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Use and categorization of Light Detection and Ranging vegetation metrics in avian diversity and species distribution research

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Abstract

Aim: Vegetation structure is a key determinant of animal diversity and species distributions. The introduction of Light Detection and Ranging (LiDAR) has enabled the collection of massive amounts of point cloud data for quantifying habitat structure at fine resolution. Here, we review the current use of LiDAR-derived vegetation metrics in diversity and distribution research of birds, a key group for understanding animal–habitat relationships.

Location: Global.

Methods: We review 50 relevant papers and quantify where, in which habitats, at which spatial scales and with what kind of LiDAR data current studies make use of LiDAR metrics. We also harmonize and categorize LiDAR metrics and quantify their current use and effectiveness.

Results: Most studies have been conducted at local extents in temperate forests of North America and Europe. Rasterization is currently the main method to derive LiDAR metrics, usually from airborne laser scanning data with low point densities (<10 points/m^2) and small footprints (<1 m diameter). Our metric harmonization suggests that 40% of the currently used metric names are redundant. A categorization scheme allowed to group all metric names into 18 out of 24 theoretically possible classes, defined by vegetation part (total vegetation, single trees, canopy, understorey, and other single layers as well as multi-layer) and structural type (cover, height, horizontal variability and vertical variability). Metrics related to canopy cover, canopy height and canopy vertical variability are currently most often used, but not always effective.

Main conclusions: Light Detection and Ranging metrics play an important role in understanding animal space use. Our review and the developed categorization scheme may facilitate future studies in the selection, prioritization and ecological interpretation of LiDAR metrics. The increasing availability of airborne and spaceborne LiDAR data and the development of voxel-based and object-based approaches will further allow novel ecological applications, also for open habitats and other vertebrate and invertebrate taxa.

KEYWORDS
airborne laser scanning, animal diversity, habitat use, LiDAR, literature review, species distribution modelling, structural heterogeneity, vertical vegetation structure

1 | INTRODUCTION

A key goal of biodiversity and conservation research is to predict and understand species distributions (Franklin & Miller, 2009) and diversity patterns (Ricklefs & Schluter, 1993). In this context, climate and habitat heterogeneity are among the most widely studied determinants of terrestrial species diversity and distribution (Hawkins et al., 2003; Stein, Gerstner, & Kreft, 2014). While climate is often thought to be the key determinant at large spatial extents (Pearson & Dawson, 2003), vegetation structure often becomes particularly relevant at small spatial extents and/or fine grain sizes (Zellweger, Braunisch, Baltensweiler, & Bollmann, 2013). Vertical and horizontal structure of vegetation has long been recognized as an important factor driving animal diversity and species distributions, especially of birds (Cody, 1985; Dunlavy, 1935; MacArthur & MacArthur, 1961). However, measuring the fine-scale habitat structure and 3-D characteristics of vegetation across large regions is difficult and labour-intensive, and hence limits most animal–habitat studies to the local or landscape scale (i.e., <200 km). Nevertheless, recent developments in remote sensing now provide unprecedented opportunities for measuring vegetation structure across broad spatial extents (Kissling, Seijmonsbergen, Foppen, & Bouten, 2017; Lausch et al., 2016; Skidmore et al., 2015).

Light Detection and Ranging (LiDAR)—an active remote sensing technique—is a technology that provides fine-grained information about the 3-D physical structure of ecosystems (Davies & Asner, 2014; Lefsky, Cohen, Parker, & Harding, 2002; Simonson, Allen, & Coomes, 2014; Vierling, Vierling, Gould, Martinuzzi, & Clawges, 2008). LiDAR sensors, for example installed on airplanes or satellites (Figure 1a), measure the return time of an emitted pulse of laser light and convert this time to a distance. Especially, airborne laser scanning (ALS) data are often used because they cover large areas and country-wide datasets are becoming increasingly available. For ALS, a plane or helicopter serves as the platform from which the LiDAR sensor is operated. In most cases, near-infrared light is used which partially penetrates the vegetation and therefore allows to measure both the canopy and subcanopy vegetation structure. LiDAR data are recorded as full waveform (FWF) or discrete echoes (i.e., returns of one or more energy reflections from the FWF; Figure 1a). The resulting dataset is called a "point cloud" (Figure 1a) and consists of the *x,y,z* coordinates of the points together with intensity values. LiDAR is widely used in forestry to measure 3-D forest structure (Maltamo, Naesset, & Vauhkonen, 2014), but applications in ecology, biodiversity and conservation planning are also increasing (Davies & Asner, 2014; Simonson et al., 2014). Nevertheless, using and processing the massive amounts of LiDAR data across large spatial extents remains challenging (Bergen et al., 2009; Kissling et al., 2017) and most current LiDAR applications are restricted to local study sites as well as forest habitats (Wulder et al., 2012).

Recent reviews on the use of LiDAR data for measuring 3-D habitats of animals show that vegetation structure can be quantified in many ways (e.g., Davies & Asner, 2014; Hill, Hinsley, & Broughton, 2014). A potential confusion for ecologists could be that a multitude of LiDAR metrics exists to quantify structural vegetation attributes. For instance, canopy height can be calculated as the maximum return, the mean height of the first returns or the height of the 95th percentile of returns in a raster cell (Ackers, Davis, Olsen, & Dugger, 2015; Coops et al., 2016; Smart, Swenson, Christensen, & Sexton, 2012). Additionally, there are also many technical, methodological and data quality aspects that may influence how LiDAR-derived vegetation structure is quantified. For instance, in many cases the point cloud is rasterized (i.e., simplified into pixels) or voxelized (i.e., into three-dimensional voxels; Figure 1b). LiDAR-derived vegetation metrics (e.g., mean canopy height) are then calculated to summarize the vegetation structural information from the point cloud within each pixel or voxel. An advantage of such area-based approaches (i.e., rasterization) and voxel-based approaches (i.e., voxelization) is that they are computationally efficient, but they also lead to information loss regarding the 3-D information of the point cloud (Ciuti et al., 2018). An alternative is to use object-based approaches (Figure 1b) where either the point cloud or a derived rasterized map is segmented into objects such as trees, forest stands, reed beds or hedges based on similarities and differences in neighbourhood information around points or grid cells (Höfle, Hollaus, & Hagenauer, 2012; Koch, Kattenborn, Straub, & Vauhkonen, 2014). This is computationally demanding, but also provides new ways of quantifying 3-D habitat structure compared to area-based or voxel-based approaches. Other specific technical and methodological constraints include point cloud density, footprint size and conditions of the flight campaign such as flight altitude and season (leaf-on vs. leaf-off). The season of LiDAR data acquisition might also be influential when mapping 3-D animal habitats (e.g., understorey in deciduous or broad-leaf forests; Hill & Broughton, 2009). Currently, there is no overview available on how LiDAR data characteristics are represented in ecological studies of animal–habitat relationships.

Diversity and distribution studies usually aggregate raw data from opportunistic observations or standardized and structured surveys to represent the presence, presence–absence, population size or richness of species across space and time (Gaston, 1996; Kissling et al., 2018). Such aggregated field observations (e.g., presence-only or atlas data) can then be mapped and used in species distribution models (SDMs; Guisan, Thuiller, & Zimmermann, 2017) or species richness analyses to quantify the relationship with environmental predictor variables, to map and predict spatial distributions, or to

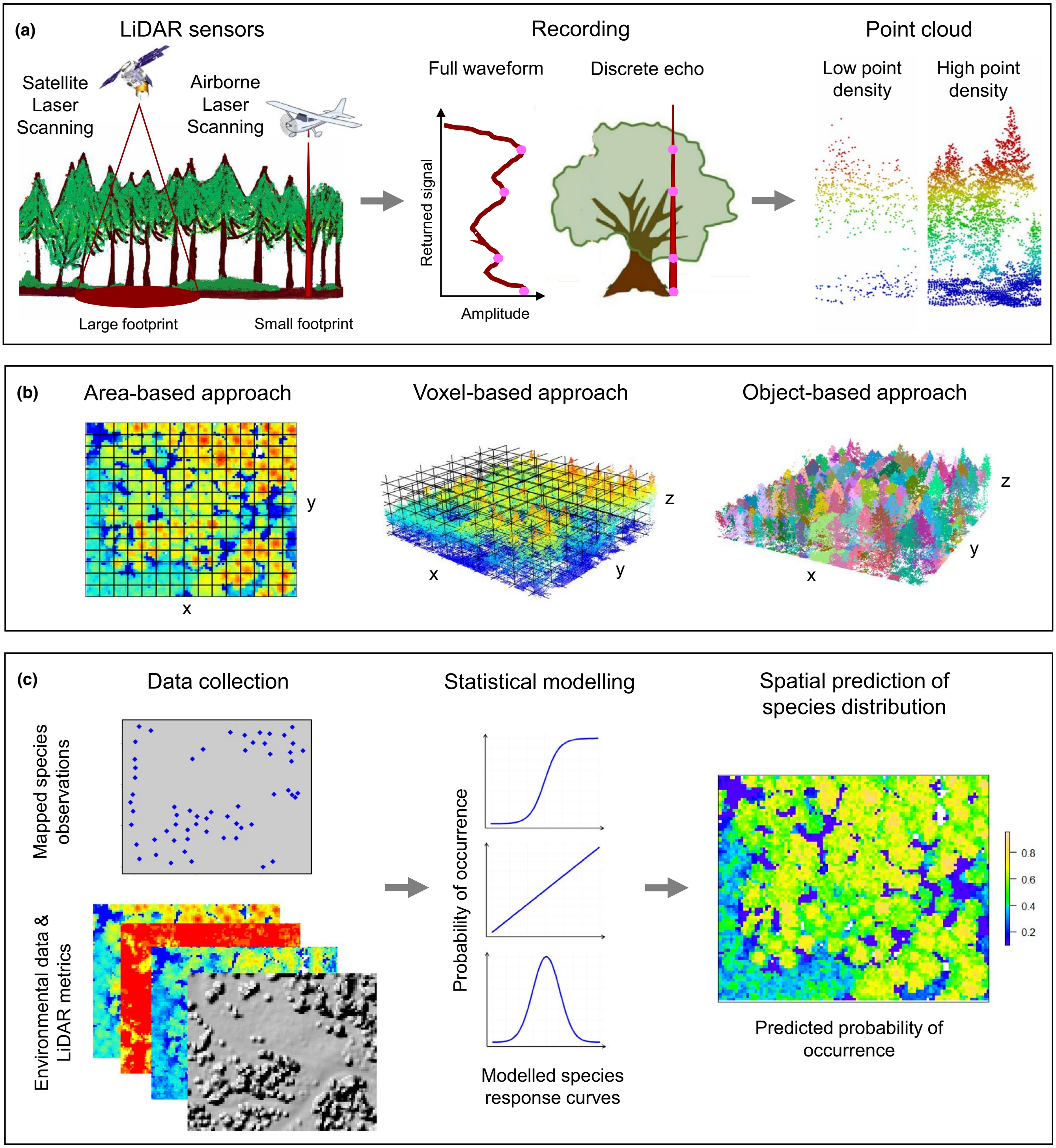

FIGURE 1 Sampling and processing of Light Detection and Ranging (LiDAR) data and its use in species distribution modelling. (a) LiDAR data can be obtained from spaceborne or airborne sensors with a certain footprint size, recorded as full waveform or discrete echo and then processed into point clouds with low or high point densities. (b) LiDAR point clouds can be further processed using area-based approaches (i.e., rasterization into grid cells), voxel-based approaches (i.e., voxelization into 3-D voxels) or object-based approaches (e.g., segmentation into objects such as trees). (c) Applications of species distribution models use mapped species observations together with environmental data and LiDAR metrics in a statistical model to predict the spatial distribution of species

test ecological hypotheses (Figure 1c). In most large-scale studies, environmental information related to climate, productivity, topography and land cover is used to quantify predictor variables (Guisan et al., 2017; Hawkins et al., 2003), but information on fine-scale habitat structure (e.g., density, cover and openness of vegetation) and 3-D vegetation distribution (e.g., vertical and horizontal distribution of biomass) is often lacking (Kissling et al., 2017). An exciting opportunity to improve statistical models of species distributions and species richness is therefore the increasing availability of airborne and spaceborne LiDAR data which allows one to derive a diversity of metrics that quantify many aspects of the 3-D structure of vegetation. This is particularly relevant because individual species show strong preferences for particular habitat structures (Cody, 1985) and because species richness tends to increase with larger available niche space in structurally heterogeneous and complex habitats (Stein et al., 2014).

Here, we provide a review on the use of LiDAR data in avian species distribution and diversity research. We focus on studies of species distributions (based on occupancy, presence-only, presence–absence and abundance data) and species richness (based on range maps, inventories or atlas data) because these are widely studied aspects in spatial ecology and biogeography (Guisan et al., 2017; Kissling et al., 2018; MacArthur & MacArthur, 1961; Stein et al., 2014). We further focus on birds because they strongly depend on 3-D habitat structure (Cody, 1985; MacArthur & MacArthur, 1961) and because they are among the most widely studied organisms in this particular research field (Davies & Asner, 2014). We first summarize the representativeness of published studies in terms of geographical coverage, habitat types and spatial study extents. We then review some of the technical, methodological and data quality characteristics of the employed LiDAR datasets (e.g., point density, footprint sizes, leaf-on vs. leaf-off data, area-based vs. voxel-/object-based approaches). Finally, we quantify which LiDAR-derived vegetation metrics are most commonly used and what relationship they show with individual species distributions and species richness, respectively. We expect that most studies have been conducted in Northern Hemisphere temperate forests (Davies & Asner, 2014; Maltamo et al., 2014), predominantly at local (1–10 km) or landscape (10–200 km) scales (Simonson et al., 2014), and with area-based rather than object-based or voxel-based approaches (Blaschke et al., 2014; Kissling et al., 2017; Maltamo et al., 2014). We further hypothesize that metrics related to canopy height and cover are most widely used (Davies & Asner, 2014) and that metrics describing vertical heterogeneity and distribution of vegetation are most effective (MacArthur & MacArthur, 1961; Stein et al., 2014). In comparison with a recent review on this topic (Davies & Asner, 2014), our study provides more detailed insights and technological background of the employed LiDAR-derived vegetation metrics and how they are currently used in avian diversity and distribution research.

2 | METHODS

2.1 | Article selection

Our review is based on a total of 50 articles which focused on analysing bird species distributions and bird species richness in relation to LiDAR-derived vegetation metrics (see Supporting Information Appendix S1). These articles were found with keyword searches in the Web of Science on 11 September 2017 (see workflow in Supporting Information Appendix S2). Included keywords were "avian" or "bird" for the bird component, "LiDAR," "ALS" or "airborne laser scanning" for the LiDAR component and "vegetation structure," "landscape structure" or "habitat structure" for the vegetation component. These keywords were used in all possible combinations for the bird and LiDAR components, with the vegetation component as an optional addition. This search initially resulted in a total of 128 articles (Supporting Information Appendix S2).

We further improved the article selection by applying several selection criteria (Supporting Information Appendix S2). Articles with a focus outside the field of ecology (e.g., LiDAR applications for urban planning) were excluded (*n* = 29). From the remaining 99 articles, we further excluded articles that were not related to birds (*n* = 24), review papers (*n* = 13), articles that used LiDAR but not for deriving specific vegetation metrics (*n* = 8), studies that did not use direct field observations of birds (*n* = 3), and studies that focused on breeding success (*n* = 2) or beta diversity (*n* = 1). Finally, we added two papers that were suggested by a reviewer and which matched our inclusion criteria. The final list included 50 articles (Supporting Information Appendix S1).

2.2 | Data extraction

From the 50 articles, we extracted publication details, biological data, information on LiDAR data and processing, and information about the calculated LiDAR-derived vegetation metrics (see workflow in Supporting Information Appendix S2). All extracted data together with a detailed metadata description are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.tm28hb6).

For recording publication details, we extracted information on first author, year, title, journal and the study location and country. This was mainly used to map the study locations and to assess their geographical distribution.

For the extraction of biological data, we recorded taxonomic information, whether the study focused on species distributions or species richness, the bird observation method (point count, transects, territory mapping, atlas data etc.), the habitat type and the extent of the study area. Taxonomic information was obtained by recording the bird species name from the species distribution and abundance studies, using the standardized taxonomy from the checklist of the birds of the world (del Hoyo, Collar, Christie, Elliott, & Fishpool, 2014; del Hoyo et al., 2016). For species richness studies, species names were not recorded because they are usually not provided, but we recorded order or family information when available. Habitat information was extracted from the articles and recorded using the standardized terms from the Habitat Classification Scheme version 3.1 of the IUCN red list (https://www.iucnredlist.org/resources/habitat-classification-scheme). This distinguished major habitat types such as forests (defined as continuous stands of trees), savannas (ecosystems dominated by a grass ground cover with an overstorey of widely spaced trees and shrubs), shrublands (scrub, bushland and thickets), grasslands (composed of grasses and broadleaved herbaceous plants), wetlands (inland aquatic habitats) and deserts (arid landscapes with a sparse plant cover). For simplification, we use the term "agriculture" for the IUCN habitat type "Artificial—Terrestrial" (which includes arable land, pastureland, plantations, rural gardens, urban areas and subtropical/tropical heavily degraded former forest). In cases where multiple habitat types were analysed in a study, we recorded all habitat types. To quantify the spatial extent of each study, we recorded the area size (km^2) covered by the LiDAR measurements if mentioned in the articles. Moreover, we quantified the spatial resolution (in m) of the raster cell or the radius around the focal bird observation point for which the LiDAR metrics were calculated. For raster data, we recorded (a) the original resolution of the LiDAR metrics; and (b) the resolution at which LiDAR metrics were aggregated when linked to the bird data.

For extracting information on LiDAR data and processing, we recorded several LiDAR characteristics. First, we extracted whether LiDAR data were obtained from ALS or spaceborne laser scanning (SLS), and at which flight altitude because both can influence LiDAR data quality and precision. Second, the echo detection mode (discrete or full waveform) was recorded because this can influence how LiDAR-derived vegetation metrics are calculated (e.g., canopy height is calculated with waveform data as the highest peak above a certain threshold, whereas it is calculated as the mean height of first returns with discrete data). Third, we recorded the LiDAR point density because it influences the calculation of LiDAR-derived vegetation metrics. With low point densities (e.g., 1 point/m^2), it is impossible to calculate vegetation complexity at a metre resolution whereas high point densities (e.g., >20 point/m^2) allow to analyse multi-layer LiDAR metrics at very fine (e.g., 5 × 5m) resolution. Fourth, we extracted footprint size which describes the diameter of the laser pulse on the ground (Figure 1a). At small footprint sizes (e.g., <1 m diameter), data points reflect measurements of single branches or parts of trees whereas at large footprint sizes (e.g., 10–25 m diameter) they represent multiple trees or even parts of vegetation stands. Fifth, we extracted in which season LiDAR data were collected (leaf-on or leaf-off) because this can have consequences for how many points are received from lower vegetation strata (e.g., in broadleaved forest). Finally, we recorded how LiDAR data were processed before calculating the metrics, that is whether studies used area-based, voxel- or object-based approaches (Figure 1b). As a special case of rasterizing, we also recorded whether studies calculated metrics for raster cells (pixels) or for areas around a focal observation point because many bird studies use point counts rather than area-based sampling methods (such as line transects or territory mapping; Bibby, Burgess, Hill, & Mustoe, 2000).

For the extraction of metric information, we recorded all metric names as mentioned in the original articles (e.g., canopy height heterogeneity, mean fractal dimension index, patch diversity, foliage height diversity based on Simpson index). We also distinguished whether metrics were derived from discrete LiDAR or from full waveform LiDAR. We further extracted the effect each metric had, that is the relationship (e.g., model parameter estimate, correlation coefficient, predictor variable importance) between the metric and the species distribution or richness variable.

2.3 | Harmonization of metric names

All metrics used in the selected articles were compared with each other in terms of metric names, structural elements of the vegetation that they describe (e.g., canopy, understorey or total vegetation), calculation method (e.g., mathematical formula) and the unit in which the metric is measured (e.g., metres, %, an index value). We then harmonized the metric names by grouping them if they had a similar meaning, using those names which were most widely used or which described the metric in terms of mathematical approach and ecological meaning of the metric. This resulted in a list of harmonized metrics (see Supporting Information Appendix S3) in which the metric name, a description, the calculation method, the unit and the articles which used this metric were summarized. We only included LiDAR metrics as used in the selected bird–habitat studies. It was not our aim to review all methodological and technical aspects of LiDAR metric calculations as used in vegetation and forestry studies (see e.g., Bergen et al., 2009; Hyyppä et al., 2008; Koenig & Höfle, 2016).

2.4 | Categorization of metric names

To facilitate a conceptual and ecological comparison and interpretation of metric names, we developed a categorization scheme based on which part of the vegetation was described (Figure 2a) and which structural type was quantified (Figure 2b).

For the vegetation part, we distinguished six categories including total vegetation, single tree, three different single layers (i.e., canopy, understorey or other layer) and multi-layer (Figure 2a). *Total vegetation* refers to metrics describing the whole vegetation without distinguishing layers. This may provide ecological information on the vertical and horizontal distribution of total vegetative biomass with relevance for explaining animal species richness. *Single-tree* metrics refer to structural metrics of single trees, which may be specifically relevant for animals that live or nest in particular trees (e.g., cavity nesters such as woodpeckers or deadwood specialists). Single layers (i.e., *canopy*, *understorey* and *other layer*) refer to calculations which focus on specific vegetation strata that might be relevant for certain species (e.g., ground-dwelling, understorey or canopy birds). Finally, *multi-layer* refers to metrics where vegetation strata were distinguished but metrics then calculated across different strata. This may allow to quantify the vertical and horizontal distribution of vegetative biomass in more detail than from total vegetation or single layers, for example as initially envisaged for quantifying foliage height diversity (MacArthur & MacArthur, 1961).

For the structural type, we distinguished four categories including height, cover, vertical variability and horizontal variability (Figure 2b). For instance, metrics describing the height of the canopy (or of another vegetation layer) were categorized into the height category and metrics describing the density of the vegetation (e.g., understorey cover) were categorized into the cover category. Vertical variability included metrics describing the vertical distribution of vegetation structure (e.g., foliage height diversity). Horizontal variability encompassed metrics describing the horizontal distribution of variation in vegetation structure (e.g., patchiness of vegetation). All

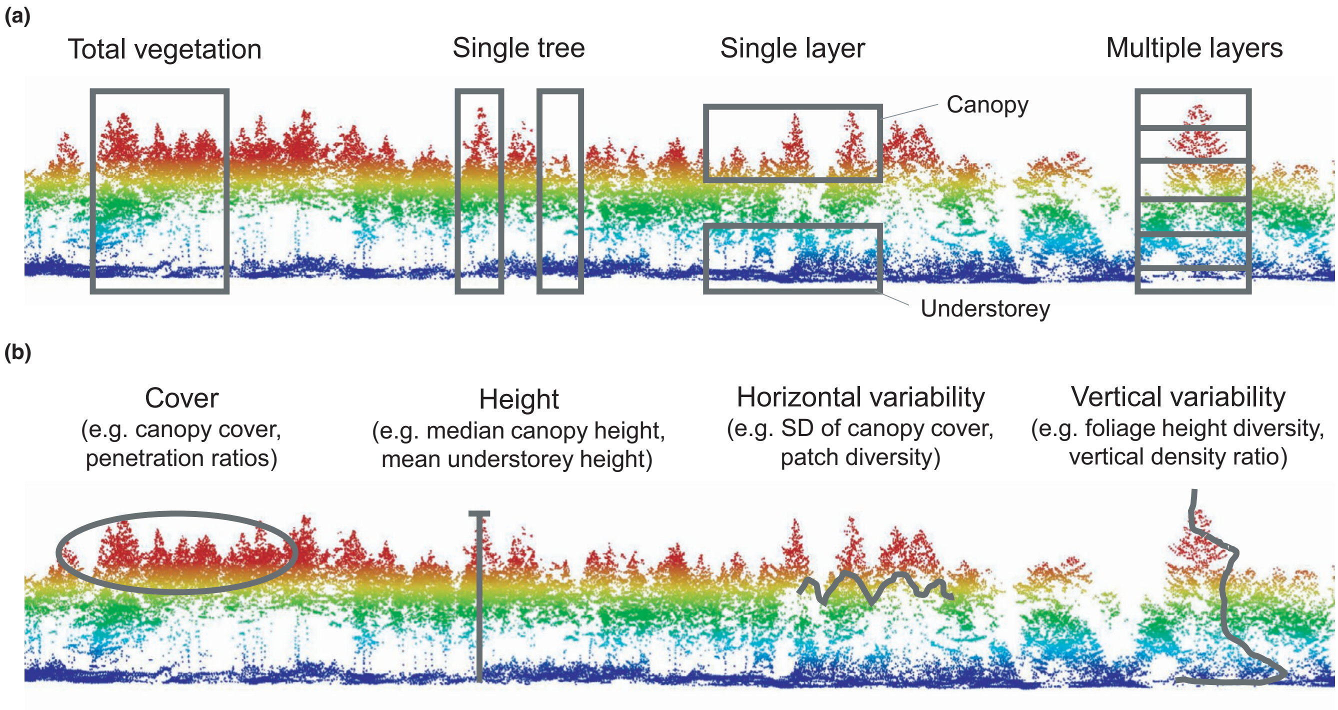

FIGURE 2 Conceptual categorization of LiDAR-derived vegetation metrics to facilitate ecological comparisons. The categorization scheme is based on (a) vegetation part (total vegetation, single tree, single layers such as canopy and understorey, and multi-layer), and (b) structural type (cover, height, horizontal variability and vertical variability). All LiDAR-derived vegetation metrics available from the literature review were grouped into this categorization scheme (see overview in Table 1). A full list of all metrics and their relation to vegetation part and structural type is provided in Supporting Information Appendix S3

four structural types describe different aspects of the 3-D distribution of vegetative biomass.

Based on the six categories of the vegetation part and the four categories of the structural type, a total of 24 metric classes were theoretically possible. These metric classes reflected the combination of both what part of the vegetation and what type of structural type was described. The 24 metric classes within the six vegetation part categories were as follows: (a) total vegetation cover, total vegetation height, total vegetation horizontal variability, total vegetation vertical variability; (b) single-tree cover, single-tree height, single-tree horizontal variability, single-tree vertical variability; (c) canopy cover, canopy height, canopy horizontal variability, canopy vertical variability; (d) understorey cover, understorey height, understorey horizontal variability, understorey vertical variability; (e) other layer cover, other layer height, other layer horizontal variability, other layer vertical variability; and (f) multi-layer cover, multi-layer height, multi-layer horizontal variability and multi-layer vertical variability. We assigned each harmonized metric name to one of these metric classes (see Supporting Information Appendix S3) to allow an overview and categorization of the currently used LiDAR-derived vegetation metrics.

2.5 | Relationship of metrics with species distribution and species richness

We used the extracted information on model parameter estimates, regression coefficients and predictor variable importance to quantify the effect of LiDAR-derived vegetation metrics on species distributions and species richness. Because the methods in the selected articles were very heterogeneous and did not consistently report the basic data needed for a meta-analysis (i.e., enabling calculation and analysis of effect sizes; Gerstner et al., 2017), we simplified the information to whether the LiDAR metric showed an "effect" or "no effect" on the bird response variable. A positive, negative or unknown direction of the bird–habitat relationship was classified as an "effect." A positive and negative direction reflected the sign of parameter estimates from the species distribution and species richness models, whereas an unknown direction reflected that information on the direction of the bird–habitat relationship was missing in a specific article. We distinguished studies of species distribution from those of species richness to test whether "effect" versus "no effect" depended on the bird response variable. Our quantification provides a coarse estimate of the effectiveness of currently used LiDAR-derived vegetation metrics.

3 | RESULTS

3.1 | Overview of articles

The 50 selected articles spanned the years 2006–2017 (Supporting Information Appendix S1). A total of 17 articles represented species richness studies, 32 articles species distribution studies, and one article contained both species richness and species distribution

TABLE 1 Categorization of LiDAR-derived vegetation metrics based on vegetation part (total vegetation, single tree, single layers such as canopy, understorey or other layer, and multi-layer) and structural type (cover, height, horizontal variability and vertical variability)

			Single layer			
	Total vegetation	Single tree	Canopy	Understorey	Other layer	Multi-layer
Cover	Ground, total vegetation volume, vegetation cover, forest stand volume, number of layers, vegetation amount	Crown diameter	Canopy cover,[a] gaps, canopy volume, *canopy cover*	Openness, shrub density index, understorey cover[b]		Density percentiles, penetration ratios between fixed heights, *density percentiles*
Height	Vegetation height,[c] *return height metrics*	Crown area weighted height, single-tree height	Canopy height,[d] *canopy height*	Mean understorey height, understorey volume	Height of dominant mode, *height of median energy*	Height percentiles, *height percentiles*
Horizontal variability	Density of large conifers, forest edge density, hardwood canopy cover, total edge length, *SD* of vertical density ratio		Canopy height heterogeneity, forest edge distance, forest gap density, nearest gap, *SD* of canopy cover		*SD* of mid-storey cover	Clumpiness of vegetation patches, CV of vegetation patch area, mean fractal dimension index, mean vegetation patch area, patch diversity, patch type nearest neighbour distance, *SD* of density percentiles, vegetation patch edge density
Vertical variability	Canopy relief ratio, Shannon evenness of height, variation in vegetation height,[e] vertical density ratio, *vertical density ratio*		Variation of canopy height,[f] Rumple index			3-D vegetation profile, foliage height diversity,[g] multi-storey profile, range between minimum and maximum mode, *SD* of height percentiles, *foliage height diversity*

Note. Metrics derived from discrete LiDAR data are shown in plain text, whereas metrics derived from full waveform LiDAR data are shown in italics. Some metrics are grouped in the table for readability (see footnotes). Colour coding reflects the number of metrics per class (□ = 0 metrics; □ = 1–2 metrics; □ = 3–4 metrics; ■ = 5–6 metrics; ■ = 7–8 metrics). A full list of all metrics with their description and calculation method is provided in Supporting Information Appendix S3.

[a]Canopy cover: multiple metrics available, for example calculating percentage of returns in canopy layer, percentage of returns above a fixed height or an estimation with combination of LiDAR and imagery data. [b]Understorey cover: returns from above ground bottom layer as percentage of all above ground returns, and returns from above ground bottom layer as percentage of all returns in that layer (with ground returns). [c]Vegetation height: mean of all returns and mean of all returns corrected for vegetation gaps. [d]Canopy height: multiple metrics available for calculating canopy height, for example based on 95 percentile of returns, with canopy surface model, corrected for gaps, mean maximum height, mean height from individual trees and median canopy height. [e]Variation in vegetation height: multiple metrics calculating standard deviation of vegetation height or vegetation height variance. [f]Variation in canopy height: multiple metrics available, for example calculating standard deviation, kurtosis, coefficient of variation, skewness and standard deviation corrected for gaps for the canopy height. [g]Foliage height diversity: calculated with Shannon–Wiener Index or Simpson Index.

analyses. The majority of studies used bird distributional information from point counts (n = 22), whereas atlas data (n = 5), territory mapping (n = 6), opportunistic observations (n = 5), bird tracking (n = 4), nest locations (n = 4), transects (n = 4) and range maps (n = 1) were less often used. In those articles focusing on species distributions, a total of 62 different bird species were studied with a total of 76 SDMs (i.e., some species were studied in multiple articles, Supporting Information Appendix S4). The majority of SDM applications focused on passerine birds (order Passeriformes, n = 54 SDM applications, 71%). The second and third most commonly studied birds were the woodpeckers (family Picidae in order Piciformes, n = 8, 11%) and the pheasants and partridges (family Phasianidae in order Galliformes, n = 8, 11%), respectively. Other bird orders such as parrots (Psittaciformes), owls (Strigiformes), pigeons (Columbiformes) and falcons (Falconiformes) were less represented (≤3%).

Most studies were located in North America (n = 26) and Europe (n = 19) (Figure 3a). The continents Asia (n = 2), South America (n = 1) and the Pacific region (n = 1) were less represented, and no studies from Africa and Oceania were detected with the keywords of our systematic literature search (Figure 3a). Most studies (n = 41) focused on a single habitat type whereas studies using multiple habitat types (n = 9) predominantly studied a combination of forest with one or more other habitat types (8 out of 9 studies). Hence, almost all studies (n = 48) included forest as a habitat type whereas grassland (n = 9), shrubland (n = 6), agriculture (n = 3) and desert (n = 2) were less represented (Figure 3b). Some habitat types (e.g., savannas, wetlands) were not represented. These results confirmed the expectation that most studies have been conducted in forest habitats of the Northern Hemisphere temperate zone.

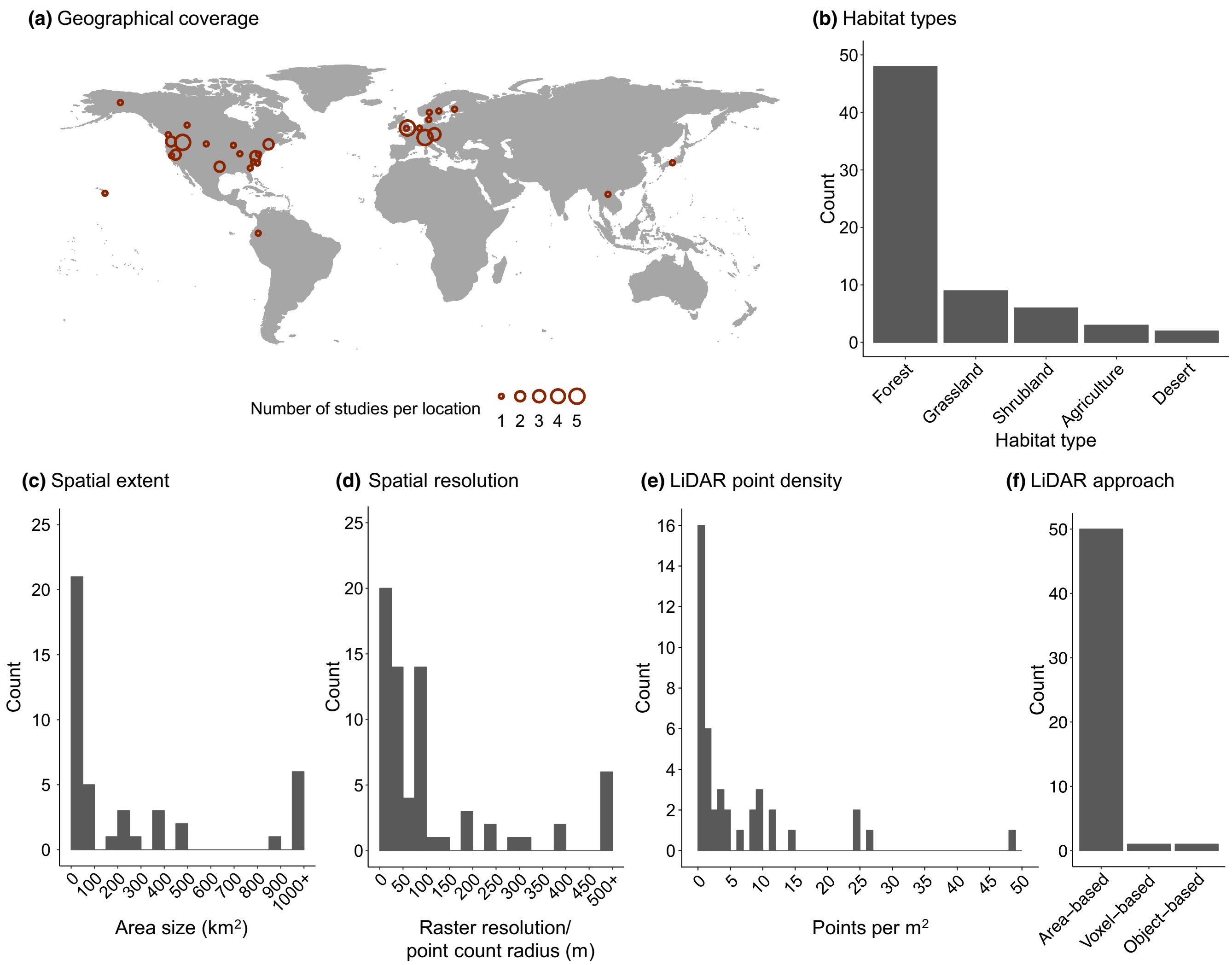

FIGURE 3 Geographical, biological and Light Detection and Ranging (LiDAR) characteristics from 50 articles included in the review. (a) Geographical coverage illustrated by the number of studies per location (n = 49 studies, with one global study not shown in the map); (b) number of times a habitat type was studied (n = 68 habitat types mentioned in 50 studies, with 9 studies reporting multiple habitat types); (c) frequency distribution of spatial extents (i.e., area sizes in km^2) available from 42 studies; (d) frequency distribution of spatial resolution (either raster resolution or point count radius for which LiDAR metrics were calculated and linked to the bird observation data, n = 69); (e) frequency distribution of LiDAR point densities available from 42 studies; and (f) the approach (area-based, voxel-based and object-based) used for processing LiDAR data (n = 50 studies)

Information on spatial extent and spatial resolution was available from 43 (86%) and 50 (100%) studies, respectively. Spatial extent ranged from local (0.1 km^2) to regional (330,000 km^2), with one study (using spaceborne LiDAR) even being conducted at a global extent (Roll, Geffen, & Yom-Tov, 2015). For studies presenting data on spatial extent, the median area size covered was 53 km^2 (Figure 3c). Thus, most studies (*n* = 26, 60%) covered areas <100 km^2, supporting the expectation that studies are predominantly conducted at local or landscape scales. Spatial resolution also varied widely from 0.25 to 9,600 m (Figure 3). Half of the studies (*n* = 25, 50%) calculated LiDAR metrics with a radius around focal bird observation points (e.g., opportunistic observations, point counts, territory mapping, bird tracking or nest location data), whereas the other half of the studies (*n* = 25, 50%) used raster cells (e.g., for atlas data, gridded range maps, bird tracking, nest locations, transect counts, point counts, territory mapping or opportunistic observations). At least 8 studies (16%) first calculated LiDAR metrics at a fine spatial resolution (e.g., 0.5, 1, 3 or 20 m grid cell size) and then aggregated (i.e., averaged) the metrics at a coarser resolution (e.g., 50, 80, 100 or even 1,000 m) when linking them to the bird data.

A total of 48 studies used LiDAR data only from ALS, one study used SLS data at a global scale (Roll et al., 2015), and one both ALS and SLS data at a landscape scale (Vierling, Vierling, Adam, & Hudak, 2013). Reported flight altitudes for obtaining the ALS data were in the range of 365–7,000 m (median = 1,550 m, *n* = 25 studies). A total of 46 studies (94%) used the discrete return signals from ALS to calculate LiDAR-derived vegetation metrics, whereas only five studies (including the two SLS studies) used full waveform measurements. Information on LiDAR point density was available from 42 studies and ranged from 0.1 to 48 points/m^2 with a median of 1.5 points/m^2 (Figure 3d). Hence, the majority of studies (79%) calculated LiDAR-derived vegetation metrics from low point densities (<10 points/m^2). Recorded footprint sizes were generally small, that is ≤80 cm (all data from ALS studies, *n* = 19). The number of studies using leaf-on LiDAR data (*n* = 31) was larger than those using leaf-off (*n* = 19), with a few studies (*n* = 5) having data available from both seasons. The area-based approach dominated, with all 50 studies applying this way of processing the LiDAR data (Figure 3e). However, one study additionally applied a voxel-based approach (Sasaki, Imanishi, Fukui, & Morimoto, 2016) and one other study additionally used an object-based approach to delineate single trees (Swatantran et al., 2012).

3.2 | LiDAR metrics

After harmonizing the 128 identified metric names from the 50 selected articles, a total of 77 unique metrics remained (see details in Supporting Information Appendix S3). This suggests that about 40% of the currently used metric names are redundant. Among the set of 77 unique metrics, many different calculation methods became evident even for metrics within the same vegetation part (see Supporting Information Appendix S3 for a full overview of all metric calculations). For instance, metrics of canopy height were derived in the reviewed studies from the mean height of a canopy surface model, from the mean height of the returns in the 95 percentile or from the maximum return in a grid cell. Canopy vertical variability was sometimes calculated from the coefficient of variation of canopy height values, but also from standard deviation, skewness or kurtosis of height. Similarly, our review revealed many ways to calculate multi-layer cover metrics, for example with density percentiles (where the percentage of returns in fixed layers is calculated) or height percentiles (where the heights at which a certain percentage of returns is recorded are calculated).

The 77 metrics fall into 18 of the 24 possible metric classes (Table 1). Most of the metrics were related to the metric classes canopy height, canopy vertical variability or multi-layer horizontal variability (eight metrics per class), followed by multi-layer vertical variability (seven metrics), canopy cover, total vegetation cover and total vegetation vertical variability (each six metrics), and canopy horizontal variability and total vegetation horizontal variability (both five metrics). The other classes included ≤4 metrics.

Quantifying the current use of the 18 metric classes indicated that a few metric classes are very popular (Figure 4). For instance, canopy metrics were most often used, especially those related to canopy height (93 times), canopy vertical variability (63 times) and canopy cover (34 times). In contrast, metric classes such as single-tree cover, single-tree height, understorey cover, understorey height, other layer height and other layer horizontal variability were rarely used (Figure 4). Studies on species distributions and species richness generally showed similar patterns in metric use, with a few exceptions (Figure 4). For instance, metrics of total vegetation cover were proportionally more often used in studies of species richness than in studies of species distributions (Figure 4).

For most metric classes, the LiDAR-derived vegetation metrics showed more often an "effect" than "no effect" (Figure 4). For instance, metrics within the most widely used canopy height metric class often showed a relationship with species distributions or species richness (*n* = 54, 58%). Canopy vertical variability (the second most widely used metric class) was less effective than other metric classes and showed less often a relationship (*n* = 28, 44%). Overall, canopy metrics were most widely used, and those related to canopy height and canopy cover also tend to effectively explain species distributions and species richness (Figure 4). It is important to note that the effectiveness and direction of the relationship (i.e., positive or negative effect) of a particular metric will depend on the ecology of the specific species.

4 | DISCUSSION

Our review provides a detailed overview and quantification of the current use of LiDAR-derived vegetation metrics in avian species distribution and species richness research. The categorization into 24 metric classes—defined by vegetation part (total vegetation, single trees, canopy, understorey, and other single layers as well as multi-layer) and structural type (cover, height, horizontal variability

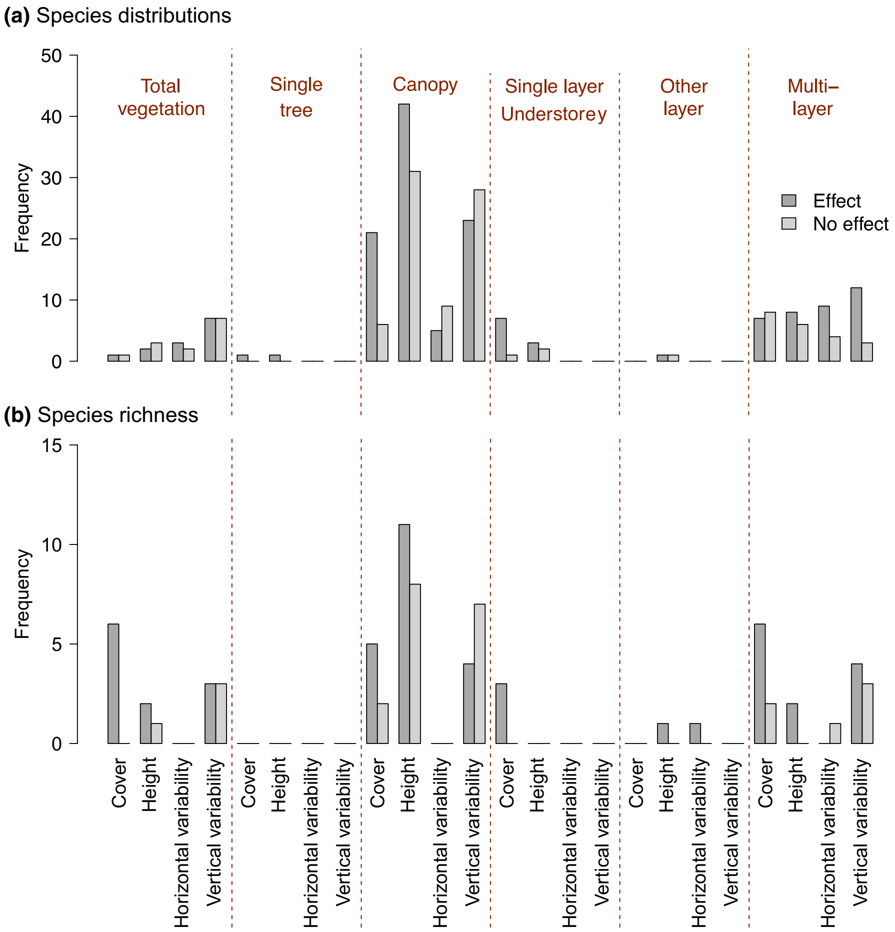

FIGURE 4 Dominant use and effectiveness of classes of Light Detection and Ranging (LiDAR)-derived vegetation metrics as currently employed in studies of (a) avian species distributions, and (b) avian species richness. The metric classes are arranged by vegetation part (total vegetation, single tree, single layers such as canopy, understorey or other layer, and multi-layer) and within that by structural type (cover, height, horizontal variability and vertical variability). Compare Table 1 and Supporting Information Appendix S3 for metrics within metric classes. Frequency indicates how often LiDAR-derived vegetation metrics within a class showed a relationship ("effect," dark grey) or no relationship ("no effect," light grey). See Supporting Information Appendix S1 for the 50 reviewed articles, and the method section for how information on relationships was extracted from the articles

and vertical variability)—provides a general conceptual framework for ecological comparisons of LiDAR metrics. While LiDAR canopy metrics of forests are currently most widely used (Figure 4), especially at local and landscape scales (Figure 3), there is great potential for future studies to extend this to other vegetation layers (e.g., understorey, multi-layer), other habitat types (e.g., non-forest ecosystems), other taxa than birds (e.g., invertebrates, other vertebrates) and broader spatial extents (e.g., >100 km^2).

The focus of our review was on bird species distribution and diversity studies which linked LiDAR metrics to the occurrence, abundance and species richness of birds as measured from opportunistic observations, point counts, transects, territory mapping, bird tracking, atlas data, range maps or nest location data. These kind of distribution data are widely investigated when using LiDAR in studies with focus on animal ecology (Davies & Asner, 2014). For other aspects of bird ecology (e.g., breeding success, acoustic diversity, beta diversity), some available studies suggest potential similarities to our findings. For instance, LiDAR-retrieved canopy height allows to predict the breeding success (measured as body mass of nestlings in occupied nestboxes) of Great Tits and Blue Tits in broadleaved woodlands in the UK (Hill et al., 2014; Hinsley, Hill, Gaveau, & Bellamy, 2002). Acoustic diversity (quantified with a diversity index based on acoustic frequency bands derived from soundscape recordings) in a Neotropical rain forest in Costa Rica is well explained by canopy height and multi-layer vertical variability (Pekin, Jung, Villanueva-Rivera, Pijanowski, & Ahumada, 2012). Beta diversity (i.e., turnover and nestedness) of birds across Switzerland can be partly explained by variation in LiDAR-derived canopy height (Zellweger, Roth, Bugmann, & Bollmann, 2017). The current use of LiDAR metrics seems to be largely consistent across different bird data sources (Figure 4), probably because canopy metrics can be reliably retrieved and also act as a potential surrogate for 3-D habitat structure below the canopy, at least in mature and old woodlands and forests. The success and effectiveness of LiDAR metrics to explain bird ecology may depend not only on the quality of the LiDAR data, but also on the quality of the ecological data, including sampling biases or inaccuracies in geo-referencing (Beck, Böller, Erhardt, & Schwanghart, 2014). Moreover, the effect of LiDAR metrics on bird distributions might also depend on whether below-canopy vegetation metrics reflect microclimatic conditions, for example in montane forest environments (Frey, Hadley, & Betts, 2016). Finally, the spatial resolution at which ecological data are linked to the LiDAR data (e.g., length of radii or grid cell size around bird observation points) could also influence the predictive performance of LiDAR metrics. These aspects should be investigated in more detail in future studies.

The revealed geographical bias in current bird-LiDAR studies towards temperate forests of North America and Europe is consistent with an earlier review (Davies & Asner, 2014) and partly caused by the commercial interest in developing LiDAR metrics for forestry applications (Maltamo et al., 2014). In a seminal paper (based on field measurements rather than LiDAR), MacArthur and MacArthur (1961) already showed that the vertical distribution of biomass in North American forests can be a good predictor of bird species richness. More recent studies using LiDAR have, for instance, demonstrated that forest stand height and density of large conifers can explain the habitat suitability of the spotted owl in North America (Ackers et al., 2015), that heterogeneity in forest canopy height and vertical structure predicts the occupancy of the ground-living hazel grouse in Central Europe (Bae, Reineking, Ewald, & Mueller, 2014; Zellweger, Morsdorf, Purves, Braunisch, & Bollmann, 2014), and that canopy height, total vegetation cover and below-canopy vegetation heterogeneity are important determinants of bird species richness in European and North American forests (Coops et al., 2016; Goetz, Steinberg, Dubayah, & Blair, 2007; Zellweger et al., 2016). Socioeconomic factors most likely explain the strong geographical bias towards North America and Europe (Kissling et al., 2018; Meyer, Kreft, Guralnick, & Jetz, 2015). Such biases towards wealthy countries and temperate forest ecosystems are widespread in ecological studies (Martin, Blossey, & Ellis, 2012) and can limit the scalability and applicability of ecological theory. We therefore recommend to conduct more animal–habitat studies with LiDAR-derived vegetation metrics in tropical forests (Davies, Ancrenaz, Oram, & Asner, 2017; Singh, Tokola, Hou, & Notarnicola, 2017; Wallis et al., 2016), savannas (Loarie, Tambling, & Asner, 2013), wetlands and aquatic reedbeds (Corti Meneses, Baier, Geist, & Schneider, 2017; Zlinszky, Mücke, Lehner, Briese, & Pfeifer, 2012), riparian habitats (Seavy, Viers, Wood, Eavy, & Iers, 2009), or in low-stature terrestrial habitats such as grasslands, tundra, shrublands or agricultural areas (e.g., Svendsen, Sell, Bøcher, & Svenning, 2015; Boelman et al., 2016).

Most bird–habitat studies using LiDAR-derived vegetation metrics have been conducted at small spatial extents (<100 km^2) using area-based approaches (e.g., rasterization with grid cells), and with ALS data that have low point densities (<10 points/m^2) and small footprint sizes (<1 m diameter). This mostly reflects the current availability of LiDAR data and the challenges related to an effective processing and data management of the massive amounts of point cloud data (Kissling et al., 2017; van Oosterom et al., 2015; Pfeifer, Mandlburger, Otepka, & Karel, 2014; Vo, Laefer, & Bertolotto, 2016). While there is a rapid growth in the availability and quality of national ALS data (e.g., an increasing open access to country-wide ALS data in Europe), only few studies have so far made use of such large-extent LiDAR datasets in bird–habitat studies. Examples include bird diversity studies at sites across entire Switzerland (Zellweger et al., 2016, 2017) or the Canadian province of Alberta (Coops et al., 2016). To date, LiDAR bird–habitat studies with a global extent have been rare because the only near-global SLS data currently available are from the NASA full waveform Geoscience Laser Altimeter System (GLAS). This laser scanner has a footprint of ca. 70 m in diameter (the size of a small stand of trees) and has been used to estimate forest canopy height at 1 km^2 resolution (Simard, Pinto, Fisher, & Baccini, 2011). These forest canopy height data have subsequently been used to analyse global bird species richness at 96 × 96 km resolution (Roll et al., 2015). A promising avenue for future research is the new Global Ecosystem Dynamics Investigation (GEDI) LiDAR installed in 2018 by NASA on the International Space Station (ISS; Stavros et al., 2017). This will further advance our ability to monitor 3-D ecosystem structure by measuring canopy heights and foliar vertical profiles with footprints of 25 m globally (between 51.6° N and 51.6° S).

Most reviewed studies used high-resolution ALS data (i.e., footprint sizes <1 m diameter), but point densities were comparably low (<10 points/m^2) and the flight season (leaf-on vs. leaf-off) varied among studies. Both point density and flight characteristics can affect the calculation of LiDAR-derived vegetation metrics, for example for the quantification of forest understories (Hill & Broughton, 2009) or in single-tree detection (Koenig & Höfle, 2016). Some metrics (e.g., those related to canopy height) might be little affected by varying point densities and flight seasons and could be relatively robust when calculated for datasets with different LiDAR measurement configurations or with varying spatial resolutions. In contrast, multi-layer metrics (e.g., foliage height diversity and penetration ratios between fixed heights) or single-layer metrics below the canopy (e.g., understorey cover) might be particular sensitive to variation in LiDAR characteristics because they will be affected by how many LiDAR returns are available from the subcanopy layers. High point density LiDAR data (>10 points/m^2) are then needed to meaningfully calculate those metrics (Holbrook, Vierling, Vierling, Hudak, & Adam, 2015; Koenig & Höfle, 2016; Müller, Moning, Bässler, Heurich, & Brandl, 2009; Müller, Stadler, & Brandl, 2010; Vierling et al., 2013). High point density data will also allow to calculate unique metrics. For instance, a study in Japan with high point densities (e.g., 48 points/m^2) allowed to voxelize the LiDAR point cloud into 1 × 1 × 1 m voxels, and the derived voxel-based metrics were especially robust predictors for the habitat use of forest birds (Sasaki et al., 2016). Other examples with high point density data (e.g., 27 points/m^2) demonstrate that LiDAR-derived vegetation metrics can be calculated for grasslands where it is particularly difficult to differentiate the ground level from the dense vegetation near the ground (Boelman et al., 2016). A systematic analysis of how the various LiDAR-derived vegetation metrics are affected by different LiDAR measurement configurations (e.g., point density, leaf-on vs. leaf-off) should be conducted in the future to better assess the robustness of each metric for up-scaling and analyses across different LiDAR datasets.

All studies used an area-based approach for processing the LiDAR data, either by rasterizing point cloud information into grid cells or by calculating LiDAR-derived vegetation metrics with a radius around focal bird observation points. The rasterization of LiDAR point clouds is computationally efficient in terms of data handling, but leads to information loss regarding the fine-scale structure of the 3-D point cloud because grid cells merge the information of various objects. Using an object-based approach would instead have the advantage to classify groups of points (e.g., based on direct neighbourhood information from the point cloud around each focal point) into objects such as structurally similar reedbeds, hedges within agricultural landscapes, or single trees and patches of dominant tree species within a forest (Kissling et al., 2017). While object-based approaches are steadily increasing in geography (Blaschke et al., 2014) and examples of object-based vegetation analysis with LiDAR data exist for urban vegetation mapping (Höfle et al., 2012) and single-tree detection within forests (Koch et al., 2014), the bird–habitat studies reviewed here rarely used an object-based approach. One exception was a study on migratory songbirds in a US deciduous forest that employed a canopy height model and an object-based approach to obtain crown radii and height of single trees which then allowed to calculate stem densities per hectare (Swatantran et al., 2012). We envisage that the further development of an object-based methodology will provide exciting new ways to quantify the 3-D vegetation structure and habitat use of animals.

Our harmonization of LiDAR-derived vegetation metrics revealed that many different metric names exist for the same metric calculation method. For instance, foliage height diversity, understorey height diversity and Shannon diversity index are three names that have been used for the same metric (Bae et al., 2014; Vierling et al., 2013; Zellweger et al., 2016). Even more confusing is that similar names are applied to metrics that differ in the way they are calculated. The most obvious example is canopy height which is calculated in myriad ways (see Supporting Information Appendix S3), including the maximum return in a grid cell, the mean of the first returns or the height of the 95th percentile of returns (Ackers et al., 2015; Coops et al., 2016; Smart et al., 2012). Most of these metrics might be strongly correlated, but their sensitivity to outliers and point cloud density might differ (e.g., maximum vs. 95th percentile canopy height). The 77 unique metric names were grouped into 24 theoretically possible metric classes defined by vegetation part and structural type. This categorization might help in future studies for the selection, prioritization and ecological interpretation of LiDAR metrics. However, choosing the right metrics is not always easy and might depend on a priori ecological knowledge of animal habitat use. In cases where such knowledge is lacking, it is also possible to condense the variability in LiDAR point clouds by generating principal components as predictors and using them in exploratory analyses with animal species distribution data to generate hypotheses about animal habitat and space use (Ciuti et al., 2018).

Our categorization of LiDAR metrics allowed a comparison of the current use and relative effectiveness of these metrics. This analysis supported our initial hypothesis that canopy metrics (related to canopy height, canopy cover and canopy vertical variability) are most widely used (Davies & Asner, 2014), although we show that they may not always be a good predictor of individual species distributions or species richness (Figure 4). One reason for their widespread use is that canopy metrics (e.g., canopy height) can be well retrieved even with low point densities (Ruiz, Hermosilla, Mauro, & Godino, 2014) or from large footprint SLS data with global coverage (Lefsky, 2010; Simard et al., 2011) and that they may act as a surrogate for 3-D habitat structure below the canopy. LiDAR metrics from below-canopy layers are more challenging to derive and require LiDAR point clouds with high point densities. For instance, single-tree segmentation is often carried out by detecting the local height maxima from raster-based canopy height models which might easily miss trees below the dominant canopy (Koch et al., 2014). Single-tree delineation is also computationally demanding and requires high point densities (Höfle et al., 2012), and is often only applied to particular forest stands (Koch et al., 2014) or in urban environments where individual trees are spatially well separated (Koma, Koenig, & Höfle, 2016). Understorey and multi-layer LiDAR metrics are also less widely used because most ALS data have low point densities and are limited in capturing information below the canopy. Nevertheless, below-canopy metrics in forest have high potential for understanding and predicting the distribution and habitat use of birds (Cody, 1985; Dunlavy, 1935; MacArthur & MacArthur, 1961) and potentially of many other taxa, and hence should be of increasing focus in the future.

5 | CONCLUSION

Our review shows that LiDAR metrics play an important role for understanding animal habitat and space use. The increasing availability of open access ALS LiDAR datasets and the forthcoming spaceborne LiDAR data from the GEDI (Stavros et al., 2017), coupled with ever increasing point densities, improved software tools and new data sharing web services (e.g., Kissling et al., 2017; Pfeifer et al., 2014; van Oosterom et al., 2015) will provide exciting new opportunities for quantifying and predicting animal species distributions and species richness across large spatial extents and with fine resolutions (e.g., 10–100 m grid cell size). Our categorization scheme may facilitate future studies in the selection of metrics that represent structural aspects of the vegetation which are complementary, and in the prioritization and ecological interpretation of LiDAR metrics. Major challenges for large-scale LiDAR applications emerge from combining ALS datasets across space (e.g., from different countries) and time (e.g., from different flight campaigns) because point densities, footprints and other technical, methodological and data quality characteristics (e.g., flight heights, season, laser return intensities, sensor angle, full waveform vs. discrete points) differ among LiDAR datasets, which may subsequently influence the calculation of LiDAR metrics. Moreover, the development of voxel-based and object-based approaches will allow novel ecological applications (e.g., via better quantification of subcanopy metrics and multi-layer vertical variability), but require high point density information and efficient software for data handling and processing. We further encourage animal–habitat studies with LiDAR in non-forest habitats, including savannas, wetlands, agricultural landscapes and other open habitats. Together, these advancements will allow unprecedented insights into species–habitat relationships, not only for birds but also for other taxa.

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DATA ACCESSIBILITY

All data extracted from the reviewed literature together with a detailed metadata description are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tm28hb6 (Bakx, Koma, Seijmonsbergen, & Kissling, 2019).

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BIOSKETCH

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Author contributions: W.D.K. and T.R.M.B conceived the study; T.R.M.B and Zs.K. collected data; T.R.M.B and W.D.K. analysed data; W.D.K. and Zs.K. supervised T.R.M.B.; T.R.M.B wrote the first draft; W.D.K. wrote the second draft with input from Zs.K.; and all authors provided ideas, comments and input. The revision was led by W.D.K., with input from T.R.M.B, Zs.K. and A.C.S.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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