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Title: Assessing the transferability of airborne laser scanning based models for predicting natural forest attributes

Year: 2026

Version: Publisher's version

Please cite the original version:

Maltamo, M., Keskinen, R., Packalen, P., Vastaranta, M., Hyyppä, J., Räty, J. and Korhonen, L. 2026. Assessing the transferability of airborne laser scanning based models for predicting natural forest attributes. Baltic Forestry 32(1): id859; https://doi.org/10.46490/BF859

https://balticforestry.lammc.lt
ISSN 1392-1355
eISSN 2029-9230

Baltic Forestry 2026 32(1): id 859
Category: Research article
https://doi.org/10.46490/BF859

Assessing the transferability of airborne laser scanning based models for predicting natural forest attributes

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Maltamo, M., Keskinen, R., Packalen, P., Vastaranta, M., Hyyppä, J., Räty, J. and Korhonen, L. 2026. Assessing the transferability of airborne laser scanning based models for predicting natural forest attributes. *Baltic Forestry* 32(1): id 859; https://doi.org/10.46490/BF859.

Received 21 April 2026
Revised 15 June 2026
Accepted 16 June 2026

Abstract

Natural forest areas which have usually been unmanaged already several decades are often small and isolated from one another. The performance of airborne laser scanning (ALS) based management forest inventory in natural forests is unknown, since ALS inventories are typically based on field reference data from managed forests. The aims of the study were to (1) Develop ALS based linear regression models for predicting forest attributes in natural forests, and (2) Assess how reliably such models can be applied across different inventory areas. The forest attributes considered were growing stock volume (m^3 ha^{-1}), volume of standing dead wood (m^3 ha^{-1}), number of stems (ha^{-1}), dominant height (m), and structural complexity by Gini coefficient (0–1).

The inventory areas were located in Southern and Eastern Finland. Data from four inventory areas were used in model development, and sample plots measured from even-aged forest area and continuous-cover forest area were used for validation. The point densities of ALS data in the inventory areas varied between 4 and 13 m^{-2}, and the number of plots in the field datasets ranged from 14 to 148. Linear regression models were fitted with field measured plot attributes as responses and two ALS features as predictors. A total of 25 forest variable models were constructed, and 150 model predictions were made. Analyses were conducted separately for each natural forest data set, but general models fusing all natural forest data sets were also constructed. The models' performances in transfers across inventory areas were quantified with relative root mean square error (rRMSE) and bias rBias values.

The accuracies of the models in their fitting datasets were in line with the previous studies. In terms of the transferability, the performance of the models was modest. On average, the rRMSE doubled and rBias increased considerably in the transfer. On average, the rRMSE increased by 9% for growing stock volume, 190% for dead wood volume, 31% for number of stems, 6% for dominant height, and 9% for Gini coefficient. If the obtained accuracy of growing stock attributes were acceptable for natural forest inventory, one could rely on model transfer or the use of general models.

Keywords: primary forest; remote sensing; airborne laser scanning; forest variable; area-based approach; regression model

Introduction

The commonly used definition of a natural or semi-natural forest by the Food and Agriculture Organization of the United Nations (FAO) states that a natural forest is a naturally regenerated forest composed of native tree species, with no obvious signs of human activity and with no obvious disturbance to its ecological processes. According to the FAO's (2020a) Global Forest Resources Assessment, natural forests currently cover about 34% of the world's forest area, or about 1.11 billion hectares, of which 1.41 million hectares are in Europe. In Finland, 203,000 hectares were designated as natural forests in 2020 (FAO 2020b).

Finland's national definition of natural forests is based on the definition used in the National Forest Inventory (NFI; FAO 2020b): Natural forests do not show clear signs of human activity and are at least 160 years old in Southern Finland or 200 years old in Northern Finland. The "naturalness" (Arnkil et al. 2024) is assessed in the NFI based on stand structure, amount of dead wood and human activity. The dominant tree layer must be old, the tree sizes must be variable, and tree locations random. The proportion of decayed wood of varying ages must be considerable (for example 50–120 m^3 ha^{-1}). The assessment of the presence of human activity must consider the management history of the stand and the presence of forest roads and ditches. Clear-cutting in the past is not an obstacle to meeting the criterion of naturalness, if it has not altered the structure, spatial distribution or species composition of the next tree generation.

Globally, the area of natural forests has decreased, which has led to many protection initiatives. The conservation of natural forests is seen as important, as they are one of the key factors in maintaining biodiversity and a rich store of carbon dioxide (Pascual et al. 2026). One of the most far-reaching actions is the European Union Biodiversity Strategy (European Commission 2020), which states that strict protection of all remaining primeval forests is one of its main objectives. Monitoring of the protected natural forests can be done with remote sensing. Particularly, the use of airborne laser scanning (ALS) data has been studied for this purpose. ALS measurements can be used to create a 3D map of the forest canopy and terrain, allowing accurate estimation of tree height, density, canopy gaps and canopy structure (White et al. 2016, Toivonen et al. 2023). Furthermore, since ALS typically provides wall-to-wall coverage of the entire inventory area, within-stand heterogeneity can be revealed. Because ALS can accurately capture differences in forest structure, it has been applied to distinguish managed old growth forests from natural forests through horizontal echo distribution features, canopy height models, and large plot sizes, since they more likely contain spatial patterns of trees and crown features indicative of forest naturalness (Sverdrup-Thygeson et al. 2016, Della Vedova and Wahde 2025, Räty et al. 2025).

In forest inventories, ALS data are commonly used to construct prediction models that describe the statistical dependence between forest attributes measured from sample plots and ALS features describing canopy height and density (Holopainen et al. 2013). This kind of forest attribute modelling with ALS is often referred to as area-based approach (ABA; Næsset 2002). Regression equations describing the statistical relationship between the forest attributes and the selected ALS features is a common way to apply ABA. Various non-parametric machine learning methods can also be used (Cosenza et al. 2021). There are no general, one-size-fits-all forest attribute prediction models, as the performance of the models is affected by the structural variability in the area of interest and the ALS acquisition parameters. For example, differences in flight altitude and scanner settings will alter the characteristics of ALS data. If a forest attribute prediction model is applied in a geographically different area, differences in forest structure will affect the accuracy of prediction (Kotivuori et al. 2016). In Finland for example, the height/diameter ratio and annual volume growth are different in the north and south, which makes using the same model less accurate.

Previous research on ALS-based forest attribute modelling using an ABA has been carried out mainly in managed forests, especially in areas where forestry is actively applied. The study published by Næsset (2002) outlined the basic principle of ABA. Since then, the method has been developed and applied on a larger scale. In Finland, for example, ABA is in widespread operational use to obtain forest attributes by species. This kind of forest information is produced annually for about 3 million hectares (Maltamo et al. 2021). The inventory covers all forested areas, but sample plots used in the modelling are intentionally placed only to managed stands (Suomen Metsäkeskus 2018). Thus, the accuracy of ABA in natural forests is unknown, but tentative research on this topic suggests that the accuracy is not good (Honkanen 2022). All in all, less modelling has been done in natural forest environments, although e.g. standing deadwood volume has been modelled in a national park (Pesonen et al. 2008).

Although in ABA it is generally best practice to conduct new plot measurements, develop new predictive models, and apply the models separately for each inventory area, there are nonetheless use cases where applying the models beyond their original calibration data may be necessary. Typically, the reason for this is that there are not sufficient sample plots available from the area of interest. Models can be transferred to another inventory area for which ALS data have been collected using the same scanner and scanning parameters. In such cases, errors may still arise from the transfer, if the forest structure differs between the training and target areas. Models can also be applied to data collected with a different scanner, in which case differences in data characteristics introduce additional uncertainty into the model predictions (Næsset 2009). Temporal transfer means that models developed for an inventory area are applied to new data collected from the same area. Transferability of prediction models has been previously investigated in some of the use cases. For example, Kotivuori et al. (2016, 2018) studied the performance of national volume, biomass and dominant height models and their transferability between the inventory areas. Fekety et al. (2018) investigated the transferability of basal area and stem volume models within one ecoregion in Idaho, USA. The prediction accuracies for the stem volume models ranged from 32.3% to 50.1% by relative root mean square error (rRMSE) values validated at the plot level. It was concluded that the predictive models can be used at sites that are similar in ecological characteristics to the target sites, but the collection of site-specific sample plots is recommended to calibrate the results. Gopalakrishnan et al. (2015) investigated how accurately ALS-based forest inventory can be conducted in the southeastern United States using ALS datasets that had been collected using different ALS sensors/systems. They concluded that sufficient accuracy was not reached due to the heterogeneity in the forest structure and ALS data. Tomasik et al. (2019) investigated the impact of predicted forest attributes, modelling methods and point cloud characteristics on the prediction accuracy of the transferred models. They found that the most relevant factors affecting accuracy were the forest attribute of interest and the modelling method, while point cloud characteristics had a smaller impact on the results. Despite the research concerning model transferability, it remains unknown how well models developed for natural forests models can be applied across natural forests located in different regions.

Since the earlier research (Honkanen 2022) indicated that the use of ABA based forest attribute prediction models constructed in managed forests may be problematic in natural forests within the same inventory area, the aims of this study were to develop ABA based forest attribute prediction models for boreal natural forests, and to test the transferability of the models between inventory areas. Thus, our research question is whether an ABA-based model constructed in natural forests can be correspondingly transferred, as has previously been done in managed stands. Examining model transferability is particularly important for natural forests, where comprehensive inventories may be lacking. The starting point for the study is the fact that the study areas of natural forests are small and isolated from one another. In these areas, some research-related field inventories and corresponding remote sensing data acquisitions have been conducted over a long-time span. This means that the properties of remote sensing data vary considerably due to the development of scanners. This has an impact especially on model transfer, where relatively simple models that use first pulse data are preferred to be used (see e.g. Maltamo et al. 2025). The forest attributes to be modelled were growing stock volume, volume of standing deadwood, number of stems, dominant height, and Gini coefficient of tree diameters (Valbuena et al. 2016). In addition to the inventory area-specific models, we also developed general models covering all the natural forest areas included in the study. Furthermore, we tested the performance of the models in two non-natural forest inventory areas: one representing even-aged managed forests, and the other continuous cover forests. This allowed us to examine the effect of forest management type.

Material and methods

Study areas

The study data consisted of six different inventory areas located in Eastern and Southern Finland (Figure 1). Field plots and ALS data are available from each area. Four of the inventory areas, namely Hiidenportti National Park in Sotkamo, Kalkkinen in Asikkala, Koli National Park in Lieksa, and Nuuksio National Park in Espoo, are in natural forests. Katajamäki area in Rautavaara and Liperi operational inventory area are used for timber production. The models are only developed in the four natural forest areas, while continuous cover forestry area Katajamäki and even-aged area Liperi areas are for testing only. It should be noted that the natural forest data sets do not meet all the criteria of a natural forest, for example in terms of age, but the plots were in protected areas that have not been subject to forestry activities for several decades. However, they are counted here as natural forests, as the trees in the plots are considered to sufficiently correspond to the characteristics of natural forest in other regards.

Figure 1. Location of the inventory areas in Finland. Red points indicate natural forest modelling sites and grey points continuous cover forestry (Katajamäki) and even-aged (Liperi) test sites

Field data

The field data are from various research projects of the University of Eastern Finland, the Geospatial Research Institute of Finland, and the University of Helsinki from 2001–2021. Since the field measurements were conducted as part of different projects across various inventory areas, the placement, size, and measurement methods of the plots varied between the measurement campaigns. However, in all campaigns, the objective was to determine the stand attributes of the plots based on tree-level measurements. The number of plots varied between 14 plots in Koli and 216 plots in Nuuksio (Table 1). The field plots were either circular or rectangular depending on the inventory area. The circular plots were measured with radii of 7.98 m or 15 m, whereas rectangular plots had a side length of 30 m.

Due to the age of the field data, details of the field measurement protocol are missing from some areas. For the Hiidenportti and Katajamäki survey plots, the University of Eastern Finland's field guide was used, which is based on the field guide of the Finnish Forest Centre. In the Katajamäki inventory area, the centres of the plots were predefined. In the Hiidenportti inventory area, the surveyors had been given the stands for the plot measurements, but the final location of the plots in a stand was decided on the basis that there was at least one dead tree in the plot. The smallest tree to be included in the inventory had to be

Table 1. Mean forest characteristics of the inventory areas

Inventory area	Inventory, year	V, $m^3\ ha^{-1}$	V_d, $m^3\ ha^{-1}$	N, ha^{-1}	H_{dom}, m	Gini, 0–1	Canopy cover, %	Proportion of deciduous species, %	Number of the plots	Type	Size, m^2
Hiidenportti	2021	266 (40–522)	17 (0–41)	841 (453–1203)	27 (14–29)	0.26 (0.13–0.38)	69.8 (25.0–88.3)	22.9	36	C	707
Kalkkinen	2001	308.8 (15–533)	11 (0–101)	911 (467–2044)	25 (8–32)	0.26 (0.15–0.36)	82.5 (60.2–97.1)	40.9	33	R	900
Katajamäki	2021	147 (61–277)	3 (0–8)	870 (382–2759)	18.8 (15–24)	0.3 (0.22–0.42)	61.9 (32.0–95.0)	12.7	25	C	707
Koli	2005	49 (286–413)	10 (0–44)	1066 (433–1556)	26.2 (25–30)	0.35 (0.27–0.45)	90.5 (74.2–97.7)	48.5	14	R	900
Liperi	2016	222 (60–651)	1 (0–25)	1079 (170–4004)	21.3 (12–33)	17.7 (0.06–0.38)	75.6 (35.8–98.0)	21.8	111	C	707
Nuuksio	2007–2008	228.8 (8–613)	9 (0–108)	773 (100–3249)	23.4 (6–35)	0.26 (0.04–0.44)	61.7 (13.9–89.2)	29.6	148	C	200

Note: V – growing stock volume, V_d –standing deadwood volume, N – number of stems, H_{dom} – dominant height, Gini – Gini-coefficient according to breast height diameter. Canopy cover is calculated as explained in the section "Calculation of ALS features". Ranges of these characteristics are given in brackets. Proportion of deciduous species is calculated from V. Also information on plots is given, type refers to circular (C) or rectangular (R) plots.

at least 50 mm in diameter at breast height (d). For each tree measured, diameter at breast height, height, species and tree class (live/dead) were recorded. The height of the trees was measured with a Vertex measuring device and the position of the plots with a Trimble Geo 7 series Global Navigation Satellite System using differential post processing. In contrast to the above-mentioned guide, in the Nuuksio inventory area, tree heights were measured in only 46 plots and tree heights in the remaining plots were predicted using a model.

The volume of growing stock (V), the volume of standing deadwood (V_D) and the number of stems per hectare (N) were calculated for each plot in each inventory area (Table 1). Volumes were calculated using species-specific functions of Laasasenaho (1982). In addition, the dominant height (H_{Dom}) and the Gini coefficient (Gini) based on the diameters at breast height were calculated (Table 1). H_{Dom} is calculated as the arithmetic mean of the 100 thickest trees per hectare. Thus, for plots, this attribute was calculated from the relative number of thickest trees, e.g. in a 30×30 m plot, the H_{Dom} is calculated from nine trees. In the smallest plots with 7.98 m radius, the H_{Dom} was calculated from the trees that were thicker than the diameter of the basal area median tree (Dgm) of the plot. This is because the traditional method would only include two trees, which would make the result inaccurate. The Gini coefficient describes the difference in size of the tree structure, i.e. the higher the value, the more uneven the tree stock is in terms of diameter (Valbuena 2016). Gini coefficient values range from 0 to 1 and is as follows

$$Gini = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\left|d_i - d_j\right|}{2n^2\bar{d}}\ , \qquad (1)$$

where d is diameter at breast height, cm.

ALS data

ALS data were collected as part of the above-mentioned projects or in the national airborne laser scanning programme led by the National Land Survey of Finland. The data were collected in leaf on conditions between 2003 and 2020. The dates of the flights fell between May and July. Riegl, Toposys, Optech and Leica ALS devices were used, and the flight altitudes varied between 400 and 1,700 m. There were also differences among the data sets in the scan angle, pulse frequency and overlapping of scanning lines, but this information was not available for all data sets. Table 2 shows the ALS acquisition parameters by inventory area.

Table 2. Properties of the Airborne laser scanning data sets: date of the data acquisition, scanner type, beam divergence, flight height, point density and scanning angle

Inventory area	Scanning year	Scanner	Beam divergence, mrad	Flight height, m	First pulse point density, m^{-2}	Scanning angle, degrees
Hiidenportti	2020	Riegl VQ-1560II	0.23	2,100	5	20°
Kalkkinen	2003	Toposys Falcon	1.00	400	10	7.1°
Koli	2005	Optech ALTM 3100	0.43	900	4	11°
Nuuksio	2006	Optech ALTM 3100	0.43	1,000	4	-
Katajamäki	2019	Leica ALS 80HP	0.22	1,700	5	-
Liperi	2016	Optech Titan, channel 2	0.50	850	13	40°

Calculation of ALS features

Lascanopy tool from the LAStools (Rapidlasso 2025) software was used to calculate the features of ALS data. The ALS echoes were classified into ground and vegetation hits using cell size 2 m and the approach presented by Axelsson (2000). Only the first echoes were used, as the first echo is known to be robust in describing the height characteristics of the vegetation, and ABA-based forest attribute prediction models can be transferred between inventory areas (Maltamo et al. 2025). In addition, the Toposys scanner used in Kalkkinen area was an early system that could only record two echoes per pulse, first and last. Thus, using only first echoes was the best option from the perspective of model transferability. Echo heights were first normalized, which meant converting the original echo heights to represent above ground heights. The ABA metrics were computed for each plot without a height threshold by using only first of many and only echoes. However, when calculating canopy cover, height threshold of 2 m was applied. Finally, ALS features describing echo heights and densities (Næsset and Gobakken 2008) according to LAStools were calculated (Table 3).

Modelling forest attributes and model transferability tests

Linear regression models were developed and used to predict forest attributes. We used linear models to keep the models simple, as the focus of this study was on the transferability. We constructed a model using ALS features as explanatory variables for each forest attribute per inventory area, as well as general models (also joint models term used), resulting in a total of 25 models. Models were fitted in the R environment using the method of ordinary least squares (R Core Team 2022). For each model, the explanatory variables were selected on the basis of the combination that gives the lowest root mean square error (RMSE) while using two predictor variables. ALS variable pool also included square root and natural logarithm transformations of the predictor variables. The set of ALS features, thus, contained 67 explanatory features (Table 3). In the case of general models, statistical significance of the inventory area specific indicator variable was tested, and these models could therefore include more than two variables. The accuracy of the prediction model within its development dataset was assessed by leave-one-plot-out cross-validation (LOOCV) using relative root mean square error (rRMSE) and relative bias (rBias). When applying the model to other inventory areas or to the test areas in Liperi and Katajamäki, the accuracy was evaluated using field plots measured in the respective areas, from which rRMSE and rBias were calculated. The equations for RMSE and Bias are as follows:

$$RMSE = \sqrt{\sum_{i=1}^{n} \frac{(x_i - \hat{x}_i)^2}{n}} , \quad (2)$$

where

n – the number of plots,

x – the observed forest attribute for plot i, and

$\hat{x}_i$ –the predicted forest attribute for plot i.

$$Bias = \sum_{i=1}^{n} \frac{(x_i - \hat{x}_i)}{n} , \quad (3)$$

Feature	original	sqrt	ln	Explanation
max	x	x	x	Maximum value of height, m
avg	x	x	x	Average height. m
qav	x	x	x	Average square height, m2
std	x	x	x	Standard deviation of height, m
p30	x	x		Cumulative height percentiles, m
p40	x	x		
p50	x	x		
p60	x	x		
p70	x	x		
p80	x	x	x	
p90	x	x	x	
p95	x	x	x	
b05	x	x	x	Cumulative densities of height percentiles, %
b10	x	x	x	
b20	x	x	x	
b30	x	x	x	
b40	x	x	x	
b50	x	x	x	
b60	x	x	x	
b70	x	x	x	
b80	x	x	x	
b90	x	x	x	
b95	x	x	x	
dns	x	x	x	Canopy cover, %

Table 3. Candidate ALS features and for which features square root (sqrt) and natural logarithm (ln) transformations were computed. The features were calculated by using only first of many and only echoes

Subsequently, rRMSE and rBias were calculated by dividing the RMSE or Bias by the observed attribute mean and then multiplying the result by 100. The accuracies of the general models, which covered all natural inventory areas, were also assessed by LOOCV and, in addition, by applying the models to the Liperi and Katajamäki areas.

Results

Forest attribute prediction models

In all models all chosen explanatory variables were statically significant (p-values lower than 0.05). The chosen ALS predictors, coefficients, the residual mean errors and the adjusted R^2 values of growing stock volume models are presented in Table 4. For the growing stock volume models, the residual mean errors ranged from 38.01 to 76.24 m^3 ha^{-1} and the adjusted R^2 values ranged between 0.64–0.90.

Correspondingly, the chosen ALS predictors, coefficients, residual mean errors and adjusted R^2 values of the standing deadwood volume models are presented in Table 5. For the standing deadwood volume models, the residual mean errors ranged from 8.77 to 17.84 m^3 ha^{-1} and the adjusted R^2 values ranged between 0.11–0.40.

The chosen ALS predictors, coefficients, residual mean errors and adjusted R^2 values of the number of stems models are presented in Table 6. For these models, the residual mean errors ranged from 166.2 to 358 stems ha^{-1} and the adjusted R^2 from 0.36 to 0.86.

The chosen ALS predictors, coefficients, residual mean errors and adjusted R^2 values of the dominant height models are presented in Table 7. For the dominant height models, the residual mean errors ranged from 0.58 to 2.59 m and the adjusted R^2 values ranged between 0.78–0.97.

The chosen Gini coefficient predictors, coefficients, the residual mean errors and the adjusted R^2 values are presented in Table 8. For the Gini coefficient models, the residual mean errors ranged from 0.022 to 0.075 and the adjusted R^2 values ranged between 0.22–0.83.

Table 4. Growing stock volume (V) models and residual standard error (RSE) and adjusted R-square (R^2) of the models

Inventory area	Model		RSE	Adjusted R^2
Hiidenportti	$V = 541.58 + 65.04 \cdot p90 - 339.01 \cdot \sqrt{p95}$	(1)	44.33	0.77
Kalkkinen	$V = -0.35 - 10.5 \cdot p30 + 1.4 \cdot qav$	(2)	44.78	0.90
Koli	$V = -1346.27 - 24.78 \cdot \sqrt{b50} + 534.75 \cdot \ln(\max)$	(3)	38.01	0.77
Nuuksio	$V = -44.58 + 11.15 \cdot p70 + 6.58 \cdot p90$	(4)	76.24	0.64
General	$V = -83.44 - 4.06 \cdot p30 + 28.28 \cdot \sqrt{gav} - 38.11 \cdot Kalkkinen$	(5)	68.70	0.70

Note: ALS features, see Table 3, *Kalkkinen* refers to inventory area specific dummy variables.

Table 5. Standing deadwood volume (V_d) models and residual standard error (RSE) and adjusted R-square (R^2) of the models

Inventory area	Model		RSE	Adjusted R^2
Hiidenportti	$V_d = -234.62 - 1.88 \cdot b40 + 87.38 \cdot ln(b50)$	(6)	8.77	0.33
Kalkkinen	$V_d = -1361.11 - 45.35 \cdot \sqrt{b80} + 394.55 \cdot ln(b90)$	(7)	17.84	0.22
Koli	$V_d = -67.84 - 358.08 \cdot ln(p90) + 375.9 \cdot ln(p95)$	(8)	9.075	0.40
Nuuksio	$V_d = -6.85 - 8.86 \cdot \sqrt{p80} + 6.98 \cdot std$	(9)	17.58	0.14
General	$V_d = -8.66 - 3.55 \cdot \sqrt{p30} + 1.91 \cdot \sqrt{qav} + 6.95 \cdot Hiidenportti$	(10)	16.89	0.11

Note: ALS features, see Table 3, *Hiidenportti* refers to inventory area specific dummy variables.

Table 6. Number of stems (N) models and residual standard error (RSE) and adjusted R-square (R^2) of the models

Inventory area	Model		RSE	Adjusted R^2
Hiidenportti	$N = 1447.62 + 212.0 \cdot \sqrt{dns} - 747.37 \cdot ln(max)$	(11)	166.20	0.46
Kalkkinen	$N = 785.84 - 66.39 \cdot b20 + 55.21 \cdot b40$	(12)	233.90	0.57
Koli	$N = 13967.28 + 374.0 \cdot avg - 3293.18 \cdot ln(qav)$	(13)	201.80	0.86
Nuuksio	$N = 456.59 + 420.98 \cdot \sqrt{dns} - 1034.58 \cdot ln(p90)$	(14)	358.0	0.40
General	$N = -1456.25 - 510.47 \cdot \sqrt{avg} + 474.38 \cdot \sqrt{dns}$	(15)	350.7	0.36

Note: ALS features, see Table 3.

Table 7. Dominant height (H_{dom}) models and residual standard error (RSE) and adjusted R-square (R^2) of the models

Inventory area	Model		RSE	Adjusted R^2
Hiidenportti	$H_{dom} = 4.53 + 0.034 \cdot p30 + 0.98 \cdot p90$	(16)	0.58	0.97
Kalkkinen	$H_{dom} = -1.77 + 0.56 \cdot max + 0.47 \cdot p95$	(17)	1.25	0.96
Koli	$H_{dom} = -71.88 - 1.75 \cdot p70 + 43.72 \cdot ln(p80)$	(18)	1.14	0.90
Nuuksio	$H_{dom} = -19.27 + 0.078 \cdot b20 + 8.89 \cdot \sqrt{p95}$	(19)	2.59	0.78
General	$H_{dom} = -9.37 - 0.83 \cdot \sqrt{dns} + 8.86 \cdot \sqrt{p95} - 1.14 \cdot Kalkkinen$	(20)	2.22	0.82

Note: ALS features, see Table 3, *Kalkkinen* refers to inventory area specific dummy variable.

Table 8. Gini coefficient (Gini) models and residual standard error (RSE) and adjusted R-square (R^2) of the models

Inventory area	Model		RSE	Adjusted R^2
Hiidenportti	$Gini = 0.44 - 0.095 \cdot \sqrt{b05} + 0.0092 \cdot b30$	(21)	0.048	0.36
Kalkkinen	$Gini = 0.097 - 0.028 \cdot p50 + 0.009 \cdot \sqrt{qav}$	(22)	0.037	0.51
Koli	$Gini = -0.21 + 0.0024 \cdot b50 + 0.009 \cdot \sqrt{max}$	(23)	0.022	0.83
Nuuksio	$Gini = -0.59 + 0.0079 \cdot b30 + 0.0078 \cdot dns$	(24)	0.075	0.22
General	$Gini = -0.55 + 0.0077 \cdot b30 + 0.0075 \cdot dns + 0.076 \cdot Koli$	(25)	0.066	0.27

Note: ALS features, see Table 3, *Koli* refers to inventory area specific dummy variable.

Model accuracy

Figures 2 and 3 illustrate the differences in prediction accuracy among the forest attributes by inventory area in terms of absolute and rRMSE and absolute Bias and rBias (see also Supplementary data Tables A1–A5).

The main observation was that the Nuuksio models (4, 9, 14, 19, 24) always produced the worst results in terms of rRMSE in their own modelling data. The Hiidenportti models (1, 6, 11, 16, 21) produced the best results in their own data for three different forest attributes. Most of the rBiases fell within 0.5% in the whole data, with the exception of the rBiases for Koli stem volume (3), standing dead volume (8) and number of stems (13) models, which exceeded the 2% limit. In addition, the rBias in Kalkkinen standing dead wood model (7) was exceptionally large. However, it should be noted that the rBiases within the modelling data were a result of cross-validation, i.e. without cross-validation the models are unbiased within their own data.

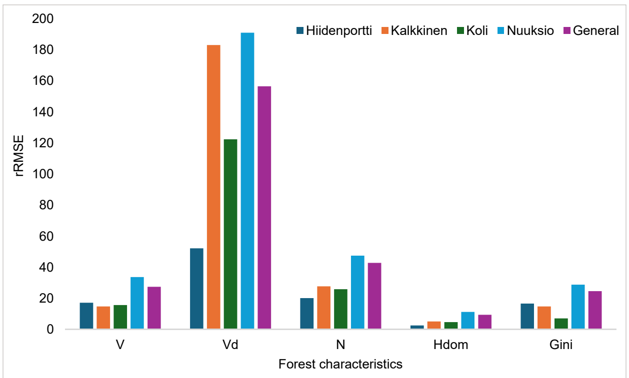

Figure 2. Cross-validated accuracies of growing stock volume (V), standing deadwood volume (V_d), number of stems (N), dominant height (H_{dom}) and Gini coefficient (Gini) models in terms of rRMSE

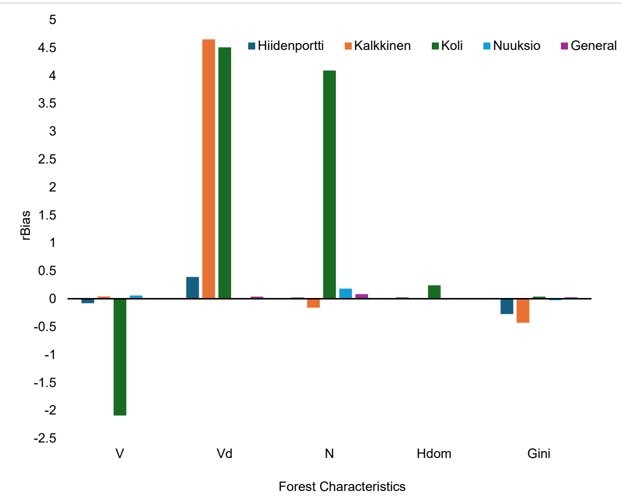

Figure 3. Cross-validated model accuracies of growing stock volumes (V), standing deadwood volume (V_d), number of stems (N), dominant height (H_{dom}) and Gini coefficient (Gini) in terms of rBias

Furthermore, from the results in Figure 2 and Tables A1–A5, it can be observed that the order of prediction accuracy of the forest attribute models according to the mean rRMSE, from most to least accurate, was as follows: dominant height (6.6%), Gini coefficient (18.4%), growing stock volume (21.8%), number of stems (32.8%) and volume of standing dead wood (141.1%). This means that on average, the dominant height model (16–20) gave results that are closest to the values measured in the field, while the standing deadwood volume modeling (6–19) deviated on average by almost one and a half times from the values measured in the field. There was a wide variation in model accuracy for different forest attributes, but the standing deadwood volume models were particularly inaccurate on average.

Looking at the results of all models averaged by inventory areas in Figure 2 and Tables A1–A5, it can be seen that the average rRMSEs from the most to the least accurate were: Hiidenportti (21.8%), Koli (35.2%), Kalkkinen (49.1%), general models (52.2%) and Nuuksio (62.5%). In other words, the predictions of the Hiidenportti models were on average closest to the observed values, while the predictions of the Nuuksio models were the most inaccurate.

Prediction accuracies of model transfers and in sub-data sets

Models for the growing stock volume

The mean rRMSE (LOOCV) of the growing stock volume models in the study areas was 18.4% and the corresponding rBbias was –2.1%. Transferred to other inventory areas, the average result was 30.7% for rRMSE and 5.8% for rBias. The order of prediction accuracy in other inventory areas based on rRMSE was, on average, as follows (Figure 4, Table A1): Nuuksio model (21.0%), joint model (23.2%), Hiidenportti model (32.6%), Kalkkinen model (36.8%) and Koli model (41.4%). In the case of joint model, it should be noted that the figures are based on model

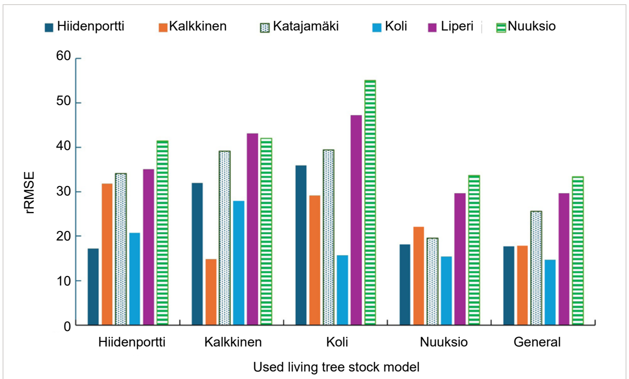

Figure 4. Model and transferred accuracies of growing stock volume models in terms of rRMSE

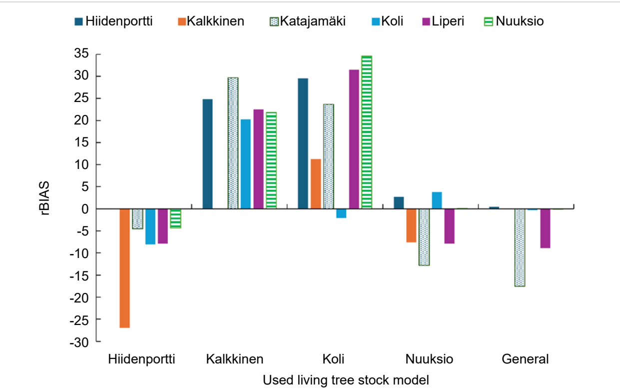

Figure 5. Model and transferred accuracies of growing stock volume models in terms of rBias

reliability in each inventory area as a part of joint model. The average rBiases (Figure 5) for the other inventory areas were in the following order, from most to least accurate: joint model (–4.4%), Nuuksio model (–4.4%), Hiidenportti model (–10.4%), Kalkkinen model (23.8%) and Koli model (26.1%). On average, the general model performed better than other models in the prediction of growing stock volumes, although the rRMSE was about 2% percentage points worse than the best model (Nuuksio).

As illustrated in Figure 4, there were no differences in the rRMSE results, except for the Nuuksio model, which produced better results for the other areas than for the modelling area. In terms of rBias (Figure 5), it can be observed that the Kalkkinen and Koli models almost invariably produced underestimates of around 20% for all data sets. The overestimates for Hiidenportti, Nuuksio and the general model were more moderate.

Models for the standing deadwood volume

In the volume models of standing dead wood, the mean rRMSE (LOOCV) of the study areas was 141.1% and the corresponding rBias was 1.9%. Transferred to other inventory areas, the average result was 337.7% for rRMSE and –86.0% for rBias. The order of prediction accuracy on average in the other inventory areas and

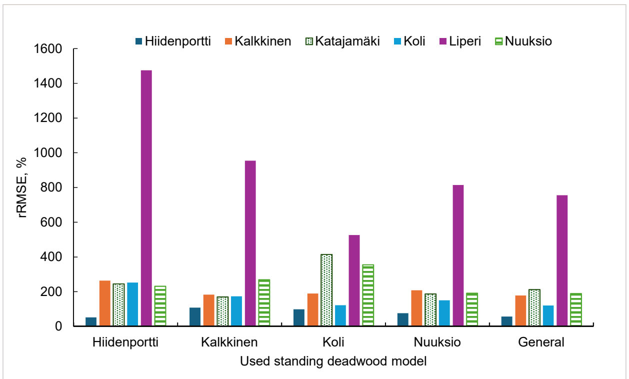

Figure 6. Model and transferred accuracies of standing deadwood volume models in terms of rRMSE

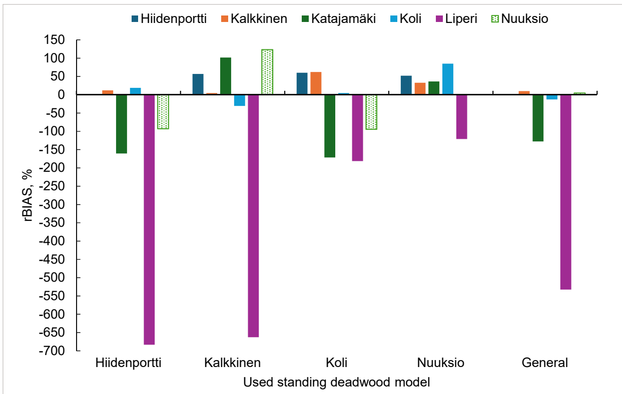

Figure 7. Model and transferred accuracies of standing deadwood volume models in terms of rBias

rRMSE according to Figure 6 and Table A2 was as follows: general model (252.6%), Nuuksio model (287.3%), Koli model (316.9%), Kalkkinen model (334.83%) and Hiidenportti model (493.5%). For the other inventory areas, the average rBiases (Figure 7) were in the following order from most to least accurate: Nuuksio model (17.0%), Koli model (–64.9%), Kalkkinen model (–82.3%), joint model (–113.0%) and Hiidenportti model (–181.2%). The joint model thus performed better than the other models on average, but the models were still highly inaccurate. In terms of Bias, the joint model produced the second worst result.

Figure 6 shows how the standing deadwood volume models are highly inaccurate in terms of rRMSE values, especially when transferred to a managed even-aged forest. Even without the Liperi managed forest data, the average rRMSE was close to 200%. In terms of rBias (Figure 6), the models transferred to the Liperi area produced overestimates of several hundred percent. When transferred to other areas, the rBias also reached tens of percentages almost without exception.

Models for the number of stems

In the models of number of stems, the mean rRMSE (LOOCV) of the study areas was 32.9% and the corresponding rBias was 0.9%. Transferred to other inventory areas, the average result was 64.1% for rRMSE and –5.1% for

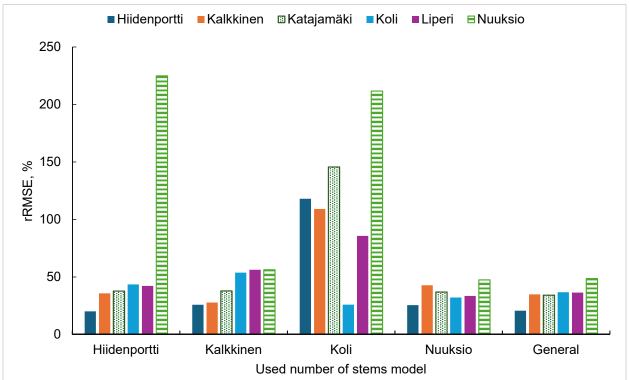

Figure 8. Model and transferred accuracies of number of stems models in terms of rRMSE

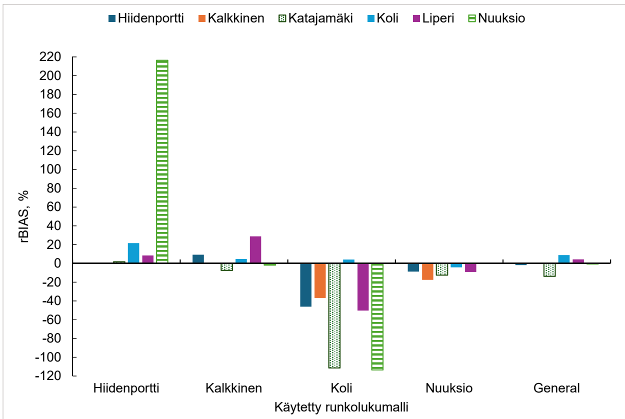

Figure 9. Model and transferred accuracies of number of stems models in terms of rBias

rBias. According to Figure 8 and Table A3, the order of prediction accuracy after transfer and average rRMSE was as follows: Nuuksio model (34.2%), joint model (35.3%), Kalkkinen model (46.0%), Hiidenportti model (76.8%) and Koli model (134.1%). In the other inventory areas, the average rBiases (Figure 9) were in the following order from most to least accurate: the general model (–0.7%), the Kalkkinen model (6.7%), the Nuuksio model (–10.4%), the Hiidenportti model (49.5%) and the Koli model (–71.6%). The general model performed second best for the number of stems, just after Nuuksio, with an rRMSE one percentage unit higher. In terms of rBias (Figure 9), the performance is average on a ranking scale, but still better than the average for the models when averaged over the figures.

Figure 8 shows that by transferring the Hiidenportti and Koli models to the Nuuksio data, the rRMSE was over 200%. With the Koli number of stems model, the rRMSE was around 100% in the other inventory areas as well. For the other models and areas, the rRMSEs were mainly between 30–50%. In terms of rBias (Figure 9), the Koli model yielded overestimates of tens of percents in all areas, except for the modelling data itself. In addition, transferring the number of stems model from Hiidenportti to the Nuuksio resulted in an underestimation of more than 200%.

Models for the dominant height

In the models of dominant height, the mean rRMSE (LOOCV) of the study areas was 6.6% and the corresponding rBias was 0.1%. Transferred to other inventory areas, the average results were 12.6% for rRMSE and –0.5% for rBias. According to Figure 10 and Table A4, the order of prediction accuracy based on the average rRMSE after transfer was as follows: joint model (8.5%), Nuuksio model (8.9%), Hiidenportti model (9.9%), Kalkkinen model (10.8%) and Koli model (26.0%). For the other inventory areas, the average rBiases (Figure 11) were in the following order from most to least accurate: Koli model (–0.91%), Nuuksio model (–1.0%), joint model (–2.2%), Hiidenportti model (–4.1%) and Kalkkinen model (6.2%). On average, the joint model produced the most accurate results for predicting the dominant height, with an overestimation of only 2.2%.

Figure 10 shows that the results are fairly even in terms of rRMSE, except for the Koli model transferred to Katajamäki and Nuuksio data, where the rRMSE was over 30%, while elsewhere the values were mostly around 10%. The values for the rBias (Figure 11) were about 10% over- and underestimates. In the Katajamäki area, almost all results were overestimates. With the Hiidenportti model, the

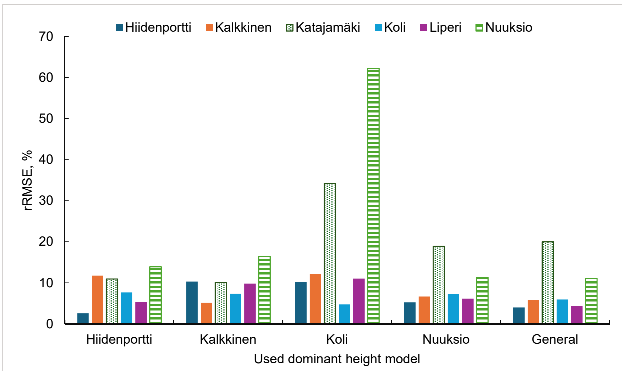

Figure 10. Model and transferred accuracies of dominant height models in terms of rRMSE

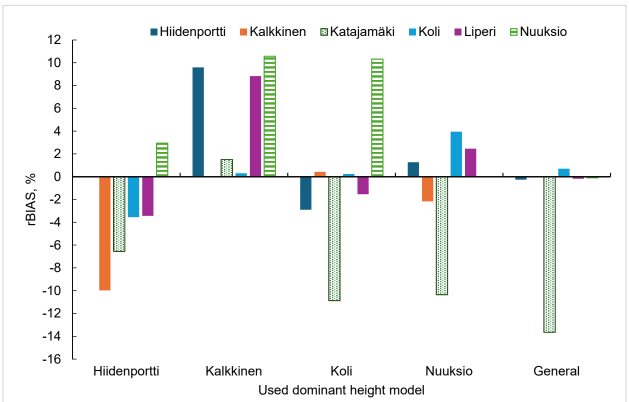

Figure 11. Model and transferred accuracies of dominant height models in terms of rBias

dominant heights were overestimated on most of the other inventory areas. On the other hand, the Kalkkinen and Koli models gave underestimates of more than 10%.

Models for the gini-coefficient

In the models of gini coefficient, the mean rRMSE (LOOCV) of the study areas was 18.4% and the corresponding rBias was 0.7%. Transferred to other inventory areas, the average results were 26.8% for rRMSE and –6.8% for rBias. According to Figure 12 and Table A5, the order of prediction accuracy based on the average rRMSE after transfer was as follows: general model (19.8%), Nuuksio model (22.0%), Hiidenportti model (27.7%), Kalkkinen model (27.6%) and Koli model (38.28%). In the other inventory areas, the average rBiases (Figure 13) were in the following order of prediction accuracy, from most accurate to least accurate: Kalkkinen model (–0.6%), joint model (0.73%), Nuuksio model (8.1%), Hiidenportti model (–13.2%) and Koli model (–29.7%). The joint model produced the best average results for Gini coefficient, and the Biases indicated underestimates of less than 1%.

Figure 12 shows that the rRMSE values were relatively similar, but slightly larger errors occurred when the models were transferred to the Liperi and Nuuksio data sets. In terms of rBias (Figure 13), Koli and Hiidenportti models overestimated the most. For the Liperi and Nuuksio datasets, overestimates occurred for each model. The underestimations were mainly due to the transfer of models to the Koli area.

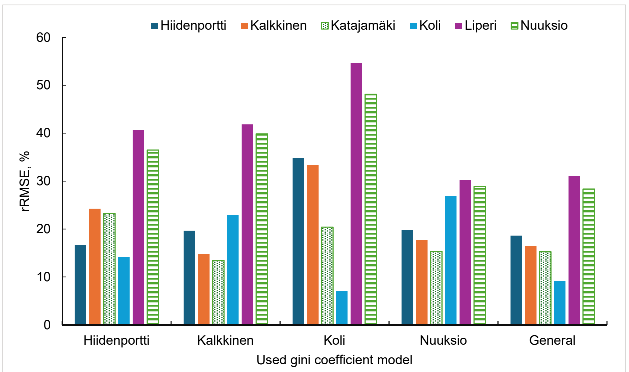

Figure 12. Model and transferred accuracies of gini coefficient models in terms of rRMSE

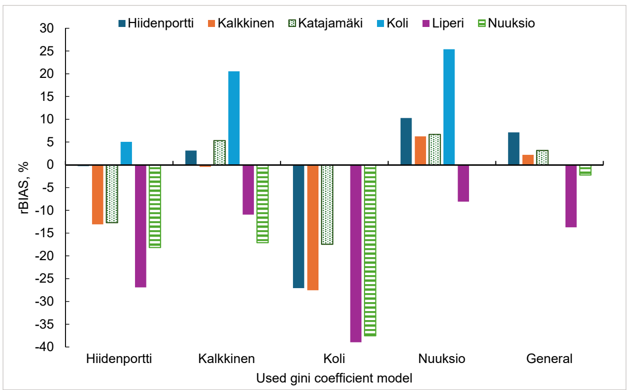

Figure 13. Model and transferred accuracies of gini coefficient models in terms of rBias

Discussion

This study examined the transferability of natural forest attribute models. Based on the previous studies (e.g. Maltamo et al. 2025) we only had two predictor variables in the models. Correspondingly, we only used first pulse data of the ALS data. This was also affected by the properties of different ALS data which were acquired during a long-time span. These aspects might have slightly decreased the model accuracy of the models but on the other hand improved transferability. The results showed that the transferability varied between forest attributes but was on average slightly worse than in the case of transferability of forest attributes in managed forests.

Comparison to other studies

Research on the modelling some of the forest attributes has already been performed on each of the individual data sets, so the results obtained with the modelling data can be directly compared with previous results. In general, the reliability of the models was worse in this study which may be due to the fact that our models were constructed aiming for best possible transferability. For growing stock volume, there are earlier results from the Kalkkinen area (Maltamo et al. 2006). In this study, the model rRMSE ranged from 10 to 14%. The pulse density of the data was not found to have an impact on the results. In the current study, the rRMSE value for the stem volume of Kalkkinen was 14.79%. The small difference in the result is probably due to the fact that cross-validated models were used in this study, as cross-validation tends to slightly increase the RMSE values. In the Maltamo et al. (2006) the form of the models differed (more predictors) from the two-predictor linear regression models used in this study, which may also contribute to the results. In addition, only the first echoes were used in this study, whereas the Maltamo et al. (2006) used both first and last echoes.

In a study by Pesonen et al. (2008), the volume of standing deadwood volume was modelled using the Koli data. Their rRMSE was 78.8% while in this study it was 122.4%. The difference is large, but the method is not exactly the same as in the Pesonen et al. (2008). In addition, the data in Pesonen et al. (2008) included also managed pine dominated plots, which were not used in this study, so the number of plots was almost doubled compared to this study. In addition, Pesonen et al. (2008) used an intensity variable to improve the accuracy of the results. In this work, the transfer of the models to other inventory areas prevented the use of intensity features. Intensity features can help to distinguish, for example, dead trees from living ones (Wing et al. 2015).

Hiidenportti data have been used to construct models for the growing stock volume, the volume of standing deadwood, and the Gini coefficient (Vänskä 2023). The rRMSE for predicting the growing stock volume was 13.8%, while in this study it was 17.2%. The rRMSE for the volume of standing deadwood was 45.34%, compared to 52.28% in this study, and the rRMSE for the Gini coefficient prediction was 12.7%, compared to 16.7% in this study. The corresponding errors in this study were therefore slightly larger, but this is because the Vänskä (2023) models were not cross-validated and the models generated by regression analysis had three explanatory variables. In addition, the Gini coefficient was calculated from basal area rather than diameter, which affected the results. The number of echo types was also higher than in this study, as ALS features from the last echoes were also used. All in all, these results are comparable to our results.

Mäkinen (2023) also predicted the volume of standing deadwood in Hiidenportti National Park. The best model achieved an rRMSE of 55.7%, whereas in the present work the rRMSE was 52.3%, so the accuracies are still fairly consistent between the two studies. The models were constructed using the cross-validation in both studies, but in Mäkinen (2023) vegetation index values calculated from aerial photographs were also used as explanatory variables.

Volume models have also been constructed in the Katajamäki continuous cover forestry area for both growing stock and standing deadwood (Maltamo et al. 2023). The models yielded rRMSE values of 8.9% for stem volume and 52.47% for standing deadwood. In this work, volume models from other regions transferred to the Katajamäki data set produced an average rRMSE of 30.7%, but the best result was obtained with the Nuuksio model, i.e. 19.5%. In the case of standing deadwood, the averaged result of all inventory area-specific models for Katajamäki in this study was 235.6%, with the best result obtained with the joint model (162.0%). The differences are partly due to the fact that the models were constructed for areas of different forest management than the Katajamäki data itself. The models were also constructed using different methods, e.g. also intermediate and last echoes were used in the Maltamo et al. (2023) study.

In the Nuuksio national park data, growing stock volume and mean height have been modelled by comparing ALS and radar data (Holopainen et al. 2010). The features used were selected using a genetic algorithm and the non-parametric K-nearest neighbour method was used for prediction. The models based on the ALS data yielded a rRMSE of 35.7% for growing stock volume. In this work, the growing stock volume model produced a rRMSE of 33.7%. The rRMSE for the mean height in the study by Holopainen et al. was 14.7%. In the present study, the rRMSE of the dominant height was 11.3%. It should be noted, however, that mean height and dominant height are different attributes, but both describe the vertical structure of the forest. The mean height may be more difficult to model, as it includes trees below the dominant height, which may be more difficult to detect from the ALS data. The volume results were relatively similar, and small differences could be due to the different modelling methods.

Kukkonen et al. (2019) predicted tree species-specific growing stock volumes using the data from the Liperi inventory area. In addition to ALS, optical data were used in the study. The prediction errors for the rRMSE ranged from 30 to 60%. The prediction accuracies in their study can be somewhat compared to the accuracy of our stem volume model, as the results were based on laser features. The rRMSEs in their study ranged from 20.9% to 33.5%. In our study, the live volume models transferred to the Liperi data yielded rRMSE values between 29.7% and 47.2%, or an average of 37.2%. The results are quite similar, but also not directly comparable due to the different tree species and the modelling method used. Compared to the Kukkonen et al. (2019), the volume prediction errors are smaller in our study. The differences are due to the species-specific nature of the Kukkonen et al. (2019) study, which makes it difficult to obtain an accurate prediction.

Different impacts on prediction accuracy

In general, the modelling of forest attributes is done on a data-by-data basis. The reason is that when ALS data are acquired under different forest structures, phenological conditions, and ALS devices, the properties of point cloud data differ from each other. This must be considered when using several different data sets in the same study and when transferring models between different data sets. The differences arise from many factors. The ALS device is a relevant factor, as there are differences between scanners, and they have evolved considerably in past 20 years. Six different ALS devices from four different manufacturers were used to acquire the data for this study. In addition, there are many data acquisition parameters that affect the properties of the ALS data. Flight altitude affects the results, as the footprint of the transmitted pulse and the laser power per footprint area (irradiance) vary with the flight altitude (Hopkinson 2007). Typically, if the irradiance is constant, pulses with larger footprints will provide more echoes from both the canopy and the ground. On the other hand, smaller irradiance leads to fewer echoes regardless of footprint area. The flight altitudes of the data used in this work ranged from 400 to 2,100 metres, which may lead to major differences in both footprint and irradiance. A second influencing parameter is the scan angle. In this study, the scanning angles varied between 7.1 and 40 degrees, which can have major effect on the number of ground echoes and canopy density variables (Holmgren et al. 2003). Finally, another parameter that affects the usefulness of the data is the pulse density. While its effects are generally small (Gobakken and Næsset 2008, Jakubowski et al. 2013), the point density ranged from 4 to 13 points per square metre, which could possibly affect the results. Sensitivity and capability of ALS devices to record multiple echoes per pulse has also improved drastically. For this reason, we used only first echoes in this study.

Model transferability

Typically, the rRMSE almost doubles and the rBias multiplied with model transfer. The results for growing stock volume were fairly consistent, but the rBiases showed that the predictions were highly underestimated when applying Koli and Kalkkinen models. This may be because both areas are slightly more rugged in their characteristics than the other areas. Both areas are at least 100 m above sea level and hilly. It can therefore be assumed that the trees in these areas are shorter than average in relation to their diameter, which affects the volume model predictions in the other areas.

It was found that the prediction errors associated with standing deadwood volume were large. This is in line with the previous studies (Pesonen et al. 2008, Maltamo et al. 2023). In particular, the errors were very large when the models were transferred to Liperi. This may be due to the fact that the managed Liperi plots, unlike the natural forest plots in training areas, have almost no deadwood, which leads to large overestimates. On the other hand, when transferred to the Hiidenportti data, the models performed somewhat tolerably. Hiidenportti plots were established so that here is always at least one large decaying tree, which improved model accuracy. The forests in the Liperi area are managed by periodic cover and have a relatively uniform structure. This highlights the problem that it is difficult for ALS features to distinguish between standing dead and living trees, as the two categories present similar structures. As mentioned in the study by Pesonen et al. (2008), prediction of the volume of standing deadwood is also inaccurate compared to the prediction accuracy of the volume of downed deadwood. The identification accuracy of standing deadwoods could possibly be improved, if a tree level approach and higher pulse density data were used instead. Deadwood dynamics could potentially be effectively monitored using ALS time series data.

The observed decreases in accuracy due to the model transfers were smaller for the number of stems, dominant height and Gini coefficient. There were no major differences in the transfer of number of stems models between inventory areas, but the Koli model had the largest errors and overestimates when transferred to other areas. In addition, the Hiidenportti model in Nuuksio causes an underestimation of the number of stems by more than 200%. The results are also fairly consistent in terms of dominant height, with the exception of applying the Koli model in Nuuksio. One notable aspect is the poor performance of these models in Katajamäki. This may be because dominant height is a different attribute in even-aged and uneven-aged forests. Using different Gini coefficient models in Liperi and Nuuksio yielded the highest rRMSE values. In addition, large overestimates were obtained for Liperi, which can be explained by the forest structure of Liperi, as the models were trained with near-natural forest plots. The phenomenon was reversed for Koli, where differences in size between trees were largest (highest Gini coefficient; Table 1). The low adjusted R-square values in Nuuksio may relate to the small plot size with larger variation in gini coefficient values.

When examining the results, it was found that all Nuuksio models performed worse in their own modelling data than when transferred elsewhere. The poor performance in the modelling data may be due to the small size of the Nuuksio plots (200 m^2) compared to the size of the plots in the other datasets (700–900 m^2). It has been noted that the small size of the plots is prone to positional errors and thus to inaccurate modelling results (Gobakken and Næsset 2009). Positioning errors are particularly likely to occur if the visibility upward from the bottom of the plot is poor, or if there are large differences in terrain height. In such conditions, the number of satellites available for positioning is typically smaller than usual. If the plots were larger, the increased size would mitigate the effects of positioning errors.

However, the good performance of the Nuuksio models in transfer was surprising. A possible explanation for this may be the large sample size of Nuuksio, with 148 plots. This may allow the construction of more robust models. The number of plots was particularly large compared to the Koli data, for example, as there were only 14 plots, so the Koli models are probably not as robust. The large number of plots in Nuuksio was also reflected in the results obtained with the general models, which are very similar to the Nuuksio models. This is because Nuuksio's characteristics dominated the models due to the large number of plots. A solution to this could have been to use weighted regression where each data set would have obtained the same proportion of the modelling data. Then the number of samples in the individual data sets would not have affected the properties of the general model so much (Maltamo et al. 2023).

There are no clear trend emerging that unambiguously indicates the transfer of models according to a specific logic. It might be assumed that the models of the Southern Finland inventory areas would work well together due to their close proximity. The same assumption applies to the inventory areas in Eastern Finland. However, such a phenomenon was not directly observed, which may be due to differences in forest silvicultural history, habitats included and other growing conditions. Similar assumptions could be made about the properties of the scanners, whereby data from older scanners would produce mutually compatible models, and vice versa. In addition, the naturalness stage of an inventory area could be expected to produce mutually compatible models. These assumptions are not completely ruled out, but there is also no clear trend in their favour.

As noted in previous studies testing transferability, the good predictive accuracy of forest attribute models in a transfer is usually observed when the stand structure is similar to that in the training data (Fekety et al. 2018, Karjalainen et al. 2019, Toivonen et al. 2021). This can be seen particularly in the case of the natural forest models in the Liperi even-aged forestry area, where the prediction accuracy was worse than elsewhere. The use of general models improves the results, as their modelling data are more diverse in structure than the individual data sets. It can also be also observed that in some cases the site-specific models provided a better accuracy than the general model in a data subset. This indicates the averaging effect of general model.

For transferability, the predictive accuracy of the models could be improved by calibrating the modeling data with a few plots from the target area that are representative of local growing conditions (Korhonen et al. 2019). In general, the use of ALS predictors specifically in natural forest environments is logical, as natural forests are generally mature and the ALS modelling results are most accurate in such forests (Suvanto et al. 2005). In the future, it is likely that more comprehensive modelling of natural forest features will be possible as more accurate laser data becomes available. High-density data could allow more accurate mapping of characteristics specific to natural forests, such as spatial distribution of stands or decaying trees.

The results of this study indicate that if accurate estimates of forest attributes are required in natural forests, prediction models specific to protected areas should be developed. However, ground truth data acquisition from protected areas may be expensive, since these areas are usually small in size and may be far from roads. Field data for protection area specific models may be acquired, if ecological information on other species than just trees are also acquired. In the case of a protection area specific models the use of more versatile ALS predictors that could utilize e.g. last and intermediate echoes and intensity information, could be also enabled. In addition, field data acquisition could include, for example, terrestrial laser scanning measurements.

In general, model transferability will much likely increase in the future due to the high field data acquisition costs. The most serious problem in transferability so far, the prediction of species-specific attributes, which was not covered in this study needs yet to be solved. From a methodological point of view, the use of deep learning approaches and very large training datasets may also be beneficial.

Conclusions

The results of this study showed that the transferability of the ABA based forest attribute prediction models is modest in natural forests. On average, model transfers increased the rRMSE of growing stock volume by about 9 percentage points, the rRMSE of standing deadwood volume by about 190 percentage points, the rRMSE of number of stems by about 31 percentage points, the rRMSE of dominant height by about 6 percentage points, and the rRMSE of Gini coefficient by about 9 percentage points. If the obtained accuracy of growing stock attributes were acceptable for natural forest inventory, one could rely on model transfer or the use of general models constructed similarly as in this study.

Acknowledgements

This work was supported by the UNITE flagship project, funded by the National Research Council of Finland (grants 337127 and 357906).

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Supplementary Table A1. Growing stock volume models absolute (m^3 ha^{-1}) RMSE and Bias and rRMSE and rBias values cross-validated in modeling data (in bold) and transferred to other inventory areas

Used model	Target area	RMSE, m^3 ha^{-1}	rRMSE, %	Bias, m^3 ha^{-1}	rBias, %
Hiidenportti	**Hiidenportti**	**45.8**	**17.3**	**–0.2**	**–0.08**
	Kalkkinen	98.1	31.8	–83.3	–27.0
	Katajamäki	57.2	34.1	–7.6	–4.5
	Koli	68.8	20.8	–26.6	–8.0
	Liperi	77.9	35.1	–17.5	–7.9
	Nuuksio	94.7	41.4	–9.9	–4.3
Kalkkinen	**Kalkkinen**	**45.7**	**14.8**	**0.1**	**0.05**
	Hiidenportti	84.9	31.9	65.9	24.8
	Katajamäki	65.6	39.2	49.7	29.7
	Koli	92.4	27.9	67.2	20.3
	Liperi	95.8	43.2	50.0	22.5
	Nuuksio	96.1	42.0	49.9	21.8
Koli	**Koli**	**51.9**	**15.7**	**–6.9**	**–2.1**
	Hiidenportti	95.5	35.9	78.6	29.5
	Kalkkinen	89.9	29.1	34.9	11.3
	Katajamäki	66.0	39.4	39.6	23.7
	Liperi	104.8	47.2	69.9	31.5
	Nuuksio	126.0	55.1	79.2	34.6
Nuuksio	**Nuuksio**	**77.1**	**33.7**	**0.1**	**0.1**
	Hiidenportti	48.2	18.1	7.1	2.7
	Kalkkinen	68.2	22.1	–23.6	–7.6
	Katajamäki	32.7	19.5	–21.4	–12.8
	Koli	50.9	15.4	12.5	3.8
	Liperi	65.9	29.7	–17.5	–7.9
General	**General**	**69.4**	**27.5**	**0.01**	**0.00**
	Hiidenportti	47.1	17.7	1.2	0.5
	Kalkkinen	55.2	17.9	0.0	0.0
	Katajamäki	37.7	25.6	–25.8	–17.5
	Koli	48.7	14.7	–1.1	–0.3
	Liperi	66.8	29.7	–20.1	–8.9
	Nuuksio	76.2	33.3	–0.1	–0.04

Appendix Table A2. Standing deadwood volume models absolute (m^3 ha^{-1}) RMSE and Bias and rRMSE and rBias values cross-validated in modeling data (in bold) and transferred to other inventory areas

Used model	Target area	RMSE, m^3 ha^{-1}	rRMSE, %	Bias, m^3 ha^{-1}	rBias, %
Hiidenportti	**Hiidenportti**	**9.1**	**52.3**	**0.07**	**0.4**
	Kalkkinen	29.9	263.9	1.4	11.9
	Katajamäki	17.8	244.8	–11.7	–160.7
	Koli	23.3	252.4	1.7	18.9
	Liperi	20.2	1474.7	–9.3	–683.1
	Nuuksio	21.6	231.5	–8.7	–93.0
Kalkkinen	**Kalkkinen**	**20.7**	**183.1**	**0.5**	**4.7**
	Hiidenportti	18.8	108.0	9.9	56.7
	Katajamäki	12.4	169.8	7.4	101.8
	Koli	16.0	173.3	–2.8	–30.4
	Liperi	13.0	954.5	–9.1	–662.7
	Nuuksio	25.0	268.5	11.5	123.3
Koli	**Koli**	**11.3**	**122.4**	**0.4**	**4.5**
	Hiidenportti	17.2	98.5	10.5	60.0
	Kalkkinen	21.5	189.8	7.05	62.4
	Katajamäki	30.2	414.5	–12.5	–171.3
	Liperi	7.2	526.6	–2.5	–181.4
	Nuuksio	33.1	355.2	–8.8	–94.3

Supplementary Table A2 (continued)

Used model	Target area	RMSE, m^3 ha^{-1}	rRMSE, %	Bias, m^3 ha^{-1}	rBias, %
Nuuksio	**Nuuksio**	**17.8**	**191.0**	**0.00**	**0.00**
	Hiidenportti	13.3	76.3	9.06	52.0
	Kalkkinen	23.6	208.4	3.7	33.0
	Katajamäki	13.6	187.2	2.6	36.3
	Koli	13.8	150.2	7.8	84.9
	Liperi	11.1	814.6	–1.7	–121.0
General	**General**	**17.0**	**156.6**	**0.00**	**0.02**
	Hiidenportti	9.9	56.9	0.00	0.00
	Kalkkinen	20.2	178.5	–0.9	–10.0
	Katajamäki	5.5	212.3	–3.3	–127.4
	Koli	11.2	120.5	–1.2	–12.9
	Liperi	9.0	755.8	–6.4	–532.6
	Nuuksio	17.7	189.3	0.4	4.7

Supplementary Table A3. Number of stems models absolute (ha^{-1}) RMSE and Bias and rRMSE and rBias values cross-validated in modeling data (in bold) and transferred to other inventory areas

Used model	Target area	RMSE, ha^{-1}	rRMSE, %	Bias, ha^{-1}	rBias, %
Hiidenportti	**Hiidenportti**	**169.6**	**20.2**	**0.2**	**0.03**
	Kalkkinen	325.6	35.8	–3.5	–0.4
	Katajamäki	324.0	37.7	15.1	1.8
	Koli	516.5	43.5	256.2	21.6
	Liperi	455.4	42.2	91.1	8.4
	Nuuksio	1739.0	224.9	1671.9	216.3
Kalkkinen	**Kalkkinen**	**253.1**	**27.8**	**–1.4**	**–0.2**
	Hiidenportti	217.4	25.9	77.8	9.3
	Katajamäki	325.4	37.9	–64.2	–7.5
	Koli	638.0	53.7	55.6	4.7
	Liperi	607.2	56.3	310.6	28.8
	Nuuksio	435.3	56.3	–14.5	–1.9
Koli	**Koli**	**307.7**	**25.9**	**48.6**	**4.1**
	Hiidenportti	992.6	118.0	–387.9	–46.1
	Kalkkinen	994.0	109.1	–335.9	–36.9
	Katajamäki	1251.0	145.7	–956.5	–111.4
	Liperi	925.2	85.8	–542.0	–50.2
	Nuuksio	1636.3	211.7	–877.8	–113.5
Nuuksio	**Nuuksio**	**367.3**	**47.5**	**1.4**	**0.2**
	Hiidenportti	214.6	25.5	–73.9	–8.8
	Kalkkinen	389.5	42.8	–160.4	–17.6
	Katajamäki	316.8	36.9	–106.9	–12.5
	Koli	381.7	32.2	–50.2	–4.2
	Liperi	361.3	33.5	–98.5	–9.1
General	**General**	**355.7**	**42.9**	**0.7**	**0.09**
	Hiidenportti	173.7	20.7	–16.1	–1.9
	Kalkkinen	317.2	34.8	–5.2	–0.6
	Katajamäki	293.6	34.2	–118.7	–13.8
	Koli	436.2	36.8	104.7	8.8
	Liperi	393.1	36.4	45.9	4.3
	Nuuksio	375.8	48.6	–5.5	–0.7

Supplementary Table A4. Dominant height models absolute (m) RMSE and Bias and rRMSE and rBias values cross-validated in modeling data (in bold) and transferred to other inventory areas

Used model	Target area	RMSE, m	rRMSE, %	Bias, m	rBias, %
Hiidenportti	**Hiidenportti**	**0.6**	**2.6**	**0.01**	**0.03**
	Kalkkinen	2.9	11.8	–2.5	–10.0
	Katajamäki	2.1	10.9	–1.3	–6.6
	Koli	2.0	7.7	–0.9	–3.6
	Liperi	1.1	5.4	–0.7	–3.4
	Nuuksio	3.3	13.9	0.7	2.9
Kalkkinen	**Kalkkinen**	**1.3**	**5.2**	**0.00**	**0.01**
	Hiidenportti	2.4	10.3	2.3	9.6
	Katajamäki	2.0	10.1	0.3	1.5
	Koli	1.9	7.4	0.1	0.3
	Liperi	2.1	9.8	1.9	8.8
	Nuuksio	3.8	16.4	2.5	10.6
Koli	**Koli**	**1.2**	**4.7**	**0.06**	**0.2**
	Hiidenportti	2.4	10.3	–0.7	–2.9
	Kalkkinen	3.0	12.1	0.1	0.4
	Katajamäki	6.7	34.2	–2.1	–10.9
	Liperi	2.4	11.0	–0.3	–1.5
	Nuuksio	14.6	62.2	2.4	10.3
Nuuksio	**Nuuksio**	**2.6**	**11.3**	**0.00**	**0.01**
	Hiidenportti	1.2	5.3	0.3	1.3
	Kalkkinen	1.7	6.7	–0.5	–2.2
	Katajamäki	3.7	18.9	–2.0	–10.4
	Koli	1.9	7.3	1.03	4.0
	Liperi	1.3	6.1	0.5	2.5
General	**General**	**2.3**	**9.5**	**0.00**	**0.01**
	Hiidenportti	0.9	4.0	–0.1	–0.3
	Kalkkinen	1.5	5.8	0.0	0.0
	Katajamäki	3.8	20.0	–2.6	–13.7
	Koli	1.6	6.0	0.2	0.7
	Liperi	0.9	4.3	–0.04	–0.2
	Nuuksio	2.6	11.1	–0.02	–0.1

Supplementary Table A5. Gini coefficient models absolute (0–1) RMSE and Bias and rRMSE and rBias values cross-validated in modeling data (in bold) and transferred to other inventory areas

Used model	Target area	RMSE, (0–1)	rRMSE, %	Bias, (O–1)	rBias, %
Hiidenportti	**Hiidenportti**	**0.04**	**16.7**	**–0.00**	**–0.3**
	Kalkkinen	0.06	24.2	–0.03	–13.1
	Katajamäki	0.07	23.2	–0.04	–12.7
	Koli	0.05	14.1	0.02	5.1
	Liperi	0.09	40.6	–0.06	–26.9
	Nuuksio	0.10	36.5	–0.05	–18.2
Kalkkinen	**Kalkkinen**	**0.04**	**14.8**	**–0.00**	**–0.4**
	Hiidenportti	0.05	19.7	0.01	3.1
	Katajamäki	0.04	13.5	0.02	5.3
	Koli	0.08	22.9	0.07	20.5
	Liperi	0.09	41.9	–0.02	–10.9
	Nuuksio	0.10	39.9	–0.05	–17.1
Koli	**Koli**	**0.03**	**7.1**	**0.00**	**0.04**
	Hiidenportti	0.09	34.8	–0.07	–27.1
	Kalkkinen	0.09	33.4	–0.07	–27.5
	Katajamäki	0.06	20.4	–0.05	–17.4
	Liperi	0.12	54.7	–0.08	–39.0
	Nuuksio	0.13	48.1	–0.10	–37.5
Nuuksio	**Nuuksio**	**0.08**	**28.9**	**–0.00**	**–0.02**
	Hiidenportti	0.05	19.8	0.03	10.3
	Kalkkinen	0.05	17.7	0.02	6.3
	Katajamäki	0.05	15.3	0.02	6.7
	Koli	0.09	26.9	0.08	25.4
	Liperi	0.06	30.2	–0.02	–8.1
General	**General**	**0.01**	**24.7**	**0.00**	**0.00**
	Hiidenportti	0.05	18.6	0.02	7.1
	Kalkkinen	0.04	16.5	0.01	2.2
	Katajamäki	0.05	15.3	0.01	3.2
	Koli	0.03	9.1	0.00	0.0
	Liperi	0.07	31.1	–0.03	–13.7
	Nuuksio	0.07	28.3	–0.01	–2.2