Improving forecasts of arctic-alpine refugia persistence with landscape-scale variables

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ABSTRACT

Refugia, sites preserving conditions reminiscent of suitable climates, are projected to be crucial for species in a changing climate, particularly at high latitudes. However, the knowledge of current locations of high-latitude refugia and particularly their ability to retain suitable conditions under future climatic changes is limited. Occurrences of refugia have previously been mainly assessed and modelled based solely on climatic features, with insufficient attention being paid to potentially important landscape-scale factors. Here, climate-only models and 'full' models incorporating topo-edaphic landscape-scale variables (radiation, soil moisture and calcareousness) were developed and compared for 111 arctic-alpine plant species in Northern Fennoscandia. This was done for both current and future climates to determine cells with resilient climatic suitability harbouring refugia. Our results show that topographic and edaphic landscape-scale predictors both significantly improve models of arctic-alpine species distributions and alter projections of refugia occurrence. Predictions of species-climate models ignore landscape-scale ecological processes and may thus provide inaccurate estimates of extinction risk and forecasts of refugia where species can persist under a changing climate.

Keywords: climate change; refugia; landscape-scale factor

Introduction

Previous research has shown the importance of refugia for species survival during past environmental changes (Taberlet, 1998; Birks & Willis, 2008; Svenning *et al.*, 2008). Refugia are sites that provide environmental conditions deviant from the regional average, thereby supporting species persistence in a changing climate (Médail & Diadema, 2009; Keppel *et al.*, 2012). Due to the rate and magnitude of global change, refugia are also likely to be among the major mechanisms assisting species persistence in the future (Reside *et al.*, 2013) and should thus be acknowledged in climate change –based conservation planning. A challenge still remains in the credible identification of present-day refugia across landscapes, and particularly in assessing their capability to retain suitable conditions under future climatic changes. Spatial information regarding future refugia is particularly important at high latitudes, as they are among the most susceptible environments to a changing climate (Root *et al.*, 2003; Ashcroft, 2010). However, little is known about which high-latitude landscapes and species are most vulnerable to projected future climatic trends. This knowledge gap calls for increased attention on robust forecasts of how the suitable areas for the species might change, which environmental factors are most critical for developing the most reliable models of this change, and how well potential future refugia are discernible from a given landscape.

Species distribution models (SDMs) are a commonly used tool to forecast the spatial changes in realized or potential species distributions (Guisan & Thuiller, 2005; Araújo & Peterson, 2012). SDMs have also been shown to complement and be spatially correlated with traditionally used phylogeographic estimates of past refugia distribution while providing less subjective and spatially more explicit predictions (Waltari *et al.*, 2007). However, it is increasingly recognized that SDMs often require both climatic variables and non-climatic variables describing landscape-scale or local environmental conditions to maximize predictive ability (Franklin, 1995; Austin & Van Niel, 2011a; Beauregard & de Blois, 2014). Such integrative modelling studies have not, however, been carried out for arctic-alpine species or their refugia in high-latitude regions. This is a shortcoming as the inclusion of landscape-scale factors into SDMs developed for high-latitude refugia may be of particular significance and help identify locations able to preserve environmental conditions reminiscent of the current climate within the surrounding changing matrix, thus leading to more robust predictions of future refugia (Austin & Van Niel, 2011a; Hodd *et al.*, 2014).

A frequently applied paradigm in the study of global change impacts on biota involves models of the distributional changes of species – or the areas environmentally suitable for them - as spatially explicit functions of projected change (Guisan & Thuiller, 2005; Botkin *et al.*, 2007). Similarly, previous studies using spatial models of predicted species distributions have mainly approached refugia from the viewpoint of a single species (Hugall *et al.*, 2002; Austin & Van Niel, 2011a), past distributions (Fløjgaard *et al.*, 2009) or coarser spatial scales (Hodd *et al.*, 2014). Here, we investigate whether the addition of landscape-scale variables to climate-only SDMs (1) leads to different interpretations of how projected changes in climate may affect the distributions of 111 arctic-alpine plant species, and (2) modifies predictions of in situ refugia for these species in N-Fennoscandia. We base these analyses on high-quality species and environmental data, and predict species distributions under contemporary climate as well as two projected future climates i.e. Representative Concentration Pathway (RCP) scenarios: the moderate RCP 4.5 (Smith & Wigley, 2006; Clarke *et al.*, 2007; Wise *et al.*, 2009) and extreme RCP 8.5 scenarios (Riahi *et al.*, 2007).

Materials and methods

Study area

Located in Northern Fennoscandia between 67°N and 70°N, the sub-arctic climate of our study region is driven by its position at the edge of the Eurasian continent, the Polar Front, the warm North Atlantic current, and proximity to the Scandes Mountains (Fig. 1) (Tikkanen, 2005; Aalto *et al.*, 2014b). The area is characterized by varying climatic, topographic and geologic gradients (Oksanen & Virtanen, 1995). Average July temperatures range from 6.1 °C to 15.2 °C and mean annual precipitation from 449 mm to 600 mm (1981 – 2010 means) (Pirinen *et al.*, 2012). Elevation ranges from 72 to 1365 m.a.s.l. The vegetation gradient varies from spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) forests in the south to mountain birch (*Betula pubescens* subsp. *czerepanovii*) in the north, with shrub-dominated tundra-like vegetation above the tree-line (Sormunen *et al.*, 2011).

Preliminary data analysis indicated that parts of our study area are predicted to have a future climate with no current equivalent within the study region. To reduce errors from predicting species responses to climatic conditions without current equivalents, and as arctic-alpine species are generally expected to move northwards as the climate warms, we used data from the whole area for training the models, but excluded the non-analogue southern- and easternmost regions of our study area from model projections (dashed line in Fig. 1) (Sætersdal *et al.*, 1998; Heikkinen *et al.*, 2006).

Species data

Species occurrence data for 1341 1 km² cells were collected by botanists and volunteers, and refined using scientific literature and herbaria. The sampling cells cover all important vegetation zones and ecosystems present in the study area, ranging from taiga to treeless tundra (Kurtto & Lampinen, 1999). Only arctic-alpine species (defined according to biogeographic distribution by professional botanists; see le Roux *et al.* (2012)) with an occurrence in a minimum of eight cells within our study area were included in the subsequent analysis (*n*=111).

Selection of predictors

We used an extensive grid of environmental data matching the resolution of the species data (1 km²) to investigate key refugia predictors. We chose to demonstrate our methodology using a set of climate and landscape-scale terrain and geological variables (Table 1) known to be important for plant species (Skov & Svenning, 2004; Austin & Van Niel, 2011a; Dobrowski, 2011; Scherrer & Körner, 2011). The chosen direct and resource variable predictors (Austin & Smith, 1990) represent growing conditions, surface temperature, light, moisture and soil conditions considered critical for high-latitude vegetation.

The climate data, comprising of observations from 61 stations in Northern Fennoscandia, were acquired from the national observation networks of Finland (Finnish Meteorological Institute), Sweden (Swedish Meteorological and Hydrological Institute) and Norway (Norwegian Meteorological Institute), and modelled to a 1 km² resolution grid (see Aalto *et al.*, 2014). Three climatic predictors with a temporal coverage of 1981–2010 were initially included in the analyses: growing degree days (GDD3; annual accumulated daily temperature sum above 3°C, i.e. growing conditions), temperature of the coldest quarter (TCQ; overwintering conditions) and water balance (WAB; moisture conditions). However, due to ecologically erroneous projections resulting from the counter effects of different climatic variables caused by variable multicollinearity, (namely strong correlations of GDD3 with TCQ and WAB [Spearman's rank correlation coefficients, rs = -0.88 and rs = -0.87, respectively]), only GDD3, which correlates the most with arctic-alpine species diversity in the study area (rs = -0.75), was ultimately included in the final models.

Landscape features exert a strong influence through numerous geomorphological, hydrological, geological and biological processes (Moore *et al.*, 1991), thus controlling the growing conditions experienced by plants (Guisan *et al.*, 1998; Ackerly *et al.*, 2010; Scherrer & Körner, 2011). Here, three topo-edaphic landscape-scale predictors were used: (1) incoming potential solar *radiation* representing surface temperature conditions (McCune & Keon, 2002); (2) digital elevation model-derived topographic wetness index (*TWI*) representing the availability of soil moisture from upslope areas (Beven & Kirkby, 1979); and (3) *calcareousness* representing the proportion of calcareous, nutrient-rich bedrock in a given 1 km² grid cell (Dubuis *et al.*, 2013). In contrast to GDD3, the relative effects of radiation, fluvial processes (e.g. TWI) and soil properties (e.g. calcareousness) should remain more constant in the future (Reside *et al.*, 2013). Radiation and TWI were based on an Aster -derived digital elevation model (NASA Land Processes Distributed Active Archive Center (2013); spatial resolution 30 m²). Radiation was calculated using the ArcView 3.2 Solar analyst extension which uses digital elevation models to generate radiation data by accounting for latitude, elevation, slope angle, slope aspect, shadows cast by surrounding topography, daily and seasonal shifts in solar angle, and atmospheric attenuation (Fu & Rich, 1999). Due to the landscape scale of this study, only one latitude value (here, 69°) for the whole digital elevation model was used. TWI, the most often used surrogate for soil moisture, was calculated using a Python script written by Prasad Pathak that accounts for slope and local upslope contributing area (Beven & Kirkby, 1979; Esri, 2013). Calcareousness was reclassified from a digital database (Geological Survey of Finland 2010; spatial resolution 20 m²). The landscape predictors were resampled by spatial averaging to a 1 km² resolution to match the species and climate data.

Climate change scenarios

Forecasts for the locations of refugia may vary between climate scenarios, thus making it imperative to consider predictions based on multiple scenarios (Reside *et al.*, 2013). Four sets of scenarios containing different emission, concentration and land-use trajectories, have been developed (Van Vuuren *et al.*, 2011). These scenario sets are referred to as Representative Concentration Pathways (RCPs) and they correspond to different greenhouse gas (GHG) concentration trajectories (Moss *et al.*, 2010). Here we explore the implications of two possible future pathways, RCP 4.5 and RCP 8.5 (where the number refers to radiative forcing in watts/m^2 by the year 2100). RCP 4.5 is an intermediate mitigation scenario where GHG emissions are stabilized at low to medium levels (Van Vuuren *et al.*, 2011). RCP 8.5, the unabated 'business-as-usual' scenario, represents the highest GHG emission profile (Riahi *et al.*, 2011; Van Vuuren *et al.*, 2011).

Statistical analyses

Observed species distributions were related to the set of predictors using five statistical modelling techniques. These included two regression methods: generalized linear modeling (GLM) (McCullagh & Nelder, 1989) and generalized additive modeling (GAM) (Hastie & Tibshirani, 1990) and three machine-learning methods: generalized boosting methods (GBM, also known as boosted regression trees (BRT)) (Elith *et al.*, 2008), random forest (RF) (Breiman, 2001) and maximum entropy (MAXENT) (Phillips *et al.*, 2004). All the models were implemented in the Biomod2 platform (Thuiller *et al.*, 2013) using R-program (R Development Core Team 2013). The models were fitted using two sets of predictors:

Occurrence of species = GDD3

[base model]

Occurrence of species = GDD3 + CALC + RAD + TWI

[full model]

Model transferability was assessed using four-fold cross-validation. We applied a commonly used approach (Zimmermann *et al.*, 2009; le Roux *et al.*, 2013b; Aalto & Luoto, 2014) to compare the predictive power of base (climate-only) and full (climate-plus-landscape) models by calculating the area under the curve of a receiver operating characteristic (AUC) plot (Fielding & Bell, 1997), true skill statistics (TSS) and Cohen's Kappa coefficient (Allouche *et al.*, 2006) based on the four evaluation runs (where the models calibrated with 75% of the data were evaluated with the withheld 25 % of the data, and repeated for each of the four quarters of the data). A non-parametric Wilcoxon's test was employed to examine whether explanatory power and predictive accuracy differed significantly between models.

All data were used for projecting species occurrences to current and future climatic conditions. Occurrence probabilities were transformed to binary presence/absence predictions using a TSS cutoff, maximizing model accuracy, defined by BioMod2. In order to account for intermodal variability and to create the final maps of predicted species distributions, we used the consensus approach (Araújo & New, 2007) to construct an ensemble of forecasts that combine the binary predictions from all models. Here we chose a majority's vote of a minimum of three out of five modelling techniques to denote a presence value for a given species inside a given 1 km² grid cell (Figure S1).

For each species, variable influence was assessed in Biomod2 by randomizing each variable individually and then projecting the model with the randomized variable while keeping the other variables unchanged. The model predictions containing the randomized variable were then correlated with those of the original models. Finally, the importance of the variable was calculated as one minus the correlation, with higher values indicating higher predictor importance (Thuiller *et al.*, 2009). This was repeated ten times for each modelling method and the resulting variable influence values were averaged.

Definition of refugia

Areas where the contemporary and future distributions of species overlap may act as refugia (Temunović *et al.*, 2013). By modelling contemporary and projected climates, we can identify these spatiotemporal species distribution overlaps (henceforth referred to as 'resilient cells'). Here, we regard these resilient cells as potential sites for *in situ* refugia where local species may be maintained, i.e. persist even under the assumption of no dispersal (Thomas *et al.*, 2004; Pearson, 2006). *In situ* refugia are more likely to function as effective refugia as reaching them requires only local or no range-shifts (Reside *et al.*, 2014) and, by remaining within the present range of a given species, they provide a robust estimate of species persistence (Shoo *et al.*, 2013).

To locate *in situ* refugia from SDM predictions we utilized a step-by-step approach as follows (Figure S1): firstly, as refugia are essentially species-specific (Provan & Bennett, 2008; Stewart *et al.*, 2010), we model the species separately to gain insights into their preferred environments. Next, the single-species predictions are projected separately into current climatic conditions and two future climate scenarios to locate cells where species occurrence is maintained both spatially and temporally (Shoo *et al.*, 2013; Temunović *et al.*, 2013). Finally, as favourable environmental conditions supporting refugia may overlap for several species (Hampe & Petit, 2005; Keppel *et al.*, 2012) and to increase prediction robustness, we stack projections of these resilient cells to locate sites where suitable conditions persist for several species. Areas with higher arctic-alpine species diversity are strong refugia candidates as they maximize available information and the probability of this diversity persisting under climate change. Consequently, sites harbouring several refugial species simultaneously are potentially very valuable for future conservation planning. Thus, we set a threshold of a minimum of five persisting species as a prerequisite for a resilient 1 km² grid cell to be classified as a refugia.

Results

The use of topo-edaphic landscape-scale predictors significantly ($p<0,001$) improves the accuracy of SDMs developed for the studied arctic-alpine species. Based on the cross-validation runs, the mean AUC values improved from 0.77 (base i.e. climate-only model) to 0.86 (full i.e. climate-plus-landscape model). The corresponding TSS values improved from 0.51 to 0.62, and Kappa values from 0.39 to 0.46 (Table 2). Lower standard deviations of the evaluation metrics in the full models also indicate greater model accuracy (Table 2).

The inclusion of landscape-scale predictors changes contemporary predictions of refugia as well as projections of species distributions and predictions of the availability of suitable environments for arctic-alpine species in a warming climate. Differences arise in both predictions of how many species are predicted to persist in a given refugia, as well as the total count i.e. spatial extent of refugial cells. The full model predicts fewer species range reductions and higher species persistence (Fig 2: b, d; Table S1): out of the 111 species, the full model locates refugia for 77 species in RCP 4.5 (climate-only model: 40 species) and 47 species in RCP 8.5. Considerably less refugia were predicted by the full model into the more extreme RCP 8.5 (207 refugia; compared to 959 in RCP 4.5; Table S1). The base model does not project any refugia into RCP 8.5 (Fig 2: c). The spatial extent of refugial cells predicted by both models into RCP 4.5 shows a 79% overlap (Fig 2: a, b). However, over 95% of the refugial cells predicted by the full model for RCP 4.5 demonstrate a higher species persistence rate than predictions from the base model (Fig 2: b, d; Table S1).

Out of the 111 species included in the analysis, GDD3 was the most influential variable for most of the species (n=69); calcareousness for 26 species; TWI for 13 species; and radiation was the most important variable for three species. An example of projected refugia for Alpine Mouse-ear (*Cerastium alpinum*) are shown in Figure S3. This small perennial herb shows a clear preference for high substrate calcareousness and cooler growing conditions offered by the regions refugia. There is a clear spatial prominence of refugial cells around the cooler, more calcareous mountainous regions of the study area (Figs 1 & 2; Table S2; Figure S4: b-d). By including topo-edaphic landscape-scale variables, suitable environments for arctic-alpine species can, however, be projected into cells with a higher GDD3 than by accounting for climate alone. Aside from climatic differences, the refugia derived from full model predictions also exhibit slightly differing landscape conditions, here higher radiation, a higher cover of calcareous substrates and lower TWI (Table S2).

Discussion

Our results demonstrate more detailed and accurate predictions of refugia following the inclusion of landscape-scale variables reflecting the topo-edaphic conditions to climate-only models. This is due to the limiting effect of using only climatic predictors that overlooks certain fine-resolution spatial and temporal (e.g. extent and persistence of suitable habitat, respectively) aspects of species distributions. In other words, consideration of landscape properties is required to capture the important topo-edaphic conditions shaping refugia distribution patterns in space and time (Austin & Van Niel, 2011b), and our study shows that this is true also for high-latitude environments.

Refugia defined using both climate and topo-edaphic parameters, compared to refugia defined by climate alone, are more likely to continue to provide suitable conditions for a greater portion of arctic-alpine species growing in a given grid cell (Dobrowski, 2011; Keppel *et al.*, 2012). The inclusion of topo-edaphic variables modifies climate-only models in a way that enables predictions of suitable future conditions into a number of cells with warmer average growing conditions. This significance of accounting for the topo-edaphic setting results partly from how it can modify the climatic conditions experienced by species (Austin & Van Niel, 2011a; Lenoir *et al.*, 2013). As seen for the example species, Alpine Mouse-ear, the climate-only model predicts species persistence in northern refugia, where temperatures are cooler (Figs S2 & S4). The refugia show a more spatially dispersed pattern of persistence in a changed climate, but the forecasts of species persistence are made more optimistic through additions of topographic and edaphic predictors. Moreover, improvements to the models and derived predictions resulting from the incorporation of landscape-scale variables also emphasize an increase in species' tolerance in confronting climatic changes via edaphic conditions (Table S2; Fig S3). The importance of calcareous substrate also shows that adjusting climate models with topographical variables only, e.g. constructing topoclimatic models, may lead to misrepresentative conclusions regarding SDMs and climate change predictions.

Possibly owing to the importance of climate as a predictor, the spatial distribution of refugia appears similar between the base and full model predictions for RCP 4.5. This is particularly evident in the northern regions of the study area where GDD3 levels remain favourably low for arctic-alpine species persistence. Areas with the least environmental change are more likely refugia candidates for most species within a grid cell (Reside *et al.*, 2013) and, indeed, considerably less refugia were predicted by the full model into the more extreme RCP 8.5 (207 refugia; compared to 959 in RCP 4.5). The spatial distribution of these 207 refugial cells is more dispersed, suggesting that refugial species in a warmer future would need to rely on more isolated habitats to provide locally favourable landscapes. Though decreased by climatic changes, forecasts of species persistence in refugia are improved by even fairly simple topo-edaphic landscape properties at the mesoscale. Examining such grid cells where species can persist is a robust way of mapping distributional changes and refugia, though dispersal abilities and possible time lags of species responses to changing landscape configurations are also likely to contribute to the effectiveness of refugia. However, accounting for circumstances of little or no spatial overlap between current and future suitable environments would require information on species dispersal capacities (Reside *et al.*, 2013; Reside *et al.*, 2014) to *ex situ* refugia (Shoo *et al.*, 2013) to enable more realistic estimates of species range-shift abilities to future refugia.

The distributions of a majority of the 111 arctic-alpine species studied here are projected to shrink following increases in temperature with most of the study region appearing as a matrix of unsuitable growing conditions for arctic-alpine species. Heterogeneous mountainous regions, such as the northern areas of our study landscape, are expected to be exceedingly important for refugia and the conservation of species (Loarie *et al.*, 2008; Luoto & Heikkinen, 2008; Scherrer & Körner, 2011), especially for endemic mountain plants at risk from range reduction by upward displacement (Rull & Vegas-Vilarrúbia, 2006). Indeed, our finding that the located refugia are offering conditions of lower soil moisture (as indicated by the variable TWI) is related to the assumption that steeper slopes, such as those found in the Scandes, are less likely to retain water (Beven & Kirkby, 1979). The significance of these mountain refugia, however, is likely to be affected by species' properties such as growth form and dispersal capacity (Engler *et al.*, 2009), and mountain refugia have been disputed to be of little avail to small, scattered populations of species (Birks, 2008). The reduction in available land area at higher elevations may also result in species' local extinctions (Patsiou *et al.*, 2014). Nevertheless, the *in situ* refugial expanse in the mountainous area of the study region is projected to be an important location for providing many arctic-alpine species with suitable conditions for persistence, and its potential to do so deserves further investigation.

More generally, it needs to be acknowledged that evaluating the capability of refugia in promoting species persistence and ecosystem resilience is difficult due to the many uncertainties involved in predicting and modelling climate, changes therein, and species responses to these changes (Wiens *et al.*, 2009; Reside *et al.*, 2013; Shoo *et al.*, 2013). For example, assuming uniform warming across a given landscape, or basing forecasts of changes in local climate on simple temperature-elevation correlations may over-emphasize the importance of relatively cool sites or higher elevations (Ashcroft, 2010). Essential aspects of future refugia research include investigating the dynamics of climatic decoupling between the atmosphere and terrain within arctic-alpine landscapes (Dobrowski, 2011; Scherrer & Körner, 2011; Hylander *et al.*, 2015), as we cannot surmise the effects of topography on climatic stability with the approach used here. A similar modelling framework could also be used to pinpoint individual at-risk species, specific areas or habitat types facing substantial changes in a warmer future (Thuiller *et al.*, 2005; Williams *et al.*, 2005; Loarie *et al.*, 2008). Furthermore, though the landscape-scale predictors used here provide a solid basis for a comprehensive set of ecologically meaningful predictors, enumerating the significance of other variables, such as geomorphological disturbances (Randin *et al.*, 2009; le Roux *et al.*, 2013a; Slaton & Linder, 2015), CO_2 effects (Rickebusch *et al.*, 2008) and biotic interactions (Godsoe *et al.*, 2015; Mod *et al.*, 2015), may also be necessary for more realistic predictions of refugia persistence (sensu Austin and Van Niel 2011b), though their relevance is likely to be further pronounced at finer spatial scales. ur results, highlighting the importance of topo-edaphic landscape-scale factors for modelling refugia as well as demonstrating changes in the extent and connectivity of suitable habitat, show there is a strong case for applying a similar approach at finer or even multiple scales to facilitate a more mechanistic approach to future refugia study.

Conclusions

Climate change projections suggest that returning to historical climatic conditions is highly improbable. Here we show that, despite forecasted future regional warming, several resilient sites found in our study landscape are predicted to maintain suitable local environments due to topo-edaphic conditions. Refugia can be found in places where locally optimal environments remain constant across timescales and in which the effects of landscape preserve environmental conditions more reminiscent of suitable contemporary climates. Predictions of species responses to climate change based on climate alone may be inaccurate in estimating extinction risk as they neglect to consider topographic and edaphic processes affecting species distributions, and may fail to identify refugia where species can persist. Thus, models of species distributions and changes therein need to account for topo-edaphic landscape-scale variables to provide information on relevant spatial and temporal responses to environmental change and should thus be explicitly accounted for in future climate change impact assessment studies.

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Table 1 Descriptions of the four focal environmental variables with their minimum (Min.), median (Med.), mean and maximum (Max.) values

Variable	Description	Min.	Med.	Mean	Max.
GDD3 (contemporary)	Growing degree days (annual accumulated daily temperature sum above 3°C; unit °C)	163	810	784	1050
(under RCP 4.5)		374	1247	1204	1489
(under RCP 8.5)		633	1620	1587	1964
Radiation	Potential annual direct radiation (MJ/cm^2/a)	0.28	0.43	0.43	0.62
TWI	Topographic wetness index	5.58	6.93	6.95	8.70
Calcareousness	Cover of calcareous substrates (%)	0	6.7	13.0	90.3

Table 2 The model evaluation statistics for the base (climate-only) and full (climate-plus-landscape) models showing the mean and standard deviation (SD) of the evaluation metrics over four cross-validation runs. Wilcoxon signed rank test p-values show change in predictive ability (*** = highly significant). AUC improved for 104; TSS for 10; and Kappa for 99 out of 111 species

	AUC		TSS		Kappa	
	Base	Full	Base	Full	Base	Full
Mean ± SD	0.77 ± 0.09	0.86 ± 0.06	0.51 ± 0.14	0.62 ± 0.13	0.39 ± 0.21	0.46 ± 0.16
p-value	< 0.001***		< 0.001***		< 0.001***	

Fig 1. The location and elevation of the study area in northern Fennoscandia. We used data from whole area for training the models, but excluded non-analogue regions from the projections (white dashed line)

Fig 2. Refugia in two Representative Concentration Pathway (RCP) scenarios (RCP 4.5 a-b; RCP 8.5 c-d) of future climate according to base models (climate-only; a, c) and full models (climate-plus-landscape; b, d). The full models predict a higher relative species persistence from contemporary to future climates. No refugia were predicted for scenario RCP 8.5 by the base model. The legend applies throughout

Supporting Information

Figure S1: An outline of the modelling framework used. We combined model predictions for 111 arctic-alpine plant species to estimate current and projected species distribution and identify refugia at a 1 km² resolution. To enable the comparison of species' distributional changes, we ran the predictions for contemporary climate as well as two Representative Concentration Pathways (RCPs 4.5 and RCP 8.5). Two sets of predictors were used: climate-only (growing degree days (GDD3)); and climate-plus-landscape, which included additional landscape-scale predictors: potential solar radiation (RAD); calcareousness (CALC); and topographic wetness index (TWI). Observed species distributions were related to the set of predictors using five statistical modelling techniques: generalized linear modeling (GLM), generalized additive modeling (GAM), generalized boosting methods (GBM), random forest (RF) and maximum entropy (MAXENT). All the models were implemented in the Biomod2 platform under R-program

Table S1: Summary statistics for arctic-alpine species persistence within refugia; the number (n) and proportion (%) of species persisting in refugia according to the two model structures used and two scenarios of future climate. No refugia were predicted for scenario RCP 8.5 by the base model. The total count of cells used in the analysis was 15 622

Figure S2: Predicted contemporary and future distributions of Alpine Mouse-ear (*Cerastium alpinum)* in the study area. The predicted distributions were modelled into two scenarios of future climates (RCP 4.5 and RCP 8.5) according to two sets of predictors: climate-only (base model) and climate-plus-landscape (full model)

Figure S3: Box-and-whisker plot showing the mean variable importance values based on the full model across all species and across the five modelling techniques utilized (boxplot represents median, first and third quartiles; the whiskers show the interquartile range). The variables included in the full model are growing degree days (GDD3), calcareousness (CALC), potential solar radiation (RAD) and topographic wetness index (TWI). See table 1 for a full description of each variable. Outliers are excluded for clarity

Table S2: Summary statistics for refugia located by the base (climate-only) and full (climate-plus-landscape) models under Representative Concentration Pathway (RCP) 4.5 and the full model for RCP 8.5 (the base-model for RCP 8.5 found no refugia). The full set of variables are growing degree days (GDD3), calcareousness, potential solar radiation (RAD) and topographic wetness index (TWI). See table 1 for a full description of each variable and for comparison with contemporary climatic conditions

Figure S4. Spatial characteristics of the predictor variables: growing degree days (GDD3; °C) for the contemporary climate 1981–2010 (a), and GDD3 for the two Representative Concentration Pathway (RCP) scenarios used: RCP 4.5 (b) and RCP 8.5 (c); calcareousness (d; %); potential solar radiation (e; MJ/cm²/a); and topographic wetness index (TWI) (f). See table 1 for a further description of the predictors

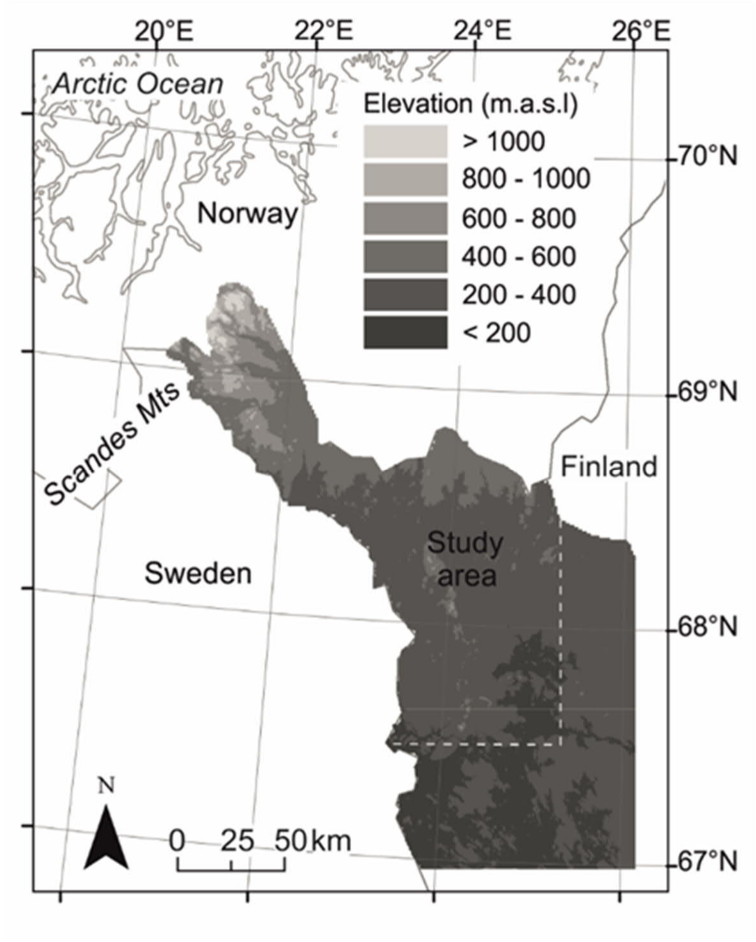
20°E
22°E
24°E
26°E
Arctic Ocean
Elevation (m.a.s.l)
> 1000
800 - 1000
600 - 800
400 - 600
200 - 400
< 200
70°N
69°N
68°N
67°N
Norway
Scandes Mts
Finland
Sweden
Study area
N
0 25 50 km

Figure 1.

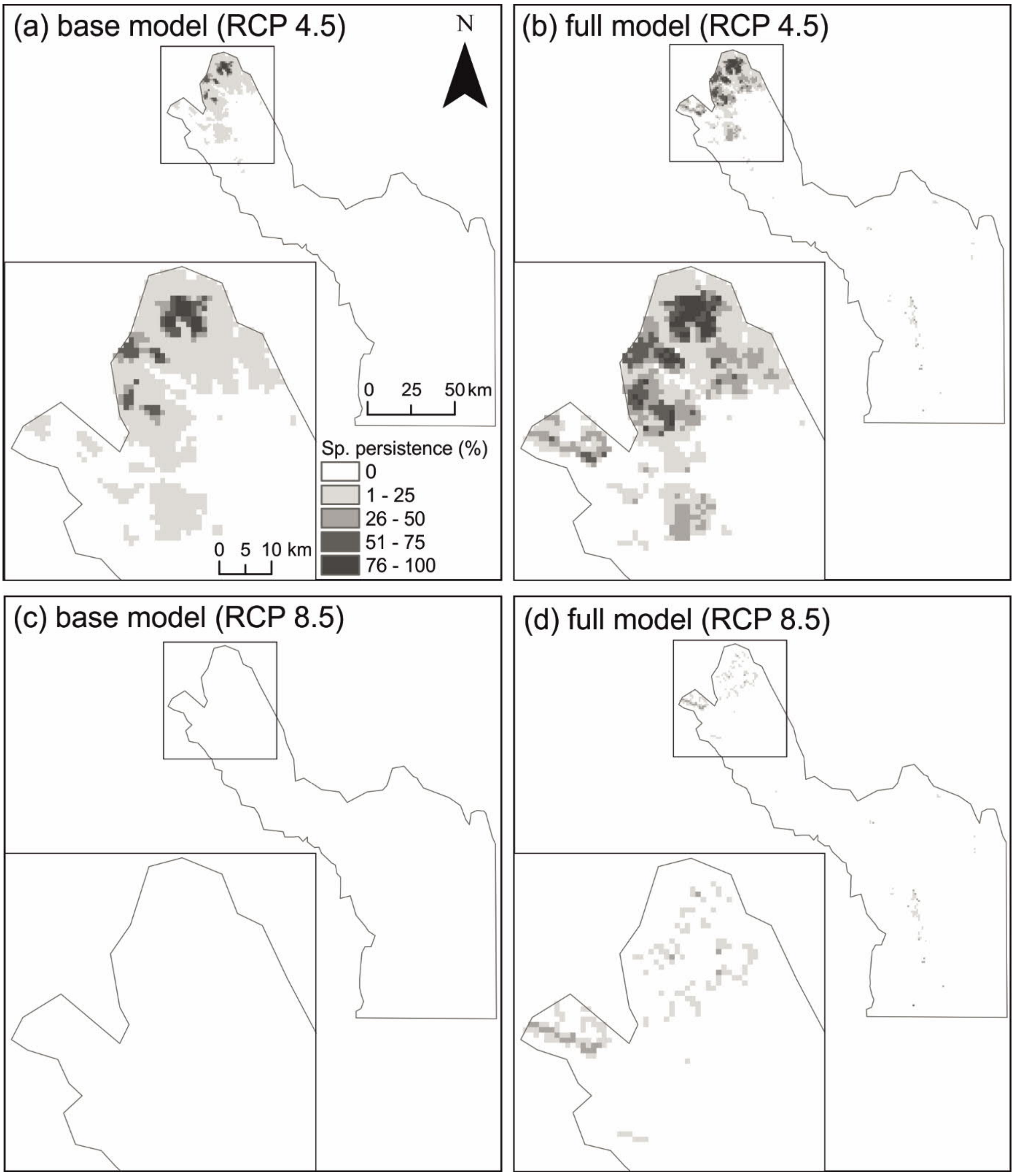
(a) base model (RCP 4.5)
N
(b) full model (RCP 4.5)
0 25 50 km
Sp. persistence (%)
0
1 - 25
26 - 50
51 - 75
76 - 100
0 5 10 km
(c) base model (RCP 8.5)
(d) full model (RCP 8.5)

Figure 2.