Hybridization mediated range expansion and climate change resilience in two conifers

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Abstract

The current global climate change is expected to affect biodiversity negatively at all scales. Population level changes in allele frequencies provide species to innovate adaptation to changing climates and prevent extinction. This is often exhibited through their adaptations to local environment and reflects species' potential for future climate change resilience. However, detecting such environment associated alleles require whole genome sequencing of many populations and/or long running common garden experiments. This is however far from being practical for species with long generation times. Here, in the present study, using exome capture sequences, we tested multiple methods to assess local adaptation and climate resilience in Norway spruce and Siberian spruce. We show that local adaptation in conifers can be detected through allele frequency variation, population level ecological preferences, and historical niche movement. Moreover, we integrated both genetic and ecological information into genetic off-set predictive models to show that hybridization plays a main role in expanding both species' niche breath and may allow both species to cope better with changing future climates. Finally, this allowed us to identify genetically isolated populations at risk under current climate change.

Keywords: *Landscape genomics, Climate change, Local adaptation, Climate change resilience*

Background

It is no secret now that species around the world face habitat loss due to human activities and the global climate change has only exacerbated the hardship (Bellard et al., 2012; Grimm et al., 2013; Walther et al., 2002). At the current rate of global warming, ecological communities need rapid changes in their structure and composition to keep up with the challenges and recent studies show that communities respond to regional rather than global changes (Altieri & Gedan, 2015; Araújo & Rahbek, 2006; Atkins & Travis, 2010; Thuiller et al., 2005; Williams et al., 2021; Wuethrich, 2000). The asymmetry in the climate change across ecosystems has created a heterogeneity of ecological dynamics leading natural communities to face stochastic changes in their local environment (Carbeck et al., 2022; Walther et al., 2002). As a result, in order for organisms to avoid complete collapse of their demography and possible extinction, they must move with their climatic niche and/or adapt to the changing environment from their standing genetic variation or through new mutations. Genetic diversity and high levels of heterozygosity, indeed increase stress resistance in populations (e.g., (Markert et al., 2010) and specially their adaptive potential to climate change (Frankham, 2005; Pauls et al., 2013). On the other hand, the decline of genetic diversity leaves species and their populations at the risk of not being able to cope with changing environments and eventually face extinction (Leroy et al., 2020). If environmental heterogeneity can promote intraspecific genetic variation, global climate change, however, can have major negative impact on a species' overall genetic diversity by affecting demographic dynamics to large extents, leading to variation in spatial and temporal distribution of genetic variation and hindering evolutionary potential through adaptation to changing environments (Pauls et al., 2013; Rellstab et al., 2016).

Plant species are probably even more affected by global change given their disadvantage of tracing suitable habitats, especially species with long generation times (Dauphin et al., 2021; Leroy et al., 2020). Therefore, the survival of the species depends critically upon the potential of the species to expand into new regions through ancestral potential for adaptations to such environments as well as the potential for populations at the edge of its distribution range to face new environmental conditions (Pfennig et al., 2016; Taylor et al., 2015).

In Western Europe for instance, the recurrent cycles of population contraction and expansion following glacial cycles shaped both genetic diversity (Milesi et al., 2023; Petit et al., 2003) and local adaptation pattern along environmental gradients that also correspond to recolonization routes (L. Li et al., 2022; Milesi et al., 2019; Savolainen et al., 2013; Tsuda et al., 2016). Genetic admixture following range expansion from refugia is a major source of genetic diversity in forest trees (Milesi et al., 2019; Tsuda et al., 2016) (Milesi et al. 2023, Tsuda et al. 2016). It can promote increased climate resilience in wild populations (e.g., (Inoue & Berg, 2017; MEESTER et al., 2018) and aid wider phenotypic plasticity against rapid climate changes (see (Catullo et al., 2019). Admixture caused by recurrent colonization by superior ecotypes can promote better resistance to environmental stress (e.g., (Hamilton & Miller, 2016; Ortego et al., 2015) and can counter extinction through population size increase (Milesi et al., 2023), persistence at the range edge and range expansion (e.g., (Gillies et al., 2016; Teukeng et al., 2022; Zalapa et al., 2010). Hybridization and admixture are thus effective mechanisms to increase overall genetic diversity but they also promote the transfer of adaptive alleles from one genetic background to another, enhancing local adaption and allowing populations to respond quickly to selective pressure (Rendón-Anaya et al., 2021; L. H. Rieseberg & Willis, 2007; Stelkens et al., 2014; Taylor et al., 2015). Here we hypothesize that the recurrent hybridization and admixture events between two closely related coniferous species through cycles of historic range shifts due to main climatic cycles help both species to better cope with future climatic changes.

Norway spruce (*Picea abies* (L.) H. Karst) and Siberian spruce (Ledeb) are two closely related species that diverged ca. 17.6 mya but have had several cycles of contacts in their distribution range (Chen et

al., 2019). Today, the two species have clear western (Western Europe) and eastern (Siberian Russia) distribution albeit with a known hybrid zone located between western and eastern Russia (See map Fig. 1). Currently, the distribution of *P. abies* is sub-divided into three main domains (Alpine, Carpathian, and Baltico-Fennoscandian, (EUFORGEN, 2009)) and seven main genetic clusters can be delineated (Chen et al., 2019; L. Li et al., 2022); they correspond to three ancestral clusters (Alpine, Carpathian, Fennoscandian) as well as the admixture between these main clusters (Chen et al., 2019; L. Li et al., 2022). Siberian spruce, on the other hand, expands from Northeast Asia to Western Russia. Following glacial cycles, the species came into contact at several occasion, leading to introgression (e.g., (Chen et al., 2019; Tsuda et al., 2016). Recently, Nota et al., (2022), using ancient DNA, and Li et al., (2022), using nuclear markers, confirmed that recolonization of Scandinavian peninsula after the last glacial maximum (LGM) by Norway spruce occured through two different entry points, a southern one, from Eastern location across the Baltic Sea and a northern one through northern Finland. Given the close genetic affinity of the two species, hybridizing zone, historic recolonization events, and the climatic gradient they are distributed along, Norway spruce and Siberian spruce serve as a unique system to study the role of hybridization in shaping climate resilience fostered by genetic variation and range expansion.

Using a combination genome scan and genotype environment association studies we first showed evidence of local adaptation and identified the main climatic variables conditioning species distributions. We then used environmental niche models with these climatic variables and species occurrences to define species ecological niche preference and their historical movement. Finally, we integrated both genetic and ecological information into genetic off-sets predictive models to show that hybridization plays a main role in expanding both species' niche breath and may allow both species to cope better with changing future climates.

Results

Populations exhibiting a high level of admixture are spread over three climatic groups

We used a Bayesian framework to investigate the co-variation pattern in allele frequencies and delineate genetic clusters. Three entities emerged. The first cluster was composed of populations located East of Ural Mountain, previously recognized as *P. obovata*. The second consisted of populations from the Western Europe recognized as *P. abies* and a the third confirmed through the hybrid nature of the populations located East of the Ural Mountain and West of the Baltic region (Fig. 1 and S1). In order to investigate if specific genetic entities were associated with given climatic zones, we used a redundancy analysis incorporating both genetic and climatic data (see materials and methods, *Genetic diversity distribution among populations*). From K-means clustering of climatic and adaptive index from RDA (se materials and methods), we recognized five major environmental clusters (i.e., climatic groups) among all the populations studied with populations in the contact zone belonging to three different clusters (supp Fig. 2). Interestingly, this divided western populations (i.e., *P. abies*) into three groups: a southern group consisting Alpine, Carpathian and central European populations, a northern group made of Fennoscandian populations and, a third group with central European and Baltic populations while eastern populations (i.e., *P. obovata*) were separated into northern and southern groups along the southern border of west Siberian taiga.

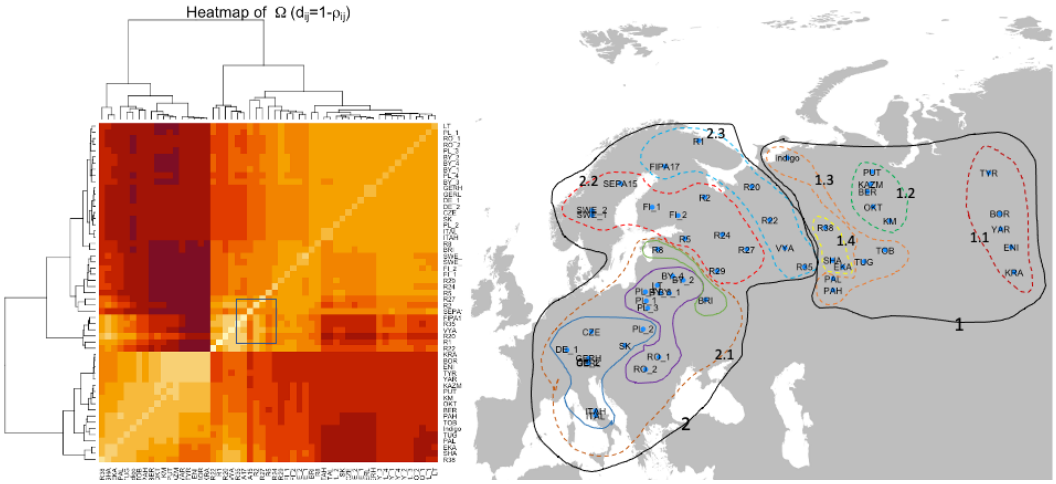

Fig. 1. Clustering of populations of *P. abies* and *P. obovata* based on Bayesian inferences. The genetic distance matrix assumes the allele frequencies of populations diverge from a

Spatial heterogeneity and environmental conditioning of genetic diversity

We first investigated changes of nucleotide diversity (π) across the whole range of the species. Globally, π ranges from 0.0019 to 0.00255, the highest values found in North-Eastern range for *P. obovata* and Southern Scandinavia for *P. abies*. Overall, *P. obovata* populations exhibit higher π values than *P. abies*, probably reflecting more stable distribution through time and more continuous distribution through space (Fig. 3). In *P. obovata*, a clear shift in π match the location of the Ural Mountain, which likely limits the geneflow. Pockets of high diversity are found in the Southernmost range of *P. obavata*, west of the Urals, probably reflecting refugia during ice age. While the overall genetic diversity within *P. abies* also ranges between 0.002 and 0.0025, the northern and southern most populations had the lowest nucleotide diversity. Despite the fact that southern locations in Italy and the Alpine mountains region have been refugia for Norway spruce during the ice ages, the current relative isolation of the populations because of the topography, probably explains the relatively lower genetic diversity. On the other hand, the northernmost populations of *P. abies* in Sweden harbor the lowest genetic diversity. These populations are also the youngest and the low π probably reflects colonization front. Nevertheless, the highest π value are found in Southern Scandinavia, also recolonized after the LGM. Besides this area harboring the optimal niche conditions for Norway spruce (see below), high genetic diversity could be the result of the numerous breeding programs that takes place in both Norway and Sweden where genotypes from the whole range of the species were planted in the 1950's. Finally, populations located in contact zones (e.g., in Scandinavia between the Northern and the Southern range) or located within the large hybrid zone between *P. abies* and *P. obovata* exhibit higher pi value than close-by populations, exhibiting the effect of introgression and/or admixture on genetic diversity.

We further investigated whether part of the observed pattern of genetic differentiation could be due to local adaptations using *pcAdapat*, a genome scan method to detect outlier SNPs exhibiting a higher degree of the differentiation than the genetic background while controlling for population structure. As expected, we detected 1650 SNPs, clustered into specific area of the genome (Supp Fig. 3) suggesting that natural selection shaped genetic diversity on top of population movement and demography history.

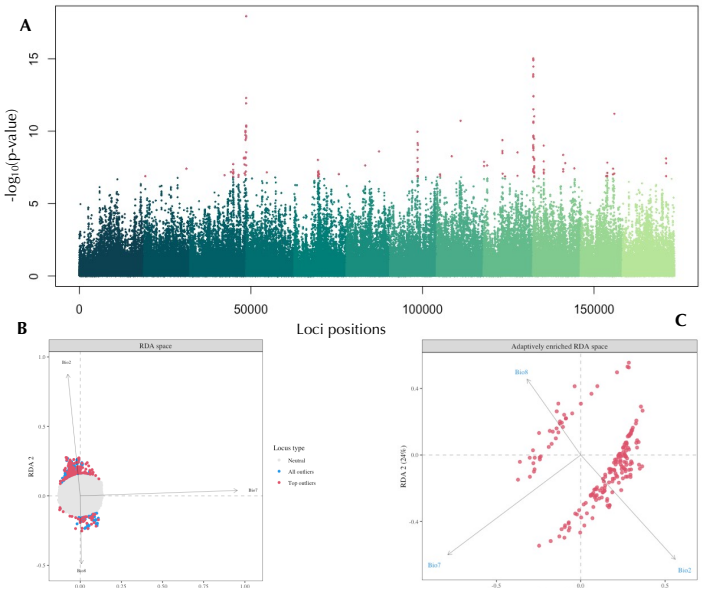

Fig. 2. The enrichment of outlier alleles associated to temperature variables; A: The significance values (-log10(p-values)) from the linear regression of allele frequencies and the environmental variables in RDA laid along the genome. The different shades of green color show linkage groups and the red points are the top outliers; B&C: Ordination of adaptive alleles with the respective environmental variables

In order to understand the role of environmental variation in shaping genetic diversity we conducted a redundancy analysis (RDA) with bioclimatic factors as predictors. After an ad-hoc selection to remove high level of correlation between climatic variables, we retained three climatic variables: Bio2, the mean diurnal range in temperature, Bio7, the temperature annual range, and Bio8, the mean temperature of the wettest quarter. While Bio2 mainly varies along latitude, Bio7 and Bio8 mainly reflect continentality and vary with longitude. Together the climatic variables explained 5.4% of the total genetic variation in the RDA. Still, we detected 1548 outlier loci significantly associated with at least one of the bioclimatic variables out of which 300 were considered top outliers based on the overlap of a simple RDA model and climatic model (see Capblancq & Forester, 2021 for details). These top outliers clustered together in various region of the genome (Fig. 2). Outlier SNPs showed substantial congruence with the enrichment observed in *pcAdapt* (82 % overlap) indicating that part of the allele frequency variation observed among populations is driven by environmental heterogeneity. Finally, we derived an *adaptive index* (see materials and methods) to capture spatial distribution of population adaptiveness (Fig. 6). While population at both extreme of the range show the highest value of adaptiveness (strongly positive or negative values, Fig. 6) populations located within the hybrid zone exhibit intermediate values indicating lower sensitivity to environmental constraints compared to the eastern and western distributions.

Environmental preference, historical niche movement and genetic refugia

Using ordination of climatic ranges of each species from the occurrence data, we defined the niche envelop of the two species in order to contextualize the niche optima of the two species. The range of environmental preferences varied substantially between the two species albeit with considerable overlap (CEG: non-parametric environmental gradient Fig. 5A). Interestingly, the peaks of the two niches were far from each other in our environmental gradient analysis although the overall niches showed small overlap. Niche modeling for the current distribution of the two species shows slight spatial overlap of the suitable niche in the North European Russia (*sensu* TDWG classification) (Fig. 4). PCAs of climatic niche space also revealed an overlap between the two species, suggesting that marginal populations of both species are adapted to similar environmental conditions (Fig. 5). Further, when hybrid populations

are considered in the analysis, the overlap becomes wider, suggesting niche expansion owing to hybridization.

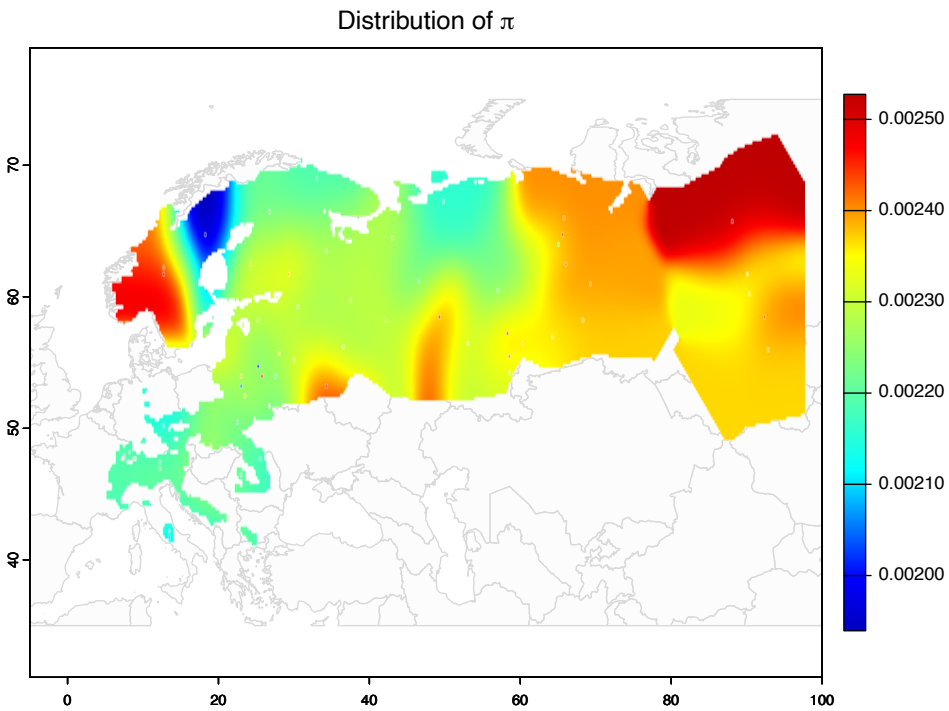

Fig. 3. The distribution of nucleotide diversity (π) throughout the complete distribution range of the two species; The points in the map show the actual π values obtained for each population which were used in nearest neighbor extrapolation to create the map (if a point is invisible on the map where there supposed to be a population, this indicates that the extrapolation completely matches the actual value).

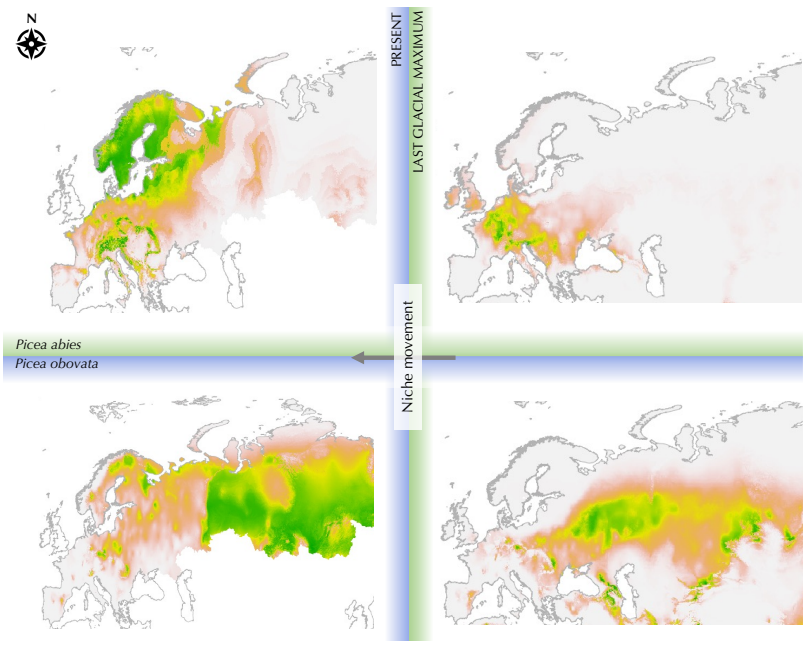

Fig. 4. Distribution of suitable habitat/niche for *P. abies* and *P. obovata* at present and during the last glacial maximum (LGM), showing the niche movement from the past to present, determined by maxent modeling of the niche optima.

To shed light on spatial variation in nucleotide diversity, we used niche modelling to infer species' suitable habitat during LGM (~25,000 years ago) and mid-Holocene (~4,000-10,000 years ago Fig. 4 & Supp. Fig. 4). It confirmed that the southern range of *P. abies* (e.g., Alpine, Carpathian and western European forests) harbored suitable habitat and must have served as refugia during the last glacial maximum. As the climate warmed up, the species recolonized the higher latitudes to the current distribution. Niche modeling for before the Last glacial maximum, specifically for the interglacial time period (i.e., ~140,000 years ago) shows that optimal habitats for *P. abies* existed in the northern most regions of the current distribution (e.g., northern Sweden and Norway) as well as in the Alpine region. The distribution of Norway spruce thus followed the movement of its niche during cycles of glaciation which drastically affected population connectivity. Contrastingly, the range of suitable habitat for *P. obovata* changed to a much lower extent during glacial cycles. It kept a wider distribution than *P. abies* and an almost continuous range. Interestingly, the range of suitable habitat for the two species overlapped regularly during glacial cycle, and in particular in the western Russian forests during LGM. This may have allowed the two species to hybridize and exchange genetic material on several occasions.

Genetic offset and resilience to climate change

Finally, we investigated the potential for current populations of both species to cope with climate change. To do so, we defined the adaptiveness of populations to future climate as the allele frequency mismatch between the present and predicted values under future climatic scenarios, hence the "genetic offset." Risk of non-adaptiveness (RONA: Restalb et al. 2016) measures the allele frequency change necessary for future climate based on a linear regression of current values. We calculated RONA for three bioclimatic variables using projection for year 2080 (i.e., Bio02, Bio07, Bio08). Overall, RONA indicates relatively high adaptiveness to all bioclimatic variables where there is high genetic diversity (Figs. 7A&B), meaning that genetic diversity sheltering adaptive potential in populations. We also identified populations from central Europe and at the Southernmost range of *P. abies* as those to be at the higher risk of extinction, except in the Alpine Mountain that clearly appears to be a refugia during, glacial period but also under warmer conditions.

More interestingly, for both species, the risk of non-adaptedness is the lowest in the hybridizing zone. This further supports the idea that admixture increases genetic diversity but also ecological niche breath facilitating species adaptation to future climatic conditions. Even though populations of the Siberian spruce have the highest overall genetic diversity (pi range 0.0022-0.0026), they still show higher risk of non-adaptiveness than the hybrid populations. Finally, we crossed the information of the genotype-environment-association study with that of the RONA. About two third of the SNPs detected as outlier in the RDA are among the SNPs with the highest RONA values. It means that the SNPs responsible for local adaptation pattern to current climatic conditions could be a disadvantage on the long term to respond to climate change.

Discussion

There is ample evidence now that the current global climate change will affect biodiversity negatively at all scales (see Altieri & Gedan, 2015; Walther et al., 2002; Williams et al., 2021). Population level changes in allele frequencies provide species to innovate adaptation to changing climates and prevent extinction (MEESTER et al., 2018). This is often observed through species' adaptations to their local environment and reflects species' potential for future climate change resilience (Sang et al., 2022). However, detecting such environment associated alleles require whole genome sequencing of many populations and/or long running common garden experiments. This is however far from being practical for species with long generation times. Here, in the present study, using exome capture sequences, we tested multiple methods to assess local adaptation and climate resilience in Norway spruce and Siberian

spruce. We show that local adaptation in conifers can be detected through allele frequency variation, population level ecological preferences, and historical niche movement. Moreover, we show evidence that recurrent admixture and hybridization between Norway spruce and Siberian spruce provided populations in the contact zone with better ability for climate change resilience, and this also allowed us to identify genetically isolated populations at risk under current climate change.

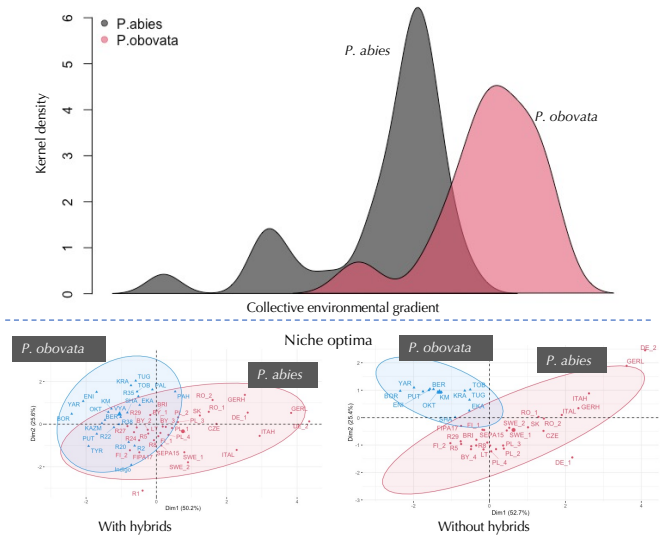

Fig. 5. Environmental preference of Norway spruce and Siberian spruce; A. Collective environmental gradient (following Karunarathne et al. 2018): the sum of transformed environmental variables (i.e., Bio2, Bio7 and Bio8) for all populations plotted against Kernel density; B&C. Niche optima of the two species (following Bronnimann et al. 2016).

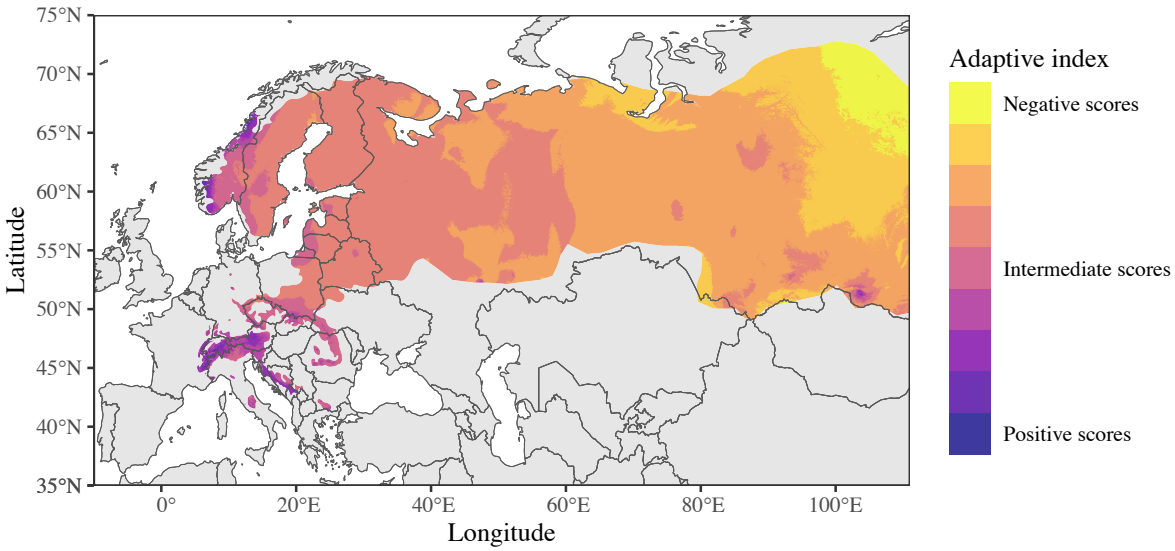

Fig. 6. The spatial distribution of genetic adaptiveness (local adaptation) of the Norway spruce and Siberian spruce. Adaptive index is the similarity/dissimilarity of genetic adaptiveness in populations; therefore, negative scores and positive score depicts the opposite adaptiveness on a continuous spectrum (Capblanqc et al. 2021).

Our analysis on niche optima movement of Norway spruce agrees with fossil records and ancient DNA analyses (Brewer et al., 2017; L. Li et al., 2022; Nota et al., 2022; Parducci et al., 2012); populations of Norway spruce and Siberian spruce traced their optimal niches during glaciation cycles and the species distribution modeling for the LGM and the mid-Holocene (see supp Fig. 4) predicted the gradual movement of the two species to and from their southern refugia. This is of course no surprise since many species in temperate regions followed the same path (Feliner, 2011; Schönswetter et al., 2005; Sommer & Nadachowski, 2006). Niche centrality suggests that a species performance is best at its optimal niche (also niche centroid) conditions (see Lira-Noriega & Manthey, 2014). Although niche center of a species may or may not be the geographical center of the species, it hypothesizes that the genetic diversity in the niche center is higher than the peripheral populations (Manel & Holderegger, 2013; Pironon et al., 2015). Our results however, show congruence to niche centrality to a certain extent, especially in the case of Norway spruce. We recognized southern Scandinavia as the niche centroid of *P. abies* (Fig. 5: see the populations in the center of eigen ellipses) and populations in this region shows the highest nucleotide diversity (Fig. 3). On the other hand, *P. obovata* did not show the same pattern; Instead, ancestral populations of Siberian spruce seem to harbor more genetic diversity while the niche centroid points to northern Ural Mountains. Nevertheless, more sampling to include as much of the distribution of Siberian species is needed to draw better inferences on the niche centrality and the genetic diversity of *P. obovata.* It is also imperative to mention that the currently observed high genetic diversity of *P. abies* in the southern Scandinavian forests is also a result of multiple breeding programs carried out by the Swedish/Norwegian governments and associated companies that brought several different gene pools from Alpine and Carpathian regions (Chen et al., 2019; Milesi et al., 2019).

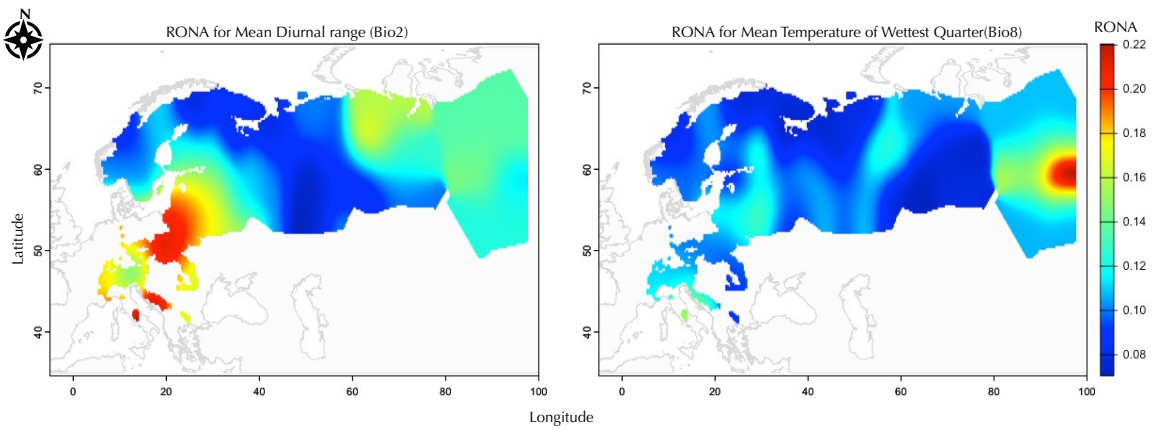

Fig. 7. The map of RONA (Risk of nonadaptedness) for Norway spruce and Siberian spruce. RONA was assessed according to Rellstab et al. 2016, using the coefficient of variation from the linear regression of present environmental variables and allele frequencies.

A crucial finding of present analysis is that recurrent admixture and hybridization between *P. abies* and *P. obovata* has resulted in high genetic diversity and climate change resilience in the contact zone (Fig. 7). Moreover, the alleles associated environmental variation and thus local adaptation from both species are also found in the hybrid zone populations. There are examples of such beneficial changes in species due to hybridization; for instance, increased diversity and infections in *Schistosoma haematobium* (Teukeng et al., 2022), northward invasion of Knotweed in North America (Gillies et al., 2016), and hybridization of *Ulmus pumila* increased genetic diversity and dispersal ability in new habitats (Zalapa et al., 2010). Hybridization can contribute to favorable traits than mutations while mutations are slow to be selected to novel conditions (Loren H Rieseberg, 1997; Taylor et al., 2015), especially in species

with long life span such as Spruce. Further, hybridization can boost range expansion of a species in two ways; 1) sustaining peripheral populations size and allow favorable variation to occur, 2) introgression can transfer favorable alleles from the resident populations to the peripheral populations (Pfennig et al., 2016). In addition, recurrent hybridization may result in parallel cases of the specific allele acquisition of loci underlying local adaptation and the subsequent spread of the species. The resulting range expansion in turn can further enhance genetic diversity in a feedback loop (Barrett & Schluter, 2008; Sexton et al., 2009). Although range expansion/niche movement initially results in higher genetic diversity than before, continuous shift may result in loss of genetic diversity due to selective pressures (Pauls et al., 2013).

Nevertheless, the genetic offset revealed by local adaptation exposed the vulnerability of spruce populations to future climatic changes, especially of the isolated populations of Norway spruce in its southern distribution where it served as refugia during glaciation. This however, needs further confirmation through assessment of the fitness changes in populations (temporal studies). Similarly, we only studied selected gene regions of interest based on their assumed role in plant adaptation. Other polygenic genes may have been involved and whole genome assessments will provide better insights on polygenic nature of the local adaptation. Furthermore, it is important to include both neutral and non-neutral alleles for local adaptation and studying genetic background for future resilience as both may carry information (Pauls et al., 2013).

Materials and methods

Sampling, genetic material, and SNP calling

The study populations come from a large-scale demographic analysis uncovering the historical demography and spatial population structure in the two closely related Norway spruce (*Picea abies*) and Siberian spruce (*Picea obovata*) (publication in preparation). Leaf needle samples of 546 individual trees from 55 populations were collected representing five predetermined geographic groups (including introgressed individuals and putative hybrid populations: following Chen et al. 2019, Li et al. 2022, and Nota et al. 2022; see map Fig. 1) and genome DNA was extracted for sequencing. Paired-end Illumina libraries were constructed and sequenced by RAPiD Genomic, USA using 40,018 exome capture probes targeting 26,219 genes (see supplementary info. for details).

Clean sequence reads were aligned to *P. abies* reference genome (Nystedt et al., 2013) with BWA (H. Li & Durbin, 2009) and individual genotypes were identified using GATK HaplotypeCaller (Van der Auwera & O'Connor, 2020) followed by SNP calling across all smaples with GenotypeGVCFs. Following hard-filtering of SNPs (QD < 2.0, MQ < 40.0, SOR > 3.0, QUAL < 20.0, MQRankSum < -12.5, ReadPosRankSum < -8.0, and FS > 60.0), variation calls with minor allele frequency higher than 0.05 were retained, which resulted in 450,000 SNPs in the final dataset. This includes both neutral and non-neutral alleles (see supplementary info. for more details).

Climatic data selection

Environmental variables for current conditions were downloaded from WorldClim 2.0 database at 30 arc seconds resolution (Hijmans et al., 2005). They are annual averages of both temperature and precipitation related variables. Climatic records at population locations were extracted with TERRA R package (Hijmans et al., 2022). In order to avoid multi-collinearity and model overfitting, we performed pairwise Pearson-correlation between all the bioclimatic variables, sequentially removing the variable with the highest correlation coefficient, r, until it reached r_{max} = 0.6. Further, to make sure multi-collinearity is minimum in the composite variables of RDA, we assessed the variance inflation factor (VIF) and retained the environmental variables for which the VIF was lower than five, as recommended

by Capblancq & Forester (2021). We used this final set of environmental variables (predictor variables hereafter) for all the other downstream analyses.

Bayesian analysis and genetic similarity/distance

We used Bayesian inference to estimate the empirical patterns of covariance in allele frequencies between populations to determine population structure and shared demographic history. Under the null model, the allele frequency in each population deviates from a hypothetical ancestral (or global) allele frequency due to genetic drift (Coop et al., 2010; Günther & Coop, 2013) (Coop et al. 2010, Günther and Coop 2013). Populations deviation may covary, allowing some populations to be more closely related to each other due to shared history or gene flow. To estimate such covariance, we assume that the population frequency transformation of an allele across populations has a multivariate normal distribution. These methods are implemented in BayPass software package and we used BayPass (v2.2 – BayPass INRA©) for generating the covariance matrix. In our analysis, to minimize the effect of linkage disequilibrium, we divided putatively neutral SNPs into subsets of 20,000 randomly selected SNPs and the covariance (omega) matrixes were generated using 50,000 MCMC iterations for all subsets. Only 1000 matrices were retained after post-burn in and they were averaged per subset followed by averaging all the sub-matrices.

Identification of alleles putatively involved in local adaptation

To study the genetic architecture of local adaptation in Norway spruce and Siberian spruce, we ran genome scans to detect outlier-loci (i.e., loci showing an excess of genetic differentiation in comparison to the rest of the genetic background) using the principal component-based outlier detection method, "pcadapt", implemented in the R package "pcadapt" v.4.3.2 (Luu et al., 2017; Privé et al., 2020). Briefly, a Z-score matrix, obtained from regressing all SNPs to PCs, is used to produce one multivariate distance for each variant. Assuming that SNPs variation along principal component axes largely reflects demographic processes, this method allows controlling for population structure when testing for local adaptation. In our analysis, in order to control for false positive risk discovery associated to multiple testing, we used FDR q-value < 0.1 to obtain the significant SNPs putatively involved in local adaptation.

Redundancy Analysis (RDA) is an asymmetric canonical analysis that combines ordination and regression, where multiple regression on the response variable (i.e., allele frequencies) and explanatory variables (climatic variables) is followed by ordination of fitted values of the regression (Van Den Wollenberg 1977). We used Redundancy Analysis (RDA) to find the main climatic variables that explain the most of variance in allele frequencies between the two species and to identify candidate loci associated to environmental variation.

In the special case of partial RDA (pRDA), additional explanatory variables (covariates) are used to control for various confounding effects (see Capblancq et al., 2018; Capblancq & Forester, 2021). This aspect of RDA is extremely useful in association analyses in order to control for the confounding effect of factors that are not the focus of the study, such as population structure and geographic distance. Thus, to isolate different drivers of genetic variation, in addition to a full model (including all predictor variables), we performed three independent pRDA models controlling for geographic distance, population structure, and environmental conditions. We adopted the method described in Capblancq & Forester (2021) where the Mahalanobis distance of each locus to the center of the RDA is calculated using two axes (K=2) of partial RDA (i.e., number of axes that explain more than 60% variation; following Capblancq et al. 2021), followed by obtaining the top outlier SNPs from this distance matrix. For geographic distance, the cartesian distance of populations was used as a proxy; to control for

population structure, we used the first three axes of a PCA performed on the set of putatively neutral loci.

Genetic diversity distribution among populations

In order to find genetically informed "climatic groups" of both species, we combined two sets of data: i) adaptively enriched genetic space scores from RDA – the RDA scores represent local adaptation in populations derived from allele frequencies, ii) bioclimatic data – this data set represents the environmental variability of populations after removing of multi-collinearity. The former was used as a proxy for population level adaptations to local climatic conditions and the latter to explain the spatial variation of local conditions. A k-means clustering was performed for total within sum of squares to determine the optimal number of genetically informed climatic clines. This was performed separately for tentative hybrid and non-hybrid populations to avoid cluster overlap that could arise from specific adaptations in hybrid populations. In non-hybrid populations, we identified five distinct climatic groups while there were only three within putatively hybrid populations. After obtaining the optimal number of clusters as five, a second k-means clustering was performed with K=5 for all populations (i.e., including hybrid and non-hybrid populations) to determine the climatic group membership of each population. This step was performed specifically to group the putative hybrid populations with their closest non-hybrid populations so as to identify their closest climatic groups.

We calculated nucleotide diversity (π: Nei and Li, 1979) to assess population-level genetic diversity using 453,278 SNPs (both neutral and non-neutral sites) with POPGENOME R package (Pfeifer et al., 2014). Extrapolation of the π values to the whole distribution of the two species was done using custom-R scripts (available in the GitHub repository) with nearest neighbor interpolation and was mapped to visualize the spatial distribution of genetic diversity of the two species.

Using the output fron the pRDA, we computed an *Adaptive index (Ai)* as implemented by Capblancq & Forester (2021) from Steane et al. (2014). *Adaptive index* is the genetic adaptive similarity or distance among populations. Basically, we used the candidate SNPs identified from the environmental RDA analysis as a multivariate response against RDA scores of the environmental variables to calculate the *Ai*. Once the climate variable score [a] (RDA loading) is obtained, the standardized climate variable value [b] for each grid cell of the range map of a species is used to calculate the *Adaptive index* using the following formula and to predict the *adaptively enriched genetic space* for the distribution range of each species:

$$Adaptive\ index = \sum_{i=1}^{n} a_i b_i$$

where i refers to one variable used at a time in the RDA of n number of significant predictor variables. The *adaptively enriched genetic space* score reflects both individual variable correlation with the genetic variation as well as the interaction between the predictor variables.

Niche expanse, species distribution modeling and historical niche optima movement analysis

The climatic niche of the two species were defined as the ordination space of all the populations with PCA eigenvalues. Therein, a PCA was performed on the selected climatic variables (i.e., Bio8, Bio9, Bio18) for all the populations of *P. abies* and *P. obovata* separately. The optimal niche was determined as the centroid of the eigenvalues and the niche breath was defined as the 95% ellipsoid of the PCA scorings. The analysis was performed with and without hybrid populations to visualize the niche breath overlap. As a complementary analysis, we also used a non-parametric method, collective environmental gradient (CEG; Karunarathne et al. 2018) to assess the total environmental aptitude of each species and

to visualize their overlap. CEG is a single value decomposition approach to determine the composite two-dimensional environmental/niche breach. We performed CEG according to Karunarathne et al., (2018) for the selected bioclimatic variables (i.e., Bio8, Bio9, Bio18).

Species distribution models for the current, mid-Holocene (ca. 6,000 ya), Last Glacial Maximum (LGM, ca. 22,000 ya), Last Inter-glacial period (ca. 120,000 - 140,000 ya), and future climatic scenarios (2021-2041 and 2041-2061) were constructed using maximum entropy (Maxent) modeling (Phillips et al., 2006). The optimal niche for separate species was determined with selected climatic variables (i.e., Bio2, Bio7, Bio8) using *maxent* function of *dismo* R package (Hijmans et al., 2016). Maxent uses presence-only data to estimate the probability distribution of occurrence based on environmental constraints (Phillips et al., 2006). In order to test the models and to facilitate more accurate prediction of species distribution, we downloaded species occurrence data for *P. abies* and *P. obovata* from GBIF (www.GBIF.org) and filtered the data to include only confirmed and natural occurrence of the species. occurrence data were then subsampled to retain only one occurrence per grid cell of 1 arc minute. The final dataset consisted of 619 occurrences (*P. abies*: 288; *P. obovata*: 331), hybrid populations have been excluded. All bioclimatic variables were downloaded from WorlClim 1.4. database at 30 arc second resolution. The climatic variables for Mid-Holocene, LGM, and Last inter-glacial were downloaded from the model CCSM4 and the future climate variables were downloaded for ACCESS-CM2 model. The projection of past and future niche distribution of the two species was done using the *predict* function of *dismo* R package. All the models were evaluated using area under the operating curve (AUC) and only the models with AUC of at least 0.85 were considered.

Assessment of genetic off set and resilience to future climatic conditions

Genetic offset of an entity (e.g., population) is the allele frequency difference between the current and required frequency in the future to survive in the future climatic scenarios. We calculated the genetic offset of our populations with risk of nonadaptedness (RONA) as in Rellstab et al. (2016). RONA is the average theoretical change in allele frequency at climate-associated loci required to match future climatic scenarios. This is established by regressing the selected loci allele frequencies with the selected environmental variables and using the regression coefficients to predict the expected allele frequencies of the respective loci to future conditions. The difference between the two allele frequencies is the risk of nonadaptedness. Here, we first performed linear regression on all loci with the selected environmental variables (i.e., Bio8, Bio9, Bio18) and kept only the loci that showed significant association (p-value < 0.05) to the three environmental variables. Then we obtained the intersection between these alleles and the top outliers from the RDA analysis for the RONA analysis. To avoid linkage between selected loci, we filtered loci within 10,000 base pairs in the same scaffold; the locus with the highest R^2 from the regression was retained. In total, ~25,000 candidate SNPs for environmental association were kept for the analysis. Finally, we used nearest neighbor interpolation (as in Rukundo & Cao 2012: custom scripts available in the GitHub repository) to predict the RONA values for the entire distribution of the two species for spatial visualization (Fig. 7).

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