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ARTICLE TITLE

Disjunct populations of European vascular plant species keep the same climatic niches

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ABSTRACT

Aim Research on how the climatic niche varies across a species range has focused on a limited number of species, mostly invasive, and has not been very conclusive so far. **Here, we assess the degree of niche conservatism between distant populations of alpine** plant species that have been established for thousands of years.

Location European Alps and Fennoscandia.

Methods **Focusing on a representative sample ($n = 389$) of the pool of terrestrial vascular plant species ($n = 888$) occurring in both the Alps and Fennoscandia, we used two complementary approaches to test for and quantify climatic-niche shifts for species with Alpine and Fennoscandian populations that are either strictly disjunct ($n = 31$) or at least distant ($n = 358$).** First, we used a species distribution modelling approach to test for a region effect on each species' climatic niche. Second, we quantified niche overlap and shifts in niche width (i.e., ecological amplitude) and position (i.e., ecological optimum) within a bi-dimensional climatic space.

Results **Only one species (3%) with strictly disjunct populations and 58 species (16%) with at least distant populations showed a region effect on their climatic niche.** Niche overlap was higher for species with strictly disjunct populations (0.50 ± 0.1) than for species with distant populations (0.42 ± 0.1), and highest for Arctic-alpine species (0.55 ± 0.06). Estimated climatic niches were, on average, larger and located towards warmer and **wetter** conditions in the Alps.

Main conclusion Climatic niches seem to be generally conserved between populations that are separated between the Alps and Scandinavia and likely have been so for 10,-15,000 years, despite the fact that populations in the Alps and Fennoscandia became adapted over time to their respective sets of regional climatic conditions. Therefore, the basic assumption of species distribution models that species' climatic niche is constant in space and time – at least one time scales 10^4 years or less – seems to be largely valid for arctic-alpine plants.

147

INTRODUCTION

148 A long-standing question in ecology is whether species populations that occupy distant
149 regions have retained similar ecological requirements, i.e. whether their environmental niche
150 remained constant over space and time (Lavergne *et al.*, 2010). This question departs from the
151 principle of phylogenetic niche conservatism, the tendency of closely related species to be
152 more similar than expected, and which involves evolutionary time scales (Losos, 2008;
153 Lavergne *et al.*, 2010; Wiens *et al.*, 2010). Determining whether or not geographically distant
154 populations have evolved to occupy distinct niches, and to what extent, and in which
155 conditions, is of paramount importance in predicting future biodiversity under climate change.
156 Indeed, most correlative models used to predict species range changes take the conservative
157 assumption that species' environmental niches are relatively constant in space and time
158 (Guisan *et al.*, 2014).

159 One difficulty when trying to address this question is that species' fundamental
160 environmental niche reflecting their physiological tolerances cannot be estimated from
161 empirical field data because other factors, such as biotic interactions and dispersal limitation,
162 often restrict the range of conditions species may encounter. The latter is often called the
163 realised ecological niche (Hutchinson, 1957; Austin *et al.*, 1990). For example, changes in
164 biotic interactions or dispersal limitation across regions may create two distinct realised
165 niches within the same global fundamental niche. Reversely, lack of change of the realised
166 niche usually indicates that the underlying fundamental niche has been largely conserved and
167 no strong regional adaptations have occurred.

168 Invasive species colonising newly separated regions have been particularly studied in
169 this context (see Guisan *et al.*, 2014 for a review). Range-filling processes in the invaded
170 range are indeed strongly **limited** or at an early stage and the potential for divergence of niche
171 requirements are largely unexploited (Williamson *et al.*, 2009). Instead, assessments of

172 climatic niche differences between distant populations originating from distinct post-
173 glaciation colonisation events are more likely to inform us about species' abilities to modify
174 their ecological requirements under future climate change. However, such comparisons have
175 rarely been undertaken (but see Pellissier *et al.*, 2013).

176 Here, we extend such niche comparison between distant populations of native species
177 by using a representative sample of the pool of vascular plants ($n = 888$) that have
178 successfully recolonised both the European Alps and Fennoscandia. These two geographically
179 distant mountainous regions have the advantage of having different recolonisation histories
180 during the last glacial-interglacial cycle and sharing analogous macroclimatic gradients.
181 During the Last Glacial Maximum (LGM, *ca* 23,000-18,000 yr BP), Fennoscandia was
182 largely covered by the Eurasian ice-sheet (Svendsen *et al.*, 2004), and largely recolonized
183 from In contrast, numerous ice-free refugial areas were located relatively close to each
184 other at the eastern and southern periphery of the much smaller ice caps that covered central
185 parts of the Alps (Schönswetter *et al.*, 2005). Thus, many high-elevation plants probably
186 survived the LGM at the margins of both the Alps (Schönswetter *et al.*, 2005) and the
187 Eurasian ice-sheet (Birks, 1994), and on the nunataks or other ice-free pockets in the Alps
188 (Stehlik *et al.*, 2002). The realised climatic niche of a given Arctic-alpine plant species should
189 thus be wider in the Alps than in Fennoscandia since the process of post-glacial recolonisation
190 of all climatically suitable sites (i.e. range-filling) has probably been less constrained by
191 dispersal limitations (Dullinger *et al.*, 2012). In addition, proximity of the Alps to the main
192 southern refugia of the temperate European flora (Iberian, Italian, and Balkan Peninsulas)
193 (Birks & Willis, 2008), with larger population sizes and genetic diversity (Hewitt, 2000), may
194 have enhanced population adaptability, and also genetic variation in the Alps. This may have
195 fostered a species' capability to exploit available post-glacial ice-free areas and thus widen its
196 fundamental climatic niche as well as shift its fundamental climatic niche towards warmer

197 conditions. In contrast, the long-distance recolonisation of Fennoscandia is likely to have
198 involved repeated founder events, successively reducing the genetic variation and most likely
199 also the fundamental climatic niche (e.g. Giesecke, 2005). Additionally, such long-distance
200 recolonisation of Fennoscandia not only originated from the main southern refugia located in
201 southern Europe, but also from eastern refugia located in Russia (Eidesen *et al.*, 2013), which
202 may have contributed to shift the fundamental climatic niche towards somewhat colder
203 conditions due to founder events from cold-adapted populations.

204 Conversely, total vascular plant species richness in the Alps is much higher than in
205 Fennoscandia (Lenoir *et al.*, 2010), generating different competition regimes, which may
206 result in different realised climatic niches between populations in the Alps and in
207 Fennoscandia (Pellissier *et al.*, 2013). The greater the number of species in a region, the
208 narrower the species' realised niche width should theoretically be (regional diversity-niche
209 width hypothesis; MacArthur, 1972), due to contraction at the least stressful margin of the
210 environmental gradient. This would lead to the expectation of narrower realised niches
211 through contraction of the warmer part of the range, resulting in the species being observed
212 towards colder conditions in the Alps.

213 Finally, potential differences in the realized climatic niche between distant populations
214 of the same species are likely to be related to its life-history traits. For instance, we can
215 assume that a generalist or opportunistic species is able to occupy wider fundamental niches
216 and thus can more easily adjust its realised niche, depending on the region, than a specialist or
217 late-successional species whose fundamental niche is too narrow to allow large shifts of the
218 realised niche (Pearman *et al.*, 2008). But we could also assume that disjunct populations of a
219 dispersal-limited species are likely to be isolated from gene flow thus favouring local
220 adaptation and increasing the chances for strong differences between their respective realized
221 climatic niches compared with distant populations of a widespread species not limited by its

222 dispersal abilities. Linking the extent to which two distant populations of the same species
223 have similar realized climatic niche (cf. niche overlap) with traits is therefore informative.

224 **Knowing all this**, we aim to answer five questions: (i) Do the realised climatic niches of
225 species native to both the Alps and Fennoscandia differ between the two regions? (ii) To what
226 extent does the realised climatic niche of a species overlap between the two regions? (iii) Is
227 there a trend towards wider (supporting the genetic diversity hypothesis) or narrower
228 (supporting the diversity-niche width hypothesis) realised climatic niches in the Alps? (iv)
229 Are the realised climatic niches of species shifting towards warmer (supporting the genetic-
230 diversity hypothesis) or colder (supporting the diversity-niche width hypothesis) conditions in
231 the Alps? (v) How much of the variation in species' niche overlap can be explained by
232 species' **life-history traits**?

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MATERIALS AND METHODS

Study area and species pool

The study area covers two geographically distant regions: the European Alps as delineated by the Alpine Convention Boundary (<http://www.alpconv.org/>) and Fennoscandia as delineated by the administrative boundaries of Norway, Sweden, Finland and Denmark (excluding islands such as the Svalbard archipelago) (Fig. 1(a)). To select the list of terrestrial vascular plant species occurring in both study regions, we assembled more than 70,000 vegetation plots from the most recent versions of two different European vegetation databases: (i) the Alps vegetation database (AVD, $n = 31,524$, <http://www.givd.info/ID/EU-00-014>) (Lenoir *et al.*, 2012) and (ii) the Nordic vegetation database (NVD, $n = 41,785$, <http://www.givd.info/ID/EU-00-018>) (Lenoir *et al.*, 2013). A total of 888 species occurred in both databases. This corresponds to the common species pool obtained by matching species lists from AVD and NVD (see Appendix S1 in Supporting Information).

Because most of the 888 species common to the Alps and Fennoscandia also occur outside this study area, it is likely that the realised climatic niche of at least one of the two studied populations will be truncated thus potentially affecting our results. To account for such effects, we screened each of the 888 species' range maps (Comparative Chorology of the Central European Flora; Meusel *et al.*, 1965, 1978, 1992) to subdivide this pool into two subsets: (i) species having disjunct distribution restricted to mountainous areas or Arctic-alpine tundra with at least one population strictly confined to the Alps and another strictly confined to Fennoscandia, hereafter referred as the "restricted" group for which the entire realised climatic niche is likely to be captured ($n = 105$); and (ii) species having either a contiguous distribution between the Alps and Fennoscandia, with these simply constituting distant populations, or a patchy distribution not restricted to mountainous areas or Arctic-alpine tundra with populations extending outside the Alps or Fennoscandia, hereafter referred

258 as the “enlarged” group for which the realised climatic niche will be truncated in at least one
259 of the two studied regions ($n = 783$). We analysed and reported all our results separately for
260 the restricted and enlarged groups.

261

262 **Climatic data**

263 We used nine bioclimatic variables expected to have direct ecophysiological impacts on plant
264 distributions (Prentice *et al.*, 1992). Three related to temperature: growing-degree-days above
265 0°C (GDD); absolute minimum temperature (AMT); and continentality index (CI). The
266 remaining six were water-related variables: annual aridity index (AI: note that higher AI
267 values represent more humid conditions); annual potential evapotranspiration (PET); annual
268 actual evapotranspiration (AET); Priestley-Taylor alpha coefficient (ALPHA = AET/PET);
269 water balance over the year (sum of monthly precipitation minus monthly potential
270 evapotranspiration) (WBAL); and soil water content of the most stressful month (SWC). All
271 variables were derived from globally available datasets at a spatial resolution of 30 arc
272 seconds which is less than one kilometre at the equator: WorldClim (Hijmans *et al.*, 2005:
273 <http://www.worldclim.org/>) and CGIAR (CGIAR-CSI: <http://www.cgiar-csi.org/>) (Appendix
274 S2).

275

276 **Presence and absence data**

277 For each of the 888 species, we followed a set of data-handling procedures (Appendix S3).
278 We first compiled geo-referenced presence records by querying AVD, NVD, and the Global
279 Biodiversity Information Facility (GBIF: <http://www.gbif.org/>) and geo-referenced absence
280 records from AVD and NVD. Presence (AVD, NVD, GBIF) and absence (AVD, NVD) data
281 were then aggregated across the study area at a 1-km resolution (cf. climatic grids) to compute
282 a probability of presence (pr) of the focal species per grid cell by dividing the number of

283 presence records found within a given grid cell by the total number of presence and absence
284 records of that species in it. Note that we could not compute a *pr* value for grid cells without
285 information on presence and absence data and thus grid cells lacking presence and absence
286 data were not used in the subsequent analyses. Finally, we subsampled all available grid cells
287 for which a *pr* value had been computed to limit spatial autocorrelation issues and to balance
288 sampling effort between regions (**Appendix S3**).

289

290 **Trait data**

291 To explain the observed differences in the realised climatic niche of species between the Alps
292 and Fennoscandia, we assembled data on species' traits according to their biogeography,
293 ecology, and biology. For biogeographic data, we extracted information on chorology (i.e.
294 biogeographic origins) from Landolt *et al.*, (2010). For ecological data, we used Ellenberg
295 indicator values (Ellenberg *et al.*, 1991) for light (L), soil nutrients (N), soil pH (R), soil
296 moisture (F), temperature (T), and continentality (K). For biological data, we collected data
297 on plant height, specific leaf area (SLA), diaspore mass and Raunkiaer's life-forms from
298 several sources (**Appendix S1**). Diaspore mass and plant height values were log-transformed
299 prior to analyses.

300

301 **Data analyses**

302 To compare the realised climatic niches between two distant populations of the same species,
303 we used two complementary approaches. First, we tested for any overall regional differences
304 (region effect) in the realised climatic niche of each species using **an environmental niche**
305 **modelling (ENM) approach based on** generalised linear models (GLMs). Second, we used a
306 bivariate analysis based on the two most statistically significant climatic layers found in the
307 GLMs, including one energy-related variable (GDD) and one water-related variable (AI) to

308 quantify the degree of niche overlap and niche shifts between regions for each species. Once
309 differences in the realised climatic niches between **distant** populations in the Alps and
310 Fennoscandia were assessed, we linked species' niche overlap **values to species' life-history**
311 **traits**.

312

313 *Region effect*

314 For each of the 888 species, all 1-km² grid cells retained after the selection process
315 (**Appendix S3**) were split into two subsets: one subset for model development (training
316 dataset) including 2/3 of the selected grid cells and one subset for model validation (test
317 dataset) consisting of the remaining 1/3 of the grid cells. Because of this splitting, 550
318 species, **of which 65 belong to the restricted group**, were sufficiently frequent (i.e. having a *pr*
319 value exceeding 0 in at least 50 grid cells within each region of the training dataset) to be
320 retained for model development.

321 For each of the 550 selected species, we ran a series of GLMs for proportion data with
322 *pr* as the dependent variable to select the most influential bioclimatic variables (GDD, AMT,
323 CI, PET, AET, WBAL, ALPHA, AI, SWC). We also evaluated the effect of the region
324 variable (Alps vs. Fennoscandia) and the potential interaction with any of the selected climatic
325 variables in the models (**Appendix S4**). Finally, we updated the model by incorporating the
326 total number of presence/absence records per grid cell as a covariate to correct for the effect
327 of sampling effort across the study area and checked for overdispersion. In those cases where
328 overdispersion was found a quasi-binomial error function was used.

329 We then evaluated the quality of the GLM using the test dataset for each species and the
330 area under the receiver-operating characteristic curve (AUC) ranging from 0.5 (poor models)
331 to 1 (perfect models) (Swets, 1988). We decided to retain only the best models by focusing on
332 species that had AUC values greater than 0.8 for further comparisons of the realised climatic

333 niche between regions. A total of 389 species, of which 31 belong to the restricted group, out
334 of 550 fulfilled this requirement (**Fig. S5 in Appendix S5**). To transform the *pr* into
335 presence/absence data (**Fig. S3 in Appendix S3**), we computed the sensitivity–specificity sum
336 maximiser criterion (MST) based on the test dataset (Jiménez-Valverde & Lobo, 2007).

337 Finally, for each of the 389 species, we merged the training and test datasets to
338 recalibrate the final model based on all the available data and extracted several model
339 statistics (coefficient estimates, *p*-values, AIC, null deviance, residual deviance). To test for
340 differences in the realised climatic niche of a given species, we focused on the significance of
341 the region effect and its interaction with the climatic variables (**Fig. 2 and Fig. S6 in**
342 **Appendix S6**).

343

344 *Observed niche overlap*

345 For each of the 389 species, we estimated niche overlap between the two regions within the
346 bi-dimensional climatic space defined by GDD and AI (**Fig. 1(b)**). These two variables were
347 selected since they were important for many of our species. We divided the bi-dimensional
348 climatic space into a grid of 500×500 cells bounded by the minimum and maximum values
349 of GDD (first axis) and AI (second axis) (**Fig. 1(b), Appendix S7**). For each region
350 separately, we mapped the occurrence data ($pr > 0$) in the bi-dimensional space defined by the
351 subset of grid cells in which the focal species was recorded as present ($pr > 0$) or absent ($pr =$
352 0) to map its realized climatic niche within the available climatic space. We applied a kernel
353 smoother to standardise species densities across the bi-dimensional climatic space
354 independently of the sampling effort and the resolution in the climatic space (**Fig. S7 in**
355 **Appendix S7**, Broennimann *et al.*, 2012).

356 We used Schoener's *D* similarity index (Schoener, 1970; Broennimann *et al.*, 2012) (see
357 formula in **Appendix S7**) to compute the observed niche overlap (D_{obs}). The *D* index was

358 calculated on the above-mentioned smoothed density of occurrences, (i.e. observed niche
359 overlap, D_{obs}), and varies from 0 (no overlap) to 1 (complete overlap). We assessed D_{obs} not
360 only across the overall climatic space including both analogue and non-analogue climates, but
361 also within the analogue climatic space alone (**Fig. 1**). *Assessing D_{obs} across the whole
362 climatic space allows to account for non-analogue climatic conditions that may become
363 analogue with future climate change, whereas focusing on the analogue climatic space solely
364 enables D_{obs} assessment to be independent of simple changes in climatic conditions thus
365 precluding to mix up apples and pears. In theory D_{obs} should be higher when focusing on the
366 analogue climatic space alone with difference in D_{obs} values between the analogue (cf.
367 baseline) and the overall climatic space indicating to what extent non-analogue climates
368 matter for D_{obs} .* To compute D_{obs} across the analogue climatic space alone, we quantified for
369 each species the part of the bi-dimensional climatic space that was shared by the two regions
370 (i.e., analogue climates) (**Fig. S7 in Appendix S7**) and then D_{obs} was computed once again as
371 above using Schoener's D similarity index (Schoener, 1970; Broennimann *et al.*, 2012).

372 *Niche overlap test*

373 To assess to what extent the realized climatic niche of a given species is conserved between
374 the Alps and Fennoscandia, we compared its empirical D_{obs} value to its simulated niche
375 overlap (D_{sim}) value obtained under a baseline scenario of climatic-niche identity. By baseline
376 scenario, we mean setting and using exactly the same climatic niche model (cf. climatic-niche
377 identity) for each of the two studied populations of the focal species to successively: (i)
378 predict each population distribution in the Alps and Fennoscandia based on climatic
379 conditions solely; (ii) project these spatial predictions into the GDD-AI climatic space; and
380 (iii) compute D_{sim} using the same approach as for D_{obs} (see **Appendix S7** for more details).

381 Comparing a species' D_{obs} value in light of its D_{sim} value help to appreciate how much
382 the realized climatic niche of this focal species is conserved. The lower the D_{obs} value

383 compared with D_{sim} , the greater the niche differentiation between the Alps and Fennoscandia.
384 Note that D_{obs} can be greater than D_{sim} , i.e. the realized climatic niche is more conserved than
385 expected under the climatic-niche identity assumption. On the one hand, D_{sim} can reach low
386 values simply because our simulations account for the potential effects of other climatic
387 variables than the one used to compute D_{sim} (cf. GDD and AI) (**Appendix S7**). On the other
388 hand D_{sim} is based on model predictions that incorporate climatic predictors only whereas D_{obs}
389 relies on empirical data that reflect not only climatic dimensions of the realised niche but also
390 other abiotic and biotic dimensions not considered in our models and which could involve
391 habitat-compensation effects. For these two reasons, it is not that odd to find greater values
392 for D_{obs} than D_{sim} . We used Student's paired t -test to assess the significance of the average
393 difference between D_{obs} and D_{sim} across all species.

394

395 *Niche width and niche optimum*

396 We used two other parameters to assess differences in the realised climatic niche of each of
397 the 389 studied plant species between the two regions: niche width (range of climatic
398 conditions suitable for a species) and niche optimum (maximum probability of presence of a
399 species within its realised climatic niche). Species niche-width and niche-optimum values
400 were computed for both the Alps and Fennoscandia from the observed density of occurrences
401 of a given species within both the overall and analogue climatic spaces.

402 We followed the method of Theodoridis *et al.*, (2013) to compute these parameters and
403 did so for the Alps and Fennoscandia, separately. Species' niche-width and niche-optimum
404 values were assessed by first extracting the scores along GDD and AI of 100 pixels sampled
405 randomly from its bi-dimensional climate space, selecting pixels with a probability according
406 to species' density of occurrences. Once extracted, the inter-decile range (80%) of these 100
407 values along GDD and AI (i.e. niche width) as well as GDD and AI coordinates of the pixel

408 where the species reached its maximum occupancy (i.e. niche optimum) were computed. This
409 randomisation procedure was repeated 100 times and the mean values of the 100 obtained
410 values for niche width and niche optimum for both the Alps and Fennoscandia were retained.
411 We used Student's paired *t*-test to assess the significance of the mean difference in species'
412 niche width and niche optimum between regions.

413

414 *Insights from plant traits*

415 Finally, we used three independent ordinary least square (OLS) regressions to assess how
416 much of the variation in D_{obs} could be explained by plant biogeography, ecology, and biology.
417 First, we fitted D_{obs} against a qualitative variable representing species' biogeographic origins
418 (Arctic-alpine, Asia, Eurasia, Europe, Holarctic, Mediterranean, North America) followed by
419 Tukey's HSD test for *post-hoc* pairwise comparisons of group means. Second, we fitted D_{obs}
420 against all six semi-quantitative Ellenberg indicator values (L, N, R, F, T, K). Third, we fitted
421 D_{obs} against plant growth, photosynthetic performances, and dispersal abilities (plant height,
422 SLA, diaspore mass) as well as Raunkiaer's life-forms. We ran all three models for both D_{obs}
423 computed across the overall climatic space including both analogue and non-analogue
424 climates, but also for D_{obs} computed within the analogue climatic space only.

RESULTS

425

426 Regional differences

427 Among the 31 species belonging to the restricted group and that were retained after the
428 modelling procedure to test for a region effect, only one species (*Epilobium alsinifolium*)
429 showed regional differences in its response curves, namely along the aridity gradient (AI)
430 (Fig. S8 in Appendix S8). Among the remaining 358 species belonging to the enlarged
431 group, only 58 species showed regional differences in their response curves along at least one
432 of the nine studied climatic variables (Table S8 in Appendix S8). Of these 58 species, 29
433 showed regional differences in response to growing degree days (GDD) (Fig. 2(b)), 26 in
434 response to soil water content during the most stressful month (SWC), 8 in response to the
435 aridity index (AI), and 5 in response to the continentality index (CI) (Fig. S8 in Appendix
436 S8).

437

438 Niche overlap

439 Based on the overall climatic space defined by GDD and AI, the observed niche overlap
440 (D_{obs}) for the 31 species belonging to the restricted group was 0.50 on average, ranging from
441 0.16 to 0.59 (Table S9 in Appendix S9). These values were higher, on average, than the D_{obs}
442 values calculated for the 358 remaining species from the enlarged group (mean = 0.42; min =
443 0.02; max = 0.66) (two-sample Student's t -tests, p -value = 0.002) (Table S9 in Appendix
444 S9). The simulated niche overlap (D_{sim}) under the baseline scenario of climatic-niche identity
445 was much lower than D_{obs} for both the restricted (mean = 0.40; min = 0.25; max = 0.52)
446 (paired two-sample Student's t -tests, $n = 27$, p -value $\ll 0.001$) and the enlarged (mean =
447 0.28; min = 0.005; max = 0.7) (paired two-sample Student's t -tests, $n = 195$, p -value \ll
448 0.001) species groups. Among the 58 species that showed regional differences in their
449 response curve along at least one climatic variable (Table S8 in Appendix S8), only 6 species

450 had distant realised climatic niches that overlapped less than under the baseline scenario (D_{obs}
451 $< D_{sim}$): *Alyssum alyssoides*, *Avenula pratensis*, *Carex ericetorum*, *Ranunculus bulbosus*,
452 *Rubus idaeus*, and *Vincetoxicum hirundinaria*. We found similar patterns for the results based
453 on the analogue climatic space solely, except that all niche overlap values were higher (**Table**
454 **S10 in Appendix S10**).

455

456 **Niche width and niche optimum**

457 Irrespective of the species group considered (i.e. restricted vs. enlarged), niche width across
458 the overall climate space was larger in the Alps than in Fennoscandia for GDD (**Figs. 3(a)**
459 **and 3(b)**) and larger in Fennoscandia than in the Alps for AI (**Figs. 3(c) and 3(d)**) (**Table S9**
460 **in Appendix S9**). The same patterns were found for the 31 species of the restricted group
461 when assessing niche width based on analogue climates alone, except that the trend was not
462 significant for AI (p -values = 0.06). However, when assessing niche width based on analogue
463 climates alone for the remaining 358 species of the enlarged group, species' realised climatic
464 niches were larger in the Alps than in Fennoscandia for both variables (**Table S10 in**
465 **Appendix S10**).

466 Niche optima results across the overall climatic space for the 31 species of the restricted
467 group showed no difference, on average, along GDD but a shift towards higher values of AI
468 (more humid conditions) in the Alps compared with Fennoscandia (**Figs. 4(a) and 4(c)**)
469 (**Table S9 in Appendix S9**). For the remaining 358 species of the enlarged group, niche
470 optima were located, on average, towards higher values of both GDD and AI (warmer and
471 more humid conditions) in the Alps than in Fennoscandia, (**Figs. 4(b) and 4(d)**) (**Table S9 in**
472 **Appendix S9**). We found the same patterns when assessing niche optima based on analogue
473 climates alone (**Table S10 in Appendix S10**).

474

475 **Insights from plant traits**

476 Whatever the species group (i.e. restricted vs. enlarged) and the climatic space (whole vs.
477 analogue) considered, we found similar patterns (**Appendices S11 and S12**). For clarity, we
478 only report results based on the full climate space (**Appendix S11**). Species' biogeographic
479 origins of the restricted and enlarged species groups explained 50% vs. 7%, respectively, of
480 the variation in D_{obs} , with Arctic-alpine species showing the highest D_{obs} values and standing
481 out of the other biogeographic groups (**Fig. 5(a) and 5(b)**). Species' ecological indicator
482 values of the restricted and enlarged species groups explained 53% vs. 21%, respectively, of
483 the variation in D_{obs} , with contrasting patterns depending on the species group. For the
484 restricted group, D_{obs} increased with increasing preference for cold temperatures and moist
485 soils (**Fig. 6(a) and 6(c)**). In contrast, for the enlarged group, D_{obs} increased with increasing
486 preference for acid soils and for fertile soils (**Fig. 6(a) and 6(c)**). There was no clear
487 relationship between D_{obs} and species' biological traits (**Appendix S11**).

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DISCUSSION

The realised climatic niche is conserved

Our findings suggest predominant niche conservatism, with only 15% of the 389 studied species displaying regional differences in realised climatic niches. Noteworthy, only one (3%) of the 31 species for which populations are clearly disjunct between the Alps and Fennoscandia showed regional differences in its climatic niche. Additionally, the fact that the observed niche overlap (50%) is higher, on average, than the simulated niche overlap (40%) obtained under a baseline scenario of climatic-niche identity suggests strong niche conservatism. Using a different approach and with a smaller set of plant species ($n = 8$), Martínez-Meyer & Peterson (2006) showed that the current species' distribution in North America predicts well their distribution at the Last Glacial Maximum (LGM) and reciprocally, suggesting an ecological niche conservatism despite changes in climate and environmental conditions over that time period. Our results confirm the general idea that niche conservatism is more likely to be the rule over short to moderate time events (thousands of year or shorter) and support results from previous studies focusing on a limited set of species (Martínez-Meyer & Peterson, 2006; Pearman *et al.*, 2008; Peterson, 2011). Over longer time periods of million to billion years, there is no study testing species niche conservatism, certainly because very few relict species have survived since the Palaeogene/Neogene without involving speciation events. However, many studies have tested phylogenetic niche conservatism between closely related species and found evidence for niche differentiation (see Table 1 in Peterson, 2011).

The observed niche overlap is greater for species with strictly disjunct populations

Niche overlap was higher for species having disjunct distribution with at least one population confined to the Alps and one population confined to Fennoscandia (cf. the restricted group:

513 0.50±0.1) than for species having contiguous or patchy distribution across Europe with
514 populations extending outside the Alps or Fennoscandia (cf. the enlarged group: 0.42±0.1).
515 This difference may stem from the fact that the entire realized climatic niche is likely to be
516 captured in the restricted group whereas in the enlarged group the realized climatic niche will
517 be truncated in at least one of the two studied regions and thus we may underestimate niche
518 overlap for the enlarged group.

519 Considering species' biogeographic affinities, niche overlap was highest for arctic-
520 alpine species (**Fig. 5**), supporting former findings of Pellissier *et al.* (2013), who found a
521 strong conservatism of the low-temperature limit of 26 arctic-alpine plant species.
522 Consistently with their findings that thermal niches are more conserved at cold than at warm
523 limits in arctic-alpine plant species, we found that niche overlap for arctic-alpine plant
524 species increased with increasing preference for cold temperatures and moist soils. On the
525 other hand, species displaying dissimilar realised climatic niche were geographically and/or
526 edaphically widespread species (e.g., *Alyssum alyssoides*, *Calluna vulgaris*, *Carum carvi*,
527 *Fragaria vesca*, *Galeopsis tetrahit*, *Juniperus communis*, *Ranunculus bulbosus*, *Rubus idaeus*,
528 *Vaccinium myrtillus*, *Viburnum opulus*) (**Table S8 in Appendix S8**). This supports the idea
529 that generalist species are tolerant of a wider range of environmental conditions given their
530 often great diversity of phenotypes and thus are more able than a specialist species to respond
531 to regional differences by exploiting a greater diversity of habitats (Colles *et al.*, 2009).
532 Generalist or opportunistic species are able to occupy wider fundamental niches and thus can
533 easily shift their realised niche depending on the region, leading to a lower niche overlap than
534 for a specialist or late-successional species whose fundamental niche is too narrow to allow
535 large shifts of the realised niche (Pearman *et al.*, 2008). This contradicts recent findings from
536 Early and Sax, (2014), who compared native vs. naturalised ranges of the same species and
537 found greater disequilibrium (cf. lower niche overlap) for species with native ranges that are

538 small and occupy a narrow range of climatic conditions. However and as suggested by Early
539 and Sax (2014), the stronger climatic disequilibrium for range-restricted species is likely due
540 to non-climatic factors such as dispersal and biotic factors constraining the native range
541 whereas in the naturalised range especially the latter biotic constraints may be alleviated (cf.
542 enemy-release hypothesis), thus leading to strong climatic disequilibrium. Here, range-
543 restricted species are arctic-alpine species whose distribution is chiefly constrained by
544 climatic factors and less so by biotic factors, which could explain such discrepancy.

545 Niche overlap also increased as plant species prefer acid grounds. Interestingly,
546 siliceous bedrock predominates across Fennoscandia and calcareous bedrock is rare and local.
547 Thus, acidic soils developed rapidly across Fennoscandia soon after deglaciation (e.g., Boyle
548 *et al.*, 2013), leading today to a larger pool of acidophilous species in Fennoscandia than in
549 the Alps (Lenoir *et al.*, 2010). Therefore, in comparison to calciphilous species, postglacial re-
550 colonisation of acidophilous species in Fennoscandia might have been less constrained by
551 dispersal limitation, leading to greater niche overlap with their distant populations in the Alps.

552 In brief, the regional imprint on of the Quaternary climate changes on is weak and
553 the realised climatic niches of terrestrial vascular plants seem largely conserved. This is
554 particularly true for specialist species like Arctic-alpine plants.

555

556 **The realised climatic niche is wider in the Alps**

557 Despite the realised climatic niche being globally conserved, we find regional differences
558 trended towards wider niches in the Alps than in Fennoscandia (**Fig. 3**), especially when
559 constraining our analyses to the analogue climatic space (**Table S9 in Appendix S9**). This
560 suggests that species have filled a greater proportion of their fundamental climatic niche in the
561 Alps and runs counter to MacArthur's (1972) hypothesis for island biogeography, which
562 proposes that species' realised-niche width is constrained by the size of the regional species

563 pool so that more intense competition in species-rich islands should lead to narrower realised
564 niches. The same reasoning for mainland biogeography does not seem to hold. Our findings,
565 however, are consistent with a recent study on the realised-niche width of plants which
566 concludes that competition from ecologically similar species plays a relatively minor role in
567 species' establishment in different habitat types (Manthey *et al.*, 2011).

568 The wider realised climatic niches in the Alps support our hypothesis that greater
569 genetic diversity due to different refugia close to the Alps, corresponding to greater habitat
570 heterogeneity, increases the likelihood for a species to fill its fundamental climatic niche.
571 Many refugia provided ice-free areas with various habitat conditions where high elevation
572 plants could survive the glacial stages in the Alps (Schönswetter *et al.*, 2005). This has likely
573 played an important role in the intraspecific diversification of many alpine plants in the Alps
574 (Alvarez *et al.*, 2009), and is also reflected by the higher levels of genetic diversity within
575 species in the Alps than Fennoscandia (Eidesen *et al.*, 2013). In contrast, cryptic glacial
576 refugia in the north (Stewart *et al.*, 2010) were probably confined to areas outside the margin
577 of the massive Fennoscandia ice-sheet (Birks, 1994) and fewer, smaller, genetically
578 depauperate populations survived, with these populations contributing little to total gene pool
579 after post-glacial population recolonisation (Edwards *et al.*, 2014), thus resulting in lower
580 genetic diversity and narrower realised climatic niches in modern populations. **However, such**
581 **differences in realised niches width may also result from time-lagged range expansion**
582 **following post-glacial warming and disequilibrium with contemporary climate for populations**
583 **in Fennoscandia (Svenning & Skov, 2004).**

584

585 **The realised climatic niche is located towards warmer and wetter conditions in the Alps**

586 The large and diverse set of terrestrial vascular plants occurring in two distant regions in the
587 present study show that species generally have their climatic optima in warmer **and more**

588 **humid** conditions in the Alps than in Fennoscandia, irrespective of the climatic space
589 considered (whole or analogue). At least two different processes could explain these inter-
590 regional differences.

591 First, shifts in the position of the fundamental niche itself may be involved through local
592 adaptation (Davis *et al.*, 2005; Leimu & Fischer, 2008). Results from common garden
593 experiments, where species' populations from different geographic areas are together in
594 several climates, reveal local adaptation of most tree and herbaceous plant species to their
595 local home environments compared to the foreign environments (Davis *et al.*, 2005; De
596 Frenne *et al.*, 2011; Alberto *et al.*, 2013).

597 Second, species may change their optimum position along one climatic axis (e.g.,
598 growing degree days or aridity index) of the *n*-dimensional niche hypervolume (*sensu*
599 Hutchinson 1957) to compensate for differences in local conditions other than climatic
600 factors. It has been shown that vascular plant species can spatially shift their realized-niche
601 optima for soil nutrients and pH (Diekmann & Lawesson, 1999; Wasof *et al.*, 2013). We did
602 not account for this process in our analyses (e.g. soil pH or land-use), thus it could be a
603 confounding...?

604 We conclude that the realised climatic niche of terrestrial vascular plants that
605 successfully recolonised northern Europe in the last glacial-interglacial cycle has largely been
606 conserved and that this is especially true for specialist species like arctic-alpine plants and
607 species less constrained by dispersal limitation. This has important consequences for
608 predicting future biodiversity under climate change. Notably, the basic assumption that
609 species' realised climatic niche is constant in space and time (thousands of years) seems to be
610 valid to a large extent. Indeed, if the aim is to track the geographic distribution of species with
611 low dispersal limitations this might well work. However, we also show that regional
612 differences in niche width and optimum are rather common. Hence, if the aim is to track

Wasof et al.

613 precisely the geographic position of some key species distribution parameters (range limit or
614 center), then the basic assumption of species distribution models is likely to be flawed, simply
615 because it does not account for regional subtleties in niche width and optimum values.

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BIOSKETCHES

Safaa Wasof is a PhD student at Jules Verne University of Picardie in France and is interested in plant community ecology and in how plant communities are affected by contemporary environmental changes. SW prepared the data, ran the analyses, interpreted the results, and wrote the first draft of the manuscript; JL designed the study, provided part of the data, analysed the data and interpreted the results; PAA, GA, VB, KAB, HJBB, HHB, CJD, MD, SD, MD, RE, JCG, BJG, JAG, AG, KK, ML, AM, BN, AO, HP, VR, SR, SMS, FHS, JS, WT, LUT, VV, LGV, RV, PV, WW, TW, NEZ, and JK, provided the data; GD, WT, AG, HJBB, IGA, MD, KH, SD, RV, JAG, WSA, VV, RE, JCS, TW, WW, MM, MZ, and JCG contributed to the design of the study and to the interpretation of the results. All authors contributed substantially to elaborate the final version of the manuscript.

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FIGURE LEGENDS

Figure 1 Delineation of the two study regions (**a, b**), i.e. the Alps in red and Fennoscandia in blue, as well as maps showing the predicted presence-absence distribution (obtained by using a species-specific threshold value based on the sensitivity–specificity sum maximiser criterion (MST) (see explanations related to model evaluation in the section on data analyses in the main text) to convert probabilities of presence into presence (1) and absence (0) data) and realised climatic niches of *Dryas octopetala* and *Fragaria vesca* (**b, c, d, e**) across both the studied geographical space (**a, c, e**) and the studied bi-dimensional climatic space represented by growing degree days above 0°C (GDD) and the aridity index (AI) (**b, d, f**). The intersection of climatic conditions (GDD and AI) shared by both the Alps and Fennoscandia corresponds to the analogue climatic space whereas climatic conditions unique to the Alps or Fennoscandia constitute the non-analogue climatic space. Climatic conditions outside the analogue and non-analogue climatic spaces are not available within the study area. The warm and cold color scales in the GDD-AI space represent kernel densities (cf. the realised climatic niches) for populations of both *Dryas octopetala* (**d**) and *Fragaria vesca* (**e**) in the Alps and Fennoscandia, respectively. Maps are depicting the digital terrain model (DTM) from the Shuttle Radar Topography Mission (SRTM) at 1-km resolution and projected into the ‘ETRS89 / ETRS-LAE; code EPSG: 3035’ projection system. *Dryas octopetala* is a typical Arctic-alpine plant with a strictly disjunct distribution across Europe and which populations in the Alps and Fennoscandia are confined to mountainous areas or Arctic-alpine tundra (cf. the “restricted” group). *Fragaria vesca* is a widespread plant which distribution is patchy across Europe but not necessarily confined to mountainous areas or Arctic-alpine tundra (cf. the “enlarged” group).

819 **Figure 1** Delineation of the two study regions (**a, b**), i.e. the Alps in black and Fennoscandia
820 in dashed, as well as maps showing the predicted presence-absence distribution (in grey,
821 obtained by using a species-specific threshold value based on the sensitivity–specificity sum
822 maximiser criterion (MST) (see explanations related to model evaluation in the section on
823 data analyses in the main text) to convert probabilities of presence into presence (1) and
824 absence (0) data) and realised climatic niches of *Dryas octopetala* and *Fragaria vesca* (**b, c**,
825 **d, e**) across both the studied geographical space (**a, c, e**) and the studied bi-dimensional
826 climatic space represented by growing degree days above 0°C (GDD) and the aridity index
827 (AI) (**b, d, f**). The intersection of climatic conditions (GDD and AI) shared by both the Alps
828 and Fennoscandia corresponds to the analogue climatic space whereas climatic conditions
829 unique to the Alps or Fennoscandia constitute the non-analogue climatic space. Climatic
830 conditions outside the analogue and non-analogue climatic spaces are not available within the
831 study area. The colour scales in the GDD-AI space represent kernel densities (cf. the realised
832 climatic niches) for populations of both *Dryas octopetala* and *Fragaria vesca* in the Alps
833 (grey scales) and Fennoscandia (from white in the center to black), respectively. Maps are
834 depicting the digital terrain model (DTM) from the Shuttle Radar Topography Mission
835 (SRTM) at 1-km resolution and projected into the ‘ETRS89 / ETRS-LAE; code EPSG: 3035’
836 projection system. *Dryas octopetala* is a typical Arctic-alpine plant with a strictly disjunct
837 distribution across Europe and which populations in the Alps and Fennoscandia are confined
838 to mountainous areas or Arctic-alpine tundra (cf. the “restricted” group). *Fragaria vesca* is a
839 widespread plant which distribution is patchy across Europe but not necessarily confined to
840 mountainous areas or Arctic-alpine tundra (cf. the “enlarged” group).

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843 **Figure 2** Response curves of *Dryas octopetala* (**a**) and *Fragaria vesca* (**b**) along the growing
844 degree days above 0°C (GDD) in both the Alps (dashed curve) and Fennoscandia (solid
845 curve), according predictions from the final model (see the section on data analyses in the
846 main text) after model calibration and model selection (**Appendix S4**) as well as model
847 evaluation (**Appendix S5**). *Dryas octopetala* is a typical Arctic-alpine plant with a strictly
848 disjunct distribution across Europe and which populations in the Alps and Fennoscandia are
849 confined to mountainous areas or Arctic-alpine tundra (cf. the “restricted” group). *Fragaria*
850 *vesca* is a widespread plant which distribution is patchy across Europe but not necessarily
851 confined to mountainous areas or Arctic-alpine tundra (cf. the “enlarged” group).

852

853 **Figure 3** Histograms showing the differences between species’ realised-niche width in Alps
854 and species’ realised-niche width in Fennoscandia across the overall climatic space (i.e. both
855 analogue and non-analogue climatic spaces together) among the 31 species belonging to the
856 restricted group (i.e. species that have disjunct distribution between two study regions; **a**, **c**)
857 and among the 358 species belonging to the enlarged group (i.e. species that are widespread
858 across Europe and found in both regions; **b**, **d**) along the growing degree days above 0°C
859 (GDD) (**a**, **b**) and aridity index (AI) (**c**, **d**) gradients. The dotted and solid vertical lines show
860 the mean differences and the zero values, respectively. *P*-values calculated from paired two-
861 sample Student’s *t*-tests were significant in all cases and means that the niche breadths are
862 significantly different between the two study regions. *P*-values are given as: *** <0.001; **
863 <0.01; * <0.05.

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865

866 **Figure 4** Histograms showing the differences between species’ realised-niche optimum in
867 Alps and species’ realised-niche optimum in Fennoscandia across the overall climatic space

868 (i.e. both analogue and non-analogue climatic spaces together) among the 31 species
869 belonging to the restricted group (**a, c**) and among the 358 species belonging to the enlarged
870 group (**b, d**) along the growing degree days above 0°C (GDD) (**a, b**) and aridity index (AI) (**c,**
871 **d**) gradients. The dotted and solid vertical lines show the mean differences and the zero
872 values, respectively. Significant *P*-values, calculated from paired two-sample Student's *t*-tests,
873 means that the niche optima are significantly different between the two study regions. *P*-
874 values are given as: *** <0.001; *n.s.* non significant.

875

876 **Figure 5** Box plots showing the distribution of observed niche overlap values across the
877 overall climate space (i.e. both analogue and non-analogue climatic spaces together)
878 according to species' biogeographic groups when considering the 31 species belonging to the
879 restricted group (**a**) and the 358 species belonging to the enlarged group (**b**). Chorology is a
880 qualitative variable representing species' biogeographic origins: Arctic-alpine (Ar.-al.), Asia,
881 Eurasia (EU), Europe (EUR), Holarctic (Hol.), Mediterranean (Med.), North America (NA)
882 (Landolt *et al.*, 2010). Numbers in brackets correspond to the number of species in each
883 biogeographic group. Box plots show median, 25 and 75% percentiles, whiskers extend to 1.5
884 x interquartile range, and points are values lying outside this range.

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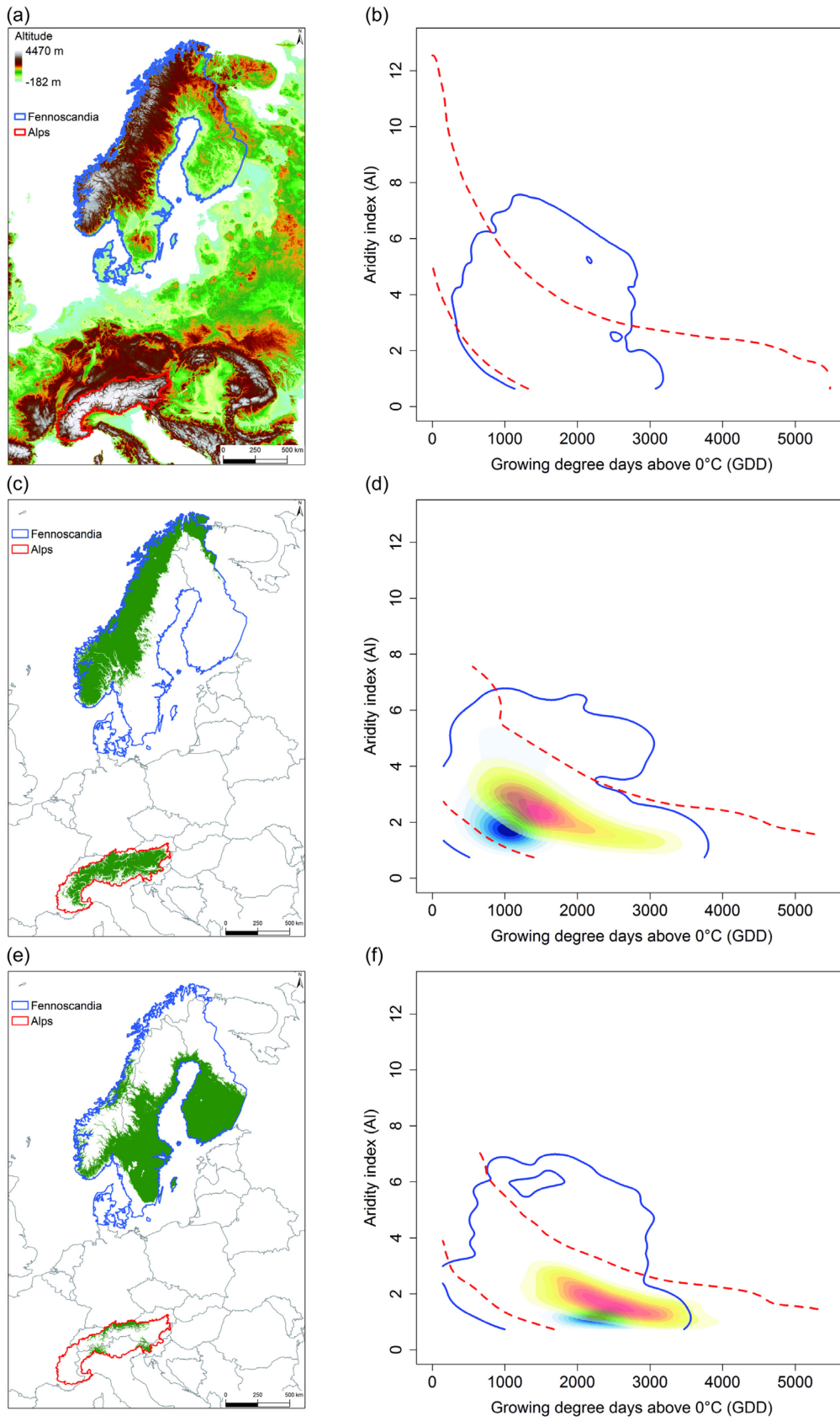
886 **Figure 6** Scatter plots showing the distribution of the observed niche overlap across the
887 overall climate space (i.e. both analogue and non-analogue climatic spaces together) among
888 the 31 species belonging to the restricted group (**a, b**) and among the 358 species belonging to
889 the enlarged group (**c, d**) along Ellenberg gradients for temperature (T) (**a**), soil moisture (F)
890 (**b**), soil nutrient (N) (**c**), and soil acidity (R) (**d**). Trend line obtained using a univariate linear
891 regression when only the ecological gradient in question was considered as the independent

Wasof et al.

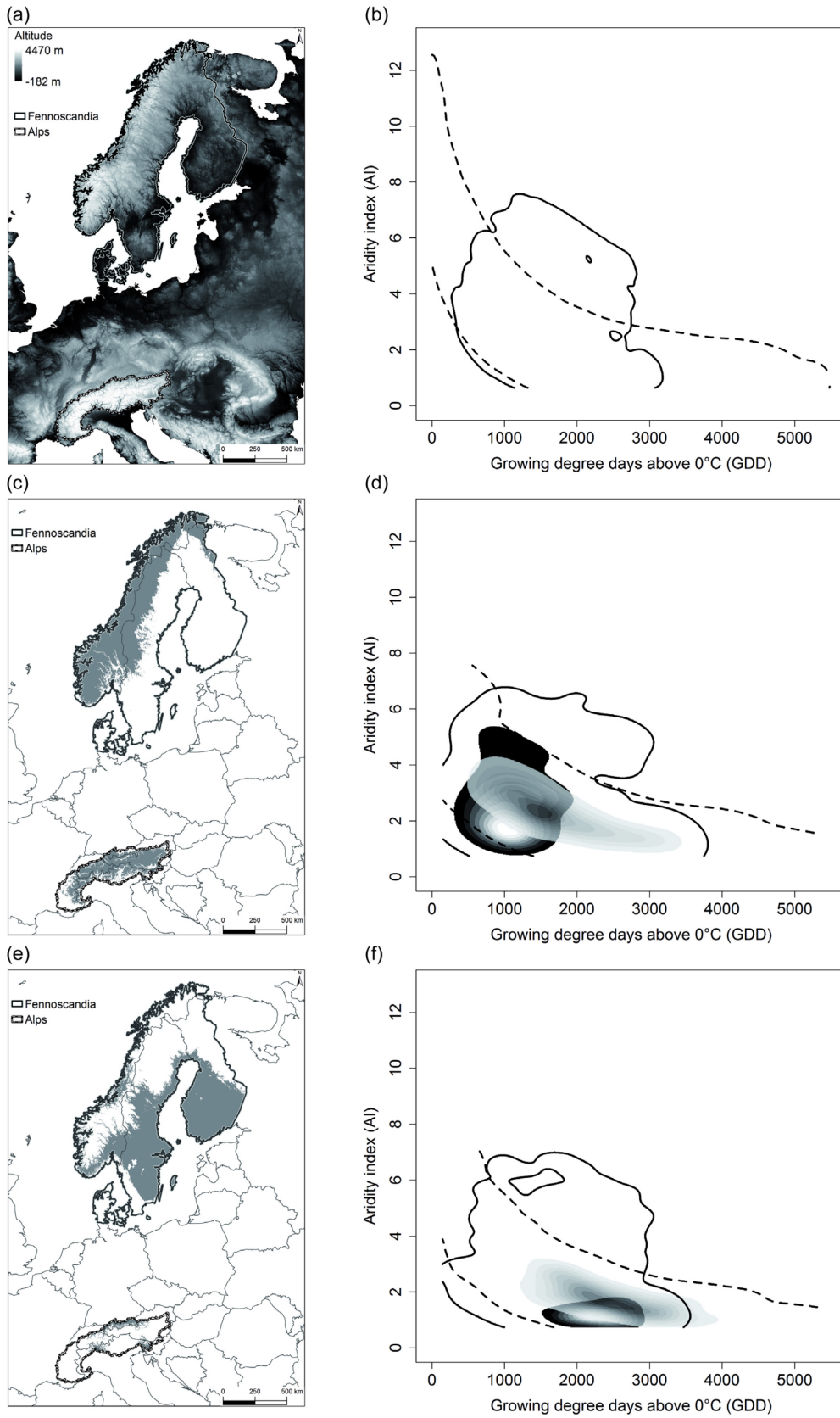
892 variable and the observed niche overlap as the response variable. For a complete multivariate
893 linear regression model, see **Appendix S11**.

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895 **Fig. 1**

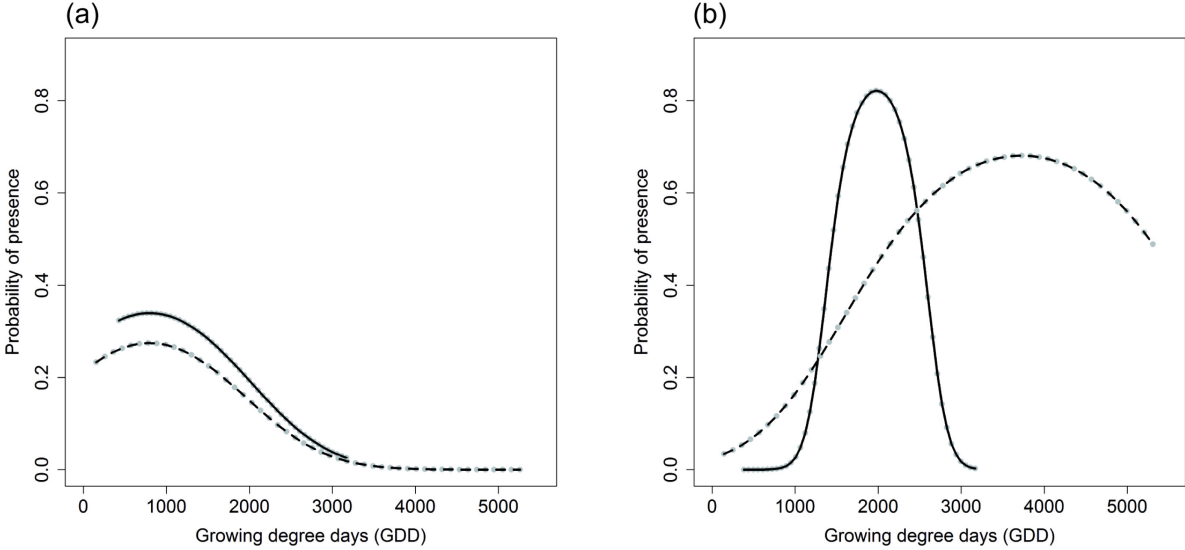


897 **Fig. 1**



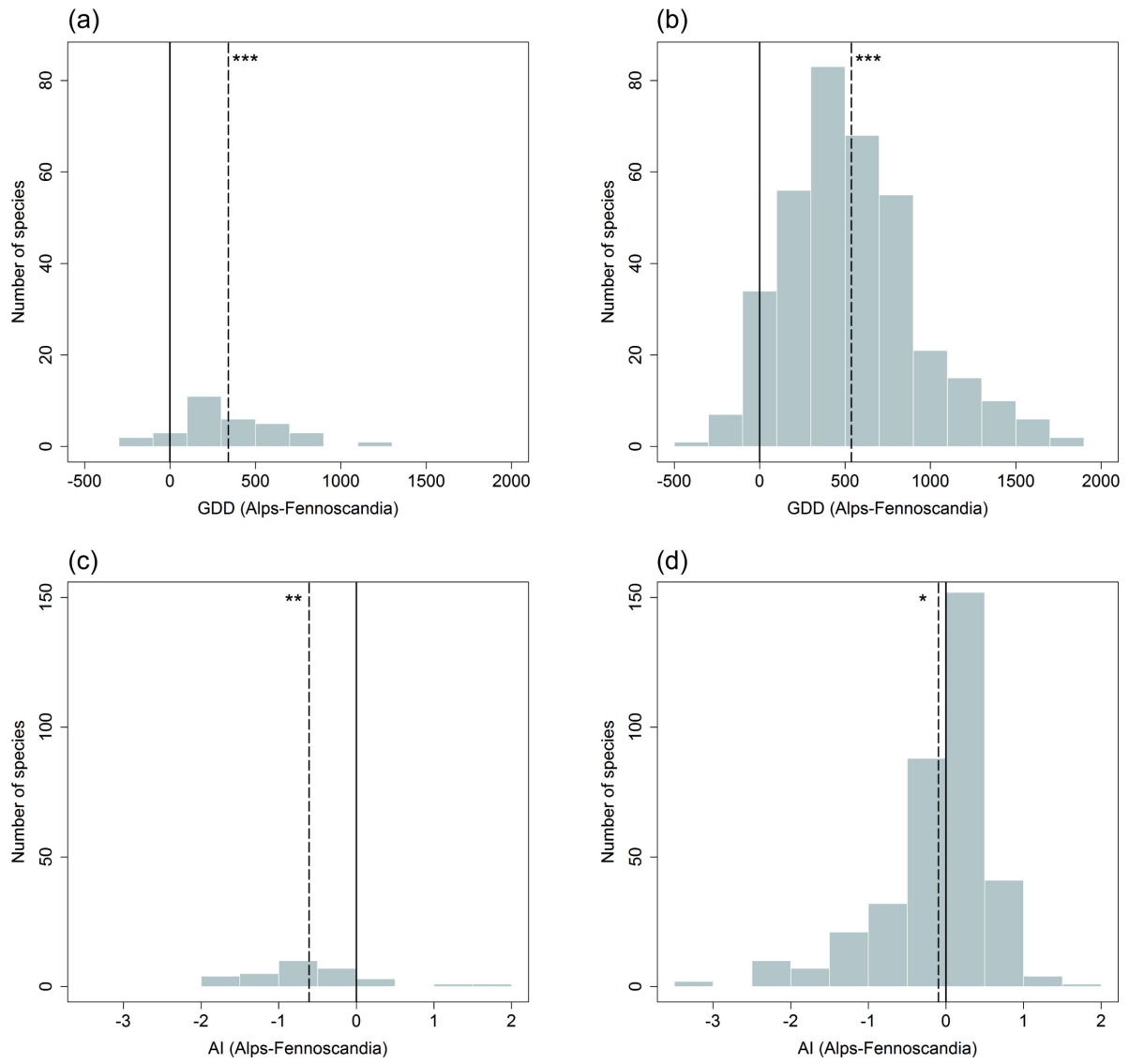
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899 **Fig. 2**



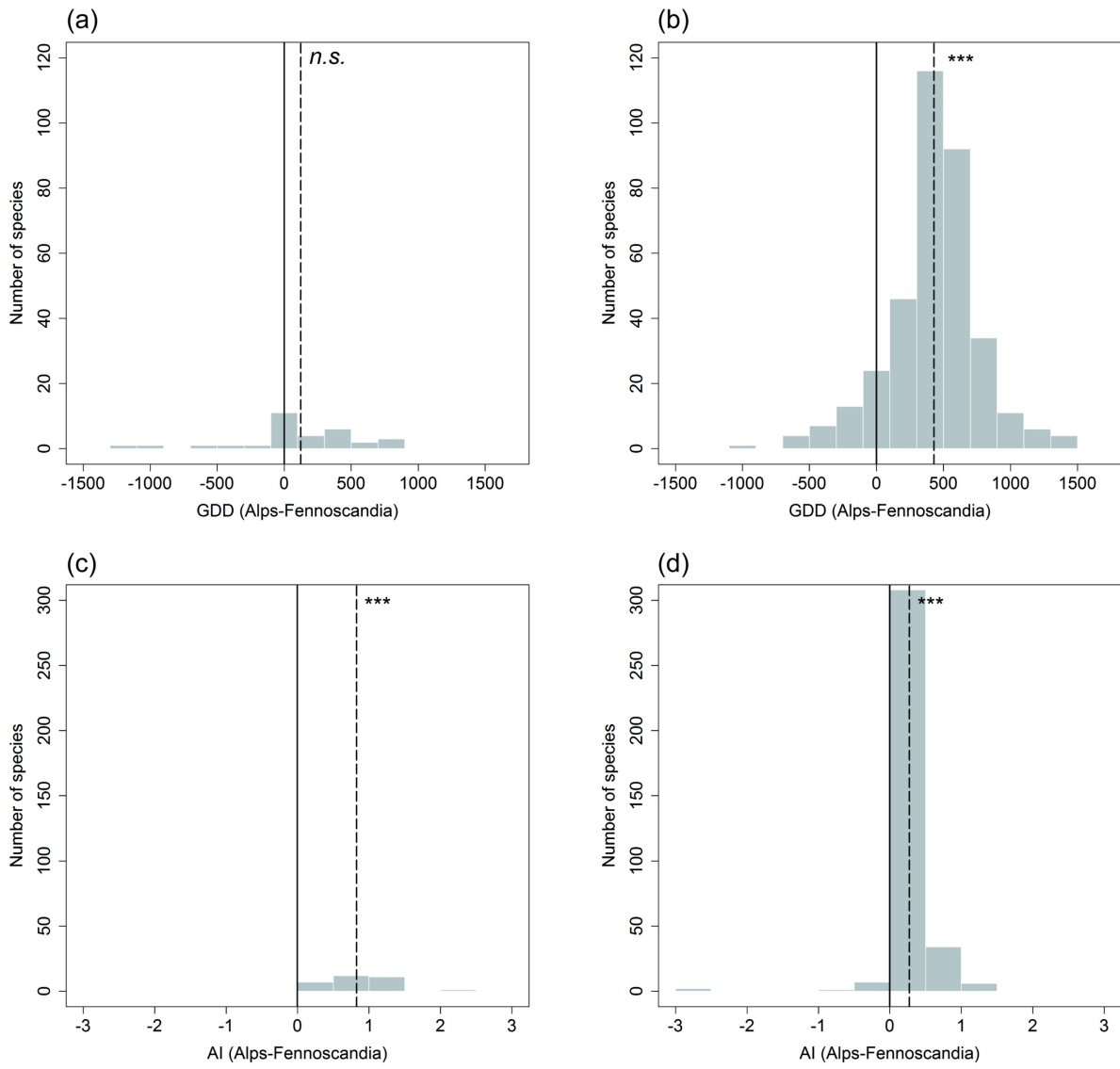
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901 **Fig. 3**



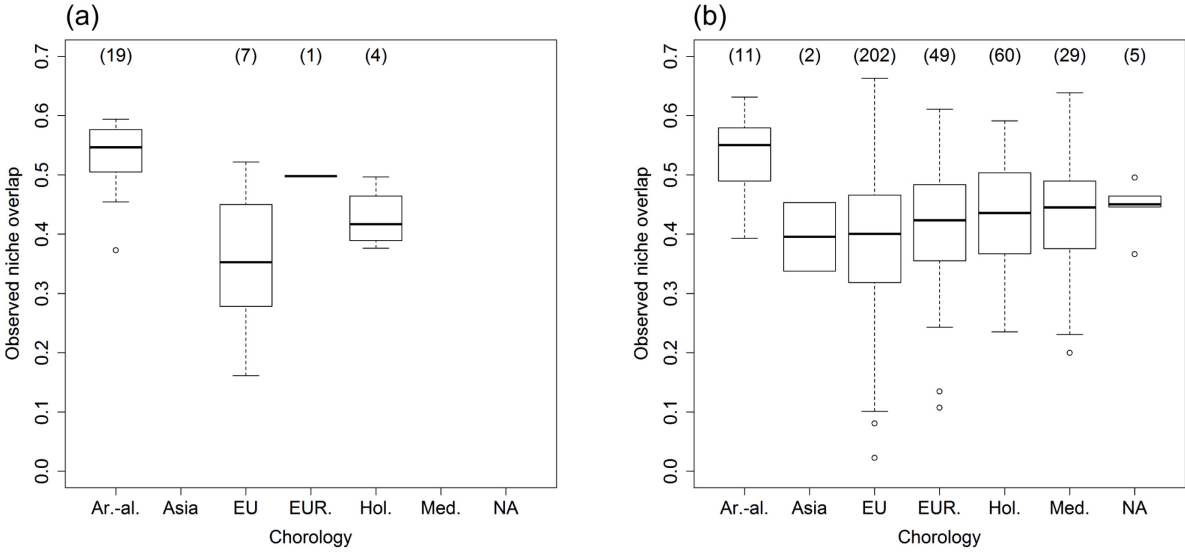
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903 **Fig. 4**



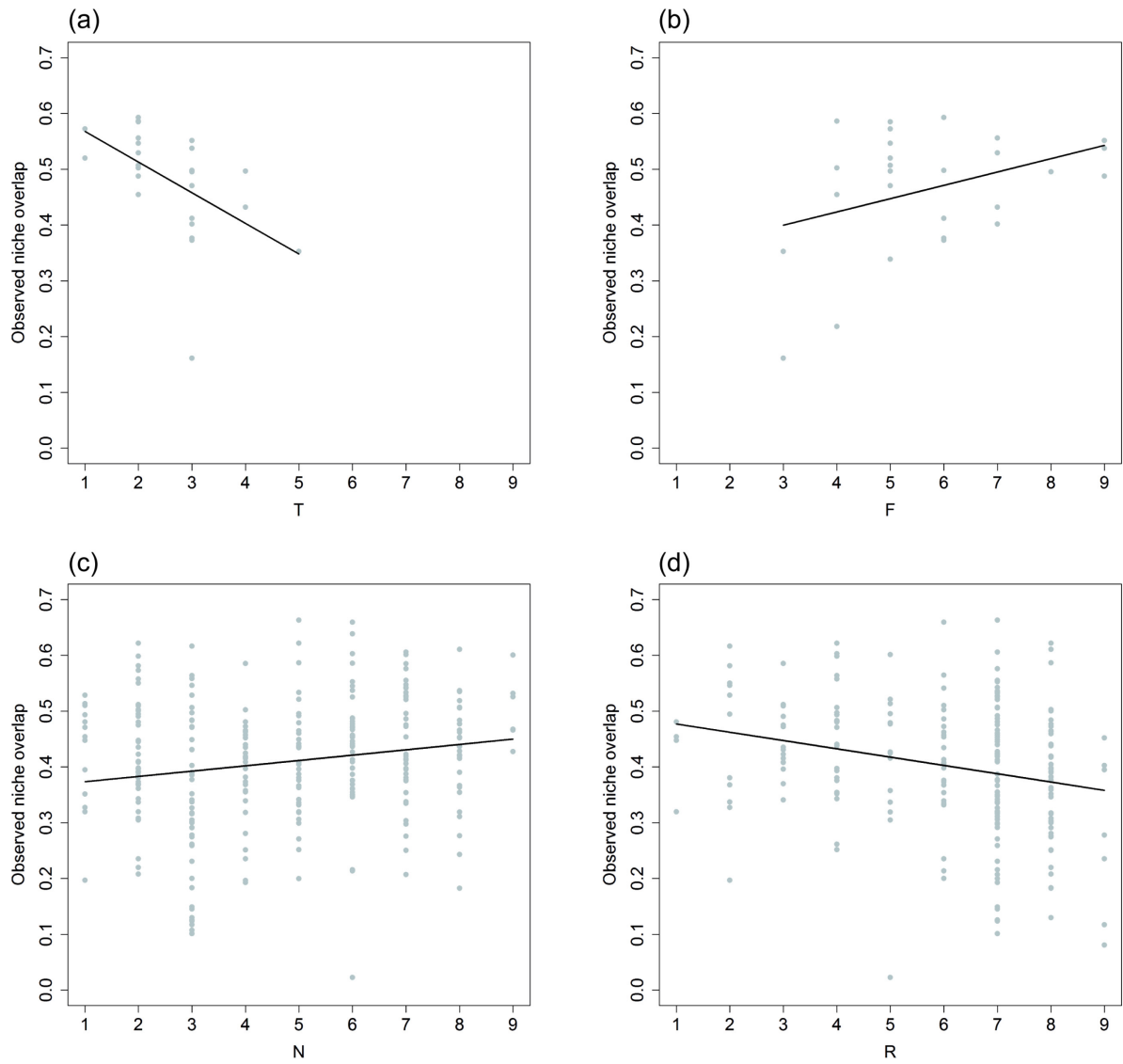
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905 **Fig. 5**



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907 **Fig. 6**



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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Pool of terrestrial vascular plant species common to the Alps and Fennoscandia.

Appendix S2 Details about the nine climatic variables considered in this study.

Appendix S3 List of data-handling manipulations on presence and absence data of each of the 888 terrestrial vascular plant species belonging to the common species pool.

Appendix S4 Model calibration and model selection.

Appendix S5 Model evaluation.

Appendix S6 Region effect.

Appendix S7 Niche overlap.

Appendix S8 Full results on region effect.

Appendix S9 Full results on niche overlap, niche width, and niche optimum across the overall climatic space.

Appendix S10 Full results on niche overlap, niche width, and niche optimum across the analogue climatic space.

Appendix S11 Full results on niche overlap and plant traits.