



## Climatic drivers of forest productivity in Central Europe



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### ABSTRACT

Climate is an important driver of forest health, productivity, and carbon cycle, but our understanding of these effects is limited for many regions and ecosystems. We present here a large-scale evaluation of climate effects on the productivity of three temperate tree species. We determine whether the National Forest Inventory data (NFI) collected in the Czech Republic (14,000 plots) and Slovakia (1,180 plots) contains sufficient information to be used for designing the regional climate-productivity models. Neural network-based models were used to determine which among 13 tested climate variables best predict the tree species-specific site index (SI). We also explored the differences in climate-productivity interactions between the drier and the moister part of the distribution of the investigated species. We found a strong climatic signal in spruce SI ( $R = 0.45\text{--}0.62$ ) but weaker signals in fir and beech ( $R = 0.22\text{--}0.46$  and  $0.00\text{--}0.49$ , respectively). We identified the most influential climate predictors for spruce and fir, and found a distinct unimodal response of SI to some of these predictors. The dominance of water availability-related drivers in the dry-warm part of a species' range, and vice versa, was not confirmed. Based on our findings, we suggest that (i) the NFI-based SI is responsive to climate, particularly for conifers; (ii) climate-productivity models should consider the differences in productivity drivers along ecological gradients, and models should not be based on a mixture of dry and moist sites; and (iii) future studies might consider the subset of influential climate variables identified here as productivity predictors in climate-productivity models.

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### 1. Introduction

The reliable assessment of forest productivity, including the effects of climatic drivers and other perturbations, has been increasingly recognized as crucial to forest management planning and climate change mitigation efforts (Hanewinkel et al., 2012; Nabuurs et al., 2013; Wamelink et al., 2009). While the effect of site climate on forest productivity has traditionally been central to the interest of foresters (Bontemps and Bouriaud, 2013; Skovsgaard and Vanclay, 2008, 2013; Socha et al., 2016), a forest's capacity to sequester carbon and exert control on climate has recently highlighted the bi-directional nature of forest-climate interactions (Becknell et al., 2015; Brovkin et al., 2009).

To investigate the environmental control of forest productivity and carbon cycle, researchers have focused on both the rule of fun-

damental ecophysiological processes (Coops et al., 2005; Zhou et al., 2005) and on the statistical associations between the environment and productivity indicators (Aertsen et al., 2010; Antón-Fernández et al., 2016). Although the latter approach provides only a limited understanding of the underlying processes (Adams et al., 2013; Pretzsch et al., 2015), it can guide management decisions, provide information about the main drivers of and changes in forest productivity (Bošel'a et al., 2014; Charru et al., 2010; Kint et al., 2012; Pretzsch et al., 2014), and support the development of empirical forest models (Pretzsch et al., 2008; Trasobares et al., 2016).

Here, we used an empirical approach to investigate the effects of climate on forest productivity in two countries in central Europe—the Czech Republic and Slovakia. To facilitate such investigation, we used extensive datasets of the National Forest Inventory (NFI) from the two countries. The NFI is a main source of forestry data in many countries and supports assessment of forest resources (Vidal et al., 2016) and research (e.g., Gasparini et al., 2013; Kováč et al., 2014). The data were also used for the development of growth-climate models and assessment of the effects of climate

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change on forests (Charru et al., 2010). The high spatial resolution of these data and the large number of inventory cycles that span many decades in some countries (e.g., from 1923 to the present in Sweden, Fridman et al., 2014) have facilitated cross-scale and interdisciplinary research through the integration with other forestry and environmental data (e.g., Kovač et al., 2014; Tomppo et al., 2008).

In Central Europe, forest productivity research has been conducted only on smaller scales (Bošel'a et al., 2013a; Socha, 2008; Socha et al., 2016), and thus the current study represents the first regional assessment of climatic effects on forest productivity. Forest productivity in this region is mainly driven by climate-orographic patterns and soil nutrient availability (Bošel'a et al., 2013a). Recent research has recognized the inter- and intraspecific differences in temperate tree growth and productivity (George et al., 2015; Suvanto et al., 2016) as well as differences in the productivity of different mixtures of species (Bošel'a et al., 2015; Pretzsch et al., 2012, 2015). Such findings have been used in forest management planning and parameterization of forest models for the region (Bošel'a et al., 2013b; Hlásny et al., 2014a; Lexer et al., 2002; Pretzsch et al., 2014). We investigate here three widespread tree species that have high commercial and ecological importance and that constitute some of the original forest communities in Central Europe: Norway spruce (*Picea abies* L. Karst), European beech (*Fagus sylvatica* L.), and silver fir (*Abies alba* Mill.).

Norway spruce has been extensively planted in Central Europe, and the so-called secondary spruce forests are for the most part currently distributed at unsuitable sites (Ellenberg, 1986; Spiecker et al., 2004; Löf et al., 2010). This is thought to greatly amplify the vulnerability of such forests to biotic and abiotic stresses (Hanewinkel et al., 2010; Hlásny and Turčáni, 2013). Although the growth response of spruce to climate was found to be variable (Andreasen et al., 2006), and although spruce growth was strongly affected by air pollution and other non-climatic effects (Bošel'a et al., 2014), spruce growth was found to significantly accelerate in recent decades in Central Europe (Pretzsch et al., 2014). On the other hand, spruce growth was found to be much more sensitive to drought than the growth of beech and fir (Zang et al., 2014). Spruce also exhibited a substantially elevated mortality under an increasingly unfavourable climate (Neuner et al., 2014).

European beech is highly sensitive to climate (Fang and Lechowicz, 2006; Fotelli et al., 2009; Mellert et al., 2016), and this has generated concerns about the sustainability of the species across a large part of its distribution under climate change (Czúcz et al., 2011; Mette et al., 2013). Beech has exhibited decreased growth since ca. 1975 near the lower range of its distribution (Jump et al., 2006; Peñuelas et al., 2007). At the same time, beech has shown accelerated growth under standard growing conditions in Central Europe (Pretzsch et al., 2014), particularly in less productive sites (Bošel'a et al., 2016). Several authors found the ratio of mean temperature of the warmest month and annual precipitation (the Ellenberg quotient) to be a powerful predictor of beech vigour, growth, and mortality (Czúcz et al., 2011; Fang and Lechowicz, 2006; Jahn, 1991).

After a serious growth decline and even a dieback of silver fir in the period of 1970–1990, fir has experienced an unprecedented growth increase in central Europe (Bošel'a et al., 2014; Elling et al., 2009). Fir growth, however, has declined in the southern range of the species' distribution since 2000, which has suggested that drought may have recently become a factor limiting fir growth in some regions (Büntgen et al., 2014; Gazol et al., 2015; Linares and Camarero, 2012). The growth decline in 1970–1990 was attributed to high levels of air pollution, whereas the recent growth increase was likely associated with climate warming when that warming has not been coupled with a significant decrease in water availability (Büntgen et al., 2014).

To increase our understanding of forest productivity and climate interactions in Central Europe, we focused here on the following objectives: (i) to identify the extent to which the species-specific site productivity in Central Europe is controlled by climatic drivers; (ii) to determine which climate variables are the most important predictors of the region's forest productivity; (iii) to evaluate differences between climate control of forest productivity in the cool-moist and the warm-dry part of the ranges of spruce, beech, and fir; and (iv) to produce maps that show the sensitivity of species productivity to climate across the Czech Republic and Slovakia.

This research will extend the current knowledge of forest-climate interactions in Central Europe because it uses a novel experimental design and novel methods of data analysis. Moreover, the used data cover a substantial part of the ranges of the three species. While most previous studies used limited sets of climate predictors to explain observed growth and productivity patterns (e.g., Albert and Schmidt, 2010; Bošel'a et al., 2013a), and while these predictors were selected based on the prior hypotheses formulated by the researchers, we evaluate here an extensive predictor set using a data mining-like approach (Zaki and Meira, 2014). Data mining has the potential to reveal patterns that might be missed by other techniques but has been used in forestry research only rarely (e.g., Hlásny et al., 2011, 2014b; Pourtaghi et al., 2016; Sanquette et al., 2013). We use neural network-based regression modelling, which has been found to have good data-fitting and predictive performance in many scientific fields including forestry (Aertsen et al., 2010; Moisen and Frescino, 2002). Given the increasing quantity of forestry data and improvements in computer performance, neural network-based modelling is likely to be increasingly used. We demonstrate here one field of application, including critical assessment of its advantages and disadvantages.

In support of the objectives, we test the hypothesis that effect of temperature and water availability-related variables is relatively balanced over the entire range of a species, while effect of water availability-related variables prevails in the warmer and drier part of the range and effect of temperature-related variables prevail in the cooler and moister part of the range (Briner et al., 2013; Walther et al., 2002). We also test the hypothesis that even though a broad set of climate variables are used as productivity predictors, there will be a substantial portion of the unexplained variance accounting for the non-climatic drivers of forest development, by the noise in the used response variable (Goelz and Burk, 1996), as well as by the conceptual limits to the use of the site index (SI) as an indicator of site productivity (Bontemps and Bouriaud, 2013).

## 2. Data and methods

### 2.1. Study area

The study area covered the territory of the Czech Republic (CZ) and Slovakia (SK) (Fig. 1). Both countries are in the temperate forest zone, with an oceanic climate prevailing in the CZ and a continental climate prevailing in SK (Rivas-Martínez et al., 2004; Table 1). A substantial climate-orographic gradient in the region has resulted in a range of zonal vegetation communities, from open woodland and semi-arid oak forests to a mountain tree line formed by conifers. Both countries apply timber-oriented forest management with a focus on softwood timber.

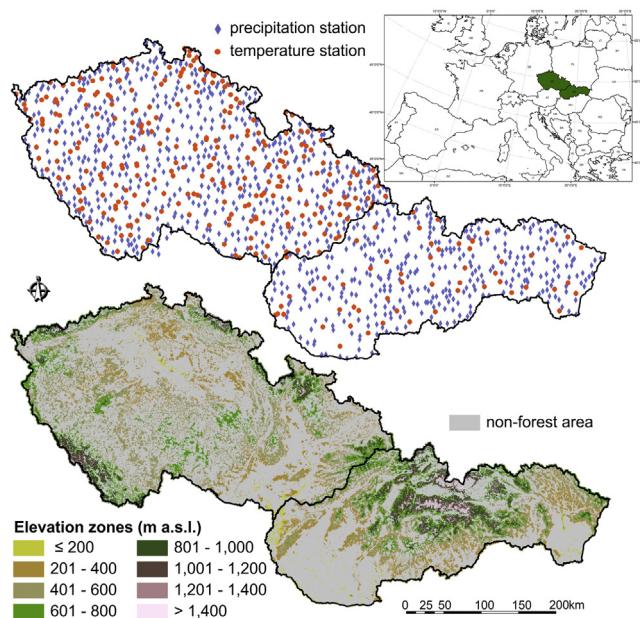
### 2.2. National forest inventory (NFI) data and used response variable

We used the data from a single cycle of the NFI conducted in the CZ (2001–2004; 14,000 plots) and SK (2005–2006; 1,180 plots). The CZ NFI has plots distributed in a grid of 2 × 2 km. Two circular

**Table 1**

Forest conditions in the Czech Republic and Slovakia.

Country	Forest cover (km <sup>2</sup> )	Forest elevation range (m a.s.l.) <sup>*</sup>	Dominant tree species (%)
CZ	26,550	262–905	Spruce (51), Pine (17), Beech (8), Oak (7), Larch (4), Fir (1)
SK	20,070	217–1122	Beech (31), Spruce (26), Oaks (14), Pine (7), Hornbeam (6), Fir (4)

<sup>\*</sup> 5–95% quantile.

**Fig. 1.** Distribution of the weather stations in Slovakia and the Czech Republic that were the sources of the temperature and precipitation data used in this study. The location of Slovakia and the Czech Republic in Europe is indicated at the top, and forest distribution along the elevation gradient is indicated at the bottom.

plots with a radius of 12.62 m are situated in each cell of the grid; one plot is in the cell's centre and second plot is 300 m from the cell's centre at the randomly selected location. The SK NFI has plots distributed regularly in a grid of 4 × 4 km. Plot diameter is 12.62 m as well. Several subplots are embedded in each plot to collect the information on smaller diameter trees and regeneration in both NFIs.

We used the so-called “site index (SI)”, a climate-sensitive variable that is the phytocentric indicator of site productivity traditionally used in forestry (Bontemps and Bouriaud, 2013; Socha et al., 2016). The SI is expressed as the stand height at a standard age for a given tree species (Skovsgaard and Vanclay, 2008). We used the standard age of 100 years, which is commonly used for the investigated tree species in Europe. The justification of this indicator's relevance is derived from Eichhorn's rule (Eichhorn, 1904), which advocates for a strong relationship between top height of a stand and total production of a species, regardless of site properties and stand density.

Age and height data measured at the NFI plots were used to calculate the SI. Stand age was assessed visually, and when necessary, age estimates were corrected by counting rings on core samples or stumps. Because the NFI plots contained stands of different ages, the regional species-specific and site-specific height-age curves (Halaj and Patráš, 1998) were used to convert the actual heights to the expected heights at 100 years. The model that was used was based on Korf's growth function (Korf, 1939; Sedmák and Scheer, 2012). More than 3000 research plots (1804 for spruce, 892 for beech, and 319 for fir) across the CZ and SK were used to estimate this function's parameters.

We used here a mean stand height instead of the commonly used top stand height because the national yield model used to estimate the SI for stands at various ages was based on the mean stand height. The use of a mean height may introduce a noise to the SI estimation because mean height is to a certain extent sensitive to the applied thinning regime. This effect, however, should not be severe, because the same thinning type is used for each species across the entire forest area in the two countries.

Because the reliability of assessing the SI for stands whose ages are substantially different from 100 years is limited (in terms of both precision and in the probability of bias, Goelz and Burk, 1996), only stands with the age of 75–125 years were investigated. Because the number of trees for a particular species differed among the plots, a plot was included in the analysis only if the SI was calculated from at least 5 trees (Table 2). To account for the different number of trees per plot, the number of trees in a plot was used to weigh the SI values in the regression modelling described below.

### 2.3. Climate data

The climate data used in this study were from the period 1980–2010, which well characterizes the conditions under which the investigated forest stands developed. Considerably less records were available before than after 1980, which prevented the use of a longer period (Source: Slovak Hydrometeorological Institute, Czech Hydrometeorological Institute). The data were obtained from 269 air temperature stations in the CZ and 55 in SK, and 788 precipitation stations in the CZ and 396 in SK (Fig. 1).

A number of climate variables that were to be evaluated as predictors of site productivity were calculated from the measured data. These derived variables were selected to describe high and low temperature-related drivers, indicators of heat and drought stress, climatic continentality, snow, precipitation, and radiation regime (Appendix A).

Because such variables are likely to be correlated and because some variables might contain little new information that could improve the performance of regression models, the redundancy test was applied. For each set of correlated variables with a Pearson's correlation coefficient ( $R$ ) > 0.9, the variable with the highest internal variability (i.e., the highest information content) was retained and used for further analyses. The applied redundancy test prevents the use of highly linearly correlated variables, and the interpretation of regression modelling outputs is more straightforward as compared with the use of, for example, an orthogonal combination of the predictors. Moreover, dimensionality reduction using techniques such as principal component analysis generates linear combinations of input variables, while NN models are primarily designed to identify complex nonlinear patterns in the data.

### 2.4. Spatial interpolation technique

We used the external drift kriging spatial interpolation technique (Goovaerts, 2000; Hudson and Wackernagel, 1994; Matheron, 1973) to produce the raster maps of 26 climate variables for the whole territory of the CZ and SK. Such maps were used to extract the climate data for each NFI plot and to thus facilitate the

**Table 2**

Statistical characteristics of the species-specific site index values and climatic limits of species' ranges in the investigated territory. The inventory plots used represent a subset of the whole inventory dataset and were selected based on an age limit and on a minimum number of trees for each species occurring in a plot.

Species	No. of plots – WR	No. of plots – MPR	No. of plots – DPR	Site Index ( $x \pm s_x$ ) (m) <sup>**</sup>	Temperature range (°C) <sup>***</sup>	Precipitation range (mm) <sup>***</sup>
European beech	1210	790	420	26 ± 5.6	2.0–5.1	585–1183
Silver fir	560	399	161	26 ± 5.5	1.7–4.2	592–1027
Norway spruce	2841	1980	861	31 ± 6.6	0.1–6.0	567–1173

WR – whole species' range; MPR – moister part of the species' range; DPR – drier part of the species' range.  $x$  denotes average;  $s_x$  denotes standard deviation.

<sup>\*\*</sup> Site Index for the WR dataset.

<sup>\*\*\*</sup> 5–95% quantiles, annual average data for period 1980–2010 are indicated.

regression modelling. Elevation was used as the supportive variable that was correlated with the interpolated climate variables. Because the method assumes a linear relationship between the target variables (climate) and the predictor variable (elevation), data transformations were applied in some cases to linearize the relationship.

We also used external drift kriging to produce the regional maps of the actual SI distribution by interpolating the SI values measured in the NFI plots. The produced maps had a resolution of 150 m.

We used the geostatistical software ISATIS v.8 for the interpolation (Geovariances, FR).

## 2.5. Regression modelling design

We used NN-based regression modelling, which is a non-parametric and non-linear technique that belongs to the data mining or machine learning family of approaches (e.g., [Zaki and Meira, 2014](#)). Such approaches were designed to extract information from and to detect patterns in large datasets. The methods are particularly useful when relationships between variables are unclear and a priori hypotheses have not been formulated ([Bishop, 1995](#)).

We used a multi-layer perceptron NN (MLP, [Bishop, 1995](#)), which consists of a set of input units (neurons), which represent the used predictors (climate variables in this study). The input neurons are fully connected using the weighted connections (synapses) with a finite number of neurons organized in one or more so-called hidden layers. There are proofs that a feed-forward NN, such as MLP (i.e. NN which transfers the signal in a forward direction only) with only a single hidden layer with a finite number of neurons, is a universal approximator (e.g. [Cybenko, 1989](#)). This means that such a network can approximate a wide variety of continuous functions. A non-linear transformation is applied in a hidden neuron on the weighted sum of inputs, and the output is forwarded to the next hidden layer or the output layer; in this study the output layer contains a single neuron only, which is SI for a given species. Then, training algorithm is used to adjust iteratively the weights of connections so as the model error (i.e. the difference between predicted and observed SI) is minimized. Testing and validation data sets are used to stop the training to prevent model overfitting and to evaluate model's performance, respectively. In the current study, the NN training was based on the back-propagation algorithm (e.g., [Haykin, 1994](#); [Patterson, 1996](#)).

The climate variables ([Tables A1, B1](#)) were used as the continuous predictors, while species-specific SI was used as the response variable. To facilitate the NN training, the input data were randomly split into a parameterization dataset (PS), a testing dataset (TS), and a validation dataset (VS) at a ratio of 70:15:15 (PS:TS:VS). Three-thousand NN models with randomly generated architectures were trained for each species, and the 15 best-performing models were retained. The trained networks contained 1–3 hidden layers with 3–15 neurons.

A correlation between predicted and observed SI evaluated based on validation dataset and testing dataset (i.e., that part of

the data that was not used for the training) was the criterion used to create the ensemble of 15 models. Even though the pre-selection of NN models was based on model performance in terms of the correlation between observed and predicted values, some models can still exhibit undesired behaviours. Therefore, additional testing was used to select the final set of models. The models were discarded when:

- The performance of any single model (as indicated by the correlation between predicted and observed SI values) was substantially lower than that of the remaining models;
- A model had substantially different correlations for training, testing, and validation datasets, while the performance of other models was balanced.

A sensitivity analysis (SA) was performed to identify the most decisive predictor variables. The SA estimated the rate of change in model output caused by changes in model inputs ([Saltelli et al., 2000](#)). The SA used in this study iteratively "discards" an input variable and assesses the network error. The measure of sensitivity is the ratio of the error produced by a model with a missing variable to the error produced by the model with the full set of input variables; this measure is referred to as a sensitivity score (SS, [Hunter et al., 2000](#)). SS will increase with the sensitivity of the network to a particular input.

Two iterations of the above procedures were used to identify the set of most influential variables. The SSs yielded by the first iteration (i.e., the training and SA) were used to identify the variables with very little effect (i.e., with SS close to 1). In the second iteration, these variables were discarded, and the reduced set of predictors was used for model training; so produced modelling outputs were used for making the inferences. The two iterations were sufficient in most of cases to avoid having a large number of predictor variables with SS close to 1.

For each of the three tree species, these analyses were conducted for the whole species' range (WR), for the drier part of the range (DPR), and for the moister part of the range (MPR). A simple approach was used to split the WR dataset into the DPR and MPR subsets; 30% of the data distributed in the warm-dry part were considered as the DPR, and rest of the data were considered as MPR. This separation used the Ellenberg climate quotient ([Ellenberg, 1986](#)), which is a useful predictor of the growth and distribution of some tree species ([Czúcz et al., 2011](#); [Fang and Lechowicz, 2006](#); [Jensen et al., 2004](#); [Mellert et al., 2016](#)).

Given that the maps of climate predictors were produced by spatial interpolation, the developed regression models were deployed using such maps, and spatial prediction maps of SI were generated to support the inferences and interpretations. In addition to the prediction maps, maps were produced showing the inter-model variability (i.e., the differences in SI values predicted by the individual NN models in the final ensemble of models) in terms of the coefficient of variation (CV%).

Statistica Neural Networks v.7 and v.13 (Dell, Inc.) was used for the analyses. The trained NN models are available for use in the Pre-

**Table 3**

Statistical description of 13 climate variables selected for the regression modelling from the initial set of 26 variables. Selection was based on inter-variable correlation. Variable codes are explained in [Appendix A](#).

Variable	T-avg	T-ColdM	DSnow_L3 .Tmin10	T-Ampl	P0- 10days	Heat Waves	Snow- March1	Heat Waves- L	Heat Waves- D	T- WarmM	EGD- RAD10	EQ	K
$x \pm s_x$	$3.4 \pm 2.1$	$-3.8 \pm 0.8$	$2.3 \pm 0.9$	$21.6 \pm 0.7$	$38.4 \pm 9.0$	$7.2 \pm 1.8$	$19.9 \pm 14.6$	$5.5 \pm 3.3$	$6.8 \pm 2.6$	$17.8 \pm 1.3$	$163 \pm 23$	$24.8 \pm 6.4$	$27.8 \pm 1.8$
5–95%	0.26–7.26	−5.4–2.7	0.6–3.7	20.4–22.8	24.4–53.0	3.9–9.1	4.5–49.9	0.4–11.4	2.9–9.2	15.6–19.6	137–183	13.9–35.0	25.0–35.1

$x$  denotes average;  $s_x$  denotes standard deviation.

**Table 4**

Average Pearson correlation coefficients between observed and predicted site index values for spruce. The coefficients were calculated based on a number of neural network-based regression models for the parameterization, testing, and validation datasets. The results are indicated separately for models designed for the whole spruce range (WR) in the investigated territory, for the moister part of the range (MPR), and for the drier part of the range (DPR).

Geographical range of the spruce datasets	No. of models	Correlation coefficients		
		Parameterization	Testing	Validation
WR	11	0.50	0.49	0.45
MPR	13	0.52	0.62	0.62
DPR	3	0.24	0.23	0.24

dictive Modelling Markup Language (PMML, [Grossman et al., 2002](#)) as a dataset accompanying this article (Supplementary material S1).

### 3. Results

#### 3.1. Climate data pre-processing

Of the initial set of 26 climate variables ([Appendix A, Table A1](#)), 13 were selected (based on the redundancy test) to be used as the predictors in the regression modelling ([Table 3](#)). The correlation matrix of the final subset of variables is provided in [Appendix B](#) ([Table B2](#)). The selected variables well represented the initial full set because they characterized high and low temperatures, drought and heat, snow regime, and climatic continentality.

#### 3.2. Climatic control of the spruce site index

The first iteration of model training and SA for the **WR dataset** led to the discarding of five climate predictors, which received SSs close to 1. The second iteration produced a set of 12 NN models (i.e. 3 of the 15 retained models were discarded for the reasons described above) with consistent performance for the PS, TS, and VS. The average performance of all models as indicated by correlations between observed and predicted SI values was  $R = 0.50$  for the PS, and 0.49 and 0.45 for the TS and VS, respectively; the inter-model variability of  $R$  was up to 2.5% of the average  $R$  ([Table 4](#)).

For the WR dataset, the SS was highest for the variable Snow-March1 (2.66), indicating that model error was 2.66 times bigger without this variable than with it ([Table 5](#)). The average rank (AR) of Snow-March1 was 2.33, which indicates a minor inter-model disagreement in this variable's importance. Variables T-ColdM (SS 1.7, AR 2.17), T-WarmM (SS 1.54, AR 3.00), and EQ (SS 1.44, AR 4.00) occupied the next positions. The response of measured and predicted SI to the most influential variables was clearly unimodal, peaking at a value of  $-4.5^{\circ}\text{C}$  for T-ColdM,  $17^{\circ}\text{C}$  for T-WarmM,  $18^{\circ}\text{C mm}^{-1}$  for EQ, and 25 cm for Snow-March1 ([Fig. 2](#)).

For the **MPR dataset**, the first modelling iteration led to the discarding of only one climate variable (HeatWaves-D). The second iteration led to the discarding of two models and the retention of 13. The retained models for the MPR dataset performed better than the retained models for the WR dataset ([Table 4](#)); the correlation coefficient ( $R$ ) for the VS and the TS was 0.62 with the inter-model variability up to 3%.

The variables that were most influential for the WR dataset were also the most influential for the MPR dataset, and these were

T-WarmM (SS 2.55, AR 1.62), T-ColdM (SS 2.19, AR 2.23), HeatWaves (SS 1.75, AR 4.62), and Snow-March1 (SS 1.67, AR 5.46). The remaining variables also received SSs significantly above 1, which indicated that the SI variability was controlled by the combined influence of the whole predictor set. The SI response to the most influential variables was unimodal as well ([Fig. 2](#)). The functions peaked at  $17.5^{\circ}\text{C}$  for T-WarmM,  $-4.5^{\circ}\text{C}$  for T-ColdM, 7 days for HeatWaves, and 28 cm for Snow-March1. The response for HeatWaves had an unnatural behaviour at low values. Because few data were distributed in this part of the range, such a response is an artefact.

For the **DPR dataset**, the first modelling iteration led to the discarding of five climate predictors, although the SSs for all variables were close to 1. Model performance with the DPR dataset (both before and after variable reduction) was significantly lower than for the WR and MPR datasets; the correlation coefficients ( $R$ ) for the three sets were low (from 0.23 to 0.24). Model performance with the DPR dataset was not improved by various modifications to the training process or by the testing of different types of neural networks or training algorithms. Because SSs were too low to allow the ranking of variables by their influence, only the SS and ranks for EQ (SS 1.02) and HeatWaves (SS 1.01), which were found to be the most influential, are indicated in [Table 5](#). Given the low performance of these models, response functions are not shown in [Fig. 2](#).

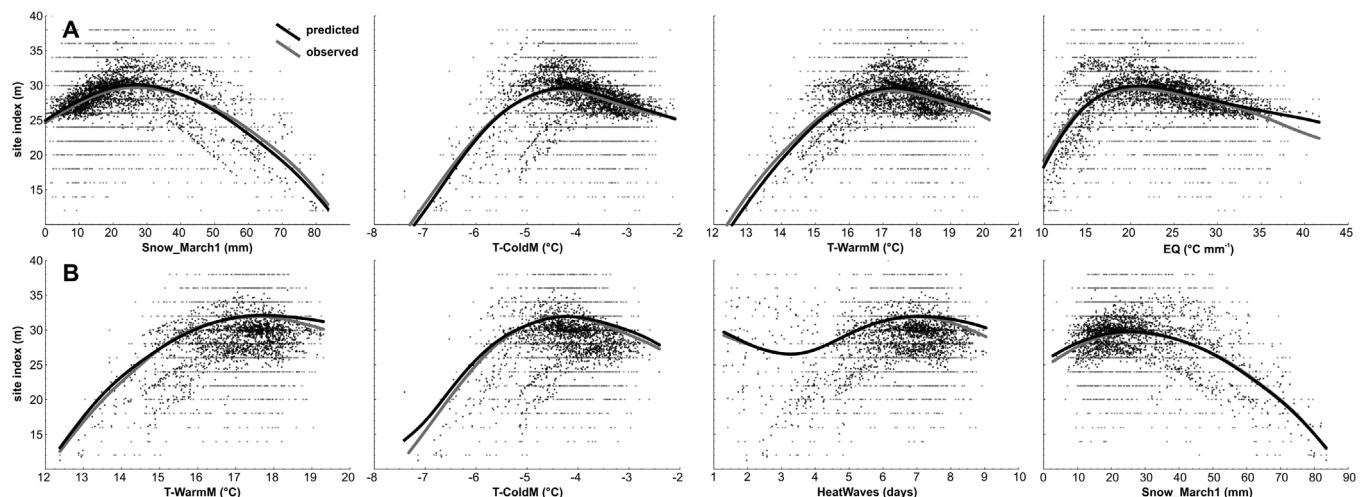
The prediction maps based on the average of 11 and 13 NN models ([Table 4](#)) parameterized using the WR and MPR datasets, respectively, are shown in [Fig. 3a–b](#). Respective CV% maps indicating the inter-model variability in SI are in [Appendix C](#). The WR-based prediction map showed small spatial variability in the west of the region (CZ) but much greater variability in the mountainous areas of SK in the east (Carpathian Mts., [Fig. 1](#)). At the same time, SI values tended to increase from west to east; SI in the CZ ranged from 25 to 30 m in most of the forest area but from 30 to 35 m in SK. In SK, regions outside the production optimum of spruce could be recognized both in the moist-cool limit in the north (High Tatras, Mts.) and in the dry-warm limit in the south (Pannonia Lowland). The MPR-based prediction map ([Fig. 3d](#)) had a pattern similar to that of the WR-based map in most of the moister part of spruce range, where the prediction could be applied. This corresponded with the finding that the most influential predictors were similar for the WR and MPR datasets.

The maps of CV% based on the inter-model differences (i.e., a difference in predictions based on 11 models for the WR dataset and 13 models for the MPR dataset; [Appendix C](#)) showed variability

**Table 5**

Average spruce sensitivity scores (SSs) for the variables, ranking of the variables based on the average SS (RA), and average ranking (AR). All indicators were calculated based on a number of neural network-based regression models. The results are indicated for the models parameterized using datasets for the whole range of spruce in the investigated territory (WR), the drier part of the range (DPR), and moister part of the range (MPR). AAR indicates the AR averaged for WR and MPR; DPR was not considered in this averaging because of the low performance of the respective regression models. — indicates that a variable's effect was insignificant.

Indicator	Dataset	Climate variables used for spruce											
		T-ColdM	T-WarmM	Snow-March1	Heat Waves	EQ	Heat Waves-L	T-AVG	Heat Waves-D	K	DSnow_L3_Tmin10	T_ampl	P0-10days
SS	WR	1.70	1.54	2.66	—	1.44	1.34	1.36	1.17	—	—	1.11	—
	MPR	2.19	2.55	1.67	1.75	1.42	1.53	1.44	—	1.38	1.26	1.19	1.14
	DPR	—	—	—	1.01	1.02	—	—	—	—	—	—	—
RA	WR	2.00	3.00	1.00	—	4.00	5.00	6.00	7.00	7.00	—	8.00	—
	MPR	2.00	1.00	4.00	3.00	5.00	6.00	8.00	—	—	9.00	10.00	11.00
	DPR	—	—	—	2.00	1.00	—	—	—	—	—	—	—
AR	WR	2.17	3.00	2.33	—	4.00	5.33	5.33	6.58	6.77	—	7.25	—
	MPR	2.23	1.62	5.46	4.62	5.46	5.62	7.00	—	—	7.77	9.15	10.31
	DPR	—	—	—	2.00	1.00	—	—	—	—	—	—	—
AAR		2.2	2.3	3.9	4.6	4.7	5.5	6.2	6.6	6.8	7.8	8.2	10.3



**Fig. 2.** Response of measured and predicted spruce site index values to the four most influential climate predictors. The responses are indicated separately for the models designated for the (A) whole range of spruce in the investigated territory (WR) and for the (B) moister part of the range (MPR). Grey – observed values, Black – average values predicted by the ensemble of the best performing neural networks. Distance-weighted least square functions are fitted to the data.

up to 5% across most of the CZ, while variability in SK ranged from 10 to 30%. In case for MPR, the variability in SK was even higher.

The prediction maps (i.e., maps showing the climatically sensitive part of the SI) closely resembled the map produced by interpolation of the original SI values (Fig. 3d) in most of the CZ and in the mountainous part of SK (see Fig. 1 for the regions' elevations). The disagreement was greatest in the non-forest areas, where no NFI data were available.

### 3.3. Climatic control of fir site index

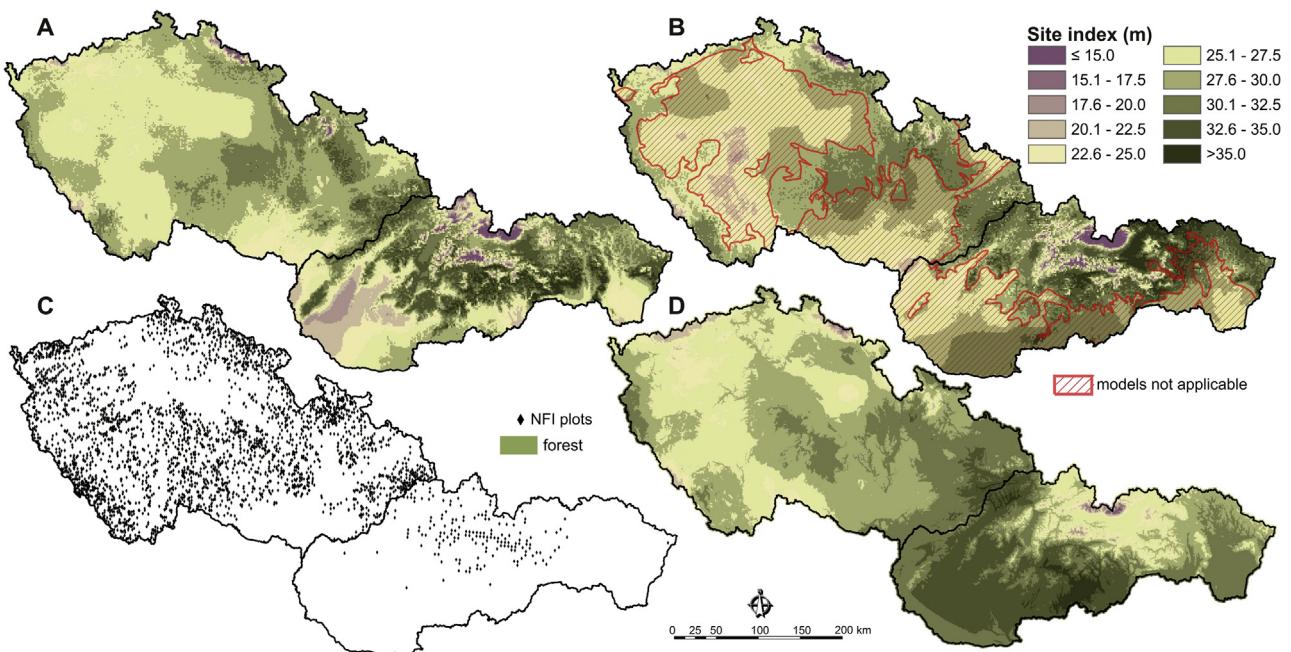
The models performed less well for fir than for spruce in terms of correlations between predicted and observed SI values, and these correlations were less consistent among PS, TS, and VS than was the case with spruce (Table 6). Many models had to be discarded for the reasons described earlier, and thus the inferences for fir were less robust than those for spruce.

The first iteration of training and SA for the fir **WR dataset** led to the discarding of only the T-WarmM variable. The second iteration showed that T-ColdM (SS 1.84, AR 2.0), HeatWaves (SS 1.27, AR 4.0), DSnow\_L3\_Tmin10 (SS 1.18, AR 3.7), and Tampl (SS 1.15, AR 4.3) were the most influential predictors (Table 7). This comparison, however, was based on only three models. SI response to these variables in fir was less distinct than in spruce (Fig. 4). Still, SI tended

to peak at 5.0–5.5 °C for T-ColdM, at 3 days for HeatWave, and at 30 cm for Snow-March1.

For the fir **MPR dataset**, the inferences were based on 10 models, whose correlation coefficients were rather unbalanced between PS, TS, and VS (Table 6). The most influential variable was the continentality index K (SS 1.61) with an AR of 1.2, which indicated very low inter-model differences in the rank of this variable. The next positions were occupied by T-WarmM (SS 1.48, AR 3.5), T-ColdM (SS 1.31, AR 7.6), and DSnow\_L3\_Tmin10 (SS 1.22, AR 4.8). The difference between RA and AR in Table 7 indicated a varying level of inter-model agreement in the importance of these variables. SI response to K indicated an increase from west to east (Fig. 4). SI peaked between −5.0 and −5.5 °C of T-ColdM, while response to the variables T-WarmM and DaySnow\_L3\_Min10 lacked a distinct peak.

Contrary to the models for spruce DPR, the models for the fir **DPR** performed well (Table 7), and the correlation coefficients for PS, TS, and VS were balanced, i.e., they ranged from 0.42 to 0.45 (Table 6). The inferences were based on only three models. The most influential variables were T-ColdM (SS 2.62, AR 1.7), T-WarmM (SS 2.61, AR 1.7), K (SS 2.33, AR 2.7), and Snow-March1 (SS 1.42, AR 4.7). The small difference between RA and AR in Table 7 indicates a consistent inter-model signal. An indistinct peak was only observed in both measured and predicted SI values at 17–18 °C of T-WarmM



**Fig. 3.** Prediction maps of the spruce site index based on the ensemble of neural network-based regression models. Prediction of models parameterized using the dataset covering (A) the whole spruce range in the investigated region, and (B) the moister part of the range (the drier part of the range, where this model is not applicable, is that area delimited by the red line). (C) The distribution of the inventory plots used in this study; and (D) a map produced by interpolation of the measured site index values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 6**  
Average Pearson correlation coefficients between observed and predicted site index values for fir. The coefficients were calculated based on a number of neural network-based regression models for the parameterization, testing, and validation datasets. The results are indicated separately for models designed for the whole range of fir in the investigated territory (WR), for the moister part of the range (MPR), and for the drier part of the range (DPR).

Geographical range of the fir datasets	No. of models	Correlation coefficients		
		Parameterization	Testing	Validation
WR	3	0.32	0.27	0.24
MPR	10	0.39	0.43	0.22
DPR	3	0.41	0.45	0.46

**Table 7**  
Average fir sensitivity scores (SSs) for the variables, ranking of the variables based on the average SS (RA), and average ranking (AR). The results are indicated for the models parameterized using datasets for the whole range of fir in the investigated territory (WR), the drier part of the range (DPR), and the moister part of the range (MPR). AAR indicates the AR averaged for WR, MPR and DPR. – indicates that a variable's effect was insignificant.

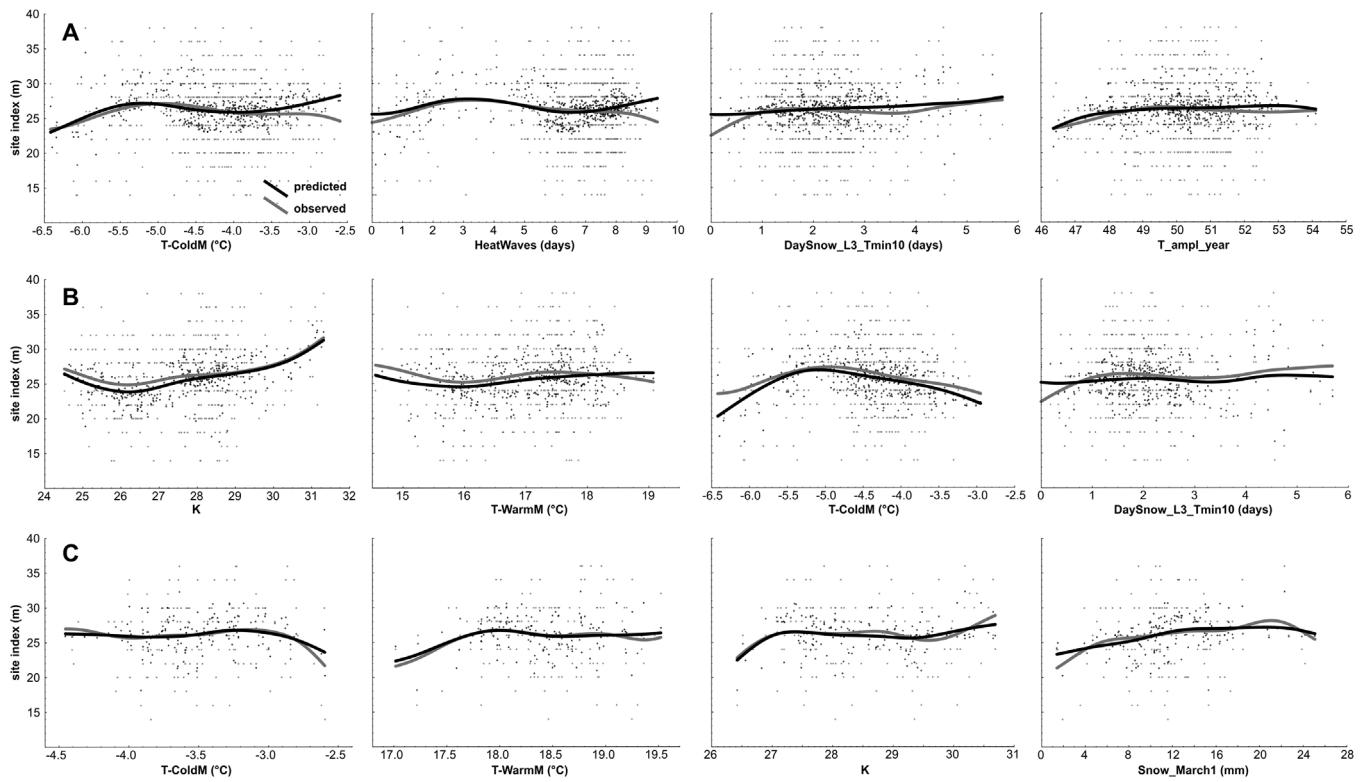
Indicator	Dataset	Climate variables used for fir											
		T-WarmM	K	T-ColdM	DSnow_L3	Snow-March1	Heat Waves	T_ampl	EQ	T-AVG	Heat Waves-D	Heat Waves-L	P0-10days
SS	WR	–	1.10	1.84	1.18	1.15	1.27	1.15	1.09	1.12	1.08	1.05	1.02
	MPR	1.48	1.61	1.31	1.22	1.14	1.13	1.09	1.21	1.17	–	1.09	1.10
	DPR	2.61	2.33	2.62	–	1.42	1.37	1.34	1.10	1.13	–	1.22	–
RA	WR	–	7.0	1.0	3.0	5.0	2.0	4.0	8.0	6.0	9.0	10.0	11.0
	MPR	2.0	1.0	3.0	4.0	7.0	8.0	11.0	5.0	6.0	–	10.0	9.0
	DPR	2.0	3.0	1.0	–	4.0	5.0	6.0	9.0	8.0	–	7.0	–
AR	WR	–	6.7	2.0	3.7	4.0	4.0	4.3	8.0	6.0	7.0	9.7	10.7
	MPR	3.5	1.2	7.6	4.8	6.0	6.4	7.3	5.7	7.2	–	7.8	8.5
	DPR	1.7	2.7	1.7	–	4.7	6.3	5.7	8.3	7.7	–	6.3	–
AAR		2.6	3.5	3.8	4.2	4.9	5.6	5.8	7.3	7.0	7.0	7.9	9.6

(Fig. 4). As was the case for MPR, SI for DPR increased slightly as K increased.

WR-, MPR-, and DPR-specific models generated rather different patterns in the SI prediction maps for fir. For WR and MPR models, SI increased from west to east (Fig. 5A, B). This trend, however, was not present in the interpolated SI (Fig. 5D), which, like the low

correlation coefficients, suggested the dominance of non-climatic drivers.

The inter-model variability of predicted SI for WR was as high as 5% of the predicted SI in most of the CZ, and was 10–20% in most of SK. Similarly, CV% maps for MPR and DPR showed an increase in variability from west to east; the highest values occurred in areas where the models were not applicable.



**Fig. 4.** Response of measured and predicted fir site index to the four most influential climate predictors. The responses are indicated separately for the models for (A) the whole range of fir in the investigated territory (WR), (B) the moister part of the range (MPR), and (C) the drier part of the range (DPR). Black – observed values; Grey – average values predicted by the ensemble of best performing neural networks. Distance-weighted least square functions are fitted to the data.

#### 3.4. Climatic control of beech site index

For beech, model performance (the correlation between observed and predicted SI values) was poor and was highly uneven among PS, VS, and TS datasets (Table 8). Because SSs did not significantly exceed 1 for any variable, SSs and response functions for beech are not presented.

#### 4. Discussion

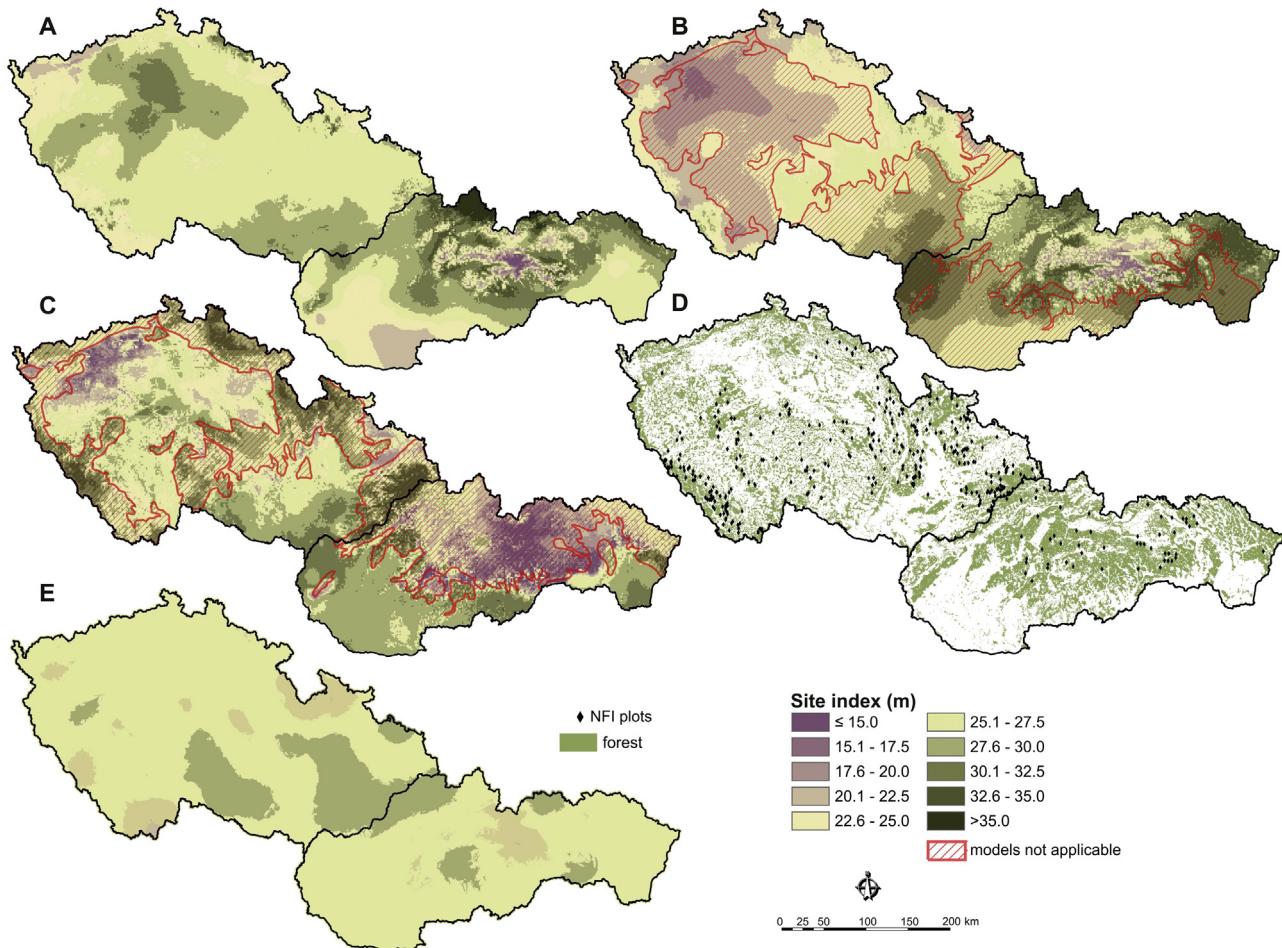
While the quantity and diversity of forestry and environmental data have been increasing, the ecological patterns in these datasets and the limits of the datasets are largely unexplored. In the current study, we attempted to identify the main climatic drivers of the productivity of three temperate tree species. We also strived to determine whether the SI values collected in the two central European NFIs are sufficiently sensitive to capture the response of site productivity to climate. The main findings, which are considered in greater detail in the remaining Discussion, were as follows:

- The sensitivity of SI to climate depended on the tree species, i.e., SI was responsive to climate for spruce and fir but not for beech. Because beech is thought to be very sensitive to climate, this result is surprising and requires explanation.
- The response of SI to climate differed in different parts of each species' range, but our hypothesis that water availability-related drivers would dominate on the dry part of the range, and vice versa, was not confirmed. Whether this result has an ecological or methodological explanation warrants consideration.
- The presented models were developed with NN-based algorithms, which are not commonly used in forestry research. Whether the advantages of using NN models (e.g. noise tolerance, robustness of predictions, etc.) outweigh their disadvantages or limits warrants consideration.

#### 4.1. Ecological inferences

##### 4.1.1. Norway spruce

For spruce, the climate predictors used in this study explained 38% of SI variability in the moister part of range (the MPR), which supports our inferences on the effect of individual predictors for a major part of the spruce range in the study region. On the other hand, the climate predictors explained very little of SI variability in the dry part (the DPR) of the spruce range. That the climatic drivers of tree growth and productivity change along ecological gradients is well recognized at many scales (Churkina and Running, 1998; Way and Oren, 2010; Nishimura and Laroque, 2011). Andreassen et al. (2006), for example, reported that spruce growth was affected by June precipitation in lowlands and by June temperatures at high elevations in Norway. Still, the poor relationship between SI and climate predictors in the DPR for spruce is surprising, especially because the data available for the analysis were abundant. Moreover, there is no reason to suspect that data quality was lower in the DPR than in the other regions or that spruce growth could have been affected by some driver that acted in DPR only (for example management practise differing from the rest of the range). We hypothesize that spruce, which is sensitive to low water availability (Zang et al., 2012; Boden et al., 2014), may have shown a more variable response in the DPR than in the MPR. The likely reason is that the DPR contains a lowland to hilly relief with high inter-plot variability in water regime, which could have overridden the main climatic signal. Spruce climatic unresponsiveness in the DPR indicates that the NFI data may have limited usefulness for assessing the effects of climate on spruce productivity in drier environments, where spruce has been extensively planted in the past (Ellenberg, 1986; Spiecker et al., 2004; Hlásny and Sitková, 2010). This is particularly disturbing given the projected expansion of the Mediterranean climates to central Europe (Alessandri



**Fig. 5.** Prediction maps of the fir site index based on the ensemble of neural network-based regression models. Prediction of models parameterized using the dataset covering (A) the whole range of fir in the investigated region, (B) the moister part of the range, and (C) the drier part of the range. (D) The distribution of the inventory plots used in this study; and (E) a map produced by interpolation of the measured site index values.

**Table 8**  
Average Pearson correlation coefficients between observed and predicted site index values for beech. The coefficients were calculated based on a number of neural network-based regression models for the parameterization, testing, and validation datasets. The results are indicated separately for models designed for the whole range of beech in the investigated territory (WR), for the moister part of the range (MPR), and for the drier part of the range (DPR).

Geographical range of the beech datasets	No. of models	Correlation coefficients		
		Parameterization	Testing	Validation
WR	15	-0.03	-0.01	0.20
MPR	15	0.24	0.13	0.20
DPR	15	-0.05	-0.09	0.49

et al., 2014), which can make spruce growth and productivity very hardly predictable.

Substantial differences in productivity drivers along climatic gradients also highlight the limits to the use of regional productivity models (Bošel'a et al., 2013a; Hägglund, 1981; Socha, 2008), which do not consider such differential responses. Relative to our results, results of ecophysiological studies (e.g., Ditmarová et al., 2010; Ježík et al., 2015) and dendroecological studies (e.g., Zang et al., 2014), which better control for inter-plot variability, indicated a strong response of spruce to both observed and simulated drought. Obviously, such a tree-scale or stand-scale response did not translate to the regional scale that was investigated in the current study.

Comparing the percentage of variance explained by the predictors in the current study and in other studies is difficult, because differences in experimental design and data quality might significantly affect the predictive power of growth-climate models (Yang

et al., 2015). In Slovakia, for example, Bošel'a et al. (2013a) found that 76% of the variability in spruce SI in the NFI plots was explained by three climate variables, soil acidity, and the carbon:nitrogen ratio. Surprisingly, a low  $R^2$  value (0.39) was reported by Albert and Schmidt (2010), who used four climatic and three non-climatic variables to predict the spruce SI in Lower Saxony, Germany.

In the current study, a combination of several temperature- and water regime-related variables was found to control spruce productivity in the MPR and to a lesser extend in the WR. Because of the moderate inter-model differences in predictor importance, no single variable could be identified as the most influential. The distinct unimodal response of the spruce SI to the four most influential predictors indicated both the substantial climatic gradient covered by the data, including the suboptimal conditions in the dry-warm and cool-moist part of the range, and strong climatic signal in the SI. This pattern was also evident in the prediction maps, which

clearly discriminated between the mountain and lowland locations where the predicted SI was as much as 15–20 m; in locations where production was highest, the predicted SI ranged from 30 to 35 m.

#### 4.1.2. Silver fir

The fir models were based on much less data than the spruce models, and this could reduce the performance of the fir models. Because fir in the study region occurs mostly as the admixture species, the distribution of NFI plots with fir was rather scattered, and the coverage of climatic gradients by the plots was poorer than for spruce. Contrary to the spruce models, the performance of fir models evaluated at the validation set indicated that the fir SI was more responsive in the DPR than in the MPR or WR, i.e., climate explained 21% of the SI variation in the validation dataset for DPR but only 5–6% of the SI variation in the validation dataset for WR and MPR. However, fir model performance for the MPR and DPR evaluated for parametrization and testing datasets was well balanced, with  $R^2$  ranging from 15% to 20%; therefore, if we relax on the performance for validation dataset, we find that the intensity of climatic effect on fir productivity is equal throughout the range of the species' distribution in the CZ and SK. The poor performance for the WR in all datasets (parameterization, testing, and validation), however, indicates that there are differences in productivity drivers along the climatic gradient and that models based on the mixture of wet and dry sites should be avoided for fir.

The most influential variables were the temperature for the coldest and the warmest months (T-WarmM and T-ColdM) and the continentality index K; the tendency for SI to increase from west to east was clearly evident in the prediction maps. Continentality was found to affect the growth and productivity of various fir species in diverse environments, including, for example, Balsam fir (*Abies balsamea* L. Mill.) and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) in Canada (Nishimura and Laroque, 2011; Splechtna, 2001). Therefore, we recommend that future studies consider some indicator of climatic continentality along with temperature-related variables as predictors of fir growth and productivity.

#### 4.1.3. European beech

The lack of relationships between the predictors used in this study and beech SI was surprising because beech climatic sensitivity and productivity responsiveness have been repeatedly documented (Fotelli et al., 2009; Mellert et al., 2016; Mette et al., 2013). In the study of Albert and Schmidt (2010) mentioned earlier, for example, the predictors accounted for the 34% of the variation in beech SI. For these reasons, we suspect that methodological difficulties related to height measurement and age identification using the increment cores may have reduced the quality of the beech data used in the current study. This suggests that SI measured in the NFI plots for beech should be used with caution and that other datasets or productivity indicators should be considered.

### 4.2. Methodological assets and limitations

Our study benefited from a dense network of NFIs that covered a substantial climate gradient. The plots, however, contained only a single observation (i.e., only one NFI cycle), and this might have introduced substantial noise related to inter-plot differences in site conditions, genotype, effect of small-scale stress pulses, etc. (Bontemps and Bouriaud, 2013; Zang et al., 2014; Cook, 1990). Moreover, the noise is likely to be amplified by measurement errors (Goelz and Burk, 1996). The length of available climate time series, which covered only a part of the lifespan of investigated forest stands, could also reduce the strength of climatic signal in the data. We attempted to reduce such effects by carefully selecting plots used for the analyses, which resulted in a substantial reduction of the original number of plots in the two NFIs. The use of NN mod-

elling, which is thought to perform well with the noise-containing data (Bishop, 1995; Minnix, 1992), was another way of coping with this problem.

The two criteria applied to select a subset of plots to be used for the analyses concerned tree age and number of trees in a plot for a particular species. Regarding the age criterion, numerous studies have revealed that SI decreases with stand age (Albert and Schmidt, 2010; Nothdurft et al., 2012; Sharma et al., 2012; Socha, 2008; Socha et al., 2016), which might limit the value of SI as an unbiased indicator of productivity. This decline in SI can be explained by changes in site and climate conditions over time (e.g., Bontemps and Bouriaud, 2013; Sharma et al., 2012), or more likely, by the fact that highly productive forest stands in rotation forestry (with rotation period ranging from 100 to 120 years) are usually removed earlier than less productive stands (Nothdurft et al., 2012; Yue et al., 2014). We attempted to reduce this effect and effect of extrapolation of the SI for stands with ages significantly different from 100 years by limiting the age of the investigated plots to 75–125 years. Regarding the plot size criterion, some plots contained too few trees of a species to enable the reliable assessment of stand height (García, 2010; Sharma et al., 2012). To cope with the trade-off between the acceptable number of trees to be used for SI assessment and the reduction in the number of plots that could be used in our analyses, we arbitrarily selected five trees per species as the minimum number, i.e., we excluded plots that had fewer than five trees of the species in question.

We identified the variables that most influenced SI variability by using sensitivity analysis, there are, however, limitations to the interpretation of so identified causal effects. Our research assessed empirical associations in the investigated system, an approach that might provide only limited insight into the processes generating the observed productivity patterns (Adams et al., 2013; Pretzsch et al., 2015). For example, Ellenberg quotient, which was among the influential variables for spruce, was highly correlated with the annual precipitation and with some snow regime-related variables (Appendix B). This suggests that variables with different physiological effects might exhibit similar spatial patterns, which is the fact that cannot be reasonably approached by statistical models. Despite this limitation, the models developed here have provided useful information on the effect of climate on forest productivity at a regional scale, and the results can help other researches select which climate predictors to consider when designing climate-productivity models. In addition, the models developed here can be embedded in empirical forest models (Pretzsch et al., 2008; Trasobares et al., 2016).

Although we have previously explained why NN models were used in this study (noise tolerance, anticipated multivariate nonlinearities, etc.), the training and interpretation phases contained several innovative or questionable aspects that should be discussed. The iterative search for optimal neuron weights that minimizes the difference between measured and predicted SI (i.e., model training) can be time-consuming, which has caused some authors to criticize NN-based approaches (e.g., Aerts et al., 2010; Moisen and Frescino, 2002). We argue, however, that this problem is not severe because computers are increasingly powerful and because NN models are well-suited for the parallel processing (Povey et al., 2015; Scanzio et al., 2010), which can be used to train a large number of complex models in a reasonable time. Moreover, training algorithms have also undergone substantial development (Askarzadeh and Rezazadeh, 2013; Taylor et al., 2016) and, for example, the training of 3000 NN models for spruce required about 40 min using a personal computer in the current study. The problem seems even less distinct in light of the benefits, which include the obtaining of a good fit to the data, good control of overfitting, and high prediction performance.

An obvious disadvantage of NN models is that the final model is in the form of a specialized script (e.g., in PMM language in the current study; Grossman et al., 2002) rather than in the form of an equation that can be directly embedded into any data-processing environment. This can limit the use of NN models for some applications.

Regarding the efficiency of NN models relative to the efficiency of other methods, Aertsen et al. (2010) compared the use of five statistical methods, including NN models, for developing a model of SI for three tree species and an array of environmental variables. Although the NN models performed best in terms of the RMSE, R<sup>2</sup>, and coefficient of efficiency (Nash and Sutcliffe, 1970), the authors finally penalized the NN models for the questionable reasons such as their “black box” nature and their high complexity. Similarly, Moisen and Frescino (2002) compared the ability of five statistical approaches to predict six forest characteristics. Although the NN models and multivariate adaptive regression splines (MARS) provided “tremendous advantages” over the remaining techniques when tested with simulated (i.e. not measured) data, the authors expressed reservations regarding the use of NN models, mainly because of the high computational demands. As we have noted, however, such demands have become less problematic as computer performance has substantially increased.

This study used a multi-model approach, i.e., we preserved a number of well-performing models and determined for each model the ranges of R<sup>2</sup> values, ranges of SSs, and the ranks of climate predictors. Finally, we used the models to produce the CV% maps that showed the inter-model variability in predicting the spatial distribution of SI values. Such a multi-model approach increased the robustness of our inferences and revealed variables or locations requiring caution because of excessive uncertainty. These benefits of a multi-model approach are seldom achieved with standard, single-model approaches. On the other hand, our multi-model approach introduced some uncertainty into the interpretations and can make the interpretation of our findings difficult.

**Table A1**

The initial set of climate variables, which were considered for the use in the analysis of climatic control over productivity of forest tree species in Central Europe.

No.	Variable	Type*	Code	Description/[units]	Used**
1.	Annual mean air temperature	T	T-AVG	-/[^°C]	+
2.	Mean temperature of the coldest month	T	T-ColdM	-/[^°C]	+
3.	Mean temperature of the warmest month	T	T-WarmM	-/[^°C]	+
4.	No. of days in July with max. daily temperature > 32 °C	T	Tmax32.July	-/[^°C]	-
5.	No. of tropical days	T	TropDays	Average no. of days with max. daily temperature > 30 °C/[^°C]	-
6.	No. of frost days	T	FrostDays	Average no. of days with min. daily temperature < 0 °C/[^°C]	-
7.	Temperature amplitude I	K	T.ampl.year	Difference between annual minimum and maximum daily temperature in a year/[^°C]	+
8.	Temperature amplitude II	K	T.ampl.month	Difference between annual temperature of the warmest and coldest month/[^°C]	-
9.	Heatwave length I	T	HeatWaves	Tmax > = 30 °C during the consecutive (at least) three days AND average Tmax during the heat wave > = 30 °C AND no single day in a heat wave is Tmax < 25 °C/[days]	+
10.	Heatwave length II	T	HeatWaves.L	Average lenght of a heat wave/[days]	+
11.	Number of days in heatwave	T	HeatWaves-D	Average no. of days in a heat wave/[days]	+
12.	Probability of heatwave	T	HeatWaves.P	Probability of heatwave occurrence in a year/[%]	-
13.	Growing season length	T	VegSeason	Average no. of days in a year with a 24-h mean temperature > 10 °C/[days]	-
14.	Annual precipitation	P	P-sum	-/[mm]	-
15.	No. of days in a dry period	P	P-0-10days	Average no. of days with precipitation 0 mm for more than 10 days/[days]	+
16.	No. of days with snow cover > 3 cm	P	DaySnow3	Average no. of days with snow depth > 3 cm/[days]	-
17.	No. of days with snow depth > 10 cm	P	DaySnow10	Average no. of days with snow depth > 10 cm/[days]	-
18.	No. of days with snow depth > 30 cm	P	DaySnow30	Average no. of days with snow depth > 30 cm/[days]	-
19.	No. of days with snow depth > 3 cm and Tmin > 10 °C	T/P	DaySnow.L3.Tmin10	Average no. of days with snow depth > 3 cm and min. daily temperature > 10 °C/[days]	+
20.	Snow depth 1st February	P	Snow.Feb1	Average snow depth on Feb. 1/[cm]	-
21.	Snow depth 1st March	P	Snow.March1	Average snow depth on March 1/[cm]	+
22.	Snow depth 1st April	P	Snow.April1	Average snow depth on April 1/[cm]	-
23.	Ellenberg climatic quotient	T/P	EQ	T-WarmM P-sum <sup>-1</sup> /[^°C mm <sup>-1</sup> ]	+

## 5. Conclusions

Although NFIs collect huge amounts of data, the use of such data for the improvement of forest management and research is generally insufficient. Therefore, we presented an innovative approach for investigating climate-productivity interactions in the under-researched environment of Central Europe. Using the NFI data concerning the productivity of spruce, fir, and beech from the Czech Republic and Slovakia, we assessed the sensitivity of the NFI data to climate, and we proposed a novel approach to analysing these data using a data mining technique. Some of the climate variables that we identified as most influential differ from the variables that are typically used in forest production research. These findings might inform other studies on suitable climate predictors and thus improve the performance of new climate-productivity models.

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## Appendix A. List of used climate variables.

Table A1 (Continued)

No.	Variable	Type*	Code	Description/[units]	Used**
24.	Gorcynski's continentality index	K	K	Ratio of T.Ampl.month and the inverse of the sine of the latitude (Gorcynski 1922)	+
25.	Effective radiation 5	R	egr_Srad_5	Average Effective Global Radiation for ETa/ETr > 0.4 AND Tmean >= 5 °C AND without snow AND SRAD > 5 mj m <sup>-2</sup> day <sup>-1</sup>	-
26.	Effective radiation 10	R	egr_Srad_10	Average Effective Global Radiation for ETa/ETr > 0.4 AND Tmean >= 5 °C AND without snow AND SRAD > 10 mj m <sup>-2</sup> day <sup>-1</sup>	+

\* T – temperature related variable, P – precipitation related variable, K – continentality related variable, R – radiation related variable.

\*\* The column indicates whether the variable was used in the regression modelling or discarded because of the redundancy with other variable(s) (+preserved, – removed).

## Appendix B. Redundancy control of the used climate variables.

Table B1

The original set of 26 climate variables, which were considered for the use in the regression modelling presented here. The table shows the results of redundancy testing. Rows contain the original 26 variables and columns contain variables with the Pearson's correlation above 0.9. Variable codes are indicated in Table A1; \*Number of redundancies; Grey cells indicate the preserved variables, empty cells indicate the discarded variables; RV1–9—Redundant Variable 1–9.

	Variable	No. of red.*	RV 1	RV 2	RV 3	RV 4	RV 5	RV 6	RV 7	RV 8	RV 9
1	T-AVG	0									
2	T-ColdM	3	FrostDays	DaySnow3	DaySnow10						
3	EGD-RAD5	1	EGD-RAD10								
4	Tmax32_July	3	TropDays	HeatWaves-P	HeatWaves-L						
5	DSnow_L3_Tmin10	0									
6	TropDays	4	Tmax32_July	HeatWaves-P	HeatWaves-L	T-WarmM					
7	T_ampl	0									
8	P-sum	5	DaySnow10	DaySnow30	Snow-Feb1	Snow-March1	EQ				
9	P-0-10days	0									
10	HeatWaves	0									
11	FrostDays	3	T-ColdM	VegSeason	T-WarmM						
12	DaySnow3	8	T-ColdM	DaySnow10	DaySnow30	Snow-April1	Snow-Feb1	Snow-March1	VegSeason	EQ	
13	DaySnow10	9	T-ColdM	P-sum	DaySnow3	DaySnow30	Snow-April1	Snow-Feb1	Snow-March1	VegSeason	EQ
14	DaySnow30	6	P-sum	DaySnow3	DaySnow10	Snow-April1	Snow-Feb1	Snow-March1			
15	Snow-April1	6	DaySnow3	DaySnow10	DaySnow30	Snow-Feb1	Snow-March1	VegSeason			
16	Snow-Feb1	6	P-sum	DaySnow3	DaySnow10	DaySnow30	Snow-April1	Snow-March1			
17	Snow-March1	6	P-sum	DaySnow3	DaySnow10	DaySnow30	Snow-April1	Snow-Feb1			
18	VegSeason	5	FrostDays	DaySnow3	DaySnow10	Snow-April1	T-WarmM				
19	HeatWaves-P	3	Tmax32_July	TropDays	HeatWaves-L						
20	HeatWaves-L	3	Tmax32_July	TropDays	HeatWaves-P						
21	HeatWaves-D	0									
22	T-WarmM	3	TropDays	FrostDays	VegSeason						
23	EGD-RAD10	1	EGD-RAD5								
24	EQ	3	P-sum	DaySnow3	DaySnow10						
25	Range_Tm	1	K(Grodzinski)								
26	K(Grodzinski)	1	Range_Tm								

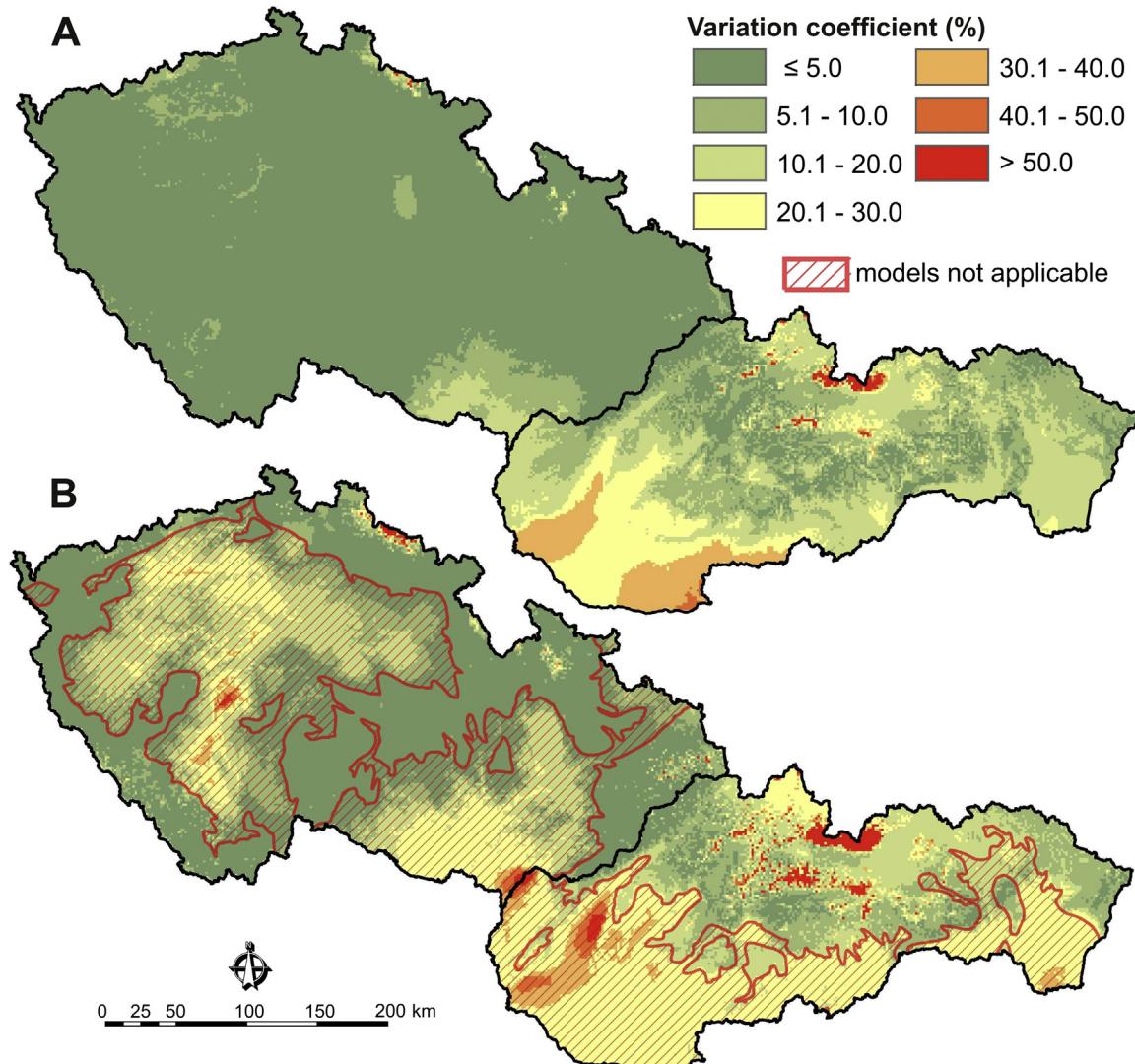
Table B2

Correlation matrix of climate variables, which passed the redundancy test and were used in the regression modelling. Colours indicate the magnitude (intensity) and direction (blue – positive, red – negative) of correlation coefficients.

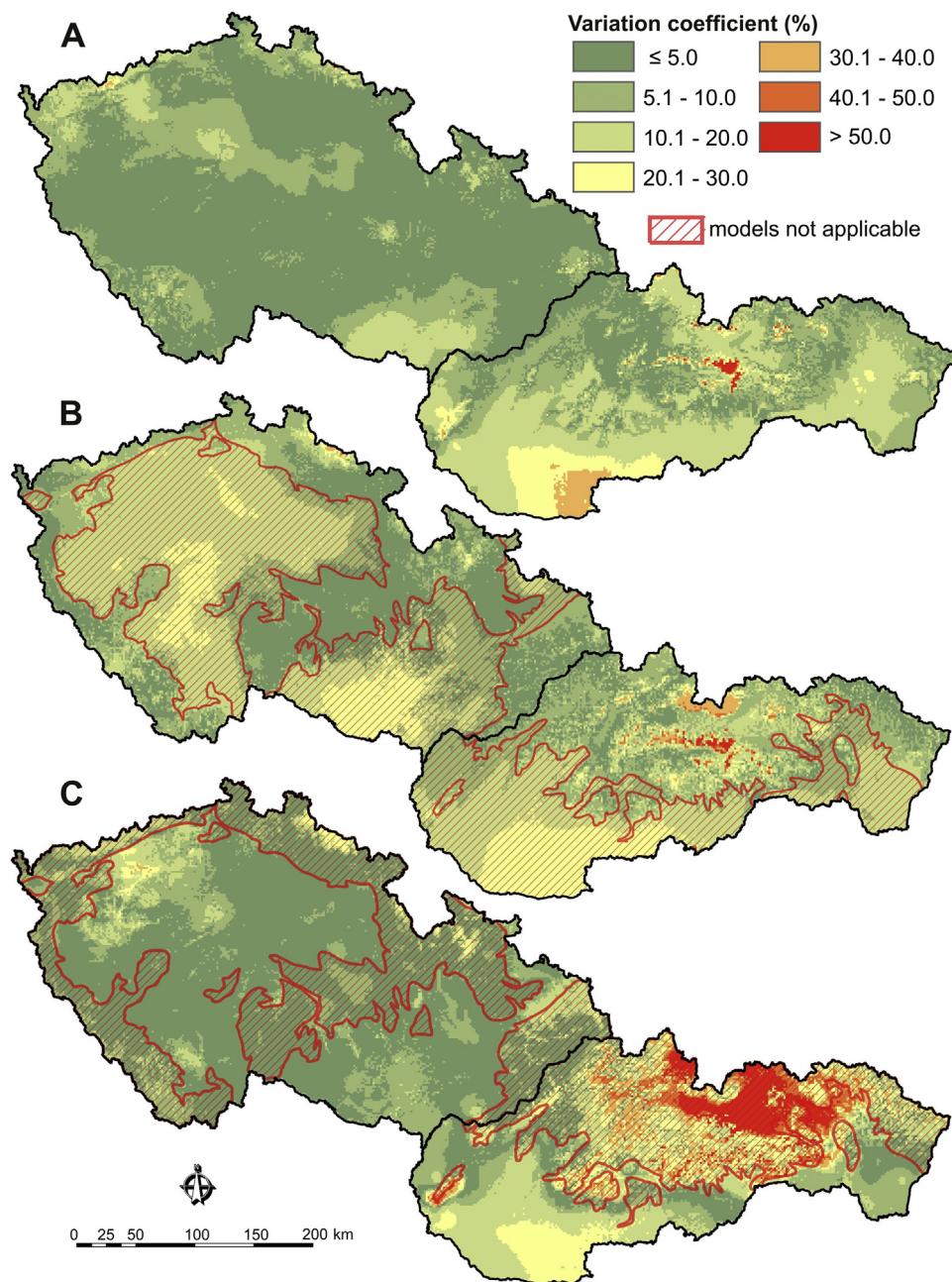
Variable	T-AVG	T-ColdM	DSnow_L3_Tmin10	T_ampl	P0-10days	HeatWaves	Snow-March1	HeatWaves-L	HeatWaves-D	T-WarmM	EGD-RAD10	EQ	K
T-AVG	1.00	0.52	0.71	0.44	0.82	0.38	-0.56	0.86	0.27	0.76	-0.30	0.64	0.76
T-ColdM	0.52	1.00	0.56	0.62	0.49	0.89	-0.84	0.79	0.51	0.86	-0.25	0.81	0.29
DSnow_L3_Tmin10	0.71	0.56	1.00	0.72	0.68	0.39	-0.72	0.67	0.23	0.63	-0.17	0.68	0.50
T_ampl	0.44	0.62	0.72	1.00	0.34	0.51	-0.71	0.54	0.35	0.57	-0.04	0.54	0.31
P-0-10days	0.82	0.49	0.68	0.34	1.00	0.44	-0.63	0.71	0.41	0.74	-0.30	0.70	0.78
HeatWaves	0.38	0.89	0.39	0.51	0.44	1.00	-0.77	0.68	0.59	0.82	-0.22	0.75	0.34
Snow-March1	-0.56	-0.84	-0.72	-0.71	-0.63	-0.77	1.00	-0.72	-0.52	-0.84	0.18	-0.87	-0.48
HeatWaves-L	0.86	0.79	0.67	0.54	0.71	0.68	-0.72	1.00	0.34	0.87	-0.36	0.82	0.59
HeatWaves-D	0.27	0.51	0.23	0.35	0.41	0.59	-0.52	0.34	1.00	0.60	-0.17	0.49	0.44
T-WarmM	0.76	0.86	0.63	0.57	0.74	0.82	-0.84	0.87	0.60	1.00	-0.29	0.85	0.72
EGD-RAD10	-0.30	-0.25	-0.17	-0.04	-0.30	-0.22	0.18	-0.36	-0.17	-0.29	1.00	-0.42	-0.20
EQ	0.64	0.81	0.68	0.54	0.70	0.75	-0.87	0.82	0.49	0.85	-0.42	1.00	0.54
K	0.76	0.29	0.50	0.31	0.78	0.34	-0.48	0.59	0.44	0.72	-0.20	0.54	1.00

### Appendix C. Inter-model variability of the predicted Site Index values.

See Figs C1 and C2



**Fig. C1.** Coefficient of variation of spruce site index calculated based on 11 and 13 SI predictions generated by the Neural Networks-based regression models. The maps are based on the regression models parameterized using the data for the whole spruce range in the investigated territory (A) and for the moister part of range (B). Map for the drier part of range is not presented because of poor models performance. The red polygon indicates the drier part of the territory, where the model is not applicable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. C2.** Coefficient of variation of fir site index calculated based on 3, 10 and 3 SI predictions generated by the Neural Networks-based regression models. The maps are based on the regression models parameterized using the data for the whole fir range in the investigated territory (A), for the moister (B) and for the drier part of range (C). The red polygon indicates that part of the territory, where the model is not applicable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### Appendix D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2016.12.024>.

#### References

- Adams, H.D., Williams, a. P., Xu, C., Rauscher, S.A., McDowell, N.G., 2013. Empirical and process-based approaches to climate-induced forest mortality models. *Front. Plant. Sci.* 4, 438.
- Aertszen, W., Kint, V., van Orshoven, J., Özkan, K., Muys, B., 2010. Comparison and ranking of different modelling techniques for prediction of site index in Mediterranean mountain forests. *Ecol. Modell.* 221, 1119–1130.
- Albert, M., Schmidt, M., 2010. Climate-sensitive modelling of site productivity relationships for Norway spruce (*Picea abies* (L.) Karst.) and common beech (*Fagus sylvatica* L.). *For. Ecol. Manage.* 259, 739–749.
- Alessandri, A., De Felice, M., Zeng, N., Mariotti, A., Pan, Y., Cherchi, A., Lee, J.I., Wang, B., Ha, K.J., Ruti, P., Artela, V., 2014. Robust assessment of the expansion and retreat of Mediterranean climate in the 21st century. *Nat. Sci. Rep.* 4, 7211.
- Andreasen, K., Solberg, S., Tveito, O.E., Lystad, S.L., 2006. Regional differences in climatic response of Norway spruce (*Picea abies* L. Karst) growth in Norway. *For. Ecol. Manage.* 222, 211–221.
- Antón-Fernández, C., Mola-Yudego, B., Dalsgaard, L., 2016. Climate sensitive site index models for Norway. *Can. J. For. Res.* 33, 1–33.
- Askarzadeh, A., Rezazadeh, A., 2013. Artificial Neural Network training using a new efficient optimization algorithm. *Appl. Soft Comput.* 13 (2), 1206–1213.
- Büntgen, U., Tegel, W., Kaplan, J.O., Schaub, M., Hagedorn, F., Bürgi, M., Brázdil, R., Helle, G., Carrer, M., Heussner, K.U., Hofmann, J., Kontic, R., Kyncl, T., Kyncl, J., Camarero, J.J., Tinner, W., Esper, J., Liebold, A., 2014. Placing unprecedented recent fir growth in a European-wide and Holocene-long context. *Front. Ecol. Environ.* 12, 100–106.

- Becknell, J.M., Desai, A.R., Dietze, M.C., Schultz, C.A., Starr, G., Duffy, P.A., Franklin, J.F., Pourmokhtarian, A., Hall, J., Stoy, P.C., Binford, M.V., Boring, L.R., Staudhammar, C.L., 2015. *Assessing interactions among changing climate management, and disturbance in forests: a macrosystems approach.* BioScience 65, 263–274.
- Bishop, C., 1995. *Neural Networks for Pattern Recognition.* University Press, Oxford.
- Bošel'a, M., Máliš, F., Kulla, L., Šeben, V., Deckmyn, G., 2013a. Ecologically based height growth model and derived raster maps of Norway spruce site index in the Western Carpathians. Eur. J. For. Res. 132, 691–705.
- Bošel'a, M., Petráš, R., Šeben, V., Mecko, J., Marušák, R., 2013b. Evaluating competitive interactions between trees in mixed forests in the Western Carpathians: comparison between long-term experiments and SIBYL simulations. For. Ecol. Manage. 310, 577–588.
- Bošel'a, M., Petráš, R., Sitková, Z., Priwitzer, T., Pajtik, J., Hlavatá, H., Sedmák, R., Tobin, B., 2014. Possible causes of the recent rapid increase in the radial increment of silver fir in the Western Carpathians. Environ. Pollut. 184, 211–221.
- Bošel'a, M., Štefančík, I., Petráš, R., Vacek, S., 2016. The effect of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. Agric. For. Meteorol. 222, 21–31.
- Boden, S., Kahle, H.P., Wilpert, K., Spiecker, H., 2014. Resilience of Norway spruce (*Picea abies* (L.) Karst) growth to changing climatic conditions in Southwest Germany. For. Ecol. Manage. 315, 12–21.
- Bontemps, J.D., Bouriaud, O., 2013. Predictive approaches to forest site productivity: recent trends, challenges and future perspectives. Forestry 87, 109–128.
- Briner, S., Elkin, C., Huber, R., 2013. Evaluating the relative impact of climate and economic changes on forest and agricultural ecosystem services in mountain regions. J. Environ. Manage. 129, 414–422.
- Brovkin, V., Raddatz, T., Reick, C.H., Claussen, M., Gayler, V., 2009. Global biogeophysical interactions between forest and climate. Geophys. Res. Lett. 36, 1–6.
- Charru, M., Seynave, I., Morneau, F., Bontemps, J.D., 2010. Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. For. Ecol. Manage. 260, 864–874.
- Churkina, G., Running, S.W., 1998. Contrasting climatic controls on the estimated productivity of global terrestrial biomes. Ecosystems 1, 206–215.
- Cook, E.R., 1990. A Conceptual Linear Aggregate Model for Tree Rings. In: Cook, E.R., Kairiukstis, L.A. (Eds.). Kluwer, Dordrecht, pp. 98–104.
- Coops, N.C., Waring, R.H., Law, B.E., 2005. Assessing the past and future distribution and productivity of ponderosa pine in the Pacific Northwest using a process model, 3-PG. Ecol. Mod. 183, 107–124.
- Cybenko, G., 1989. Approximations by superpositions of sigmoidal functions. Math. Control Signals Syst. 2 (4), 303–314.
- Czúcz, B., Gálhidy, L., Mátyás, C., 2011. Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in Central Europe. Ann. For. Sci. 68, 99–108.
- Ditmarová, L., Kurjak, D., Palmroth, S., Střelcová, K., 2010. Physiological responses of Norway spruce (*Picea abies*) seedlings to drought stress. Tree Physiol. 30, 205–213.
- Eichhorn, F., 1904. Beziehungen zwischen bestandshöhe und bestandsmasse. All. For. Jagd-Zeit. 80, 45–49.
- Ellenberg, H., 1986. *Vegetation Mitteleuropas Mit Den Alpen*, 4th ed. Fischer, Stuttgart.
- Elling, W., Dittmar, Ch., Pfaffelmoser, K., Roetzer, T., 2009. Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. For. Ecol. Manage. 257, 1175–1187.
- Fang, J., Lechowicz, M.J., 2006. Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. J. Biogeogr. 33, 1804–1819.
- Fotelli, M.N., Nahm, M., Radoglou, K., Rennenberg, H., Halyvopoulos, G., Matzarakis, A., 2009. Seasonal and interannual ecophysiological responses of beech (*Fagus sylvatica*) at its south-eastern distribution limit in Europe. For. Ecol. Manage. 257, 1157–1164.
- Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A.H., Ståhl, G., 2014. Adapting National Forest Inventories to changing requirements – the case of the Swedish National Forest Inventory at the turn of the 20th century. Silva Fenn. 48, 1–29.
- García, O., 2010. Dynamical implications of the variability representation in site-index modelling. Eur. J. For. Res. 130, 671–675.
- Gasparini, P., Di Cosmo, L., Cenni, E., Pompei, E., Ferretti, M., 2013. Towards the harmonization between National Forest Inventory and Forest Condition Monitoring. Consistency of plot allocation and effect of tree selection methods on sample statistics in Italy. Environ. Monit. Assess. 185, 6155–6171.
- Gazol, A., Camarero, J.J., Gutiérrez, E., Popa, I., Andreu-Hayles, L., Motta, R., Nola, P., Ribas, M., Sangüesa-Barreda, G., Urbinati, C., Carrer, M., 2015. Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. J. Biogeogr. 42, 1150–1162.
- George, J.P., Schueler, S., Karanitsch-Ackerl, S., Mayer, K., Klumpp, R.T., Grabner, M., 2015. Inter- and intra-specific variation in drought sensitivity in *Abies* spec and its relation to wood density and growth traits. Agric. For. Meteorol. 214–215, 430–443.
- Goetz, J.C.G., Burk, T.E., 1996. Measurement error causes bias in site index equations. Can. J. For. Res. 26, 1585–1593.
- Goovaerts, P., 2000. Geostatistical approaches for incorporating elevation into the spatial interpolation of rainfall. J. Hydrol. 228, 113–129.
- Grossman, R.L., Bailey, S., Ramu, A., Qin, X., 2002. The management and mining of multiple predictive models using the predictive modelling markup language. Inf. Softw. Technol. 41, 589–595.
- Hägglund, B., 1981. Evaluation of forest site productivity. For. Abst. 42, 516–527.
- Halaj, J., Patrás, R., 1998. *Growth Tables of Main Tree Species* (in Slovak). Slovak Academic Press, Bratislava.
- Hanewinkel, M., Hummel, S., Cullmann, D.A., 2010. Modelling and economic evaluation of forest biome shifts under climate change in Southwest Germany. For. Ecol. Manage. 259, 710–719.
- Hanewinkel, M., Cullmann, D.A., Schellhaas, M.J., Nabuurs, G.J., Zimmermann, N.E., 2012. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Change 3, 203–207.
- Haykin, S., 1994. *Neural Networks: A Comprehensive Foundation.* Macmillan Publishing, New York.
- Hlásny, T., Sitková, Z., 2010. Spruce Forests Decline in the Beskids. National Forest Centre – Forest Research Institute Zvolen & Czech University of Life Sciences Prague & Forestry and Game Management Research Institute, Jílově – Stradný, Zvolen, Slovakia.
- Hlásny, T., Turčáni, M., 2013. Persisting bark beetle outbreak indicates the unsustainability of secondary Norway spruce forests: case study from Central Europe. Ann. For. Sci. 70, 481–491.
- Hlásny, T., Kříšek, Š., Holuša, J., Trombík, J., Urbaňcová, N., 2011. Snow disturbances in secondary Norway spruce forests in Central Europe: regression modelling and its implications for forest management. For. Ecol. Manage. 262, 2151–2161.
- Hlásny, T., Barcza, Z., Barka, I., Merganičová, K., Sedmák, R., Kern, A., Pajtik, J., Baláz, B., Fabrika, M., Churkina, G., 2014a. Future carbon cycle in mountain spruce forests of Central Europe: modelling framework and ecological inferences. For. Ecol. Manage. 328, 55–68.
- Hlásny, T., Barka, I., Sitková, Z., Bucha, T., Konopka Lukáč, M.M., 2014b. MODIS based vegetation index has sufficient sensitivity to indicate stand-level intra-seasonal climatic stress in oak and beech forests. Ann. For. Sci. 72, 109–125.
- Hudson, G., Wackernagel, H., 1994. Mapping temperature using kriging with external drift: theory and an example from Scotland. Int. J. Climatol. 14, 77–91.
- Hunter, A., Kennedy, L., Henry, J., Ferguson, I., 2000. Application of neural networks and sensitivity analysis to improved prediction of trauma survival. Comput. Methods Prog. Biomed. 62, 11–19.
- Jahn, G., 1991. Temperate deciduous forests of Europe. In: Rohrig, E., Ulrich, B. (Eds.), *Ecosystems of the World*. Elsevier, London, pp. 377–502.
- Ježík, M., Blaženec, M., Letts, M.G., Ditmarová, L., Sitková, Z., Střelcová, K., 2015. Assessing seasonal drought stress response in Norway spruce (*Picea abies* (L.) Karst.) by monitoring stem circumference and sap flow. Ecohydrology 8, 378–386.
- Jensen, L.U., Lawesson, J.E., Balslev, H., Forchhammer, M.C., 2004. Predicting the distribution of *Carpinus betulus* in Denmark with Ellenberg's climate quotient. Nord. J. Bot. 23, 57–67.
- Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Global Change Biol. 12, 2163–2174.
- Kint, V., Aertsen, W., Campioli, M., Vansteenkiste, D., Delcloo, A., Muys, B., 2012. Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. Clim. Change 115, 343–363.
- Korf, V., 1939. Contribution to mathematical definition of the law of stand volume growth (in Czech). Lesnická práce 18, 339–379.
- Kovač, M., Bauer, A., Ståhl, G., 2014. Merging national forest and national forest health inventories to obtain an integrated forest resource inventory – experiences from Bavaria, Slovenia and Sweden. PLoS One 9 (6), e100157.
- Löf, M., Bergquist, J., Brunet, J., Karlsson, M., Welander, N.T., 2010. Conversion of Norway spruce stands to broadleaved woodland – regeneration systems, fencing and performance of planted seedlings. Ecol. Bull. 53, 165–173.
- Lexer, M.J., Hönniger, K., Scheifinger, H., Matulla, C., Groll, N., Kromp-Kolb, H., Schadauer, K., Starlinger, F., Englisch, M., 2002. The sensitivity of Austrian forests to scenarios of climatic change: a large-scale risk assessment based on a modified gap model and forest inventory data. For. Ecol. Manage. 162, 53–72.
- Linares, J.C., Camarero, J.J., 2012. From pattern to process: linking intrinsic water-use efficiency to drought-induced forest decline. Global Change Biol. 18, 1000–1015.
- Matheron, G., 1973. The intrinsic random functions and their applications. Adv. Appl. Probab. 5, 439–468.
- Mellert, K.H., Ewald, J., Hornstein, D., Dorado-Liñán, I., Jantsch, M., Taeger, S., Zang, C., Menzel, A., Kölling, C., 2016. Climatic marginality: a new metric for the susceptibility of tree species to warming exemplified by *Fagus sylvatica* (L.) and Ellenberg's quotient. Eur. J. For. Res. 135, 137.
- Mette, T., Dolos, K., Meinardus, C., Bräuning, A., Reineking, B., Blaschke, M., Pretzsch, H., Beierkuhnlein, C., Gohlke, A., Wellstein, C., 2013. Climatic turning point for beech and oak under climate change in Central Europe. Ecosphere 4 (12), 145.
- Minnix, J.I., 1992. Fault-tolerance of the back propagation neural network trained on noisy inputs. In: Proceedings of the International Joint Conference on Neural Networks, Baltimore, MD, pp. 847–852.
- Moisen, G.G., Frescino, T.S., 2002. Comparing five modelling techniques for predicting forest characteristics. Ecol. Model. 157, 209–225.

- Nabuurs, G.-J., Lindner, M., Verkerk, P.J., Gunia, K., Deda, P., Michalak, R., Grassi, G., 2013. First signs of carbon sink saturation in European forest biomass. *Nat. Clim. Change* 9, 792–796.
- Nash, J.E., Sutcliffe, J.V., 1970. River flow forecasting through conceptual models 1: a discussion of principles. *J. Hydrol.* 10, 282–290.
- Neuner, S., Albrecht, A., Cullmann, D., Engels, F., Griess, V.C., Hahn, W.A., Hanewinkel, M., Härtl, F., Kölling, C., Staupendahl, K., Knoke, T., 2014. Survival of Norway spruce remains higher in mixed stands under a drier and warmer climate. *Global Change Biol.* 21, 935–946.
- Nishimura, P.H., Laroque, C.P., 2011. Observed continentality in radial growth-climate relationships in a twelve site network in western Labrador, Canada. *Dendrochronologia* 29, 17–23.
- Nothdurft, A., Wolf, T., Ringeler, A., Böhner, J., Saborowski, J., 2012. Spatio-temporal prediction of site index based on forest inventories and climate change scenarios. *For. Ecol. Manage.* 279, 97–111.
- Patterson, D., 1996. *Artificial Neural Networks*. Prentice Hall, Singapore.
- Peñuelas, J., Ogaya, R., Boada, M., Jump, A.S., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* 30, 829–837.
- Pourtaghhi, Z.S., Pourghasemi, H.R., Aretano, R., Semeraro, T., 2016. Investigation of general indicators influencing on forest fire and its susceptibility modelling using different data mining techniques. *Ecol. Indic.* 64, 72–84.
- Povey, D., Zhang, X., Khundanpur, S., 2015. Parallel training of DNNs with natural gradient and parameter averaging. *Neural Evol. Comput.*, arXiv.1410.7455.
- Pretzsch, H., Grote, R., Reineking, B., Rötzer, T., Seifert, S., 2008. Models for forest ecosystem management: a European perspective. *Ann. Bot.* 101, 1065–1087.
- Pretzsch, H., Dieler, J., Seifert, T., Rötzer, T., 2012. Climate effects on productivity and resource-use efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in stands with different spatial mixing patterns. *Trees* 26, 1343.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* 5, 4967.
- Pretzsch, H., Forrester, D.I., Rötzer, T., 2015. Representation of species mixing in forest growth models: a review and perspective. *Ecol. Modell.* 313, 276–292.
- Rivas-Martínez, S., Penas, A., Díaz, T.E., 2004. *Bioclimatic Map of Europe Bioclimates*. Cartographic Service, University of León, Spain.
- Saltelli, A., Chan, K., Scott, E.M., 2000. *Sensitivity Analysis*. John Wiley & Sons Publishers, New York.
- Sanquetta, C.R., Wojciechowski, J., Corte, A.P.D., Rodrigues, A.L., Maas, G.C.B., 2013. On the use of data mining for estimating carbon storage in the trees. *Carbon Balance Manage.* 8, 6.
- Scanzio, S., Sumani, S., Gemello, R., Mana, F., Laface, P., 2010. Parallel implementation of Artificial Neural Network training for speech recognition. *Pattern Recogn. Lett.* 31 (11), 1302–1309.
- Sedmák, R., Scheer, L., 2012. Modelling of tree diameter growth using growth functions parameterised by least squares and Bayesian methods. *J. For. Sci.* 58, 245–252.
- Sharma, R.P., Brunner, A., Eid, T., 2012. Site index prediction from site and climate variables for Norway spruce and Scots pine in Norway. *Scand. J. For. Res.* 27, 619–636.
- Skovsgaard, J.P., Vanclay, J.K., 2008. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. *Forestry* 81, 13–31.
- Skovsgaard, J.P., Vanclay, J.K., 2013. Forest site productivity: a review of spatial and temporal variability in natural site conditions. *Forestry* 86, 305–315.
- Socha, J., Coops, N.J., Ochal, W., 2016. Assessment of age bias in site index equations. *iForest* 9, 402–408.
- Socha, J., 2008. Effect of topography and geology on the site index of *Picea abies* in the West Carpathian, Poland. *Scand. J. For. Res.* 23, 203–213.
- Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J.P., Sterba, H., von Teuffel, K. (Eds.), 2004. Brill, Leiden.
- Splechtna, B.E., 2001. Height growth and site index models for Pacific silver fir in southwestern British Columbia. *B.C. J. Ecosyst. Manage.* 1, 1–14.
- Suvanto, S., Nöjd, P., Henttonen, H.M., Beuker, E., Mäkinen, H., 2016. Geographical patterns in the radial growth response of Norway spruce provenances to climatic variation. *Agric. For. Meteorol.* 222, 10–20.
- Taylor, G., Burmeister, R., Xu, Z., Singh, B., Patel, A., Goldstein, T., 2016. Training neural networks without gradients: a scalable ADMM approach. In: *Proceedings of the 33rd International Conference on Machine Learning*, New York, NY, USA, pp. 1–10.
- Tomppo, E., Olsson, H., Ståhl, G., Nilsson, M., Hagner, O., Katila, M., 2008. Combining national forest inventory field plots and remote sensing data for forest databases. *Remote Sens. Environ.* 112, 1982–1999.
- Trasobares, A., Zingg, A., Walther, L., Bigler, C., 2016. A climate-sensitive empirical growth and yield model for forest management planning of even-aged beech stands. *Eur. J. For. Res.* 135, 263–282.
- Vidal, C., Alberdi, I., Redmond, J., Vestman, M., Lanz, A., Schauder, K., 2016. The role of European National Forest Inventories for international forestry reporting. *Ann. For. Sci.* 73, 793–806.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Wamelink, G.W.W., Wiegers, H.J.J., Reinds, G.J., Kros, J., Mol-Dijkstra, J.P., van Oijen, M., de Vries, W., 2009. Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition on carbon sequestration by European forests and forest soils. *For. Ecol. Manage.* 258, 1794–1805.
- Way, D.A., Oren, R., 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiol.* 30, 669–688.
- Yang, J., Pedlar, J.H., McKenney, D.W., Weersink, A., 2015. The development of universal response functions to facilitate climate-smart regeneration of black spruce and white pine in Ontario, Canada. *For. Ecol. Manage.* 339, 34–43.
- Yue, C., Mäkinen, H., Klädtke, J., Kohnle, U., 2014. An approach to assessing site index changes of Norway spruce based on spatially and tempo – rally disjunct measurement series. *For. Ecol. Manage.* 323, 10–19.
- Zaki, M.J., Meira, W., 2014. *Data Mining and Analysis Fundamental Concepts and Algorithms*. Cambridge University Press.
- Zang, C., Pretzsch, H., Rothe, A., 2012. Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. *Trees – Struct. Funct.* 26, 557–569.
- Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., Menzel, A., 2014. Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. *Global Change Biol.* 20, 3767–3779.
- Zhou, X., Peng, C., Dang, Q.L., Chen, J., Parton, S., 2005. Predicting forest growth and yield in Northeastern Ontario using the process-based model of TRIPLEX 1.0. *Can. J. For. Res.* 35, 2268–2280.