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Evaluating the performance of stochastic distribution models for European beech at low-elevation xeric limits

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Abstract—Projection for future climate conditions is an increasingly popular application of distribution modeling. However, good performance of a model under current climate does not guarantee similar performance under future climate, particularly where prediction is outside the range of environmental conditions on which the original model was set up. The objective of this study was to model the habitat suitability for beech forests during three terms (2025, 2050, and 2100) in the 21st century in Hungary using species distribution models (SDMs).

Six out of the eight methods were unsuited for predicting climate change effects on the future distribution of beech. This underlines that predictions for conservation and management issues should be based on multimodel assessments. Spatial inconsistency appeared mainly in regions, where beech is situated close to its distributional range limit (xeric limit). This suggests that the basic theoretical assumption of species distribution models may not hold at the trailing edge.

Key-words: beech, Hungary, climate change, xeric limit, Ellenberg's climate quotient

1. Introduction

Fagus sylvatica L. is one of the dominant tree species in central European temperate forests with high physiological tolerance and competitiveness

(*Ellenberg et al.*, 1992). Drought sensitivity is assumed to be a key factor limiting growth and distribution of beech close to its lower distributional limit (xeric limit) (*Mátyás et al.*, 2009) in southern and south-eastern Europe (*Backes* and *Leuschner*, 2000).

Several studies suggested a decline in beech regeneration (*Rennenberg et al.*, 2004*; Penuelas et al.*, 2007) or extensive beech dieback (*Berki et al.*, 2009*; Czúcz et al.,* 2010*; Kramer et al.*, 2010*; Lindner et al.*, 2010) under increasingly adverse climatic conditions (*Gálos et al.,* 2007). Consequently, modeling the vitality response of beech to predicted changes of climate is a critical issue (*Franke* and *Köstner,* 2007; *Mátyás,* 2009).

For management and conservation issues (*Hannah et al.*, 2002), species distribution models (SDMs) have been extensively used. SDMs derive the species' environmental envelope from the observed conditions at the localities where it is currently known to occur. They can be evaluated for their ability to predict current distributions, but it is not tested whether models that are successful in predicting current distributions are equally powerful in predicting distributions under different climates. Studies comparing modeling algorithms are now common (*Segurado* and *Araujo*, 2004; *Elith et al.*, 2006; *Tsoar et al.*, 2007), but *Thuiller et al.* (2004) have pointed out the problem of strong variation between SDM predictions for future distributions. SDMs are 'statistical' models without specific ecological knowledge, they do not describe 'cause and effect' between model parameters and response (*Guisan* and *Zimmermann*, 2000; *Pearson* and *Dawson,* 2003; *Kearney* and *Porter,* 2004).

In this study, we compared and evaluated the results of eight SDMs for beech (*Fagus sylvatica* L.). Beech is considered a climate sensitive species, which is uniquely vulnerable in south-eastern Europe and, therefore, well suited for modeling. Another advantage is that compared to other tree species in Hungary, its populations are in a relatively undisturbed condition as they were rarely regenerated artificially, and the species' reproductive material was not subject to commercial relocations (*Mátyás et al.*, 2010). Modeling focused on its distribution in Hungary, since here the retreat of the species is imminent. This ecologically and climatically specific area has been largely neglected by European studies (*Jump et al.*, 2009; *Lindner et al.*, 2010; *Mátyás*, 2010).

We address the following questions:

1. Which SDM can best describe the present distribution of beech in Hungary?
2. What are the projections for the potential future distribution of beech using SDMs?

To answer the research questions we modeled the current and potential future distribution of beech in Hungary using SDMs, and compared the performance of the different methods.

2. *Material and methods*

There are many environmental niche modeling packages available; for example, MaxEnt (*Phillips et al.,* 2006), GARP (*Stockwell* and *Peters,* 1999), ModEco (*Guo* and *Liu,* 2010), BIOMOD (*Thuiller et al.,* 2009), and Openmodeller (*Munoz et al.,* 2009).

The primary reason to choose ModEco (*Guo* and *Liu*, 2010) was that it contains models for dealing with presence-only and presence/absence data. Additional advantages of ModEco are tools for feature analysis, and model performance evaluation, as well as an accuracy assessment tool. As ModEco incorporates several modeling methods, the training, analyses, and assessments can be carried out on the same platform supporting consistent comparisons.

A disadvantage of the platform is that a trained model needs new environmental surfaces for climate change predictions, which slows down the process (*Fig. 1*).

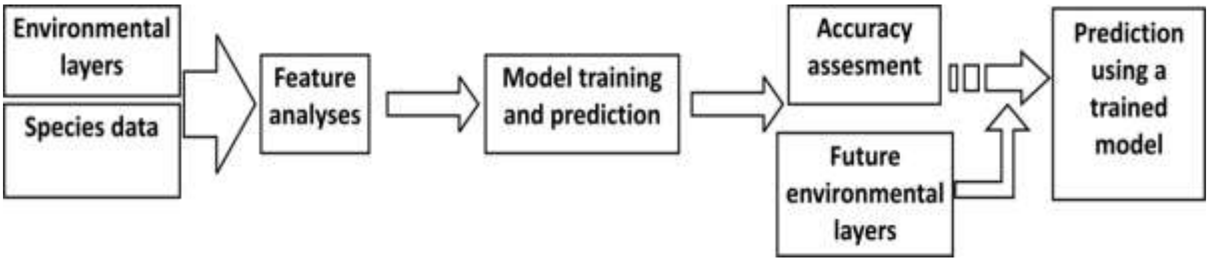

Fig. 1. General workflow of the modeling process.

2.1. *Environmental variables*

96 different environmental predictor surface maps were used as input, all with a spatial resolution of 0.0083 (appr. 1×1 km). Environmental variables were selected according to their relevance to tree survival and growth. Climatic variables were taken as surrogates for variables having more direct physiological roles in limiting the ability of plants to survive.

Although the main environmental data used were climate data, soil and geomorphological factors were also included. Soil texture and moisture regimes are indirect variables considered as surrogates for soil type, with direct impacts on nutrient and water availability for plant growth (*Austin* and *Smith, 1989*). Geomorphological factors were used as surrogates for sites in non-zonal positions.

2.2. *Soil data*

Three soil variables (soil texture, soil moisture regime, and genetic soil type – *AGROTOPO,* 2002) and three topographical factors (mean altitude, slope, and dominant orientation) were applied.

2.3. Climatic data

The dataset included monthly maximum, minimum, and mean temperatures, and monthly precipitation (48 variables in total); and a set of 19 climate-derived variables obtained from the "worldclim" database (*Hijmans et al.,* 2005).

2.4. Bioclimatic indices

12 bioclimatic factors (23 variables in total) computed from minimum and maximum monthly averaged temperatures and monthly precipitations were used (*Table 1.*). These bioclimatic predictors are: thermicity index (*Rivas-Martínez,* 1996), ombrothermic indices (*Rivas-Martínez,* 1990), de Martonne aridity index (*de Martonne,* 1942), Ellenberg quotients (*Ellenberg,* 1986; *Ellenberg,* 1996), monthly potential evapotranspiration (*Thornthwaite,* 1948), Box moisture index of precipitation/evapotranspiration (*Box,* 1981), continentality indices (*Gorczinski,* 1920; *Emberger,* 1930), forest aridity index (*Führer,* 2010; *Führer et al.,* 2011), and beech tolerance index (*Berki et. al,* 2009).

2.5. Species data

Species data for the habitat modeling were derived from the Hungarian Forest Inventory database provided by the Central Agricultural Office. The database incorporates every forest subcompartment containing beech. (A tree species is registered in a forest subcompartment, if the mixture ratio of the given tree species exceeds the 5% threshold limit.) These subcompartments were considered in the model as "true - presence" observation points (in total 11,332 subcompartments). For the presence-absence methods, "pseudo-absence" points were created randomly throughout the country with a buffer zone of 1000 m around the presence points. The size of the buffer zone was determined according to the spatial resolution of the environmental layers. The amount of pseudo-absence points was equal to the number of the presence points. As the environmental data were given in a 1×1 km grid, distribution maps were also converted to a raster format with the same resolution.

At this point it should be emphasized, that forests in Hungary are managed forest, and therefore, the presence/absence of beech is human influenced.

2.6. Future climate

The downscaled "Climate Limited Area Modeling" (CLM) regional climate model was applied for simulation of future vitality condition of beech using the A1B scenario (mean of two runs) with a grid size of 0.2 for the period 2000–2100 (*Keuler et al.,* 2009). Downscaling to regional level requires some assumptions, e.g., GCM biases are small at boundary locations or regional dynamics are non-linear and add uncertainty or biases or both due to detailed parameterizations (*Wu et al.*, 2005)).

CLM model data were corrected using the delta change approach (*Hay et al.*, 2000), based on the mean deviation of the observed and simulated variables between 1960 and 2000 for each grid box. Corrected long-term averages from monthly air temperature and precipitation were derived by kriging interpolation considering the elevation for the periods 2011–2040, 2036–2065, and 2066–2095.

Table 1. Bioclimatic variables

Bioclimatic predictors	Formula or reference
Beech tolerance index (BTI)	$= (0.2P_3+0.5P_4+P_5+P_6+P_7+0.8P_8) / T_{6–8}$
Box moisture index (BMI)	$= \mathrm{P/PET}$
Continentality index (CONTINENTY)	$= \mathrm{T_{max}–T_{min}}$
De Martonne aridity index (DMI)	$= [(P/T+10)+12p/(t+10)]/2$
Ellenberg index (EQ)	$= (T_{max}/P)1000$
Forest Aridity Index (FAI)	$= 100(\mathrm{T}_{7–8})/(\mathrm{P}_{5–7}+\mathrm{P}_{7–8})$
Gorczinski’s continentality index (GCT)	$= ((1.7A)/(\sin L)) – 20.4$
Modified Ellenberg index (EQm)	$= (T_{max}/P_{veg})\ 1000$
Ombrothermic index (Io)	$= (P_p/T_p)10$
Ombrothermic index of the summer quarter (Iosq)	$= (\mathrm{P}_{6–8}/\mathrm{T}_{6–8})/10$
Thermicity index (It)	$= (T + m + M)10$
Thornthwaite’s formula (PET)	$= 16N_m\left(\frac{10\bar{T}_i}{I}\right)^a, \quad I = \sum i_m = \sum\left(\frac{\bar{T}_i}{5}\right)^{1.5}$ $\mathrm{a} = 6.7*10^{–7}*I^3 – 7.7*10^{–5}*I^2 + 1.8*10^{–2}*I + 0.49$

T_{max}: mean temperature of the hottest month [°C]
T_{min}: mean temperature of the coldest month [°C]
P: annual precipitation [mm]
T: mean annual temperature [°C]
P_i: precipitation sum of the given month [mm]
P_{ii}: precipitation sum of the given months [mm]
T_{ii}: mean temperature of the given months [°C]
p: precipitation of the driest month [mm]
t: mean temperature of the driest month [°C]
PET: annual accumulated potential evapotranspiration calculated by the Thornthwaite equation [mm]
A: mean annual air temperature amplitude [°C]
L: latitude of the site [absolute value]
P_{veg}: precipitation sum of the vegetation period [mm]
P_p: Yearly Positive Precipitation [mm] (total average precipitation of those months whose average temperature is higher than 0°C)
T_p: Yearly Positive Temperature [°C] (sum of the monthly average temperature of those months whose average temperature is higher than 0°C)
m: average minimum temperature of the coldest month of the year [°C]
M: average maximum temperature of the coldest month of the year [°C]
N_m: monthly adjustment factor related to hours of daylight [–]
I: heat index for the year [–]

2.7. Modeling algorithms

We evaluated and compared the following eight methods: “presence-only” methods such as BioClim (*Nix*, 1986; *Busby*, 1991), Domain (*Carpenter et al.*, 1993), and one-class support vector machine (SVM) (*Vapnik*, 1995); „presence-absence” classification methods such as generalized linear model (GLM), artificial neural network using back-propagation algorithm (BP-ANN, *Maravelias et al.*, 2003), maximum likelihood classification (*Richards* and *Jia*, 1999), maximum entropy (MAXENT, *Phillips et al.*, 2006), and classification tree (CTree, *Breiman et al.*, 1984).

2.8. Accuracy assessment

Cross-validation accuracy, area under the receiver operator curve (AUC), receiver operating characteristic (ROC), error matrix and maximum kappa values were used to assess the accuracy of presence/absence-based models (*Wiley et al.*, 2003; *Elith et al.*, 2006). For presence-only models, the above mentioned measures are not applicable, therefore, the true positive rate (TPR) vs. the factional prediction area (FPA) as a proxy for true positive rate vs. false positive rate, and the area under TPR vs. FPA were used (*Guo et al.*, 2005; *Phillips et al.*, 2006).

2.9. Factor analyses

Factor importance analysis was carried out to examine the contributions of different environmental factors (with-only and without a specific environmental factor) to the overall classification accuracy of SDMs, based on the kappa values (*Forman*, 2003). This importance analysis is designed to evaluate the change of classification accuracy of the model (*Phillips*, 2006).

Some models (i.e., Maximum likelihood, Domain) are sensitive to the number of the predictors therefore, the reduction of environmental factors was essential in some cases. Redundant environmental layers were identified via pairwise correlations. Variables with a correlation higher than 0.8 were considered redundant. Between any two redundant variables, those related to climate extremes were preferred.

3. Results

3.1. Performance of presence-only methods

3.1.1. Potential current distribution

Presence-only methods showed marked variation in modeling success. Although *TPR* was very similar, the predicted area varied a lot among the models. Using the accuracy measures of presence-only data, the one-class SVM performed better (*TPR*: 0.794) for predicting current distribution than BioClim and Domain, but the predicted area was also greater. If we also consider the specifically generated pseudo-absence points during the assessment and penalize the false negative predictions by using the *ROC* score (true positive rate vs. true negative rate), Domain showed the best performance (*Table 2*).

Table 2. Parameters and statistical performance of presence-only methods for predicting potential current distribution of beech in Hungary

Models	**Parameters**	**Number of layers**	**True positive rate (TPR)**	**Predicted area**	***TPR* vs. predicted area**	***ROC***
BioClim	percentile: 96%	88	0.708	1.004	0.8924	0.898
Domain	similarity: 0.995	64	0.765	0.987	0.7264	**0.933**
One-class SVM	Nu:0.064 Gamma: 27.6	65	**0.794**	**1.318**	**0.9046**	0.909

There were significant regional differences between the modeled potential and the actual distribution. While BioClim, the simplest climate envelope model, predicted in total almost the observed suitable area, there still were regional biases. BioClim notably overpredicted in the Southwest (Zala county, south from Szombathely) and Northeast (Cserhát, north from the Mátra Mountains), but also a smaller patch north form the lake Balaton (Balaton-felvidék) was predicted as suitable for beech. BioClim systematically excluded the marginal sites (Mátra, Bükk, Zemplén, Kőszeg, Sopron, and Börzsöny Mountains, Mura Valley) and also failed in the Őrség and Aggtelek Karst. One-class SVM performed regionally similarly to BioClim, only the magnitude of the overprediction was greater. Domain predicted very precisely the current distribution of beech, almost all observation point were enclosed in the potential area (*Fig. 2–3*).

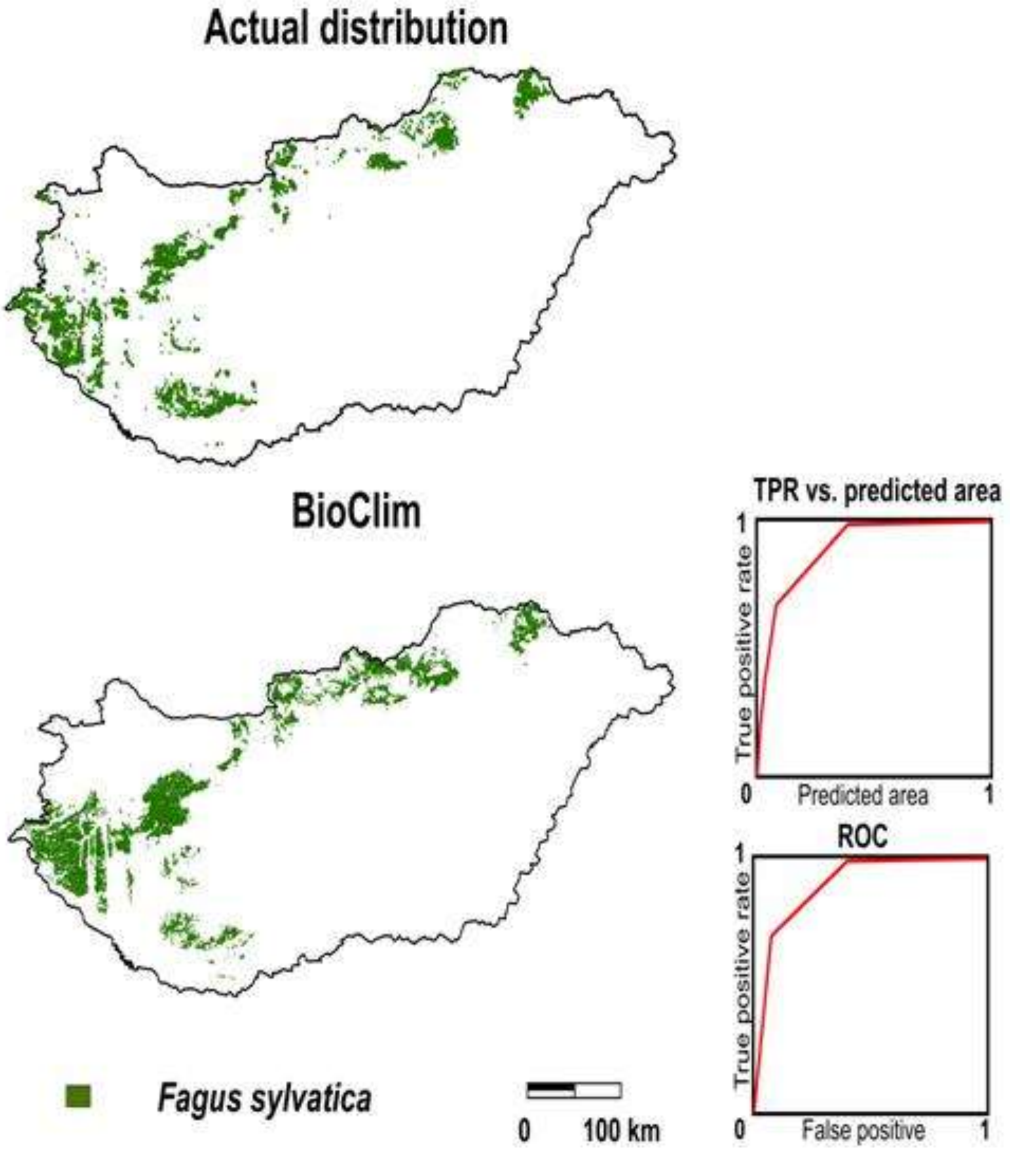

Fig. 2. Actual distribution and potential current distribution modeled by BioClim and the related operating curves. Green color represents observed localities of beech in the first map and areas modeled as suitable in the potential maps.

3.1.2. Future distribution

While the presence-only methods performed fairly well describing the current distribution of beech, all three methods were unsuited for predicting climate change impacts. BioClim and Domain removed all beech even for the near future (2011–2040), while one-class SVM predicted potential occurrence only for regions under sub-Mediterranean and subcontinental influences.

Prediction with Domain and BioClim was only possible when the number of the environmental predictors was strongly reduced.

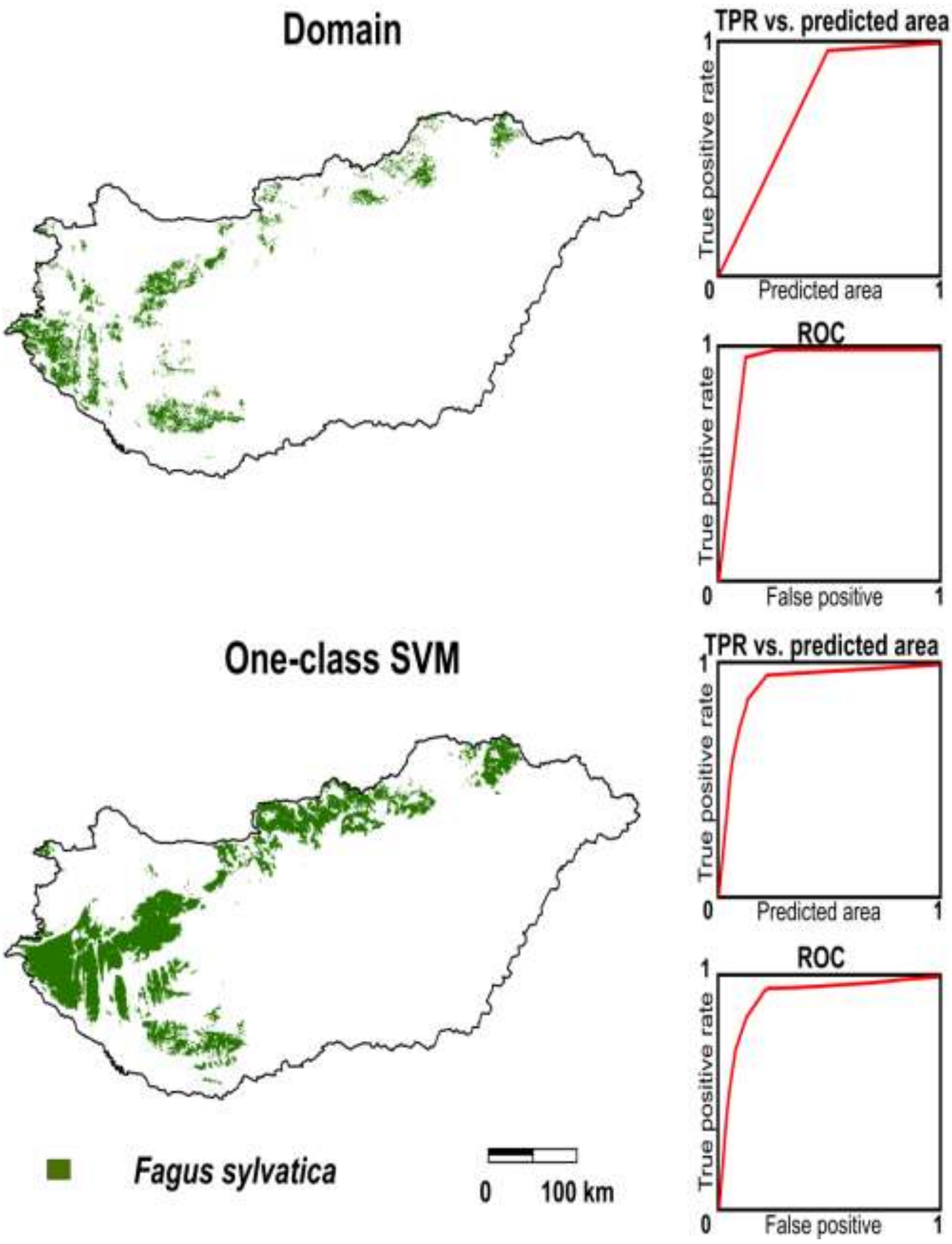

Fig. 3. Potential current distribution modeled by Domain and one-class SVM and the related operating curves. Green color represents areas modeled as suitable for beech.

3.2. Performance of presence/absence classification methods

3.2.1. Potential current distribution

Presence/absence classification methods outperformed presence-only models, the TPR and also the kappa score was higher in all cases (*Table 3*).

Table 3. Parameters and statistical performance of presence/absence models

Model	**Parameters**	**True positive rate (*TPR*)**	**Predicted area**	**Kappa index**
Artificial neural network with backpropagation (BP-ANN)	Momentum: 0.3 Learning rate: 0.1	0.9425	1.2096	**0.8336**
Classification tree (CTree)	Number of trails: 10 Window size: 20 Pruning confidence level: 0.25	0.9493	1.3196	**0.8431**
General linear model (GLM)	Link function type: LOGIT Threshold: 0.426	0.9592	1.6237	0.8174
Maximum entropy (MAXENT)	Omission rate: 0.05	0.9395	1.4362	0.8145
Maximum likelihood (MLC)	No parameter required	0.9415	1.5205	0.8076

MAXENT, MLC, and GLM performed relatively poorly, only GLM had high TPR (0.959), which was due to its strong overprediction of the species area (1.623). CTree and BP-ANN methods performed significantly better than the other models. The high *TPR*, the smaller predicted potential area, and the high kappa score indicated that these models are able to capture non-linear responses and can handle interactions between the variables.

Visually, the CTree model created a more dispersed potential area, while the BP-ANN model produced a less fragmented distribution with more distinct boundaries (*Fig. 4*).

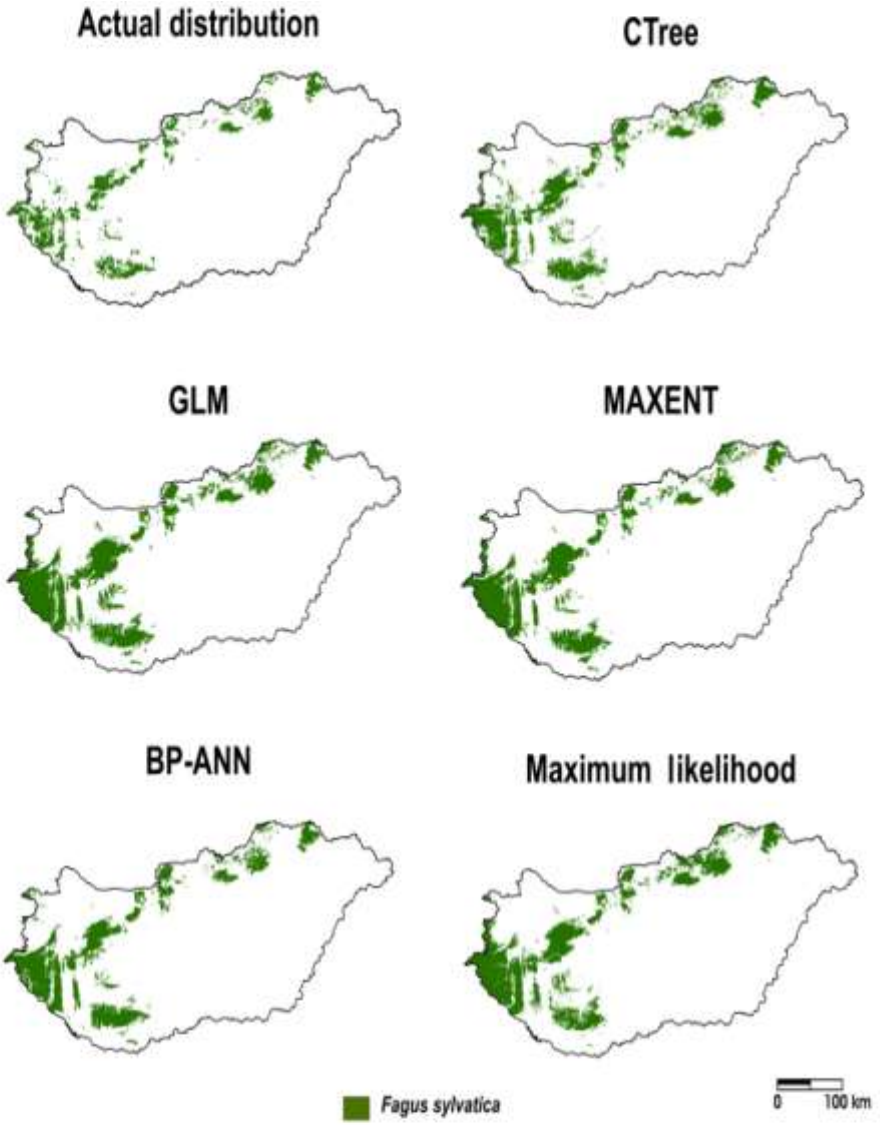

Fig. 4. Actual distribution and potential current distribution modeled by BP-ANN, CTree, GLM, MAXENT, and Maximum likelihood methods. Green color represents observed localities of beech in the top left map and areas modeled as suitable in the potential maps.

3.2.2. Future distribution

The Maximum likelihood method predicted complete extinction of beech for the whole country for the period 2011–2040. GLM overpredicted the distribution of beech in the near future, and marked regions as potential area, which are already out of the current distribution range. MAXENT predicted a considerable dieback even for the near future removing more than 91.6% of the current stands.

BP-ANN predicted almost no reduction in the potential area for the period 2011–2040 and a very slight (8.0%) for 2036–2065. A considerable shrinkage (56.8%) of the potential area was predicted only to the end of this century, which results that 45.2% of the current stands will be out of the potential area. Regionally, the most serious decrease was predicted for the sub-Mediterranean region in the Southwest.

CTree predicted a more pronounced shrinkage in all regions of Hungary by losing 37.3%, 67.5%, and 74.7%, respectively (*Fig. 5*).

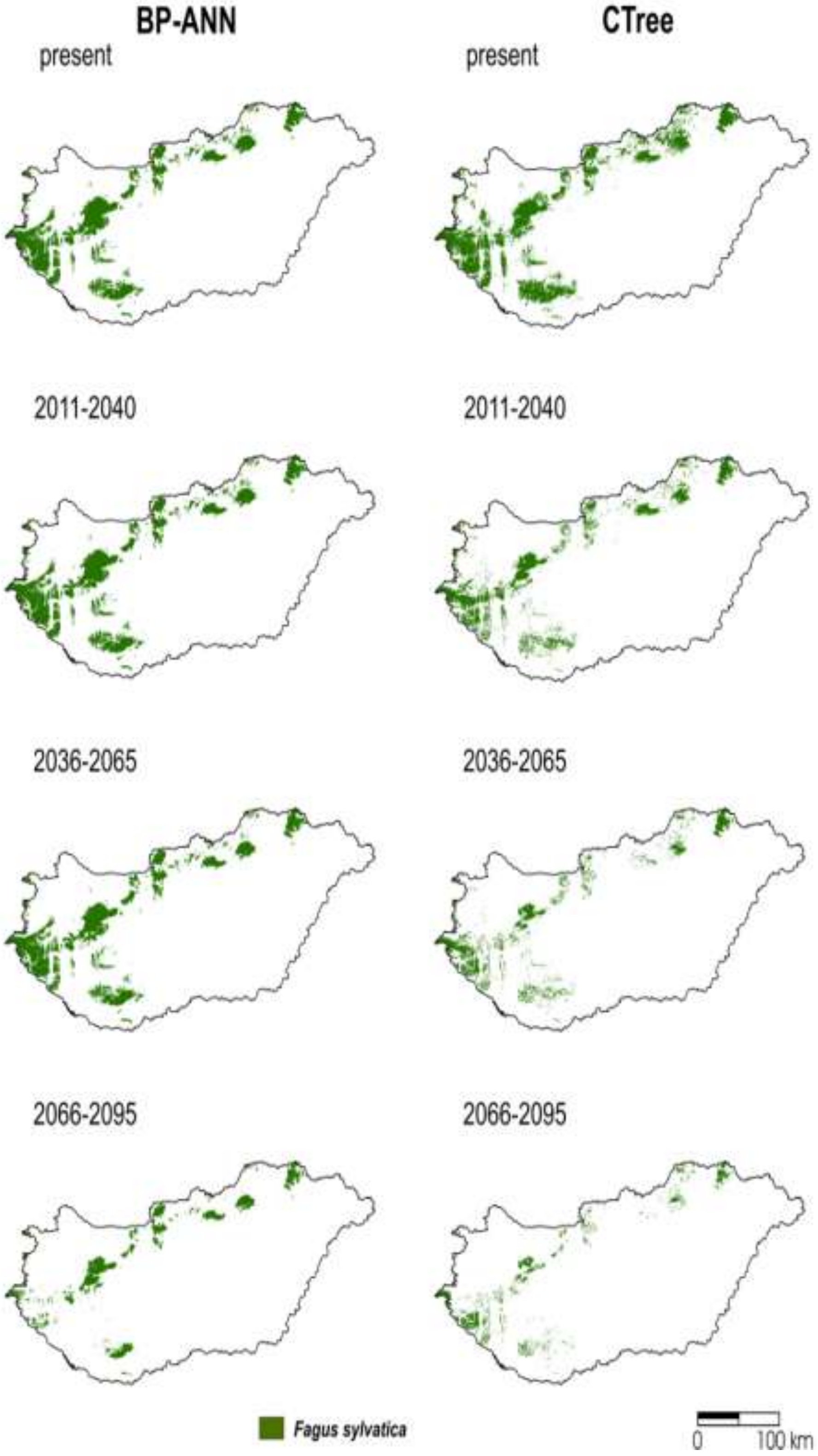

Fig. 5. Potential distribution modeled by BP-ANN and CTree for present and future conditions (2011–2040, 2036–2065, and 2066–2095, respectively). Green color represents areas modeled as suitable for beech during the given periods.

3.3. Factor importance analysis

Factor importance analysis is algorithm-sensitive, but among the environmental variables, the maximum temperature of May and the modified Ellenberg quotient appeared repeatedly as the most influential predictor. In addition, maximum temperatures of summer and precipitation of late summer played a significant role in determining the presence of beech (*Table 4*).

A climate quotient to characterize the humidity conditions of beech and oak forests was first suggested by *Ellenberg* (1986). He defined the climate quotient *EQ* as the quotient of the mean air temperature of the long-term hottest month per year and the annual precipitation sum. Later this quotient was changed to include a definition of the forest's growing period *(EQm),* taking into account only the precipitation of the growing season (*Ellenberg, 1996*). This climate quotient has been successfully applied to separate areas dominated by beech from areas of boreal or thermophilic species (*Schlüter, 1968; Hofmann, 1968; Jensen et al., 2004; Czúcz et al., 2010*). *EQ* has been also used to evaluate sites of mixed beech-oak stands for studies of carbon and water relations (*Franke* and *Köstner, 2007*).

Table 4. The overall classification accuracy of the models and the most predictive five factors with their related kappa values resulting from the factor importance analyses. The repeatedly occurring predictors are in bold

Rank	Models							
	BioClim		**One-Class SVM**		**CTree**		**GLM**	
	Predictor	**kappa**	**Predictor**	**kappa**	**Predictor**	**kappa**	**Predictor**	**kappa**
	overall	0.611	overall	0.788	overall	0.843	overall	0.817
1.	**EQm**	0.570	**EQm**	0.533	**Tmax_05**	0.717	**Tmax_05**	0.708
2.	**Tmax_05**	0.565	Prec_09	0.511	Tmax_06	0.707	Tmax_06	0.697
3.	BMI	0.555	**Tmax_05**	0.491	Tmax_08	0.704	Tmax_07	0.673
4.	Prec_09	0.544	Tmax_08	0.544	Tmax_04	0.704	**EQm**	0.670
5.	IO	0.534	Prec_08	0.451	**EQm**	0.673	Tmean_05	0.664

4. Discussion

Overall, the BP-ANN method showed the highest model performance, whereas similarity- and ordination-based models (DOMAIN, BioClim, one-class SVM) showed the lowest performances by predicting the potential future distribution of beech. While some authors (e.g., *Mastrorillo et al.,* 1997; *Pearson et al.,* 2002) also consider BP-ANN to be advantageous to model species occurrences, these observations are not supported by other studies, where BP-ANN showed overall performances comparable to GLM (*Manel et al.,* 1999). Other studies also showed that similarity and ordination-based methods perform less well than advanced techniques, namely CTree and BP-ANN (*Elith* and *Burgman,* 2002). Since these studies did not always use the same parameterization, they are, however, not fully comparable.

4.1. Actual and potential current distribution

BioClim treats the environmental data values at the locations of species occurrence as multiple one-tailed percentile distributions. It creates hyperboxes to include a given percentile for each variable so that, for example, the fifth percentile is treated the same as the 95th percentile. This results in an approach in which locations with extreme conditions (wettest – driest, hottest – coldest, etc.) are considered as outliers. This is the reason, why BioClim obviously failed at the top of the mountains in the Northwest (coldest sites of Börzsöny, Mátra, Bükk, and Zemplén Mountains) and at low elevation sites in Zala (Mura Valley).

Domain is a similarity based model, which uses the Gower distance method to classify the suitability of any new sites. The more variables are incorporated, the more accurate is the similarity assessment of a new site. The calculation was very time consuming, but resulted in a very precise prediction with a high accuracy rate.

BioClim uses only hyperboxes to contain the presence data. Thus this model is often unsuitable for other forms of data that have irregular distributions in feature space. Therefore, one-class SVM was also applied. One-class SVMs seek to find an optimal hypersphere which contains all or most of the training points, at the same time tightly constraining the presence data in feature space. Originally, SVMs are designed for 2-class problems (separating two types of data) and optimized for working with low number of predictors. The relatively high number of the environmental variables produced a very complex distribution pattern which resulted in greater overprediction.

Although CTree has clear advantages over classic climate envelope methods, certain disadvantages emerged. CTree appeared to be very sensitive to the number of predictors. Even small changes produced highly divergent results. The dispersed potential map of CTree could be a sign of overfitting, which means, that the model is too specific (unbalance of specificity and sensitivity).

Except Domain, all models predicted larger potential area than the current distribution. The systematic overprediction of the models might be explained mainly by the following factors:

Human interaction: After the post-glacial recolonization, a general reduction of the distribution of tree species occurred as a result of deforestation and land use change. Due to the low-altitude occurrence of beech in the Southwest, beech forests were often transformed through human land use (plough-land, populated places). In the mountainous areas, human impact on beech forests has been traditionally low (cold and moist areas are unsuitable for agriculture), however, the low-elevation beech forests were often converted into oak forests (pasture).

Lack of soil data: Beech can be found on a wide scale of soil types from acidic to calcareous. However, beech is not able to tolerate quick changes of dry and wet soil conditions. Although, soil data were considered in the study, fine-scale soil information for forests was not available. Therefore, some models (BioClim, one-class SVM, GLM) assessed the macroclimate as suitable for beech in the west part Hungary. Nevertheless, its occurrence is often hindered by reduced aeration or unfavorable physical and textural characteristics of the soil.

Competition and other biotic interactions: Competition is an important mechanism that is absent from SDMs. Competitive tree species as predictors were not included in this work. Even if applying occurrence data of competitive species could enhance model performance by predicting current potential distribution, such reliable information is not available for the future (future distribution of competitors). We hypothesized that the occurrence of competitive tree species could be surrogated by applying a wide range of environmental predictors during the modeling.

Beside competition, other biotic interactions should be also considered, such as facilitation, pollination, herbivory, or symbiosis. However, databases for these factors do not exist.

Extreme events: Most SDMs are calibrated under the assumption that range margins are formulated by climatic means. The association of range margin and climatic mean may not hold when climatic extremes occur with a skewed frequency distribution, thus, predictions based on climatic means alone could overestimate ranges. The inclusion of real extreme measures could be especially important along the trailing edge (xeric limit) of the distribution (*Zimmermann et al.,* 2009).

4.2. Future potential distribution

The mathematical properties of the models can help to explain the differences in their predictive performance. The most important reason for the underprediction of BioClim is that the model is very sensitive to the occurrence of variables that are outside of what was observed as the current climate, even if this is not truly a limiting factor (*Tsoar et al.,* 2007). In Domain, all occurrence points are treated separately and, unlike in the other models, there is no generalization (creation of response functions). Domain is, therefore, very sensitive to the occurrence of new combinations of the environmental predictors, and this negatively affects its predictive ability. One-class SVMs are able to represent very irregular data distribution shapes without making assumption on the probability density of the data (*Tax* and *Duin,* 2002), which allowed better performance during prediction.

Presence-absence classification models seemed to be able to predict species distributions better under current and novel combinations of climate than presence-only methods. GLM performed relatively poorly due to the lack of flexibility (*Austin,* 2002). MAXENT uses an exponential model for probabilities, and gave very large predicted values for environmental conditions outside the range present in the training set (*Phillips et al.*, 2006). CTree provided the best statistical performance describing the current distribution among all models, although the predictions for the future showed regional inconsistency, especially in the Southwest and Northeast. The relatively good predictive performance of CTree could be explained by the ability of finding interactions and hierarchical relations among environmental variables (*Hastie* and *Tibshirani,* 1990; *Austin,* 2002).

BP-ANN significantly outperformed CTree in the domain of predicting the future potential distribution of beech. Although BP-ANN performed slightly poorer than CTree by predicting the current potential distribution, the predictions for the future were more realistic without regional inconsistency. The larger predicted area and the distinct boundaries in the future potential maps of BP-ANN indicated that the generalization ability of BP-ANN was clearly superior to that of CTree. One possible explanation for the difference in the predictive performance is that complex features that are constructed allow non axis-parallel and nonlinear decision boundaries.

The results of this investigation provide clear support to the preference for neural networks in at least this type of bio-informatics problems.

4.3. Regional differences

Model accuracy can be measured not only on the country scale (overall model performance), but also at a finer (regional) scale. Accuracy measures like *TPR, AUC,* Kappa values and predicted area can be assessed also across different forest regions. The regional analyses of the model performance enable the assessment of SDMs under different climatical/ecological conditions.

Hungary stretches across three climate regions. Southwest Hungary is under strong Mediterranean influence, northwest Hungary is subatlantic, while the north-eastern part is more continental. The soil and hydrological conditions that sustain the forest vary greatly. As a result, Hungary features 6 main forest regions and 54 forest regions, each supporting characteristic tree species and forest types.

The breakdown of the accuracy measures for forest regions indicated that false negative rates (overprediction) of the BP-ANN and CTree model were higher in Mecsek Mountains, Göcsej Hills, Őrség, east Zala Hills, Marcali Ridge, and west Zselic than the overall false negative rate by predicting the current potential distribution (*Fig. 6*). Beech in the above mentioned forest regions reaches its lower xeric distribution limit (trailing edge). The Mecsek Mountains, east Zala Hills and west Zselic were already affected with large-scale beech decline after 2003,(*Lakatos* and *Molnár,* 2009).

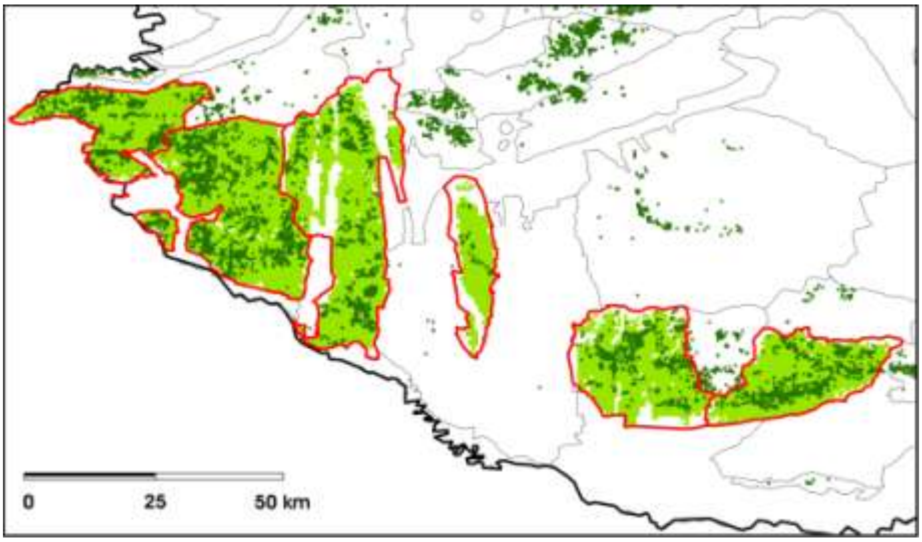

Fig. 6. Beech dominated forest regions (indicated with red contours) in southwest Hungary with high false negative values (overprediction) during the simulations under current climate conditions with the BP-ANN model. The potential area predicted by the BP-ANN method is colored with light green, observed localities with beech occurrence are indicated with dark green.

False negatives typically are due to the violation of the fundamental equilibrium assumption of static models (*Guisan* and *Zimmermann,* 2000). Accordingly, in the present study they suggest that beech at its trailing edge is not in equilibrium with the climate characterized by long-term means.

After the extreme dry and hot 2003, widespread beech decline was observed in several forest regions where beech reaches its lower distributional limit. This suggests that range margins of beech in Hungary are formulated by short-term dry periods – rather than by long-term climatic means.

4.4. Correlates of beech distribution

Beech trees show a rapid increase of radial increment from mid-May to July as soon as leaf expansion starts. Until the end of June 30–70% of annual growth is achieved (*Lebaube et al.,* 2000, *Bouriaud et al.,* 2003). In conclusion, beech appears particularly sensitive to weather conditions at the beginning of the growing season.

The factor importance analysis ranked the maximum temperature of spring and early summer and the modified Ellenberg quotient among the most influential factors. Our results, underlining the importance of May-June weather conditions in the presence of beech, are coherent with results obtained from dendrochronological analyses (*Lebourgeois et al.,* 2005; *Di Filippo et al.,* 2007).

Using climatic predictors, only the current distribution of beech could be easily predicted under optimal conditions, but models failed in the Southwest and Northeast. Including soil data and continentality indices improved model performance in these regions. This suggests that soil conditions could play an important role in determining the presence of beech at the edge of its distribution range.

An example of better prediction accuracy improved by the addition of soil parameters can be seen in *Fig. 7*.

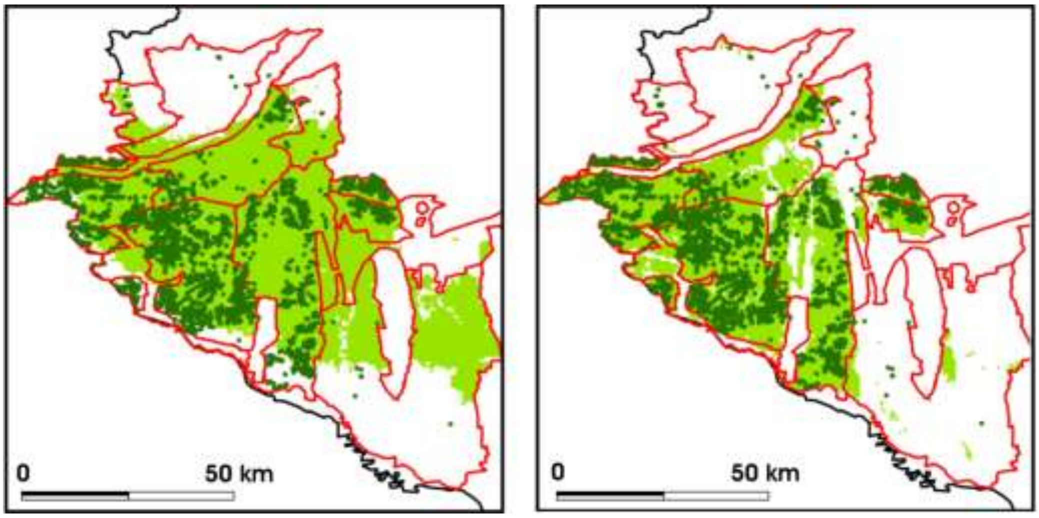

Fig. 7. Predicted potential distribution of beech by the BP-ANN method in southwest Hungary using climate predictors only (left) and using climate, soil, and geomorphological predictors (right). Forest regions are indicated with red.

5. Conclusions

The aim of this study was to test the performance of species distribution models predicting the potential future distribution of beech (*Fagus sylvatica* L.) near to the xeric limit in Hungary. To achieve this aim eight different stochastic algorithms were compared and evaluated.

Most of the species distribution models performed fair or good description of the current distribution of beech, but machine learning methods like classification trees and artificial neural networks with backpropagation algorithm, generally outperformed the established ones. Six out of the eight methods were unsuited for predicting climate change effects on the future distribution of beech. This confirms that a good model performance in predicting the current distribution does not guarantee success in predicting distribution under different climates. The relative failure of some methods underlines that predictions for conservation and management issues should be based on multimodel assessments.

Even machine learning methods like artificial neural networks with backpropagation algorithm failed in regions where beech reaches its distributional limit. The results of the present study suggest that:

- beech in Hungary at its trailing edge (xeric limit) is not in equilibrium with the climate and
- range margins of beech in Hungary are formulated by short-term dry periods rather than long-term climatic means.

The factor importance analysis of the species distribution models ranked the maximum temperature of May and the modified Ellenberg quotient repeatedly as the most influential predictors. In addition, maximum temperatures of summer and precipitation of late summer played a significant role in determining the presence of beech. The ranking suggests that the distribution of beech in Hungary is determined mainly by the maximum temperatures during springtime and it is secondly related to precipitation.

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