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Modelling the potential carbon storage capacity of forests dominated by *Pinus sylvestris* across European ecological zones

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Abstract

Background

Forests are vital carbon sinks, and accurately assessing their maximum capacity to store carbon in absence of disturbances, further called as Potential Carbon Storage Capacity (PCSC), is essential for national greenhouse gas inventory (NGHGI) and effective forest

management. Estimating PCSC at large scales is challenging due to ecological variability, which can be addressed through a site-quality-dependent approach that accounts for local environmental and management conditions. Characterization of PCSC through a site quality gradient as a reference for comparing the current value of aboveground carbon (AGC), in both absolute and relative terms, could therefore enable comparable estimates across regions. This study presents a methodology for *Pinus sylvestris* L. forests across Europe, linking site quality to AGC stocks.

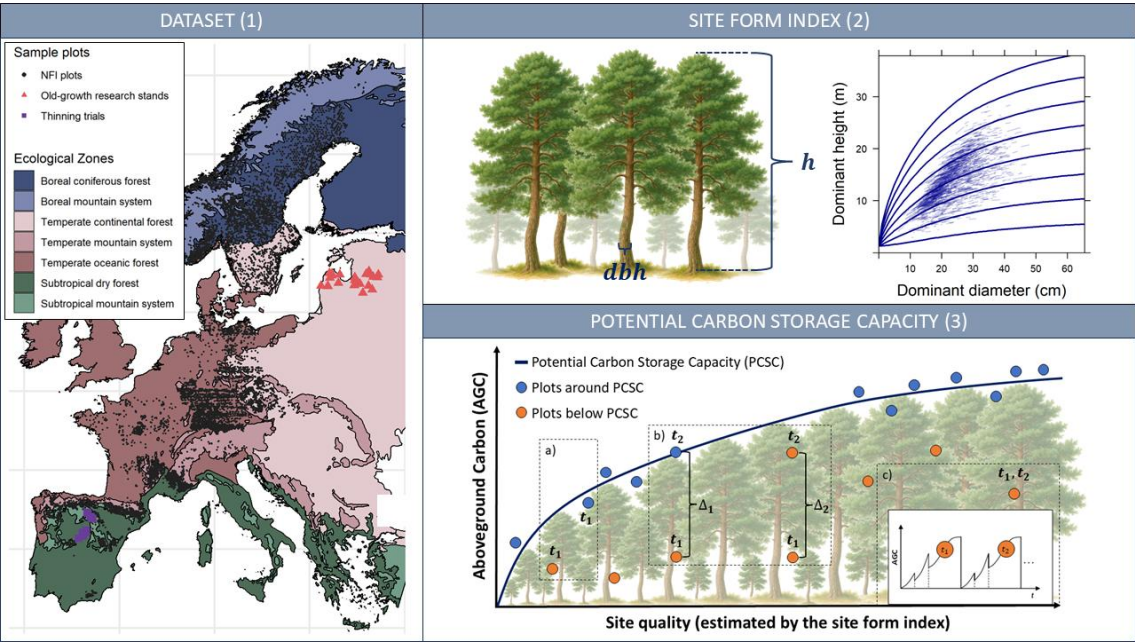
Results

Site quality was quantified using the site form (SF) index, which corresponds to the dominant height at a reference dominant diameter. PCSC was estimated by fitting *AGC – SF* curves at the FAO Global Ecological Zone level. Results show that SF effectively reflects productivity, with different PCSC reference levels for the different ecological zones. The PCSC fitted models were used as a baseline for case studies in Latvia and Spain, confirming their value as reference conditions for characterizing disturbance intensity in both old-growth and managed forests.

Conclusions

This study presents a methodology for estimating the PCSC of forests dominated by *Pinus sylvestris* L. across European ecological zones, with potential applicability to other forest types. The framework provides a baseline for PCSC estimation, supporting NGHGs and policies such as the Paris Agreement and EU Forest Strategy. In addition, the study findings also highlighted that using the PCSC for forest ecosystems is crucial to ensure consistent information regarding (i) evaluation of past carbon stock losses due to human and natural disturbances, (ii) prediction of potential carbon stock gains through changes in forest management, and (iii) assessment of mitigation benefits lost when forests are managed with carbon reserves below their maximum capacity.

Keywords: Biomass stock, Carbon carrying capacity, Carbon reservoirs.



Summary of the idea developed in this work. (1) Dataset constructed with data from the networks of plots of the national forest inventories (NFIs) in the Czech Republic, France, Germany, Italy, Norway, Slovakia, Spain, Sweden and Switzerland, as well as two sets of plots located in old-growth and managed *Pinus sylvestris* forests in Latvia and Spain, respectively. (2) Estimation of the site form (SF) index, defined as the dominant height (H_0) at a reference dominant diameter ($D_{0_{ref}}$). (3) Theoretical graphical representation of the aboveground carbon stock along a site-quality gradient, including plots close to PCSC (shown in blue) and plots below their PCSC (shown in orange). Cases are observed in which (a) only one AGC estimate is available, (b) the AGC increment (Δ_1) reaches the PCSC between two measurements of the same plot, and the AGC increment (Δ_2) does not reach the PCSC between two measurements of the same plot, and (c) the AGC remains the same (or decreases) between two consecutive measurements.

1. Background

According to major climate change mitigation policies and agreements (e.g. the Paris Agreement and the European Green Deal), reducing deforestation and forest degradation and improving forest management are recognized as key mitigation strategies (1,2). These actions contribute to reducing greenhouse gas (GHG) emissions by enhancing carbon dioxide (CO_2) sequestration and long-term storage (3). Forests already play a role as carbon sinks and reservoirs globally: they harbor approximately 870 gigatons of carbon (4), absorb nearly one third of human-induced CO_2 emissions (4,5) and influence climate by exchanging energy, water and chemical compounds with the atmosphere (6). In this context, aboveground biomass (AGB) -and by extension aboveground carbon (AGC)-

represents the most dynamic carbon pool in forests (7). AGB can be estimated using allometric equations, from variables commonly surveyed in forest inventories (8–12). These estimates can be used with carbon content values per tree fraction to estimate AGC (4,5). Land Use, Land-Use Change, and Forestry (LULUCF) data are reported in the National Greenhouse Gas Inventories (NGHGs) submitted by countries under the United Nations Framework Convention on Climate Change (UNFCCC). According to CO₂ flux data, global CO₂ sequestration has largely been driven by carbon sinks in forest land (13). In the period 2000–2020, these sinks accounted for approximately -6.4 Gt CO₂ year⁻¹ globally, primarily within the forest land carbon pool, which includes harvested wood products (13). Notably, forests that have existed for 20 years or more constitute most of this forest carbon sink, contributing about 87% globally (13). Therefore, monitoring and tracking the potential of forests to mitigate climate change through carbon sequestration requires greater transparency and also improved cooperation between scientists and policymakers to increase confidence in and harmonization of national statistical reporting across countries (14,15).

In carbon accounting, reference levels or baselines are needed to assess emissions reductions and removals by comparing observed or projected carbon stock changes against a defined benchmark, including past, existing, or future changes in carbon stocks (16). By one hand, the carbon carrying capacity (CCC), defined as the maximum amount of carbon that can be stored in a forest ecosystem under prevailing environmental conditions and natural disturbance regimes (17), has been considered as an ecologically based reference level in previous works (18). However, because this definition relies on primary forests, it may lead to unrealistic outcomes, such as areas where intact forests exhibit lower carbon storage potential than managed forests (19). This pattern may arise because intact and managed forests are not fully comparable. For instance, forest management may have preferentially targeted the most fertile sites, increased the maximum attainable biomass

through the establishment of highly productive monospecific stands, or e.g. reduced natural disturbance regimes through active or passive fire suppression (19). In addition, the use of CCC as a benchmark remains controversial. Some researchers claim that CCC is reached in primary and old-growth forests in the absence of major disturbances (20–22). However, others have found that mature forests with lower degrees of naturalness can also reach CCC levels (23–29). Conversely, other studies show that forest reserves -even where management has been abandoned for decades- do not necessarily reach their CCC (30). These divergent findings underscore the complexity of defining CCC rigorously. Therefore, the potential carbon storage capacity (PCSC), defined as the theoretical upper limit of carbon an ecosystem like a forest can hold under optimal and in the absence of disturbances, both natural and anthropic (31), may help overcome these issues.

The PCSC is known to depend on site quality (32), where site quality refers to the capacity of a forest area to produce wood or biomass with a given genotype and a specified management regime (33). Characterization of PCSC through a site quality gradient as a reference for comparing the current value of AGC in relative terms, could therefore enable comparable estimates across regions. This approach may also help estimate the potential for additional carbon storage under different forest conditions, including unmanaged forests and forests managed under alternative schedules (19). Moreover, it has the advantage of requiring only a single measurement because it focuses on carbon stock. By contrast, the biomass stock-change approach used in NGHGs (34) requires several measurements because changes in biomass stocks are assessed by comparing biomass at a given time with a reference value determined in the past.

From a methodological perspective, site quality can be estimated by means of the site form (SF) index, defined as the dominant height (H_0) at a reference dominant diameter ($D_{0_{ref}}$) (35), which performs similarly to the well-known site index (H_0 at a reference age) in comparable situations (36). The SF index has the advantage of being a reliable, age-

independent site quality index that is suitable for National Forest Inventory (NFI) data (37,38), as stand age is often not available or is only very roughly estimated in NFIs (39). This property of SF makes it appropriate for most forest types, including plantations, uneven-aged/size stands, multispecies forests, continuous cover forestry (CCF) and unmanaged forests. The idea of estimating the PCSC in relation to site quality has been evaluated by Molina-Valero et al. (2021) for several major forest species in Spain. In these studies, data from the Spanish NFI and plots under conditions of maximum AGB capacity were used to validate the methodology, considering only living aboveground biomass. Nevertheless, the methodology requires some fine-tuning, and its suitability must be demonstrated at larger scales, such as global ecological zones (GEZ) (40).

By using an approach based on site-quality-dependent PCSC, we can aim to answer the following questions: (i) How can the AGC be estimated relative to the PCSC when only one measurement is available? (Fig. 1a); (ii) If the AGC has increased between two measurements, will this trend continue or has the PCSC already been reached? (Fig. 1b); (iii) If the AGC remains constant between two consecutive measurements (e.g. if those measurements occur at the same time of the forest management schedule), what does this mean in terms of reaching the PCSC? (Fig. 1c); And finally, (iv) how can we compare the AGC in forests with different site qualities? Defining a reference PCSC baseline could help to overcome these challenges, complementing the biomass stock-change approach used in NGHGs.

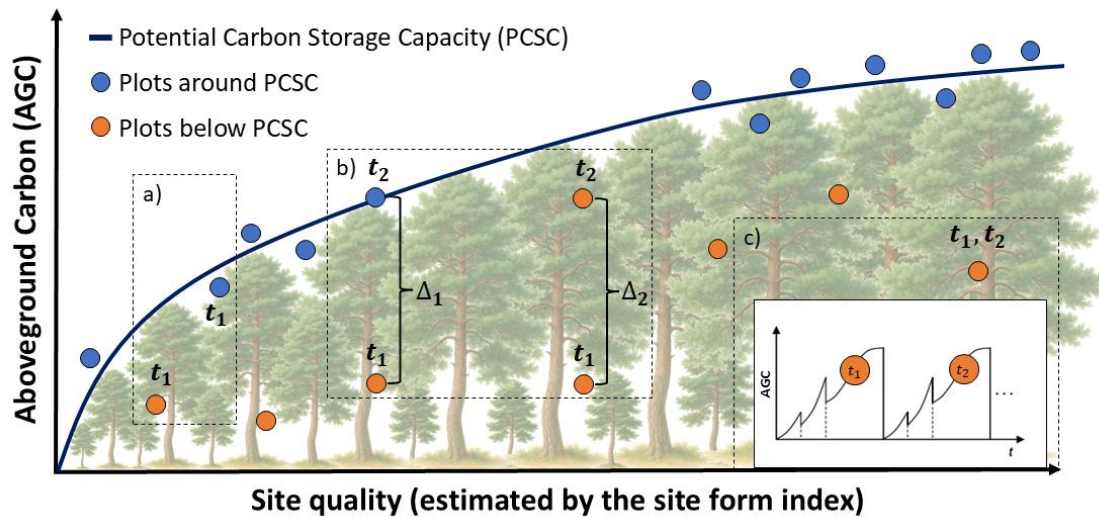


Fig. 1. Theoretical graphical representation of the aboveground carbon stock in a hypothetical forest type as a site quality gradient, including plots close to PCSC (shown in blue) and plots further from their PCSC (shown in orange). Cases are observed in which (a) only one AGC estimate is available, (b) the AGC increment (Δ_1) reaches the PCSC between two measurements of the same plot, and the AGC increment (Δ_2) does not reach the PCSC between two measurements of the same plot, and (c) the AGC remains the same (or decreases) between two consecutive measurements.

This study aimed to introduce and evaluate a framework to estimate PCSC in relation to site quality, while also proposing a baseline for estimating carbon gains and losses in NGHGs. We further compared the estimated PCSC with two contrasting case study scenarios: old-growth forests and thinning trials established in even-aged managed forests. In this study, we focused on *Pinus sylvestris* L., as this is the most widespread species in Europe and therefore has a high potential for carbon storage (41). Moreover, *P. sylvestris* stands represent a substantial source of income; use of the species has been increasing over the years, and it is distributed over six environmental zones and includes units designated for genetic conservation management (42). In addition to NFI data, we analyzed a network of plots located in old-growth forest stands in Latvia and another in managed forests in Spain as comparative case studies. We developed a model to predict SF for *P. sylvestris* in Europe and fitted a curve to the $AGC \sim SF$ scatter plot, thus defining the PCSC of the AGC through SF values at the level of GEZ in Europe.

2. Methods

2.1. Study area

The study area covers a broad latitudinal gradient (approximately 37° N - 70° N), including all global ecological zones (GEZ) where *Pinus sylvestris* L. occurs (Fig. 2). The GEZ framework, established by the FAO (40), uses a hierarchical approach to stratify the Earth into zones. It first divides the planet into climatic domains, i.e. tropical, subtropical, temperate, boreal and polar, and further refines these domains into GEZs based on regional variations in climate, vegetation composition and structural characteristics. The following GEZs were included in the study: coniferous forest, mountain system and tundra woodland in the boreal domain; dry forest and mountain system in the subtropical domain; and continental forest, mountain system and oceanic forest in the temperate domain. The forest inventory dataset was constructed with data from the networks of permanent plots of the national forest inventories (NFIs) in the Czech Republic, France, Germany, Italy, Norway, Slovakia, Spain, Sweden and Switzerland, as well as two sets of plots located in old-growth and managed *Pinus sylvestris* forests in Latvia and Spain, respectively (Fig. 2).

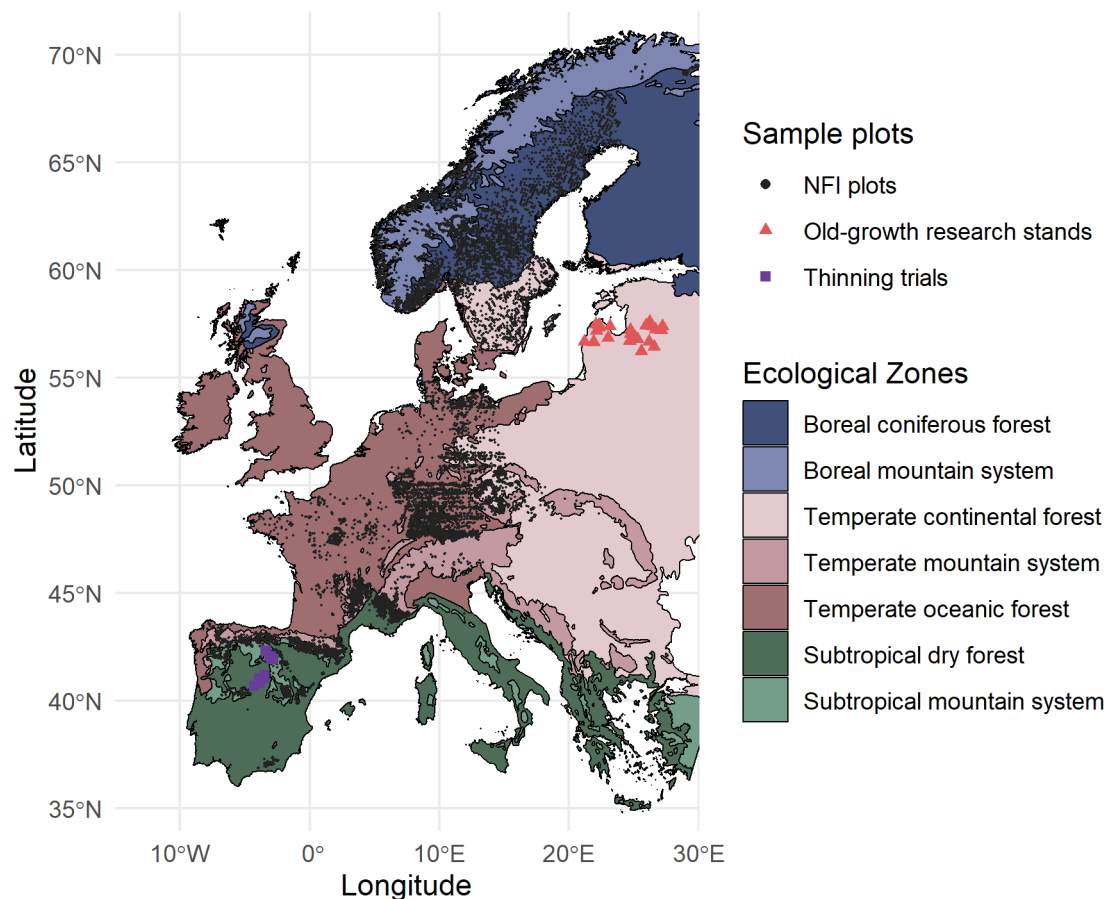


Fig. 2. Dataset constructed with data from the networks of permanent plots of the national forest inventories (NFIs) in the Czech Republic, France, Germany, Italy, Norway, Slovakia, Spain, Sweden and Switzerland, as well as two sets of plots located in old-growth and managed *Pinus sylvestris* forests in Latvia and Spain, respectively.

2.2. Dataset

2.2.1. National Forest Inventories

Our methodologies for fitting site quality models require up-to-date NFI data to derive growth trajectories from two consecutive measurements. Therefore, we used the two most recent surveys from NFI. Since the study focused on forests dominated by *P. sylvestris*, only plot measurements with at least 90% dominance of this species in basal area (G , $\text{m}^2 \text{ha}^{-1}$) were considered. This produced a total of 34,948 measurements of plots that met the conditions of *P. sylvestris* dominance (Table 1). From these measurements, a total of 16,406 (8,203 plots) were used to fit the site form models, as only plots including a minimum of 10

trees at both inventories were retained, to guarantee a minimum tree density adequate for fitting the SF models (see section 2.3 Data processing).

Table 1. Number of observations (plots and plot measurements) by NFI.

NFI	Total data		Data used for SF fitting	
	Plots	Measurements	Plots	Measurements
Czech Republic (CZ)	762	1104	624	312
France (FR)	2553	3213	356	712
Germany (DE)	5805	11371	2714	5428
Italy (IT)	46	74	24	48
Norway (NO)	1927	5288	874	1748
Slovakia (SK)	26	48	16	32
Spain (ES)	5240	7812	1944	3888
Sweden (SE)	3308	6009	1955	3910
Switzerland (CH)	22	36	8	16
Total	19689	34948	8203	16406

Plots: number of NFI plots included in this work. Measurements: total number of measurements across all plots that met the conditions of *P. sylvestris* dominance.

National Forest Inventories across Europe are highly diversified and employ different sampling and measurement designs to monitor forests. While all NFIs rely on grid-based sampling and circular plots, they differ in grid spacing, plot structure, diameter threshold of measurements, and remeasurement cycles. For example, Spain uses a nested plot design, which has been shown to produce biased estimates of some stand attributes, species diversity, and spatial forest structure (43,44). However, these designs have been found to provide unbiased estimates of basal area per hectare, a variable closely related to AGC (44). Further methodological details for each NFI are provided in Supplementary material 1.

2.2.2. Case study scenarios

Old-growth forest stands in Latvia

Old-growth stands were identified through a two-stage selection process. First, stands were randomly pre-selected from the forest inventory database if no management information was available for at least 40 years and were therefore assumed to be ‘unmanaged’. Second, the stands were visited and examined in situ; only those that met all eligibility criteria based on the Buchwald classification (class n6, old-growth forest) (45) were selected and included in the study. These criteria included no previous logging, dominance of large trees of the target species, a high amount of large deadwood in different decomposition stages (both standing and lying), multiple canopy layers, and a minimum distance of 5 km from settlements to avoid human influence. Signs of former human activity were accepted only where they were minor and no longer significantly affecting natural processes. Old-growth stands in three different forest site types were assessed – *Hylocomniosa* (described as fertile, productive forests on dry mesotrophic mineral soil), *Caricoso-phragmitosa* (described as forests of moderate productivity on mesotrophic peat soil) and *Myrtillosa turf. mel.* (described as fertile, very productive forests on mesotrophic drained peat soil). Data were collected in 2017 and re-measurements were conducted in 2022. The size of the old-growth forest stands sampled varied from 1.2 to 4.9 ha (on average 2.4 ha). For this study, only plots with at least 80% dominance by *P. sylvestris*, in terms of basal area (G , $m^2 ha^{-1}$), were selected, to ensure that all plots represented *P. sylvestris* dominated forests in the hemiboreal region. Altogether, data from 31 old-growth stands (86 sample plots) were used. Stand age is an estimate of the oldest cohort of trees in mixed-aged stands (144 to 223 years). Each sample stand included six to eight systematically established sampling plots of 0.05 ha (radius = 12.62 m). In each of these, the tree species were recorded and the $dbh \geq 6.1$ cm of all the live and dead standing trees were measured. Tree biomass was calculated using species-specific allometric equations for Latvia (46,47).

Managed forest stands in Spain

We used data from ten thinning trials established in even-aged, monospecific *P. sylvestris* stands in inland Spain. In each trial, between two and four treatments, including an unthinned control, were tested. The thinning treatments varied in intensity, which was based on the percentage of basal area removed at the onset of the trial. Thinning intensity was thus defined as follows: light thinning (< 15% basal area removal), moderate thinning (15% to 25% basal area removal) and heavy thinning ($\geq$ 25% basal area removal). Within each trial, both the control and thinning treatments were applied to at least two square plots of 1000 m² per experimental site. For example, in a trial with three treatments (control, moderate, and heavy thinning) there would be three plots per treatment. The thinning trials were established between the 1960s and 1990s. At the start of each experiment, we measured the *dbh* and *h* of all trees with a *dbh* of 7.5 cm or greater. Individual trees were numbered and labelled for identification purposes in subsequent inventories. Inventories were typically conducted every five years between establishment of the trial and the beginning of regeneration felling, at which point the trial concluded. Thinning was implemented at intervals of 10 to 15 years.

2.3. Data processing

For the development of site quality models (based on the site form index - SF) only plots with two consecutive measurements and positive growth trajectories were included. This approach avoided considering cases where the second measurement reflected an earlier stage of development, such as e.g. those caused by significant disturbances. In addition, only plots including a minimum of 10 trees at both inventories were retained, to guarantee a minimum tree density adequate for fitting the SF models. This is because dominant height (H_0) may be underestimated in stands that are not sufficiently dense. In some cases, H_0 tends to increase rapidly at low stand densities but stabilizes as density increases (48). By contrast, dominant diameter (D_0) typically exhibits similar growth across stands with wider

spacing, regardless of density (49). The 10-tree threshold was determined as follows: between 1 and 20 trees per plot measurement were assessed for a random subsample of 50 plots for each NFI, in order to establish a minimum number of trees per plot (i.e. tree density) where H_0/D_0 ratios were stable (Supplementary material 2 Fig. 1). Therefore, as mentioned above, plot measurements including at least 10 trees were used to fit SF models. Applying all these criteria resulted in a total of 8,203 plots (16,406 measurements) suitable for fitting the SF models based on growth trajectories from two consecutive measurements (Table 1).

In most NFIs, h measurements are only available for a sample of trees within the plot, whereas dbh measurements are available for all trees. Therefore, H_0 was predicted using Assmann's criterion (50), which is based on a $h \sim dbh$ logarithmic relationship (Eq. 1). The D_0 is calculated as the arithmetic mean of the 100 trees per hectare with the largest dbh (or proportional for plots, as these have an area of less than 1 ha), and H_0 is predicted as h when the independent variable dbh takes the value of D_0 (Eq. 2):

$$h = \beta_0 + \beta_1 \cdot \log_{10} \cdot dbh \quad (1)$$

$$\hat{H}_0 = \hat{\beta}_0 + \hat{\beta}_1 \cdot \log_{10} \cdot D_0 \quad (2)$$

where β_0 and β_1 are parameters to be estimated ($\hat{\beta}_0$ and $\hat{\beta}_1$) for each sample plot.

2.4. Site form (SF)

In this study, the Generalized Algebraic Difference Approach (GADA) methodology developed by Cieszewski & Bailey (2000) was used to fit the SF curves. This technique is used to derive dynamic equations that have the general form $Y = f(D_0, D_{0_i}, Y_i)$, where Y is the value of the function (H_0 in this case) at dominant diameter D_0 , and Y_i is the reference variable defined as the value of the function at dominant diameter D_{0_i} . The GADA methodology enables expansion of base equations according to theories about the growth

characteristics of forest stands, such as asymptotic behaviour. This approach also enables the inclusion of more than one site-specific parameter, resulting in dynamic equations that are flexible, polymorphic and capable of exhibiting different asymptotes (51–53). We used the Bertalanffy-Richards equation (Eq. 3) to fit the SF curves. An additional constant of 1.3 was added to the right-hand side of the equation to force the curves to pass through the point ($D_0 = 0$ cm, $H_0 = 1.3$ m), as D_0 is estimated from *dbh* and, therefore, trees must be taller than 1.3 m.

$$H_0 = 1.3 + a(1 - e^{(-bD_0)})^c \quad (3)$$

The parameters a and c of the equation are site specific. These were replaced with explicit functions of X (an unobservable independent variable that describes site productivity as a summary of management regimes, soil conditions, and ecological and climatic factors) and new parameters (Eq. 4). Thus, the initially selected two-dimensional base equation $Y = f(D_0)$ is expanded into an explicit three-dimensional site equation $Y = f(D_0, X)$, which describes both cross-sectional and longitudinal changes using two independent variables, D_0 and X . Since X cannot be reliably measured or even functionally defined, the final step involves replacing X with equivalent initial conditions representing snapshot observations of the two observable variables D_0 and Y (e.g. D_{0_i} and Y_i), so that the model can be implicitly defined and is practically applicable (51,53).

$$H_0 = 1.3 + \exp(X_0)(1 - e^{(-bD_0)})^{d/X_0}$$

$$a = \exp(X_0) \quad (4)$$

$$c = d/X_0$$

This resulted in the final expression of the fitted SF model, as follows:

$$SF = 1.3 + \exp(X_0) \left(1 - e^{(-bD_{0ref})}\right)^{d/X_0}$$

$$X_0 = 0.5 \left[\ln(H_{0i} - 1.3) + \sqrt{\ln(H_{0i} - 1.3)^2 - 4dL_0} \right] \quad (5)$$

$$L_0 = \ln(1 - \exp(-bD_{0i}))$$

315 Dummy variables were then included to expand the parameters b and d by GEZ,
 316 incorporating an associated parameter and a dummy variable to differentiate the three
 317 main GEZs (boreal, subtropical and temperate) as follows:

$$SF = 1.3 + \exp(X_0) \left(1 - e^{(-(b_1 + b_2 \cdot I_{su} + b_3 \cdot I_{te})D_{0ref})}\right)^{(d_1 + d_2 \cdot I_{su} + d_3 \cdot I_{te})/X_0}$$

$$X_0 = 0.5 \left[\ln(H_{0i} - 1.3) + \sqrt{\ln(H_{0i} - 1.3)^2 - 4(d_1 + d_2 \cdot I_{su} + d_3 \cdot I_{te})L_0} \right] \quad (6)$$

$$L_0 = \ln(1 - \exp(-(b_1 + b_2 \cdot I_{su} + b_3 \cdot I_{te})D_{0i}))$$

318 where I_{su} , and I_{te} are the dummy variables for the subtropical and temperate GEZs,
 319 respectively. These dummy variables take a value of 1 for the corresponding GEZ and 0 for
 320 the other GEZ. To select the best model, an F-test comparing the simplest model (Eq. 5)
 321 against the more complex model (the one including dummy variables, Eq. 6) was
 322 performed. Finally, the reference dominant diameter (D_{0ref}) was selected so that it was a
 323 reliable predictor of H_0 at other D_0 (55). A different reference D_0 and the corresponding
 324 observed H_0 were used to estimate H_0 at other D_0 (both forward and backward) for each
 325 plot. The results were compared with the values obtained from plot data, after which the
 326 relative error in predictions (RE%) was calculated.

We fitted the nonlinear models with the `nls` function in the R software environment (56). Two goodness-of-fit statistics were calculated: the coefficient of determination (R^2 , referred to as pseudo- R^2 when applied in nonlinear regression), which indicates the proportion of the variance of the dependent variable explained by the model, and the root mean square error ($RMSE$), which assesses the precision of the estimates. In addition, a leave-one-out cross-validation method was applied to validate the fitted model in terms of R^2 and $RMSE$. Finally, graphical analysis of the residuals and the appearance of the fitted curves overlaid on the trajectories of the H_0 of the plots was also conducted to test the assumptions of homoscedasticity and correct model specification, respectively. The assumption of independence in the residuals did not require to be tested as there are only two consecutive data points in time.

2.5. Potential carbon storage capacity (PCSC)

The aboveground biomass (AGB), defined as the total amount of organic matter in leaves, branches, stem and bark, was estimated using country species-specific allometric models for individual trees. These allometric models use dbh and h as explanatory variables, which are either directly available in the NFI databases or can be predicted, as is the case for h (Eq. 1). Whenever models incorporating both variables (dbh and h) were available, they were preferred over those that only use dbh . Additionally, in rare cases where models for specific species were not available, models for species with similar allometry were used. The bibliographic sources of the equations used for each NFI are summarized in Supplementary material 1 Table 1. Subsequently, AGB was estimated at the stand level ($Mg\ ha^{-1}$) by aggregating the AGB of individual trees at the plot level while scaling it to surface area units (ha) using expansion factors.

Carbon values were predicted using the carbon fraction coefficients outlined in the 2006 IPCC guidelines for national greenhouse gas inventories (34). Since some AGB values were

directly provided by the NFIs, without the possibility of distinguishing between different biomass fractions, the default value of 0.47 was used in all cases (57). Thus, the aboveground carbon (AGC) was calculated as $AGC = AGB \cdot 0.47$. As stand biomass depends on site quality and development stage, the PCSC models were based on the relationship between AGC (Mg ha^{-1}) and SF (m), i.e. the $AGC \sim SF$ scatter plot. This is consistent with the findings of Molina-Valero (28), who demonstrated that SF is a key determinant for adequately estimating the upper limits of potential biomass storage. The guide curve methodology (49) and the Bertalanffy-Richards base model were used to fit the model, with AGC as the dependent variable and SF as the independent variable (Eq. 7). Based on the analysis of maximum AGC values, a distinct asymptote (represented by parameter a) was applied for the boreal zone, while a common asymptote value was used for the subtropical and temperate zones. This was achieved by incorporating dummy variables to expand parameter a . Parameter b was considered site-dependent (Eq. 8) to obtain the PCSC curves, which were defined by the maximum reference AGC values (AGC_{ref_i}) for an SF_{ref} of 15 m (Supplementary material 2 Fig. 2).

$$AGC = a[1 - \exp(-b \cdot SF)]^c \quad (7)$$

$$b = \frac{-\ln\left(1 - \left(\frac{AGC_{ref_i}}{a}\right)^{1/c}\right)}{15} \quad (8)$$

$$a = a_{bo} \cdot I_{bo} + a_{su} \cdot I_{su} + a_{te} \cdot I_{te}$$

where AGC_{ref_i} are the maximum AGC values for $SF_{ref} = 15$ m at their respective GEZs, and I_{bo} , I_{su} , and I_{te} are the dummy variables for the boreal, subtropical and temperate GEZs, respectively. The fitting process was carried out by fitting the base model of AGC (Eq. 7) as a function of SF. The AGC_{ref_i} values are shown in Table 2.

To select the asymptotic parameters (a_{bo} , a_{su} and a_{te}), a sequence of values ranging from 50 to 300 Mg ha⁻¹ was used to fit the PCSC model for the different GEZs, and the R^2 was obtained for each fit. The a values were then selected on the basis of visual comparison of the fitted curves overlaid on the maximum values of AGC through the SF gradient and the highest possible R^2 values (Supplementary material 2 Fig. 3), yielding the estimates showed in Table 2.

Table 2. Maximum AGC values for $SF_{ref} = 15$ and asymptotic values (parameter a).

Global Ecological Zones		AGC_{ref}	a
Boreal	Coniferous forest	70.5	190
	Mountain system	82.0	
Temperate	Continental forest	82.0	260
	Mountain system	117.5	
	Oceanic forest	105.5	
Subtropical	Dry forest	94.0	260
	Mountain system	117.5	

3. Results and discussion

3.1. Site quality

We first demonstrated that the use of SF as a proxy for site quality prediction is effective, with robust results at the global ecological zones (GEZs scale). To select the best model for estimating the site form (SF) index, we compared two models incorporating different sets of explanatory variables. The first model (the GADA model without dummy variables) revealed that all parameters were significant at the 5% confidence level, yielding an R^2 of 0.999 and a root mean square error ($RMSE$) of 0.204 m (Table 3). Conversely, the initial GADA model with dummy variables for the subtropical and temperate GEZs (see methods) included non-significant parameters, prompting their removal and adjustment of the model to retain only significant parameters (b_1 , b_3 , d_1 , d_2 , d_3). This refinement resulted in all parameters being significant at the 5% confidence level, with an R^2 of 0.999 and a slightly improved $RMSE$ of 0.193 m (Table 3). The F-test yielded a value of 327.34 (p-value of $2.2e^{-16}$), supporting the null hypothesis that the more complex model explains more variability. This model

corresponds to the GADA specification, incorporating GEZs as auxiliary variables. Visual comparison of the fitted curves against the observed dominant height trajectories further confirmed the strong performance of the model (Fig. 3). Consequently, the GADA model with dummy variables was selected for estimating SF. It was found that a reference dominant diameter of 32 cm was superior for predicting the dominant height (Supplementary material 2 Fig. 4), and the residuals were homoscedastic (Supplementary material 2 Fig. 5a). The final expression is shown as Eq. 9.

Table 3. Estimated parameters and goodness-of-fit statistics for fitted models.

Model	Parameters		Fit statistics		Cross-validation statistics	
	Estimated	p-value	R^2	$RMSE$	R^2	$RMSE$
Eq. 5	$b = 0.0295$	<0.001	0.999	0.204		
(without dummy variables)	$d = 2.2075$	<0.001				
Eq. 6	$b_1 = 0.0358$	<0.001	0.999	0.193	0.999	0.194
(with dummy variables)	$b_3 = -0.0018$	<0.001				
	$d_1 = 2.4628$	<0.001				
	$d_2 = 0.2622$	<0.001				
	$d_3 = -0.4221$	<0.001				
PCSC	$b = 0.0421$	<0.001	0.578	45.336		
(Eq. 7)	$c = 2.3957$	<0.001				

R^2 : coefficient of determination (pseudo- R^2); $RMSE$: root mean square error.

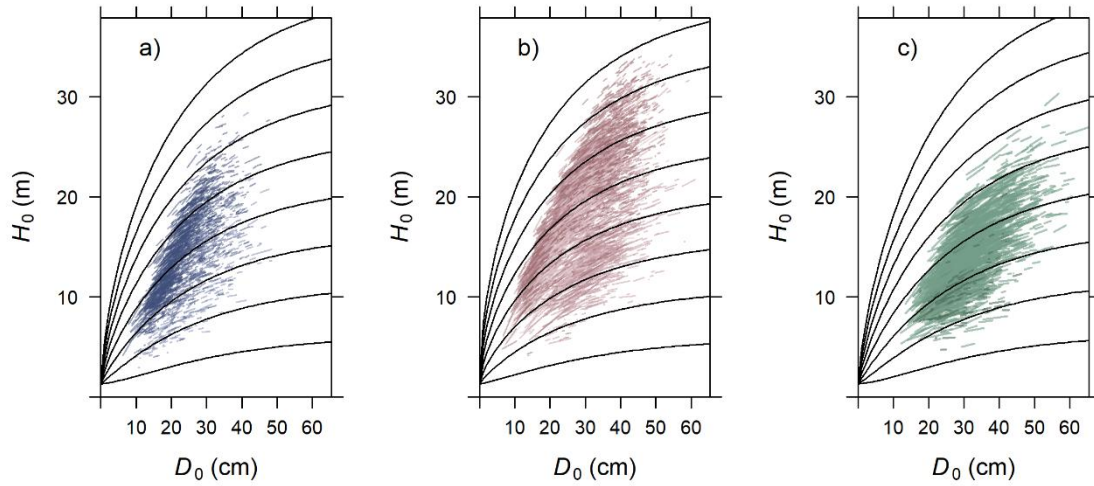


Fig. 3. Site form (SF) curves for dominant heights of 4, 8, 12, 16, 20, 24, 28 and 32 m at a reference dominant diameter (D_{0ref}) of 32 cm overlaid on the observed data for the Global Ecological Zones (GEZ) boreal (a), temperate (b) and subtropical (c).

$$SF = 1.3 + \exp(X_0) \left(1 - e^{-(0.0358 - 0.0018 \cdot I_{te}) \cdot 32} \right)^{(2.4628 + 0.2622 \cdot I_{su} - 0.4221 \cdot I_{te}) / X_0}$$

$$X_0 = 0.5 \left[\ln(H_{0i} - 1.3) + \sqrt{\ln(H_{0i} - 1.3)^2 - 4(2.4628 + 0.2622 \cdot I_{su} - 0.4221 \cdot I_{te})L_0} \right] \quad (9)$$

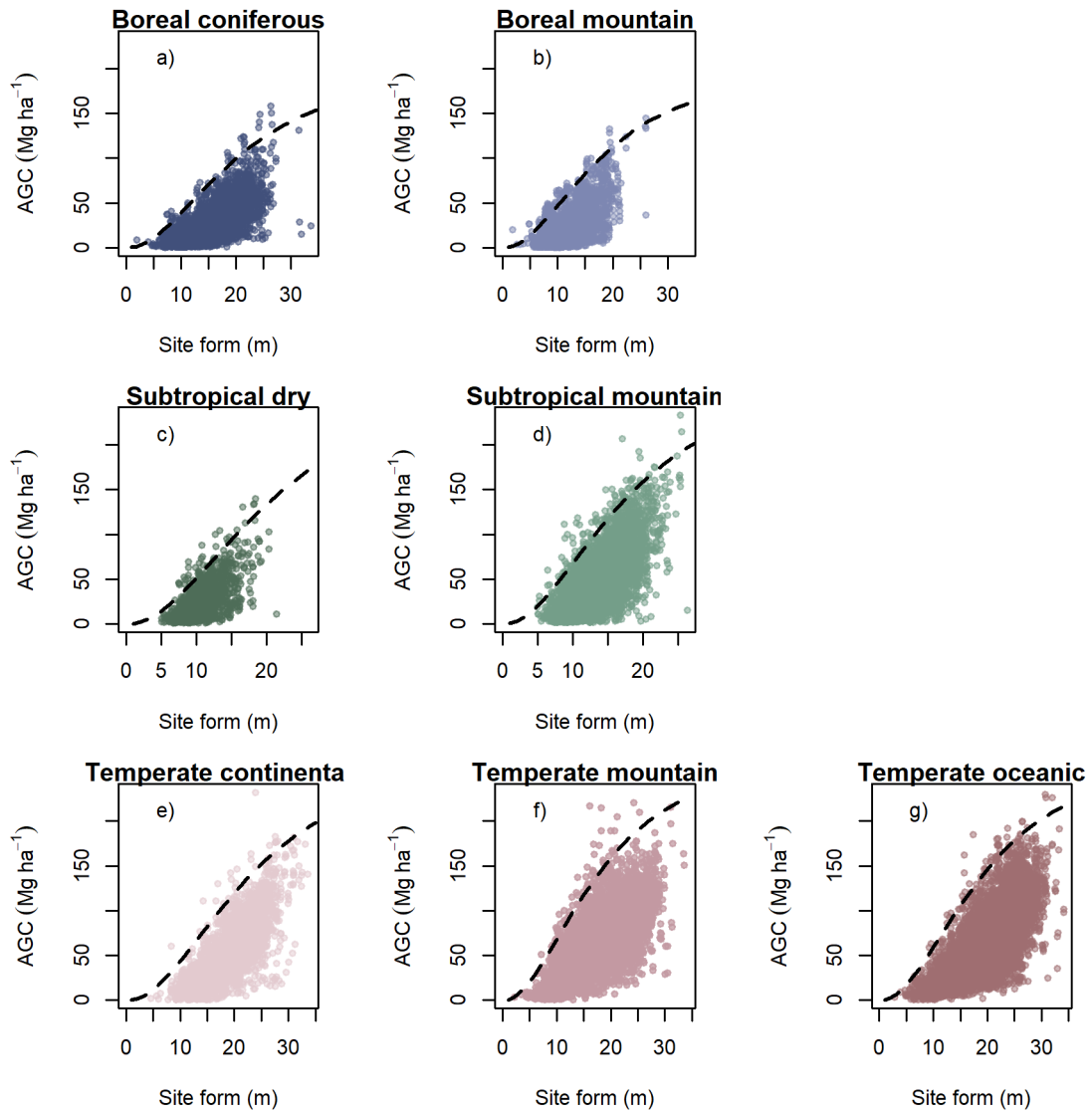
$$L_0 = \ln(1 - \exp(-(0.0358 - 0.0018 \cdot I_{te})D_{0i}))$$

where H_{0i} and D_{0i} are the dominant height and diameter respectively for the plot i , and I_{su} , and I_{te} are the dummy variables for the subtropical and temperate GEZs, respectively. These dummy variables take a value of 1 for the corresponding GEZ and 0 for the other GEZ. Compared to previous studies showing that SF estimates at national scale based on NFIs are consistent with species' autoecology (37,38), the present study covers a larger scale and also applies an improved methodology for model fitting using GADA relative to the guide curve method. Consequently, the use of SF continues to be strengthened in increasingly broad contexts and across diverse forest stand types dominated by *P. sylvestris*.

Furthermore, as the estimation of forest potential was included in the "Forest Principles" for sustainable forest management at the Earth Summit (58), SF serves as a practical and operational estimator. SF can effectively guide silvicultural strategies related to timber yield at the stand level (59) and can be used in broader forest policy decisions. Notably, it has applications in international initiatives such as the FAO's REDD+ program, which aims to reduce emissions from deforestation and forest degradation (17). Additionally, SF facilitates site quality estimation using remote sensing products (60), as both height (61) and diameter (62) can be estimated using various remote sensing sensors at scales ranging from local to national. As SF does not require age information but only values for tree height and diameter, it can be directly derived from field data collected in conventional forest inventories. Consequently, SF models could be developed for other species beyond *P. sylvestris* to estimate site quality using existing NFI data in most countries.

3.2. Potential carbon storage capacity

As expected, the PCSC was found to increase with site quality (estimated as SF) and can also be modelled using the proposed approach. Parameterized and representative PCSC curves were thus obtained for each GEZ (Fig. 4), which were used to map carbon stocks according to the dataset used here (Fig. 5). In the fitted models, all parameters were significant at the 5% confidence level, with an R^2 of 0.578 and a $RMSE$ value of 45.336 Mg C ha⁻¹ for the PCSC model (Table 3). The residuals were found to be homoscedastic (Supplementary material 2 Fig. 5b).



435

436 Fig. 4. Predicted potential carbon storage capacity (PCSC) curves (black dashed lines) overlaid on the observed
 437 data (colored dots) for the Global Ecological Zones (GEZ) boreal mountain systems (a) and coniferous forests
 438 (b); subtropical dry forest (c) and mountain systems (d); and temperate continental forest (e), mountain system
 439 (f) and oceanic forests (g).

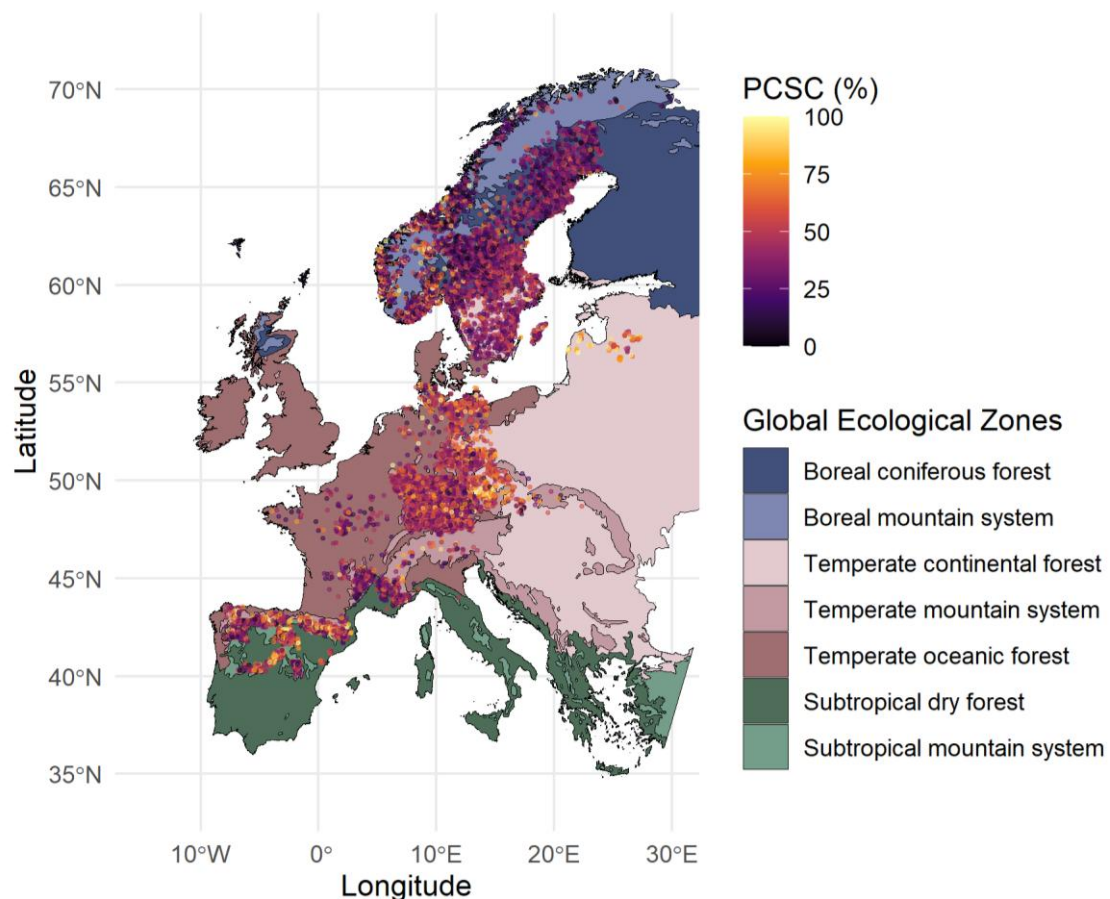


Fig. 5. Predicted carbon carrying capacity (PCSC) of the network of NFI *Pinus sylvestris* forest plots used in this study. Plots correspond to the most recent NFI survey in the respective countries. The various global ecological zones (GEZ) are represented by different colors.

The PCSC values shown for coniferous forests across different European GEZs are lower in boreal forests than in temperate and subtropical zones, with the latter two achieving similar PCSC values (Fig. 4). Thus, these last two zones have a similar potential carbon stock, as reported by Keith et al. (2024). Another example of PCSC estimation is found in old-growth *Pinus sylvestris* forests in Latvia, classified as temperate forests under the GEZ framework, estimated with AGC values in living trees values of $172 \pm 7.0 \text{ MgC ha}^{-1}$ (25,26). These values are consistent with the PCSC curve values for an SF of approximately 22.5 m (Fig. 4). However, as comparisons are not based on site quality, it is not possible to assess these values accurately. Moreover, it is important to note that this study did not consider belowground or dead biomass, which can account for on average 16% and 22% of the total

carbon stock, respectively (18). This is particularly relevant for dead biomass, which constitutes a potentially large carbon pool in old-growth forests (63).

From a methodological point of view, there are some discrepancies with other methodologies in which the PCSC was estimated based exclusively on forests under natural disturbance regimes, with managed forests excluded from the estimates (19).

However, this methodology produced some unexpected results, with boreal regions showing higher carbon storage potential in managed forests than in unmanaged forests.

Roebroek et al. (2023) proposed the following possible explanations for that: “(i) in these regions, intact forests are not fully comparable to the managed forests because of the preferred selection of the most fertile sites for forest management; and (ii) management has increased the maximum potential realized biomass (for example, through the introduction of highly productive monospecific stands) or has deliberately decreased the natural disturbance regime (for example, active and passive suppression of forest fires)”. In addition, Keith et al. (2024) also reported aboveground biomass carbon stock values in primary forests that were lower than the 100 MgC ha⁻¹ reported in our results for conifer forests in boreal zones. The reasons for this discrepancy cannot be accurately determined, for the following reasons: (i) this study focused exclusively on *Pinus sylvestris* forests, whereas Keith et al. (2024) included additional conifer species; and (ii) the old-growth boreal forests analyzed by Keith et al. (2024) were situated in mountainous areas of Sweden characterized by low site quality. This highlights the limitations of focusing solely on old-growth forests for establishing the PCSC, as the site quality gradient may not be adequately represented. For all the reasons mentioned above, it is important to consider plots in managed forests as well as to focus on different types of forests for developing a robust methodology. Using a site quality estimator (e.g. SF) that is sensitive to the site potential and also to the genotype and specific management regime is also important (33).

3.3. Case study scenarios

Old-growth forests in Latvia

Hemiboreal old-growth forests are specific ecosystems, which may have only some of the structural attributes of similar forest types in the temperate continental forest zone. However, they still host a variable mixture of coniferous and deciduous trees and a diverse biota (64). This is evidenced by the higher SF values of some of the sites than in the other temperate continental sites, especially in the mesotrophic mineral soils with normal moisture regime (Fig. 6a). Our results show that PCSC values can potentially be reached in these old-growth forests (Fig. 6), despite variability in AGC among sample plots within stands (Fig. 6b), likely reflecting differences in past natural disturbance regimes and ongoing successional processes. This variability is also influenced by the regeneration strategies and lifespans of the dominant tree species, as well as by stand species composition and soil properties within and between the old-growth stands (65,66). This suggests that status of old-growth stand alone does not necessarily imply that a stand has reached its maximum carbon storage potential. Instead, PCSC should be interpreted as a reference upper boundary against which the strength of the natural disturbance regime can be estimated (19).

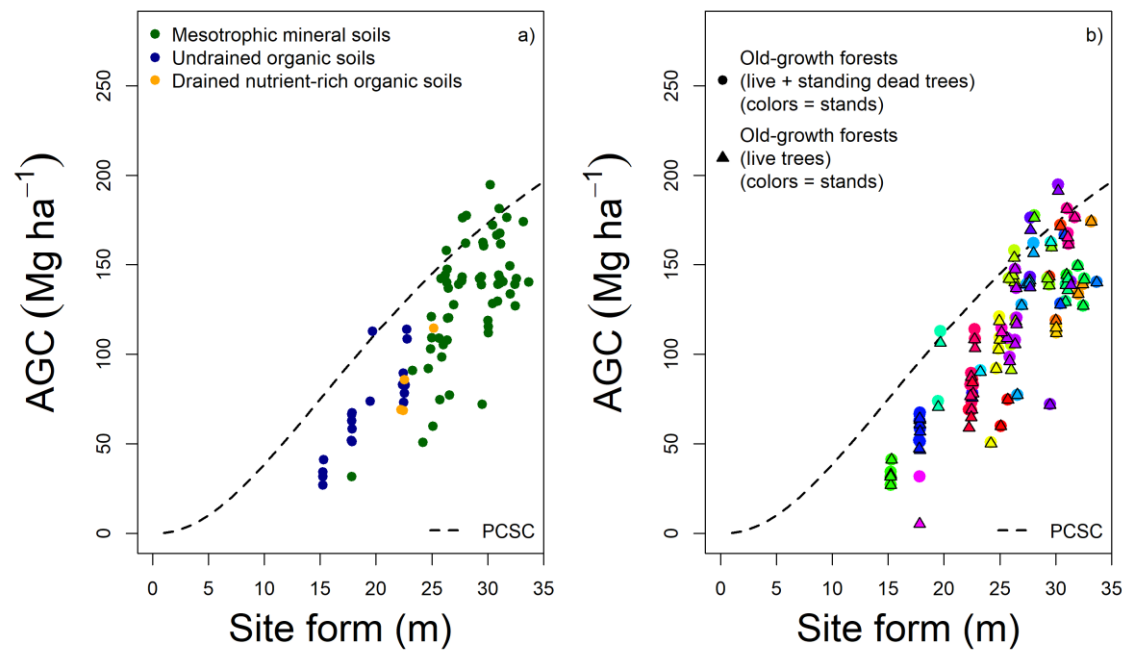


Fig. 6. PCSC of *Pinus sylvestris* old-growth forests in Latvia. In a), mesotrophic mineral soils with normal moisture regime; naturally wet (undrained) organic soils; and drained nutrient-rich organic soils. In b), old-growth forests including live and standing dead trees. Each dot represents a plot.

Managed forests in Spain

We found that the PCSC cannot be reached under intensive harvesting where the extracted volume per rotation is optimized. In the thinning trials conducted in Spain, we found that AGC reached maximum values in the control plots (i.e. unmanaged) and decreased with management intensity (control > light > moderate > heavy thinning; Fig. 7). This is consistent with the expectation that heavier thinning leads to more open, less well stocked stands. However, it is important to note that the AGC removed through thinning operations was not accounted for as carbon stock in this study. According to Assman (1970) and Langsæter (1941) plateau rule, within a specific range of thinning intensity, the enhanced growth of the remaining trees could compensate for the stock removed by thinning. Thus, by the end of the rotation period, control plots are expected to have similar AGC stocks as the sum of the extracted and standing stocks in thinned plots for each trial. Another important aspect here is that the stand age at which maximum AGC values are reached differs according to the intensity of management. Thus, for older ages in the control plots (i.e. unmanaged plots)

and lower ages as management intensity increases, a gradient is again established (control > light > moderate > heavy thinning; Supplemental material 2 Fig. 6). This also seems to be consistent with the compensation theory mentioned above. Furthermore, we found that AGC is positively related to age in the four treatments, although this is more evident in control plots than in thinned plots. This is due to a reduction in tree density in control plots exclusively due to natural mortality, while thinning alters tree density and therefore AGC stands over the rotation period, indicating the observed lower correlations between AGC and age.

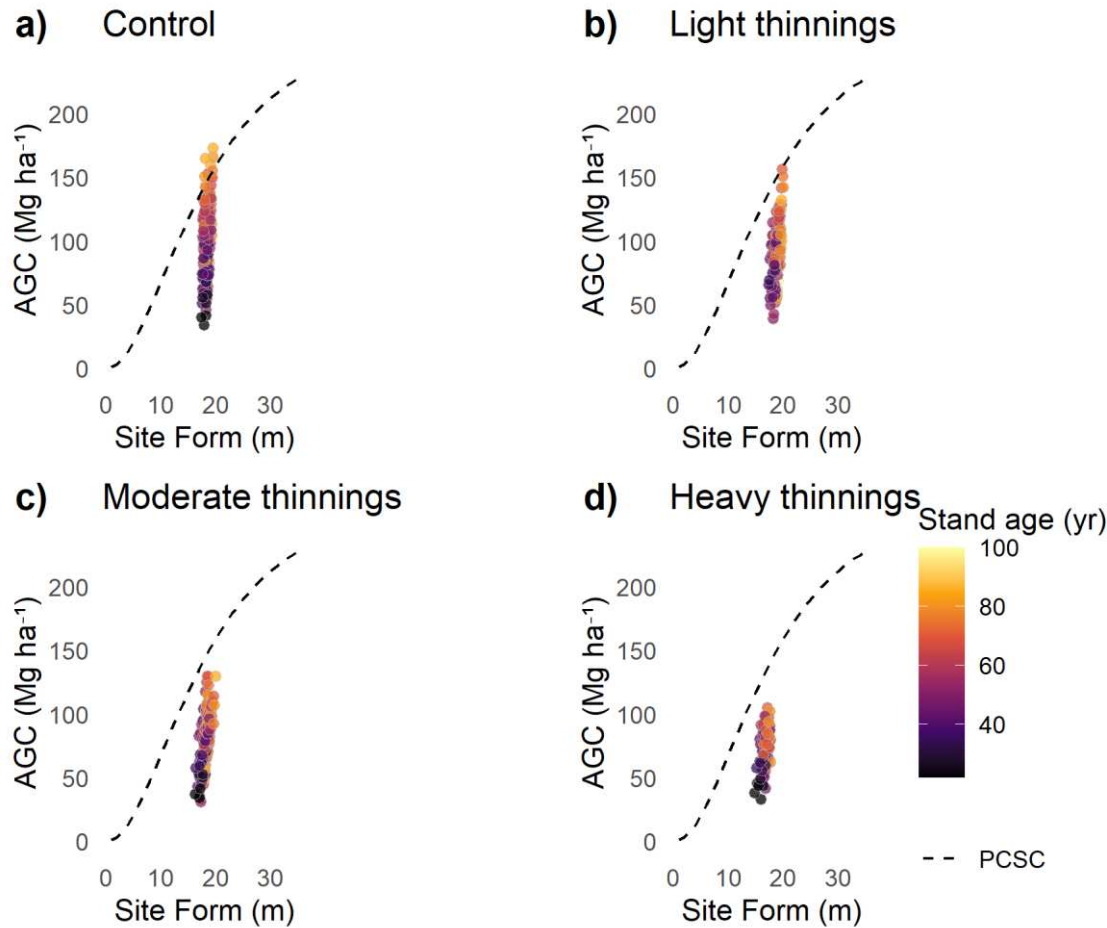


Fig. 7. PCSC in managed *Pinus sylvestris* thinning experiment trials forests in subtropical stands (Spain). In a) control (0% basal area removal), b) light thinning (< 15% basal area removal), c) moderate thinning (15% to 25% basal area removal), and d) heavy thinning ($\geq$ 25% basal area removal).

4. Conclusions

The findings of this study are highly relevant to international carbon monitoring agreements, as forest ecosystems play a critical role as carbon stores, holding approximately 870 Pg C in live biomass, dead biomass and soil organic carbon (4). Furthermore, forests represent the largest component of the terrestrial carbon sink (4,5) and have a high potential for additional carbon sequestration (68). This is particularly important considering that large carbon reserves in primary forests have been underestimated (18), both by global biomass models such as GlobBiomass (Santoro et al., 2018) and by default values provided by the Intergovernmental Panel on Climate Change (34). The reference level currently used by the UNFCCC to assess the target reduction in emissions by each country projects future net annual emissions on the basis of current carbon reserves and ongoing management dynamics. These dynamics are influenced either by the continuation of documented historical practices or the implementation of approved future policies (70). However, this approach cannot predict the potential carbon reserves that forests could store if management were modified to restore maximum reserves based on site conditions, given the natural potential of forest ecosystems. This limitation highlights that the methodology developed in this study, based on carbon reserves, offers a complementary accounting solution that can be applied within the framework of the Paris Agreement (2).

The proposed methodology would be particularly relevant in continuous cover forestry (CCF) and unmanaged systems because, unlike in the case of rotation forest management, maximum carbon potential is not defined by the rotation age. In addition, CCF systems like close-to-nature approaches are considered strategic in the New EU Forest Strategy for 2030 to ensure long-term environmental and socio-economic viability of forests (71). Thus, estimating the management intensity based on the PCSC may help to establish sustainable forest management targets. This approach also aligns with the principles of the Paris agreement to “conserve and enhance, as appropriate, sinks and reservoirs of greenhouse gases” (2, Art. 5 Section 1); by “reducing emissions from deforestation and forest

degradation, and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries; and alternative policy approaches, such as joint mitigation and adaptation approaches for the integral and sustainable management of forests” (2, Art. 5 Section 2). Hence, forest protection and management are key factors in the global ambition to limit anthropogenic climate change (72). In fact, climate change mitigation strategies (i.e. promoting PCSC) may conflict with efforts to adapt to changing environmental conditions (i.e. reducing tree density to lower resource competition). Forest management can be particularly important in regions and forest types where active management is the most effective strategy for preventing wildfires (73). Such disturbances lead to CO₂ emissions, contributing to the decline in the land carbon sink observed in 2023 (74). Another important point is to promote mixed conifer-broadleaf stands through management to increase forest resilience e.g. to drought events (75–77). However, this may be incompatible with the high density of *P. sylvestris* trees, especially in relation to more light-demanding broadleaf species. Therefore, retaining high proportions of stands close to PCSC in forests dominated by *P. sylvestris* could limit the regeneration and especially the recruitment of e.g. beech, oak and birch (78).

Overall, the study findings also highlighted that using the PCSC for forest ecosystems is crucial to ensure consistent information regarding (i) evaluation of past carbon stock losses due to human activities, (ii) prediction of potential carbon stock gains through changes in forest management, and (iii) assessment of mitigation benefits lost when forests are managed with carbon reserves below their maximum capacity.

Declarations

Availability of data and materials

The datasets generated and/or analyzed during the present study are available from the corresponding author or from the respective National Forest Inventories, depending on their origin, upon reasonable request.

Consent to Publish declaration

All authors consent to the publication of this manuscript.

Competing interests

The authors declare that they have no competing interests.

Ethics and Consent to Participate declarations:

Not applicable.

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Authors' contributions

J.A.M.V. wrote the original draft. J.A.M.V., J.G.A.G., and C.P.C. contributed to the conceptualization, methodology, and formal analysis. V.M., P.S., and R.M. supported the work through the provision of resources. J.A.M.V., L.K., D.M.F., A.L., C.R., F.M., H.C., I.C., J.P., T.G., V.S., P.S., and R.M. participated in data curation, either by providing the raw datasets or processing them. All authors contributed actively to the writing, review, and editing of the manuscript. J.A.M.V. and A.L. were responsible for the preparation, creation, and

visualization of the published work. P.S. and R.M. supervised the study. Funding was acquired by J.A.M.V., P.S., and R.M.

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