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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

24 **Abstract**

25 Identifying the factors determining the abundance and distribution of species is a fundamental
26 question in ecology. One key issue is how similar the factors determining species'
27 distributions across spatial scales are (here we focus especially on spatial extents). If the
28 factors are similar across extents, then the large scale distribution pattern of a species may
29 provide information about its local habitat requirements, and vice versa. We assessed the
30 relationships between landscape and national optima as well as landscape and continental
31 optima for growing degree days, maximum temperature and minimum temperature for 96
32 bryophytes and 50 vascular plants. For this set of species, we derived landscape optima from
33 abundance weighted temperature data using species inventories in central Sweden and a fine-
34 grained temperature model (50 m), national optima from niche centroid modelling based on
35 GBIF data from Sweden and the same fine-grained climate model, and continental optima
36 using the same method as for the national optima but from GBIF data from Europe and
37 Worldclim temperatures (*c.* 1000 m). The landscape optima of all species were positively
38 correlated with national as well as continental optima for maximum temperature ($r=0.45$ and
39 0.46 , respectively), weakly so for growing degree days ($r = 0.30$ and $r = 0.28$), but sometimes
40 absent for minimum temperature ($r=0.26$ and $r = 0.04$). The regression slopes of national or
41 continental optima on local optima did not differ between vascular plants and bryophytes for
42 GDD and T_{max} . However, the relationship between the optima of T_{min} differed between
43 groups, being positive in vascular plants but absent in bryophytes. Our results suggest that
44 positive correlations between optima at different spatial scales are present for some climatic
45 variables but not for others. Moreover, our results for vascular plants and bryophytes suggest
46 that correlations might differ between organism groups and depend on the ecology of the
47 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

52 **1. Introduction**

53 Identifying the factors determining the abundance and distribution of species, and and if those
54 environmental factors remain important across spatial scale (grain and extent) are key
55 objectives in global change ecology (Hurlbert et al., 2005; Hess et al., 2006; Azaele et al.,
56 2015). Given that populations in different parts of the distribution range are genetically
57 similar and experience the same range of environmental conditions, we would expect that the
58 relationship between environmental factors and distributions should be similar in different
59 parts and over different spatial extents (e.g. Brown, 1984; Guisan and Zimmermann, 2000;
60 Thuiller et al. 2005; Wiens et al., 2010; Wasof et al., 2015). Yet, there are several reasons
61 why we should instead expect relationships to differ among different parts of the distribution
62 range or among different spatial extents. First, populations in different part of the distribution
63 range might be genetically differentiated and locally adapted with regard to the relationship
64 between environmental conditions (including biotic interactions) and individual performance
65 (Lavergne et al., 2010; Pellissier et al., 2013). For example, Alberto et al. (2013) found
66 genetic differentiation of many adaptive traits when comparing populations of many tree
67 species across geographically separated common gardens. Second, the frequency distribution
68 and range of environmental parameters influencing organism performance as well as the
69 correlation between parameters will often vary among different parts of the distribution range
70 and between extents of different sizes (Hylander et al. 2015). Third, distributions might not be
71 in equilibrium with current environmental conditions. For example, environmental conditions
72 might have changed but changes in distribution are time-lagged due to dispersal limitation or
73 delayed extinctions (Svenning et al. 2015) and such processes are likely to vary among spatial
74 scales. Moreover, changing the grain size of environmental predictors often results in changes
75 in which environmental variables that best predict distributions. For example, structural
76 habitat variables were more important predictors than climate variables in predicting the

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

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

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

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

113

114 **2. Materials and Methods**

115 *2.1 Study areas*

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

127 The whole of Sweden (450 000 km²) was used to examine the national scale. Sweden
128 is extending over a substantial latitudinal and altitudinal gradient (latitudes 55.3 - 69.1°N and
129 0-2100 m.a.s.l.). The continental scale study area comprises a large part of Europe, is more
130 than 5100 km from west to east and 2800 km from south to north, and cover a land area of
131 4.40×10^6 km² (Fig. 1b, between the latitudes 27°38' and 81°48' N). It covers a wide range of
132 altitudes (up to 4810 m.a.s.l.) and climatic conditions from Mediterranean climate in the south
133 to cold climates with long winters in the north and at high altitudes. There is also an east-west
134 climatic gradient across the temperate zone ranging from maritime climates along the Atlantic
135 Ocean to continental climates in the eastern inlands (Peel et al., 2007; Europe, 2014).

136

137 **2.2 Study design and species occurrences**

138 In the focal landscape, we selected 24 south-facing and 25 north-facing forested slopes
139 distributed across the whole area. Within each slope, we randomly selected one 25 × 25m plot
140 within mature forest (at least 50 years old, estimated from aerial pictures). To reduce
141 environmental heterogeneity, selected plots were located > 25 m from open areas, > 50 m
142 from streams, > 10 m from vertical cliffs (> 5 m high), and were situated on mesic soils. Most
143 of the plots were dominated by Norway spruce (*Picea abies* L. Karst.), but at some sites also
144 birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth), Aspen (*Populus tremula* L.) or
145 Scots pine (*Pinus sylvestris* L.) co-dominated the tree layer. The plots were oriented between
146 159° and 214° at south-facing slopes (180° = S) and between 333° and 56° at north facing
147 slopes (360°/0° = N). The slope inclination varied between 7° and 35°, and the altitude ranged
148 from 39 m to 385 m. We assessed the local area species composition within each of the 49
149 chosen 25 × 25 m plots by recording the abundance of all occurring species of bryophytes and
150 vascular plants. We estimated the abundance in three categories 1 = sporadic (few
151 occurrences covering < 5 %), 2 = common (covering 5 – 50 %), and 3 = dominant (covering ≥

152 50 %). For analyses of optima, we included all bryophyte and vascular plant species occurring
153 in at least 5 of the plots (Appendix S1), resulting in 96 bryophytes and 50 vascular plant
154 species.

155 For the national scale we compiled occurrences of the study species from Swedish
156 Artportalen (www.artportalen.se) and for the continental scale also from GBIF
157 (www.gbif.org), and Norwegian Artsobservasjoner (www.artsobservasjoner.no). In GBIF, we
158 included observations, literature data and herbarium specimens. We restricted the GBIF
159 occurrence data sets to the time period 1950 to 2014. Information on the precision of
160 coordinates was lacking for large parts of the GBIF data sets and to include as many
161 observations as possible, we did not apply any restrictions on precision. In the continental
162 scale data we included only countries that had an average density of at least 1 observation per
163 1000 km² of the 146 study species pooled to avoid biasing estimates of species' continental
164 range optima due to scarce reporting from these areas (Fig. 1b).

165

166 ***2.3 Temperature variables***

167 For both the landscape and national scale, we extracted decadal averages (2000-2010) of
168 growing degree days (base 5°C, GDD5), minimum temperature (the yearly 5th percentile of
169 the daily min temperature, T_{min}, °C) and maximum temperature (the yearly 95th percentile of
170 the daily max temperature, T_{max}, °C) from freely available modelled fine-grained layers at a
171 50 m resolution covering the whole of Sweden (Meineri & Hylander 2017). For the
172 continental area we retrieved the same variables from Worldclim v1.4 (period 1960-1990;
173 www.worldclim.org; Hijmans et al., 2005) at a 30 seconds resolution (~1 km). At this scale,
174 T_{min} and T_{max} were monthly means derived from daily minimum and maximum
175 measurements averaged for the period 1960-1990. We set the lowest of the twelve monthly
176 T_{min}- and the highest of the twelve monthly T_{max}-values as our continental T_{min} and T_{max},

177 respectively. We calculated GDD5 following Synes and Osborne (2011) and Nieto et al.
178 (2015) by using the formula: $GDD5 \text{ for each month} = ((\text{monthly } T_{\text{max}} + \text{monthly } T_{\text{min}}) / 2 -$
179 $T_{\text{base}} [\text{in our case } 5]) \times \text{Days per month}$, and then summing up GDD5 for each month (those
180 above zero) to a yearly GDD5. Thereby, we approximated a yearly heat accumulation for the
181 chosen time period.

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

188

189 *2.4 Temperature optima*

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

193 Equation 1:

$$194 \text{ Landscape optima} = \frac{(\sum_{i=1}^n (\text{ith site abundance} \times \text{ith site value of climatic variable}))}{(\sum_{i=1}^n (\text{ith site abundance}))}$$

195

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

202 three focal climate variables as a proxy for the species' optima. We used the R package
203 "hypervolume" version 2.0.11 (Blonder 2018). We used the one-class support vector machine
204 algorithm with default tuning parameter settings, and number of random points used to assess
205 the species-specific hypervolumes was set to $10^5 + \sqrt{\frac{\text{number of climate variables}}{\text{number of observations}}}$. This parameter
206 ensures equal sampling effort of species with different number of observations, and the higher
207 the number, the more robust results you get with a trade-off of computer power (Blonder et al.
208 2017). The niche centroid was calculated as the mean of the random points, giving one value
209 for each niche axes.

210

211 *2.5 Statistical analyses*

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

226

227 **3. Results**

228 *3.1 Correlations between species landscape, national and continental optima*

229 Species with higher landscape optima for Tmax also had on average higher national and
230 continental optima (landscape vs national: $r = 0.45$, $P < 0.001$; landscape vs continental: $r =$
231 0.46 , $P < 0.001$, Fig. 2b and e, Appendix 2). For GDD5, there were also positive, albeit
232 weaker, correlations between landscape and national, and landscape and continental optima
233 (landscape vs national: $r = 0.30$, $P < 0.001$; landscape vs continental: $r = 0.28$, $P < 0.001$, Fig.
234 2b, Appendix 2b). For Tmin, the correlation between landscape and national optima was even
235 weaker ($r = 0.26$, $P = 0.002$, Fig. 2c, Appendix 2c), and there was no correlation between
236 landscape and continental optima ($r = 0.04$, $P = 0.65$, Fig. 2f, Appendix 2f).

237

238 *3.2 Differences between bryophytes and vascular plants*

239 The relationships between the landscape and national optima and landscape and continental
240 optima for the three temperature variables showed similar patterns for bryophytes and
241 vascular plants in most cases (Fig 3, $p > 0.05$ for the interaction effect, Appendix 3). However,
242 for the model between landscape and continental optima of minimum temperatures there was
243 a significant effect if the interaction between organism group and temperature (Ancova, $P =$
244 0.0023). For vascular plants, but not for bryophytes, Tmin optima were positively correlated
245 across extents (Fig 3c, f, i and l, Appendix 3). Correlation coefficients did not differ
246 significantly between the two groups, except between Tmin at landscape and continental
247 scales where vascular plants had a higher coefficient than bryophytes ($r = 0.36$ vs. $r = -0.13$;
248 Fisher r-to-z test, $P = 0.004$).

249

250 *3.3 Within-scale relationships*

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

254

255 Correlations between the three examined temperature variables differed among the three
256 spatial extents. GDD5 and Tmax were positively correlated at all extents (landscape: $r = 0.40$,
257 $P = 0.005$; national: $r = 0.89$, $P < 0.001$; and continental: $r = 0.83$, $P < 0.001$, Appendix 4
258 and 5), while Tmin was correlated to GDD5 only at the national and continental extents
259 (landscape: $r = 0.26$, $P = 0.07$; national: $r = 0.91$, $P < 0.001$; continental: $r = 0.78$, $P < 0.001$).
260 There were no correlation between Tmin and Tmax at the landscape ($r = -0.21$, $P = 0.15$), but
261 a positive correlation at the national and continental extents (national: $r = 0.67$, $P < 0.001$;
262 continental: $r = 0.39$, $P < 0.001$) (Appendix 4 and 5).

263

264 **4. Discussion**

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

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

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

301 al., 2000). Still, data from larger grid cells might generate downscaled distribution maps that
302 are quite accurate in some cases, as shown for several species groups in Britain (Barwell et al.
303 2014, Fernandes et al. 2014), and the field is developing fast (Keil et al. 2013, Groom et al.
304 2018). We found very similar patterns when correlating the landscape optima to fine-gridded
305 national data and to coarse-gridded continental scale data. This suggest that our larger scale
306 datasets quite well describe the distributional optima for the species, despite the difference in
307 both extent and grain size. A likely reason for this pattern is that both dataset covers long
308 latitudinal gradients, which are more important to estimate optima than within grid-cell
309 variation. Thus, for studies focusing on niche hypervolume size or shape there is a larger risk
310 for biases due to different grid sizes than in studies focusing on niche centroids (Kambach
311 2019).

312 The correlations between landscape and continental optima were strongest for
313 maximum temperature, weaker but significant for growing degree days, and even weaker or
314 not significant for minimum temperature. Both growing degree days and maximum
315 temperature characterize the climatic conditions during the plant growing season, suggesting
316 that these variables should have an important effect on plant performance. However,
317 minimum temperature has also been highlighted as important for species distributions at
318 different spatial scales (Aschcroft et al., 2011; Dobrowski, 2011; Scherrer and Körner, 2011;
319 Illán et al., 2014), including the range limits of tree species towards cold conditions (Sakai,
320 1979; Körner, 2012, Kreyling et al. 2015). Niche conservatism has been higher for the cold
321 than warm thermal limit for a number of alpine plant species (Pellissier et al., 2013).
322 However, a majority of our studied species might not be affected by yearly minimum
323 temperature in northern regions such as in our focal landscape, since they are resting and
324 protected by snow cover during winter periods there (cf. Vercauteren et al., 2013). Trees and
325 shrubs that extend above the snow cover are more affected by winter frosts than for example

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

344 Several factors may contribute to weak correlations between landscape and larger
345 scale optima. A likely ecological explanation to this is that several factors interact, in a
346 species-specific way, to determine where a species can occur in the landscape (e.g. Gaston,
347 2009, Zellweger et al., 2016). For example, while two species might have similar high
348 continental optima for growing degree days, this might be due to a direct dependence on
349 longer growing season in one of the species but due to dependence on humid conditions,
350 which are correlated with growing degree days, for the other species. As a consequence, they

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

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

391 In conclusion, the correlations between landscape optima and optima at larger spatial
392 extents suggest that there is sufficient climatic variation also in topographic heterogeneous
393 landscapes for the distribution of sessile species to be regulated by climate (Scherrer and
394 Körner, 2011; Ashcroft and Gollan, 2012; Meineri et al., 2015). In our study system, optima
395 of maximum temperature had relatively strong correlations between the scales, while optima
396 for minimum temperature were correlated for vascular plants but not bryophytes. We may
397 thus to some extent infer the drivers of distributions of species at larger spatial extents by
398 studying landscape climatic optima, and vice versa. However, the fact that the strength of
399 correlations differed between the three examined temperature variables suggest that it is not
400 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

417 **References**

- 418 1. Alberto, F.J., Aitken, S.N., Alia, R., Gonzalez-Martinez, S.C., Hanninen, H., Kremer, A.,
419 Lefevre, F., Lenormand, T., Yeaman, S., Whetten, R., Savolainen, O. 2013. Potential
420 for evolutionary responses to climate change evidence from tree populations. *Global*
421 *Change Biology* 19, 1645-1661.
- 422 2. Araújo, M., Thuiller, M., Williams, P.H., Reginster, I. 2005. Downscaling European
423 species atlas distributions to a finer resolution, implications for conservation planning.
424 *Global Ecology and Biogeography* 14, 17–30.

- 425 3. Azaele, S., Maritan, A., Cornell, S.J., Suweis, S., Banavar, J.R., Gabriel, D., Kunin, W.E.
426 2015. Towards a unified descriptive theory for spatial ecology, predicting biodiversity
427 patterns across spatial scales. *Methods in Ecology and Evolution* 6, 324-332.
- 428 4. Ashcroft, M.B., French, K.O., Chisholm, L.A. 2011. An evaluation of environmental
429 factors affecting species distributions. *Ecological Modelling* 222:24-531.
- 430 5. Ashcroft, M.B., Gollan J.R. 2012. Fine-resolution (25 m) topoclimatic grids of near-surface
431 (5 cm) extreme temperatures and humidities across various habitats in a large (200 x
432 300 km) and diverse region. *International Journal of Climatology* 32, 2134–2148.
- 433 6. Austin M.P., Van Niel K.P. 2011. Improving species distribution models for climate
434 change studies, variable selection and scale. *Journal of Biogeography* 38, 1–8.
- 435 7. Barwell, L.J., Azaele, S., Kunin, W.E., Isaac, N.J.B. 2015. Can coarse-grain patterns in
436 insect atlas data predict local occupancy? *Diversity and Distributions* 20, 895-907.
- 437 8. Blonder, B. 2018. hypervolume: High Dimensional Geometry and Set Operations Using
438 Kernel Density Estimation, Support Vector Machines, and Convex Hulls. R package
439 version 2.0.11.
- 440 9. Blonder, B., Morrow, C. B., Maitner, B., Harris, D. J., Lamanna, C., Violle, C., Enquist, B.
441 J., Kerkhoff, A. J. 2017. New approaches for delineating n-dimensional hypervolumes.
442 *Methods of Ecology and Evolution* 9, 305-319.
- 443 10. Brown J.H. 1984. On the Relationship between Abundance and Distribution of Species.
444 *The American Naturalist* 124, 255–279.
- 445 11. Collingham Y.C., Wadsworth R.A., Huntley B., Hulme P.E. 2000. Predicting the spatial
446 distribution of non-indigenous riparian weeds, issues of spatial scale and extent.
447 *Journal of Applied Ecology* 37, 13–27.

- 448 12. Connor, T., Hull, V., Vina, A., Shortridge, A., Tang, Y., Zhang, J.D., Wang, F., Liu, J.G.
449 2019. Effects of grain size and niche breadth on species distribution modelling.
450 *Ecography* 41, 1270-1282.
- 451 13. Dahlberg C.J., Ehrlén J., Hylander K. 2014. Performance of forest bryophytes with
452 different geographical distributions transplanted across a topographically
453 heterogeneous landscape, *PLoS ONE* 9, e112943.
- 454 14. Dobrowski S.Z. 2011. A climatic basis for microrefugia, the influence of terrain on
455 climate. *Global Change Biology* 17, 1022–1035.
- 456 15. Dynesius, M., Hylander, K., Nilsson, C. High resilience of bryophyte assemblages in
457 streamside compared to upland forests. *Ecology* 90, 1042-1054.
- 458 16. Europe 2014. Continent. Available at,
459 <http://www.britannica.com/EBchecked/topic/195686/Europe> [Accessed 29 July 2014]
- 460 17. Fernandes, R.F., Vicente, J.R., Georges, D., Alves, P., Thuiller, W., Honrado, J.P. 2014. A
461 novel downscaling approach to predict plant invasions and improve local conservation
462 actions. *Biological Invasions* 16, 2577-2590.
- 463 18. Franklin J., Davis F.W., Ikegami M., Syphard A.D., Flint L.E., Flint A.L., Hannah L.
464 2013. Modeling plant species distributions under future climates, how fine scale do
465 climate projections need to be? *Global Change Biology* 19, 473–483.
- 466 19. Fridley J.D. 2009. Downscaling climate over complex terrain, high finescale < 1000 m.
467 spatial variation of near-ground temperatures in a montane forested landscape (Great
468 Smoky mountains) *Journal of Applied Meteorology and Climatology* 48, 1033–1049.
- 469 20. Gaston, K.J. 2009. Geographic range limits, Achieving synthesis. *Proceedings of the*
470 *Royal Society B Biological Sciences* 276, 1395–1406.

- 471 21. Gotsch, S.G., Davidson, K., Murray, J.G., Duarte, V.J., Draguljic, D. 2017. Vapor
472 pressure deficit predicts epiphyte abundance across an elevational gradient in a
473 tropical montane region. *American Journal of Botany* 12, 1790-1801.
- 474 22. Groom, Q.J., Marsh, C.J., Gavish, Y., Kunin, W.E. 2018. How to predict fine resolution
475 occupancy from coarse occupancy data. *Methods in Ecology and Evolution* 9: 2273-
476 2284.
- 477 23. Guisan A. and Zimmermann N.E. 2000. Predictive habitat distribution models in ecology.
478 *Ecological Modelling* 135, 147-186.
- 479 24. Hampe A., Rodríguez-Sánchez F., Dobrowski S., Hu F.S., Gavin D.G. 2013. Climate
480 refugia, from the last glacial maximum to the twenty-first century. *New Phytologist*
481 197, 16–18.
- 482 25. Hannah L., Flint L., Syphard A.D., Moritz M.A., Buckley L.B., McCullough I.M. 2014.
483 Fine-grain modeling of species' response to climate change, holdouts, stepping-stones,
484 and microrefugia. *Trends in Ecology and Evolution* 29, 390–397.
- 485 26. Herrero, A. Almaraz, P. Zamora, R., Castro, J., Hodar, J.A. 2016. From the individual to
486 the landscape and back, time-varying effects of climate and herbivory on tree sapling
487 growth at distribution limits. *Journal of Ecology* 104, 430-442.
- 488 27. Hess, G.R., Bartel, R.A., Leidner, A.K., Rosenfeld, K.M., Rubino, M.J., Snider, S.B.,
489 Ricketts, T.H. 2006. *Biological Conservation* 132: 448-457. Hijmans R.J., Cameron
490 S.E., Parra J.L., Jones P.G., Jarvis A. 2005. Very high resolution interpolated climate
491 surfaces for global land areas. *International Journal of Climatology* 25, 1965–1978.
- 492 28. Hurlbert, A.H., White, E.P. 2005. Disparity between range map- and survey-based
493 analyses of species richness: patterns, processes and implications. *Ecology Letters*
494 8:319-327. Hylander K. 2005. Aspect modifies the magnitude of edge effects on
495 bryophyte growth in boreal forests. *Journal of Applied Ecology* 42, 518–525.

- 496 29. Hylander K., Dynesius M., Jonsson B.G., Nilsson C. 2005. Substrate form determines the
497 fate of bryophytes in riparian buffer strips. *Ecological Applications* 15, 674–688.
- 498 30. Hylander K., Ehrlén J., Luoto M., Meineri E. 2015. Microrefugia, Not for everyone.
499 *AMBIO* 44, 60–68.
- 500 31. Illán J.G., Thomas C.D., Jones J.A., Wong W.-K., Shirley S.M., Betts M.G. 2014.
501 Precipitation and winter temperature predict long-term range-scale abundance changes
502 in Western North American birds. *Global Change Biology* 20, 3351–3364.
- 503 32. Kambach, S., Lenoir, J., Decocq, G., Welk, E., Seidler, G., Dullinger, S., Gégout, J.-C.,
504 Guisan, A., Pauli, H., Svenning, J.-C., Vittoz, P., Wohlgemuth, T., Zimmermann,
505 N.E., Bruelheide, H. 2019. Of niches and distributions: range size increases with niche
506 breadth both globally and regionally but regional estimates poorly relate to global
507 estimates. *Ecography* 42, 467-477.
- 508 33. Kreyling, J., Schmid, S., Aas, G. 2015. Cold tolerance of tree species is related to the
509 climate of their native ranges. *Journal of Biogeography* 42, 156–166.
- 510 34. Lembrechts, J., Ivan, N., Lenoir, J. 2018. Incorporating microclimate into species
511 distribution models. *Ecography* 42, 1-13.
- 512 35. Lenoir J. et al. 2013. Local temperatures inferred from plant communities suggest strong
513 spatial buffering of climate warming across Northern Europe. *Global Change Biology*
514 19, 1470-1481.
- 515 36. Lenoir, J. et al. 2017. Climatic microrefugia under anthropogenic climate change,
516 implications for species redistribution. *Ecography* 40, 253–266.
- 517 37. Keil, P., Belmaker, J., Wilson, A.M., Unitt, P., Jetz, W. 2013. Downscaling of species
518 distribution models: a hierarchical approach. *Methods in Ecology and Evolution* 2013:
519 4: 82-94. Keppel, G. et al. 2012. Refugia, identifying and understanding safe havens
520 for biodiversity under climate change. *Global Ecol. Biogeogr.* 21, 393–404.

- 521 38. Körner C. 2012. *Alpine Treelines*. Springer, Basel.
- 522 39. Lavergne S., Mouquet N., Thuiller W., Ronce O. 2010. Biodiversity and climate change,
523 Integrating evolutionary and ecological responses of species and communities. *Annual*
524 *Review of Ecology, Evolution, and Systematics* 41, 321–350.
- 525 40. Mascher J.W. 1990. *Ångermanlands flora*. SBT-redaktioner, Lund.
- 526 41. Meineri E., Dahlberg C.J., Hylander K. 2015. Using Gaussian Bayesian networks to
527 disentangle direct and indirect associations between landscape physiography,
528 environmental variables and species distribution. *Ecological Modelling* 313, 127–136.
- 529 42. Meineri, E. and Hylander, K. 2017. Fine-grain, large-domain climate models based on
530 climate station and comprehensive topographic information improve microrefugia
531 detection. *Ecography* 40, 1003–1013.
- 532 43. Menke, S.B., Holway, D.A., Fisher, R. N., Jetz, W. 2009. Characterizing and predicting
533 species distribution across environments and scales: Argentine ant occurrences in the
534 eye of the beholder. *Global Ecology and Biogeography* 18:50-63
- 535 44. Muffler, L., Beierkuhnlein, C., Aas, G., Jentsch, A., Schweiger, A.H., Zohner, C.,
536 Kreyling, J. 2016. Distribution ranges and spring phenology explain late frost
537 sensitivity in 170 woody plants from the Northern Hemisphere. *Global Ecology and*
538 *Biogeography* 25, 1061-1071.
- 539 45. Pearman P.B., Guisan A., Broennimann O., Randin C.F. 2008. Niche dynamics in space
540 and time. *Trends in Ecology and Evolution* 23, 149–158.
- 541 46. Pearson R.G. and Dawson T.P. 2003. Predicting the impacts of climate change on the
542 distribution of species, are bioclimate envelope models useful? *Global Ecology and*
543 *Biogeography* 12, 361–371.
- 544 47. Peel M.C., Finlayson B.L., McMahon T.A. 2007. Updated world map of the Köppen-
545 Geiger climate classification. *Hydrology and Earth System Sciences* 4, 439–473.

- 546 48. Pellissier L., Bråthen K.A., Vittoz P., Yoccoz N.G., Dubuis A., Meier E.S., Zimmermann
547 N.E., Randin C.F., Thuiller W., Garraud L., Van Es J., Guisan A. 2013. Thermal
548 niches are more conserved at cold than warm limits in arctic-alpine plant species.
549 *Global Ecology and Biogeography* 22, 933–941.
- 550 49. Phillips S.J., Anderson R.P., Schapire R.E. 2006. Maximum entropy modeling of species
551 geographic distributions. *Ecological Modelling* 190, 231–259.
- 552 50. Proctor M.C.F. 2009. Physiological ecology. *Bryophyte Biology* ed. by B. Goffinet and J.
553 Shaw., pp. 237–268. Cambridge University Press, New York.
- 554 51. Proctor M.C.F. 2011. Climatic responses and limits of bryophytes, comparisons and
555 contrasts with vascular plants. *Bryophyte Ecology and Climate Change*. ed. by Z.
556 Tuba, N.G. Slack, L.R. Stark., pp. 35–54. Cambridge University Press, New York.
- 557 52. Randin C.F., Engler R., Normand S., Zappa M., Zimmermann N.E., Pearman P.B., Vittoz
558 P., Thuiller W., Guisan A. 2009. Climate change and plant distribution, local models
559 predict high-elevation persistence. *Global Change Biology* 15, 1557–1569.
- 560 53. Ratcliffe D.A. 1968. An ecological account of Atlantic bryophytes in the British Isles.
561 *New Phytologist* 67, 365–439.
- 562 54. Revelle, W. 2018. psych: Procedures for Personality and Psychological Research,
563 Northwestern University, Evanston, Illinois, USA. R package version 1.8.12.
- 564 55. R Core Team 2014. R, A language and environment for statistical computing. R
565 Foundation for Statistical Computing, Vienna.
- 566 56. Sakai A. 1979. Freezing tolerance of evergreen and deciduous broad-leaved trees in Japan
567 with reference to tree regions. *Low temperature science. Ser. B, Biological sciences*
568 36, 1–19.

- 569 57. Scherrer D. and Körner C. 2011. Topographically controlled thermal-habitat
570 differentiation buffers alpine plant diversity against climate warming. *Journal of*
571 *Biogeography* 38, 406–416.
- 572 58. Svenning JC, Eiserhardt WL, Normand S, Ordonez A, Sandel B 2015. The influence of
573 paleoclimate on present-day patterns in biodiversity and ecosystems. *Annual Review*
574 *of Ecology, Evolution and Systematics* 46, 551-572.
- 575 59. Swedish Meteorological and Hydrological Institute 2016. Klimatdata. Available at,
576 <http://www.smhi.se/klimatdata> [accessed 29 January 2016]
- 577 60. Synes N.W. and Osborne P.E. 2011. Choice of predictor variables as a source of
578 uncertainty in continental-scale species distribution modelling under climate change.
579 *Global Ecology and Biogeography* 20, 904–914.
- 580 61. Thuiller W., Richardson D.M., Pyšek P., Midgley G.F., Hughes G.O., Rouget M. 2005.
581 Niche-based modelling as a tool for predicting the risk of alien plant invasions at a
582 global scale. *Global Change Biology* 11, 2234–2250.
- 583 62. Trivedi M.R., Berry P.M., Morecroft M.D., Dawson T.P. 2008. Spatial scale affects
584 bioclimate model projections of climate change impacts on mountain plants. *Global*
585 *Change Biology* 14, 1089–1103.
- 586 63. Ureta, C., Martorell, C., Cuervo-Robayo, A.P., Mandujano, M.A.C., Martinez-Meyer, E.
587 2018. Inferring space from time, On the relationship between demography and
588 environmental suitability in the desert plant *O. rastrera*. *PlosONE* 8, e0201543.
- 589 64. Vercauteren N., Lyon S.W., Destouni G. 2013. Seasonal influence of insolation on fine-
590 resolved air temperature variation and snowmelt. *Journal of Applied Meteorology and*
591 *Climatology* 53, 323–332.
- 592 65. Walter H. and Breckle S.-W. 1989. *Ecological systems of the geobiosphere, 3 temperate*
593 *and polar zoniomes of northern Eurasia*. Springer-Verlag, Berlin Heidelberg.

594 66. Wasof S., Lenoir J., Aarrestad P.A., et al. 2015. Disjunct populations of European
595 vascular plant species keep the same climatic niches. *Global Ecology and*
596 *Biogeography* 24, 1401–1412.

597 67. Wiens J.J., Ackerly D.D., Allen A.P., Anacker B.L., Buckley L.B., Cornell H.V.,
598 Damschen E.I., Jonathan Davies T., Grytnes J.-A., Harrison S.P., Hawkins B.A., Holt
599 R.D., McCain C.M., Stephens P.R. 2010. Niche conservatism as an emerging principle
600 in ecology and conservation biology. *Ecology Letters* 13, 1310–1324.

601 68. Woodward F.I. and Williams B.G. 1987. Climate and plant distribution at global and local
602 scales. *Vegetatio* 69, 189–197.

603 69. Zellweger, F., Baltensweiler, A., Ginzler, C., Roth, T., Braunisch, V., Bugmann, H.,
604 Bollmann, K. 2016. Environmental predictors of species richness in forest landscapes,
605 abiotic factors versus vegetation structure. *Journal of Biogeography* 43, 1080-1090.

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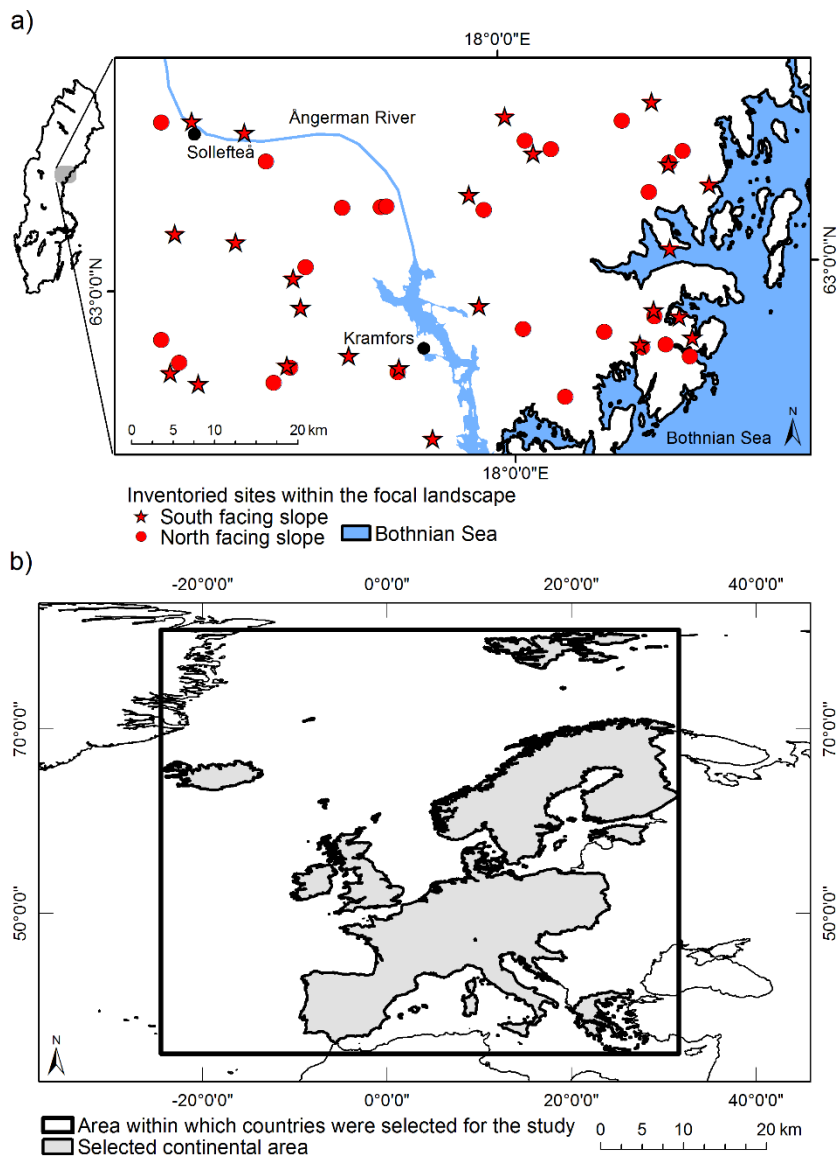
608 Supplementary material Appendix 1-5.

609 Additional data and R-code deposited at XXX

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611 Figures

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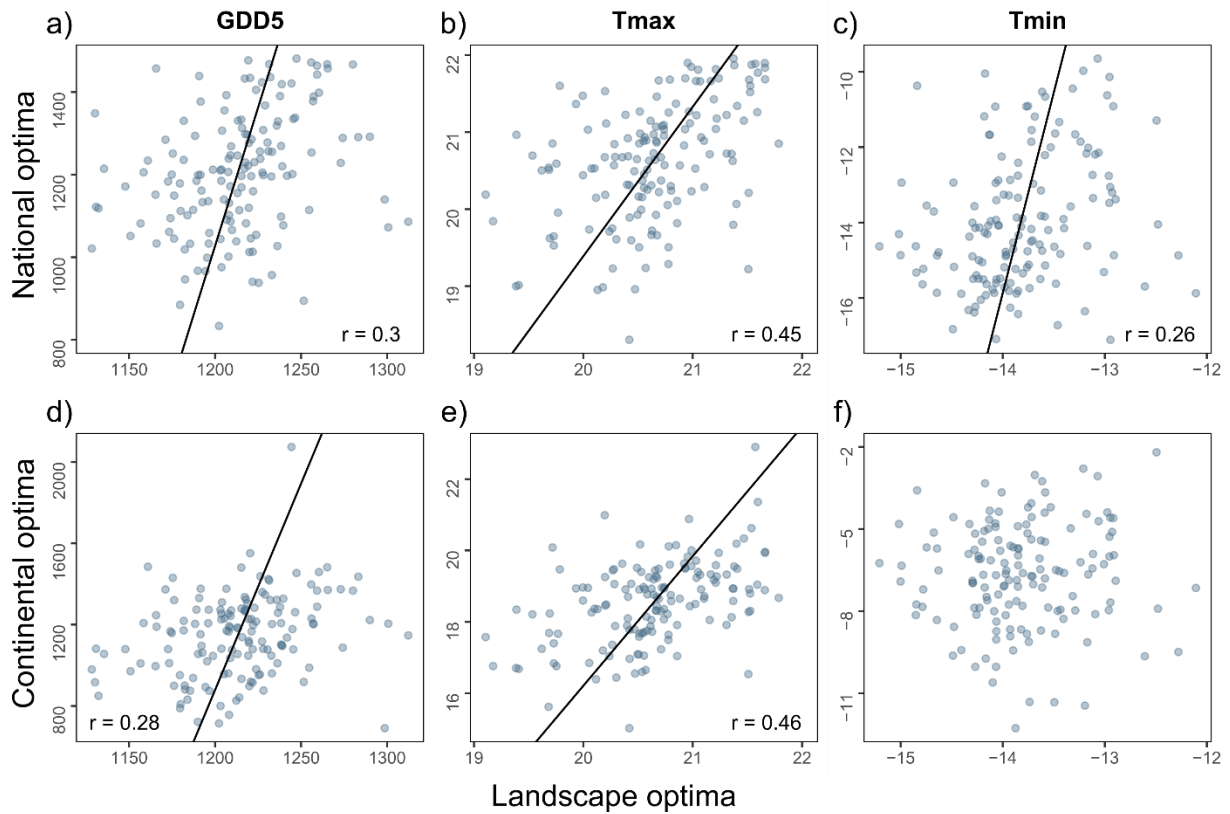


613

614 Figure 1 a) Location of the focal landscape with the 49 inventoried sites in the middle of
615 Sweden between the latitudes 62°50' and 63°12' N. The national data was for the whole of
616 Sweden (small map in the left of the panel) b) The location of the continental area in Europe.

617 Background overview maps, © Lantmäteriet Gävle 2014 I2014/00691.

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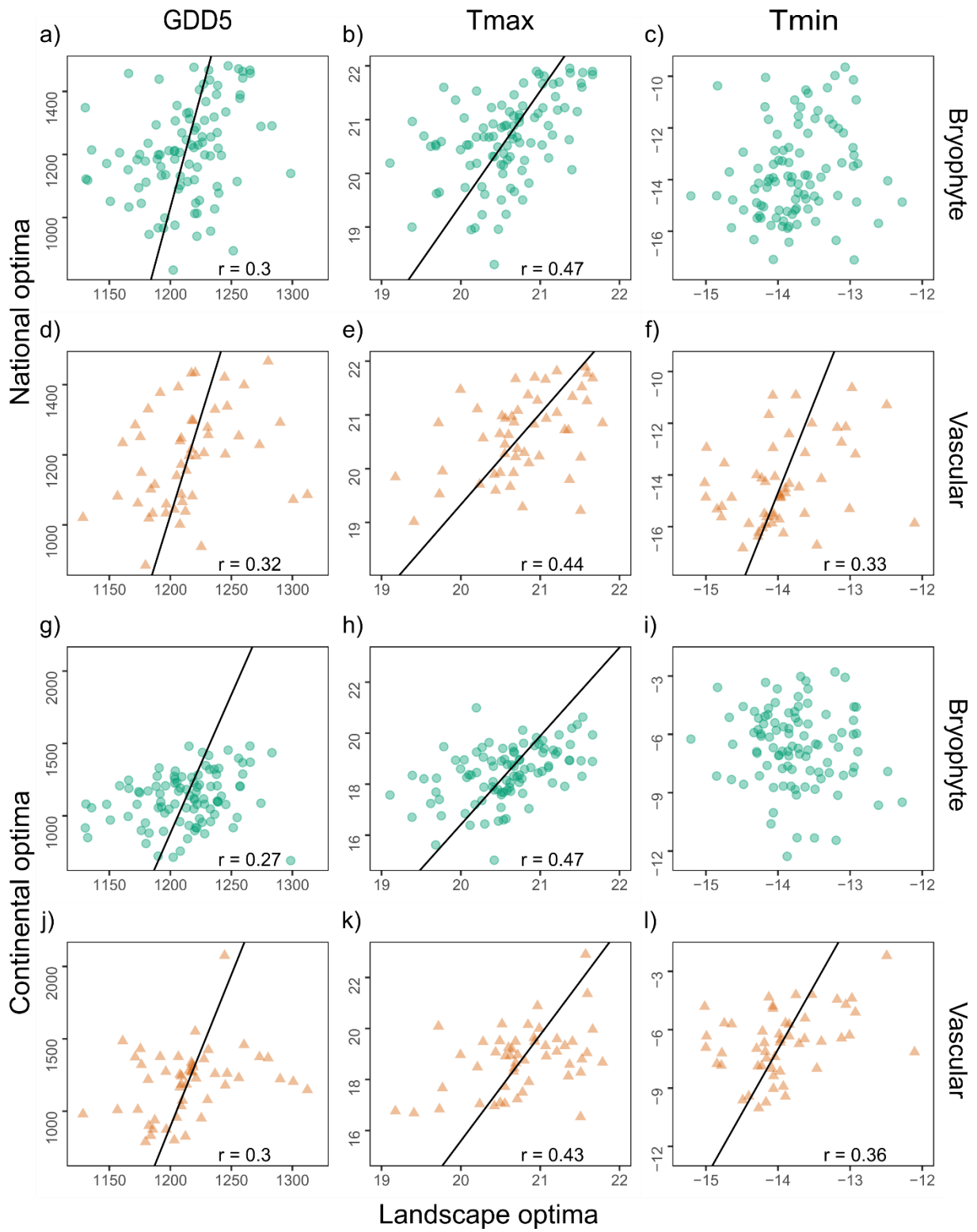
620

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

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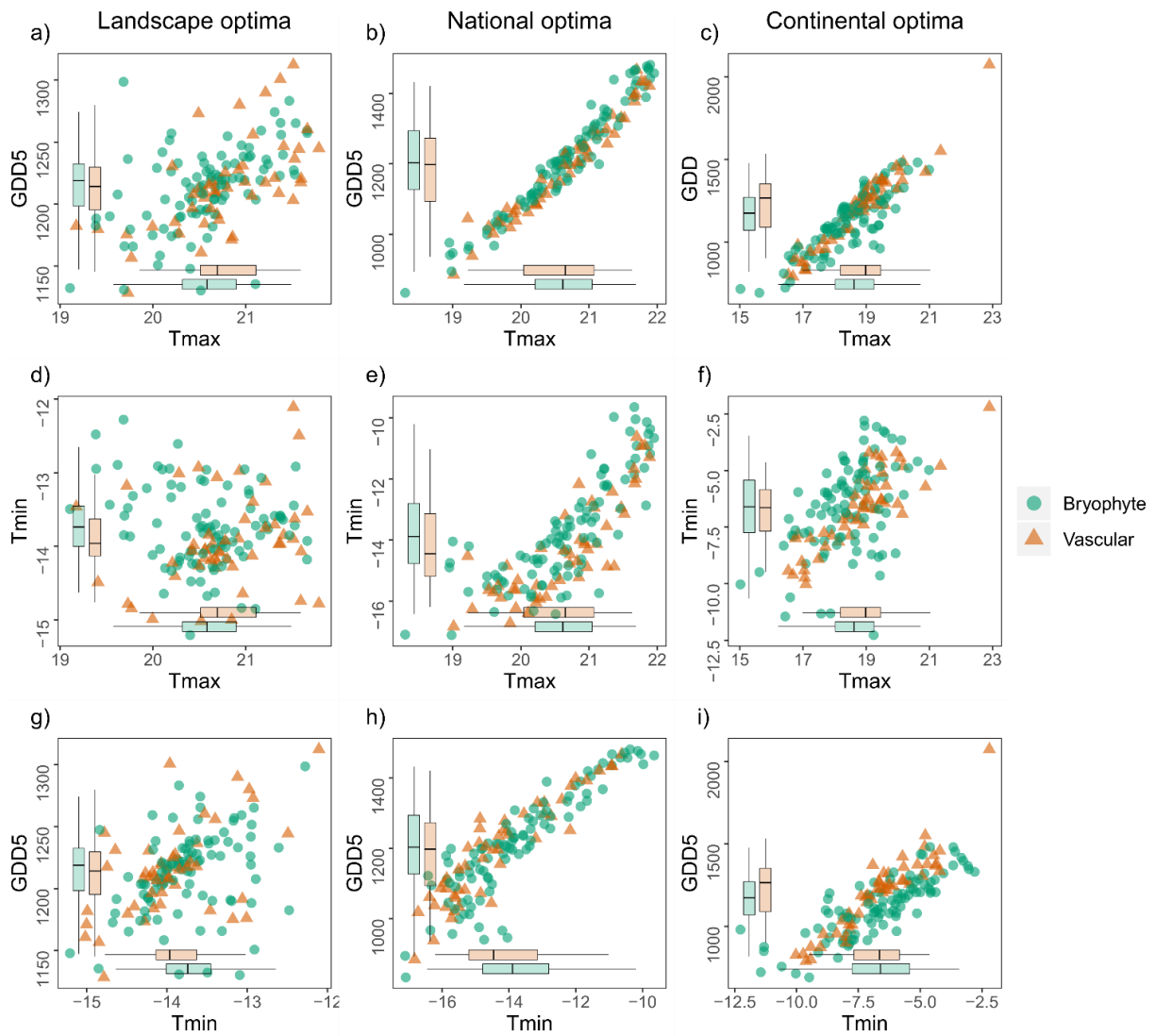


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631 Figure 3. The correlations between landscape and continental climatic optima of (a-c)

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).
638



640

641 Figure 4. Variation in optima of growing degree days GDD5, maximum temperature Tmax

642 °C and minimum temperature Tmin °C within three different scales a-c) landscape, d-f)

643 national and g-i) continental scales. Bryophytes (96 species) are shown with green circles and

644 vascular plants (50 species) with orange triangles. Boxplots indicate the median and variation

645 for the optima of bryophytes grey and vascular plants light grey, where significant differences

646 at $P < 0.05$ between the two groups are indicated with the symbols a–b.

647