



Palaeoclimatic models help to understand current distribution of Caucasian forest species

DAVID TARKHNISHVILI*, ALEXANDER GAVASHELISHVILI and LEVAN MUMLADZE

Biodiversity Research Center, Institute of Ecology, Ilia State University, 3/5 K. Cholokashvili Ave., Tbilisi 0162, Georgia

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Spatial and temporal constraints on dispersal explain the absence of species from areas with potentially suitable conditions. Previous studies have shown that post-glacial recolonization has shaped the current ranges of many species, yet it is not completely clear to what extent interspecific differences in range size depend on different dispersal rates. The inferred boundaries of glacial refugia are difficult to validate, and may bias spatial distribution models (SDMs) that consider post-glacial dispersal constraints. We predicted the current distribution of 12 Caucasian forest plants and animals, factoring in the effective geographical distance from inferred glacial refugia as an additional predictor. To infer glacial refugia, we tested the transferability of the current SDMs based on the distribution of climatic variables, and projected the most transferable ones onto two climate scenarios simulated for the Last Glacial Maximum (LGM). We then calculated least-cost distances from the inferred refugia, using elevation as a friction surface, and recalculated the current SDMs incorporating the distances as an additional variable. We compared the predictive powers of the initial with the final SDMs. The palaeoclimatic simulation that best matched the distribution of species was assumed to represent the closest fit to the true palaeoclimate. SDMs incorporating refugial distance performed significantly better for all but one studied species, and the Model for Interdisciplinary Research on Climate (MIROC) climatic simulation provided a more convincing pattern of the LGM climate than the Community Climate System Model (CCSM) simulation. Our results suggest that the projection of suitable habitat models onto past climatic conditions may yield realistic boundaries of glacial refugia, and that the current distribution of forest species in the study region is strongly associated with locations of former refugia. We inferred six major forest refugia throughout western Asia: (1) Colchis; (2) western Anatolia; (3) western Taurus; (4) the upper reaches of the Tigris River; (5) the Levant; and (6) the southern Caspian basin. The boundaries of the modelled refugia were substantially broader than the refugia boundaries inferred solely from pollen records. Thus, our method could be used to: (1) improve models of current species distributions by considering the dispersal histories of the species; and (2) validate alternative reconstructions of palaeoclimate with current distribution data. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **105**, 231–248.

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INTRODUCTION

Spatial and temporal constraints on dispersal may be important in shaping the ranges of species, in addition to habitat suitability (Pulliam, 2000; Guisan & Thuiller, 2005). Species may be absent from suitable habitats because of limited dispersal ability, preventing full recolonization after historical reduction of

their ranges (Pulliam, 2000; Araújo *et al.*, 2005; Guisan & Thuiller, 2005; Marsico, 2009).

The Last Glacial Maximum [LGM; *c.* 21 thousand years (ky) BP] was a crucial event that determined the current landscape and species diversity throughout the Earth. In temperate zones, forests were confined to isolated refugia during the LGM (Van Andel & Tzedakis, 1996), and their current distribution reflects post-glacial expansion from these refugia. One can expect that the expansion rates of different species were dependent on several factors, such as

*Corresponding author. E-mail: davitar@gmail.com

dispersal ability, physiological tolerances and competitive ability. It has been suggested that post-glacial dispersal patterns should be considered when explaining current distributions (Svenning & Skov, 2004; Graham, Moritz & Williams, 2006). The analysis of the distribution of multiple forest plant species shows that the distance from glacial refugia may be more important than the current climatic conditions in explaining species diversity (Willner, Di Pietro & Bergmeier, 2009).

The incorporation of post-glacial dispersal patterns into current spatial distribution models (SDMs) requires a good knowledge of the geographical ranges of species during the LGM. Traditional methods for the reconstruction of ancient ranges, based on the analyses of fossils, provide a limited and biased picture, because dead organisms tend to decompose, and conditions favouring fossilization are unevenly distributed in space and time (e.g. Signor, 1985). This is particularly true for the reconstruction of glacial refugia: they can often be overlooked if molecular genetic data are not considered (Provan & Bennett, 2008; Tarkhnishvili *et al.*, 2008). Since gridded palaeoclimatic data became widely available (Braconnot *et al.*, 2007), researchers have been trying to reconstruct ancient distributions of plants and animals by projecting SDMs, based on present occurrence data, onto past conditions (Graham *et al.*, 2006; Martínez-Meyer & Peterson, 2006; Davies, Purvis & Gittleman, 2009). Palaeovegetation data suggest that, since the LGM, the ecological requirements of long-lived, temperate tree species have not changed considerably (Martínez-Meyer & Peterson, 2006), and the projection of current SDMs onto past conditions may provide a realistic output.

The consideration of dispersal history may improve current distribution models for plants (Svenning, Normand & Skov, 2008; Willner *et al.*, 2009; Normand *et al.*, 2011). Because the precision of the shape, size and location of glacial refugia was not the primary objective of these studies, the authors did not discuss different palaeoclimatic simulations, or species–climate modelling algorithms, and the studies were applied at coarse spatial resolutions. Normand *et al.* (2011), who inferred glacial refugia and included as many as 1016 plant species in their study, only indicated the consistency of the results without addressing the issue of model transferability before inferring the location of glacial refugia.

Nogués-Bravo (2009) emphasized that the majority of palaeodistribution reconstructions have not been tested using independent data. Indeed, it is difficult to validate the models inferring future or past distributions because of a lack of test occurrence locations. Sometimes palaeodistribution data, e.g. pollen records, are used for validation (Martínez-Meyer &

Peterson, 2006), but known occurrences may not capture the full extent or climatic diversity of the ancient range, leading to poor predictive performance.

Palaeodistribution models can be validated indirectly through an examination of which of the competing LGM climate simulations best explains the current distribution of the species. This approach considers the incorporation of the spatio-temporal autocorrelation of an inferred ancient distribution into current distribution models, followed by a test of the predictive power of a corrected current SDM.

In this article, we predict the current distribution of several plants and animals in the Caucasus and western Asia at a high spatial resolution by the incorporation of the least-cost distance from the inferred species-specific location of glacial refugia as an additional predictor in the modelling of species distributions. We infer the glacial refugia by projecting the current species–climate models onto available palaeoclimatic simulations. We assume that the palaeoclimatic simulation that best matches the species distributions represents the closest fit to the true palaeoclimate. Thus, our method could be used to: (1) improve models of current species distributions by considering the distribution histories of the species; and (2) validate palaeoclimatic simulations using current distribution data.

METHODS

STUDY AREA AND TARGET SPECIES

The Caucasus Ecoregion and surrounding parts of western Asia and eastern Europe (latitudinal range, 32–48°N; longitudinal range, 26–54°E) were selected as a study area. Most of this region has a dry continental or Mediterranean-type climate and a forestless landscape. Forests are associated with distinct areas of mesic climates. The largest continuous mesic forest landscapes are located along the southern and eastern Black Sea coast, north-west of the Greater Caucasus, and along the southern coast of the Caspian Sea (Fig. 1). They support biological communities with several dominant trees, including oriental beech (*Fagus orientalis*) (Denk *et al.*, 2002). The area harbours multiple glacial relict populations, which survived the LGM in forest refugia (Kikvidze & Ohsawa, 1999; Denk, Frotzler & Davitashvili, 2001; Milne & Abbott, 2002). The ranges of many forest plants and animals overlap, either throughout western Asia, or in its larger subsections, although the extent of such overlap varies from species to species.

For our study, we selected 12 species for which we had sufficiently accurate distribution data and that only coexist in the eastern Black Sea region known as Colchis. Selecting the species from the Colchis, which

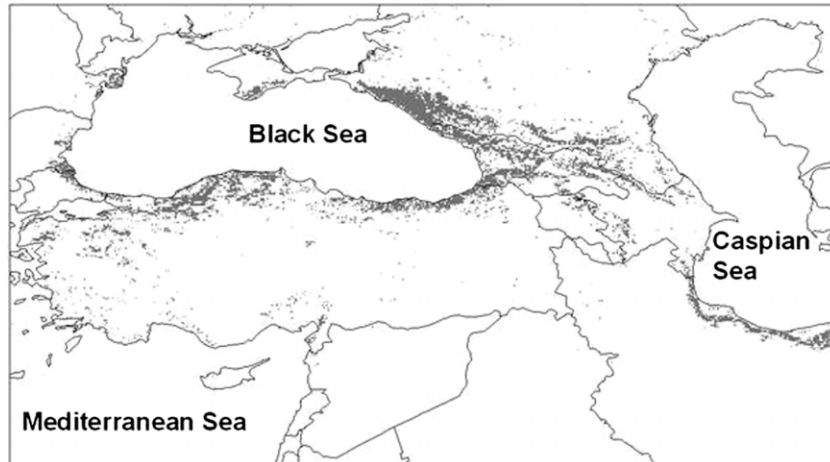


Figure 1. Current distribution of forests in western Asia, extracted from Land Cover Type 1 of the MODIS Land Cover Yearly L3 Global 500-m dataset coded MCD12Q1 (EOS Data Gateway, 2010).

is traditionally associated with glacial refugia, made it possible to compare the extents of post-glacial dispersal for diverse life forms. The selected species represent taxonomic groups with different life cycles, physiologies, reproduction and dispersal potential. The list includes five trees typical for the Caucasian forests (*Abies nordmanianna*, *Picea orientalis*, *Castanea sativa*, *Fagus orientalis*, *Carpinus betulus*), common rhododendron (*Rhododendron ponticum*), an endemic snail (*Helix buchi*), Caucasian salamander (*Mertensiella caucasica*), northern banded newt (*Ommatotriton ophryticus*), Caucasian parsley frog (*Pelodytes caucasicus*), Ajarian lizard (*Darevskia mixta*) and Robert's snow vole (*Chionomys roberti*). *Helix buchi* and *D. mixta* have parapatric sister species with very similar habitat requirements: *H. goderdziana* and *D. clarkorum*, respectively (Murphy *et al.*, 2000; Mumladze *et al.*, 2008). In our analyses, each pair of sister species was treated as a single taxon. For each of these study taxa, our datasets included 31–1000 presence locations covering the extent of occurrence of each taxon throughout the Caucasus. The datasets of species occurrence were from published data, the Soviet military topographical maps at a scale of 1 : 50 000 (for data on tree species) and field data collected by the authors since the early 1980s (Darevskii, 1967; Tarkhishvili & Gokhelasvili, 1999; Tarkhishvili *et al.*, 2008; Bukhnikashvili, 2004; Kryštufek & Vohralík, 2004. Supporting Information Table S1 and Fig. S1).

We paid particular attention to the accuracy of the presence locations of the studied species (Table S1). In mountain areas such as the Caucasus, climate changes abruptly with horizontal distance, and inaccurate locations can strongly bias the modelling output. This explains the relatively small number of species used in our analyses.

GENERAL METHODOLOGICAL REMARKS

Niche-based SDMs with the best predictive power are commonly based on many predictors and consider interactions among them (McPherson, Jetz & Rogers, 2006; Cordellier & Pfenninger, 2009). A number of commonly used modelling techniques, including logistic regression (Hosmer & Lemeshow, 1989), maximum entropy (Phillips & Dudik, 2008), neural networks (Fitzgerald & Lees, 1992) and simple or partitioned Mahalanobis distance (MD) (Rotenberry, Preston & Knick, 2006; Griffin *et al.*, 2010) estimate the strength and type of association between predictors. Some of these methods help to estimate the relative importance of predictors in distinguishing between presence and absence locations.

However, these methods have major limitations that result in poor transferability of the respective models. SDMs rarely perform well outside the extent of training locations (Barry & Elith, 2006; Hijmans & Graham, 2006), and one could expect similar problems with SDMs projected into different geological periods. There are two potential reasons for this issue. First, the association between environmental predictors may be specific to a particular area (Pearson & Dawson, 2003; Randin *et al.*, 2006), causing loss of model accuracy elsewhere. Second, predictors that separate presence and absence locations within the extent of training data may be unimportant elsewhere (Guisan & Thuiller, 2005). To estimate the transferability of SDMs, several approaches have been applied (Thomas & Bovee, 1993; Randin *et al.*, 2006; Vanreusel *et al.*, 2006), based on a comparison of SDM predictive power within and outside the extent of training locations.

There are also ways of increasing transferability. It has been suggested that only mechanistic SDMs, based on an a priori knowledge of the ecophysiological

requirements of a species, provide a reliable basis for the potential niche (Kearney & Porter, 2004; McPherson *et al.*, 2006; Zarnetske, Edwards & Moisen, 2007), although relevant knowledge is very limited (Guisan & Thuiller, 2005). If an SDM is based on empirical occurrence data, one should expect higher transferability for simple models, not including assumptions whose relevance is difficult to test – such as interactions between the predictors. One example of this simple approach is climatic envelope analysis (Hijmans & Graham, 2006; Pearson *et al.*, 2006), a straightforward methodology linking the suitability of a habitat with empirically identified tolerance limits, or its modifications, such as fuzzy envelope (FE) analysis (Skov & Svenning, 2004; Svenning & Skov, 2004). Bioclimatic envelope models provide a good first approximation on large geographical scales (Pearson & Dawson, 2003). In addition, transferable SDMs should be based only on the environmental predictors whose impact on a species has a simple and straightforward explanation.

We applied two approaches for inferring sufficiently powerful and, simultaneously, transferable suitable habitat models, prior to correcting the models using the post-glacial dispersal constraints: one focused on the increasing predictive power of a model within the training extent, and the other on a simple intuitive approach, based on fixed, expert-selected environmental predictors.

The purposes of our study included: (1) the development of sufficiently transferable suitable habitat models of the study species, based on the current distribution of climates; (2) the projection of the models for each species onto LGM conditions, according to two different palaeoclimatic simulations, and inferring the extent of LGM refugia; (3) refinement of the current SDMs by the incorporation of post-glacial dispersal constraints; and (4) testing of the predictive power of the refined SDMs, based on different palaeoclimatic simulations, within the geographical extent of the analysis, in order to identify which palaeoclimatic simulation was in better accordance with current species distributions (Fig. 2).

SELECTION OF THE MOST TRANSFERABLE DISTRIBUTION MODELS

As environmental predictors for SDM development, we used climatic grids downloaded from WorldClim Version 1.4 (<http://www.worldclim.org/>), a set of global climate layers with a spatial resolution of 5 km², which provide various parameters of temperature and precipitation at a global scale (Hijmans *et al.*, 2005).

We applied two algorithms requiring presence-only datasets: FE analysis (Skov & Svenning, 2004) and the MD method (Clark, Dunn & Smith, 1993).

The analyses were based on two alternative approaches – an ‘iterative’ approach and an approach based on the expert selection of environmental predictors. In the ‘iterative’ approach, multiple models were developed, based on various combinations of climatic variables, with MD considering correlations among the predictors and FE excluding these correlations. For the iterative approach, we used six predictors: (1) mean annual temperature; (2) isothermality; (3) maximum temperature of the warmest month; (4) minimum temperature of the coldest month; (5) annual precipitation; and (6) precipitation seasonality. We developed multiple models including one to all six climatic variables in different combinations, such that all combinations with two or more predictors included at least one that described temperature (1, 2, 3, 4) and at least one that represented precipitation (5, 6). Thus, we had 45 combinations in total (Appendix). Based on each predictor combination, we developed 90 spatial models for each combination of the predictors and selected the MD and FE models with the highest predictive power for the training extent (hereafter referred to as ‘iteratively fitted models’) for further analyses.

As an alternative approach, we selected three predictors with a straightforward impact on the ecological performance of a wide range of biological species and applied the FE algorithm based on these predictors (fixed-predictor models). The predictors were the maximum temperature of the warmest month, minimum temperature of the coldest month and annual precipitation. Annual precipitation is routinely used as an important predictor in spatial models developed for both animals and plants. Temperature extremes may have lethal effects, and may be important at long time intervals (Barry & Elith, 2006).

Three-quarters of the occurrence locations of each species (training locations) were used for the development of the models, and the remaining presence locations (test locations) were used for model validation at a local scale. In order to test the predictive power of the derived models, we estimated the area under the curve (AUC) of the receiver operating characteristic (ROC) curve (Fielding & Bell, 1997; Hand & Till, 2001) based on the predicted probabilities of presence for test occurrence locations and 5000 random (‘pseudo-absence’) locations, generated within the study extent using the random point generator extension for ArcView GIS 3.x (Jenness, 2004). We applied shuffling (1000 permutations) to randomly subdivide the original occurrence datasets into test vs. training locations, and selected subsets of the test pseudo-absence locations equal in size to a set of test presence locations. For each permutation, the predicted probabilities of the test presence and test pseudo-absence locations and respective AUC values

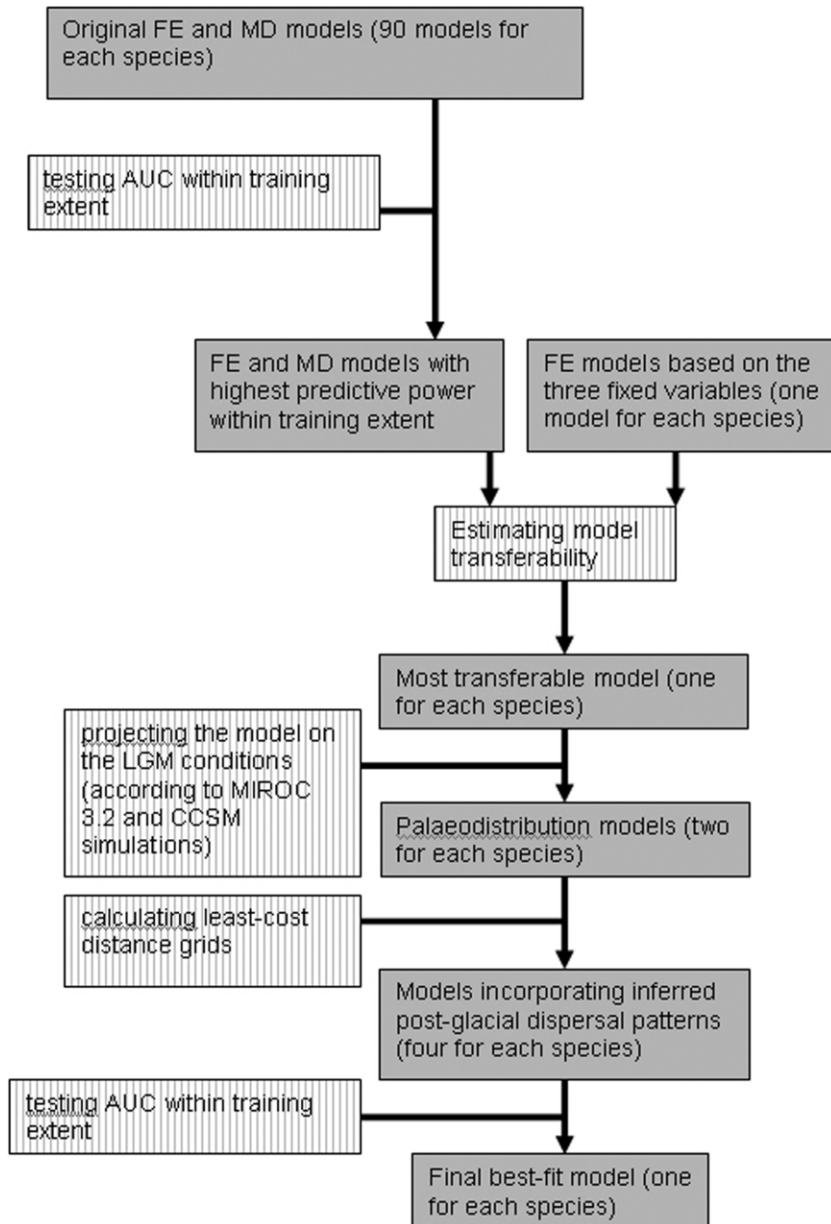


Figure 2. Diagram showing sequential steps in the modelling (see Methods section for explanations). AUC, area under the curve; CCSM, Community Climate System Model; FE, fuzzy envelope; LGM, Last Glacial Maximum; MD, Mahalanobis distance; MIROC, Model for Interdisciplinary Research on Climate.

were estimated, using Microsoft Excel; the mean AUC value over 1000 permutations was used as a final output. For the permutation procedure, we used ‘shufflerows’ and ‘MonteCarlo methods’ options in the Microsoft Excel application PopTools (Hood, 2010).

Based on test presence data from Europe, we tested the transferability level of iteratively fitted MD and FE models with the highest predictive power, and that of the fixed-predictor models. This was performed in order to select the model with the best transferability – that is, that which performed best in

areas distant from the training extent. The best transferable model in space would be highly likely to retain its predictive power over time, which is important when considering making inferences in the remote past, typically with no validation data.

As a test European dataset, we downloaded or generated occurrence locations of the target species and their closest relatives/ecological counterparts (Supporting Information Table S2). *Abies alba*, *Picea abies*, *Fagus sylvatica*, *Helix pomatia* and *Chioglossa lusitanica* are closest or very close relatives of *A. nor-*

dmanianna, *P. orientalis*, *F. orientalis*, *H. buchi* + *H. goderdziana* and *M. caucasica*, respectively (Farjon, 1990; Veith *et al.*, 1998; Denk *et al.*, 2002; Schütt, 2005), and were used as their ecological counterparts in Europe. *Castanea sativa*, *C. betulus* and *R. ponticum* form natural or invasive populations in Europe. We did not test the transferability of the SDMs for *P. causicus*, *O. ophryticus*, *D. mixta* and *C. roberti*, because they do not have single, unequivocal ecological counterparts in the regions remote from western Asia. Because the test occurrence locations from Europe did not always cover the entire ranges of the species or their equivalents, we did not apply AUC analysis, but used omission error as an indicator of SDM transferability. We calculated median probability values and applied a Kruskal–Wallis nonparametric test in order to compare mean ranks of estimated probabilities for test European locations, based on the three competing models. A model with the highest mean rank/highest median value was assumed to be the most transferable. The significance of the difference between the competing models of the same species was tested with the Mann–Whitney nonparametric test.

Model projections were visualized using the ArcView GIS module *Spatial Analyst* (ESRI, Redlands, CA, USA) and the MD extension for ArcView GIS 3.x (Jenness, 2003).

CONSIDERATION OF POST-GLACIAL DISPERSAL PATTERNS

We identified the 95th percentile cut-off of the most transferable models and projected the output onto LGM climatic conditions to infer the spatial distribution of glacial refugia. We used grids based on two palaeoclimatic models downscaled to a resolution of 5 km²: the Community Climate System Model (CCSM) and the Model for Interdisciplinary Research on Climate (MIROC) (Braconnot *et al.*, 2007). We selected these two climate models because of their high resolution and availability at the time of our study. The areas suitable for the target species under LGM conditions were defined as ‘refugia’. Subsequent analyses were based on the incorporation of spatio-temporal autocorrelation into the current, most transferable models by including the distance from the boundaries of the refugia as an additional predictor in order to explain the current distribution of the study species.

Two sets of polygons of potential post-glacial dispersal sources were used for each species: (1) all continuous refugia throughout western Asia and the Caucasus region; and (2) only the refugia that fell within, overlapped or were geographically closest to the current distribution of the species. We derived least-cost distances from refugial polygons (hereafter

referred to as REFDIST) based on the cost-distance algorithm in the ArcGIS module *Spatial Analyst* (ESRI). This algorithm considers a friction or cost grid that is a raster map in which each cell indicates the relative difficulty (cost) of moving through that cell. A least-cost path minimizes the sum of frictions of all cells along the path, and this sum is the least-cost distance (Adriaensen *et al.*, 2003). In the calculation of cost-distances, we incorporated information about climate suitability to provide more realistic distances regarding the dispersal. We used elevation (source: the SRTM 1-km grid of elevation available at Global Land Cover Facility, 2010) as the surrogate for climate at a regional level to derive the cost-distance from the refugia. We assumed that the cost-distance between a refugium and a certain point accounted for not only the straight-line distance, but also the additional effort made by the species population to expand through inclement terrain to reach or colonize that point. The cost-distance grids were calculated separately for each studied species, and for CCSM and MIROC palaeoclimatic models. We developed one-sided fuzzy envelopes for REFDIST at four different settings for each studied species (Table 1). We tested a set of each of the four REFDIST predictors and climatic variables included in potential climatic niche models to validate our SDMs against the current distributions of the study species.

Finally, we estimated AUC of the spatial models by incorporating spatio-temporal autocorrelation, using the described permutation procedure. The models were not tested with the occurrence data outside the study extent, because distributions of the studied species in distant geographical areas relate to glacial refugia outside the western Asian region.

Figure 2 shows the interrelations between the sequential steps of the analysis.

RESULTS

PREDICTIVE POWER AND TRANSFERABILITY OF ITERATIVELY FITTED MODELS

For most species, the highest AUC value at the training extent was obtained for either the MD or FE model that included three or more predictors. For each species, different combinations of the predictors produced the best statistically fitted models (Table 1, Appendix).

However, the transferability of most of the iteratively fitted FE and MD models was moderate or low (Table 1), as the respective spatial projections onto the whole of Europe and western Asia underpredicted the presence of the species in many regions in which they or their closest relatives occurred (Supporting Information Fig. S2). The omission error was particularly high for the MD-based models, but also substantial for iteratively fitted FE models (Table 1).

Table 1. Predictive power (area under the curve, AUC) and transferability (mean rank, MR, according to a Kruskal–Wallis test, and median probability, MP) of suitable spatial distribution models (SDMs) of the studied species inferred from a fixed-predictor fuzzy envelope (FE) model, iteratively fitted FE model and iteratively fitted Mahalanobis distance (MD) model

Model	An	Po	Cs	Cb	Fo	Rp	Hb	Mc	Pc	Oo	Dm	Cr
Fixed FE (variables)	T_{max}	T_{max}	T_{max}	T_{max}	T_{max}	T_{max}	T_{max}	T_{max}	T_{max}	T_{max}	T_{max}	T_{max}
	T_{min}	T_{min}	T_{min}	T_{min}	T_{min}	T_{min}	T_{min}	T_{min}	T_{min}	T_{min}	T_{min}	T_{min}
	AP	AP	AP	AP	AP	AP	AP	AP	AP	AP	AP	AP
Iteratively fitted FE (variables)	IT	MT	T_{min}	MT	T_{min}	IT	T_{max}	IT	IT	IT	IT	IT
	T_{max}	IT	AP	IT	IT	T_{max}	IT	T_{max}	T_{max}	T_{max}	AP	T_{max}
	AP	AP	P_{var}	AP	AP	P_{var}	AP	P_{var}	AP	AP	P_{var}	AP
Iteratively fitted MD (variables)	MT	MT	MT	MT	MT	MT	MT	MT	MT	MT	IT	MT
	IT	IT	IT	IT	IT	IT	IT	IT	IT	IT	IT	IT
	T_{min}	T_{max}	T_{min}	T_{max}	T_{min}	T_{max}	T_{min}	T_{max}	T_{min}	T_{max}	T_{min}	AP
	P_{var}	P_{var}	AP	AP	AP	AP	P_{var}	P_{var}	AP	AP	AP	P_{var}
Fixed FE (AUC)	0.892	0.884	0.840	P_{var}	0.661	0.709	0.823	0.836	0.829	0.852	0.878	0.851
Iteratively fitted FE (AUC)	0.923	0.938	0.914	0.749	0.784	0.857	0.864	0.881	0.856	0.893	0.886	0.875
Iteratively fitted MD (AUC)	0.896	0.911	0.898	0.815	0.806	0.845	0.885	0.855	0.836	0.881	0.865	0.867
Fixed FE (MR)	14 497	11 202	5275	12 906	26 171	3693	8232	1039				
Iteratively fitted FE (MR)	6737	8524	4619	10 848	24 232	3583	7118	271				
Iteratively fitted MD (MR)	6226	9794	2487	3801	8404	1504	3471	772				
Fixed FE (MP)	0.497	0.134	0.396	1.000	1.000	1.000	0.499	1.000				
Iteratively fitted FE (MP)	0.000	0.100	0.286	1.000	0.950	1.000	0.236	0.000				
Iteratively fitted MD (MP)	0.000	0.001	0.000	0.000	0.001	0.001	0.000	0.000				

An, *Abies nordmanniana*; Cb, *Carpinus betulus*; Cr, *Chionomys roberti*; Cs, *Castanea sativa*; Dm, *Darevskia mixta* + *D. clarkorum*; Fo, *Fagus orientalis*; Hb, *Helix buchi* + *H. goderdziana*; Mc, *Mertensiella caucasica*; Oo, *Ommatriton ophryticus*; Pc, *Picea orientalis*; Po, *Picea orientalis*; Rp, *Rhododendron ponticum*. Climatic predictors: 1, mean annual temperature (MT); 2, isothermality (IT); 3, maximum temperature of warmest month (T_{max}); 4, minimum temperature of coldest month (T_{min}); 5, annual precipitation (AP); 6, precipitation seasonality (P_{var}).

FIXED-PREDICTOR FE MODELS

The AUC values of the fixed-predictor FE models, based on the maximum temperature of the warmest month, minimum temperature of the coldest month and annual precipitation, exceeded 0.82 for all studied species except *F. orientalis*, but were lower than those of the iteratively fitted models (Table 1). Even minor differences were highly significant ($P < 0.001$), given 1000 permutations.

However, the transferability index of the FE models, based on the three fixed predictors, was higher than that of the iteratively fitted models (Table 1). The differences were significant for all studied species ($P < 0.001$, Mann–Whitney test).

Visually, the predicted suitable areas for the selected species covered the entire ranges of the studied species in western Asia and Europe, although the presence of some species or their relatives was overpredicted in northern and/or eastern Europe (Fig. S2).

In addition, spatial projection of the models onto the Caucasus and western Asia showed large areas beyond the actual distribution of some species, expanding the predicted ranges eastwards and southwards from their actual ranges (Fig. 4, left panel).

PROJECTION OF THE MOST TRANSFERABLE MODELS ONTO LGM CONDITIONS

The refugia, defined as projections of the most transferable models onto LGM land surfaces, showed similar ranges for all studied species. Throughout the Caucasus and western Asia, a large refugium with a suitable climate was concentrated along the southern and eastern Black Sea coast (Colchis), and smaller refugia occurred in the southern Caspian basin, at the eastern Mediterranean coast (the Levant) and throughout different parts of Anatolia (Fig. 3). The refugia were more fragmented according to the MIROC model than the CCSM model. The MIROC model, unlike the CCSM model, identified large refugia in western Anatolia, the westernmost Taurus Mountains and the upper reaches of the Tigris River, but showed fewer refugial areas at the southern Black Sea coast (Fig. 3).

MOST TRANSFERABLE MODELS INCORPORATING SPATIO-TEMPORAL AUTOCORRELATION

The inclusion of refugial distance in the most transferable models increased significantly the values of AUC for most of the species, relative to the original models. The AUC gain was particularly high when the distance was calculated from the refugia that spatially matched the current distributions (Table 2).

The REFDIST calculated from MIROC-based refugia yielded a greater increase in model predictive power than that based on the CCSM-based refugia. The increase in the predictive power of the SDMs, incorporating the distance from the MIROC-based refugia, was significant ($P < 0.001$) in all species except *O. ophryticus*; the corrected models of *A. nordmanianna*, *P. orientalis* and *C. sativa* had the highest predictive power. The increase in the predictive power of SDMs incorporating the distance from the CCSM-based refugia was not significant for *R. ponticum*, *P. caucasicus* and *O. ophryticus*, and the predictive power of all corrected models (except *O. ophryticus*) was lower than the models corrected using MIROC-based refugia.

Comparison of the models with the actual distribution maps (Fig. S1) showed qualitative improvement of the most transferable models with spatio-temporal autocorrelation, when compared with the models in which autocorrelation was not incorporated (Fig. 4). For all species, the SDMs incorporating refugial distance based on the MIROC climatic simulation showed higher specificity than the models that incorporated refugial distance based on the CCSM climatic simulation. The models calculated from the CCSM-based refugia overpredicted the presence of animals endemic to the Caucasus (*H. buchi* + *H. goderdziana*, *M. caucasica*, *P. caucasicus*, *D. mixta* + *D. clarkorum*, *C. roberti*) on the south-western Black Sea coast, whereas the models based on the MIROC simulation did not (Fig. 5).

DISCUSSION

The potential niche of a species, which defines the spatial distribution of suitable environments, only partly explains the observed distribution patterns (Pulliam, 2000; Guisan & Thuiller, 2005). In order to increase the predictive power of SDMs based on the analysis of abiotic environmental predictors, we should consider biotic interactions, metapopulation dynamics and dispersal limitations (Legendre, 1993; Gavashelishvili, 2004; Hampe, 2004; Svenning & Skov, 2004; Barry & Elith, 2006). The last two factors can be incorporated into SDMs by accounting for spatial or temporal autocorrelation patterns (Lichstein *et al.*, 2002; Araújo *et al.*, 2005; Randin *et al.*, 2006). Our results show that factoring in a few environmental predictors and modelling post-glacial dispersal patterns improves the predictive power of spatial models for Caucasian forest species, whose ranges were reduced during glacial advances in the Pleistocene. The results also suggest that the distribution models based on different simulations of palaeoclimate are not equally powerful in explaining current distribution patterns, and that forest distri-

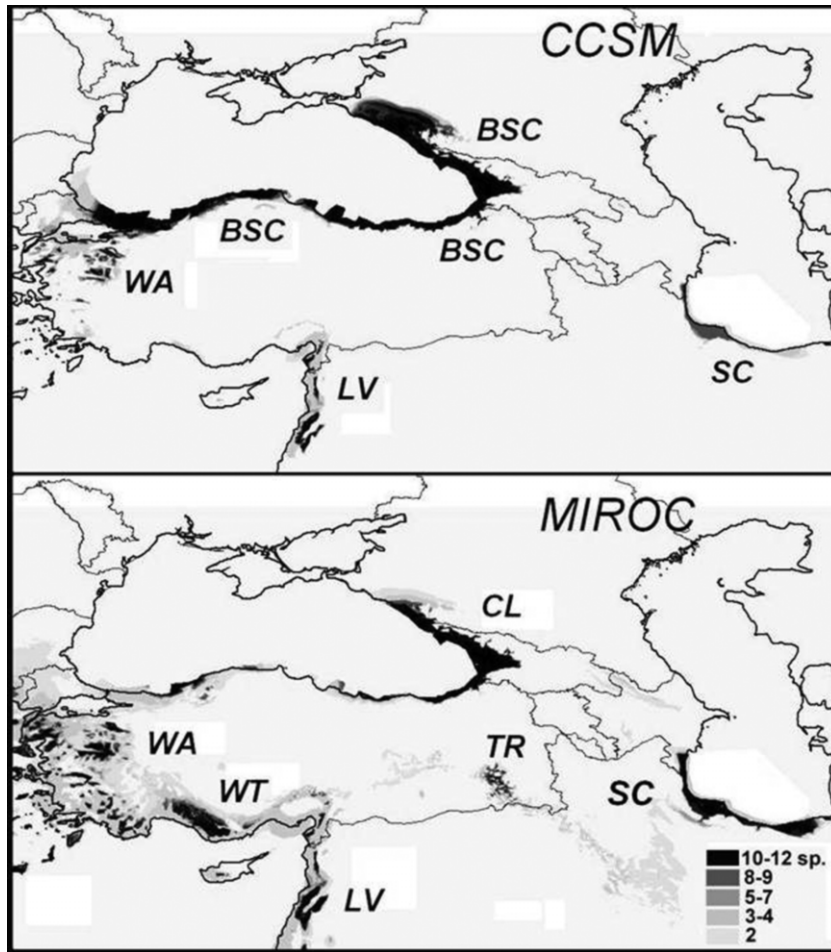


Figure 3. The distribution of climates suitable for the 12 forest plants and animals during the Last Glacial Maximum (LGM) throughout the Caucasus and western Asia. Shade intensity indicates the number of species out of the 12 for which the LGM climate was suitable. Our data show that the Model for Interdisciplinary Research on Climate (MIROC) climatic simulation provides a more realistic pattern of the LGM climate than the Community Climate System Model (CCSM) simulation. The CCSM-based inference indicates a large refugium throughout most of the Black Sea coast (BSC) and smaller refugia in western Anatolia (WA), the southern Caspian basin (SC) and the Levant (LV). The MIROC-based inference suggests that major refugia existed in Colchis (CL), the southern Caspian basin (SC), western Anatolia (WA), the western Taurus Mountains (WT), the upper reaches of the River Tigris (TR) and the Levant (LV). Contours in the maps show the current sea surface line and political borders.

Table 2. Predictive power (area under the curve, AUC) of the most transferable models (MTMs), based solely on habitat suitability and corrected by incorporating the post-glacial dispersal pattern. The Community Climate System Model (CCSM) and Model for Interdisciplinary Research on Climate (MIROC) are two different reconstructions of the palaeoclimate (see the text for details); ‘alref’ refers to all inferred continuous refugia for one species, whereas ‘specref’ refers to those refugia that overlap with the current range of the species. See Table 1 for abbreviations of the studied species. The standard error is below 0.001 for all cases at 1000 permutations. The highest AUC values are shown in bold type

Model	<i>An</i>	<i>Po</i>	<i>Cs</i>	<i>Cb</i>	<i>Fo</i>	<i>Rp</i>	<i>Hb</i>	<i>Mc</i>	<i>Pc</i>	<i>Oo</i>	<i>Dm</i>	<i>Cr</i>
MTM	0.892	0.884	0.840	0.661	0.709	0.823	0.836	0.829	0.852	0.878	0.851	0.860
CCSM_alref	0.909	0.894	0.872	0.746	0.732	0.806	0.841	0.863	0.858	0.874	0.863	0.870
MIROC_alref	0.911	0.897	0.864	0.762	0.787	0.820	0.832	0.873	0.845	0.870	0.863	0.858
CCSM_specref	0.912	0.913	0.891	0.746	0.732	0.818	0.869	0.870	0.857	0.872	0.881	0.879
MIROC_specref	0.918	0.920	0.904	0.762	0.787	0.833	0.883	0.883	0.870	0.870	0.885	0.885

Figure 4. Spatial projection of the most transferable models on the Caucasus and western Asia under current climatic conditions: left, uncorrected models; right, models corrected with the refugial distance. Dotted outlines indicate the areas in which the presence of a species is overpredicted. *An*, *Abies nordmanianna*; *Cb*, *Carpinus betulus*; *Cr*, *Chionomys roberti*; *Cs*, *Castanea sativa*; *Dm*, *Darevskia mixta* + *D. clarkorum*; *Fo*, *Fagus orientalis*; *Hb*, *Helix buchi* + *H. goderdziana*; *Mc*, *Mertensiella caucasica*; *Oo*, *Ommatotriton ophryticus*; *Pc*, *Pelodytes caucasicus*; *Po*, *Picea orientalis*; *Rp*, *Rhododendron ponticum*.

bution in western Asia during the LGM was considerably broader than is reflected in the existing pollen record (Van Andel and Tzedakis, 1996; Arslanov, Dolukhanov & Gei, 2007; Connor & Kvavadze, 2008).

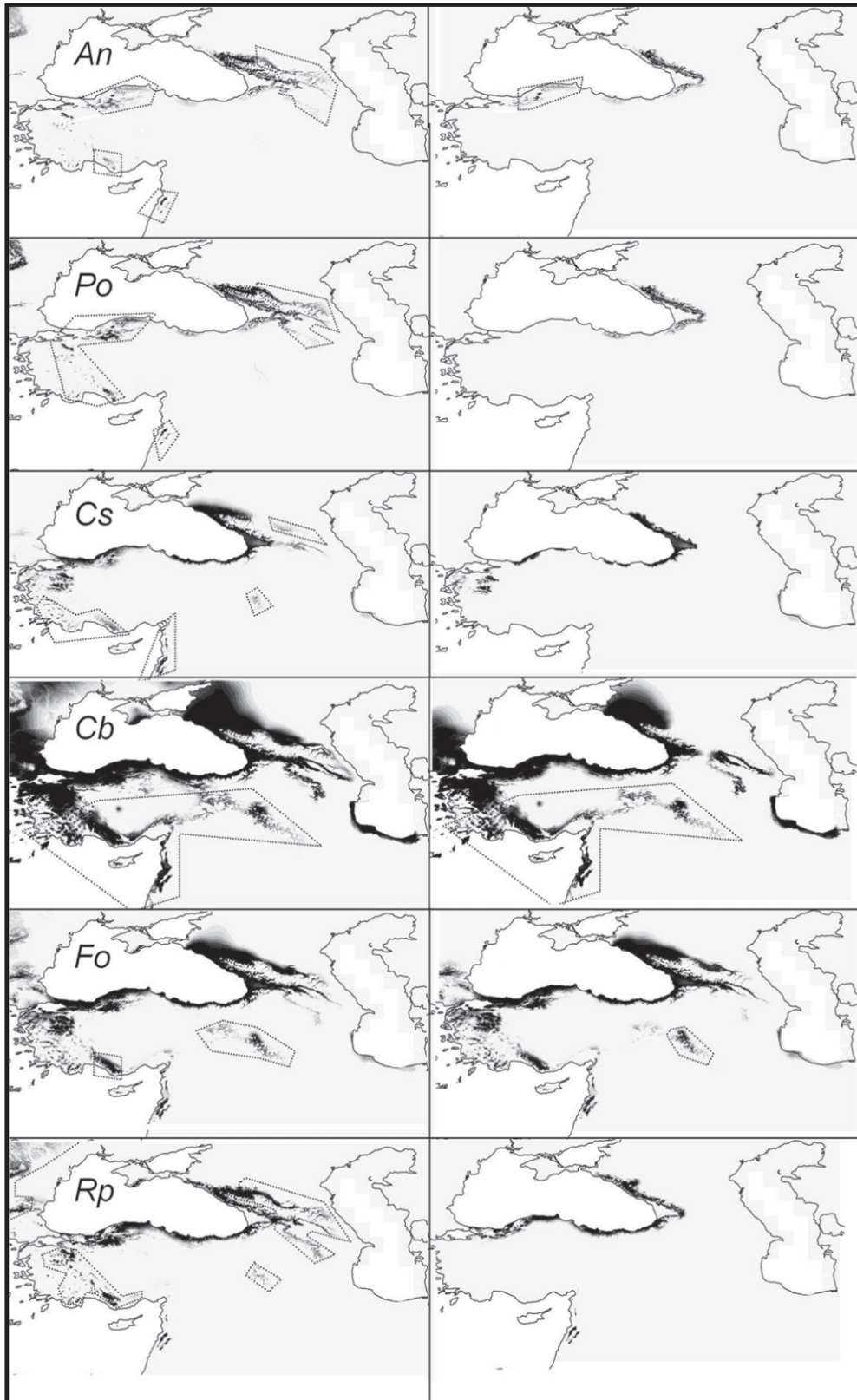
FE models, which do not consider interactions between variables, had a higher predictive power within the training extent than the models that considered these interactions for all species except *F. orientalis* and *H. buchi* (Table 1). Fixed-predictor FE models had a higher transferability than the iteratively fitted models, but somewhat lower predictive power within the training extent. Apparently, this outcome is a result of overfitting of the training dataset. The selection of predictors based on expert ecological knowledge has clear advantages (Midgley *et al.*, 2002; Kearney & Porter, 2004). This approach is commonly used for modelling suitable habitats (Hijmans & Graham, 2006; Pearson *et al.*, 2006). Increased interest in the models of ancient ranges (Martínez-Meyer & Peterson, 2006; Davies *et al.*, 2009) requires the availability of environmental variables for a sufficiently wide temporal and spatial scale. Climatic variables important for the survival of species (Midgley *et al.*, 2002; Skov & Svenning, 2004) are not always available for distant geological periods. The three simple predictors selected for this study have an obvious impact on a broad range of living organisms, and the respective climatic grids are freely available for both present and glacial time (as well as for the predicted future).

Although the fixed-predictor FE models had only moderate predictive power on a local spatial scale, the incorporation of palaeoclimatic information into these models provided a reasonable improvement. The explanations of the observed distribution patterns, based on the dispersal hypothesis, appear to be more plausible in many cases than those based on complex hypotheses on the interaction between an organism and its environment. The Caucasian ranges of *R. ponticum*, *A. nordmanianna* and *P. orientalis* extend only slightly east to the boundaries of the inferred Colchis refugium. In contrast, the ranges of *F. orientalis* and *C. betulus* go far beyond this area, to the eastern Caucasus (Nakhutsrishvili, 1999). The forests of Colchis (where all listed species are sympatric) generally have a higher annual rainfall than the forests of eastern Georgia, where only beech and hornbeam are found. One can obtain an impression that the last

two species are more resistant to the lack of humidity than the others. This is not true. The areas in the southern Black Sea coast west of Trabzon, where all five species coexist, have lower annual rainfall and colder winters than many areas of the eastern Caucasus. This also applies to variables more directly reflecting summer drought, including the ratio of the rainfall level to the sum of positive temperatures throughout the year. The simplest explanation of the observed distribution patterns is that all included species survived during the LGM at the Black Sea coast, but some failed to recolonize the central and eastern Caucasus during the Holocene.

In general, the diversity of species increases rapidly near the sources of post-glacial dispersal. The expansion of forests in the Caucasus was directed from the west to the east (Connor & Kvavadze, 2008), and more competitive trees and shrubs might have prevented the dispersal of the less competitive ones. This is in line with the suggestion that the distribution of plants typical for temperate rainforests, such as rhododendrons, is largely limited by the presence of competitors (Vetaas, 2002). Similarly, congeneric species have a substantial impact on the realized niche of *D. mixta* (Tarkhnishvili *et al.*, 2010), and this may explain why this species failed to recolonize the areas east of the LGM refugium.

MIROC climatic grids better describe the current distribution patterns than do CCSM grids. Although the former model suggests the presence of isolated refugia in Colchis, the latter expands the boundaries of suitable climates west to the Bosphorus with limited interruptions (Fig. 4). Consequently, the CCSM model fails to explain the presence of multiple species endemic to the western Caucasus (Zazanashvili *et al.*, 2004), whereas the MIROC model explains this phenomenon well. Molecular genetic data also support the presence of isolated refugia in the western Caucasus. A number of Caucasian endemics have been isolated from their relatives throughout the world since the Pliocene, such as the Caucasian rhododendron (Milne, 2004), Caucasian salamander (Weisrock *et al.*, 2001), Caucasian parsley frog (García-Paris, Buchholz & Parra-Olea, 2003) and Caucasian grouse (Lucchini *et al.*, 2001). All of these species have sister taxa in distant parts of Europe, East Asia and North America, but none in geographically close and potentially suitable habitats in western Turkey. A broad



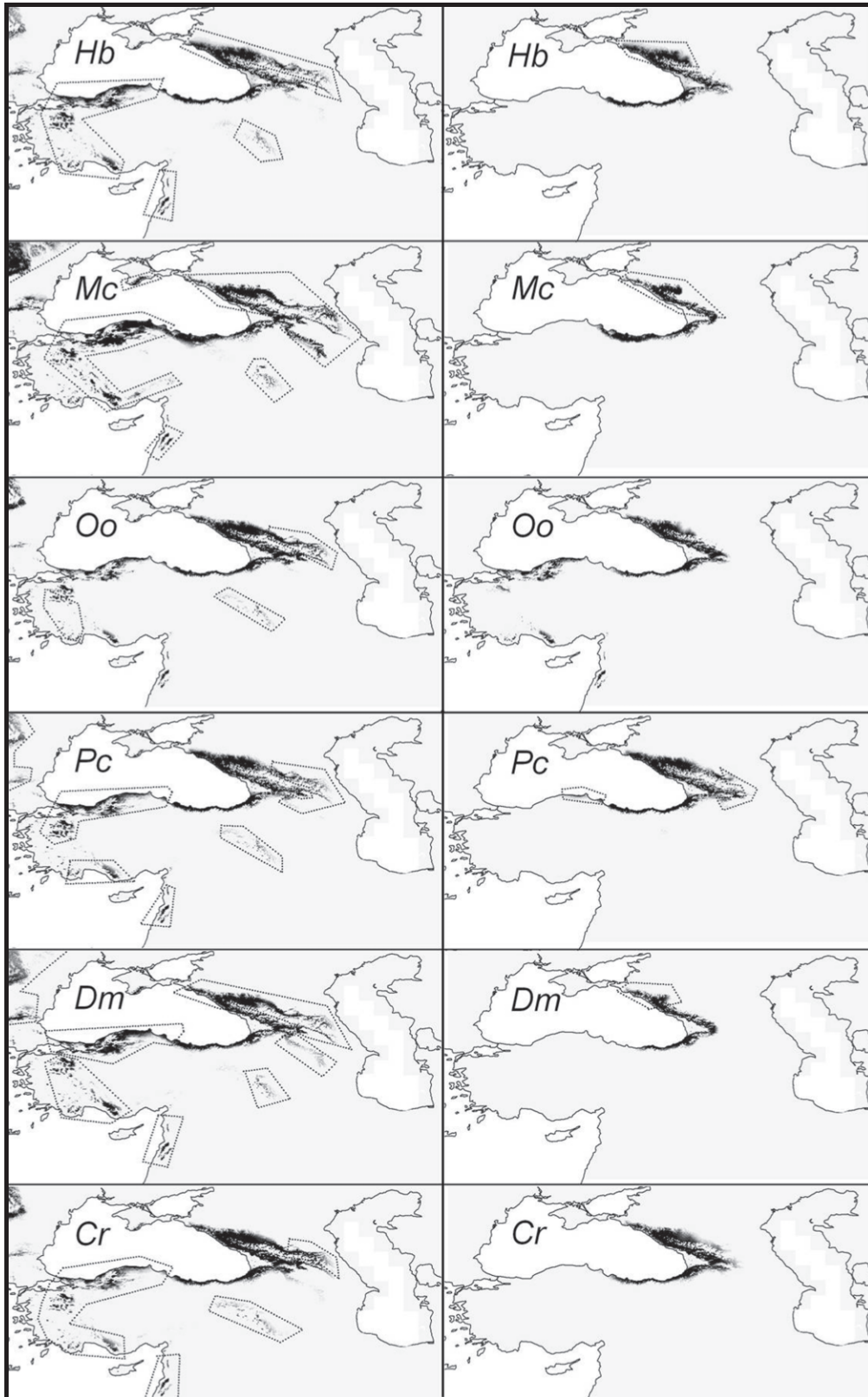


Figure 4. Continued

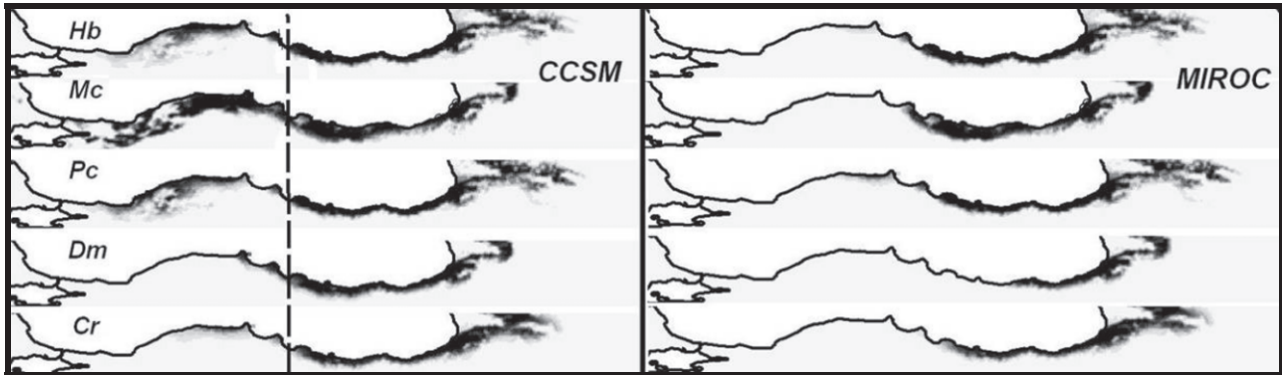


Figure 5. Southern coast of the Black Sea, with the predicted distribution of five endemic Caucasian animals, incorporating the distance from the Last Glacial Maximum (LGM) refugia, according to Community Climate System Model (CCSM) and Model for Interdisciplinary Research on Climate (MIROC) climate simulations. For abbreviations see Figure 3. The broken line indicates the current westernmost limit of the distribution of the species. CCSM simulation overpredicts the presence of all species at the south-western Black Sea coast, whereas MIROC simulation does not.

gap with unfavourable climate, which existed between the Colchis and western Anatolia during the LGM according to our MIROC-based model (Fig. 4), explains the limited current distribution of the listed species. Currently, a dry segment of the southern Black Sea coast between Ordu and Sinop in Turkey, where annual rainfall at the coast is below 700 mm and forest vegetation is scarce (Fig. 1), hinders the dispersal of the Caucasian endemics into north-western Anatolia. However, if the CCSM-based model is considered, we should expect a continuous distribution of suitable habitats along the southern Black Sea coast in LGM, and the absence of a number of Caucasian endemics from the south-western Black Sea coast becomes difficult to explain.

The reconstruction of the ancient suitable areas provides us with improved insight into the spatial position of glacial refugia, where forest-associated biological communities could survive the glacial period. Palynology suggests the presence of forests during the LGM in limited parts of Europe and western Asia (van Andel & Tzedakis, 1996). These areas are concentrated in the Alps, the Carpathians and along the south-eastern Black Sea coast. Beyond these major refugia, pollen records (Arslanov *et al.*, 2007; Connor & Kvavadze, 2008) provide evidence of uninterrupted forest cover at the north-eastern Black Sea coast. However, there is a lack of pollen diagrams which could either confirm or reject the occurrence of forests in the rest of the modelled Colchis refugium earlier than 10 ky BP (Connor & Kvavadze, 2008). Did the forests actually occur in the areas predicted by the palaeodistribution models? Genetic studies support a pattern in line with the modelling results. *Mertensiella caucasica*, which is found exclusively in forests or near

the timberline, has two evolutionary lineages isolated from each other since pre-glacial time (Tarkhnishvili *et al.*, 2000, 2008). The eastern lineage is limited to the eastern part of the western Caucasus, i.e. the area outside the palynologically confirmed refugia. The same applies to *D. mixta* (Murphy *et al.*, 2000). This means that the allopatric evolutionary lineages of the salamander and rock lizard independently survived the LGM in the south-western and eastern parts of the western Caucasus, and that the east of the inferred Colchis refugium had forests undetected so far in pollen profiles. The genetic data suggest that the actual distribution of forests in Colchis was more fragmented than predicted by the palaeodistribution models, but confirm that forests did exist in parts of Colchis, where palynological evidence is still lacking.

Our inference of the broader distribution of forests than that obtained from the available pollen records is in accordance with the outcomes of phylogeographical and vegetation studies. Van Zeist & Bottema (1991) postulated the presence of woodland during the LGM in parts of the Near East where the current forest distribution is limited (e.g. Levantine Mountains), based on the analysis of the current distribution of plants and the synthesis of palaeoecological data. The presence of multiple cryptic refugia in Europe (Provan & Bennett, 2008) and the isolation of evolutionary lineages of forest frogs and banded newts from the southern Caspian area and the Levant from their close relatives in Colchis since the Tertiary period support the presence of multiple, mesic, glacial refugia in western Asia (Veith *et al.*, 2003; Litvinchuk *et al.*, 2005). Our study suggests that, in all potential refugia, shown in Figure 4B, suitable climates existed during the LGM for temper-

ate forest species, and this pattern provides a plausible explanation for their current distributions.

A comparison of the current distribution of suitable climates (Fig. 3) with the actual distribution of forests in western Asia (Fig. 1) suggests that the area of the potentially suitable climates for some tree species, including beech and hornbeam, is wider than the actual distribution. Even distribution models for these two species, corrected by the post-glacial dispersal constraints (Fig. 3, right panel), predict their presence in the western Taurus and in the upper reaches of the Tigris. The most likely explanation of their absence in the indicated areas is deforestation caused by human activity, especially in the areas in which the human population has remained dense for thousands of years. In particular, the inferred refugium in the upper reaches of the Tigris River, where mesic forests are currently absent, is located in the specific small region of the Fertile Crescent, which has been suggested to be the cradle of agriculture (Diamond, 1997; Abbo, Lev-Yadun & Gopher, 2010). The human-caused deforestation in the Caucasus was less extensive in the past than in the south of the Middle East, although substantial transformation of forests in the historical past has been suggested for this area as well (Dolukhanov, 1966). The palynological record of the mid-Holocene suggests that forests existed in many potentially suitable, but nowadays treeless, agricultural areas (Connor & Kvavadze, 2008). The current vegetation of areas such as the upper reaches of the Tigris does not encourage vegetation scientists to hypothesize the presence of forest refugia there. Conversely, spatial modelling suggests the presence of a climate suitable for forest vegetation in a number of currently treeless regions.

The results of the present study suggest that, during the LGM, climates suitable for forest vegetation existed in six regions of western Asia: Colchis, western Anatolia, western Taurus, the upper reaches of the Tigris River, Levant and the southern Caspian basin. Figure 4B roughly outlines the spatial positions of these forest refugia, which could help to better understand the geographical distribution of plants and animals throughout the Near and Middle East. Further palaeobiological and phylogeographical studies may verify the exact position of the predicted refugia and add more details to the inferred pattern.

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SUPPORTING INFORMATION

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

Figure S1. Maps of occurrence locations for 12 plants and animals, used as training locations for spatial modelling. *An*, *Abies nordmanianna*; *Cb*, *Carpinus betulus*; *Cr*, *Chionomys roberti*; *Cs*, *Castanea sativa*; *Dm*, *Darevskia mixta* + *D. clarkorum*; *Fo*, *Fagus orientalis*; *Hb*, *Helix buchi* + *H. goderdziana*; *Mc*, *Mertensiella caucasica*; *Oo*, *Ommatotriton ophryticus*; *Pc*, *Pelodytes caucasicus*; *Po*, *Picea orientalis*; *Rp*, *Rhododendron ponticum*.

Figure S2. Iteratively fitted and fixed-predictor models of suitable climates for four plant and two animal species projected on Europe: *A*, iteratively fitted Mahalanobis distance models; *B*, iteratively fitted fuzzy envelope (FE) models; *C*, fixed-predictor FE models; *D*, European range of a species or its ecological equivalent. 1, *Abies nordmanianna*; 2, *Picea orientalis*; 3, *Castanea sativa*; 4, *Carpinus betulus*; 5, *Fagus orientalis*; 6, *Rhododendron ponticum*; 7, *Helix buchi* + *H. goderdziana*; 8, *Mertensiella caucasica*. See Table 1 for transferability estimates.

Table S1. Species occurrence data from the Caucasus Ecoregion.

Table S2. Data sources for testing model transferability (occurrence data for the target species or their ecological equivalents from Europe).

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