

Thermal niche predictors of alpine plant species

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Abstract. Within the context of species distribution models, scrutiny arises from the choice of meaningful environmental predictors. Thermal conditions are not the sole driver, but are the most widely acknowledged abiotic driver of plant life within alpine ecosystems. We linked long-term measurements of direct, plant-relevant, near-surface temperatures to plant species frequency. Across 47 sites located along environmental gradients within the Scandinavian mountain chain, the thermal preferences of 26 focal species of vascular plants, lichens, and bryophytes were explored. Based on partial least-squares regression, we applied a relative importance analysis to derive inductively the thermal variables that were best related to a species' frequency. To discover potential seasonal variability of thermal controls, analyses were both differentiated according to meteorological season and integrated across the entire year. The pronounced interspecies and temporal variability of thermal constraints revealed the thermal niches were much more nuanced and variable than they have commonly been represented. This finding challenges us to present, interrogate, and interpret data representing these thermal niches, which seems to be required in order to move beyond purely probabilistic and correlative descriptions of species' range limits. Thus, this information will help improve predictions of species distributions in complex arctic-alpine landscapes.

Key words: *arctic-alpine ecosystems; boundary-layer climatology; bryophytes; climate envelope modeling; lichens; near-ground temperatures; thermal threshold hours; vascular plants.*

INTRODUCTION

Niche modeling in climate change studies

In a rapidly changing world, there is a critical need to predict the future geographical ranges of species (Anderson 2013, Yackulic et al. 2015). For this prediction, it is necessary to know the potential range limits of a given species and the factors determining those limits (Wellenreuther et al. 2012). Indeed, a profound understanding of the distribution boundaries of a species is pivotal in regard to projecting potential species distributions, especially under novel environmental conditions (Körner and Hiltbrunner 2018). The use of species distribution models (SDMs) is a common tool to make inferences on species' range limits and to project how the distribution of species might change (Morin and Lechowicz 2008, Wellenreuther et al. 2012, Yackulic et al. 2015).

Ecological niche models are the cornerstones of such distributional modeling. These models are built upon information on the environmental features that define the current niche (i.e., the environmental requirements) of a species. Future distributions of those features, derived from climate change scenarios, are then used to

predict where the species' niche requirements might be satisfied in the future (Wiens et al. 2009). Most approaches like these are correlative, linking environmental data to species distribution records. An alternative strategy is to incorporate explicitly the mechanistic links between the functional traits and the environments of organisms into SDMs (Kearney and Porter 2009). Building on knowledge about the dominant processes that underlie survival and reproduction to predict a geographic range, a mechanistic SDM is likely to predict range dynamics better than a correlative model. However, this approach has the disadvantage of requiring an accurate *a priori* (but still lacking) understanding of a species' fitness relationship with the environment (Buckley et al. 2010). As such, various examples indicate that correlative SDMs perform well when characterizing the natural distributions of species within their current range; these SDMs provide useful ecological insights and strong predictive capabilities when well-designed survey data and functionally relevant predictors are used (Elith and Leathwick 2009).

There is, however, growing concern about how SDMs are being used to predict the impact of climate change on biodiversity. These results, for instance, may be derived from implausible assumptions or may disregard the appropriate scales of plant–environment and biotic interactions (Austin and Van Niel 2011). Indeed, the choice of meaningful explanatory variables and the spatial scale at which these models are applied are of

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fundamental importance (Pearson and Dawson 2003, Araújo and Peterson 2012, Körner and Hiltbrunner 2018). We acknowledge the importance of the entire set of primary environmental factors (e.g., thermal conditions, soil moisture, and nutrient availability) when quantifying a species' niche. In the following research, however, we will explicitly focus on the thermal niche and its predictors. Thermal conditions are frequently reported as having a dominant effect on species distributions (Scherrer and Guisan 2019) and are widely used. They still serve, however, as representatives to illustrate the challenges associated with obtaining a thorough description of the ecological niche of a species.

The alpine thermal niche and associated challenges

Opposed to the fundamental (i.e., physiological) niche of a species, which is defined by the abiotic environment, in nature, we inevitably observe the realized niche, which additionally reflects the constraining effects of biological interactions and dispersal (Hutchinson 1957). Considering the asymmetric abiotic stress limitation hypothesis (Normand et al. 2009), however, the effect of biotic interactions on fluctuations in the realized niche diminished toward the more stressful ends of environmental gradients (Connell 1961, Austin 1990, Pellissier et al. 2013). Here, species distributions were primarily limited by physiological tolerance to dominant environmental drivers. Hence, under extreme conditions, the margins of the realized niche approximated the limits of the fundamental niche. In arctic-alpine landscapes, thermal conditions are likely to represent such a dominant environmental driver (Scherrer and Körner 2011). In this study, "thermal niche" refers to the *realized* thermal niche of a species, which might, under certain conditions, also approximate its fundamental thermal niche.

It is a long-established idea that climatic conditions govern species' ranges at broad extents (Humboldt and Bonpland 1805, Woodward 1990, Araújo et al. 2013). In general, temperature has been identified as the most prominent determinant of the fundamental ecological niche of organisms. Temperature may be the most widely acknowledged abiotic driver of plant life, at least in alpine ecosystems (Körner and Hiltbrunner 2018). It is a common and insightful practice to assess the thermal requirements of a species (i.e., its thermal niche) to model the distribution of a plant species under arctic-alpine conditions (Thuiller et al. 2005, Dullinger et al. 2012, Pellissier et al. 2013). Consequently, the most pressing question is that related to explaining and defining the thermal range limits of species (Körner and Hiltbrunner 2018). However, the data on these forcing variables are often unavailable at the spatial and temporal scales that are most critical for alpine plant life.

This problem is due to data availability and convenience, as data typically come from a single weather station or are interpolated grid data based on station records (e.g., WorldClim; Hijmans et al. 2005). Within regions with a sparse station network, such as regions at

higher elevations, such data are prone to high uncertainties (Hijmans et al. 2005, Pepin et al. 2015). Moreover, the information provided is about ambient air temperature, measured at the standard meteorological screen height of 2 m above the ground. It is well documented, however, that the ambient thermal regime is decoupled from the near-surface conditions commonly experienced by small-stature, arctic-alpine plants (Fig. 1; see also Pape et al. 2009, Scherrer and Körner 2010, Graae et al. 2012). During the snow-free period, this decoupling is, to a high degree, controlled by micro-topography and soil moisture; during winter, this decoupling is controlled by snow cover (Löffler et al. 2006, Wundram et al. 2010, Graae et al. 2018). Such a mismatch between ambient air and near-surface conditions renders any description of the thermal niche of alpine plant species based on ambient air temperatures problematic, as there is a lack of information about the thermal conditions at the critical location of action, that is, the actual growing site of the plant species.

Moreover, the mean annual temperature has become the most widely used measure to describe thermal conditions (Körner and Hiltbrunner 2018), although it completely neglects the central role of seasonality, which is well pronounced, especially in alpine environments. It is the multifaceted nature of thermal conditions (including extremes, accumulated heat sums, and length of growing season) that affects the different stages in the life cycle and phenology of a plant species to various extents (Graae et al. 2018). However, the mean temperatures are associated with plant growth; acting mainly in a gradual manner, extreme temperatures and their timing trigger threshold responses, such as mortality (Körner et al. 2016). Additionally, it is not just the period of major plant physiological activity that needs to be considered: winter conditions—in particular, soil temperatures mediated by snow—have been recognized to play a major role in determining biodiversity patterns and ecosystem functioning in snow-governed alpine ecosystems (Pauli et al. 2013, Petty et al. 2015). However, winter conditions are still a missing dimension in most studies (Choler 2018, Niittynen and Luoto 2018). As such, the critical time scale relevant for plant growth is insufficiently reflected within the temperature data commonly used to characterize a species' thermal niche.

In addition to the well-known concept of heat units (Wang 1960), such as growing degree days (GDD) or growing degree hours (GDH) and their application in SDMs (Thuiller et al. 2005), the use of freezing degree days (FDD) has recently been proposed to determine the thermal niche of alpine species (Choler 2018). All of these concepts use a certain predefined thermal threshold temperature (such as 0°C or 5°C), which is then quantified by accumulating the respective number of days or hours above this chosen threshold. Sometimes, the threshold values are empirical findings from specific studies that are then transposed to other groups of organisms. As such, Körner and Paulsen (2004) found a global 5.6°C root zone

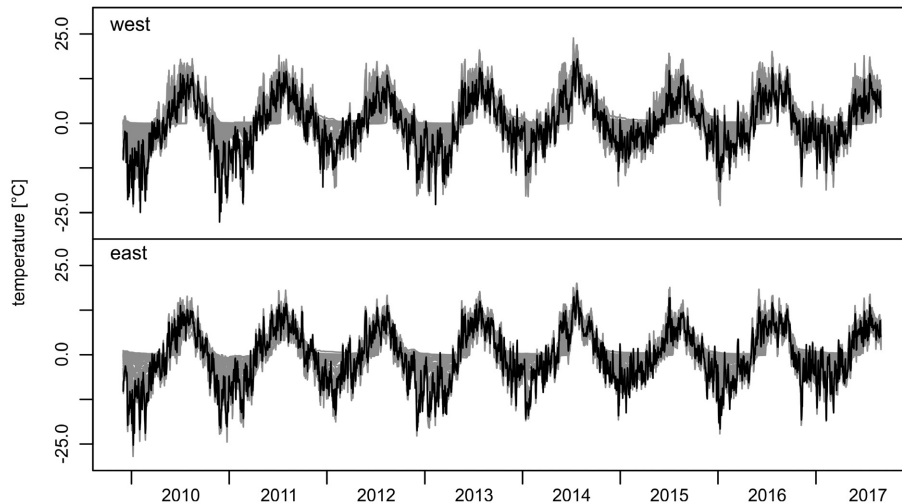


FIG. 1. Near-surface thermal regimes (expressed as daily mean data) across all sites (gray) within the west (upper diagram) and east (lower diagram) compared to the ambient air temperature (black), which was derived from gridded data at a spatial resolution of 1 km (www.senorge.no). The near-surface maxima in the west are underestimated by those of the ambient air during summer. During winter, snow cover at these sites leads to a total decoupling of the near-surface thermal regime from the ambient air.

threshold for tree growth along alpine tree lines. Based on the variety of different life forms in the alpine vegetation, however, it can be assumed that the distribution limits of different species are determined by different thermal thresholds. Consequently, a species-specific approach that screens the entire range of occurring temperatures for potential thermal thresholds is needed.

Aims and objectives

In our study, we aimed to explain and define the thermal range limits of alpine plant species, which was a question raised by Körner and Hiltbrunner (2018). Following Körner et al. (2016), knowing the actual drivers and responses would help move beyond purely probabilistic and correlative descriptions towards more mechanism-based definitions of range limits. Using the Scandinavian mountain chain as an example, our objective was to characterize the realized thermal niches of 26 circumpolar-distributed alpine plant species. We used a unique multiyear temperature data set acquired at those locations and at time scales critical for plant growth to search for species-specific thermal thresholds and their ecological justification.

MATERIALS AND METHODS

Study sites

We conducted our study in two alpine mountain regions of central Norway, covering one of the steepest regional climate gradients in Europe. To the west, the Geiranger/Møre og Romsdal region (62°03' N; 7°15' E) is located within the slightly to markedly oceanic climate section (O1–O2; Moen 1999) of the inner fjords. It is

characterized by humid conditions, with a total annual precipitation of 1,500–2,000 mm in the valleys (Aune 1993). To the east, the Vågåmo/Oppland region (61°53' N; 9°15' E) is located within the continental climate section (C1; Moen 1999). The total annual precipitation is low, ~300–500 mm in the valleys, which corresponds to the highest aridity found in Norway (Kleiven 1959). Within the alpine area, our own measurements indicate the annual liquid precipitation is 900 mm in the west and 375 mm in the east. The additional amount of solid precipitation and its snow water equivalent remains unknown, but snow drift leads to an uneven distribution of the snowpack within the complex alpine topography (Löffler 2005, 2007, Löffler and Finch 2005). The mean annual ambient air temperatures in the alpine area are 1.9°C (range: –23.2 to 17.2°C) in the west and –1.2°C (range: –29.2 to 16.7°C) in the east (Löffler 2003).

Across the western and eastern regions, we used alpine sites that were stratified randomly chosen along elevational and microtopographical gradients within the frame of our long-term alpine ecosystem research project (LTAER; Löffler 2002, Hein et al. 2014, Weijers et al. 2018). The elevational gradient was stratified into six elevational levels from the tree line upwards. In the oceanic region we used 700, 900, 1,000, 1,200, 1,300, and 1,400 m above sea level (a.s.l.); in the continental region we used 900, 1,100, 1,300, 1,400, 1,500, 1,600 m a.s.l. Within each elevational level, we sampled along the microtopographical gradient ridge (Fig. 2A), the south-facing slope (Fig. 2C), the depression (Fig. 2B), and the north-facing slope (Fig. 2D), as these topographical positions are likely to represent the thermal regime extremes. This design resulted in a total of 2 (region) × 6 (elevation) × 4 (topography) = 48 sites.

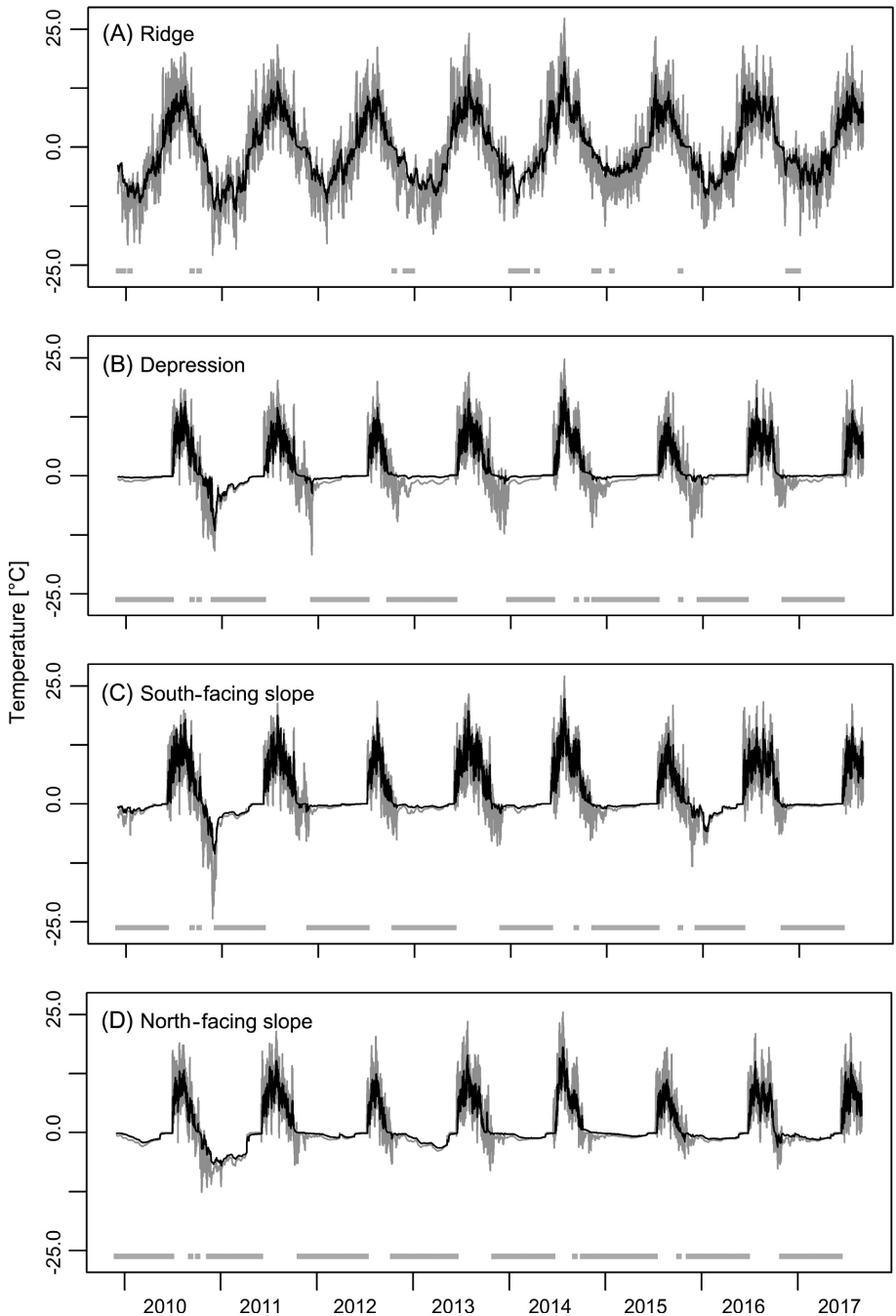


FIG. 2. Near-surface thermal regimes along a middle-alpine microtopographical gradient within our eastern study region at 1,400 m above sea level. Root-zone temperatures at -15 cm are shown in black, and shoot-zone temperatures at $+15$ cm are shown in gray. The light-gray lines at the bottom of each diagram indicate the period of snow cover, which corresponds to dampened temperature fluctuations.

Field data

The frequency of vascular plant species, macrolichens, and bryophytes per site was recorded based on four spatially independent plots that were each 1 sq. m in size, with 25 subsamples (5×5 , each 20×20 cm² in size)

within each. Any occurrence of a species within a subsample was counted as 1, resulting in frequency values per site within the range of 0 to 100 after the aggregation of count data across the four plots. Nomenclature and taxonomy followed that in Lid and Lid (2007) for vascular plants, that in Moberg and Hultengren (2016) for

lichens, and that in Hallingbäck (2016) for bryophytes. Field identification of *Sphagnum* moss was, in most cases, possible to the genus level only, which led to the exclusion of this genus from further analysis. We found 110 species, which were grouped into six plant functional types: deciduous shrubs, evergreen shrubs, graminoids, macrolichens, bryophytes, and forbs. The latter were excluded in our species-specific assessments of the thermal niche because of their overall low abundance ($\ll 5\%$ relative frequency; with relative frequency calculated as the ratio of observed frequency to the maximum achievable frequency across all sites).

To identify the thermal constraints of plant life at the critical location of action, we measured the temperatures at a depth of 15 cm below the soil surface within the root zone (hereafter RZ) and the temperatures at a location 15 cm above the soil surface, which was within the shoot zone (hereafter SZ), at all sites. Temperatures were measured at 1-min intervals and recorded as hourly means using ONSET's HOBO loggers (type H21-002) and temperature sensors of type S-TMB-002 ($\pm 0.2^\circ\text{C}$ accuracy). For the SZ measurements, the sensors were equipped with passively ventilated radiation shields. Our data covered the period of eight full meteorological years from 1 December 2009 to 31 August 2017. Missing data occurred at only one site, a depression in the west, and led to the omission of that site from further analysis. Thus, there were 47 sites analyzed within this study. The different near-surface temperature regimes of our microtopographical sites are illustrated in Fig. 2, showing the paramount effect of snow coverage and its insulation.

Data analysis

From our data set of 110 species, we extracted 26 focal species for further analysis based on Isopam analysis (Schmidt et al. 2010). With Isopam, a hierarchical partitioning of an ordination space is performed, which results in the generation of sample classes (four in our case), along with post hoc identification of indicator species (i.e., our 26 focal species), which were significantly typical for the classes found (cf. Table 1).

To avoid generalizations of the thermal regime that might arise from data averaging into mean values (likely to neglect relevant time scales) or the utilization of heat units above a pre-defined threshold (likely to be irrelevant for the species under consideration), we introduce "thermal threshold hour" (hereafter TTH) to be used in further analysis. We set the range of occurring temperatures (-25 to $+25^\circ\text{C}$) in 0.1°C steps as "thresholds," and used our raw hourly temperature data to calculate the sum of hours each threshold was either below (for temperatures $\leq 0^\circ\text{C}$) or above (for temperatures $> 0^\circ\text{C}$). TTHs were calculated separately for (a) each meteorological season, where winter was "s1" (DJF), spring was "s2" (MAM), summer was "s3" (JJA), and autumn was "s4" (SON), and (b) the entire year ("a"). We used the following principle of abbreviations: the number of hours

during the summer season (s3: June to August) in which root zone temperature was higher than 0.6°C was hereafter referred to as "s3.TTH_{RZ} $> 0.6^\circ\text{C}$." This abbreviation scheme was used throughout the study.

Relations between the frequencies of our 26 focal species and site-specific thermal regimes (expressed as the set of TTHs) across our 47 sites were analyzed by applying partial least squares regression (PLSR; Wold 1975). Combining elements from principal-component analysis (PCA) and multiple linear regression (MLR), this technique is also known as "projection on latent structures" (Abdi 2010). As a limited information approach, which was introduced by Wold as a soft modeling technique to handle various modeling problems in situations where the hard assumptions of more traditional statistics could not be met, PLSR has the advantage in that it works without distributional assumptions (Wold 1980, Dijkstra 1983, Vinzi et al. 2010). Moreover, PLSR efficiently deals with unreliability and heteroscedasticity issues (Martens and Naes 1989) and is a useful tool if the number of predictors exceeds the number of observations or if the predictors are highly correlated (Carrascal et al. 2009)—both of which were true for our data. Instead of using all independent variables simultaneously, which would inevitably result in model overfitting, PLSR extracts only a few components (latent factors; in our case 2–4(7), dependent on the species being analyzed) from the independent variables to be used as predictors. Unlike PCA regression, these latent factors are derived to maximize the explained variance not only in the independent variables, but also in the dependent variables. Comparing multiple regression, PCA regression and PLSR, PLSR was found to be most reliable in identifying relevant variables, especially in cases with a small sample size (Carrascal et al. 2009). Moreover, PLSR is strongly shielded against both type I (false positive) and type II (false negative) errors. Thus, PLSR is very useful where the emphasis is on theory development rather than on testing, in a confirmatory sense, how well a theoretical model fits observed data (Sosik et al. 2009). Our motivation to apply PLSR was based on the need to screen the entire range of occurring temperatures (expressed as TTHs) for those that were best related to the variation in the response (cf. Mehmood et al. 2012) based on relative importance analysis. In this context of variable selection, a PLSR model was built, and its output was solely used to assess the (relative) importance of each explanatory variable, that is, the focus was to determine the influential explanatory variables rather than the response (Mehmood and Ahmed 2016).

PLSR in its original form had no intention of being used to assess the importance of each single independent variable within a model to guide variable selection; however, a large number of methods have been proposed for variable selection in PLSR (Farrés et al. 2015; see also the review by Mehmood et al. 2012). The two most frequently used methods, variable influence on projection (VIP; Wold et al. 1993) and target projection with a selectivity ratio

TABLE 1. List of the 26 focal plant species selected by Isopam.

Species name	Isopam cluster number	Plant functional type	Relative frequency (%)				
			Overall	A	B	C	D
<i>Betula nana</i>	1	De	17.2	12.1	6.4	26.3	23.1
<i>Salix glauca</i>	2	De	3.9	0.0	16.0	0.1	0.4
<i>Salix herbacea</i>	4	De	34.8	21.9	33.5	58.2	25.7
<i>Vaccinium myrtillus</i>	1	De	22.3	2.2	0.0	44.4	40.9
<i>Empetrum hermaphroditum</i>	1	Ev	29.3	38.4	0.8	36.1	39.6
<i>Harrimanella hypnoides</i>	4	Ev	8.4	0.0	0.0	14.3	18.5
<i>Loiseleuria procumbens</i>	3	Ev	4.6	11.3	0.0	3.2	3.6
<i>Vaccinium vitis-idaea</i>	1	Ev	18.9	45.5	0.0	8.6	19.8
<i>Carex bigelowii</i>	3	Gr	20.2	12.9	22.5	25.0	20.4
<i>Deschampsia flexuosa</i>	1	Gr	16.2	3.2	2.5	36.8	21.3
<i>Eriophorum angustifolium</i>	2	Gr	11.8	0.0	49.7	0.0	0.5
<i>Juncus trifidus</i>	3	Gr	7.4	12.8	0.1	8.8	7.4
<i>Luzula confusa</i>	4	Gr	5.9	6.4	5.0	2.8	9.4
<i>Poa vivipara</i>	4	Gr	0.8	0.0	1.4	0.3	1.6
<i>Alectoria ochroleuca</i>	3	Li	18.9	74.0	0.0	0.0	0.0
<i>Bryocaulon divergens</i>	3	Li	14.3	56.1	0.0	0.0	0.0
<i>Cetraria ericetorum</i>	3	Li	35.1	64.1	1.6	35.4	36.5
<i>Cetraria islandica</i>	1	Li	8.7	6.0	0.2	13.5	14.3
<i>Flavocetraria cucullata</i>	3	Li	16.1	60.6	0.0	0.3	2.3
<i>Flavocetraria nivalis</i>	3	Li	31.7	82.8	13.6	12.9	16.1
<i>Cladina arbuscula</i>	3	Li	34.1	54.7	1.7	47.8	29.5
<i>Solorina crocea</i>	4	Li	6.7	1.3	0.0	10.8	14.3
<i>Anthelia juratzkana</i>	4	Br	9.3	0.0	20.0	2.0	15.9
<i>Conostomum tetragonum</i>	4	Br	37.9	28.3	35.2	39.8	48.0
<i>Dicranum fuscescens</i>	1	Br	14.6	5.1	0.1	23.9	27.9
<i>Kiaeria starkei</i>	4	Br	26.6	10.9	28.8	36.2	30.8

Notes: Their attribution to Isopam clusters and plant functional types as well as their overall and site-specific (A = ridge, B = depression, C = south-facing slope, and D = north-facing slope) relative frequencies are provided. The relative frequency was calculated as the ratio of the observed frequency to the maximum achievable frequency across all sites.

(SR; Rajalahti et al. 2009), have been compared by Farrés et al. (2015) and Frindte et al. (2019). These authors found the SR method to be more reliable for variable selection purposes. The SR is defined as the ratio of explained to residual (unexplained) variance for each variable in the target projection vector. This target projection utilizes both the predictive ability (regression vector) and the explanatory ability (variance/covariance matrix) for the calculation of the SR (Farrés et al. 2015). To restrict the resulting SR values to a range between 0 and 1, we applied a modification to the original SR and provided the SR as the proportion of the explained variance. Moreover, to enhance the interpretative ability of the resulting SR plots further, we multiplied the SR of each variable by the sign of its corresponding regression coefficient, making it easy to identify which variables were positively or negatively related to the dependent variable (cf. Rajalahti et al. 2009).

Prior to PLSR, the variables were centered, and those exhibiting a near-zero variance were removed; the remaining variables were left untransformed. Following Wold's approach (Wold et al. 2001, Eriksson et al. 2006) to test whether a multi- or single-response PLSR would be appropriate, we ran a preliminary PCA on the

matrix of dependent variables (i.e., the frequency per plant species across our sites). The apparent high variance among species frequencies revealed that species-specific, single-response PLSR models were appropriate. To estimate the PLSR models, we used the SIMPLS algorithm (de Jong 1993), which was implemented in the package mdatools (Kucheryavskiy 2015) for R 3.3.1 (R Development Core Team 2016). The optimal number of components in the PLSR model was found using Wold's R criterion (Wold 1978). The results were differentiated according to root and shoot zone as well as meteorological seasons and the entire year. Tenfold cross-validation was used to assess the explained variance during model calibration (indicating goodness-of-fit) and validation (indicating model robustness).

From the PLSR and the subsequent assessment of the SR, we obtained a thermal response curve (actually a bar plot; cf. Fig. 3) for each focal plant species. The x-axis represents our explanatory variables, i.e., the thermal threshold in 0.1°C steps along the range of occurring temperatures between −25 and +25°C, measured as exceedance (or lower) time. For each threshold, along the y axis, its linear relation to the species' frequency is shown as the proportion of variance explained

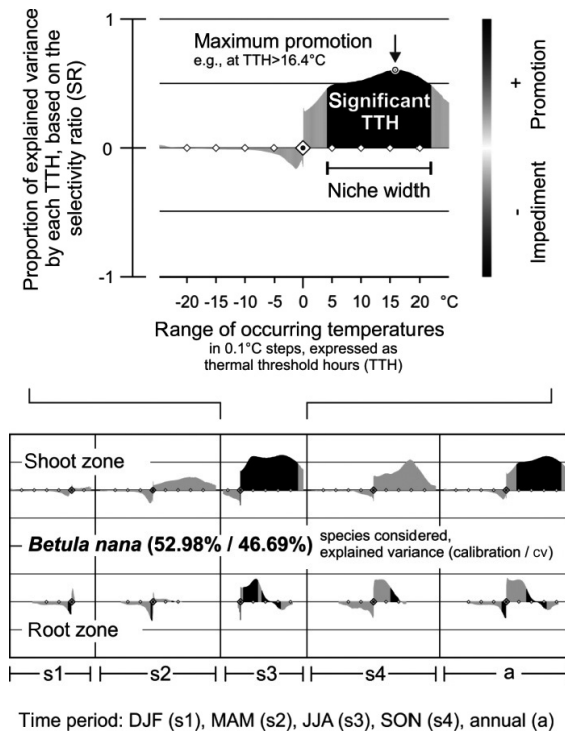


Fig. 3. Schematic illustration of the thermal niche model of a plant species. Thermal thresholds in 0.1-K steps across the range of occurring temperatures are displayed along the x -axis for the shoot and root zone, and they are differentiated by season (s1–s4) and the annual (a) context. Along the y -axis, for each threshold, its linear relation to the observed frequency of species' occurrence is shown, expressed as the proportion of the explained variance based on the selectivity ratio (SR). Positive values correspond to a thermal promotion of the species under consideration, and negative values correspond to an impediment of this species. Significant thresholds ($P < 0.05$) are shown in black. Based on the context of all thresholds, their range has been interpreted to illustrate the width of the thermal niche.

by that specific threshold. Negative values correspond to an impediment of a species by that threshold, and positive values indicate a promotion. The thermal thresholds found to have a significant ($P < 0.05$) effect are shown in black. Based on this thermal response curve, information about the thermal niche of a species can be inferred. Because we used thresholds, inferences about niche width and optima must always be based on the context and relation of all thresholds. We interpret the range of the significant bars, that is, those thresholds that can provide linear fits of exceedance (or lower) time to the frequency of occurrence, as reflecting the niche width. That approach is justified when the thresholds are regarded in relation to one another. At the upper edge of the niche, the threshold immediately above (upper edge of the niche plus 0.1 K) includes all values that showed a nonsignificant effect on the frequency. At the lower edge, the threshold immediately below (lower edge of the niche minus 0.1 K) includes a temperature outside and below the niche of the species, adding noise and thus

causing the model results to be nonsignificant. Furthermore, the thermal optimum of each species is related to the threshold showing the highest proportion of explained variance. Thresholds lower than the optimum additionally include less relevant (but still significant if within the niche) temperatures, adding noise that leads to less explanatory power. Thresholds higher than the optimum, though still significant if within the niche, exclude the optimum, again leading to less explanatory power.

For example, for *Betula nana* in Fig. 3, the thresholds within the range from >4.8 to $>22.0^{\circ}\text{C}$ (measured as the time span these temperatures were exceeded) were found to be significantly related to the species' frequency of occurrence, and the exceedance times of >4.7 and $>22.1^{\circ}\text{C}$ were not significantly related to its frequency of occurrence. Combining these significant and nonsignificant thresholds, as described above, where the niche is pragmatically defined as the range of temperatures showing a significant relation to the frequency of occurrence, reveals a thermal niche width of 17.2 K, ranging from 4.8 to 22.0°C for *B. nana*.

Within that range, all temperatures showed a positive relation ("promotion"), but the effect culminated at temperatures $>16.4^{\circ}\text{C}$ (the best linear relation with $\sim 60\%$ of explained variance). As the threshold immediately above ($>16.5^{\circ}\text{C}$) and immediately below ($>16.3^{\circ}\text{C}$) showed less effect, *B. nana* has an optimum temperature of 16.4°C ; for example, when the 16.4°C temperature is not included, the variance explained by the remaining higher temperatures is smaller than that when 16.4°C is included in the threshold, and when 16.3°C is included, the noise in the model grows, again resulting in less explained variance.

RESULTS

Our thermal variables explained 1–97% of the observed variance in the individual species' frequencies, indicating the general extent of thermal control was highly variable among our 26 focal alpine plant species. Moreover, we observed thermal controls to be highly species specific, with the strongest promoting and impeding thermal drivers per species listed in Table 2. Finally, considering the seasonal and annual variability, species-specific characteristics of the realized thermal niche emerged (Fig. 4A–E).

For all but one of our deciduous shrub species, summer warmth, especially within the shoot zone, showed the highest effect on a species' frequency (Fig. 4A). A gradual differentiation among the thermal niches, however, was revealed by the respective ranges and the maximum promoting TTH. We found the widest thermal niche for *B. nana* (42.3% explained variance after 10-fold cross-validation), showing a significant promotion throughout almost the entire range of positive temperatures that culminated at a maximum of $s3.TTH_{SZ} > 16.4^{\circ}\text{C}$. Both *Salix glauca* (cv: 8.2%) and *Vaccinium myrtillus* (cv: 45.9%)

TABLE 2. Most promoting and impeding temperatures for our 26 focal species.

Species	Shoot zone		Root zone	
	Promotion	Impediment	Promotion	Impediment
<i>Betula nana</i>	s3 > 16.4	s3 ≤ 0.0	s3 > 6.2	s2 ≤ −0.4
<i>Salix glauca</i>	s3 > 10.7	s2 ≤ −0.3	s4 > 0.8	s2 ≤ −0.3
<i>Salix herbacea</i>	–	a > 1.0	s3 ≤ 0.0	a > 2.6
<i>Vaccinium myrtillus</i>	s3 > 21.7	s4 ≤ 0.0	–	–
<i>Empetrum hermaphroditum</i>	a > 15.5	s4 ≤ 0.0	a > 0.7	s4 ≤ −0.2
<i>Harrimanella hypnoides</i>	–	s2 > 0.1	s4 ≤ −0.1	a > 0.1
<i>Loiseleuria procumbens</i>	a > 0.5	–	s3 > 4.3	–
<i>Vaccinium vitis-idaea</i>	s2 > 0.5	–	s3 > 3.9	–
<i>Carex bigelowii</i>	–	–	–	–
<i>Deschampsia flexuosa</i>	s4 > 11.1	s2 ≤ −0.8	s4 > 0.6	s2 ≤ −0.7
<i>Eriophorum angustifolium</i>	–	s1 ≤ −0.6	–	a ≤ −0.1
<i>Juncus trifidus</i>	s1 ≤ −0.4	s4 > 5.1	s1 ≤ 0.0	–
<i>Luzula confusa</i>	s4 > 5.5	s2 ≤ −1.4	a ≤ −0.9	s4 > 0.1
<i>Poa vivipara</i>	–	s1 ≤ −2.4	–	s1 ≤ 0.0
<i>Alectoria ochroleuca</i>	a ≤ −7.5	–	s1 ≤ −4.7	s4 > 0.1
<i>Bryocaulon divergens</i>	s2 ≤ −9.5	–	a ≤ −5.8	–
<i>Cetraria ericetorum</i>	a ≤ −2.7	s4 > 5.5	a ≤ −1.3	s4 > 0.1
<i>Cetraria islandica</i>	–	–	a > 6.2	–
<i>Flavocetraria cucullata</i>	a ≤ −7.3	–	a ≤ −5.3	s4 > 0.1
<i>Flavocetraria nivalis</i>	s1 ≤ −10.3	s3 > 19.7	s1 ≤ −4.3	–
<i>Cladina arbuscula</i>	s1 ≤ −0.5	–	s1 > 0.1	s3 > 6.4
<i>Solorina crocea</i>	s4 ≤ 0.0	a > 0.9	s3 > 0.0	a > 2.2
<i>Anthelia juratzkana</i>	–	s3 > 1.8	s3 ≤ 0.0	s3 > 3.3
<i>Conostomum tetragonum</i>	s4 ≤ 0.0	a > 3.6	s3 ≤ 0.0	a > 4.3
<i>Dicranum fuscescens</i>	s3 > 16.8	s2 ≤ −4.7	s4 > 4.5	s2 ≤ −1.0
<i>Kiaeria starkei</i>	–	s3 > 1.4	–	s3 > 0.3

showed a much narrower thermal niche around their respective maximum promotions at $s3.TTH_{SZ} > 10.7^{\circ}\text{C}$ and $s3.TTH_{SZ} > 21.7^{\circ}\text{C}$. Thus, *B. nana* seemed to be more of a thermal generalist, whereas *S. glauca* and *V. myrtillus* were confined to cooler and the warmer habitats, respectively. For all three species, frost sensitivity outside the summer season was displayed by the impeding effects of subzero temperatures. From an annual perspective, the summer thermal constraints were well reflected, indicating the paramount effect of summer conditions for these three species. In contrast, *Salix herbacea* was almost unexplained thermally, with just 5% of explained variance during model calibration and 0% after cross-validation, though our model indicated a significant impediment from above-zero temperatures, and summer temperatures at the freezing point were the only promoting temperatures. This finding aligns with the preference of *S. herbacea* for sites where snow lasts long into the summer.

For our focal evergreen shrub species, the thermal conditions outside the summer season gained importance (Fig. 4B, Table 2). This result suggests that evergreen species might take advantage of favorable thermal conditions outside the summer season, when their deciduous congeners are snow-covered and/or physiologically inactive. The rather robust model for *Empetrum hermaphroditum*

(51% of explained variance after cross-validation) revealed a wide thermal niche, with promotion by comparatively high temperatures in the shoot zone throughout summer and autumn ($13.3^{\circ}\text{C} < s3.TTH_{SZ} < 22.6^{\circ}\text{C}$ and $0.1 < s4.TTH_{SZ} < 7.7^{\circ}\text{C}$, respectively), transferred into a maximum promotion at $TTH_{SZ} > 15.5^{\circ}\text{C}$ in the annual context. The RZ temperatures showed less importance. Its wide thermal niche is in line with the distribution of *E. hermaphroditum* along all major topographic positions and with elevation. *Vaccinium vitis-idaea* and *Loiseleuria procumbens* remained almost unexplained by thermal constraints. Nevertheless, their respective models also indicated significant thermal promotion outside the summer season. For *L. procumbens*, even subzero temperatures during winter (and to a lesser extent also autumn) were indicated to have a promoting effect. In contrast with the thermal promotion of the aforementioned evergreen species, *Harrimanella hypnoides* (cv: 31.7%) was found to be largely disfavored by positive temperatures throughout spring, summer, and autumn. It was only promoted within a very narrow range of subzero temperatures within the shoot zone during autumn ($-0.3^{\circ}\text{C} < s4.TTH_{SZ} < -0.1^{\circ}\text{C}$), which indicates *H. hypnoides* has similar extreme habitats (i.e., late snow beds) as those of its deciduous counterpart *S. herbacea*.

Our six focal graminoid species revealed a clear separation in terms of their thermal niches, although the specific models were the least robust of all plant functional types (Fig. 4C, Table 2). *Deschampsia flexuosa* (cv: 10.8% of explained variance) and *Luzula confusa* (cv: 22.4%) had a wide thermal niche but also had antagonistic thermal drivers. *Deschampsia flexuosa* was promoted by fairly high temperatures during summer and autumn (maximum promotion at $s4.TTH_{SZ} > 11.1^{\circ}\text{C}$) and was impeded by light frosts outside the summer season; *L. confusa* was promoted by frosts throughout all seasons but was impeded by shoot-zone temperatures exceeding 3.8 and 0°C during summer and autumn, respectively. In contrast to the aforementioned species, *Eriophorum angustifolium* (cv: 3.5%) and *Juncus trifidus* (cv: 7%) revealed less thermal dependence. *Poa vivipara* (cv: 26%) showed an extremely narrow thermal niche, without any significant promoting drivers but with a significant impediment from shoot-zone temperatures above 0°C during spring and below 0°C during autumn. This result indicates *P. vivipara* thrives in habitats with an early and long-lasting snow cover, which is typical for the oceanic western region. With only 2.0% of thermally explained variance during calibration, our last graminoid species *Carex bigelowii* was revealed to be a thermal generalist.

The thermal niches of our eight focal lichen species showed a distinct differentiation into snow-avoidant (chionophobic) and snow-preferring (chionophilous) species, with the former being characterized by the most robust models found in this study (Fig. 4D, Table 2). *Alectoria ochroleuca* (cv: 51.3% of explained variance), *Bryocaulon divergens* (cv: 40.4%), *Cetraria ericetorum* (cv: 18.8%), *Flavocetraria cucullata* (cv: 52.5%), and *Flavocetraria nivalis* (cv: 88.7%) were promoted throughout a wide range of sub-zero temperatures within the shoot and root zone (down to severe frosts below -15°C) outside the summer season, resulting in all these species being described as strongly chionophobic, though they had a gradual differentiation in terms of frost hardness. Compared to the aforementioned species, *Cladina arbuscula* (cal: 11.6%) was promoted by less extreme frosts during winter ($s1.TTH_{SZ/RZ} < -0.1^{\circ}\text{C}$), making it a slightly chionophobic species in a relatively narrow thermal niche, and it was further promoted by higher soil temperatures during summer. Our model for *Cetraria islandica* was even less robust (cal: 5.2% of explained variance) but indicated warmer soils were important (maximum SR at $a.TTH_{RZ} > 6.2^{\circ}\text{C}$), regardless of the winter conditions. The model for *Solorina crocea* (cv: 4.7%) revealed a wide range of both above-zero temperatures (outside the winter season) and subzero temperatures (during the winter season) were impeding, with the maximum impediment reached at $a.TTH_{SZ} > 0.9^{\circ}\text{C}$. These thermal characteristics subscribe *S. crocea* to habitats with a high frequency of freeze–thaw action at higher elevations and in late snow beds.

For all but one of our four focal bryophyte species, thermal impediment was shown to be the dominant issue, which led to narrow thermal niches (Fig. 4E, Table 2). *Conostomum tetragonum* (cv: 61.5% of explained variance) was promoted only within a narrow range of sub-zero temperatures from spring to autumn (maximum promotion at $TTH_{SZ/RZ} < 0^{\circ}\text{C}$), but was impeded by temperatures exceeding 4°C . Additional impediment by frost below -5°C restricted the primary occurrence of *C. tetragonum* to late snow beds. The same general principle became evident for *Anthelia juratzkana* (cv: 18.4%) and *Kiaeria starkei* (cv: 38.5%), although they had gradual differences. In contrast to the aforementioned, the more cold-adapted species *Dicranum fuscescens* (cv: 5.6%) was favored by the combination of summer temperatures within the shoot zone (maximum promotion at $s3.TTH_{SZ} > 16.8^{\circ}\text{C}$) and autumnal above-zero temperatures within the root zone. Similar to the aforementioned species, frost hardness was found to be an issue for *D. fuscescens*, with impediment by frosts, especially during spring (maximum impediment at $s2.TTH_{SZ} < -4.7^{\circ}\text{C}$ and $s2.TTH_{RZ} < -1.0^{\circ}\text{C}$). The requirement of summer warmth in combination with frost protection suggests the spatial restriction of *D. fuscescens* to early-melting snow beds at lower elevations.

DISCUSSION

Species-specific thermal niche predictors

In our study, deciduous shrubs were generally promoted by $TTH_{SZ/RZ} > 0^{\circ}\text{C}$, except for *S. herbacea*, which was significantly impeded by above-zero temperatures during summer. Because of its low stature, *S. herbacea* is restricted to habitats affected by either extreme snow beds or extreme exposure, leading to open communities in which this species, as a poor competitor, exploits the absence of more vigorous species (Birks 1993, Beerling 1998). As such, the only promotion by $TTH_{RZ} \leq 0^{\circ}\text{C}$ expresses the species' restriction to extreme snow beds. Hence, neither its optimum photosynthetic temperature of $10\text{--}20^{\circ}\text{C}$ (Beerling 1998) nor its assumed limit at the $+26^{\circ}\text{C}$ maximum summer temperature isotherm (Dahl 1951) would help describe the realized distribution of this species. In contrast to *S. herbacea*, we found *B. nana* was promoted within a wide thermal range of above-zero temperatures during summer, encompassing most of its photosynthetic optimum temperature range of $10\text{--}30^{\circ}\text{C}$ (Johnson and Tieszen 1976, Semikhatova et al. 1992). Our upper threshold of $\sim 22^{\circ}\text{C}$ was in good agreement with the finding of Rodwell (1991) for British *B. nana* communities, where the mean maximum temperature was $< 21^{\circ}\text{C}$. In accordance with its wide thermal niche, *B. nana* generally occupies exposed ridges, more sheltered midslopes, and swampy habitats (de Groot et al. 1997). Stretching from 12.6 to 23.7°C during summer, *Vaccinium myrtillus* shows a much narrower thermal niche that is clearly shifted toward the highest

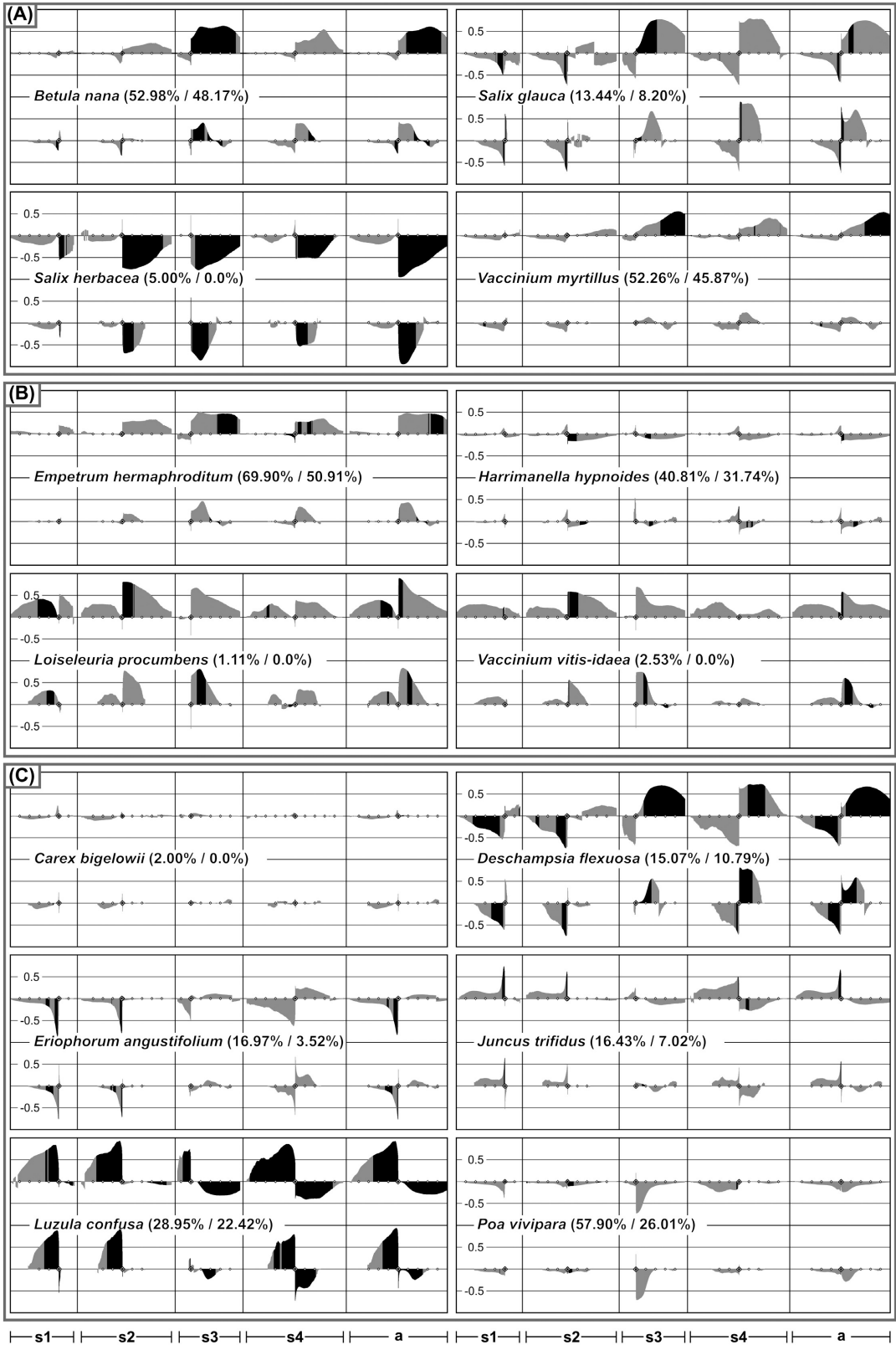


FIG. 4. Thermal niche characteristics of the selected 26 focal plant species, differentiated by the plant functional types: (A) deciduous shrubs, (B) evergreen shrubs, (C) graminoids, (D) macrolichens, and (E) bryophytes; see also the legend of Fig. 3.

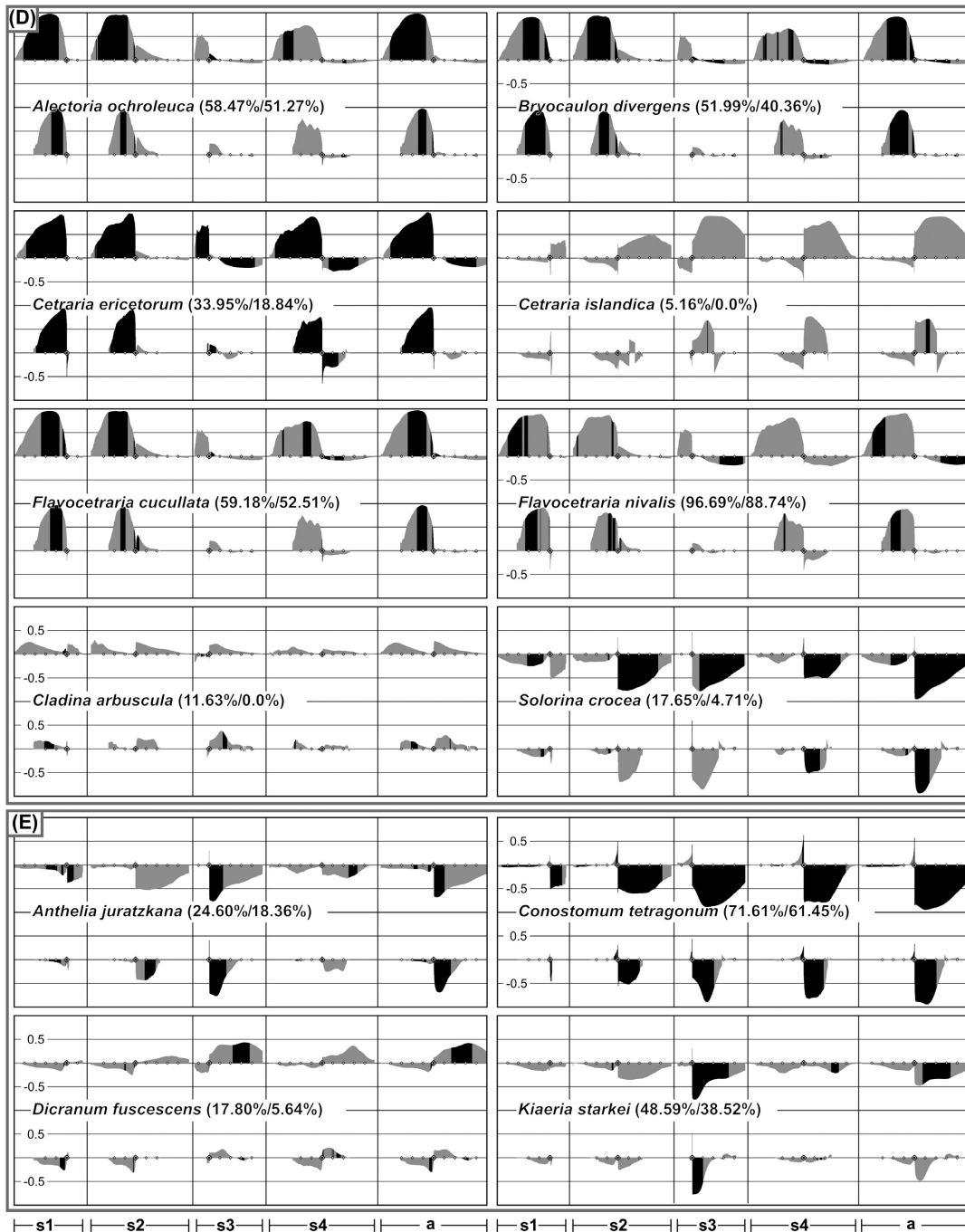


FIG. 4. Continued.

alpine summer temperatures. This finding is in accordance with the high photosynthetic optimum temperature of 27°C reported by Skre (1975). We found *V. myrtillus* was impeded by severe soil frosts ($a.TTH_{RZ} < -9.6^{\circ}\text{C}$), which were not as low as but were still in line with the minimum temperature of approximately -20°C stated by Green (2009) and the observed frost hardness of leaf buds down to -35°C during winter (Stushnoff and Junttila 1986). During autumn, however, our results revealed an impediment of *V. myrtillus* by the occurrence of frosts, despite its reported frost hardness of leaves down to approximately -6°C by the end of the growing season (Beerling et al. 2001). Our finding is in better agreement with the -2°C minimum given by Dahl (1998) and the actual occurrence patterns of *V. myrtillus* in the Scandes, resulting from a trade-off wherein the snow cover is sufficient to provide protection against frost but not deep enough to shorten the growing period too drastically (Dahl 1956, 1975).

Like their deciduous congeners, we found most evergreen shrub species were promoted by positive temperatures during summer. Their evergreen habits and the resulting ability to be physiologically active throughout the seasonal cycle whenever permitted by the environmental conditions, however, allowed them to capitalize on additional time windows of photosynthetic opportunities when the potentially competing deciduous species were leafless (Wyka and Oleksyn 2014). Consequently, our thermal niche predictors outside the summer season gained importance. In agreement with its wide distributional range, *E. hermaphroditum* showed the widest thermal niche with regard to near-surface air temperatures ($15.4^{\circ}\text{C} < a.TTH_{SZ} < 21.6^{\circ}\text{C}$), but there was a surprisingly narrow thermal niche of $9.4^{\circ}\text{C} < a.TTH_{RZ} < 10.2^{\circ}\text{C}$ for soil conditions. Silvola and Heikkinen (1979) reported the optimum temperature for photosynthesis to be at $\sim 10^{\circ}\text{C}$, which falls well below our observed thermal niche, although their reported maximum temperature of 25°C is not reached either. The lack of impediment of *E. hermaphroditum* by low winter temperatures is in line with the observed frost hardness of the species down to -35°C (Stushnoff and Junttila 1986, Ögren 2001). During autumn, however, we found frosts to impede and positive temperatures to promote the occurrence frequencies of *E. hermaphroditum*. Although Bär et al. (2008) found no correlation between annual growth increments of *E. hermaphroditum* and autumn temperatures, the growth of *E. nigrum* in Britain was reported to continue until September or October (Bell and Tallis 1973), making it likely that at least nonstructural carbohydrates in the form of cryoprotective sugars are built during autumn. Whereas thermal conditions during spring had no significant effect on *E. hermaphroditum*, we found *V. vitis-idaea* to be promoted by temperatures close to or even above 0°C during spring ($-0.9^{\circ}\text{C} < TTH_{SZ} < 4.6^{\circ}\text{C}$, $TTH_{RZ} > 0.6^{\circ}\text{C}$). This finding likely corresponds with the observed ability of the species to utilize favorable subnivean conditions during

spring for photosynthesis (Starr and Oberbauer 2003), which is facilitated by a low minimum temperature for photosynthesis of approximately -3.5°C (Pisek et al. 1967). Moreover, Karlsson (1985) estimated that sub-Arctic *V. vitis-idaea* might gain $\sim 22\%$ of its annual photosynthetic production in the early and late parts of the snowless season. Early activation of the photosynthetic apparatus, while still being under snow, enables the plants to reach their maximum capacity quickly after snowmelt, forming an important adaptive trait to the rather short growing season (Starr and Oberbauer 2003). Spring activity is indicated by the significant drivers $0.2^{\circ}\text{C} < s2.TTH_{SZ} < 4.6^{\circ}\text{C}$ also for *Loiseleuria procumbens*, a specialist of windswept ridges with little or no snow cover during winter (Grabherr 1980), also noted for its extreme frost hardness down to -40°C during winter (Pisek and Schießl 1946, Körner 2003). In fact, we found *L. procumbens* to be promoted by severe frosts during autumn and winter, which is in line with observations of a positive correlation between frost occurrence and shoot growth (Wipf et al. 2009), resulting in a competitive advantage of this species over potentially co-occurring species. From an annual perspective, these findings result in a bimodal thermal niche of the species providing both the occurrence of severe frosts to exclude competitors and sufficient temperatures during the growing season. Despite optimum temperatures for photosynthesis of $10\text{--}30^{\circ}\text{C}$ (Semikhatova et al. 1992), our niche model describes $0.4^{\circ}\text{C} < TTH_{SZ} < 1.2^{\circ}\text{C}$ and $4.7^{\circ}\text{C} < TTH_{RZ} < 5.9^{\circ}\text{C}$ to be sufficient, possibly because of the low minimum temperature for net photosynthesis of -6°C reported by Larcher and Wagner (1976). In contrast to the aforementioned evergreen species, we found *H. hypnoides* to be impeded by positive temperatures and only promoted by $s4.TTH < -0.1$. As such, *H. hypnoides* is the evergreen analog to *S. herbacea* and is restricted to extreme snow beds.

As one of our focal graminoid species, *D. flexuosa* has a wide distribution across plant communities of the Deschampsieto-Myrtilletalia alliance (Dahl 1956), which are all chionophilous communities of the low-alpine belt. Thus, as *D. flexuosa* is dependent on sufficient snow cover, we found its occurrence to be impeded by frosts below -1°C , but promoted throughout a wide range of positive temperatures, where the comparably high promoting air temperatures are in line with the $5\text{--}17^{\circ}\text{C}$ thermal optimum of photosynthesis reported by Nygaard (1975). *Eriophorum angustifolium* is mostly restricted to depressions, with high soil moisture as the superior environmental driver (Phillips 1954). Wet peat effectively hinders the soil from being frozen, explaining our observed impediment of the species by soil temperatures below zero. Shoots were reported to survive frost (Phillips 1954), which is reflected in our findings by a somewhat lower threshold in the shoot zone of -0.6°C , although an insulating snow cover seems to be important. In contrast to the aforementioned chionophilous species, we found *Juncus trifidus* and *Luzula confusa*

to be promoted by frosts, with *L. confusa* even being significantly impeded by above-zero near-surface temperatures. Addison and Bliss (1984) reported high photosynthetic rates for *L. confusa*, especially at low temperatures, with leaf temperatures being enhanced by energy-trapping characteristics, such as tufted growth form and persistence of dead leaves. As a slow-growing species, these adaptations give the species a competitive advantage over other species under harsh environmental conditions. Another graminoid species, *Carex bigelowii*, showed neither impeding nor promoting effects within the range of our observed thermal conditions, which likely reflect its wide ecological amplitude (Gjærevoll 1956) stretching from wind-exposed ridges to late snow beds.

The physiological adaptation of lichens, such as their extremely high freezing tolerance while still maintaining photosynthetic capacity (Dahl 1954, Kappen and Lange 1972), allow colonization of (and, despite their slow growth, dominance within) areas where higher plant competition is lessened by rigorous environmental conditions (Lechowicz and Adams 1974). In fact, we found most of our lichen species to be promoted throughout a wide range of subzero temperatures, even at lower temperatures than we observed to be promotional for chionophobic vascular plants such as *L. procumbens*. Having a low photosynthetic temperature optimum of 0–10°C (Lange 1965, Kappen and Lange 1972, Kappen and Friedmann 1983), the range of apparent photosynthesis for lichens extends well into subzero temperatures, even down to –20°C for *Flavocetraria nivalis* (Kallio and Heinonen 1971). In contrast, we found *F. nivalis* (but also *C. ericetorum*, *B. divergens*, and *S. crocea*) to be impeded by higher temperatures, which is in line with the reported strong decline in net assimilation at higher temperatures, leading to lichens being less heat tolerant than vascular plants when they are in an active, nondesiccated state (Lange 1965). However, the self-engineering of favorable cool conditions is facilitated by a high reflectance in combination with a low thermal and hydrological conductivity of the lichen thalli (Odland et al. 2017).

Like lichens, bryophytes are well adapted to severe environmental conditions (e.g., Kallio and Heinonen 1973, Löscher et al. 1983, Glime 2017). The optimum photosynthetic temperature is reported to be ~5–10°C for most northern species, but activity continues at subzero temperatures (Kallio and Valanne 1975). Unlike our lichen species, however, we found the bryophyte species *Anthelia juratzkana* and *Conostomum tetragonum* to be impeded by both subzero temperatures and summer warmth, confining the thermal niche in case of *C. tetragonum* to a narrow range at ~0°C, typically found in late snow beds. For *A. juratzkana*, investigations by Löscher et al. (1983) revealed the lower temperature compensation point to be reached at –4°C and net-photosynthesis not to be sustained beyond 30°C. Its capability to make use of low light intensities and its low-temperature

demand to achieve optimal photosynthetic rates makes *A. juratzkana* well adapted to grow in the border zone along permanent snow patches. *Dicranum fuscescens* revealed more “temperate” thermal niche characteristics, especially promoted by $s3.TTH > 16.8^{\circ}\text{C}$ and impeded by $s2.TTH < -4.7^{\circ}\text{C}$ in the shoot zone. As such, it is mainly restricted to the chionophilous low-alpine *Vaccinietum* communities (Dahl 1956).

Conceptual strengths, limitations, and arising challenges

The large spread in explanatory power and robustness of thermal niche models among our 26 focal species pinpoints the need to consider not just one but all ecophysiological relevant variables when attempting to quantify a species’ ecological niche. Centering at a well acknowledged and commonly used environmental factor, that is, the thermal conditions and the associated thermal niche of a species, however, showcases the myriad ways a single factor varies with respect to species, above- and belowground conditions, magnitude of thresholds, and temporal variability. Though this was actually to be expected, our findings reveal general challenges within the context of species distribution modeling that urgently need to be addressed because—correct and simply put by Mod et al. (2016)—“what we use is not what we know.”

In general, our findings align with the wide acknowledgment of climate and especially temperature as a prominent abiotic driver of (alpine) plant life and the natural distribution of species (Pearson and Dawson 2003, Körner and Hiltbrunner 2018). Consequently, the “bioclimatic envelope” of a species can be identified to facilitate modeling of its biogeographical distribution by using niche-based species distribution models (Randin et al. 2006, Dullinger et al. 2012, Pellissier et al. 2013). As such, utilizing thermal conditions to describe species distribution is not *per se* an implausible assumption (sensu Araújo and Peterson 2012), given that—based on knowledge about the biogeographical and ecological theory—sound eco-physiological predictors are chosen (Araújo and Guisan 2006, Elith and Leathwick 2009).

Addressing the consequential critique of, for example, Franklin et al. (2013) and Körner and Hiltbrunner (2018), we selected physiologically and ecologically meaningful measures of temperature related to (1) *the critical location* of plant enzyme activity, phenology, and growth by choosing on-site RZ and SZ temperatures; (2) *the microtopographical constraints* of the thermal regime that result from the interplay of soil moisture, snow cover, and solar radiation by choosing a site-based approach along multi-scale spatial gradients; and (3) *the critical time scales* of the above physiological aspects by choosing near-surface, hourly temperature recordings within a seasonal and annual perspective. As such, our approach addresses the obvious mismatch between the resolution of climatic data and the scale at which species experience this climate (Randin et al. 2009a, Harwood

et al. 2014, Pape and Löffler 2017). Moreover, the central role of seasonality of life in alpine environments (Körner and Hiltbrunner 2018) is considered because the seasonality of climate has already been proven to be of primary importance in defining the niche of plant species (Chuine and Beaubien 2001, Morin et al. 2007, Chuine 2010).

Moreover, by identifying species-specific thermal threshold hours (TTH) as a measure of biologically relevant temperatures, derived from the comparison between the entire set of temperatures and the frequency of a species, our approach overcomes the criticism of Thuiller et al. (2005) against the common approach of using a hypothetical set of generic variables, such as annual mean temperature, maximum temperature of the warmest month, or heat units above or below a fixed threshold (GDD, FDD) for niche-based modeling (Lenoir et al. 2017, Choler 2018, Lany et al. 2018). Whereas temperature response functions behind those physiological processes actually determining species distribution might best guide the choice of bio-climatically limiting variables (Bykova et al. 2012), as a compromise, here we promote the use of thermal threshold hours as a useful tool to quantify a plant species' realized thermal niche. Although still correlational, we expect our TTH and their physiological valuation to assist the step proposed by Körner et al. (2016) to move beyond probabilistic and correlational descriptions and toward mechanism-based definitions of range limits.

It is a challenge, however, to provide such truly ecophysiological meaningful predictors for large-domain SDMs. Downscaling of available climate data based on high-resolution topography is a first step, but major limitations remain (Meineri and Hylander 2017), as the decoupling between ambient air and near-surface conditions is still not considered (cf. Fig. 1). As such, increasing solely the spatial resolution does not help, if the functional relationships are not more finely resolved as well (Pradervand et al. 2014, Pape and Löffler 2017). Attempts to use spatial correlates instead of assessing the thermal regime directly reveal the paradox that this might work reasonably well over small spatial extents, but becomes increasingly inaccurate across those spatial extents these surrogates are actually sought for (Randin et al. 2009b). Instead, we propose that the only way to move a step forward would be to rely more on extensive field measurements conducted within a stratified design to represent a range of environmental conditions across a large spatial domain. This would be logistically challenging (Meineri and Hylander 2017) but not impossible (Körner and Paulsen 2004, Pradervand et al. 2014). Gained species-specific knowledge about (thermal) range limits then extends the general idea of species-specific ecological indicator values (Ellenberg 1974) and especially trait catalogs (Dahl 1998, Kattge et al. 2011), providing a basis for a more quantitative and predictive ecology (Kattge et al. 2011, Scherrer and Guisan 2019).

CONCLUSION

Assessing the realized thermal niches of 26 arctic-alpine plant species from the plant's ground-level perspective revealed an obvious challenge in species distribution modeling. Thermal niches are much more nuanced and variable than they are commonly represented, challenging us to improve the way we present, interrogate, and interpret data representing those thermal niches. Although we theoretically know about the importance of ecophysiological relevant predictors, the actual choice of predictors is more often based on the most convenient data source. This study used a widely acknowledged environmental factor with seemingly good data availability, but data limitations become a more important issue for other factors that are more difficult to obtain. Here, we propose a wider utilization of in situ measurements of the environmental factors at the actual growing site of a plant species, as this would allow a step forward to move beyond purely probabilistic and correlative descriptions of species' range limits and improve predictions of species distributions in complex arctic-alpine landscapes.

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