then stored in a cold room in the laboratory before measuring the other traits. A total of 80 samples were thus collected in the scree core zone and 80 others in the control zone.

Following the protocols of Pérez-Harguindeguy et al. (2016), we measured Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC). Once done, the 10 replicates corresponding to each population of each species were pooled to obtain sufficient material for analysing leaf nitrogen concentration (N), leaf carbon concentration (C), and leaf pH (pH). There is therefore only one measurement per population for

these traits, which correspond to the mixture of the 10 replicates. Finally, we calculated the leaf C/N ratio.

For bryophytes, all traits were measured by adapting protocols from Pérez-Harguindeguy et al. (2016) to the whole green ramets. Although these measurements technically relate to ramets rather than individual leaves, we retained the standard trait terminology (*e.g.*, SLA, LDMC, etc.) for ease of reference.

Statistical analyses

The aim of this work is to study intraspecific variability and thus the difference in functional trait values of plants between the cooled zone of the scree and the surrounding forests (control zone). For traits with replicates (height, SLA and LDMC), we first performed a Shapiro-Wilk test to assess the normality of the distribution and a Leven test for the homogeneity of variance. We then used a Student's t-test (if variances were homogeneous and the distribution normal, $p > 0.05$) or a Welch t-test (if not $p < 0.05$) to compare the cold zone and the control zone

3. Results

All studied species displayed intraspecific variability between the cold scree slope and the control zone for at least one of the measured traits. Yet, the responses were highly contrasted, with some species presenting considerable differences in some trait values between the two zones, while others showed minimal to no variation, or differed in other traits.

Intraspecific variation of height, SLA and DMC

Overall, the trend toward smaller species with higher LDMC in the cold scree was consistent across species displaying a significant difference, while for SLA, three species exhibited significantly lower values, and one a higher value (Fig. 3). Five species showed a different height between the cold and the control zone, and four species had a difference in at least SLA or LDMC.

Specifically (see S1 for detailed results of t-tests), the two shrubs studied, *Vaccinium myrtillus* and *Rhododendron ferrugineum*, had a lower height in the cold scree but no significant difference in the other traits. The herb *Maienthemum bifolium* was smaller and had a much lower SLA in the cold zone, and a much higher LDMC. Among the bryophytes, *Hylocomium splendens* displayed a far smaller SLA, a far higher LDMC, but a similar height in the cold scree slope. Other bryophytes species displayed a milder response overall with only *Pleurozium schreberi* being slightly smaller in the cold scree slope. The SLA was lower in the cold zone for *Rhytidiadelphus loreus*, while it was higher for *Pleurozium schreberi* and not significantly different for *Ptilium crista-castrensis* and *Rhytidiadelphus triquetrus*. Finally, the LDMC was higher in the cold microrefuge for *Pleurozium schreberi* and *Rhytidiadelphus triquetrus*, while it showed no significant difference for *Rhytidiadelphus loreus* and *Ptilium crista-castrensis*.

Intraspecific variation of leaf C, N, C/N ratio and leaf pH

The C leaf content differences were minimal for every species, while N leaf content, and C/N ratio accordingly, showed sharp and contrasting species-specific differences between cold and control zone (Fig. 4). Interestingly, *Ptilium crista-castrensis* which showed no differences in Height, SLA or LDMC displayed a much lower N leaf content and thus much higher C/N in the cold scree slope (60.44 vs 28.80). The two shrubs species exhibited similar although milder trend, whereas *Pleurozium schreberi* had much lower C/N in the cold zone (46.88 vs 62.62). *Maienthemum bifolium* and the three other bryophytes did not show differences. Finally, the leaf pH of the eight studied species was either similar or lower in the cold scree compared to the control zone (Fig. 4). The differences were generally larger for bryophytes, with, for example, a pH 0.5 units higher in the control zone for *Pleurozium schreberi*, yet differences were minimal for vascular species and absent for *Rhytidiadelphus triquetrus*.

4. Discussion

The ventilation system cooling cold scree slopes generates, through both direct and indirect processes, an abiotic filter driving most of the differences in environmental conditions with adjacent forests: colder temperatures, higher humidity, nutrient limitation, lower soil pH, and, due to the dwarfism of trees, more abundant light resources for the moss and shrub layers (Celi et al., 2010; Körner and Hoch, 2006). Some plant species are nevertheless abundant both in the cold scree slope and in the warmer, drier and shaded adjacent forest floor.

In our observations, the eight species we studied exhibited significant intraspecific variability for at least one of the measured traits between cold scree slopes and neighbouring forests. However, our results suggest that the adaptation strategies to the environmental factors specific to cold scree slopes differ among the generalist species able to establish there. As we expected, several species seem to adopt a more resource-conservative strategy in the cold zone (*i.e.* overall lower size, SLA and N leaf content, higher LDMC), which probably allows the herbaceous plant *Maienthemum bifolium* to persist in cold scree slopes, at the edge of the abiotic conditions favourable to its development. However, the intraspecific variability we observed does not appear to be solely due to adaptations directly related to cold temperatures. Some species seem to react to the openness of the environment and thus to a decrease in competition for light in the cold scree slopes. *Rhododendron ferrugineum* and *Vaccinium myrtillus*, the two shrubs in our study, were only smaller in the cold zone. Contrasting with our observations, in a previous study in the Italian alps, Tonin et al. (2020) found that leaf N was higher in a low altitude microrefugia compared to subalpine populations of four species including *Rhododendron ferrugineum* and *Vaccinium myrtillus*. For these two species, SLA was higher and LDMC lower in the microrefugia, accounting for a more resource acquisitive strategy. But it was in shaded microrefugia, compared to open subalpine environments. These divergent results emphasise that such different cold microrefugia provide specific abiotic filtering resulting in various biotic interactions. Height is a trait that can express growth or competition, particularly for light (Moles et al., 2009). The absence of a response in traits typically linked to the resource acquisition strategy in our study, such as SLA, leaf C/N, or LDMC, combined with a lower height in cold scree slope, suggests a change in the competitive context rather than growth in these two species. Unlike the surrounding forests, the dwarfism of trees and their low

density in the cold scree slopes provide more abundant light resources to plant communities compared to the adjacent forest floor, while the lack of light is a strong limiting factor for *Vaccinium myrtillus* and *Rhododendron ferrugineum* (Malicki et al., 2019; Montané et al., 2016). Additionally, the dominance of low-height bryophytes, lichens, and dwarf shrubs on cold scree slopes likely shifts competitive dynamics from vertical growth to lateral expansion. These two species are indeed capable of emitting creeping branches under the bryophyte carpet, emerging several meters away and allowing them to expand spatially without sexual reproduction (Bjedov et al., 2015; Pornon and Escaravage, 1999).

The varied responses observed among bryophyte species emphasise the difficulty of extending the vascular plant resource acquisition-conservation trade-off model to bryophyte communities, as previously documented (Roos et al., 2019; van Zuijlen et al., 2022). One of the reasons, when compared to vascular flora, is the importance of water conservation strategies associated with this poikilohydric growth form, with a bryophyte economic spectrum greatly relating on water regulation (Grau-Andrés et al., 2022). As such, SLA is supposed to be linked with water holding capacity (Roos et al., 2019). A previous study suggested that the increase in temperature and evapotranspiration with decreasing altitude leads to a decrease in SLA, while the water retention capacity increases significantly at the bryophyte community scale (Henriques et al., 2017). Although this relationship remains poorly understood, it could notably explain the higher SLA in the cold zone for *Pleurozium schreberi*, in response to the increase in humidity in cold scree slopes. Yet, the SLA is lower in the cold zone for *Hylocomium splendens* and *Rhytidiadelphus loreus*. While some species respond mainly to lower temperatures and increased humidity, it is possible that an increase in light resource interacts with these two factors differently between species and could partly explain these contrasting responses. It has indeed been suggested that for certain bryophytes developing in cold ecosystems, such as the widespread species *Hylocomium splendens*, competitive exclusion, humidity, and light intensity are the main limiting factors, indirectly related to temperature (Busby et al., 1978; Greiser et al., 2021; Stewart and Mallik, 2006). Measurements of bryophyte water retention capacity and light intensity would be interesting in this regard, as would investigations along an environmental gradient allowing intermediate observations between the extremely cold, humid, and unshaded conditions of cold scree slopes, and the surrounding forests. In any case, while Arctic tundra studies have highlighted species turnover as the primary driver of bryophyte functional responses to warming at the community level, with intraspecific variability playing a secondary role unlike in vascular species (Roos et al., 2019; van Zuijlen et al., 2022), our results demonstrate that it can still be substantial at the species level for this growth form in cold environments.

The spectacular differences we recorded in *Maianthemum bifolium* and *Hylocomium splendens* for SLA and LDMC, and in *Pleurozium schreberi* and *Ptilium crista-castrensis* for N leaf content and thus C/N ratio highlight how phenotypic plasticity facilitates persistence in harsh marginal environments such as cold scree slopes microrefugia (Niu et al., 2020; Wellstein et al., 2013), with strong species-specific adaptations. We also point out the critical role of the unique abiotic filters in each cold microrefugia, particularly the strong influence of light, water, and soil nutrient availability. These factors shape diverging biotic interactions, driving generalist species such as *Rhododendron ferrugineum* and

Vaccinium myrtillus to adopt distinct adaptive strategies, as evidenced by our contrasting observations on these species compared to those reported by Tonin et al. (2020).

Declarations

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Author Contribution

Simon Meynier and Grégory Loucougaray conceived the research idea, protocol, and collected field data together. Simon Meynier performed the analysis and wrote the paper. Grégory Loucougaray revised the manuscript and provided countless suggestions through iterations.

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Data Availability

The data that support the findings of this study are openly available as Supplementary information n°2.

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Figures

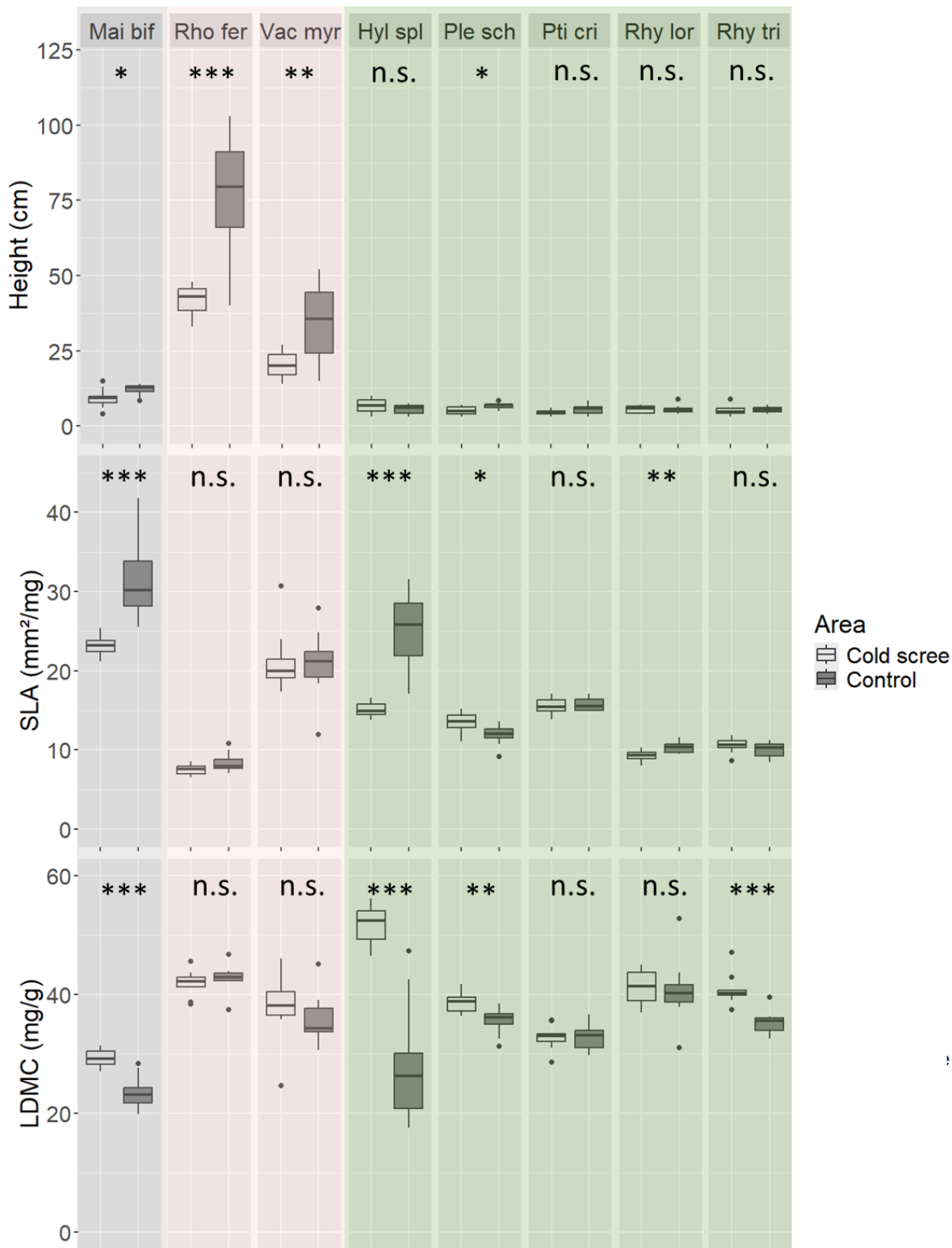


Figure 1

Figure 3: Intraspecific variation between the cooled zone and the control zone for height, Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC). The result of the t-test corresponding to each trait-species pair is indicated as follows: *** : $p < 0.001$; ** : $0.001 < p < 0.01$; * : $0.01 < p < 0.05$; n.s.: not significant. The herbaceous plant is represented in grey, the shrubs in red, and bryophytes in green.

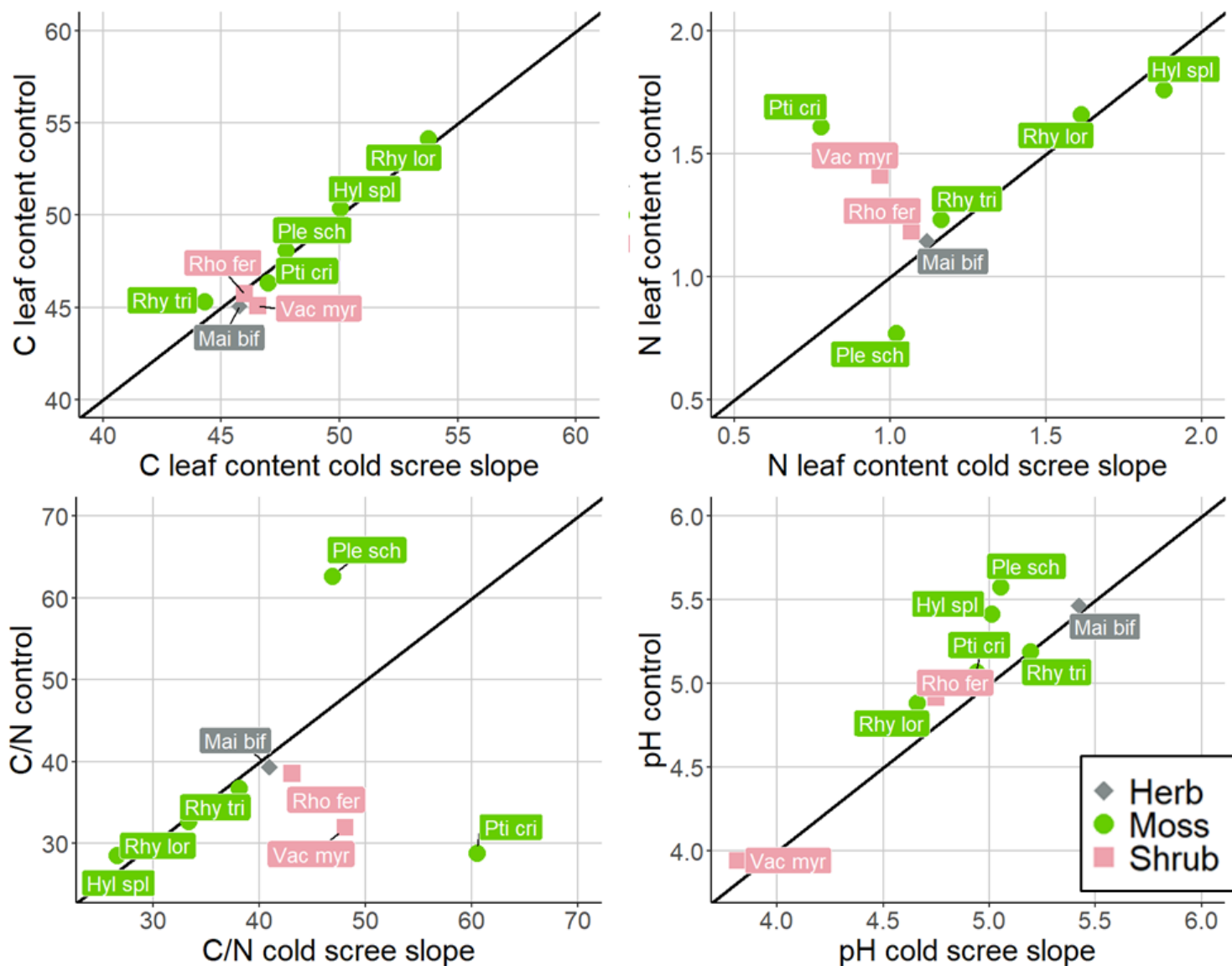


Figure 2

Figure 4: Differences in the leaf C, N, C/N ratio and leaf pH between the cold scree slope and the control zone.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [S1Detailedstatisticaltests.docx](#)
- [S2Data.csv](#)