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Correlations between plant climate optima across different spatial scales

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Short running heading: Correlations between climatic optima across scales

Abstract

Identifying the factors determining the abundance and distribution of species is a fundamental question in ecology. One key issue is how similar the factors determining species' distributions across spatial scales are (here we focus especially on spatial extents). If the factors are similar across extents, then the large scale distribution pattern of a species may provide information about its local habitat requirements, and vice versa. We assessed the relationships between landscape and national optima as well as landscape and continental optima for growing degree days, maximum temperature and minimum temperature for 96 bryophytes and 50 vascular plants. For this set of species, we derived landscape optima from abundance weighted temperature data using species inventories in central Sweden and a fine-grained temperature model (50 m), national optima from niche centroid modelling based on GBIF data from Sweden and the same fine-grained climate model, and continental optima using the same method as for the national optima but from GBIF data from Europe and Worldclim temperatures (*c.* 1000 m). The landscape optima of all species were positively correlated with national as well as continental optima for maximum temperature ($r=0.45$ and 0.46 , respectively), weakly so for growing degree days ($r = 0.30$ and $r = 0.28$), but sometimes absent for minimum temperature ($r=0.26$ and $r = 0.04$). The regression slopes of national or continental optima on local optima did not differ between vascular plants and bryophytes for GDD and T_{max} . However, the relationship between the optima of T_{min} differed between groups, being positive in vascular plants but absent in bryophytes. Our results suggest that positive correlations between optima at different spatial scales are present for some climatic variables but not for others. Moreover, our results for vascular plants and bryophytes suggest that correlations might differ between organism groups and depend on the ecology of the focal organisms. This implies that it is not possible to routinely up- or downscale distribution

48 patterns based on environmental correlations, since drivers of distribution patterns might
49 differ across spatial extents.
50 **Keywords:** bryophyte; climatic optima; distribution; microclimate; spatial scale; vascular
51 plant

1. Introduction

Identifying the factors determining the abundance and distribution of species, and and if those environmental factors remain important across spatial scale (grain and extent) are key objectives in global change ecology (Hurlbert et al., 2005; Hess et al., 2006; Azaele et al., 2015). Given that populations in different parts of the distribution range are genetically similar and experience the same range of environmental conditions, we would expect that the relationship between environmental factors and distributions should be similar in different parts and over different spatial extents (e.g. Brown, 1984; Guisan and Zimmermann, 2000; Thuiller et al. 2005; Wiens et al., 2010; Wasof et al., 2015). Yet, there are several reasons why we should instead expect relationships to differ among different parts of the distribution range or among different spatial extents. First, populations in different part of the distribution range might be genetically differentiated and locally adapted with regard to the relationship between environmental conditions (including biotic interactions) and individual performance (Lavergne et al., 2010; Pellissier et al., 2013). For example, Alberto et al. (2013) found genetic differentiation of many adaptive traits when comparing populations of many tree species across geographically separated common gardens. Second, the frequency distribution and range of environmental parameters influencing organism performance as well as the correlation between parameters will often vary among different parts of the distribution range and between extents of different sizes (Hylander et al. 2015). Third, distributions might not be in equilibrium with current environmental conditions. For example, environmental conditions might have changed but changes in distribution are time-lagged due to dispersal limitation or delayed extinctions (Svenning et al. 2015) and such processes are likely to vary among spatial scales. Moreover, changing the grain size of environmental predictors often results in changes in which environmental variables that best predict distributions. For example, structural habitat variables were more important predictors than climate variables in predicting the

distribution of an ant species at finer scales (grain), while the reversed was true at larger spatial grain sizes (Menke et al. 2009). Since organisms always interacts with their local environment, it is important to use fine grained data, and this is not least true for climate variables (Keppel et al 2012; Lenoir et al. 2013; Lenoir et al. 2017; Hannah et al., 2014; Meineri et al., 2015; Lembrechts et al 2018). However, also when we have access to such fine-grained environmental data, it is not trivial to downscale organisms distributions since high resolution occurrence data are still uncommon (Menke et al. 2009, Keil et al. 2013).

Given that the relationship between environmental factors and distributions might differ over different spatial scales, a key task is to empirically assess if the factors governing distributions (and optima) are similar over different spatial grains and extents, as well as how such relationships differ among species and environmental variables. One important question regards how the strength of the relationships between distributions and environmental factors (e.g. species optima) differ among spatial grains and extents. If the relationship is strong, then the large scale distribution pattern of a species may provide information about its local habitat requirements, and vice versa. Another important question is if relationships, and thus the predictive capacity, are stronger for some environmental variables than for others. Lastly, relationships with a given environmental factor can vary between groups of species with different physiology. For example, moisture conditions are probably more important for bryophytes than for vascular plants, since bryophytes cannot regulate water uptake and loss (cf. Woodward and Williams, 1987; Hylander, 2005; Proctor, 2011), or winter conditions might be more important for trees than for herbs in areas with snow cover (Walter and Breckle, 1989).

In this study, we investigated how strongly temperature optima of 50 vascular plant species and 96 bryophyte species were correlated between spatial scales. We compared optimqfrom a landscape consisting of 3000 km² forested area in central Sweden, with the

optima calculated at the national extent using a fine-grain climate data, and with optima at a continental extent including most of Europe with a more coarse-grain climate data. Three temperature variables were examined: growing degree days, minimum temperature and maximum temperature. We retrieved the species' landscape optima, defined as the most favorable climate in the focal landscape, by calculating abundance-weighted temperature averages for georeferenced species occurrences from 49 inventoried field sites. The national and continental optima were retrieved from niche centroid modelling (Blonder et al. 2017), and reported occurrences in Europe of the same species' in a database. Using these three optima from different geographic extents, we examined the strength of correlations for the three climate variables, for all species pooled as well as for vascular plants and bryophytes separately.

2. Materials and Methods

2.1 Study areas

The study area used for the landscape scale data is located in the county of Ångermanland in central Sweden (Fig. 1a; between the latitudes 62°50' and 63°12' N). This area ranges 73 km westward from the Baltic Sea and 42 km from north to south. The area is hilly with a moderate altitudinal variation (0 – 470 m). The bedrock consists mostly of gneiss covered by podzolic soils of sandy loamy or silty materials. It is a mainly forested landscape situated in the middle boreal subzone, and, along the coast, in the southern boreal subzone. In July, the mean temperature is 15.6 °C, and the annual mean precipitation reaches 671 mm (Swedish Meteorological and Hydrological Institute, 2016). The heterogeneous topography and the fact that this area hosts the range margins of both southern and northern species (Mascher, 1990) make this a particularly suitable landscape to study the influence of microclimate on species distributions.

The whole of Sweden (450 000 km²) was used to examine the national scale. Sweden is extending over a substantial latitudinal and altitudinal gradient (latitudes 55.3 - 69.1°N and 0-2100 m.a.s.l.). The continental scale study area comprises a large part of Europe, is more than 5100 km from west to east and 2800 km from south to north, and cover a land area of 4.40×10^6 km² (Fig. 1b, between the latitudes 27°38' and 81°48' N). It covers a wide range of altitudes (up to 4810 m.a.s.l.) and climatic conditions from Mediterranean climate in the south to cold climates with long winters in the north and at high altitudes. There is also an east-west climatic gradient across the temperate zone ranging from maritime climates along the Atlantic Ocean to continental climates in the eastern inlands (Peel et al., 2007; Europe, 2014).

2.2 Study design and species occurrences

In the focal landscape, we selected 24 south-facing and 25 north-facing forested slopes distributed across the whole area. Within each slope, we randomly selected one 25 × 25m plot within mature forest (at least 50 years old, estimated from aerial pictures). To reduce environmental heterogeneity, selected plots were located > 25 m from open areas, > 50 m from streams, > 10 m from vertical cliffs (> 5 m high), and were situated on mesic soils. Most of the plots were dominated by Norway spruce (*Picea abies* L. Karst.), but at some sites also birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth), Aspen (*Populus tremula* L.) or Scots pine (*Pinus sylvestris* L.) co-dominated the tree layer. The plots were oriented between 159° and 214° at south-facing slopes (180° = S) and between 333° and 56° at north facing slopes (360°/0° = N). The slope inclination varied between 7° and 35°, and the altitude ranged from 39 m to 385 m. We assessed the local area species composition within each of the 49 chosen 25 × 25 m plots by recording the abundance of all occurring species of bryophytes and vascular plants. We estimated the abundance in three categories 1 = sporadic (few occurrences covering < 5 %), 2 = common (covering 5 – 50 %), and 3 = dominant (covering ≥

50 %). For analyses of optima, we included all bryophyte and vascular plant species occurring in at least 5 of the plots (Appendix S1), resulting in 96 bryophytes and 50 vascular plant species.

For the national scale we compiled occurrences of the study species from Swedish Artportalen (www.artportalen.se) and for the continental scale also from GBIF (www.gbif.org), and Norwegian Artsobservasjoner (www.artsobservasjoner.no). In GBIF, we included observations, literature data and herbarium specimens. We restricted the GBIF occurrence data sets to the time period 1950 to 2014. Information on the precision of coordinates was lacking for large parts of the GBIF data sets and to include as many observations as possible, we did not apply any restrictions on precision. In the continental scale data we included only countries that had an average density of at least 1 observation per 1000 km² of the 146 study species pooled to avoid biasing estimates of species' continental range optima due to scarce reporting from these areas (Fig. 1b).

2.3 Temperature variables

For both the landscape and national scale, we extracted decadal averages (2000-2010) of growing degree days (base 5°C, GDD5), minimum temperature (the yearly 5th percentile of the daily min temperature, T_{min}, °C) and maximum temperature (the yearly 95th percentile of the daily max temperature, T_{max}, °C) from freely available modelled fine-grained layers at a 50 m resolution covering the whole of Sweden (Meineri & Hylander 2017). For the continental area we retrieved the same variables from Worldclim v1.4 (period 1960-1990; www.worldclim.org; Hijmans et al., 2005) at a 30 seconds resolution (~1 km). At this scale, T_{min} and T_{max} were monthly means derived from daily minimum and maximum measurements averaged for the period 1960-1990. We set the lowest of the twelve monthly T_{min}- and the highest of the twelve monthly T_{max}-values as our continental T_{min} and T_{max},

respectively. We calculated GDD5 following Synes and Osborne (2011) and Nieto et al. (2015) by using the formula: $GDD5 \text{ for each month} = ((\text{monthly } T_{\text{max}} + \text{monthly } T_{\text{min}}) / 2 - T_{\text{base}} [\text{in our case } 5]) \times \text{Days per month}$, and then summing up GDD5 for each month (those above zero) to a yearly GDD5. Thereby, we approximated a yearly heat accumulation for the chosen time period.

Although GDD5, T_{min} and T_{max} were calculated differently at the landscape/national and continental scales, we believe that the results would be highly correlated and rank similarly across sites. For example, the 5th percentiles of the coldest days of the year (T_{min} at landscape and national scale) is expected to rank similarly to the average of minimum daily values over the coldest month across sites since the coldest days of the years (landscape/national scale) often occurs during the coldest month (continental scale).

2.4 Temperature optima

We derived the landscape climatic optima for each species as the mean value of GDD5, T_{min} and T_{max} at the sites where the species occurred, weighted by the abundance (1, 2 or 3, see equation 1).

Equation 1:

$$\text{Landscape optima} = \frac{(\sum_{i=1}^n (\text{ith site abundance} \times \text{ith site value of climatic variable}))}{(\sum_{i=1}^n (\text{ith site abundance}))}$$

To calculate the national and continental climate optima we used a recently developed method for calculating niche hypervolumes (Blonder et al. 2017). The method calculates the niche in a multidimensional space, and produces many geometry statistics including the total volume of the niche and the niche centroid (see also Ureta et al. 2018 for the use of niche centroids as a successful measure of plant fitness). For each species we ran the model two times, for the national and continental scales respectively, and extracted the niche centroid for each of the

three focal climate variables as a proxy for the species' optima. We used the R package “hypervolume” version 2.0.11 (Blonder 2018). We used the one-class support vector machine algorithm with default tuning parameter settings, and number of random points used to assess the species-specific hypervolumes was set to $10^5 + \sqrt{\frac{\text{number of climate variables}}{\text{number of observations}}}$. This parameter ensures equal sampling effort of species with different number of observations, and the higher the number, the more robust results you get with a trade-off of computer power (Blonder et al. 2017). The niche centroid was calculated as the mean of the random points, giving one value for each niche axes.

2.5 Statistical analyses

We evaluated the relationships between landscape and national species optima as well as between landscape and continental species optima for GDD5, Tmin and Tmax, for all species pooled, using Pearson correlation tests, and visualized the relationships with a trend line from a type II regression.. To investigate if these two relationships (i.e. between landscape and national as well as between landscape and continental) differed between bryophytes and vascular plants, we carried out an ANCOVA for each climate variable with organism group as a fixed factor, the landscape climate variable as a continuous predictor, and their interaction. Moreover, we tested if there was any difference between the correlation coefficients of bryophytes and vascular plants using the Fisher r-to-z transformation test with the R package “psych” (Revelle 2018). Lastly, we tested if the mean optima of vascular plants and bryophytes differed within the different scales using Student's t-test. We also evaluated the relationships between the three examined temperature variables within each spatial scale dataset using Pearson correlation tests, and visualized them with type II regression lines. All analyses were done in R 3.6.0 (R Core Team, 2019).

3. Results

3.1 Correlations between species landscape, national and continental optima

Species with higher landscape optima for Tmax also had on average higher national and continental optima (landscape vs national: $r = 0.45$, $P < 0.001$; landscape vs continental: $r = 0.46$, $P < 0.001$, Fig. 2b and e, Appendix 2). For GDD5, there were also positive, albeit weaker, correlations between landscape and national, and landscape and continental optima (landscape vs national: $r = 0.30$, $P < 0.001$; landscape vs continental: $r = 0.28$, $P < 0.001$, Fig. 2b, Appendix 2b). For Tmin, the correlation between landscape and national optima was even weaker ($r = 0.26$, $P = 0.002$, Fig. 2c, Appendix 2c), and there was no correlation between landscape and continental optima ($r = 0.04$, $P = 0.65$, Fig. 2f, Appendix 2f).

3.2 Differences between bryophytes and vascular plants

The relationships between the landscape and national optima and landscape and continental optima for the three temperature variables showed similar patterns for bryophytes and vascular plants in most cases (Fig 3, $p > 0.05$ for the interaction effect, Appendix 3). However, for the model between landscape and continental optima of minimum temperatures there was a significant effect if the interaction between organism group and temperature (Ancova, $P = 0.0023$). For vascular plants, but not for bryophytes, Tmin optima were positively correlated across extents (Fig 3c, f, i and l, Appendix 3). Correlation coefficients did not differ significantly between the two groups, except between Tmin at landscape and continental scales where vascular plants had a higher coefficient than bryophytes ($r = 0.36$ vs. $r = -0.13$; Fisher r-to-z test, $P = 0.004$).

3.3 Within-scale relationships

There were few differences in the mean optima between the two groups (boxplots in Fig 4). The largest difference was a lower value for growing degree days for bryophytes than for vascular plants in the continental data ($P = 0.042$, Fig. 4c,i).

Correlations between the three examined temperature variables differed among the three spatial extents. GDD5 and Tmax were positively correlated at all extents (landscape: $r = 0.40$, $P = 0.005$; national: $r = 0.89$, $P < 0.001$; and continental: $r = 0.83$, $P < 0.001$, Appendix 4 and 5), while Tmin was correlated to GDD5 only at the national and continental extents (landscape: $r = 0.26$, $P = 0.07$; national: $r = 0.91$, $P < 0.001$; continental: $r = 0.78$, $P < 0.001$). There were no correlation between Tmin and Tmax at the landscape ($r = -0.21$, $P = 0.15$), but a positive correlation at the national and continental extents (national: $r = 0.67$, $P < 0.001$; continental: $r = 0.39$, $P < 0.001$) (Appendix 4 and 5).

4. Discussion

Our study provided evidence of clear positive correlations between plant species landscape climatic optima and their optima at larger, national and continental extents for two of three examined climate variables. Species growing under locally warm conditions with high maximum temperatures, on average tended to have more equator skewed distributions, and vice versa. In this context the landscape optima can in fact be closer to a species thermal limit for species at their distribution margins, and the broader implication of our results is that knowledge about a species wider geographic distribution can suggest where in a focal landscape it is most likely occurring. At the same time, it is important to note that the highest observed correlation coefficient between landscape and a larger scale optima was 0.47, suggesting that the relationships are relatively weak. Also notable is that the pattern observed for maximum temperature was largely absent for minimum temperature. Few studies have

specifically tested if it is possible to upscale or downscale distributions across areas of different spatial extents, while the question of upscaling and downscaling distributions in relation to grain size has received more attention (see below). However, the question of up- or downscaling across spatial extent resembles the more investigated question of how well future species distributions can be predicted based on current species distributions (e.g. Austin and Van Niel, 2011; Franklin et al. 2013), and if species niches are consistent across areas (Wasof et al., 2015). However, Kambach et al. (2019) studied different extents and demonstrate that the niche breadth plants in the Alps is a poor predictor of the global niche breadth of the same species. Our results showed that correlations between optima at different spatial extents differed among environmental variables, which suggest that some relationships might be more linked to causal drivers, while others are mostly correlative. Thus, the success of upscaling and downscaling between different spatial extents or predictions of distributions in new areas may sometimes be good and sometimes misleading, depending on whether the identified variables representing causal drivers of distributions (see also Menke et al. 2009).

One problem with comparing models at different geographical extents is that the grain size often is larger in larger areas. Larger grid cells fail to detect more of the within grid heterogeneity (Randin et al., 2009, Meineri and Hylander 2017), and as a result different sets of variables, varying over different spatial scales, might explain the distribution at different grain sizes (Pearson and Dawson, 2003; Menke et al., 2009; Connor et al. 2018). However, Collingham et al. (2000) did not find that the influence of different environmental variables varied among grain size, and was optimistic regarding the possibility of upscaling to coarser resolutions, especially when holding the spatial extent constant. In contrast, models calibrated at larger grid cells did not produce realistic downscaled distribution maps for three invasive plant species in Britain, although this might have been partly due to the fact that distributions were not in equilibrium with environmental conditions at either spatial scale (Collingham et

al., 2000). Still, data from larger grid cells might generate downscaled distribution maps that are quite accurate in some cases, as shown for several species groups in Britain (Barwell et al. 2014, Fernandes et al. 2014), and the field is developing fast (Keil et al. 2013, Groom et al. 2018). We found very similar patterns when correlating the landscape optima to fine-gridded national data and to coarse-gridded continental scale data. This suggest that our larger scale datasets quite well describe the distributional optima for the species, despite the difference in both extent and grain size. A likely reason for this pattern is that both dataset covers long latitudinal gradients, which are more important to estimate optima than within grid-cell variation. Thus, for studies focusing on niche hypervolume size or shape there is a larger risk for biases due to different grid sizes than in studies focusing on niche centroids (Kambach 2019).

The correlations between landscape and continental optima were strongest for maximum temperature, weaker but significant for growing degree days, and even weaker or not significant for minimum temperature. Both growing degree days and maximum temperature characterize the climatic conditions during the plant growing season, suggesting that these variables should have an important effect on plant performance. However, minimum temperature has also been highlighted as important for species distributions at different spatial scales (Aschcroft et al., 2011; Dobrowski, 2011; Scherrer and Körner, 2011; Illán et al., 2014), including the range limits of tree species towards cold conditions (Sakai, 1979; Körner, 2012, Kreyling et al. 2015). Niche conservatism has been higher for the cold than warm thermal limit for a number of alpine plant species (Pellissier et al., 2013). However, a majority of our studied species might not be affected by yearly minimum temperature in northern regions such as in our focal landscape, since they are resting and protected by snow cover during winter periods there (cf. Vercauteren et al., 2013). Trees and shrubs that extend above the snow cover are more affected by winter frosts than for example

herbs (Walter and Breckle, 1989). Thus, the correlation between minimum temperature and species landscape scale distribution may not be so informative for continental scale distribution and vice versa when part of the distribution is including winters with snow cover. Yet, perhaps minimum temperatures during late spring, which we did not include in this study, might have a stronger effect on distributions (Muffler et al. 2016). Although both growing degree days and maximum temperature might influence distributions, it is difficult to disentangle their independent effects since they are correlated and correlations are similar at all the scales. In contrast, the correlations between minimum and maximum temperature were in different directions at the different spatial scales; notably even with a tendency to be negatively correlated at the landscape scale (Appendix 4c and f). This difference in correlations among climatic variables between scales may explain why we found less of landscape-large scale optima correlations for minimum temperature than for growing degree days and maximum temperature (Hylander et al., 2015, Meineri et al., 2015). Similarly, Menke et al. (2009) suggested that differences in the distribution of environmental conditions between areas greatly reduces the predictive power of species distribution models parameterized in different areas. Such difference in distribution of environmental conditions might apply also to our case, even if our focal landscape is nested within the other areas, partly explaining different patterns for maximum and minimum temperatures.

Several factors may contribute to weak correlations between landscape and larger scale optima. A likely ecological explanation to this is that several factors interact, in a species-specific way, to determine where a species can occur in the landscape (e.g. Gaston, 2009, Zellweger et al., 2016). For example, while two species might have similar high continental optima for growing degree days, this might be due to a direct dependence on longer growing season in one of the species but due to dependence on humid conditions, which are correlated with growing degree days, for the other species. As a consequence, they

might differ in landscape optima for growing degree days if the correlation between growing degree days and humidity is different at the landscape scale than at the continental scale (Hylander et al. 2015). In our study many species, especially of bryophytes, with a high maximum temperature landscape optima also had a low minimum temperature optima at landscape scale (Fig 4d), reflecting the tendency of a negative correlation between these variables in this particular landscape (Appendix 4d). This fact constrains the possibility for strong simultaneous correlations for both maximum and minimum optima between landscape and larger scales optima, since the two variables at larger scales were strongly positively correlated (Appendix 4e and f). Also, local adaptation, biotic interactions and dispersal limitation are likely to decrease the strength of the correlations between spatial scales (Lavergne et al. 2010; Svenning et al. 2015; Herrero et al. 2016). Still, the optima correlations for maximum temperature found in our study lend support to the notion that populations of the same species to some extent are influenced similarly by climatic variables across their geographical range (e.g. Pearman et al., 2008; Wiens et al., 2010; Wasof et al., 2015). Given that many of the species are close to their poleward distribution limit in the focal landscape, we might have expected a clustering of species landscape optima at the warmest end of the climate gradients. Yet, a visual inspection of the graphs does not reveal any such clustering (Fig 2 and 3). The regression slopes and correlation coefficients were overall very similar for vascular plants and bryophytes. This was somewhat surprising given that these groups have quite different ecophysiological traits and it could be expected that the distribution of vascular plants would be mostly influenced by growing degree days while the distribution of bryophytes is more influenced by maximum temperatures, affecting moisture conditions (Dynesius et al. 2009; Gotsch et al. 2017). The reproduction of bryophytes is facilitated by water and the poikilohydric state of bryophytes causes them to easily dry up (Proctor, 2009). In particular, many forest bryophytes are likely to be favoured by moist conditions (Hylander

et al., 2005; Gotsch et al. 2017). Higher incoming solar radiation, and thus warmer maximum temperature, might lead to shorter periods of net assimilation and reproduction due to drought (Hylander, 2005; Proctor, 2009). This is perhaps the reason for the somewhat colder maximum temperature optima at the landscape scale for bryophytes than for vascular plants (cf. Ratcliffe, 1968). The vascular plants in this study had somewhat higher values of growing degree days at the continental scale compared to bryophytes, which indicate the possible importance of a warm and long growing season for their performance. Yet, the only difference found between vascular plants and bryophyte correlations was a significant correlation of minimum temperature optima between landscape and continental scales for vascular plants that was not detected for bryophytes. Thus, even if most vascular plants are under the snow in the winter it seems like the southern species still to some extent have a higher chance of finding a suitable site in places with mild winter conditions. It would be interesting to find out to what extent there is a stronger co-occurrence pattern of southern vascular plants than southern bryophytes in the rare type of places with a combination of warm long summers and mild winters in the focal landscape.

In conclusion, the correlations between landscape optima and optima at larger spatial extents suggest that there is sufficient climatic variation also in topographic heterogeneous landscapes for the distribution of sessile species to be regulated by climate (Scherrer and Körner, 2011; Ashcroft and Gollan, 2012; Meineri et al., 2015). In our study system, optima of maximum temperature had relatively strong correlations between the scales, while optima for minimum temperature were correlated for vascular plants but not bryophytes. We may thus to some extent infer the drivers of distributions of species at larger spatial extents by studying landscape climatic optima, and vice versa. However, the fact that the strength of correlations differed between the three examined temperature variables suggest that it is not possible to routinely upscale or downscale species distributions across geographical extents.

401

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410

411 ***Author contributions***

412 JD, KH and JE designed the study. JD collected the field data and downloaded most of the
413 data from databases. JD and DMC did the majority of the analyses with supervision from EM.
414 JD wrote the first draft of the ms and all authors contributed to the interpretation of the data,
415 revision of the text and final approval.

416

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608 Supplementary material Appendix 1-5.

609 Additional data and R-code deposited at XXX

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Figure 1 a) Location of the focal landscape with the 49 inventoried sites in the middle of Sweden between the latitudes 62°50' and 63°12' N. The national data was for the whole of Sweden (small map in the left of the panel) b) The location of the continental area in Europe. Background overview maps, © Lantmäteriet Gävle 2014 I2014/00691.

Figure 2. The correlations between landscape versus national climatic optima (a-c) and landscape versus continental climatic optima (d-f) of all species for the three temperature variables growing degree days GDD5, maximum temperature Tmax °C, and minimum temperature Tmin °C., respectively. A major axis type II regression is projected on significant correlations $p < 0.05$ with corresponding r-values. Note that the ranges on the axes as well as the metrics are different in the different data sets (see methods).

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631 Figure 3. The correlations between landscape and continental climatic optima of (a-c)

632 bryophytes and (d-f) vascular plants for the three temperature variables growing degree days

633 GDD5, maximum temperature T_{max} °C and minimum temperature T_{min} °C., respectively.
634 Panels (g-l) show the same for correlations between landscape and national climatic optima.
635 A major axis type II regression is projected on significant correlations $p < 0.05$ with
636 corresponding r-values. Note that the ranges on the axes as well as the metrics are different in
637 the different data sets (see methods).
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Figure 4. Variation in optima of growing degree days GDD5, maximum temperature Tmax °C and minimum temperature Tmin °C within three different scales a-c) landscape, d-f) national and g-i) continental scales. Bryophytes (96 species) are shown with green circles and vascular plants (50 species) with orange triangles. Boxplots indicate the median and variation for the optima of bryophytes grey and vascular plants light grey, where significant differences at $P < 0.05$ between the two groups are indicated with the symbols a–b.