

Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing

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Abstract

Aim: Although species distribution models (SDMs) traditionally link species occurrences to free-air temperature data at coarse spatio-temporal resolution, the distribution of organisms might instead be driven by temperatures more proximal to their habitats. Several solutions are currently available, such as downscaled or interpolated coarse-grained free-air temperatures, satellite-measured land surface temperatures (LST) or in-situ-measured soil temperatures. A comprehensive comparison of temperature data sources and their performance in SDMs is, however, currently lacking.

Location: Northern Scandinavia.

Time period: 1970–2017.

Major taxa studied: Higher plants.

Methods: We evaluated different sources of temperature data (WorldClim, CHELSA, MODIS, E-OBS, topoclimate and soil temperature from miniature data loggers), differing in spatial resolution (from 1" to 0.1°), measurement focus (free-air, ground-surface or soil temperature) and temporal extent (year-long versus long-term averages),

and used them to fit SDMs for 50 plant species with different growth forms in a high-latitudinal mountain region.

Results: Differences between these temperature data sources originating from measurement focus and temporal extent overshadow the effects of temporal climatic differences and spatio-temporal resolution, with elevational lapse rates ranging from -0.6°C per 100 m for long-term free-air temperature data to -0.2°C per 100 m for in-situ soil temperatures. Most importantly, we found that the performance of the temperature data in SDMs depended on the growth forms of species. The use of in-situ soil temperatures improved the explanatory power of our SDMs (R^2 on average +16%), especially for forbs and graminoids (R^2 +24 and +21% on average, respectively) compared with the other data sources.

Main conclusions: We suggest that future studies using SDMs should use the temperature dataset that best reflects the ecology of the species, rather than automatically using coarse-grained data from WorldClim or CHELSA.

KEY WORDS

bioclimatic envelope modelling, bioclimatic variables, climate change, growth forms, land surface temperature, microclimate, mountains, soil temperature, species distribution modelling

1 | INTRODUCTION

Species distribution models (SDMs) are widely used to describe and forecast the spatial distribution of species (Elith & Leathwick, 2009). Species distribution models relate species occurrence data to information about the environmental conditions at these locations (Elith & Leathwick, 2009; Guisan & Thuiller, 2007; Jiménez-Valverde et al., 2011). The most common strategy is to work with long-term (e.g., 30 years) interpolated averages of a set of bioclimatic variables at 30" resolution (c. $1 \times 1 \text{ km}$ at the equator; e.g., WorldClim or CHELSA; Gonzalez-Moreno, Diez, Richardson, & Vila, 2015; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Karger et al., 2017; Sears, Raskin, & Angilletta, 2011; Slavich, Warton, Ashcroft, Gollan, & Ramp, 2014; Warren, Glor, & Turelli, 2008). Although such macroclimate data might be sufficient to capture the conditions on flat terrain, many environments host a heterogeneous topography (e.g., across steep elevational gradients in mountain regions) that makes the microclimate near the ground vary noticeably over short distances (Gottfried, Pauli, Reiter, & Grabherr, 1999; Holden, Abatzoglou, Luce, & Baggett, 2011; Opedal, Armbruster, & Graae, 2015; Scherrer & Körner, 2011; Sears et al., 2011; Stewart, Simonsen, Svenning, Schmidt, & Pellissier, 2018). In order to make realistic forecasts of species distributions and distribution shifts in such heterogeneous environments, it has been suggested that climate data at finer spatio-temporal resolutions are needed (Graae et al., 2012, 2018; Illan, Gutierrez, & Wilson, 2010; Lenoir et al., 2013; Opedal et al., 2015; Scherrer & Körner, 2011). Such new climate datasets, including in-situ logging and remote sensing, are now increasingly becoming available (Bramer et al., 2018). Nonetheless, an evaluation

of their performance in SDMs is necessary to provide guidance for future studies; in particular, for those predicting the responses of species to climate change (Stewart et al., 2018).

In the high-latitude and high-elevation areas of northern Europe, local temperatures have been found to vary up to 6°C within 1 km^2 spatial units, reflecting the local topography (Lenoir et al., 2013). This high temperature variation depends, for instance, on the interaction between temperature and snow distribution and, consequently, affects the length of the local growing season (Aalto, Scherrer, Lenoir, Guisan, & Luoto, 2018; Körner, 2003). Local temperatures also vary greatly between seasons, and short-term extreme weather conditions have been shown to be more relevant for species distributions than the average climatic conditions (Ashcroft & Gollan, 2012). Including this variation in SDMs is likely to be crucial, for instance in the context of stepping stones, holdouts or microrefugia (Dobrowski, 2011; Meineri & Hylander, 2017; Opedal et al., 2015). Stepping stones refer to areas with microclimates that facilitate shifts in species ranges (e.g., upward or poleward movement during climate change or after non-native species introductions; Hannah et al., 2014; Lembrechts, et al., 2018; Pauchard et al., 2009). Holdouts and microrefugia, in contrast, are areas with a relatively stable microclimate where isolated populations can persist for a certain time (Ashcroft, 2010; Hannah et al., 2014; Lenoir, Hattab, & Pierre, 2017; Meineri & Hylander, 2017). Climatic variability within an area can indeed considerably buffer effects of climate warming (Lenoir et al., 2013, 2017), which often remain undetected using macroclimate data, possibly leading to the overestimation of rates of extinction and range expansion (Willis & Bhagwat, 2009).

Moreover, many organisms (particularly small-stature plants, certain types of insects and soil microbes) experience temperatures at ground or sub-surface level, which can differ greatly from ambient air temperatures that are usually measured at 2 m above the soil surface (Aalto et al., 2018; Körner & Hiltbrunner, 2018; Poorter et al., 2016). Especially in high-latitude and high-elevation regions, snow cover, for example, acts as an insulator, thereby strongly decoupling soil and air temperatures (Pauli, Zuckerberg, Whiteman, & Porter, 2013; Poorter et al., 2016; Thompson, Zuckerberg, Porter, & Pauli, 2018), and biophysical processes owing to vegetation cover may also decouple upper atmospheric conditions from boundary layer conditions (Geiger, 1950).

In order to overcome this spatio-temporal mismatch between climate data and species ecology and to improve predictions of species' current and future distributions, four main approaches are commonly used: (a) to downscale existing coarse-grained (i.e., $1,000 \times 1,000$ m resolution) climate data (McCullough et al., 2016); (b) to interpolate climate station data (Aalto, Riihimäki, Meineri, Hylander, & Luoto, 2017); (c) to gather local climate data through field measurements (Lenoir et al., 2017; Potter, Woods, & Pincebourde, 2013; Slavich et al., 2014); or (d) to monitor climatic conditions continuously in space and time through remote sensing technologies (e.g., satellite-measured land surface temperatures; Metz, Rocchini, & Neteler, 2014; Wan, 2008).

In the first two approaches, a high spatial resolution can be obtained using topographic variables derived from digital elevation models, which are available at much finer resolutions (e.g., 1", which is c. 30×30 m at the equator). Such downscaled or interpolated climate data have been found to be a significant improvement over macroclimatic variables for modelling species distributions (Dobrowski, 2011; Meineri & Hylander, 2017; Randin, Engler, et al., 2009; Slavich et al., 2014).

In the third approach, one uses in-situ measurements to provide fine-grained climatic conditions with high spatial accuracy (microclimate) (Meineri & Hylander, 2017; Opedal et al., 2015). Such field measurements can also be interpolated to the level of regional climate using topographical information (Ashcroft, Chisholm, & French, 2008; Greiser, Meineri, Luoto, Ehrlén, & Hylander, 2018; Maclean, Suggitt, Wilson, Duffy, & Bennie, 2017), yet usually cover short temporal and small geographical extents only. In addition to a fine spatial resolution, in-situ measurements provide the opportunity to adapt the measurement focus to the ecology or life-form of the species (e.g., by measuring near-surface soil temperature instead of air temperature). Gathering in-situ temperature data, however, requires considerably more resources than the previously mentioned downscaling approaches (Meineri & Hylander, 2017; Opedal et al., 2015). Increasing the spatio-temporal resolution and extent of such field measurements generally refines the predictions, but also presents a logistical challenge (Meineri & Hylander, 2017; Wundram, Pape, & Löffler, 2010).

Finally, the fourth approach (i.e., using remotely sensed data) is now more frequently used in SDMs (Pottier et al., 2014), for instance through remotely sensed snow cover data or by using

the normalized difference vegetation index (NDVI) (Yannic et al., 2014). One such remotely sensed source of data, for which the spatio-temporal resolution, extent and accuracy is rapidly improving, is satellite-based land surface temperatures (LSTs; Wan, 2008; Wan et al., 2015). Remotely sensed LSTs are now freely available at the global scale at the vegetation canopy or land surface level, with a temporal resolution of days over a period of decades and with a spatial resolution ranging from 30" (c. $1,000 \times 1,000$ m at the equator) to as fine as 1" (c. 30×30 m) (Cook, 2014). This type of data does have the advantage over free-air temperature datasets, such as WorldClim or CHELSA, of being a direct and contiguous measurement in space and time, as opposed to data interpolation and temporal averaging from a network of weather stations, yet might be affected strongly by land surface characteristics and cloud cover in the area (Zellweger et al., 2019). Thanks to the increasing availability of these long-term and accurate time series, such satellite-based LST datasets offer very promising research avenues to fill the gap between local temperature measurements and global-scale climatic datasets.

These different approaches to obtain suitable climate data have been extensively explored and applied in SDMs (Bramer et al., 2018), yet a comparative study of all of these (downscaled and interpolated macroclimate data, field measurements and satellite-based LST) together, concerning both their inherent characteristics and their role in SDMs, has been missing until now. Such a comparison is nevertheless needed urgently in order to quantify the progress that can be made by replacing the traditional global climate models with other temperature data sources. We hypothesize in that regard that the best result depends mainly on two critical factors: (a) the climatic characteristics of the study region; and (b) the growth forms of the study organisms.

Here, we use a case study along steep climatic gradients in the Northern Scandes, a mountain range in northern Scandinavia, to assess both factors and to provide guidelines for the use of temperature data in SDMs in topographically challenging regions. We compare the characteristics of different temperature datasets within the region, in addition to the descriptive and predictive power of SDMs for 50 plant species with different growth forms: forbs, graminoids, (dwarf) shrubs and trees. We compare global climate datasets (i.e., WorldClim and CHELSA) with datasets of remotely sensed LSTs (MODIS), a topographic downscaling and interpolation approach, and soil temperature obtained with miniature data loggers, and use three widely applied and ecologically relevant (i.e., bioclimatic) temperature variables: mean annual temperature, and mean temperature of the warmest and the coldest quarter. We hypothesize a significant effect of the spatial resolution of the climate data and of measurement focus (free-air, surface or soil) and temporal extent on temperature patterns across topographic gradients. Increasing spatio-temporal accuracy of temperature data, especially through the use of in-situ measurements, is expected to improve the descriptive and predictive power of the SDMs, despite the associated reduction in temporal extent. The optimal resolution, extent and measurement focus

are, however, likely to depend on the growth forms of the assessed species (i.e., the spatio-temporal framework in which they operate).

2 | METHODS

2.1 | Study region

The study was conducted in the Northern Scandes mountain range in Norway and Sweden, between $67^{\circ}46'23.5''$ N, $16^{\circ}30'52.6''$ E (south-west) and $68^{\circ}40'33.6''$ N, $18^{\circ}58'40.4''$ E (north-east), covering an area of 100×100 km and an elevation range from 0 to 2,097 m above sea level (a.s.l.). The area ranges from the Norwegian coast, with a relatively mild and wet climate dominated by birch forests with heathland understorey, to the significantly drier and colder eastern side of the Northern Scandes, typically vegetated by subarctic, alpine dwarf shrub vegetation (Lembrechts, Milbau, & Nijs, 2014). The region was chosen for its strong climatic gradient, with large macro- and microclimatic

variation owing to a distinct topography and high-latitude location (Graae et al., 2012; Lenoir et al., 2013; Scherrer & Körner, 2011). In total, 106 temperature measurement locations were spread across the study area (Figure 1).

2.2 | Climate data

For this area, we obtained eight different types of climate data encompassing a wide range of measurement foci, spatio-temporal resolutions and temporal extents (Table 1). For each of these datasets, we extracted or calculated the mean annual temperature and mean temperature of the warmest and coldest quarter [bioclimatic variables Bio1, Bio10 and Bio11, following the definition of WorldClim (Hijmans et al., 2005), hereafter called mean annual, summer and winter temperature, respectively]. These ecologically relevant variables belong to the set of physiologically most pertinent bioclimatic determinants of spatial plant species distribution and are thus commonly used in SDMs (e.g., Austin & Van Niel, 2011; Cord & Rödder, 2011; Distler, Schuetz, Velásquez-Tibatá, &

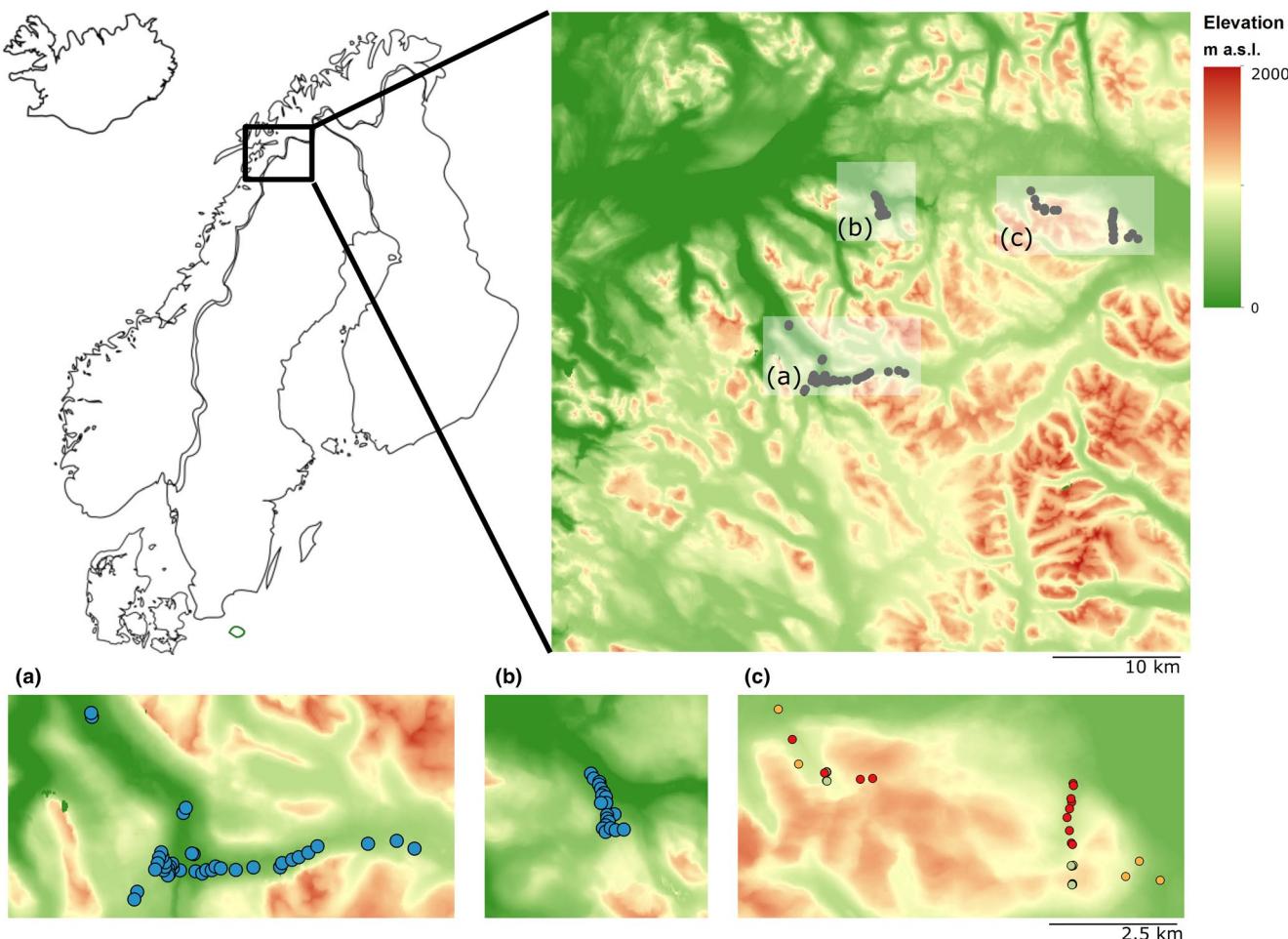


FIGURE 1 Study area and measurement locations. Location of the study area in Scandinavia (left) and digital elevation model (DEM) at $1''$ resolution (c. 30×30 m at the equator) across the study area (right). Dots on the DEM show locations of the 106 soil temperature measurements. Species data sampling was done in the locations marked with blue dots (a,b). See Table 2 for datasets (blue = 1; orange = 2; green = 3; red = 4). Elevational gradients range from 0 to 700 m a.s.l. (a,b) and from 400 to 1,200 m a.s.l. (c)

TABLE 1 The eight climate datasets studied and their geographical and temporal extent, spatial resolution and measurement focus

Dataset	Initial source	Geographical extent	Spatial resolution	Measurement focus	Temporal coverage
WorldClim	WorldClim	Global	30"	Free-air	1970–2000
CHELSA	CHELSA	Global	30"	Free-air	1979–2013
Downscaled	CHELSA	10,000 km ²	1"	Free-air	1979–2013
Topoclimate	Aalto et al. (2017)	10,000 km ²	1"	Free-air	1981–2010
MODIS LST	MODIS	Global	30"	Surface	2015–2017
EuroLST	MODIS	Europe	c. 7.5"	Surface	2001–2011
E-OBS	E-OBS	Europe	0.1°	Free-air	2015–2017
Soil temperature	iButtons	10,000 km ²	1"	Soil	2015–2017

Langham, 2015), and they allow us to take into account seasonal differences in climate accurately. The different datasets are discussed in detail below.

2.2.1 | WorldClim

The WorldClim database (v.2.0) provides globally interpolated free-air temperature conditions over a 30-year time period (1970–2000) at a spatial resolution of 30" (c. 1,000 × 1,000 m at the equator) (Fick & Hijmans, 2017). The studied bioclimatic variables were directly downloaded from the website (www.worldclim.org).

2.2.2 | CHELSA

The climatologies at high resolution for the earth's land surface areas (CHELSA, v.1.2) is a global dataset based on quasi-mechanistic statistical downscaling of free-air temperatures from the ERA Interim (ECMWF) global circulation model (Dee et al., 2011), over a period of 34 years (1979–2013) and with the same spatial resolution as WorldClim (30", c. 1,000 × 1,000 m at the equator), yet for a more recent time period (Karger et al., 2017). Bioclimatic variables were again downloaded directly from the website (www.chelsa-climate.org).

2.2.3 | Downscaled CHELSA data (hereafter called "downscaled")

We used the bioclimatic variables downloaded from CHELSA, at an original resolution of 30" (c. 1,000 × 1,000 m at the equator), and downscaled them statistically even further, to a 1" (c. 30 × 30 m at the equator) resolution based on topographic variation, using a physiographically informed model fitted with a geographically weighted regression (GWR) technique (Fotheringham, Brunsdon, & Charlton, 2003). In short, GWR extends the traditional regression approach by allowing estimated regression parameters to vary across space. Therefore, GWR models are particularly relevant for exploration of the scale-dependent and spatial non-stationary relationships between free-air temperatures and physiographic variables (here: elevation, slope, eastness, northness, distance to the ocean and

clear-sky solar radiation) (Su, Foody, & Cheng, 2012). For more details, see Supporting Information Appendix S1.

2.2.4 | Topoclimate

Fine-resolution gridded climate data for the region were obtained from Aalto et al. (2017), who included topography-driven small-scale climate heterogeneity in a topoclimatic interpolation of weather station data across northern Scandinavia, using generalized additive modelling at a resolution of 1" (c. 30 × 30 m at the equator). They modelled monthly average temperatures from 1981 until 2010 using geographical location, elevation, water cover, solar radiation and cold-air pooling. Bioclimatic variables were calculated based on these monthly averages.

2.2.5 | MODIS LST

The moderate resolution imaging spectroradiometer (MODIS) satellite TERRA (Wan et al., 2015) from the National Aeronautics and Space Administration (USA) provides global LST. We extracted data from MOD11A2: 8-day averages based on the clear sky day- and night-time records at a 30" (c. 1,000 × 1,000 m at the equator) resolution, for a period of 2 years corresponding to the in-situ measurements (from August 2015 to July 2017; see below). Mean annual temperature was calculated in ArcGIS by averaging the temperature per pixel for 2015–2016 and 2016–2017, separately, from day of the year (DOY) 209 in year *n* (e.g., 27 July 2015) to DOY 208 in year *n* + 1 (e.g., 26 July 2016), which was the set of 8-day averages corresponding most closely to the period used for the in-situ temperature measurements described below (see sub-section below on Soil temperatures). Mean summer and winter temperatures were calculated in a similar manner, but for DOY 185 (e.g., 3 July 2015) to 272 (28 September 2015) and from DOY 1 (e.g., 1 January 2016) to 88 (28 March 2016), respectively.

2.2.6 | EuroLST

The EuroLST dataset is a gap-filled dataset at the European scale of LST derived from MODIS (see the sub-section above on MODIS LST)

at a spatial resolution of 250×250 m and averaged over a temporal extent of 10 years (Metz et al., 2014). This dataset has been created using a combination of weighted temporal averaging with statistical modelling and spatial interpolation to fill in the gaps in the MODIS LST dataset and to improve its spatial resolution. Relevant bioclimatic variables were downloaded directly from the website (courses.neteler.org/eurost-seamless-gap-free-daily-european-maps-land-surface-temperatures).

2.2.7 | E-OBS

The E-OBS dataset (v.17.0) provides daily gridded climate data of free-air temperature for Europe at a 0.1° (*c.* $10,000 \times 10,000$ m at the equator) spatial resolution, interpolated from weather stations (Haylock et al., 2008), used here over the study period from August 2015 to July 2017 (as in the subsection on MODIS LST). The gridded dataset is created by first interpolating the monthly mean temperature from the weather stations using three-dimensional thin-plate splines, interpolating the daily anomalies using a spatial kriging approach with an external drift for temperature, and then combining these monthly and daily estimates. Temperature data were downloaded directly from the website (<https://www.ecad.eu/download/ensembles/download.php>) and subsequently used to generate the three studied bioclimatic variables in R.

2.2.8 | Soil temperatures

Near-surface soil temperatures were logged every 1.5 or 2 h (iButtons: DS1922L or DS1921G, with an accuracy of 0.5°C , www.maximintegrated.com, San José, CA, USA) at a depth of 3 cm below the soil surface in 106 locations along several elevational gradients in Norway and Sweden (Figure 1; Table 2). Loggers were wrapped in parafilm and put in a small zipper bag to prevent water damage. The loggers were originally established for several different projects (Lembrechts et al., 2018, 2014, 2016) along seven elevational gradients, together ranging from 0 to 1,200 m a.s.l., of which three were in Norway and four in Sweden. The three bioclimatic variables were calculated in R (R Core Team, 2015) for each 106 locations and for

each year (from 2015 to 2017, corresponding to the periods used in the sub-section above on MODIS LST) from daily averages. Based on these soil temperature data, we made predictions for each bioclimatic variable for the whole study area of 100×100 km for the period from August 2016 to July 2017 using GWRs (as in the sub-section above featuring the downscaling approach) based on the same physiographic variables (i.e., elevation, slope, eastness, northness, distance to the ocean and clear-sky solar radiation). The models were used to predict the bioclimatic variables for every $1''$ (*c.* 30×30 m at the equator) pixel in the study area. For more details on the interpolation approach, see Supporting Information Appendix S1.

2.3 | Plant species observations

Plant species data were obtained during summer 2017 in the framework of the Mountain Invasion Research Network (www.mountaininvasions.org) long-term monitoring effort, and specifically as a follow-up to the survey of Lembrechts et al. (2014) in the Norwegian study plots (59 out of the 106 plots with in-situ soil temperature measurements; see Figure 1; Table 2). Within the framework of this survey, three elevational gradients were selected (spanning on average 700 m in elevation). The elevation range covered by each gradient was divided into 19 equally spaced elevation bands, resulting in 20 sampling sites per gradient. At each elevation, presence/absence of all vascular plant species was recorded in plots of 2×50 m in natural vegetation. At one end of each of these plots, the temperature logger (see dataset described in the sub-section on Soil temperatures above) was buried. We used data for the 50 most common plant species in the survey (i.e., ≥ 10 occurrences). Species were grouped based on their growth forms (Supporting Information Table S1): forbs ($n = 25$); graminoids ($n = 7$); dwarf shrubs ($n = 15$); and trees ($n = 3$). All species were native to the region.

2.4 | Direct comparison of climatic variables

2.4.1 | Relationship to elevation

To assess differences in the behaviour of the eight climate datasets along an elevational gradient, the three bioclimatic variables derived

TABLE 2 Overview of in-situ soil temperature measurement plots in Sweden and Norway ($n = 106$)

Region	Number of gradients	Number of sites	Number of plots	Surface area	Temporal extent	Elevation (m a.s.l.)	Species data
1. Norway	3	59	59	2×100 m	1 August 2015 to 31 July 2017	0–700	Yes
2. Sweden	2	4	23	0.6×1.2 m	1 August 2015 to 31 July 2016	900–1,100	No
3. Sweden	2	6	11	0.6×1.2 m	1 August 2015 to 31 July 2017	400–900	No
4. Sweden	2	13	13	2×10 m	1 August 2015 to 31 July 2017	400–1,200	No

Note. For each region (numbered from 1 to 4; refer to the map in Figure 1), we present the number of elevational gradients (i.e., different mountains monitored), sites and plots (with more plots than sites indicating repeated temperature measurements in a $<20 \times 20$ m area), in addition to the temporal extent, the length of the elevational gradient, and whether species data are available to run species distribution models (SDMs).

from these climate datasets were plotted separately against the elevation of the 106 locations of the in-situ soil temperature data loggers. For the gridded climate datasets, we extracted a value for each bioclimatic variable for each location. We used linear models (function *lm* in R; R Core Team, 2015) to assess the lapse rate (i.e., the slope, in degrees Celsius per 100 m) of decrease in temperature with elevation. For MODIS LST, E-OBS and the soil temperature measurements, data were plotted and modelled separately for the two study years (2015–2016 and 2016–2017).

2.4.2 | Paired comparisons

For each of the 106 studied locations, we compared the values for each climatic dataset (and each of the three bioclimatic variables) against the others, to investigate consistent temperature deviations between datasets. Trends for each bioclimatic variable and each dataset were visualized with general additive models (GAMs), with a cubic regression line and without a pre-set smoothing value (function *gam*, R package *mgcv*; Wood, 2006), following procedures described by Zuur, Ieno, Walker, Saveliev, and Smith (2009). General additive models were used because we did not want to make restrictive assumptions about the relationships of the datasets with each other.

2.4.3 | Correlative dendograms

For all 106 locations, we made correlative dendograms ($\text{distance} = 1 - \rho$, where ρ is Pearson's product-moment correlation) to visualize correlations among and relationships between the different datasets, using the function *hclust* from the package *spatstat* (Baddeley, Rubak, & Turner, 2015).

2.4.4 | Regional climate predictions

We generated regional maps for the different climate datasets (see the Climate data section and Supporting Information Appendix S1 for more details on how the maps were generated for the in-situ measurements), and calculated for each pixel the absolute temperature difference between the respective dataset and the regionally modelled soil temperature at a 1" (c. 30×30 m at the equator) spatial resolution.

2.4.5 | Temporal correction

For a more formal comparison between the datasets with different temporal windows, we calculated, for each climatic dataset, its difference from the "background climate", taken as temperatures for the window in question from the ERA Interim (ECMWF) 2 m free-air temperature database (Dee et al., 2011). This is a time series of monthly means of daily means from 1979 to 2018 (hence covering the time period for all studied datasets except WorldClim), for which we calculated average Bio1, Bio10 and Bio11 over the whole 100×100 km study area (based on the original $0.75^\circ \times 0.75^\circ$

resolution grid). We then re-ran the paired comparisons (see Paired comparisons section) with the temperature off-set (i.e., the difference between the bioclimatic value, for each observation and for each dataset, and the average bioclimatic value from ERA Interim for the corresponding period), using Student's paired *t*-tests to test for potential differences, such as differences between Bio1(soil temperature_(2016–2017)) and Bio1(ERA Interim_(2016–2017)) and between Bio1(CHELSA_(1979–2013)) and Bio1(ERA Interim_(1979–2013)).

Use of this off-set of temperatures from a standardized and common time series allowed us to correct, to some extent, for differences in the temporal scope among the climatic datasets, and thus climate change and interannual weather variation. Although this does not take into account possible decoupling of climate change between soil, surface and air temperature, it does allow the estimation of the size of the temporal effect in the dataset, and thus more precise quantification of the difference between in-situ soil temperature and the other datasets.

2.5 | Species distribution modelling

The regional distribution of the 50 plant species was modelled using species-specific generalized linear mixed-effect models [GLMMs; function *glmer*, package *lme4* (Bates, Maechler, Bolker, & Walker, 2015), family = binomial] as a function of mean annual, summer and winter temperature, and their quadratic terms. Gradient (plant data were available from three different elevational gradients; Table 2) was used as a random intercept term in these models to account for structural variation between gradients. This was repeated for each climate dataset (except for E-OBS, because owing to the limited climate variation measured within the region, species distributions could not be modelled), resulting in a total of 350 SDMs (50 species \times seven datasets). For both MODIS LST and soil temperature, only the data from the measurement year before the species observations (2016–2017) were used, whereas the bioclimatic variables from 2015–2016 were highly correlated with those of 2016–2017 and thus excluded. The variance inflation factor (VIF; function *vif*, package *car*; Fox & Weisberg, 2011) was calculated for each of the climatic datasets to test the correlation between the different bioclimatic variables. Given that the VIF (a value between zero and infinity) exceeded five (indicating a strong correlation) for some datasets (specifically, those with long-term climatic averages), separate models including only Bio1 as explanatory variables were made, and results were compared between both approaches.

The explained variance in the present distribution of the species (R^2 of the fixed effect, i.e., the marginal R^2 ; Nakagawa & Schielzeth, 2013) was then calculated for each model and compared across all species between the different datasets with an ANOVA and Tukey's HSD post-hoc test [differences in R^2 between growth forms (factor with four levels), model assumptions were met]. We also compared the increase in R^2 values obtained by using soil temperature versus the other climate datasets for the different growth forms (forbs, graminoids, shrubs and trees) separately.

Finally, we assessed the predictive power of the different SDMs using a leave-one-out method, each time calibrating the model with 58 data points (plots) and predicting for the remaining one. We calculated the area under the curve (AUC) of the receiver operating characteristic (ROC), using the function *performance* from the package *ROCR* (Sing, Sander, Beerenwinkel, & Lengauer, 2005), in addition to the sensitivity (presences correctly predicted as presences) and the specificity (absences correctly predicted as absences) metrics. A value of .5 was used to binarize predictions. This was repeated for each species and for each climate dataset, and differences in AUC, sensitivity and specificity between SDMs using the different climatic datasets were again assessed with an ANOVA and a post-hoc Tukey's HSD test. We also compared the increase in AUC, sensitivity and specificity obtained by using soil temperature versus the other climate datasets for the different growth forms separately. Note that this predictive approach is limited for three reasons. First, the restricted dataset size is likely to constrain the predictive power of the models. Second, for comparative purposes, our SDMs are only calibrated using bioclimatic predictors, and thus predictive power (as estimated here using AUC values) will be relatively low. Third, when using predictive modelling in small-sized plots (i.e., 100 m² here, versus 1 km² traditionally), one can expect a high accuracy in correctly predicting presences as presence (i.e., if a species is observed, the model will also predict its presence), but low accuracy in predicting absences as absence [i.e., if a species is absent, this could be attributable either to the plot falling outside its niche (correctly predicted absence) or to random absences owing to the limited plot size or microscale non-climatic factors (incorrectly predicted absence)]. Of course, incorrect absences can also be attributable to observation bias, identification uncertainties and incomplete detection, further lowering predictive power. We thus expect high sensitivity, but relatively low specificity and AUC values, and encourage interpretation of these different evaluation metrics together to assess the predictive power of the models (Jiménez-Valverde, 2012).

All analyses were performed in R (R Core Team, 2015).

3 | RESULTS

3.1 | Direct comparison of climatic variables

All three studied bioclimatic variables (Bio1 = mean annual temperature; Bio10 = mean summer temperature; and Bio11 = mean winter temperature) showed a consistent negative correlation with elevation in almost all temperature datasets in the region, but with large differences in lapse rate (Figure 2). The lapse rate ranged for mean annual temperature from c. -0.6°C per 100 m for CHELSA, downscaled CHELSA and Topoclimate, to c. -0.4°C per 100 m for WorldClim, EuroLST and MODIS LST, -0.2°C per 100 m for soil temperature and -0.1°C per 100 m for E-OBS. Mean annual temperatures in both years were consistently higher for the soil temperature than for all other datasets [i.e., both the long-term temperature data (WorldClim, CHELSA, downscaled CHELSA, Topoclimate and EuroLST; Figure 3a–e) and the

surface (MODIS LST; Figure 3f) and free-air (E-OBS; Figure 3g) temperature measurements from the same time period ($p < .001$ from a linear model)], but differences were larger at low than at high temperatures. Differences of 3–6°C between soil temperature and all other datasets remained even after correcting for possible interannual and climate change effects (Table 3; Supporting Information Figure S1a–f). Significant differences of ≤3°C in mean annual temperature could also be observed between all other datasets (Table 3; Supporting Information Figure S2).

Despite the higher mean annual temperature in the soil, mean summer soil temperature in both years was similar (compared with WorldClim, Topoclimate, EuroLST and E-OBS) or even lower (CHELSA, downscaled CHELSA and MODIS LST) than air and surface temperature (Figure 3h–n). After correcting for interannual and climate change effects, differences between soil temperature and most other datasets (except MODIS LST) remained limited to c. 1–1.5°C (Table 3; Supporting Information Figure S1g–l). Summer temperature recordings were highest in MODIS LST (Figure 2n; Supporting Information Figure S2i,k,l). The relationship with elevation was again the strongest for (downscaled) CHELSA (-0.6°C per 100 m) and weakest for E-OBS and MODIS LST. Winter temperature showed the largest discrepancy between soil, free-air and surface temperatures (Figure 3), with soil temperatures being close to 0°C from sea level up to ≥900 m a.s.l., and as such, driving the higher mean annual temperatures in the soil (Figure 2x). Part of this variation was attributable to relatively warm winters with plenty of snow in the area in the period 2015–2017, but the difference remained as high as 4–11°C after correcting for the temporal mismatch (Table 3; Supporting Information Figure S1n–r). Surface temperatures were, in addition, colder than free-air temperatures (Supporting Information Figure S2n–r) owing to an extended frost period (Supporting Information Figure S3). Temperature differences between years were relatively small, except for mean annual and mean summer surface temperatures from MODIS (Figure 2f,n).

The above-mentioned differences along the elevational gradient, combined with additional effects from local topography, resulted in large regional differences between the different climate datasets in general (Figure 4), and between interpolated soil temperature and the other datasets in particular (Figure 5). The correlation analyses (Figure 4) showed that the climate datasets were nested, with the strongest relationships (across all bioclimatic variables) between the datasets with long-term averages: (downscaled) CHELSA, Topoclimate, WorldClim and EuroLST. The datasets with short-term measurements (in-situ soil, MODIS LST and free-air E-OBS) differed more from each other than from the long-term averages. Modelled mean annual temperature in the soil was, as expected, several degrees warmer than in all other datasets, especially at higher elevations (Figure 5), whereas in summer the soil temperature was warmer than CHELSA climate and MODIS LST at high elevations, but colder at low elevations (Figure 5). Winter temperature predictions were ≤17°C higher in the soil than in the other datasets, except at the highest elevations. Owing to the large local variation in snow

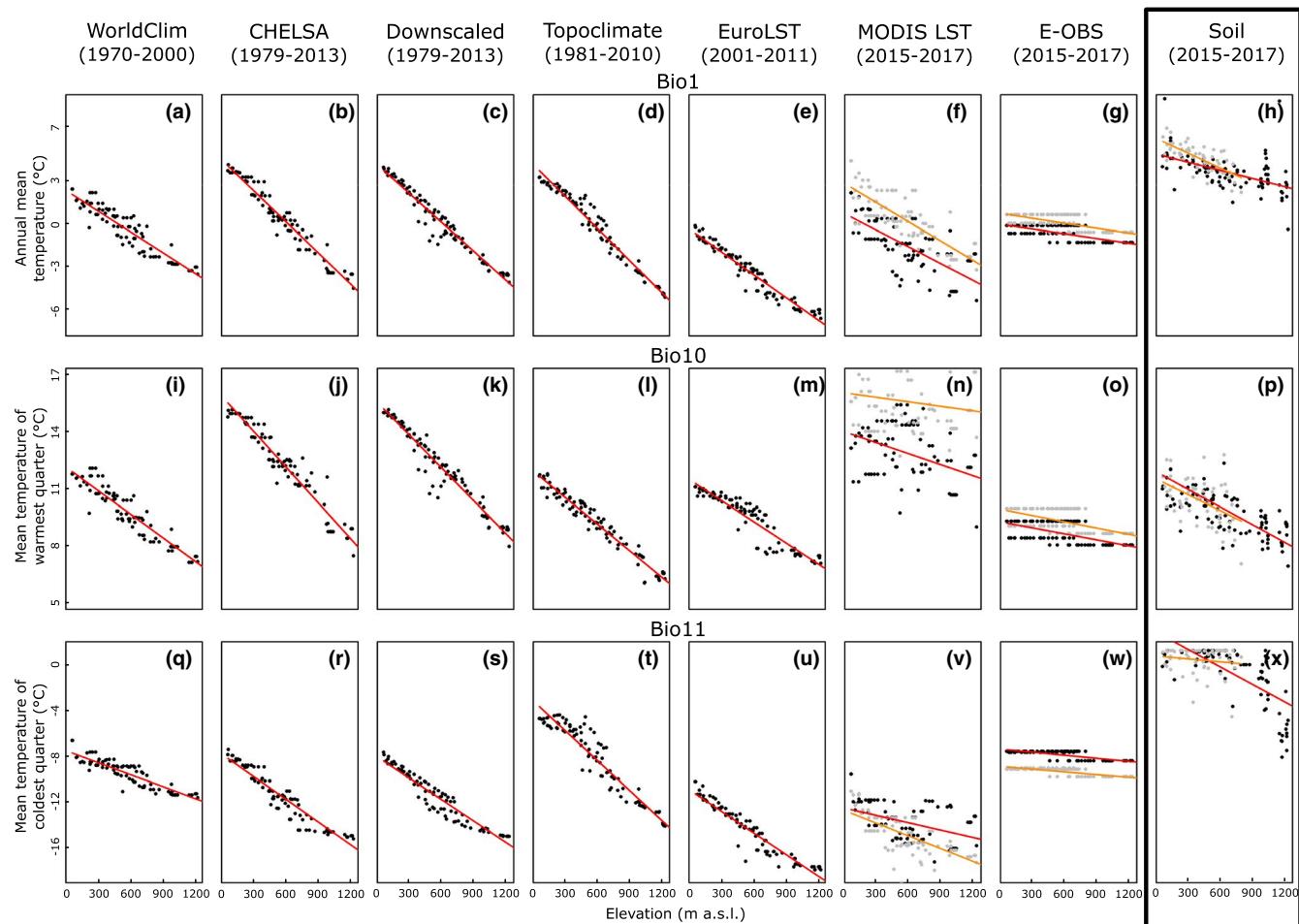


FIGURE 2 Temperature patterns against elevation for the different temperature datasets. Average annual (Bio1; a–h), summer (Bio10; i–p) and winter (Bio11; q–x) temperature for the eight climate datasets (columns, with temporal extent in parentheses) against elevation of the 106 measurement locations. Orange (2015–2016) and red (2016–2017) lines are fitted with linear models

cover, however, winter soil temperature predictions were unreliable (Figure 5; Supporting Information Figure S4), in contrast to annual and summer temperatures, for which the local R^2 (indicating the local spatial regression fit) of the regional interpolations was highly consistent across space, albeit only moderately high (i.e., on average 50% for Bio10 and 37% for Bio1).

3.2 | Species distribution modelling

Species distribution models using soil temperatures explained, on average, 80% of variance (48% if only Bio1 was used), which was, on average, 18% (15% for models with Bio1 only) more than the models using other climate datasets (Figure 6; significant differences with most datasets after correcting for multiple testing). Differences in explained variance among SDMs based on these other datasets were much smaller. Differences in predictive power were not significant between models [highest for Euro-LST and downscaled CHELSA (AUC c. .70), and between .61 and .64 for the other datasets (Supporting Information Figure S5)]. As expected, sensitivity

was high (c. .85), but specificity was low (c. .27) for all datasets. Predictive modelling was nearly impossible with models having Bio1 only (AUC c. .5, specificity c. .20), even though sensitivity was still high (c. .81).

Model performances depended strongly on growth forms (i.e., forbs, graminoids, dwarf shrubs and trees; Figure 6b,c). We observed a significant net improvement in marginal R^2 values (as an indicator of descriptive power of the models) for SDMs based on soil temperature in the case of forbs and graminoids compared with the other datasets (on average +24 and +21% for the full model, respectively, and +20 and +25% for the model with Bio1 only), and moderately so for shrubs (full model = +8%, Bio1 = +25%). However, there was no such net increase for trees (+2 and +8% only). On the contrary, we observed a significant net decrease in predictive values for shrubs and trees when using soil temperature compared with most of the other datasets (AUC, on average, −.12 and −.11, respectively, for both models; −.06 and −.08 for Sensitivity), but not so for forbs and graminoids (Supporting Information Figure S5b,c).

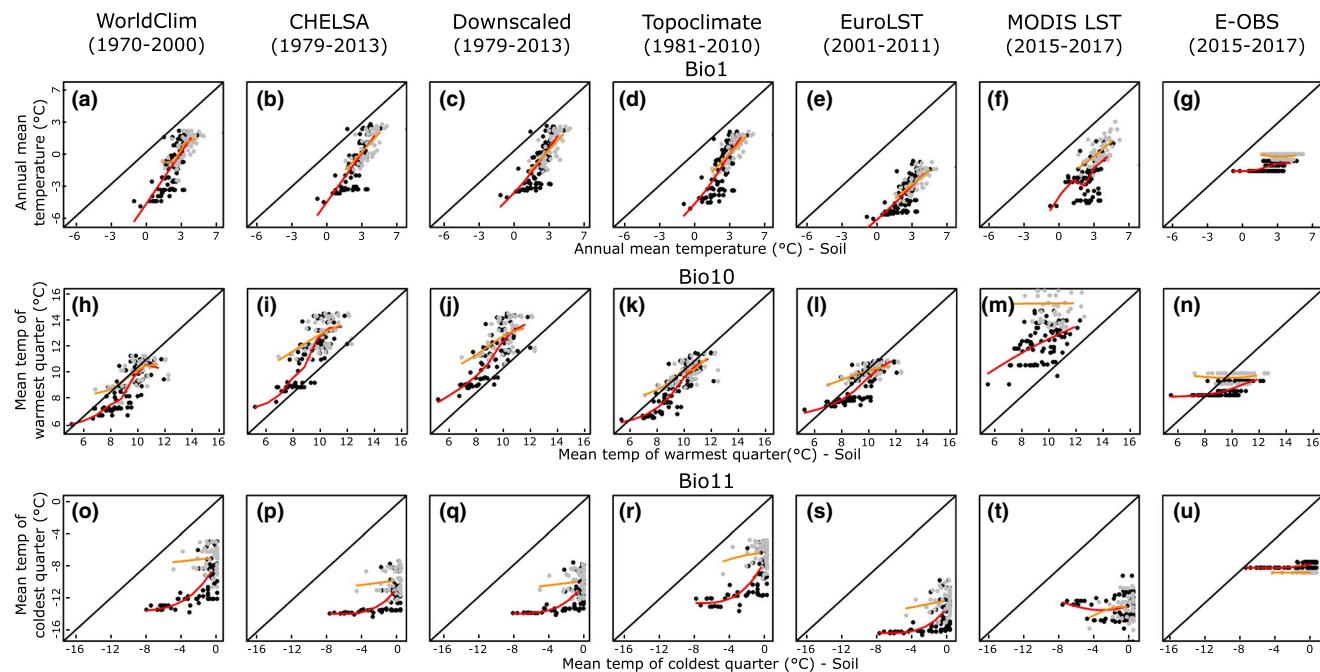


FIGURE 3 Plot-by-plot comparisons of soil temperature data against seven other sources of temperature data. Mean annual (Bio1; a–g), summer (Bio10; h–n) and winter (Bio11; o–u) temperature, for all 106 measurement locations for 2015–2016 (orange lines, grey dots) and 2016–2017 (red lines, black dots). Black lines show first bisectors (a hypothetical perfect match); red and orange lines are fitted with generalized additive models for each year of temperature measurements separately. Measurement periods are given in parentheses

4 | DISCUSSION

Our comparison of different climate datasets highlights that the use of a specific source of climate data is species and region specific and can have strong repercussions on the outcome of SDMs, as exemplified here for the distributions of 50 plant species along steep climatic gradients in a cold-climate region. Our data indeed revealed a strong sensitivity of SDMs to the climate dataset used, depending on the growth form of the species. In general, the use of in-situ soil temperature instead of surface or free-air temperature did improve the explanatory power of our SDMs. It did so much more for forbs and graminoids, to a lesser degree for shrubs, but not for trees (Figure 6). This outcome confirms recent studies arguing for the use of more local climate variables in distribution modelling (e.g., Ashcroft et al., 2008; Pradervand, Dubuis, Pellissier, Guisan, & Randin, 2014; Slavich et al., 2014; Opedal et al., 2015; Meineri & Hylander, 2017) and proves the validity of this concept across a whole range of possible temperature data sources. Nevertheless, our results also indicate that an increased accuracy of climate data does not necessarily improve distribution models for all species or in all circumstances (Bennie, Wilson, Maclean, & Suggitt, 2014; Pradervand et al., 2014), because it will depend on the growth forms of the species and perhaps also the regional climate characteristics. The differences in the explanatory power of SDMs could result from differences in measurement focus and spatio-temporal resolution or extent, related to the different spatio-temporal framework in which different species groups operate, as discussed below.

4.1 | Measurement focus

The most critical differences observed between the climate datasets in the present study were probably driven by measurement focus (free-air, land surface or soil), with consistently higher average annual temperatures observed in the soil resulting, to a large extent, from differences in winter temperatures (Bio11). Even though free-air temperature predictions (WorldClim, CHELSA and E-OBS) for winter temperature easily dropped below -7°C , and surface temperature measurements (EuroLST, MODIS LST) were even lower, winter temperatures immediately below the soil surface were close to 0°C along most of the elevational gradient (Figure 2). Only in those locations where global climate models predicted an average winter temperature below -10°C did measured soil temperatures drop below 0°C (Figure 2). These differences remained even after correcting for the temporal mismatch in the different datasets (Table 3; Supporting Information Figure S1). Although some of the earliest studies on soil temperature reported a strong relationship with air temperature across all seasons (Shanks, 1956), it is clear that both a dense vegetation cover and a thick snow pack can provide effective insulation and protection against freezing events in the subnivium (Aalto et al., 2017; Dorrepaal, Aerts, Cornelissen, Callaghan, & Logtestijn, 2004; Geiger, 1950; Pauli et al., 2013; Thompson et al., 2018) and that snow in the Arctic is a crucial explanatory variable for the distribution of plant species (Niittynen & Luoto, 2018; Randin, Vuissoz, Liston, Vittoz, & Guisan, 2009). In northern Norway, especially, the relatively mild climate and humid

TABLE 3 Differences in average temperature between the climatic datasets

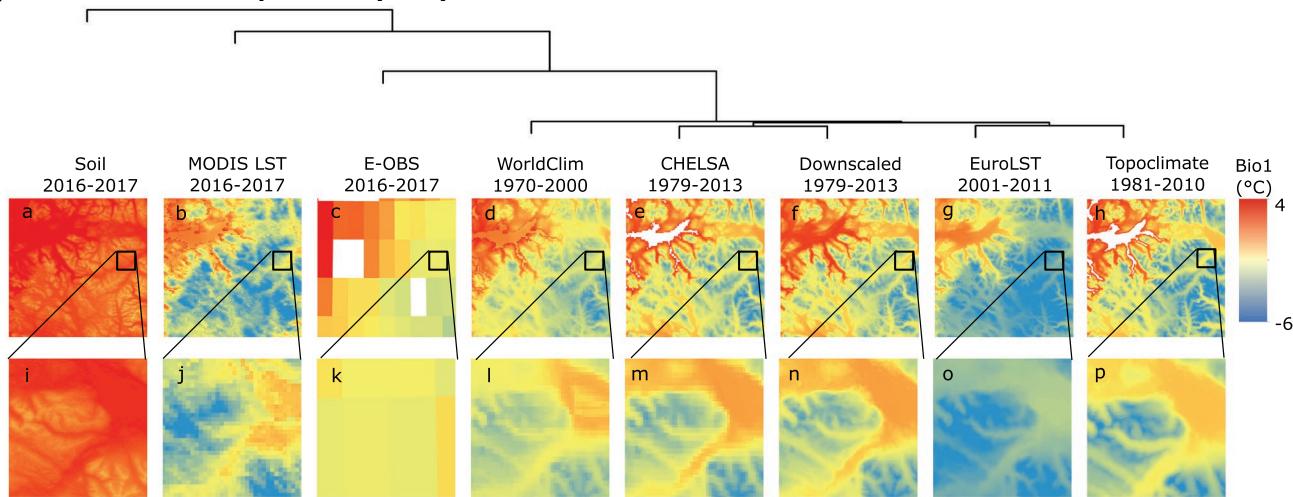
	CHELSA down	Topoclimate	EuroLST	MODIS LST	E-OBS	In-situ soil
Bio1						
CHELSA	-0.03	-0.36	-3.19	-1.96	-1.11	2.67
CHELSA down	-	-0.33	-3.16	-1.92	-1.08	2.68
Topoclimate	-	-	-2.84	-1.59	-0.75	3.00
EuroLST	-	-	-	1.22	2.08	5.77
MODIS LST	-	-	-	-	0.91	4.53
E-OBS	-	-	-	-	-	3.53
Bio10						
CHELSA	-0.03	-2.86	-3.28	1.45	-2.85	-1.48
CHELSA down	-	-2.83	-3.25	1.49	-2.81	-1.48
Topoclimate	-	-	-0.42	4.30	0.01	1.24
EuroLST	-	-	-	4.70	0.43	1.67
MODIS LST	-	-	-	-	-4.23	-3.15
E-OBS	-	-	-	-	-	1.12
Bio11						
CHELSA	-0.03	2.60	-2.47	-4.82	0.02	6.30
CHELSA down	-	2.63	-2.44	-4.78	0.05	6.29
Topoclimate	-	-	-5.07	-7.39	-2.58	3.74
EuroLST	-	-	-	-2.35	2.49	8.72
MODIS LST	-	-	-	-	4.89	10.99
E-OBS	-	-	-	-	-	6.06

Note. Two-by-two comparisons between the three studied bioclimatic variables (Bio1 = mean annual temperature; Bio10 = mean temperature of the warmest quarter; Bio11 = mean temperature of the coldest quarter) for the different climatic datasets (except WorldClim) after correcting for interannual and climate change effects using ERA Interim (for details, see Methods). Analysis is based on data from all 106 measurement locations; for MODIS LST, E-OBS and in-situ soil temperature, only the data from 2016–2017 are tested. Values show the differences in average temperature in degrees Celsius between the two datasets, with positive values indicating higher temperatures in the variable in the column than in the row. Values in bold are significant at $p < .05$ from Student's paired t-tests. Relationships with in-situ soil temperature are visualized in the Supporting Information Figure S1, whereas some relationships among the other variables are visualized in Supporting Information Figure S2.

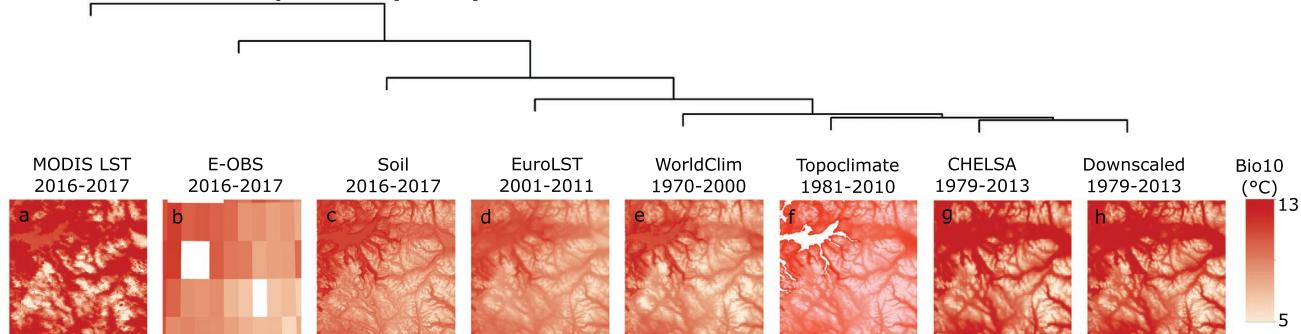
air from the ocean result in thick winter snow packs that can provide a significant decoupling between air, surface and soil temperature (Pauli et al., 2013; Thompson et al., 2018). Such an insulating snow pack can affect plant life in several ways, through its effects on overwintering survival, productivity, reproductive success and nutrient and water availability (Niittynen & Luoto, 2018), with both positive (e.g., fewer frost events) and negative effects (e.g., limited growing season) observed. For many species in the region, especially low-growing forbs and graminoids, we have shown that using near-surface soil temperatures instead of free-air temperatures, which allows the incorporation of these snow cover effects, is crucial to describe the distribution of small-stature plants accurately (Niittynen & Luoto, 2018; Randin, Vuissoz, et al., 2009). For trees, however, the absence of model improvement through the use of soil temperature might result from a stronger correlation with air than with soil temperature owing to higher maximal canopy heights, at least in later life stages. In winter and early spring, trees are likely to be much more affected by air temperatures and freezing events affecting their buds above the snow than by temperatures in the soil (Körner, 2003).

These results also indicate that the relative importance of using soil temperature in SDMs will depend on the topography and large-scale climate of the region. Most importantly, the amount of fresh snow in winter will define the strength of the discrepancy between winter (and thus indirectly annual) mean temperatures in the soil and in the air (Cohen, 1994; Zhang, 2005). The mismatch is, in our study, indeed significantly larger in the warmer but snowier (Norwegian) plots at low elevations than in the colder yet drier (Swedish) plots at high elevations (Figure 3). For summer temperature, our data overall showed a more consistent match between the different datasets, although with minor buffering effects of the vegetation. Even though the discrepancy between measurement foci is thus region specific (and probably even more different in tropical regions), we suggest that the use of climate data in close proximity to the study species is always recommended. Importantly, however, the use of soil temperature does not resolve this measurement mismatch fully, because only part of the plants is belowground. Although our data demonstrate a significant improvement in the use of soil temperature over free-air temperature data for species groups entirely covered by snow in winter, an optimal approach would incorporate in-situ

(a) - Mean annual temperature (Bio1)



(b) - Mean summer temperature (Bio10)



(c) - Mean winter temperature (Bio11)

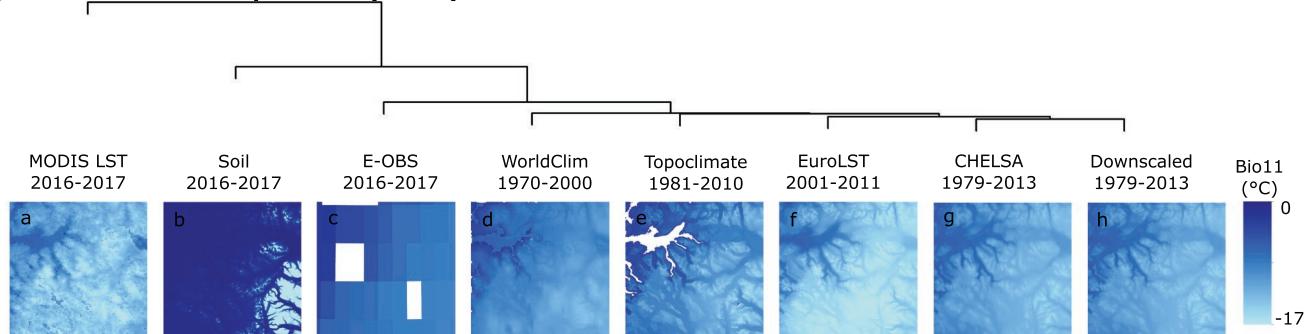


FIGURE 4 Dendrograms of collinearity between different temperature datasets. Data from the 106 measurement locations for mean annual (Bio1; a), summer (Bio10; b) and winter (Bio11; c) temperature. Measurement periods are given in parentheses. Maps show the regional (100×100 km) predictions for each dataset and bioclimatic variable. For Bio1, cut-outs of the maps are shown (location specified by black squares)

climate measurements both above and below the soil surface. The latter can be achieved, for example, with the temperature and soil moisture plant simulator sensors as described by Wild et al. (2019), measuring temperatures at, above and below the surface.

Despite the clear benefits of using soil temperature data in SDMs, a major drawback (next to the cost associated with obtaining in-situ soil temperature measurements) lies in the increased local-scale heterogeneity, especially in winter. The soil temperatures in our study were hard to predict accurately using a 50×50 m DEM-based interpolation approach. More in-situ temperature measurements, in addition to the inclusion of other microclimate-related variables, such

as snow cover maps, might be needed to improve interpolations of microclimate at fine spatial resolution. This is also a prerequisite for better predictive performances of SDMs. Follow-up studies with larger datasets and in-situ measurements of more environmental variables (e.g., soil moisture, air temperature, precipitation or snow cover) are thus recommended to investigate this further.

Although satellite-measured land surface temperature data (MODIS LST and EuroLST) resulted in mean annual temperatures within the same range as those obtained with free-air temperature measurements, the LSTs were, throughout the measurement period, significantly higher in summer and lower in winter, thus resulting in

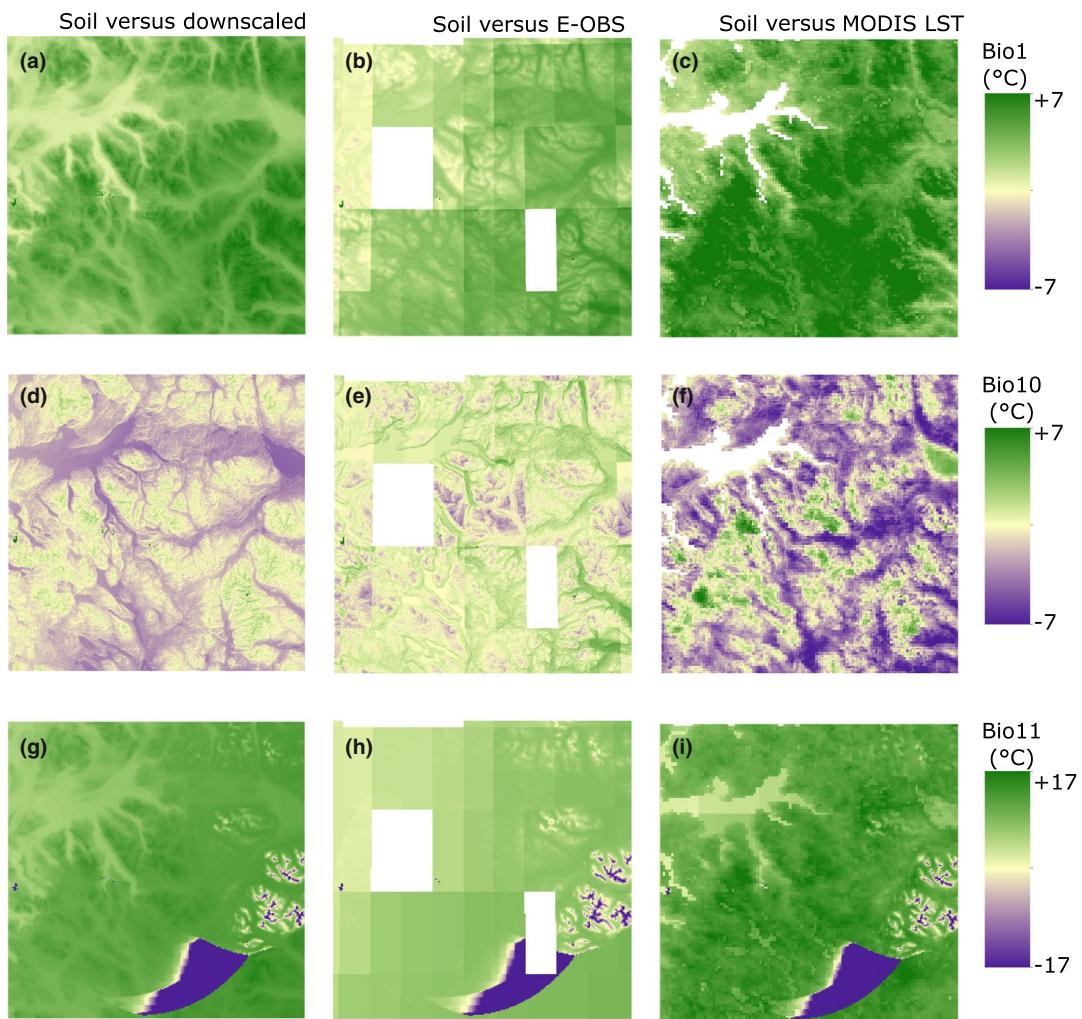


FIGURE 5 Differences (in degrees Celsius) between regionally modelled soil temperature and other temperature data sources. Differences in annual average temperature (Bio1), mean temperature of the warmest quarter (Bio10) and mean temperature of the coldest quarter (Bio11) are shown for soil temperature versus downscaled CHELSA (left), E-OBS (middle) and MODIS LST (right). Comparisons between soil temperature and CHELSA, WorldClim and EuroLST are not shown, because trends were similar. Values below zero indicate a lower value for the soil temperature compared with the other dataset; values above zero a higher value

an increased overall annual temperature range (Figure 2; Table 3; Supporting Information Figure S1). These extremes were smoothed out, however, when using the EuroLST temperature averages over a 10-year period. Although the use of satellite-based LSTs for SDMs has been largely underexplored until now, our study adds to the growing list of recent studies indicating the potential of these untapped data resources for accurately predicting species distributions (see e.g., Bisrat, White, Beard, & Richard Cutler, 2012; Cord & Rödder, 2011; Neteler et al., 2013). We expect that LST timeseries with an even higher spatial resolution, such as Landsat (Cook, 2014), will turn out to be the crucial link between local-scale temperature measurements and global climate models. Our results, however, indicate that smoothed, long-term averages, such as EuroLST, are preferable to short-term measurements, especially for predictive modelling. Similar to the issue of spatial heterogeneity for in-situ soil temperature data, averages over long-term time series are, by

nature, more likely to increase the predictive performances of SDMs compared with more erratic fluctuations based on short-term data.

4.2 | Temporal extent

Differences between the climate datasets used could also be attributed to variation in temporal extent, with the datasets building on long-term historical averages (WorldClim, CHELSA, Topoclimate and EuroLST) showing the strongest correlation with each other (Figure 4). Correlations were weakest for the three datasets with only 2 years of data, but with different measurement foci, as described above (MODIS LST, E-OBS and soil temperature). Although patterns over time for these datasets were relatively consistent between measurement years (Figure 2), they did reveal more variation between air and surface temperature than between EuroLST and the other datasets with long-term climatic averages. The discrepancy in

temporal extents might also explain why the performance of our predictive models decreased in some cases for shrubs and trees when using short-term soil (or surface) temperatures (Supporting Information Figure S5). These long-lived species are likely to be

relatively inert to short-term changes in their environment (Körner, 2003), which might make it harder to predict their distribution based on locally measured short-term temperatures (Ashcroft et al., 2008). Long-lived organisms, such as most arctic-alpine species in the study

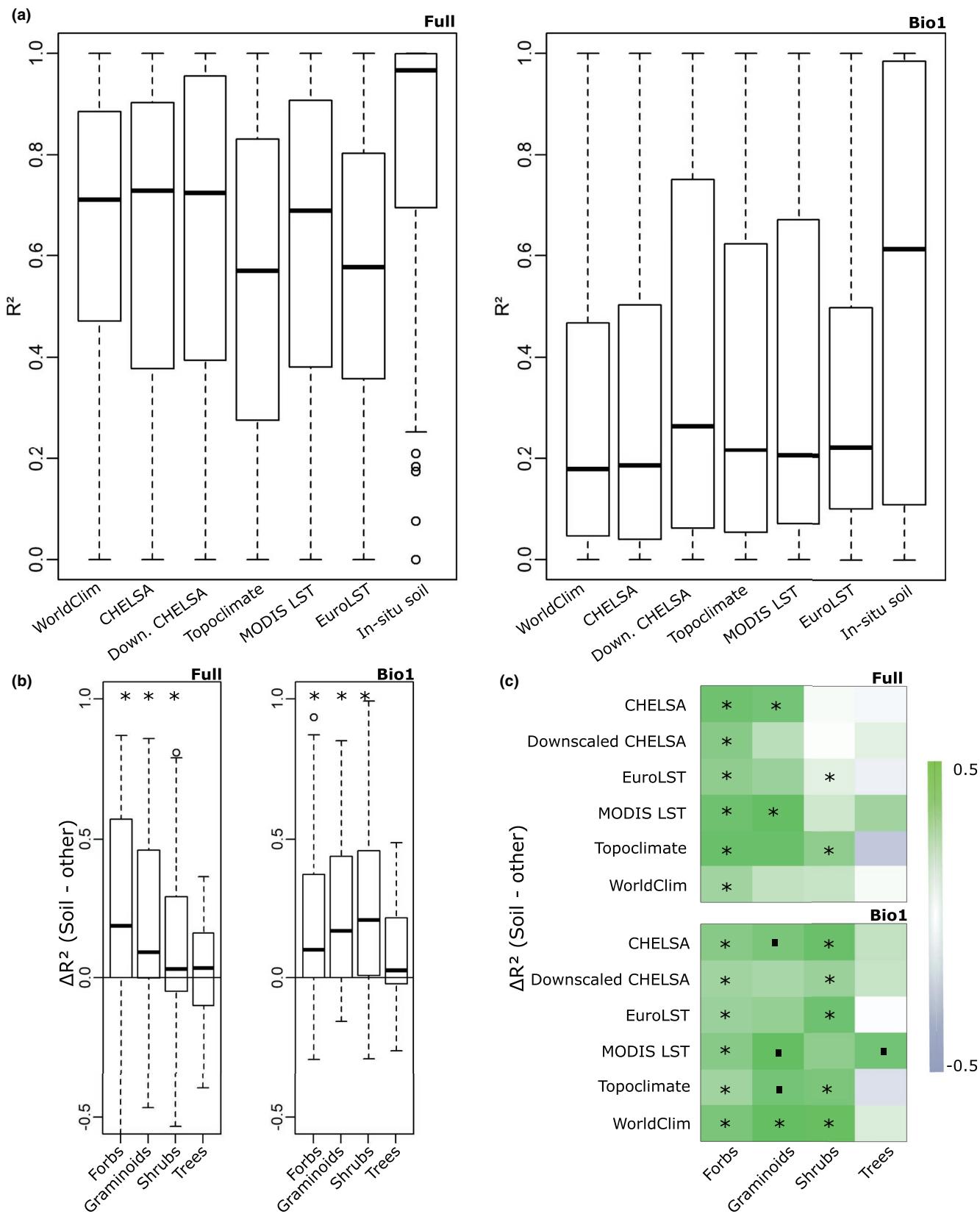


FIGURE 6 Proportion of explained variance (marginal R^2) by species distribution models (SDMs) using the different temperature datasets. (a) Boxplots of the marginal R^2 of distribution models for 50 plant species in a subset of 59 plots, based on binomial generalized linear mixed-effect models (GLMMs) built with the different temperature datasets: using Bio1, Bio10 and Bio11 together (left, "Full") or Bio1 only (right, "Bio1"). (b) Differences in marginal R^2 between the models using soil temperature and all other datasets for forbs ($n = 25$), graminoids ($n = 7$), (dwarf) shrubs ($n = 15$) and trees ($n = 3$). (c) Heatmaps visualizing the differences in marginal R^2 between the models using soil temperature and each of the other climatic datasets for the different growth forms. Green (positive values) indicates better performance of soil temperature models, blue a better performance of the other dataset in question. ** and * respectively indicate significant ($p < .05$) and marginally significant (.05 $< p < .1$) differences from zero as obtained with Student's two-tailed t-test

region, could also persist outside their niche for considerable parts of their life (Bond & Midgley, 2001), adding to the complexity of predicting their distribution using short-term temperature data.

4.3 | Spatial resolution

Our comparative approach indicates that the downscaling or interpolation of climate data, as applied here respectively to global datasets such as CHELSA and the in-situ soil temperature data and topoclimatic dataset from Aalto et al. (2017), was rather successful. Downscaling of CHELSA from $1,000 \times 1,000$ m to 30×30 m based on the physiography worked well, as indicated by the high local R^2 values ($.90 \pm .06$ for Bio1 and Bio10; $.89 \pm .06$ for Bio11; Supporting Information Figure S4), but nevertheless resulted in only minor improvements of the regional SDMs compared with coarse-grained CHELSA data (3.7% and .035 for the R^2 and AUC values, respectively). This lack of improvement is in disagreement with several other studies (e.g., Gillingham, Huntley, Kunin, & Thomas, 2012; Slavich et al., 2014). Part of this could be attributable to the inherent limitations in the original CHELSA dataset; unlike elevation, small-scale topographic variables, such as slope and aspect, are not taken into account in the original CHELSA model, and their inclusion in the downscaling approach is thus unlikely to have major effects. Small-scale topographic effects on microclimate are more correctly taken into account in the topoclimatic dataset from Aalto et al. (2017), however, making the latter approach recommendable above the former. The fact that the topoclimatic dataset did not perform significantly better in the SDMs than CHELSA ($\Delta R^2 = -7\%$ and +5%, and AUC = -0.01 and +.06, depending on the model) might suggest again that an increased level of detail is not better by default, but depends on the context of the study (Bennie et al., 2014). The most likely explanation for this lack of improvement in model performance in this case is that the distribution of the studied alpine species might be less driven by small-scale topoclimatic variation in air temperature than by snow-cover-induced variation in soil temperature.

Interpolation of the soil temperature data worked well across the whole study region, except for winter temperature, where the strong local variation and the highly non-linear correlation with elevation probably resulted in inaccurate predictions (Figure 4; Supporting Information Figure S3; Ashcroft et al., 2008). The large differences in winter temperatures between measurement locations (and the low predictability of soil winter temperature in the region) thus suggest that caution is needed, because in many regions winter temperatures

are likely to be crucial for the distribution of species (Williams, Henry, & Sinclair, 2015). A larger dataset and more accurate predictor variables (e.g., related to the duration of snow cover; Niittynen & Luoto, 2018) might be needed to improve these interpolation efforts.

4.4 | Implications

The observed differences in the climate datasets and SDMs at the regional scale advocate for a careful selection of the climate data source when modelling species distributions, based on a priori ecological assumptions about the relationship of the studied organism with the regional environment, and the comparison (or joint use) of different datasets (Buermann et al., 2008; Rebaudo, Faye, & Dangles, 2016). Measurement focus, temporal extent and spatio-temporal resolution should all be taken into account with regard to the studied species and area. Is the species affected by snow cover? Is it an annual or a perennial species? Is the focal species mobile or sessile? Does the study area reach above the tree line? Is it in topographically challenging terrain?

Our study highlights the importance of growth forms. Soil temperature was highly important for forbs and graminoids and, to a certain extent, for shrubs, but not so for trees. Only when making ecologically meaningful a priori decisions and when comparing the performance of different datasets, and perhaps their interactions, can one be sure that the observed trends relate to the real (micro) climate experienced by the study species or species group(s) in the study region. Understanding these processes in the current climate is a crucial step before model projections can be improved under climate change. In order to advance towards this goal, there is an urgent need for large-scale datasets of microclimate data; ecologists and climatologists should consider in-depth on-the-ground, long-term microclimate monitoring along climatic gradients to be able to improve our microclimatic models for use in SDMs (Lembrechts, Nijls, & Lenoir, 2019). Nevertheless, our case study suggests that SDMs can be relatively robust to several characteristics of different types of climate datasets, such as spatial and temporal resolution, especially in the relatively stable, slow-reacting vegetation types of high-latitude mountains. Additionally, there is a need to improve our abilities to forecast microclimate data in the future, because climate change is likely to affect soil, surface and air temperatures differently (Ashcroft & Gollan, 2013; De Frenne et al., 2019). Significant progress has been made in this regard; for example, by integrating microclimatic dynamics and processes such as microclimatic buffering in predictions (Keppel et al., 2015; Lenoir et al., 2017; Wason,

Bevilacqua, & Dovciak, 2017), but there is still a need for improvement before the same diversity and quality of climate datasets will be available for SDM projections into future climate as we have now for current climate.

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DATA AVAILABILITY STATEMENT

Most climate datasets used are freely available (see Methods section). Plot-level climate and species distribution data is available open access at 10.5281/zenodo.3302639.

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BIOSKETCH

This study was performed in the framework of: (a) the Mountain Invasion Research Network (MIREN, www.mountaininvasions.org), a global consortium of plant ecologists focusing on species redistributions in mountain regions; and (b) SoilTemp (<https://soiltemp.weebly.com>), a global effort to create a database of in-situ soil temperature measurements for use in ecology.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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