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Terrestrial lidar reveals new information about habitats provided by large old trees

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ABSTRACT

Large old trees have been described as keystone habitats for several species. However, current research does not fully explain why these species show a preference for such trees. In this study, we combined field observations of birds with terrestrial lidar scans and computational feature-recognition to describe habitats provided by trees at an unprecedented level of detail. We conducted field observations of birds at 62 trees and used parameters including branch angle, branch diameter, branch state (living or dead), and trunk diameter at breast height (DBH) to develop a generalised linear mixed model (GLMM) that could predict which types of branch birds are more likely to visit. We then quantified angles, diameters, and states of 78,006 branch objects representing the complete canopies of 16 trees. By combining these two models we predicted that large trees (>80 cm DBH) contained, on average, 383 m of branches that were highly suitable for birds (i.e., the predicted probability of observing a bird was ≥0.5), which was more than seven times the average length of highly suitable branches provided by medium trees (51–80 cm DBH). Only one of the sampled medium trees contained highly suitable branches. Small trees (<50 cm DBH) contained none. Our analysis provides new knowledge about characteristics that make large old trees disproportionately attractive to birds and presents a novel method of assessment that can apply to other complex habitat structures.

1. Introduction

Large old trees have been described as keystone structures (Hunter et al., 2017; Manning et al., 2006; Prevedello et al., 2018) because they are disproportionately important as habitats for many animals in comparison to smaller and younger trees (Lindenmayer and Laurance, 2016). Over 300 vertebrates in Australia (Gibbons and Lindenmayer, 2002) and 1000 bird species worldwide (van der Hoek et al., 2017) depend on large old trees for nesting, roosting, and shelter.

One explanation for the disproportionate use of large old trees by animals is that older trees are more likely to develop hollows or cavities. Hollows are habitat structures that provide nesting sites for many mammals, birds, herpetofauna, and invertebrates (Lindenmayer and Laurance, 2016). However, many species that depend on large old trees do not use hollows but rely on branches for perching, nesting, and other activities (Le Roux et al., 2015a; Lindenmayer, 2017). Therefore, taken alone, the presence of hollows cannot explain why many organisms prefer large old trees.

There are other significant aspects that make tree habitats preferable to animals. One of those factors is the spatial arrangements of branches in tree crowns. Complex patterns of tree canopies result from centuries of growth, aging, lightning strikes, wind damage, insect assaults, fungal proliferation, and fires (Pretzsch, 2009). Features that are common in large old trees but are absent or rare in younger trees include diverse branch arrangements (Sillett et al., 2015), fissured bark (Lindenmayer et al., 2000), and many dead and lateral branches (Le Roux et al., 2018). These structures provide sites for crucial activities, including nesting and perching (Le Roux et al., 2015a).

Low-resolution methods cannot measure such complex aggregations of branches. Conventional approaches for assessing trees rely on relatively coarse naked-eye observations from the ground (Harper et al., 2004; Koch, 2008; Rayner et al., 2011), aerial and satellite sensing (Corona et al., 2010), or measurements taken through tree climbing or from crane gondolas (Lindenmayer and Laurance, 2016). Some of these techniques can account for structures that are relatively large and few in number, for example major tree limbs (Sillett et al., 2015), hollows (Gibbons and Lindenmayer, 2002), or structures located on the ground including fallen logs (Killey et al., 2010) and leaf litter (Mcelhinny et al., 2010). However, the measurements obtained in this way provide unreliable estimates of habitat features in tree canopies (Rayner et al., 2011; Stojanovic et al., 2012). For example, they can overlook properties of branch aggregations (Seidel et al., 2011) or interiors of hollows (Harper et al., 2004).

When the number of features such as small branches increases,

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assessment becomes challenging (Malhi et al., 2018). Given this difficulty, surveyors can inappropriately assume an equivalence between large and small trees in terms of habitat structures such as dead and lateral branches (Vesk et al., 2008). By failing to account for features that are unique to large old trees, this assumption can contribute to the loss of significant habitat structures in managed landscapes (Le Roux et al., 2015b; Lindenmayer, 2017).

Better analysis of trees as habitats requires approaches that can exceed human visual acuity and capture ecologically meaningful features (Calders et al., 2020b). The scale of relevant ecological interactions is a more meaningful threshold for the fidelity of data representations (Gámez and Harris, 2022; Olsoy et al., 2015). To illustrate, animals operate within perceptual worlds determined by their sensory abilities, cognition, and learning (Dyck, 2012; Greggor et al., 2014). They ascribe meaning to structures when they recognise and choose to use them as habitats (McGarigal et al., 2016). Better measurement can reveal properties of habitat structures in ways that reflect such perceptions (Aben et al., 2018; Russo et al., 2023) including the preference for large old trees (Prevedello et al., 2018).

Recent developments in sensing and analysis has improved accuracy, precision, repeatability, and traceability of measuring the structures in trees (Calders et al., 2020b). For example, terrestrial lidar scanning senses structures by emitting laser pulses, which offers higher-resolution data, permitting detailed descriptions of structural elements beneath and within the canopies of trees (Camarretta et al., 2019).

Most techniques for assessing scans of trees are adaptations from methods originally devised for the analysis of less spatially detailed samples such as forest stands (Calders et al., 2020b). Better assessments of individual trees can be done with emerging feature-recognition techniques developed for high-resolution point-cloud data provided by terrestrial lidar devices. For example, quantitative structure models can register 99 % of branches with millimetre accuracy (Hackenberg et al., 2015). The typical use of such models is to estimate biomass for harvesting or carbon sequestration (Disney et al., 2018). Some studies have also used these models to understand relationships between branches, for example, in trees under wind loads (Malhi et al., 2018). To our knowledge, none of these approaches model how fauna use trees.

In response, we: 1) develop a statistical model that uses field observations to predict patterns of branches that birds are more likely to visit; 2) recognise every occurrence of these branches in high-resolution three dimensional scans; and 3) compare habitat suitability of trees for birds by combining steps one and two. This approach allows us to compare the importance of trees as habitats across sizes and ages.

2. Methods

To develop this approach, we focus on a 50km^2 area in the Australian Capital Territory (35°17′35.64″S; 149°07′27.36″E), near Canberra. This case typifies challenges that apply to the conservation of large old trees (Schnell et al., 2015) in Australia and globally. In south-eastern Australia, temperate eucalypt woodlands have declined by 95 % since European settlement, leaving isolated large old trees being the only remnants over much of the area where this ecological community once occurred (Department of Environment, Climate Change and Water NSW, 2011).

2.1. Use field observation to predict which birds are more likely to visit

To identify branches that are significant to birds, we observed birds visiting locations in tree crowns and recorded characteristics of visited branches including diameter, angle relative to the horizontal plane, as well as whether visited branches were dead or alive. To achieve this, our process had to:

1. **Define tree classes.** To observe branches in trees of different ages, we used size as a proxy for age and categorized trees into three classes using trunk diameter at breast height (DBH). Although many factors affect the formation of individual trees, age of trees in the genus *Eucalyptus*, including (*E. melliodora*) in our study (Banks, 1997), correlate with DBH (Gibbons et al., 2000; Whitford, 2002). The classes were: small (20–50 cm DBH), medium (51–80 cm DBH), and large (>80 cm DBH). We adopt this classification to demonstrate the contrast between smaller and larger trees.
2. **Select sample trees and schedule bird observations.** To represent various land uses and management practices, we selected 62 trees from four different areas: reserves, agricultural zones, urban parks, and streets. The sample size included a selection of small, medium, and large trees for each land use (see Fig. 1, Supplementary Materials Appendix A). All trees were from the genus *Eucalyptus*, primarily from four species *(E. blakeleyi, E. melliodora, E. polyanthemos, and E. bridgesiana)*.

   We recorded birds visiting these trees twice per year during the Austral spring (September to November) over two years (2017 and 2019), surveying each tree four times in total. Each ‘observation period’ involved standing 5–10 m away from the canopy edge for 20 min between sunrise and 10 am. The ‘total observation period’ was 96 h (5760 min).
3. **Record types of branches visited by birds.** We recorded the branch type that birds visited in each tree. A ‘visit’ is a binary value (0,1) indicating whether a bird was observed perching, feeding, or nesting on one of 54 possible branch types within each tree across the total observation period. We counted multiple uses of a branch type within a tree across all observation periods as a one and no visits to a branch type across all observation periods as a zero.

   ‘Branch type’ is a combination of characteristics as follows:
   - Size (three conditions: <5 cm, 5–20 cm, >20 cm diameter estimated from the ground).
   - State (two conditions: dead or alive).
   - Angles (nine conditions: 1–10°, 11–20°, 21–30°, 31–40°, 41–50°, 51–60°, 61–70°, 71–80°, 81–90° relative to the horizontal plane estimated from the ground).

   Classification based on these characteristics yielded 54 *branch types* $= 3$ *sizes* $\times$ 2 *states* $\times$ 9 *angles*.

   For each visit, we also recorded: tree trunk diameter measured at breast height over bark (DBH) and assigned a “Tree ID” to each surveyed tree.

   In total, we observed 482 bird visits (see Fig. 2, Supplementary Materials Appendix A).
4. **Predict branch types likely to attract visits.** Using Generalised Linear Mixed Models (GLMMs), we examined the relationship between the probability a bird visited a branch type and potential explanatory variables including branch diameter, branch angle relative to the horizontal plane, branch state, tree DBH, and tree ID. We used the binomial distribution for the probability of a bird visit to a branch and represented DBH as a continuous variable. In all GLMMs:
   - branch diameter, state, angle, and tree diameter at breast height (DBH) were fixed effects and
   - Tree ID was a random effect because our data contained multiple observations from the same trees.
5. **Confirm significance of characteristics that define branch types.** To identify the types of branches visited by birds, we found the best model in a set of five candidate models that contained distinct combinations of fixed effects (see Table 4, Supplementary Materials Appendix D). The best model fit observations using the fewest number of variables ensuring that we did not overfit the model to the observed visits. We applied Akaike's Information Criterion (AIC) to select the best model (Anderson and Burnham, 2002). We completed these analysing using the glmmTMB and MuMIn packages in R (Barton, 2009; Brooks et al., 2017).

Together, the steps described in this section produced a statistical model that linked bird visits to characteristics of branches. The next

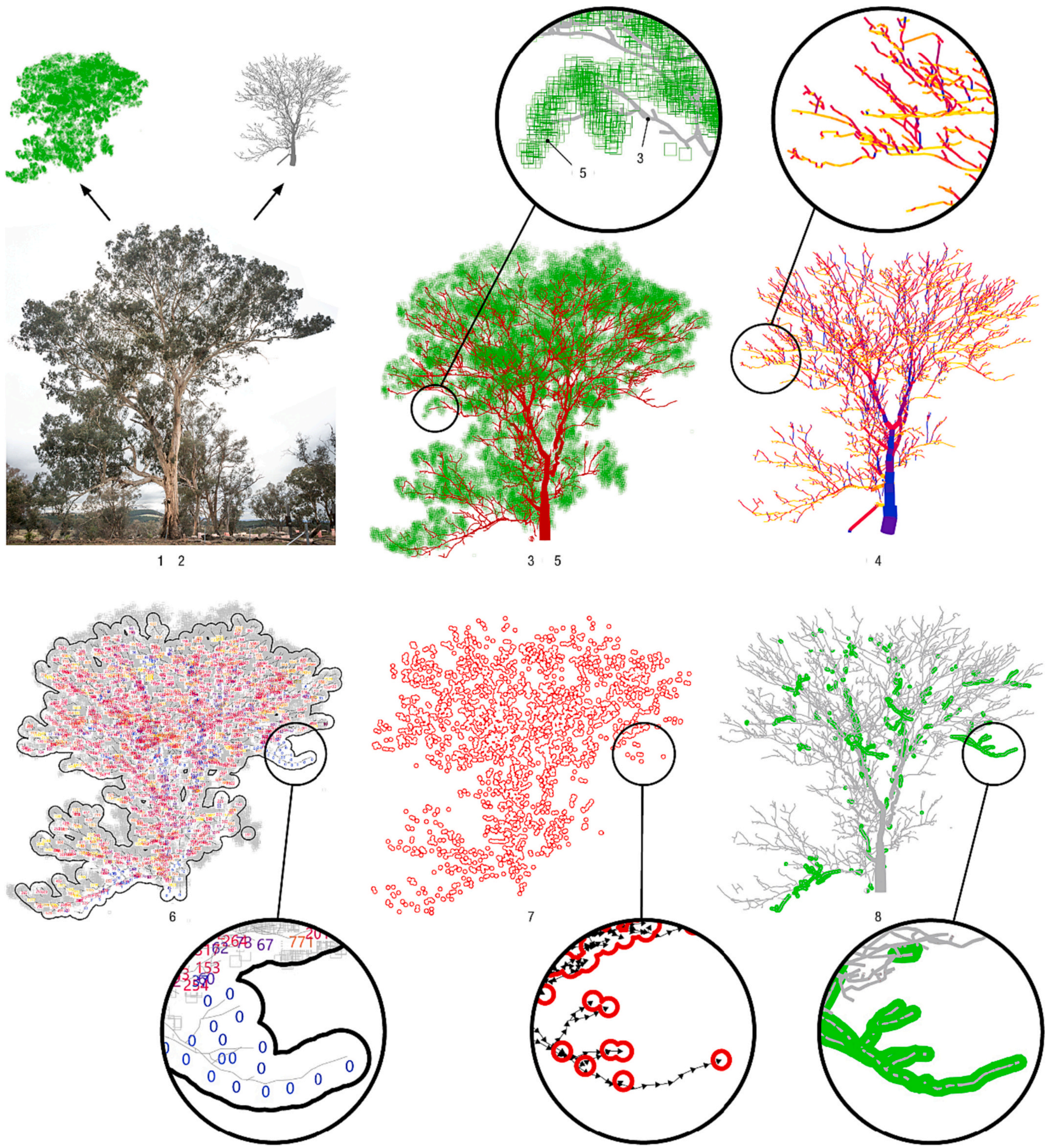

Fig. 1. Computational feature-recognition routines used to recognise branch objects. 1) Sample tree scanned; 2) Separated leaf (green) and wood (grey) points; 3) recognised branch objects(red); 4) branch-object angles (low-angle branches relative to the horizontal plane in yellow); 5) canopy voxels (green boxes); 6) branch-object exposure values (coloured numbers); 7) branch-object connections (black arrows) with terminal branch objects (red circles); and 8) branch object states (dead branch-objects in green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

step searched for these characteristics in high-resolution lidar scans of trees.

2.2. Recognise branch characteristics in high-resolution scans

We next used a custom feature recognition workflow (Fig. 1) to recognise all ‘branch objects’ in scanned trees, measure their diameter, their angles relative to the horizontal plane and assess their states because we identified the significance of these characteristics on bird visits (see Results 6.1). We refer to the recognised structures as ‘branch objects’ to distinguish these numerical representations from physical branches. These objects represent branches as cylinders differentiated

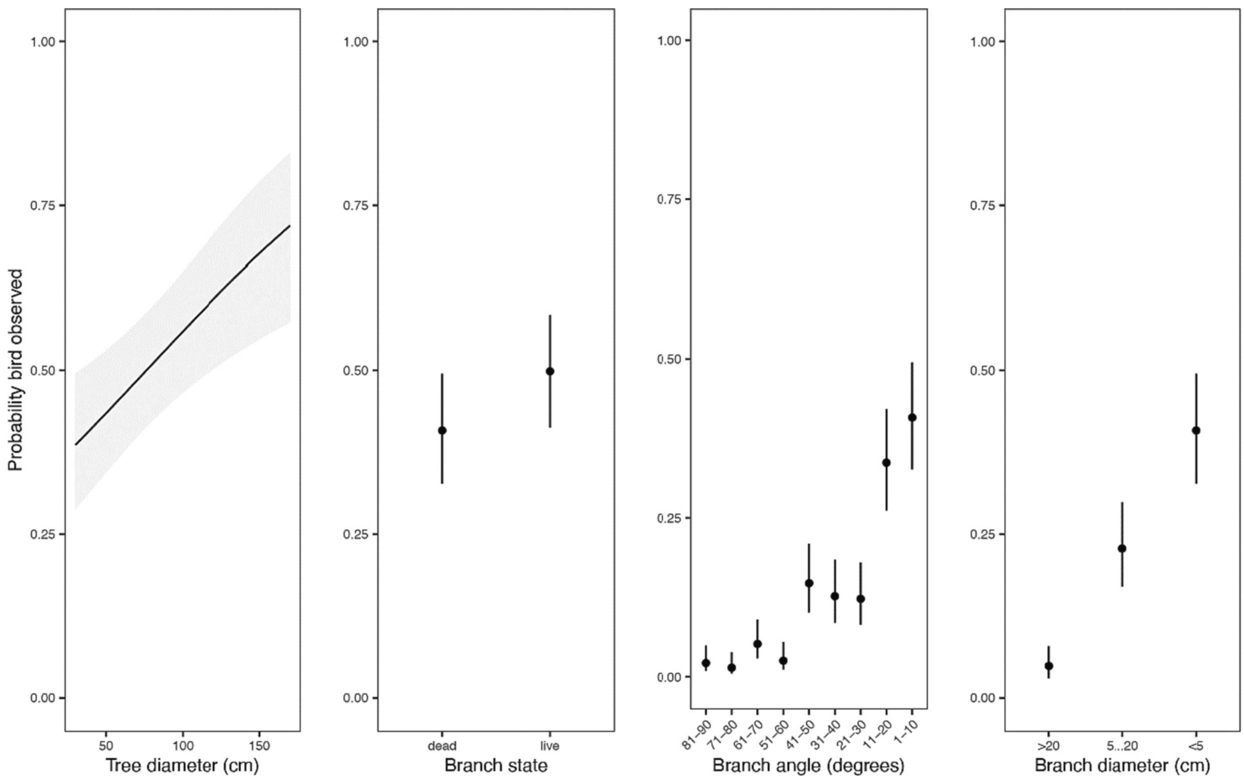

Fig. 2. Field observations of birds at trees. The probability of a bird visit at an observed branch in response to changes in tree diameter (cm DBH), branch state (alive dead), branch angle (degrees from horizontal) and branch diameter (small, medium, and large). We plotted predictions for each variable while holding the other values at their mean (for continuous variables) or their mode (for categorical variables).

by their length, radii, position, orientation, and connectivity to other branch objects.

Below, we outline the steps of this recognition workflow (for additional detail, see Supplementary Materials Appendix B):

1. **Scan trees.** To obtain the datasets for feature recognition, we scanned 16 trees using a Z + F IMAGER 5016 terrestrial lidar scanner. These trees were either surveyed in our bird observation study or of the same species within the study site (see Fig. 1, Supplementary Materials Appendix A). Into this scanning, we included trees of varying ages and growing under differing land management practices. We selected: four small, five medium, and seven large trees. The environments included reserves (n = 7), agricultural land (n = 6), and urban areas such as parks and streets (n = 3). The distribution by size class was as follows: urban (S = 0, M = 1, L = 2), reserve (S = 2, M = 1, L = 4), and agricultural land (S = 2, M = 3, L = 1) (Fig. 1, Step 1).
2. **Separate points into clusters representing leaves and branches.** To define these clusters, we measured surface irregularity using a Gaussian mixture model (Belton et al., 2013) that operates on point cloud information (Fig. 1, Step 2).
3. **Recognise and connect branch objects.** For each tree, we generated a quantitative structure model using the points from the branch cluster and the cylinder-fitting method in SimpleTree (Hackenberg et al., 2015). This method found three-dimensional positions, radii, and lengths of all branch objects within tree scans (Fig. 1, Step 3). The algorithm also connected adjacent objects forming a connectivity graph of the whole tree. We standardised the branch objects into 20 cm–50 cm lengths by merging smaller or splitting larger branch objects using a custom script written in Grasshopper 3D.
4. **Find branch diameters and angles.** We used a custom script in Grasshopper 3D to classify branches diameters into small, <5 cm; medium, 5–20 cm; and large, >20 cm. This script also used the start and end points of all branch objects to find their inclination relative to the horizontal plane that we grouped into nine conditions: 1–10°, 11–20°, 21–30°, 31–40°, 41–50°, 51–60°, 61–70°, 71–80°, 81–90°) (Fig. 1, Step 4).
5. **Define leaf objects**. To prepare the leaf cluster for further analysis we sampled the points as 10 cm × 10 cm × 10 cm voxels using CloudCompare (Fig. 1, Step 5).
6. **Find exposure values**. To estimate the extent by which the leaves obscured branches in trees, we defined an 'exposure' characteristic for each branch object using Grasshopper 3D. We defined this characteristic as the number of canopy voxels within a sphere of 1 m radius and its centre at the centroid of the object. (Fig. 1, Step 6).
7. **Find terminal branch-objects using connectivity information.** To identify branch objects representing the termini of tree limbs, we found all objects with only one connecting neighbour using the connectivity graph (Fig. 1, Step 7).
8. **Classify branch states**. We used a custom Grasshopper 3D script to classify states of branch objects as either 'living' or 'dead' (Fig. 1, Step 8). To do so, we defined a dead branch as a branch object that: 1) had the exposure value <50 and 2) was a terminal branch or had a connecting branch object that was also dead. We determined the value of 50 as appropriate through visual inspection of recognised dead branches. The second step of the process ensured that we did not misclassify exposed living limbs such as the tree trunk as dead.

By completing this step, we obtained numerical descriptions of the complete tree crowns for selected small, medium, and large trees. This information served as the basis for the next step where we predicted the suitability of trees for birds.

2.3. Predict branches that birds are more likely to visit in scanned trees and compare trees

This section describes the process we used to predict which branches within scanned trees match branch types likely to be visited by birds. We used these predictions to compare the lengths of highly suitable branches for small, medium, and large trees. To perform this comparison, we:

1. **List significant explanatory characteristics of branch objects.** First, we listed characteristics of branch objects that have a demonstrated association with bird visits, as outlined in Section 3.1. These variables were: tree diameter at breast height (DBH), branch angle, branch diameter, and branch state. This step allowed us to match recognised branch objects in the scanned trees to branch types on which we could perform predictive analyses.
2. **Predict which branch objects are likely to receive bird visits.** For each branch object, we used the GLMM to predict the probability of observing at least one bird visit to a branch with the same characteristics in a tree of corresponding trunk diameter over the total observation period ('visit likelihood').

   The outcome of this prediction yielded a mean probability value for each branch object ranging from zero (indicating that no bird visits) to one (indicating that at least one bird visit would be observed).
3. **Classify highly suitable branches.** Based on these predictions, we classified branch objects into two conditions: 'highly suitable' (visit likelihood ≥ 0.5) or 'minimally suitable' (visit likelihood <0.5) for birds.
4. **Quantify the total length of highly suitable branches for each tree and the mean length of such branches in small, medium, and large size classes.** For each tree, we summed the lengths of branch objects classified as highly suitable to calculate the mean length of highly suitable branches. We then computed the mean length of highly suitable branches per size class.

Comparisons of these values between trees and size classes enabled us to understand why large (and therefore old) trees are disproportionately vital as bird habitats by contrasting the total lengths of branches associated with bird visits in larger and smaller trees.

3. Results

3.1. Branch angle, branch diameter, and DBH predict bird visits

The best Generalised Linear Mixed Model (GLMM) based on field observations showed that bird visits were more likely at branches that have a lower angle relative to the horizontal plane (<20°), are smaller in diameter (<5 cm), and found in trees with larger DBH values. The analysis also indicated a modest preference for living branches (Fig. 2).

3.2. Characteristics of every branch in tree canopies become measurable

In 16 scanned trees, we recognised 78,006 individual branch objects (see Table 3, Supplementary Materials Appendix C). Small trees had a mean total branch length of 159 m (range 67–356 m), medium trees had a mean total branch length of 888 m (range 650–1246 m), and small trees had a mean total branch length of 1329 m (range 851–2054 m). We classified these branch objects based on their angle, diameter, and state (Table 1).

In scanned trees, branch objects had an average angle of 34° (Table 1, Fig. 3). Trees in the small (20–50 cm DBH), medium (51–80 cm DBH) and large (>80 cm DBH) size classes had mean branch angles of 35°, 37°, and 33° respectively.

The total length of lateral branches (defined as branches with an angle <20° relative to the horizontal plane) on which birds are more likely to be observed (Fig. 2) in each size class of trees differed substantially. The mean length of lateral branches in large, medium, and small trees was 513 m (range 290–579 m), 211 m (range 94–414 m), and 60 m (range 14–170 m) respectively. Large trees therefore contained, on average, 2.4 times greater length of lateral branches than medium-sized trees and 8.5 times greater length of lateral branches than the smallest trees.

Table 1
Structural properties of branches, feature-recognition routines, and estimated quantities.

Characteristics identified	Feature recognition routines applied to scans of trees produced by terrestrial lidar		Estimated quantities
Tree ID	1	Scan trees	Up to 5 million unclassified points per tree. 78,006 total branch objects.
	2	Separate points into clusters representing leaves and branches	
	3	Recognise and connect branch objects	
Branch angles and diameters	4	Find angles and diameters of branch objects	Mean angle relative to horizontal 34.1° (range 0–89.7°). 74,784 branch objects <5 cm diameters, 2054 objects with diameters between 5 and 20 cm, 1168 objects with diameters >20 cm.
Branch states (dead or alive)	5	Define leaf objects	975,226 canopy voxels.
	6	Find exposure values	5498 dead branch-objects.
	7	Find terminal branch-objects	62,508 living branch objects.
	8	Find dead and living branch-objects	

To build on these findings, we performed a comparative analysis focusing on the lengths and orientations of dead and living branches (Table 1, Fig. 3). We describe results for dead branches below and provide a similar breakdown for living branches as well as for branch diameters in the Supplementary Materials Appendix C.

Across 16 scanned trees, we identified 62,508 living and 5498 dead branch objects. Large, medium, and small trees had mean dead-branch lengths of 114 m (range 55–396 m), 48 m (range 3–139 m), and 4 m (range 0–14 m), respectively. This meant that large trees had, on average, 2.5 times greater length of dead branches than medium-sized trees and 32.9 times greater length than small trees.

Large trees had dead branches with an average angle of 28°, while medium and small trees had average angles of 37° and 38°, respectively. Large trees had a mean length of lateral dead branches of 50 m (range 16–179 m), medium trees of 11 m (range 1–21 m), and small trees just 1 m (range 0–3 m). Thus, large trees contained four times greater length of dead and lateral dead branches than medium-sized trees, and 59 times greater length of such branches than small trees.

3.3. Suitability of trees for birds changes with tree sizes

We defined "highly suitable" branches as those for which the mean predicted probability of observing a bird was ≥0.5 (Fig. 4). Our GLMM (Fig. 2) predicted that large trees supported, on average, 383 m (range 209–609 m) of highly suitable branches. By contrast, only one medium-sized tree (Tree 9, DBH 79 cm) supported any lengths of highly suitable branches, amounting to 266 m. This led to an average of 53 m (range 0–266 m) of such branches for medium-sized trees. Small trees had no highly suitable branches.

We also compared the ratio of highly suitable branches to minimally suitable branches (i.e., mean predicted probability of observing a bird was <0.5). On average, large trees contained 1.1 times greater length of

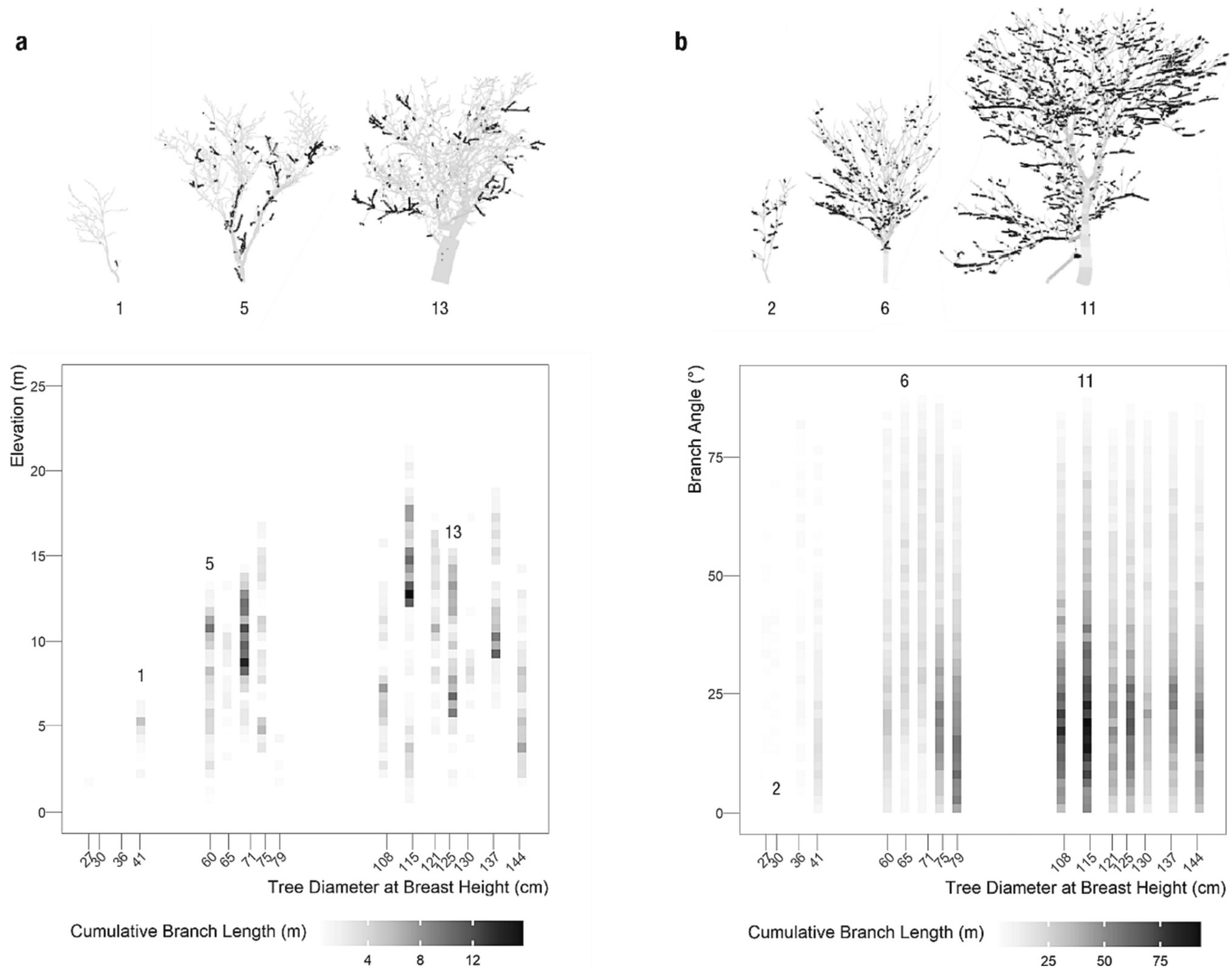

Fig. 3. Recognised branch structures. Darker shading in the tree icons shows structural features for select large, medium, and small trees. Lines in the graphs show distributions of these branches for all sampled trees. Clusters of lines correspond to trees of small (27–41 cm DBH), medium (60–79 cm DBH) and large (108–144 cm) DBH sizes. A, Dead-branch availability relative to the DBH and elevation of sample trees. Each vertical line in the graph represents the aggregate distribution of dead branches in one tree. Darker shading in tree icons shows recognised dead branches. B, Branch angle plotted relative to the DBH. Each vertical line shows the distribution of angles in one tree. Darker shading in the tree icons shows lateral branches with angles <20°.

minimally suitable branches than medium trees but 7.2 times greater length of highly suitable branches than these trees. We could not compare large trees to small trees because small trees had no highly suitable branches. Such findings clearly demonstrate that large trees substantially outperform their smaller counterparts in providing highly suitable branches for birds.

Furthermore, only large trees had dead branches predicted to be highly suitable for birds. Large trees had, on average 25 m (range 6–81 m) of such branches. That is, on average, 15 % of the highly suitable branches provided by large trees were dead branches. We present metrics for individual trees and also include comprehensive results for various combinations of branch characteristics, delineating their distribution across highly suitable and minimally suitable branches in Supplementary Materials Appendix E.

4. Discussion

This research introduced a novel approach that quantified the lengths of branches that are highly suitable for birds in large old trees. We demonstrated that the canopies of large old trees contained on average 383 m of branches that are highly suitable for birds, which is more than seven times the average of 53 m for medium size trees. Only one of the sampled medium trees contained highly suitable branches, while small trees contained none. Here, we discuss our results in three points to show that the examination of branch properties can aid the understanding of tree use by animal communities. We conclude the discussion by demonstrating the broader implications and scalability of our workflow.

4.1. Field observations identify relationships between branch structures and bird use

First, we discuss the study's field observations of bird visits to branches. Our observations modelled the likelihood of visits and ranked preferences of birds relative to branch types (see Fig. 4, Supplementary Materials Appendix D). Modelled patterns consistently demonstrated that birds have the strongest preference for small diameter branches that occur at low angles relative to the horizontal plane and in trees with larger trunk diameters (Fig. 2).

Our predictions of such preferences are consistent with existing research. Perching preferences result from various relationships between birds and habitat structures, including interactions between bird physiology and perch surfaces (Roderick et al., 2019) as well as landing behaviours in vertical and horizontal space (KleinHeerenbrink et al., 2022). Many birds – including passerines – spend most of their time perching. Mechanically, perching is easier on branches with lower

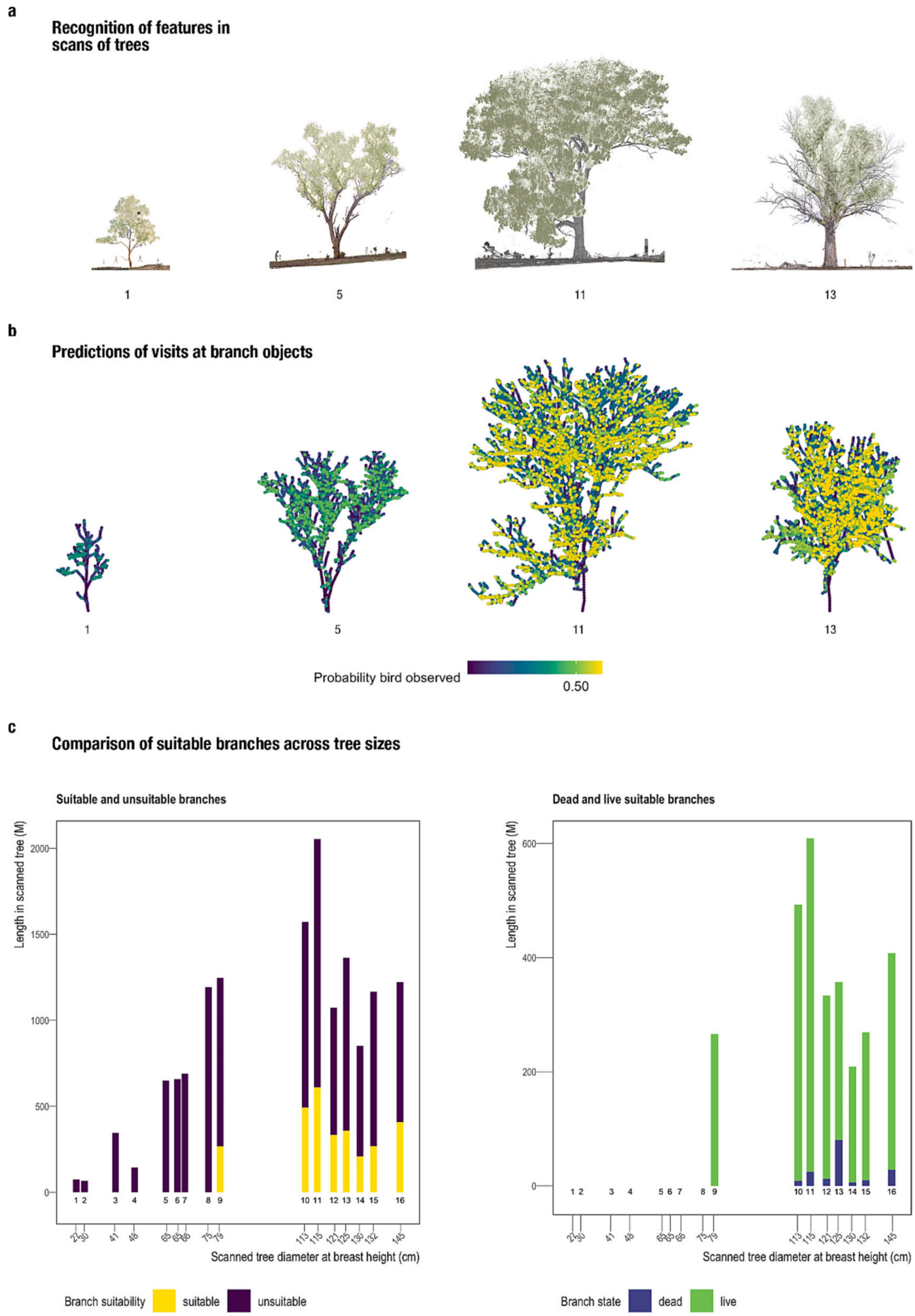

Fig. 4. Comparison of trees through the synthesis of lidar scanning, feature recognition, and field observations. a, Lidar scans of trees. Recognised leaves coloured in green. B, Predicted probabilities of observing birds on branch objects. Circles represent recognised branch objects. Colours show the probability a bird was observed at branch types in trees of different sizes. C, Cumulative lengths of highly suitable branches (i.e., mean probability a bird was observed is $\geq$0.5) in trees of different sizes. The left panel shows lengths of highly suitable and minimally suitable branches. The right panel shows length of highly suitable dead and living branches. For an expanded set of images corresponding to this figure across all 16 scanned trees, refer to Supplementary Materials Appendix E. (For the interpretation of colours in this figure legend, refer to the web version of this article.)

angles relative to the horizontal plane (Granatosky et al., 2022). Furthermore, smaller diameter branches may offer easier gripping, enhancing their suitability as perches.

The major constraint of naked-eye observations is that they cannot account for most branches. For example, during field observations, we recorded only visited types of branches and assigned zero values to all other types. The analysis of scanned data demonstrated that each of Trees 8–13, 15, and 16 (DBH 75–145) had more than one kilometre of branches and Tree 11 (DBH 115 cm) had more than two kilometres. Tree 11 had 11,217 branch objects with varying properties and all scanned 16 trees had 78,006 objects (Table 3, Supplementary Materials Appendix C). Typical field observations can only hope to record a small portion of the totals in such complex tree crowns. The next section explains how digital imaging and analysis can extend such observations.

4.2. Use of numerically defined branch objects results in more complete descriptions of tree crowns

This second subsection shows that datasets produced by terrestrial lidar and feature recognition can offer significant improvements to assessments based on field observations by creating detailed numerical descriptions of complex tree canopies.

Techniques of feature recognition can identify individual branches and other tree organs. Improved completeness and resolution provided by this workflow are important for studying large old trees because their canopies produce especially dense and varied structures (Hunter et al., 2017; Lindenmayer, 2017; Prevedello et al., 2018). Non-computational approaches for recording individual branches do exist (Sillett et al., 2015), but they are laborious when applied to larger trees. To illustrate this challenge, Tree 11 (DBH 115 cm) had 777 m of lateral branches (Table 3, Supplementary Materials Appendix C). Such large numbers only loosely correlate with measurements such as trunk diameters at breast height, canopy footprints, canopy strata, and tree heights (Seidel et al., 2011). Alternative methods that predict complete canopy structures via allometric equations (Köhl et al., 2017), algorithms (Prusinkiewicz et al., 2018), or tree-architecture models (Barthélémy and Caraglio, 2007) are also insufficient when assessing large old trees because these techniques focus on general principles and cannot capture unique and highly varied patterns of individual trees.

We use a subclass of feature recognition methods known as object-oriented metrics to assess complete tree canopies. These metrics generate numerically defined descriptions of irregular and complex spatial objects by characterizing them with real-world attributes, such as three-dimensional shapes or surface textures (Glad et al., 2020). This approach offers improvements over techniques that capture only one- or two-dimensional measurements because biota interact with habitat structures in three dimensions and respond to functional properties at the scale of branches (Malhi et al., 2018; Calders et al., 2020a; Gámez and Harris, 2022). Other studies have used feature recognition to assess complex habitat features and associate them with animal use (Glad et al., 2020; Varin et al., 2020). However, these studies rely on airborne lidar and evaluate habitat suitability at landscape scales (Glad et al., 2020). Resulting datasets have point spacings between 0.2 and 30 m (Beland et al., 2019), which is sufficient for recognizing tree boundaries but not branches and other smaller features.

By contrast, our workflow recognises lateral, dead, exposed, and terminal branches (as lines that range from 20 cm to 50 cm), leaves (as cubes with 10 cm edges), voids, and other features. To obtain this additional detail, we use terrestrial lidar scanning, which offers resolutions between 0.005 and 0.05 m (Beland et al., 2019), resulting in millions of sample points per tree. Some studies do apply terrestrial lidar scanning to assess habitats in woodlands and individual trees (Ashcroft et al., 2014; Calders et al., 2020a; Krishna Moorthy et al., 2019). However, existing approaches do not generate connected branch structures of whole canopies from these data or recognise objects such as individual branches using quantitative structure models. Other studies represent individual branches and the topology of canopies using these models, but apply the results to assess wood volumes for harvesting or carbon sequestration without considering trees as habitats (Disney et al., 2018; Lau et al., 2018). Thus, datasets produced by terrestrial lidar scanning and analysed through feature recognition offer significant improvements on existing approaches.

4.3. Feature recognition linked with field observations quantifies the significance of large old trees for birds

Part three of our discussion relates field observations to feature recognition. Existing research on habitat complexity already emphasises the need to assess features that are meaningful for wildlife in addition to measuring geometrical properties such as size, variation, and scale (Kovalenko et al., 2012; Loke and Chisholm, 2022). Our workflow responds to this need by using branch angles, lengths, radii, and 3D positions to identify branch types. It then matches branches with observed animal use to determine their relative significance. This assessment integrates field observations and structural measurements to clarify why birds prefer large trees using outcomes that neither technique can provide in isolation. The resulting workflow assesses the suitability of trees by comparing totals across size classes and comparing individual trees.

Our comparison of complete tree crowns demonstrates that birds have a strong preference for larger trees because these trees offer greater numbers of highly suitable branches. For instance, our best-performing large tree (Tree 11, DBH of 115 cm) had over 600 m of highly suitable branches. This contrasts with our largest medium tree (Tree 9, DBH 79 cm), which had 266 m of such branches. This contrast is overwhelming with every other tree in the small and medium classes, which had no highly suitable branches.

Our model also confirmed that the inclination of branches relative to the horizontal plane significantly influenced their suitability for birds. This result shows that low-inclination branches are much more common in large old trees, a trait likely attributable to the loss of apical dominance in older trees (Munné-Bosch, 2018). For instance, Trees 10 (DBH 113 cm), 11 (DBH 115 cm), and 12 (DBH 121 cm) in the large class all had >500 m of lateral branches (ie. branches with angles lower than 20°), compared to as little as 14 m of such branches in smaller trees (Tree 2, DBH 30 cm). This difference shows that the abundance of lateral branches in large old trees makes them uniquely equipped to meet the needs of birds.

Moreover, while existing studies highlight that birds prefer perching on dead branches (Becker et al., 2009; Fröhlich and Ciach, 2020), our research augments this understanding. Other things being equal, we found that lateral dead branches are more likely to be highly suitable for birds. A comparison of angles across trees of varying sizes showed that the average orientation of dead branches in larger trees was nearly ten degrees closer to the horizontal plane than in smaller trees. Consequently, the average large tree contained 59 times more lateral dead branches compared to the average small tree. Examining individual large trees further illuminates this disparity. For instance, Tree 13 (DBH 115 cm) had a total 179 m of lateral dead branches. This was over three times the combined 59 m length of lateral dead branches in all medium ($n = 5$) and small ($n = 4$) trees. The length of such branches in this one large tree also surpassed the combined total of all lateral dead branches in the other large old trees ($n = 6$) put together (171 m). Although all trees produce more dead branches as they age and senesce, our modelling demonstrates that stochastic events impacting trees of similar ages and sizes can result in trees with significantly different structures. Some of these tree structures better align with bird preferences, confirming the need for techniques that can capture complex patterns within tree crowns.

Our modelling successfully extended field observations with novel numerical methods of lidar-scanning and analysis. For example, we found that, on average, a large tree has 1.5 times greater length of branches compared to a medium tree, but 7.2 times greater length of branches highly suitable for birds. These estimates indicate that larger and older trees function as keystone habitat structures because their branches have many concurrent characteristics. These attributes collectively influence which branches birds choose to visit and are rarely found together in smaller and younger trees. Measuring the lengths of all branches in a tree crown cannot be done with other techniques and this assessment shows the disproportionate significance of large old trees for birds.

4.4. Proposed methods have wider applications

In addition to the improved understanding, our modelling can support assessments of arboreal features for planning and restoration. In these domains, many models assume equivalence between younger and older trees or focus on more easily distinguishable characteristics such as hollows (Le Roux et al., 2015b). These simplified models inform development scenarios that clear mature, well-established trees and seek to offset such losses by installing nest boxes (Lindenmayer, 2017) or planting young and small trees to replace the old (Gibbons et al., 2010). To our knowledge, current assessments have not considered complex arrangement of branches in tree crowns (Seidel, 2018). Numerical evidence provided by our modelling supplies strong reasons for the retention of large old trees and preservation of their complex canopy structures.

Better numerical descriptions can also contribute to larger scale evaluations. For example, computational objects specified in our approach can serve as building blocks for a variety of ecological assessments. In carbon accounting, detailed data about individual trees can refine forest models (Disney et al., 2018). Similarly, our methods could integrate with landscape-level models, computing "kilometres of highly suitable branches" to describe woodlands at larger scales.

Furthermore, our approach can reveal how animals perceive their arboreal habitats and use this understandings to inform innovative methods in design for biodiversity (Aben et al., 2018; Dominoni et al., 2020). Detailed digital models can evaluate what a bird can see from every branch it can access. Some studies already use terrestrial lidar scans to assess how structures aid or impede animals' ability to detect hazards (Olsoy et al., 2015). Our workflow has the potential to integrate techniques such as path finding and collision detection to further strengthen the link between perception and habitat geometries (Lennon et al., 2021). Future work can link our modelling with improved observations by tracking animal movement through drones, video recordings and rapid 3D modelling (Koger et al., 2023). Quality of this data is improving swiftly (D'Urban Jackson et al., 2020).

Our techniques can apply to other microhabitats in trees, including bark or epiphyte plants (Frey et al., 2020). They can work with other sites and species including trees in urban areas, conifer plantations, and exceptionally large individual organisms surviving in undisturbed forests (Malhi et al., 2018). Broader still, these approaches can be adapted to work with other important habitat structures including reefs and rocks (Hunter et al., 2017). Beyond efforts to understand existing patterns of habitation, they can also inform designs of artificial habitats in degraded landscapes (Holland and Roudavski, n.d.; Mirra et al., 2022; Roudavski, 2021).

5. Conclusion

This study addresses the acute need to understand and measure the significance of large old trees. Such understanding is lacking because tree canopies are complex and assessments typically have coarse resolution. In response, our study employed an innovative approach that combined field observations of birds with terrestrial lidar scans and computational feature-recognition. The resulting modelling could describe habitats provided by trees at an unprecedented level of detail. To obtain such detailing, we first observed birds at 62 trees and measured characteristics of visited branches. We then used angle, diameter, state (living or dead), and diameter at breast height to develop a generalised linear mixed model that could predict which types of branches birds are more likely to visit. To extend these predictions, we calculated angles, diameters, and states of 78,006 branch objects in lidar scans of 16 trees. By combining the two models, we demonstrated that large old trees have branch structures that do not occur in smaller, younger trees. Our comparative modelling estimated that the length of highly suitable branches in large trees was seven times greater than in medium trees, while small trees possessed no highly suitable branches. Our methods can apply to a variety of sites and work with complex habitat structures other than trees. To conclude, this work contributes to knowledge by developing a novel approach to the evaluation of complex habitat structures and providing an improved understanding of the large old trees' disproportionate significance as habitats for birds.

Credit authorship contribution statement

Alexander Holland generated the dataset of trees and developed the feature recognition workflow used to produce the results. Phil Gibbons undertook the bird surveys and processed the data identifying bird use. Alexander Holland developed the literature review, designed the research study, and drafted the text. Stanislav Roudavski devised and led the overarching research program. Phil Gibbons, Stanislav Roudavski and Jason Thompson guided the conception and design of the experiment and contributed to the article writing and editing. All authors approved the final version of the manuscript.

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

Source data and code for data preparation, statistical analyses and figures are available at https://github.com/alexrfholland/assessing-trees-for-birds

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110507.

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