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

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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 (Espíndola 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; Espindola *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 palaeo-climatic 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 www.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 microrefugia 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 mcmcglmm 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 cespitosa*) 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. herbacea* 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* ($-85\% \times 1000$ km^{-1}), *Micrantes stellaris* ($-40\% \times 1000$ km^{-1}) and *Arabis alpina* ($-22\% \times 1000$ 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).
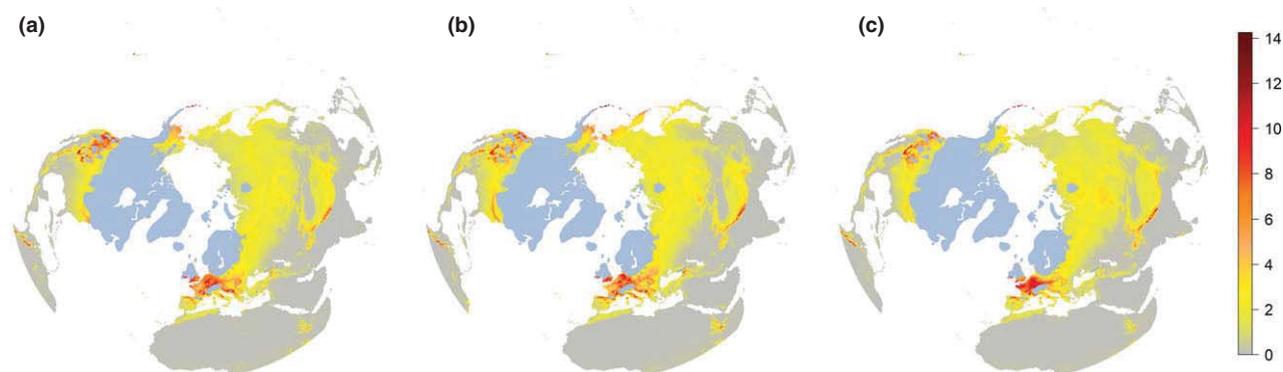
Figure 1 Stacked climatic suitability (probability of occurrence) of the 30 investigated species during the Last Glacial Maximum (−21 Ky) provided by the 30 model ensembles, with the three general circulation models (GCMs) (a) CCSM4, (b) MPI-ESM-P, (c) MIROC-ESM. Model hindcasting indicates four main 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 suitabilities for eastern North America and Beringia.
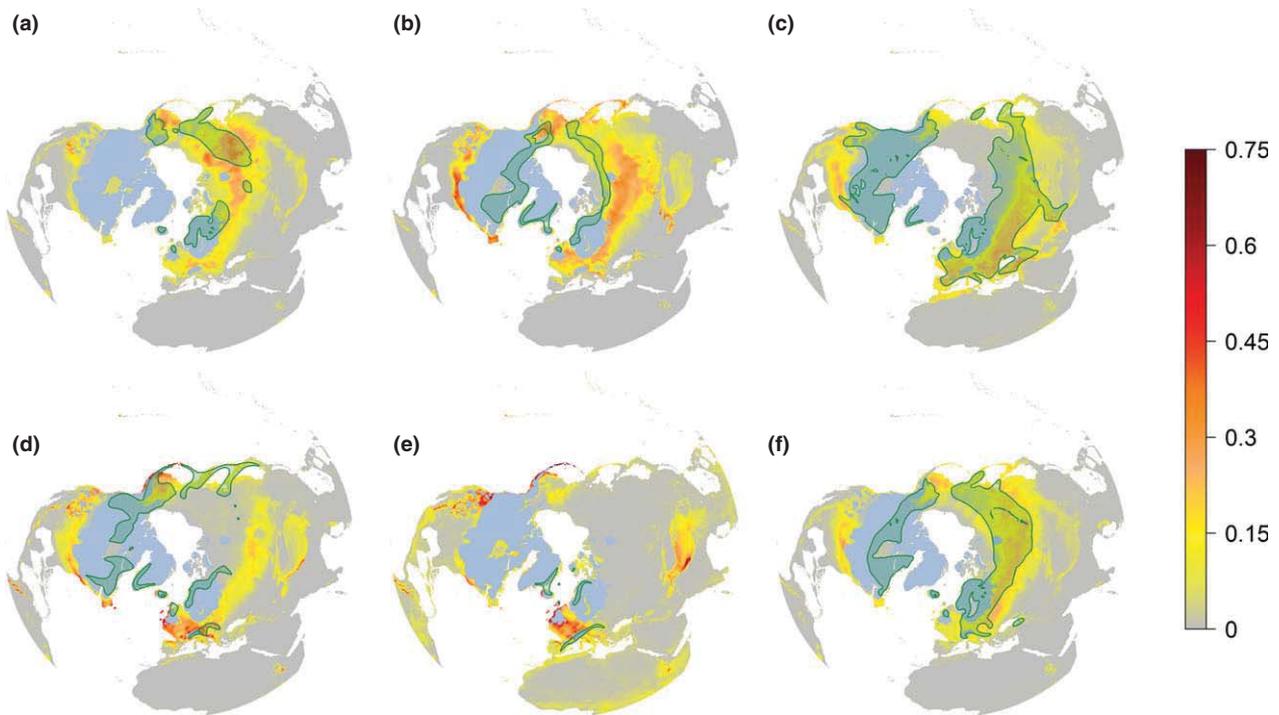
Figure 2 Maps of species current distribution (in green), together with hindcasted climatic suitability for the species during the Last Glacial Maximum (LGM) computed as the average between the projections using the three general circulation models. Shown are: (a) *Betula nana*, (b) *Carex bigelowii*, (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.
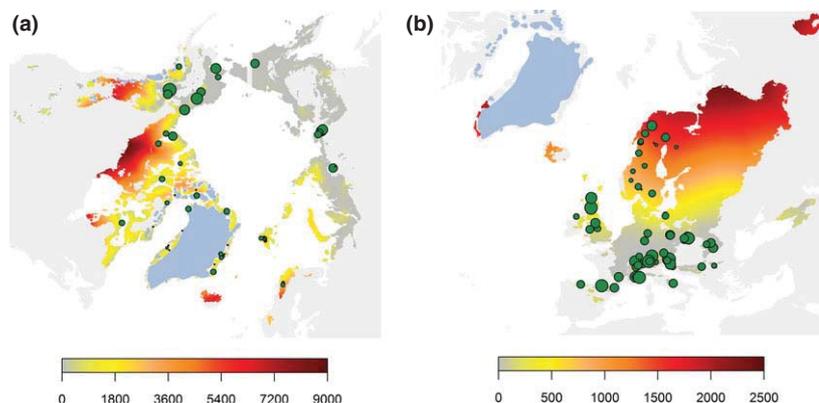
We found no spatial autocorrelation in the SAR model residual of each species.

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.

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.

	Pollination	Isolation	P	Migration	P	Rate
Angelica archangelica L.	Insect	-0.44 ± 0.08	*	-0.27 ± 0.05	*	-14.27 ± 1.59
Arabis alpina L.	Insect	0.05 ± 0.10		-0.44 ± 0.09	*	-21.58 ± 1.47
Arctous alpinus (L.) Nied.	Insect	0.46 ± 0.09		-0.26 ± 0.09		
Arenaria humifusa	Insect	0.36 ± 0.08		-0.08 ± 0.09		
Avenella flexuosa (L.) Drejer	Wind	-0.17 ± 0.05		0.31 ± 0.04		
Betula nana L.	Wind	-0.58 ± 0.02	*	-0.01 ± 0.02		
Carex atrofusca Schkuhr	Wind	-0.37 ± 0.04		-0.37 ± 0.03		
Carex bigelowii Torr. ex. Schwein.	Wind	0.00 ± 0.03		-0.08 ± 0.11		
Cassiope tetragona (L.) D.Don	Insect	-0.36 ± 0.02	*	-0.34 ± 0.01	*	-39.91 ± 5.00
Chamerion angustifolium (L.) Holub	Insect	-0.18 ± 0.04		-0.19 ± 0.04		
Dryas octopetala L.	Insect	0.36 ± 0.09		0.04 ± 0.01		
Empetrum nigrum L. s.lat.	Wind	-0.17 ± 0.02		-0.28 ± 0.06	*	-12.72 ± 3.20
Juncus biglumis L.	Wind	0.19 ± 0.13		0.38 ± 0.13		
Juniperus communis L.	Wind	-0.36 ± 0.02	*	-0.06 ± 0.02		
Loiseleuria procumbens (L.) Desv.	Insect	-0.11 ± 0.06		-0.15 ± 0.02		
Minuartia biflora (L.) Schinz & Thell.	Insect	-0.20 ± 0.38		-0.37 ± 0.22		
Micranthes foliolosa (R.Br.) G.	Insect	0.31 ± 0.41		-0.33 ± 0.08		
Micranthes stellaris (L.) G.	Insect	-0.07 ± 0.02		-0.40 ± 0.06	*	-39.69 ± 8.50
Pedicularis oederi Vahl	Insect	0.12 ± 0.15		-0.07 ± 0.03		
Ranunculus glacialis L.	Insect	-0.05 ± 0.02		-0.06 ± 0.04	*	-85.12 ± 6.49
Ranunculus pygmaeus Wahlenb.	Selfing	-0.59 ± 0.19	*	-0.59 ± 0.47	*	-3.51 ± 2.70
Rubus chamaemorus L.	Insect	-0.33 ± 0.10	*	-0.12 ± 0.23	*	-8.29 ± 5.22
Sagina cespitosa	Insect	0.67 ± 0.84		-1.07 ± 0.79	*	-17.07 ± 8.54
Salix herbacea L.	Insect	-0.50 ± 0.06	*	-0.22 ± 0.15		
Saxifraga rivularis L.	Selfing	0.10 ± 0.07		0.61 ± 0.03	*	21.67 ± 0.76
Sibbaldia procumens	Insect	-0.11 ± 0.25		-0.09 ± 0.08		
Thalictrum alpinum L.	Insect	-0.18 ± 0.04		-0.14 ± 0.12		
Trollius europaeus	Insect	0.01 ± 0.04		-0.49 ± 0.01	*	-9.58 ± 2.03
Vaccinium uliginosum L.	Insect	-0.25 ± 0.07		0.14 ± 0.01		
Vaccinium vitis-idaea L.	Insect	-0.10 ± 0.06		-0.54 ± 0.01	*	-20.17 ± 0.09

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 (Matteodo *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 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

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 colonizations 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.

REFERENCES

Abbott, R.J. & Brochmann, C. (2003) History and evolution of the arctic flora: in the footsteps of Eric Hultén. *Molecular Ecology*, **12**, 299–313.

Alsos, I.G., Eidesen, P.B., Ehrich, D., Skrede, I., Westergaard, K., Jacobsen, G.H., Landvik, J.Y., Taberlet, P. & Brochmann, C. (2007) Frequent long-distance plant colonization in the changing Arctic. *Science*, **316**, 1606–1609.

Alsos, I.G., Alm, T., Normand, S. & Brochmann, C. (2009) Past and future range shift and loss of genetic diversity in dwarf willow (*Salix herbacea* L.) inferred from genetics, fossils, and modelling. *Global Ecology and Biogeography*, **18**, 223–239.

Alsos, I.G., Ehrich, D., Thuiller, W., Eidesen, P.B., Tribsch, A., Schönswetter, P., Lagaye, C., Taberlet, P. & Brochmann, C. (2012) Genetic consequences of climate change for northern plants. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2042–2051.

Alsos, I.G., Ehrich, D., Eidesen, P.B., Solstad, H., Westergaard, K.B., Schönswetter, P., Tribsch, A., Birkeland, S., Elven, R. & Brochmann, C. (2015) Long-distance plant dispersal to North Atlantic islands: colonization routes and founder effect. *AoB Plants*, **7**, plv036.

Barton, K. (2011). *MuMIn: multi-model inference*. R package version 1.0. 0. R Foundation for Statistical Computing, Vienna, Austria. See http://CRAN. R-project. org/package= MuMIn.

Bialozyt, R., Ziegenhagen, B. & Petit, R.J. (2006) Contrasting effects of long distance seed dispersal on genetic diversity during range expansion. *Journal of Evolutionary Biology*, **19**, 12–20.

Binney, H.A., Willis, K.J., Edwards, M.E., Bhagwat, S.A., Anderson, P.M., Andreev, A.A., *et al.* (2009) The distribution of late-Quaternary woody taxa in northern Eurasia: evidence from a new macrofossil database. *Quaternary Science Reviews*, **28**, 2445–2464.

Birks, H.J.B. & Willis, K.J. (2008) Alpines, trees, and refugia in Europe. *Plant Ecology and Diversity*, **1**, 147–160.

Blomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.

Brubaker, L.B., Anderson, P.M., Edwards, M.E. & Lozhkin, A.V. (2005) Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of Biogeography*, **32**, 833–848.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., *et al.* (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.

Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Corlett, R.T. & Westcott, D.A. (2013) Will plant movements keep up with climate change? *Trends in Ecology and Evolution*, **28**, 482–488.

Dlugosch, K.M. & Parker, I.M. (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, **17**, 431–449.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., *et al.* (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, **2**, 619–622.

Durka, W. & Michalski, S.G. (2012) Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology*, **93**, 2297–2297.

Eidesen, P.B., Ehrich, D., Bakkestuen, V., Alsos, I.G., Gilg, O., Taberlet, P. & Brochmann, C. (2013) Genetic roadmap of the Arctic: plant dispersal highways, traffic barriers and capitals of diversity. *New Phytologist*, **200**, 898–910.

Espíndola, A., Pellissier, L., Maiorano, L., Hordijk, W., Guisan, A. & Alvarez, N. (2012) Predicting present and future intra-specific genetic structure through niche hindcasting across 24 millennia. *Ecology Letters*, **15**, 649–657.

Excoffier, L., Foll, M. & Petit, R.J. (2009) Genetic consequences of range expansions. *Annual Review in Ecology, Evolution and Systematics*, **40**, 481–501.

Forester, B.R., DeChaine, E.G. & Bunn, A.G. (2013) Integrating ensemble species distribution modelling and statistical phylogeography to inform projections of climate change impacts on species distributions. *Diversity and Distributions*, **19**, 1480–95.

Frankham, R. (2005) Genetics and extinction. *Biological Conservation*, **126**, 131–140.

Frenzel, B. (1968) The Pleistocene vegetation of northern Eurasia. *Science*, **161**, 637–649.

Friedman, J. & Barrett, S.C.H. (2009) Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. *Annals of Botany*, **103**, 1515–1527.

Gavin, D.G., Fitzpatrick, M.C., Gugger, P.F., Heath, K.D., Rodriguez-Sanchez, F., Dobrowski, S.Z., *et al.* (2014) Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytologist*, **204**, 37–54.

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modeling*, **135**, 147–186.

Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, **33**, 1–22.

Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

Hamrick, J.L. & Godt, M.J.W. (1996) Effects of life history traits on genetic diversity in plant species. *Philosophical Transaction of the Royal Society B: Biological Sciences*, **351**, 1291–1298.

Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, **58**, 247–276.

Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907–913.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, **199**, 142–152.

Hoffmann, A.A. & Sgrò, C.M. (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

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 Equiformal Progressive Areas of Present Plant Species*, Vol. 1. Bokförlags Aktiebolaget, Thule.

Hultén, E. & Fries, M. (1986) *Atlas of North European vascular plants,* vols. I – III. Koeltz Scientific Books, Kö nigstein, Germany.

Ingvarsson, P. (2002) A metapopulation perspective on genetic diversity and differentiation in partially self-fertilizing plants. *Evolution*, **56**, 2368–2373.

Jump, A.S., Marchant, R. & Penuelas, J. (2009) Environmental change and the option value of genetic diversity. *Trends in Plant Science*, **14**, 51–58.

Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59–71.

Körner, C. (2003) *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer.

Kosman, E. (2003) Nei' gene diversity and the index of average differences are identical measures of diversity within populations. *Plant Pathology*, **52**, 533–535.

Lenoir, J., Gégout, J.C., Marquet, P.A., De Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.

Lorenzen, E.D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K.A., *et al.* (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature*, **479**, 359–364.

Maiorano, L., Cheddadi, R., Zimmerman, N.E., Pellissier, L., Petitpierre, B., Pottier, J., *et al.* (2012) Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. *Global Ecology and Biogeography*, **22**, 302–317.

Matteodo, M., Wipf, S., Stöckli, V., Rixen, C. & Vittoz, P. (2013) Elevation gradient of successful plant traits for colonizing alpine summits under climate change. *Environmental Research Letters*, **8**, 024043.

McCauley, S.J., Davis, C.J., Werner, E.E. & Robeson, M.S., II (2014) Dispersal, niche breadth, and population extinction/colonization ratios predict range size in North American dragonflies. *Journal of Animal Ecology*, **83**, 858–865.

McLachlan, J.S., Hellmann, J.J. & Schwartz, M.W. (2007) A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, **21**, 297–302.

Mitchell, T. D., Carter, T. R., Jones, P. D., Hulme, M. & New, M. (2004) A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). *Tyndall Centre for Climate Change Research Working Paper*, **55**, 25.

Pauls, S.U., Nowak, C., Bálint, M. & Pfenninger, M. (2013) The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology*, **22**, 925–946.

Pellissier, L., Leprieur, F., Parravicini, V., Litsios, G., Olesen, S., Wisz, M.S., Kulbicky, M., Cowman, P., Belwood, D. & Mouillot, D. (2014) Quaternary coral reef refugia preserved fish diversity. *Science*, **344**, 1016–1019.

Petit, R.J., Bialozyt, R., Garnier-Géré, P. & Hampe, A. (2004) Ecology and genetics of tree invasions: from recent introductions to Quaternary migrations. *Forest Ecology and Management*, **197**, 117–137.

Prugnolle, F., Manica, A. & Balloux, F. (2005) Geography predicts neutral genetic diversity of human populations. *Current Biology*, **15**, R159–R160.

Reed, D.H. & Frankham, R. (2003) Correlation between fitness and genetic diversity. *Conservation Biology*, **17**, 230–237.

Reed, D.H., Lowe, E.H., Briscoe, D.A. & Frankham, R. (2003) Fitness and adaptation in a novel environment: effect of inbreeding, prior environment, and lineage. *Evolution*, **57**, 1822–1828.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.C. (2011) The influence of Late Quaternary climate-change velocity on species endemism. *Science*, **334**, 660–664.

Schönswetter, P., Stehlik, I., Holderegger, R. & Tribsch, A. (2005) Molecular evidence for glacial refugia of mountain plants in the European Alps. *Molecular Ecology*, **14**, 3547–3555.

Singarayer, J.S. & Valdes, P.J. (2010) High-latitude climate sensitivity to ice-sheet forcing over the last 120kyr. *Quaternary Science Reviews*, **29**, 43–55.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.G. & Cosson, J.F. (1998) Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, **7**, 453–464.

Tarasov, P.E., Volkova, V.S., Webb, T., Guiot, J., Andreev, A.A., Bezusko, L.G., *et al.* (2000) Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. *Journal of Biogeography*, **27**, 609–620.

Thiel-Egenter, C., Gugerli, F., Alvarez, N., Brodbeck, S., Cieślak, E., Colli, L., *et al.* (2009) Effects of species traits on the genetic diversity of high-mountain plants: a multispecies study across the Alps and the Carpathians. *Global Ecology and Biogeography*, **18**, 78–87.

Thomson, F.J., Moles, A.T., Auld, T.D. & Kingsford, R.T. (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, **99**, 1299–1307.

Waltari, E., Hijmans, R.J., Peterson, A.T., Nyari, A.S., Perkins, S.L. & Guralnick, R.P. (2007) Locating pleistocene refugia: comparing phylogeographic and ecological niche model predictions. *PLoS ONE*, **2**, e563.

Westergaard, K.B., Jørgensen, M.H., Gabrielsen, T.M., Alsos, I.G. & Brochmann, C. (2010) The extreme Beringian/Atlantic disjunction in *Saxifraga rivularis* (Saxifragaceae) has formed at least twice. *Journal of Biogeography*, **37**, 1262–1276.

Westergaard, K.B., Alsos, I.G., Popp, M., Engelskjon, T., Flatberg, K.I. & Brochmann, C. (2011) Glacial survival may matter after all: nunatak signatures in the rare European populations of two west-arctic species. *Molecular Ecology*, **20**, 376–393.

Willi, Y., Van Buskirk, J. & Hoffmann, A.A. (2006) Limits to the adaptive potential of small populations. *Annual Review in Ecology, Evolution and Systematic*, **37**, 433–458.

Wisz, M.S. & Guisan, A. (2009) Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecology*, **9**, 8.

Yannic, G., Pellissier, L., Ortego, J., Lecomte, N., Couturier, S., Cuyler, C., *et al.* (2014) Genetic diversity in caribou linked to past and future climate change. *Nature Climate Change*, **4**, 132–137.

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.