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PAPER

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

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## ABSTRACT

**Aim** Previous research on how climatic niches vary across species ranges has focused on a limited number of species, mostly invasive, and has not, to date, been very conclusive. Here we assess the degree of niche conservatism between distant populations of native alpine plant species that have been separated for thousands of years.

**Location** European Alps and Fennoscandia.

**Methods** Of the studied pool of 888 terrestrial vascular plant species occurring in both the Alps and Fennoscandia, we used two complementary approaches to test and quantify climatic-niche shifts for 31 species having strictly disjunct populations and 358 species having either a contiguous or a patchy distribution with distant populations. First, we used species distribution modelling 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%) of the 31 species with strictly disjunct populations and 58 species (16%) of the 358 species with distant populations showed a region effect on their climatic niche. Niche overlap was higher for species with strictly disjunct populations than for species with distant populations and highest for arctic–alpine species. Climatic niches were, on average, wider 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 Fennoscandia and have probably been so for 10,000–15,000 years. Therefore, the basic assumption of species distribution models that a species' climatic niche is constant in space and time – at least on time scales 10<sup>4</sup> years or less – seems to be largely valid for arctic–alpine plants.

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## Keywords

Alpine plants, arctic plants, climatic niche, disjunct distribution, distant populations, niche conservatism, niche optimum, niche overlap, niche width, species distribution modelling.

## INTRODUCTION

A long-standing question in ecology is whether species populations that occupy distant regions have retained a similar environmental niche over space and time (Lavergne *et al.*, 2010). Determining whether geographically distant populations have evolved distinct niches, to what extent and under 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 assumption that species environmental niches are relatively constant in space and time (Guisan *et al.*, 2014).

A challenge in predictive modelling is that a species' fundamental environmental niche reflecting its physiological tolerances cannot be estimated from empirical field data because other factors, such as biotic interactions and dispersal limitations, often restrict the range of conditions the species may encounter. The latter is often called the realized ecological niche (Hutchinson, 1957; Austin *et al.*, 1990). For example, changes in biotic interactions or dispersal limitations across regions may create two distinct realized niches within the same global fundamental niche. Conversely, lack of change of the realized niche usually indicates that the underlying fundamental niche remained the same across regions but does not exclude directional selection and local adaptation to occur within each region separately. Assessments of differences in climatic niche between distant populations originating from distinct post-glaciation colonization events are particularly informative about species abilities to modify their ecological requirements under climate change. However, such comparisons have rarely been undertaken (but see Pellissier *et al.*, 2013).

Here, we extend a niche comparison between distant populations of native species by using a large sample of vascular plants ( $n = 888$ ) that have successfully recolonized both the European Alps and Fennoscandia. These two geographically separated mountainous regions have the advantage of having different recolonization histories during the last glacial–interglacial cycle and share analogous macroclimatic gradients. During the Last Glacial Maximum (LGM, c. 23,000–18,000 yr BP), Fennoscandia was largely covered by the Eurasian ice sheet (Svendsen *et al.*, 2004), while much smaller ice caps covered parts of the Alps with numerous ice-free refugial areas located relatively close to each other (Schönswetter *et al.*, 2005). Thus, the process of post-glacial recolonization of all climatically suitable sites (i.e. range-filling) by high-elevation plants surviving the LGM at the margins of both the Alps (Schönswetter *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), was probably

less constrained by dispersal limitations in the Alps (Dullinger *et al.*, 2012) than in Fennoscandia.

In addition, population adaptability, and also genetic variation, may have been enhanced in the Alps because of the 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). 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 (genetic diversity hypothesis). In contrast, the long-distance recolonization 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 recolonization 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 shifted the fundamental climatic niche towards colder conditions due to founder events from cold-adapted populations.

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 realized 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 a 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 realized 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 can be related to its traits. For instance, a generalist species may have a wider fundamental niche and thus more easily adjust its realized niche to peculiarities of different regions than a specialist whose fundamental niche is too narrow to allow pronounced regional shifts of the realized niche (Pearman *et al.*, 2008). Dispersal traits may also cause disjunct populations of a dispersal-limited species to be more genetically isolated, favouring local adaptation and hence fostering niche differentiation. Linking traits with the extent of niche overlap between two distant populations of the same species could therefore be informative.

With this background, we aim to answer five questions. (1) Do the realized climatic niches of species native to both the Alps and Fennoscandia differ between the two regions? (2) To what

extent does the realized climatic niche of a species overlap between the two regions? (3) Is there a trend towards wider (supporting the genetic diversity hypothesis) or narrower (supporting the diversity-niche width hypothesis) realized climatic niches in the Alps? (4) Are the realized climatic niches of species shifting towards warmer (supporting the genetic diversity hypothesis) or colder (supporting the diversity-niche width hypothesis) conditions in the Alps? (5) How much of the variation in species niche overlap can be explained by species 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. 1a). To select the list of terrestrial vascular plant species occurring in both regions, we assembled about 70,000 vegetation plots from two different European vegetation databases: (1) the Alps Vegetation Database (AVD;  $n = 31,524$ , <http://www.givd.info/ID/EU-00-014>) (Lenoir *et al.*, 2012), and (2) the Nordic Vegetation Database (NVD;  $n = 41,785$ , <http://www.givd.info/ID/EU-00-018>) (Lenoir *et al.*, 2013). The 888 species occurring in both databases correspond to the common species pool (see Appendix S1 in Supporting Information).

Because most of these 888 species also occur outside our study area, it is likely that the estimates of the realized climatic niche will be truncated for at least one of the two studied populations, thus potentially affecting our results. To account for such effects, we screened each of the 888 species range maps (Meusel *et al.*, 1965, 1978, 1992) to subdivide the species into two subsets: (1) species having a 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 group of 'disjunct' distribution for which the entire realized climatic niche is assumed to be captured ( $n = 91$ ); and (2) 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 group of 'widespread' distribution, for which the realized climatic niche will be truncated in at least one of the two studied regions ( $n = 797$ ). For this latter group we still assume that the populations are so widely separated that they are genetically separated. We analysed and reported all our results separately for the disjunct and widespread 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, higher AI values represent more humid conditions); annual potential evapotranspiration (PET); annual actual evapotranspiration (AET); the Priestley–Taylor alpha coefficient (ALPHA = AET/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 1 km: WorldClim (Hijmans *et al.*, 2005: <http://www.worldclim.org/>) and CGIAR (CGIAR-CSI: <http://www.cgiar-csi.org/>) (Appendix S2).

### Presence and absence data

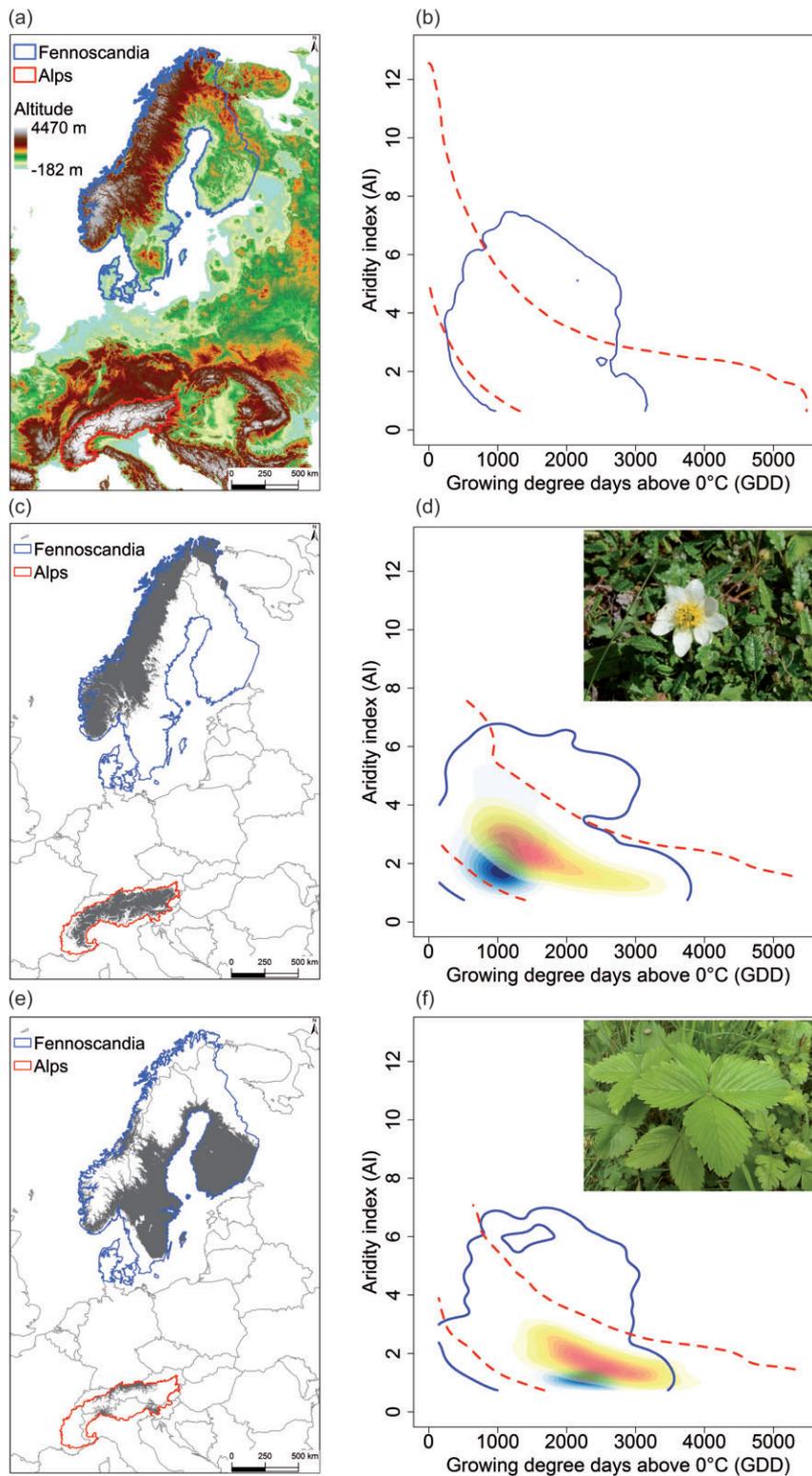
For each of the 888 species, we followed a set of data-handling procedures (Appendix S3). We first compiled geo-referenced presence records by querying AVD, NVD and the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>) and geo-referenced absence records from AVD and NVD. Presence (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 these 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 realized 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-form from several sources (Appendix S1). Diaspore mass and plant height values were log-transformed prior to analyses.

### Data analyses

To compare the realized 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 realized climatic niche of each species using an environmental niche modelling (ENM) approach



**Figure 1** Geographic (a) and climatic (b) delineations of the two study regions: the Alps and Fennoscandia. Range maps as well as realized climatic niches of *Dryas octopetala\** (c, d) and *Fragaria vesca+* (e, f) are depicted 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). Dashed and solid lines within the GDD–AI space delineate climatic conditions (cf. background data) for the Alps and Fennoscandia, respectively. 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. Colour ramps in the GDD–AI space represent kernel densities (cf. the realized climatic niches) for populations of both *D. octopetala* and *F. vesca* in the Alps (cf. the yellow-to-red colour ramp in the online version or the light-to-dark grey colour ramp in the printed version) and Fennoscandia (cf. the light-to-dark blue colour ramp in the online version or the black-to-white colour ramp in the printed version). The digital terrain model (DTM) is based on data from the Shuttle Radar Topography Mission (SRTM). All maps are projected into the ‘ETRS89/ETRS-LAEA; code EPSG: 3035’ projection system and aggregated at 1-km resolution. For more information on the predicted species distributions depicted in grey, see explanations related to model evaluation and prediction in the section ‘Data analyses’ in the main text. Note that background data for *D. octopetala* and *F. vesca* are based on 1-km grid cells for which we have information on presence or absence data and thus slightly differ from the full background data based on all 1-km grid cells available across each region.

\**Dryas octopetala* is a typical arctic-alpine plant with a strictly disjunct distribution across Europe and whose populations in the Alps and Fennoscandia are confined to mountainous areas or arctic-alpine tundra (cf. the ‘disjunct’ group).

+*Fragaria vesca* is a widespread plant whose distribution is patchy across Europe but not necessarily confined to mountainous areas or arctic-alpine tundra (cf. the ‘widespread’ group).

based on generalized linear models (GLMs). Second, we used a bivariate analysis based on the two most statistically significant climatic layers found in the GLMs, one temperature-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 realized climatic niches between distant populations in the Alps and Fennoscandia were assessed, we linked species niche overlap values to species traits.

### Region effect

For each of the 888 species, all 1-km<sup>2</sup> grid cells retained after the selection process (Appendix S3) were split into two subsets: one subset for model development (training dataset) including two-thirds of the selected grid cells and one subset for model validation (test dataset) consisting of the remaining grid cells. Because of this splitting, 550 species, of which 55 belong to the disjunct 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 (binomial distribution) with *pr* as the dependent variable to select the most influential bioclimatic variables (GDD, AMT, CI, PET, AET, WBAL, ALPHA, AI, SWC). We then added the region variable (Alps versus Fennoscandia) and tested its 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. When overdispersion was detected 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 realized climatic niche between regions. A total of 389 species, of which 31 belong to the disjunct group, out of 550 fulfilled this requirement (Fig. S5 in Appendix S5). To transform the predicted probability of presence into presence-absence data (Fig. S3 in Appendix S3), we computed the sensitivity-specificity sum maximizer 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. To test for regional differences in the realized climatic niche of a given species, we focused on the significance of the interaction terms (Fig. 2 & Fig. S6 in Appendix S6).

### Observed niche overlap

We estimated niche overlap between the two regions within the bi-dimensional climatic space defined by GDD and AI (Fig. 1b, Appendix S7). These two variables were selected since they were

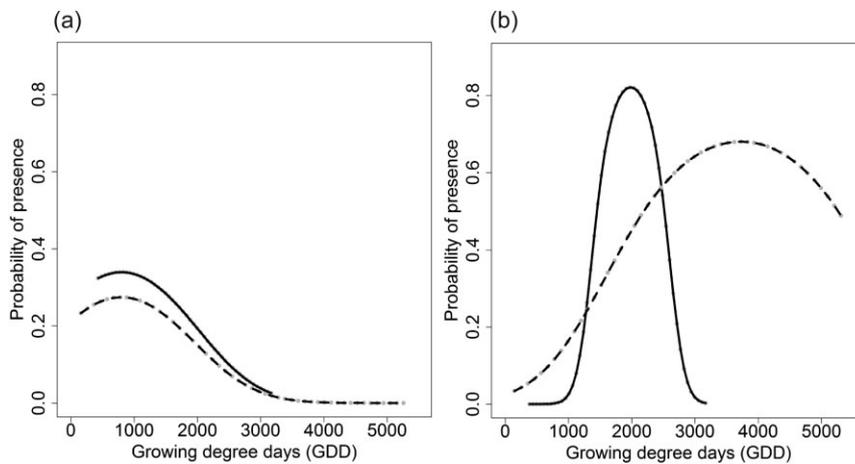
important for many of our species (Table S8 in Appendix S8). We divided the bi-dimensional climatic space into a grid of 500 × 500 cells bounded by the minimum and maximum values of GDD (first axis) and AI (second axis) (Fig. 1b, Appendix S7). For each region separately, we mapped the occurrence data (*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 standardize 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 us to account for non-analogue climatic conditions that may become analogues with future climate change, whereas focusing solely on the analogue climatic space enables assessment of  $D_{obs}$  to be independent of simple differences in climatic conditions. In theory  $D_{obs}$  should be higher when focusing on the analogue climatic space alone, with difference in  $D_{obs}$  values between the analogue 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 the part of the bi-dimensional climatic space that was shared by the two regions for each species (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 with 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: (1) predict each population distribution in the Alps and Fennoscandia based on climatic conditions solely; (2) project these spatial predictions into the GDD–AI climatic space; and (3) 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 helps to assess how much the realized climatic niche of this focal species is conserved. The lower the  $D_{obs}$  value is 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. indicating that the realized climatic niche is more conserved than



**Figure 2** Response curves of *Dryas octopetala* (a) and *Fragaria vesca* (b) along the growing degree days above 0 °C (GDD) gradient in both the Alps (dashed curve) and Fennoscandia (solid curve) after model calibration and model selection (Appendix S4) as well as model evaluation (Appendix S5). *Dryas octopetala* and *F. vesca* depict a non-significant regional difference and a significant regional difference, respectively, along the GDD gradient.

expected under the assumption of climatic-niche identity.  $D_{sim}$  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 realized niche but also other abiotic and biotic dimensions not considered in our models and which could involve habitat-compensation effects. For this reason, it is not surprising 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 regional differences in the realized climatic niche: niche width (the range of climatic conditions that are suitable for a species) and niche optimum (the maximum probability of presence of a species within its realized climatic niche). Values of species niche width and niche optimum 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. Values for each species niche width and niche optimum 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 the 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 randomization procedure was repeated 100 times, and the mean values of the 100 values obtained 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 honestly significant difference (HSD) test for post-hoc pairwise comparisons of group means. Second, we fitted  $D_{obs}$  against all six semi-quantitative Ellenberg indicator values. Third, we fitted  $D_{obs}$  against plant height, SLA, diaspore mass and 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 in the disjunct group, only one (*Epilobium alsinifolium*) showed regional differences along only one particular gradient (AI) (Fig. S8 in Appendix S8). Among the remaining 358 species of this widespread group, only 58 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, 26, 8 and 5 showed regional differences in response to GDD (Fig. 2b), SWC, AI and CI, respectively (Fig. S8 in Appendix S8).

### Niche overlap

Based on the overall climatic space defined by GDD and AI, the observed niche overlap ( $D_{obs}$ ) of the disjunct group (mean 0.5; range 0.16–0.59) was higher than for the widespread group (mean 0.42; range 0.02–0.66) (two-sample Student's *t*-test,  $P = 0.002$ ) (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 disjunct (mean 0.4; range 0.25–0.52) (paired two-sample Student's *t*-test,  $n = 27$ ,  $P \ll 0.001$ ) and widespread (mean 0.28; range 0.005–0.7) ( $n = 195$ ,  $P \ll 0.001$ ) groups. Among the 58 species that showed regional differences in their response curves along at

least one climatic variable (Table S8 in Appendix S8), only six had distant realized climatic niches that overlapped less than under the baseline scenario ( $D_{\text{obs}} < D_{\text{sim}}$ ): *Alyssum alyssoides*, *Avenula pratensis*, *Carex ericetorum*, *Ranunculus bulbosus*, *Rubus idaeus* and *Vincetoxicum hirsutinaria*. We found similar patterns when calculations were based on the analogue climatic space, except that niche overlap values were higher throughout (Table S10 in Appendix S10).

### Niche width and niche optimum

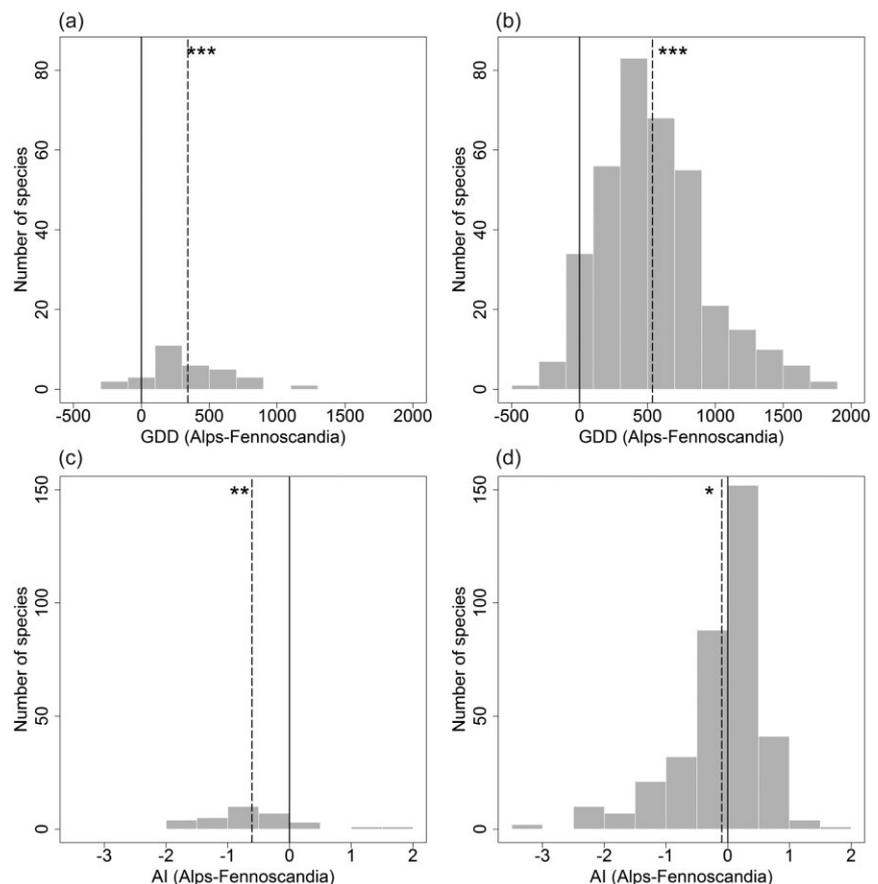
Irrespective of the species group considered (i.e. disjunct versus widespread), niche width across the overall climate space was larger in the Alps than in Fennoscandia for GDD (Fig. 3a, b) and larger in Fennoscandia than in the Alps for AI (Fig. 3c, d) (Table S9 in Appendix S9). The same patterns were found for the disjunct group when assessing niche width based on analogue climates alone, except that the trend was marginally not significant for AI ( $P = 0.06$ ). However, when assessing niche width based on analogue climates alone for the widespread group, species realised climatic niches were larger in the Alps than in Fennoscandia for both variables (Table S10 in Appendix S10).

Results for niche optima across the overall climatic space for the disjunct group showed no difference along GDD but a shift towards higher values of AI in the Alps compared with Fennoscandia (Fig. 4a, c) (Table S9 in Appendix S9). For the

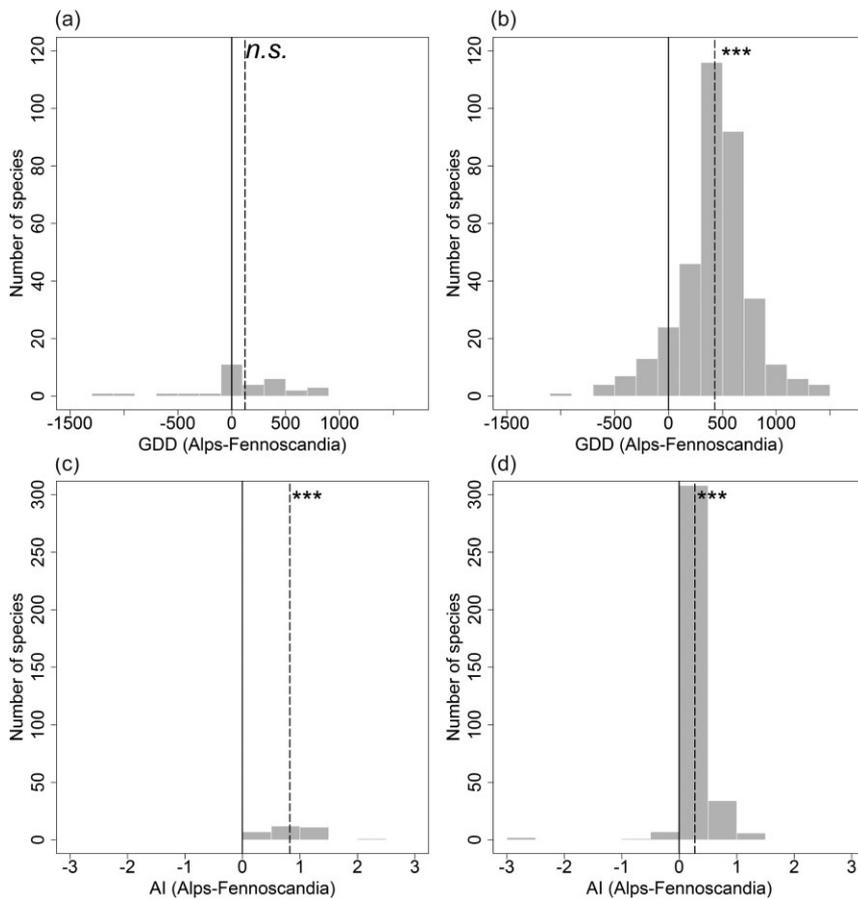
widespread group, niche optima were located, on average, towards higher values of both GDD and AI in the Alps than in Fennoscandia, (Fig. 4b, d) (Table S9 in Appendix S9). We found the same patterns when assessing niche optima based on analogue climates (Table S10 in Appendix S10).

### Insights from plant traits

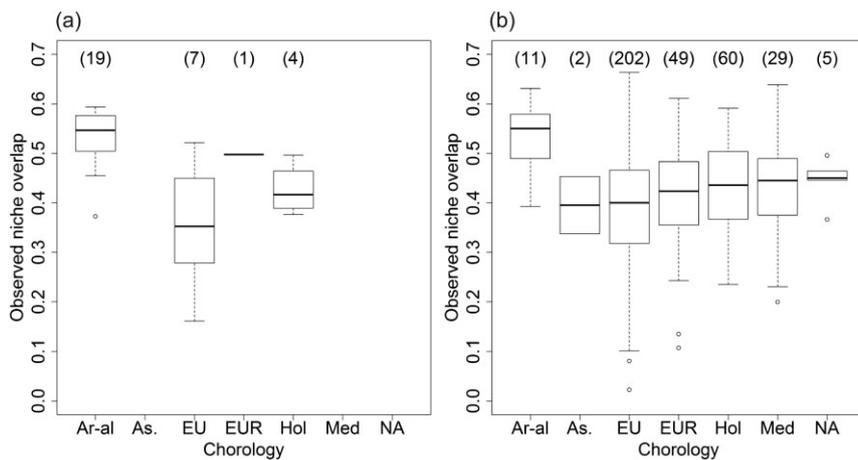
Whatever the species group (i.e. disjunct versus widespread) and the climatic space (whole versus analogue) considered, we found similar patterns (Appendices S11 & S12). For clarity, we only report results based on the full climatic space (Appendix S11). The biogeographic origin of species in the disjunct and widespread groups explained 50% versus 7%, respectively, of the variation in  $D_{\text{obs}}$ , with arctic-alpine species showing the highest  $D_{\text{obs}}$  values and standing out from the other biogeographic groups (Fig. 5a, b). Ecological indicator values for species of the disjunct and widespread groups explained 53% versus 21%, respectively, of the variation in  $D_{\text{obs}}$ , with contrasting patterns depending on the species group. For the disjunct group,  $D_{\text{obs}}$  increased with increasing preference for cold temperatures and moist soils (Fig. 6a, c). In contrast, for the widespread group,  $D_{\text{obs}}$  increased with increasing preference for acid soils and for fertile soils (Fig. 6a, c). There was no clear relationship between  $D_{\text{obs}}$  and species biological traits (Appendix S11).



**Figure 3** Histograms of paired differences in species realized-niche width between distant populations from the Alps and Fennoscandia for both the disjunct (a, c) and widespread (b, d) groups along the growing degree days above 0 °C (GDD) (a, b) and aridity index (AI) (c, d) gradients. Species realized-niche width values were computed across the overall climatic space. The dotted and solid vertical lines show the mean difference and zero values, respectively.  $P$ -values are based on paired two-sample Student's  $t$ -tests.  $P$ -values are given as: \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$ .



**Figure 4** Histograms of paired differences in species realized-niche optimum between distant populations from the Alps and Fennoscandia for both the disjunct (a, c) and widespread (b, d) groups along the growing degree days above 0 °C (GDD) (a, b) and aridity index (AI) (c, d) gradients. Species realized-niche optimum values were computed across the overall climatic space. The dotted and solid vertical lines show the mean difference and zero values, respectively. *P*-values are based on paired two-sample Student's *t*-tests. *P*-values are given as: \*\*\**P* < 0.001; n.s. non significant.



**Figure 5** Box plots of the distribution of observed niche overlap values according to species biogeographic origins or chorology for both the disjunct (a) and widespread (b) groups. Niche overlap values were computed across the overall climatic space. Chorology is a factor variable with seven levels or biogeographic origins: Arctic-alpine (Ar-al); Asia (As.); Eurasia (EU); Europe (EUR); Holarctic (Hol.); Mediterranean (Med.); and North America (NA) (Landolt *et al.*, 2010). Numbers in brackets indicate the total number of species for each biogeographic origin. Box plots show median, 25th and 75th percentiles. The whiskers extend to 1.5 × interquartile range and points are values lying outside this range.

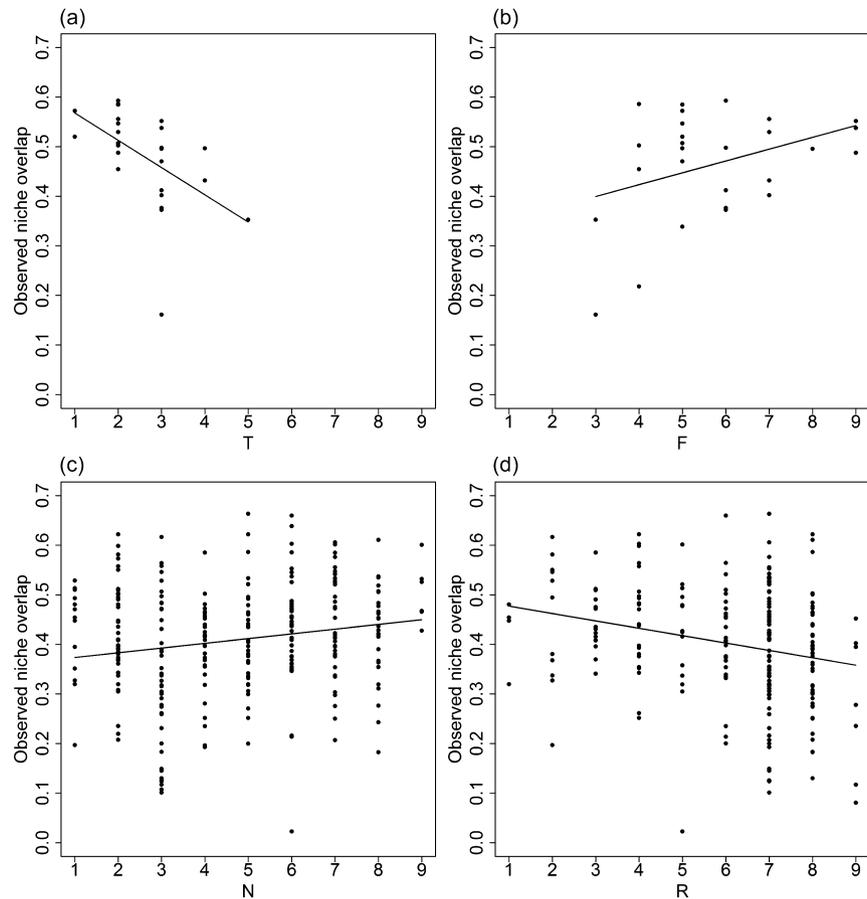
## DISCUSSION

### The realized climatic niche is conserved

Our findings suggest predominant niche conservatism, with only 15% of the 389 studied species displaying regional differ-

ences in realized climatic niches. 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 with a smaller set of plant species ( $n = 8$ ), Martínez-Meyer & Peterson (2006) showed that

**Figure 6** Scatter plots of the distribution of observed niche overlap values for both the disjunct (a, b) and widespread (c, d) groups along Ellenberg gradients for temperature (T) (a), soil moisture (F) (b), soil nutrient (N) (c) and soil acidity (R) (d). Niche overlap values were computed across the overall climatic space. Regression lines are based on univariate linear regression models. See Appendix S11 for multivariate linear regression models. Note that Ellenberg indicator values are semi-quantitative variables that group species into categories according to their position along the main ecological gradients. These variables do not have units and were considered as continuous in our models.



current species distributions in North America predict their distribution well at the LGM and vice versa, suggesting ecological niche conservatism despite changes in climate and environmental conditions over that time period. Our results confirm the general idea that niches are conserved over time spans of millennia and support results from previous studies focusing on a limited set of species (Martínez-Meyer & Peterson, 2006; Pearman *et al.*, 2008; Peterson, 2011).

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

Niche overlap was higher for species having a disjunct distribution with at least one population confined to the Alps and one population confined to Fennoscandia than for species having contiguous or patchy distribution across Europe with populations extending outside the study area. This may be due to methodological reasons because the entire realized climatic niche is likely to be captured in the disjunct group whereas in the widespread group the realized climatic niche will be truncated in at least one of the two regions studied and thus we may underestimate niche overlap for the widespread group.

Considering species' biogeographic affinities, niche overlap was highest for arctic-alpine species (Fig. 5), supporting strong conservatism as found by Pellissier *et al.* (2013) for the low-temperature limit of 26 arctic-alpine plant species. Consistent

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 climatic niches were geographically and/or edaphically widespread (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 more able than specialist species to respond to regional differences by exploiting a greater diversity of habitats (Colles *et al.*, 2009). However, it contradicts recent findings of Early & Sax (2014), who compared native versus 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 they also suggested that the stronger climatic disequilibrium for range-restricted species is probably due to non-climatic factors such as dispersal and biotic factors constraining the native range, whereas in the naturalized range especially the latter biotic constraints may be alleviated (cf. the enemy release hypothesis), thus leading to strong climatic disequilibrium. In our study, the range-restricted arctic-alpine species are 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 substrates. 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, post-glacial re-colonization of acidophilous species in Fennoscandia might have been less constrained by dispersal limitations, leading to greater niche overlap with their distant populations in the Alps.

### The realized climatic niche is wider in the Alps

Despite the realized climatic niche being globally conserved, we found a trend 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 supports the genetic diversity hypothesis and invalidates the diversity-niche width hypothesis based on MacArthur's (1972) assumption for island biogeography which proposes that a species' realized-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 realized niches. Greater genetic diversity due to different refugia close to the Alps (Schönswetter *et al.*, 2005), corresponding to greater habitat heterogeneity, increases the likelihood of a species filling its fundamental climatic niche. This has probably played an important part 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 in Fennoscandia (Eidesen *et al.*, 2013).

However, such regional differences in realized niche width may also result from time-lagged range expansion following post-glacial warming and disequilibrium with current climate for populations in Fennoscandia (Svenning & Skov, 2004). Notably, the difference may also stem from the rather coarse resolution of the climatic data we used and the fact that climatic heterogeneity within a 1-km<sup>2</sup> spatial unit (Lenoir *et al.*, 2013) is likely to be greater in the Alps than in Fennoscandia. Therefore, our approach might overestimate niche width in the Alps relatively more than in Fennoscandia.

### The realized 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 populations of a species from different geographic areas are grown together, reveal local adaptation of most tree and

herbaceous plant species to their local home 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. GDD or AI) 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), and thus it could be a confounding factor.

## CONCLUSIONS

We conclude that the realized climatic niche of terrestrial vascular plants that successfully recolonized 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. This has important consequences for predicting future biodiversity under climate change. Notably, the basic assumption that species' realized climatic niche is constant in space and time (thousands of years) seems to be valid to a large extent. However, we also show that regional differences in niche width and optimum are rather common. Hence, if the aim is to track precisely the geographic position of some key species distribution parameters (the range limit or centre), then the basic assumption of species distribution models is likely to be flawed, simply because it does not account for regional subtleties in niche width and optimum values.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1** Supplementary information describing how the pool of terrestrial vascular plant species common to the Alps and Fennoscandia was built and Table S1 listing the 888 studied terrestrial vascular plant species occurring in both regions.

**Appendix S2** Supplementary information providing full details on the nine climatic variables considered in this study.

**Appendix S3** Supplementary information listing all the data-handling procedures on presence and absence data of each of the 888 terrestrial vascular plant species belonging to the common species pool and Fig. S3 illustrating the case of *Rubus idaeus*.

**Appendix S4** Supplementary information detailing model calibration and model selection steps.

**Appendix S5** Figure S5 showing results on model evaluation for the 550 species being sufficiently frequent to be retained for model calibration and model selection.

**Appendix S6** Figure S6 illustrating the region effect for *Rubus idaeus*.

**Appendix S7** Supplementary information detailing computations of the observed and simulated niche overlap and Fig. S7 illustrating the case of *Rubus idaeus*.

**Appendix S8** Figure S8 and Table S8 showing results on the contribution of the region effect for both the 31 species belonging to the 'disjunct' group and the 358 species belonging to the 'widespread' group.

**Appendix S9** Table S9 listing niche overlap, niche width, and niche optimum across the overall climatic space for both the 31 species belonging to the 'disjunct' group and the 358 species belonging to the 'widespread' group.

**Appendix S10** Table S10 listing niche overlap, niche width, and niche optimum across the analogue climatic space for both the 31 species belonging to the 'disjunct' group and the 358 species belonging to the 'widespread' group.

**Appendix S11** Supplementary analyses on the link between the observed niche overlap computed across the overall climatic space and plant traits.

**Appendix S12** Supplementary analyses on the link between the observed niche overlap computed across the analogue climatic space and plant traits.

## BIOSKETCH

**Safaa Wasof** is a PhD student at Jules Verne University of Picardie, France and is interested in plant community ecology and in how plant communities are affected by contemporary environmental changes.

S.W. prepared the data, ran the analyses, interpreted the results and wrote the first draft of the manuscript; J.L. designed the study, provided part of the data, analysed the data and interpreted the results; P.A.A., G.A., V.B., K.A.B., H.J.B.B., J.B., H.H.B., C.J.D., M.D., S.D., M.D., R.E., J.C.G., B.J.G., J.A.G., A.G., K.K., M.L., A.M., B.N., A.O., H.P., V.R., S.R., S.M.S., F.H.S., J.S., W.T., L.U.T., V.V., L.G.V., R.V., P.V., W.W., T.W., N.E.Z. and J.K. provided the data; G.D., W.T., A.G., H.J.B.B., I.G.A., M.D., K.H., S.D., R.V., J.A.G., W.S.A., V.V., R.E., J.C.S., T.W., W.W., M.M., M.Z. and J.C.G. contributed to the design of the study and to the interpretation of the results. All authors contributed substantially to the final version of the manuscript.

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