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Bayesian calibration of a carbon balance model PREBAS using data from permanent growth experiments and national forest inventory

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ABSTRACT

Policy-relevant forest models must be environment and management sensitive and provide unbiased estimates of predicted variables over their intended areas of application. While empirical models derive their structure and parameters from representative data sets, process-based model (PBM) parameters should be evaluated in ranges that have a biological meaning independently of output data. At the same time PBMs should be calibrated against observations in order to obtain unbiased estimates and an understanding of their predictive capability. By means of model data assimilation, we Bayesian calibrated a forest model (PREBAS) using an extensive dataset that covered a wide range of climatic conditions, species composition and management practices. PREBAS was calibrated for three species in Finland: Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* [L.] H. Karst.) and Silver birch (*Betula pendula* L.). Data assimilation was strongly effective in reducing the uncertainty of PREBAS parameters and predictions. A country-generic calibration showed robust performances in predicting forest variables and the results were consistent with yield tables and national forest statistics. The posterior predictive uncertainty of the model was mainly influenced by the uncertainty of the structural and measurement error.

1. Introduction

Management for climate change mitigation and other environmental targets alongside with wood production have become important objectives of national and continental forest policies (e.g. Forest Europe 2015, Council of the European Union 2017). This has emphasized the need for models that are capable of incorporating both climate change impacts and variable forest management responses. In order to produce realistic, policy relevant results, such models must provide unbiased estimates of growth and production (e.g., gross primary production, net primary production, CO_2 budgets, stemwood growth) over the area intended for application. In empirical models this has been ascertained by deriving model equations and parameters from data sets that are representative of the area in question (Vanclay and Skovsgaard, 1997). In process-based models, on the other hand, most parameters are evaluated in focused measurements of physiological, structural and functional plant traits independently of model output data. Because all such parameter estimates include some degree of uncertainty, and some parameters are even impossible to measure directly (Korzukhin et al., 1996; Mäkelä et al., 2000), process model parameters need to be calibrated to make model outputs comply with measurements.

The significance of calibration is that it allows us to estimate the parameters inversely from a comparison of model outputs with observed data and thus constrain process parameters through observations of outputs (Hartig et al., 2012; Van Oijen et al., 2005). From a theoretical perspective, the downside of model calibration is that it makes model outputs dependent on output data in the same way as in statistical models. On the other hand, it also makes model predictions more reliable at least in conditions similar to the data. This aspect underlines the importance of the dataset used in model calibration; a comprehensive dataset that covers a wide range of processes and environmental conditions will lead to a more robust calibration and the model will be more generally applicable. Most importantly, data assimilation opens up extensive forest mensuration and national forest inventory (NFI) data sources for process-based parameter estimation. Similar to empirical models, the inventory data could ascertain regionally representative parameterisation, while data from permanent experiments would support adequate parameterisation in relation to stand dynamics and management responses (Nagel et al., 2012).

Several studies have been published over the last decade that

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calibrated process-based forest models against forest inventory and mensuration data using either "trial and error" or statistical fitting of selected parameters against output variables. For example, Lasch et al. (2005), Blanco et al. (2007) and Kalliokoski et al. (2017) calibrated process-based forest models for sites over large regions in Germany, Canada and Finland, respectively, then tested the effects of thinning on stand growth and diameter distributions against data from permanent growth experiments. Gonzalez-Benecke et al. (2016) parameterised the 3-PG model for loblolly pine over its natural range in the US and also beyond that in Uruguay, then tested its performance against standard forestry variables at independent sites in the same areas. Mäkelä et al. (2016) parameterized the PipeQual model for Norway spruce stands in Fennoscandia and tested its performance against long-term data from selected sites as well as against an empirical model, focusing on both site productivity and management impacts on diameter distributions.

A more systematic approach to calibration is provided by inverse model-data assimilation methods such as Bayesian calibration (BC) (van Oijen et al., 2005; Hartig et al., 2012; Thomas et al., 2017). The Bayesian method offers a means, on the basis of probability theory, for incorporating prior information about the parameter values, and later reducing the prior uncertainty by systematic comparisons of model predictions with available data on outputs. Furthermore BC allows to continuously update parameter distributions every time new available data are assimilated. Bayesian calibration can also be combined with sensitivity analysis, error propagation and uncertainty estimation (Van Oijen et al., 2011; Minunno et al., 2013a; 2013b). BC has been used before to calibrate the parameter distributions of process-based forest models for selected sites (Green et al., 1999; Van Oijen et al., 2005; Luo et al., 2009). Van Oijen et al. (2013) calibrated six forest models of different complexity with NFI and long-term growth experiment data from four countries in Europe and used Bayesian model comparison and averaging to assess the models and methods. In their study, models of medium complexity were those to provide the most likely representation of the data. Country-wise calibrations did not significantly improve the within-country predictions compared to generic calibration. The study indicated that models capable of initialising the simulation with measured data provided more accurate results than those initialised with a localised spin-up run.

One of the models included in the study by Van Oijen et al. (2013) was the CROBAS model (called the BRIDGING model in Van Oijen et al., 2013) (Mäkelä, 1997, Valentine and Mäkelä, 2005) combined with a semi-empirical procedure for estimating Gross Primary Productivity (GPP) from daily weather data and stand structure (Härkönen et al., 2010). The model behaved fairly well in the test, especially considering its simplicity and modest input data needs (Van Oijen et al., 2013). Although limited to a few example sites, these results gave promise of the possibility of generic parameterisation of CROBAS, given sufficiently informative data.

The environmental effects in CROBAS are expressed as annual effective means of physiological rates and morphological ratios and can be estimated from lower-level process models or direct measurements. A key climate-dependent parameter of the model is the annual photosynthetic capacity of a site, which is also used for estimating the respective respiration and turnover rates (Mäkelä et al., 2016). Here we determined annual GPP by coupling CROBAS with a daily canopy photosynthesis model, PRELES (Peltoniemi et al., 2015), which has already been parameterised for boreal coniferous stands using BC (Minunno et al., 2016). Site fertility affects below-ground allocation in CROBAS and was made operational through existing site-type classification, following Mäkelä et al. (2016). After these extensions, the coupled PRELES-CROBAS model is both climate and management sensitive and, owing to its minimal input requirements, potentially feasible for predictions over large geographical areas.

The objective of this study was to Bayesian calibrate the growth model CROBAS against empirical data on mean tree variables available from forestry experiments and monitoring. The parameters of the coupled PRELES model were taken from the previous, independent calibration (Minunno et al., 2016), and similarly, the below-ground allocation parameters were left outside the calibration and fixed to estimates obtained from previous literature (Helmisaari et al., 2007; Mäkelä et al., 2016). We utilised data from 229 permanent growth and yield experiments (spanning over 10–84 years each) and 137 NFI permanent sample plots (two measurements separated by 10 years each) from southern and central Finland to parameterise CROBAS for Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* [L.] H. Karst.) and Silver birch (*Betula pendula* L.). Gridded climate data was used to estimate the climatic inputs to PRELES for each site. The specific objectives of the study were (1) to ascertain if a generic, species-specific parameterisation can be found for PRELES-CROBAS, (2) to estimate the parameter distributions and their uncertainty ranges, (3) to analyse any differences between the parameter sets implied by the two different data sets, and (4) to demonstrate the use of the coupled PRELES-CROBAS model for stand growth and carbon balance prediction. The new model obtained by coupling PRELES and CROBAS will be called PREBAS from now on.

2. Material and methods

2.1. The growth model

CROBAS is an individual tree growth model that can be applied in different stand configurations, climates and sites, provided the effect of these on model parameters is specified. Below, we summarise the basic individual tree model (Mäkelä, 1997; Valentine and Mäkelä, 2005; Kokkila et al., 2006), describe how stand structure affects photosynthesis, crown rise and mortality, and outline the linkages of the model to climate and site variation. The latter includes the coupling of CROBAS with PRELES. More details on model structure are provided in Appendix A; in Appendix D the reader will find instructions on how to install and run a version of the model written in *R* language.

Growth in CROBAS is based on the acquisition and allocation of carbon and calculated at annual time resolution. Total tree growth hence equals annual net photosynthetic production. Gross photosynthesis is calculated as a product of foliage mass and mass-specific annual photosynthetic rate (dependent on climatic factors and local interactions). Respiration is divided into growth and maintenance components, where maintenance is assumed proportional to live biomass and growth respiration is a proportion of growth. Total growth is allocated annually to the biomass components that comprise foliage, fine roots and three sapwood fractions, stems, branches and coarse roots. Carbon allocation between wood and foliage is based on the pipe model with dynamic crown rise, and allocation between fine roots and foliage assumes that fine-root to foliage ratio depends on nutrient availability (see Appendix A for details and definitions).

CROBAS can be applied to different stand structures (e.g. Kokkila et al., 2006) but it is here used as a mean-tree model by species in an even-aged stand. The stand is defined by multiplying the tree-level biomass variables by the number of stems per unit area, (ha^{-1}). Basal-area weighted means of dimensional variables are used. Stand density affects light available to the mean tree and hence the foliage-specific photosynthesis and crown rise. In addition, it affects tree mortality. Species interaction for light competition is also implemented. (see Appendix A for details and definitions).

Climate influences all metabolic rates of forests, including photosynthesis, respiration, nutrient and water uptake and tissue turnover. Here we use the PRELES model (Mäkelä et al., 2007; Peltoniemi et al., 2015; Minunno et al., 2016) to estimate the potential photosynthetic production of a stand (P_0 see Eq. (A.1) in Appendix A). We further use P_0 to derive the geographic variation of the other relevant metabolic parameters, following the procedure proposed by Mäkelä et al. (2016) (Appendix A).

The model has 19 parameters (Table 1). Out of these, we consider

Table 1
Parameters of the PREBAS model. Those indicated with (*) vary with environmental factors in this study. The parameter ranges (min, max) were different for the tree species (pine (p), spruce (sp) and birch (b)) if indicated.

Name	Meaning	Definition	min	max	Reference
(*)P_0	*maximum annual photosynthetic production of stand*	Eq. A(1), Eq. A(7)	–	–	–
$m_{F,ref}$	maintenance respiration rate of foliage	Table A.1, Eq. A(8)	0.2	0.5	Ryan (1995, 2013)
$m_{R,ref}$	maintenance respiration rate of fine roots	Table A.1, Eq. A(8)	0.2	0.5	Ryan (1995, 2013)
$m_{S,ref}$	maintenance respiration rate of sapwood	Table A.1, Eq. A(8)	0.03	0.05	Ryan (1995, 2013)
c	growth respiration rate (kg C / kg C / yr)	Table A.1	0.2	0.3	
$\nu_{F,ref}$	Leaf longevity (yr)	Table A.1, Eq. A(9)	2.5 (p); 7 (sp); 0.8 (b)	4 (p); 10 (sp); 1.2 (b)	Tupek et al. (2015)
ν_R	Fine root longevity (yr)	Table A.1	0.5 (p,sp); 0.6 (b)	1.5 (p,sp); 1.8 (b)	Leppälammi-Kujansuu et al. (2014)
k_H	homogeneous extinction coefficient	Eq. A(3), Eq. A(5)	0.25	0.32	Duursma and Mäkelä (2007)
s_{LA}	specific leaf area (m^2/kg C) (all-sided)	Eq. A(2)	20 (p,sp); 35 (b)	30 (p); 35 (sp); 50 (b)	Ilomäki et al. (2003), Kantola et al. (2006), Oker-Blom (1985)
s_1	parameter relating to reduction of photosynthesis with crown length	Eq. A(1)	0.01(p); 0.005 (sp); 0.015 (b)	0.06 (p,b); 0.15 (sp)	Mäkelä and Valentine (2001)
ρ_F	ratio of foliage mass to cross-sectional area at crown base (kg C/m^2)	Table A.2	180 (p); 200 (sp); 100 (b)	250 (p); 300 (sp); 150 (b)	Berninger et al. (2005), Ilomäki et al. (2003), Kantola and Mäkelä (2006)
ρ_W	wood density (kg C / m^3)	Table A.2	190 (p); 180 (sp); 200 (b)	210 (p); 220 (sp); 300 (b)	Kärkkäinen (2007)
(*)α_{Rs}	*ratio of fine roots to foliage*	Table A.2, Eq. (A10)	–	–	Helmisaari et al. (2007)
z	foliage allometry parameter	Table A.2	1.6 (p); 1.7 (sp, b)	1.9 (p); 1.95 (sp, b)	Valentine and Mäkelä (2005)
β_0	ratio of total sapwood to above-ground sapwood biomass	Table A.2	1.25 (p,sp); 1.4 (b)	1.35 (p,sp); 1.6 (b)	Valentine and Mäkelä (2005)
β_B	ratio of mean branch pipe length to crown length	Table A.2	0.2 (p,sp); 0.35 (b)	0.4 (p); 0.5 (sp); 0.6 (b)	Valentine and Mäkelä (2005)
β_S	ratio of mean pipe length in stem above crown base to crown length	Table A.2	0.2	0.5	Valentine and Mäkelä (2005)
χ	parameter for relating branch length to crown length	Table 1	–	–	Ilomäki et al. (2003), Kantola and Mäkelä. (2006) Mäkelä and Vanninen (1998)
C_R	Light level at crown base that prompts full crown rise	Table A.1	0.15 (p, b); 0.075 (sp)	0.25 (p); 0.225 (sp); 0.2 (b)	Educated guess
N_0	Stand density at which mortality begins when diameter is 25 cm	Eq. A(6)	350	1200	Pretzsch (2006)

18 as temporal constants and 17 as spatial constants. The site-dependence is aggregated in the ratio of fine roots to foliage, (Eq. A.10 (Appendix A)). The environmental impact parameters are not included in the model calibration; PRELES parameters were taken from a previous calibration (Minunno et al., 2016) and the fine root to foliage ratios are evaluated on the basis of site type from existing empirical results using the method by Mäkelä et al. (2016).

2.2. Data

For PREBAS calibration we used two dataset available for Finnish commercial forests: permanent plots of the Finnish National Forest Inventory (pNFI) and

permanent growth and yield experiments (PGE).

2.2.1. NFI data

We used data from two consecutive measurements, 1985 and 1995, from permanent plots of the Finnish National Forest Inventory, established by the Finnish Forest Research Institute (now part of Natural Resources Institute Finland, Luke). The data set contained a total of 137 sample plots (Table 2), including 223 species-plot subsets of Scots pine, Norway spruce and deciduous trees. About 33% of the pNFI where mono-specific stands, in 41% of the plots two of the three species were present and the remaining 26% of the plots were mixed stands of pine, spruce and birch. This was a subsample of the entire NFI data set and came from a previous study (Härkönen et al., 2010) where it had been prepared to provide as reliable information as possible about the growth rate of the mean tree variables. The plots where located in central and southern regions of Finland as mapped in Fig. 2 of Härkönen et al. (2010). The following criteria had been applied: (1) the sample plot was located on mineral soil, (2) it was regarded as part of one and only one management unit at both measurements, (3) the plot had not been subject to thinnings, cuttings or mortality during the measurement interval, (4) the data contained all sample tree measurements that were required for estimating mean tree volume growth for all the tree species strata (Scots pine, Norway spruce and deciduous) found in the plot, (5) the plot site type was *Oxalis-Myrtillus* (OMT, fertile and moist), *Myrtillus* (MT, medium fertility), *Vaccinium* (VT, lower fertility and moisture) or *Calluna* (CT, poor and dry) site type (Cajander, 1949) and (6) the data were free of obvious measuring/coding errors.

In this study, we used information about basal-area-weighted tree height (H, m), crown length (L_C, m), diameter at breast height (D, cm)

Table 2
Description of the calibration datasets. In the last column ("Number of data points") the total number of measured variables of all plots at all measurement times are provided.

Symbol	Dataset	Species	Variables	Number of plots	Number of data points
PGEcal	Permanent Growth experiments	Pine, spruce	B, D, H, Hc, V	785	9368
pNFIcal	National forest inventory data	Pine, spruce and birch	B, D, H	137	1233
PGEcal50	50% of the plots of the Permanent Growth experiments	Pine, spruce	B, D, H, Hc, V	392	4784

and basal area (B, m^2 ha^{-1}). The diameter measurements had been taken on all trees while height and crown base height (H_C, m) were measured on sample trees and modelled for the other trees on the basis of diameter. The details of the procedure are provided in Härkönen et al. (2010). For mixed stands the model was initialized for each species, i.e., multiple coexisting species-specific layers were considered.

2.2.2. Growth experiment data

The second dataset came from long-term growth and yield experiments established by the Finnish Forest Research Institute to investigate the effects of thinning intensity on growth and yield of the stands. Treatments covered unthinned control plots and thinnings from below with intensities ranging from low intensity thinnings to ~40% removal of stand basal area. The data set consisted of 125 stands of which 21 were Norway spruce dominated and 104 were Scots pine dominated (Table 2 and Mäkinen and Isomäki, 2004). The average area of the plots was 1000–1600 m2 (range 500–2500 m2). The experiments were located in southern and central Finland and contained altogether 785 plots, 657 were dominated by Scots pine and 128 by Norway spruce. The sites were classified as from *Oxalis-Myrtillus* to *Calluna* forest site type (Cajander, 1949), as in the pNFI data set. Stands were even-aged, pure or almost pure stands growing on mineral soil.

The experiments were measured 2–9 times, the longest measurement period being 84 years. The data were collected between 1928 and 2014. In each plot, the tree species, social position in the stand and stem diameter were measured on all trees. Tree height and crown base height were measured on randomly selected sample trees (~20 – 40 per plot) and modelled for the other trees on the basis of stem diameter. In addition, crown base heights were not measured in the earliest measurement of some experiments. Most of the experiments were established at the first thinning stage in young stands, but some experiments were also established in older stands. Stand age at the first measurement ranged from 12 to 116 yrs, stand density from 160 to 14360 ha^{-1}. In the last measurement, stand age ranged from 37 to 143 yrs.

2.2.3. Weather data

The weather inputs for PREBAS were daily values of mean temperature (T, °C), vapour pressure deficit (VPD, kPA) estimated from daily mean T and relative humidity (RH%), precipitation (R, mm day^{-1}) and photosynthetic photon flux density (PPFD, Φ, μmol m^{-2} day^{-1}). The weather observations from meteorological stations were spatially downscaled to uniform 10 km grid in Venäläinen et al. (2005). For each plot, we used data from the closest grid point. Data covered years from 1971 until 2010; for those sites were forest measurements were available before 1971 we sampled the weather data from the period 1971–2010.

2.3. Model calibration

Data assimilation is a framework to integrate information from observations into ecosystem models (Niu et al., 2014; Williams et al., 2005). The Bayesian approach is a statistical method often used for data assimilation and it has been increasingly applied to forest model calibration (van Oijen et al., 2005; Xenakis et al., 2008; Thomas et al., 2017; Augustynczik et al., 2017) and model comparison (van Oijen et al., 2013; Minunno et al., 2013a). The calibration produces parameter estimates and their probability ranges that make model predictions consistent with the observations. Bayesian statistics also allow us to account for observational and parametric uncertainties, and multiple types of data at different temporal scales can be used in the assimilation process (Hartig et al., 2012; van Oijen et al., 2005). Sensitivity and uncertainty analyses are often used to complement BC and improve the understanding of model behavior, identifying weaknesses in model calibration and/or model structure (van Oijen et al., 2005; Minunno et al., 2013a; 2013b).

Details on PREBAS Bayesian calibration are given in the following paragraphs. We also carried out global sensitivity and uncertainty analyses (SUA) on the prior and posterior parameter space of PREBAS. SUA details and results are provided in Appendix C.

2.3.1. Bayesian calibration settings

Bayesian calibration requires definitions of prior parameter distributions, likelihood of outputs, choice of methods for estimating posterior distribution and testing parameter convergence. Since this was the first attempt with Bayesian methods to calibrate PREBAS we used uninformative priors, delimited by the minimum and maximum values of the parameters involved in the calibration (Table 1) and assigning a uniform distribution. The ranges varied for the different species and were determined on the basis of expert knowledge and evidence from the literature (Table 1).

The stand variables used for model calibration were basal area (B, m^2 ha^{-1}), diameter at breast height (D, cm), tree height (H, m), height of the crown base (H_C, m) and stand volume (V, m^{-3} ha^{-1}). We assumed that the data were normally distributed and that the data uncertainty was linearly related to the magnitude of the predictions:

$$\sigma_m = a_m + b_m sim(\theta) \tag{1}$$

where σ_m = standard deviation. The coefficients a_m and b_m were included in the calibration and were assumed to vary for each data type (m).

The posterior distribution was numerically sampled using the Differential Evolution Markov Chain Monte-Carlo algorithm (DEMCzs) (ter Braak and Vrugt, 2008). We used the DEMCzs sampler implemented in the Bayesian Tools R package (Hartig et al., 2018).

To evaluate if the sample drawn by DEMCzs was a representative approximation of the target distribution we computed the Gelman-Rubin diagnostic (Gelman and Rubin, 1992).

2.3.2. Model calibration and validation

As noted above, two types of datasets were available for the calibration: PGE and pNFI. PGE data covered monospecific even-aged stands of Scots pine and Norway spruce (see Section 2.2.2); pNFI data covered monospecific and mixed even-aged stands of Scots pine, Norway spruce and Silver birch (see Section 2.2.1). We calibrated the model with the whole PGE dataset (PGEcal) and with the pNFI data (pNFIcal) (Table 2). pNFIcal was tested using the PGE data and, *vice versa*, PGEcal was tested using the pNFI data. We also carried out a cross-validation of the model using the PGE data; i.e., we calibrated the model with 50% of the plots randomly selected (PGEcal50) and we validated the model with the remaining 50% of the data (Table 2).

To evaluate the predictive capacity of the model we ran PREBAS with 1000 parameter vectors sampled from the posterior distribution and computed the average simulated value for each data point. We used these average values to evaluate the root mean squared error (RMSE), normalized root mean squared error (NRMSE, Eq. (3)) and the percentage bias (PBIAS, Eq. (4)) as follows

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}(\hat{y}_i - y_i)^2}{n}} \tag{2}$$

$$\text{NRMSE} = \frac{RMSE}{(y_{max} - y_{min})} \tag{3}$$

$$\text{PBIAS} = 100\frac{\sum_{i=1}^{n}(\hat{y}_i - y_i)}{\sum_{i=1}^{n} y_i} \tag{4}$$

where n is the number of data points; $\hat{y}$ and y are the predicted and the observed data, respectively; y_{max} and y_{min} are the maximum and minimum of the observed data.

2.4. Model testing

For assessing the geographic trends in growth potential predicted with the PREBAS model, we made simulations from an initial seedling stand (with $H = 1.5$ m; D = 0.5 cm; stand density = 2200 ha^{-1}) over the whole rotation for pine and spruce stands on sites of four different fertility classes each as described in Section 2.2.1, over a country-wide grid with resolution of 1 km × 1 km. The model was driven by the weather input data at a resolution of 1 × 1 km grid (see Section 2.2.3). Thinning and clearcut were modelled according to the instructions for forestry practice in Finland as described in Appendix A.

From these simulations, we calculated the mean annual increment (MAI, m^3 ha^{-1} y^{-1}) at the end of the rotation. MAI is defined as the mean cumulative stemwood production per year and is used as a standard productivity indicator in forestry (Skovsgaard and Vanclay, 2008).

We compared the simulations of pine and spruce at 7 selected points over a North-South transect with yield tables (Vuokila and Väliaho, 1980) and national forestry statistics (Yearbook of Forestry Statistics, 2014). The yield tables are based on an empirical model developed for Finland using data from southern Finland for spruce and from southern and northern Finland for pine. They include tables classified by species (pine and spruce) and site index, defined as dominant height at stand age 100 years, with a number of different thinning schedules each. The thinning schedules define the rotation length, the number of thinnings and the volume percentage removed at each thinning. The yield tables also specify a conversion between the height-based site index and the ground-vegetation based site type used here. We chose the appropriate yield table for each example site on the transect, then found the minimum and maximum values of mean annual increment (MAI) at the end of rotation among all the treatments. This was taken as the yield-table uncertainty range that was compared with the PREBAS results.

The national forestry statistics (Finnish Forest Research Institute, 2014) report the mean annual growth (measured during 2009–2013) per hectare of 13 forestry districts in Finland. These include the mean of all species in the district, representing the actual age class, site class and species distribution in each district. We computed a comparable value with PREBAS by taking a weighted average of pine and spruce, weighted with the area of site classes and species in the district. Age class distribution was not accounted for, as this was considered less important for the mean. The calculation of mean growth (G_{MAI}) for each district was as follows:

$$G_{MAI} = \left(\sum_{i\in I_P} A_i G_{P_i} \tilde{A}\cdot \sum_{i\in I_P} A_i\right) \times A_P \tilde{A}\cdot (A_P + A_S) + \left(\sum_{i\in I_S} A_i G_{S_i} \tilde{A}\cdot \sum_{i\in I_S} A_i\right) \times A_S \tilde{A}\cdot (A_P + A_S) \tag{5}$$

where A_i is the reported area of site type i, I_P and I_S are the index sets referring to site types assumed to be occupied by pine and spruce, respectively, G_{P_i} and G_{S_i} are PREBAS estimates of pine and spruce MAI on site type i, respectively, and A_P and A_S are reported areas covered by pine and spruce, respectively. The area of other species (*Betula* spp. and other deciduous species of minor commercial importance) is about 10% of total forest area but was ignored in this calculation.

3. Results

3.1. PREBAS calibration

3.1.1. Parameter estimates and sensitivity & uncertainty analyses

We were able to reduce the parametric uncertainty of PREBAS (Fig. 1) achieving three species specific calibrations. The parameters that remained most uncertain in the PGE calibration were some of the respiration rates (c (in the spruce calibration (PGEcal_sp) (Fig. 1)) and m_r), the ratio between total and aboveground sapwood biomass (β_0) and the wood density (ρ_W) (Fig. 1). In the pNFI calibration also the parameters related with light absorption and crown length were less constrained (c_R, k, $s_1$and β_S) as well as the mortality parameter (N_O) (Fig. 1). The marginal distributions give an incomplete picture of the parameter uncertainty because they don't take into account parameter interactions. In the pNFI calibration, the correlations between parameters were generally higher than those of the PGE calibrations (data not shown) and this partially contributed to the reduction of model output uncertainty (Fig. 2).

The main differences in the parameter estimates between pNFIcal and the PGEcal were encountered in the crown length related parameters (c_R (mainly for spruce), β_B, β_S and s_1), the light absorption parameter (k) and, to a lesser extent, the respiration parameters (m_w, m_f, m_r) (Fig. 1).

Bayesian calibration reduced model output uncertainty significantly (Fig. 2). The standard deviations of the posterior distribution of the average annual variation of the model outputs (B, D, H, H_C, and V) were about 90% lower than those of the prior output distribution in the PGE calibration and about 75% lower in the pNFI calibration (Fig. 2). Output uncertainties and sensitivities to parameters varied significantly across the plots (see Appendix C for the detailed results of the sensitivity and uncertainty analyses).

The error parameters of Eq. (1) were calibrated for each data type in each calibration (PGEcal pine, PGEcal spruce and pNFIcal) (Fig. 3). The slopes of the standard deviation (parameter b of Eq. (1)) were significantly higher in the pNFI calibration than in the PGE calibrations (Fig. 3). Therefore the error of the pNFI calibration increased rapidly for higher values of B, D and H. We also analysed the weight that the error uncertainty had on the predictive uncertainty of the model (Table 3). The predictive uncertainty of a model depends on the uncertainty given by the parameters plus the error uncertainty. The result was that the error was by far the most dominant component of the predictive uncertainty (Table 3).

3.1.2. Goodness of fit and PGE calibration vs pNFI calibration

PREBAS reliably predicted the data from pNFI and PGE (Fig. 4). The goodness of fit was better for average stand height and average D predictions than those for basal area, stemwood volume and height of the crown base (Figs. 5–7). Furthermore, the PGE calibration performed better than the pNFI calibration, especially for the spruce stands of the PGE validation dataset. The normalized root mean squared errors were below 10% in most of the cases, and the absolute values of the PBIAS were always below 5% for the PGE calibration (Fig. 4). The pNFI calibration was less robust, underestimating all the stand variables in the spruce forests, especially for the mature-older stands (Figs. 4–6). In the pine stands both calibrations reproduced well the D and H developments (Figs. 8 and 10), but both were less accurate in predicting B (Fig. 7) and V (Fig. 10). In fact, in the pine stands of the growth experiments, the highest measurements of basal area and volume ($B > 45\,m^2\,ha^{-1}$ and $V > 500\,m^3\,ha^{-1}$) were systematically underestimated by the model (Fig. 5).

Both model calibrations provided similar performances in predicting the forest variables at the pNFI plots (Fig. 7). The differences between the NRMSEs of pNFIcal and PGEcal were below 1% for all the variables (Fig. 4). Also the PBIAS were quite close and for D and H the PGEcal had lower PBIAS than the pNFIcal.

3.2. Country level predictions

PREBAS was run for the whole country using the PGE pine and spruce calibrations in order to evaluate the regional pattern of timber production estimates. The country level simulations were repeated 3 times for each species (Fig. 8) using three site fertility classes. For forest growth and timber production a latitudinal gradient was found moving from North to South, due to the climatic conditions. The South-West part of the country was the most productive area in the results. MAI estimates were sensitive to site fertility class; in fact, the average country MAI decreased by about 1 m^3 ha^{-1} y^{-1} per site class from the more fertile to the less fertile soils (Fig. 8).

PREBAS and Yield table estimates of MAI showed similar trends across the country (Fig. 9), however the MAI predicted by PREBAS were higher than the yield table predictions, especially for spruce. PREBAS estimates of MAI were consistent with the national forest statistics for timber production (Fig. 10). PREBAS overestimated only the two northernmost points of the transect, while the remaining points were in close agreement with the national forest statistics, showing a higher peak of MAI in central Finland.

4. Discussion

We calibrated and tested a process-based forest model using an extensive dataset that covered a wide range of climatic conditions, species composition and management practices (in particular thinnings and tree density). In the following sections we discuss the main findings in relation to our stated objectives.

4.1. Generality of PREBAS parameterisation

For large-scale applications of any model it would be beneficial if model parameters were generic, i.e, identical for all sites, or at least for all sites within a category, such as species and site index, that are easily identifiable from the input data. Previous studies have found that even if site-specific parameterisations provide a better fit to data, the benefit may be marginal in relation to the cost of acquiring the additional data (Blanco et al., 2015; Minunno et al., 2016). Here we did not attempt site-specific parameterisations, but differences in parameters between the PGE and pNFI sets provide cues of the generality of the calibration and possible needs for additional data and model development.

The photosynthesis part of PREBAS was not calibrated in this study, but an existing calibration to boreal eddy flux data was used which has provided reasonable estimates of the carbon inputs at a regional scale (Minunno et al., 2016). The pipe-model related structural parameters were similarly well constrained in the prior on the basis of previous

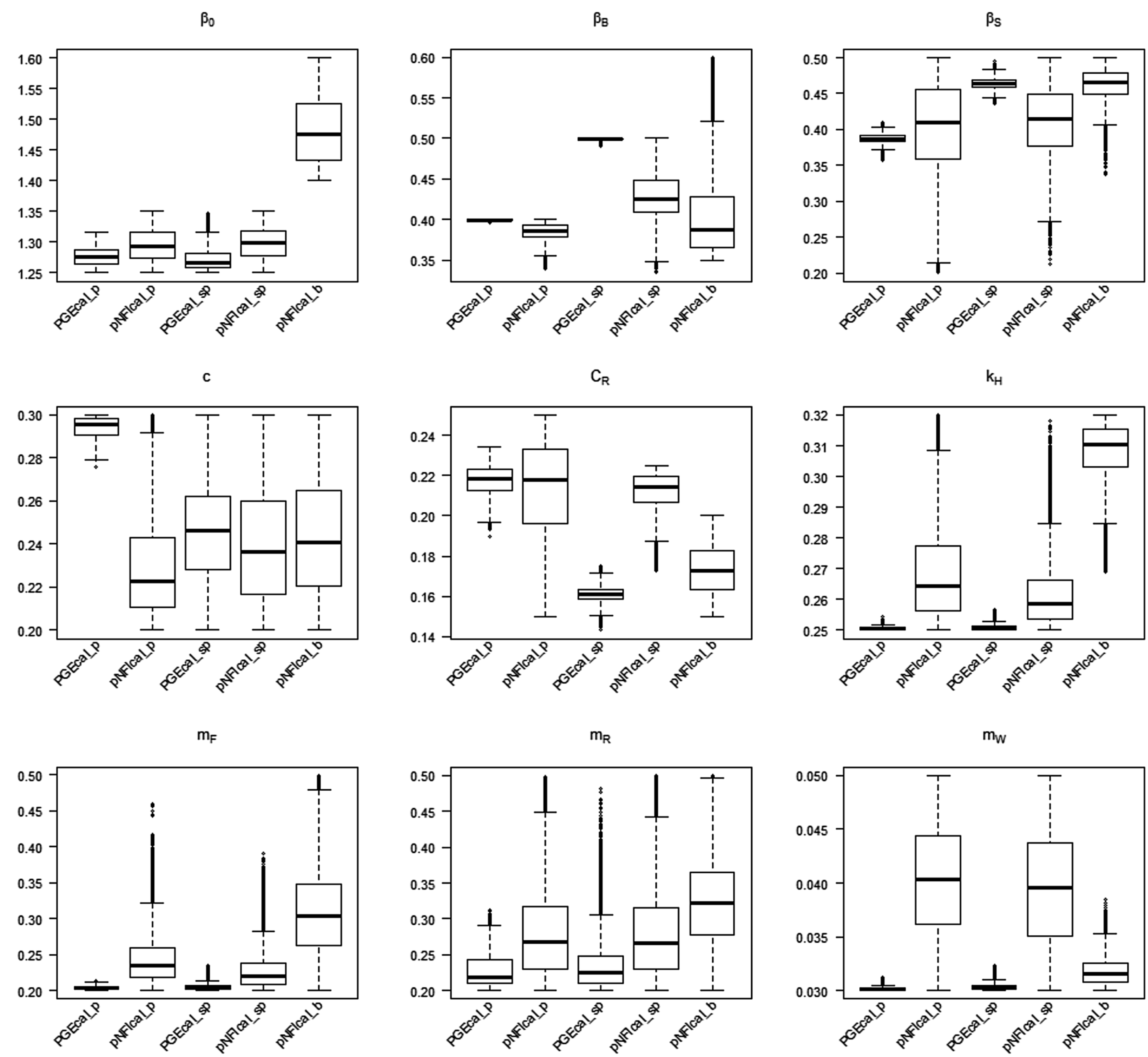

Fig. 1. Marginal distributions of PREBAS model parameters (Table 1). The boxplots in the graphs refer to the calibration for pine (p), spruce (sp) and birch (b) species obtained using the two datasets (PGE and pNFI data).

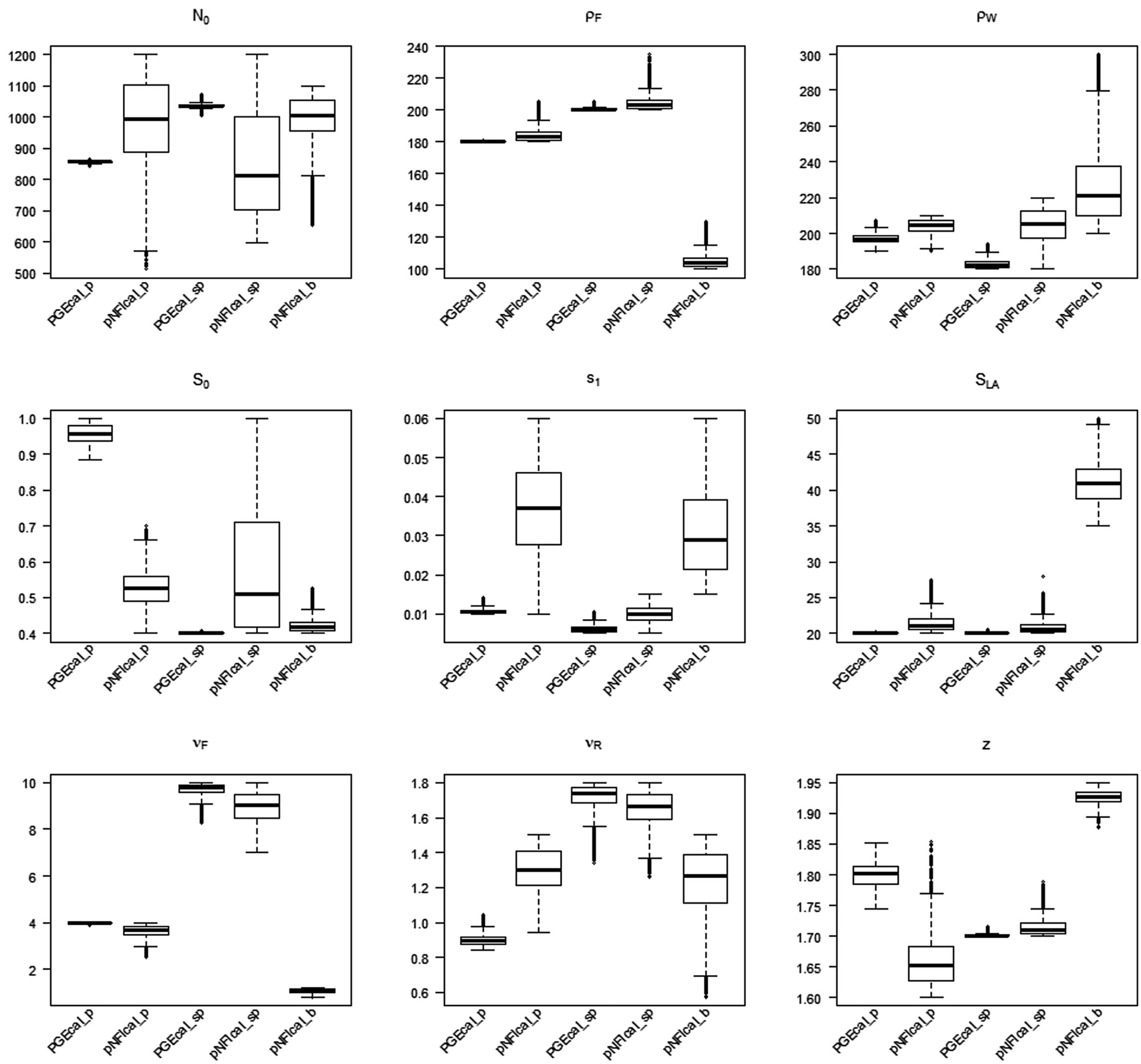

Fig. 1. (*continued*)

measurements on Scots pine (e.g. Berninger et al., 2005; Vanninen and Mäkelä, 2005), Norway spruce (Kantola and Mäkelä 2004, 2006) and Silver birch (Ilomäki et al., 2003), and some parameters, such as wood density, are well known from forestry literature. In contrast, parameters related to respiration, tree mortality, crown rise and the reduction of photosynthetic capacity with crown size were uncertain *a priori*, because direct measurements are generally not available. These parameters and the related assumptions also include structural uncertainty, because the submodels related to these processes have not been evaluated independently. The datasets used here, especially the PGE data, did provide constraints to these parameters, but uncertainty still remains. This was particularly evident from the fact that the two calibration data sets led to different behaviours of the model in mature stands (Figs. 6 and 7).

The parameters that contributed to reduced growth in mature and old stands in the pNFI calibration compared with the PGE calibration include higher maintenance respiration rates (m_f, m_r, m_w), higher reduction of photosynthesis with crown length (s_1), higher stemwood density (ρ_w) and higher coarse root allocation (b_0). The differences between the calibrations in the mature stands could be due to the higher average age of the pNFI plots, including several stands older than 100 years. This calls for an analysis of possible additional, explicit age effects on growth (Meinzer et al., 2011) Differences were also detected in the mortality parameter N_0 between the two data sets, the pNFI-based parameter showing large uncertainty. This is evident, however, because the pNFI plots were selected to exclude any harvests and mortality between the two measurement times, to allow for an accurate estimation of volume and basal area growth (Härkönen et al., 2010). The mortality functions derived from the pNFI data are therefore likely inaccurate.

One source of error in model calibration could come from the fact that weather inputs before 1971 were not available and annual weather data where sampled from the period 1971–2010 (see Section 2.2.3). We opted to include in the calibration data collected before 1971 because we believe that since forest data were collected on average at a distance of 5 years the annual weather variability of each site should be well represented in a 5 year range and the contribution of the sampled weather inputs to the model calibration error should be negligible.

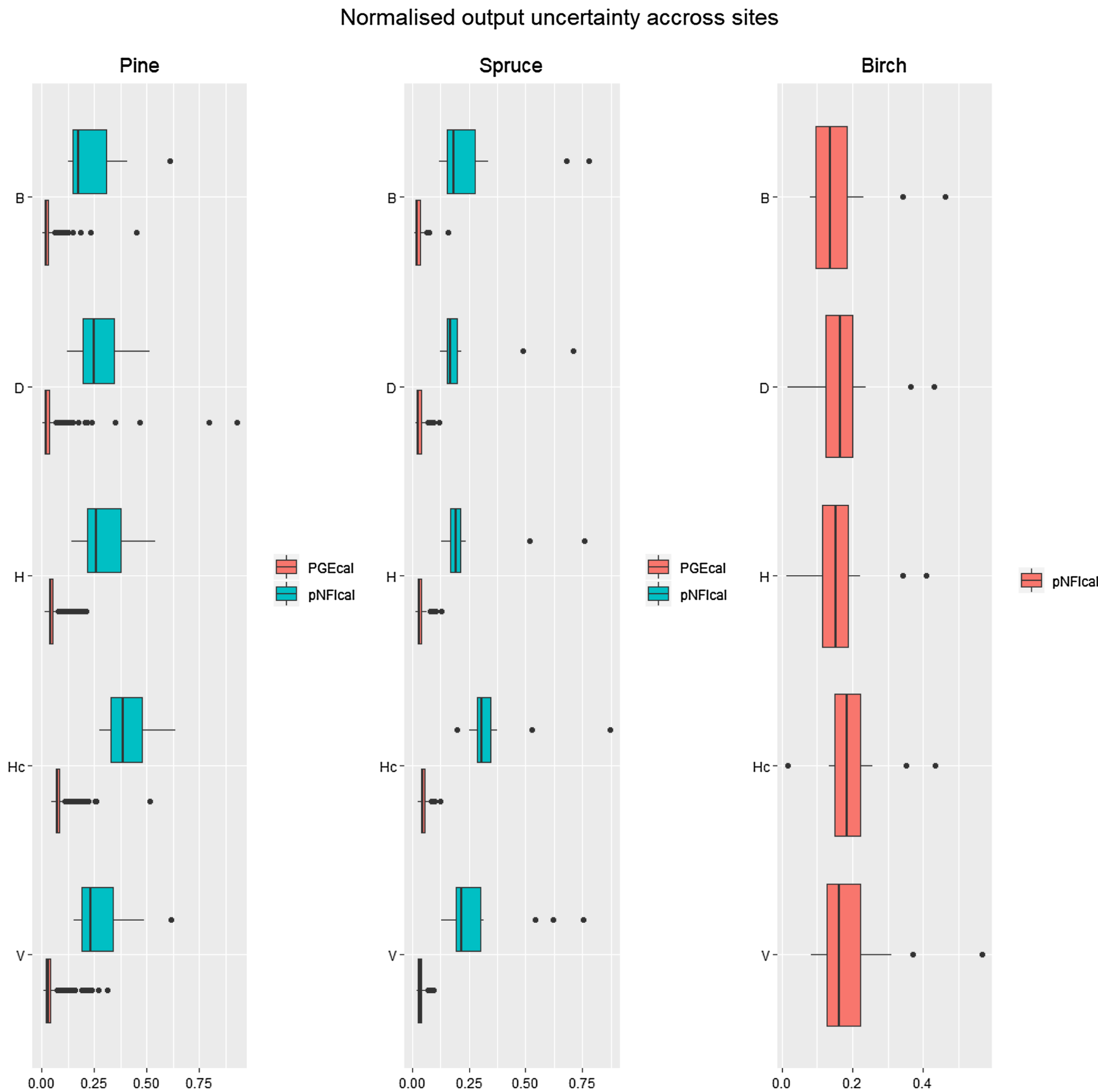

Fig. 2. Model output uncertainty. On the *x*-axis the posterior standard deviation of model outputs (B = basal area, D = diameter at breast height, H = height, H_C = height to crown base, V = volume) divided by the prior standard deviation. The metrics were computed at each plot and the boxplots show the distribution across the plots. In blue the results of the PGEcal for pine and spruce, in red the results of pNFIcal for pine, spruce and birch.

4.2. Parameter distributions and their uncertainty ranges

Bayesian calibration was strongly effective in reducing the uncertainty of PREBAS parameters and predictions. The parameters with the highest a priori uncertainty were estimated most accurately, and therefore the output variability due to parametric uncertainty was strongly reduced. Prior uncertainty was dominated by β_B and N_O because both parameters were *a priori* sensitive and uncertain. By means of Bayesian calibration the uncertainty of those parameters was strongly reduced, therefore the posterior uncertainty was much less dominated by β_B and N_O. However, the mortality parameter (N_O) still remained one of the most important parameters for basal area and volume uncertainty in the pNFI calibration. This reflects the fact that the pNFI data were constrained to sites with no mortality and only spans over ten years, whereas the PGE data were collected over 10–80 years, including several mortality events.

In general, the PGE data were able to constrain the posterior distributions much more than the pNFI data. The key parameters that remained uncertain in the PGE calibration were those for which direct data were not available, e.g., the respiration parameters, the coarse root ratio, and wood density. Correlations between parameters related to processes that are not directly measurable may mask their influence on the measurable variables, such that multiple combinations provide equally good results. Although not critical for the available forest growth variables, these parameters might play an important role if the model was to be used for carbon balance estimates. The Bayesian approach allows to update parameter estimates every time new data become available, therefore the uncertainty of PREBAS posterior

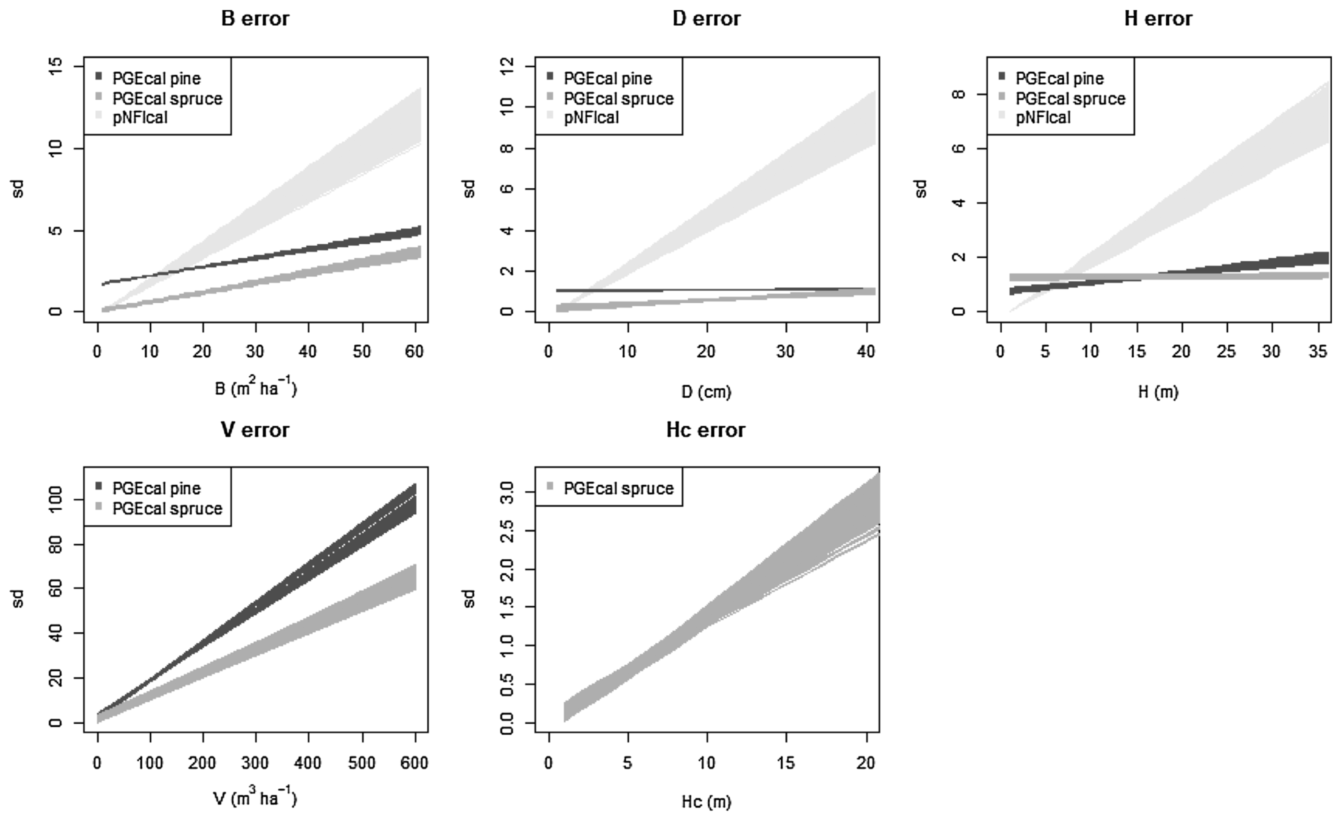

Fig. 3. Error magnitude (Eq. (1)) as function of stand variables (i.e., B = basal area, D = diameter at breast height, H = height, V = volume, H_C = height to crown base). The errors were computed for the different calibrations (pNFIcal and PGEcal for pine and spruce).

Table 3
Partitioning of the predictive uncertainty into error uncertainty and parameter uncertainty. The values represent the fraction of the output standard deviation explained by the two components. B = basal area, D = diameter at breast height, H = height, H_C = height to crown base, V = volume.

		pNFIcal		PGEcal	
species	variables	Error	Parameters	Error	Parameters
pine	H	0.996	0.004	1.00	0.00
	D	0.998	0.003	1.00	0.00
	B	0.983	0.017	1.00	0.00
	V	NA	NA	1.00	0.00
spruce	H	0.997	0.003	1.000	0.000
	D	0.998	0.002	0.999	0.001
	B	0.975	0.024	0.999	0.001
	Hc	NA	NA	0.998	0.002
	V	NA	NA	0.999	0.001
birch	H	0.997	0.003	NA	NA
	D	0.997	0.003	NA	NA
	B	0.983	0.017	NA	NA

distributions could be reduced in the future. Additional data on process-related variables, such as foliage and fine roots, should prove useful for improving the parameter estimates for the carbon balance.

We found that the predictive uncertainty (i.e. parameter uncertainty + error uncertainty) was dominated by the error uncertainty. However, in our representation of the error, the model structural error (discrepancy) and the data error are lumped together, leading to an overestimation of the uncertainty since we are including the stochastic error of the measurements in the predictions (van Oijen, 2017). It is difficult to disentangle the two error components, and just a few works have outlined how to decompose the error (Kennedy et al., 2001; Rougier, 2007). Our results suggest that to reduce the predictive uncertainty we should improve the structure of the model, reducing the discrepancy, and also we could collect more accurate data reducing the measurement uncertainty.

The variability of the SUA results across sites (see Appendix C) are due to the variability of factors like climatic conditions, management practices and initial state. This emphasizes the fact that output uncertainty strongly depends, not only on climatic inputs like e.g. in most dynamic global vegetation models and land surface models, but also on forestry inputs, pressing the need to include these in ecological forecasts under climate change. Kalliokoski et al. (2018) found that, under changing climatic conditions, the uncertainty of weather inputs and the air CO_2 concentration strongly contributed to PRELES output uncertainty. In PREBAS also the uncertainty in management practices can be taken into account since management routines (thinnings and clearcuts) have been implemented in the model.

4.3. On the impact of the calibration dataset on model performances

The calibration process is a key step in model development; more than 50% of model performance can depend on model calibration (Dietze et al., 2014). To date only few studies were able to integrate rich forest datasets into process-based forest models through data assimilation (Thomas et al., 2017). In our work we compared the performance of PREBAS calibrated with data collected at permanent national forest inventory plots and at permanent growth experiment plots in order to understand what characteristics of data are crucial for a robust calibration.

Based on results from empirical modelling, we expected that PGE data could be more valuable for estimating generic parameter values important for stand dynamics, whereas pNFI data could ascertain the regional representativeness of the parameters (Nagel et al., 2012). Regarding the datasets used herein, a limitation of the PGE data used in this work is that they were not representative of very old stands where especially we found parameter discrepancies between the two data sets

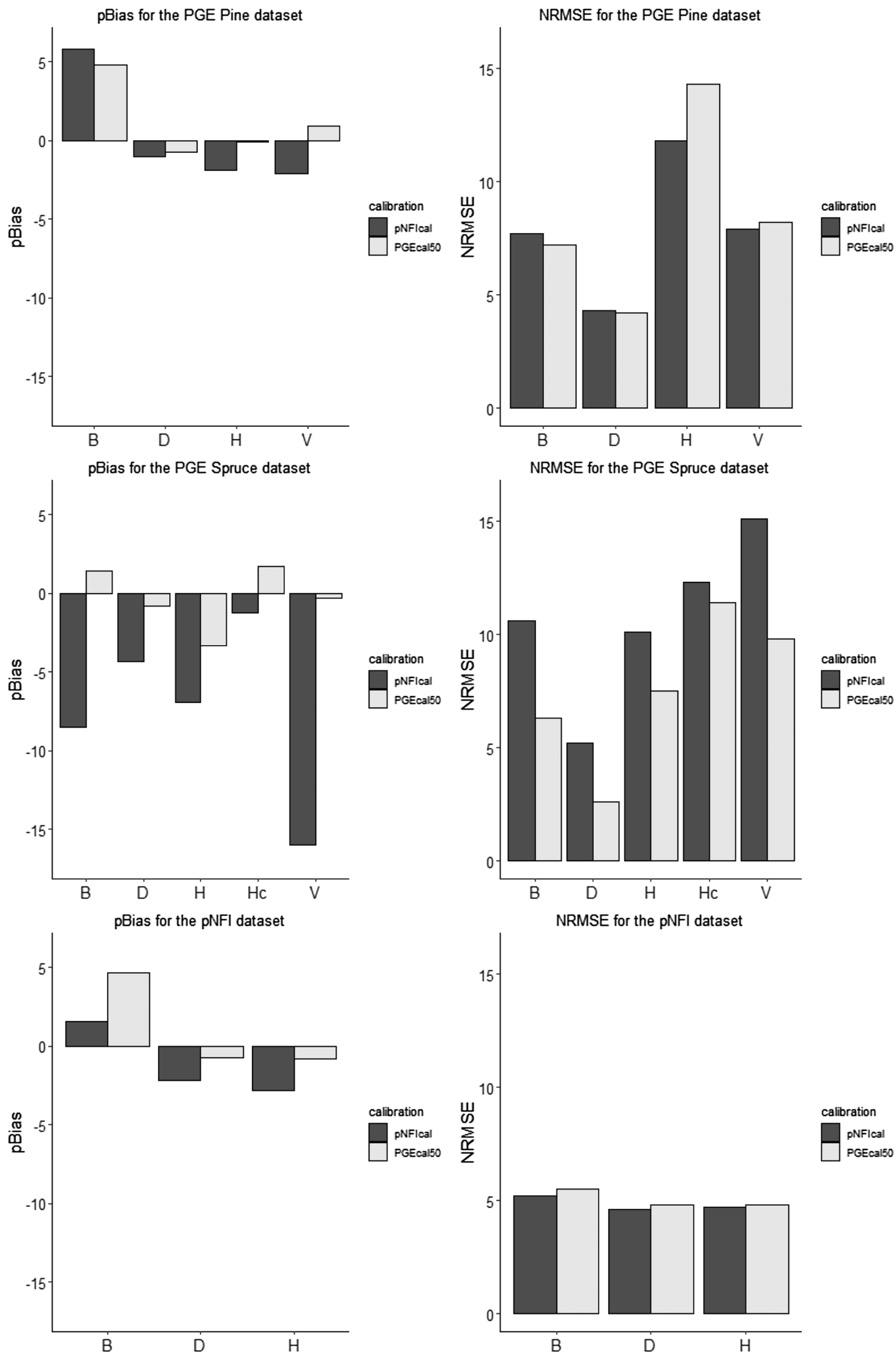

Fig. 4. Percentage bias (left panels) and normalized root mean squared error (right panels). Light and dark grey colours refers to PGE and pNFI calibrations respectively. On the x-axes the output variables (B = basal area, D = diameter at breast height, H = height, H_C = height to crown base, V = volume) are reported. PBIAS and NRMSE of the PGE datasets (first two lines panels) were computed on the validation plots using the pNFI calibration (pNFIcal) and the PGE calibrations obtained using 50% of the PGE plots (PGEcal50). PBIAS and NRMSE for the pNFI dataset were computed using the PGE calibrations (i.e. the calibrations obtained using the whole PGE datasets, PGEcal) and the pNFI dataset itself (pNFIcal). See Table 2 and Section 2.3.2 for further details on the calibrations.

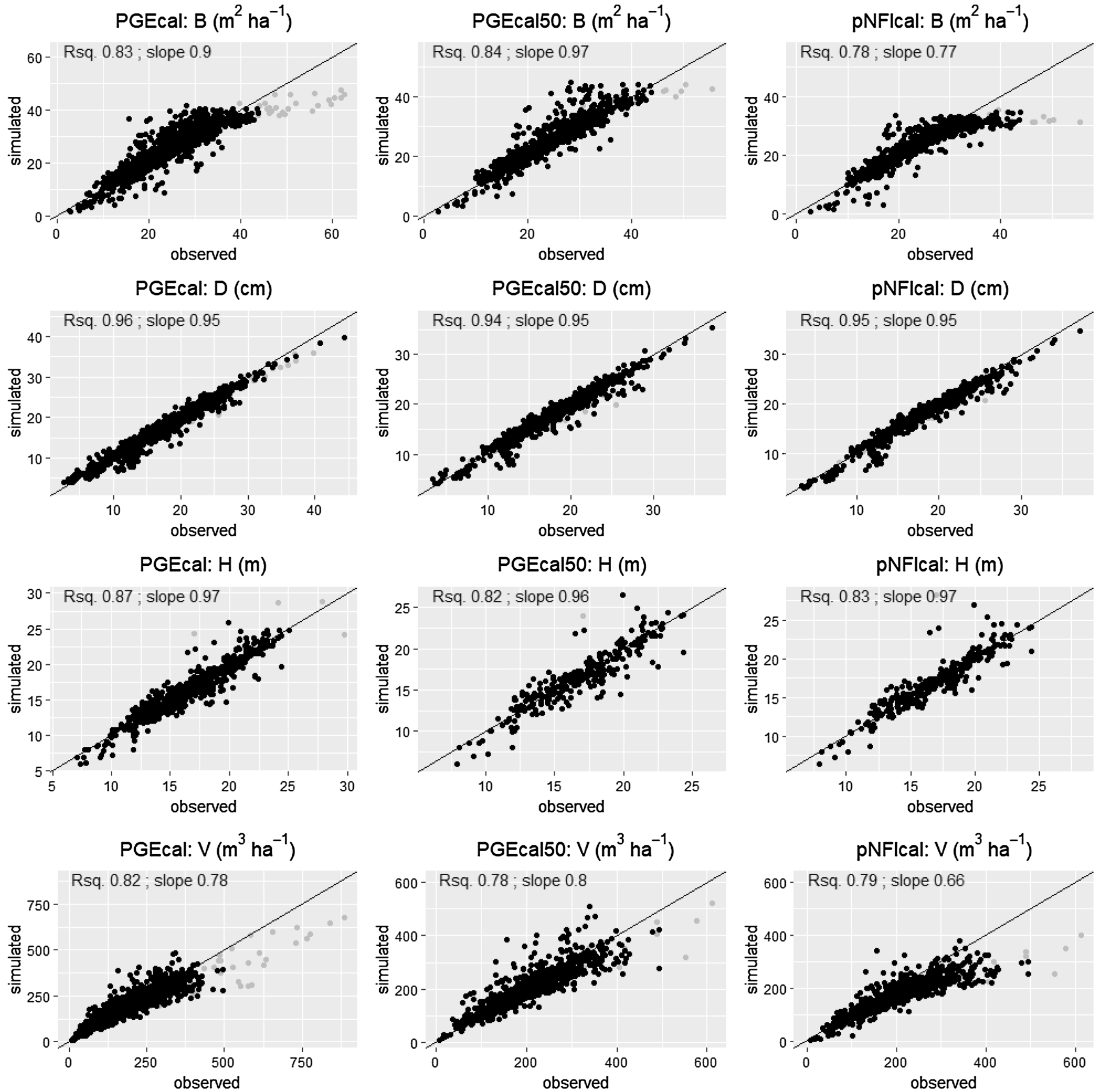

Fig. 5. Observed vs. simulated data from the PGE dataset of pine stands. Each row refers to a different data type (B = basal area, D = diameter at breast height, H = height, H_C = height to crown base, V = volume). Each column refers to results obtained for different calibrations (PGEcal, PGEcal50, pNFIcal (Table 2). In the first column the simulated data were generated for the PGE pine dataset using the *maximum a posteriori* (MAP) parameter set of the PGE pine calibration (PGEcal); in the second column the simulated data were generated for the PGE validation dataset using the MAP parameter set of the PGEcal50 pine calibration; in the third column the simulated data were generated for the PGE validation dataset using the MAP parameter set of the pNFIcal calibration. Grey dots are data points from plots where V and B were unusually high for the Boreal region (i.e., $V > 500\,m^3\,ha^{-1}$ and $B > 45\,m^2\,ha^{-1}$).

(as already noted above). While, the NFI dataset was limited compared to the full national NFI database.

PREBAS calibrated with the PGE data provided good estimates of the pNFI data; in contrast the pNFI calibration was less accurate in predicting high values of basal area and volume of the PGE plots. These results were consistent with the estimates of our error model of Eq. (1) (Fig. 3). In the pNFI calibration, the slope of the standard deviation (b in Eq. (1)) was higher, leading to a higher increase of the error when the magnitude of the variable also increases. In the pNFI calibration, we think that observation error and process error are higher. The process error might be higher because some of the pNFI plots were located in mixed stands, having different species competing for light and soil resources. This also partially explains the differences in the parameter estimates of the pNFI and PGE calibrations especially for the light absorption related parameters; as well as the higher uncertainties and correlations in the pNFI calibration.

As regards the accuracy of the measurements, Minunno et al., (2016) showed that when running the flux model PRELES for a site, a version of the model calibrated with long term, high quality data from a different site could lead to better performance than a version of the model calibrated with less accurate or shorter term data collected at the same site of the simulations. In forest modelling it is also crucial to

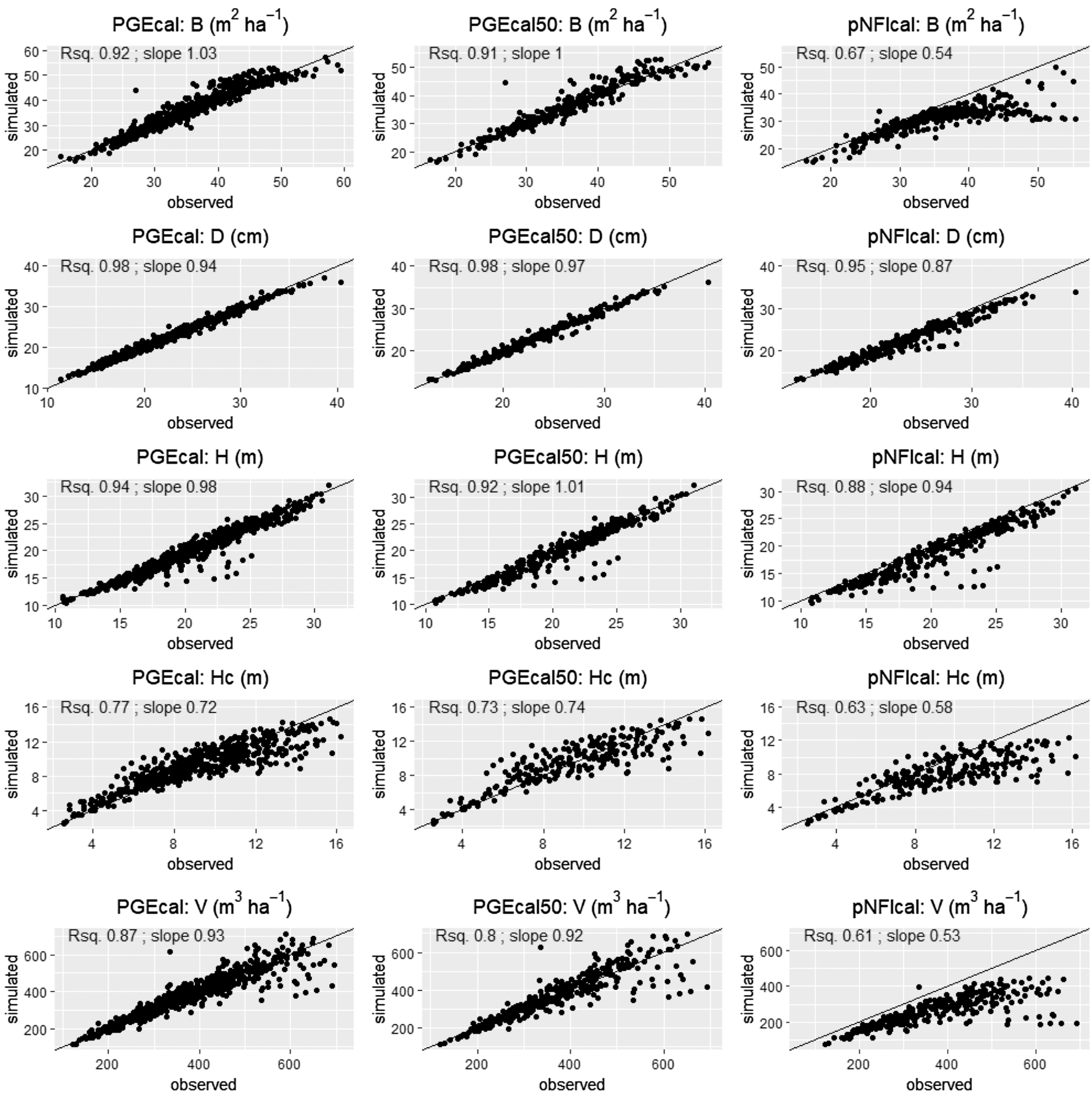

Fig. 6. Observed vs. simulated data from the PGE dataset of spruce stands. Each row refers to a different data type (B = basal area, D = diameter at breast height, H = height, H_C = height to crown base, V = volume). Each column refers to results obtained for different calibrations (PGEcal, PGEcal50, pNFIcal (Table 2). In the first column the simulated data were generated for the PGE spruce dataset using the *maximum a posteriori* (MAP) parameter set of the PGE spruce calibration (PGEcal); in the second column the simulated data were generated for the PGE validation dataset using the MAP parameter set of the PGEcal50 spruce calibration; in the third column the simulated data were generated for the PGE validation dataset using the MAP parameter set of the pNFIcal calibration.

include accurate information about management practices. PGE data usually contain detailed information of management practices that took place between two consecutive measurements. Furthermore, long-term measurements better capture phenomena like tree mortality and growth decline; conversely, these processes might remain latent if data are collected over a short time range. For instance, pNFI data are somehow limited for model calibration because in most cases, between any two measurements, information about management practices are vague or unavailable. Even if the occurrence of thinnings or clearcuts can be detected, we don’t know exactly when they took place, nor if natural mortality was responsible for some of the removal of trees. In the future, remotely sensed data can probably help acquire the missing information.

Van Oijen et al. (2013) concluded that, according to the data used in their study, permanent experiment data proved more useful for model calibration than pNFI data. A limitation of their work was that the calibration and validation of the models were data limited. Consistently with van Oijen et al. (2013), but supported by a more extensive dataset, we concluded that PGE data were better for model calibration because they were more detailed and covered a longer time period. However our findings must be considered strictly contingent to the data used in this study, since the accuracy of NFI data can vary across time and space (mainly by country); so, more detailed and larger NFI datasets would lead to as reliable model performance as long-term PGE data.

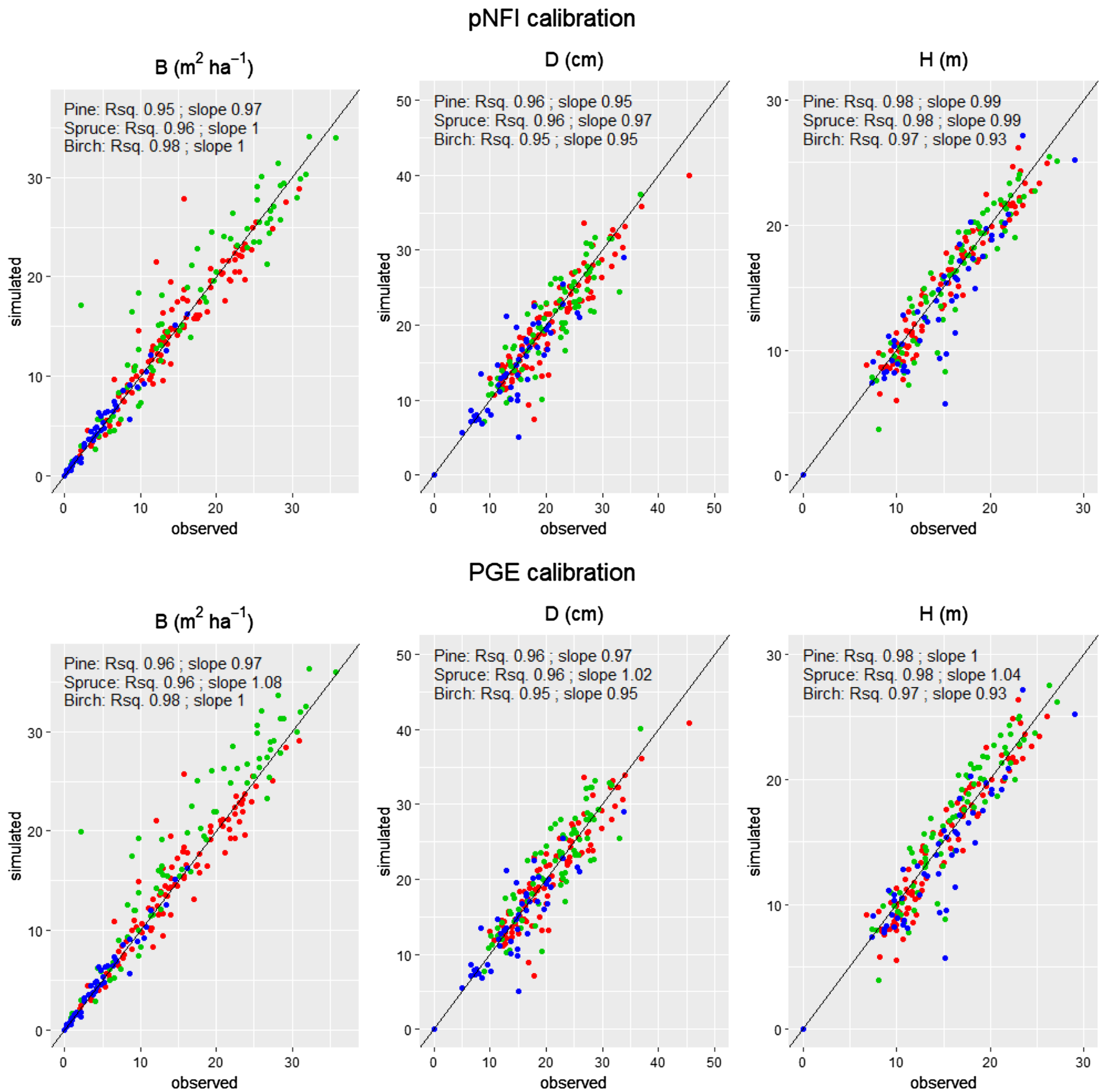

Fig. 7. Observed vs. simulated basal area (*B*, column 1), diameter at breast height (*D*, column 2) and stand height (*H*, column 3) of the pNFI dataset. In the first row the simulated data points were generated using the pNFI calibration; in the second row the simulated data were generated using the PGE calibration. The colours red, green and blue refers to pine, spruce and birch data respectively. Note that PGE calibrations were available only for pine and spruce, when we run the model for stands with birch trees we used for this species the parameter set obtained in the pNFI calibration.

Regardless of the purpose of the data collection, our results highlight how the quality of the dataset used in calibration is decisive for achieving a robust model performance.

4.4. Performance of PREBAS across Finland

PREBAS showed reliable performance in predicting forest growth in Finland. The PGE calibrations were robust in reproducing the validation plots of the growth experiment dataset as well as the pNFI data. Model predictions of basal area and volume were reasonable although less accurate than diameter and height variables. The B and V are more sensitive to processes such as natural mortality and disturbances that are more difficult to predict; furthermore B and V measurements are generally characterized by higher error. The highest values of B and V in PGE pine stands were underestimated by the model, however values of B above 45 m^2 ha^{-1} and V above 500 m^3 ha^{-1} are unusual in the Boreal zone and probably these stands are growing at exceptionally fertile sites. In the future, a more accurate evaluation of the model should be carried out for mature/old stands.

The country-level runs and comparison with yield tables and national forest statistics should not be considered as a rigorous test of the model. However they provide useful insights about PREBAS predictions across the country, considering also the fact that the data used in the calibration where not representative for the northern area of Finland. The yield-table estimates of mean annual increment were in general lower than PREBAS MAI estimates especially in the north of the

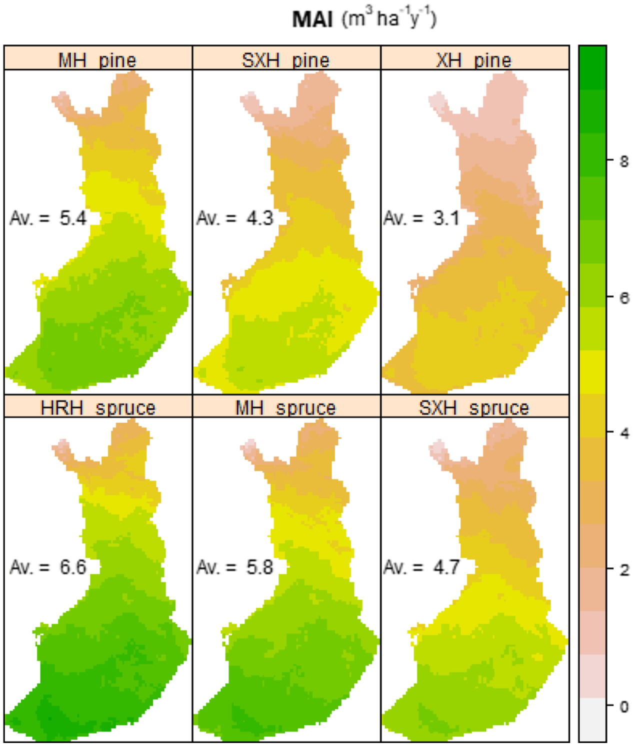

Fig. 8. Mean annual increment (MAI) estimates for pine and spruce stands, simulated for different soil types: herb-rich heath forests (HRH), mesic heath forests (MH), sub-xeric heath forests (SXH) or xeric heath forests (XH). Country averages (Av.) are reported in the maps.

country, even though the spatial growth trend from South to North was similar. The discrepancy of MAI predictions between the yield-table and PREBAS might be explained by numerous factors, such as the details of thinning and clearcut routines and site conditions variability. Moreover during the last few decades the forests have been experiencing changes in climatic conditions that are causing in general an increase of forest growth in the boreal region (Henttonen et al., 2017). The effects of those changes are not captured by the yield tables that are not sensitive to weather inputs.

PREBAS predictions were consistent with the national forest statistics. PREBAS simulations also caught the peak of MAI in central Finland (Fig. 10) that is due to a more extensive cover of spruce stands and more fertile sites. The deviation encountered for the northern transect points might be explained either by an uneven age distribution of the stands in this area or by poor model performance in the northern part of the country where data for the calibration were not available.

An area where the current data proved to be insufficient for a regional calibration of PREBAS parameters was the belowground carbon allocation. In PREBAS, the belowground carbon demand consists of growth, determined by the fine-root to foliage ratio and foliage and fine root turnover, and fine root and coarse root respiration. Since we only had data on above-ground stem growth, the calibration did not allow us to identify the different belowground parameters separately, as the key influence on aboveground growth was the total belowground allocation. Therefore we fixed the fine-root to foliage ratios using values available from boreal empirical studies (Helmisaari et al., 2007; Ostonen et al., 2011; Mäkelä et al., 2016). Combining PREBAS with a soil carbon model, such as Yasso (Liski et al., 2005; Tuomi et al., 2009), and using regional data on litter fall and soil carbon pools (Lehtonen et al., 2016) as additional constraints, could help to solve this problem and will be the focus of our work in the near future.

PREBAS, thanks to its structure, is able to reproduce the light absorption processes of multi-layered forests. Even though in this work the data came mainly from even aged stands, the model has the potential to be applied to mixed and uneven aged forests. However, prediction of species mixtures still remains a key structural uncertainty in the model, as the growth of the species of the mixture seems overly sensitive to stand initial conditions (not shown). Satisfactory description of species mixtures has been found problematic also in other modelling studies, probably because of insufficient data, but advances have recently been made with the 3-PG model that could prove useful for PREBAS development as well (Forrester et al., 2017). In the future,

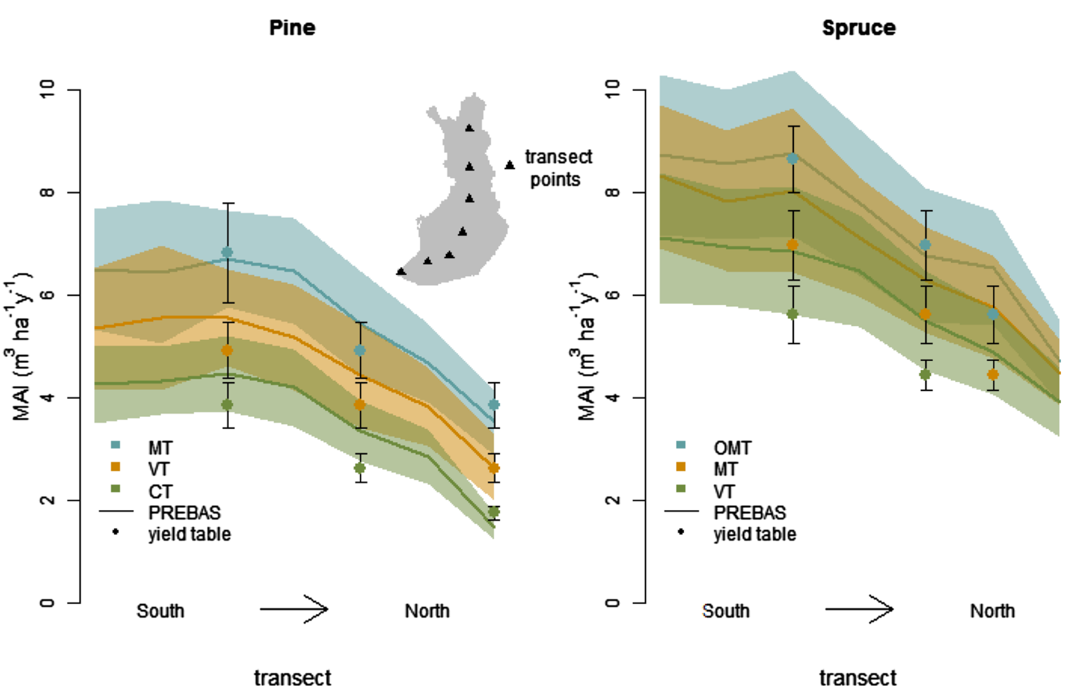

Fig. 9. Comparison between the mean annual increment (MAI) of the rotation estimated by PREBAS (lines) and by Yield tables (dots) along a North-South transect. The different colors refer to different site types. The shaded areas represent the predictive uncertainty of the model; the bars of the points provide the variability reported in the Yield tables (see Section 2.4. for details). Black triangles in the map are the location of the transect points.

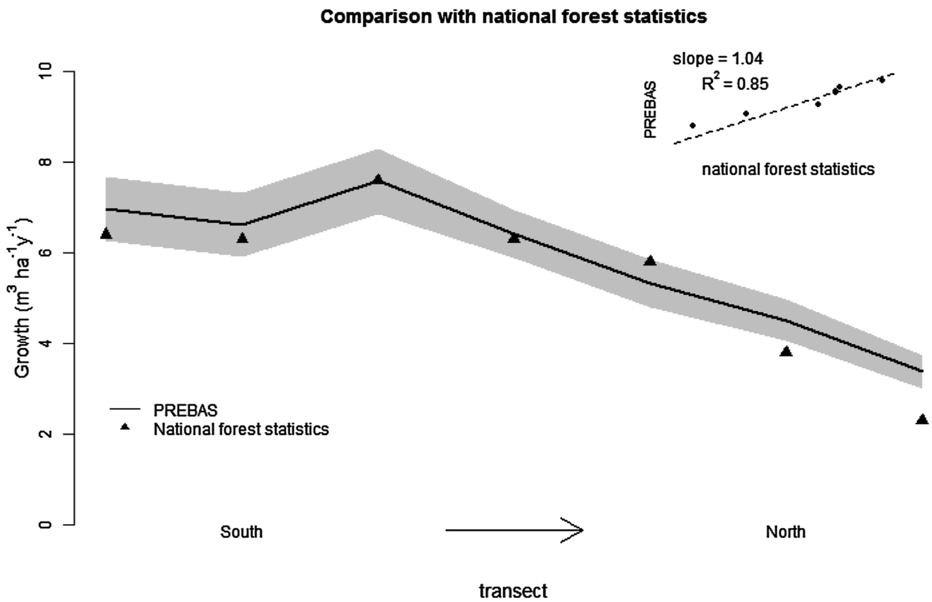

Fig. 10. Comparison between Finnish national statistics of forest annual growth (triangles) and PREBAS predictions (black line). The shaded grey area represents model predictive uncertainty. National statistics estimates were taken from the regions where the transect points were located and were computed for pine and spruce. Model predictions were the weighted average MAI of pine and spruce at different growth sites, where the weights were obtained from the National statistics on the basis of respective areas covered in each region (See Section 2.4 for details).

we plan to test the model for uneven aged mixed stands. Moreover natural regeneration is not yet incorporated in the model, as well as the understory vegetation, and they will be implemented in future model developments.

The PGE data covered different thinning regimes and tree densities; PREBAS showed robust results for stands under a variety of management actions and climatic conditions (within the study region). These properties have been assessed important for models intending to evaluate optimal management under changing climate (Fontes et al., 2011). In the long term, processes that are not represented in the model (e.g., nutrient cycle, pest attacks, etc.) might become important for predictions of carbon cycle and forest growth. However, on short to medium term (50–80 years) PREBAS is readily applicable, e.g., for verifying the impacts of interventions aimed to mitigate climate change.

5. Conclusions and outlook

By means of Bayesian statistics we were able to calibrate and test a simple forest growth model based on carbon acquisition and allocation. The data assimilation of multiple data types, sites and species allowed us to make use of tree measurements collected over decades. Furthermore, owing to the Bayesian framework, our posterior distribution can be the prior for a new calibration when new data become available.

The uncertainty of model parameters and output variables was strongly reduced after the calibration. The posterior predictive uncertainty was mainly influenced by the uncertainty of the structural and measurement error.

The permanent growth experiment dataset led to a more robust calibration than the fairly limited national forest inventory dataset available to this study. PGE calibrated PREBAS showed better predictive performance and less uncertain estimates of forest growth variables. The model reliably predicted stand variables of pine, spruce and birch forests across Finland under a wide range of management and environmental conditions, proving to be a robust tool for regional analysis and forest forecasts. However, some subroutines of the model, such as the respiration rates and the belowground allocation, were not extensively investigated in this work because data directly related to these model components were not available. Estimating these parameters with a more versatile data set remains a challenge for our future work and will be conducted by coupling PREBAS with a soil carbon model in order to complete the carbon cycle at ecosystem level.

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Appendix A. PREBAS model structure

In this section we describe all the processes implemented in PREBAS and we report all the fundamental equations.

A.1. Growth modelling (CROBAS)

The allocation procedure is the core of the model and is based on the pipe model with dynamic crown rise. The key assumptions for deriving the allocation scheme are, (1) that foliage mass is proportional to stem cross-sectional area at crown base (the pipe model, Shinozaki et al. 1964), and (2) that an allometric relationship exists between crown length and foliage mass (Mäkelä and Sievänen, 1992; West et al. 1999; Duursma et al., 2010). In addition to these, the cumulative sapwood areas of branches and coarse roots are assumed proportional to stem sapwood area, and mean branch and coarse root lengths are assumed derivable from stem and crown length, implying that the biomasses of all sapwood components are derivable from crown length and sapwood area at breast height and crown length (Ilomäki et al., 2003; Kantola et al., 2006). - A third focal assumption controlling growth allocation in the model is that (3) fine root mass is proportional to foliage mass.

These assumptions imply that all biomass components of the tree crown and fine roots are related to foliage mass through structural equations involving crown length and stem sapwood area (see a list of variables in Table 2), and these two are also inter-connected. In addition, the above

Table A1
Key process rates and their definitions in CROBAS. For explanatory variables see Table 2; for parameters see Table 3.

Variable	Meaning	Definition
P_T	Tree photosynthetic production (kg C yr^{-1})	σW_F
σ	foliage-specific photosynthesis (yr^{-1})	$P/(NW_F) \times 10000$
P	Canopy photosynthesis (kg C m^{-2} yr^{-1})	Eq. (1)
R_M	Maintenance respiration (kg C yr^{-1})	$m_F W_F + m_R W_R + m_S(W_S + W_B + W_T)$
G	Total growth of tree (kg C yr^{-1})	$(P_T - R_M)/(1 + c)$
$\frac{dW_i}{dt}$	Growth rate of mass i (kg C yr^{-1})	$\lambda_i G - W_i/\nu_i$
λ_i	Allocation of growth to mass$i$	From structural constraints
$\frac{dH_C}{dt}$	Rate of "crown rise" (m yr^{-1})	$\frac{c_R}{f_C}\frac{dH}{dt}$
f_C	Relative light level at crown base	From canopy light distribution

Table A2
Tree structure variables and their mutual relationships in CROBAS.

Variable	Meaning	Relationships
W_F	Foliage mass (kg)	$W_F = \rho_F A_S$
W_R	Fine root mass (kg)	$W_R = \alpha_R W_F$
W_B	Branch sapwood mass (kg)	$W_B = \rho_W A_S \beta_B L_C^x$
W_S	Stem sapwood mass (kg)	$W_S = \rho_W A_S(H_C + \beta_S L_C)$
W_T	Coarse root sapwood mass (kg)	$W_T = \frac{\beta_0 - 1}{\beta_0}(W_B + W_S)$
A_S	Basal area of stem sapwood at crown base (m^2)	Primary variable
H	Tree height (m)	$H = H_C + L_C$
L_C	Crown length (m)	$L_C \propto A_S^{\frac{1}{2z}}$
H_C	Crown base height (m)	Primary variable
H_B	Mean branch length (m)	$H_B = \beta_B L_C{}^x$
W_C	Mass of bole below crown (kg)	$W_C = (A_S + B_{13} + \sqrt{A_S B_{13}})x\frac{H_C}{2.9}$
W_H	Stem heartwood mass (kg)	$W_H = (W_C - \rho_W A_S H_C)$
D	Diameter at breast height (m)	Primary variable
B	Stem basal area at breast height (m^2)	$B_{13} = \frac{\pi}{4}D^2$
N	Stocking density (ha^{-1})	Primary variable
L	Leaf area index (m^2 m^{-2})	$L = s_{LA} N W_F/10000$

assumptions define a growth and allocation scheme where crown rise determines sapwood turnover below the crown, allowing us to calculate the development of heartwood area and mass in the stem below crown and hence diameter at breast height, (Mäkelä, 2002, Valentine and Mäkelä, 2005). It thus remains to define a rule for crown rise in the tree. Here, we relate crown rise to height growth (Valentine and Mäkelä, 2005) with a coefficient that depends on the level of light available at the crown base: crown rise accelerates when the light level reduces (Kalliokoski et al., 2017) (Table 1).

Stand level photosynthesis, P (g C m^{-2} yr^{-1}) is calculated following the Light Use Efficiency (LUE) approach

$$P = (1 - s_1 L_C)P_0 f_{APAR} \tag{A1}$$

where f_{APAR} is the proportion of incoming radiation absorbed by the canopy and P_0 is potential photosynthetic production of a stand with $f_{APAR} = 1$, L_C is crown length and s_1 is a parameter. The L_C-dependent term represents the reduction of photosynthesis with impaired water transport in the crowns (Valentine and Mäkelä, 2005). P_0 is environment-dependent and may also indirectly depend on f_{APAR} as described in Appendix A.2. This allows us to evaluate the foliage-specific photosynthetic rate for the mean tree. Because the foliage-specific rate has a maximum, canopy photosynthesis is scaled down for very sparse canopies. This is done using the factor σ_0.

We calculate f_{APAR} as the minimum of two different estimates, $f_{APAR,1}$ and $f_{APAR,2}$. The first one is based on the Lambert-Beer law:

$$f_{APAR,1} = \left(1 - e^{-k_{eff} L}\right) \tag{A2}$$

Here, L is leaf area index and k_{eff} is effective light extinction coefficient (Duursma and Mäkelä, 2007) which modifies the homogenous canopy extinction coefficient k_H due to clumping in randomly distributed crowns and depends on tree leaf area relative to crown envelope area. Crown envelope areas are assumed conical (spruce) or ellipsoidal (pine, birch) and crown radius is estimated with the basal-area weighted mean branch length. Eq. (A.2) may overestimate canopy photosynthesis in very sparse canopies where a significant part of radiation falls onto the ground. To account for this, we adopt the model of f_{APAR} used in the LPJ model (Sitch et al., 2003) which gives lower values than Eq. (A.2) in sparse canopies:

$$f_{APAR,2} = \left\{1 - exp\left(-k_H \frac{L}{A_{TOT}}\right)\right\} A_{TOT} \tag{A3}$$

where k_H is the homogenous extinction coefficient, L is leaf area index and A_{TOT} is crown coverage. When crown coverage is high, $f_{APAR,2} > f_{APAR,1}$, because Eq. (A.3) then approaches the homogeneous canopy assumption, while Eq. (A.2) accounts for clumping in dense stands. Therefore, we choose to use the smaller of the two:

$$f_{APAR} = min\{f_{APAR,1}, f_{APAR,2}\} \tag{A4}$$

In practise, $f_{APAR,2}$ is preferred over $f_{APAR,1}$ when both reach values near to 0.3–0.4.

For mixed stands, we calculate the proportions of absorbed radiation by (mean tree of) species in a one-dimensional canopy, assuming that all species are randomly distributed in space and all have a parabolic vertical effective leaf area distribution between tree height and crown base with maximum at half crown. Effective leaf area is defined as

$$L_{eff} = \frac{k_{eff}}{k_H}L \tag{A5}$$

(Duursma and Mäkelä, 2007). In this mixed canopy, we calculate light absorption by species using the Lambert-Beer law. This procedure also allows us to calculate the remaining proportion of light at the crown base of each species.

Mortality is modelled using the Reineke self-thinning model (Reineke 1933). It defines the maximum number of trees for stand mean breast height diameter, D, as follows:

$$N_c = N_0\left[\frac{0.25}{D_{BH}}\right]^{1.66} \tag{A6}$$

where N_0 is a parameter indicating maximum stand density when $D = 0.25m$. Mortality is modelled with a switch function to start as the density approaches the critical density such that this density is not exceeded. These parameters are species-specific.

A.2 Incorporating climate and site effects (PRELES)

Climate influences all metabolic rates of forests, including photosynthesis, respiration, nutrient and water uptake and tissue turnover. Here we use the PRELES model (Mäkelä et al., 2007; Peltoniemi et al., 2015; Minunno et al., 2016) to estimate P_0 of Eq. (A.1). We further use P_0 to derive the geographic variation of the other relevant metabolic parameters, following the procedure proposed by Mäkelä et al. (2016).

PRELES is a light-use-efficiency (LUE) based model, which predicts daily (k) GPP (P_k, kg C m^{-2} day^{-1}), evapotranspiration (ET, E_k, mm day^{-1}) and soil water content (θ_k, mm). The photosynthesis sub-model is a separable model that calculates the LUE of a stand as the product of absorbed photosynthetically active radiation (f_{APAR}), a species-specific potential LUE and a set of independent environmental modifiers that vary between 0 and 1. These depend on photosynthetic photon flux density, mean temperature, vapour pressure deficit, and soil water content. The latter is calculated from precipitation and evapotranspiration in the water-balance submodel of PRELES. It considers water stored in three pools: intercepted water (mainly on canopy surfaces), snow/ice and soil water storage. All components are described by simple bucket models. ET is calculated by means of a simple empirical equation that links the predicted daily photosynthesis and soil water content (Peltoniemi et al., 2015).

We link PRELES to CROBAS by computing whole-canopy f_{APAR} in CROBAS and running PRELES for the entire year with this value, returning the annual sum of daily GPP to CROBAS:

$$P = \sum_{k=1}^{365} P_K \equiv P_0 f_{APAR} \tag{A7}$$

This also defines the parameter P_0 that aggregates the effect of climate on stand photosynthesis as the production of a stand with $f_{APAR} = 1$ while all other modifiers are as given for the actual f_{APAR} (see Eq. (A.1)) (Note that estimating with PRELES for a stand with $f_{APAR} = 1$ may not give the same result as stand density has an impact on the availability of water).

In addition to photosynthesis, other metabolic rates also depend on climate. Following Mäkelä et al. (2016) and based on the widely held view (Dewar et al., 1999; Högberg et al., 2001; Wertin and Teskey, 2008; Medlyn et al., 2011) that long-term mean respiration rates are related to the respective photosynthetic production rates, we set

$$m_i = m_{i,ref}\frac{P_0}{P_{0ref}} \tag{A8}$$

where m_i is the biomass-specific maintenance respiration of foliage, fine roots or sapwood, P_{0ref} is a reference rate of potential photosynthesis, $m_{i,ref}$ is the corresponding maintenance respiration rate for the reference stand, and P_0 is as in Eq. (A.7).

The mean lifetime of foliage, ν_F, and fine roots, ν_R, also depend on climate. Tissue lifespan has been functionally attributed to general tissue activity (Kikuzawa and Lechowicz, 2011; Reich et al., 2014). Based on this and following Mäkelä et al. (2016) we assumed that the photosynthetic parameter P_0 reflects foliar tissue activity, so

$$\nu_F = \nu_{F,ref}\frac{P_{0,ref}}{P_0} \tag{A9}$$

where $\nu_{F,ref}$ is tissue lifetime at $P_{0,ref}$. As proposed by Mäkelä et al. (2016), fine root lifetime was kept independent of P_0 to account for the opposite trends with climate in the carbon requirement for mycorrhiza and other exudates on one hand, and fine root lifetime on the other hand. Sapwood turnover is controlled by crown rise (Valentine and Mäkelä, 2005).

Site effects are described as an impact on the fine-root to foliage ratio, α_R, which has been found empirically to depend on site fertility (Helmisaari et al., 2007; Ostonen et al., 2011). Mäkelä et al. (2016) developed a procedure to relate α_R to the site type classification system used in Finland (Cajander, 1949). We therefore relate a value α_{Rs} to each site type and evaluate fine root mass on this basis:

$$W_R = \alpha_{Rs} W_F \tag{A10}$$

Here, we ignore any other edaphic site effects, such as impacts on photosynthesis, respiration and turnover rates and impacts on foliage density in the crown, as their role is smaller than that of below-ground allocation (Mäkelä et al., 2016).

Appendix B. Standard management practices implemented in PREBAS

Following the standard management routines applied to Finnish forests we implemented clearcuts and thinning rules in the PREBAS model.

The clearcut occurred if the diameter at breast height (D) or stand age exceeded certain thresholds (Table B.1).

Thinning rules were based on a basal area thresholds (B_{limit}); if the B of a stand exceeded B_{limit} the stand was thinned in order to lower the basal area to a prescribed value ($B_{thinned}$). B_{limit} and $B_{thinned}$ were dependent on the average stand height (H). If H is lower than 20 m B_{limit} and $B_{thinned}$ were defined by the following equation:

$$B_{xx} = a * H^2 + b * H + c \tag{B1}$$

where $B_{xx}$is either B_{limit} and $B_{thinned}$; a, b and c are parameters that change for B_{limit} and $B_{thinned}$ and vary for conifers and deciduous species and for site type.

If H is higher than 20 m B_{limit} *and* $B_{thinned}$ were equal to a constant that is different according to the forest type and the site type (Table B.2).

Table B1
D and Age thresholds for clearcut. The ranges are depends on the site type of the forests and the location (north vs. south of the country).

species	D (cm)	Age (y)
pine	23.5–29	70–100
spruce	26.5–30	60–80
birch	27–30	60

Table B2
Ranges for basal area thresholds (B_{limit}) for thinnings and basal area of thinned stands ($B_{thinned}$) when the average stand height is higher or equal to 20 m. The ranges are depends on the site type of the forests and the location (north vs. south of the country).

forest type	B_{limit} (m^2 ha^{-1})	$B_{thinned}$ (m^2 ha^{-1})
conifers	23–33	16–24
deciduous	21	15

Appendix C. Sensitivity and uncertainty analysis results

In this section we describe the sensitivity and uncertainty analysis (SUA) performed for PREBAS. In total 6 SUAs were carried out. For the prior SUAs the parameter space was defined by the uniform distribution (Table 1); we drew a sample of 100.000 parameter sets using the Latin hypercube sampling strategy. For the posterior SUAs we extracted 100.000 parameter sets equidistantly from the posterior distributions. The output variables for the SUAs were basal area, average diameter at breast height, average stand height, average height of the crown base and stand volume. We considered the average annual variation of the variables (i.e., the difference between the model output at the end and at the beginning of the simulation divided by the number of years of the simulation) and performed the SUA at each plot (842 plots × 5 variables × 2 calibrations (pNFIcal and PGEcal) for a total of 8420 SUAs). For the SUA of the pNFI dataset, in order to account for species interaction, we considered only the 36 plots where all the tree species were present.

For a comparison of model output sensitivities to different parameters we quantified parameter *elasticity*, defined as the sensitivity standardized using the average parameter value ($\bar{X}$) and the average output ($\bar{Y}$) (i.e., *sensitivity* × $\bar{X}/\bar{Y}$). An elasticity of 1 means that a unit relative increase of the parameter causes a unit relative increase in the output.

Bayesian calibration was effective in reducing parametric uncertainty and model output uncertainty. The standard deviations of parameter marginal posterior distributions were on average 40% less than the prior *sd* in the pNFI calibration and between 80% and 85% less in the PGE calibrations (Fig. C1).

In the following graphs (Figs. C2 - C26) we report the elasticities and uncertainty contribution of PREBAS parameters to each variable and each calibration. The horizontal boxplot correspond to the distributions of the sensitivity and uncertainty metrics across the plots. The colors blue and red refers to the prior and posterior (post) analysis, respectively. The parameters were ranked according to the median value of the posterior uncertainty analysis over the plots.

The NFI SUA results are reported for each variable of each species. The suffixes _P, _SP, _B at the end of the parameter names (y axes of Figs. C12 - C26) refer to the different species (i.e., pine, spruce and birch).

The parameters that contributed the most to the output uncertainty (i.e., higher R^2 values) were also those that had the highest variability of R^2 across the sites (Figs. C2 to C26). The ratio of mean branch length to crown length (β_B) was the parameter that dominated the prior uncertainty of model outputs (Figs. C2 to C26). The Reineke parameter (N_0) strongly contributed to basal area and volume prior uncertainty. Both parameters ($\beta_B$and N_0) had a much lower weight on the posterior uncertainty and the posterior sensitivity of the model to these parameters was strongly reduced compared to the prior sensitivity. An array of parameters contributed to the output posterior uncertainty, where c_R, v_R, z, m_R and ρ_F were the parameters with the strongest contribution. However the standard deviation of model outputs explained by each of these parameters was only 20–30% (Figs. C2 to C26).

The posterior parameter elasticities showed similar patterns for the different calibrations (NFI, PGE pine and PGE spruce), i.e. most of the elasticities were consistently positive or negative across the calibrations and also the magnitudes of the values were similar (Figs. C1–C25). In the NFI calibration most of the stands were mixed forests characterized by the presence of the three species (pine, spruce and birch) and there was a strong interaction between the parameters of the different species. For instance, an increase of the specific leaf area of pine (s_{LA_P}) causes an increase of the pine basal area, but at the same time, an increase of specific leaf area of spruce (s_{LA_SP}) has a negative impact on pine basal area (Fig. C12).u

SUA results for PGE pine calibration

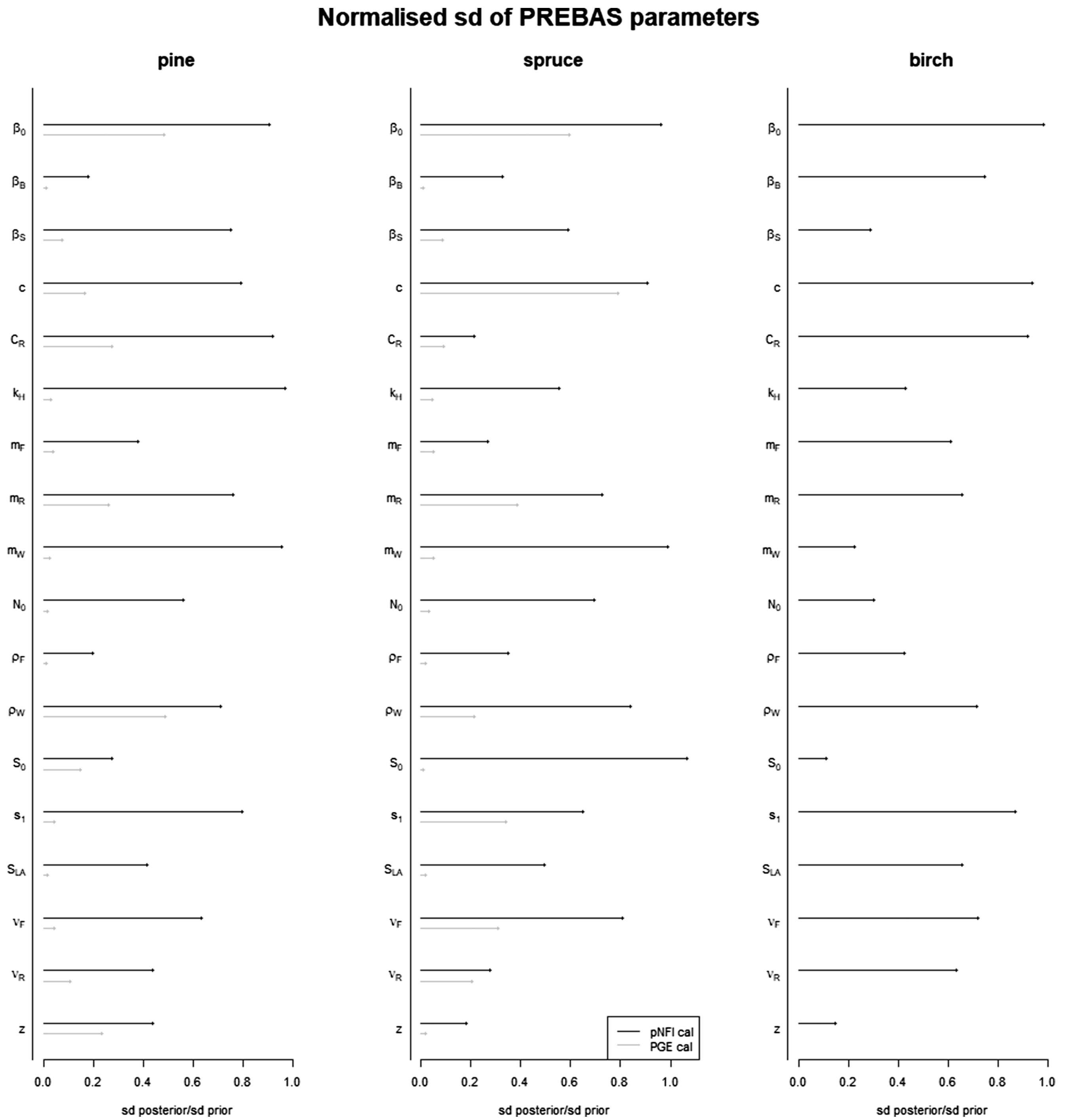


Fig. C1. Standard deviation of the posterior marginal distributions of PREBAS parameters (Table 1) normalised using the standard deviation of the prior distributions (sd posterior/ sd prior). Values below 1 indicate a reduction on the posterior parameter uncertainty compared to the prior. In grey the results for the PGE pine and spruce calibrations, in black the results for the pNFI calibration for pine, spruce and birch.

B

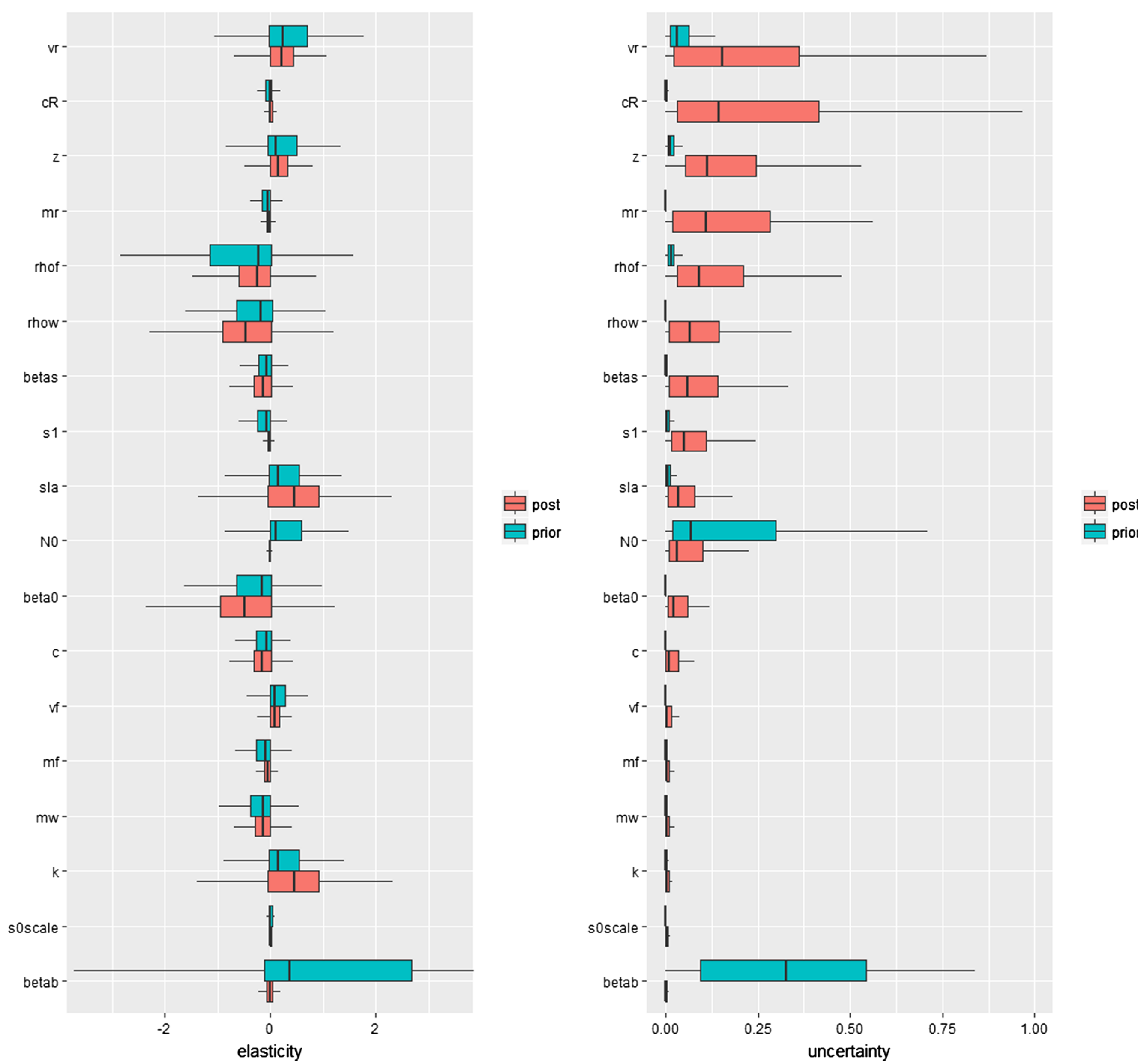


Fig. C2. Basal area sensitivity and uncertainty analysis results for the PGE pine calibration.

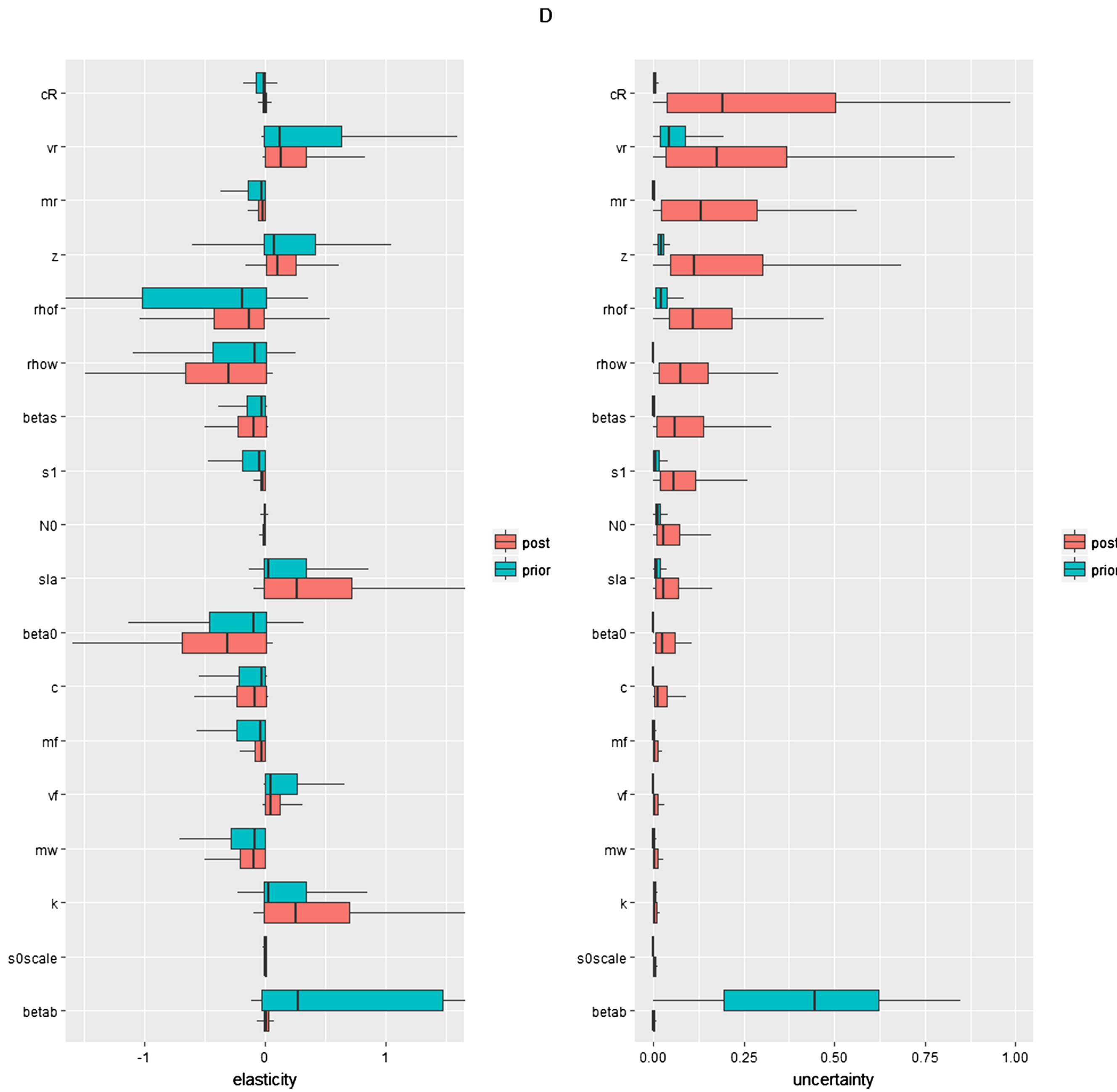


Fig. C3. Average stand diameter at breast height sensitivity and uncertainty analysis results for the PGE pine calibration.

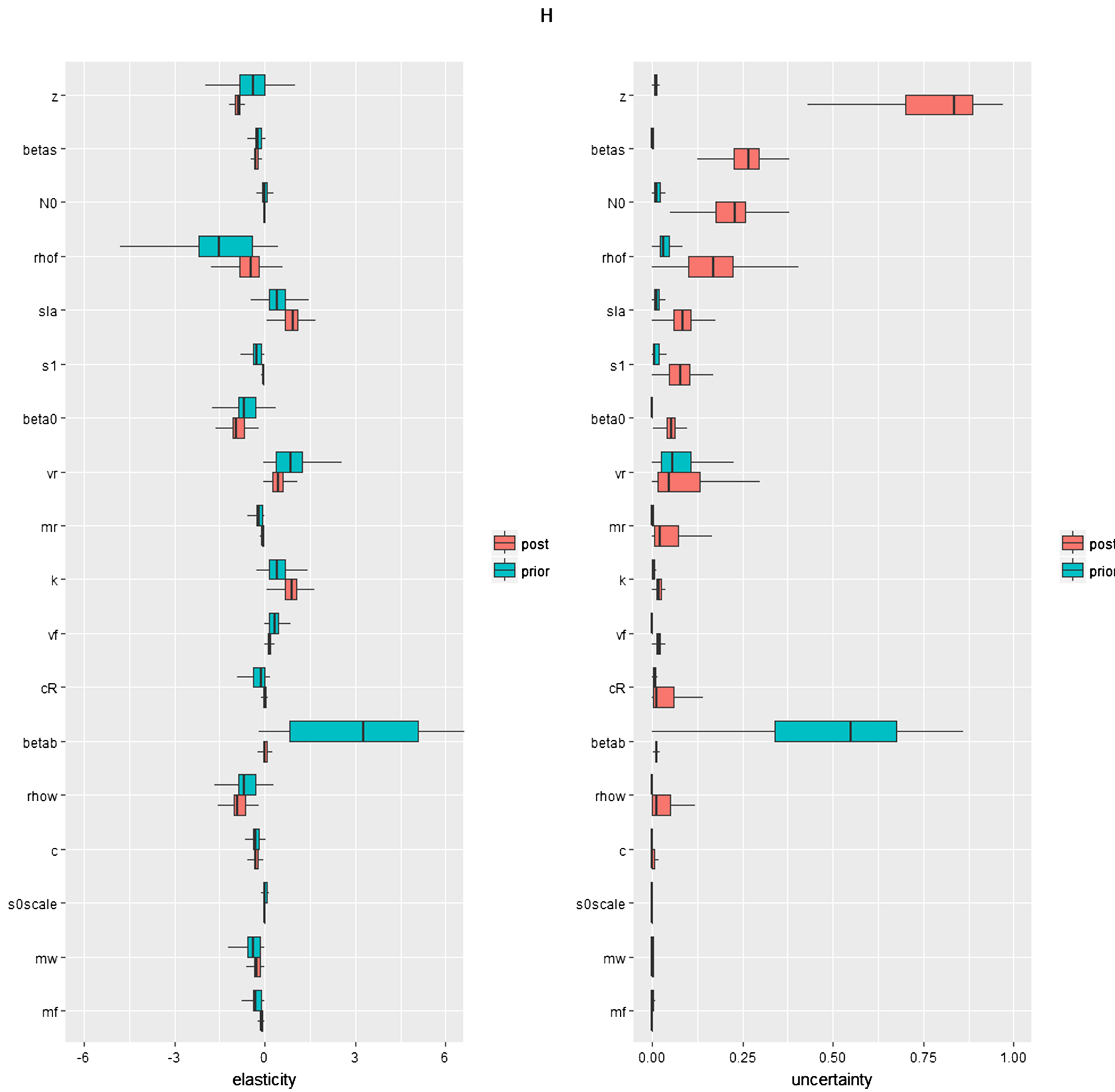


Fig. C4. Average stand height sensitivity and uncertainty analysis results for the PGE pine calibration.

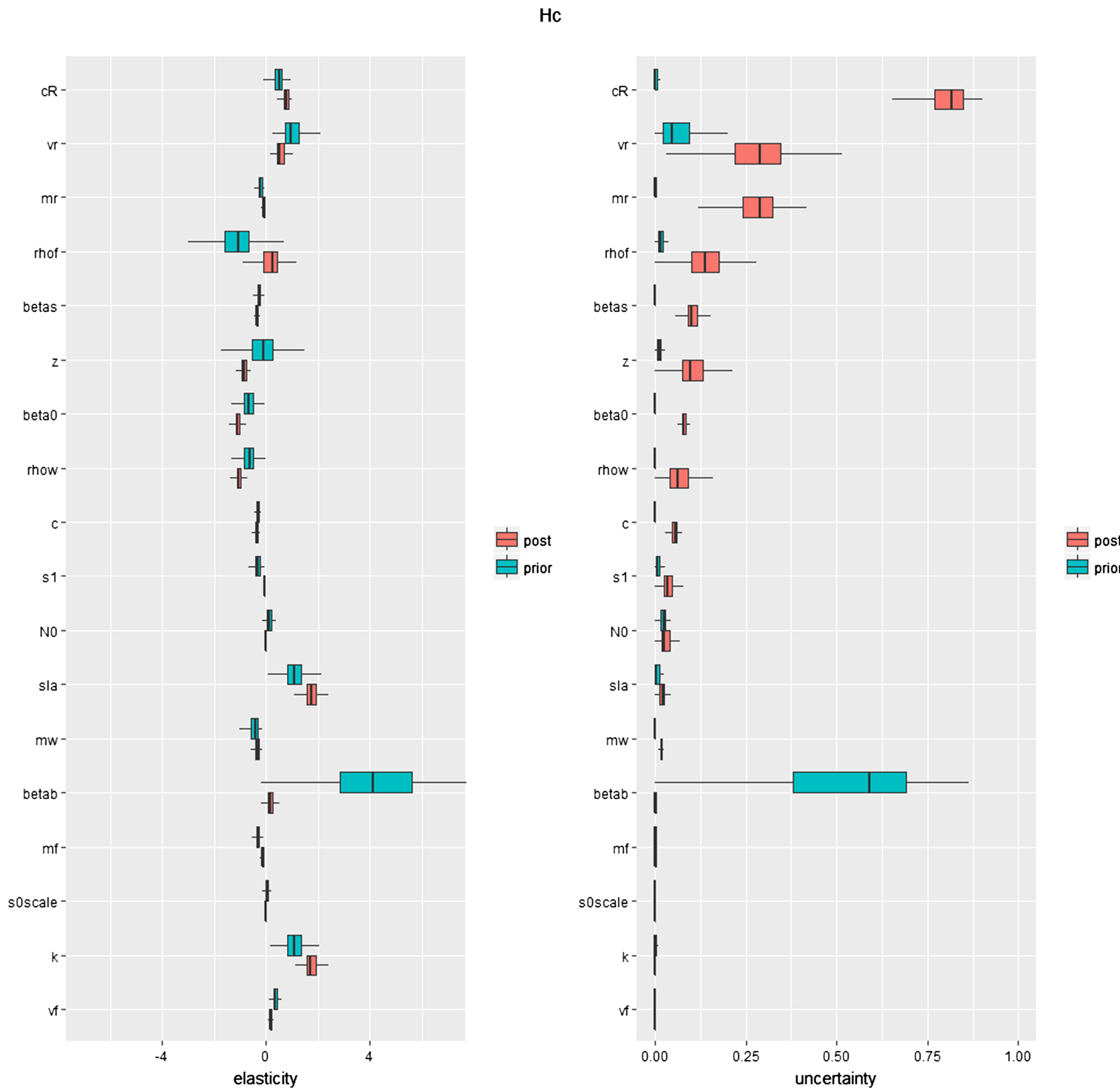


Fig. C5. Average stand height of crow base sensitivity and uncertainty analysis results for the PGE pine calibration.

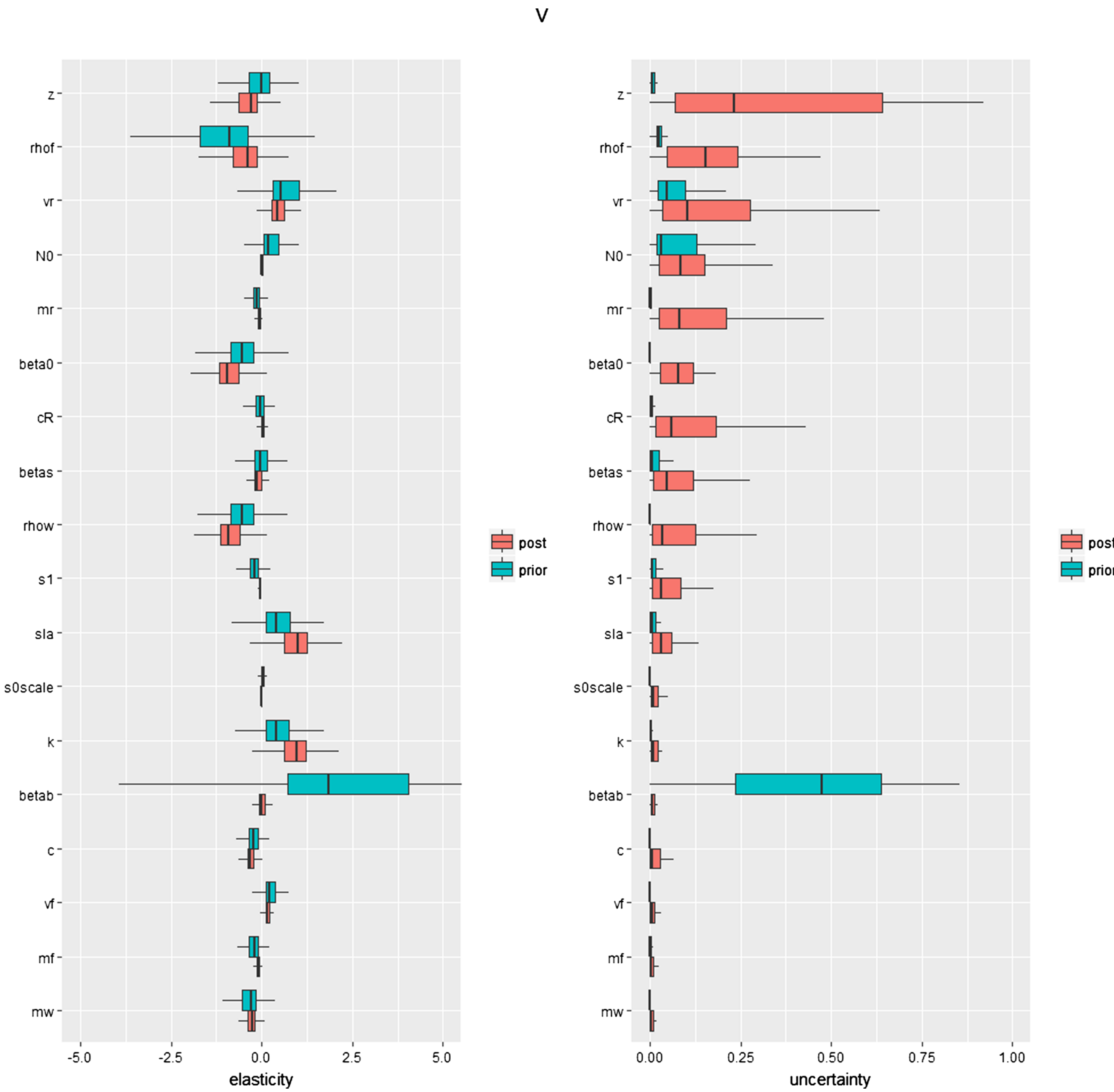


Fig. C6. Stand volume sensitivity and uncertainty analysis results for the PGE pine calibration.

SUA results for PGE spruce calibration

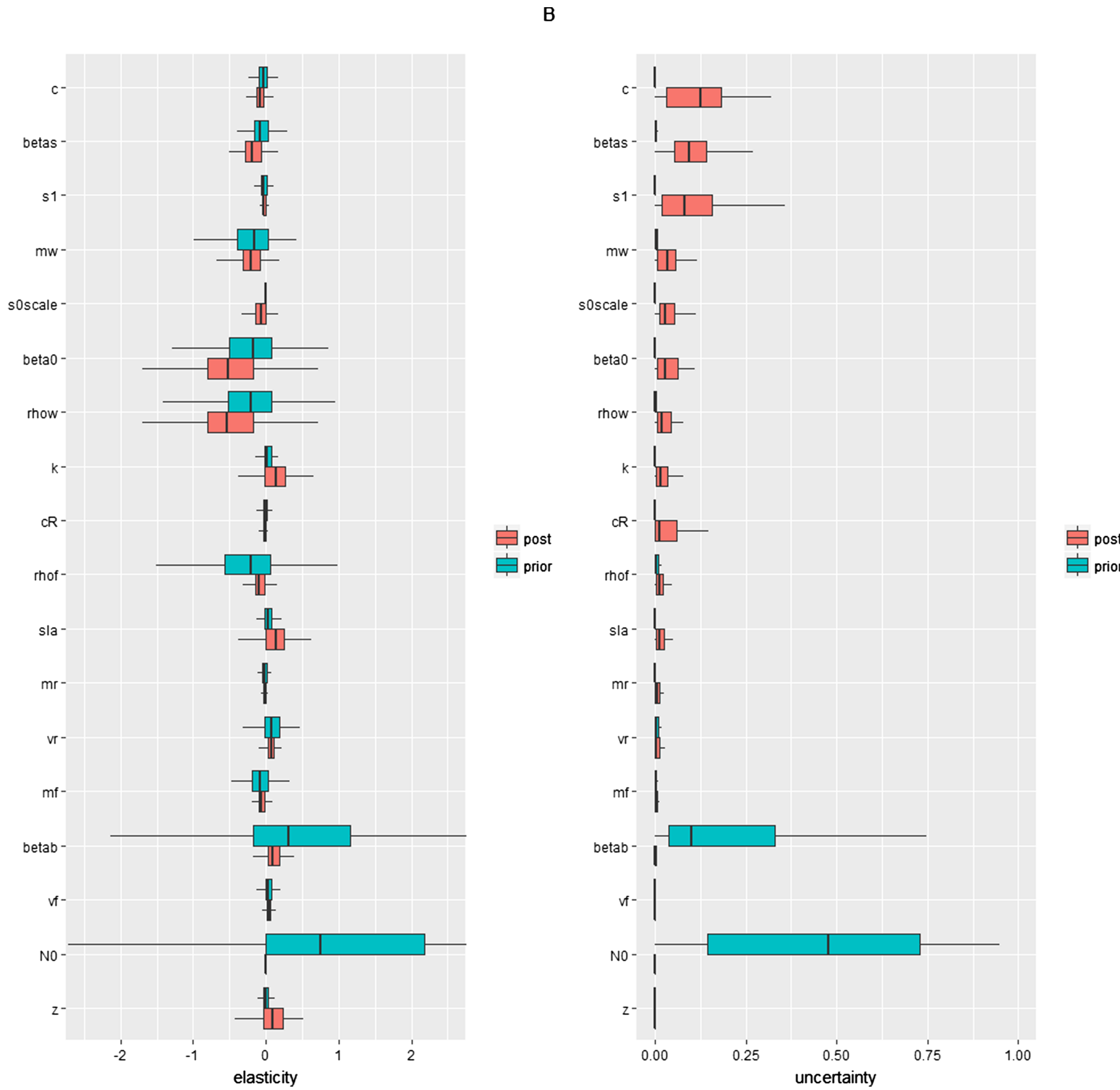


Fig. C7. Basal area sensitivity and uncertainty analysis results for the PGE spruce calibration.

D

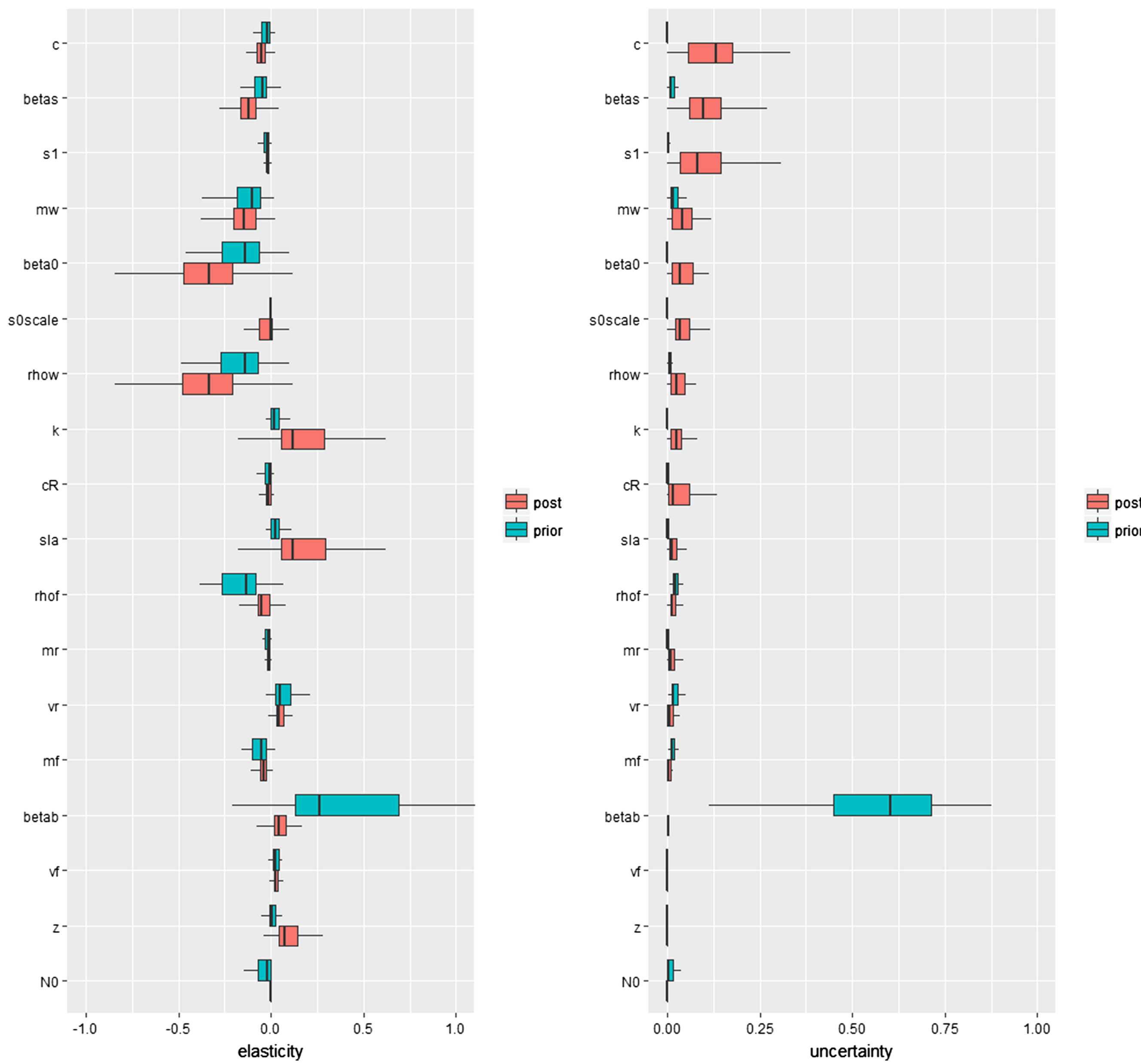


Fig. C8. Average stand diameter at breast height sensitivity and uncertainty analysis results for the PGE spruce calibration.

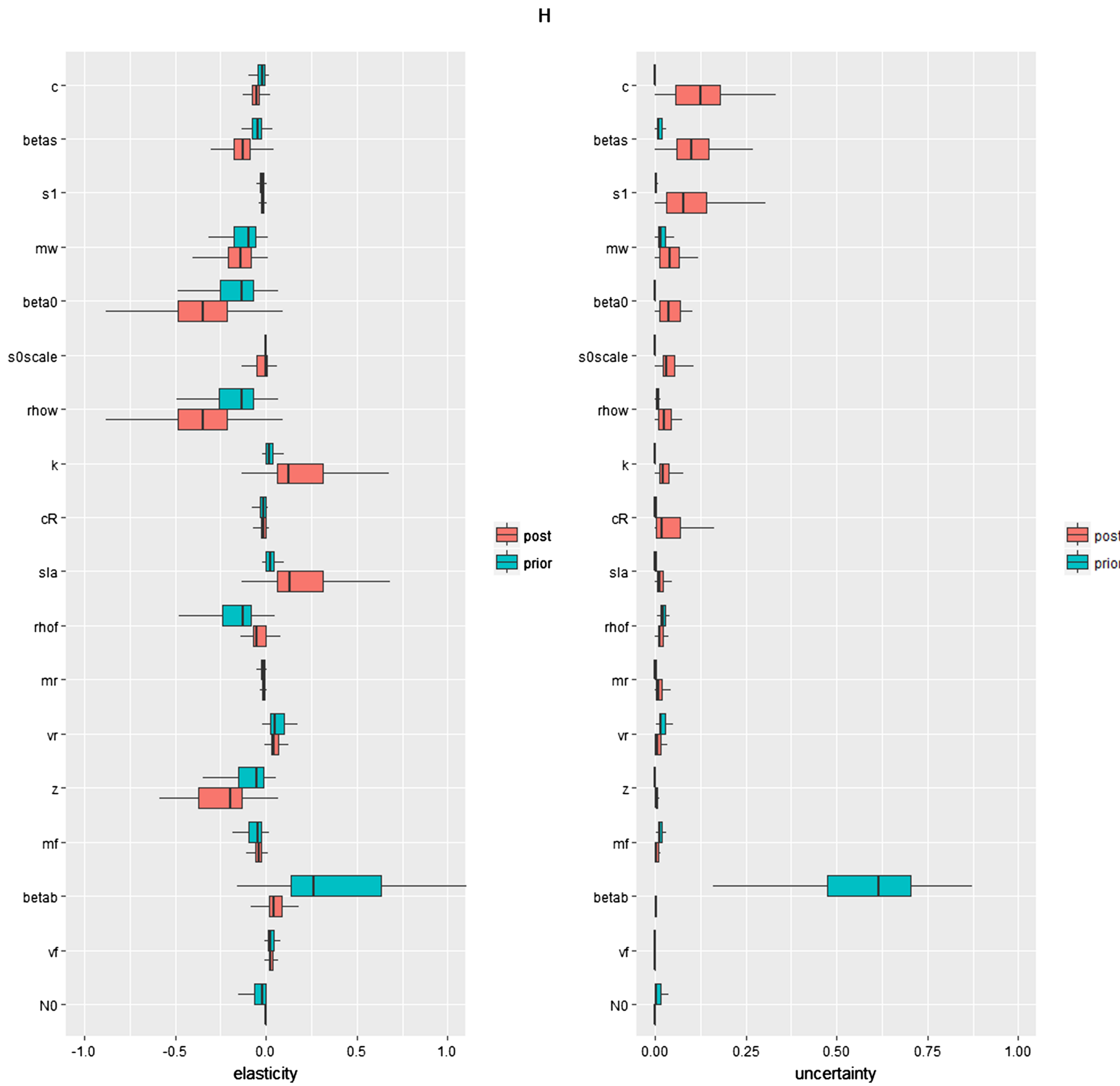


Fig. C9. Average stand height sensitivity and uncertainty analysis results for the PGE spruce calibration.

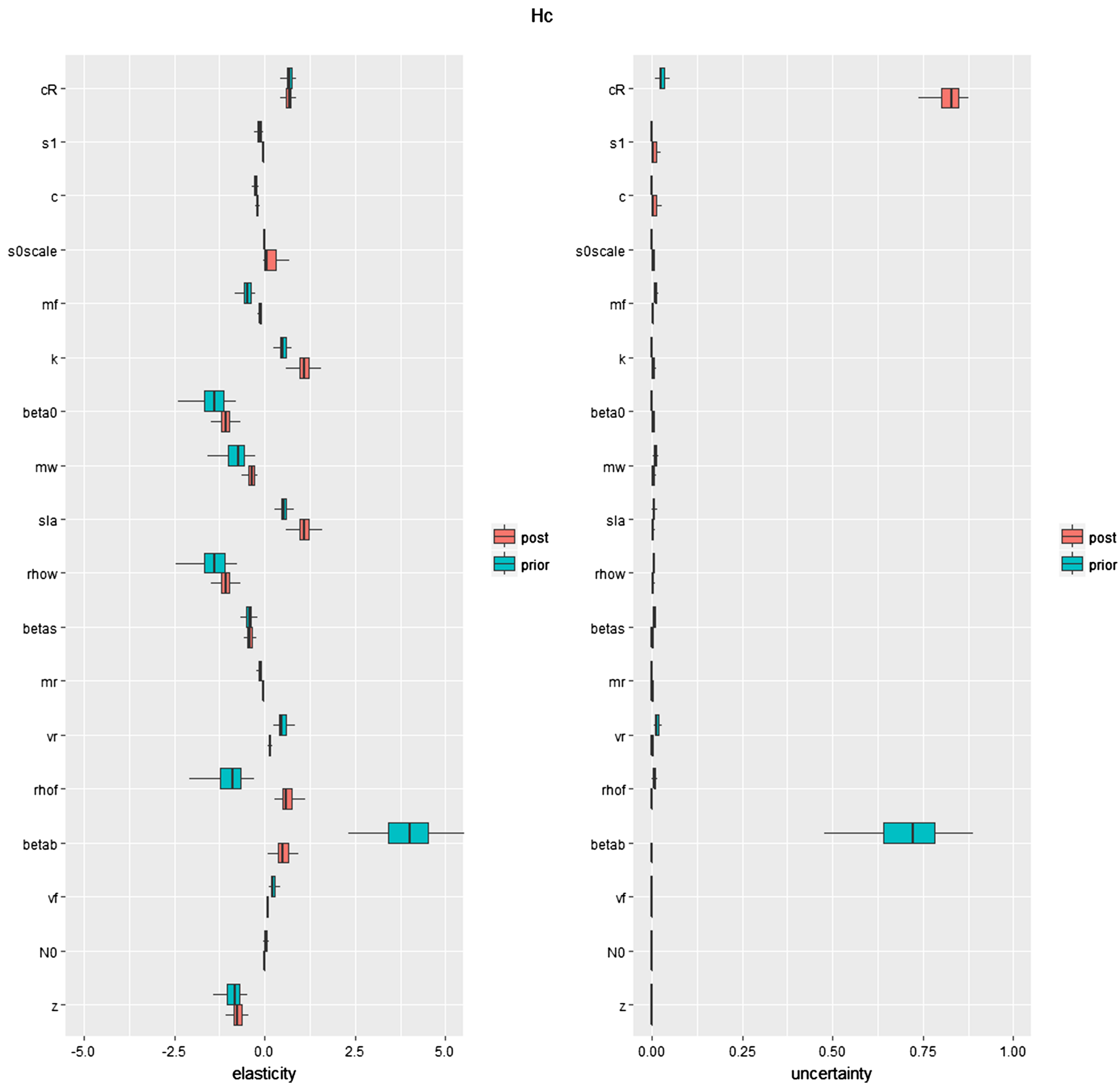


Fig. C10. Average stand height of crow base sensitivity and uncertainty analysis results for the PGE spruce calibration.

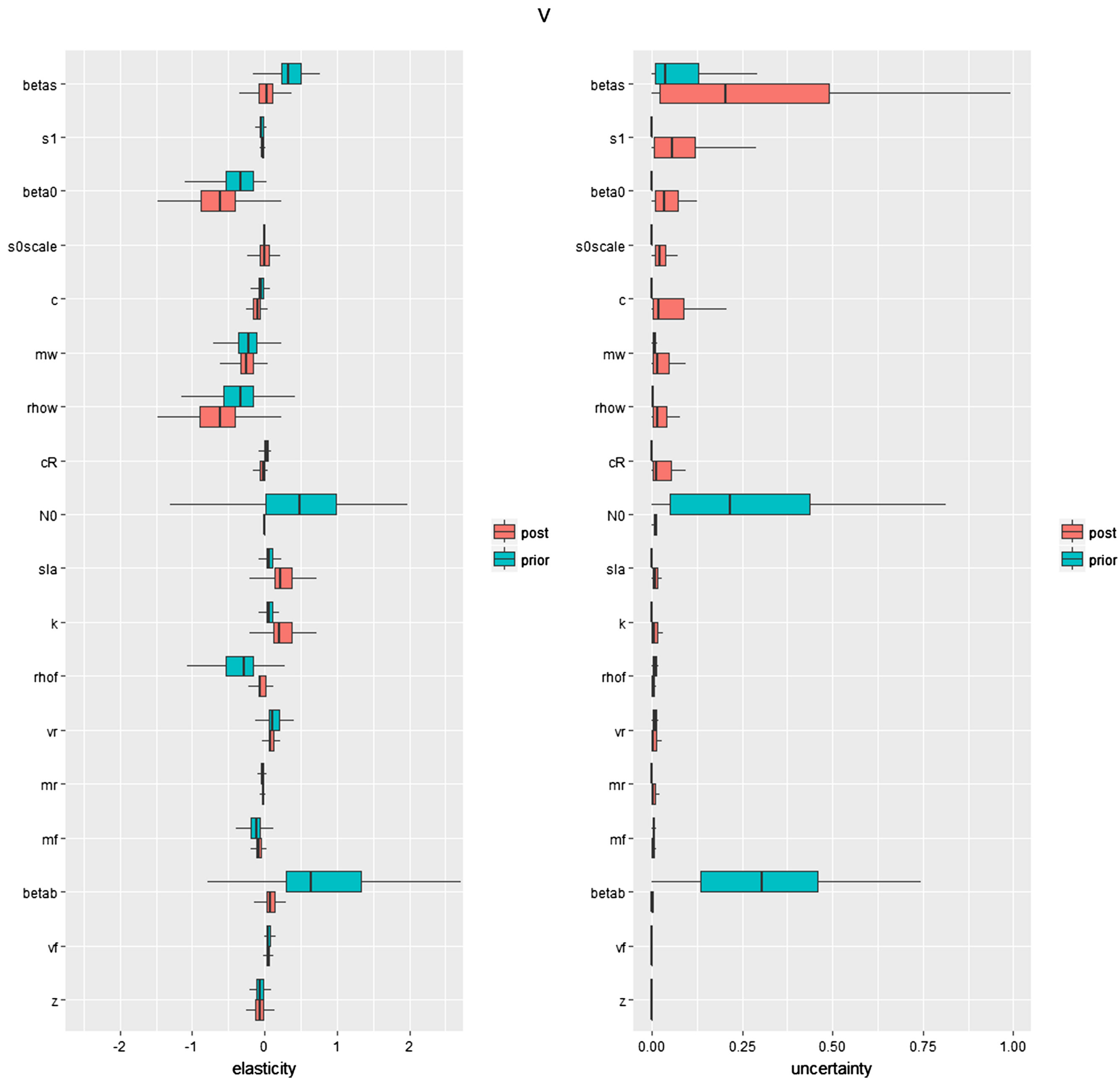


Fig. C11. Stand volume sensitivity and uncertainty analysis results for the PGE spruce calibration.

SUA results for NFI calibration

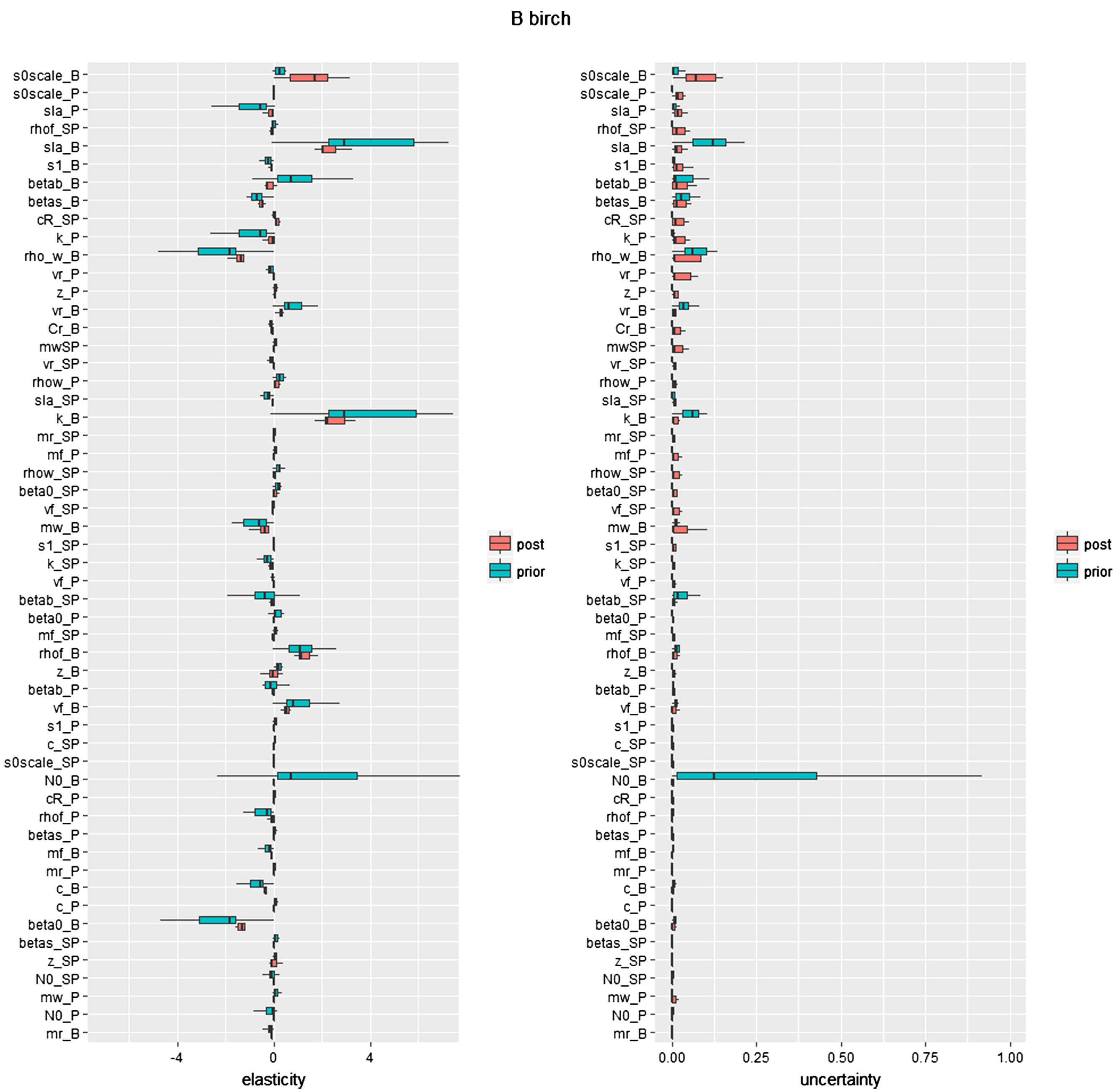


Fig. C12. Birch basal area sensitivity and uncertainty analysis results for the NFI calibration.

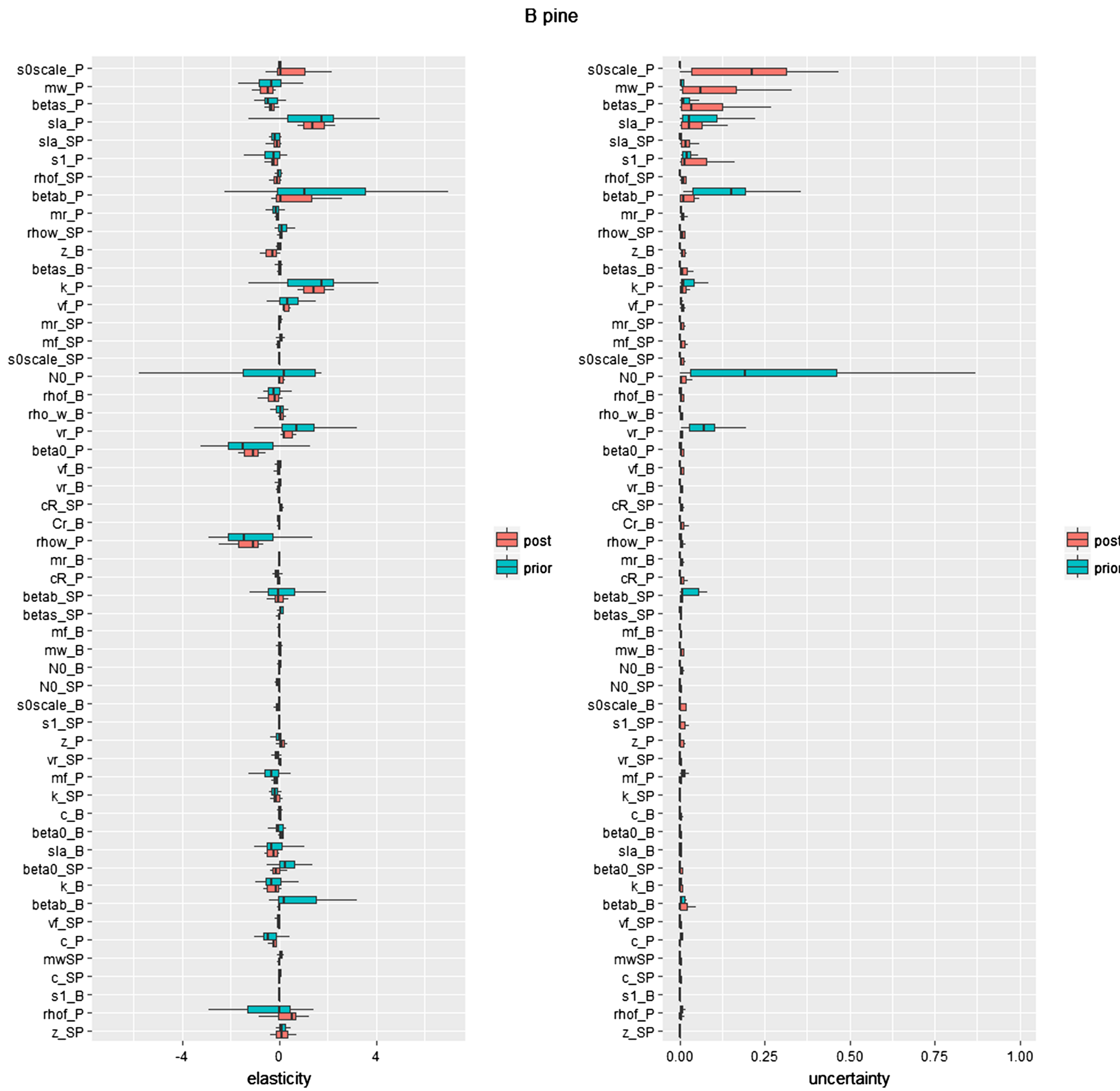


Fig. C13. Pine basal area sensitivity and uncertainty analysis results for the NFI calibration.

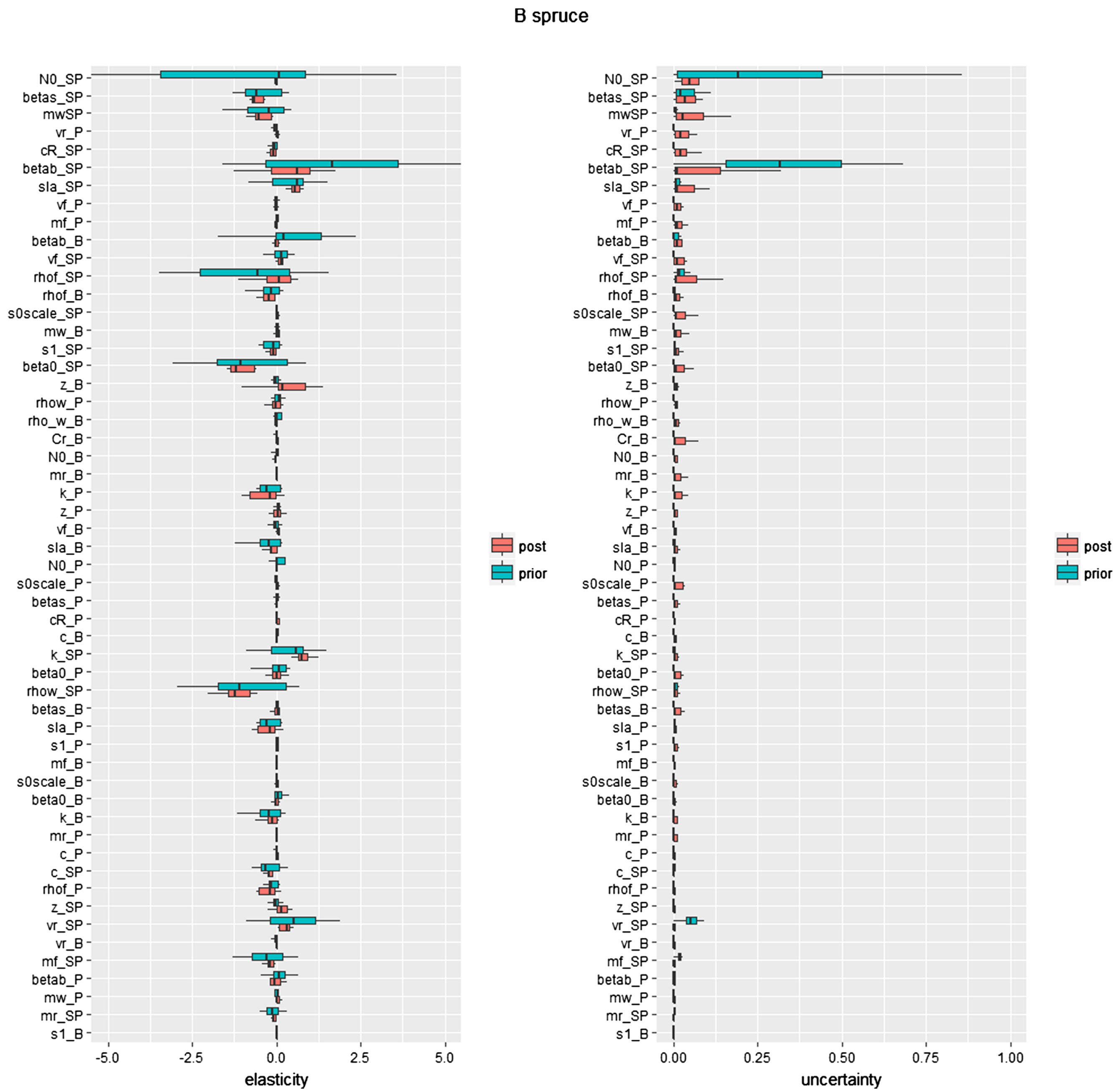


Fig. C14. Spruce basal area sensitivity and uncertainty analysis results for the NFI calibration.

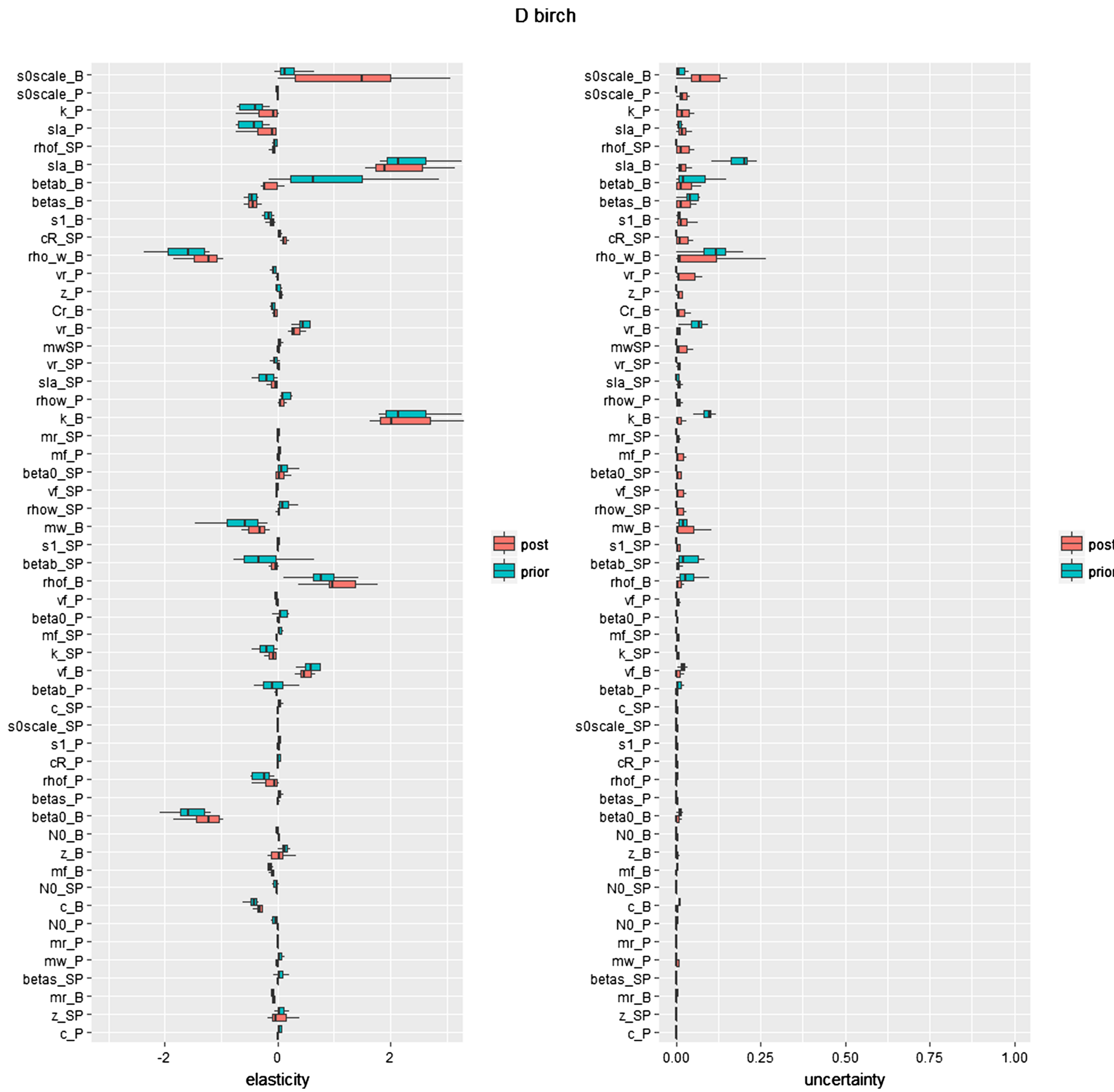


Fig. C15. Birch average stand diameter at breast height sensitivity and uncertainty analysis results for the NFI calibration.

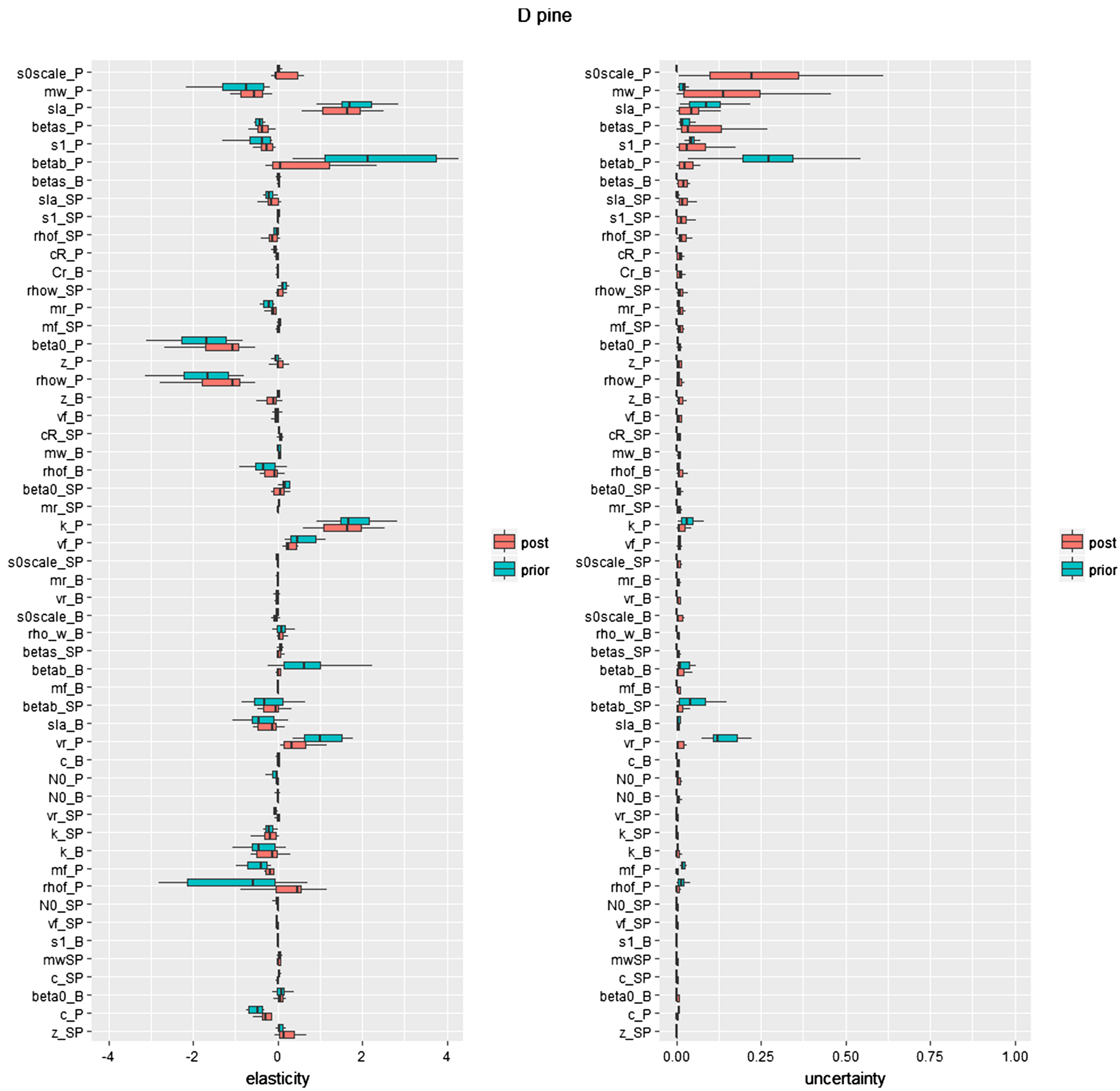


Fig. C16. Pine average stand diameter at breast height sensitivity and uncertainty analysis results for the NFI calibration.

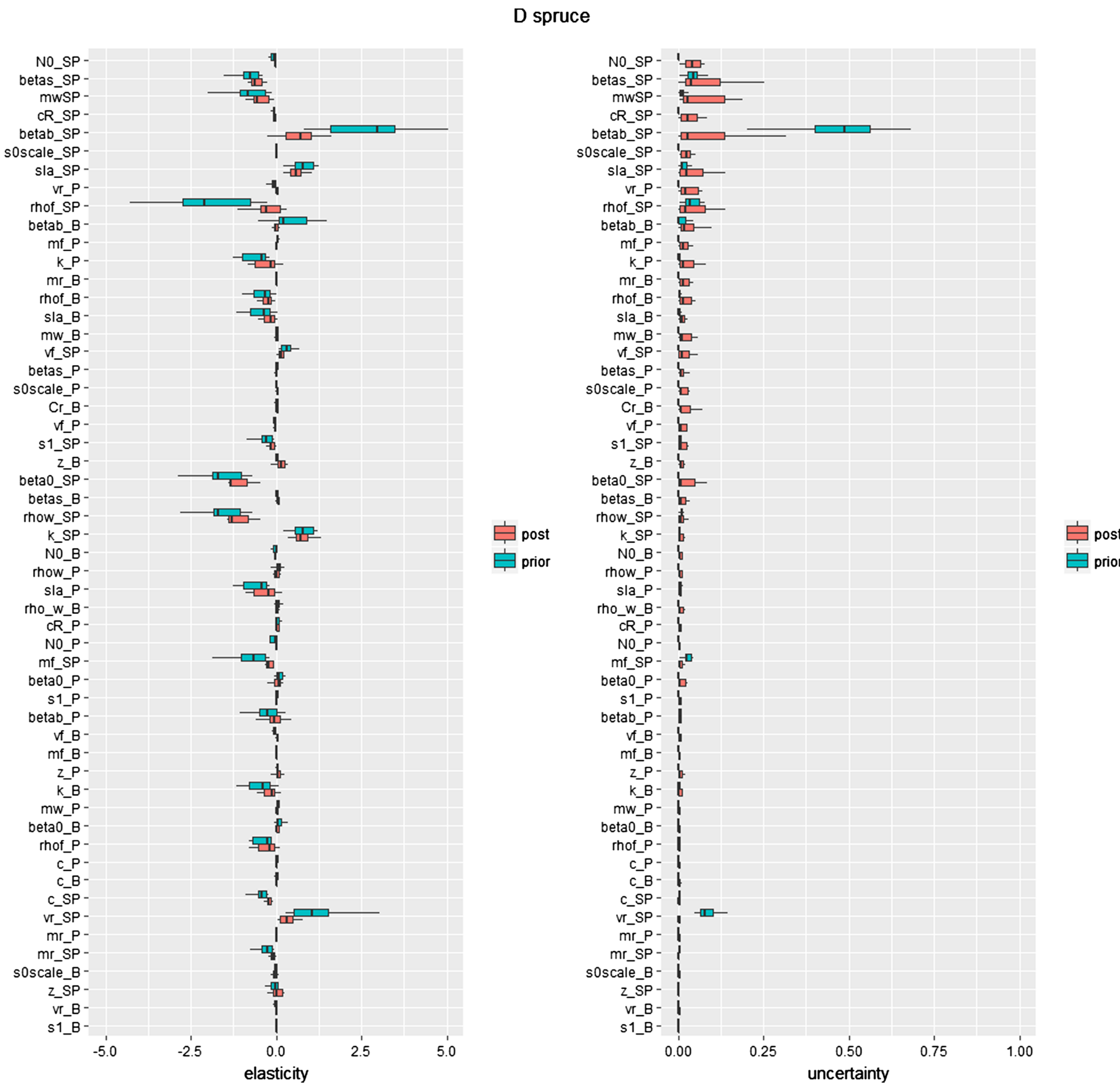


Fig. C17. Spruce average stand diameter at breast height sensitivity and uncertainty analysis results for the NFI calibration.

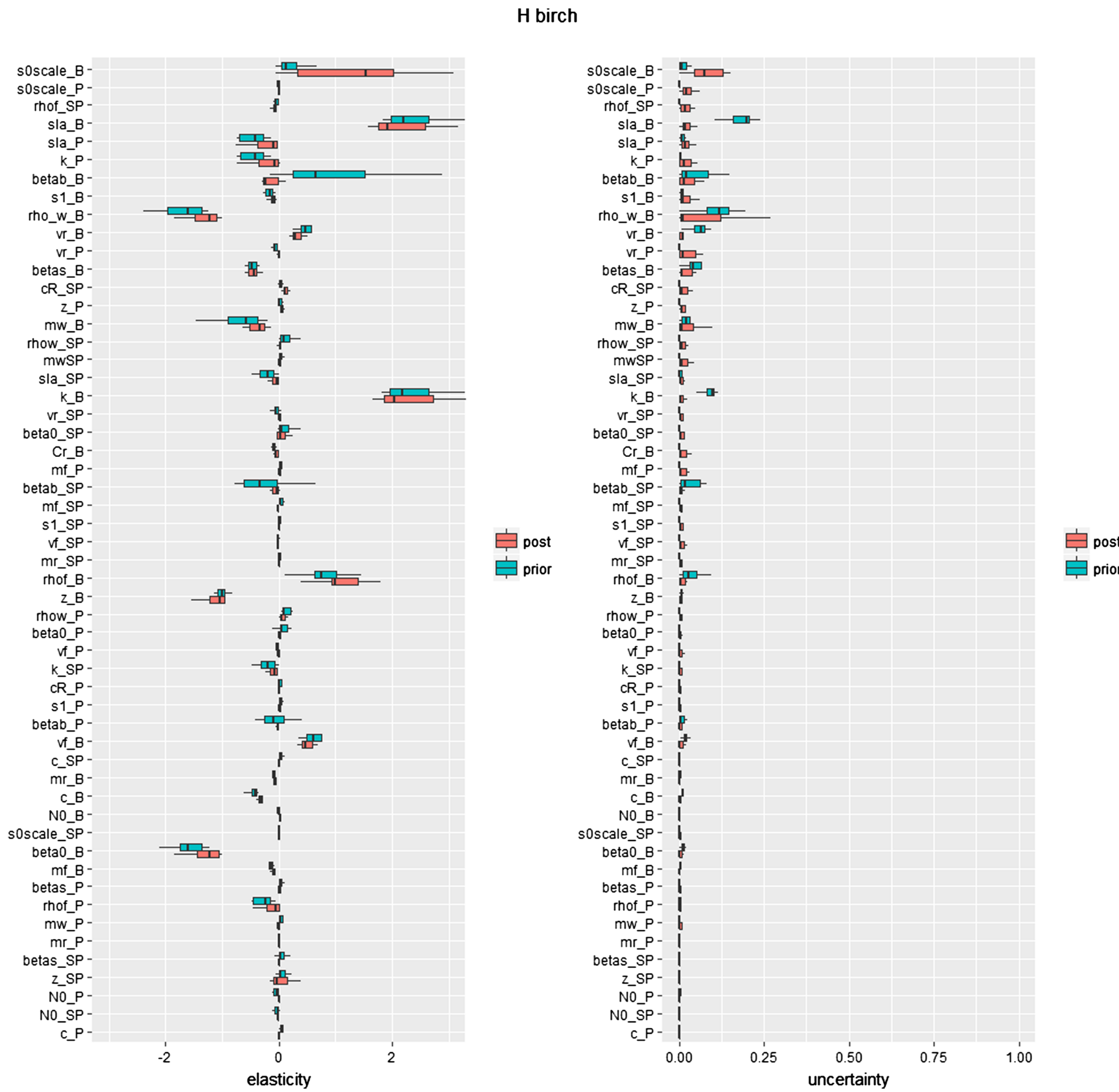


Fig. C18. Birch average stand height sensitivity and uncertainty analysis results for the NFI calibration.

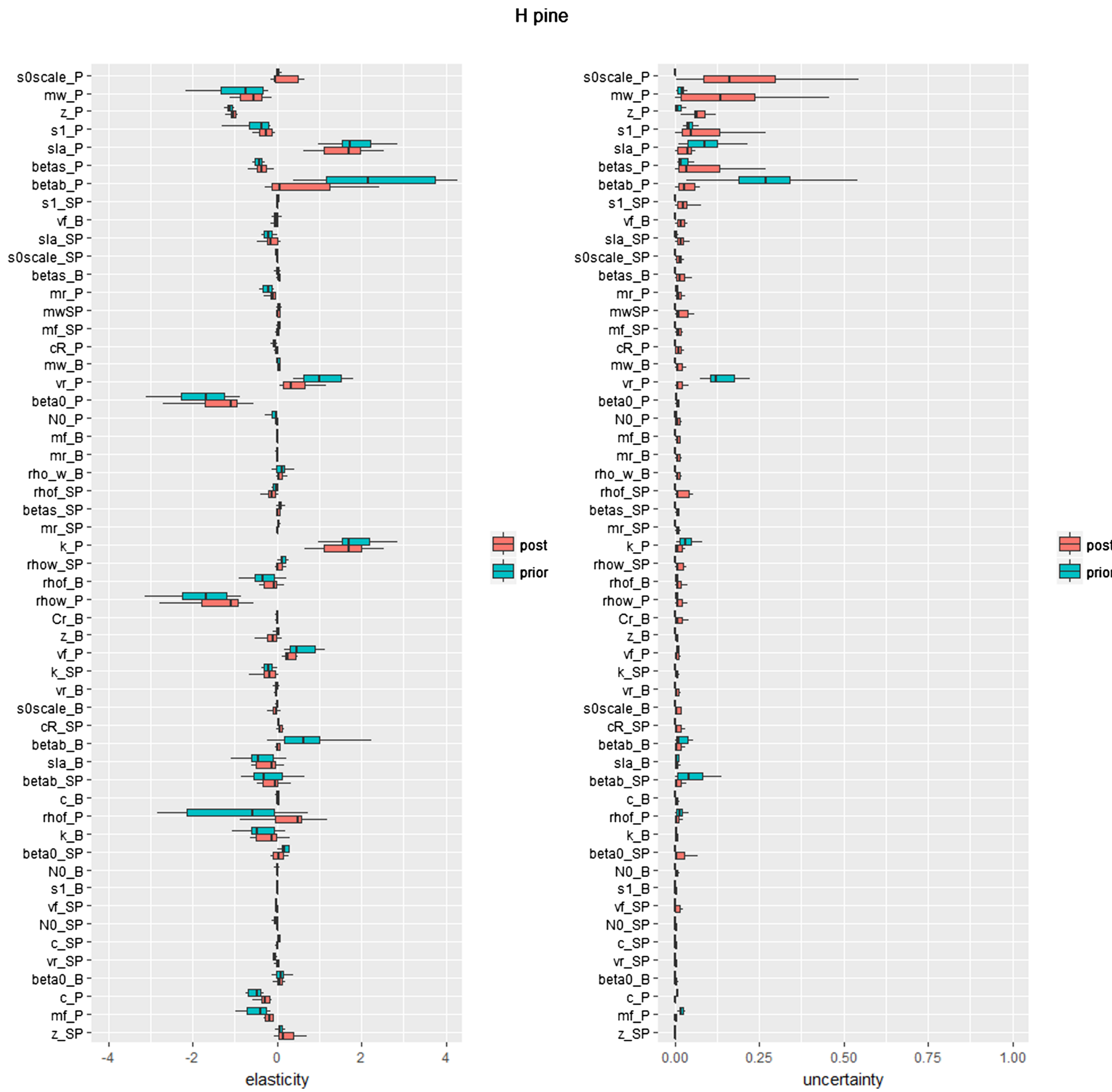


Fig. C19. Pine average stand height sensitivity and uncertainty analysis results for the NFI calibration.

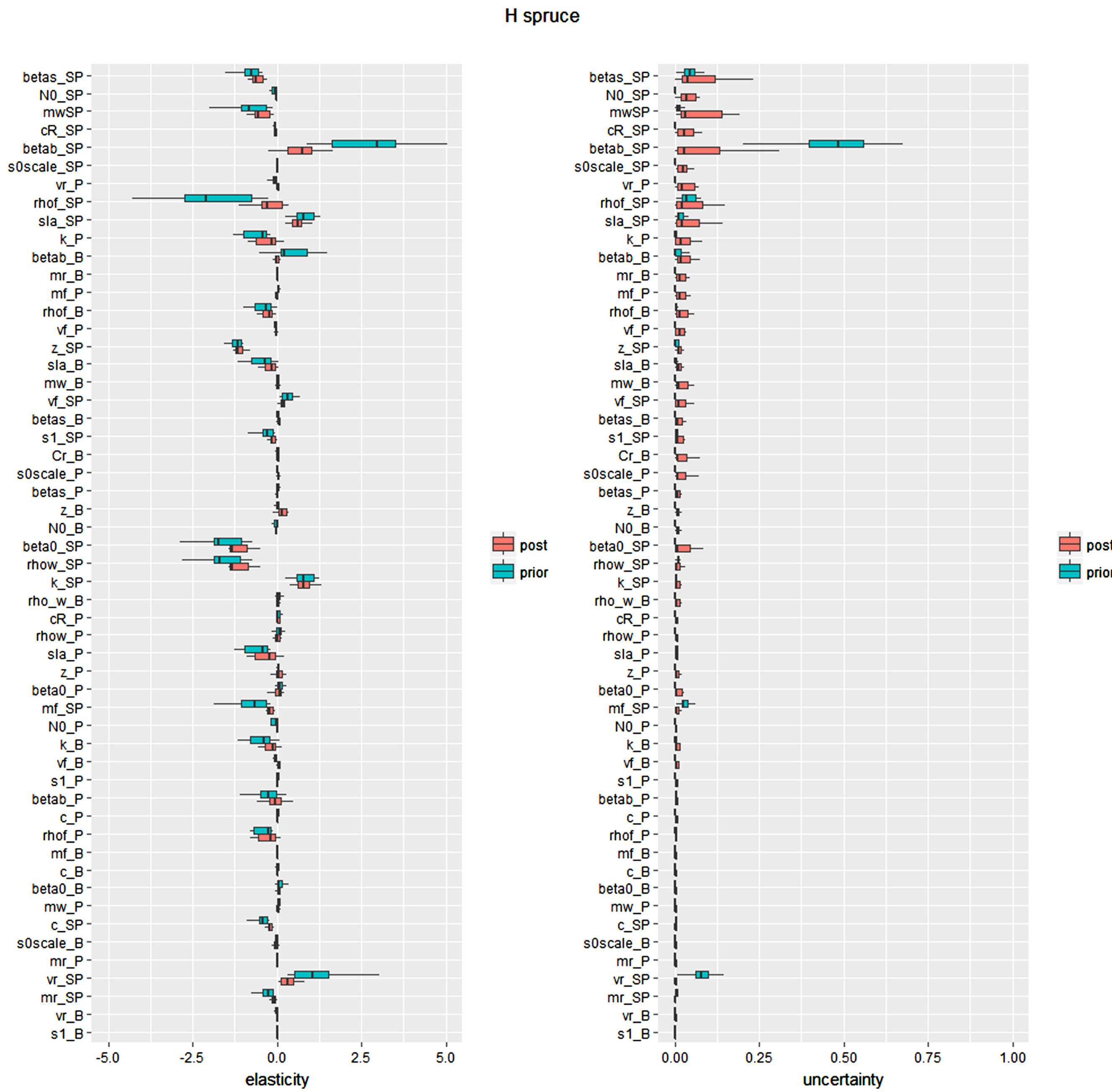


Fig. C20. Spruce average stand height sensitivity and uncertainty analysis results for the NFI calibration.

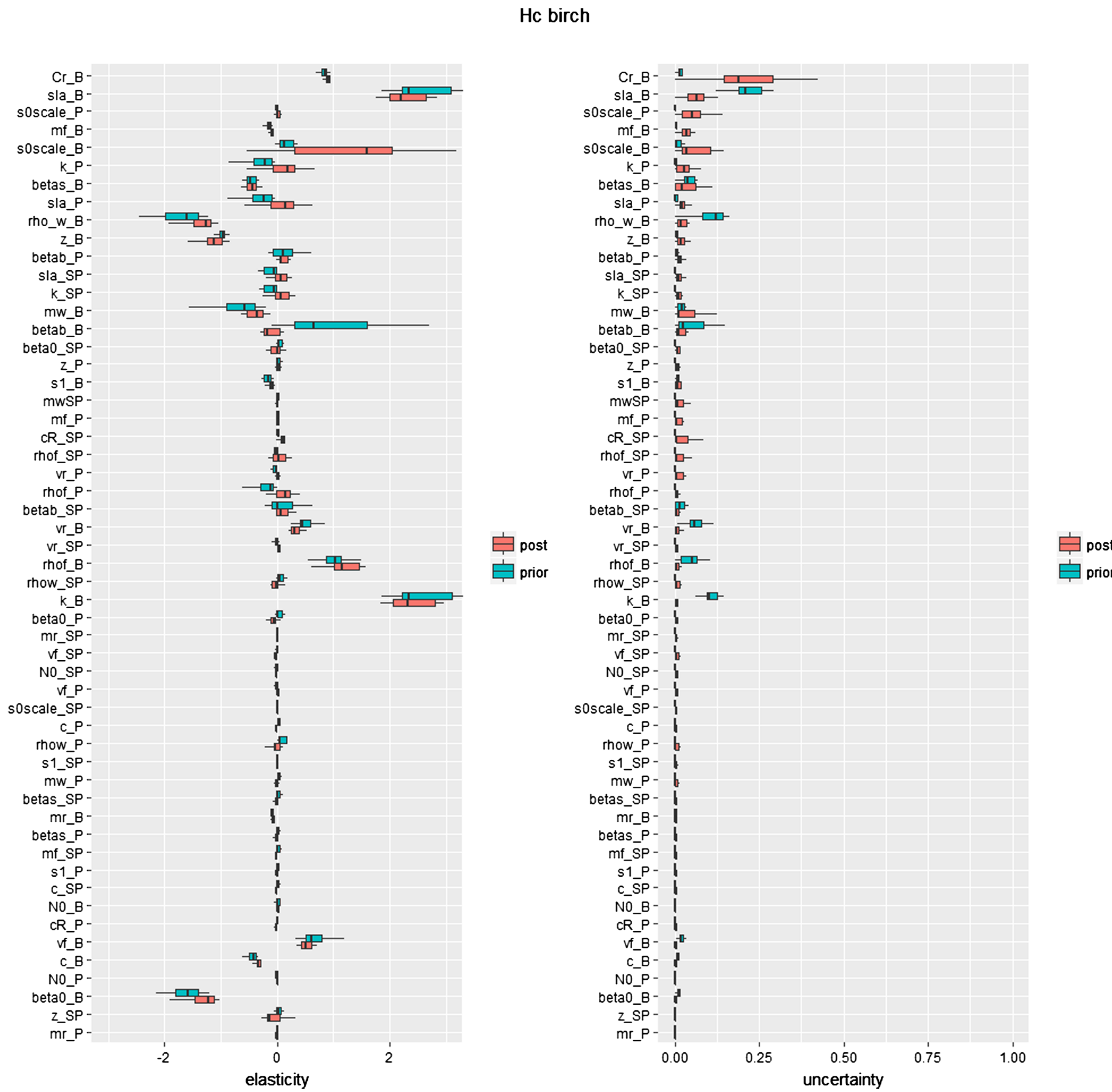


Fig. C21. Birch average stand height of the crown base sensitivity and uncertainty analysis results for the NFI calibration.

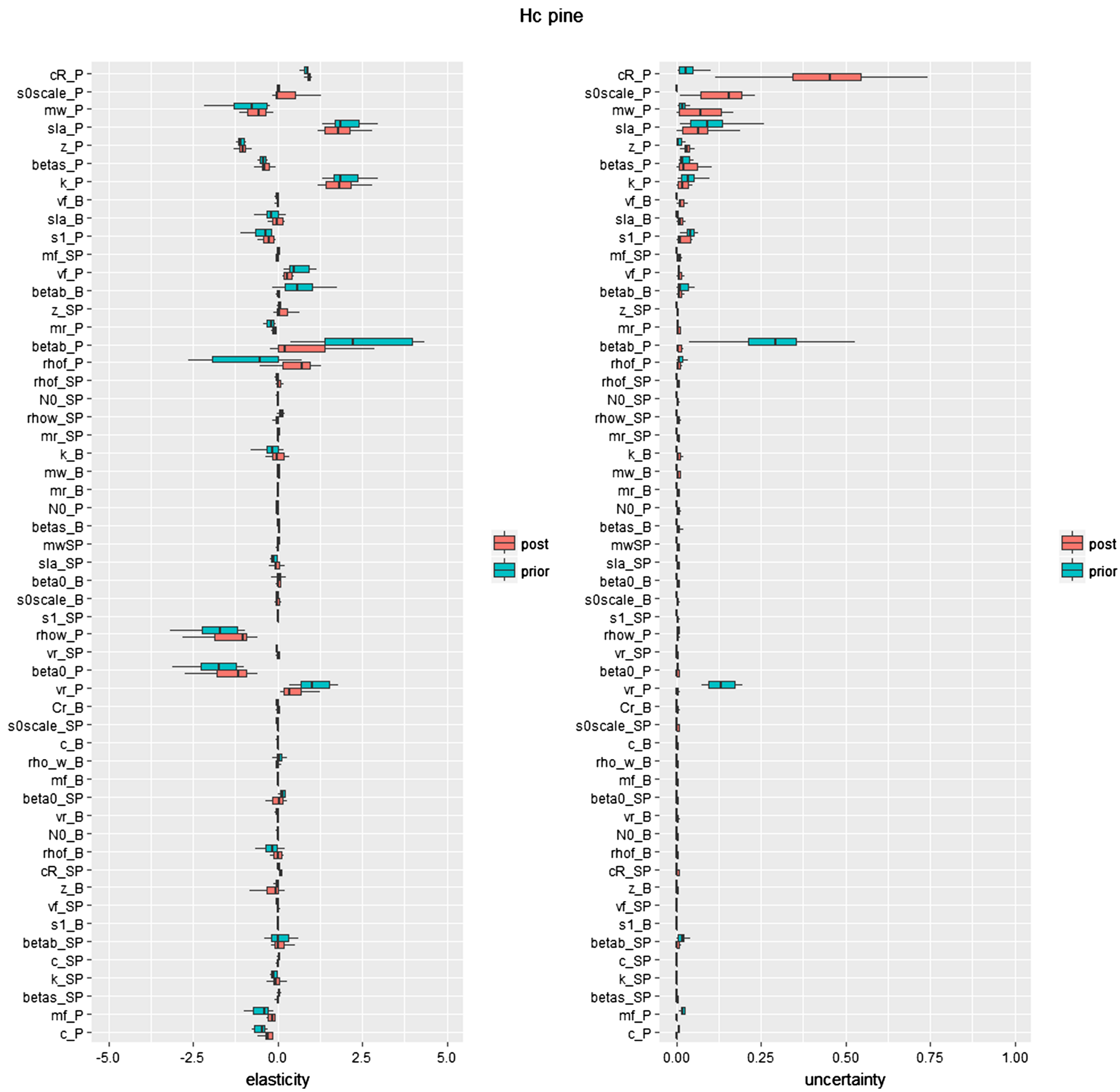


Fig. C22. Pine average stand height of the crown base sensitivity and uncertainty analysis results for the NFI calibration.

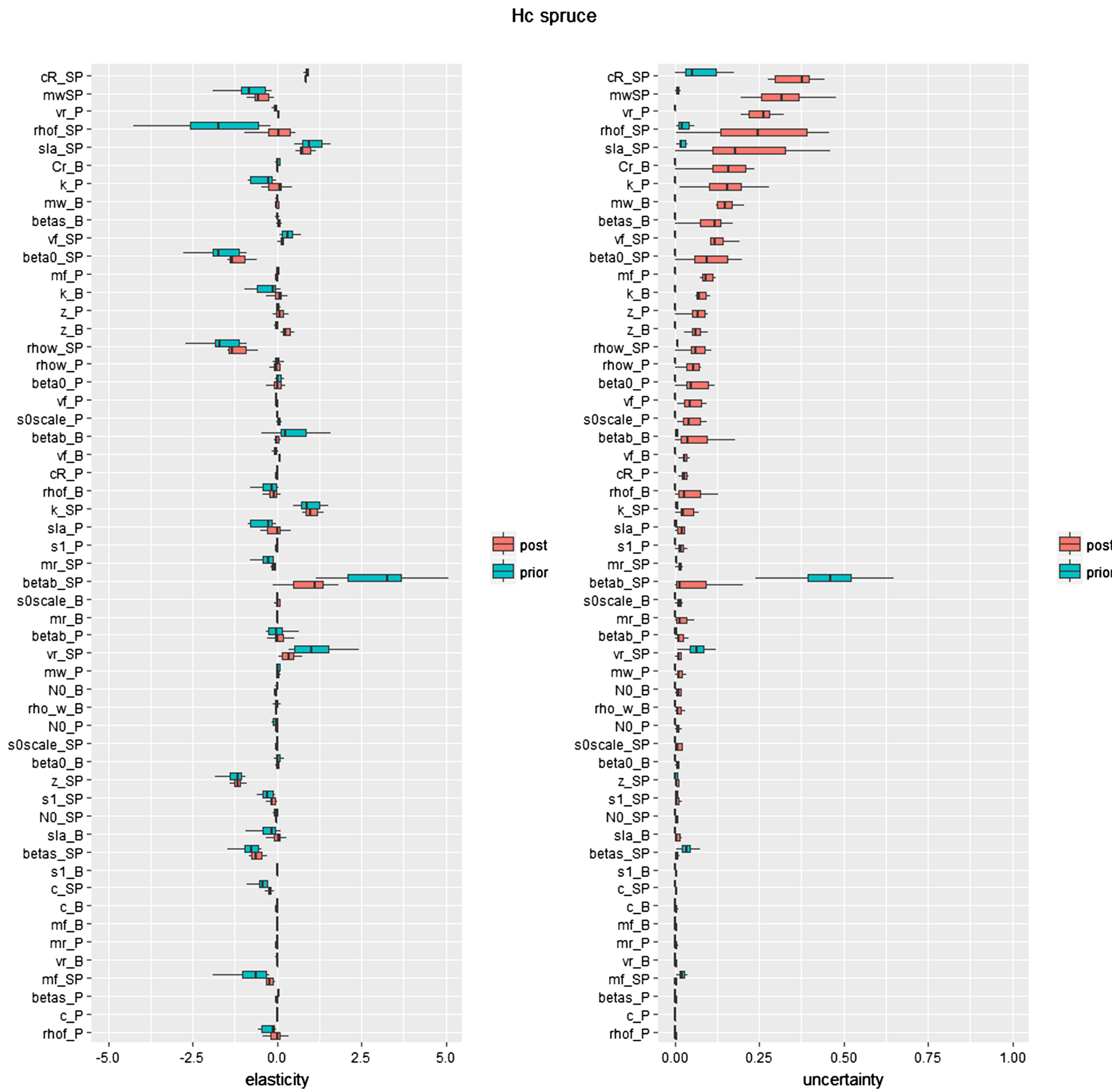


Fig. C23. Spruce average stand height of the crown base sensitivity and uncertainty analysis results for the NFI calibration.

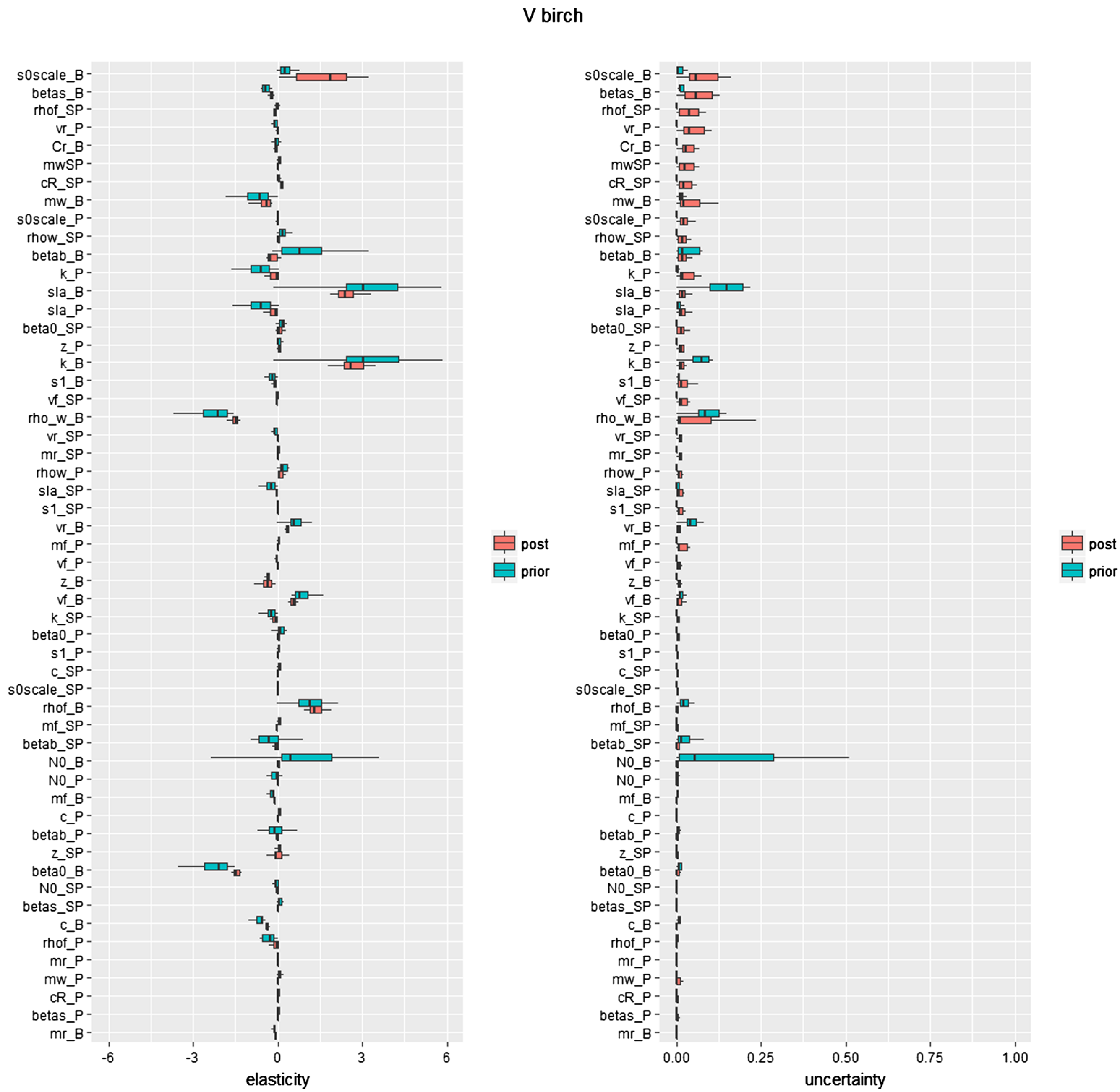


Fig. C24. Birch average stand volume sensitivity and uncertainty analysis results for the NFI calibration.

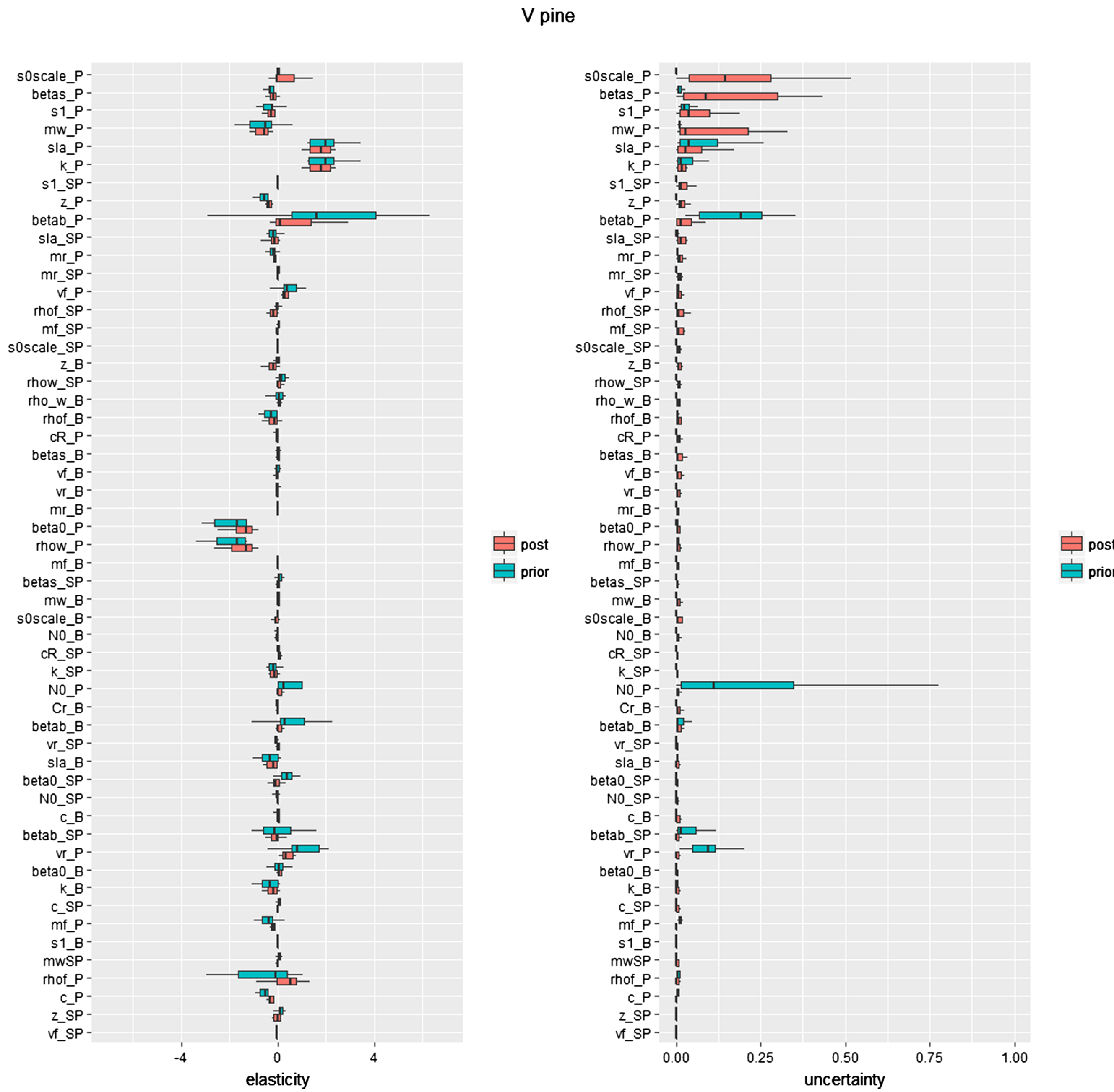


Fig. C25. Pine average stand volume sensitivity and uncertainty analysis results for the NFI calibration.

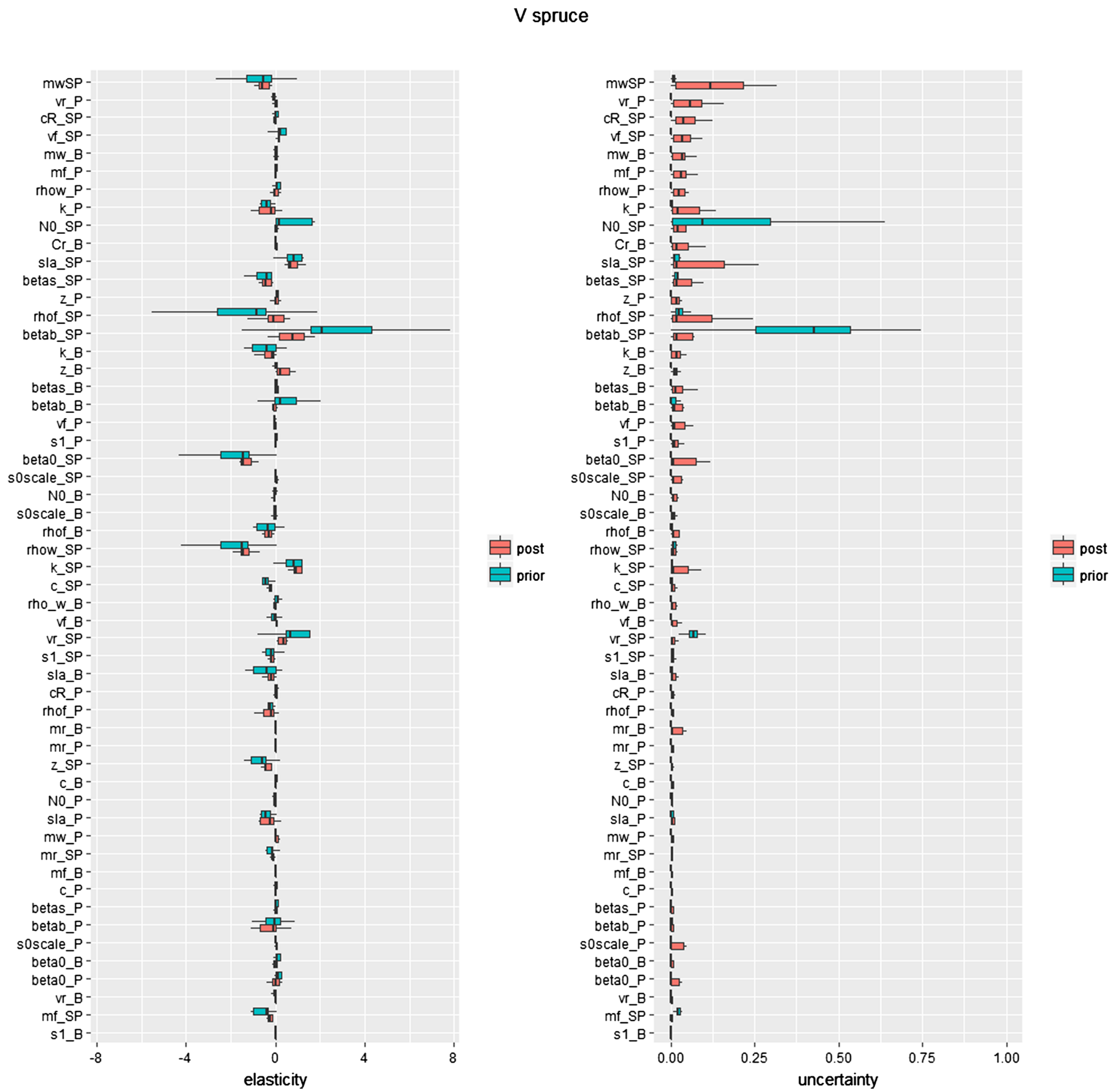


Fig. C26. Spruce average stand volume sensitivity and uncertainty analysis results for the NFI calibration.

Appendix D. Manual on PREBAS installation and examples

PREBAS have been coded in R and an R package (Rprebas) is available on GitHub. Here we provide guidelines on how to install the package and run examples on an R environment.

The Rprebas package can be downloaded here: https://github.com/checcomi/Rprebas; while the example code and files are at https://github.com/checcomi/Rprebas_examples.

Install the package

Install and load the package

```
library(devtools)
install_github("MikkoPeltoniemi/Rpreles@v1.0")
install_github("checcomi/Rprebas@v1.0")
```

```
library(Rprebas)
```

Loading required package: Rpreles

Loading required package: sm

Package 'sm', version 2.2-5.4: type help(sm) for summary information

Function prebas

The function that calls the model is prebas(). See the help for a description of the input arguments and the outputs.

```
?prebas
```

starting httpd help server ... done

Example 1

This first example uses the minimal inputs for the prebas function: the number of years of the simulations (nYears) and the weather inputs (PAR,TAir,VPD,Precip,CO2). In this example weather inputs are read from a .csv file. The stand it's initialized from plantation.

Read the weather inputs from an .csv file (https://github.com/checcomi/Rprebas_examples)

```
weather <- read.csv("inputs/weather.csv",header = T)
PAR = c(weather$PAR,weather$PAR,weather$PAR)
TAir = c(weather$TAir,weather$TAir,weather$TAir)
Precip = c(weather$Precip,weather$Precip,weather$Precip)
VPD = c(weather$VPD,weather$VPD,weather$VPD)
CO2 = c(weather$CO2,weather$CO2,weather$CO2)
DOY = c(weather$DOY,weather$DOY,weather$DOY)
```

Run the model

```
PREBASout <- prebas(nYears = 100, PAR=PAR,TAir=TAir,VPD=VPD,Precip=Precip,CO2=CO2)
```

Plot model outputs

```
# plot.prebas(PREBASout,layerNam = c("pine","spruce","birch"))
```

Example 2

In this example PREBAS inputs are read from .csv files are in the inputs folder at

"https://github.com/checcomi/Rprebas_examples".

Read the initial state of the stand (initVar), weather, site information (sietInfo), thinning and observed

data (obsData).

```
nYears = 100
siteInfo <- read.csv("inputs/siteInfo.csv",header = T)
thinning <- read.csv("inputs/Thinning.csv",header = T)
initVar <- read.csv("inputs/initVar.csv",header = T, row.names = 1)
obsData <- read.csv("inputs/obsData.csv",header = T)

weather <- read.csv("inputs/weather.csv",header = T)
PAR = c(weather$PAR,weather$PAR,weather$PAR)
TAir = c(weather$TAir,weather$TAir,weather$TAir)
Precip = c(weather$Precip,weather$Precip,weather$Precip)
VPD = c(weather$VPD,weather$VPD,weather$VPD)
CO2 = c(weather$CO2,weather$CO2,weather$CO2)
DOY = c(weather$DOY,weather$DOY,weather$DOY)
```

Run PREBAS

```
PREBASout <- prebas(nYears=nYears, pCROBAS = pCROB, pPRELES = pPREL,
            pAWEN = parsAWEN, siteInfo = siteInfo, thinning = thinning,
            PAR = PAR, TAir=TAir,VPD=VPD,Precip=Precip,CO2=CO2,
            initVar = as.matrix(initVar), defaultThin = 0., ClCut = 1.)
```

Plot model outputs

The function to plot prebas objects is plot.prebas. It is possible to provide and plot the observed data.

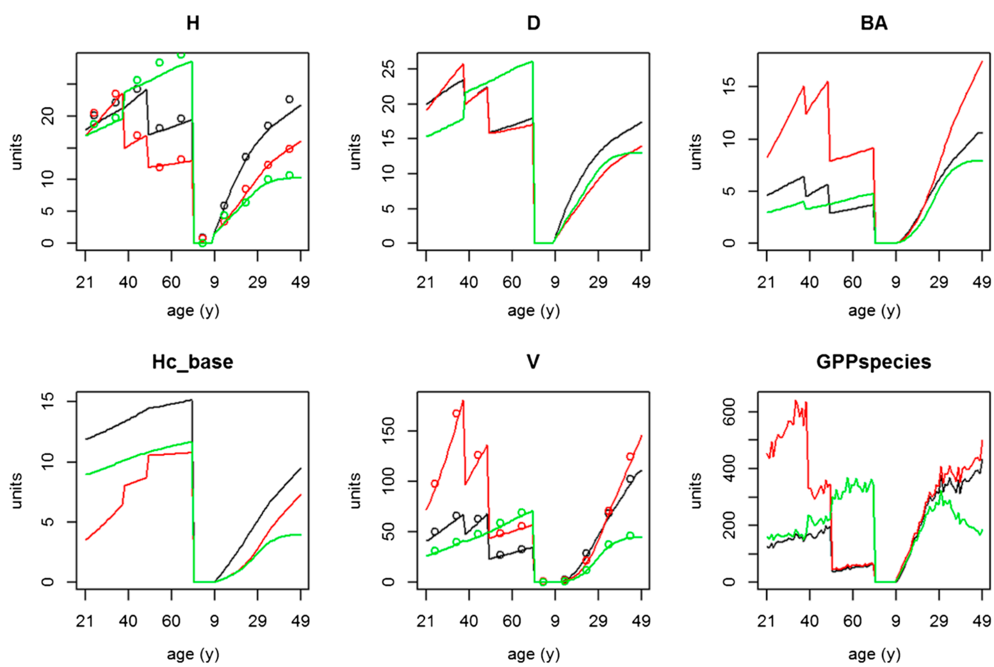
```
?plot.prebas
```

Select some variables to plot.

```
variableIDs=c(11:14,30,44);siteIDs=NA;leg=T;layerNam = c("pine","spruce","birch")
```

Plot PREBAS output and observed data.

```
plot.prebas(PREBASout,variableIDs,siteIDs,leg = F,layerNam =layerNam,obsData = obsData)
```



Appendix E. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.02.041.

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