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PERSPECTIVE

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Vegetation structure derived from airborne laser scanning to assess species distribution and habitat suitability: The way forward

Abstract

Ecosystem structure, especially vertical vegetation structure, is one of the six essential biodiversity variable classes and is an important aspect of habitat heterogeneity, affecting species distributions and diversity by providing shelter, foraging, and nesting sites. Point clouds from airborne laser scanning (ALS) can be used to derive such detailed information on vegetation structure. However, public agencies usually only provide digital elevation models, which do not provide information on vertical vegetation structure. Calculating vertical structure variables from ALS point clouds requires extensive data processing and remote sensing skills that most ecologists do not have. However, such information on vegetation structure is extremely valuable for many analyses of habitat use and species distribution. We here propose 10 variables that should be easily accessible to researchers and stakeholders through national data portals. In addition, we argue for a consistent selection of variables and their systematic testing, which would allow for continuous improvement of such a list to keep it up-to-date with the latest evidence. This initiative is particularly needed not only to advance ecological and biodiversity research by providing valuable open datasets but also to guide potential users in the face of increasing availability of global vegetation structure products.

1 | INTRODUCTION

Understanding the interactions of species with their environment is fundamental to predicting species distribution patterns and habitat use, and thus to improving biodiversity conservation and management. Early studies of species–environment relationships focused on measuring environmental variables at species observation points. From this, relationships were inferred that could, however, not be used to predict species occurrence at other locations where these explanatory variables were not available. This has changed markedly with the use of remote sensing data for assessing and modelling the distribution of species (e.g., Cord et al., 2013). An example that perhaps best illustrates the contrast between the methods used in the past and the present to collect data on species–environment relationships, is the study by MacArthur and MacArthur (1961), in which they demonstrated that bird species diversity is more affected by the physiognomy (physical structure) of the habitat than by plant composition. The method they used to measure vegetation structure was extremely laborious and virtually precluded the collection of such environmental data for large areas—they looked through an aluminium tube and counted the numbers of visible leaves. Nowadays, laser altimetry, commonly referred to as Light Detection and Ranging (LiDAR), can easily collect vegetation structure information. Airborne laser scanning (ALS), i.e., a LiDAR sensor onboard an airplane, has now become the main method for collecting accurate terrain and vegetation structure over large areas (e.g., Evans et al., 2009; Melin et al., 2017; Wehr & Lohr, 1999).

Laser altimetry is an active remote sensing method that uses laser beams to measure distances between the sensor and a target surface and thus determine the positions of objects in three-dimensional space (Wehr & Lohr, 1999). Lasers are used for measuring distances due to their unique properties such as coherence and the ability to emit a large number of photons in a defined direction in very short pulses at a predefined wavelength (Shan & Toth, 2018). Commercial systems for general topographic and vegetation mapping usually work with infrared radiation (at a wavelength of approx. 1064 nm; Baltsavias, 1999). A typical ALS output is represented by an irregular distribution of the returns (i.e., points) in three-dimensional space, referred to as a point cloud. Vegetation structure can also be estimated using synthetic aperture radar (SAR) or digital aerial photogrammetry (DAP) that can be acquired with various mapping

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platforms (drones, airborne, or spaceborne) (Bergen et al., 2009; Valbuena et al., 2020). Of the possible combinations of sensors and platforms, using an aircraft as a LiDAR sensor carrier has, for most applications and habitat types, a major advantage over other methods, as it provides a continuous and dense coverage of relatively large study areas. This is in contrast to spaceborne laser altimeters, such as GEDI or ICESat-2, which provide greater coverage but sparse discrete measurements; further, GEDI is limited to the area between 51.6° N and 51.6° S (Dubayah et al., 2020; Marselis et al., 2022; Moudrý et al., 2022). Drones and terrestrial laser scanning, on the other hand, provide greater detail but can only cover small areas (Calders et al., 2020; Kuželka et al., 2020; Štroner et al., 2021). A key advantage of LiDAR (in comparison to DAP and SAR) is its ability to capture the terrain under the vegetation canopy (Stereńczak et al., 2016; Stereńczak & Kozak, 2011). LiDAR pulses can penetrate gaps in the vegetation canopies and register multiple returns. In vegetated areas, the laser beams are usually reflected by several layers of vegetation. The interaction of the laser beam with the canopy is then characterized by multiple returns from different depths in the vegetation. The first return usually comes from the vegetation canopy surface, followed by the intermediate returns from leaves and branches, and the last one ideally being a return from the ground. Ground returns are, however, not always detected—the chance of their recording depends on the spatial distribution of the vegetation canopy (or gaps therein), scan angle, laser beam divergence, and reflectivity of the surface for the wavelength of the laser beam (Hofton et al., 2002; Næsset et al., 2004). It is common that the laser beam does not reach the ground, especially in dense forests, and the last return may in some cases even originate from the tree canopy. However, for deriving high-quality terrain models and, consequently, valid vegetation metrics, a certain density of ground returns is necessary.

Over the past two decades, the availability of ALS data has steadily increased due to direct investments in data acquisition by international, national, or regional agencies. For instance, many European countries make their national ALS data publicly available (Table 1; Melin et al., 2017). In parallel with the data availability, there has been considerable development in the field of available software (McGaughey, 2016; Meijer et al., 2020; Roussel et al., 2020; Silva et al., 2022). This has enabled the development of several LiDAR-based applications in ecological research and contributed significantly to improving our understanding of species–environment relationships (Bakx et al., 2019; Davies & Asner, 2014). The increasing availability of ALS data has the potential to significantly improve ecological research, and in particular species distribution modelling (SDM) and habitat quality assessments, by providing detailed information on vegetation structure. However, this potential is currently not fully exploited as the only product describing vertical vegetation structure, which is usually provided by national authorities, is the ALS point cloud (Table 1). This leads to the curious fact that although the datasets as such are often available, access to ecologically meaningful information that can be derived from such data is practically denied to many (Assmann et al., 2022). Processing ALS data requires specialized knowledge (e.g., filtering and classifying point clouds; Klápště et al., 2020; Moudrý et al., 2020) and also places high requirements on storage space and computing power (Vo et al., 2016). Besides, there is no consensus on which variables should be produced for ecological research. Here, we propose 10 variables (Table 2) that can be derived from ALS point clouds and that could be made easily available to researchers and stakeholders with limited experience with ALS point clouds—preferably in common raster formats via already existing data portals (Table 1). In addition, we advocate a consistent selection of variables and a continuous and systematic assessment of their relevance for ecological research in order to regularly update the list of such variables to reflect technological developments and user requirements.

2 | ROLE OF VEGETATION STRUCTURE IN THE DISTRIBUTION OF SPECIES

Species distribution modelling is a rapidly evolving field in biogeography and spatial ecology, and the need for clear concepts and standards for modelling has long been acknowledged and advocated (Araújo et al., 2019; Austin & Van Niel, 2011; Jiménez-Valverde et al., 2008; Zurell, Franklin, et al., 2020). The selection of appropriate explanatory variables is crucial, as the variables chosen should adequately represent the main factors affecting species' distributions, e.g., climate, land cover, or topography (Gábor et al., 2022; Gardner et al., 2019; Moudrý et al., 2019; Santini et al., 2021) and should be tailored to the species ecology and habitat requirements. SDM encompasses two quite distinct lines of research (Ferrier et al., 2017). The first, 'explanatory modelling', aims to explain the relationships between a biodiversity-related response variable (such as the distribution of individual species) and the explanatory variables (e.g., Bazzichetto et al., 2018; Moudrý & Šímová, 2013). The other one is 'predictive modelling', which aims to predict unknown values of the biodiversity response variable based on pre-specified relationships. Predictive SDM is especially useful in supporting conservation decision-making, such as in selecting protected areas; identifying critical habitats that contain essential features for endangered species conservation; or predicting the impacts of climate or land use change on biodiversity (Araújo et al., 2019; Fricker et al., 2021; Guisan et al., 2013; Morris et al., 2020).

Habitat heterogeneity is one of the most important factors affecting species distributions and diversity. It is determined by the variability of environmental conditions (e.g., habitat types, species dominance and composition, vegetation density, soil types, or topographic variability). According to the habitat heterogeneity hypothesis, more complex environments can provide more niches and thus increase species diversity (see reviews by Stein et al., 2014; Tews et al., 2004). Here, we focus on only one aspect of habitat heterogeneity—vegetation structure, a fundamental physical element of habitat, which affects species by providing shelter, foraging, and nesting sites. The Ecosystem Vertical Profile, i.e., the vertical distribution of biomass in ecosystems, is one of 20 essential

TABLE 1 Examples of European countries or administrative areas that provide ALS data free of charge.

Country or administrative area	Link to download data portal	Available products
Austria	https://data.bev.gv.at/	DTM, DSM
Belgium	https://download.vlaanderen.be/Producten/Detail?id=937&title=Digitaal_Hoogtemodel_Vlaanderen_II_DSM_raster_1_m https://remotesensing.vlaanderen.be/apps/openlidar/	DTM, DSM, point cloud
Denmark	https://download.kortforsyningen.dk/content/dhmpunktsky	DTM, DSM, point cloud
England	https://environment.data.gov.uk/DefraDataDownload/?Mode=survey	DTM, DSM, point cloud
Estonia	https://geoportaal.maaamet.ee/eng/Spatial-Data/Elevation-data-p308.html	DTM, DSM, point cloud
Finland	https://www.maanmittauslaitos.fi/en/e-services/open-data-file-download-service	DTM, point cloud
France	https://geoservices.ign.fr/lidarhd	point cloud
North-Rhine Westfalia (Germany)	https://www.opengeodata.nrw.de/produkte/geobasis/hm/3dm_l_las/	DTM, DSM, point cloud
Saxony (Germany)	https://www.geodaten.sachsen.de/downloadbereich-lsc-4667.html	DTM, DSM, point cloud
Thuringia (Germany)	https://www.geoportal-th.de/de-de/Downloadbereiche/Download-Offene-Geodaten-Th%C3%BCringen/Download-H%C3%B6hendaten	DTM, DSM, point cloud
Ireland	https://data.gov.ie/dataset/open-topographic-lidar-data	DTM, DSM
Italy	http://www.pcn.minambiente.it/mattm/en/online-the-new-procedure-for-the-request-of-lidar-data-and_or-interferometric-ps/	DTM, DSM, point cloud
Latvia	https://www.lgia.gov.lv/en/Digit%C4%81lais%20virsmas%20modelis	point cloud
Luxembourg	https://data.public.lu/fr/datasets/lidar-2019-releve-3d-du-territoire-luxembourgeois/	point cloud
Netherlands	https://www.pdok.nl/	DTM, DSM, point cloud
Norway	https://hoydedata.no/LaserInnsyn/	DTM, DSM, point cloud
Poland	https://mapy.geoportal.gov.pl/imap/Imgp_2.html	DTM, DSM, point cloud
Portugal	https://geocatalogo.icnf.pt/geovisualizador/agil.html	point cloud
Scotland	https://remotesensingdata.gov.scot/data#/list	DTM, DSM, point cloud
Slovakia	https://zbgis.skgeodesy.sk/mkzbgis/en/teren?pos=48.800000,19.530000,8	DTM, DSM, point cloud
Slovenia	http://www.geoportal.gov.si/eng/viewers/	point cloud
Spain	http://centrodedescargas.cnig.es/CentroDescargas/index.jsp	DTM, DSM, point cloud
Catalonia (Spain)	http://www.icgc.cat/en/Downloads/Elevations	DTM, point cloud
Sweden	https://www.lantmateriet.se/en/	DTM, point cloud
Switzerland	https://www.swisstopo.admin.ch/en/geodata/height/surface3d.html	DTM, DSM, point cloud
Wales	https://lle.gov.wales/GridProducts#data=LidarCompositeDataset	DTM, DSM

Note: Additional information on the individual datasets, such as resolution, point density, etc. can be found in the recent technical report by Kakoulaki et al. (2021).

Abbreviations: ALS, airborne laser scanning; DSM, digital surface model; DTM, digital terrain model.

biodiversity variables (EBVs) defined by GEO BON (Group on Earth Observations Biodiversity Observation Network) and belongs to the EBV class Ecosystem Structure (https://geobon.org/ebvs/what-are-ebvs/). In addition, vegetation and topographic variability can generate local climatic refugia, which, play an important role in light of climate change (Austin & Van Niel, 2011; Kašpar et al., 2021; Macek et al., 2019).

Several studies have shown that ALS data can serve as useful proxies for habitat heterogeneity (Bakx et al., 2019; Burns et al., 2020; Davies & Asner, 2014; Guo et al., 2017; Lefsky et al., 2002; Torresani et al., 2020; Vierling et al., 2008; Vogeler & Cohen, 2016). The pioneering studies mainly focused on investigating (i.e., demonstrating) the effectiveness of ALS-derived variables in describing species–environment associations (Bradbury et al., 2005; Broughton et al., 2006; Goetz et al., 2007; Hill et al., 2004; Hinsley et al., 2002). Since then, the focus of exploratory studies has shifted to assessing relationships between vegetation structure and the distribution of individual species (e.g., Farrell et al., 2013; Graf et al., 2009; Huber et al., 2016; Seavy et al., 2009; Sillero & Goncalves-Seco, 2014), species diversity (e.g., Clawges et al., 2008; Eldegard et al., 2014; Lesak et al., 2011; Müller et al., 2010), and rarity (Moudrý et al., 2021). Several studies explored differences in the applicability of ALS-derived variables with respect to different functional guilds (e.g., nesting, foraging, and habitat), showing that the importance of individual variables as well as the predictability of species occurrence using

TABLE 2 List of 10 ALS metrics proposed as standard structural variables for analysing species distributions and habitat quality.

Class	Variable name (units)	Variable description	Calculation
Height	Maximum vegetation height (m)	The maximum vegetation height provides information about the tallest vegetation, for example a tree or shrub. In the case of trees, height is an indicator of tree diameter and age, which are important factors for species diversity (Bae et al., 2014; Müller et al., 2010)	Highest LiDAR vegetation return in a cell (H_{max})
Height	Mean vegetation height (m)	Average vegetation height in the cell. For example, well-developed canopies would be expected to have high values of the mean vegetation height, while with the increasing representation of understorey and mid-storey, the value will decrease (Zellweger et al., 2016)	The arithmetic mean of the height of all above-ground vegetation returns in a cell (H_{mean})
Vertical variability	Standard deviation of vegetation height (m)	Vertical variability of the vegetation within the cell. Small values arise from areas with homogenous vegetation, while high values reflect vertically heterogeneous vegetation (Melin et al., 2019; Müller & Brandl, 2009; Vogeler et al., 2014)	The standard deviation of vegetation returns heights above ground (H) in a cell. $SD = \sqrt{\frac{\Sigma\left(H-\bar{H}\right)^2}{N}}$
Cover	Canopy cover (%)	The extent/percentage of the ground covered by vegetation. A Canopy cover value of 85 means that 85% of returns were reflected above x meters. The higher the value, the denser the canopy (closed stands). Low values reflect open or scattered stands (Singh et al., 2017; Tweedy et al., 2019)	The number of returns above a given height cutoff (N_P) divided by the total number of returns (N_{TF}). $(N_P/N_{TF}) \cdot 100$
Height	Height percentiles (m)	Heights at which a certain percentage of returns in a cell has been recorded, usually from 5% to 95% in steps of 5%. It shows the vertical distribution of points. (Singh et al., 2017; Vaglio Laurin et al., 2016)	Cumulative height of certain percentages of returns
Cover	Density proportions (%)	Vertical distribution of points (vegetation architecture); usually at least ten density bins are calculated (Eldegard et al., 2014; Lesak et al., 2011)	Fixed height bins between the minimum and maximum height are used for calculating the proportion of returns in a certain bin to the total number of returns (N_T)
Vertical variability	Foliage height diversity (FHD) based on Shannon-Wiener index	A measure of canopy layering (MacArthur & MacArthur, 1961). The maximum possible value increases with the increasing number of layers and the maximum value occurs when all layers have the same number of returns (i.e., the Shannon-Wiener index increases with a more even distribution of points over the layers). The number of used layers varies slightly in existing studies (Bae et al., 2014; Clawges et al., 2008; Weisberg et al., 2014). From the producer's perspective and for maintaining simplicity, it is reasonable to use the same bins as for the Density proportions	Vertical structure complexity using the Shannon-Wiener index (i.e., the proportion of returns p_i in each vertical layer i; n is the total number of layers). $FHD = \sum_{i=1}^{n} p_i \ln p_i$
Cover	Cover of the herbaceous layer (Understorey density) (%)	The amount of vegetation in the herbaceous/understorey layer. A cover value of 10 means that of all vegetation returns, 10% came from herbaceous vegetation (Jones et al., 2013; Moudrý et al., 2021)	The number of returns at the lowest vegetation layer (N_U) divided by the total number of vegetation returns (N_{TV}). $(N_U/N_{TV}) \cdot 100$
Cover	Cover of the shrub layer (Mid-storey density) (%)	The amount of vegetation in the shrub/mid-storey layer. A cover value of 25 means that of all vegetation returns, 25% came from shrub vegetation (Jones et al., 2013; Moudrý et al., 2021)	The number of returns at the middle vegetation layer (N_M) divided by the total number of vegetation returns (N_{TV}). $(N_M/N_{TV}) \cdot 100$
Cover	Cover of the tree layer (Canopy density) (%)	The amount of vegetation in the tree/canopy layer. A cover value of 65 means that of all vegetation returns, 65% came from trees (Jones et al., 2013; Moudrý et al., 2021)	The number of returns at the top vegetation layer (N_C) divided by the total number of vegetation returns (N_{TV}). $(N_C/N_{TV}) \cdot 100$

Abbreviation: ALS, airborne laser scanning.

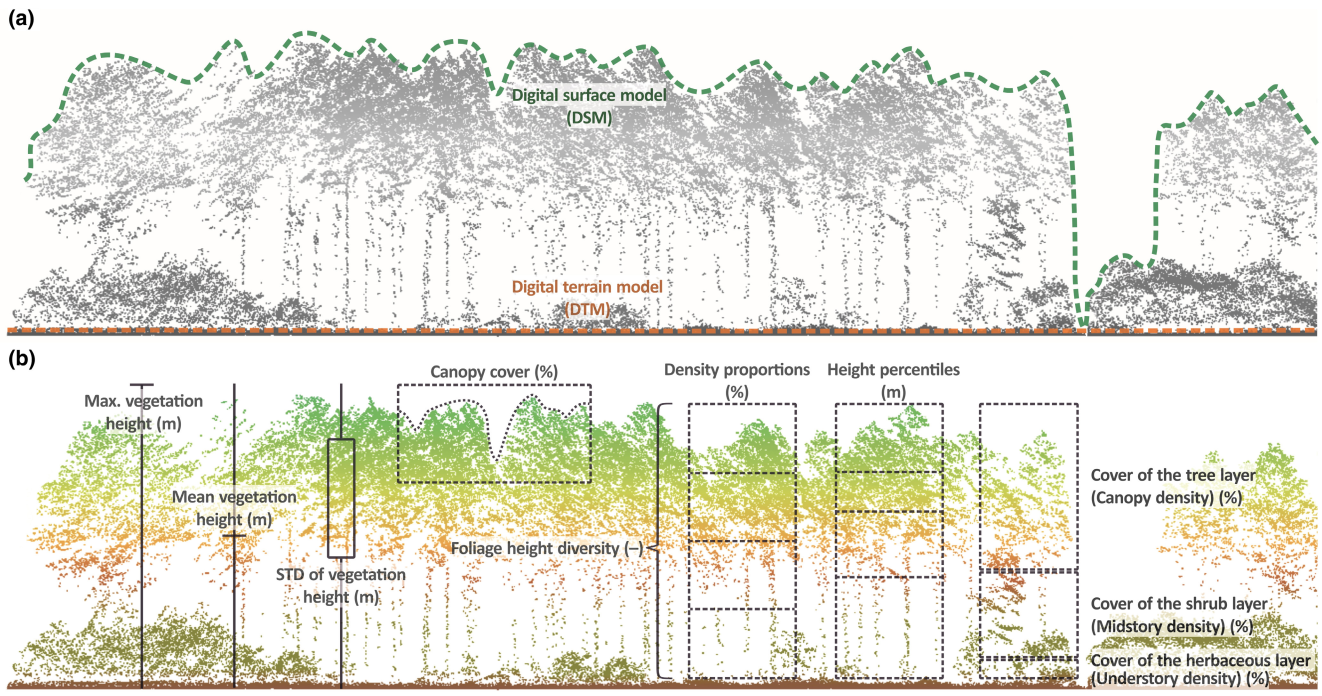

FIGURE 1 Example of an ALS point cloud profile. The top figure (a) illustrates that digital terrain and surface models (typical raster products derived from ALS point clouds offered by the data providing authorities), can be used to derive information on vegetation height and horizontal variation in canopy cover, but do not adequately describe the vertical variability of vegetation structure. The bottom figure (b) shows suitable variables to describe the vertical structure of the vegetation, which are proposed as standard structural variables in this study. Note that this figure is for illustrative purposes only and the density of the point cloud is considerably higher (75 points/m^2) than the typical density of point clouds available in Europe. Details on the variables in (b) are given in Table 2. Colours indicate vegetation height. ALS, airborne laser scanning

vegetation structure differ between guilds (Cooper et al., 2020; Goetz et al., 2007; Jones et al., 2013; Peura et al., 2016; Vogeler et al., 2014; Weisberg et al., 2014). Recently, ALS-derived vegetation structure data proved useful for quantifying niche overlap/separation (Koma, Grootes, et al., 2021).

Species distribution model studies often simultaneously encompass many species (Zurell, Zimmermann, et al., 2020). Hence, the selection of environmental variables based on the known ecological requirements of individual species is often neglected and instead commonly available variables (that are generally considered important for modelling species occurrence) are used. Consequently, the variables used are often derived from a limited pool of available products (Araújo et al., 2019). Typical raster products, derived from ALS point clouds and provided by the government agencies along with the ALS data, comprise only digital terrain and surface models (Table 1). Subtracting a digital terrain model (DTM) from a digital surface model (DSM) results in a normalized digital surface model (nDSM), which represents the objects present (e.g., buildings, vegetation) on top of the relief. A special form of the nDSM, the so-called canopy height model (CHM), contains only the vegetation heights. As it is comparatively easy to obtain, metrics calculated from the CHM are the most commonly used variables in modelling species diversity and distribution (e.g., Bakx et al., 2019; Müller et al., 2010; Müller & Brandl, 2009; Rada et al., 2022); nevertheless, they only describe horizontal variation in canopy cover (Figure 1a). However, variables describing the vertical structure of vegetation are at least as important for the modelled species (Figure 1b). These characteristics can be derived from ALS point clouds as easily as the aforementioned digital elevation models (i.e., DTM, DSM, and CHM). The first attempt to provide a ready-to-use, standardized product that contains also vegetation structure variables was recently presented by Assmann et al. (2022), who processed Danish national ALS data and made eight vegetation structure variables available for free download in raster format at 10 m resolution. The authors also provide documentation and source code for the processing workflow, which allows the methods to be applied to other ALS datasets (note, however, that they used commercial software). Similarly, Meijer et al. (2020) mention the calculation of vegetation structure variables at a resolution of 10 m for the entire Netherlands. These pioneering examples should be followed by more systematic efforts that lead to ALS-derived variables being available to a wider audience and standardized for use in ecological research.

3 | WHICH VEGETATION STRUCTURE VARIABLES SHOULD BE PROVIDED AS STANDARD?

After a period of intensive research that has shown the irreplaceability of ALS-derived vegetation structure variables for understanding species–environment relationships, it is now time to make them available to a wider audience which will allow incorporating them as common variables in predictive models. Finding new ways to make ALS data easily accessible is a priority to accelerate ecological research (Assmann et al., 2022; Stereńczak et al., 2020). It would be valuable to have a list of several standardized variables recommended for use in SDM and ecological research, so that scientists or authorities generating ALS-derived products know which to focus on. The chosen variables should be both ecologically relevant as well as easy to interpret and understand (Glad et al., 2020).

Variables that are difficult to interpret from an ecological point of view but have been used in previous research, such as the standard deviation of the 10th percentile (Zellweger et al., 2013) or height skewness of the returns located between 1.5 and 5 m (Kortmann et al., 2018), may be less useful in this sense. A prime example of ecologically relevant and standardized variables are the 19 bioclimatic variables (introduced by Hijmans et al., 2005) that describe various physiological mechanisms limiting species occurrence, such as seasonality and extreme climatic conditions related to temperature and precipitation. These variables are widely used by ecologists and are nowadays provided as standard by the data-providing institutions (Fick & Hijmans, 2017; Title & Bemmels, 2018; Vega et al., 2017).

LiDAR-derived variables can be grouped into four structural categories (cover, height, horizontal variability, and vertical variability) (Bakx et al., 2019). We propose 10 variables from the above classes as standard structural variables for ecological research (Table 2; Figure 1). Note, however, that we have not included horizontal vegetation variability metrics, as these can be easily calculated from the proposed variables (e.g., standard deviation of canopy cover). The proposed standard structural variables were selected based on the following criteria, building on previous work by Bakx et al. (2019): (i) their applicability and ecological relevance have already been proven in several studies. Fifty-two of the 77 variables reviewed by Bakx et al. (2019) were used in only one study and 10 more were used in two to four studies. Only 13 variables were used in at least five studies (out of 50 studies reviewed by Bakx et al., 2019), and from those we selected variables that (ii) are easy to interpret.

The maximum, mean, and standard deviation of vegetation returns are among the simplest metrics for describing the vertical structure of vegetation. Tree height is a useful indicator of tree diameter and, to some extent, of tree age, which are important factors for species diversity. Hence, maximum height should be particularly useful in predicting the occurrence of species associated with mature, old-growth forests. For example, a positive relationship between the maximum canopy height and species richness has been reported for birds (Flaspohler et al., 2010; Lesak et al., 2011) as well as vascular plants (Mao et al., 2018). Mean height of vegetation returns is particularly useful in combination with variability in return heights. For example, Vogeler et al. (2013) found a positive relationship between mean height, vertical variability of vegetation, and Brown Creeper (*Certhia americana*) occupancy. Similarly, Aguirre-Gutiérrez et al. (2017) found that butterfly diversity increased with average vegetation height and vertical variability of vegetation. Together with vegetation height, vertical height variability reflects key structural differences between land cover and habitat types and is important for their differentiation (Koma, Seijmonsbergen, et al., 2021; Prošek et al., 2020). For example, lower mean height and high vertical variability could indicate forests with sparse canopy and dense understorey vegetation.

Vertical height variability is often characterized by a single variable (e.g., the standard deviation of vegetation returns or foliage height diversity index based on the Shannon-Wiener index; MacArthur & MacArthur, 1961). For example, Moudrý et al. (2021) and Weisberg et al. (2014) reported positive associations between bird species richness and the standard deviation of vegetation returns or foliage height diversity, respectively. On the other hand, Vogeler et al. (2014) found that foliage height diversity was not a strong predictor of bird species richness. This could be due to the fact that these individual variables may not fully capture the complex layering of vegetation. Other metrics characterizing the vertical vegetation profile as the proportions of returns within different vegetation layers (e.g., understorey, mid-storey, canopy) may be more useful. Such vertical stratification describes the presence of different age classes or life forms existing at certain heights (e.g., herbs, shrubs, and trees). In particular, understorey vegetation in forests (Clawges et al., 2008; Vogeler et al., 2014) and shrub vegetation such as hedgerows in agricultural landscapes (Pelletier-Guittier et al., 2020) are often considered important factors for species richness, as they provide nesting and foraging habitats, affect visibility and prey abundance, and alter the near-surface microclimate (Stickley & Fraterrigo, 2021). On the other hand, vegetation can also act as an obstacle, and it has been shown that forest-dwelling aerial insectivores, such as some bird species or bats, prefer forests without a shrub layer as an optimal foraging habitat (Lesak et al., 2011; Rauchenstein et al., 2022). Similarly, Torre et al. (2022) have shown that the diversity of Mediterranean small mammal communities is negatively affected by the structural complexity of vegetation. On the other hand, herbaceous and shrub vegetation serve as important refuge for wildlife in landscapes heavily influenced by humans, such as agricultural and urban areas (Choi et al., 2021; Melin et al., 2018; Moudrá et al., 2018). Canopy cover can serve as a proxy for light availability on the ground. Open canopy stands are often associated with dense understorey layers. Closed canopies, on the other hand, buffer microclimatic conditions such as temperature and moisture content (Davis et al., 2019).

We assume that stratifying the vegetation vertical structure into three basic layers (i.e., herbs, shrubs, and trees) is usually sufficient for modelling species distributions in temperate forests (e.g., Jones et al., 2013; Lesak et al., 2011; Müller et al., 2010; Rauchenstein et al., 2022), agricultural landscapes (Melin et al., 2018), as well as in early successional habitats (Moudrý et al., 2021). For Europe, we suggest calculating the cover of the herbaceous layer from returns below 1 m, the cover of the shrub layer from returns between 1 and 3 m, and the cover of the tree layer from returns above 3 m

(Moudrý et al., 2021). However, the height of herbs/understorey, shrubs/mid-storey, and trees/canopy can vary considerably among different ecosystems even within Europe. Therefore, the proposed ranges may not be the best in certain situations, and the use of more detailed stratification of vegetation architecture may be helpful. For example, this could be the case when characterizing the structure of linear woody features such as hedgerows (Broughton et al., 2021), or vegetation density in urban parks (Choi et al., 2021). We therefore recommend that users are also provided with height percentiles and density proportions, which describe vertical vegetation structure in more detail (Table 2). Height percentiles indicate the height (in meters) below which a certain percentage of returns has been recorded, usually from 5% to 95% in 5% increments. For instance, if the 70th height percentile is 10 m, it means that the lowest 70% of the vegetation returns are below 10 m. Density proportions reflect the proportion of points within a certain height bin to the total number of returns. We suggest the use of at least 10 proportional density bins with larger distances at greater heights and smaller distances at lower heights (interval boundaries can be, for example, 0.5, 1.0, 2.0, 3.0, 5.0, 10, 20, 30, 40, and 50 m; Bae et al., 2014; Eldegard et al., 2014; Lesak et al., 2011).

The list of 10 proposed variables presented here is a starting point rather than a definitive list. The number of variables that can be calculated from ALS point clouds is infinite and new metrics are constantly being proposed, making the selection of standard variables a challenge (Carrasco et al., 2019; Glad et al., 2020; Hagar et al., 2020). However, there is currently insufficient evidence to suggest that any vegetation structural variable is the "universal best" for SDM (see reviews by Bakx et al., 2019; Davies & Asner, 2014). For this reason, we suggest that the above-mentioned variables should be routinely tested as part of ecological studies (e.g., SDM, habitat suitability), which focus on relevant spatial scale, target species, habitat, etc. Such testing would allow their systematic and dynamic refinement based on their individual relevance in explaining species occurrences. When variables are freely available, they are likely to be tested by the scientific community in different settings and cases. Although it is difficult to orient such testing, it is to be expected that—as for other variables or remote sensing products—the results of individual independent studies will be synthetized in reviews or meta-analyses, providing testing information that can guide the user community (e.g., Zolkos et al., 2013 review on above ground biomass estimation by LiDAR). The variables proposed in Table 2 should be derived in a standardized way from national airborne scanning campaigns (Valbuena et al., 2020) and be available to users as ready-to-use open access products (i.e., in a common raster format) through already existing data portals (Table 1). We propose 10–20 m as the optimal resolution for calculating these variables, which is a compromise between the grains usually used in studies on species distributions and habitat suitability and the typical density of national point clouds. For example, SDM studies typically use an analysis grain (i.e., the spatial unit in which the species occurrence is modelled) between 10 m and 10 km (Mertes & Jetz, 2018; Moudrý & Šímová, 2012); however, environmental data should be available at an even more detailed resolution, sufficient to capture the smallest habitat patches suitable for a given species (Gottschalk et al., 2011; Koma, Seijmonsbergen, et al., 2021; Šímová et al., 2019). In addition, the resolution of the proposed standard structural variables needs to reflect the density of point clouds. While many European countries provide point clouds with a density of more than 4 points/m^2 (e.g., Denmark, Netherlands, Switzerland, Slovenia, Slovakia, Latvia, and Poland), which is sufficient to obtain accurate estimates of vegetation structure at a resolution of 10 m (Assmann et al., 2022; Meijer et al., 2020), others have a relatively low density (e.g., Spain and Sweden have average point density between 0.5 and 2 points per square meter; Kakoulaki et al., 2021); when point clouds with such low density are used as a basis for modelling, it is preferable to use coarser resolutions for calculating these variables. Forestry applications using point clouds with similar densities typically adopt a resolution of 20 m to calculate vegetation metrics (e.g., Woods et al., 2011), and a resolution of 20–25 m has been shown to be sufficient to reduce potential errors in vegetation structure estimation due to low point cloud density (Ruiz et al., 2014; Treitz et al., 2012; Wilkes et al., 2015). In addition, countries may already provide other spatial datasets that the ALS-based rasters could be aligned with (Finland, for instance, provides nationwide rasters derived from the National Forest Inventory with a spatial resolution of 16 m).

It is advisable that an authoritative institution takes the responsibility for the production and the provision of vegetation structural variables. A coordinated international effort on this topic could be beneficial, as is the case with other remote sensing products, but the road in this direction might be long. In the meantime, it would be beneficial if the same governmental agencies that are now responsible for storing and managing lidar data would also take on the responsibility of creating and openly providing lidar-based vegetation structure data.

4 | CONCLUSION

The EBV Ecosystem structure, and in particular vegetation structure, is a fundamental physical element of habitat and as such is essential for ecological research. However, to realize its full potential, data must be available in a form that can be accessed by users with average GIS experience. The need to create such variables based on ALS data is even greater because vegetation height is now available globally at a 10 m resolution (Lang et al., 2022). It is only a matter of time until other variables representing the vegetation structure become available (Dubayah et al., 2020). However, these global vegetation height products are based on predictive models combining spaceborne laser altimeters (e.g., GEDI) and optical remote sensing data (e.g., Sentinel-2) (Lang et al., 2022) and are therefore usually subject to significant errors. Their use in local scale modelling and biodiversity studies may lead to erroneous results (Meyer & Pebesma, 2022). Nevertheless, because they are readily available in a raster format, there is a risk that users will prefer global products to the tedious processing of much more accurate ALS data.

An one example, Lewis et al. (2022) calculated the mean and variance of canopy height from the 2019 Global Canopy Forest Height database (Potapov et al., 2021), even though ALS data for Georgia were available for the same period (opentopography.org). This example once again underlines the importance of providing vegetation structure variables (and not only point clouds). In this article, we proposed variables that could be used as a standardized set for SDM and habitat analyses. Namely, we call for (i) the easy availability of such variables through existing data portals of national authorities in a common raster format (e.g., GeoTiff) together with DTMs and DSMs (the only raster products commonly derived from ALS) and (ii) their consistent selection and systematic testing. In the past, the standardization and improved availability of bioclimatic variables has had a major positive impact on ecological modelling. For this reason, we believe that similar efforts will have the same effect in the case of variables describing vegetation structure.

KEYWORDS

habitat heterogeneity, LiDAR, niche, point cloud, predictors, SDM

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CONFLICT OF INTEREST

The authors have declared no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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BIOSKETCHES

The authors of this publication work at different European universities and research centres. While they have a professional background in different disciplines such as spatial ecology, botany, geography, forestry, or ecosystem services, they share a common interest and have extensive experience in the use and processing of remote sensing data, especially airborne laser scanning point clouds.

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