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Models of arctic-alpine refugia highlight importance of climate and local topography

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Abstract:	This study aims to determine the effects of environmental factors on the distribution and species richness of refugia for arctic-alpine vegetation. We will assess the main drivers for the arctic-alpine refugia in our study areas in N Europe, defined as isolated pockets with multiple species occurrences outside their main distribution area, and how well they can be modelled. The study is based on a comprehensive vascular plant distribution data set combined with abiotic environmental data at a resolution of 1 km². Cross-validated Boosted Regression Tree (BRT) modelling was employed to examine the effects of the climatic, topographic and geologic variables on refugia distribution and refugia species richness. Model testing was performed incrementally, i.e. first climate alone, then with additions of topography or geology, and concluding with a model including all predictors. All refugia distribution models (climate-only and different predictor combinations) performed well with mean area under curve (AUC) values higher than 0.85 and true skill statistics (TSS) values higher than 0.57. The inclusion of topography significantly improved model performance for both refugia distribution and refugia species richness. Climate has a central role in controlling the occurrence of refugia. However, topographic variables aid in recognizing the locally heterogeneous environments that sustain refugia. Refugia are thus driven by joint impacts of climatic and topographic factors that determine local thermal and moisture conditions. Our study demonstrates that the spatial patterns of refugia can be successfully modelled but emphasizes a need for high-quality data sampled at resolutions reflecting significant environmental gradients.
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Models of arctic-alpine refugia highlight importance of climate and local topography

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Abstract

This study aims to determine the effects of environmental factors on the distribution and species richness of refugia for arctic-alpine vegetation. We will assess the main drivers for the arctic-alpine refugia in our study areas in N Europe, defined as isolated pockets with multiple species occurrences outside their main distribution area, and how well they can be modelled. The study is based on a comprehensive vascular plant distribution data set combined with abiotic environmental data at a resolution of 1 km². Cross-validated Boosted Regression Tree (BRT) modelling was employed to examine the effects of the climatic, topographic and geologic variables on refugia distribution and refugia species richness. Model testing was performed incrementally, i.e. first climate alone, then with additions of topography or geology, and concluding with a model including all predictors.

All refugia distribution models (climate-only and different predictor combinations) performed well with mean area under curve (AUC) values higher than 0.85 and true skill statistics (TSS) values higher than 0.57. The inclusion of topography significantly improved model performance for both refugia distribution and refugia species richness. Climate has a central role in controlling the occurrence of refugia. However, topographic variables aid in recognizing the locally heterogeneous environments that sustain refugia. Refugia are thus driven by joint impacts of climatic and topographic factors that determine local thermal and moisture conditions. Our study demonstrates that the spatial patterns of refugia can be successfully modelled but emphasizes a need for high-quality data sampled at resolutions reflecting significant environmental gradients.

Keywords: General Boosted Model; GBM; spatial modelling; species distribution models; refugium; high-latitude environments.

INTRODUCTION

Climate change is predicted to cause notable changes in high-latitude environments, causing fragmentation and structural changes in habitats and ultimately leading to local extinctions and range shifts of plant species (Ashcroft 2010; IPCC 2007; Root et al. 2003). Some species may, however, be able to persist in refugia (Skov and Svenning 2004). In general, refugia are considered as suitable locations for species to retreat to in unfavorable periods and re-disperse from if suitable environmental conditions return (Dobrowski 2011; Keppel et al. 2012). Projected climatic changes in high-latitude environments call for increased attention to the identification of locations that act as present-day refugia or could function as refugia in the future.

Two main lines of reasoning are relevant here. First, a number of studies call for the protection of contemporary and future refugia (Bush 1996; Noss 2001; Mawdsley et al. 2009) as they are increasingly considered as a means to reduce the impacts of environmental change on biota (Médail and Diadema 2009; Dobrowski 2011) and biodiversity (Barnosky 2008; Rull 2009; Ashcroft 2010; Vegas-Vilarrúbia et al. 2012). Second, identifying the main drivers of refugia occurrence and species richness, and developing models for these relationships, is of particular importance in the preservation of arctic ecosystems (Reside et al. 2013; Shoo et al. 2013) as the distribution of contemporary refugia can also provide decisive clues for determining the most probable locations of future refugia.

Despite growing interest in the supportive role of refugia in the face of climate change, our knowledge remains insufficient in regards to a number of research issues. In particular, refugia for cold-adapted species have not been well documented (Bennett and Provan 2008; Stewart et al. 2010) and there is great uncertainty regarding the conditions governing their subsistence (Dobrowski 2011; Moritz and Agudo 2013). The importance of filling this gap in knowledge is enhanced by the fact that there are no on-going attempts to quantify contemporary refugia in arctic-alpine northern Europe, a region likely to experience notable changes in climate (ACIA 2004). This study aims to fill in such research gaps by incorporating extensive data sets with modern geoinformatics and spatial modelling tools to investigate the spatial patterns of contemporary refugia and their predictability. For the purposes of this study, we define refugia as isolated pockets of multiple species occurring outside a main distribution area. Based on this definition we will model and quantify the effects of climatic, topographic and geologic variables on the distribution and species richness of refugia for arctic-alpine plant species outside their main range area, starting with baseline climate-only models and building up to more complicated models, ultimately including predictors from all three variable categories. To achieve this we analyzed an extensive data set collected in north-western Finland and Norway, a region where refugia may be expected to strongly influence current and future vegetation patterns.

MATERIALS AND METHODS

Study area

The study area is located in northern Fennoscandia between 67°N and 69°N (Fig. 1 a). The climate in the region is sub-arctic and strongly affected by its location at the edge of the Eurasian continent, the influence of the Polar Front and the warm North Atlantic current, and the proximity of the Scandes Mountains (Fig. 1 b: Tikkanen 2005; Aalto et al. 2014). Mean July temperature varies from 1.3 °C to 12.6 °C and mean annual precipitation from 423mm to 593mm (1981 – 2010 averages) (Aalto et al. 2014). Along with the noticeable climatic gradients, the area is characterized by strong topographic and geologic gradients. Elevational differences range from 72 to 1365 m.a.s.l. The vegetational gradient of the study area runs from spruce and Scots pine dominated forests in the south to mountain birch in the north, with tundra-like shrub-dominated vegetation above the tree-line (Sormunen et al. 2010; Aalto and Luoto 2014).

Data

Refugia species

A vegetation data set consisting of 2081 1 km² cells in north-western Finland served as the basis for this study. The species data was collected by professional and voluntary amateur botanists and refined using scientific literature and herbaria (Ryttäri and Kettunen 1997; Rassi et al. 2001). Two dependent variables were derived from the species data: (1) binomial refugia distribution and (2) refugia species richness.

Though refugia are species specific (Bennett and Provan 2008; Stewart et al. 2010), the favourable environmental conditions supporting refugia may overlap for several species (Keppel et al. 2012). Consequently, sites harbouring several refugia species simultaneously are potentially very valuable for future conservation planning. Arctic-alpine species (hereafter called refugia species) were inferred from our floristic data set as species with more than two thirds of their study area distribution in the arctic-alpine Scandes Mountains (Fig. 1; see Online Resource 1 for species list). This set of refugia species was then used to detect contemporary arctic-alpine refugia in the study region outside their main distribution area in the Scandes Mountains. As our focus was in building models for the refugia, the 1 km² cells located in the Scandes Mountains (which were used to infer refugia species) were disregarded from the subsequent model building (grey points in Fig. 1). Consequently, a total of 1552 cells were included in the calibration of our refugia models modelling (white points in Fig. 1). From the retained 1552 cells we appointed those with observations of multiple (≥5) refugia species as refugia cells. The presence of multiple refugia species is a way of repeatedly identifying them as refugia and enables us to determine the most important predictors.

Environmental predictors

We used an extensive environmental 1 x 1 km data grid matching the species data and encompassing the entire study area to quantify dominant refugia predictors. A total of 11 ecologically appropriate and theoretically meaningful climatic, geologic and topographic variables (Körner 1999; Skov and Svenning 2004; Dobrowski 2011; Scherrer and Körner 2011; Graae et al. 2012; Reside et al. 2013) were chosen for modelling both refugia distribution and species richness (Table 1). We assume refugia distribution to be linked to the physical environment represented by these variables and, consequently, refugial species to show distinct relationships with one or more of the environmental factors considered here (Guisan et al. 1998).

The climate data set, comprising of observations from 61 stations in northern Fennoscandia, was acquired from the national observation networks of Finland (Finnish Meteorological Institute), Sweden (Swedish Meteorological and Hydrological Institute 2012) and Norway (the Norwegian Meteorological Institute 2012). The temporal coverage corresponds to the recording period of the species data (1971 – 2000). Three mean climatic variables were calculated from monthly mean temperature and precipitation values (see Aalto et al. 2014): (1) growing degree days (*GDD3;* growing conditions); (2) freezing degree days (*FDD;* overwintering conditions) and; (3) water balance (*WAB;* available moisture). Two variables describing extreme temperatures were constructed alongside mean conditions as they may be especially characteristic of high-latitude environments (Aalto et al. 2014). The predicted rapid increase in extreme temperature events (Meehl and Tebaldi 2004) make them increasingly relevant for studies of ecological systems (Pimm 2009). In our study, daily minimum and maximum temperatures were used to delineate annual measures of extreme absolute temperatures. Lowest absolute minimum temperatures (T_{min}; coolest within-cell sites) represent winter conditions, where colder temperatures are needed for the persistence of cold-adapted northern species. Lowest absolute maximum temperatures (T_{max}; the coolest within-cell sites within a warmer matrix) represent sites that remain relatively cool when the surrounding area warms up in the summer, i.e. conditions that are necessary for the survival of northern species under the warming climate.

Topography can also exert a strong influence on growing conditions and the distribution of potential refugia (Ackerly et al. 2010; Austin and Van Niel 2011; Scherrer and Körner 2011; Keppel et al. 2012). The topographic variables used here were based on an Aster -derived digital elevation model (DEM; spatial resolution 25 m²; Land Survey of Finland, 2013) and calculated following Aalto and Luoto (2014). Three topography-based variables were selected: (1) incoming potential solar *radiation* (surface temperature conditions (McCune and Keon 2002)); (2) topographic wetness index (*TWI;* availability of soil moisture from upslope areas (Beven and Kirky 1979)); and (3) *slope* angle (slope processes). These variables are good proxies for the microclimates of rugged terrain (Guisan and Zimmermann 2000; Dobrowski 2011) and geomorphological processes (Randin et al. 2009) affecting species distributions in high-latitude landscapes.

Slope and *TWI* have also been found to be good predictors of soil moisture (Penna et al. 2009), which is a key driver of vegetation properties (le Roux et al. 2013).

Geology influences vegetation through soil properties (Guisan et al. 1998; Austin and Van Niel 2010). Three geologic variables were chosen for this study: (1) *calcareousness* (soil pH, shown to improve the predictive power of species distribution models (Dubuis et al. 2012)), (2) *soil diversity* (variability of growing substrate: rock, sand, peat, till) and (3) *rock cover* (cliffs, rocky outcrops, scree; considered here as its own variable as it can be significant in predicting species distributions in harsh environments (Guisan et al. 1998)). The geological predictors used here were reclassified from a digital database (Geological Survey of Finland: 2010) and transformed following Aalto and Luoto (2014).

Data analysis

We combined species distribution data with environmental predictors to determine the drivers of refugia and their species richness in our study area. Predictor and response variable relationships were quantified using boosted regression tree (BRT) modelling, a form of regression capable of modelling complex nonlinear functions (Elith et al. 2008). Comparative analyses have rated BRT performance highly (Elith et al. 2006; Heikkinen et al. 2012). BRTs simultaneously use numerous trees and consider all predictors as well as interactions to improve model performance and predictive ability (Elith et al. 2006, 2008; De'ath 2007; Leathwick et al. 2008). BRTs compute the relative influence of each variable based on capacity to reduce overall model deviance and contribution to predictive ability. Higher relative influence values point to stronger effects of the predictor on the response variable (De'ath et al. 2007; Elith et al. 2008). In the first phase of the modelling process, models were calibrated using only 1 km² grid cells with available vegetation data. All statistical analyses were performed using the statistical software R (version 3.0.2; R Foundation for Statistical Computing, Vienna, AT).

The BRT models (interaction depth = 4, number of iterations/ trees = 3000) were run using the *gbm* -package (Ridgeway 2013). Models were built to assess the importance of different environmental variable groups and to evaluate the relative influence of individual variables on refugia. The response variables, (a) refugia distribution and (b) refugia species richness, were fitted with identical sets of environmental predictors (Fig. 2) using Bernoulli and Poisson distributions, respectively.

Eight different models were run following the methodology of Guisan and Zimmermann (2000) and le Roux et al. (2012; 2013) to assess model transferability: projections were cross-validated with 999 runs, each time selecting a different 70% random data sample while verifying model accuracy against the remaining 30%. We assessed the predictive power of the refugia distribution models by comparing the observed and predicted refugia occurrences by calculating the mean values of the area under the curve of a receiver operating characteristic plot (AUC; Fielding and Bell 1997) and the true skill statistics (TSS; Allouche et al. 2006) based on the evaluation runs. AUC values generally range from a random (AUC 0.5) to a perfect fit (AUC 1.0), with AUC values higher than 0.7 deemed a fair fit (see Swets 1988). A TSS value of 1 indicates perfect agreement; zero or below indicates a performance no better than random (Allouche et al. 2006). The models for refugia species richness were examined with the same cross-validation procedure but using Spearman's rho (ρ) analysis. A non-parametric Wilcoxon’s test was employed to examine whether explanatory power and predictive accuracy differed significantly between models.

With the exception of temperature extremes (T_{max} and T_{min}) and *soil diversity*, all variables are expressed as mean values, as calculated for the 1 km² cells included in the study. Some correlations exist between the extreme temperature variables, *GDD3* and *WAB*. *Slope* is also strongly correlated with *TWI*, as the former is used to calculate the latter (Online Resource 2).

In the second phase of the modelling process, we produced final prediction maps to illustrate the spatial predictions of the contemporary refugia for a wider area, i.e. the region in which the 1552 1 km² cells used in model calibration are embedded. Here, the derived models were fitted to the environmental data covering the entire study area with 1 km² grid cells (n=25 766), thus enabling us to predict refugia occurrence for the whole area.

RESULTS

Refugia distribution

We identified 109 1 km² grid cells harbouring refugia based on the species data available for our study area (Fig. 3). Refugia occurrence resembles a proximal distribution with few outliers situated diffusely in the south, thus showing a gradual decrease in refugia with distance to the main distribution area (Fig. 3).

The mean AUC values for all models are higher than 0.85, indicating that all combinations of predictor variables are fairly good at predicting refugia distribution (Fig. 4a). Model TSS values demonstrate a moderately good explanatory power for the studied variables (Allouche et al. 2006). However, statistically significant differences between the models were evident. Adding topography to the climate-only model significantly improved predictive power, making the climate + topography model (Fig. 4a ii) the best combination of predictors for refugia distribution according to AUC values. The full model (Fig. 4a iv), however, has the highest mean TSS value. Additions of geologic variables improve the climate model only according to TSS values (Fig. 4a iii).

The importance of climatic predictors is pronounced (Fig. 5). *WAB* was constantly shown as the most influential variable within all models of refugia distribution, with areas of high *WAB* promoting extreme habitats (Online Resource 4: Fig. 1). Refugia are located in 1 km² cells which have sites that become neither too hot in summers nor too cold during winters, i.e. they host less extreme environments in regards to T_{max} and T_{min} (Fig. 5; Online Resource 4: Fig. 1). Correlations are also evident between refugia distribution and topographic predictors. The importance of *slope* indicates that refugia are more often found in steeper than flatter terrain (Fig. 5; Online Resource 4: Fig. 1). Improvements to model performance from the inclusion of geologic variables were indistinct and minor (Fig. 5). Model projections for refugia occurrence across the entire study area are visualized in Figure 6. These prediction maps mirror results seen in Figures 4a and 5. They visually demonstrate climatic significance at this scale of analysis, similarities between models, and a slight increase in the detail of the spatial pattern of refugia distribution, especially to the south, resulting from the addition of local topographic predictors to climate-only models.

Refugia species richness

The environmental variables studied here fare better in explaining refugia species richness than refugia distribution (mean Spearman's rho (ρ) values 0.53 and 0.37, respectively) (Online Resource 4: Fig. 2). All mean Spearman's rho (ρ) values are higher than 0.50, suggesting that all variable combinations are fairly good predictors of refugia species richness with marginally significant differences between models (Fig. 4b). The sole exception to significantly improve predictive power was the addition of topography to the climate model (Fig. 4b ii).

Refugia species richness is prolifically affected by the *WAB* gradient (Fig. 5), the most important variable in the full model. T_{max} is the most important climatic variable when effects of topography are not directly accounted for, with more species favouring less extreme temperatures in regards to both extreme temperature variables. The topographic variable *slope* has the most relevant influence on refugia species richness, followed by the effects of climatic conditions (Fig. 5). A clear threshold exists with topographically heterogeneous areas where slopes steeper than 15° display greater refugia species richness (Online Resource 4: Fig. 2). The geological variables consistently showed the weakest overall explanatory power for refugia species richness (Fig. 5).

DISCUSSION

To decipher where refugia might be located in the future and why, we must develop robust models to predict their current distributions and ascertain the key drivers underlying them. This study provides promising results for this task as we were successfully able to locate and model contemporary refugia, as well as infer factors affecting their suitability for multiple refugia species based on climatic, topographic and geologic parameters. Our results suggest that useful predictive models for refugia distribution can be developed by relating key environmental features with species occurrences, thus highlighting the significance of spatially explicit species' data and reliable, fine-resolution climate and environmental data (Austin and Van Niell 2010, 2011). We echo notions put forth by Luoto and Heikkinen (2008) and Austin and Van Niell (2011) concerning the inclusion of topography leading to more robust estimates of species distributions.

Noticeable trends and the pronounced contributions of certain variables enabled us to distinguish suitable physical drivers of contemporary refugia. Trends included refugia preference to environments differing from regional means (e.g. Taberlet and Cheddadi 2002; Ackerly et al. 2010), locations with steep slopes or moist soil conditions (e.g. Rull 2009; Dobrowski 2010), cooler or shorter growing seasons and coolest within-cell meso-climates (e.g. Dobrowski et al. 2010), all landscape features supporting refugia development and boosting refugial biodiversity in the studied arctic-alpine region. Variables indicating suitable moisture conditions and the presence of relatively cool sites (Olson et al. 2012) and slopes were constantly identified as the most controlling and influential factors for both refugia distribution and species richness with a pooled variable influence between 63 – 79% in all models.

Our results suggest that climate is a key determinant of refugia at the meso-scale. Derived prediction maps show that the probabilities of refugia occurrence over the whole study region are mainly low (<5%). This, along with the high relevance of climatic variables, reinforces the cautionary remarks on how well climate trajectories will enable the re-dispersal of refugia species (Hannah et al. 2014). Still, refugia provide one of the most promising means to support species survival under adverse climates (Birks and Willis 2008; Keppel et al. 2012). In our results, all climate-only model predictions were improved by the incorporation of topography and the importance of the most influential variables relies on the inclusion of both climatic and topographic predictor sets. This provides clear support for the complementary significance of local factors for refugial persistence (Sormunen et al. 2010). Moisture conditions were the most important predictors of refugia distribution while the effects of slope was integral to explaining refugia species richness, suggesting that while climate is key in controlling where refugia occur, topographic factors enable the persistence of multiple species in these refugia.

Cells with refugia in our study area are characterized by moister conditions resulting from high precipitation or low evapotranspiration, which is in agreement with a number of earlier studies (Armbruster et al. 2007; Thomas Fickert 2007; Ackerly et al. 2010). Growing season temperatures were of higher relative importance than overwintering temperatures, suggesting that the avoidance of summer time temperature highs is critical for arctic-alpine refugia. Despite the significance of mean growing conditions, the refugia in our study appear to be more affected by climatic extremes. The relative influence of growing conditions is surpassed by the presence of relatively cooler sites in all models, possibly displaying the climatic stability offered by more oceanic climates (Aalto et al. 2014) and reflected in the proximal distribution of the refugia. These results, concordant with research in different climatic conditions (Noss 2001; Shoo et al. 2010; Ashcroft and Gollan 2013), show that refugia may thus be more susceptible to changes in climatic extremes than fluctuations in seasonal temperatures. Refugia provide species with cooler locales when temperatures reach their maximum: lowest maximum temperatures of refugia are, on average, 2.2°C cooler than non-refugial cells (Online Resource 2).

Topography has a clear effect on the extreme temperatures of the region (Aalto et al. 2014), seen in our results through the importance of the lowest maximum temperatures when topography is not taken into account. Our results showcase the importance of refugial cooling effects for arctic-alpine species, possibly resulting in increased temperature gradients and thereby leading to more diverse habitats (Fridley 2009; Ashcroft 2010). Consequently, the importance of refugia can be seen as two-fold: protecting species from environmental change as well as increasing environmental diversity.

Steeper slopes provide ideal habitats for many refugia species (Online Resource 4: Figs. 1 and 2). Slope-related factors have been shown to effect biodiversity (Körner 2005; Bennie et al. 2006), possibly manifesting through topographic influence on climate, such as steeper slopes decoupling local climates from the regional (Hampe et al. 2013). The role of steep landforms in the study area as well as in the adjacent Scandes Mountains may become increasingly vital for species persistence in the future. This issue is linked with the question on how earth surface processes (ESPs; e.g. active geomorphic processes related to slope) might influence refugia, especially as they have been shown to improve species richness and distribution model accuracy for arctic–alpine species in particular (Luoto and le Roux 2014). Improvements to model performance from the inclusion of geologic predictors were minor and indistinct, suggesting that geologic data is not essential for refugia modelling at the meso-scale (here, resolution of 1 km²) (Anderson and Ferree 2010). Another potential explanation is that the effect of geological conditions may be imperative only for individual refugia species and thus remain undetected in multi-species analyses.

More generally, due to the spatial scale of this study it cannot be determined whether the significance of the factors deemed here as important for refugia is direct or indirect. Though both coarse and fine scale processes are relevant for assessing changes in species' distributions under changing climates, fine scale analysis would capture more precise effects of current and forthcoming changes on biota. Refugia species richness was more accurately predicted than occurrence, emphasizing the importance of considering refugia in terms of biodiversity conservation (Taberlet and Cheddadi 2002) and yet, adversely, underlining difficulties in locating refugia for individual species and the need to prioritise species at greatest risk (Skov and Svenning 2004). Our results support the notion that single refugia are not necessarily suitable for multiple at-risk species, so potential differences between refugia must be carefully considered.

The moderate explanatory power of the refugia distribution models might be explained by issues of temporality and spatiality: firstly, our models do not capture refugia dynamics (see Hannah et al. 2014) and secondly, occurrences of some refugia, particularly those inhabited by threatened species or including particularly sensitive habitats, may be governed by factors operating at finer scales than those employed here (Brown 2010). Though our use of meso-scale climate data goes some way in addressing issues of scale, our quantification of contemporary refugia relies on the identification method used, and as such cannot be used to address issues of long-term climate change (Ashcroft et al. 2012). Refugia connectivity is greater in areas closer to the main distribution area (Fig. 3), but whether this is due to limitations by environmental conditions or poor species' dispersal ability is difficult to judge. The ability of species to disperse into previously unoccupied *ex situ* refugia should also be addressed, especially in light of the proximal nature of refugia occurrence in the area.

CONCLUSIONS

Climate alone has significant control on arctic-alpine plant refugia, though refugia species also appear to favour topographically heterogeneous environments. Modifications to broader environmental conditions through local features create fundamental environmental conditions that support refugia species, such as cooler climates resulting from a high water balance, as well as steep slopes and avoidance of extreme temperatures. As predictor effects on refugia species richness are bound to include species-specific responses, it is important to predict which species are most likely to be restricted to refugia in the future. Our results provide interesting avenues for further research, in which finer scale species data combined with measures of local climate, topography and other appropriate variables could give a more detailed outlook on the futures of these arctic-alpine species. However, already the findings of this study demonstrate the importance of appropriately scaled species' and environmental data at suitable resolutions and, by mapping contemporary refugia, provide a template for developing a better understanding of the processes governing refugia in changing arctic-alpine landscapes.

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Supplementary material

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

Online Resource 1 List of the refugia species (species with more than two thirds of their study area distribution occurring in the arctic-alpine Scandes Mountains) used in this analysis

Online Resource 2 Variable correlation matrix showing Spearman's rho (ρ) values between explanatory variables

Online Resource 3 Table showing variable coefficients

Online Resource 4 Response curves predicted by the full models for refugia distribution (Fig. 1) and refugia species richness (Fig. 2)

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Figure captions

Fig. 1 The location and average temperature conditions (1971 – 2000: Finnish Meteorological Institute) of the study area in northern Fennoscandia with the locations of the sites with available plant distribution data: sites within the Scandes Mountains (dark grey points) were used to infer refugia species based on species distribution data (white points) and were subsequently excluded from analysis. The dashed line in the main map shows the study area subset seen in Fig. 3

Table 1 Descriptions of the environmental variables used in this study showing mean, minimum (Min) and maximum (Max) values

Fig. 2 The structure of the models (i. – iv.) used to explain (a) refugia distribution and (b) refugia species richness

Fig. 3 The locations of the refugia (black points) in relation to the three most influential variables: (a) mean water balance (*WAB*: mm), (b) lowest maximal temperatures (T_{max}: °C) and (c) mean slope (*Slope*: degrees). The subset of the study area used in this visualization can be observed in the dashed line in the main map of Fig. 1

Fig. 4 Model accuracy in **a)** predicting refugia occurrence. Mean AUC (area under the curve of a receiver operating characteristic plot), TSS (true skill statistic) and Wilcoxon signed rank test p-values indicating change in the models predictive ability when adding either or both the topography/geology group to the climate model; and, **b)** predicting refugia species richness. Spearmans rank correlation coefficients (rs) and Wilcoxon signed rank test p-values indicating change in the models predictive ability when adding either or both the topography/geology group to the climate model. Change in predictive ability is indicated by asterisks. *** Highly significant change in predictive ability ($p < 0.001$); ** significant change ($p < 0.01$); * marginally significant change ($p < 0.05$); ns, no significant change

Fig. 5 Variable influence (%) for all BRT models (i – iv) for refugia distribution (a) and refugia species richness (b). The y-axis for each panel shows the relative influence of each variable within the model. Clim., Topo. and Geo. indicate the individual variables comprising the climatic, topographic and geologic factors. High relative influence corresponds to a strong influence of a predictor on the response variable

Fig. 6 The predicted occurrence of refugia across the whole study area using (a) climatic; (b) climatic and topographic; (c) climatic, topographic and geologic variables. Red indicates cells where model predictions indicate a high probability of refugia occurrence; blue specifies cells where the model predicts a low probability of refugia occurrence. Black marks indicate the refugia discovered in this study

Figure

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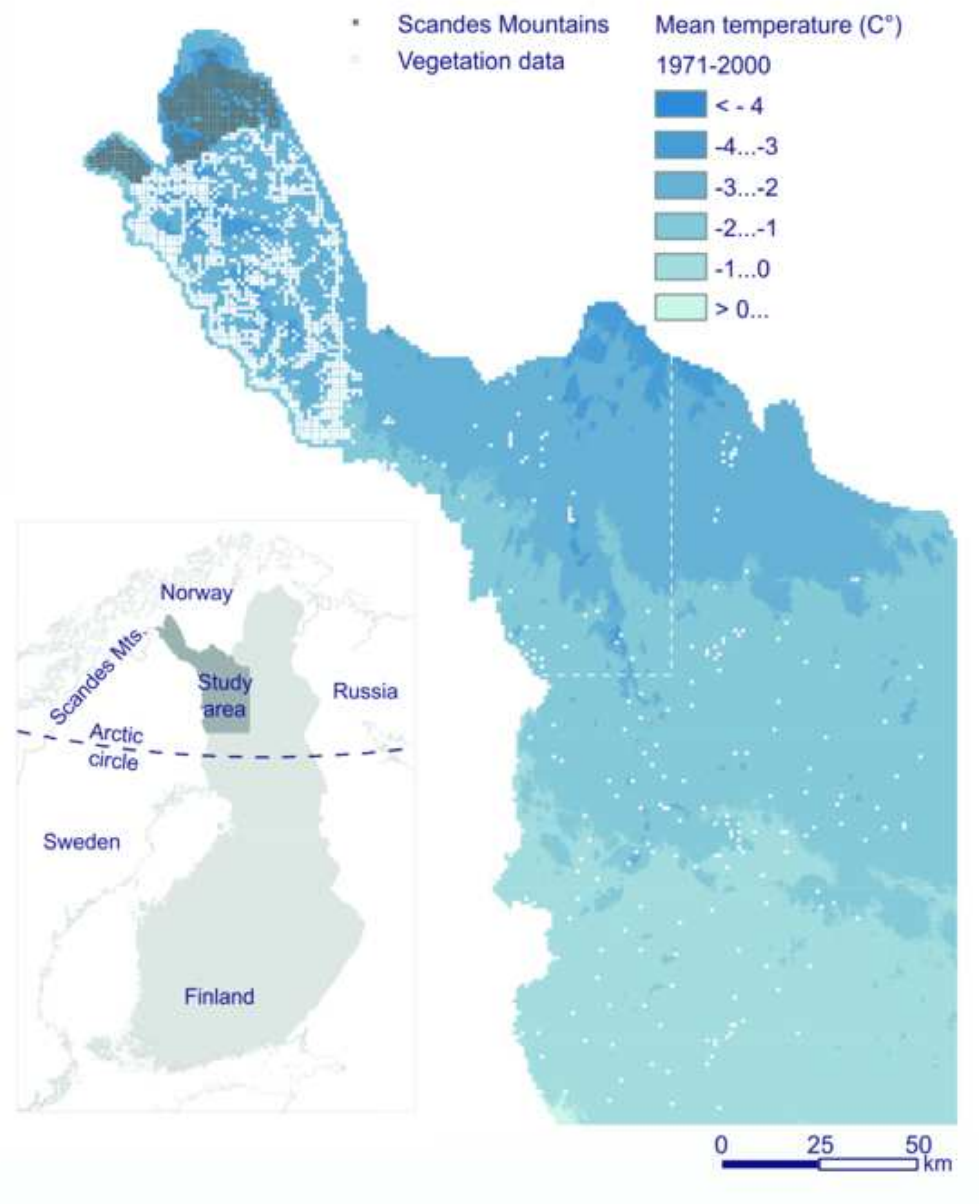
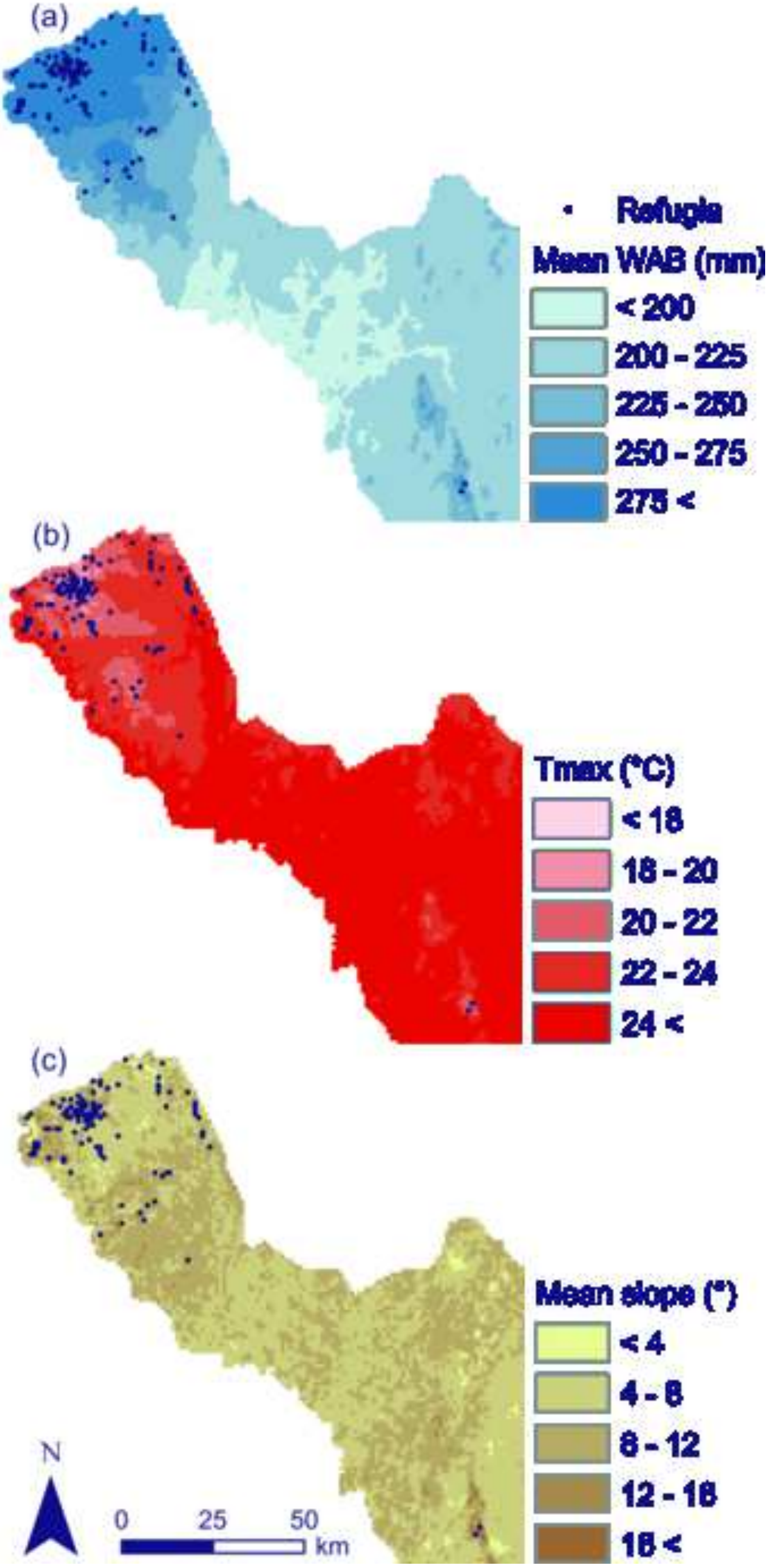


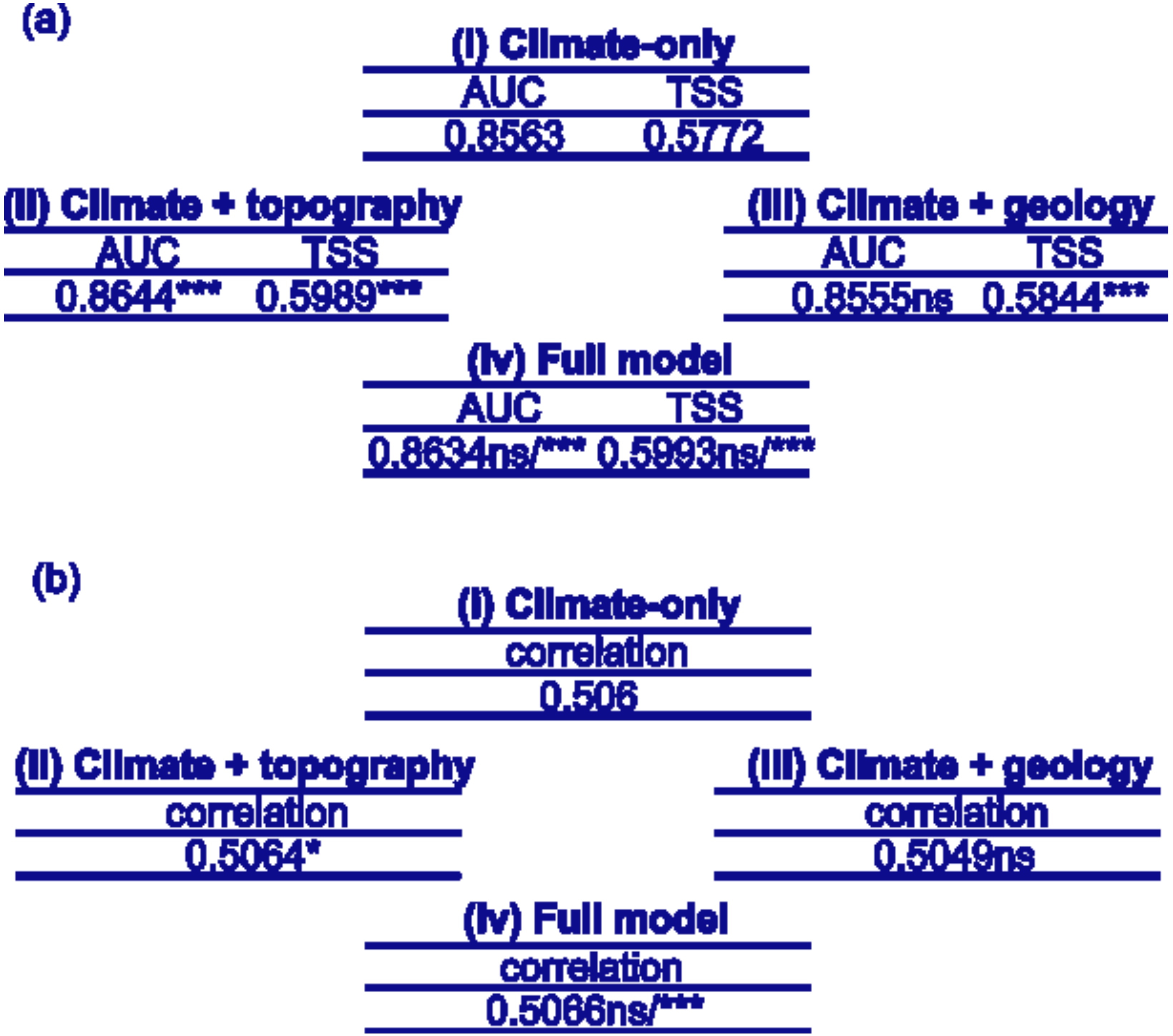
i) Refugia a) distribution, b) species richness =
GDD3 + FDD + WAB + Tmax + Tmin
(climate model)

ii) Refugia a) distribution, b) species richness =
climate model + *TWI + slope + radiation*
(climate + topography model)

iii) Refugia a) distribution, b) species richness =
climate model+ *rock cover + soil diversity + calcareousness*
(climate + geology model)

iv) Refugia a) distribution, b) species richness =
climate model + *TWI + slope + radiation +*
rock cover + soil diversity + calcareousness
(full model)


(a)
Refugia
Mean WAB (mm)
< 200
200 - 225
225 - 250
250 - 275
275 <
(b)
Tmax (°C)
< 18
18 - 20
20 - 22
22 - 24
24 <
(c)
Mean slope (°)
< 4
4 - 8
8 - 12
12 - 16
16 <
N
0
25
50
km



(a)

(i) Climate-only

AUC	TSS
0.8563	0.5772

(ii) Climate + topography

AUC	TSS
0.8644***	0.5989***

(iii) Climate + geology

AUC	TSS
0.8555ns	0.5844***

(iv) Full model

AUC	TSS
0.8634ns/***	0.5993ns/***

(b)

(i) Climate-only

correlation
0.506

(ii) Climate + topography

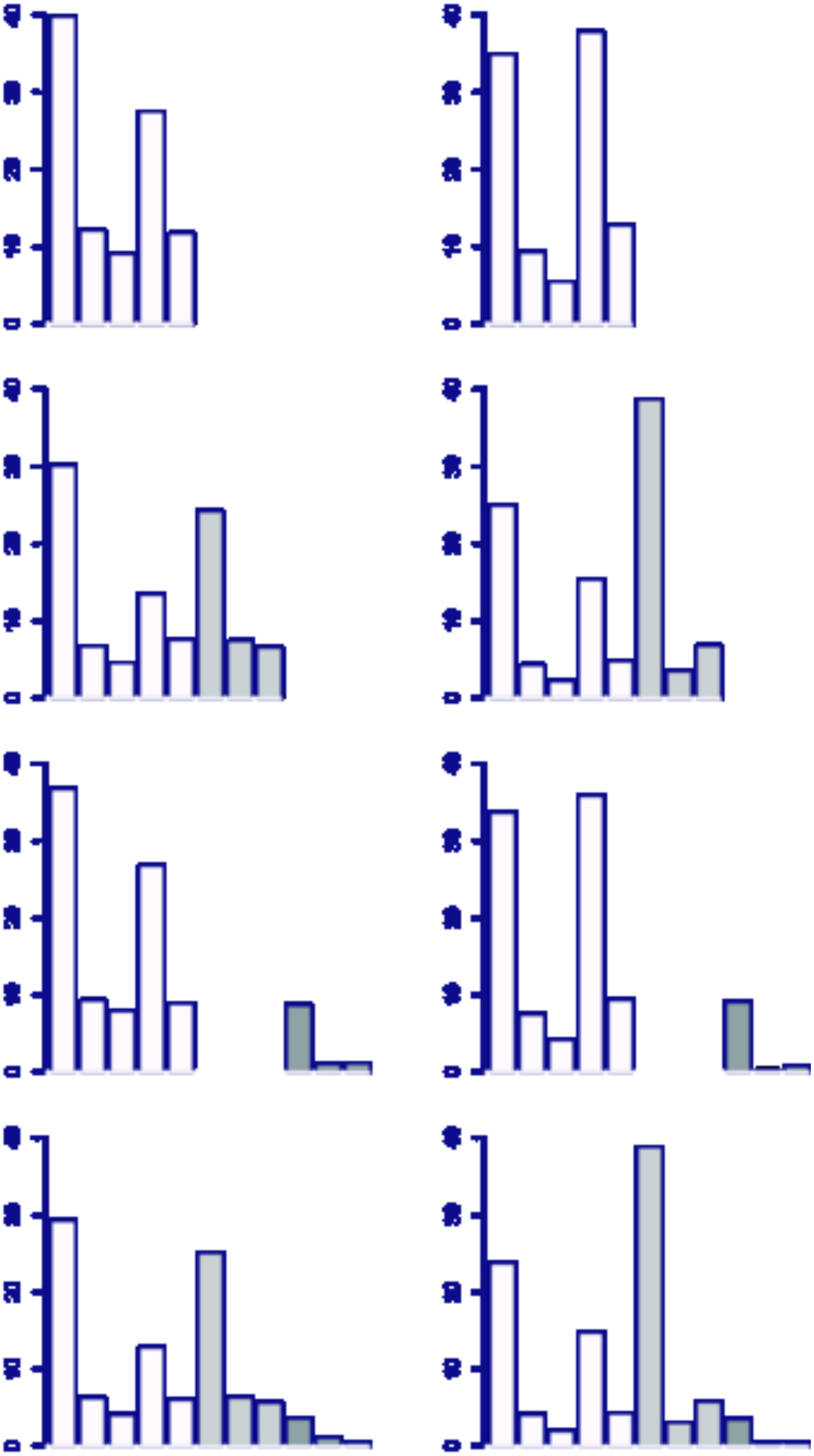
correlation
0.5064*

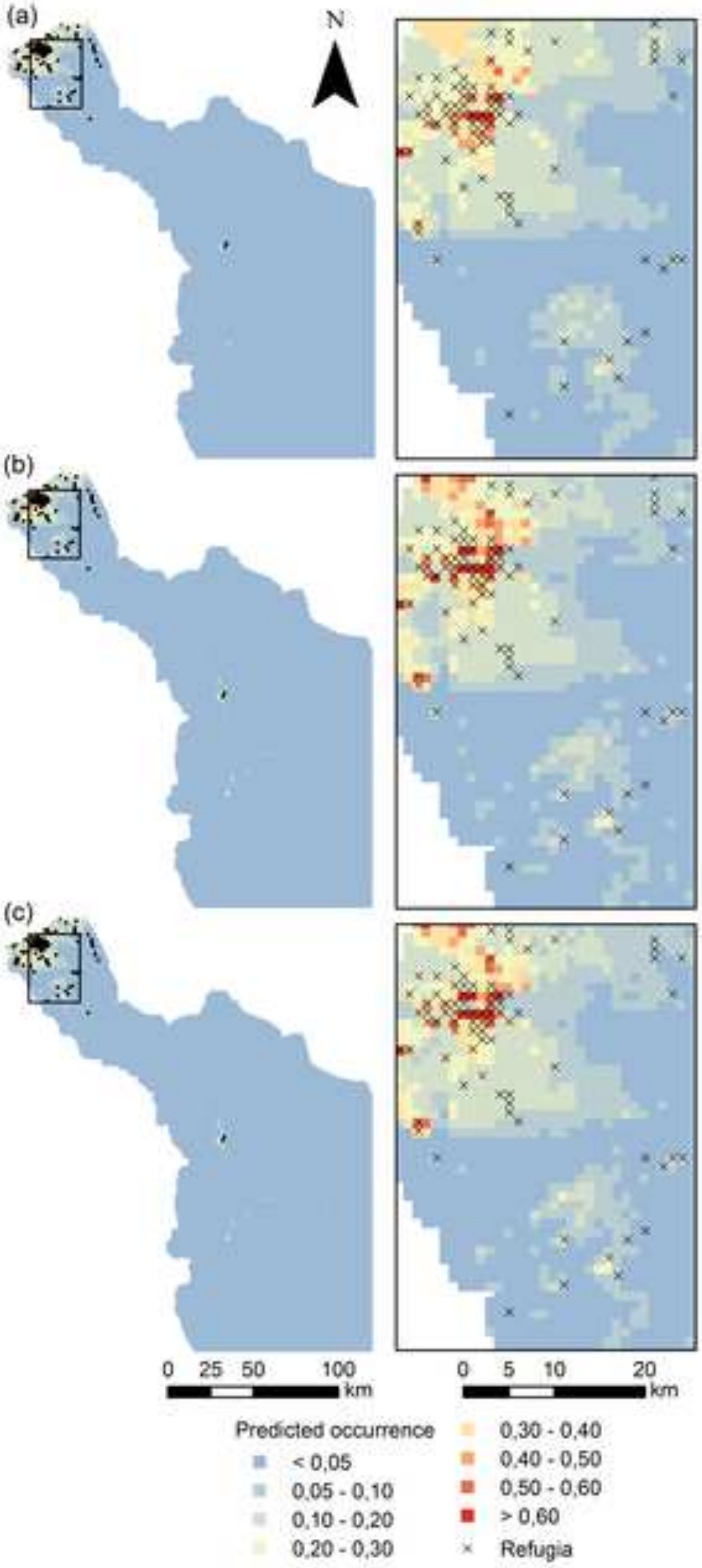
(iii) Climate + geology

correlation
0.5049ns

(iv) Full model

correlation
0.5066ns/***




(a)
N
(b)
(c)
0
25
50
100
km
0
5
10
20
km
Predicted occurrence
< 0,05
0,05 - 0,10
0,10 - 0,20
0,20 - 0,30
0,30 - 0,40
0,40 - 0,50
0,50 - 0,60
> 0,60
× Refugia

Table

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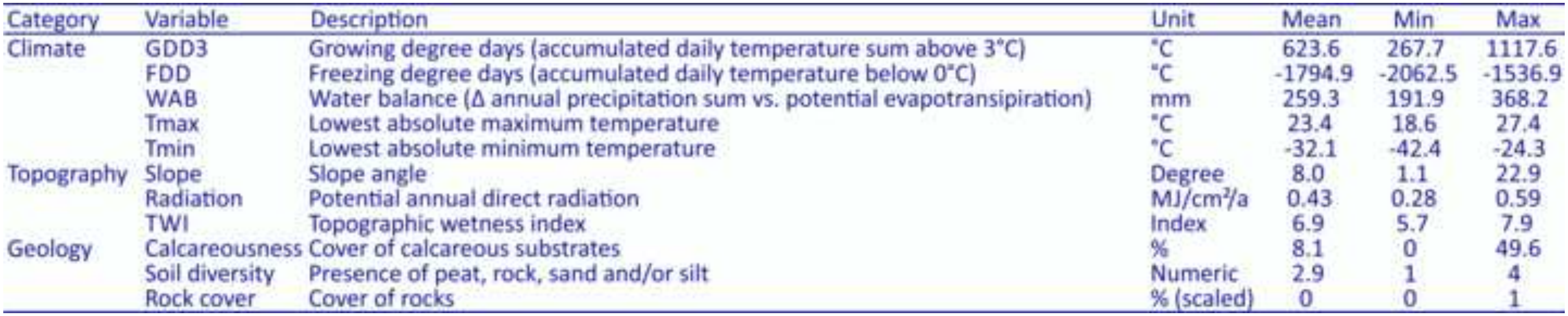

Category	Variable	Description	Unit	Mean	Min	Max
Climate	GDD3	Growing degree days (accumulated daily temperature sum above 3°C)	°C	623.6	267.7	1117.6
	FDD	Freezing degree days (accumulated daily temperature below 0°C)	°C	-1794.9	-2062.5	-1536.9
	WAB	Water balance (Δ annual precipitation sum vs. potential evapotransipiration)	mm	259.3	191.9	368.2
	Tmax	Lowest absolute maximum temperature	°C	23.4	18.6	27.4
	Tmin	Lowest absolute minimum temperature	°C	-32.1	-42.4	-24.3
Topography	Slope	Slope angle	Degree	8.0	1.1	22.9
	Radiation	Potential annual direct radiation	MJ/cm²/a	0.43	0.28	0.59
	TWI	Topographic wetness index	Index	6.9	5.7	7.9
Geology	Calcareousness	Cover of calcareous substrates	%	8.1	0	49.6
	Soil diversity	Presence of peat, rock, sand and/or silt	Numeric	2.9	1	4
	Rock cover	Cover of rocks	% (scaled)	0	0	1