**Predicting late Quaternary distribution and future refugia of oriental beeches (*Fagus sylvatica*** **subsp. *orientalis*) in Asia Minor**

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Text, inclusive of abstract and reference list, should not exceed 7000 words.

**Abstract [max300 words]334**

**Aim:** European beech (*Fagus sylvatica*) has been widely used as model organism for late Quaternary vegetation reconstruction and modelling past and future distributions to understand responses of temperate tree species to changing climate. In contrast, little is known about its eastern counterpart *F. orientalis*. We investigated the late Quaternary history of this taxon, its refuge area(s), and projected distribution ranges under climate warming using a combined palaeobotanical, phylogeographic, and modelling approach.

**Location:** Western Eurasia

**Taxon:** Oriental beeches, *Fagus sylvatica* subsp. *orientalis*

**Methods:** Five species distribution modelling (SDM) algorithms were used to predict distributions under present, past (last glacial maximum, LGM, at 21 ka, mid-Holocene, MH, at 6 ka), and future (scenarios RCP 4.5, RCP 8.45) climates obtained from MIROC-ESM and CCSM4 climate models. Two modeling methods, *MaxEnt* and biomod2, were used. Models were compared to palaeobotanical and phylogeographic evidence and outcomes were compared to published accounts on European beech.

**Results:** Genetically distinct entities of *F. orientalis* predate the LGM and colonized their current ranges from different refugia. Pollen data indicate northern Turkey and western Caucasus as refugia for oriental beeches during LGM. Data are missing for northern Iran where sea level of the Caspian Sea dropped by 50 m during LGM. However, molecular data unambiguously point to LGM refugia in this area. Pollen data indicate presence of beeches during the MH in the entire area. SDM predicted modern and LGM distribution of *F. orientalis* moderately well, but underestimated MH ranges. Future predictions under various climate scenarios indicate the Caucasus region as major refuge for beeches. Predictions from the biomod2 package performed better than *MaxEnt*.

**Main conclusion:** A combined palaeobotanical, phylogeographic and model approach is useful when making predictions about past and future distributions of beeches in Asia Minor. Palaeobotanical and molecular evidence rejects some of the model predictions. Nevertheless, the projected reduction in distribution to the Caucasus area highlights the difference of this area to the northern Turkish and northern Iranian one. European and oriental beeches had different evolutionary histories since the late Quaternary.

**Keywords:** Species distribution modeling, last glacial maximum, Mid-Holocene, future climates, model bias, bioclimatic variables, pollen, isozymes, abiotic factors, biotic factors, competition, range shift

**1. Introduction**

Climate has been changing continuously through Earth’s history. However, at present, climate changes more rapidly than ever: Since 1880, global temperature had increased by ~1°C in 2013 (IPCC, 2013) and already had severe impacts on Earth. Additionally in early 2019 temperature reached upto 1.9°C (https://climate.nasa.gov/). Among the most apparent impacts is that on living organisms across the globe; organisms adapt to climate change by changing their behavior, physical features, and shifts in geographical distribution (Walther et al., 2002; Scheffers et al., 2016; Parmesan, 2006). Among all biomes, forests are one of the most affected by the recent changes, especially when terrestrial productivity is taken into account which is crucial for life on Earth (Boisvenue, C., & Running, S. W., 2006). These changes not only unbalance the survival rate of tree species, but also force plants to respond to extreme events, such as severe droughts, floods, wildfires etc. (Lindner et al., 2010, 2014). Since trees are the dominant species of forest ecosystems, any influence on them would leave marks on the environment in terms of resource supply, shelter, local and regional climate stability, as well as ecosystem services. Changes in dominant tree species would force the whole ecosystem and dependent organisms to alter their lifestyle and even cause extinction (Dyderski, 2017).

Broadleaf deciduous forests of Asia Minor are located adjacent to two major biodiversity hotspots, the Mediterranean Basin and the Caucasus hotspot (Myers et al., 2000) and the Euxine-Colchic broadleaf forests of Turkey and Georgia and the Hyrcanian forests of north Iran are among the most diverse forest ecosystems in western Eurasia (<https://www.worldwildlife.org/biomes/temperate-broadleaf-and-mixed-forests>). Great landscape diversity in northern Turkey, Transcaucasia and northern Iran is buffering the effects of climate change and has created refugia for plant species during past glacial periods (Médail & Diadema, 2009; Şekercioğlu et al., 2011). However, relatively little is known about how future climates will affect the distribution of broadleaf forests in these regions.

The most popular approach to investigate the impacts of climate change on distributions is through construction of species distribution models (SDMs) (Pearson & Dawson, 2003; Pearson, 2007). These models help to identify regions in an area with changing environmental variables that have similar environments to localities where the species has been observed (and hence these models do not take into account niche evolution). For this purpose, models use occurrence data (mostly in presence/absence format) and environmental data (such as climate, elevation and slope, etc.) provided for the designated area (Elith & Leathwick, 2009; Pearson, 2007). SDMs provide predictions of distributions of species by using abiotic factors such as environmental data. Hence, SDM is mainly a tool for estimating the extent of a species’ range in the future or in the past and is highly relevant for ecology and conservation purposes. Many of the known statistical classification algorithms which are in use can also be applied to build SDMs, they only differ in terms of the type of the distribution data, which is either presence-absence (GLM, GAM, RF) or presence-only (*MaxEnt*, BIOCLIM).

Climate change involves many challenges in terms of fitness of the plant species and pushes them to adapt to severe conditions or shift their geographical distribution (Parmesan, 2006; Root & Schneider, 2006; Lindner et al., 2014).

In this study, five SDM algorithms were used to model potential distributions of oriental beeches, *Fagus sylvatica* subsp. *orientalis* L.(Lipsky) Greuter & Burdet (hereafter *Fagus orientalis*) under the present, past (LGM and MH), and future (RCP 4.5, RCP 8.45) climatic conditions obtained from MIROC-ESM and CCSM4 climate models. *Fagus orientalis* is particularly well suited for SDM as it is a strongly niche conserved taxon (Pearman et al., 2007). One focus was on testing the species distribution to explore the most effective bioclimatic variables in the dataset and to investigate the responses of *F. orientalis* to climate change.

Oriental beeches are widely distributed across Eurasia, where environments with sufficient rainfall, absence of summer drought, and mild temperatures occur (Yaltırık, 1982a; Fang & Lechowicz, 2006; Kottek et al., 2006; Caudullo et al., 2017). Beech in western Eurasia plays an important role in forming monodominant or mixed beech-conifer forests. It has a narrow ecological niche being sensitive to late spring frosts and summer droughts (Peters, 1997). Several studies indicate that *F. orientalis* is vulnerable to climate change especially because of increasing temperature and decreasing precipitation (Köse & Güner, 2012; Haghshenas et al., 2016). SDM in order to better understand past and future distributions of tree species has extensively been applied to European woody species (e.g. Benito Garzón et al., 2007; Giessecke et al., 2007; Svenning et al., 2008; Maiorano et al., 2013). Likewise, a great number of palaeobotanical studies investigated the late Quaternary history of *Fagus* in Europe (e.g. Magri, 1998, 2008; Willis & van Andelt, 2004; Magri et al. 2006; Bradshaw et al., 2010) and these studies were integrated with phylogeographic investigations of *Fagus* (e.g. Magri et al., 2006). In contrast, SDM has rarely been applied to Minor Asian tree taxa (e.g. Tarknishvili et al., 2012; Ülker et al., 2018). The aims of the present study therefore are, **(*i*)** to investigate the late Quaternary history of *Fagus* in Asia Minor using published palynological data, **(*ii*)** to assess available phylogeographic data and their bearing on the location and presence of ice age refuges for beeches in Asia Minor, **(*iii*)** to model the present distribution range of *Fagus* in Asia Minor, **(*iv*)** to model the distribution during the LGM (21,000 a) and MH (6,000 a), and finally **(*v*)** to predict the future distribution of *Fagus* in Asia Minor under different climate change scenarios.

**2. Materials and methods**

**2.1 Study location and species distribution**

The location of our study was defined by the distribution range of *Fagus orientalis* plus some extension, to account for possible future or past expansions. We defined an area within longitudes of 18°–62° E and latitudes of 33°–51° N. A grid system with 2.5ˊ resolution with 457,681 raster cells was used. Forest management plans from General Directorate of Forestry (GDF) were used to determine the distribution of the species in Turkey and European Forest Genetic Resources Program (2009; EUFORGEN) distribution data (http://www.euforgen.org/species/fagus-orientalis/) were used for the remaining areas. Then, these two shapefiles were merged to create a distribution map (Figure 1).

All occurrence points were transformed into 2.5ˊ resolution (WGS-84 coordinate system) in ArcGIS (version 10.3.1) providing 10,493 presence points in total across the study area which is sufficient for our target modeling methods. These datasets have slight differences; however due to their similar datings and since the distribution would not change within close dates, results would not be biased. Two merged occurrence data of the *F. orientalis* distribution are shown on a satellite map in Figure 1.

**2.2 Environmental parameters**

We used 19 bioclimatic variables aggregated with elevation data obtained from WorldClim 1.4 (http://www.worldclim.org/; Hijmans et al., 2005) as environmental data (Appendix 1). Climate is the main abiotic factor shaping species distribution (Pearson & Dawson, 2003); thus it was used as the main environmental parameter. In the WorldClim database, past and future GCMs are available in order to investigate the climate change influence on species. We used two different GCMs, MIROC-ESM (Watanabe et al., 2011) and CCSM4 (Gent et al., 2011) from the available ones in WorldClim. For the past, Last Glacial Maximum (LGM) and Mid–Holocene (MH) time periods were simulated. Future simulations cover average values from 2041–2080 with different scenarios according to representative concentration pathways (RCPs) as defined by IPCC, which refer to the level of radiative forcing between preindustrial era and 2100 (Harr et al., 2014; IPCC, 2013). According to IPCC’s AR4 guideline, scenarios differ in CO2 concentration and the increase in global mean temperature between the preindustrial era and 2100. In the optimistic scenario – RCP2.6 – in 2100, CO2 concentration will be 450 ppm with an increase in global mean temperature between 0.2 –1.8 °C; moderate scenario (B1) – RCP4.5 – in 2100, CO2 concentration will be 650 ppm with an increase in global mean temperature between 1.0 – 2.6 °C; pessimistic scenario (A1F1) – RCP8.5 – in 2100, CO2 concentration will be 1350 ppm with an increase in global mean temperature between 2.6 – 4.8 °C (Harris et al., 2014; van Vuuren et al., 2011; Weyant et al., 2009). All data from WorldClim 1.4 were used at 2.5ˊ resolution and cropped according to the extent of the study region in ArcGIS. Since all bioclimatic variables are derived from monthly temperature and precipitation records, the correlation between them would cause bias in the model. We provided a correlation matrix (Table 2) between 19 bioclimatic variables to eliminate the highly correlated ones; as a result, we only used nine of them (Table 1).

**2.3 Model development and analysis**

We modeled and obtained potential distribution maps of *Fagus orientalis* using two different modeling methods, Maximum Entropy (*MaxEnt*) from its Java platform (Phillips et al., 2006) and biomod2 R package which is designed for species distribution modeling, calibration, and evaluation, through an ensemble of models (Thuiller et al., 2007). Since its first occurrence, *MaxEnt* became one of the most popular SDM methods. We chose *MaxEnt* as our main method since it needs presence-only data and, in contrast to other algorithms, does not require absence data; instead, it runs with background data pseudo-absences (Phillips, Anderson, Schapire, 2006; Elith et al., 2011). The advantage of using presence-only data is avoiding the risks of unreliable absence records (Jimenez-Valverde et. al., 2008). We modelled the distribution using *MaxEnt*’s default settings, with 30% random test percentage; that means 70% of the raster cells were used as training data to construct the model and the remaining 30% is used as testing data to evaluate the model. Background points make the results more accurate since it gives the model uniformity while still subjected to climatic constraints (Elith et al., 2011). Jackknife analyses and response curves were also performed in order to see which parameter affects distribution the most.

In addition to the *MaxEnt* method, we also used biomod2 package by Thullier et al. (2007) in R version 3.5.1 with RStudio. We performed 5 different algorithms within this package, including General Linearized Model (GLM), General Additive Model (GAM), Random Forest (RF), BIOCLIM, and Maximum Entropy (*MAXENT*). Again, default settings were used for data formatting, 780% of the input data was used as training sample and 20,796 background points were created randomly since GLM, GAM and RF algorithms require both presence and absence data. The code sheets are given in the supplementary (Appendix 2).

To evaluate and compare the models, area under the Receiving Operator Curve (AUC) was used; it depends on the true positive and true negative overlapping rates between the current and projected models. AUC range is in between 0 and 1; when the value is 0.50, it highlights that the model is equal to random, whereas 1.0 indicates the best separation. The higher the AUC value, the better the model performance (Swets, 1988; Fielding & Bell, 1997). Model outputs from both methods are based on the probability of the presence values of the species. For display and evaluation purposes, a threshold needed to be set. We used both lowest predicted value (Pearson et al., 2006; Phillips et al., 2006) and sensitivity – specificity equality (Pearson et al., 2004) methods to set the threshold, which was calculated as 0.585. With this approach, we aimed zero omission by setting the threshold to a minimum predicted value of observed occurrences, at the same time we tried to equalize sensitivity and specificity for increasing accuracy.

**3. Results**

**3.1 Late Quaternary palynological records of *Fagus* in Asia Minor** (Table 3)

A general feature of the 25 pollen profiles containing *Fagus* is the sparse occurrence or absence of *Fagus* during the LGM and its more or less continuous presence since about 10 ka. LGM values usually are low indicating long distance dispersal (LDD). One exception is the profile from the Marmaris area (core MD01-2430) that records beech with moderate abundance during the LGM. No suitable sediments recording LGM are known from the southern Caspian area. This might be due to the marked drop in sea level (-50 m) of the Caspian Sea during the LGM (Kislov et al., 2014). In contrast, MH distribution of *Fagus orientalis* was continuous and abundant throughout its present distribution range from eastern Bulgaria, the Marmaris region, northern Turkey, the western Caucasus and the southern Caspian Sea region (Table 3). Percentages commonly are way above the proposed threshold values indicating local presence of *Fagus* reported in Lisitsyna et al. (2011).

There is no convincing evidence for the presence of beech during MH outside its modern distribution range. Two pollen profiles from Cappadocica and Lake Van have sporadic occurrences of *Fagus* pollen but these are very few pollen grains and most likely indicate LDD. This is also suggested by the overall composition of these pollen floras (open oak woodland in the Acıgöl area of Cappadocia, Woldring & Bottema, 2003; forest steppe in the Lake Van area, Wick et al., 2003).

**3.2 Phylogeographic and taxonomic framework and inferred glacial refugia**

In general, populations of *Fagus orientalis* are markedly more differentiated than *F. sylvatica* with FST being 0.157 in the former and 0.032 in the latter (Gömöry et al., 2007). In addition, these authors found much higher levels of allelic richness in *F. orientalis* indicating that Pleistocene bottlenecks did not deplete the gene pool to the extent they did in the European *F. sylvatica*. Geographical subgroups of *Fagus orientalis* are genetically and morphologically highly distinct (Denk 1999a, b; Denk et al., 2002; Gömöry et al., 2007, 2018; Gömöry & Paule, 2010). Populations ranging from eastern Bulgaria to northern Turkey and the Amanos Mountains form one cluster. Two additional highly distinct clusters involve the western, eastern and Transcaucasian populations on the one hand and the populations south of the Caspian Sea on the other hand. In contrast, the European *F. sylvatica* forms a single cluster. In a recent study, Gömöry et al. (2018) tested speciation scenarios in subgroups of *Fagus orientalis* under an approximate Bayesian framework. Number of generations were used to estimate divergence times between genetically distinct regional populations. Divergence times suggest that European populations of *F. sylvatica* diverged from Asian Minor populations (*F. orientalis*) at c. 1.222–0.7 Ma. The Crimean beeches are of hybrid origin between Caucasian *F. orientalis* and *F. sylvatica*. They might have originated at around the Eemian interglacial (130–114 ka). Differentiation among the eastern populations happened much earlier: Caspian populations became isolated from Caucasian ones at 2.2–1.6 Ma, and from Turkish ones at 1.9–1.8 Ma. Finally, genetic isolation between populations of *F. sylvatica*  from the Balkans and Central Europe and Apennine occurred much later, at 100 ka and 70 ka.

This has important implications for inferring Pleistocene refugia for beeches in western Eurasia. Essentially, when considering the LGM and MH, *in situ* refugia must have existed for all geographical subgroups of *F. orientalis* because these regional groups had been isolated long before these events.

**3.3 Environmental parameters relevant for *Fagus* growth in Asia Minor**

Jackknife results from *MaxEnt* show which parameters (among the nine selected bioclimatic variables) are most important for *F. orientalis* survival in the defined region. Temperature seasonality (BIO4) was suggested to be most important and mean diurnal range (BIO2) least important (Figure 2). AUC values varied from 0.79 to 0.99 (Table 4) and hence performance of the values was successful, since all of them were above 0.7 (Elith et al., 2011). In Figure 3 we provide the ROC curve from the *MaxEnt* model to show the suitability of the model, which was satisfactory to move on.

Models were applied to four time periods, namely, the past (MH and LGM) and the future (2050 and 2070). Climate change scenarios and GCMs also differed in possible distribution ranges, also the number of shifts (Appendix 3, 4). Combined results from both GCMs and average of the scenarios show that the main geographical shift of *F. orientalis* will be towards the northeast of its present distribution in the future. Also, the past reconstructions are consistent with each in different GCMs. All of the simulation models were projected through the trained model (Figure 4) with present conditions based on the distribution data (Figure 1).

**3.4 Past reconstructions**

The past reconstructions are going back to 21,000 BP (LGM) and 6,000 BP (MH). The *MaxEnt* outputs of past simulations show that the possible distribution of *F. orientalis* is found mainly from the mid Black Sea region to Caucasia and northern Iran during LGM (Figure 5a), whereas in MH, the Iranian region lost the population and species distribution shifted slightly towards the west (Figure 5b).

Past reconstructions were also done with other algorithms via the biomod2 package. Here, we present the most successful one according to the AUC values, RF (Figure 6a-c). Comparing with the *MaxEnt*’s reconstructions, RF is a bit more ‘pessimistic’. There are more threats on the individual amount, yet overall the distribution range is similar. Other algorithms from the biomod2 package are given in Appendix 5 to 9.

**3.5 Future projections**

One of the main aims of this study was to evaluate responses of *F. orientalis* to ongoing climate change. Figure 7 shows *MaxEnt* results of the current distribution (Figure 7a) and future projections with three different climate scenarios (Figures 7b-d; here shown for the year 2070 from MIROC – ESM GCM; for more future projections see Appendix 3 and 4). According to this projections, there will be a severe contraction in the geographical range of the species both compared with the trained model and the input distribution data. The numbers of the influences of different scenarios are given in Table 5. The more pessimistic the scenario, the percentage of presence cells are decreasing and shifting from south to north. Also, *Fagus orientalis* starts to disappear from eastern parts, especially Iran region. According to RF MIROC ESM results in optimistic scenario, the proportion of presence numbers are 1.49 % of all cells, in the moderate scenario it is 0.95 % and in the pessimistic scenario, it is 0.42 % (Table 5). Same pattern is observed for *MaxEnt* outcomes. Presence cell numbers are decreasing whereas absence cell numbers are increasing in overall future simulations; the absence numbers are elevating with the pessimistic scenario. The models predict that in the future, *Fagus orientalis* will shift its range towards the northeast, the Caucasian region.

**4. Discussion and conclusions**

**4.1 Comparison of SDMs with real world data: choice of the “best” model**

SDMs are models that “describe or predict the probability of the presence or absence of a species across environmental gradients or in a specified geographical area” (Pearman et al., 2007). A key assumption of bioclimatic SDM is that the ranges of the modelled species are in equilibrium with climate (Pearson, 2007; Svenning et al., 2008; Hanspach et al., 2010).

*MaxEnt* MIROC ESM descriptions of the present distribution of *Fagus orientalis* (Figs. 4, 7a) roughly include the known range of this taxon but suggest large additional areas as suitable for growth of oriental beeches. Among these, the range expansion in Georgia-Armenia-Azerbaijan are plausible because climate conditions would favour growth of beeches in these regions (Cf and Df climates according to Köppen; see Kottek et al., 2006; Peel et al., 2007). Extensions into distinct Mediterranean climates (Cs climates) in the inner Aegean region and on the Peloponnese of Greece includes areas where the species has never been detected. Extensions into the Balkans are also plausible (cf. Yaltırık, 1982) although these areas are currently inhabited by *Fagus sylvatica*. Likewise, area extensions involving the distribution range of *F. orientalis* have been predicted in SDMs for *Fagus sylvatica* (Maiorano et al., 2013).

*MaxEnt* did consider the presence of oriental beech in the Amanos Mountains as unexpected. In contrast mountainous areas north of the Amanos Mountains were identified as probable habitats for beeches. It is noteworthy that a small area at c. 34°N corresponding with Mount Lebanon was designated as probable habitat for *Fagus*. This is plausible in view of the distribution in the Amanos Mountains. Finally, a further range expansion would include the eastern extension of the northern Iranian (Caspian) range of *Fagus orientalis*. This extension involves arid steppe regions (Bsk Köppen climate type) and is highly unrealistic. It has been noted previously that *MaxEnt* systematically overestimates occurrence probability in regions where the species has never been detected (Royle et al., 2012; Huntley, 2014).

Estimates of probability of occurrences of oriental beeches during the LGM by *MaxEnt* (Fig. 5a) are to some extent congruent with known pollen records. Unambiguous occurrences of beech pollen from LGM deposits are known from the Sea of Marmara, off the central northern Turkish Black Sea coast, and from Sukhumi (Table 3). While estimates on presence in Transcaucasia and south of the Caspian Sea are sensible, a major refuge area at 60°E east of the Caspian Sea is highly unrealistic in view of the present arid climate in this region. During the LGM, a cold continental climate would not have provided suitable conditions for growth of beech. The core region of *Fagus orientalis* estimated for the MH includes the eastern part of the Turkish Black Sea Coast and the Caucasus. While unambiguous pollen records are known from this area, the model entirely misses the western Black Sea area and the south Caspian region, from where abundant records of beech are known as well.

In contrast, biomod2 with RF and MIROC-ESM predicts probable distributions of beech for the MH that are congruent with the distribution known from the pollen record (Fig. 6c, Table 3).

As mentioned before all of the models ran successfully according to their AUC values (Table 4). The most successful among the algorithms was RF. RF works with a combination of classification trees to produce more accurate classifications, create complex interactions with model predictors and data, perform several statistical data analyses, such as regression, classification, survival and unsupervised learning (Cutler et al., 2007). Comparing the other algorithms, combination of regression and classification approaches, as well as in-algorithm verification provided more accurate outcome in RF and ed this algorithm to be the most successful one. On the other hand, the BIOCLIM algorithm is the most primitive method for SDM studies (Booth et al., 2014). It was the first developed model to apply the spatial analysis of species. It was expected from other algorithms to give better results than BIOCLIM with their advanced characteristics and calculations. In addition to that, present time projections fitted well with the present distribution data, thus our model is verified by the observation data, this means trained model is reliable to do further projections for past and future. The only critical problem with the model algorithms is seen in GAM (App. 6.) with its overfitted distribution in the past projections. Since it is not reliable to have such a wide distributional area in the past climatic conditions and also no information was found on past distribution of the species, we interpreted this outcome as an error in the algorithm (even GAM has the second-best AUC value). It is known that GAM algorithm is highly sensitive to large sample size since the fitted functions are not constrained to any functional form when sample size increases. Our study area is considered as a very large sample for a default SDM, thus it is likely that GAM results would be biased (Pearce & Ferrier, 2000).

Apart from this, a main finding of this study is that biomod2 performed better than *MaxEnt* in case of oriental beeches. We assume that the match of modelled MH distribution with the observed pollen record from this time period will give a clue about how distribution projections under future climates will perform (cf. Giessecke et al., 2007).

**4.2 Comparison with SDMs of *Fagus sylvatica***

Giessecke et al. 2007 … could be done later

**4.3. The future of beech in Asia Minor**

xxx… could be done later as a sort of Conclusion

**Acknowledgments**

We are thankful to Abbas Şahin and General Directorate of Forestry, Turkey, for providing us the *Fagus* distribution data within Turkey. TD acknowledges funding from the Swedish Research Council (VR grant no. 2015-03986).

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**Figure and Table captions**

**Fig. 1.** *Fagus orientalis* distribution data, A) from EUFORGEN, B) from GDF and C) from the merged data.

**Fig. 2.** The Jackknife results from *MaxEnt* depicting the relative importance of the environmental parameters for *Fagus orientalis.* (BIO 1 is annual mean temperature, BIO12 is annual precipitation, BIO15 is precipitation seasonality, BIO19 is precipitation of coldest quarter, BIO2 is mean diurnal range, BIO3 is isothermality, BIO4 is temperature seasonality, BIO8 is mean temperature of the wettest quarter and BIO 9 is mean temperature of driest quarter.)

**Fig. 3.** The ROC curve from *MaxEnt* showing AUC values above 0.7, indicating the model is successful. (The red line, training data, shows the fitness of the model to the training data. The blue line, test data, shows the fitness of the model to testing data and is the real one to evaluate the success of the model.)

**Fig. 4.** The trained model with present climatic conditions. The model was successful (AUC: 0.84), thus it could be used for the past and future projections. The output of trained model is mapped by the probability range from *MaxEnt*, from blue to red, occurrence probability of the species is increasing, where blue is absent and red is present.

**Fig. 5.** Past reconstructions from *MaxEnt*, here only MIROC – ESM GCM is shown (for CCSM4 see Appendix 4.) The map is printed by the probability range from *MaxEnt*, from blue to red, occurrence probability of the species is increasing, where blue is absent and red is present.

**Fig. 6.** Past reconstructions by the biomod2 method, RF algorithm; here only MIROC – ESM GCM is shown (for CCSM4 see Appendix 4.) Maps are printed using the probability range from biomod2 package’s default settings, from grey to green, they indicate increasing presence probability percentage\*10.

**Fig. 7.** Current and future projected distribution maps of *Fagus orientalis* from *MaxEnt* model with three different climate scenarios, **A**) represents current **B**) represents the optimistic-RCP2.6 scenario, **C**) represents the moderate-RCP4.5 scenario, and **D**) represents the pessimistic-RCP8.5 scenario. Blue areas represent overlap of current and future projected ranges, whereas green areas show potential range expansion in the model, orange pink areas show expected range contraction and red area shows expected range contraction in the model. Spatial resolution: 2.5 ˊ

**Table 1.** Selected bioclimatic variables to use as environmental input in the models.

**Table 2.** Correlation matrix between 19 bioclimatic variables.

**Table 3 ADDITIONAL TABLE.**

Palaeobotanical records for the LGM and MH.

**1**, Filipova Marinova et al. (2013); **2**, Filipova Marinova et al. (2016); **3**, Atanassova (2005); **4**, Margari et al. (2009); **5, 6**, Mudie et al. (2002, 2007); **7**, Valsecchi et al. (2012); **8**, van Zeist & Bottema (1991); **9**, Shumilovskikh et al. (2012); **10**, Shumilovskikh et al. (2013); **11**, Shumilovskikh et al. (2014); **12**, Woldring & Bottema (2003); **13**, Wick et al. (2003); **14**, Shatilova et al. (2011); **15**, Arslanov et al. (2007); **16**, Marret et al. (2019); **17, 18**, Tarasov et al. (1999, 2000); **19** Connor & Kvavadze (2009); **20**, Bottema (1986); **21**, Djamali et al. (2008); **22**, Leroy et al. (2007); **23**, Leroy et al. (2016); **24**, Leroy et al. (2013); **25**, Shumilovskikh et al. (2016).

**Table 4.** AUC values of all the models performed.

**Table 5.** Coordinate, cell numbers and presence percentages of the future projections from Fig. 7. From optimistic to pessimistic scenario, species are shifting to north and east according to coordinates, presence cell numbers (cell number (1)) are decreasing, whereas absence cell number (cell number (0)) are increasing. This also means the percentage of the cells which species are present is decreasing.