DISTRIBUTION MODELLING OF THE CAUCASIAN ENDEMIC *FRITILLARIA LATIFOLIA* AGAINST THE BACKGROUND OF CLIMATE CHANGE

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Current climate change, habitat degradation, pastoralism, shoot and bulb harvesting pose serious threats to the rare Caucasian endemic *Fritillaria latifolia* throughout its range. Knowledge of the limiting factors, species range dynamics in relation to climate change and the role of Protected Areas in species distribution are necessary to develop an effective conservation system at present and in the future. This was aimed (1) to determine the most suitable set of abiotic predictors for modelling *Fritillaria latifolia* localisation, (2) to formalise environmental and anthropogenic factors in species distribution models, (3) to predict the possible changes in the species range in relation to climatic changes, (4) to identify refugia with a consistently high probability of the species occurrence despite climatic changes. We applied Maxent software for species habitat modelling to build current and climatic models of the *Fritillaria latifolia* distribution, considering the abiotic variables and anthropogenic predictors such as the distance to Protected Areas and grasslands. Distances to anthropogenic infrastructure were calculated with the Path Distance measure considering the horizontal straight-line distance, surface distance and vertical factor. We also formalised the area accessibility (movement factor) through the distance to optimal sites (plots with 0.8 threshold of habitat suitability), where the probability of species occurrence was higher than 0.5. The most important abiotic variables in the species distribution were the Emberger's pluviothermic quotient, with optimal values corresponding to humid and perhumid climates, and the terrain roughness index, with optimal values ranging from nearly level (81–116) to intermediately rugged (162–239) slopes. Distance to Protected Areas (0–1 km) was the third important predictor of the *Fritillaria latifolia* current distribution, while the distance to grasslands contributed less to the model. The distance of suitable areas from optimal habitats (area accessibility) was 15 km. The species current core ranges are localised in the Western and Central Caucasus, Western and Central Transcaucasia, and the northwestern ridges of the Lesser Caucasus within a network of Protected Areas covering most of the highlands. The optimistic socio-economic pathway SSP1-2.6 predicted a 1.6-fold decrease in the area of species optimal habitats from 2021 to 2100. The pessimistic SSP5-8.5 scenario predicted 122-fold habitat area reduction. According to SSP1-2.6 climatic models, by 2100 the refugia area would be 172.4 km^2 in the highlands of the western and central parts of the Greater Caucasus, including the Caucasus State Nature Reserve and Teberda National Park. These areas should be prioritised for the conservation of *Fritillaria latifolia* populations.

Key words: Biotic-Abiotic-Movement concept, Maxent, Protected Area, refugia, socio-economic pathways

Introduction

Current climate change poses a serious threat to the global biodiversity (Banag et al., 2015; Mazangi et al., 2016) and reduces the effectiveness of local and regional conservation and management strategies (Van Dyke, 2008). Climate change is a pressing issue for the Caucasus Mountains, where the average annual air temperature increased by 0.2–0.4°C between the 1960s and 2010 (Atayev & Bratkov, 2014). Biodiversity of mountain ecosystems is particularly sensitive to climate change (Guerrina et al., 2016). Endemic species, with their localised populations and low dispersal rates, are considered among the most vulnerable components of the mountain flora (Van Dyke, 2008; Banag et al., 2015; Guerrina et al., 2016; Christmas et al., 2016). One of the rare Caucasian endemics is *Fritillaria latifolia* Willd. It is native to the mountain meadow ecosystems of the ecoregion. Despite a number of population-based studies (e.g. Thazaplizheva & Chadaeva, 2012; Tania & Abramova, 2013; Yamalov et al., 2014; Pshegusov et al., 2019), the current knowledge about the factors limiting *Fritillaria latifolia* distribution remains extremely scarce. Information on the species range dynamics in relation to climate change and the role of Protected Areas in its predicted distribution is also still lacking. However, knowledge of the distribution predictors and location of refugia is necessary to develop an effective conservation system for *Fritillaria latifolia* at present and in the future.

The issue can be addressed through Species Distribution Models (SDMs). Based on the statistical processing of geographic species records and layers of topographic and climate information, SDM is considered an efficient method for studying the species potential distribution (Elith et al., 2006; Peterson et al., 2011; Duarte et al., 2019; Bowen & Stevens, 2020; Sillero et al., 2021). This is particularly useful in mountainous areas with complex, inaccessible basin-and-range terrain. Within «bioclimate envelope» modelling, SDMs typically include only abiotic environmental predictors of the species distribution. At the same time, interspecific interactions, as well as the widespread impact of human activity, represent integral components of species ecological niches and influence species distribution. Accounting for biotic and anthropogenic factors in the models remains a relevant methodological challenge in SDM. Our study therefore is focused on the Biotic-Abiotic-Movement (BAM) concept, which integrates three key sets of factors (namely B-factors (biotic predictors including anthropogenic factors in this study), A-factors (abiotic environmental variables), and M-factors (movement, dispersal capability or area accessibility)) into single-species models (Soberón & Peterson, 2005; Peterson, 2006; Peterson et al., 2011; Peterson & Soberón, 2012). This concept allows an analysis of the «occupied distributional area», which corresponds most closely to the actual species distribution (Soberón & Peterson, 2005; Peterson & Soberón, 2012).

In this context, this study was aimed to investigate the abiotic and anthropogenic factors, and area accessibility, which could affect the distribution of *Fritillaria latifolia* in the Caucasus. This knowledge is important, as it can form the basis for an effective system of species preservation. The research objectives were (1) determining the most suitable set of abiotic predictors for modelling the species localisation, (2) formalising environmental and anthropogenic factors in SDMs, (3) predicting the possible changes in the species range in relation to climatic changes, and (4) identifying refugia with a consistently high probability of the species occurrence despite climatic changes. We hypothesised that the distance to Protected Areas is one of the key factors in the species distribution at present and in the future.

Material and Methods

Target species and study area

Fritillaria latifolia is a striking, well recognised bulbous geophyte species distributed in mountain grasslands of the Ciscaucasia, the North Caucasus, Western and Eastern Transcaucasia (Tania & Abramova, 2013; Batsatsashvili et al., 2017; Pshegusov et al., 2019). The species belongs to the psychrophytes, which prefer cold and wet habitats (Red Data Book of the Chechen Republic, 2020). As a hydrophilic species (Yamalov et al., 2014; Batsatsashvili et al., 2017), it occurs mainly on gentle river terraces (Tania & Abramova, 2013) and couloirs with long-lasting snow cover (Pshegusov et al., 2019) in subalpine and alpine wet and marshy meadows, often on peaty soils (Yamalov et al., 2014; Batsatsashvili et al., 2017). The decline in populations of this Caucasian endemic throughout its range is caused by pastoralism, habitat degradation, and shoot and bulb harvesting (Tania & Abramova, 2013; Pshegusov et al., 2019). This species has been classified as «Rare species» in the Red Data Book of the Republic of Kabardino-Balkaria (2018) and the Red Data Book of the Chechen Republic (2020).

The Caucasus ecoregion (about 390 000 km^2 between 38–47° N and 36–50° E) was considered the study area. It comprises several climate-orographic parts, namely the Ciscaucasia, the North Caucasus and Transcaucasia (parts of the Greater Caucasus), the Colchis and Kura-Araks Lowlands, the Lesser Caucasus, and the Transcaucasian Highland (Fig. 1a).

The Caucasus ecoregion includes the territories of the Russian Federation, Azerbaijan, Georgia, and Armenia. The Ciscaucasia is dominated by a warm continental climate (Dfa according to the Köppen-Geiger classification) (Fig. 1b). The prevailing climate of the Greater Caucasus is warm summer continental (Dfb) in the middle mountains and cool summer continental (Dfc) or alpine (ET) in the highlands. The North-Western Caucasus and Western Transcaucasia have a predominantly humid subtropical (Cfa) and oceanic (Cfb) climate. Aridity of the climate increases towards the southeast of the Greater Caucasus. A humid subtropical and oceanic climate also prevails in the Colchis Lowland and the northwestern part of the Kura-Araks Lowland. In the southeastern part of the Kura-Araks Lowland, the climate is cold semi-arid (BSk). The mountainous areas of the Lesser Caucasus and Transcaucasian Highland have a warm summer continental climate with increasing aridity towards the southeast. In the southern part of the Transcaucasian Highland, a cold semi-arid climate prevails. The main tree species in the foothills and middle mountains of the Caucasus are *Fagus orientalis* Lipsky, *Carpinus betulus* L. and *Quercus* spp. *Pinus sylvestris* L. and *Betula* spp. are widespread in the middle mountains and highlands. *Picea orientalis* (L.) Peterm. and *Abies nordmanniana* (Steven) Spach occur in the North-Western Caucasus and Western Transcaucasia, while *Juniperus* spp. are common mainly in the Transcaucasian Highland and Lesser Caucasus. The plains, foothills and lowlands of the Caucasus ecoregion are mainly used for agriculture. Subalpine and alpine grasslands historically serve as grasslands.

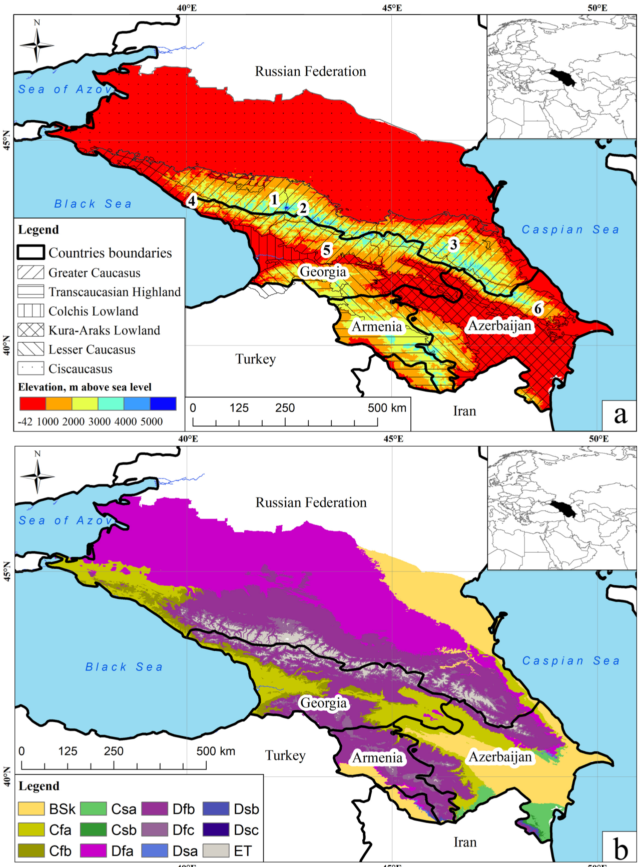

Fig. 1. The geographic location, orography (a) and climate classification scheme (b) of the study area. The climate classification scheme was built based on monthly mean temperature and precipitation data from WorldClim2 using the Saga Gis v. 7.8.2 algorithm of Conrad et al. (2015). Köppen-Geiger climate classification and colour scheme were sourced from Peel et al. (2007). Designations: 1 – Western Caucasus, 2 – Central Caucasus, 3 – Eastern Caucasus (parts of the North Caucasus), 4 – Western Transcaucasia, 5 – Central Transcaucasia, 6 – Eastern Transcaucasia; BSk – cold semi-arid climate, Cfa – humid subtropical climate, Cfb – oceanic climate, Csa – Mediterranean hot summer climate, Csb – Mediterranean warm or cool summer climate, Dfa, Dfb and Dfc – hot, warm and cool summer continental climate respectively, Dsa, Dsb and Dsc – hot, warm and cool dry summer continental climate respectively, ET – alpine climate.

Geographic records and environmental variables

The study design, including assessment and manipulation of spatial data (presence points, environmental layers), model development and evaluation, was summarised in Electronic Supplement 1. We used 57 geographic records of *Fritillaria latifolia* from the 2013–2022 expedition surveys and 82 occurrence data from the Global Biodiversity Information Facility (GBIF.org, 2023). To address the problem of spatial clustering of presence points, we applied spatial thinning as one of the popular correction methods (Petrosyan et al., 2020) (Electronic Supplement 1). Based on the removal of geographic records, spatial thinning produces an occurrence dataset, from which efficient SDM models are constructed (Kramer-Schadt et al., 2013; Syfert et al., 2013; Aiello-Lammens et al., 2015; Sillero et al., 2021). Accordingly, geographic records were checked for duplicates and sparse to one data per 1 km^2 grid cell. As a result, 122 presence points remained after the spatial thinning. Then, the dataset was tested for spatial clustering using the Average Nearest Neighbour Index (Clark & Evans, 1954), which revealed a clustered distribution of 122 presence points (Electronic Supplement 2: Table S1, Fig. S1). When rethinning over a distance of 14 km, 113 randomly distributed presence points remained (Electronic Supplement 2: Table S1, Fig. S1). The R packages (R Core Team, 2023) used for spatial thinning and testing for spatial clustering were specified in Electronic Supplement 3.

To determine the most suitable abiotic predictors for modelling *Fritillaria latifolia* localisations (Electronic Supplement 1), we used two sets of environmental variables for comparative predictor analysis: 1) WorldClim2 bioclimatic parameters (Fick & Hijmans, 2017; WorldClim2, 2023) and GMTED2010 topographic data (Danielson & Gesch, 2011; GMTED2010, 2023); 2) ENVIREM (ENVIronmental Rasters for Ecological Modeling) climatic and topographic variables (Title & Bemmels, 2018; ENVIREM, 2023). To select uncorrelated environmental layers, we applied the VIF (Variance Inflation Factor) test in R (VIF threshold ≤ 3) (Electronic Supplement 1). As a result, five ENVIREM variables and eight WorldClim2+GMTED2010 predictors were involved in the analysis (Electronic Supplement 2: Table S3).

To check, whether sampling bias is a problem (Kramer-Schadt et al., 2013; Merow et al., 2013; Sillero et al., 2021), we compared the distribution of predictor values for both ENVIREM and

WorldClim2+GMTED2010 datasets (Electronic Supplement 1). According to Mann-Whitney U-test for two independent samples, the distributions of predictor values were similar only in the pair of presence points and background points for the ENVIREM set, indicating the absence of bias (Electronic Supplement 2: Table S2). High similarity was also identified when comparing biased and unbiased ENVIREM A-models using the agreement coefficient (Ji & Gallo, 2006; Riemann et al., 2010) and Pearson correlation coefficient r (Electronic Supplement 2). Thus, no sampling bias problem was revealed when using 113 occurrence points (obtained after spatial thinning), background biased points and ENVIREM dataset. Therefore, already at this stage of the study, the ENVIREM A-model was prioritised for further analysis.

In this study, we considered anthropogenic factors as a part of the biotic predictors of the species distribution. Given the susceptibility of *Fritillaria latifolia* populations to overgrazing and direct human destruction, we used the distances to grasslands and Protected Areas as the main anthropogenic factors. Estimating distances from target species to anthropogenic infrastructure is a common method of accounting for human activity in SDMs (Ortiz-Urbina et al., 2020; Vignali et al., 2021; Sharma et al., 2023). However, Euclidean distance, as the most popular tool in this process, is obviously not suitable for studying mountainous areas, as it does not consider the altitude gradient. Therefore, we used the Path Distance measure (path_landuse and path_PAs) calculated with horizontal straight-line distance, surface distance and vertical factor (McCoy et al., 2001). Path Distance was estimated for each grid cell as the distance to the nearest object, considering altitude gradient (McCoy et al., 2001). The input data were represented by a spatial feature class from the NextGIS vector map sets (NextGIS, 2023) and the digital altitude model GMTED2010 (Amatulli et al., 2018).

The area accessibility (movement factor) is an important concept in SDM, irrespective of the algorithm used (Soberón & Osorio-Olvera, 2023). Our approach to formalising the movement factor was to represent area accessibility through the distance to optimal sites (plots with 0.8 threshold of habitat suitability), on which the probability of species occurrence was higher than 0.5 (Pshegusov et al., 2022).

BAM concept allows the effects of the three factors to be studied separately by building A-, BA- and BAM-models. In the A-models, we used the abiotic variables selected by the VIF test. In the BA-models, we considered the abiotic variables and anthropogenic predictors (VIF $\leq$ 3) such as the distance to grasslands (path_landuse) and Protected Areas (path_PAs). The raster of distances to optimal areas (sites with 0.8–1.0 probability of species occurrence), where the probability of *Fritillaria latifolia* occurrence remained above 0.5, was used as a movement-layer in the BAM-model. The resolution of the resulting layers was 1 km per pixel.

Model development and evaluation

The modelling procedures were described in ODMAP protocol (Electronic Supplement 4). The R packages used for model development and evaluation were specified in Electronic Supplement 3.

In this study, we applied Maxent v. 3.4.3 (Phillips et al., 2017) for species habitat modelling. It is considered one of the most robust and efficient modelling methods based on presence-only data (Elith et al., 2006; Phillips & Dudík, 2008), especially when rare species with a small sample size are involved (Elith et al., 2011; Qin et al., 2017; Vignali et al., 2021). Identification of the optimal set of Maxent model parameters was shown in Overview/SDM algorithms/Model complexity of the ODMAP protocol (Electronic Supplement 4). Selection of optimal model settings was also shown in Overview/SDM algorithms/Selection of optimal models in the ODMAP protocol (Electronic Supplement 4).

We calculated the percentage contribution of predictors (Phillips et al., 2017) to assess their importance in Maxent models. The optimal variable values were obtained from the response curves by cutting off at a threshold of 0.8. Different thresholds are used to convert continuous probabilities calculated in Maxent into discrete presence/absence predictions (Liu et al., 2013), and there is no uniform method for defining the habitat suitability threshold (Glover-Kapfer, 2015). To reduce the risk of misidentification, it is advisable to choose a high threshold for habitats with a high degree of suitability (Pearson et al., 2004). In this study we used a fixed high threshold of 0.8 for optimal habitats. Such a threshold reduces the possibility of false-positives (Buhl-Mortensen et al., 2019). For potentially suitable habitats, we used a fixed threshold of 0.5 (Elith et al., 2010; Kramer-Schadt et al., 2013). The complementary log-log (cloglog) transform was used to build the models as the best fit for estimating the occurrence probability (Phillips et al., 2017). Distribution maps were generated with a scale of species occurrence probability from 0 to 1 in the Maxent palette colour gradations.

The climatogenic distribution dynamics of *Fritillaria latifolia* was considered in four time periods, namely 2021–2040, 2041–2060, 2061–2080, 2081–2100. We used the UKESM1-0-LL (UK Earth System Model) developed in the United Kingdom at the CMIP6 project (Sellar et al., 2019). This is the second highest priority model in the ISIMIP3b modelling protocol (Lange & Büchner, 2020). For this model, we considered two general socio-economic pathways (SSP), in particular the optimistic scenario SSP1-2.6 and the worst-case scenario SSP5-8.5. The calculation of ENVIREM layers for these scenarios were shown in Data/Predictor variables/Data processing of the ODMAP protocol (Electronic Supplement 4). In total, we built eight climatic BA-models of *Fritillaria latifolia* future distribution under two scenarios in four time periods. The anthropogenic and orographic predictors were assumed constant.

The localisation of *Fritillaria latifolia* refugia with a consistently high probability of the species occurrence despite climatic changes was determined in several steps. First, we converted into points the optimal sites of the species occurrence at present. Second, at these points we extracted values of the species occurrence probability in future time periods. Third, on the raster layers of the climatic BA-models, we cut off points with the occurrence probability below 0.8. Finally, we mapped areas where the probability of *Fritillaria latifolia* occurrence exceeded 0.8 throughout the prediction period.

Results

Selection of the most suitable set of environmental variables. A-models

The performance statistics of the resulting WorldClim2+GMTED2010 and ENVIREM A-models indicated their high predictive accuracy (Electronic Supplement 2: Table S4). According to the first A-model, the current *Fritillaria latifolia* distribution was influenced by climatic factors such as maximum mean temperature in February, precipitation in November, and by altitude (Table 1). Predicted altitude values (0.8 threshold) corresponded to the altitude values in *Fritillaria latifolia* habitats, reported previously, namely 1600–2300 m a.s.l. in Abkhazia (Tania & Abramova, 2013), 1700–2500 m a.s.l. in Armenia (Batsatsashvili et al., 2017), 2100–2500 m a.s.l. in the Central Caucasus (Pshegusov et al., 2019).

As reported in the Red Data Book of the Chechen Republic (2020), *Fritillaria latifolia* occurs at altitudes up to 3000 m a.s.l. in the Eastern Caucasus. The main processes of underground morphogenesis and growth of the species occur in late winter, while the main processes of aboveground vegetation (sprouting, shoot growth, flowering) take place in spring (Thazaplizheva & Chadaeva, 2012). This probably explains the importance of maximum mean temperature in February in the *F. latifolia* distribution. A suitable temperature range during this critical vegetation period is typical for the mountainous regions of the Western Caucasus and Western Transcaucasia. Accordingly, the model predicted the *F. latifolia* core range in these areas (Fig. 2a), which is consistent with field observations (Pshegusov et al., 2019). At the same time, an interpretation of the November precipitation influence, i.e. precipitation during the species dormancy period, was difficult.

According to the ENVIREM A-model, the most important variable in the species distribution was Emberger's pluviothermic quotient, with optimal values corresponding to humid and perhumid climates (Daget et al., 1988) (Table 1). The model predicted the core ranges of this hydrophilic species in the Western Caucasus, Western and Central Transcaucasia, and the western ridges of the Lesser Caucasus (Fig. 2b), i.e. in areas with humid subtropical and oceanic climate (Fig. 1b).

Table 1. Contribution of the main abiotic variables (percentage contribution of more than 10%) to the WorldClim2+GMTED2010 and ENVIREM A-models of *Fritillaria latifolia* ecological niche

WorldClim2+GMTED2010			ENVIREM		
Variable	PC, %	Optimal values	Variable	PC, %	Optimal values
tmax2, °C	31.6	from -4 to +0	embergerQ	54.7	150–190
prec11, mm	29.5	135–155	TRI	20.8	75–250
Alt, m a.s.l.	11.4	1800–2100	PETColdestQuarter, mm/month	14	7–14

Note: Predictor abbreviations: tmax2 – maximum mean temperature in February, prec11 – precipitation in November, Alt – altitude, embergerQ – Emberger's pluviothermic quotient, TRI – terrain roughness index, PETColdestQuarter – mean monthly potential evapotranspiration of the coldest quarter. Variable importance is represented as a percentage contribution (PC, %) in the Maxent models. Optimal values of variables were sourced from the response curves by cutting off at the threshold of 0.8.

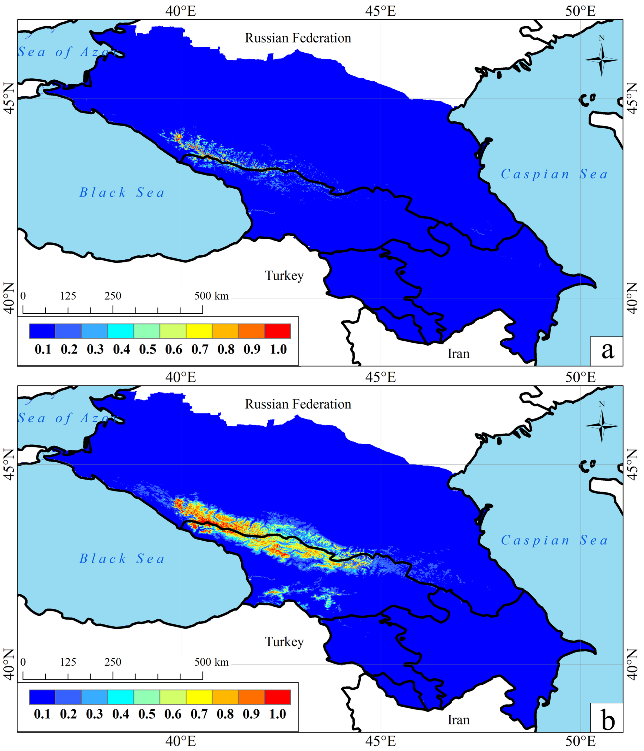

Fig. 2. Predictive maps of the *Fritillaria latifolia* distribution in the Caucasus by A-models based on WorldClim2+GMTED2010 (a) and ENVIREM (b) sets of environmental variables. Designations: 0–1 scale indicates the probability of species occurrence.

Less suitable habitat conditions were predicted in the humid Central Caucasus, while unsuitable habitats were expected in the arid areas of the Ciscaucasia, the eastern part of the Greater and Lesser Caucasus, the Transcaucasian Highland and the Kura-Araks Lowland. The second most important predictor of *Fritillaria latifolia* distribution was the terrain roughness index, with optimal values ranging from nearly level (81–116) to intermediately rugged (162–239) slopes (Riley et al., 1999). This is in line with field studies showing that the species is mainly distributed in relatively gentle terrain (Tania & Abramova, 2013; Pshegusov et al., 2019).

As a result, in both A-models (WorldClim2+GMTED2010 and ENVIREM) the contribution and optimal values of environmental predictors were largely consistent with the ecological features of *Fritillaria latifolia*, and the predictive distribution maps were in line with the actual localisation of species populations. In both A-models, the three most important predictors were temperature, humidity and orographic parameters. Despite similar results, we concluded that the ENVIREM cartographic model was more consistent with the actual distribution of *Fritillaria latifolia* in the Caucasus. Compared to the more «strict» WorldClim2+GMTED2010 A-model, it predicted large suitable areas in Transcaucasia, which is in agreement with literature data on *Fritillaria latifolia* occurrence in northern parts of Abkhazia and Georgia and in northwestern part of Armenia (Tania & Abramova, 2013; Batsatsashvili et al., 2017). Furthermore, ENVIREM predictors are not difficult to interpret from available scales, and they have a direct link to physiological and ecological processes in vegetation cover (Title & Bemmels, 2018). Emberger's pluviothermic quotient and terrain roughness index combine highly correlated variables in mountainous areas (altitude and slope steepness, temperature and evapotranspiration). In our view, their use contributes to addressing the high collinearity of environmental variables that have coherent variability on the altitude gradient in mountains. In addition, as shown above, no sampling bias problems have been identified for ENVIREM A-model only. Accordingly, we used the set of ENVIREM variables to build the models of *Fritillaria latifolia* distribution (Electronic Supplement 1).

BA- and BAM-models of Fritillaria latifolia distribution

High values of AUCtest, CBItest and TSStest were obtained for the models (Table 2). These values indicated high predictive accuracy of the resulting models (good balance between model accuracy and complexity, and model sensitivity and specificity in discriminating occurrence data from random data).

As shown in Table 1, the main abiotic predictors in the A-model of *Fritillaria latifolia* distribution were embergerQ and TRI, which determine the location of optimal habitats on near-level and intermediately rugged slopes in humid and perhumid climate. These climatic and orographic parameters also contributed most to the BA-model (Table 2). Accordingly, the differences in areas of suitable and optimum habitats predicted by the A-model and BA-model were only 0.44% and 0.02% of the study area (1700 km^2 and 80 km^2), respectively (Table 3).

In terms of the percentage contribution to the BA-model, the distance to Protected Areas was the third important factor with optimal values of 0–1 km. This probably explains the increase in the species optimal habitats according to the BA-model (Table 3, Fig. 3a). The grazing factor, formalised through the distance to grasslands, contributed less to the model. *Fritillaria latifolia* populations could be found both within grasslands and 40 km away from grasslands (Table 2).

Table 2. Model performance and contribution of the main variables to the Maxent models of *Fritillaria latifolia* distribution in the Caucasus

Environmental variables	A-model		BA-model		BAM-model	
	PC, %	Optimal values	PC, %	Optimal values	PC, %	Optimal values
embergerQ	54.7	150–190	48.7	160–180	28.1	160–180
TRI	20.8	75–250	19.8	80–250	15.9	80–250
PETColdestQuarter, mm/month	14.0	7–14	8.7	5–14	2.6	5–14
path_PAs, km	–	–	14.7	0–1	5.3	0–1
path_landuse, km	–	–	1.5	0–40	0.3	0–20
Movement factor, km	–	–	–	–	44.5	0–15
AUCtest ± SD	0.95 ± 0.02		0.97 ± 0.01		0.97 ± 0.01	
CBItest	0.93		0.96		0.93	
TSStest	0.82		0.85		0.86	

Note: Predictor abbreviations: embergerQ – Emberger's pluviothermic quotient, TRI – terrain roughness index, PETColdestQuarter – mean monthly potential evapotranspiration of the coldest quarter, path_Pas – distance to Protected Areas, path_landuse – distance to grasslands. Model performance was assessed by AUCtest (area under the curve from validation datasets) values averaged over five replications, CBItest (continuous Boyce index from validation datasets), and TSStest (true skill statistics from validation datasets).

Table 3. Areas of suitable and optimal habitats of *Fritillaria latifolia* based on the Maxent models

Suitable areas, percentage of the study area			Optimal areas, percentage of the study area		
A-model	BA-model	BAM-model	A-model	BA-model	BAM-model
2.04	1.60	1.85	0.71	0.73	0.94

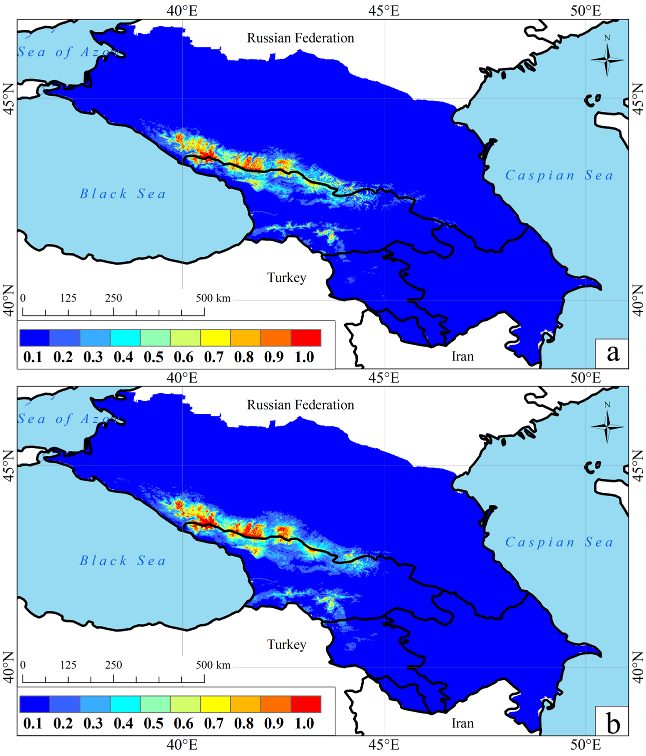

Fig. 3. Predictive maps of *Fritillaria latifolia* distribution in the Caucasus based on BA-model (a) and BAM-model (b).

According to the BAM-model, an important predictor of *Fritillaria latifolia* distribution was the movement factor (area accessibility) with a percentage contribution equal to the combined contribution of abiotic variables (Table 2). The distance of suitable areas to optimal habitats was 15 km, and the area of suitable and optimal areas increased by 0.25% and 0.21% of the study area (980 km^2 and 830 km^2), respectively, compared to the BA-model (Table 3, Fig. 3b).

Climatogenic dynamics of the Fritillaria latifolia range

Optimistic SSP1-2.6 models predicted a 1.6-fold decrease in the area of suitable and optimal habitats of *Fritillaria latifolia* from 2021 to 2100. The pessimistic (worst-case) SSP5-8.5 models predicted a 103-fold reduction in suitable habitat areas and a 122-fold reduction in optimal habitat areas (Table 4).

According to both scenarios, the reduction in habitat area was particularly pronounced in the western part of the current species range with the most humid (subtropical and oceanic) climate (Electronic Supplement 2: Fig. S2). The climatic models predicted less habitat reduction in the Central Caucasus with a humid continental climate. In the pessimistic scenario, only a small core range of *Fritillaria latifolia* would remain here by 2080 and 2100. The optimistic models predicted that the species core ranges would remain in the highlands of the Western and Central Caucasus (Electronic Supplement 2: Fig. S2).

Given the species dependence on the climatic parameters (Table 2), the predicted reduction in its range is explained by a decrease in embergerQ and annual precipitation with a simultaneous increase in mean annual temperature (Fig. 4). By 2060 and 2100, the worst-case SSP5-8.5 scenario predicted an increase in average annual temperature of 6°C and 9°C and a decrease in annual precipitation of 30 mm and 40 mm, respectively. The SSP5-8.5 scenario predicted only 7 km^2 (0.002% of the study area) of *Fritillaria latifolia* refugia by 2060 and no consistently optimal areas by 2080 (Electronic Supplement 2: Table S5).

Table 4. Habitat areas of *Fritillaria latifolia* according to the climatic models based on the optimistic (SSP1-2.6) and the worst-case (SSP5-8.5) socio-economic pathways during 2021–2100

Climatic models	SSP1-2.6				SSP5-8.5			
	2021–2040	2041–2060	2061–2080	2081–2100	2021–2040	2041–2060	2061–2080	2081–2100
Suitable areas, percentage of the study area	1.20	0.84	0.85	0.76	1.06	0.26	0.06	0.01
Optimal areas, percentage of the study area	0.37	0.22	0.27	0.23	0.31	0.05	0.01	0.002

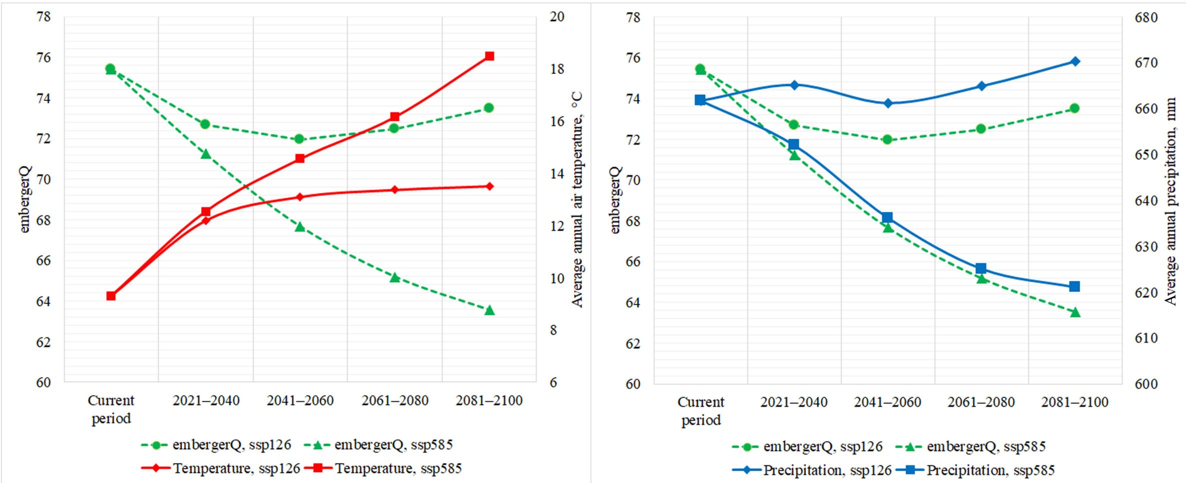

Fig. 4. Dynamics of embergerQ, average annual temperature and average annual precipitation in the Caucasus according to the climate change scenarios (socio-economic pathways) SSP1-2.6 and SSP5-8.5.

According to the optimistic SSP1-2.6 model, by 2100 the refugia area would be 172.4 km^2 (0.05% of the study area) (Electronic Supplement 2: Table S5), and three main refugia of *Fritillaria latifolia* will remain in the highlands of the Western and Central Caucasus (Fig. 5). The refugia will be partly located within Protected Areas.

Discussion

Previous studies covered various aspects of *Fritillaria latifolia* ecology, such as orographic and climatic requirements for habitats (Tania & Abramova, 2013; Yamalov et al., 2014; Batsatsashvili et al., 2017; Pshegusov et al., 2019), seasonal vegetation (Thazaplizheva & Chadaeva, 2012), the actual localisation of the species in the Caucasus (Zernov, 2006; Zernov & Onipchenko, 2011; Tania & Abramova, 2013; Pshegusov et al., 2019), its population biology (Thazaplizheva & Chadaeva, 2012; Tania & Abramova, 2013; Pshegusov et al., 2019). Although most of these surveys were carried out using field observations, our study can be seen in the context of previous investigations. We assessed the potential distribution of *Fritillaria latifolia* in relation to abiotic and anthropogenic factors, area accessibility and climate changes. This provided new insights into the importance of Protected Areas as the species refugia in the Caucasus.

Current distribution of Fritillaria latifolia

According to the A-, BA- and BAM-models, the optimal habitats of *Fritillaria latifolia* in the Caucasus were located on relatively gentle, wet slopes (Table 2), which is consistent with field observations (Tania & Abramova, 2013; Yamalov et al., 2014; Batsatsashvili et al., 2017; Pshegusov et al., 2019). The occurrence of this hydrophilic species was predicted mainly in areas with humid subtropical and oceanic climate, such as the Western Caucasus, Western and Central Transcaucasia, and the western ridges of the Lesser Caucasus (Fig. 2, Fig. 3). The lack of suitable sites in the Colchis Lowland with a humid climate was probably due to the species preference for highlands (Tania & Abramova, 2013; Yamalov et al., 2014; Pshegusov et al., 2019; Batsatsashvili et al., 2017).

The optimal habitats of *Fritillaria latifolia* predicted within 0–1 km of the Protected Areas (Table 2). Actually, the main reported habitats of this species in Abkhazia were concentrated within the Ritsa Relict National Park (Tania & Abramova, 2013), while species populations in northwestern Armenia were localised in the Lake Arpi National Park (Batsatsashvili et al., 2017). In the North Caucasus, *Fritillaria latifolia* was also mainly found within a network of Protected Areas covering most of the highlands. There are the Sochi National Park and Teberda National Park (Zernov, 2006; Zernov & Onipchenko, 2011), Prielbrusye National Park

(Pshegusov et al., 2019), Erzi State Nature Reserve, and Argun State Museum-Reserve (Red Data Book of the Chechen Republic, 2020). Suitable species habitats in northern Georgia, particularly in Racha-Lechkhumi Region, Svaneti Region and Mtiuleti Region (Batsatsashvili et al., 2017), were mostly located outside Protected Areas. This probably explains the considerable reduction in the species optimal habitats in this area according to the BA-model (Fig. 3a), although in the total area of optimal habitats it is increased based on the A-model (Table 3).

The low contribution of the grazing factor in the tested models (Table 2) may be associated with the resistance of *Fritillaria latifolia* to trampling by animals. This resistance is probably related to the protected underground bulbs (Yamalov et al., 2014) and the early vegetation season before cattle moving to summer pastures (Taniya & Abramova, 2013). Moderate grazing may also positively affect the species population parameters (bulb and seed reproduction, population density) by reducing vegetation coverage and the level of interspecific competition in the plant community (Thazaplizheva & Chadaeva, 2012; Pshegusov et al., 2019).

The species mobility (area accessibility) was 15 km to optimal habitats (Table 2). Ecologically, the area accessibility (the vastness of suitable subalpine grasslands) explains the species dispersal capacity on a 15-km scale. Biologically, the species distribution ability is related to seed spreading by wind and water. Despite the abundance of geographical barriers in the mountains, this species mobility resulted in an increase in the area of suitable and optimal habitats of *Fritillaria latifolia* in the BAM-model.

Future species distribution against the background of climate changes*. *Climatic refugia

Fritillaria latifolia belongs to the psychrophytes, which prefer cold and wet habitats (Red Data Book of the Chechen Republic, 2020). Therefore, an increase in climate aridity (Fig. 4) is considered a major limiting factor for the species, which is consistent with our results. The Central Caucasus, with its humid continental climate, is probably more resistant to climate changes than the Western Caucasus, Western and Central Transcaucasia, and the western ridges of the Lesser Caucasus with the most humid climate. The main future core ranges of the species were predicted in the Central Caucasus under both worst-case and optimistic socio-economic pathways (Electronic Supplement 2: Fig. S2).

Species refugia (areas with a consistently high probability of *Fritillaria latifolia* occurrence despite climate change) by 2100 under the SSP1-2.6 scenario were projected in the highlands of the Western and Central Caucasus (Fig. 5). The Western Caucasus refugia are partly located within the Caucasus State Nature Reserve and Teberda National Park. The Central Caucasus refugia are located within the Prielbrusye National Park. These areas should be prioritised for the conservation of *Fritillaria latifolia* populations in the Caucasus.

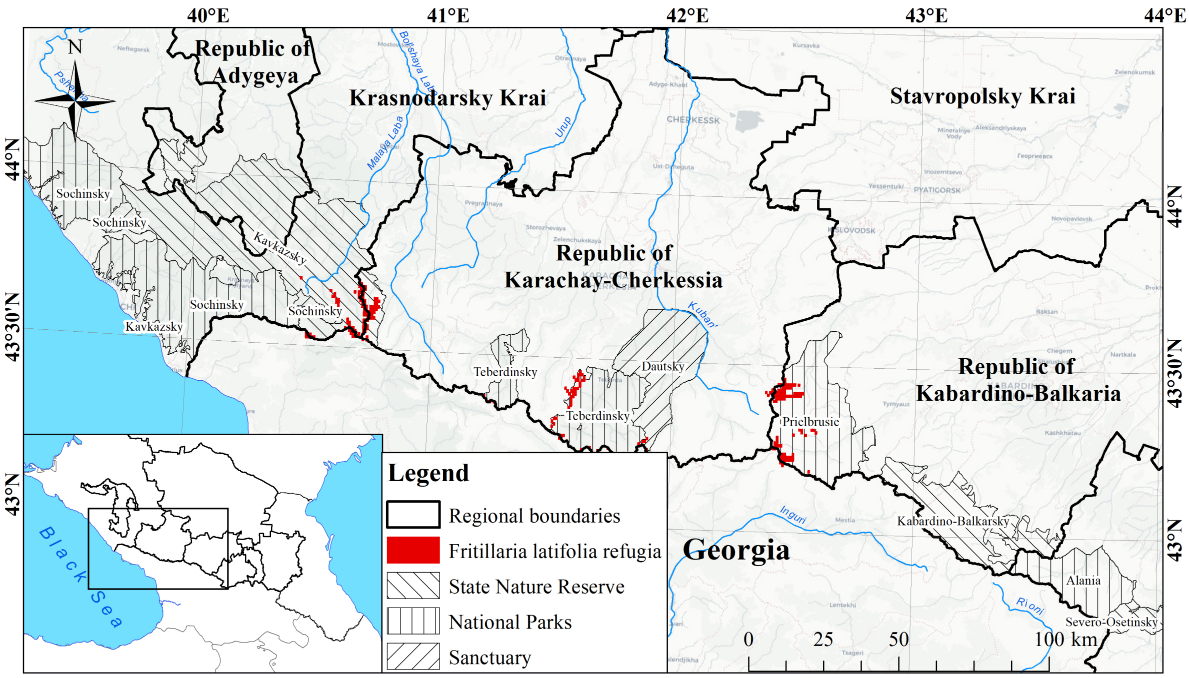

Fig. 5. The predicted location of *Fritillaria latifolia* refugia in the Caucasus by 2100 according to the optimistic SSP1-2.6 scenario.

Conclusions

For the first time using SDM, the influence of abiotic, anthropogenic factors and area accessibility on the current and future distribution of *Fritillaria latifolia* in the Caucasus was studied, and the territories prioritised for the species conservation were identified. ENVIREM and WorldClim2+GMTED2010 models of the *Fritillaria latifolia* ecological niche had good performance indicators and were largely consistent with the ecological and biological characteristics of the species. However, the ENVIREM model was more in line with the actual localisation of the species and had no sampling bias problem. Accordingly, we used the ENVIREM set of variables to construct BAM-models.

The main abiotic predictors of *Fritillaria latifolia* distribution in the Caucasus were Emberger's pluviothermic quotient and terrain roughness index. The importance (percentage contribution) of these predictors was also high in the BA-model, which considered distances to Protected Areas and grasslands, and in the BAM-model, which included an area accessibility factor. Optimal *Fritillaria latifolia* habitats occurred on nearly level to intermediately rugged mountain slopes in humid and perhumid climates no more than 0–1 km to the Protected Areas, and the area accessibility of the species was about 15 km. At present the potential area of optimal habitats for the species is 3680 km^2 or 0.94% of the study area. Optimistic models predicted a 1.6-fold decrease in the area of optimal *Fritillaria latifolia* habitats by 2100, while pessimistic models predicted a 122-fold decrease, respectively.

The results also confirmed our hypothesis that distance to Protected Areas is one of the key factors in the current and future distribution of *Fritillaria latifolia*. Species core ranges are localised in the Western and Central Caucasus, Western and Central Transcaucasia, and the northwestern ridges of the Lesser Caucasus within a network of Protected Areas covering most of the highlands. Given the extensive tourism development in the Caucasus, strict monitoring of the environmental regime in these territories is required. According to the optimistic models, refugia with a consistently high probability of *Fritillaria latifolia* occurrence by 2080–2100 would remain in the highlands of the Western and Central Caucasus, including the Caucasus State Nature Reserve and Teberda National Park. These Protected Areas are a priority for the species conservation in the Caucasus, and their identification constitutes the practical importance of the study. Future studies should be aimed at monitoring of the condition of *Fritillaria latifolia* populations, searching for new species localities in the predicted areas, as well as adjusting forecasts to new climate change scenarios.

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Supporting Information

Additional data for the paper by Phegusov & Chadaeva (2024), with four Electronic Supplements, may be found in the **Supporting Information**.

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МОДЕЛИРОВАНИЕ ПРОСТРАНСТВЕННОГО РАСПРОСТРАНЕНИЯ КАВКАЗСКОГО ЭНДЕМИКА *FRITILLARIA LATIFOLIA* НА ФОНЕ КЛИМАТИЧЕСКИХ ИЗМЕНЕНИЙ

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Современные изменения климата, деградация местообитаний, перевыпас скота, сбор побегов и луковиц представляют серьезную угрозу для редкого кавказского эндемика *Fritillaria latifolia*. Изучение лимитирующих факторов и динамики ареала вида в связи с изменением климата и роли особо охраняемых природных территорий в распространении необходимо для разработки эффективной системы сохранения вида в настоящее время и в будущем. Целями данного исследования были: (1) определить наиболее подходящий набор абиотических предикторов для моделирования локализации *Fritillaria latifolia*, (2) формализовать абиотические и антропогенные факторы в моделях пространственного распределения, (3) спрогнозировать возможные изменения ареала вида на фоне климатических изменений, (4) выявить рефугиумы с постоянно высокой вероятностью обнаружения вида, несмотря на климатические изменения. Мы использовали Maxent для моделирования современного и климатогенного ареалов *Fritillaria latifolia* с учетом абиотических переменных и антропогенных предикторов (расстояние до особо охраняемых природных территорий и пастбищ). Расстояния до антропогенной инфраструктуры рассчитывались с помощью показателя Path Distance, учитывающего горизонтальное расстояние по прямой, расстояние по поверхности и вертикальный фактор. Доступность территории (movement factor) формализовали через расстояние от оптимальных участков (с порогом пригодности местообитаний 0.8), на которых вероятность появления вида была выше 0.5. Наиболее важными абиотическими переменными в распределении видов были плювиотермический коэффициент Эмбергера, оптимальные значения которого соответствуют влажному и пергумидному климату, и индекс шероховатости рельефа с оптимальными значениями, варьирующими от почти ровных (81–116) до средне крутых (162–239) склонов. Расстояние до особо охраняемых природных территорий (0–1 км) было третьим значимым предиктором современного распространения *Fritillaria latifolia*, в то время как расстояние до пастбищ не внесло значительного вклада в модель. Расстояние пригодных территорий от оптимальных местообитаний (доступность территории) составило 15 км. Центры современного ареала вида локализованы на Западном и Центральном Кавказе, в Западном и Центральном Закавказье и на северо-западных хребтах Малого Кавказа в пределах сети особо охраняемых природных территорий, охватывающей большую часть высокогорий. Оптимистичный климатический сценарий SSP1-2.6 прогнозировал с 2021 по 2100 гг. уменьшение площади оптимальных для вида местообитаний в 1.6 раза, пессимистичный сценарий SSP5-8.5 – в 122 раза. Согласно климатическим моделям SSP1-2.6, к 2100 г. площадь рефугиумов составит 172.4 км^2 в высокогорных районах западной и центральной частей Большого Кавказа, включая территории Кавказского государственного природного биосферного заповедника и Тебердинского национального парка. Эти территории должны стать приоритетными для сохранения природных популяций *Fritillaria latifolia*.

Ключевые слова: Maxent, климатические сценарии, концепция Biotic-Abiotic-Movement, особо охраняемая природная территория, рефугиумы