Past climate-driven range shifts and population genetic diversity in arctic plants

Loïc Pellissier1,2,3,a, Pernille Bronken Eidesen4,a, Dorothee Ehrich5, Patrice Descombes1,2,3, Peter Schönswetter6, Andreas Tribsch7, Kristine Bakke Westergaard8, Nadir Alvarez9, Antoine Guisan9,10, Niklaus E. Zimmermann2,3, Signe Normand11, Pascal Vittoz10, Miska Luoto12, Christian Damgaard11, Christian Brochmann13,3, Mary S. Wisz14,b and Inger Greve Alsos15,b

ABSTRACT

Aim High intra-specific genetic diversity is necessary for species adaptation to novel environments under climate change, but species tracking suitable conditions are losing alleles through successive founder events during range shift. Here, we investigated the relationship between range shift since the Last Glacial Maximum (LGM) and extant population genetic diversity across multiple plant species to understand variability in species responses.

Location The circumpolar Arctic and northern temperate alpine ranges.

Methods We estimated the climatic niches of 30 cold-adapted plant species using range maps coupled with species distribution models and hindcasted species suitable areas to reconstructions of the mid-Holocene and LGM climates. We computed the species-specific migration distances from the species glacial refugia to their current distribution and correlated distances to extant genetic diversity in 1295 populations. Differential responses among species were related to life-history traits.

Results We found a negative association between inferred migration distances from refugia and genetic diversities in 25 species, but only 11 had statistically significant negative slopes. The relationships between inferred distance and population genetic diversity were steeper for insect-pollinated species than wind-pollinated species, but the difference among pollination system was marginally independent from phylogenetic autocorrelation.

Main conclusion The relationships between inferred migration distances and genetic diversities in 11 species, independent from current isolation, indicate that past range shifts were associated with a genetic bottleneck effect with an average of 21% loss of genetic diversity per 1000 km−1. In contrast, the absence of relationship in many species also indicates that the response is species specific and may be modulated by plant pollination strategies or result from more complex historical contingencies than those modelled here.

Keywords

Arctic plants, climate change, climatic niche, Last Glacial Maximum, migration, species distribution models

INTRODUCTION

Climate warming is shifting the geographical ranges of many species to higher latitudes or elevations. Meta-analyses have estimated a median poleward animal species migration rate of 16.9 km decade−1 over the last century (Chen et al., 2011). Estimates for plants have been documented only along elevation with up to 29 meters decade−1 (Lenoir et al., 2008). Terrestrial isotherms have been displaced at an even faster rate with a median velocity of 27.3 km decade−1 over the last 50 years (Burrows et al., 2011), and it is foreseen that many species will not be able to track the similar or
faster pace of climate change expected in the future (Corlett & Westcott, 2013). To remain viable, many species will depend on both migration and their potential to adapt to novel climatic conditions (Corlett & Westcott, 2013; Jump et al., 2009; Hoffmann & Sgrò, 2011; Pauls et al., 2013). Migration and adaptive potential are tightly linked (Reed & Frankham, 2003) since adaptive potential depends on genetic diversity, which is related to species’ demographic history, range contractions and expansions following climate changes (Excoffier et al., 2009). A better understanding of species vulnerabilities to genetic erosion is needed to evaluate demographic consequences of climate change (Pauls et al., 2013). Investigating species historical responses might provide clues on future outcomes of ongoing climate change.

Migration allows movement of alleles, both among existing populations and at the advancing front of a species range when colonizing new areas (Bialozyt et al., 2006; Excoffier et al., 2009). Successive founder events during colonization of new areas typically lead to decreasing genetic diversity in the leading edge populations (Hewitt, 1996; Excoffier et al., 2009; Dlugosch & Parker, 2008; Yannic et al., 2014). Such genetic erosion is predicted as a consequence of recolonization after the Quaternary glaciations (Espindola et al., 2012; Yannic et al., 2014). Since the Last Glacial Maximum (LGM), when massive ice sheets covered large parts of North America and Eurasia, many species, which survived in ice free refugia, progressively colonized the distribution range they currently occupy as the ice retreated (Taberlet et al., 1998; Hewitt, 2000; Eidesen et al., 2013). Historical range expansions left a signature of decreasing genetic diversity, which is expected to be more marked with increasing migration distance (Excoffier et al., 2009; Yannic et al., 2014). In contrast, populations in or close to areas where the species has persisted over long periods of time, including the glacial periods, usually have preserved more genetic diversity (Hampe & Petit, 2005; Yannic et al., 2014). While the link between migration distance and genetic erosion has been evaluated in a few species (Prugnolle et al., 2005; Yannic et al., 2014), our knowledge regarding the variability of responses among species remains limited.

All species are generally expected to lose genetic diversity during range shift (Excoffier et al., 2009). Nevertheless, genetic erosion will be influenced by the level of gene flow, which can be highly species specific (Thiel-Egenter et al., 2009). In plants, gene flow results from both pollen and seed dispersal, and differences in genetic diversity among populations are expected to be related to both the frequency of reproduction and the distances over which pollen and seeds typically disperse (Hamrick & Godt, 1996; Bialozyt et al., 2006; Thiel-Egenter et al., 2009). Also, local conditions affecting establishment and survival will influence demographic processes and thus levels of genetic diversity (Thiel-Egenter et al., 2009). Gene flow will also be indirectly influenced by factors like growth form, as plant height strongly influence dispersal distance (Thomson et al., 2011), and niche breadth, which influence dispersal efficiency (McCauley et al., 2014). As a consequence, variable degree of genetic erosion among species might be related to different life-history traits, including reproduction, morphology and species abundance patterns. Previous studies have shown that the spatial variability in genetic diversity among populations is linked to plant life-history traits (Thiel-Egenter et al., 2009). However, there is no empirical comparison across a large number of plant species to assess the generality of the theoretical prediction of loss of diversity via post-glacial migration.

To calculate a species’ post-glacial migration distance, the location of putative glacial refugia needs to be identified. Classically, the location of glacial refugia have been inferred from fossils (e.g. Frenzel, 1968; Tarasov et al., 2000; Birks & Willis, 2008) or molecular phylogeographical evidence (e.g. Schönswetter et al., 2005; Eidesen et al., 2013). However, most species do not have fossil records with sufficient spatial or taxonomic resolution (e.g. species-level identification of pollen) to identify glacial distribution. Moreover, sampling for molecular phylogeography studies are usually limited to extant populations (Gavin et al., 2014; but see Lorenzen et al., 2011). In contrast, species distribution models (SDMs) relate species range information to current climatic conditions (Guisan & Zimmermann, 2000) and model forecasts can accommodate high-resolution, species-specific responses to climatic change (Waltari et al., 2007; Yannic et al., 2014; Gavin et al., 2014). Although SDMs rely on assumptions of causal species-climate relationships, and that these relationships remain static despite changed environment and biotic interactions (Guisan & Thuiller, 2005; Gavin et al., 2014), SDMs provide useful approximations of the potential distribution of the species under past climatic conditions (Waltari et al., 2007; Forester et al., 2013).

Here we investigated the relationship between genetic diversity at the population level and migration distance since the LGM in 30 cold-adapted plant species with distinct tolerance to temperature and precipitations conditions. We calibrated the climatic niche of each species, using SDMs, which were used to infer the location of glacial refugia. We computed the inferred migration distances from refugia to current location of the populations and tested whether the genetic diversity loss per unit of migration distance was related to plant traits associated with important demographic and ecological functions (including life-form, seed dispersal, and pollination mode). We expected a general decrease in within-population genetic diversity with increased migration distance since the LGM, but that this loss would vary across species according to their life-history traits. Finally, we discuss how examining the way species have responded to past climate change can provide novel insights into ongoing climate change.

**MATERIALS AND METHODS**

**AFLP data**

We analysed 30 plant species typically occurring in the bio-climatic zones at the tree line and above, i.e. the alpine and Arc-
tic zones. For each species, leaf samples were collected from 5–11 individuals per population and dried in silica gel (see Table S1 in Appendix S1 in Supporting Information). A standard amplified fragment length polymorphisms (AFLPs) procedure was followed (Alsos et al., 2012, 2015). In total, we analysed 10,073 individual plant samples across 1295 populations for genetic diversity. On average, 336 individuals (range: 73–958), from 43 populations (range: 14–131) were collected per species (see Table S1 in Appendix S1). The full details of data collection and genetic structuring have been published elsewhere (Alsos et al., 2012; Espíndola et al., 2012; Alsos et al., 2015). Intra-population genetic diversity was estimated as the average proportion of pairwise differences (a measure identical to gene diversity/expected heterozygosis for binary markers such as AFLPs; Kosman, 2003).

Species distribution modelling

Using SDMs coupled with past climatic reconstructions (Hijmans et al., 2005), we modelled species-specific climatic niches and reconstructed the migration distance from inferred glacial refugia. Species distribution models were calibrated using the Hultén and Fries distribution maps (Hultén & Fries, 1986) or occurrences from Global Biodiversity Information Facility (www.gbif.org) when ranges were unavailable (i.e. for Arenaria humifusa, Juncus biglumis, Sagina cespitosa, Saxifraga rivularis, see Figs S1 & S2 in Appendix S2). Range maps were related to Worldclim bioclim parameters including (1) total annual precipitation, (2) summer precipitation (months 6, 7, 8), (3) winter precipitation (months 12, 1, 2), (4) annual mean temperature, (5) summer mean temperature, and (6) winter mean temperature as done in Espíndola et al. (2012). Those variables represent known physiological limits to alpine plant distribution including water and energy availability during the growing season and protective snow cover during the winter season (Körner, 2003). One thousand presence points were selected randomly across the species ranges and pseudo-absences were generated by selecting 10,000 random points across the Northern Hemisphere following the recommendation of Wisz & Guisan (2009) and as implemented in Yannic et al. (2014).

Four statistical methods were used to calibrate SDMs: generalized linear models, generalized additive models, boosted regression trees and random forest. To evaluate the models, we calculated the Boyce index (Hirzel et al., 2006) by random split sampling of 70% of the data for calibration and 30% for evaluation, and this was repeated 10 times. Calibrated models were then used to project species’ potential distribution under current and past climates. We used palaeoclimatic maps at a 15 km spatial resolution from three Earth-System Model coupling the ocean, the atmosphere and the land surface (general circulation model, GCMs, CCSM4, MIROC-ESM, MPI-ESM-P available from http://cmip-pcmdi.llnl.gov/cmip5/ processed on worldclim.org) hindcasted to LGM (21,000 years ago) and the mid-Holocene (6,000 years ago). We calculated an average of the four modelling techniques for each projection. We transformed the projected probabilities into presences/absences using the thresholds that maximize percentage of presences and absences correctly predicted. In addition, we considered as unsuitable those regions known to have been covered by ice during each time period (thus ignoring potential micro-refugia on e.g. nunataks). We obtained the putative location of the refugia for each of the three GCMs considered. For two species with available fossil records at the LGM (Dryas octopetala from the European pollen database, Binney et al., 2009; Salix herbacea from Alsos et al., 2009), we evaluated the model performance to predict the location of fossils records using the Boyce index (Yannic et al., 2014).

Predictors of genetic diversity

We computed the migration distance from refugia needed to track suitable habitat from the LGM, through the mid-Holocene and to current distribution range for each of the GCM considered. For each time-step (LGM, mid-Holocene, current), once a given cell became suitable for the species in the time frame (t + 1), we summed the minimum distance from the closest cell suitable at time t. We obtained the total distance required to recolonize a given cell from the LGM refugia through the Holocene and to the current distribution. Because difference in genetic diversities among populations may result from current limited gene flow and not necessarily be associated with post-glacial range dynamic, we computed a variable representing the current level of isolation of populations. For each cell of the current species potential distribution, we computed the mean distance to the 1000 closest suitable cells. For each population with genetic information, we extracted the value of past migration and current isolation from the rasters.

For each species, we computed linear regressions between genetic diversity and distance from refugia and current population isolation accounting for spatial non-independence among sampled locations using spatial autoregressive models (SARs) as suggested by Kissling & Carl (2008). We used a spatial weight matrix with neighbourhoods defined as all cells within 2000 km of the focal cell, and applied a Moran’s I global test to determine whether residual autocorrelation persisted in the SAR models. We calculated the standardized slope coefficient (beta) of each predictor in the SAR models.

In addition, we quantified the relative loss of genetic diversity per distance unit for each species with a significant relationship in the SAR models. Because maximum intrapopulation genetic diversity differed between species, we standardized the slope coefficient by the maximum genetic diversity for each species to obtain the relative decrease in genetic diversity (%) per unit of distance expressed per 1000 km.

Meta-analysis of association with species traits

To test for the effect of plant traits on the species-specific association between migration distance and genetic diversity,
we related the standardized slope of the distance from refugia from the SAR models to those plant traits that are expected to influence population size or genetic exchange through seed dispersal or pollen (growth form, reproduction, pollination, dispersal, see Table S2 in Appendix S1) using the mcmcgglmm package in R (Hadfield, 2010), which accommodates random effects. Because we had three estimates per species (one for each GCM), we included species as the random effect in the models and GCM as a fixed effect. We further checked that the relationship between slope coefficients and relevant traits was robust to phylogenetic relatedness by adding species phylogenetic autocorrelation as a second random effect in the model. We used the ‘Daphne’ phylogeny of central European flora (Durka & Michalski, 2012). Four species (Arenaria humifusa, Cassiope tetragona, Saxifraga foliolosa, Sagina caespitosa) were missing in the phylogeny, and thus they were replaced with a congeneric species. We estimated the mean of the posterior distribution of each factor coefficient as well as of the phylogenetic signal ‘lambda’.

RESULTS

Model performances and hindcasted distributions

Most models showed good predictive power when validated using repeated split samples (see Table S1 in Appendix S1) and predicted accurately the fossil distribution of D. octopetala (CCSM4: boyce index bi = 0.71, MIROC-ESM: bi = 0.61, MPI-ESM-P: bi = 0.54). The fossil distribution of S. herbaecea was also well predicted, but with higher variability associated with the GCMs (CCSM4: bi = 0.41, MIROC-ESM: bi = 0.68, MPI-ESM-P: bi = 0.39, see Figs S1 & S2 in Appendix S2 and S3 in Appendix S3). We found considerable variation among hindcasted suitable areas at the LGMs for the 30 Arctic, Arctic-alpine and north boreal species (Figs 1 & 2). North-western Europe was suitable for most species during LGM. Beringia and northern Asia, on the contrary, were inferred to be unsuitable for many of the presently amphi-Atlantic species such as Micranthes stellaris, Sagina caespitosa or Ranunculus glacialis. The area south of the ice in North America, including some locations both in the west and in the east, was inferred to have been suitable for many species during the LGM (Fig. 1, see Figs S1 & S2 in Appendix S2). Distance from refugia was low, where current suitable ranges are close to locations that were suitable and not covered by ice during the LGM such as in Beringia. In contrast, Eastern North America and Greenland, together with Svalbard or Iceland showed high values of distances from refugia as those regions were covered by ice during glacial periods (Fig. 3). We found low variability in migration distance among estimates from the three different GCMs (Table 1, Fig. 1) except for S. caespitosa, which could be explained by a more fragmented extant range possibly more difficult to model.

Relationship between genetic diversity and migration distance

Among the 30 species analysed, 25 showed a negative relationship between migration distance from inferred refugia and level of genetic diversity (11 of them significantly so), indicating genetic erosion (Table 1). Across the species with a significant relationship, on average 21% of genetic diversity was lost per 1000 km of range shift from their LGM. In the most extreme negative cases, migration distance was associated with severe genetic bottlenecks, as in Ranunculus glacialis (−85% × 1000 km⁻¹), Micrantes stellaris (−40% × 1000 km⁻¹) and Arabis alpina (−22% × 1000 km⁻¹), with no diversity left in populations most distant from LGM refugia. In contrast, many species showed no significant relationships with inferred migration distance, with flat relationships and a few positive ones (Table 1). In addition, seven species had a significant relationship between population genetic diversity and current isolation (Table 1).

Figure 1 Stacked climatic suitability (probability of occurrence) of the 30 investigated species during the Last Glacial Maximum (−21 Ky) provided by the 30 model ensembles, with the three general circulation models (GCMs) (a) CCSM4, (b) MPI-ESM-P, (c) MIROC-ESM. Model hindcasting indicates four main disconnected refugia: Central Europe, Beringia, eastern North America and western North America. Blue colour indicates surfaces covered by ice. The numbers on the bar represent the summed suitability values across all species. The three GCMs are largely congruent for Central Europe and western North America, but show more variability in the summed suitability for eastern North America and Beringia.
We found no spatial autocorrelation in the SAR model residual of each species.

**Association with species traits**

Among the different life-history traits tested, we found that only pollination mode was associated with interspecific differences in the rate of genetic diversity shift along a migration gradient (in: post.mean = −0.29; se: post.mean = 0.27, P = 0.23; wi: post.mean = 0.29, P = 0.03), with no effect of GCM (me: post.mean = −0.05, P = 0.28; mr: post.mean = 0.007, P = 0.89). We also ran the models excluding the self-pollination category with low sample size (n = 2), and the significant differences between insect- and wind-pollinated species persisted (in: post.mean = −0.29; wi: post.mean = 0.29, P = 0.03). Nevertheless, the relationship between pollination mode and the rate of genetic diversity shift was only marginally significant in the MCMCglmm model when accounting for phylogenetic dependency among species (in: post.mean = −0.29; wi: post.mean = 0.29, P = 0.0501, λ = 0.27), indicating that the effect of pollination mode is partially associated with a phylogeny signal.

**Figure 2** Maps of species current distribution (in green), together with hindcasted climatic suitability for the species during the Last Glacial Maximum (LGM) computed as the average between the projections using the three general circulation models. Shown are: (a) Betula nana, (b) Carex bigelowii, (c) Epilobium angustifolium, (d) Loiseleuria procumbens, (e) Ranunculus glacialis, (f) Vaccinium uliginosum. The ice cover at the LGM is shown in blue. The figures illustrate how distance between current distribution and past suitable area differs across current species ranges. Other species maps are provided in Appendix S2. Shown observed ranges are based on central distribution shapes of Hultén & Fries (1986).

**Figure 3** Maps of migration distance (expressed in kilometres) since the Last Glacial Maximum (LGM) and sampled genetic locations. Variation in estimated range shifts since the LGM, exemplified with two species (a) Cassiope tetragona, (b) Trollius europaeus. Darker shades of red indicate larger migration distances from refugia. Symbol sizes in green are proportional to intrapopulation genetic diversity. The current ice cover is shown in blue.
them appear to be unable to carry large amounts of genetic variation and to homogenize diversity across their ranges. In the most extreme cases, populations at the forefront of the range expansion have almost no genetic variation left (e.g. populations of *R. glacialis*, *A. alpina*, *M. stellaris*). For those species, our results corroborate the role of successive founder events during migration under past climate change leading to decreasing genetic diversity (Hewitt, 1996; Excoffier et al., 2009). Populations currently close to areas climatically suitable during the LGMs show a much higher genetic diversity, such as populations near the large LGM unglaciated Arctic regions in Beringia (Fig. 2). In agreement with a stronger founder effect in insect-pollinated species colonizing Arctic islands (Alsos et al., 2015), we found that genetic erosion was more pronounced for insect- than wind-pollinated species, although this was only marginally independent from a phylogenetic signal. Ten of the eleven species showing significant genetic erosion (the exception is the selfing *R. pygmaeus*) are insect pollinated. Wind pollination may promote more frequent and more massive genetic exchange over larger distances than insect pollination, and therefore be

**Table 1** Summary of the spatial autoregressive model parameters relating population genetic diversity and the distance from the refugia (migration) as well as current level of isolation (isolation). The means and standard deviations across the three general circulation models (GCMs) of the standardized regression slopes coefficient (beta) are provided. The statistical significance of the relationships computed with a slope z-test (*, < 0.05, when significant for the three GCMs) are shown. For significant relationships, the decrease in genetic diversity per 1000 km relative to the most diverse population observed (rate) is provided.

<table>
<thead>
<tr>
<th>Species or clade</th>
<th>Pollination</th>
<th>Isolation</th>
<th>Migration</th>
<th>Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Angelica archangelica</em> L.</td>
<td>Insect</td>
<td>−0.44 ± 0.08 *</td>
<td>−0.27 ± 0.05 *</td>
<td>−14.27 ± 1.59</td>
</tr>
<tr>
<td><em>Arabis alpina</em> L.</td>
<td>Insect</td>
<td>0.05 ± 0.10</td>
<td>−0.44 ± 0.09 *</td>
<td>−21.58 ± 1.47</td>
</tr>
<tr>
<td><em>Arctous alpinus</em> (L.) Nied.</td>
<td>Insect</td>
<td>0.46 ± 0.09</td>
<td>−0.26 ± 0.09</td>
<td></td>
</tr>
<tr>
<td><em>Arenaria huinifusa</em></td>
<td>Insect</td>
<td>0.36 ± 0.08</td>
<td>−0.08 ± 0.09</td>
<td></td>
</tr>
<tr>
<td><em>Avenella flexuosa</em> (L.) Drejer</td>
<td>Wind</td>
<td>−0.17 ± 0.05</td>
<td>0.31 ± 0.04</td>
<td></td>
</tr>
<tr>
<td><em>Betula nana</em> L.</td>
<td>Wind</td>
<td>−0.58 ± 0.02 *</td>
<td>−0.01 ± 0.02</td>
<td></td>
</tr>
<tr>
<td><em>Carex bigelovii</em> Schkuhr</td>
<td>Wind</td>
<td>−0.37 ± 0.04</td>
<td>−0.37 ± 0.03</td>
<td></td>
</tr>
<tr>
<td><em>Cassiope tetragona</em> (L.) D.Don</td>
<td>Insect</td>
<td>−0.36 ± 0.02 *</td>
<td>−0.34 ± 0.01 *</td>
<td>−39.91 ± 5.00</td>
</tr>
<tr>
<td><em>Chamerion angustifolium</em> (L.) Holub</td>
<td>Insect</td>
<td>−0.18 ± 0.04</td>
<td>−0.19 ± 0.04</td>
<td></td>
</tr>
<tr>
<td><em>Dryas octopetala</em> L.</td>
<td>Insect</td>
<td>0.36 ± 0.09</td>
<td>0.04 ± 0.01</td>
<td></td>
</tr>
<tr>
<td><em>Empetrum nigrum</em> L. s.lat.</td>
<td>Wind</td>
<td>−0.17 ± 0.02</td>
<td>−0.28 ± 0.06 *</td>
<td>−12.72 ± 3.20</td>
</tr>
<tr>
<td><em>Juncus biglumis</em> L.</td>
<td>Wind</td>
<td>0.19 ± 0.13</td>
<td>0.38 ± 0.13</td>
<td></td>
</tr>
<tr>
<td><em>Juniperus communis</em> L.</td>
<td>Wind</td>
<td>−0.36 ± 0.02 *</td>
<td>−0.06 ± 0.02</td>
<td></td>
</tr>
<tr>
<td><em>Loiseleuria procumbens</em> (L.) Desv.</td>
<td>Insect</td>
<td>−0.11 ± 0.06</td>
<td>−0.15 ± 0.02</td>
<td></td>
</tr>
<tr>
<td><em>Minuartia biflora</em> (L.) Schinz &amp; Thell.</td>
<td>Insect</td>
<td>−0.20 ± 0.38</td>
<td>−0.37 ± 0.22</td>
<td></td>
</tr>
<tr>
<td><em>Microstelius fiofolia</em> (R.Br.) G.</td>
<td>Insect</td>
<td>0.31 ± 0.41</td>
<td>−0.33 ± 0.08</td>
<td></td>
</tr>
<tr>
<td><em>Microstelius stellaris</em> (L.) G.</td>
<td>Insect</td>
<td>−0.07 ± 0.02</td>
<td>−0.40 ± 0.06 *</td>
<td>−39.69 ± 8.50</td>
</tr>
<tr>
<td><em>Pedicularis oederi</em> Vahl</td>
<td>Insect</td>
<td>0.12 ± 0.15</td>
<td>−0.07 ± 0.03</td>
<td></td>
</tr>
<tr>
<td><em>Ranunculus glacialis</em> L.</td>
<td>Insect</td>
<td>−0.05 ± 0.02</td>
<td>−0.06 ± 0.04 *</td>
<td>−85.12 ± 6.49</td>
</tr>
<tr>
<td><em>Ranunculus pygmaeus</em> Wahlenb.</td>
<td>Selfing</td>
<td>−0.59 ± 0.19 *</td>
<td>−0.59 ± 0.47 *</td>
<td>−3.51 ± 2.70</td>
</tr>
<tr>
<td><em>Rubus chaamaenorus</em> L.</td>
<td>Insect</td>
<td>−0.33 ± 0.10 *</td>
<td>−0.12 ± 0.23 *</td>
<td>−8.29 ± 5.22</td>
</tr>
<tr>
<td><em>Sagina cepitosae</em></td>
<td>Insect</td>
<td>0.67 ± 0.84</td>
<td>−1.07 ± 0.79 *</td>
<td>−17.07 ± 8.54</td>
</tr>
<tr>
<td><em>Salix herbacea</em> L.</td>
<td>Insect</td>
<td>−0.50 ± 0.06 *</td>
<td>−0.22 ± 0.15</td>
<td></td>
</tr>
<tr>
<td><em>Saxifraga rivularis</em> L.</td>
<td>Selfing</td>
<td>0.10 ± 0.07</td>
<td>0.61 ± 0.03 *</td>
<td>21.67 ± 0.76</td>
</tr>
<tr>
<td><em>Sibbaldia procumbens</em></td>
<td>Insect</td>
<td>−0.11 ± 0.25</td>
<td>−0.09 ± 0.08</td>
<td></td>
</tr>
<tr>
<td><em>Thalictrum alpinum</em> L.</td>
<td>Insect</td>
<td>−0.18 ± 0.08</td>
<td>−0.14 ± 0.12</td>
<td></td>
</tr>
<tr>
<td><em>Trollius europaeus</em></td>
<td>Insect</td>
<td>0.01 ± 0.04</td>
<td>−0.49 ± 0.01 *</td>
<td>−9.58 ± 2.03</td>
</tr>
<tr>
<td><em>Vaccinium uliginosum</em> L.</td>
<td>Insect</td>
<td>−0.25 ± 0.07</td>
<td>0.14 ± 0.01</td>
<td></td>
</tr>
<tr>
<td><em>Vaccinium vitis-idaea</em> L.</td>
<td>Insect</td>
<td>−0.10 ± 0.06</td>
<td>−0.54 ± 0.01 *</td>
<td>−20.17 ± 0.09</td>
</tr>
</tbody>
</table>

**DISCUSSION**

Species or clade responses to past (Sandel et al., 2011; Pellissier et al., 2014) or ongoing climate change (Lenoir et al., 2008; Chen et al., 2011) are highly variable. Some species or species groups are more able to track suitable climatic conditions than others. Our results indicate the genetic consequence of species range shift under climate change is also highly variable among the species considered in the study. In 11 species, we found evidences of serious genetic erosion associated with species range shifts since the LGM. In contrast, many others showed no relationship to inferred migration distance. Variability in species response may arise from several reasons, including differences among species life-history traits (Matteo et al., 2013), differences in historical contingencies (including admixture, nunataks and non-linear dispersal routes), or differences in the accuracy of the hindcasted suitable glacial refugia among species.

Although many arctic species seem to be able to track their suitable habitats and demonstrate remarkable capability of long-distance dispersal (Alsos et al., 2007, 2015), some of
associated with lower loss of genetic diversity under range shifts. This would corroborate previous results of pollination system as a major driver of genetic exchange and genetic variation among populations (Thiel-Egenter et al., 2009; Friedman & Barrett, 2009). In addition, wind-pollinated species are not dependent on the presence of pollinators for colonization and establishment in a new area. Nevertheless, our sample contained a higher number of insect- than wind-pollinated species and future studies on wind pollination are required to make firm conclusions on this point.

Distinct historical contingencies might also have promoted differential genetic responses to past range shifts among species. In our estimations, we considered the shortest migration distance for each population, although species do not always follow the shortest route when tracking shifting climatic conditions (e.g. long-distance dispersal) and may also use multiple routes (Alsos et al., 2007; Espíndola et al., 2012; Eidesen et al., 2013). For instance, Alsos et al. (2015) showed that species colonized North Atlantic islands post-glacially via multiple dispersal routes from several source regions. Such complex and multiple colonization routes may lead to admixture effects (Petit et al., 2004), which may blur the pattern between genetic diversity and minimal distance from refugia as quantified in our study. In addition, we found a significant positive relationship between genetic diversity and migration distance in the case of Saxifraga rivularis. The genetic structure of this species indicates glacial survival in northern glacial nunatak microrefugia (Westergaard et al., 2010, 2011), a possibility not accounted for in our coarse resolution estimates of refugia. Therefore, more complex historical contingencies than those modelled here such as multiple colonizations, admixture effects or nunatak refugia might have given rise to the large variability in responses observed in our study.

Finally, difference may arise from variation among the model predictive power and quality of the reconstruction of species past ranges. In our validations with fossil records, while the reconstruction of D. octopetala matched fossil records well, only the glacial refugia of S. herbacea modelled using the MPI-ESM-P was able to correctly predict fossil occurrences in eastern North America at the LGM (see Fig. S3 in Appendix S3). While we found generally low variability among reconstructed migration distances from the three GCMs, we cannot exclude that uncertainty in both reconstructed ice distribution and climatic conditions may have led to poor identification of glacial refugia for some species generating uncertainty in the modelled responses. Nevertheless, the areas that were identified as refugia corresponded to areas formerly considered as refugia based on phytogeographical (Hultén, 1937; Abbott & Brochmann, 2003), fossil record (Brubaker et al., 2005) and genetic evidence (Eidesen et al., 2013, see Figs S1 & S2 in Appendix S2).

Because the observed velocity of ongoing climate change is faster than that observed in the Holocene (Burrows et al., 2011), we can expect that future range shifts will cause erosion of genetic diversity at an even higher rate than observed for the past. This increased velocity of climate change is also occurring on top of other anthropogenic disturbances, such as habitat fragmentation, which will also impact rates of genetic erosion beyond what we can model from the past. Nevertheless, our results indicate a complex relationship between population genetic diversity and historical species range shift. Therefore, it is not trivial to understand and predict species demographic response to climate change that may vary according to species traits or historical contingency (Dullinger et al., 2012). Care should be taken when forecasting the demographic and genetic consequences for species under climate change. Our result indicate that a portion of the species conserve the highest level of genetic diversity in populations of southern latitudes, whereas expanding populations at the leading edges often show low genetic diversity (Fig. 2). High diversity populations at the trailing edge of species range shift under ongoing climate change have the best raw genetic material to adapt to new climatic conditions, but might also be the most threatened with local extinction if climate change velocity is too high compared to adaptation abilities. This raises conservation questions, as to whether it is important to transplant individuals from high diversity populations to the expanding front as higher standing genetic diversity offer better possibility for long-term survival under changing environments (Reed et al., 2003; Hampe & Petit, 2005). Ethical problem of moving individuals within the same species to preserve genetic diversity might be less pronounced that moving species into new locations (McLachlan et al., 2007). Together, our study highlights how understanding species historical responses might bring new insights into the consequence of ongoing climate change on biodiversity.

ACKNOWLEDGEMENTS

We thank the two anonymous referees for careful reading and constructive comments on a previous version of the manuscript. This work was supported by the Danish Council for Independent Research Natural Sciences (grant no. 10-085056 to S.N. and grant no. n° 12-126430 to L.P.), by the grant ‘Felix Bonjour’ 2013 of the Société Académique Vaudoise, and by the Research Council of Norway (grant nos. 150322/720 and 170952/V40 to C.B.). The work was initiated at a workshop for the TFI Networks ‘Effect Studies and Adaptation to Climate Change’ under the Norforsk Initiative (2011–2014). We thank S. Birkeland and A.K. Brysting for use of genetic data of Sibbaldia procumbens.

REFERENCES


Hultén, E. (1937) Outline of the History of Arctic and Boreal Biota during the Quaternary Period: their Evolution during and after the Glacial Period as indicated by the Equisetum Progressing Areas of Present Plant Species, Vol. I. Bokförlags Aktiebolaget, Thule.


**SUPPORTING INFORMATION**

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

**Appendix S1** Boyce index of model validation together with species trait information.

**Appendix S2** Maps of species current distribution together with hindcasted climatic suitability for the species during the LGM.

**Appendix S3** Maps of hindcasted climatic suitability of *S. herbacea* for the LGM together with fossil records.

**BIOSKETCH**

Loïc Pellissier’s research interests lie in the investigation of the ecological and evolutionary mechanisms that determine the spatial distribution of species and biodiversity across the earth. The ultimate goal is to inform on the consequences of ongoing climate change on biodiversity.

Author contributions: I.G.A. and L.P. designed the study, I.G.A, P.B.E, P.S., A.T., K.B.W., N.A. and C.B. provided genetic data, A.G, N.Z. and S.N. provided the data for species distribution modelling, P.V. and I.G.A. provided collected the species trait data, and LP conducted the analyses and lead the writing of the manuscript with the help of all co-authors.

Editor: Stephen Cavers