Development of Individual Tree Growth and Yield Model Across Multiple Contrasting Species Using Non-parametric and Parametric Methods in the Hyrcanian Forests of Northern Iran

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Development of individual tree growth and yield model across multiple contrasting species using non-parametric and parametric methods in the Hyrcanian forests of northern Iran

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Abstract

Background

The Hyrcanian forests of Iran contain many species-rich communities that can only be maintained through an understanding of the renewal and development of these forests. Located in the Jojadeh section of the Farim forest in northern Iran, individual tree growth of five distinct species [(Oriental beech (*Fagus orientalis* Lipsky), chestnut-leaved oak (*Quercus castaneifolia* Coss. ex J.Gay), Persian maple (*Acer velutinum* Boiss.), common hornbeam (*Carpinus betulus* L.) and Caucasian alder (*Alnus subcordata* C.A.Mey.)] were measured on 313 permanent sample plots (0.1 ha) over a 10-year period (2003-2013).

Methods

In this analysis, various tree-level predictions were investigated using the available data with application of parametric models and two artificial neural networks (i.e., the multilayer perceptron (MLP) and radial basis function (RBF) networks).

Results

Individual tree diameter growth models showed a robust negative relationship with basal area in larger trees (BAL), which was relatively consistent across species. A total height model

indicated that the examined species did not differ for a given set of covariates. In the survival model, the survival probability of Oriental beech was lower than the other species, while the ingrowth model revealed sapling density of all species increased with the greater basal area. The artificial neural network based on the MLP was superior for all models and predicted more accurately than the RBF. Furthermore, the models based on the MLP were also superior to the parametric individual tree models developed using mixed-effect regression.

Conclusion

The use of these developed models in forest planning and management is imperative, but assessment of long-term projection behavior across the contrasting statistical approaches used is warranted despite the general superiority of the non-parametric models.

Keywords: diameter growth, height, survival, ingrowth, Artificial Neural Network, Mixed models, Permanent sample plots.

1. Introduction

Hyrcanian forests are the only commercial forests where temperate broad-leaved tree species exist today in Iran. Covering an area of approximately 1.85 million ha, the Hyrcanian forests account for approximately 15% of Iranian forests and 1.1% of the country's total area. These forests range from sea level up to an elevation of 2,800 m and comprise various forest types with no less than 80 woody species (trees and shrubs). Of these, Oriental beech (*Fagus orientalis* Lipsky), chestnut-leaved oak (*Quercus castaneifolia* Coss. ex J.Gay), Persian maple (*Acer velutinum* Boiss.), common hornbeam (*Carpinus betulus* L.) and Caucasian alder (*Alnus subcordata* C.A.Mey.) are among the main tree species in these forests. The Hyrcanian forests have been forestland since the third geological era and are considered to be one of the oldest forests in the world (Ahmadi et al., 2020). These forests thus are of significant concern to forest planners and policy makers charged with maintaining the

resilience of this important forest ecosystem to support and benefit human livelihoods in the 53
region. Whereas economic planning without consideration for sustaining renewable natural 54
resources can lead to their degradation that can ultimately contribute to the extinction of 55
nations and civilizations (Hatfield, 2015), decision-makers are no longer solely concerned 56
about economics and do increasingly take a broader, more holistic management perspective 57
(Vanclay, 1994). 58

In forestry, decision-making is the essence of a management plan that includes 59
prescribed activities, a schedule, and control measures aimed at achieving the stated 60
management objectives in a forest area (Bayat et al., 2013). Because multiple forest 61
management objectives often conflict at the landscape scale, a spatial approach to planning 62
uses a modeling technique that adapts spatially explicit stand management objectives to 63
minimize the conflicts at the landscape scale (Baskent & Keles, 2005). In addition to high- 64
quality inventory and survey data that describe the current forest condition, both planners and 65
managers thus require a description of the desired future conditions and acceptable alternative 66
future states. 67

To obtain the most reliable information on the likely future state of a forest, planners rely 68
on forecasts from growth and product models that are widely employed in forest management 69
(Bettinger et al., 2005; Weiskittel et al. 2011). Growth and product models predict the 70
dynamics of forests, including future forest growth and products that enable the study of 71
alternative management options/scenarios and have thus become a key element in sustainable 72
forest management planning (Burkhart, 1990; Vanclay, 1994; Bayat et al., 2013). For 73
example, sub-models for individual tree diameter/height growth, survival, and ingrowth 74
enabled the predictions of stand density and diameter distributions needed to guide the 75
management of uneven-aged forests in Finland (Pukkala et al., 2009, 2012). Further, harvest 76
intensities were based on height, survival, and growth of the regeneration in uneven mixed 77

softwood stands in Finland to ensure sufficient survival and growth of small spruces (*Picea* spp.), intolerant birch (*Betula* spp.) and pine (*Pinus* spp.) to maintain the species composition of the current selection stands (Eerikainen et al., 2014). Finally, mixed-effects regression models were recently developed to project the distance-independent individual tree growth and yield for uneven-aged forests in northern Iran managed under selection systems (Kalbi et al., 2019). In addition to the mentioned studies, other researches such as Ahmadi et al. (2016, 2020) have developed additional tree-level statistical models for the Hyrcanian forests.

To more fully understand the dynamics of forests, it is often not sufficient to solely model the overall growth of forest stands, but commonly more detailed individual-based modeling approaches are needed that effectively discriminate among several growth components (Vanclay 1994). This is especially true to support uneven-aged forest management in mixed natural stands, the following set of individual tree growth models is essential: diameter/height growth, tree mortality or survival, and estimates of ingrowth (Trasobares et al. 2004; Bayat et al., 2013). The models can be developed using a variety of statistical techniques, which are further explained below.

The mixed-effects model is a parametric method for addressing hierarchical data. Examples of grouped data are individuals within spatially explicit subgroups, such as sample trees within forest sample plots; observations of a split-plot or a block in a controlled experiment; and repeated measurements of any subjects, such as plants or permanent sample plots. It is quite common that the groups of the data represent only a sample from a population of groups, while general interest is often in making the inference about the entire population of groups. In those situations, the group effects are naturally treated as random variables, which leads to the mixed-effects model, also called mixed or random-effects regression. These mixed models have been extensively used and have now become the standard for growth and yield modeling (Weiskittel et al. 2011). Additional benefits of

random group effects over the fixed effects are that the number of observations per group can be small; even one observation per group may be enough for satisfactory estimation accuracy, provided some groups have several observations. As groups get larger, the estimated group effects from the mixed-effects model approach those of the fixed-effects model. Mixed-effects models also enable modeling of variability between groups using fixed predictors that are defined at the group level. Furthermore, prediction is also possible for groups that were not present in the modeling data (Mehtätalo & Lappi, 2020). For growth modeling, use of species as hierarchical level in a mixed model has been shown to result in more robust predictions (Kuehne et al. 2020).

In addition to mixed-effects regression techniques, artificial neural networks (ANNs) is a form of artificial intelligence (AI) and are used for a wide range of complex multivariate problems in various fields, including communication memory, optimization, prediction, diagnosis, control, and forestry (Nandy et al, 2017; Da Rocha et al, 2018; Vieira et al. 2018; Zhu et al, 2018, Zhou et al, 2019). ANNs form a subset of AI whose structure and function generally mimic the human brain and consist of a number of simple structural components with complex connections, analogous to neurons in the brain (Strobl & Forte, 2007;). ANNs have recently gained increased traction in forestry with applications in the mapping of forest structure (Ingram et al. 2005), predicting site index (Aertsen et al. 2010), estimating forest growth and yield (Ashraf et al. 2013), modeling tree diameter and height (Reis et al. 2016; Vieira et al. 2018), determining volume and biomass of individual trees (Pereira et al, 2019), predicting the probability of tree survival (Bayat et al., 2019a), and estimation of tree heights (Bayat et al., 2020).

Few studies have investigated how well traditional parametric mixed-effects compare to AI/ANN-based growth and yield models. A recent study comparing the estimation of volume and biomass of individual trees of different species in the Brazilian central savanna derived

using both approaches clearly demonstrated the great potential of AI techniques compared to mixed models and underscored the utility of ANN-based models to handle manifold information to accurately predict tree-level attributes (Pereira et al. 2019). However, nonparametric methods like ANN may have important limitations for application in a regional forest growth and yield modeling context, namely inability to extrapolate beyond the fitting data, potential inconsistency with biological expectations, and more difficult transferability to other potential users. To our knowledge, no comprehensive study has compared the tree-level growth and yield results from parametric mixed-effects regression models to those from ANNs to date, particularly in uneven-aged and mixed forests like those in the Hyrcanian forests of Iran.

ANNs used in this study consisted of two architectures that are commonly used for solving difficult engineering problems (Walling et al., 2001; Zhu et al, 2007; Bayat et al., 2020): the feedforward multilayer perceptron (MLP) and the radial base function (RBF) networks. Both methods give robust estimates (Reis et al., 2018; Van Dao et al., 2020) and are able to approximate a variety of nonlinear functions (Benali et al. 2019). The number of layers and neurons in each hidden layer is of great importance in designing the network. The number of neurons in the input and output layers is equal to the number of input and output variables under investigation. The challenging task is to determine the number of hidden layers and the number of neurons in each hidden layer. The ANNs in this study were trained with back-propagation algorithms that used 70% of input-output data records for model training and the remainder for model testing (Benali et al. 2019).

To manage mixed uneven-aged forests with the selection system, reliable predictive models of diameter/height growth, survival/mortality rates of trees, and ingrowth of regeneration are needed to guide harvest intensities and residual basal areas to ensure a sustainable development of trees through the diameter distribution. In this study, we

parameterized these various individual tree growth models using mixed models and ANN to
determine which approach provided the best model accuracy. Further, the primary goal was
an accurate and appropriate method for predicting diameter/height growth, survival /mortality
rates of trees, and ingrowth of regeneration for the most important and economically valuable
species in the forests of northern Iran.

2. Materials and methods

2.1. Study area

This study was carried out in the Jojadeh district, which is one of five sections covered
by forestry development projects in the Farim forest. The Jojadeh section is located on the
southern part of the Sari, the capital city of the Mazandaran province on the slopes of the
northern Alborz Mountains in the Dodangeh district (Figure 1). The section covers an area of
3550.2 ha with minimum and maximum altitudes of 782 and 1750 m, respectively. The
climate of this forest is classified as humid with an annual rainfall of 832.9 mm and an
average annual temperature of 11.2°C. This forest is composed of an uneven-aged and mixed
forest, and in most parts has at least three stories. The primary species of this section are
Oriental beech (*Fagus orientalis* Lipsky), chestnut-leaved oak (*Quercus castaneifolia* Coss.
ex J.Gay), Persian maple (*Acer velutinum* Boiss.), common hornbeam (*Carpinus betulus* L.)
and Caucasian alder (*Alnus subcordata* C.A.Mey.) (Hamidi et al, 2019). These primary
species often occur together in a variety of mixtures and forest types throughout the region.

Figure 1. Overview of the study area in northern Iran and approximate location of plots used in this analysis. Variations in color indicate different elevations (m, AMSL; see legend).

2.2. Study method

In 2003, 313 circular permanent sample plots (0.1 ha) were systematically laid out using an inventory grid (200 m $\times$ 150 m) in the Jojadeh district. After locating the plot centers in the field, the slope of each plot was determined, and the radius of the sample plot was slope corrected. In each plot, the center was permanently monumented and each tree within the plot received a number that was painted at breast height (1.3 m). The DGPS device (RTK model - with an accuracy of approximately 1–5 cm (RMS)) was used to record the position of all sample plots (Bettinger et al., 2019). The DBH of all live trees with a diameter >12.5 cm was measured using a caliper and recorded by species and All data, including slope, aspect, etc., were measured in the field. Measurements were re-taken after 10 years in 2013 and the

mortality of any previously tallied tree and ingrowth of trees beyond the diameter threshold 188
 were noted. 189

Data 190

A total of 4832 trees of which 2878 were Oriental beech, 838 common hornbeam, 187 191
 oak, 417 Caucasian alder, 80 Persian maple and 432 Other trees predominantly *Acer* 192
cappadocicum, *Tilia spp.*, *Ulmus minor*, *Ulmus glabra*, *Fraxinus excelsior*, and *Zelkova* 193
carpinifolia. All of these observations across the five primary species were available for 194
 modeling diameter growth. Height was modeled using 626 pairs of diameter and height, 195
 while a total of 5852 and 1340 trees were used for survival and regeneration modeling, 196
 respectively. 197

Due to the uneven structure of most stands in this forest, the thickest and closest tree to 198
 the center of the plot were selected for measurement, which was accomplished using a Sunto 199
 clinometer and calculated from the following formula (Equation. 1): 200

$$H = d [\tan \alpha - (\tan \beta)] \quad (1) \quad 201$$

Where H: the height of the tree (m), d: the horizontal distance to the tree (m), $\tan \alpha$ and $\tan \beta$: 202
 The slope of the tip and the bend of the tree, respectively, are relative to the horizontal 203
 surface (%). 204

Modeling approaches 205 206

For modeling the 10-year diameter increment ($DBH_{2013} - DBH_{2003}$) in this study, the 207
 following parameters were included in the model: (1) tree size (DBH); (2) competition (total 208
 basal area (BA) and basal area of trees larger than the subject tree (BAL) as well as its 209
 transformation, $\ln(BAL)$). BAL has been suggested as a proxy for the ability of trees to 210
 compete for light (Schwinning and Weiner 1998). Other studies have posited that tree 211
 competitive position, determined using BAL or modifications of BAL, may be the strongest 212

predictors of diameter growth in both even-aged (Adame et al. 2008, Uzoh and Oliver 2008) 213
and uneven-aged stands (Pukkala et al. 2009); and (3) physiographic factors including slope, 214
aspect, altitude and transformation of these variables with natural log-transformed diameter 215
growth as the dependent variable (Vanclay, 1994), Linear mixed-effect regression was used 216
to model the diameter increment following Lhotka, and Loewenstein (2011) that incorporated 217
species as the random variable (Kuehne et al, 2020). 218

Due to errors in tree height measurements associated with the first inventory, only a 219
static total height model associated with the second inventory could be developed. The static 220
height models were developed based on the relationship between tree height and DBH from 221
626 trees (i.e., the largest diameter and nearest tree to the center in each sample plot). Twenty 222
alternative nonlinear DBH to height model types were fitted and evaluated in this study from 223
which 11 models were two-parameter and nine were three-parameter models. 224

The mortality model was based on the number of trees that survived or died between 225
2003 and 2013 and modeled by species using logistic regression. The explanatory variables 226
evaluated were tree size (DBH and different derivatives) and competition factors (BA, BAL, 227
N); only significant variables ($p < 0.05$) were retained in the final model (Equation. 2): 228

$$Pi = \frac{1}{1+e^{-[b(0)+b(1)\times x(1)+b(2)\times x(2)+\dots+b(n)\times x(n)]}} \quad (2) \quad 229$$

Where P_i represents the possibility of tree mortality for threshold i , b_0 – b_n are parameters to 230
be estimated and $x_{(1)}$ – $x_{(n)}$ are descriptive variables. 231

The regeneration/ingrowth model used the number of trees that exceeded the diameter 232
threshold of 12.5 cm DBH as the response variable and that was regressed against stand total 233
basal area. Based on the data availability and desired use in future projections, some 234
additional explanatory variables for predicting the number of ingrowth trees per hectare were 235
selected: (i) total basal area ($m^2 ha^{-1}$); (ii) number of trees per ha; (iii) average DBH of each 236

plot; (iv) physiographic factors; and (v) transformations of basal area ($\text{m}^2 \text{ha}^{-1}$). These were
all used in a Poisson generalized linear model (GLM) (Equation. 3).

$$\ln(\text{IN}) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n \quad (3)$$

The systematic linear predictor is a multiplication of a parameter vector β and an explanatory
variable design matrix X (Li et al, 2011). All computations and modeling were done
employing the R software using the lme and nlme packages (Pinheiro et al. 2020) similar to
Bayat et al. (2020).

Artificial Neural Network (ANN)

Prior to training, all input and output data were normalized (Nagy et al., 2002). The
ANN-structure was iteratively altered by changing the number of hidden nodes. The structure
that produced the least amount of error (difference between modeled and observed values)
was selected for further testing at a later stage. All calculations were analyzed in
STATISTICA software.

Model Evaluation

Common criteria for assessing the goodness-of-fit of model predictions are the
coefficient of determination (R^2), the root mean squared error (RMSE), the relative RMSE,
BIAS, and relative BIAS (Lumbres et al, 2016; Bayat et al., 2019b). An important advantage
of the relative RMSE (in %) is that it enables comparisons among predictions produced by
different models (Pulido-Calvo et al., 2007; Janizadeh et al., 2019). In addition to the above
evaluation metrics, the mortality was evaluated with the Nagelkerke R-square criteria, Chi-
square (Hann et al., 2003), Hosmer-Lamshaw test (Padilla, 2010) and ROC subsurface levels
(Lei et al., 2004).

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (\text{est}_i - \text{obs}_i)^2}{n}} \quad (4)$$

$$\text{Relative RMSE} = 100 * (\text{RMSE} / \text{mean observation value}) \quad (5)$$

$$\text{BIAS} = \frac{\sum_{i=1}^n (est_i - obs_i)}{n} \quad (6) \quad 261$$

$$\text{Relative BIAS} = 100 * (\text{BIAS} / \text{mean observation value}) \quad (7) \quad 262$$

where est_i and obs_i are the i^{th} estimate and observation, respectively, and n is the number of observations. For evaluation, we performed cross-validation by randomly selecting 70% of the data as the training dataset and 30% as the evaluation dataset. 263
264
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Results 266

The data covered a wide range of conditions typical for the region with the descriptive statistics given in Table 1. 267
268
269

Table1. Descriptive statistics of data used in the growth model 270

Variable	Mean	Maximum	Minimum	Standard deviation
Tree-level				
Diameter (cm)	37	160	12.5	22
Total height (m)	16.55	33.32	13.82	2.66
Diameter growth (cm yr ⁻¹) (train)	1.94	7.45	0	1.16
Diameter growth (cm yr ⁻¹) (test)	1.98	8	0	1.17
Survival (train)	0.98	1	0	0.02
Survival (test)	0.98	1	0	0.02
Stand-level				
Stem density (# ha ⁻¹)	212	560	60	91.7
Ingrowth (# ha ⁻¹ yr ⁻¹) (train)	7.5	12	6	1.13
Ingrowth (# ha ⁻¹ yr ⁻¹) (test)	8	12	5	1.15
Total basal area (m ² ha ⁻¹)	22.8	48.8	3.8	10.3
Elevation	1178.2	1650.0	815.0	234.1
Slope	31.9	70.0	5.0	12.6

Individual tree Diameter growth model

The diameter growth of most trees ranged between 0–8 cm in the 10-year period. A linear mixed-effect model was employed for modeling of the diameter growth and the best performing model is presented in Equation 8:

$$Id = -1.64 + u_j + 0.03(DBH) - 0.00015(DBH^2) + 0.0032(BA) - 0.010(BAL) - 0.00016 (DBH \cdot BAL) + 0.00014 (Slope) - 0.03 \sin(Aspect) + 0.14 \cos(Aspect) + e_{ij} \quad (\text{Equation 8})$$

Where Id is the diameter growth in a 10-year period; $u_j \sim N(0, \sigma_u^2)$ represents the random effect species; DBH is the diameter at breast height (cm); Square of DBH (cm), BA is the stand basal area ($m^2 ha^{-1}$); BAL is the basal area of larger trees in the plot when compared to the subject tree ($m^2 ha^{-1}$). The variance and standard deviation for the random factor of species were 1.79 and 2.83, respectively. Results also showed that the correlation between growth rate and BAL was negative i.e. the diameter growth decreased with an increase in this index. The RMSE, bias, and R^2 were 1.11, 0.12, and 0.20, respectively

Results of five MLP- and RBF-based ANNs showed that the RBF-based models gave better results the superior MLP-based model resulted in an RMSE of 0.06 cm, indicating that the predicted average diameter growth is close to the measured diameter growth (Table 2). In Table 2, only the models with high accuracy are given, while all ANNs fitted are given in the Supplemental Materials (Table S1 and S2). Also, Fig. 2 shows the relationship between the actual and predicted diameter growth for all species by the parametric (mixed-effect regression) and non-parametric methods (ANN).

Table 2. Characteristics of the superior MLP-based ANNs for individual tree diameter growth and associated goodness-of-fit criteria for model performance.

sample	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
Train	MLP 13-6-1	BFGS 57	SOS	Tanh	0.55	0.93	4.79	0.1	0.51
Test	MLP 13-6-1	BFGS 57	SOS	Tanh	0.53	0.79	3.98	0.06	0.30

MLP = multilayer perceptron (10-4-1 implies 10 = number of input layers; 4 = number of hidden layers; and 1 = number of output layer); RBF = radial basis function; BFGS = Broyden-Fletcher-Goldfarb-Shanno; RBFT = Radial Basis Function Training; SOS = Symbiotic Organisms Search

Figure 2. Graphical presentation of measured and predicted tree diameter growth by the parametric (mixed-effect regression (red line)) and non-parametric methods (ANN (black line))

Individual tree height growth model

The following individual tree data were used to fit tree height models using tree diameter as the main predictor (Table 3). The best obtained height model is shown in Equation 9:

$$H_{ij} = (1.3 + 65.52 / (0.029d_{ij}^{-0.55} + 0.024 (BA) + 0.027 (BAL))) + e_{ij} \quad \text{Equation 9}$$

Where H is the tree height and d_{ij} is the diameter at the breast height of the tree, BA is the stand basal area ($\text{m}^2 \text{ ha}^{-1}$); BAL is the basal area of the larger trees in the plots ($\text{m}^2 \text{ ha}^{-1}$) and $e \sim N(0, \sigma_u^2)$ represents the residuals. In addition, modeling was performed for all species separately, but a better model was achieved when all species were combined and species was treated as a random factor. Residual standard error, RMSE, RMSE %, bias, bias %, and R² were 4.10 m, 4.91 m, 18.45, 0.15 m, 0.27%, and 73%, respectively (Fig. 3).

Table 3. Descriptive statistics of trees' DBH (cm) and height (m) by species in the study area

Descriptive statistics	DBH (cm)						Height (m)					
Species	<i>Fagus</i>	<i>Carpinus</i>	<i>Quercus</i>	<i>Alnus</i>	<i>Acer</i>	Other trees	<i>Fagus</i>	<i>Carpinus</i>	<i>Quercus</i>	<i>Alnus</i>	<i>Acer</i>	Other trees
Mean	63.2	67.5	68.1	71.6	57.2	53.4	27.7	24.5	26.6	27.6	22.3	19.5
Maximum	138	122	110	135	130	122	40.5	36	39	40.5	36.3	38.4
Minimum	13	25	18	10	13	14	7.5	12.5	8	7	10	7
Standard Deviation	29.3	23.1	23.4	30.8	42.9	33.9	7.3	5.2	6.6	7.3	8.9	8.3
Number	398	98	51	78	19	33	398	98	51	78	19	33

Of the ANN models evaluated for tree height, the MLP-based ANN that contained seven hidden layers was the superior model that resulted in an RMSE of 4.81 m (Table 4). In Table 4, only the models with high accuracy are given, while the results of all ANN are given in the Supplemental Materials (Table S3 and S4). However, predictions using the best ANN and mixed model were nearly identical across the range of tree sizes examined (Figure 3).

Table 4. Characteristics of the superior MLP-based ANNs for individual tree height and associated

goodness-of-fit criteria for model performance.

Sample	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
Train	MLP 3-4-1	BFGS 15	SOS	Identity	0.74	4.89	18.53	0.0003	0.001
Test	MLP 3-4-1	BFGS 15	SOS	Identity	0.86	2.86	10.55	0.09	0.34

MLP = multilayer perceptron (3-7-1 implies 3 = number of input layers; 7 = number of hidden layers; and 1 = number of output layer); RBF = radial basis function; FGS = Broyden-Fletcher-Goldfarb-Shanno; RBFT = Radial Basis Function Training; SOS = Symbiotic Organisms Search

Figure 3. Regression model of diameter-height by the parametric (mixed-effect regression (red line)) and non-parametric methods (ANN (black line))

Individual tree survival growth (mortality) model

In the mortality model, we considered the survival of trees to be a one and dead trees are a zero with a binary logistic regression was used to estimate the survival model. Equation 10 is the individual tree survival growth (mortality) model

$$Y = \frac{1}{1 + \exp^{(4+0.17DBH-8.01BA-1.10BAL)}} \quad \text{Equation 10}$$

The results of the neural network show that the MLP-based network of tree survival had an RMSE of 0.28 and a bias of 0.011 and performed better than the RBF-based network (Table 5 and Fig 4). In Table 5, only the models with high accuracy are presented, while all of neural network determined are given in the Supplemental Materials (Table S5 and S6)).

Table 5. Characteristics of the superior RBF and MLP-based ANNs for individual tree survival and associated goodness-of-fit criteria for model training.

Sample	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
Train	MLP 5-7-1	BFGS 132	SOS	Logistic	0.27	0.35	35.77	0.005	0.01
Test	MLP 5-7-1	BFGS 132	SOS	Logistic	0.36	0.28	28.01	0.011	1.19

MLP = multilayer perceptron (5-7-1 implies 5 = number of input layers; 7 = number of hidden layers;

and 1 = number of output layer); RBF = radial basis function; BFGS = Broyden-Fletcher-Goldfarb-

Shanno; RBFT = Radial Basis Function Training; SOS = Symbiotic Organisms Search

Figure 4. Model of survival by the parametric (mixed-effect regression (red line)) and non-parametric methods (ANN (black line)) with observed probabilities by 5 cm diameter class.

Evaluation results of survival model are given in Table 6, which suggest that the ANN were slightly better in terms of ROC and R². The better performance achieved for the ANN was primarily at the ends of the distribution in terms of smaller and larger trees (Figure 4).

Table 6. Evaluation results of survival model by modeling approach.

Test	Mixed-effects	ANN
Chi-Square value	2862	5882
Hosmer & Lemeshow Chi-square test	0.070	0.092
ROC	0.54	0.81

Nagelkerke R^2	0.43	0.40
Cox & Snell R^2	0.41	0.37

Ingrowth model

The average rate of ingrowth (number of trees that passed the diameter threshold of 12.5 cm) over a 10-year period was 42.8 ± 6.4 (mean $\pm$ SD) trees per ha, which was unequally distributed among the different species (Table 7). The average diameter of ingrowth trees in the 10-year period was 17.1 ± 2.21 cm. Equation 11 shows the ingrowth model:

$$\ln(\text{IN}) = 10.70 - 0.35 (\text{mDBH}) + 0.47 (\text{BA}) - 0.0043(\text{BA}^2) + 0.01 (\text{BA}_{Fagus})$$

Equation 11

Where IN is the ingrowth of a 10-year period (number of trees that passed the diameter class of 12.5 cm) mDBH is the stand-level mean diameter at breast height (cm), BA is the total basal area ($\text{m}^2 \text{ha}^{-1}$), BA^2 is the squared basal area ($\text{m}^2 \text{ha}^{-1}$) of each plot, and BA_{Fagus} is the basal area ($\text{m}^2 \text{ha}^{-1}$) of *Fagus* species.

Table 7. Average number of trees passed the diameter threshold of 12.5 cm over a 10-year period

Species	Number of trees per ha that exceed the diameter threshold of 12.5 cm	Maximum number of trees per ha
Beech	21.21	110
Hornbeam	7.76	60
Oak	3.09	40
Alder	3.19	70
Maple	2.17	40
Other Species	5.36	60
Total	42.81	380

The results of the ANN show that the MLP-based network of ingrowth had an RMSE of 0.54 trees per ha, a bias of 0.027 trees per ha, and performed better than RBF-based network (Tables 8; Fig 5). In Table 8, only the models with high accuracy are given, while the performance of all determined ANNs are provided in the Supplemental Materials (Table S7 and S8). However, predictions of ingrowth using both ANN and mixed-effects were relatively similar across a range of basal areas (Figure 5).

Table 8. Characteristics of the superior MLP-based ANNs for the number of ingrowth trees per ha that exceed the DBH threshold of 12.5 cm over 10 years and associated goodness-of-fit criteria for model predictions.

Sample	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
Train	MLP 10-5-1	BFGS 95	SOS	Logistic	0.99	0.55	1.3	0.029	0.061
Test	MLP 10-5-1	BFGS 95	SOS	Logistic	0.99	0.54	1.2	0.027	0.054

MLP = multilayer perceptron (10-5-1 implies 10 = number of input layers; 5 = number of hidden layers; and 1 = number of output layer); RBF = radial basis function; BFGS = Broyden-Fletcher-Goldfarb-Shanno; RBFT = Radial Basis Function Training; SOS = Symbiotic Organisms Search

Figure 5. Predictions of the mixed-effects ingrowth model (Eqn. 11; number of trees passed the diameter class of 12.5 cm) (red line)) and non-parametric methods (ANN (black line)) over total stand-level basal area (m² ha⁻¹) with observed values.

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Comparison of modeling approach

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A general comparison of the R^2 and RMSEs from the parametric (mixed-effects) and non-parametric (ANN) prediction methods indicated that the ANN resulted in the best performance in this analysis (Table 9). For R^2 , the % improvement by ANN ranged from 3.1 to 157.1%, while % improvement for RMSE was between 10.0 and 94.9%. The largest improvements were primarily observed for the diameter increment model. However, as noted above, many of the predictions using either ANN and mixed-effects were generally consistent across the range of the data and both well aligned with observed trends.

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Table 9. Comparison of various model fit statistics for parametric (mixed-effect regression) and non-parametric methods (ANN) by equation.

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Model	Parametric			Non-parametric			% Improvement		
	R^2	RMSE	BIAS	R^2	RMSE	BIAS	R^2	RMSE	BIAS
Diameter increment	0.20	0.11	0.12	0.53	0.079	0.06	165.0	-28.2	-50.0
Height	0.73	4.91	0.15	0.86	2.86	0.09	17.8	-41.8	-40.0
Survival	0.24	0.38	0.043	0.36	0.28	0.011	50.0	-26.3	-74.4
Ingrowth	0.96	0.60	2.17	0.99	0.54	1.2	3.1	-10.0	-44.7

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Discussion

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Evaluation of the structure and dynamics of natural forests helps to determine the possibility of optimal forest management in achieving a desirable structure so that the implementation of appropriate silviculture operations in the stands under management can help to preserve the biological diversity and sustainability of forests (Ashraf et al, 2013, Zhao et al., 2019). Forest structure and composition are very imperative factors for assessing forest health and sustainability. Hyrcanian forests also have a variety of functions that require an integrated and comprehensive management such as wood production, biodiversity, aesthetics,

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recreation and habitat. It appears that uneven-aged and mixed species management is an efficient and efficacious way of attaining these varying goals (Bourque and Bayat. 2015, Yang et al., 2019). However, lack of suitable decision-support tools for the proper implementation of uneven management in mixed broad-leaved forests has delayed the scientific and efficient implementation of this technique (Bourque et al, 2019).

In this study, some models have been presented that can be employed in forest management. The models for uneven-aged, mixed forest presented in this study include individual tree diameter growth, height, and survival (mortality) as well as ingrowth. According to the results, the individual tree diameter growth had a robust performance across the species examined (Equation 8). Results of a sensitivity analysis indicated that the most important independent variables used in the best model for diameter growth was the logarithm of DBH. Stand basal area and BAL were used to account for competition. BAL is the most common tool for quantifying one-sided competition because it is an absolute value, a simple calculation, and correlates well with the growth rate (Vanclay, 1994, Weiskittel, 2011, Kweon & Comeau, 2019, Kuehne et al, 2020).

Results also showed that increased competition greatly reduced diameter growth across the species examined. In addition, the ANN based on the Multilayer Perceptron network (MLP) provided a better fit to the data than the RBF-based ANN (Tab 2, fig 3). The results of the ANN sensitivity analysis showed in both cases that DBH and stand basal area were the most influential variables whose effects were further modified by physiographic factors in the form of altitude, slope, and aspect. The parametric model for diameter growth indicated that highest growth was observed on northwest aspects (300-340°), but declined as the slope steepened. Weiskittel et al. (2007) found a similar influence of altitude, slope, and aspect on individual tree diameter growth of species in the US Pacific Northwest.

In this study, the static technique was employed for modeling height growth. The descriptive statistics of trees' DBH and height indicated that observations were selected from a wide range of values (12.5 - 138 cm for DBH and 8.0 – 40.5 m for height; Table 3). This suggests that nearly the full range of tree diameter and height for this area were considered. In the height model, species had no effect on the model, which was obtained when the model was fitted for all species separately and the difference was not statistically significant. The developed mixed effect regression height models from our work expressed tree height as a function of DBH and the best model we produced resulted in a RMSE value equal to 18.5%, which was noticeably lower in the present study than reported by Trasobares et al. (2004), where it ranged from 21 to 24%. This high accuracy is important as height models are needed for predicting tree volume. For the ANN method, the R^2 and RMSE % values were lower than the parametric method, which were 0.79 and 18.2%, respectively. The MLP network had higher accuracy than RBF network. In addition, the important variable in this model included diameter, basal area, and basal area in larger trees.

The mortality of individual trees is an important event in the development of a forest stand and has significant applications in forest growth and product modeling (Bourque et al, 2019). In determining the survival model (mortality), despite the predictive difficulties of mortality at the stand level, there are many equations for estimating it at the tree level, and the logistic regression was used in this study similar to several previous studies (e.g. Hann et al., 2003; Monserud and Sterba, 1999). Guan and Gertner (1991) in their assessment of using ANN and the logistic function showed the former was an effective technique for tree mortality modeling, which other studies have also found (King et al, 2000; Metcalf et al., 2009). However, when the model is used on independent data, the difference between logistic regression and other fitting methods may be less obvious. As a result, logistic regression is

generally appropriate due to its simplicity, robustness, and easy application for many practical purposes of mortality modeling (Yagi & Primicerio, 2014).

Results of the developed survival model showed that trees with a diameter of 20 to 150 cm had the highest survival (Fig. 6). With an increase in competition (BAL), tree survival rate decreased rapidly. According to the analysis, beech trees also had a lower survival probability than others. Assessment and validation of tree mortality models was difficult because of its discontinuous and discrete nature (Han et al., 2006). According to our results, ANN was able to better estimate survival probability and to identify the predictors that contribute the most. ANN uses non-linear network connections and allows an analysis that explores the efficacy of all input variables at the same time, which may lead to an improved quality of the results. In this study, the validation of models was determined using Nagelkerke R^2 and its value was 0.40 (Table 6). According to studies, this parameter represents a good fit of the model if the value is between 0.2 and 0.4 (Wilson et al., 2005). In this study, the validity of the model was further assessed using Hosmer-Lemeshow test and its value was 0.092. Given the fact that the value of this parameter is greater than 0.05, the model obtained is valid (Pukkala and Kellomäki, 2012). In addition, the other criterion was ROC, which was 0.81 and indicates relatively robust predictions. The correct prediction of the survival model was 92% if 0.5 was used as a threshold for survival. In this model, the diameter and basal area and their transformations were among the factors that had a high impact on the model, respectively, while the physiographic factors in this model had no effect.

Models of ingrowth predict the development of trees from the sapling stage instead of predicting seedling development or trying to evaluate the variety of factors that influence the process of forest stand rejuvenation (Ma et al., 2019). One of the benefits of this approach is that the time needed for establishment of regeneration in the stand after the reduction of stand

density due to harvesting allows it to be more realistic (Gould et al., 2006, 2007). Regarding the results, the ingrowth model was generally reasonable and was more reliable than other models (Fig. 8). The ANN showed that MLP approach had highest accuracy and lowest bias (Table 8). Ingrowth increased with the basal area of stand, which is a similar finding to results of Trasobares et al., (2004) who showed that the basal area had a major role in regeneration modeling. In this study, the ANN trial and error procedure showed that, depending on the input variables, four to ten hidden layers resulted in the best performance. However, the number of neurons on the hidden layer varied based on the number of input variables. Some researchers have suggested that the number of neurons on the hidden layer should be more than twice that of the input neurons (Liu et al. 2013; Zhu et al. 2018). Although other researchers found that, the number of hidden layers and their neurons is totally dependent on the size of the data, which always leads to a trial and error procedure or application of optimization techniques (Karaboga and Kaya, 2018).

Considering the potential of ANN in forest measurements and modeling, studies like Vendruscolo et al. (2017), Çatal and Saplıoğlu (2018), Reis et al. (2018a, 2018b), Sanquetta et al. (2018) and Vieira et al. (2018) have found that they generally perform better than regression models, while they can be estimated with higher speeds and result in more precise models. Thereby, in order to minimize the errors in growth models estimation in uneven-aged forest, such as the Hyrcanian forest, the use of artificial intelligence techniques is very important, (Aerts et al., 2010; Breiman, 2001; Kano et al., 2017; Gorgens et al., 2015; Özçelik et al., 2013, 2010; Reis et al., 2018; Siminsky, 2017; Simões and Shaw, 2007). In particular, ANNs represent powerful methods for data analysis that can enhance estimation skill (Xu et al., 2014). However, it is important to recognize many potential limitations of non-parametric methods like ANN as they may overfit the data, cannot extrapolate beyond the available training data, and do not guarantee biologically plausible behavior.

Consequently, the assessment and evaluation of long-term growth projections from both parametric and non-parametric is needed. This is important as improved model fit statistics like R^2 and RMSE does not necessitate better long-term (25+ years) growth projections (e.g. Russell et al. 2011), which underscores the need and importance of robust model forms that might be challenging for non-parametric approaches to ensure.

Conclusion

Today, a logical solution cannot be achieved in many planning and policy formulation processes without modeling and simulation. Consequently, this study was aimed at providing a growth model for the primary species in the Hyrcanian forest in order to determine the best condition and the most important factors for their growth that can be used in forest management. In this study, tree-level diameter growth, height, and survival as well as stand-level ingrowth were developed using mixed effects and artificial neural networks. Individual tree growth models are needed in order to determined suitable management regimes for the uneven- aged and mixed Hyrcanian forests. Results showed the MLP model was more accurate than RBF and we found the ANN approach relatively easy to use and powerful as they significantly outperformed the traditional approaches for predicting diameter growth, height, survival, and ingrowth. Overall, results indicated that growth and yield model performance was consistent with expectations, and that the general fit to the validation data was acceptable. The results also indicated that the models performed relatively well in terms of amount of the variation explained (36-99%). Therefore, they seem quite suitable for predicting tree growth and survival in uneven-aged hardwood stand types in the region where the study area was situated.

According to the general findings, ANNs were capable of accurately and robustly predicting the different tree-level variables needed for effective forest modeling. Therefore,

ANN can likely be considered a very promising alternative technique when sufficient data is available for analysis. Suggestions for future studies include applying ANN to other forest regions and using other types of ANN to maximize the accuracies involved. In addition, it is important to compare long-term projections using ANNs with actual field data to ensure robust model behavior and performance that is well aligned with biological expectations. Ultimately, the best approach for growth and yield modeling might be the hybridization of parametric and non-parametric methods like ANN that can fully capitalize on the advantages of each method.

Abbreviations

AI: Artificial intelligence;	
ANN: Artificial Neural network;	
b_0 – b_n : parameters to be estimated;	
BA: Basal area;	
BAL: basal area in larger trees;	
DBH: diameter at breast height;	
GLM: Generalized linear model	
m: meter	
MLP: multilayer perceptron;	
P_i : the possibility of tree mortality for threshold i ;	
RBF: Radial basis function;	
RMSE: root mean squared error;	
$x_{(1)}$ – $x_{(n)}$: descriptive variables;	

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the
corresponding author on reasonable requests.

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Table S1. Characteristics of RBF and MLP-based ANNs for individual tree diameter growth	810
and associated goodness-of-fit criteria for model performance. The superior model is shown	811
in bold.	812

Index	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
1	MLP 13-6-1	BFGS 57	SOS	Tanh	0.55	0.93	4.79	0.10	0.51
2	MLP 13-12-1	BFGS 72	SOS	Logistic	0.53	0.97	5	0.12	0.61
3	MLP 13-11-1	BFGS 55	SOS	Tanh	0.49	0.95	4.89	0.17	0.87
4	MLP 13-13-1	BFGS 32	SOS	Logistic	0.54	0.98	5.05	0.12	0.61
5	MLP 13-7-1	BFGS 27	SOS	Exponential	0.51	0.96	4.94	0.11	0.56
6	RBF 13-30-1	RBFT	SOS	Gaussian	0.36	2.76	14.22	0.43	2.21
7	RBF 13-26-1	RBFT	SOS	Gaussian	0.07	4.86	25.05	9.02	46.49
8	RBF 13-27-1	RBFT	SOS	Gaussian	0.05	4.81	24.79	8.18	42.16
9	RBF 13-31-1	RBFT	SOS	Gaussian	0.04	4.83	24.89	11.01	56.75
10	RBF 13-28-1	RBFT	SOS	Gaussian	0.39	2.14	11.03	0.87	4.48

Table S2. Characteristics of RBF and MLP-based ANNs for individual tree diameter growth	814
and associated goodness-of-fit criteria for model evaluation. The superior model is shown in	815
bold.	816

Index	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
1	MLP 13-6-1	BFGS 57	SOS	Tanh	0.53	0.79	3.98	0.06	0.30
2	MLP 13-12-1	BFGS 72	SOS	Logistic	0.47	0.81	4.09	0.07	0.35
3	MLP 13-11-1	BFGS 55	SOS	Tanh	0.51	0.97	4.89	0.09	0.45
4	MLP 13-13-1	BFGS 32	SOS	Logistic	0.48	0.99	5	0.08	0.40
5	MLP 13-7-1	BFGS 27	SOS	Exponential	0.48	0.86	4.34	0.08	0.40
6	RBF 13-30-1	RBFT	SOS	Gaussian	0.38	1.36	6.86	0.83	4.19
7	RBF 13-26-1	RBFT	SOS	Gaussian	0.05	2.64	13.33	1.46	7.37
8	RBF 13-27-1	RBFT	SOS	Gaussian	0.08	2.83	14.29	1.32	6.66
9	RBF 13-31-1	RBFT	SOS	Gaussian	0.06	2.56	12.92	1.41	7.12
10	RBF 13-28-1	RBFT	SOS	Gaussian	0.38	1.16	5.85	0.89	4.49

Individual tree height growth model

Table S3. Characteristics of RBF and MLP-based ANNs for individual tree height and associated goodness-of-fit criteria for model performance. The superior model is shown in bold.

Index	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
1	MLP 3-3-1	BFGS 14	SOS	Identity	0.74	4.90	18.59	0.0003	0.001
2	MLP 3-9-1	BFGS 13	SOS	Exponential	0.74	4.90	18.55	0.026	0.1
3	MLP 3-4-1	BFGS 15	SOS	Identity	0.74	4.89	18.53	0.0003	0.001
4	MLP 3-5-1	BFGS 10	SOS	Identity	0.74	4.91	18.59	0.001	0.007
5	MLP 3-10-1	BFGS 14	SOS	Exponential	0.74	4.91	18.60	0.19	0.72
6	RBF 3-22-1	RBFT	SOS	Gaussian	0.28	26.27	99.50	3.99	15.11
7	RBF 3-23-1	RBFT	SOS	Gaussian	0.04	41.16	155.90	9.14	34.62
8	RBF 3-27-1	RBFT	SOS	Gaussian	0.02	57.59	218.14	12.23	46.32
9	RBF 3-29-1	RBFT	SOS	Gaussian	0.05	39.54	149.77	8.31	31.47
10	RBF 3-21-1	RBFT	SOS	Gaussian	0.16	36.52	138.33	5.14	19.46

Table S4. Characteristics of RBF and MLP-based ANNs for individual tree height and associated goodness-of-fit criteria for model evaluation. The superior model is shown in bold.

Index	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
1	MLP 3-3-1	BFGS 14	SOS	Identity	0.85	2.89	10.63	0.17	0.63
2	MLP 3-9-1	BFGS 13	SOS	Exponential	0.86	2.86	10.54	0.17	0.63
3	MLP 3-4-1	BFGS 15	SOS	Identity	0.86	2.86	10.55	0.09	0.34

4	MLP 3-5-1	BFGS 10	SOS	Identity	0.85	2.88	10.60	0.16	0.61
5	MLP 3-10-1	BFGS 14	SOS	Exponential	0.85	2.89	10.64	0.18	0.67
6	RBF 3-22-1	RBFT	SOS	Gaussian	0.19	24.33	89.48	8.14	29.93
7	RBF 3-23-1	RBFT	SOS	Gaussian	0.12	36.67	134.86	10.23	37.62
8	RBF 3-27-1	RBFT	SOS	Gaussian	0.22	21.75	79.99	4.84	17.80
9	RBF 3-29-1	RBFT	SOS	Gaussian	0.22	21.73	79.91	4.65	17.10
10	RBF 3-21-1	RBFT	SOS	Gaussian	0.11	39.11	143.83	11.12	40.89

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Individual tree survival growth (mortality) model

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Table S5. Characteristics of RBF and MLP-based ANNs for individual tree survival and associated goodness-of-fit criteria for model train. The superior model is shown in bold.

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Index	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
1	MLP 5-5-1	BFGS 1000	SOS	Exponential	0.13	0.36	36.91	0.0014	0.11
2	MLP 5-11-1	BFGS 46	SOS	Logistic	0.12	0.36	36.96	0.0012	0.12
3	MLP 5-7-1	BFGS 132	SOS	Logistic	0.27	0.35	35.77	0.005	0.01
4	MLP 5-4-1	BFGS 65	SOS	Tanh	0.16	0.36	36.70	0.008	0.14
5	MLP 5-7-1	BFGS 188	SOS	Logistic	0.16	0.36	36.71	0.009	0.31
6	RBF 5-21-1	RBFT	SOS	Gaussian	0.08	0.43	43.71	0.0021	1.42
7	RBF 5-27-1	RBFT	SOS	Gaussian	0.11	0.38	38.74	0.0011	0.23
8	RBF 5-23-1	RBFT	SOS	Gaussian	0.12	0.36	36.72	0.0012	0.12
9	RBF 5-23-1	RBFT	SOS	Gaussian	0.10	0.39	39.23	0.009	1.09
10	RBF 5-22-1	RBFT	SOS	Gaussian	0.12	0.36	36.39	0.0012	0.14

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Table S6. Characteristics of RBF and MLP-based ANNs for individual tree survival and associated goodness-of-fit criteria for model evaluation. The superior model is shown in bold.

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Index	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
1	MLP 5-5-1	BFGS 1000	SOS	Exponential	0.11	0.39	39.28	0.023	2.39
2	MLP 5-11-1	BFGS 46	SOS	Logistic	0.09	0.39	39.35	0.023	2.32
3	MLP 5-7-1	BFGS 132	SOS	Logistic	0.36	0.28	28.01	0.011	1.19
4	MLP 5-4-1	BFGS 65	SOS	Tanh	0.13	0.39	39.21	0.020	2.09
5	MLP 5-7-1	BFGS 188	SOS	Logistic	0.16	0.39	39.02	0.020	2.09
6	RBF 5-21-1	RBFT	SOS	Gaussian	0.10	0.41	41.71	0.025	2.56
7	RBF 5-27-1	RBFT	SOS	Gaussian	0.08	0.45	45.57	0.12	1.23
8	RBF 5-23-1	RBFT	SOS	Gaussian	0.04	0.76	76.98	0.23	2.34
9	RBF 5-23-1	RBFT	SOS	Gaussian	0.14	0.39	39.26	0.045	4.58
10	RBF 5-22-1	RBFT	SOS	Gaussian	0.17	0.40	40.11	0.043	4.37

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Ingrowth model

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Table S7. Characteristics of RBF and MLP-based ANNs for the number of trees per ha
ingrown beyond the DBH threshold of 12.5 cm over 10 years and associated goodness-of-fit
criteria for model predictions. The superior model is shown in bold.

Index	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
1	MLP 10-4-1	BFGS 192	SOS	Exponential	0.99	0.56	1.33	0.044	0.10
2	MLP 10-13-1	BFGS 109	SOS	Logistic	0.99	0.58	1.38	0.043	0.10
3	MLP 10-9-1	BFGS 79	SOS	Logistic	0.99	0.56	1.33	0.038	0.09
4	MLP 10-5-1	BFGS 95	SOS	Logistic	0.99	0.55	1.30	0.029	0.061
5	MLP 10-8-1	BFGS 157	SOS	Logistic	0.99	0.58	1.38	0.051	0.12
6	RBF 10-32-1	RBFT	SOS	Gaussian	0.95	0.61	14.52	0.12	0.285
7	RBF 10-27-1	RBFT	SOS	Gaussian	0.92	0.73	17.38	0.14	0.33
8	RBF 10-25-1	RBFT	SOS	Gaussian	0.95	0.60	14.28	0.091	0.21
9	RBF 10-26-1	RBFT	SOS	Gaussian	0.96	0.62	14.76	0.084	0.2
10	RBF 10-21-1	RBFT	SOS	Gaussian	0.94	0.71	16.90	0.11	0.26

Table S8. Characteristics of RBF and MLP-based ANNs for the number of trees per hectare
ingrown beyond the DBH threshold of 12.5 cm over 10 years and associated goodness-of-fit
criteria for model evaluation. The superior model is shown in bold.

Index	Structure	Algorithm	Error Function	Hidden activation	R ²	RMSE	%RMSE	BIAS	%BIAS
1	MLP 10-4-1	BFGS 119	SOS	Exponential	0.99	0.56	1.32	0.029	0.059
2	MLP 10-13-1	BFGS 219	SOS	Logistic	0.99	0.55	1.33	0.033	0.056
3	MLP 10-9-1	BFGS 104	SOS	Logistic	0.99	0.55	1.54	0.030	0.065
4	MLP 10-5-1	BFGS 95	SOS	Logistic	0.99	0.54	1.2	0.027	0.054
5	MLP 10-8-1	BFGS 95	SOS	Logistic	0.99	0.59	1.85	0.028	0.098
6	RBF 10-32-1	RBFT	SOS	Gaussian	0.96	0.76	12.41	-0.01	-1.13
7	RBF 10-27-1	RBFT	SOS	Gaussian	0.95	0.73	14.76	-0.02	-2.11
8	RBF 10-25-1	RBFT	SOS	Gaussian	0.96	0.77	12.61	0.05	3.73
9	RBF 10-26-1	RBFT	SOS	Gaussian	0.94	0.78	15.19	-0.9	-0.60
10	RBF 10-21-1	RBFT	SOS	Gaussian	0.94	0.81	16.29	-0.07	-0.65

Figures

Figure 1

Overview of the study area in northern Iran and approximate location of plots used in this analysis. Variations in color indicate different elevations (m, AMSL; see legend).

Figure 2

Graphical presentation of measured and predicted tree diameter growth by the parametric (mixed-effect regression (red line)) and non-parametric methods (ANN (black line))

Figure 3

Regression model of diameter-height by the parametric (mixed-effect regression (red line)) and non-parametric methods (ANN (black line))

Figure 4

Model of survival by the parametric (mixed-effect regression (red line)) and non-parametric methods (ANN (black line)) with observed probabilities by 5 cm diameter class.

Figure 5

Predictions of the mixed-effects ingrowth model (Eqn. 11; number of trees passed the diameter class of 12.5 cm) (red line) and non-parametric methods (ANN (black line)) over total stand-level basal area (m² ha⁻¹) with observed values.