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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.

INTRODUCTION

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

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

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

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

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

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

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

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

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

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

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

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

Climatic data

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

Presence and absence data

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

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

Trait data

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

Data analyses

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

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

Region effect

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

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

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

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

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

Observed niche overlap

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

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

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

Niche overlap test

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

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

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

Niche width and niche optimum

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

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

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

Insights from plant traits

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

RESULTS

Regional differences

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

Niche overlap

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

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

Niche width and niche optimum

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

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

Insights from plant traits

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

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:

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

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

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

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

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

The realised climatic niche is wider in the Alps

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

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

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

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

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

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

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

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

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

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.

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).

Figure 1 Delineation of the two study regions (**a, b**), i.e. the Alps in black and Fennoscandia in dashed, as well as maps showing the predicted presence-absence distribution (in grey, 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 colour scales in the GDD-AI space represent kernel densities (cf. the realised climatic niches) for populations of both *Dryas octopetala* and *Fragaria vesca* in the Alps (grey scales) and Fennoscandia (from white in the center to black), 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).

Figure 2 Response curves of *Dryas octopetala* (**a**) and *Fragaria vesca* (**b**) along the growing degree days above 0°C (GDD) in both the Alps (dashed curve) and Fennoscandia (solid curve), according predictions from the final model (see the section on data analyses in the main text) after model calibration and model selection (**Appendix S4**) as well as model evaluation (**Appendix S5**). *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).

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

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

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

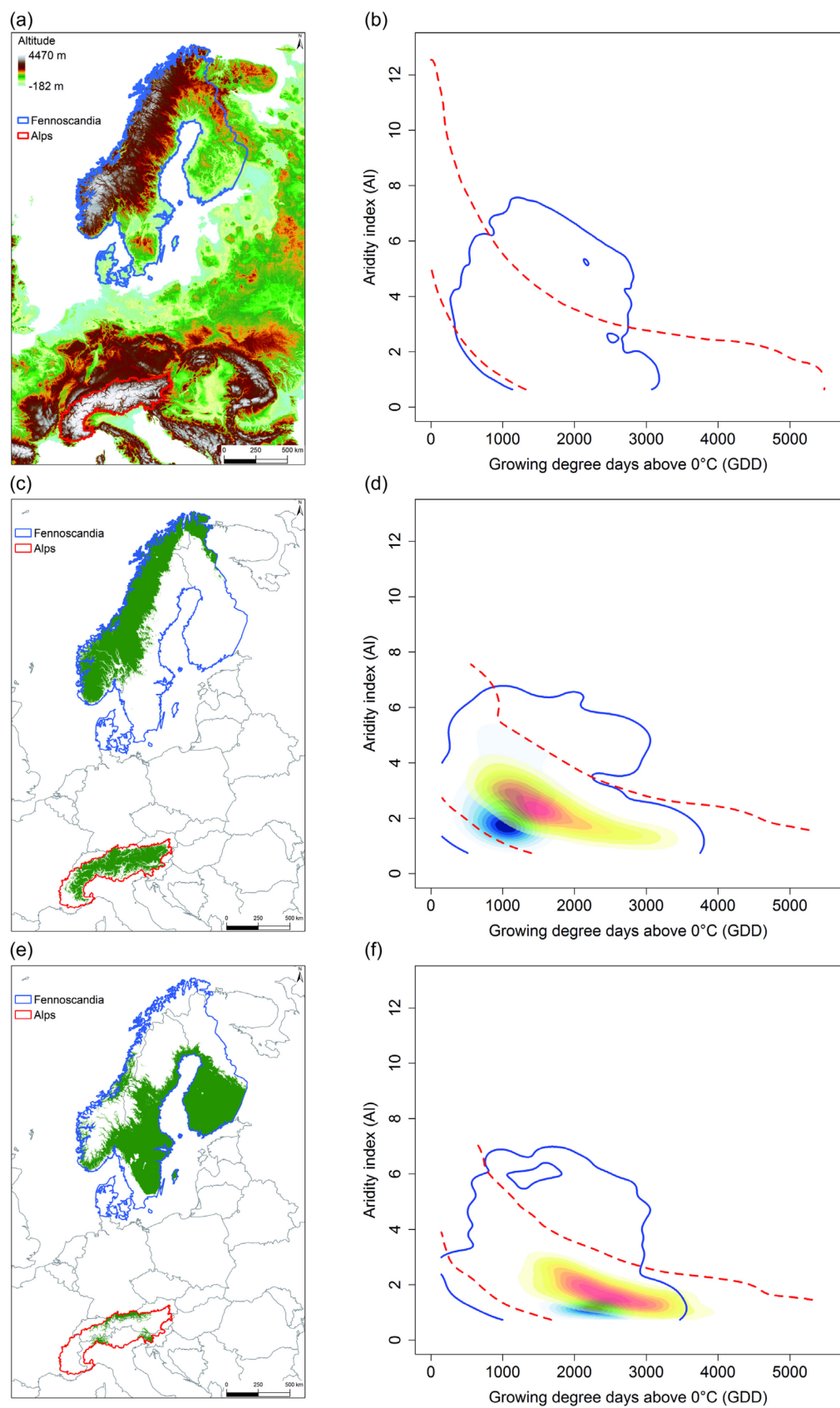
Figure 5 Box plots showing the distribution of observed niche overlap values across the overall climate space (i.e. both analogue and non-analogue climatic spaces together) according to species' biogeographic groups when considering the 31 species belonging to the restricted group (**a**) and the 358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

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

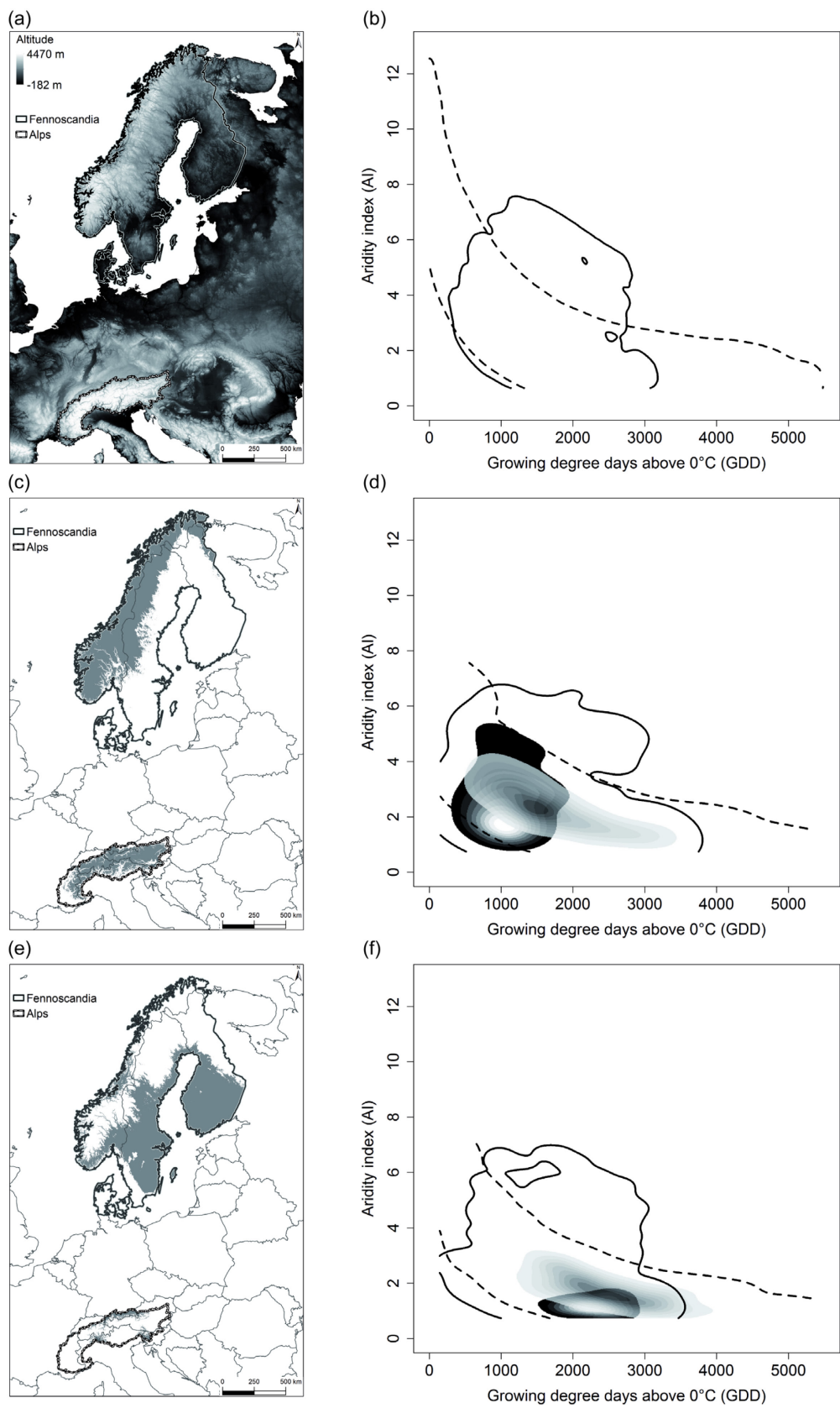
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892 variable and the observed niche overlap as the response variable. For a complete multivariate
893 linear regression model, see **Appendix S11**.

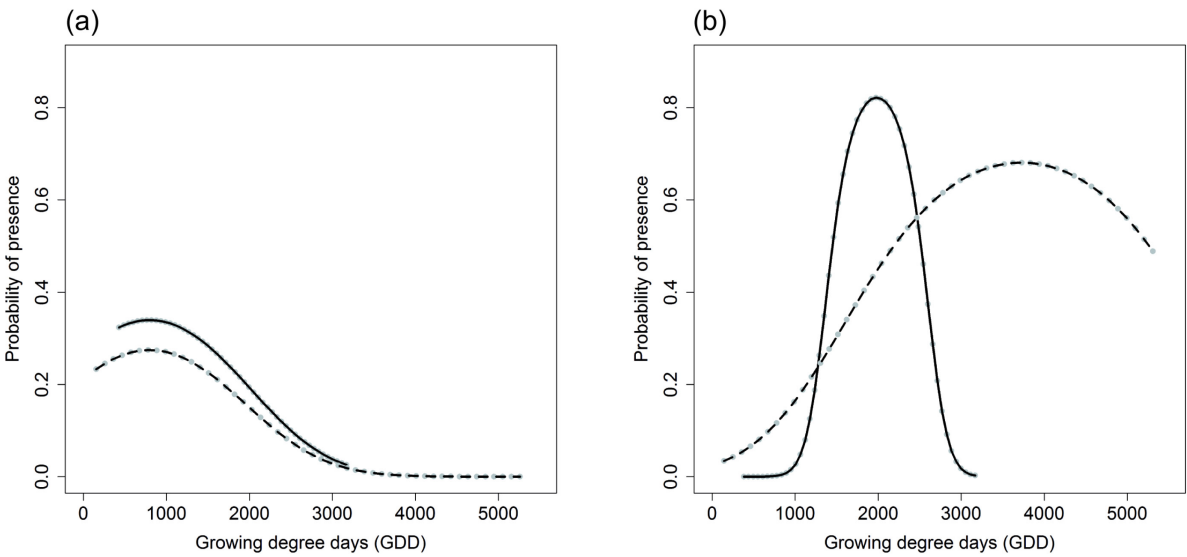
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895 **Fig. 1**

897 **Fig. 1**

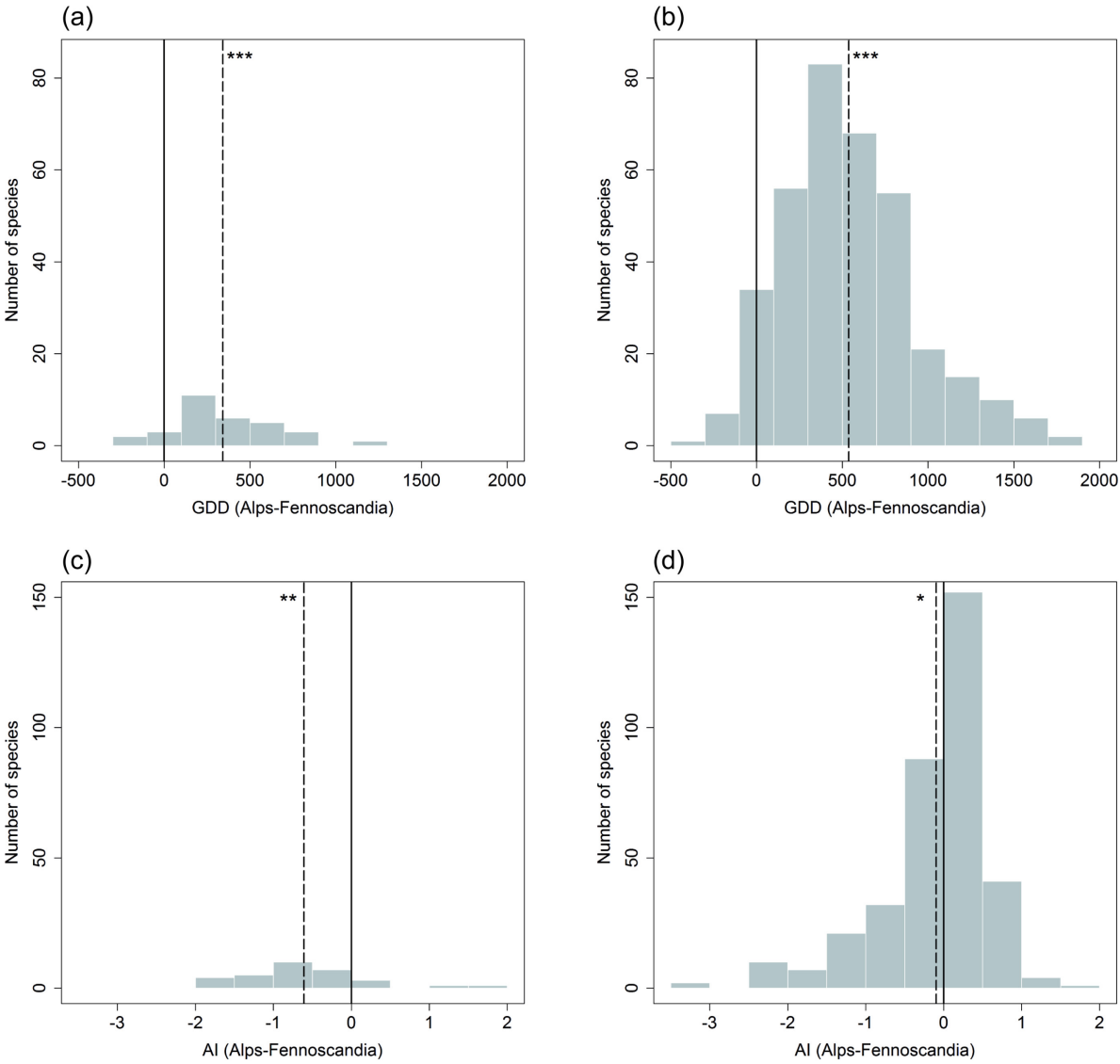


899 **Fig. 2**



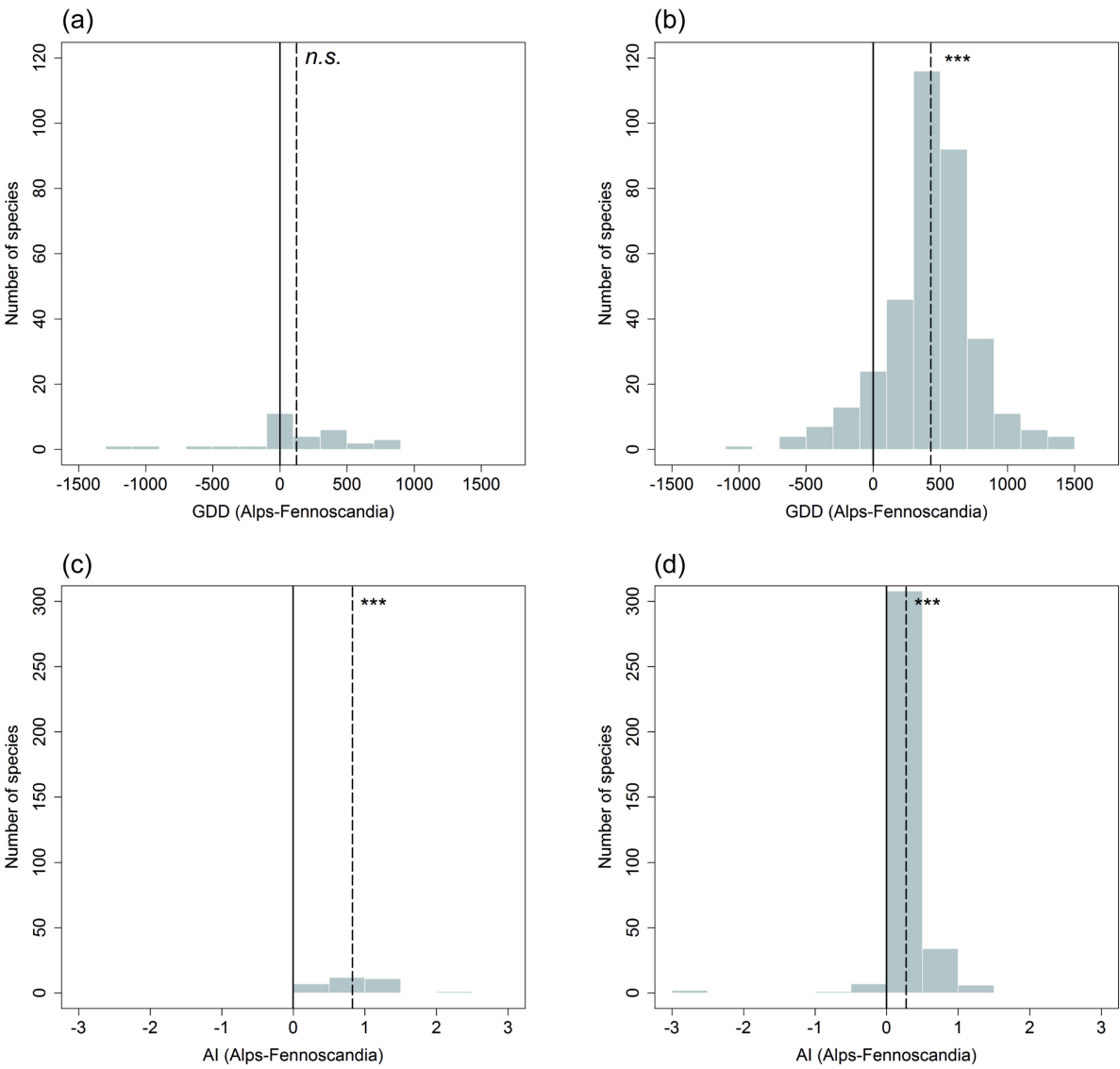
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901 **Fig. 3**



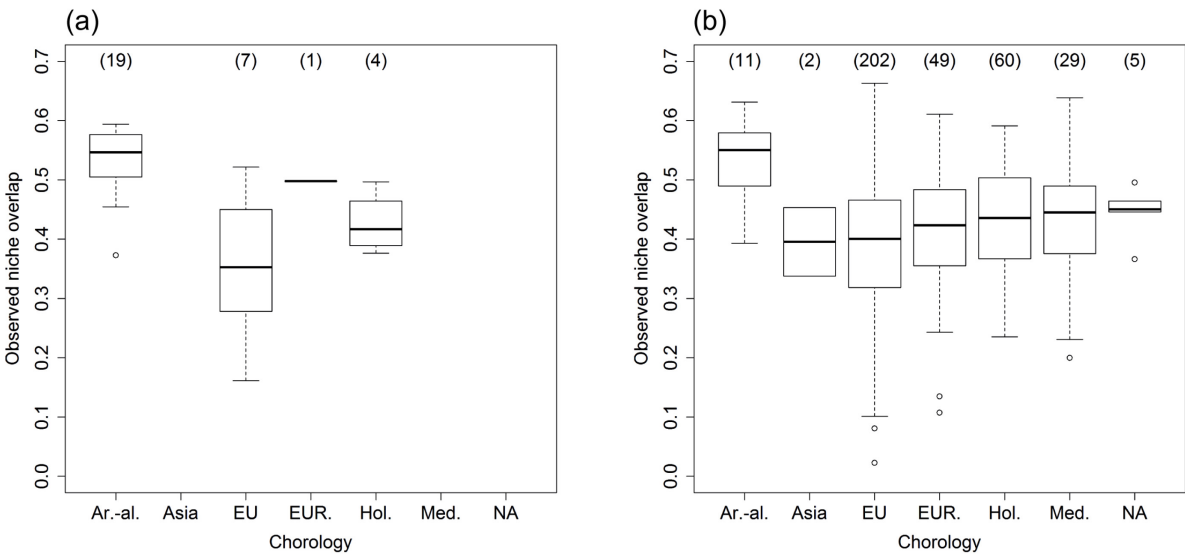
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903 **Fig. 4**



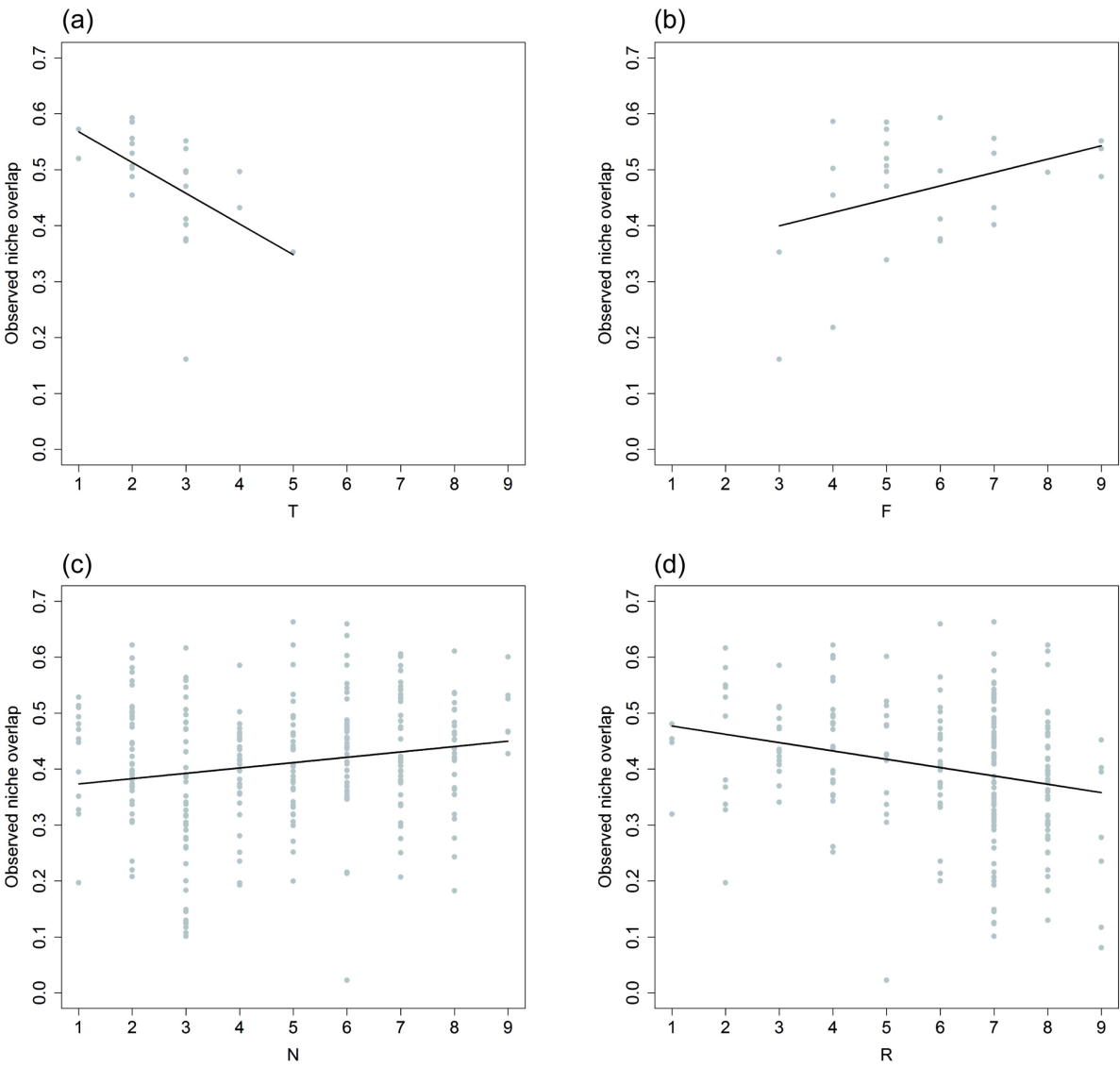
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905 **Fig. 5**



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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.