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Review

Assessing biodiversity using forest structure indicators based on airborne laser scanning data



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ABSTRACT

The role of forests in biodiversity assessment and planning is substantial as these ecosystems support approximately 80% of the world's terrestrial biodiversity. Forests provide food, shelter, and nesting environments for numerous species, and deliver multiple ecosystem services. It has been widely recognised that forest vegetation structure and its complexity influence local variations in biodiversity. As forests are facing threats globally caused by human activities, there is a need to map the biodiversity of these ecosystems. The main objective of this review was to summarise the use of airborne laser scanning (ALS) data in biodiversity-related assessment of forests. We draw attention to topics related to animal ecology, structural diversity, dead wood, fragmentation and forest habitat classification. After conducting a thorough literature search, we categorised scientific articles based on their topics, which served as the basis for the section division in this paper. The majority of the research was found to be conducted in Europe and North America, only a small fraction of the study areas was located elsewhere. Topics that have received the most attention were related to animal ecology (namely richness and diversity of forest fauna), assessment of dead trees and tree species diversity measures. Not all studies used ALS data only, as it were often fused with other remote sensing data – especially with aerial or satellite images. The fusion of spectral information from optical images and the structural information provided by ALS was highly advantageous in studies where tree species were considered. Relevant ALS variables were found to be case-specific, so variables varied widely between forest biodiversity studies. We found that there was a lack of research in geographical areas and forest types other than temperate and boreal forests. Also, topics that considered functional diversity, community composition and the effect of spatial resolution at which ALS data and field information are linked, were covered to much lesser extent.

1. Introduction

Biodiversity refers to all the variation in lifeforms found at different scales of biological organisation on Earth, ranging from genes to ecosystems. It is divided into genetic, species and ecosystem diversity components (United Nations, 1992). The variability between the elements within each level of organisation can be quantified as richness (the number of elements), evenness (the equitability of elements) and heterogeneity (the difference in the element form and function) (Balvanera et al., 2014). Biodiversity is seen as a fundamental part of the Earth system as it offers a vast range of ecosystem services from which society obtains direct or indirect benefits (Duffy 2009). Much of the global biodiversity is in danger because of human-induced changes on

ecosystems. Consequently, conservation, and future- and current-state assessment of biodiversity have caught both scientific and political interest in recent decades (e.g. Millennium Ecosystem Assessment, 2005).

Forests have a significant role in biodiversity-related assessment and planning because they support approximately 80% of global terrestrial biodiversity. They provide fundamental ecosystem services to society, such as provisioning services, e.g. timber, recreation and climate regulation (Balvanera et al., 2014). While large scale biodiversity is understood to be determined by climatic conditions, vegetation structure also has an influence on diversity and species distribution at smaller scales, such as within forested ecosystems (Zellweger et al., 2013a). Forest structure as a 3D complex is typically divided into two components: horizontal and vertical structures (Franklin and van Pelt, 2004;

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McElhinny et al., 2005). Vertical structure highlights the distribution of the vertical vegetation profile and horizontal structure describes the distribution of vegetation in the horizontal dimension of a forest. Forest structure (and its complexity) influences species occurrence and distribution in several ways: it modifies microclimatic conditions, provides breeding sites, affects the distribution and availability of resources and niches, and provides shelter from predators (Brokaw et al., 1999; LaRue et al., 2019; MacArthur and MacArthur 1961; Melin et al., 2014). When there is a greater number of niches and more resources available in a forest (i.e. more structural diversity), there is more likely to be greater diversity of species than in a forest with less of these features (Stein et al., 2014). For example, uneven-aged multi-species forests provide more micro habitats than even-aged forests (Gilbert and Lechowicz, 2004; Savilaakso et al., 2021). In addition, the variation in terrain elevation (i.e. topography) has been found to influence species diversity at the local scale (Vogeler et al., 2014; Zhou et al., 2015). One relevant concept of the mutual relationship between the environment and individuals of a species is niche theory (e.g. Chase and Leibold 2003). It has numerous definitions, which include the requirement-based concept of an ecological niche that links the fitness of an individual to environmental variables (e.g. Hutchinson 1957). As the large-scale measurement of habitat structure and the reconstruction of 3-D vegetation characteristics using ground sampling is both time consuming and resource demanding, there is an evident need for more efficient methods of data collection.

Current remote sensing (RS) methods, which include active and passive sensors, offer ecologically relevant data for large-scale biodiversity assessment of forests (Turner et al., 2003; Miura and Jones, 2010; Álvarez-Martínez et al., 2018). Remote sensing-based approaches to biodiversity mapping can generally be divided into modelling of habitats and modelling of biodiversity distribution. The use of passive optical RS sensor data for biodiversity assessment has been studied extensively in recent decades and offers relevant data for the classification of vegetation types or for the definition of the horizontal structure of the landscape (Turner et al., 2003). However, the diversity of many taxa is also dependent on the vertical structure, which cannot be measured using solely optical sensor data (Vierling et al., 2008). One such technique to overcome this limitation is light detection and ranging (lidar) as it can be used to map both the horizontal and vertical vegetation structures at the landscape scale (Bergen et al., 2009).

Lidar is an active remote sensing technology. As such, it does not require sunlight to offer reflected measurements of the targets (Dubayah and Drake, 2000; Wehr and Lohr, 1999). Instead, the lidar sensor emits light pulses (usually in the near-infrared wavelength) that reflect from the objects back to a detector in the sensor. Lidar systems can be spaceborne, airborne or terrestrial. Airborne laser scanning (ALS; or airborne lidar) is often used in 3D ecosystem assessments because these surveys cover large areas and such datasets have become increasingly available (Bakx et al., 2019). In general, ALS pulses penetrate the vegetation partially, thereby allowing the measurement of canopy and subcanopy conditions. Lidar data can be recorded either as discrete returns (DR), full-waveform (FW) or single photons. In DR-ALS systems, a fixed number of returns is recorded for each laser pulse (Wagner et al., 2004). The FW-ALS system records the distribution of returned light energy and often contains more information than DR-ALS data (e.g. Adams et al., 2012). DR is the most often used form of ALS data. Information offered by FW-ALS has been found to be useful in forestry applications that concentrate on species classification, single tree modelling and extraction of biophysical parameters (Maltamo et al., 2014). In DR lidar systems, multiple (hundreds or thousands) photons are needed for the reliable detection of a single object. The much less studied single photon lidar is relatively new technology and it offers refined efficiency in photon collection (Yu et al., 2020). It has been shown to be suitable for the estimation of traditional stand attributes (Räty et al., 2022). Its greatest advantage over previous lidar systems is a larger coverage during a flight, which is due to a higher flying altitude

(Matikainen et al., 2020). In most of the ALS systems, distance from object to the sensor can be calculated by determining the time interval between the sending of the laser pulse and the backscattered echo (Baltsavias 1999; Wehr and Lohr, 1999). The 3D-coordinates are provided for each echo by integrating the time measurement and information from the GPS-IMU system, which measures the exact location and orientation of the ALS-platform for each submitted lidar pulse. In forest-related ALS analysis, the first processing step is typically the modelling of the ground surface, i.e. the generation of a digital terrain model (DTM). After this, the height of vegetation with respect to the ground is calculated by subtracting the DTM from height values of the original echoes.

The ALS data offers multiple metrics to quantify the structural attributes of forest habitats (Bakx et al., 2019; Davies and Asner, 2014; Hill et al., 2013). In general, they are statistics associated with the height and/or intensity values of the ALS echoes, which can be linked to attributes of interest. These metrics can be roughly categorised into height, density and intensity metrics. Height metrics can further be divided into distribution metrics that describe the central tendency (e.g. mean), shape (e.g. skewness), dispersion (e.g. standard deviation) and percentiles of the ALS height distribution. Density metrics account for the proportion of returns in the fixed layers of a canopy or above/below a certain height limit. The intensity metrics represent the amplitude of a backscattered ALS echo or pulse, and they are dependent, for example, on the geometry and reflectance of a target. Metrics calculated from FW-ALS are mostly similar to DR lidar data. However, information on waveform enables the calculation of metrics that are inaccessible with DR lidar data, such as echo width.

The two main approaches used to derive forest information from ALS data are the area-based approach (ABA) (e.g. Naesset 2002) and individual tree detection (ITD) (e.g. Hyyppä et al., 2001). In ABA, ALS-metrics are calculated at the raster cell- or plot-level, and are used as predictor variables for the estimation of the attribute of interest. The most suitable metrics vary with regard to the variable of interest. Canopy height, for example, can be predicted by the mean height of the first echoes, maximum height or by using the height of the 95th percentile of echoes (Coops et al., 2016; Smart et al., 2012). In the ITD approach, the derivation of tree- or stand attributes is based on the prediction of tree characteristics from the segmented ALS data. It is also possible to segment the ALS echoes or a rasterised map into objects, such as trees or logs, for instance (Blanchard et al., 2011). This type of method is called the object-based approach and is more demanding both from a computational and technical basis than previous approaches (e.g. Blanchard et al., 2011). The required scale of information may also determine the method to be used (Maltamo et al., 2014), for example, it may be useful to detect dead standing trees at the tree-level. Similarly, when the structure of the forest stand is of interest, one could select ABA over ITD.

Lidar technologies have become increasingly popular in the fields of ecology, biodiversity and conservation because they can characterise vertical and horizontal forest structures (Bergen et al., 2009; Davies and Asner 2014; Simonson et al., 2014). Bergen et al. (2009) suggested that information derived from ALS data can serve as a relevant proxy for species richness in vertically complex ecosystems, such as forests. Numerous studies have focused on the utilisation of ALS-based forest structural and topographical information to predict the diversity and richness of forest fauna, such as birds, mammals and insects (e.g. Klein et al., 2020; Vierling et al., 2011). Some studies have detected and classified dead wood (Chirici et al., 2018; Polewski et al., 2015b), which is an inseparable component of the diversity in forests. Furthermore, structural classification of a forest in terms of land cover (Botalico et al., 2014), canopy layering (Moran et al., 2018) and successional stage (Martinuzzi et al., 2013) can serve in habitat suitability assessments, for example. Tree size variation in the plant community is a known issue in forest inventories (Gobakken and Næsset 2004) and has been described in many studies by the coefficient of variation, standard deviation

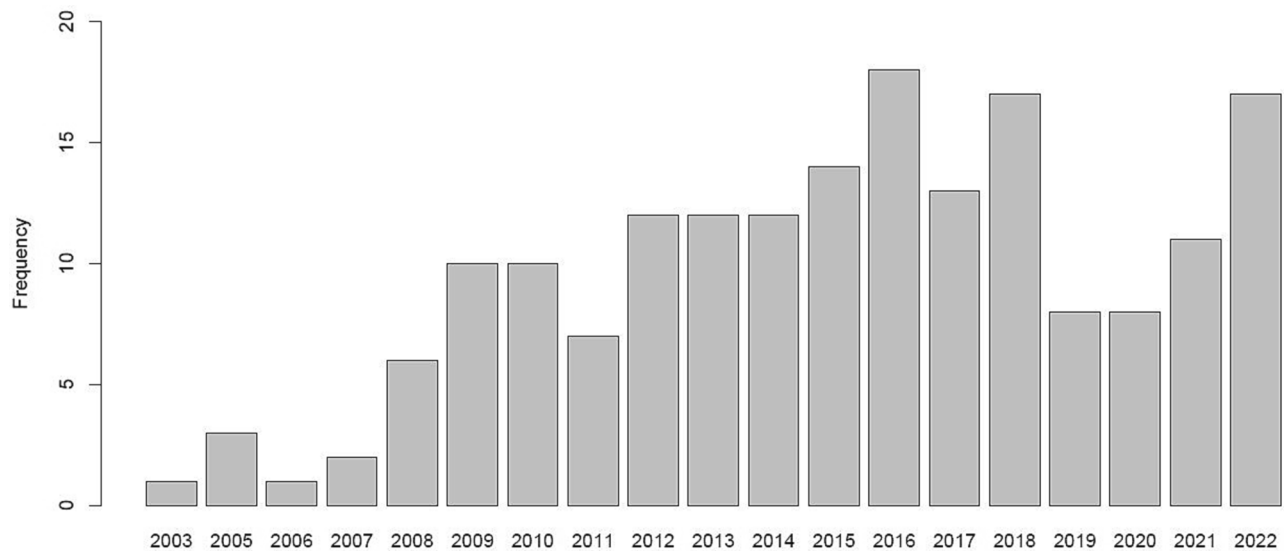


Fig. 1. Histogram showing the annual frequency of forest diversity studies. Bars represent the total number of publications per year.

(Bottalico et al., 2017) and the Gini coefficient (GC) (Valbuena et al., 2016a).

In this paper, we provide a review of the use of ALS data in forest biodiversity assessment. We review studies where the main interest is the assessment of dead wood, lower canopy layers, fragmentation, gap dynamics, forest structural diversity and structural classification in terms of the different canopy layers, land cover classes and forest successional stage. Also, we review topics concerning the richness and diversity of flora and fauna found in different types of forests and includes birds, mammals, insects, invertebrates, plants and trees. By structural diversity, we focus on variations in tree and crown heights and tree diameters, as well as on the spatial patterns of the trees in the forest. In the first stage, we describe the material gathering process and sum up the published studies in terms of their publication year, journal domain, the spatial extent and location of the study areas in order to highlight “hotspot areas” of research on this topic. We also present the distribution of study areas within ecoregions. In the second stage, we systematically examine the studies categorized by research topics (sections 3–9). Some studies covered more than one aspect and were, therefore, included in multiple categories. In the third stage, we summarise the current use of ALS data in assessments of forest biological and structural diversity and discuss prospects for its use in future studies.

2. Material and methods

In this review, literature searches in Scopus, Google Scholar and UEF Primo (search service for electronic materials at the University of Eastern Finland) were conducted between May 2021–July 2023. Keywords used in the searches were carefully chosen to represent the topic of the review and to minimise the potential of excluding relevant studies. The selected keywords were “ALS”, “airborne lidar” or “airborne laser scanning” for the lidar component, “forest” or “forest structure” for the vegetation component and “biodiversity”, “forest type”, “dead wood”, “fragmentation”, “species diversity”, “species richness”, “successional stage”, “understorey” and “animal ecology” were used separately on each for the last component. These keywords were used in all possible combinations for the vegetation, lidar and last components. After the search, the number of articles was reduced by screening the articles, first by their title and then by abstract. Finally, the selected articles were verified by the full text. Also, a study could be included in this review if it was included in the references of another suitable study even though it was not found through a literature search. We excluded studies where the primary data were acquired with terrestrial,

spaceborne or profiling lidar systems, and studies that used photogrammetric point clouds derived from aerial and satellite image data. In addition, studies where the main interest was the assessment of leaf-area index (LAI), canopy cover, primate habitats or were conducted in aquatic ecosystems, were excluded from this review. This was to limit the length and complexity of this paper. In total, 182 scientific articles were included in this review and all articles were published between 2003 and 2022 (Fig. 1). Most of the research was conducted between 2009 and 2018, with a peak occurring in 2016 when 17 studies were published (Fig. 1). There was a slight decline in the number of published articles during 2019 and 2020, although by 2022, the number of studies had rose to 2018 levels.

The most common domain for publications was in remote sensing-oriented journals, which accounted for 45% of the studies (Fig. 2a). Approximately, one quarter of the studies were published in either ecology or forestry-related journals. A total of 134 studies (approximately 75%) only utilised ALS data (Fig. 2b). Both ALS and terrestrial laser scanning data were used in four studies, and approximately one quarter of studies used optical image data with ALS (Fig. 2b). There was a clear trend in the type of ALS data used: A total of 171 studies used discrete return signals from ALS in metrics calculation (Fig. 2c). Between 2010 and 2022, FW-ALS was used only in 12 studies. Clear trends with regard to the use of this type of ALS data were not found. We classified study areas by their spatial extent, defined here as the spatial unit on which the study was conducted (Fig. 2d). Here, landscape level denotes a large heterogeneous area that consists of multiple different land-uses (e.g. different forest types). Stand level is defined as a rather homogeneous, small forest unit.

The majority of the study areas was located in Europe and North America (Fig. 3). Note that there are more study areas than study articles, since some studies included data from numerous locations. A full list of studies categorised by their topics and the continent of the study areas is presented in Appendix A.

Approximately 42% of the study areas were located in temperate broadleaved and mixed forests (Fig. 4). Both boreal and temperate coniferous forests were hosts for approximately 20% of the study areas. The remainder of the study areas were mainly located in Mediterranean and tropical forests – each accounting for < 10% of the study areas.

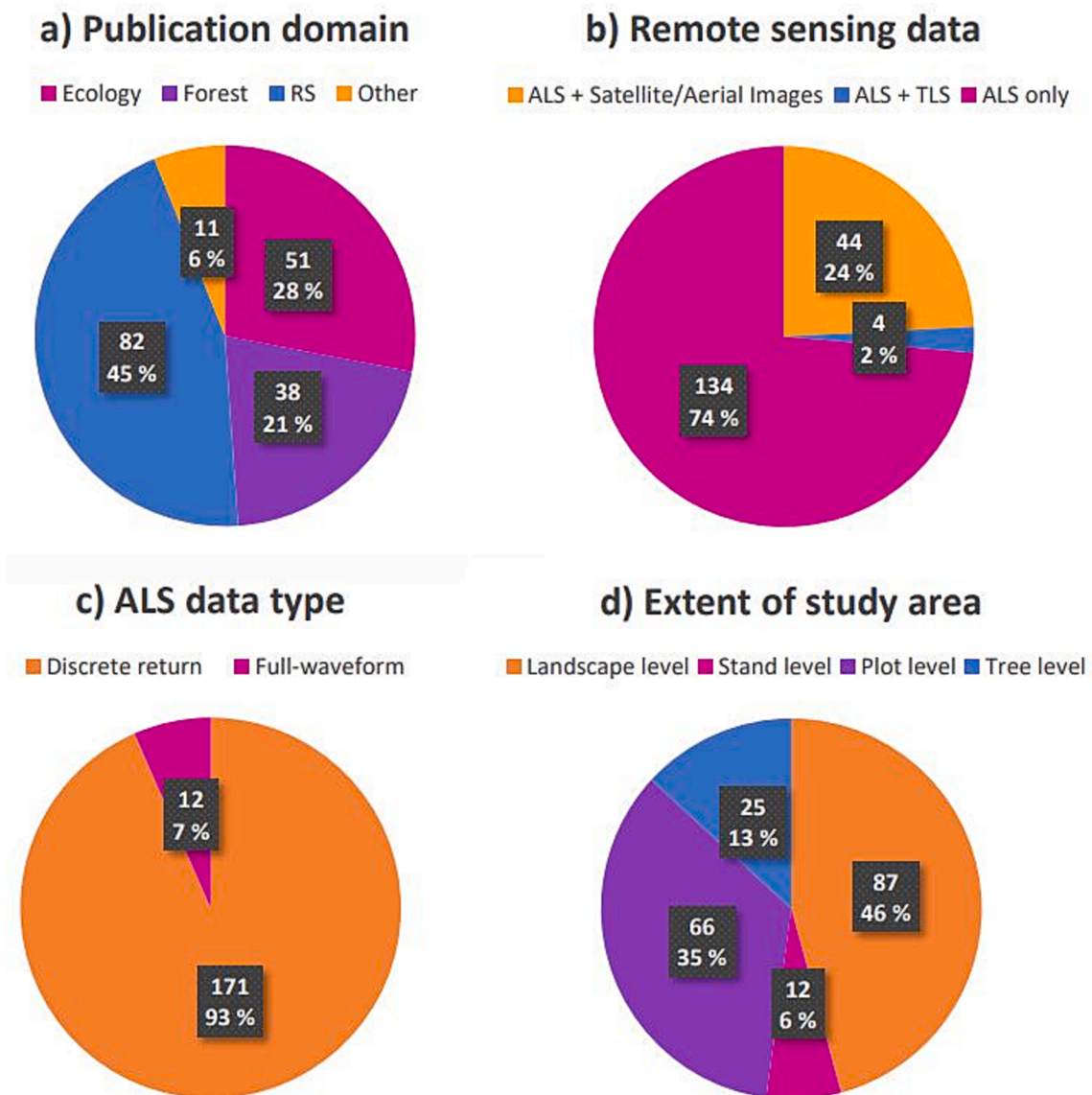


Fig. 2. Reviewed articles by (a) domain of the publication journal, (b) type of remote sensing dataset, (c) type of airborne laser scanning (ALS) dataset, and (d) spatial extent of study area. Numbers above the percentages denote the actual number of the articles per class. Note that some studies belong to more than one class (c and d).

3. Forest type and successional stage

3.1. Land cover classification

The distribution of habitat types across large areas reflects potential species richness but its mapping has been a challenge for conservation practitioners. High-resolution maps that depict habitat distribution have mostly been derived from resource-consuming field inventories and from visual interpretation of aerial images (Evans 2006).

In our review, the classification schemes of land covers varied between studies, but classes were typically named after the main tree species or the species group that was most representative of a landscape (Dalponte et al., 2008; Shoot et al., 2021; Simonson et al., 2013; Su et al., 2016). Some studies defined the classes very precisely. For example, Hill and Thomson (2005) used the National Vegetation Classification scheme for woodlands and scrub of Great Britain and Bässler et al. (2010) used the Natura 2000 habitat classification scheme. Bottalico et al. (2014) employed a broader scheme as they classified forests as high forests, young and adult coppices. Sverdrup-Thygeson et al. (2016) used only

two classes as they aimed to distinguish old managed and old near-natural forests. One study classified forests into four classes of forest naturalness (Sinclair 2021), while Vehmas et al. (2009 and 2011a) employed a very distinctive scenario with the aim to classify mature stands based on site fertility types. Pippuri et al. (2016) also classified forest plots based on site fertility, but they also used other classification scenarios, such as peatland type (spruce, pine and open), drainage status (drained vs. undrained), land use/land cover (forest vs. non-forest) and main soil type (mineral vs. peat).

Terrestrial biomes in these study areas were mostly temperate broadleaved/coniferous and boreal forests. Two studies concentrated on the mapping of forest land cover classes in the tropics (Marselis et al., 2018; Martinuzzi et al., 2013). Most of the study areas were located in a national park or in a protected site (e.g. Natura 2000 site).

Methods differed to some extent between studies, although the classification of habitat types was generally based on supervised machine learning algorithms, such as maximum likelihood, k-NN, Random Forest (RF), boosted regression trees (BRT) and support vector machines (SVM). Álvarez-Martínez et al. (2018) used a slightly different approach

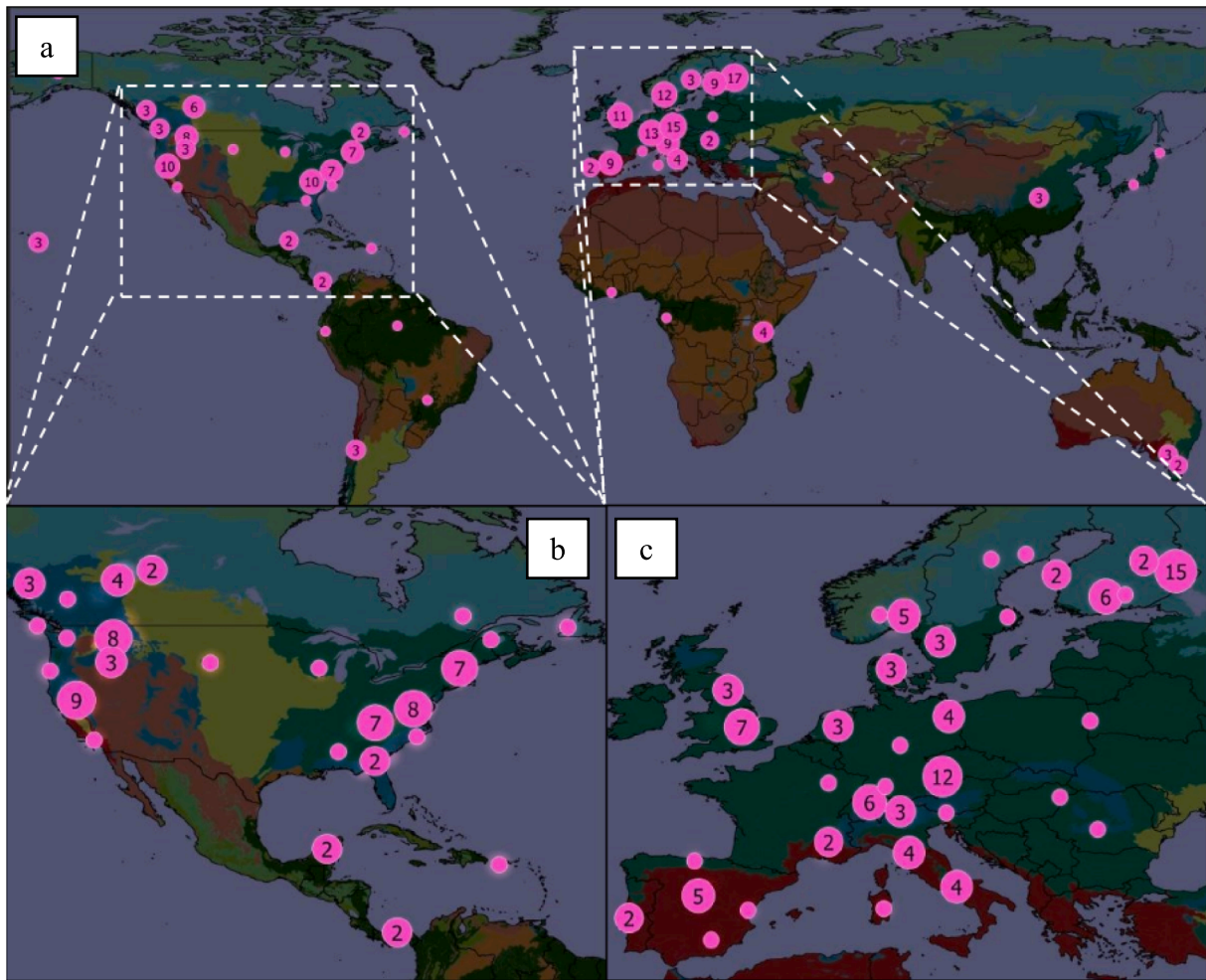


Fig. 3. Locations of reviewed study areas (a) globally, (b) in North and Central America, and (c) in Europe. Number of clustered studies is presented inside the dots. Colouring of the world map is based on the global terrestrial biome classification as presented by Olson et al. (2001). Map: WWF, 2021.

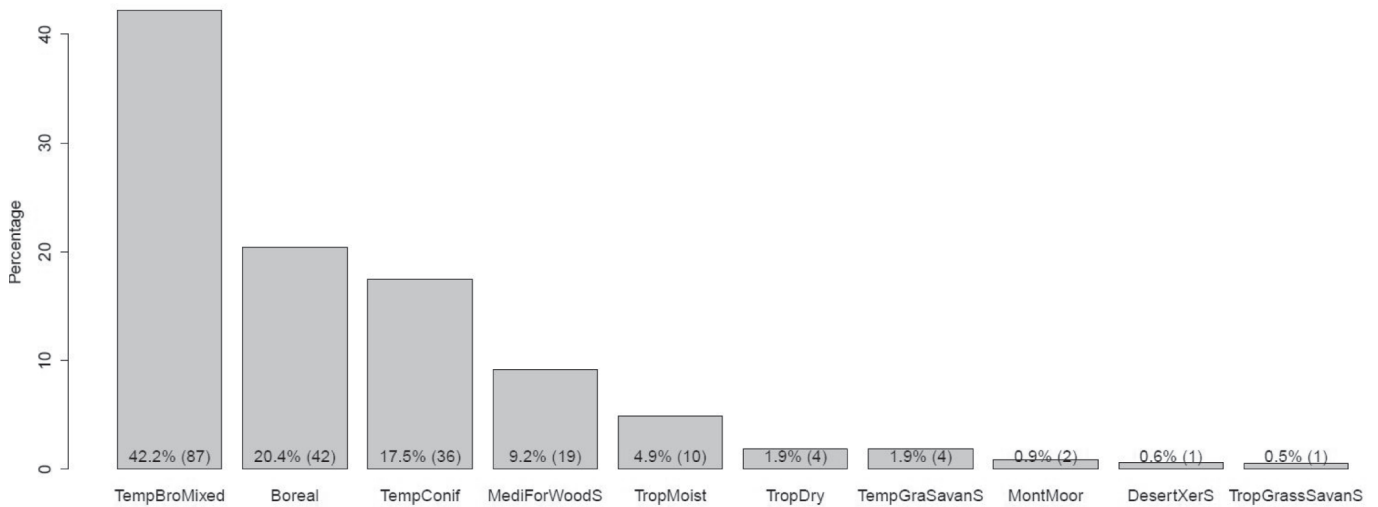


Fig. 4. Histogram showing the percentage distribution of study areas in terms of the terrestrial biome, as shown in the Fig. 3. Number in parentheses denotes the actual number of study areas in the specific ecoregion. Abbreviations are as follows: TempBroMixed = Temperate Broadleaf and Mixed Forests, Boreal = Boreal Forest/Taiga, TempConif = Temperate Coniferous Forests, MediForWoodS = Mediterranean Forests, Woodlands and Scrub, TropMoist = Tropical and Subtropical Moist Broadleaf Forests, TropDry = Tropical and Subtropical Dry Broadleaf Forests, TempGraSavanS = Temperate Grasslands, Savannas and Shrublands, MontMoor = Montane Moorlands, DesertXerS = Deserts and Xeric Shrublands, TropGrassSavanS = Tropical and Subtropical Grasslands, Savannas and Shrublands.

for their supervised classification as they implemented a 3-stage classification strategy. At each stage, the area occupied by each habitat type was predicted at a finer spatial scale, which resulted in a map that depicted the most probable habitat type for each pixel. Unsupervised classification was implemented by Hill and Thomson (2005) and Su et al. (2016). Some studies used only one classification algorithm, and others compared classification results between two or more algorithms. For instance, Shoot et al. (2021) compared five machine learning algorithms.

In general, distribution-free machine learning algorithms performed better than parametric classifiers, especially with the fusion of ALS and hyperspectral imagery when the number of explanatory variables was relatively high (Dalponte et al., 2008). When only ALS data was used, no significant differences were reported in the performance of the classifiers (e.g. Sverdrup-Thygeson et al., 2016; Vehmas et al., 2009).

In general, the overall accuracy was greater when the number of habitat types to be classified was small, as expected. For example, Sverdrup-Thygeson et al. (2016) obtained an overall accuracy of approximately 94% in their 2-class scenario, whereas Álvarez-Martínez et al. (2018) mapped 11 forest-related habitat types with an overall accuracy of approximately 66%. Poor class-level accuracies were attributed in some studies to the small number of training samples for a specific class (Álvarez-Martínez et al., 2018; Pippuri et al., 2016; Shoot et al., 2021) and to incorrect labelling of the training data (Vehmas et al., 2009). Also, leaf-off ALS data were found to result in poorer overall accuracies than leaf-on data, which would indicate that the mixed use of ALS data acquired under different conditions may not be favourable in this use case (Bottalico et al., 2014). In addition, low point cloud density ($\sim 0.5\text{pt./m}^2$) was indicated as a potential cause for low classification accuracy (Tijerín-Triviño et al., 2022). An increase in overall accuracy when using optical aerial imagery in combination with ALS data was reported by Shoot et al. (2021), Simonson et al. (2013) and Dalponte et al. (2008). The inclusion of Landsat and radar metrics were found to have minimal or no effect on the classification accuracy of forest types when used in combination with ALS metrics (Martinuzzi et al., 2013).

Vertical ALS metrics were used in most studies and were found to perform well in the classification of forest habitat types, even when the point density was as low as 0.05pt./m^2 (Martinuzzi et al., 2013). In general, the most powerful vertical ALS metrics were average/mean values (Álvarez-Martínez et al., 2018; Bottalico et al., 2014) and the coefficient of variation associated with vegetation height (Bottalico et al., 2014; Sinclair 2021; Sverdrup-Thygeson et al., 2016). Other useful vertical ALS metrics included penetration rate and height percentiles (80th, 90th, 95th, max. value) of the vegetation. In an assessment of old forest naturalness Sverdrup-Thygeson et al. (2016) observed that the ALS metrics that described the horizontal variation of the vegetation performed better than those that reflected the vertical structure. Martinuzzi et al. (2013) and Shoot et al. (2021) listed topographical variables as important in the classification of forest habitat types. The best performing FW-ALS metrics in the discrimination of vegetation types were related to canopy height, canopy cover, total plant area index (PAI) and PAI profile (Marselis et al. 2018).

When broadleaved trees were used in classification, the addition of spectral variables (Dalponte et al., 2008) and/or ALS intensity features (Pippuri et al., 2016; Vehmas et al., 2011a) were found to be favourable. However, Dalponte et al. (2008) stated that the elevation information of ALS data offered much more explanatory power than ALS-intensity.

3.2. Successional stages

Most long-term processes in forests, such as carbon sequestration, are driven by successional dynamics (Shugart 2000). The precise determination of the forest successional stage in a large area helps to achieve many goals of sustainable forest management, although this determination is not always easy, e.g. in uneven-aged forest management, which

is regarded as an effective way to increase structural and species diversity at the stand-level (Savilaakso et al., 2021). Information on the forest successional stage can also be used to predict future forest conditions via succession models (Busing et al., 2007).

In our review, determination of the stage to be classified was either based on an existing classification scheme used in forest management (e.g. Alberti et al., 2013; Valbuena et al., 2016b) or was tailored by the authors of the study (Martin and Valeria 2022; Martinuzzi et al., 2013). The number of successional stages to be classified ranged from 2–8. Shao et al. (2018) used a 2-class scenario where the purpose was to classify forests as early or later-stage forests. In contrast, Martinuzzi et al. (2013) only considered forests >30 years of age in their classification and classified those into three secondary forest classes (taking into consideration previous land-use) and primary forests. Kane et al. (2010) did not classify forests by age, but examined whether young secondary forests could be separated from primary forests by ALS metrics. Differences in the description of successional stages were evident between studies. For example, Martinuzzi et al. (2013) defined stands >90 years old as primary forests, whereas Kane et al. (2010) used an age threshold value of 220 years for primary forests. In three studies, the aim was to derive old-growth index at the landscape-level as an indicator of old-growth forest conditions (de Assis Barros and Elkin 2021, Fuhr et al., 2022, Hevia et al., 2022). These indices were based on field measurements of forest maturity attributes, such as the basal area of large dead standing trees.

Study areas in the terrestrial biomes were mostly temperate coniferous (Alberti et al. 2013; Falkowski et al., 2009) and contained trees from *Abies*, *Picea* and *Tsuga* genera. One study was conducted in a subtropical broadleaved dry forest (Martinuzzi et al., 2013).

The classification of successional stages was most often based on machine learning algorithms. Fuhr et al. (2022), Martin and Valeria (2022), Martinuzzi et al. (2013) and Falkowski et al. (2009) used a RF algorithm in their studies, while Torresan et al. (2016) first defined the structural patterns in the desired classes with unsupervised clustering, and then used the resulting features as a basis for a supervised classification of successional stages. Other machine learning algorithms that were used included SVM (Valbuena et al., 2016b) and the classification and regression tree (CART) (Weber and Boss 2009). Alberti et al. (2013) and Shao et al. (2018) used a classification based on height threshold values of an ALS canopy height model (CHM).

Classification accuracy was greater in older successional stages (Alberti et al., 2013; Torresan et al., 2016). Errors were most common in forests that exhibited significant structural variability. Examples of this included multi-layered stages (Alberti et al., 2013; Torresan et al., 2016), stages with a distinct understorey (Falkowski et al., 2009) and younger successional stages that contained a large number of small trees (Valbuena et al., 2016b). Small trees in the understorey were found to be difficult to assess using low point density ALS data (2.8pt./m^2), especially with the ITD approach (Alberti et al., 2013). Moreover, ALS data were found to offer better classification accuracy than classification based on Landsat imagery (Martinuzzi et al., 2013). Kane et al. (2010) found no significant relationship between ALS metrics and the age of the primary stands, although metrics for secondary forests showed significant relationships with stand age. The main outcome in their study was that stand age did not automatically indicate a specific stage of canopy structure (i.e. canopy structure does not develop in a linear fashion). A similar conclusion was reported by Weber and Boss (2009), while de Assis Barros and Elkin (2021) also found that tree age did not improve classification accuracy. Studies that predicted continuous old-growth indices (e.g. de Assis Barros and Elkin, 2021; Hevia et al., 2022) reported moderate goodness-of-fit measures for their models (R^2 : 0.35–0.77).

The studies used a number of different ALS metrics as explanatory variables for successional stage classification, although the most often used and important metrics were those that described the vertical canopy structure. For example, standard deviation (Fuhr et al., 2022),

median absolute deviation (Martinuzzi et al., 2013) and average absolute deviation of vegetation height (Valbuena et al., 2016b) were found to perform well with ALS metrics. Other similar metrics included the difference between the 90th and 10th percentiles (Torresan et al., 2016) and the median of the absolute deviations from the overall median of vegetation height (Valbuena et al., 2016b). Metrics related to canopy cover were also reported as important in the modelling of forest maturity (Falkowski et al., 2009; Hevia et al., 2022). Some studies only used the predicted CHM-based canopy height, and these studies often utilised a height threshold to classify successional stages (Alberti et al., 2013; Shao et al., 2018). Martin and Valeria (2022) reported that the ALS metrics commonly associated with structural complexity in old-growth boreal forests showed differing patterns compared to temperate forests (de Assis Barros and Elkin 2021; Kane et al., 2010).

4. Canopy assessment

4.1. Overall canopy structure

Overall canopy structure assessment refers here to the separation of forests into classes that describe height, openness or layering of the canopy. This diverges from the classification scenarios presented in the previous section by concentrating on the structural arrangement of a canopy. Canopy structure (e.g. layering) is an especially important component of the forest ecosystem as it influences the energy fluxes between the atmosphere and the forest stand (Shugart et al., 2010).

In our review, the most common attribute of interest was canopy layering; either single- or multi-storey (Leiterer et al., 2015; Wilkes et al., 2016). For example, Zimble et al. (2003) used a 2-class scenario where the intention was to classify forests as either single- or multi-storey, while Wilkes et al. (2016) predicted the actual number of canopy strata and Morsdorf et al. (2010) defined the extent and height of each stratum. Some studies derived canopy structural types, which included information on canopy layering (single, two-, and multi-layered), canopy type (broadleaved or evergreen) (Jayathunga et al., 2018; Leiterer et al., 2015) and age (Adnan et al., 2019). A more complex classification based on the proportional cover of predefined over-, mid- and under-storey layers was proposed by Whitehurst et al. (2013). They also examined canopy layering using continuous foliage area profiles. Some studies also predicted the crown coverage of different canopy layers in the classification (Guo et al., 2017; Morsdorf et al., 2010; Pascual et al., 2008). In a study by Moran et al. (2018), the premise was to aggregate ecoregion-specific classes of a predominant canopy structure to more general meta-classes at the landscape-scale without using field training data.

Study areas in terrestrial biomes were mostly temperate broadleaved forests that comprised of aspen, poplar or beech species (Guo et al., 2017; Leiterer et al., 2015). Other common regions were temperate coniferous (Zimble et al., 2003) and Mediterranean forests (Pascual et al., 2008).

A wide range of modelling and classification methods were used across the reviewed studies. The most used unsupervised classification method was k-means clustering (Guo et al., 2017; Jayathunga et al., 2018; Pascual et al., 2008). Unsupervised classification was also utilised by Moran et al. (2018), although they used RF for this task in two separate stages, firstly to identify natural groupings within the ALS data, and secondly to classify landscapes using cluster labels in a supervised fashion. A similar approach was used by Adnan et al. (2019) and Morsdorf et al. (2010), although they used different algorithms. Wilkes et al. (2016) utilised the gap probability function, which determines the probability that there is a gap above a certain height in the canopy, and Zimble et al. (2003) classified canopies as single- or multi-storey using a threshold value for tree height variance. Leiterer et al. (2015) used a hierarchical, multi-scale classification approach with Bayesian robust mixture modelling.

Overall classification accuracy in the reviewed studies varied

between 66.9% and 97%. The studies of Zimble et al. (2003) and Leiterer et al. (2015) demonstrated the importance of class number for classification accuracy, i.e. a smaller number of classes will result in greater overall accuracy in general. Also, classification was more accurate for structurally simpler forests and for the dominant layers of multi-layered forests (Morsdorf et al., 2010). Most misclassification occurred in classes with an open canopy structure and those that were multi-layered (Adnan et al., 2019; Guo et al., 2017; Leiterer et al., 2015; Morsdorf et al., 2010; Wilkes et al., 2016). Some studies observed that broadleaved canopies tended to be classified less accurately than evergreen canopy types (Leiterer et al., 2015; Morsdorf et al., 2010). Small training sample size (Guo et al., 2017; Morsdorf et al., 2010; Wilkes et al., 2016), minor differences between classes (Adnan et al., 2019), and the low point density of ALS data (Zimble et al., 2003) were listed as possible reasons for poor classification accuracy for some canopy structure classes.

Suitable ALS metrics for canopy structure classification were those that represented the vertical distribution of the canopy material. Metrics in this category include, for example, the median and standard deviation (Pascual et al., 2008; Guo et al., 2017), second population L-moment (L-scale) (Moran et al., 2018) and the coefficient of variation (Zimble et al., 2003) associated with vegetation height. However, some studies used ALS canopy height to account for the classification of canopy layering (Morsdorf et al., 2010; Whitehurst et al., 2013). Other potential explanatory variables were ALS-predicted canopy cover (Adnan et al., 2019; Guo et al., 2017; Wilkes et al., 2016) and canopy density (Guo et al., 2017; Jayathunga et al., 2018; Moran et al., 2018). Horizontal ALS metrics (e.g. horizontal standard deviation of canopy density) were found to offer supplementary information that aided in the characterisation of the overall canopy structure, although they were not utilised that frequently (Leiterer et al., 2015; Moran et al., 2018). The use of ALS intensity was tested in one study and was found to be a powerful feature in the separation of layers of two different tree species with similar heights (Morsdorf et al., 2010). Aerial imagery metrics were also found to be valuable in distinguishing coniferous from deciduous canopies (Jayathunga et al., 2018). Wilkes et al. (2016) reported that the increment of ALS plot size provided a more robust estimate for the number of canopy strata.

4.2. Understorey description

Understorey is defined here as the vegetation layer where suppressed trees and shrubs exist under a dominant canopy. Understorey trees are fundamental components for ecosystem functioning as they influence stand development, fire behaviour, and provide habitats for many wildlife species (Hamraz et al., 2017a).

The aims of the reviewed studies can be loosely divided into two groups: studies that predicted the existence of an understorey or its trees (Hamraz et al., 2017a; Hill and Broughton 2009; Miura and Jones 2010) and studies that predicted the forest features that describe the understorey (Crespo-Peremarch et al., 2018; Dees et al., 2012; Jarron et al., 2020; Lindberg et al., 2012). The most commonly predicted features were height, cover and volume of the understorey trees, although other aims were evident. For example, Bollandsås et al. (2008) were interested in depicting the growth and regeneration success of young trees in an uneven-aged forest, while Hamraz et al. (2017b) analysed the occlusion effect of higher canopy layers on the lower layers in terms of ALS point density, and investigated how this affected tree segmentation quality. Vehmas et al. (2011b) identified the differences between understoreys of canopy gap types in semi-natural and managed forests.

Temperate broadleaved forest was the most abundant terrestrial biome studied in our review, followed by temperate coniferous forest. Most of the forests were in a natural or near-natural state. One study area was located in a pine plantation (Sumnall et al., 2017).

In assessing the forest understorey, there were essentially two ways to process the ALS data: include all canopy points (Bollandsås et al.,

2008) or remove the dominant canopy layer for further processing (Hill and Broughton 2009; Sumnall et al., 2017; Wing et al., 2012). Jarron et al. (2020) compared the use of these two approaches and noted that the dominant canopy and sub-canopy layers could be separated by multiple methods. A common method was histogram thresholding based on various height measures (Dees et al., 2012; Hamraz et al., 2017a; Jarron et al., 2020; Maltamo et al., 2005). This phase was usually followed by derivation of models between field-measured variables and ALS data to estimate variables for the forest understory. Crespo-Peremarch et al. (2018) employed a different approach and used voxelised FW metrics to predict various understory attributes. Lindberg et al. (2012) compared the estimated vegetation volume profiles between FW and DR-ALS data. Two of the estimated vegetation volume layers were vegetation below 10 and 3 m above ground level. Variables that depict the forest understory in these studies were mostly predicted at the plot-level. Some studies created models at the plot-level and applied those to the whole study area (e.g. Jarron et al., 2020).

The studies in our review reported moderate and substantial R^2 values for the models that estimated understorey volume (0.88–0.95), the number of trees (0.55–0.87) and the different height measures (0.76–0.96). In general, the volume of the understorey was predicted more accurately than height features. Segmentation of the canopy layers was found to increase the prediction performance of derived models (Crespo-Peremarch et al., 2018; Hamraz et al., 2017a; Jarron et al., 2020), especially with variables related to understorey height. Here, segmentation of canopy layers refers to the removal of the upper canopy layers based on a field-derived height threshold of the understorey, for example. Lindberg et al. (2012) reported that vegetation volume estimates for lower canopy layers were more accurate when FW-ALS was utilised over the DR-ALS. Hill and Broughton (2009) reported that both leaf-on and leaf-off ALS data could be used to predict absence or presence of the understorey with almost equal accuracy (72% vs. 77%). For point density, Hamraz et al. (2017b) noted that both understorey and overstorey trees could be segmented equally accurately when the overall point density was approximately 170/m². Bollandsås et al. (2008) reported that ALS data was able to describe regeneration success better than measures related to vitality (e.g. leader length). Vehmas et al. (2011b) found that canopy gaps with dense undergrowth could be distinguished from other types of gaps using spatial metrics and ALS return heights.

Sumnall et al. (2017) reported cases where the understorey layer intersected the dominant canopy layer. This resulted in an over-estimation of sub-dominant heights, especially in older coniferous stands. Hill and Broughton (2009) emphasised that the modelling of understorey information must consider the structure of the overstorey and the penetration of the laser pulse through this layer. Therefore, the use of simple height thresholds is not adequate under such conditions and will likely lead to false discrimination of the canopy layers (Hill and Broughton 2009).

5. Diversity measures of trees

5.1. Tree species

Species richness and diversity are often reported measures of biodiversity, and their assessment is of major global interest as they contribute to ecosystem (here forest) health. This section covers the studies that have utilised ALS data as the main remote sensing data in the assessment of tree species diversity. We also reviewed studies that used ALS data in the inventory of ecologically important tree species.

Some studies defined species richness (i.e. the number of species within a defined region) or diversity indices (e.g. Shannon diversity index) based only on the trees (e.g. Fricker et al., 2015; George-Chacon et al., 2019; Mauya 2015), although some studies also considered shrub and herb species (e.g. Ceballos et al., 2015; Leutner et al., 2012). A small number of studies concentrated on the amount of ecologically important

tree species, for example, aspen (Maltamo et al., 2015; Sankey, 2012) within the forest stand.

Study areas were most often located in boreal coniferous and temperate broadleaved forests. Also, tropical and sub-tropical forests were often studied (Hernández-Stefanoni et al., 2015; Martins-Neto et al., 2021). One study area was located in the urban forests of Los Angeles (Gillespie et al., 2017).

Tree species diversity measures were most often predicted using regression techniques, such as linear regression (Ceballos et al., 2015; Gillespie et al., 2017; George-Chacon et al., 2019) and generalised least squares regression (Dalponte et al., 2018; Fricker et al., 2015; Wolf et al., 2012). Non-parametric methods, including RF (Leutner et al., 2012; Mohammadi et al., 2020), k-NN (Mauya 2015; Mohammadi et al., 2020) and Multivariate Adaptive Regression Spline (Vaglio Laurin et al., 2016) were also used. Martins-Neto et al. (2021) tested multiple machine learning methods for the prediction of tree species richness and diversity among other stand variables. Sankey (2012) utilised quantile regression, and Säynäjoki et al. (2008) used linear discriminant analysis in the classification of individual deciduous canopies.

In general, studies reported that the correlation of tree species richness and ALS metrics was greater than the correlation of tree species diversity and ALS metrics (Leutner et al., 2012; Mauya, 2015). Martins-Neto et al. (2021) reported contradictory results, mainly because of the large number of tree species found in tropical forests. Leutner et al. (2012) reported the lowest R^2 value (0.30) for species richness of all canopy layers, and the best performing model of all studies ($R^2 = 0.89$) was obtained by George-Chacon et al. (2019) for the Shannon diversity index of tree species, which utilised both ALS metrics and satellite imagery. Similar model performance was reported by Zhao et al. (2018) and Dalponte et al. (2018) for the Shannon diversity index and tree species richness. Kamoske et al. (2022) reported that the taxonomic diversity model yielded a greater explanatory power (R^2 : 0.46) than the phylogenetic (R^2 : 0.33) and functional diversity (R^2 : 0.31) models. Mapping of aspen was found to be difficult as it shared similar intensity metric values with spruce and birch (Korpela et al., 2010). Yet, other ecologically important species, such as *Alnus incana* and *Salix caprea*, could be separated based on high intensity values. However, when aspen trees are relatively large, they are distinguishable from other deciduous tree species when both intensity and height percentiles are used (Säynäjoki et al., 2008). Moreover, ALS-based vegetation height was found to improve the overall accuracy of Landsat-based aspen presence/absence detection (Sankey, 2012), while Maltamo et al. (2015) reported that a balanced sample obtained with ALS-guided probability proportional sampling generally improved the predictions of stand volume estimates for aspen.

In general, studies that used both optical and ALS data reported that the latter provided the best performance for diversity models (Ceballos et al., 2015; Fricker et al., 2015; Kamoske et al., 2022; Mohammadi et al., 2020). The standard deviation associated with vegetation height was found to correlate more with tree species richness than with the mean value (Fricker et al., 2015; Hernández-Stefanoni et al., 2015; Mohammadi et al., 2020). Leaf-on ALS data were reported to explain slightly more of the variation in tree species richness than leaf-off data: $R^2 = 0.49$ vs. 0.42 (Hernández-Stefanoni et al., 2015). Leutner et al. (2012) clarified that ALS provided the best predictors for total species richness predictions across all forest canopy layers (including herb and shrub species), although tree species richness was predicted most accurately using a fusion of hyperspectral and ALS data. Improved R^2 values when two datasets were combined were also reported by other studies (George-Chacon et al., 2019; Kamoske et al., 2022). Wolf et al. (2012) demonstrated that the inclusion of ALS terrain metrics improved the model performance for tree species richness in tropical forests. In urban forests, ALS metrics were not found to be associated with tree species diversity (Gillespie et al., 2017). Dalponte et al. (2018) reported that multispectral ALS data offered a slightly more accurate prediction of the Shannon diversity index for tree species compared to single

spectral ALS data ($R^2 = 0.85$ vs. 0.80), although there were differences in the explanatory power between the multispectral ALS channels.

5.2. Understorey species

Studies that assessed understorey plant species most often predicted species richness and/or the diversity index (Shannon, Simpson, Pielou) associated with these species. In some cases, predictions were calculated separately for a different species group; for example, shrub and herb species (Ceballos et al., 2015; Leutner et al., 2012; Lopatin et al., 2016), bryophyte species (Bourgouin et al., 2022), or species-wise (Nijland et al., 2014), or all vascular plants were examined together (Zellweger et al., 2016). Moeslund et al. (2022) had a divergent objective for their study as they modelled the dark diversity of plant species, which denotes the absence of suitable species. Some studies predicted the actual yield of specific species, for example, fruit production (berries) (Barber et al., 2016; Bohlin et al., 2021; Nielsen et al., 2020) or mushroom production (dry mass per hectare) (Pascual and de-Miguel 2022; Peura et al., 2016). Pascual and de-Miguel (2022) showcased the use of ALS data in various forest management scenarios where the aim was to increase mushroom yield. Korpela (2008) tested the use of ALS intensity information for the detection of lichen mats on a small test plot. The most commonly used methods in the reviewed studies were RF and Generalised Linear Models.

The study areas in this topic covered different terrestrial biomes, from mixed mountainous to broadleaved Mediterranean forests. However, the most common terrestrial biome was temperate forests with a mixture of tree species.

Model fits (R^2) for understorey species richness and diversity ranged between 0.2–0.6. Martinuzzi et al. (2009) reported a classification accuracy of 83% for the presence/absence of understorey shrub species, while lichen mats could be detected with an overall accuracy of 65–75% (Korpela 2008). Richness models usually exhibited better R^2 values than the diversity (Leutner et al., 2012) or yield models (Peura et al., 2016). When all vascular plants in the understorey layer were considered (including trees), model accuracies did not improve noticeably. One possible reason could be that R^2 values for species richness in the herb and shrub layers were greater than for the tree layer (Leutner et al., 2012; Lopatin et al., 2016). The presented approach of using ALS data to guide forest management actions towards optimal mushroom yields was found to be informative for forest managers at the landscape scale and provided evidence for meaningful decision making (Pascual and de-Miguel 2022).

The ALS metrics related to heterogeneity in the lower parts of the vegetation layers were considered the most important by the reviewed studies. These included proportions of returns from lower heights (e.g. Thers et al., 2017) and low percentiles of vegetation heights (Bourgouin et al., 2022; Vauhkonen, 2018). Mean canopy height was often identified as an important variable in the modelling of species richness (Lopatin et al., 2016). Information provided by ALS data was found to be especially important on sites that showed extensive heterogeneity in topography, for example, mountainous areas (Bouvier et al., 2017; Ceballos et al., 2015). Normalised ALS intensity information was found to be useful for the detection of lichen mats on the forest floor (Korpela 2008). Variables related to local terrain structure were especially important when predicting richness and diversity of understorey species (Barber et al., 2016; Bourgouin et al., 2022; Moeslund et al., 2019; Nielsen et al., 2020; Nijland et al., 2014). Another important variable that was used in combination with ALS was climate (Mao et al., 2018; Zellweger et al., 2016). The ALS metrics were found to have greater explanatory power than metrics computed from aerial (Leutner et al., 2012) and satellite images (Bouvier et al., 2017; Peura et al., 2016). The vegetation height information from ALS was the most important factor that affected dark plant diversity in forests (Moeslund et al., 2022). The combination of variables from both ALS and imagery data did not significantly improve model performance or the overall classification

accuracy related to the understorey assessment (Singh et al., 2015).

Some of the reviewed studies reported that there were issues with the suitability of ALS to assess the species richness and diversity of the understorey species. For example, Barber et al. (2016) reported that the diversity and yield prediction of buffaloberry (*Shepherdia canadensis*) with ALS data was not successful. One reason may be the randomness of the distribution of this species and other factors, such as competition. Bohlin et al., (2021) reported that their ALS-based mixed effects model for bilberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitis-idaea* L.) yields exhibited R^2 values of 0.40 and 0.53, respectively, although the fixed part of the models exhibited R^2 values of only 0.05. Most of the random variation was found in the National Forest Inventory cluster level in both models (Bohlin et al., 2021) where the ALS predictions provided valuable information on the spatial location of substantial berry yields, a finding also supported by Nielsen et al. (2020). Martinuzzi et al. (2009) reported that some of the vertically lower ALS metrics were problematic in understorey related assessments, as they indicated the presence of lower branches and saplings instead of shrubs.

5.3. Structural diversity

Structural diversity is regarded as a fundamental component of biodiversity assessment in forests (Chirici et al., 2011). Structurally diverse forests exhibit substantial variation in tree diameter and height, which results in more tree species and age classes within the stand.

In our review, structural diversity was most often measured by the Gini coefficient (GC) (identical to coefficient of variation of L moments) associated with tree size inequality with respect to diameter at breast height (dbh) or tree height (Adhikari et al., 2020; Valbuena et al., 2014). Some studies utilised the standard deviation associated with tree height and dbh (e.g. Mura et al., 2015), or employed variations in crown dimensions (Davison et al., 2020; Ozdemir and Donoghue, 2013) and/or crown surfaces (Kukunda et al., 2019) as measures of structural diversity. In three studies, the main focus was on the functional diversity of trees (Kamoske et al., 2022; Zheng et al., 2021; Zheng et al., 2022).

The main objectives of the studies can be divided into two main groups: studies that only predicted structural diversity measures using ALS variables (Dalponte et al., 2018; Mura et al., 2016) and others that investigated the effects of different components (e.g. ALS pulse density or plot size) in the modelling and prediction of these measures (Bottalico et al., 2017; Davison et al., 2020). Some studies also investigated the use of derived structural diversity measures in the characterisation of forest structural types (Valbuena et al., 2013; Valbuena et al., 2016a). Regression was the most used statistical method to estimate field-derived structural diversity measures from ALS variables. Other commonly used methods were RF (Kukunda et al., 2019) and k-NN (Mura et al., 2016).

Study areas were most often located in temperate broadleaved and mixed, boreal, and Mediterranean forests. An African study area was located in tropical forests in a mountainous region (Adhikari et al., 2020). Two study areas were located on mixed sub-tropical forests (Zheng et al., 2021; Zheng et al., 2022).

The studies reported a wide range of fits (R^2) for the models that assessed tree size inequality (e.g. GC_{dbh} : 0.33–0.89). The poorest fits were related to forests with a very diverse structure. For example, Adhikari et al. (2020) obtained a GC_{dbh} R^2 value of 0.40 in tropical mountainous forests. In general, models for tree height diversity exhibited better fits (R^2 : 0.62–0.86). However, models for the standard deviation associated with tree height and dbh produced a better overall fit than GC models (Bottalico et al., 2017). Models that depicted crown dimensional diversity (crown length and width) did not perform as well as the tree height and diameter-related diversity models (R^2 : 0.20–0.52) (e.g. Ozdemir and Donoghue, 2013). Individual tree detection in tree size inequality assessments proved to be inferior to the ABA, mostly because of the poor tree detection rate of the understorey trees (Valbuena et al., 2014). On the other hand, the ITD approach for the

mapping of trait-based functional diversity was more robust than ABA, as the larger pixel size in ABA was led to the capture of less variation (Zheng et al., 2022).

The most often selected explanatory ALS variables were coefficient of variation, standard deviation and skewness of ALS heights, L-skewness, and canopy cover metrics. Other potential variables included percentiles of vegetation heights (Bottalico et al., 2017; Dalponte et al., 2018; Mura et al., 2016) and standard deviation of heights in ALS-CHM (Ozdemir and Donoghue, 2013). The predictive power of ALS variables was found to be superior to Landsat metrics, although incorporation of these variables improved model R^2 values from ~ 0.45 to ~ 0.60 (Adhikari et al., 2020). Dalponte et al. (2018) reported that a model from multispectral ALS data, which included metrics from three channels, had a slightly poorer fit for GC_{dbh} than a model based on single spectral ALS data. They also found that GC_{dbh} did not correlate with ALS intensity information. Leaf-on and leaf-off ALS data performed equally well, but the combined use of leaf-on and leaf-off data in structural diversity models explained over 10% more variance than either dataset used alone (Davison et al., 2020).

Valbuena et al. (2013) reported that the GC_{dbh} could be used to separate uneven- and even-sized forests. In the former, Lorenz asymmetry (Lorenz curve indicator) was found to characterise the understorey development. However, the assessment of understorey establishment yielded the most uncertainty, as the model fit for Lorenz asymmetry was significantly poorer (R^2 : 0.25) than for GC (R^2 : 0.89). More recently, Valbuena et al. (2017) showed that the direct estimation of two L-moment ratios that describe ALS return distributions, the L-coefficient of variation (=GC) and L-skewness (=Lorenz asymmetry), were well-suited to separate forests in a manner similar to their earlier study (Valbuena et al., 2013). The use of GC was also found to be applicable in separating forests under different management regimes (Valbuena et al., 2016a).

6. Dead wood

The existence of dead wood in forests is important for many reasons as it affects forest carbon storage, nutrient cycling, and provides habitats and resources for many species (Harmon et al., 1986; Siitonen 2001; Smallman et al., 2017). In particular, large-diameter dead wood is considered ecologically valuable as the increment in the diameter is positively correlated with forest biodiversity (Jönsson and Jonsson 2007).

The viewpoints of the reviewed studies differed. Some studies focused on fallen trees (Heinero et al., 2021; Lindberg et al., 2013), others on standing dead trees (Amiri et al., 2019; Hardenbol et al., 2022; Stitt et al., 2022a), and some took both types into consideration (Pesonen et al., 2008). The objective was often to identify single standing trees or fallen dead trees (Blanchard et al., 2011; Dobre et al., 2021; Yao et al., 2012), although characteristics of the dead wood, such as volume (Chirici et al., 2018), diameter (Stitt et al., 2022b) and the proportion of standing dead tree (decay) classes (Bater et al., 2009), were also estimated. Pesonen et al. (2010a) investigated the use of ALS-based probability layers as auxiliary information in the design and estimation phase of a dead wood field inventory. These were found to increase the sampling efficiency of both standing and fallen dead wood (Pesonen et al., 2010a). The reviewed studies also employed widely differing minimum dbh threshold values for dead wood. For example, Mücke et al., (2013) used 300 mm and Nyström et al., (2014) 69 mm in their respective studies. In most cases, study areas were located within protected forests in the temperate and boreal ecoregions, which naturally exhibit a large amount of fallen and/or standing dead wood.

Detection of fallen and standing dead trees differed from a classification perspective. Fallen tree detection relied on the identification of line-like features (Lindberg et al., 2013; Nyström et al., 2014; Polewski et al., 2015a), whereas standing dead trees were generally detected based on their altered intensity distribution and the structure that

resulted from missing branches and reduced foliage (Wing et al., 2015; Yao et al., 2012). Height-filtering of a point cloud was an important initial stage in the detection of fallen trees (Pesonen et al., 2008; Jarron et al., 2021). Then, the line-like features of the filtered point cloud were detected using direct line detection (Heinero et al., 2021), raster-based line template matching (Lindberg et al., 2013; Nyström et al., 2014) or other less demanding methods, such as shape context descriptor (Polewski et al., 2015b) and the normalised cut approach (Yao et al., 2012). In some studies, standing trees were classified as living or dead (Martinuzzi et al., 2009). Stitt et al. (2022a) distinguished living and dead standing trees by determining the canopy gaps around stems and snags. In the same study area, Stitt et al. (2022b) classified standing dead trees by their diameter and intactness (intact or a broken top). Estimation of dead wood volume and the proportion of different dead wood classes were typically based on the use of regression between the ALS features and the variables of interest (Bater et al., 2009; Pesonen et al., 2008). However, Jarron et al., (2021) estimated the volume of dead fallen trees using the actual dimensions of segmented logs, while Chirici et al., (2018) estimated the volume of windthrown trees using mean height and dbh of the stand where the fallen trees were found.

Detection accuracies for both standing and fallen dead trees varied considerably between studies (overall accuracy: $\sim 40\%$ to $>90\%$). Detection accuracy clearly increased with increasing diameter and length of the stem (Hardenbol et al., 2022; Heinero et al., 2021; Nyström et al., 2014; Wing et al., 2015) but clear differences in detection accuracies between fallen or standing trees were not apparent. However, there was some evidence that the volume of fallen dead wood could be predicted with greater accuracy than the volume of standing dead wood when low pulse density ALS data (~ 4 pt./m²) were utilised (Pesonen et al., 2008). In studies where standing dead trees were detected by tree species, dead spruce trees were reported to be easier to identify than deciduous or pine trees (Amiri et al., 2019; Kamińska et al., 2018). Also, detection of late-stage decomposition fallen trees proved to be more difficult than earlier decay stage trees, mostly due to reduced height of the stem objects above the ground (Mücke et al., 2013; Jarron et al., 2021). Stitt et al. (2022b) reported that the classification between standing dead trees and snags was difficult. Moreover, fallen trees in old-growth forests were detected with greater accuracy than trees in young forests (Heinero et al., 2021).

There was considerable variation in ALS point densities between the studies. The greatest point densities were used in studies that focused on the detection of fallen dead trees. In these studies, densities ranged between 10 and 69pt./m². The use of point densities > 30 pt./m² did not seem to result in a noticeable improvement of the detection accuracy. For example, Polewski et al., (2015b) used an ALS point density of approximately 30pt./m² and were able to detect fallen trees with overall accuracy of 80–90%. On the other hand, Lindberg et al., (2013) used an ALS point density of 69pt./m² but their overall accuracy for fallen dead tree detection was 41%. One must note that these studies were located in different types of forests, and therefore it is difficult to draw conclusions from the effect of point density in the detection of fallen dead trees.

Structural variables related to canopy heterogeneity, such as coefficient of variation and median absolute deviation of ALS heights, were most often used in the detection of dead trees (Bater et al., 2009; Martinuzzi et al., 2009). It was observed that the variables that describe the geometrical structure of the canopy surface were beneficial (Amiri et al., 2019; Hardenbol et al., 2022; Yao et al., 2012) and waveform metric information, such as return width and amplitude, increased the detection accuracy (Mücke et al., 2012). The use of multi-wavelength ALS data was found to improve the accuracy of dead standing tree detection compared to cases when only one wavelength channel was used (Amiri et al., 2019). The ALS intensity features were particularly useful when the species of the dead trees was of interest (Amiri et al., 2019; Kamińska et al., 2018; Pesonen et al., 2008). Information provided by ALS showed a greater correlation with both standing and fallen dead trees than stand register data or aerial imagery (Hardenbol et al., 2022; Pesonen et al.,

2010b).

In general, clusters of fallen trees and dense understorey vegetation were considered to be the main reason why dead trees were falsely detected (Blanchard et al., 2011; Mücke et al., 2013; Wing et al., 2015). Also, roads, stone walls and ditches were problematic when line-like features of fallen trees were identified (Lindberg et al., 2013; Nyström et al., 2014). Data-related issues included insufficient density of the ALS point cloud (here <10 pt./m²) (Hardenbol et al., 2022; Stitt et al., 2022b; Wing et al., 2015) and poor location accuracy of the trees measured in the field (Nyström et al., 2014).

7. Forest fragmentation

Forest fragmentation and its effects on structure, function and biodiversity are important issues as they are closely connected to changes in land use (Laurance et al., 2017). The microclimate on the forest edge differs from the interior of the forest, as the air is both drier and warmer and wind effects are much more prominent (Didham and Lawton 1999).

Despite the relatively small number of forest fragmentation studies, the aims of these studies varied widely. Aims were classified into two categories: studies that focused on within-fragment properties (e.g. Almeida et al., 2019; MacLean 2017; Vaughn et al., 2014), and studies that investigated inter-fragment connections (e.g. Guo et al., 2018). Two studies investigated the long-term effects of fragmentation on canopy structure (Almeida et al., 2019; Vaughn et al., 2014) and one study investigated the effects of fragmentation and fragment area on bird species richness (Flaspohler et al., 2010). Shao et al. (2018) delineated interior forests and investigated the effect of considering forest successional stage in the delineation procedure. Study areas were mainly located in tropical moist (3 studies) and temperate broadleaved (2 studies) forests.

In general, ALS information was found to be suitable to expand understanding of fragmentation effects on forest structure and function (e.g. Vaughn et al., 2014). Almeida et al. (2019) reported that ALS information on mean canopy height showed clear differences between near-edge and inner forests: canopy height decreased by 30% on the edges of the larger fragments (>10 ha) and in the interior of smaller fragments (<3 ha). Vaughn et al. (2014) reported similar results related to canopy height and stated that fragment area was strongly related to the development of canopy structure. Minimum span variable, which defines “the minimum straight-line distance that is required to bisect the fragment while passing through a given point location”, was found to explain variations in the depth and magnitude of edge effects for canopy structural variables (Vaughn et al., 2014). Flaspohler et al. (2010) found that native and exotic bird species richness in Hawaiian forests exhibited a different response in the fragmented area; exotic species were more area-sensitive, and smaller fragments were dominated by native species. For the definition of edge depths, ALS-derived estimates did not differ significantly from the field data (MacLean, 2017). Lastly, accounting for forest successional stages in the delineation process of forest interiors proved to be well-founded as it improved the total area estimations of forest interiors by approximately 10% (Shao et al., 2018).

8. Animal ecology

Habitat structural heterogeneity has long been recognised as the main component that affects local variations in biodiversity (MacArthur and MacArthur, 1961). In forested ecosystems, this heterogeneity is caused by plant communities, and it has been shown to affect diversity and richness of multiple species including birds and mammals (Bergen et al., 2009).

8.1. Species richness (α -diversity)

To date, most of the research on faunal species richness has been

focused on birds (Carrasco et al., 2019; Lesak et al., 2011; Melin et al., 2018; Vogeler et al., 2022). A minority of studies were interested in the richness of other forest-dwelling taxa, which included butterflies (Zellweger et al., 2016), spiders (Vierling et al., 2011), bats (Renner et al., 2018; Vogeler et al., 2022) and beetles (Lindberg et al., 2015; Müller and Brandl 2009). There was a wide range of objectives across the studies. Most of the studies predicted the total and/or group-wise species richness using ALS (and possibly other remote sensing data) and compared the importance of explanatory variables and datasets (Eldegard et al., 2014; Ziegler et al., 2022). Some studies concentrated on the changes in species richness near the forest edges (Melin et al., 2019), the change in species richness under different forest management conditions (Klein et al., 2020; Renner et al., 2018) and the scale dependency in the heterogeneity-diversity-relationship (Weisberg et al., 2014). Earlier studies that predicted bird species richness with ALS used a broad habitat-based grouping of species (e.g. Goetz et al., 2007). More recently, this has shifted towards the utilisation of a grouping based on the nesting practises of the species (Vogeler et al., 2014; Weisberg et al., 2014). Some bird-related studies focused on specific species that were presumed to be sensitive to vegetation structure (Lesak et al., 2011). One study predicted both taxonomic richness and the functional richness of bird species (Tew et al., 2022). In general, species richness was modelled using regression analysis.

The most often encountered terrestrial biomes were temperate broadleaved forests. Other common ecoregions were coniferous temperate and boreal forests with a mixed set of tree species. Two study areas were located in the tropical ecoregion. A small number of studies took place in mountainous areas (Vogeler et al., 2022; Zellweger et al., 2016; Ziegler et al., 2022) and one study was focused on urban forests (Sasaki et al., 2016).

The coefficient of determination (R^2) for total species richness models ranged from 0.18 to 0.96 across all taxa. Group-specific accuracies among bird species varied widely and were in some cases much greater (R^2 : ~ 0.50) than total bird species richness. Spider species richness could be predicted with similar accuracy as birds. Also, the explanatory power of bat (R^2 : 0.96) and bird species (R^2 : 0.93) richness models were found to be similar (Vogeler et al., 2022). The R^2 values for forest beetles and butterflies were generally lower (Lindberg et al., 2015; Zellweger et al., 2016). Tew et al. (2022) reported that functional richness model for bird species exhibited a slightly lower explanatory power than model for taxonomic richness (0.78 vs. 0.89).

The use of ALS data and satellite/aerial images in combination as predictors was found to improve model predictive performance only slightly for bird species richness (Goetz et al., 2007; Melin et al., 2019), and was most beneficial for species strongly associated with deciduous trees (Eldegard et al., 2014). In many studies, climatic variables (e.g. temperature, precipitation) were found to be more strongly related to bird species richness than ALS metrics (Carrasco et al., 2019; Coops et al., 2016; Vogeler et al., 2022; Zellweger et al., 2016). In addition, Vogeler et al. (2022) reported similar dependencies for bat species richness: mean annual temperature explained 93% and ALS canopy density 20% of the variation in bat species richness. Significantly lower predictive power of ALS metrics compared to field metrics was reported by Tew et al. (2022), who found that total area and age class of a compartment explained more variation in the models of bird species taxonomic richness and functional richness.

Bird species richness was often found to increase with increasing density in the forest understorey (e.g. Klein et al., 2020). Therefore, metrics that describe lower vegetation density (e.g. Lindberg et al., 2015; Melin et al., 2018; Vogeler et al., 2014), and mid-storey height and density, were found to be important (Lesak et al., 2011). In mountainous tropical forests in Tanzania neither bird nor bat species richness were related to understorey or mid-storey density, but the greatest predictive power was observed with canopy density (Vogeler et al., 2022). In the same study area, Ziegler et al. (2022) reported that ground elevation was a more important metric than ALS structural metrics in the

prediction of species richness for 17 taxa. Moreover, the standard deviation associated with vegetation height and other metrics related to canopy vertical heterogeneity (e.g. foliage height diversity) were found to be highly efficient in predicting bird species richness (Flaspohler et al., 2010; Melin et al., 2019; Sasaki et al., 2016). Canopy height variables were found to be the most important for forest beetles (Müller and Brandl 2009) and spider richness (Vierling et al. 2011).

8.2. Species diversity indices

The most often predicted diversity index with regard to forest fauna was the Shannon diversity index (also known as the Shannon-Wiener index). This index estimates the diversity of a population through entropy by considering the number of species in a habitat and their relative abundance (MacArthur and MacArthur 1961). Another common diversity index used by the studies in our review was Simpson's diversity index, which signifies the probability of two randomly chosen individuals as belonging to different species (Lande 1996). As previously stated, most of the research concentrated on bird species, although in some studies, spiders (Vierling et al., 2011), arthropods (Müller et al., 2014) and butterflies (Zellweger et al., 2017) were of interest. A range of regression methods (generalised linear, mixed effects, best subsets) were used in the modelling phase.

Temperate broadleaved and coniferous forests were the most studied terrestrial biomes. Other ecoregions included urban (Sasaki et al., 2016) and tropical moist forests (Wallis et al., 2016).

Modelling species diversity indices yielded moderate fits: R^2 values ranged between 0 and 0.34. Studies that modelled both indices commonly reported that Simpson's diversity index was more accurately predicted than the Shannon diversity index (Müller et al., 2014). Taxa of the modelled species or forest terrestrial biome did not have any notable effect on model accuracy.

In general, the ALS predictions were reported to be superior to, or at least as accurate as, field-derived explanatory variables (Müller and Brandl 2009; Sasaki et al., 2016; Vierling et al., 2011). Inclusion of aerial or satellite imagery variables in the modelling had little effect on modelling accuracy (e.g. Melin et al., 2019). The most powerful ALS metrics were similar to those with species richness: lower vegetation height and density metrics, and metrics that describe the vertical heterogeneity in the canopy (e.g. standard deviation associated with vegetation height), were most often selected. These metrics were suitable for various taxa, although bird and arthropod diversity displayed a different response to these metrics.

Wallis et al., (2016) reported that optical texture metrics derived from satellite data had much more explanatory power than ALS metrics in tropical forests; the optical texture model for the Shannon diversity index of bird species had a R^2 value of 0.57 and the ALS model a R^2 value of 0.26. The poor performance was partly explained by the fact that a dense overstorey leads to poor penetration of laser pulses into the lower canopy. Tew et al. (2022) reported that in their model for Shannon diversity index of bird species (R^2 : 0.62), field-measured total area explained 39% of the variation and the age class of a forest compartment explained 15%. Moreover, climatic variables at the country-scale were found to be more effective than ALS variables for the prediction of diversity indices of birds and butterflies (Zellweger et al., 2017).

8.3. Habitat suitability for forest fauna

With regard to the occurrence of fauna, the studies in this review expressed different objectives. In some studies, the objective was to map the occurrence of old-growth forest species and to use their occurrence as indicators of suitable habitats for a specific animal or animals (e.g. Vogeler et al., 2013). Some studies mapped the occurrence of forest animal species using their priori-known habitat preferences and then extracting the forest areas that fulfilled these features (Coops et al., 2010; Garabedian et al., 2014; Rada et al., 2022). There were also

studies that compared the structure of ALS-predicted occurrence areas with known habitat preferences (Koma et al., 2021; Mononen et al., 2018) and studies that predicted habitat quality classes for specific species (Hinsley et al., 2006). For example, the mean body mass of birds (Bradbury et al., 2005; Hinsley et al., 2006), and the basal area and tree density (Garabedian et al., 2014) have been utilised as measures for habitat quality. Most of the research focused on birds (e.g., Bradbury et al., 2005; Herniman et al., 2020; Koma et al., 2022; Zellweger et al., 2013b), although bats (Jung et al., 2012), butterflies (de Vries et al., 2021), saproxylic beetles (Rada et al., 2022) and deer (Lone et al., 2014; Melin et al., 2013) were also covered.

Study areas focused on numerous terrestrial biomes that ranged from mountainous ecosystems (Zellweger et al., 2013a) to riparian forests (Seavy et al., 2009) and wetlands (Koma et al., 2021; Koma et al., 2022). However, most of the study areas were located in the boreal and temperate ecoregions, and included both broadleaved and coniferous forests.

By far the most often adopted statistical method to model species occurrence was logistic regression, although RF was also commonly used (de Vries et al., 2021; Eldegard et al., 2014; Koma et al., 2022). Only one study employed a different modelling approach: Vauhkonen and Imponen (2016) utilised an unsupervised k-means algorithm to locate the potential habitats for two grouse species.

In general, ALS information was considered suitable for the mapping of species occurrence. The prediction of species occurrence achieved AUC (area under the receiver operating characteristic curve) values that ranged between 0.7 and 0.9 (de Vries et al., 2021; Hagar et al., 2014; Koma et al., 2022; Seavy et al., 2009; Vogeler et al., 2013). These values indicate "acceptable" and "excellent" model discrimination, respectively (Hosmer et al., 2013). There was a clear variation in the response to ALS variables between bird species, and species-wise models exhibited variable performance (Eldegard et al., 2014; Koma et al., 2022). In general, specialist bird species models were highly significant (Eldegard et al., 2014; Herniman et al., 2020) and low accuracy models were often found for generalist bird species. For the prediction of habitat quality, ALS variables were reported to explain between 5 and 82% of the observed variation in habitat quality variables (Garabedian et al., 2014; Hinsley et al., 2006). The greatest difference in the explained variation was found in the relationship between mean canopy height and mean chick body mass, which was used as the measure of habitat quality in different years (Hinsley et al., 2006). The variation was not related to point density of ALS data or other remote sensing characteristics, but it was highly related to the local climatic conditions in different years. The highest R^2 values (up to 82%) were observed in exceptionally warm or cold springs, while the smallest R^2 values (as low as 5%) were observed in average springs. The unsupervised classification approach was deemed unsuitable for habitat mapping of forest birds (Vauhkonen and Imponen 2016).

The ALS variables that were selected most often to map occurrence and habitat quality for forest fauna were related to canopy vertical structure and heterogeneity. Examples include mean, standard deviation, and both low and high percentiles associated with vegetation height. Also, canopy cover and its variants were often selected in these models (e.g. Graf et al., 2009; Koma et al., 2022; Lone et al., 2014). The addition of optical image data was reported to lead to only slight improvements in model performance, with the improvement more pronounced for species related to deciduous trees (e.g. Eldegard et al., 2014). The explanatory power of ALS variables outperformed radar data (Koma et al., 2022; Swatantran et al., 2012). The most often selected variable outside ALS in occurrence prediction of forest fauna was the proportion of deciduous trees, which was reported by many studies (e.g. Coops et al., 2010; Garabedian et al., 2014; Goetz et al., 2010). Two studies reported that variables other than ALS, especially elevation, had the most explanatory power (Herniman et al., 2020; Smart et al., 2012).

9. Discussion

Forests contain a wide range of lifeforms, and provide food, shelter and nesting sites for numerous species. Heterogeneity in the vegetation structure has long been recognised to play a significant role in biological diversity patterns. As forested habitats and overall biodiversity face threats caused by human activities, there is an urgent need to map the 3-D structure of forested environments. Quantifying the 3-D vegetation structure on the ground has major drawbacks related to generalisation and is labour-intensive. As ALS is applicable over broad spatial extents and offers fine-scale 3D information on both vegetation structure and topography, it provides a great opportunity to bridge this gap.

In this paper, we reviewed 182 scientific articles that used ALS data as the main remote sensing data to assess the numerous aspects of biological diversity of forested ecosystems. Most of the research was clustered in North America and Europe, especially in the temperate and boreal ecoregions, on Northern Hemisphere. This is because there is a lot of expertise in this domain and ALS data is also widely available from these areas. These findings are similar to those reported in earlier ALS-reviews of forest ecosystem assessments (Acebes et al., 2021; Bakx et al., 2019; Davies and Asner 2014). Topics that received the most research attention were related to animal ecology, tree species diversity, dead trees and the assessment of forest undergrowth species. Forest fragmentation was the least studied topic in the review. The most often applied forest inventory method was ABA, which was utilised in every topic of the review. The ITD approach seemed to be a useful method, mainly in the assessment of dead trees.

The ALS data were often combined with other types of remote sensing data, especially with optical satellite or aerial data. The purpose was to create complementary information on both the structural and spectral structures of a forest. These fusions were most often related to studies where information on tree species was important either directly or indirectly. The prediction of tree species diversity measures and forest land cover classes that considered tree species were found to benefit from the fusion of ALS and optical data (e.g. Dalponte et al., 2008; George-Chacon et al., 2019; Jayathunga et al., 2018). Also, the prediction of faunal species richness, especially those associated with deciduous trees, benefited from the inclusion of optical predictor variables (Eldegard et al., 2014). However, the assessment of forest successional stages (Martinuzzi et al., 2013), dead wood (Pesonen et al., 2010b) and understorey (Bouvier et al., 2017) did not benefit from the addition of spectral data. Radar data were also combined with ALS to assess bird species distributions (Swatantran et al., 2012) and to classify forest land cover classes (Martinuzzi et al., 2013), although information provided by ALS outperformed radar in both cases. A few studies tested the use of citizen science (CS) data in ALS-based assessment of bird habitats. They reported that the fusion of these datasets yielded meaningful results despite drawbacks related to the collection of the CS data (Mononen et al., 2018; Vihervaara et al., 2015).

Relevant ALS metrics were often case-specific, as there is no single, universal metric that is suitable for all ALS-based forest biodiversity assessments. A full list of the most important ALS metrics, categorised by type and topic, are presented in Appendix B. The ALS metrics that are often used in the assessment of traditional stand attributes (e.g. volume or dominant height) were generally found to be sub-optimal for forest biodiversity studies. The vertical ALS point cloud metrics most often used to assess forest biodiversity were measures that described dispersion and the central tendency of vegetation height. In particular, standard deviation, mean and coefficient of variation were often utilised across studied topics (Appendix B). Higher and lower height percentiles were also important in the assessment of understorey shrubs and herbs in structural diversity studies and in the habitat assessment of birds. Other ALS metrics that were commonly found to be important in structural diversity studies were skewness and coefficient of variation of height of ALS echoes. Foliage height diversity was only used in animal ecology studies, but it was often regarded as an important ALS metric.

Density metrics were regarded as important in the assessment of understorey and overall canopy structure. The importance of understorey density on bird and bat species assessment was demonstrated in many studies. Among the density metrics, canopy cover was employed across nearly all study topics, and it was found to be important, especially in the assessment of habitat suitability, understorey description and in studies related to structural diversity. Distance measures (e.g. to the forest edge) were utilised in studies related to forest fragmentation and bird species richness or diversity measures. The explanatory power of horizontal measures of vegetation structure were, in most cases, outperformed by variables that described the vertical vegetation structure.

However, it is important to note that the derived ALS metrics are dependent on the sensor, acquisition parameters and dominant forest type, and so the relevant metrics and relationships in one study might not be the same elsewhere. It is also notable that none of the studies included all possible ALS metrics. Therefore, it is possible that there are important metrics that were not tested. The calculation of ALS metrics also differed between studies.

Information on ALS intensity is known to be useful in the classification of land cover types (Yan et al., 2015). In this review, we found intensity information to be useful in studies that considered tree species (broadleaved vs. coniferous). Examples included the classification of certain forest habitats and canopy types, and the identification of standing dead trees by species. The FW-ALS data was not used in many studies, but it was reported to be useful in the assessment of understorey description and forest fragmentation. Metrics that described terrain properties formed another group of ALS-derived metrics that were often used in the assessment of undergrowth species and their properties. Altitude and slope were most often utilised to describe local topography and were used more often in the assessment of non-flying mammals and arthropods (Müller and Brandl 2009; Zellweger et al., 2017) than for birds. This can be explained by the fact that these variables are associated with solar radiation and hydrography, which have a greater effect on these taxonomic groups. In an earlier review on ALS-assisted modelling of species-vegetation structure, Acebes et al. (2021) reported that topographical metrics were not used as often as conventional ALS metrics to describe vegetation structure. Despite their relatively lesser usage, topographical metrics were found to be important whenever they were employed (Acebes et al., 2021). Therefore, full integration of terrain metrics, in addition to ALS structural variables in the assessment of forest species diversity, is recommended.

Historically, the high cost of acquiring ALS data was often regarded as one of its drawbacks. However, that is not the case nowadays as numerous ALS campaigns have already been completed in many countries and cover the whole country. At the same time, the pulse densities have increased, and the processing of raw data has become more established. Most of the national level ALS datasets have point densities <5 pt./m². Typically, low point density ALS data (<2 pt./m²) is mainly suitable for ABA. In the ITD method or in the object-based detection of fallen trees, point densities of >2 pt./m² are required (Heinano et al., 2021; Kaartinen and Hyypä 2008; Kaartinen et al., 2012). The technological development in lidar systems has been rapid and the point densities will further increase in the near future – expanding the usability of the data.

There are inherent difficulties related to ALS information that was described in some of the reviewed studies. One issue was related to the penetration rate; the increase in the complexity of vegetation structure and forest cover decreases the possibility of detecting understorey returns (Goodwin et al., 2007). This can decrease the explanatory power of the ALS metrics. For example, Torresan et al. (2016) reported that older successional stages, which contain the most of trees in the overstorey layer, were predicted more accurately than other stages. Another issue is related to the point density of the ALS data: As the top of the vegetation usually has little surface area, the probability that a pulse will hit a tree top decreases as the distance between single points increases (i.

e. point density decreases). Lower-point density further decreases the potential number of returns that reach the lower canopy layers and may cause issues in ground classification. Poor ground models further decrease the accuracy of tree height prediction and related attributes. Some studies reported that a relatively low point density (<4 pt./m²) causes difficulties in the classification of forests that differ between their understorey types (Valbuena et al., 2016b), in the determination of canopy layer heights (Zimble et al., 2003) and in the detection of fallen and standing dead trees (Wing et al., 2015). High-point-density ALS data allows for a better description of the lower canopy structures and enables new approaches to retrieve information from ALS data. For example, Sasaki et al. (2016) utilised high-point-density data (48 pt./m²) to voxelise the point cloud at 1 m resolution. Voxel-based metrics were derived and were found to offer considerable explanatory power in the assessment of habitat use by forest birds (Sasaki et al., 2016). In this review, we found that many studies reported reasonable results even though point density was relatively low (<2 pt./m²). High point density data does not directly imply “better results” as there are many other factors that determine the feasibility of the data.

The ALS datasets were typically acquired in leaf-on conditions. Leaf-off ALS data were most commonly utilised in dead wood assessment. In some studies, the two types of ALS data were compared, but, in general, only minor differences were observed between them. For example, Yao et al. (2012) classified standing trees as living and dead with an overall accuracy of 71% for leaf-off and 73% for leaf-on ALS. However, Lesak et al. (2011) and Bottalico et al. (2014) observed that the use of leaf-off ALS data leads to poor results in the prediction of bird species richness and classification of forest habitat types, respectively. Moreover, ALS data acquired during both leaf-on and leaf-off conditions were not favourable for the prediction of species richness for three taxa at a country-level (Zellweger et al., 2016).

The suitability of ALS data to map forest land cover types was found to be mixed. When the goal was to map vegetation types that included the definition of tree species, the structural information provided by ALS was often insufficient (Bässler et al., 2010). In these cases, the use of multi- or hyperspectral imagery produced significantly better classification accuracies as the spectral response of the tree species can vary considerably (Dalponte et al., 2008). It was also shown that the ALS data provided meaningful measures for the classification of forested areas based on the number of canopy layers and successional stages. In their review, Ganivet and Bloomberg (2019) showed that lidar data is an excellent option, with regard to the quality of information, for the mapping of tropical forest structure and tree species diversity. Coupling lidar data with hyperspectral image data in tropical areas would potentially help in species discrimination (Féret and Asner 2012; Ganivet and Bloomberg 2019).

Most of the research with regard to ALS-assisted animal ecology has been focused on bird species. Research interest on bird vs. habitat structure remains strong, although other taxonomic groups (including non-flying mammals and arthropods) have received scant attention. This is not surprising as bird diversity was investigated in the earliest studies that assessed the effect of vegetation structure on animal ecology. In our review, we identified that insects, such as butterflies and saproxylic beetles, have received an increasing amount of attention in recent years, in particular with regard to biodiversity conservation and climate change mitigation. Similar trends were also recognised by Acebes et al. (2021) in their review.

There were some issues in animal ecology studies that were not inherently related to ALS data. For example, some species were too rare or clumped for successful modelling (Eldegard et al., 2014), while in other cases, the span of habitat types in a study area was too narrow for modelling (Mononen et al., 2018). Also, the relationships between ALS-derived vegetation structure were not always straightforward and consistent, even with the same species. For example, chick body mass (measure of breeding success) of the great tit (*Parus major*) was found to increase with increasing canopy height during an abnormally warm

spring season, but a contrary relationship was noted during colder springs (Bradbury et al., 2005).

Most focus on the assessment of dead wood has been on the detection of fallen or standing dead trees, volume and their dimension. Species and decay stage, which are also important factors that determine the suitability of dead wood for species that are dependent on dead wood, have received little attention. These aspects should be considered in future studies.

Reviewed studies provided various approaches on how to use ALS data in forest conservation and planning. These included research on potential hotspots for saproxylic beetles (Rada et al., 2022), the provisioning potential of mushrooms (Pascual and de-Miguel 2022) and forest berries (Bohlin et al., 2021), research on endangered species (Smart et al., 2012) and hotspots for forest structural diversity (Mura et al., 2015). Maps that depict spatially explicit information from forests (e.g. structural diversity or mushroom yield potential) can support decision making in forest management planning (e.g. Simonson et al., 2014; White et al., 2013). This type of usage was highlighted by Guo et al. (2018), who integrated ALS information into scenarios for forest conservation planning. Moreover, this type of information is practical for researchers who are organising forest biodiversity-oriented studies. We suggest that more research resources are allocated to tropical forests, as these forests are the most species-rich areas in the world and their ecological characteristics differ substantially from those of the temperate and boreal regions. In addition, they are notably vulnerable to climate change.

Studies that link ALS information to species richness, an iconic measure of biodiversity, were common in our review. A drawback of the species richness measure is that it does not deliver information on the abundance of species, i.e. there can be many sites that have same number of species but not necessarily the same species. Moreover, ALS studies on community composition assessment were also rare and should receive more attention in future studies. In the last few years, the assessment of functional diversity (e.g. Kamoske et al., 2022; Lozanovska et al., 2018), i.e. the range of functional variation in a population, has received some attention but it still requires more research. Soundscape ecology is a relatively new and fast-developing field that could assist remote sensing-based assessment of forest biodiversity (Rappaport et al., 2020). Lastly, many studies have emphasised the effect of the spatial resolution at which ALS information and field data are linked as an important future research topic (e.g. Tew et al., 2022).

10. Conclusion

In this review, we summarised the use of ALS data as the main remote sensing material in the assessment of different components of forest biodiversity. In total, 182 scientific articles were evaluated and categorised into 12 biodiversity-related features, each comprising a specific biodiversity topic. Most of the studied topics were related to animal ecology (richness and occurrence of forest fauna) and the assessment of tree species diversity/richness and dead wood. Studies related to forest fragmentation and successional stage assessment were covered to a lesser extent. Most study areas were located in temperate or boreal ecoregions of North America and Europe. We found that there was no unique ALS variable that could be used in the assessment of forest biodiversity, although some variables were used more often than others. These were mainly variables related to dispersion and central tendency of vegetation height; standard deviation, mean and coefficient of variation, for example. In addition, height percentiles and canopy cover were often used. The fusion of ALS data with other remote sensing datasets, especially with spectral images, was reported to be beneficial, especially in studies that considered tree species directly or indirectly. Based on the reviewed studies, we conclude that ALS data provide valuable information on the horizontal and vertical vegetation structures and can assist in the assessment of biodiversity in forested environments, at both fine and broad spatial scales.

Table A1
Reviewed studies categorised by their features and the continent of the study area.

Feature	Europe	North America	Central and South America (CSA), Asia (AS), Africa (AF), Oceania (OC)
Land cover classification	Álvarez-Martínez et al., 2018; Bottalico et al., 2014; Bässler et al., 2010; Dalponte et al., 2008; Hill and Thomson 2005; Pippuri et al., 2016; Simonson et al., 2013; Sinclair 2021; Sverdrup-Thygeson et al., 2016; Tijerín-Triviño et al., 2022; Vehmas et al., 2009; Vehmas et al., 2011a	Martinuzzi et al., 2013; Shoot et al., 2021; Su et al., 2016	AF: Marselis et al., 2018
Successional stages	Alberti et al., 2013; Fuhr et al., 2022; Hevia et al., 2022; Torresan et al., 2016; Valbuena et al., 2016b	de Assis Barros and Elkin 2021; Falkowski et al., 2009; Kane et al., 2010; Martin and Valeria 2022; Martinuzzi et al., 2013; Shao et al., 2018; Weber and Boss 2009	
Overall canopy structure	Adnan et al., 2019; Leitterer et al., 2015; Morsdorf et al., 2010; Pascual et al., 2008	Guo et al., 2017; Moran et al., 2018; Whitehurst et al., 2013; Zimble et al., 2003	AS: Jayathunga et al., 2018. OC: Wilkes et al. 2016
Understorey description	Bollandsås et al., 2008; Crespo-Peremarch et al., 2018; Dees et al., 2012; Hill and Broughton 2009; Lindberg et al., 2012; Maltamo et al., 2005; Moeslund et al., 2022; Pascual and de-Miguel 2022; Vehmas et al., 2011b	Bourgouin et al., 2022; Hamraz et al., 2017a; Hamraz et al., 2017b; Jarron et al., 2020; Sumnall et al., 2017; Wing et al., 2012	OC: Miura and Jones 2010
Tree species	Dalponte et al., 2018; Korpela et al., 2010; Leutner et al., 2012; Maltamo et al., 2015; Simonson et al., 2012; Säämäjoki et al., 2008	Gillespie et al., 2017; Kamoske et al., 2022; Sankey, 2012	CSA: Ceballos et al., 2015; Fricker et al., 2015; George-Chacon et al., 2019; Hernández-Stefanoni et al., 2015; Martins-Neto et al., 2021; Wolf et al., 2012 AS: Mohammadi et al., 2020; Zhao et al., 2018 AF: Mauya 2015; Vaglio Laurin et al., 2016
Understorey species	Bohlin et al., 2021; Bouvier et al., 2017; Leutner et al., 2012; Moeslund et al., 2019; Moeslund et al., 2022; Pascual and de-Miguel 2022; Peura et al., 2016; Simonson et al., 2012; Teobaldelli et al., 2017; Thers et al., 2017; Vauhkonen, 2018; Zellweger et al., 2016	Barber et al., 2016; Bourgouin et al., 2022; Mao et al., 2018; Martinuzzi et al., 2009; Nielsen et al., 2020; Nijland et al., 2014; Singh et al., 2015	CSA: Ceballos et al., 2015; Lopatin et al., 2015; Lopatin et al., 2016
Structural diversity	Bottalico et al., 2017; Dalponte et al., 2018; Davison et al., 2020; Kukunda et al., 2019; Mura et al., 2015; Mura et al., 2016; Ozdemir and Donoghue, 2013; Valbuena et al., 2013; Valbuena et al., 2014; Valbuena et al., 2016a; Valbuena et al., 2017	Kamoske et al., 2022; Listopad et al., 2015	AS: Zheng et al., 2021; Zheng et al., 2022 AF: Adhikari et al., 2020
Dead wood	Amiri et al., 2019; Chirici et al., 2018; Dobre et al., 2021; Hardenbol et al., 2022; Heinaro et al., 2021; Kamińska et al., 2018; Lindberg et al., 2013; Mücke et al., 2012; Mücke et al., 2013; Nyström et al., 2014; Pesonen et al., 2008; Pesonen et al., 2010a; Pesonen et al., 2010b; Polewski et al., 2015b; Yao et al., 2012	Bater et al., 2009; Blanchard et al., 2011; Jarron et al., 2021; Martinuzzi et al., 2009; Stitt et al., 2022a, Stitt et al., 2022b, Wing et al., 2015	OC: Miltiadou et al., 2020
Forest fragmentation		Flaspohler et al., 2010; Guo et al., 2018; MacLean, 2017; Shao et al., 2018; Vaughn et al., 2014	CSA: Almeida et al., 2019
Species richness	Eldegard et al., 2014; Klein et al., 2020; Lindberg et al., 2015; Melin et al., 2018; Melin et al., 2019; Müller and Brandl 2009; Müller et al., 2009; Müller et al., 2010; Müller et al., 2014; Renner et al., 2018; Tew et al., 2022; Vierling et al., 2011; Zellweger et al., 2016	Boelman et al., 2007; Carrasco et al., 2019; Coops et al., 2016; Flaspohler et al., 2010; Goetz et al., 2007; Lesak et al., 2011; Swift et al., 2017; Vogeler et al., 2014; Weisberg et al., 2014	AS: Sasaki et al., 2016 AF: Vogeler et al., 2022; Ziegler et al., 2022
Species diversity indices	Melin et al., 2018; Melin et al., 2019; Müller and Brandl 2009; Müller et al., 2014; Tew et al., 2022; Vierling et al., 2011; Zellweger et al., 2017	Clawges et al., 2008	CSA: Wallis et al., 2016 AS: Sasaki et al., 2016
Habitat suitability	Bradbury et al., 2005; de Vries et al., 2021; Eldegard et al., 2014; Graf et al., 2009; Hinsley et al., 2006; Jung et al., 2012; Koma et al., 2021; Koma et al., 2022; Lone et al., 2014; Melin et al., 2013; Melin et al., 2016; Mononen et al., 2018; Rada et al., 2022; Vihervaara et al., 2015; Zellweger et al., 2013a; Zellweger et al., 2013b	Coops et al., 2010; Garabedian et al., 2014; García-Feced et al., 2011; Goetz et al., 2010; Hagar et al., 2014; Herniman et al., 2020; Seavy et al., 2009; Smart et al., 2012; Swatantran et al., 2012; Vogeler et al., 2013	

Table B1

The most important ALS metrics related to vegetation categorised by type in each reviewed section. Numbers in the table describe the number of studies where these metrics were reported to be among the most important. Abbreviations for predictor categories are as follows: h = height predictor, v. var = vertical variability, density = density metrics, h.var. = horizontal variability, h & v = horizontal and vertical variability, intensity = ALS intensity predictor, fw = waveform-lidar predictor. Abbreviations for predictor names are as follows: max = maximum, pXX = XXth percentile of vegetation heights, min = minimum, std = standard deviation, kurt = kurtosis, skew = skewness, cv = coefficient of variation, hmad = median absolute deviation of vegetation heights, hmad_mode = median absolute deviation from overall mode, hmad_med = median absolute deviation from overall median, l_cv = L-moment coefficient of variation, l_skew = L-moments skewness of return height, FHD = foliage height diversity, CRR = canopy relief ratio, %_below Xm = percent of returns below certain height limit, %_betw X-Xm = percent of returns between certain height limits, %_above Xm = percent of returns above certain height limit, veg = returns from vegetation, ground = returns from ground, first = first returns, third = third returns, LAD = leaf area density, LAD_max_h = maximum leaf area density height, int_pXX = accumulated intensity at XXth percentile, canopy_VDR = canopy vertical distribution ratio, PAI = plant area index, max energy = maximum energy of a return, quantile energy = similar to height percentile but for return energy, underst. Vox. = filled voxels at understorey.

Metric category	Metric name	Land cover class.	Succes. Stages	Overall canopy struct.	Underst. descr.	Tree species	Underst. Species	Struct. Div.	Dead wood	Forest fragm.	Species rich.	Species div.	Habitat suitab.
h	canopy height	2		2	7	4	5	2		2		1	2
h	max		1	1	4	1		4	1	1	3	1	3
h	p55 – p95	4	4	1	2	2	4	5	4		1		6
h	mean	6	3		2	1	4	1	1	1	6	1	6
h	p05 – p45	2	2		2	1	2	4	1		1		5
h	min		3					2	1				
h	median			1									
v. var.	h_std	3	2	2	2	4	2	3	4	2	9	4	7
v. var.	h_kurt	1	1					1					
v. var.	h_skew			1				5					1
v. var.	h_cv	3		1				5	2	1			1
v. var.	h_entropy							1					
v. var.	hmad	1							1				
v. var.	hmad_mode							1					
v. var.	hmad_median							1					
v. var.	l_cv							2					
v. var.	l_skew							2					
v. var.	FHD						1				3	2	1
v. var.	CRR		1		1				1				
v. var.	rumple index		1										
density	%_below 0.5 m												1
density	%_below 2 m				1		1						
density	%_betw 0.15–1.37 m						1						
density	%_betw 1.0–2.5 m						1				1		
density	%_betw 0.3–3 m		1								1		
density	%_betw 0-8 m										1	1	
density	%_betw 12-17 m		1										
density	%_above 0.5 m												1
density	%_above 1 m	1	1										
density	%_above 2 m	1											
density	%_above 6 m											1	
density	%_above_mean												1
density	%_veg				2						1	1	
density	%_ground						2		1				
density	%_first								1				
density	%_third								1				
density	cover	2	1	1	3		1	5			2		4
density	gap_area_2m						1						
density	gap_area_5m	1											

(continued on next page)

Table B1 (continued)

	Land cover class.	Success. Stages	Overall canopy struct.	Underst. descr.	Tree species	Underst. Species	Struct. Div.	Dead wood	Forest fragm.	Species rich.	Species div.	Habitat suitab.
density	1			1		1		1	1	1	2	1
density			3	4		1	1			3	1	2
h & v	LAD_cv				2					1		
intensity		1		1	1	1		1				1
intensity					1	1						1
intensity								1				
intensity								1				
intensity								1				
intensity								1				
fw	canopy VDR									1		
fw	PAL1 - 2 m								1			
fw	PAL > 4 m								1			
fw	PAL9 - 12 m		1									
fw	max energy											
fw	quantile energy			1				1				1
fw	underst. Vox			1								

CRediT authorship contribution statement

Janne Toivonen: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization. **Annika Kangas:** Validation, Writing – original draft, Supervision. **Matti Maltamo:** Validation, Writing – original draft, Supervision. **Mikko Kukkonen:** Validation, Writing – original draft, Supervision. **Petteri Packalen:** Conceptualization, Methodology, Software, Validation, Resources, Writing – original draft, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Review article.

Appendix A

Appendix B

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