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Aboveground biomass estimates from UAV LiDAR improved via contextual learning in a Norway spruce forest

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Forest structure and aboveground biomass (AGB) analyses are key for advancing forest trait-based ecology and management. Surveys using Unmanned Aerial Vehicles (UAV) and Light Detection and Ranging (LiDAR) systems have contributed to this field with increased accuracy in tree phenotyping. Moreover, methods harnessing the flexibility of machine learning (ML) are now common tools to enhance estimates of AGB. Here, we evaluated the capacity of shallow learning methods to leverage local information from the surrounding context of the tree of interest to improve predictions of stem diameter and tree-level biomass, over 33 ha of a Norway spruce forest (Davos, CH). Our objectives have been (i) to gain insights into variation and gradients of tree heights and (ii) to evaluate whether such gradients may prove useful as contextual information to improve predictions. We segmented the point cloud data scene into individual canopies and focused the LiDAR-derived tree canopy features. We then used local indicators of spatial association to determine the influence of local context on tree height, and used this to define tree neighborhoods within the forest. Then, we extracted metrics from the neighborhoods and introduced them in a ML regression experiment to evaluate predictions of individual tree diameter. The focus was on comparing performance of tree diameter predictions between twin regression models that either consider neighborhood metrics (i.e. context-aware models), or not. Then, the improvements provided by context awareness were assessed in terms of accuracy gained in estimating AGB. We obtained results of three different shallow learning methods and evaluated these based on nested cross-validation. We applied this approach to two separate data sets within the same site, one being clustered and continuous; the other discontinuous and scattered in separate sampling plots. In both cases, we found enhanced AGB prediction performance in context-aware regressions, where the RMSE was reduced by 4.0% and by 9.1%, respectively. These findings indicate that gradients in tree heights across the ecosystem may proxy for local microclimate, edaphic conditions and biotic factors that influence tree growth, which can be leveraged to enhance predictions of AGB. The method proposed is fully native to UAV LiDAR data.

KEYWORDS

aboveground biomass, UAV LiDAR, forest structure, functional trait mapping, machine learning, contextual learning, quantitative ecology

Code and/or data are made available for peer review, uploaded as separate files for reviewers and editors.

1 | INTRODUCTION

Forest aboveground biomass (AGB) is an important component in determining global carbon budgets (C), and they are considered essential to understand the exchange of C between the atmosphere and the biosphere [1, 2]. A large body of environmental remote sensing research has advanced our understanding of it. However, current assessments of C-cycling in forest ecosystems present uncertainties, and contrasting findings exist [3], partly caused by the limited accuracy of AGB estimates [4, 5]. This underscores the need to advance methods to improve quantitative estimates of forest AGB [6] from remotely sensed data.

Predictive analyses in forest AGB and phenotyping from remote sensing surveys have traditionally been focused on regressions considering only individual tree attributes as predictors (e.g. tree height, canopy metrics) [7, 8] and fitted allometric models [9]. Such tree-level analyses have been crucial to improve the characterization of e.g. optical vegetation traits [10], tree dendrometry [11], or species composition [12]. However, these approaches generally do not account for the influence of the spatial context on the individual tree trait under investigation, be it abiotic factors (e.g. terrain condition, soil depth) or biotic interactions (e.g., light interception, nutrient competition), although it is established knowledge that the local context (microclimatic, edaphic and biotic conditions) condition tree traits. In this regard, the mixed effect of abiotic conditions and biotic interactions on individual tree performance has been long hypothesized [13, 14]. Moreover, a line of empirical research has aimed to measure tree performance components (e.g. stature, dominance) across environmental gradients, while monitoring local biotic interactions [15]. Indeed, an increasing number of empirical studies, have proposed different methods to use the information of neighboring trees to enhance individual tree trait regressions (i.e. metrics derived from monitoring inventory plots), such as non-linear mixed effects (NLME) methods [16, 17, 18], or competition-based methods [19, 20, 21]. This line of research has shown that considering neighborhood information can improve trait estimates, and its positive impact has been documented in various tree-level regression analyses, e.g. productivity [22, 23], fuel potential [24] or structural metrics [18, 25, 26].

However, despite the utility of current methods that leverage neighborhood metrics such as tree stand information, from a remote sensing perspective they result suboptimal in some respects. Many of such methods are not directly transferable to a remote sensing framework because they use understory metrics as predictors (e.g. stem diameter of neighboring trees), which are difficult to survey reliably from an above-canopy perspective [19, 20]. Additionally, questions remain about the optimal scale at which such neighborhood metrics become relevant and therefore should be retrieved [22, 23]. A common procedure is to consider the trees contained in an arbitrarily delineated inventory plot, whose size is defined to fit management purposes [23]. This approach, although useful for monitoring tasks, can pose the shortcoming of overlooking the spatial scale at which relevant ecological phenomena operate (e.g. the appropriate range at which tree competition effects are significant), so the analysis remains constrained by the effects observed at the scale of the plot size [16, 17, 18, 19, 20]. To the best of our knowledge, tree-level AGB and trait assessments considering neighborhood information are currently limited due to one or more of the following reasons: (i) they characterize the spatial context with uniquely process-specific indices (e.g. competition pressure from immediate neighbors) [19, 20, 21]; (ii) they calibrate models with neighborhood-metrics retrieved from artificially-bounded inventory plots (e.g. NLME methods) [16, 17, 18]; or (iii) they overlook the spatial scale at which an ecological phenomenon affects the trait under investigation. Moreover, when the relationship between the plot-level predictors used and any ecological phenomenon is described, often ancillary data sources are incorporated (e.g. tree stand age) [20, 27] or roughly quantified forest management metrics, e.g. "stand quality", "site index", "dominance index" [17, 20, 27]. These shortcomings are constrained by the specific data collection protocol, and currently hinder transferring such methods to an integrated remote sensing framework, which would offer greater flexibility for conducting standardized, scalable, and replicable forest analyses.

Unstaffed Aerial Vehicles (UAV) equipped with Light Detection and Ranging (LiDAR) monitoring systems are regarded as particularly versatile [28], accurate and cost-effective tools [29] to contribute to the task of extensive phenotyping, bridging scales in AGB mapping, particularly covering the scale between *in situ* field-based inventories (approx. 0-1 ha) and airborne LiDAR datasets (approx. 1-10^4 km^2) [30, 31]. With a surveying accuracy comparable to field-based measurements, UAV LiDAR monitoring provides datasets (i.e. point cloud data, PCD) that allow individual tree phenotyping at an intermediate spatial scale (approx. 1-40 ha).

While it is commonly argued that understanding local ecological processes in forests requires monitoring biomass of individual trees [20, 22, 23, 32], the opposite idea is seldom discussed: how and to what extent can community ecology processes be harnessed in tree-level AGB regression experiments? Earlier works have proposed to account for the effects of immediate competition pressure on tree growth with either distance-based [21] or distance-independent metrics [19, 33], generally finding such approaches beneficial to improve regression results [19, 20]. However, these studies are based on the premise that competition indices are the determining factor conditioning tree development, while overlooking other potential regulation factors. In this scenario, nonparametric ML regression methods, which do not assume preexisting distributions or premises, are a sound approach to incorporate a contextual analysis, and have been proposed in previous forest mapping studies [34].

Context-based regression studies [35, 36] have shown in the last decade that the inclusion of information of local context (i.e. information about the surroundings of the target object) may improve model performance [37, 38]. This information can be included in a learning model by either enlarging the receptive field size (i.e. widening the field of view) [34, 38, 39] or by incorporating context-aware features that encode neighboring information into the target object [40] (i.e. a specific tree in forestry applications). However, context-based studies typically rely on deep learning architectures and large datasets [34], which may obfuscate the explainability of model performance improvement, which make them suboptimal for ecological applications, where the focus is on explaining regulation factors. In contrast, when interpretability and dataset size limitations are critical, shallow learning methods (e.g. ensembles of decision trees and regularized linear models) are preferred [41, 42].

Here, we developed a fully integrated UAV LiDAR framework to provide context information into regression experiments to predict tree-level AGB, over 33 ha of a Norway spruce forest. We did so only using shallow learners to maintain the focus on the context regulation factors on tree-level AGB (which are ecosystem-dependent), instead of on the specific model architecture (which is ecosystem-independent). Moreover, the method we present is independent of ancillary data sources and metrics obtained from artificially bounded inventory plots. To that end, we i) collected close-range PCD via UAV LiDAR surveying in a Norway spruce forest, ii) retrieved contextual information based on the geographic spatial association of tree heights, iii) integrated context into pairs of twin regression experiments (i.e. identical except on the fact of context), and iv) evaluated the effect of introducing context-awareness in tree-level AGB estimates. The findings show that the prediction enhancement caused by including context-awareness, is robust across three different shallow learning methods for two separate datasets within the same coniferous forest. The proposed method is conceived to not rely on additional data sources beyond the UAV LiDAR datasets, in order to ease applicability.

2 | MATERIALS AND METHODS

2.1 | Study Area

The Seehornwald Davos research site (46° 48’ 55.2"N, 9° 51’ 21.3" E, 1640 m a.s.l.) is located in a managed subalpine coniferous forest on the western flank of the Seehorn mountain, near Davos, in the Swiss Alps. The site is labeled as a class-1 forest ecosystem station of the Integrated Carbon Ecosystem Station (ICOS) network [43] where regular forest inventory measurements are collected following standardized protocols. The site is covered by spruce trees

(*Picea abies (L.) Karst*., > 99.5 %) with an average height and age of 14 m and 100 years, respectively, while some trees reach a height of 40 m and an age of 300 years. The stand parameters at the research site include tree density: 639 ± 311 tree/ha; basal area: 27.6 ± 16 m^2/ha; mean crown area of dominant canopy: 13.2 m^2; and mean DBH: 17.7 cm.

The site has not been affected by infrastructure development during the 20th-21st centuries. Since 1930, grazing livestock in the forest was abandoned, and the site is sustainably managed according to the Swiss Forest Law (1876, revised until 2017) [44]. Maps dating back to 1845 reveal minimal changes within the Davos-Seehornwald forest site, while slight effects of local harvests are noticeable, particularly on steeper slopes of the easter flank, and forest regrowth at the timberline can also be observed [45]. Patchy vegetation (i.e. dwarf shrubs and mosses) covers around 30% of the forest floor (acidic ferralic podzols), which lies on a mixed silicious and dolomitic bedrock. The research site is part of national (LWF [46], TreeNet [47], SwissFluxNet [48]) and international research networks (ICOS [49], ICP Forests [50], eLTER [51]). The study area spans over 33 ha (Figure 1, b) and the terrain conditions are representative of the Alps around the Landwasser valley, i.e. a varying steepness of 23 ± 14°. The site lies on the eastern flank of the valley, so most of the slopes face west-southwest (mean slope aspect is 230° SW).

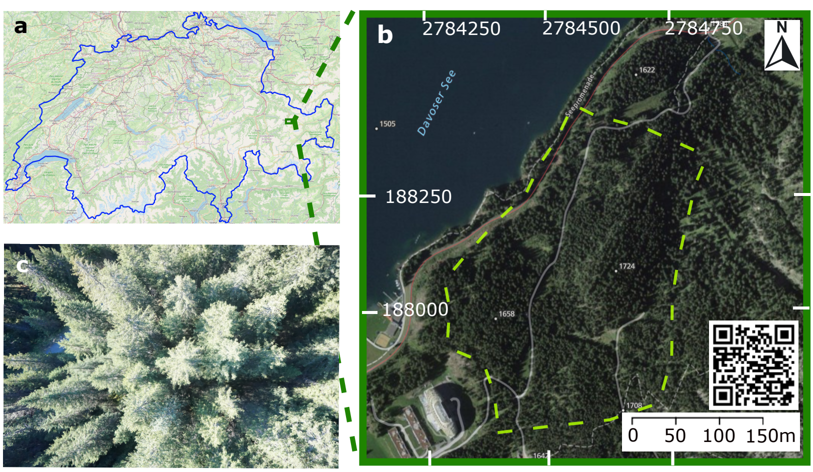

FIGURE 1 **a:** Location of the study site; the blue outline delineates the national territory of Switzerland (adapted from open.sourcemap.com). **b:** Orthoimage of the study site (adapted from swisstopo.admin.ch); coordinate units are in m, with LV95 as a projected reference system; the QR code links to additional information of the study site. The dashed yellow line shows the boundaries of the research site. **c**: Ortophoto of the study site.

2.2 | UAV LiDAR Survey and Field-Based Measurements

We used a UAV-borne LiDAR system mounted to a DJI Matrice 600 Pro payload at a 90° pitch angle, and same heading and roll as the UAV platform. The system included a discrete infrared LiDAR scanner (M8 sensor, Quanenergy Systems, Inc. Sunyvale, CA, USA) and the corresponding state-of-the art inertial and navigation systems. In addition, we used a ground based Global Navigation Satellite System (GNSS, Trimble R8) during the UAV LiDAR survey, set up in post-positioning kinematic (PPK) mode, which logged real-time satellite coverage (cf. Revenga et al. 2022 [52] for details on the airborne and ground system). The coupling of the satellite coverage data with the UAV-based laser and navigation data produced, allowed the generation of georeferenced point clouds, following Davidson et al. (2019) [53].

Data were acquired with a UAV flight height adapted to the terrain and tree height (Figure 2, a), ensuring a >20% overlap between individual LiDAR scans of approx. 50 m width and 250 points/m^2. The surveys were conducted in October 2021, coinciding with the end of the forest growing season. Figure 2 (a) shows the trajectories of the UAV LiDAR flights during the survey campaign. While the standard survey coverage followed a regular auto-pilot flight grid, certain flight lines had to be manually piloted to adapt to sudden topographic features and canopy structure. The digital elevation model of the study area is provided in Annex VI, to help to understand differences in flight heights.

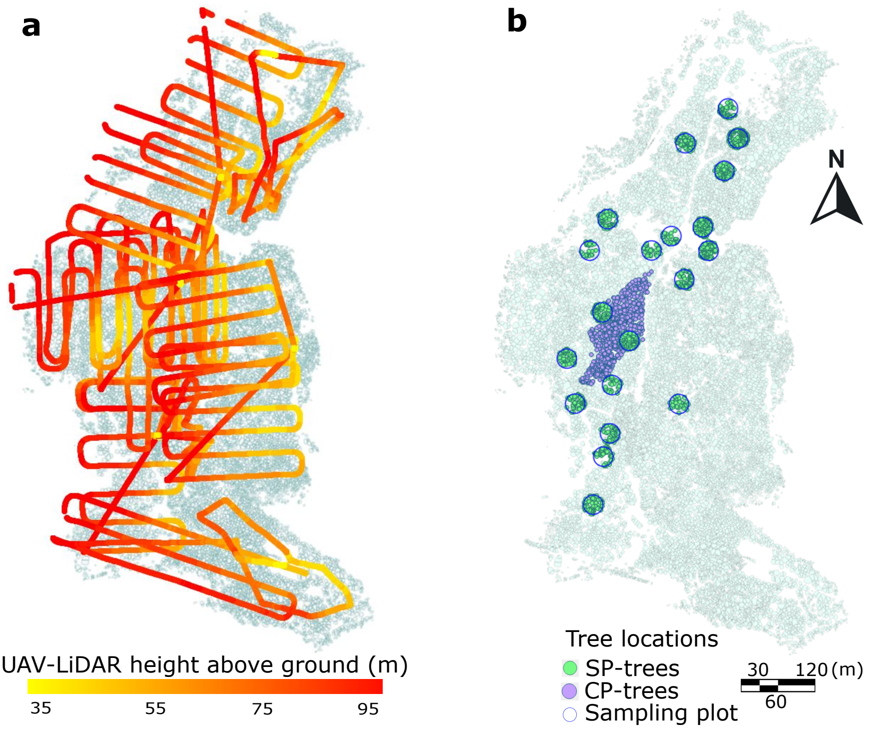

FIGURE 2 **a:** Trajectories of individual flights during survey of the Unstaffed Aerial Vehicle (UAV) Light Detection and Ranging (LiDAR) sensor; color gradient indicates height above ground during survey. Only the trajectories during LiDAR data acquisition are shown (take off and landing trajectories not shown); the variable height corresponds to the difference between a horizontally stable UAV survey and the variable terrain elevation. **b:** Spatial distribution of field-based forest inventory. Dots represent the locations of the ground truth labels. The sampling plot-trees (SP-trees, N = 1635 trees) are shown in green; the control plot-trees (CP-trees, N = 845 trees) are shown in purple. In both **a** and **b**, the underlying polygon dataset shows the individual tree canopies after the canopy height model segmentation.

The field-based measurements (shown in Figure 2, b) are taken on a yearly basis as part of a long-term ecosystem monitoring initiative—jointly organized by ICOS [49] and the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) [46]. Following a standardized protocol [54], expert field workers monitor tree crown status, focusing on three groups of indicators: variations in size, density and color. The number of trees that have died since the previous survey, as well as the new ones that reached a minimum DBH of 5 cm are also recorded [55]. Tree height and DBH are monitored with a high-precision digital rangefinder (i.e. Vertex Laser Geo) and a standard calliper, respectively.

We treated two different datasets separately as ground truth measurements within the same study area: control plot trees (CP-trees, 4 adjacent monitoring units) and sampling plot trees (SP-trees, 20 scattered units of 15 m radius). The two datasets (i.e. CP- and SP-trees) are monitored by different research groups on the field and protocols presented minor differences between both datasets. Two main factors led us to consider both datasets separately: (i) the CP-dataset is clustered and spatially continuous, while the SP-dataset is spatially discontinuous and distributed along the study site (Figure 2, b); and (ii) the two datasets present differences in morphological trait distribution (Annex V). Figure 2 (b) shows the spatial distribution of the field-based forest inventory. The CP tree position was recorded using a Leica GPS1200 total station. The location and size of the sampling plots were defined according to ICOS protocols [56]. The center location of the SP plots was determined using a GNSS Leica CS20 (antenna GS15) with a real-time kinematic (RTK) signal (accuracy measurements ranges from 0.03 m to 0.7 m). Next, the trees in the SP plots were positioned by measuring the azimuth with a field goniometer, while the horizontal distance of each tree and the inclination from the plot centers was determined using a Vertex Laser Geo meter. The accuracy of foot location of trees in the SP plots is within 0.5m and 1.2 m. The field-based inventories used as ground truth contain measurements taken between October 2019 and July 2021. The changes in structural traits of max. two years between field-based measurements and UAV LiDAR data acquisition were considered negligible for the purposes of this study and no major disturbance events were registered during this period.

2.3 | Method setup

The workflow followed in this study is presented in Figure 3. Initially, the PCD generation followed the approach described in Revenga et al. (2022) [52]. The resulting PCD scene was normalized and rasterized to obtain a canopy height model (CHM), which in turn was subject to individual tree crown segmentation producing a two-dimensional polygon dataset. For the CHM segmentation, we utilized a watershed algorithm specifically designed for coniferous forests [57]. The match between field-based measurements and individual tree crown (ITC) polygons was conducted based on the closest distance between the field-based GNSS point measurement and the ITC polygon centroid.

In order to ensure that only the LiDAR-detected trees would be accounted for in the regression experiment, a pre-processing task was required (marked * in Figure 3, the details of the preprocessing tasks involved are given in Annex II). Afterwards, using the LiDAR-derived height as polygon attribute, we calculated the distance at which the spatial autocorrelation of tree height was most significant in order to define the optimal neighborhood size (as explained in Section 3.1). Once the optimal neighborhood size had been defined, we conducted the local indicators of spatial association (LISA) analysis [58, 59] and outlier analysis [60, 61] to retrieve neighborhood metrics. Finally, two separate supervised regression experiments were performed, in order to predict DBH based on LiDAR-derived metrics: one including the neighborhood metrics (context-aware regression), the other without taking those metrics into account (context-unaware regression). Finally, AGB was estimated from the predicted DBH via an allometric function (as defined in Eq. 5).

Finally, we conducted a second task to characterize the morphometry of tree assemblages (i.e. groups of adjacent trees fulfilling a specific criterion of height similarity, as explained in Section 2.3) stemming from the ITC polygon dataset. Prior to the morphometric analysis of tree assemblages, a second pre-processing task was conducted (details are given in Annex II).

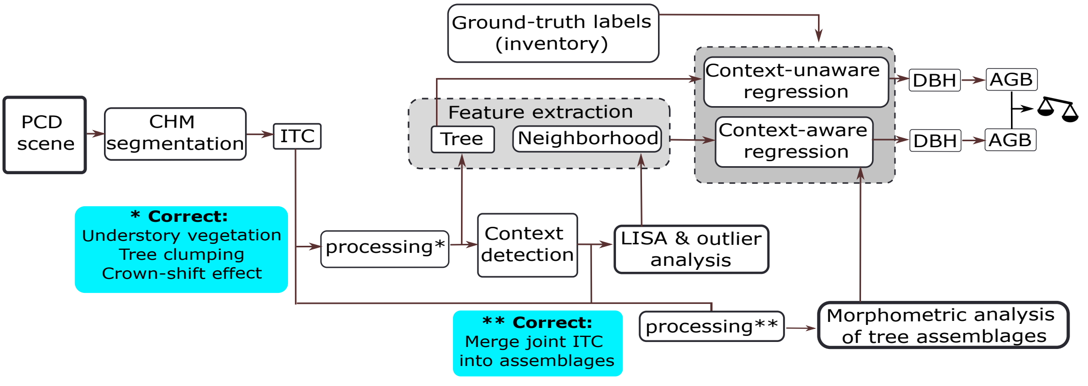

FIGURE 3 Workflow followed in this study. PCD: point cloud data, CHM: canopy height model, ITC: individual tree crown, LISA: local indicators of spatial association, DBH: diameter at breast-height, AGB: aboveground biomass. The two blue boxes describe the subtasks constituting each of the processing steps, marked * and ** in the diagram.

| Definition of Context Via Tree Heights in the Neighborhood

We determined the distance at which neighborhood metrics should be calculated (i.e. how many surrounding trees should be accounted as neighbors) based on local similarity of tree height. Accordingly, the selection of an appropriate neighborhood size around each individual tree (i.e. context detection) [62] was calculated through the analysis of spatial autocorrelation of tree height as function of incremental distance, as in previous studies [63]. Based on the global peak in the significance of spatial autocorrelation, we defined a characteristic distance within which all included trees should be considered as neighbors. Then, all so-defined neighbor trees were accounted for to compute context-aware metrics.

The local context information was encoded as metrics derived from the distance-weighted individual tree heights in each neighborhood, calculated at each tree location. Specifically, the metrics computed to define the local context were: local Moran's I [58] (i.e. an estimate of local significance of tree height similarity with respect to the global variance); and (SL_i) of tree height (i.e. a weighted average of heights calculated entirely locally) [64].

Local Moran's I_i is a well-established distance statistic in spatial data analysis [65], used for detecting local spatial autocorrelation and included within the family of LISA methods [58, 59, 64]. Similarly to other geostatistics methods [66], it relates attribute similarity with locational similarity, mapping autocorrelation across the geographic space. In the following definitions, σ is the global sample standard deviation of tree height; n and m represent the total number of instances (i.e. all trees in the forest) and the number of neighbors to each tree, respectively; y_i indicates the magnitude of interest at a particular point of interest (i.e. tree height) while the overline (i.e. $\overline{y}$) indicates the global average; $w_{i,j}$ indicates the distance weighting of each neighboring tree (here defined as inverse distance weighting); subindexes i and j indicate the tree of interest and a neighbor tree, respectively. Let $y_1, \ldots, y_n$ be the tree height values of all the n trees in the dataset. Then, the Local Moran's I_i [58] is defined as

$$I_i = \frac{y_i - \overline{y}}{\sigma^2} \sum_{j \in N_i, j \neq i} w_{i,j} (y_j - \overline{y}), \quad (1)$$

where $\mathcal{N}_i \subset \{1,...,n\}$ is the set of indices corresponding to the nearest neighbors of tree $i \in \{1,...,n\}$ in the overall set, where

$$\overline{y} = \frac{1}{n}\sum_{i=1}^{n} y_i, \tag{2}$$

and

$$\sigma = \sqrt{\frac{\sum_{i=1}^{n}(y_i - \overline{y})^2}{n-1}}, \tag{3}$$

are the global average height and the global sample standard deviation, respectively. It should be noted that insofar I_i includes global metrics (such as n, σ and $\overline{y}$), it is not entirely locally computed, but may present correlation with global features (i.e. characteristics derived from the entire dataset; cf. Westerholt et al. 2018) [67].

The Spatial Lag (SL_i) of tree height for a tree i is a spatial smoother [68] defined as

$$SL_i = \sum_{j \in \mathcal{N}_i, j \neq i} w_{i,j} y_j \tag{4}$$

where the elements of the spatial weights matrix ($w_{i,j}$) are row-standardized, so that $\sum_{j \in \mathcal{N}_i, j \neq i} w_{i,j} = 1$. Therefore, SL_i can be seen as a weighted average of the heights of neighboring trees [69].

The neighborhood metrics finally chosen as context-aware predictors are the following: local Moran's Index (I_i), z-score of I_i, p-value of I_i, z-transformed value of I_i and SL_i—computed at 20 m, 30 m , 40 m and 50 m distance bands. Additionally, the mean heights of the k-nearest trees, with k $\in (5-75)$, were also included as predictors. Likewise, we also included the topographic wetness index (TWI) [70] in order to evaluate the relative predictive performance of neighborhood metrics with respect to a well-established environmental variable as tree-growth predictor [71] (details are given in Annex VII).

Finally, we included in the regression experiments predictive features informing of local neighbor dissimilarity, i.e. local outliers of tree height. We detected local outliers using Local Outlier Factor [60] and Isolation Forest [61] algorithms. The evaluation of these features allowed us to discern between the contribution of local similarity features (i.e. Local Moran's I_i and SL_i) and that of the local outliers.

| Tree Assemblages' Morphometry

In order to define the tree assemblages, both local Moran's I_i and SL_i were computed at the optimal distance band to obtain neighborhood metrics, i.e. based on the global peak in the significance of spatial autocorrelation of tree height as a function of distance (using ArcGIS Pro) [72].

Tree assemblages were therefore defined as geographically continuous groups of trees delineated according to either (i) variation of local Moran's I_i of tree height, or (ii) according to quantiles of SL_i of tree height. The rationale for using two different statistics to calculate tree neighborhood metrics and thus delineate different tree assemblages was that while SL_i is entirely locally calculated, local Moran's I_i includes global features (and is therefore sensitive to the statistical characteristics of the dataset as a whole), as explained in Section 2.3. In order to discern which of the two approaches resulted most convenient in delineating tree assemblages (the former *entirely* local; the latter only *partially* local), both were included.

Tree assemblages defined according to local Moran's I_i are geographically continuous groups of trees with significantly different heights than the global tree height average, and they also lie in a region with significantly different neighbors. Local Moran's I_i identifies regions where the clustering of either high or short trees occurs. In the standard notation [64] (i.e. *High-High* or *Low-Low*), the first term refers to the individual tree and the second to the neighborhood (e.g. a tree belonging to a *High-High* assemblage is a "significantly high tree" in a "significantly high neighborhood"). The areas not showing statistical significance (a p-value $\geq$ 0.002 was considered sufficient) were labeled as *Not-Significant*. The significance test is based on random permutations (n = 499) of neighboring tree-height values at each step in the computation. The number of permutations and p-value indicate that, under the null hypotesis (i.e. tree heights being randomly distributed), a single tree canopy is likely to be wrongly classified with a probability of 0.002, which was deemed sufficient for the purpose of evaluating tree assemblage morphometry (i.e. if 1 out of 499 trees is wrongly attributed to a neighborhood, the morphometry of the assemblage will not change markedly). Then, for every permutation, a local Moran's I_i value was calculated by randomly rearranging the tree heights of neighboring values. The result is a randomly generated reference distribution of expected local Moran's I_i that is compared against the observed local Moran's I_i (Eq. 1) [59]. In this way, tree assemblages defined according to local Moran's I_i are classified as: *High-High*, *Low-Low*, or *Not-Significant*.

Likewise, tree assemblages defined according to SL_i of tree height are geographically continuous groups of trees delimited according to the local weighted average of tree height [69], as defined above (Eq. 4). For the purpose of this study, 5 subdivisions based on quantiles were deemed convenient, rendering a classification of tree assemblages based on SL_i ranking as: *Highest*, *High*, *Mid*, *Low* and *Lowest*.

The morphometric analysis examined the outer boundaries of the tree assemblages as defined above. Twenty basic morphometric parameters as well as 20 derived parameters were calculated for each type of tree assemblage. The 20 basic morphometric variables are simple parameters obtained by fitting elemental geometric shapes to each tree assemblage polygon (e.g. area of maximum inscribed circle), and basic positional parameters (e.g. XPOL, which is the X coordinate of the centroid of the tree assemblage polygon). The 20 derived parameters are adimensional metrics (except for concavity [73], measured in m) computed from the 20 basic morphometric variables, as explained in Güler et al. 2021, [74] (details are given in Annex III). The morphometric analysis of tree assemblages was conducted using PolyMorph-2D algorithm [74], which is a toolbox for the morphometric analysis of vector-based polygon objects, available as a plug-in for the open source JumpGIS software [75].

| Regression Models Selected

The regression experiments were designed to predict DBH, since AGB is a variable determined by the combination of DBH, height and wood density [9]. Instead, DBH is directly measured in the field, which makes it a better defined regression target. Therefore, the model estimates of AGB were derived from the DBH prediction outputs by means of an allometric fit (Eq. 5). Predicting DBH, instead of AGB directly was chosen as more suitable, as it avoids burdening the learning models with the statistical error contained in the allometric fit. Three feature-based shallow learning regression methods were selected: namely AdaBoost [76, 77, 78], Lasso [79] and Random Forest [80] regressors. The AdaBoost regressor is a tree-based gradient-boosting method that relies on stage-wise additive expansions. Its effectiveness stems from combining weak learners to form a generalized prediction hypothesis. Random Forest is a well established tree-based ensemble regression method. Finally, Lasso, on the other hand, is a linear model with an *L1* prior penalty acting as a regularizer [81]. In our case, all three shallow regression methods utilize the features derived from the ITC polygon dataset resulting from the CHM segmentation.

Context-unaware regressions were defined as those in which a learning model performs DBH regression by taking as predictors only individual tree attributes derived from the ITC polygon dataset (i.e. tree height, canopy area and canopy perimeter), as it is a common approach [8]. On the other hand, we defined context-aware regressions as those regressions in which context-aware features are additionally introduced as input in the predicting feature space. These were either neighborhood metrics, e.g. SL_i of tree height, or TWI at different spatial resolutions (Section 2.3) . For every model predicting DBH from individual tree attributes (i.e. context-unaware conditions) we implemented a context-aware counterpart. This allowed us to evaluate the impact of context on regression model performance.

| Model Training and Validation of Results

A hard validation of AGB is not possible without harvesting trees destructively, which raises obvious ethical, legal and economic issues. Instead, non-invasive methods that use remote sensing data and allometric functions are the standard procedure for estimating AGB [82]. Here, we estimated AGB from tree height, DBH, wood density and an allometric function Norway spruce trees (eq. 5). Therefore, the regression analyses conducted focused on comparing performance of predictions on DBH between twin shallow learning methods (i) "context-unaware" and their (ii) "context-aware" counterparts.

We chose DBH as the variable to test model predictions, which is a tree morphological trait contained in the field-based forest inventory, and therefore directly measured by *in situ* monitoring. Next, in order to assess the benefits of including context in the regression models, we compared results using AGB of individual trees. Specifically, AGB estimates were derived via species-specific allometric and wood density functions, tree height retrieved via UAV LiDAR, and DBH predicted via ML regression. Specifically, the allometric model used was the one proposed by Dalponte and Coomes (2016) [9]:

$$AGB_{tree} = \alpha \cdot WD_{spruce}^{\beta} \cdot (DBH - d_0)^{\gamma} \cdot H^{\delta}, \tag{5}$$

where the wood density value (WD_{spruce}) was taken from Alpine spruce dendrometric models [83], *DBH* was predicted via ML regression and height (*H*) was extracted from the UAV LiDAR data. $\alpha, \beta, \gamma, \delta$ and d_0 are species-specific fitted allometric parameters [84], obtained from allomeric fits to harvested spruce trees by the Forestry and Wildlife Service Agency of the province of Trento (an Italian neighbouring province southeast from the study site, also used in Dalponte and Coomes, 2016) [9], and we consider them applicable to the Seehornwald Davos research site. At all events, for the purpose of assessing the benefits of a context-aware approach, the specific characteristics of the allometric fit used are negligible, as it is only used to quantify a difference in terms of AGB, and both types of predictions (unaware and aware) take the same equation. Therefore, the predicted value of DBH (in either aware or unaware conditions) was input into Eq. 5, in order to obtain model predictions of AGB. This allowed to compare AGB predictions with the ground truth values of AGB, which were similarly obtained via the field-based measurements (provided by the regular tree-monitoring campaigns of ICOS [49] and WSL [46]) and Eq. 5.

The technique used to estimate model prediction error consisted of a nested cross-validation (NCV) scheme [85]. Following the NCV scheme, we divided the input dataset into 10 inner and 10 outer folds. In NCV, the results in the inner folds report of the training performance, and they are used for model optimization, while the mean performance on the outer folds is the one used for model evaluation. The model inspection technique used to evaluate predictors' influence on the DBH regression results was the permutation importance method as proposed by Altmann et al. (2010) [86]. The feature-elimination procedure consisted of eliminating progressively those predictors that presented a negative mean importance, as they were considered harmful to the model's performance. The significance of the enhancement in context-aware predictions and effect size was assessed using Wilcoxon signed-rank test [87] and Cliff's Delta analysis [88], respectively.

3 | RESULTS

3.1 | Context Detection and Tree Assemblages

The analysis of spatial autocorrelation of tree height as function of incremental distance resulted in a maximum significance of clustering at a distance of 40 m. Figure 4 (a) shows the calculation of local Moran's index (I_i) of tree height at different distance bands. Figure 4 (b) shows the standard score (i.e. z-score) of I_i obtained at each distance band, resulting from comparing the observed I_i and the expected I_i under the tree height randomness assumption (details included in Annex I). As a precaution, we ran context-aware regression experiments including also context features retrieved at shorter (i.e. 20 m, 30 m) and larger (i.e. 50 m) distances than the optimal range (i.e. 40 m). The context features retrieved at these distances (i.e. 20, 30, 40 and 50 m) which contributed to improve the predictions of DBH were all included in the final regression models.

In Figure 5, panels a and b show the spatial distribution of tree assemblages calculated using either local Moran's I_i or SL_i of tree height, respectively, at 40 m range. While both types of assemblages show similarities as regards extent, morphometry and location, SL_i captures more local variability. This is not only due to a higher discretization (5 groups in SL_i, vs. 3 groups in local Moran's I_i), but also to the fact that SL_i is insensitive to the variance in the dataset beyond the range of its neighborhood, as explained in Section 2.3.

The morphometric analysis provided 40 additional features that were evaluated as potential predictors of DBH. In Figure 6, panels a and b visualize the results of the morphometry analysis of tree assemblages defined by local Moran's I_i and by SL_i, respectively. The circular barplots show the average magnitude as bar lengths, and the standard deviation as dots. Both mean and standard deviation values are shown as min-max scaled (across assemblage types) to present all variables on the same radial axis and to ease visual comparison, i.e. for every morphometric variable, the highest value is replaced by 1, the minimum is replaced by 0, and the intermediate values are linearly interpolated between 0-1. It can be observed (Figure 6) that the morphometric variables follow very similar trends when tree assemblages are defined based on local Moran's I_i or SL_i. However, an observed difference between SL_i and local Moran's I_i was found in the heteroscedasticity of the morphometric variables calculated, where only in the former case variance of all metrics scaled with magnitude.

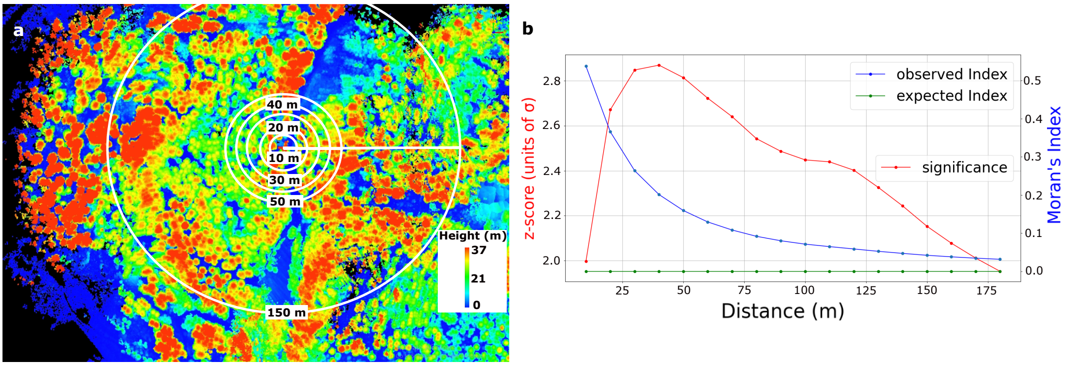

FIGURE 4 Context detection. **a:** Normalized point cloud data (PCD) scene colored by tree height overlaid with a selection of the appropriate radii for defining the neighboring context. **b:** Autocorrelation of tree height as function of distance. The red line shows the number of standard deviations (σ) that an observation is away from the expected value (under the assumption of heights being randomly distributed). The blue and green lines show the actually observed local Moran's Index and the expected value under randomness assumption, respectively.

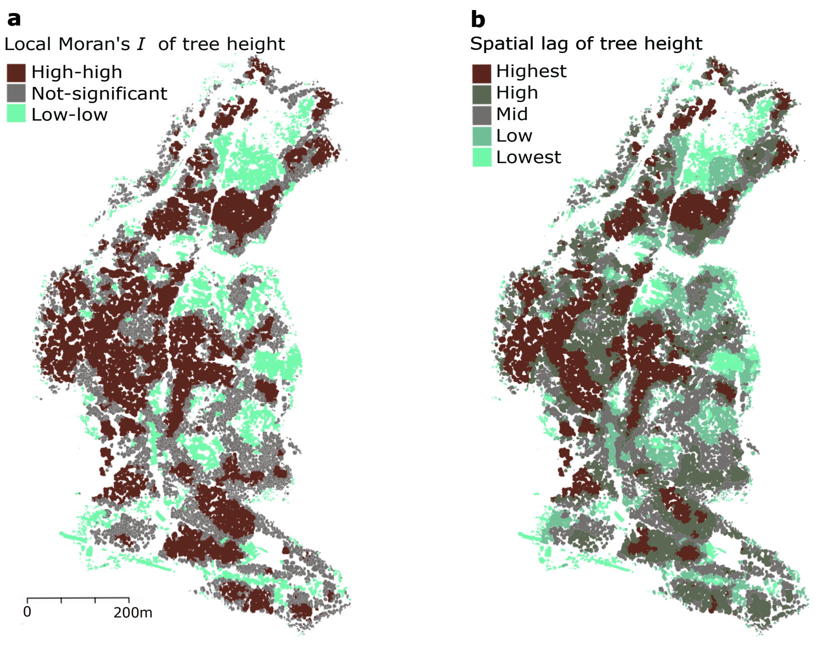

FIGURE 5 Tree assemblages defined by local similarity of tree height. **a:** Delineated according to local Moran's I_i of tree height. **b:** Delineated according to spatial lag of tree height.

While not for all variables a systematic trend was found, for several basic morphometric variables a linear positive correlation between them and SL_i was observed, as shown by the Pearson coefficient (ρ). This is the case for polygon

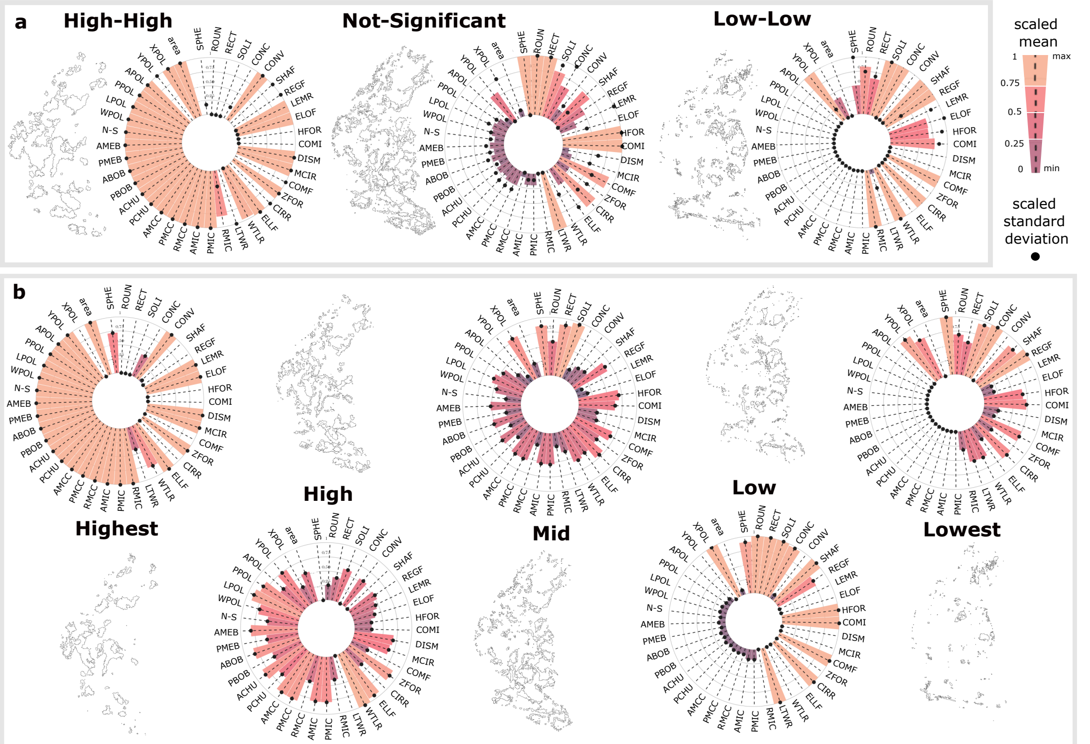

FIGURE 6 Morphometric analysis of tree assemblages grouped by **(a)** local Moran's I_i, and **(b)** by spatial lag of tree height. Bar length and color gradient represent the mean value, while black dots represent the standard deviation (SD) over all tree assemblages. Both mean and SD are scaled (min-max) to allow comparison of all metrics across assemblage types on the same axis—i.e. for every morphometric variable, the highest value of a certain assemblage type is replaced by 1, the minimum value is replaced by 0, and the intermediate values are linearly interpolated in between the range (0-1). YPOL: northing of centroid of the tree assemblage; XPOL: easting of centroid of the assemblage; APOL: area of polygon (P); N-S: defined as $|sin(azimuth)|$, shows the alignment of the main axis of P with the North-South direction; PPOL: perimeter of P; LPOL: major axis length (L) of P; WPOL: minor axis length (W) of P; ABOB: area of the bounding box fully containing P; PBOB: perimeter the bounding box fully containing P; AMEB: area of the minimum enclosing box fully containing P; PMEB: perimeter of the minimum enclosing box fully containing P; ACHU: area of containing hull ; PCHU: perimeter of convex hull fully containing P; AMCC: area of the minimum circumscribed circle (MCC); PMCC: perimeter of MCC; RMCC: radius of MCC; AMIC: area of maximum inscribed circle (MIC); PMIC: perimeter of MIC; perimeter of MCC; RMIC: radius of MCC; LTWR: length-to-width ratio [89]; WTLR: width-to-length ratio [90]; ELLF: ellipticity factor [91]; CIRR: circularity ratio [92]; ZFOR: Zavoianu's form factor [93]; COMF: compactness factor [74]; MCIR: Miller's circularity ratio [94]; DISM: dispersion measure [92]; COMI: complexity index [74]; HFOR: Horton's form factor [89];ELOF: elongation ratio [95]; LEMR: lemniscate ratio [96]; REGF: regularity factor [91]; SHAF: shape factor [91]; CONV: convexity [97]; CONC: concavity [73]; SOLI: solidity [98]; RECT: rectangularity [99]; ROUN: roundness [97]; SPHE: sphericity [100]. Correlation coefficients of the most prominent variables are given in Annex III.

area (ρ= 0.95), perimeter of polygon (PPOL; ρ=0.98) and radius of the minimum circumscribed circle (RMCC; ρ=0.98). Additionally, a positive correlation was found for some derived morphometric variables, namely: length-to-width ratio (LTWR; ρ=0.75) [89], circularity ratio (CIRR; ρ=0.88) [92], compactness factor (COMF; ρ=0.89) [74], dispersion measure (DISM; ρ=0.90) [92], complexity index (COMI; ρ=0.88) [74], lemniscate ratio (LEMR; ρ=0.81) [96], regularity factor (REGF; ρ=0.82) [91], and concavity (CONC; ρ=0.96) [73]. Conversely, other morphometric variables showed a decreasing trend with increasing SL_i. A clearly negative correlation between SL_i and the following derived morphometric variables was found: Miller's circularity ratio (MCIR; ρ=-0.88) [94], Horton's form factor (HFOR; ρ=-0.88) [89], elongation factor (ELOF; ρ=-0.83) [95], shape factor (SHAF; ρ=-0.95) [91], rectangularity (RECT; ρ=-0.85) [99] and roundness (ROUN; ρ=-0.69) [97].

3.2 | AGB Predictions: Aware vs. Unaware of Local Context

Regression experiments including context-aware features improved predictions of DBH consistently (Figure 7, Tables 1 and 2), resulting in enhanced tree-level AGB predictions via allometry (Eq. 5). All shallow learning methods improved prediction performance w.r.t R^2, RMSE and MAE in both SP- and CP-datasets. For each pairwise comparison, the improvements were consistent, although the degree of prediction enhancement differed between the two datasets considered. Predictions in the CP-dataset observed a lower enhancement in comparison to predictions in the SP-dataset. For instance, RMSE was reduced by 9.1% (SP-dataset) vs. 4.0% (CP-dataset), and R^2 increased by 3.5% (SP-dataset) vs. 3.2% (CP-dataset). This was expected, due to less variability in context in the CP-dataset, and may be indicative that capturing higher variability by the additional context features make them more effective.

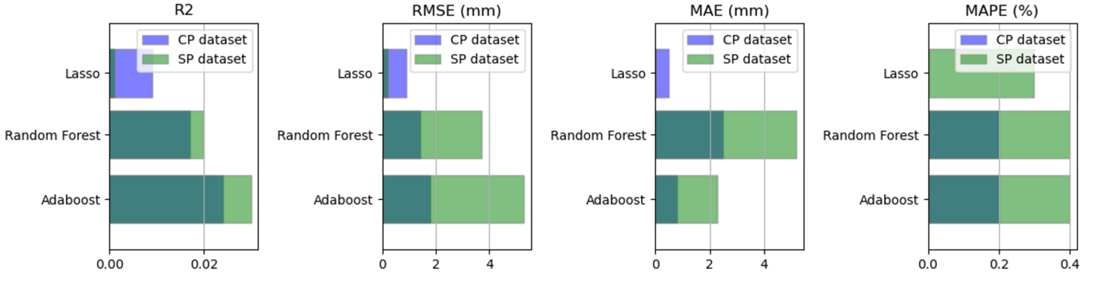

FIGURE 7 Enhancement of predictions of diameter at breast height per model type as a result of including context-based predictor variables (zero-reference corresponds to the prediction performance without including context-based predictors).

Figure 8 (a) shows the ground truth labels (i.e. field based estimates of AGB), which were derived from the field measurements and a species-specific allometric fit (i.e. Eq. 5). The central panel (b) shows the spatial distribution of residuals (i.e. $\epsilon = AGB_{ground\_truth} - AGB_{prediction}$) of the AdaBoost context-aware regression results. The mean values converge towards zero (i.e. $\overline{\epsilon}_{SP}$ = 3.8 kg , $\overline{\epsilon}_{CP} = -3.2$ kg), while the spread of the error distribution varies between SP and CP-datasets (i.e. $\sigma(\epsilon_{SP})$ = 123 kg, $\sigma(\epsilon_{CP})$ = 140 kg).

Figure 8 (b) shows the lack of high spatial autocorrelation of errors (i.e. low clustering of errors), indicating that predictions do not seem geographically biased. Figure 8 (c) displays the error distributions in both datasets. SP-errors show a unimodal distribution with a slight overestimation of DBH of -28 mm. CP-errors present a similar overestimation bias (-25 mm) with a bimodal distribution (the second mode is located at 25 mm of underestimation). The second mode of the bimodal pattern in the CP-dataset may correspond to the more frequent occurrence of larger trees, which tend to be underestimated (Figure 8, c, lower panels). It can be observed that, generally, smaller and thinner trees tend to be slightly overestimated (i.e. in the first two quantiles) compared to the largest trees, which tend to be underestimated.

Figure 9 presents the analysis of the relative importance of all predictors considered in the context-aware DBH regression with the AdaBoost regression model (i.e. the best performing one). The analysis reveals that in both SP- and CP-datasets, the most important context-based predictors are the average heights of the 5, 10, and 15 nearest neighboring trees, outperforming some individual-tree metrics, such as the crown metrics.

TWI made a marginal contribution to enhanced predictions, which was less than that of any neighborhood metric. Moreover, although modest, TWI exhibited a greater impact on improved predictive performance at finer spatial resolutions in both datasets (Figure 9), whereas its contribution decreased at coarser resolutions (e.g. it did not significantly contribute as a predictor at 10 m^2 resolution). This observation may indicate that the spatial resolution at which TWI is most informative of individual tree height, is similar to the usual tree crown size (i.e. 2-5 m^2 resolution), while at a coarser spatial resolution its contribution as predictor becomes negligible.

TABLE 1 Results (on test set) of the SP-dataset, for each pairwise model comparison (aware vs. unaware of context features). Predictor variables are entirely LiDAR-derived; the target variable is diameter at breast-height (DBH, in mm). The values are presented as mean ± standard deviation of the 10 outer CV folds of the nested scheme. One asterisk (*) marks results where the enhancement introduced by context-awareness is statistically significant with "small" size effect, while ** and *** mark "medium" and "large" size effect, respectively. The best results are shown in bold.

Regression model	R^2	RMSE (mm)	MAE (mm)	MAPE (%)
AdaBoost (unaware)	0.830 ± 0.05	58.0 ± 9.0	43.3 ± 4.4	19.1 ± 1.9
AdaBoost (aware)	**0.860** ± **0.03** ***	**52.7** ± **5.3** ***	**41.0** ± **3.1** **	**19.5** ± **1.7**
Random Forest (unaware)	0.818 ± 0.04	60.2 ± 7.3	46.8 ± 4.5	22.8 ± 5.8
Random Forest (aware)	0.838 ± 0.05 *	56.5 ± 9.2 *	41.6 ± 5.4 ***	22.4 ± 5.1
Lasso (unaware)	0.851 ± 0.02	54.6 ± 4.9	4.20 ± 3.3	19.1 ± 1.4
Lasso (aware)	0.852 ± 0.02	54.4 ± 4.9	4.17 ± 3.5	18.8 ± 1.7

TABLE 2 Results (on test set) of the CP-dataset, for each pairwise model comparison (aware vs. unaware of context features). The predictive variables are entirely LiDAR-derived; the target variable is diameter at breast-height (DBH, in mm). The values are presented as mean ± standard deviation of the 10 outer CV folds of the nested scheme. One asterisk (*) marks results where the enhancement introduced by context-awareness is statistically significant with "small" size effect. The best results are shown in bold.

Regression model	R^2	RMSE (mm)	MAE (mm)	MAPE (%)
AdaBoost (unaware)	0.713 ± 0.07	54.7 ± 5.98	43.0 ± 5.26	15.5 ± 2.4
AdaBoost (aware)	0.737 ± 0.05 *	52.9 ± 5.28 *	42.2 ± 4.43 *	15.7 ± 3.1
Random Forest (unaware)	0.688 ± 0.07	57.0 ± 5.9	43.8± 5.1	15.7 ± 3.1
Random Forest (aware)	0.705 ± 0.04	55.6 ± 5.3	41.3 ± 5.5 *	15.9 ± 4.3
Lasso (unaware)	0.741 ± 0.09	51.3 ± 6.6	39.1 ± 5.2	13.6 ± 1.6
Lasso (aware)	**0.750** ± **0.08**	**50.4** ± **5.9**	**38.6** ± **4.1**	**13.6** ± **1.1**

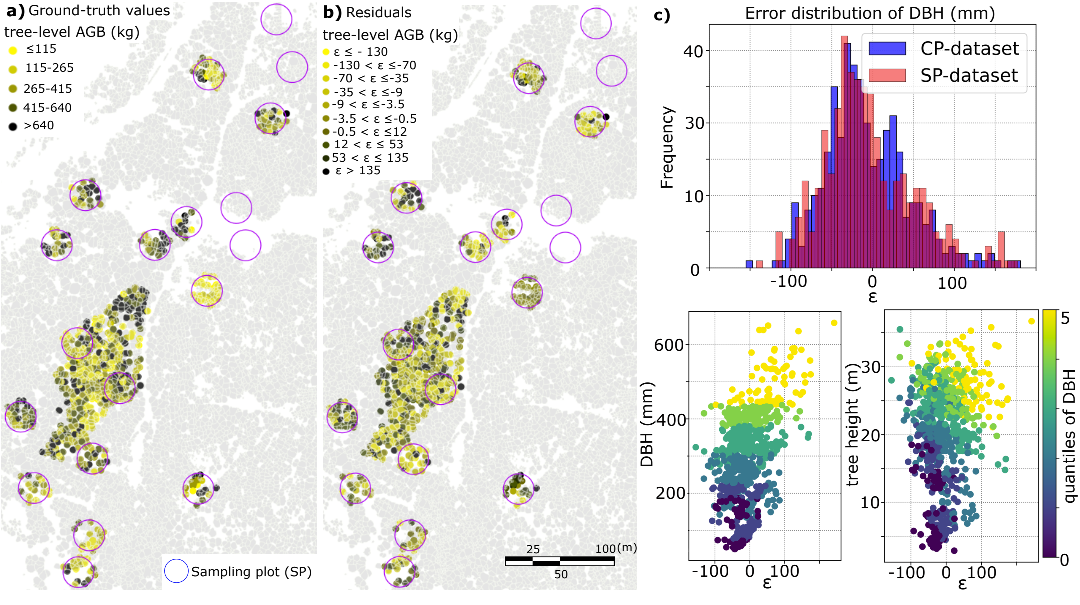

FIGURE 8 **a**: Spatial distribution of tree-level aboveground biomass (AGB) according to ground truth measurements. **b:** Spatial distribution of residuals ($\epsilon = AGB_{ground-truth} - AGB_{prediction}$) of AGB predictions with AdaBoost context-aware regression, grouped by quantiles (negative values indicate overestimation). The four empty SP-plots (and the southernmost one not included) correspond to areas where the quality of the UAV LiDAR data collection was compromised (Annex VI). **c**: Error distributions of diameter at breast-height (DBH) in sampling plot (SP) and control plot (CP) datasets. The two bottom-right panels show the error distribution of DBH (in x-axis) vs. field-measurements of DBH and tree height. The color scheme refers to the quantiles of each dataset separately, which are differently distributed (Annex V).

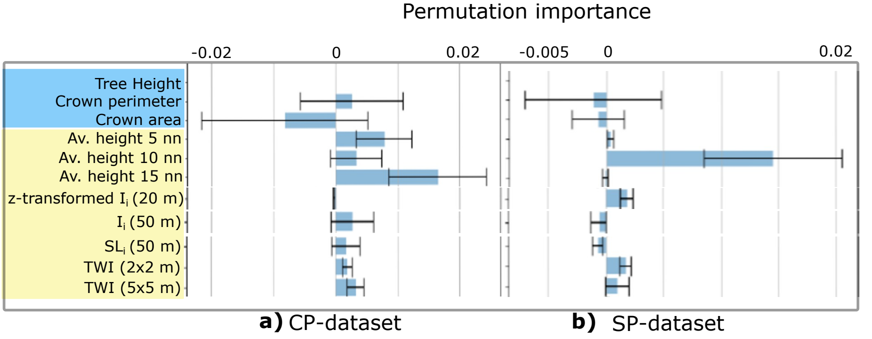

FIGURE 9 Inspection of predictors' permutation importance [86] in the AdaBoost regression experiment in context-aware conditions. The left panel **(a)** shows results in the control plot (CP) dataset, and the right panel **(b)** shows results in the sampling plot (SP) dataset. Bar length and error bar show the mean and standard deviation of a predictor's importance, respectively. Predictors highlighted in blue are individual tree traits; predictors highlighted in yellow are context-based. In both datasets, it can be noted how the average heights of the 5-15 nearest neighbors (nn) stand out as the strongest predictors, outperforming crown perimeter and crown area. In both plots (**a** and **b**), individual tree height (with importance: 0.85 in CP-dataset; 1.3 in SP-dataset) has been removed to facilitate visual comparison of the remaining predictors. Only the 11 most significant predictors are included; an extended figure is shown in Annex VII.

4 | DISCUSSION

4.1 | Enhancement of Tree-Level AGB Prediction

This study presents a method to enhance tree-level AGB estimates for coniferous forests using UAV LiDAR surveying and context-aware shallow learning regression methods. Our findings are consistent with established context learning literature [35, 36, 37, 38, 39, 40], remote sensing trait mapping studies [16, 34], and methodological advances on forest modelling—namely, NLME methods [17, 18] and competition-based studies [19, 20, 21]. We further extend this approach to a fully integrated UAV LiDAR framework. The pairwise comparison of twin methods consistently showed that context-aware regressions outperformed context-unaware regressions across models (except for Lasso in the SP-dataset, where performance virtually stagnated), and in no case adding context information became detrimental. This finding may indicate that gradients in tree heights across the ecosystem proxy for hidden environmental and biotic mechanisms (e.g. windstorm disturbance, nutrient and soil moisture abundance, light harvesting competition) [101, 102] that influence tree growth, and can therefore be leveraged to enhance predictions of AGB at the single tree level. The results showed a consistently improved performance in AGB prediction when including context. The improvements were tested as statistically significant in four of the six pairwise experiments, with size effect raging from small to large (Tables 1 and 2).

The accuracy enhancement gained from including context-aware features in the regression experiments varied between the two datasets considered (i.e. SP-trees and CP-trees). Context-aware regressions of DBH in SP-trees experienced greater enhancement than in CP-trees. This is consistent with the fact that the CP-dataset contains less variability of context, since it is a locally clustered and more homogeneous dataset, while the SP-dataset includes more variability in context features (Figure 2, b). The investigated Norway spruce forest presents a heterogeneous landscape, where the distribution of tree heights varies in space (Figure 5). Hence, the UAV LiDAR survey gives rise to a non-homogeneous dataset [62], which is a non-trivial question in automated tree phenotyping and functional trait mapping with ML methods [30, 34]. As SP-trees are grouped in scattered plots across the forest, their spatial distribution spans hundreds of meters, making them subject to a more diverse context than the very local CP-dataset.

4.2 | The Role of Neighboring Context in AGB Prediction Performance

Most shallow learning models achieved enhanced predictions when contextual information was included, with results consistently showing no deterioration (Tables 1 and 2). The average heights of the 10 and 15 nearest neighbors wer the most important context based predictore for SP- and CP-trees, respectively (Figure 9). Moreover, the degree of local similarity of tree height (i.e. SL_i, local Moran's I_i) was most important and, to a lesser extent, the LiDAR-based TWI, indicating that although TWI may be a good predictor of tree growth [71], the neighborhood information resulted more useful significant, which lies in agreement with previous literature [23]. In contrast, including features informing about neighbor dissimilarity, such as local outliers of tree height detected using Local Outlier Factor [60] and Isolation Forest [61] algorithms did not result in enhanced predictions (thus not shown here). We hypothesize that metrics containing information about the degree of local similarity may reveal the combined effect of ecological processes that are specific to the immediate neighboring context. In contrast, metrics that proxy for dissimilarity do not help to uncover such processes, although they remain useful in detecting outstanding trees (i.e. local outliers).

Context-based features at closer distances generally showed larger predictive power but also larger variance (as less neighboring trees were computed). For instance, the p-value of Local Moran's I_i at a 20 m range in the CP-dataset has an average positive effect but is not a stable predictor (Figure 9, a). This can be observed in the general trend of larger standard deviations in the permutation importance of predictors retrieved at short ranges than at greater distances (Annex VII). In accordance with competition-based studies [19, 20, 21], we observe that the strongest context-based predictors are those retrieved from the immediate neighboring trees in both datasets, i.e. the average height of 5, 10 and 15 nearest neighbors. However, our method additionally allows to compare the relative importance of competition-derived metrics and other context-based metrics operating at larger scales. For instance, in Figure 9 (a) it is shown that local Moran's I_i retrieved at a 50 m range is comparable in importance to the average height of the closest 10 neighboring trees A general difference observed between the CP and the SP-datasets is that the predictors' importances in the CP-dataset fluctuate more (i.e. larger standard deviations). Further, in the SP-dataset, predictors rarely become negative and if they do, it is to a lesser extent. Including morphometric variables calculated from the tree assemblages (shown in Figure 6) in the regression experiments did not result in improved predictions of DBH and therefore were not included in the final modelling of DBH.

Considering context metrics to enhance estimates of DBH at the individual tree level in coniferous forests has been suggested in seminal works [25, 103] and been adopted subsequently for various applications in forest research [24, 26, 21]. Moreover, recent investigations on tree morphology and productivity in coniferous forests [19, 20] have motivated the further development of competition-aware approaches to improve the prediction accuracy of individual tree traits (e.g. growth), leveraging tree canopy metrics.

In forest biomass research, a commonly recognized approach is calibrating regression models with plot-level metrics for predicting tree-level structural traits (e.g. plot-level random effects in NLME methods), which has been pointed out as a methodological limitation [23]. Indeed, the results of such approaches are constrained by the artificially-delineated plot size, and it has been observed that accuracy increases with a progressively larger plot size [16, 18]. Our method to select context based on the spatial autocorrelation of tree heights (Figure 4) may indicate the range of saturation of such improvement (40 m in this research site). Furthermore, our results show that the variability and extent of context determines its beneficial leverage for prediction of tree-level traits (e.g. DBH, AGB).

This study continues this line of work and sheds light on how the local spatial context can be defined and leveraged in tree-level structural trait predictions (i.e. DBH), making a case for AGB estimates in a Norway spruce forest. The analysis shows that there is an optimal range to computing neighborhood metrics. In the study case considered here, this corresponded to a 40 m range distance, based on the spatial autocorrelation of tree heights. Further, we found that the predictive power of context-based metrics is sensitive to context extent (i.e. the range at which such metrics are calculated). This observation may indicate that defining context based on plot-level metrics retrieved from artificially bounded units [16, 17, 18] may be seen as a constrained approach, as observed previously [23, 104]. Likewise, in the light of this observation, and in line with recent studies [105], determining the significant contextual extent of individual functional traits based on units of fixed size (e.g. pixel size) appears to be a suboptimal technique. Therefore, future forest research would probably benefit from including context-awareness determined by spatial association of tree traits, bearing in mind that context-detection is trait-dependent and may vary depending on dataset source—e.g. spatial autocorrelation as a function of distance (Figure 4) is sensitive to CHM segmentation quality—and method applied—e.g. delineation of tree assemblages varied slightly between local Moran's I_i, and SL_i, as we show in Figure 5.

Lastly, we note that optical remote sensing studies usually define the optimal scale of analysis as a trade-off between the observational extent (i.e. area surveyed) and the unit resolution (i.e. pixel size) [105, 106]. Also, in ecological research, it is common to subsample datasets using natural subregions based on ancillary ecological criteria (e.g. ecoregions, conservation status) [107]. Conversely, here we defined the range of influence of context-based metrics (i.e. the extent of tree neighborhoods) using a dataset-native approach, based entirely on the spatial association of individual tree heights. This permitted us to determine the context of influence unhampered by the remote sensing technique and not using external data sources. Furthermore, as local context was defined based on the spatial association of a real physical attribute (i.e. tree heights), and not defined by an artificially bounded unit (e.g. pixel size or plot size) the resulting distance could be considered characteristic of the forest ecosystem.

4.3 | Tree Assemblages

The analysis of morphometric variables for different tree assemblages (Figure 6) permitted to examine whether trees—grouped by local association of tree heights—persistently show different shapes at the group level, shedding light on the relationship between context-based traits (e.g. concavity of a tree assemblage) and single-tree heights. This analysis revealed certain patterns of trait convergence [108], which was specially remarkable for some metrics, which showed a strong correlation with tree height (e.g. concavity [73] and length-to-width ratio [89]). Nevertheless, none of the morphometric variables obtained from the tree assemblage analysis proved useful to improve predictions of DBH.

Remarkably, it was observed that tree assemblages delineated according to the spatial lag of tree height (i.e. SL_i, Figure 6, b) presented clear positive correlations with two-dimensional morphometric features at the tree assemblage level. For instance, assemblages with higher trees (i.e. labeled as *Highest* according to SL_i, or *High-High* according to local Moran's I_i) are consistently rounder, larger and more regular in shape. As visualized in Figure 6, SL_i correlates positively with shape regularity [91], two-dimensional concavity [73], length-to-width ratio [89] and size, indicating a consistent trait-convergence assembly pattern [108]. Higher trees seem to converge in most sheltered areas (i.e. thalwegs and local sub-basins) so that tree assemblages with highest SL_i tend to adopt the morphological features of the drainage network's shape (Annex III). Interpretation of this observation would go beyond the scope of this study. However, it may indicate that both the shape and location of tree assemblages of different heights are conditioned by underlying environmental and biotic driving mechanisms.

In the coniferous forest studied here, a significant degree of clustering of tree heights takes place (Figure 5, a), while spatial gradients of tree height present preferential shapes and directions (Figure 5, b). These observations indicate that there is tree-height convergence and a tendency toward optimal phenotype expression (i.e. maximum growth performance) around the runoff drainage network (in Annex III). Higher trees are found in sheltered regions and concave channels—which generally benefit from more frequent runoff events and deeper soils [109, 110]. This may indicate that favorable environmental conditions (e.g. deeper soil, lower soil moisture recession rates, greater availability of soil nutrients due to leaching) allow individuals to reach their optimal phenotype. Conversely, a lower SL_i of tree height in more exposed terrain (e.g. ridges, hilltops) may indicate that environmental filtering (e.g. windstorm disturbance) or a reduced competition for light could play a significant role in determining the location of low SL_i tree assemblages (Annex III). Thus, the relatively reduced tree height in exposed areas could indicate a passive adaptation of tree height to harsher environmental conditions [111], an active adaptation to higher light availability [101], a limitation to tree growth caused by other local factors, such as lower soil depth or nutrients availability [1, 110], or the effect of these factors combined. Nevertheless, we cannot provide an interpretation of such observations, as shifts in the variance of functional traits across environmental gradients, such as gradients in the spatial patterns of trait similarity, do not bring strong evidence of either biotic or environmental filtering on their own [112].

4.4 | Methods Applied and Limitations

We have aimed at preserving a fully-native UAV LiDAR approach, so that the applicability of the method proposed is not compromised by lacking local ancillary data (e.g. conservation status, edaphic conditions), whose availability may become a limiting factor in forest monitoring. We note that the these findings are specific to the mountainous Norway spruce forest considered here. Caution is advised when contemplating a direct application of this approach to more complex canopy structures and terrains, such as those found in deciduous, multilayered or broadleaf forests. The strength of our results is currently limited by the lack of replicates at different forest sites, so that we cannot yet confirm these findings to be generally applicable to a wider range of forest types and canopy configuraitons. Furthermore, the pre-processing tasks (marked * in Figure 3, Section 2.3) required as part of our experimental design, simplifies the actual PCD scene representing the real forest scenario. This simplification hampers a fully-automated, streamlined application, and case-specific considerations are still required. In sum, further research is needed to evaluate the transferability of the method.

5 | CONCLUSIONS

This study introduces and evaluates a fully integrated UAV LiDAR method that utilizes context information to improve the accuracy of AGB estimates of individual trees with shallow learning methods, making a case for a coniferous forest. The prediction performance demonstrated improvements in AGB prediction when incorporating context-aware features. The exception was the Lasso model, which stagnated in one of the datasets considered (SP-dataset). Importantly, in no case did contextual features have a detrimental effect. The results show that the use of context-aware features as predicting variables can substantially improve estimates of AGB in coniferous forests—i.e. the best performing model showed a reduction of RMSE of 9.1 % and 4.0 %, and an increase in R^2 by 3.5 % and 3.2 %, in the SP- and CP-dataset, respectively. For the best performing method (AdaBoost regression), the strongest context-based predictors were the average heights of the nearest 5-15 neighboring trees. Features that provide information about the tree neighborhood (e.g. SL_i of tree height, average height of k-nearest trees) contain useful information which can be leveraged by shallow learning methods to improve predictions of diameter at breast height, and aboveground biomass. This finding may suggest that the information retrieved from the local context serves as a proxy for underlying ecological mechanisms that exert influence on the individual tree aboveground biomass as a result of local adaptations to microclimate, edaphic conditions and biotic factors. We conclude that the use of UAV LiDAR surveys and the integration of the spatial associations of tree heights is an efficient approach to incorporate context and thus enhance forest biomass surveying.

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