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# Forecasting changes in population genetic structure of alpine plants in response to global warming

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## Abstract

**Species range shifts in response to climate and land use change are commonly forecasted with species distribution models based on species occurrence or abundance data. Although appealing, these models ignore the genetic structure of species, and the fact that different populations might respond in different ways because of adaptation to their environment. Here, we introduced ancestry distribution models, *that is*, statistical models of the spatial distribution of ancestry proportions, for forecasting intra-specific changes based on genetic admixture instead of species occurrence data. Using multi-locus genotypes and extensive geographic coverage of distribution data across the European Alps, we applied this approach to 20 alpine plant species considering a global increase in temperature from 0.25 to 4 °C. We forecasted the magnitudes of displacement of contact zones between plant populations potentially adapted to warmer environments and other populations. While a global trend of movement in a north-east direction was predicted, the magnitude of displacement was species-specific. For a temperature increase of 2 °C, contact zones were predicted to move by 92 km on average (minimum of 5 km, maximum of 212 km) and by 188 km for an increase of 4 °C (minimum of 11 km, maximum of 393 km). Intra-specific turnover—measuring the extent of change in global population genetic structure—was generally found to be moderate for 2 °C of temperature warming. For 4 °C of warming, however, the models indicated substantial intra-specific turnover for ten species. These results illustrate that, in spite of unavoidable simplifications, ancestry distribution models open new perspectives to forecast population genetic changes within species and complement more traditional distribution-based approaches.**

*Keywords*: Alpine plants, ancestry distribution models, climate change, intra-specific variation, landscape genetics.

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## Introduction

The impact of both climate and land use changes on biodiversity and more specifically on species distribution is widely acknowledged (Parmesan & Yohe 2003; Jump & Peñuelas 2005; Thuiller *et al.* 2008). For alpine plants, available evidence includes range shifts that trigger the movement of plants to higher elevations or latitudes (Grabherr *et al.* 1994; Walther *et al.* 2002; Walther 2003). Modification of range limits, however, may occur not only among species (Thuiller *et al.* 2005), but also among genetically differentiated clusters of populations within species (Aitken *et al.* 2008). This study

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introduces a new approach to forecasting effects of climate change by studying its potential impact on population structure based on species ecological characteristics and multi-locus genotypes. This approach proposes a fine-grained analysis of the impact of climate change on allele distributions and will provide indirect estimates of gene migration within species ranges (Jump & Peñuelas 2005; Storfer *et al.* 2007; Sork *et al.* 2010).

Predictions of the effects of climate change commonly rely on species distribution models (SDM) (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). Species distribution models are correlative models relating field observations to environmental predictors. Field observations are usually occurrence or abundance observations that are used to infer the realized niche of a species. Geographic locations that satisfy the habitat requirements of a given species can then be identified by projecting the niche on a map. With environmental data modified according to some specified climate change scenarios, the impact of climate change can be evaluated by comparing the locations where niche requirements are presently satisfied to those where they could be satisfied in the future. Despite their obvious appeal, there are many shortcomings to species distribution models for predicting future distributions (Aitken *et al.* 2008). In particular, these models do not account for genetic variation within the species range and for adaptation of populations to past and contemporary environments. Environmental changes not only affect the limits of species distributions but also the centres of these distributions. Because distribution centres may support genetically inhomogeneous populations, considering effects of environmental changes at the gene level is essential to our understanding of their impact on population structure.

Association of genetic variation with environmental variables has been frequently reported in the recent literature (Hedrick *et al.* 1976; Aitken *et al.* 2008; Balkenhol *et al.* 2009). For example, Duminil *et al.* (2007) tested the influence of a set of life-history traits on population genetic structure and gene flow in seed plants. Richardson *et al.* (2009) analysed climate-related genetic patterns in the western white pine suggesting that divergent climatic selection has influenced phenotypic traits associated with tree growth. Several methods can be used to identify environmental factors determining population structure, for example, through estimates of population divergence (Foll & Gaggiotti 2006). Alternatively, other approaches identify loci with clear correlations between allele frequencies and ecological variables and interpret these loci as being potentially involved in local adaptation (Joost *et al.* 2007; Coop *et al.* 2010; Poncet *et al.* 2010; Manel *et al.* 2010a,b). Among the climatic variables that contribute to genetic differentiation in plant species, the influence of temperature has recurrently been demonstrated since the pioneering work of Turesson (1925). An example of the influence of climatic conditions is the timing of phenological events, such as flowering, which depend on temperature, and which are obvious targets for natural selection (Stanton & Galen 1997; Stinson 2004; Jump *et al.* 2009a,b; Wang *et al.* 2009; Doi *et al.* 2010; Scherrer & Körner 2011). From this perspective, appropriate standing variation and the ability of long-distance gene dispersal are key factors for plant species to keep track with rapidly changing environments (Davis & Shaw 2001; Salamin *et al.* 2010).

The objective of this study is to introduce a model-based approach to forecasting changes in intra-specific genetic variation in alpine plants in response to climate change, based on correlations between environmental variables and individual ancestry. More specifically, we developed Bayesian models that incorporate hidden spatial regression models of genetic admixture (ancestry) on climatic and topographic variables. The motivation behind ancestry distribution models is that individual ancestry can be correlated with environmental variables and that estimates of change in individual ancestry can provide indirect estimates of future rates of gene migration. Implemented in the computer program POPS (Jay 2011), ancestry distribution models simultaneously estimate spatially varying genetic admixture from $K$ ancestral groups based on genetic markers and the effects of environmental covariates on population genetic structure. The need for those models was underlined in two recent reviews (Storfer *et al.* 2007; Thomassen *et al.* 2010), and a related approach was applied to California valley oaks where regional distribution models were fitted to genetically differentiated groups with distinct responses to climate change (Sork *et al.* 2010).

To illustrate our approach, we considered a set of 20 widespread, mostly perennial alpine plant species genotyped using amplified fragment length polymorphism (AFLPs; Gugerli *et al.* 2008; Alvarez *et al.* 2009; Thiel-Egenter *et al.* 2011). Plant populations can avoid extinction by tolerating climate change through phenotypic plasticity, adapting to new conditions through selection on genetic standing variation or favourable mutations, or migrating to locations with favourable conditions (Davis *et al.* 2005; Aitken *et al.* 2008). Regarding these three alternatives, ancestry distribution models assume that gene migration represents the main component in the response of plant populations to environmental change. One mechanism for migrating populations to track moving environments is through the dispersal of alleles adapted to the local environments prior to climate

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change (Davis & Shaw 2001). Given that adaptation to local environments contributes to shape current population genetic structure, the models will use associations between spatial population structure and environmental variables to forecast future spatial population structure following environmental changes. Thus, a careful interpretation of ancestry distribution model predictions will ask for an evaluation of adaptation to local environments in the *K* inferred genetic clusters.

With these caveats in mind, we addressed the following questions. (i) Which changes in spatial population genetic structure of alpine plants could be forecasted if temperatures rise from 2 °C up to 4 °C (IPCC 2007)? (ii) What is the rate of forecasted gene migration for clusters of populations adapted to warmer environments? To answer these questions, we measured the extent of intra-specific turnover, defined by the correlation between current and predicted ancestry coefficients, and the magnitude of displacement of contact zones, where individuals with mixed ancestry were found, along a central transect of the European Alps. Regarding future environments, the level of turnover indicates the importance of change in population genetic structure, and contact zone shift is used as an indirect way to quantify gene migration through projections of ancestry coefficients on geographic maps. Finally, we attempted to disentangle the relative contributions of past adaptations vs. demography in ancestry distribution model estimates.

## Materials and methods

### Plant material and data

Plant genotypes and environmental covariates were extracted from the INTRABIODIV data base (Gugerli *et al.* 2008). We considered the set of 20 mostly perennial plant species studied by Alvarez *et al.* (2009) on the basis of their extensive geographic coverage of the Alps: *Androsace obtusifolia* All., *Arabis alpina* L., *Campanula barbata* L., *Cerastium uniflorum* Clairv., *Dryas octopetala* L., *Gentiana nivalis* L., *Geum montanum* L., *Geum reptans* L., *Gypsophila repens* L., *Hedysarum hedysaroides* (L.) Schinz & Thell. s.l., *Hypochaeris uniflora* Vill., *Juncus trifidus* L., *Ligusticum mutellinoides* (Cr.) Vill., *Loiseleuria procumbens* (L.) Desv., *Luzula alpinopilosa* (Chaix) Breistr., *Phyteuma hemisphaericum* L., *Rhododendron ferrugineum* L., *Saxifraga stellaris* L., *Sesleria caerulea* (L.) Ard. and *Trifolium alpinum* L. Individual-based sampling was performed within a rectangular grid system with cell surfaces of 22.3 × 25 km (12′ latitude and 20′ longitude). Only cells with areas of elevation higher than 1500 m above sea level were considered. Three individuals per species were sampled within cells. To avoid closely related individuals, plants were sampled at least 10m apart (Gugerli *et al.* 2008). All plant samples were genotyped using amplified fragment length polymorphisms (AFLPs) as detailed in (Gugerli *et al.* 2008). In the INTRABIODIV database, habitats are modelled by using DAYMET, a computer program that analyses daily records of climate variables in a spatial context (Thornton *et al.* 1997; Gugerli *et al.* 2008). A set of geographic and environmental covariates, common to all species, was extracted from the INTRABIODIV database. We selected covariates that grouped into geographic, topographic and climatic sets of variables unambiguously and that are usually considered as important determinant of plant phenology. These covariates included latitude and longitude, additional topographic variables (slope, orientation), and annual average of minimum and maximum daily temperatures (years 1980–1989), spring and summer seasonal precipitations (years 1980–1989) measured for each cell. Using the same set of eight covariates for all plants, we likely included habitat variables generating weak gene-environment associations in some cases. We checked this does not influence our estimates of regression coefficients seriously. A short description of the data set used in this study, including the number of sampled cells and individuals, and the number of loci genotyped is provided in Table 1.

### Ancestry distribution models

To identify environmental variables that influence individual ancestry and use these variables to forecast responses to climate change, we developed POPS, a Bayesian algorithm that incorporates genetic and geographic data and infers admixture coefficients based on correlation with environmental variables (Durand *et al.* 2009; Jay 2011; Jay *et al.* 2011). More specifically, for each individual, the admixture coefficients represent the fraction of ancestry shared between *K* putative source populations or clusters. The POPS algorithm includes a hidden regression framework where admixture coefficients are regressed on geographic and ecological data. Using standard notations, admixture coefficients are stored in a matrix, $Q$, with elements, $q_{ik}$, corresponding to the genome proportion of individual $i$ that originates from the source population $k$ ($k = 1, \ldots, K$). In addition to admixture coefficients, POPS estimates a multidimensional vector of regression coefficients, $\beta$, measuring the effects of each covariate on individual ancestry. For the parameters of interest, $Q$ and $\beta$, the posterior distribution is given by

$$\Pr(Q, \beta | X, \widetilde{X}) = c \Pr(X|Q) \Pr(Q|\widetilde{X}, \beta) \Pr(\beta),$$

where $X$ is the matrix of genotypes, $\widetilde{X}$ is the matrix of geographic and environmental covariates, and $c$ is a

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**Table 1** Sampling design, number of amplified fragment length polymorphism, average minimal daily temperature, mean elevation for 20 alpine species from INTRABIODIV

| | Number of cells | Number of individuals | Number of markers | Temperature (°C) | Altitude (m a.s.l.) |
|---|---|---|---|---|---|
| *Androsace obtusifolia* | 45 | 131 | 138 | 0.48 | 2280 |
| *Arabis alpina* | 129 | 385 | 140 | 2.99 | 1874 |
| *Campanula barbata* | 104 | 307 | 114 | 2.75 | 1857 |
| *Cerastium uniflorum* | 44 | 130 | 93 | −0.42 | 2445 |
| *Dryas octopetala* | 124 | 370 | 100 | 2.62 | 1934 |
| *Gentiana nivalis* | 74 | 218 | 158 | 1.45 | 2155 |
| *Geum montanum* | 122 | 363 | 86 | 2.43 | 1982 |
| *Geum reptans* | 51 | 153 | 57 | 0.12 | 2404 |
| *Gypsophila repens* | 107 | 319 | 94 | 3.58 | 1759 |
| *Hedysarum hedysaroides* | 66 | 144 | 123 | 2.13 | 1984 |
| *Hypochaeris uniflora* | 59 | 177 | 74 | 2.43 | 1951 |
| *Juncus trifidus* | 91 | 269 | 86 | 1.74 | 2109 |
| *Loiseleuria procumbens* | 80 | 239 | 199 | 1.31 | 2191 |
| *Luzula alpinopilosa* | 42 | 92 | 93 | 0.85 | 2213 |
| *Ligusticum mutellinoides* | 90 | 270 | 116 | 1.50 | 2088 |
| *Phyteuma hemisphaericum* | 76 | 225 | 234 | 1.54 | 2111 |
| *Rhododendron ferrugineum* | 126 | 377 | 111 | 2.89 | 1891 |
| *Saxifraga stellaris* | 113 | 265 | 70 | 3.13 | 1816 |
| *Sesleria caerulea* | 100 | 283 | 187 | 2.15 | 1984 |
| *Trifolium alpinum* | 39 | 76 | 97 | 2.13 | 2060 |

constant of proportionality. In this model, the likelihood function, the prior distribution of allele frequencies and the conditional distribution of cluster labels given $Q$ are described by the same statistical models as implemented in the software STRUCTURE (Pritchard *et al.* 2000). To define the conditional probability distribution, $\Pr(Q|\widetilde{X},\beta)$, we used a hierarchical regression model. For each individual ($i$) and each cluster ($k$), we introduced a parameter ($\alpha_{ik}$) proportional to the expected value of the ancestry coefficient ($q_{ik}$) under a Dirichlet distribution (Durand *et al.* 2009). Separating $\widetilde{X}$ into a set of geographic variables, $\widetilde{X}_g$, and a set of habitat variables, $\widetilde{X}_h$, the hierarchical model was defined by $K$ hidden regression equations

$$\log(\alpha_{ik}) = \widetilde{X}_{ih}\beta_{hk} + g(\widetilde{X}_{ig})\beta_{gk} + \varepsilon_{ik},\ \ i=1,\ldots,n, k=1,\ldots,K,$$

where $\beta_{hk}$ and $\beta_{gk}$ are vectors of regression coefficients modelling environmental and geographic effects, respectively, $g(\widetilde{X}_{ig})$ represents a nonlinear spatial trend surface, $\varepsilon_{ik}$ is a zero-mean spatially auto-correlated residual (Besag 1975), and $n$ is the sample size. In the right-hand side of the regression equations, the last two terms account for broad-scale and local spatial patterns in unobserved ancestries. The first term models the effects of habitat variables once the spatial effects have been removed. Similar approaches—separating habitat and spatial covariates—have been adopted in landscape ecology where the responses consist of abundance or occurrence data (Lichstein *et al.* 2002). Using a landscape genetic framework (Holderegger & Wagner 2008), individual ancestry coefficients are used instead of species distribution data in ancestry distribution models. A Markov chain Monte Carlo algorithm allowed us to estimate the ancestry coefficients and the effects of the environmental variables. Like species distribution models, POPS also provides routines to project ancestry coefficients on geographic maps under scenarios of environmental change. These projections were used to estimate changes in population genetic structure and the magnitudes of shift for areas of mixed ancestry separating pairs of genetic clusters (i.e. contact zones). Forecasts from regression models were obtained by varying the climatic variables under various scenarios, considering temperatures increasing from 0 to 4 °C by increments of 0.25 °C (IPCC 2007). The projections of the future distributions of ancestry coefficients were displayed on geographic maps using a kriging method in R (R Development Core Team 2010).

Note that the POPS algorithm differs from a procedure that would first apply a clustering algorithm to the genetic data to infer $K$ genetic clusters and then fit SDMs to each inferred cluster, treating them as independent species. This procedure is prone to two types of errors: (i) SDMs would not be fitted from directly observed occurrence data, but from statistical estimates of cluster membership. Using these estimates, statistical errors would remain unevaluated. (ii) Clustering algorithms do not always model intra-specific hybridization accurately. The Bayesian implementation of the POPS

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algorithm provides a direct solution to these issues by using a single procedure that jointly estimates admixture coefficients and fits $K$ interdependent distribution models to these variables.

Population genetic structure estimates obtained under current environmental conditions were controlled by applying the Bayesian program TESS 2.3 (Chen *et al.* 2007) and the Neighbour-Joining algorithm using shared allele distance (Saitou & Nei 1987). The conditional auto-regressive model of TESS was applied to confirm the detection of contact zones in the geographic range of each plant species (Durand *et al.* 2009; François & Durand 2010). In TESS and POPS, we set the number of clusters to values <4, thus only retaining population clusters that corresponded to the most divergent clades in NJ trees. To evaluate whether or not the assignment of plant populations into well-defined geographic clusters could explain the high proportion of species with warm genetic clusters, we used random partitions of the study area to create geographically structured clusters (10 000 replicates).

### *Measures of contact zone shifts and intra-specific turnover*

To interpret ancestry distribution model predictions in terms of gene migration and population structure changes, we first measured the shift of contact zones between pairs of geographically adjacent clusters from projections on geographic maps. The magnitude of displacement was computed for temperatures increasing from 0.25 to 4 °C along a south-west–north-east transect paralleling the alpine axis. This was achieved by following the projections of contact zone points (sharing 50% of ancestry in each cluster) and monitoring displacements on the geographic map. In addition, we assessed the extent of intra-specific turnover by measuring the correlation between ancestry coefficients estimated using genetic data and current temperatures and those predicted for increased forecasted temperatures. The closer to 1 is this correlation, the smaller are expected changes in population structure. While contact zone shifts between clusters are calculated pairwise, intra-specific turnover can be viewed as a global measure of change in the population genetic structure of a given species.

### *Evidence supporting the existence of adaptive variation*

When applying our niche models, we implicitly assumed that plant populations were adapted to their local climatic conditions previous to climate warming. In particular, we supposed that genetic differentiation between clusters was—at least partly—explained by genetic barriers reflecting local adaptation to past and contemporary environments. To test this hypothesis, we applied an outlier locus approach based on generalized linear models (GLMs, Joost *et al.* 2007) to evaluate the evidence for local adaptation to contemporary environmental conditions in each plant species. For each locus, we fitted a model of allele distribution via logistic regression of the binary alleles on latitude and analysed the clines corresponding to extreme values of the empirical distribution of $z$-statistics. Note that we used latitude because we were interested in identifying which clusters harbour appropriate genetic variation because of local adaptation to climatic conditions (We did not examine which genes are targeted by natural selection). In this respect, latitude was more robust than temperature, which exhibits high levels of variability within small geographic areas. To overcome multiple testing issues, we controlled the false discovery rate at the level of 1% (Benjamini & Hochberg 1995). For all species with four or more outlier loci detected, we displayed the fitted allele frequency gradients corresponding to the four lowest $P$-values. We reported latitudes for which the gradients exhibited a point of change in curvature. To control for spatial auto-correlation in the sampling design of INTRABIODIV, we applied tests using generalized estimating equations (GEE; R Development Core Team 2010) as proposed in (Poncet *et al.* 2010).

### *Spatially explicit models of demographic history*

To test whether the clines observed at outlier loci could result from purely demographic processes, we performed computer simulations of a coalescent model of migration incorporating geographic information (SPLATCHE, Currat *et al.* 2004). The demographic history of plant populations was simulated using a model of range expansion defined on a lattice of demes reproducing the sampling design of the data used here. The source of expansion was located in regions of maximal genetic diversity identified as potential refugia during the ice age (Schönswetter *et al.* 2005). Genetic diversity was computed in each grid cell using Nei's estimator for AFLPs (Bonin *et al.* 2007). In simulations, the onset of expansion was either located in the south-west of the Alps (SW, 44°N, 6°E) or in the north-east of the Alps (NE, 47°N, 12°E). The simulation parameters were calibrated so that the Alps were colonized in <600 generations (Higgins & Richardson 1999). Within each cell, population size grew according to a logistic equation with carrying capacity equal to $C = 50$ effective individuals. Using cell locations and number of loci equal to those of the data used here, we tested differences between simulated and empirical data for two statistics. The first test statistic was defined by the correlation

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between ancestry proportions estimated from the genetic data and those predicted from the geographic and environmental covariates (without change). The second statistic corresponded to the amplitude of the latitudinal allele frequency cline estimated for the most extreme locus. The amplitude of a cline was computed as the difference between the minimum and maximum of the allele frequency cline within the latitudinal range of a species' distribution.

## Results

### *Population genetic structure*

When used as an assignment method, POPS split the samples into geographically well-defined clusters which agreed with the results obtained from TESS, hierarchical clustering and previous analyses (Alvarez *et al.* 2009). One striking feature shared by 18 (90%) of the 20 plant species studied was the existence of 'warm' genetic clusters (Figs 1 and S1, Supporting information; Table 2). 'Warm' clusters, as inferred by POPS, were characterized by temperatures significantly higher for the individuals assigned to this cluster than for individuals assigned to other clusters (two-sample *t*-tests, Table 2). To evaluate whether the assignment of individuals into well-defined geographic clusters could explain the high proportion of species with warm genetic clusters, we used a simulation approach. Significant differences in average temperature among artificial geographic clusters were observed in 49% of the replicates. Thus, the high proportion of warm clusters observed in the study data set (90%) was not a mere outcome of the association between geography and climate.

For 15 species, the warm clusters were located in the south-west (SW) of the Alps, south of latitude 46°N and west of longitude 8°E in France and Italy (Table 2). Proportions of ancestry in warm clusters exhibited a gradual decrease in a north-eastern direction suggesting contact and gene flow with 'colder' clusters (first row in Fig. 2, Movie S1, Supporting information). The contact zones, associated with clines of admixture around 45.5°N of latitude, reflected a potential intrusion of genes from lower latitude regions and provided evidence that the geographic boundaries between warmer and colder populations were highly permeable. Other warm clusters were identified in the south of Austria (around 46.5°N, 14°E) for two species (*Saxifraga stellaris* and *Hypochaeris uniflora*). Two species (*Luzula alpinopilosa* and *Phyteuma hemisphaericum*) showed no evidence of differentiation with respect to temperature. For one species (*Dryas octopetala*), the warm cluster was spread over the western Alps at longitudes lower than 10°E.

### *Model predictions of contact zone shifts*

The POPS ancestry distribution model enabled forecasts of genetic admixture under various climate change scenarios of similar magnitude as projected by the IPCC (2007). Starting from current average temperature values, changes in genetic admixture were computed

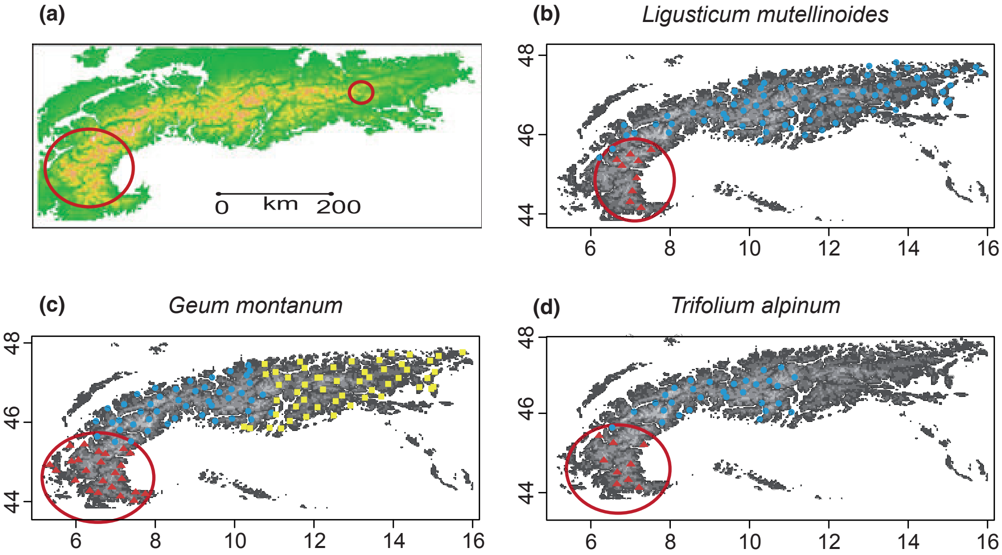

**Fig. 1** Population structure and location of warm genetic clusters in alpine plant species. (a) Geographic map of the study area showing elevations > 1000 m.a.s.l and localization of warm clusters in the south-west and east (circles). Population structure inferred by POPS for (b) *Ligusticum mutellinoides*, (c) *Geum montanum*, (d) *Trifolium alpinum*. Sample locations in warm clusters are represented by red triangles. Population structure for all species is displayed in Fig. S1 (Supporting information).

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**Table 2.** Maxima of genetic diversity, warm cluster locations and latitudinal clines for 20 alpine plant species

| | | Warm cluster[A] | | | | |
|---|---|---|---|---|---|---|
| Species name | Maximum of genetic diversity | Location of the warm cluster | Mean temperature within | Mean temperature outside | *P*-value | Latitude of the most outlier cline[B] |
| *Androsace obtusifolia* | SW[1] | SW (45.4°N, 6.95°E) | −2.13 | −3.24 | 0.00171 | 45° |
| *Arabis alpina* | SW | SW (44.9°N, 6.87°E) | 2.60 | −1.31 | 1.91e–16 | 45°/46.2° |
| *Campanula barbata* | N[1] | SW (45.5°N, 7.43°E) | −0.27 | −1.08 | 0.00292 | 45.2°/46.6° |
| *Cerastium uniflorum* | SW | SW (45.9°N, 8.74°E) | −3.21 | −3.81 | 0.0252 | 45°/46° |
| *Dryas octopetala* | NE[1] | W (45.7°N, 7.68°E) | −0.34 | −1.42 | 3.37e–06 | – |
| *Gentiana nivalis* | NE | SW (45.2°N, 7.22°E) | −1.22 | −2.29 | 0.00346 | 45°/46.2° |
| *Geum montanum* | SW | SW (44.9°N, 7.05°E) | 0.68 | −1.61 | 1.64e–09 | 45°/46° |
| *Geum reptans* | NE | SW (45.3°N, 7.04°E) | −2.30 | −3.71 | 1.78e–07 | 46.2° |
| *Gypsophila repens* | SW | SW (44.6°N, 6.79°E) | 3.19 | −0.88 | 2.64e–14 | 45° |
| *Hedysarum hedysaroides* | SW | SW (44.9°N, 7.95°E) | 1.43 | −1.80 | 1.07e–06 | 45° |
| *Hypochaeris uniflora* | E[1] | E (47.0°N, 14.4°E) | −0.61 | −1.24 | 0.0211 | – |
| *Juncus trifidus* | SW | SW (44.7°N, 7.06°E) | 1.28 | −2.23 | 1.22e–09 | 45°/46.5° |
| *Ligusticum mutellinoides* | NE | SW (45.0°N, 7.03°E) | −0.18 | −2.10 | 0.000151 | 45° |
| *Loiseleuria procumbens* | NE | SW (44.7°N, 7.13°E) | 0.65 | −2.37 | 0.000138 | 45°/46.5° |
| *Luzula alpinopilosa* | SW | – | – | – | NS[3] | – |
| *Phyteuma hemisphaericum* | SW | – | – | – | NS | 45.7° |
| *Rhododendron ferrugineum* | SW | SW (44.5°N, 6.76°E) | 2.03 | −1.09 | 1.93e–08 | 45°/46.5° |
| *Saxifraga stellaris* | –[2] | E (46.5°N, 13.4°E) | 1.58 | −0.99 | 1.54e–09 | – |
| *Sesleria caerulea* | E | SW (45.4°N, 7.66°E) | −0.33 | −1.71 | 0.00019 | 46°/47° |
| *Trifolium alpinum* | E | SW (44.9°N, 6.92°E) | 0.14 | −2.09 | 0.00172 | 45° |

1: SW = south-west, N = north, NE = north-east, E = east. 2: '–' indicates absence of results. 3: NS stands for non significant *P*-value. A: Location, mean temperature within and outside warm clusters, *P*-value for two-sample *t*-tests. B: For each species, latitudes correspond to the points where allele frequency clines crossed the 50% threshold (four most extreme *P*-values).

over the alpine range for all individuals in all species and for temperatures increasing by steps of 0.25 °C up to 4 °C. Figure 2 shows model predictions of the movement of the contact zone between warm and cold clusters for three representative species (*Ligusticum mutellinoides*, *Geum montanum and Trifolium alpinum*). Among the 18 species that exhibited a warm cluster, 16 species were predicted to experience significant movement of contact zones in response to temperature increase (Movie S1, Supporting infomation). For all these species, the ancestry distribution models predicted that genes from warm clusters would invade colder clusters by progressively moving toward a north-eastern direction with increasing temperature (Figs 2 and 3a). One species, *H. uniflora*, was predicted to behave in a different way as its warm cluster was located in the east, and thus the movement was predicted to prevail in a reverse direction, from east to the south-west. Two species with high altitudinal ranges, *Androsace obtusifolia* and *Cerastium uniflorum*, exhibited no significant changes. In these two species, warm clusters were more weakly defined than in other species: They were significantly warmer according to average daily minimum temperature ($P < 0.05$ for both species) but not according to maximum temperature ($P = 0.06$ and $P = 0.45$, respectively).

To further quantify our predictions of gene migration under increased temperature, we estimated the displacement of the contact zones for species exhibiting warm clusters in the south-west. Figure 3a reports the magnitudes of contact zone shift estimated by tracking a contact point along a south-west–north-east transect. While a global trend of movement toward a north-eastern direction was observed, the magnitude of displacement was highly species-specific. For a temperature increase of 2 °C, contact zones were predicted to shift in the north-east direction by 92 km (minimum of 5 km, maximum of 212 km, SD = 68 km) and by 188 km (minimum of 11 km, maximum of 393 km, SD = 139 km) for an increase of 4 °C. For the species *L. mutellinoides*, *G. montanum*, *T. alpinum*, we quantified the uncertainty of model predictions for a temperature increase of 2 °C (Fig. 2) and obtained posterior predictive standard deviations equal to SD = 78, 42 and 74 km, respectively. Note that these estimates of cluster interface movement are only coarse summaries of model predictions: gene migration is expected to follow the complex topography of the alpine mountain range. A more accurate descrip-

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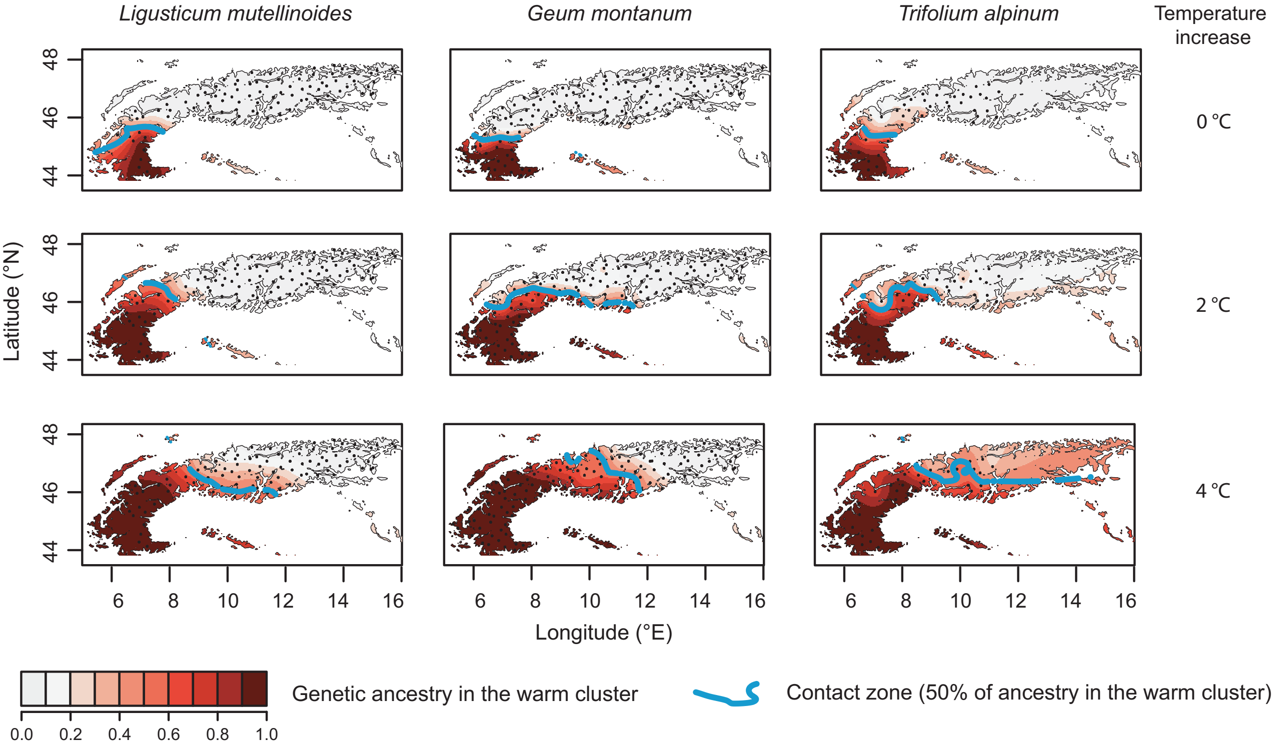

**Fig. 2** Predictions of contact zone movements in alpine plant species under increased temperature scenarios. The predictions were obtained from the POPS model for mean annual temperatures increasing by 0, 2 and 4 °C. For each location on the maps, the colour intensities represent the amounts of genetic ancestry (or individual admixture coefficients) in the warm clusters. The blue line represents the contact zone between warm and cold populations, defined as 50% of ancestry in each cluster. Maps are given for *Ligusticum mutellinoides*, *Geum montanum* and *Trifolium alpinum*. Predictions for all species are displayed in Supplementary Movie SM1.

tion of the forecasted movements of contact zones is given in the Movie S1 (Supporting information).

### *Intra-specific turnover*

For each incremental increase in mean annual temperature, the extent of intra-specific turnover was measured by the correlation between current and predicted ancestry coefficients for future temperatures (Fig. 3b). For temperature increases of <2 °C, the correlation remained larger than 70% in 18 of the 20 species. Thus, a modest impact of climate change on intra-specific structure was predicted for most species. For greater changes in temperature, histograms of correlation between current and predicted ancestry coefficients exhibited two modes, and species responses divided into two categories. For a temperature increase of 4 °C, correlations were >60% for ten plant species. For those species, intra-specific turnover remained moderate. However, for the ten remaining species, the correlations dropped below 60%, meaning that the changes in genetic population structure were substantial for these species.

### *Evidence of adaptation in warm clusters*

Existence of populations already adapted to a warmer climate is a precondition for interpreting contact zone displacements as a consequence of gene migration to track shifting environments. To examine this hypothesis, we applied two models of allele distribution, respectively, based on GLMs (Joost *et al.* 2007) and GEEs (Poncet *et al.* 2010), to detect loci for which allele frequency gradients exhibited strong correlations with latitudinal gradients. The detected outlier loci were likely to be associated with genes under selection by environmental factors linked to climate (Haldane 1948; Slatkin 1973; Coop *et al.* 2010; Manel *et al.* 2010a,b). GLMs and GEEs led to almost equal cline estimates, and we used the outlier loci of GLMs to identify geographic regions where adaptation to higher temperature could have occurred. More specifically, the models detected outlier loci exhibiting sharp latitudinal clines in 17 of 20 species including all species with warm clusters in the south-west of the Alps (Table 2; Figs 4 and S3, Supporting information). Figure 4 displays examples of 'extreme' allele frequencies at four outlier loci in three representative species (examples for 17 species is

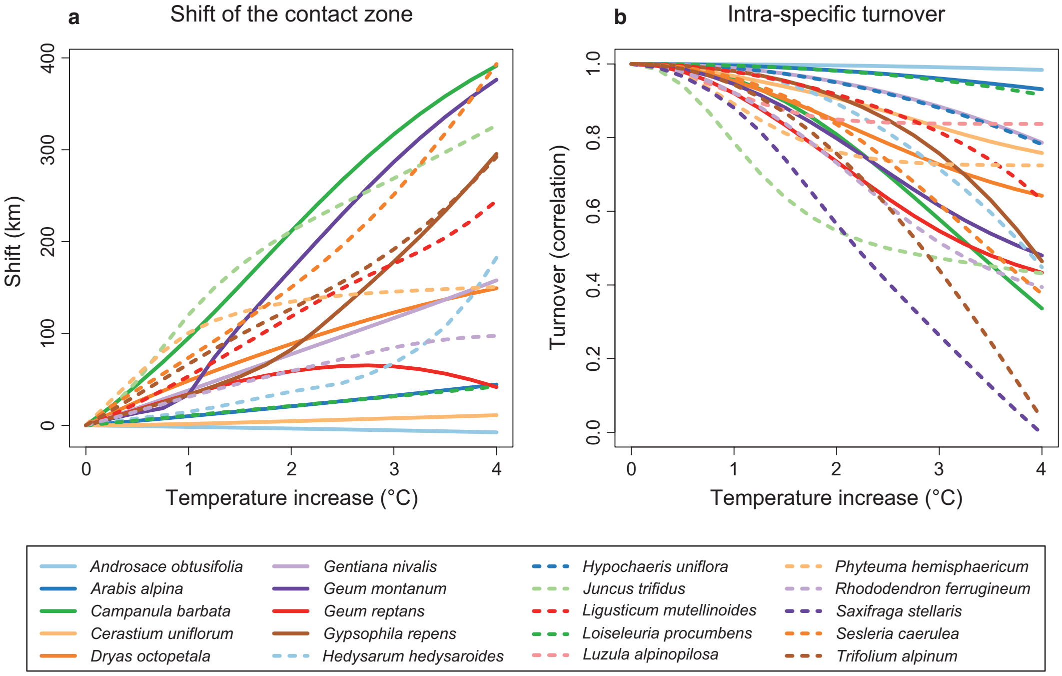

**Fig. 3** Predictions of shifts and intra-specific turnover in Alpine plant species under increased temperature scenarios. Ancestry coefficients and contact zone locations were predicted for temperatures increasing from 0 to 4 °C in steps of 0.25 °C (*x*-axes). (a) Contact zone displacement: distance (km) measured along a south-western to north-eastern transect. (b) Intra-specific turnover measured by the correlation between inferred and predicted ancestry coefficients for all individuals and all clusters.

given in Fig. S3, Supporting infomation). Sharp changes in allele frequency gradients were observed around latitudes 45–46°N, which also correspond to the location of the contemporary contact zones observed between warm and cold clusters.

## *Demographic history*

To identify the relative contribution of adaptation vs. demographic history in shaping the contemporary population genetic structure of alpine plant species, we evaluated signatures of demographic events in our data sets. Alpine plant phylogeography is strongly influenced by postglacial expansion after the ice age (Schönswetter *et al.* 2005). During range expansions, recurrent founder effects and genetic drift at the expansion front are expected to generate gradients in diversity decreasing from the source of expansion (Austerlitz *et al.* 2000; François *et al.* 2008). In agreement with previous observations (Thiel-Egenter *et al.* 2009), we found that the locations of areas of maximal diversity were species-specific (Fig. S2, Supporting infomation). This indicated that plant species probably followed distinct postglacial colonization routes, associated with distinct ecological constraints during dispersal (Alvarez *et al.* 2009). Therefore, the clusters observed in the south-western Alps for 18 species can hardly be explained by shared demographic history. This lack of association indicated that local adaptation contributed in shaping population genetic structure during the history of the species studied.

To test whether gradients in allele frequencies and high correlations between population genetic structure and environment could be explained by demographic history, we performed simulations of postglacial recolonization scenarios based on spatially explicit neutral coalescent models. In simulations, the source of expansion was either located in the south-west or the north-east of the Alps. For most species, these two areas contained the maximum of their genetic diversity and thus could correspond to putative glacial refugia. For the simulated data sets, the distribution of correlations between estimated admixture coefficients and those predicted from the current environmental covariates had their mean around 0.64 (SD = 0.13), whereas the actual mean was around 0.91 (SD = 0.04) for the 20 plant species studied here. The test based on those correlations was significant in 19 of the 20 species ($P < 0.01$ in all cases). For the demographic simulations, these results indicated that the environmental variables did not provide good explanations for the inferred population genetic structure. In contrast, the environmental variables provided high predictive power in the empirical plant data used here. In conclusion, neutral range expansion processes generated significantly lower levels

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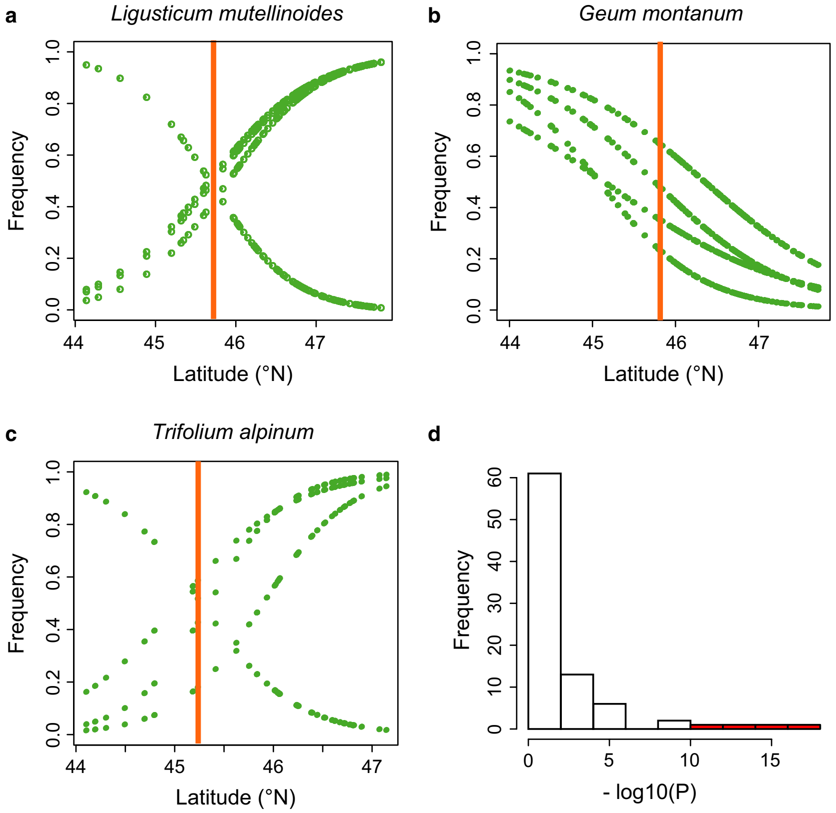

**Fig. 4** Latitudinal clines at outlier loci of alpine plant species. Allele frequency gradients at loci detected as outliers exemplified in the three species (a) *Ligusticum mutellinoides*, (b) *Geum montanum* and (c) *Trifolium alpinum*. Each dotted line represents one locus, the vertical bars correspond to the 50% frequency value. (d) Histogram of *P*-values for *Geum montanum*. The shaded area in the histogram corresponds to the four loci displayed in panel b. Latitudinal clines for other species are displayed in Fig. S3 (Supporting information).

of gene/environment associations than those observed in the data set.

Finally, we further examined the differences in amplitude between the observed allele frequency clines and those obtained from demographic simulations. Differences were significant in 15 (83%) of the 18 species exhibiting warm clusters when expansion started from the north-east. The differences were significant in eight (44%) of the 18 species when expansion started from the south-west (Fig. S4, Supporting information).

## Discussion

We combined the philosophy of species distribution models with population genetic methods to predict the neutral component of the intra-specific response of alpine plants to global warming.

### *Modelling assumptions*

As with species distribution models, the results obtained with ancestry distribution models rely on simplifications. First, biotic interactions (e.g. competition with other species) are supposed to be constant in space and time. This simplification is also present in species distribution models (Guisan & Thuiller 2005) and implies that species are studied separately. Second, no adaptation to changing conditions occurs by new mutations during the period of environmental change. This assumption means that environmental change occurs within short timescales. In addition, while ancestry distribution models consider genotypes, phenotypes are not included in analyses. Thus, the effects of phenotypic plasticity cannot be measured.

While niche modelling predicts the geographic distribution of a species (Guisan & Zimmermann 2000), ancestry distribution models forecast habitat tracking at the intra-specific level. Standard species distribution models assume a global niche and niche conservatism over time (Gallien *et al.* 2010). Ancestry distribution modelling examines the impact of climate change at the gene level and is thus complementary to niche modelling of species distributions. By substituting species occurrence data with genetic data and applying ancestry distribution models, the global niche assumption is replaced by the intra-specific niche variation assumption. Regarding temperature warming, the ancestry models predict that resident genes gradually move to locations which are suitable for their carriers in a way that conserves the realized niches of genetic clusters. In this perspective, forecasts of gene movements in response to changes in environmental variables are expected to reflect the association between population structure and these variables.

Ancestry coefficients summarize genetic admixture which is often recognized to arise in consequence of changing environments (Buggs 2007, Bierne *et al.* 2011, Verhoeven *et al.* 2011). A benefit of using ancestry distribution models is their capacity to incorporate intraspecific hybridization in species responses to such changes. The method proposed in our study is, however, not exactly comparable to considering distribution models for each of *K* clusters, because *K* independent SDMs would not be capable of representing clines of admixture correctly. More importantly, fitting independent distribution models would lead to inappropriate interpretations of clines as artificial barriers that impede habitat tracking after environmental modifications.

Based on presumably neutral markers, our approach supposes that current population structure inferred from these markers reflects isolation-by-adaptation in addition to isolation-by-distance (Nosil *et al.* 2009; Thibert-Plante & Hendry 2010) and more specifically the variation of alleles that played a role in local adaptation to climate (Davis & Shaw 2001). The ancestry distribution models presented here were, however, not designed to predict future adaptive genetic variation. In fact, forecasts of resident gene movement rely on contemporary levels of adaptive standing variation and on species dispersal abilities. Alleles involved in past adaptations, allowing populations to keep track with environmental change, may not be observable directly from the data used in our study. Because adaptation to a warming climate may be triggered by gene flow from populations already adapted to areas of warm climate within the species range (Holderegger & Wagner 2008), it would be important to identify alleles involved in past adaptations. These adaptive alleles are, nevertheless, expected to follow the same patterns of migration as those forecasted for neutral alleles (Bierne *et al.* 2011).

In summary, ancestry distribution models assume that gene migration represents the main component in the response of plant populations to environmental modifications. Biotic interactions, phenotypic plasticity and new adaptive mutations might reduce the relative importance of gene flow. Thus, the estimates obtained via ancestry distribution models should be anticipated as providing upper bounds on the rate at which genes are required to migrate in order for populations to track their rapidly changing environment (see also Aitken *et al.* 2008).

## *Interpretations of results*

In 18 of the 20 species studied here, populations in warmer environments showed higher predisposition to disperse out of their natural range in response to rapid climate change. For example, one of these species, *Rhododendron ferrugineum*, was partitioned into three genetic clusters. The warm cluster, having its centre at around 44.5°N, 6.76°E, showed a difference of 3 °C in average annual minimum daily temperatures with the other two clusters. Projections of ancestry coefficients on a geographic map predicted gene migration around 0.9 km per year for 4 °C of temperature warming in the next century. As ancestry distribution models favoured a migration hypothesis, the magnitude of shift estimated for *R. ferrugineum* and for other species is likely to represent only an upper bound of future rates of migration of neutral alleles. With the mean annual temperature rising by 2 °C, the plant populations studied showed a transversal shift within the range 5–212 km in the next 100 years. For all species, the migration process will create changes in population genetic structure that are species-specific and that could imply considerable changes in ecological interactions within plant communities (Engler *et al.* 2011). A limitation of neutral population genetic models, however, is that they ignore the selective pressures encountered during plant migration. For example, two species, *Luzula alpinopilosa* and *Phyteuma hemisphaericum*, did not exhibit differentiated clusters with respect to climate. For these two species, contact zone shifts were more difficult to predict than for species exhibiting significantly warmer clusters, and the corresponding results could be interpreted as examples of population structure rather being shaped by demographic history or unknown environmental factors (soil, microenvironment) than by climatic gradients.

## *Are patterns of neutral variation linked to adaptive variation?*

Our interpretations of results are valid if plant populations are locally adapted to the climatic conditions that occurred before climate started to warm. Implicitly, these interpretations suppose that local adaptation is detectable from neutral variation (Thibert-Plante & Hendry 2010). We applied outlier detection approaches based on generalized linear models to evaluate the evidence for local adaptation to contemporary environmental conditions in alpine plant species. The outlier detection methods detected latitudinal clines in allele frequencies for all species exhibiting a warm cluster. In addition, the zone of sharp variation of these clines coincided geographically with the contact zone between warm and cold clusters. Simulation-based tests rejected the hypotheses that clines observed at outlier loci could result from spurious association with geography, postglacial re-colonization of the European Alps or shared demographic history. Put together our results suggest that population genetic structure observed from neutral loci reflected the combined effects of demographic

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processes and past local adaptation to climate on plant genetic variation.

### Phenotypic plasticity and rapid adaptation in a historical perspective

As phenotypic plasticity and rapid adaptation are not included either in ancestry distribution models or in traditional species distribution models (Chevin *et al.* 2010, Gienapp *et al.* 2008), it is not yet possible to track the competitive and adaptive abilities of invaded gene pools and their subsequent capacity to reduce the level of introgression by the invading clusters. However, from a theoretical perspective, when assuming that central or northern alpine genotypes could quickly adapt to a changing climate and/or are plastic with respect to warmer conditions, it could be likely that the range expansion of what we describe here mainly as the northward expansion of south-western warm clusters would be more limited. Such limitation might be partly supported by the Pleistocene history of alpine plants, in which survival of gene pools during cold periods occurred all along the southern margin of the Alps (and not only in the south-west), followed by progressive re-colonization of de-glaciated areas towards the North during warmer periods (Schönswetter *et al.* 2005). Evaluating whether this is a rational scenario would only be possible by modelling the past history of a species' gene pool backwards until the last glacial maximum, a task whose realistic implementation in our models is currently not possible given the lack of precise data on the location of realized glacial refugia for each of the 20 studied species (Alvarez *et al.* 2009).

### Long-distance dispersal

In plants, dispersal occurs through seeds, while gene flow and allele migration may occur both by seed and pollen dispersal. Despite the evidence of adaptation to a relatively warm environment in alpine plants, it is not assured that the migration rates of plant species could keep pace with fast rates of environmental change (Malcolm *et al.* 2002), particularly if northern gene pools show little phenotypic plasticity and/or slow local adaptation to warmer temperatures. Long-distance dispersal ability is thus seen as a key parameter for plant species to respond to climate change (Higgins & Richardson 1999). Although long-distance dispersal events might be rare and difficult to observe, they are known to have a strong impact on population structure and adaptation (Nathan 2006; Kunstler *et al.* 2007). A prominent role of wind dispersal has been recognized in alpine habitats (Tackenberg & Stöcklin 2008), and alpine species have thus a good chance to be dispersed by wind or animals over long distances. The required level of dispersal per generation, estimated within the range of 0.5–2.1 km by our ancestry distribution models, represents realistic rates for alpine species (Tackenberg & Stöcklin 2008), especially given that this estimates might be tempered by phenotypic plasticity or existing adaptation of resident populations.

### Genetic admixture

Dispersal creates opportunities for moving populations to interbreed with resident populations at higher latitudes. The ancestry distribution models predict genetic admixture of plant populations from warm areas with populations from currently colder environments. Invasion by south-western populations certainly has the potential to increase local standing genetic variation and allowing for new adaptive potentials in invaded areas. We are, however, cautious about interpreting replacement of resident populations by invading ones for two reasons. First, local plants often perform significantly better than foreign plants at their site of origin (Leimu & Fischer 2008). Although better adapted to a warmer climate, there is no evidence that south-western populations could adapt swiftly to the conditions encountered in newly colonized environments (Walther *et al.* 2009). Ancestry distribution models accounted for differences in habitat between distinct clusters and favoured migration toward similar environments, but they did not assess the adaptive potential of organisms in those environments. Second, during population movement, the genomes of invaders are theoretically predicted to be massively introgressed by resident alleles (Petit 2004; Jump & Peñuelas 2005; Currat *et al.* 2008), which would slow down the migration process. On the other hand, invasions by south-western populations also have the potential to increase local standing genetic variation in invaded areas, which could balance the previous effect (Verhoeven *et al.* 2011). Examining these questions would require further investigations using a higher density of genetic markers and a more precise modelling of genetic drift.

### Trailing and altitudinal edges

The prediction of the presence of plant species at the edge of their distribution ranges was rendered difficult by an absence of data for species in these areas (individual genotypes were mainly sampled from species' altitudinal distribution centres). The predictions of population genetic models may thus underestimate the risk of extinction at the trailing edge of the migration of plant populations (Hampe & Petit 2005) and at the upper altitudinal edge (Jump *et al.* 2009b). Drought and

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dieback events occurring at the trailing edge of shifting clusters have a high likelihood to distort population structure (Jump *et al.* 2009a). Because selection pressures acting on trailing edge populations may be intense, species harbouring high levels of standing genetic variation in the south-west should have a greater chance to adapt than species with low levels of adaptive genetic diversity in this geographic area (Table 2). Examining these questions in further details will require coupling ancestry distribution models with more traditional species distribution models using absence–presence or abundance data and stratified niche sampling (Albert *et al.* 2010).

## Conclusions

Rising global temperatures alter the distribution of plant species (Dukes & Mooney 1999; Walther *et al.* 2009; Pereira *et al.* 2010). Here, we predicted that global change would also create intra-specific turnover impacting intra-specific genetic variation within plant communities. As migration within a species range would be followed by admixture with resident populations, local levels of genetic diversity might not experience a decrease, and some populations might even increase in genetic diversity. Although distributional changes are inevitable for most alpine plant species, intra-specific variation seems to be weakly affected by global warming at least considering a scenario in which the increase in the mean annual temperature is lower than 2 °C. For changes >2 °C, however, our ancestry distribution models predicted higher levels of intra-specific turnover in many plant species, corresponding to low correlations between actual and projected population genetic structure. Although the predictions of population genetic models do not account for rapid adaptation, phenotypic plasticity or biotic interactions, they agreed with the tolerance to temperature increase predicted by nongenetic observations (Theurillat & Guisan 2001). It is, however, important to keep in mind that anthropogenic changes in land use and land cover will surely affect migration patterns as climate change in the coming century.

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## Data accessibility

Marker data, geographic, topographic and climatic information for all 20 species: Dryad Digital Repository doi:10.5061/dryad.777jk760.

## Supporting information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Population structure for 20 alpine plant species. Sample locations in warm clusters are given in red.

**Fig. S2** Interpolated gradients of genetic diversity for 20 alpine plant species.

**Fig. S3** Latitudinal clines at outlier loci for 20 alpine plant species.

**Fig. S4** Null distribution of the shape parameter of the cline at the strongest outlier locus for 18 alpine plant species under scenarios of range expansion from the north-east and the south-west.

**Movie S1** Movement of contact zones for 18 alpine plant species.

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