We thank reviewer for acknowledging the impact of this paper and their comments which we have discussed below and think have significantly improved the manuscript.

2.1 I think this article's first and foremost improvement point is that the research goal is not clear and in-depth enough.

We apologise for a lack of clarity here, and agree that the twin goals of methodology comparison and ecological insight are not presented in as clear a manner as they could be. We have edited the wording in section 1.3 to improve their readability and enhance the communication of their importance (L132-133):

"The aims of this study are twofold: the first aim is to compare three TLS methods for estimating PAI with traditional DHP. The second aim of this study is to use TLS to understand drivers of individual tree α variation."

2.2 The presentation of the results is not complete, which makes it difficult for readers to capture their needed information, such as the WAI variation trend (functions) among 5 tree species related to their height and density.

We apologise that our analysis of WAI was not clear to the reviewer. We chose to compare methods based on PAI estimates, and not WAI or LAI, to avoid introducing additional processing steps and complexity and therefore to more directly compare the chosen methodological approaches. Differences in PAI between different TLS and DHP estimates can be attributed to differences in processing approaches, whereas comparison of WAI introduces additional error from separation approaches.

To improve clarity, we have added the following (L241-242):

"We chose to compare PAI values rather than WAI or LAI as each method corrects for non-photosynthetic elements in different ways and would introduce bias, limiting the ability to directly compare metrics."

See also our response to comment 2.4 below.

2.3 Referring to the DHP results, authors evaluated the error of WAI and PAI analyzed by point clouds. I would like to know if the authors use the TLS data to improve the LAI evaluation accuracy. TLS can support assessing the single tree and plot-level WAI more accurately.

We agree completely that the combination of TLS and DHP might improve analyses, and this has been developed in methods not tested in this paper (e.g. Kamoske et al., 2019).

Here we did not use the two datasets together, preferring instead to retain the ability to compare them as independent estimates of the indices of interest. We note that neither should be viewed as the 'truth', and therefore using them in combination could introduce additional biases that would be challenging to disentangle. Nevertheless, others could use our data to perform the analyses suggested.

2.4 More importantly, whether the WAI of different Mediterranean trees has similarities between the same species, as well as providing specific information (maybe list in thematic tables to show the relationship among species, tree height, density, and PAI), will make readers benefit greatly. I think the measured data of this study can

support this research goal, while they are not fully presented in the current edition.

Although these are not the focus of this study, we agree that additional information could prove useful to some readers. We thank the reviewer for their suggestion of including WAI analysis, which we think has significantly improved the manuscript. We have added Figure C2 and Tables C3, C4 to the supplementary information and refer to this in the main manuscript, section 3.4 (L320 – 322):

"To understand drivers of variance in WAI we carried out additional analysis to test the relationship between WAI and species, height, CAI and PAI, and presented these results in Appendix C."

2.5 In addition, the presentation of the results is incomplete. I did not find the location, site conditions and tree species appearance of the measured plots shown in the manuscript.

We apologise for this omission. This information is presented in the cited study Owen et al. (2021), but we have added a detailed site map to the supplementary materials, Figure B1, which is referred to in L145 of the main text.

Please see also our response to comment 2.14

2.6 The segmentation results of different tree species and the statistical information on PAI and WAI of trees grown in different site conditions were also not provided.

We thank the reviewer for their comment and apologise for lack of clarity around the segmentation process. Individual tree segmentation was carried out by the authors for a separate study (Owen et al., 2021). We have amended section 2.5 (L218 – 222) to clarify the segmentation process and have signposted (Owen et al., 2021).

Please see also our response to comment 2.17.

2.7 In addition, critical mathematical functions and quantitative conclusions are also lacking in the current edition.

We apologise for this lack of completeness. We are not entirely clear to which functions the reviewer refers, but for reasons of clarity and brevity we chose to primarily describe the various processing methods we used rather than repeat their original descriptions, which are extensive within the cited literature. Where equations have been used from other studies, we have cited the original equation number along with the paper in-text (but see response to 2.8 below).

2.8 I suggest authors reconsider whether it is necessary to study the CAI. This parameter can be easily analyzed using remote sensing images without using TLS.

In this study we used CAI as a proxy measure of stand density (L248), which was a necessary within our model to both understand and correct for the effect of stand density on wood to plant ratio, α. Controlling for stand density (using CAI as a proxy) is important as trees growing in dense plots have lower water availability per tree (see L75-77). We chose to use CAI as Owen et al., (2021) showed that the metric is also indicative of plot-level competition and the metric accounts for crown overlap which cannot be estimated from imagery in closed forests. Furthermore, Coomes et al., (2012) showed CAI to be better than traditional metrics such as basal area, as it is more intuitive to non-specialists and strongly predicts productivity.

We apologise for the lack of clarity when describing this metric and its intended use in the study, which was also commented on by reviewer 1 (comment 1.7).

We have therefore amended our description of the key metric, CAI, for quantifying stand density and local competition in section 2.6 L245-248:

"To further understand observed drivers of variance in PAI, we tested the relationship between PAI and TLS estimated whole plot crown area index, CAI, calculated as the sum of projected crown area divided by the plot area (Owen et al., 2021)*, and a proxy measure of stand density and local competition* (Caspersen et al., 2011; Coomes et al., 2012)*, using SMA."*

2.9 Furthermore, is it applicable to use a fixed voxel size when analyzing WAI? After all, different tree species have various canopy shapes and branch structure features. Adaptive adjusting the voxel size according to the point cloud density and the branch distribution trend may be more reasonable.

We thank the reviewer for their comment on voxel size and agree that finding an appropriate voxel size a complex problem (discussed extensively in the response to the other reviewer). We chose the method of voxel classification rather than a radiative transfer approach as it has a definitive method for choosing voxel size based on matching the voxel size to the resolution of the point cloud, which was tested against voxel sizes based on individual tree leaf size, and distance of beam, using destructive samples in Li et al., (2016). Using a radiative transfer approach, the methodology for choosing the "correct" voxel size is not clear, and others' work (and our own additional, unpublished analyses) has shown that estimated PAI values are highly sensitive to voxel size choice.

We have amended our discussion of voxel size in section 1.2 to reflect the contentious debate around voxel size choice, L108-113:

"However, PAI estimates derived using the voxel method are highly dependent on voxel size (Calders et al., 2020). Using a radiative transfer approach, Béland et al., (2014) demonstrated that voxel size is conditional on canopy clumping, radiative transfer model assumptions and occlusion effects, making a single, fixed choice of voxel size within methods for all datasets impossible. To test various approaches to selecting voxel size using a voxel classification approach, Li et al., (2016) matched voxel size to point cloud resolution, individual tree leaf size, and minimum beam distance and tested against destructive samples, finding that voxel size matched to point cloud resolution had the closest PAI values to destructive samples."

To clarify our justification for use of a voxel classification approach over a radiative transfer approach, also commented on by reviewer 1, we have added to section 2.4 (L197-199):

"We chose a voxel classification approach as this method is widely applicable to a range of TLS systems and levels of processing as well as providing explicit guidance on voxel size selection, which is known to impact derived PAI estimates (Li et al., 2016).*"*

2.10 Optimizing the TLS-based WAI assessment methods, summarizing the regulation of interspecific WAI variation, and using these rules to improve the LAI

assessment will make this article more attractive to better support research in related fields.

We thank the reviewer for their suggestion of including analysis of interspecific WAI variation, which we think is a valuable addition to the paper, and refer to our response to previous comments (2.2, 2.4, 2.11), where we have included these new analyses.

Here, we've focussed on interspecific variation in alpha and PAI, rather than WAI and LAI, but recognise that there would be value in such an additional set of analyses. We agree that developing new methods to correct for WAI in LAI estimates using approaches assessed in this paper would make for exciting work, however we think that to do this well we would require further testing and validation, ideally using destructive samples or multitemporal leaf on/leaf off remote sensing data, which is beyond the scope of this paper.

The following are some detailed points. I hope they will help improve the current edition.

2.11 I suggest authors clarify their research goal in the initial section of the manuscript. As a reader, I am more interested in how to use TLS to analyze WAI. However, authors did not briefly introduce the WAI extraction methods in the abstract but focused on comparing point cloud extraction methods of PAI and LAI.

We apologise for the lack of clarity in explaining our research goals. As in our response to comment 2.1, we have restated our primary and secondary research goals in section 1.3 (L132-133).

We thank the reviewer for their suggestion of analysing WAI, which we think has significantly improved the manuscript. As for comment 2.4, we have now included this analysis. We have chosen to keep the focus on comparing α, as this value is widely discussed in the literature. We have added a statement to this effect (L234-235):

"To allow a comparison with existing literature estimating α, (Sea et al., 2011; Woodgate et al., 2016) we focused on α values."

2.12 They focused on the wood to total plant area (α). I wonder if it is feasible to measure the plant area because of the occlusion effect during scanning. TLS may be more suitable for analyzing WAI.

We apologise not clearly stating the reasons for comparing PAI rather than WAI. All remote sensing methods evaluated in this paper (three TLS methods and DHP) more directly measure PAI than WAI or LAI as sensors are measuring the whole plant. Correcting for wood/ leaf to derive WAI/ LAI requires additional processing steps, which vary according to sensor (wood/ leaf separation algorithms for TLS and image masking for DHP, as these systems are not deciduous, and therefore leaf-off scans can't be made), introducing bias and limiting our ability to compare output. We have added a statement to this effect to section 2.6 (L241-242):

"We chose to compare PAI values rather than WAI or LAI as each method corrects for non-photosynthetic elements in different ways and would introduce bias, limiting the ability to directly compare metrics."

Please see also our response to comment 2.2

We agree that occlusion is a known problem with TLS data in closed canopy forests, however we have minimised the potential occlusion effects by following a dense scanning strategy following the widely cited Wilkes et al., (2017).

2.13 Section 1.3 It will be more interesting to add some research topics on integrating the fine-scale WAI (or α) assessed based on TLS to correct the large-scale LAI extracted from the multi-source remote sensing images. Based on the high-quality field dataset, it should be feasible to use this research in optimizing the large-scale LAI distribution evaluation.

We agree this is an exciting idea and could be the focus of follow-on work. We think that the work presented and, as the reviewer points out, our dataset provides a foundation for a more robust comparison of LAI and new insights from multi-source RS datasets, but that this would be an additional methodological development beyond the scope of our current study.

Following your suggestion, we have added a comment to this effect on L429-430:

"The work presented here provides a foundation for future work combining multi-source and multi-scale remote sensing datasets to correct largescale LAI products."

2.14 In Sections 2.1 and 2.2, the location map of study plots and some images showing the scene of plots should be provided. The pictures of tree species also need to be added to show their phenotypic characteristics, which is beneficial to evaluate their drought tolerance (L323-324).

We agree with the reviewer that a location map of the study plots would be beneficial to the manuscript and thank them for the suggestion. We have therefore added a new figure, B1 to Appendix B showing the locations of plots within the two field sites, Alto Tajo and Cuellar in central Spain.

We believe that the plots used in this study are well studied and documented in the literature and therefore a detailed description of individual plot characteristics would repeat information already available. We have added signposting to this is section 2.1 (L143-144):

"We collected TLS and DHP data from 29 plots in Alto Tajo Natural Park (40°41'N 02°03'W; FunDIV plots; see Baeten et al., (2013) for detailed description of plots)"

The five focus species of this manuscript are widely studied and known species and therefore believe that adding individual images of each species is unnecessary.

2.15 L 191 When setting this threshold (> 0 points) to identify the filled voxels, did you filter noisy points out from the tree TLS datasets? It is not easy to identify and filter all noise in TLS data. I am worried the noise would lead to a lower P_{gap} and cause inaccurate LAI and PAI.

We apologise for not making explicit the noise filtering process of our data. We denoised individual-tree point clouds using height dependant statistical filtering as outlined in Owen et al., (2021), and combined individual tree point clouds into whole plots. We have added a statement to this effect to section 2.4 (L199-200):

"We re-combined individually segmented trees, filtered for noise using a height-dependent statistical filter (see Owen et al., 2021) back into whole plot point clouds"

While any remaining noise may indeed lead to lower P_{gap}, we followed standard processing procedure for this voxel classification method outlined in Hosoi and Omasa, (2006) and tested using destructive samples in Li et al., (2016). Similarly, we followed standard protocol in the published literature for the other two methods (LiDAR Pulse and 2D intensity Image), and therefore consider that our work is a fair representation of each methods' ability to accurately derive PAI and allows a comparison of each methods' merits and drawbacks.

2.16 L203-204 Some structure features of woody and foliage materials can be analyzed based on the pointset-, height bin-, and patch-based models. Please revise this sentence.

We apologise for the lack of clarity in this statement, and thank the reviewer for their suggestion. What we meant to say was that the voxel-based approach was the only method compared in this study capable of analysing PAI, WAI and LAI of segmented individual tree point clouds. We have reworded to make this clear and L215-216 now reads:

"As the only method using multiple co-registered scans, the Voxel-Based method is the only method compared in this study capable of deriving PAI, WAI and LAI of segmented individual tree point clouds."

2.17 L206 The principle of TLS segmentation methods needs to be briefly introduced before the voxelization step. It is beneficial to improve the readability of the manuscript.

We thank the reviewer for their suggestion of providing an explanation of the segmentation process. Trees were not segmented for this paper; we used data that had already been segmented by the authors for a separate study (Owen et al., 2021), and we apologise for the lack of clarity. We have amended the description of tree segmentation in section 2.5 (L218 – 221):

"We used individual tree point clouds downsampled to 0.05 m, to aid computation time, and segmented using the automated tree segmentation program treeseg (Burt et al., 2019), implemented in C++, by Owen et al., (2021) for that study. Individual segmented tree data are available in Owen et al., (2022)."

2.18 L216 How to analyze the WAI after voxelizing woody point clouds? Some details should be introduced, which is key to calculating É‘ .

We thank the reviewer for their comment and apologise for the lack of clarity in our methods for calculating individual tree WAI. Individual tree WAI was calculated in the same way (voxel classification method) as individual tree PAI, but using the wood-only cloud from the wood – leaf separation step. We have changed L232-233 in section 2.5:

"In the same way as for PAI, we calculated WAI using the separated wood point cloud within the projected crown area of the whole tree (Figure 2d; using the whole crown and not just the wood point cloud)"

2.19 L225 Why explore the relationship between PAI and CAI in this study? The CAI assessment seems to deviate from the research topic, as it is not highly related to LAI and WAI but to the crown projection area, except the canopy gap area. Moreover, using images for CAI analysis is sufficient.

We apologise for not clearly stating our justification for the use of CAI in this study. CAI is used in this study as an indicative measure of both stand density and local competition, and is included to both explore how PAI is affected by competition, but also to correct for anticipated competitive affects that would otherwise impact our conclusions on species' differences in alpha. We thank the reviewer for their comment, and have amended our manuscript section 2.6 (L245 – 248).

Please see also our response to comment 2.8.

In closed canopies or canopies with crown overlap imagery would not capture CAI, since CAI is calculated using the sum of all projected crown area, not only that visible from imagery. We used TLS to measure CAI as CAI estimates are generated from the sum of all tree crown projected area and so requires individual tree measurements, either from segmented TLS or from ground measurements.

2.20 L245 As shown in Figure 3, PAI estimated using the LiDAR Pulse method more strongly agreed with DHP PAI than the Intensity Image method. However, I found their correlation (R^2) is not particularly significant.

We believe this is a misreading of our meaning, and therefore apologise for not using clear language in reporting our statistical results. We have therefore amended section 3.1 (L266-268):

"Of the two single scan TLS methods tested (LiDAR Pulse method and 2D Intensity Image method), we found that the relationship between PAI estimated using the LiDAR Pulse method and DHP PAI, had a higher R^2 than the 2D Intensity Image method"

2.21 L248 Please carefully recheck the description of the results is correct according to Figure 3. As shown in Figure 3a, the Pulse-based method overestimates the PAI, while the intensity-based method underestimates the PAI.

We apologise for the lack of clarity in explaining these results and meant to say that both methods underestimate relative to DHP at larger values. We have therefore amended the sentence in section 3.1 (L270 -271):

"At larger PAI values, relative to DHP, both TLS methods underestimated PAI compared with DHP (Figure 3b)."

2.22 L264 You did not label Voxel-Based PAI in Figure 3. Do you mean the TLS PAI

We apologise for the lack of clarity in this sentence. Section 3.2, L286 is referring to whole plot plant area index (Figure 4), which does include Voxel-Based PAI. We have now removed the reference to Figure 3 from this sentence.

2.23 L269 Maybe you did not set a suitable threshold when defining blank voxels. Merely my speculation!

We thank the reviewer for their speculation on why we may be experiencing overestimation from Voxel-Based PAI estimates. We followed standard protocol as described in the published literature for the Voxel-Based, LiDAR Pulse and 2D Intensity Images methods, which has allowed us to draw a fair comparison between derived PAI values from each method. Although threshold values could be influencing PAI estimates, we have made a 'best choice' to classify non-zero point containing voxels as vegetation and believe that, while important research, further exploration of threshold values would be beyond the scope of this study.

Please see also response to comment 2.15.

2.24 L282 and 257 You forget to mark the 1:1 dash line in these figures.

This graph (Figure 4b) presents the variation in PAI against CAI in order to understand how competition and stand density affects PAI so we would not assume a 1:1 relationship. Dashed line on Figure 3b is at 0 to highlight systematic variation in the residuals.

We apologise for the lack of clarity and have amended L308 to make this clearer:

"Dashed line in panel a represents 1:1 relationship"

In Figure 3b, the dashed line represents 0, as this panel is showing the relationship between TLS residuals and DHP PAI. We apologise for the lack of clarity and have amended L280:

"Dashed line in panel a represents 1:1 relationship."

And L281:

"dashed line in panel b represents 0"

2.25 Although authors used the published woody-and-foliage separation methods, it is necessary to display some examples of TLS separation results scanned from diverse plots grown with different species. Due to the lack of validation data, it may be challenging to evaluate the segmentation accuracy. However, presenting the separation results is still available to support visual evaluation.

We agree that showing an example visual assessment of wood/ leaf separation is beneficial to the reader and have included an example of a wood/ leaf separated *P. sylvestris* in Figure 2, panels a and b. We have now included signposting in the figure caption, L212-213:

"Panels a and b show wood and leaf separation of an example P. sylvestris, carried out using TLSeparation (Vicari et al., 2019)."

We also note that wood – leaf separation was carried out by the authors for a separate published study (Owen et al., 2021). We apologise for the lack of clarity and have changed our description of the wood – leaf separation process accordingly in section 2.5 (L223-225). Please see our response to comment 2.33 below.

2.26 It is not easy to accurately separate the branch and leaf point clouds of trees except those of broadleaf. More importantly, I am worried about whether it is applicable to use the same voxel size to calculate the WAI of different tree species, which is crucial to the conclusion.

Although we agree it may theoretically be more difficult to separate wood and leaf in needleleaf trees, we note that TLSeparation was developed with applicability to both types of trees, with separation difficulties attributable to scanning strategy rather than separation algorithm (Vicari et al., 2019b). We note that this problem was minimised to the best of our ability in our dataset, as we followed a dense scanning strategy as outlined in Wilkes et al., (2017). As for comment 2.25 above, we have included an example visual assessment of a wood – leaf separated (needleleaf) *P. sylvestris* and included signposting in L212-213:

"Panels a and b show wood and leaf separation of an example P. sylvestris, carried out using TLSeparation (Vicari et al., 2019)."

2.27 L294-297 These sentences are not clear. How to assess tree-specific drought tolerance? You would better add some description about its evaluation methods and list the metrics to evaluate the drought tolerance of different tree species in this figure and the related references.

We agree the source of drought tolerance rankings needs to be clear and apologise for omitting this in the figure caption. Drought tolerance are taken from the widely-cited Niinemets and Valladares, (2006). We have amended L326:

"Drought tolerance rankings are taken from Niinemets and Valladares, (2006)"

2.28 In section 4.1, why did you discuss the plot-scale CAI variation? The topic of this section is comparing diverse approaches to deriving PAI.

We apologise for the lack of clarity around the role of CAI in this study. As CAI was used as an indicative measure of stand density and local competition, it was discussed in this section as plots with higher CAI (and therefore greater stem density) showed greater variation in estimated PAI values from each method/ sensor. We note that we have now updated our description of CAI and its role in this study in section 2.6 (L245 – 248) and hope that the discussion in section 4.1 is now more clear.

Please see also our response to comment 2.8.

2.29 The title of Section 4.2 is a phenomenon that you need to analyze. Sections 4.2 and 4.3 still belong to Section 4.1 to discuss the LiDAR-extracted metrics with that of DHP.

The titles of sections 4.2 and 4.3 were intended to emphasise findings of particular interest and relevant to the initial aims of this manuscript. We agree, however, with the reviewer that these sections belong with 4.1 and have removed these section titles to make this more clear.

2.30 L320 According to the field data and Figure 3, what is a very low PAI value? Providing a quantitative indicator will significantly improve the manuscript's readability than using adjective words.

We thank the reviewer for the comment and agree that more quantitative language would improve the manuscript. We have therefore amended L342 to say:

"except at very low PAI values ($PAI_{TLS} < 0.5$)."

2.31 L348 The highest R^2 does not show a strong correlation.

We thank the reviewer for their comment and agree that we have not used clear statistical language. We have therefore changed the wording in L377 – 378:

"The relationship between the LiDAR Pulse method and TLS derived CAI had the highest R^2"

2.32 L374 This sentence is not clear. "Although species explain some variation in α, tree height and plot CAI were stronger predictors for all species…." According to the principle of these parameters, it is hard for me to agree that CAI and WAI have a strong correlation.

We agree with the reviewer that we have not used clear statistical language. We have therefore changed this sentence in section 4.5 (L403):

"Although species had a weak relationship with α, tree height and plot CAI had a statistically significant relationship with α ($p<0.001$ – $p<0.05$) for all species, showing the importance of local stand structure on leaf and woody allocation."

2.33 L390-392 This is an interesting point. I prefer you to provide some figures and statistical information to prove your finding, especially in different plots with variable growing patterns (growing density, CAI, and WAI related to the tree species, as you mentioned in the Conclusion section). It is beneficial to deepen this study topic.

We thank the reviewer for finding this point interesting and their suggestion of including quantitative results of wood – leaf separation. The discussion point the reviewer refers to is a reference to the published paper describing the wood – leaf separation algorithm. Due to the lack of validation data, evaluating quantitatively the effectiveness of the wood – leaf separation algorithm over the different tree sizes/ growing conditions is not possible for this study.

We note that the wood leaf separation process was carried out by the authors, for a separate study (Owen et al., 2021), in which the results are discussed in more detail and segmented tree files made available online, cited as Owen et al., (2022). We apologise for the lack of clarity here and have reworded our description of the wood – leaf separation process in section 2.5 (L223-229):

"To estimate PAI, WAI and α for each tree, we used individual tree point clouds wood – leaf separated by Owen et al., (2021) using the open source Python library TLSeparation (Vicari et al., 2019a)*, and then used the separated wood point clouds to calculate WAI. TLSeparation assigns points as either leaf or wood, iteratively looking at a predetermined number of nearest neighbours (knn). The knn of each iteration is directly dependent on point cloud density, since high density point clouds will require higher a knn* (Vicari et al., 2019a)*. The utility package in TLSeparation was used to automatically detect the optimum knn for each tree point cloud."*

2.34 L 398 I agree that correcting WAI can improve the LAI assessment. The TLS-extracted data can support calibrating LAI based on WAI and PAI. The WAI may be similar among single trees of the same tree species. According to your results, the WAI shows a more evident relationship to tree height and stand density. I think the assessed WAI and plot-level PAI can be used to correct regional LAI for the plot or large-scale forests that were growing with limited tree species.

We agree with the reviewer that interspecific WAI values will be of interest to some readers and thank the reviewer for their suggestion, which we think has significantly improved our manuscript. We have included these additional analyses in Appendix C as also discussed in response to comments 2.4 and 2.10. We hope this work sparks further research on improving LAI estimates at large scale.

Some text errors that needed to be corrected are listed as follows:

Thank you for pointing out these errors.

- **Do not use an abbreviation in the title of your manuscript, as many readers in other fields do not know the meaning of TLS.**

We agree with the reviewer that abbreviations should not be used in titles and have amended our title accordingly.

- **I suggest authors unify the reference format throughout their manuscript. Different citation formats appear in the same paragraph may confuse readers.**

We thank the reviewer for their comment and have checked and corrected referencing throughout.

- **L135 What are FunDIV plots?**

Added "Functional Diversity"

- **L142 I do not understand "altitudinal gradient 840 – 1400 m.a.s.l.".**

Changed to "altitudinal range"

- **L167 compare –ï¼ž compared**

Changed to "compared"

- **L169 and 180 Please note the font size of the subscript in the Pgap. This abbreviation can also be used in line 162.**

Changed to subscript and moved abbreviation to first use.

- **L176 Please add a comma to this sentence.**

Comma added

- **L199 Where are the solid black voxels in Figure 2?**

Changed to "Coloured voxels (green represents leaf and brown represents wood) are filled voxels and grey lines are empty voxels."

- **L209 wood only point clouds?**

Change to “separated wood cloud”

- **L210 TLSeparation classifies points as leaf or wood? This sentence is not clear.**

Changed to “*TLSeparation* assigns points as either leaf or wood”

- **L219 TLS PAI and DHP PAI? (Using PAI_{TLS} and PAI_{DHP} instead)**

Changed throughout.

- **L234 Please add a comma to this sentence.**

Comma added.

- **L246-248, L264-265 You can mark these metrics in the insets of Figure 3.**

We think it is important to refer to statistical results in the main text of the manuscript for emphasis, however have included them in the figure captions as well for completeness.

- **Points in Figure 3 can be denoted as different marks or colors, such as circles or crosses, red or blue, to make this chart clearer (like the style of Figure 4).**

Changed to circles and triangles.

- **L262 Please unify the term throughout the manuscript. I think TLS whole plot PAI means TLS PAI(PAI_{TLS}).**

Changed to “whole plot PAI_{TLS}”

- **L274-276 You would better mark these metrics in the subfigures of Figure 4.**

We think it is important to refer to statistical results in the main text of the manuscript, however have included them in the figure captions as well for completeness.

- **In Figures 3 and 4, please delete the unit of PAI. The PAI, LAI and WAI are all ratio-type parameters (no need to denote unit).**

Removed units and changed axis labels to new subscript (PAI_{TLS} / PAI_{DHP})

- **L318 TLS – DHP comparisons?**

Changed to “studies comparing PAI_{TLS} with PAI_{DHP}”

- **In this article, authors used lots of open-source software to support their analysis. I suggest they list all applicable packages and download links to make readers easy to use these tools.**

We thank the reviewer for their suggestion of providing a summary of all open-source software used for this manuscript. We have cited all the software used in text and in the reference list at the end of the manuscript. We believe that citing packages in the main bod, readers are able to get a more detailed and contextualised explanation of the use in individual software packages.

- **Please carefully check the format of all references according to the manuscript preparation guidelines and the latest published papers in Biogeosciences. The current reference format needs to be optimized.**

We thank the reviewer for their comment and have checked the reference format.

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Quantifying vegetation indices using Terrestrial Laser Scanning: methodological complexities and ecological insights from a Mediterranean forest

William Rupert Moore Flynn[1], Harry Jon Foord Owen[2], Stuart William David Grieve[1,3] and Emily Rebecca Lines[2]

[1]School of Geography, Queen Mary University of London, Mile End Rd, Bethnal Green, London E1 4NS

[2]Department of Geography, University of Cambridge, Downing Place, Cambridge, CB2 3EN

[3]Digital Environment Research Institute, Queen Mary University of London, New Road, London, E1 1HH

Correspondence to: W. R. M. Flynn (w.r.m.flynn@qmul.ac.uk)

Abstract. Accurate measurement of vegetation density metrics including plant, wood and leaf area indices (PAI, WAI and LAI) is key to monitoring and modelling carbon storage and uptake in forests. Traditional passive sensor approaches, such as Digital Hemispherical Photography (DHP), cannot separate leaf and wood material, nor individual trees, and require many assumptions in processing. Terrestrial Laser Scanning (TLS) data offer new opportunities to improve understanding of tree and canopy structure. Multiple methods have been developed to derive PAI and LAI from TLS data, but there is little consensus on the best approach, nor are methods benchmarked as standard.

Using TLS data collected in 33 plots containing 2472 trees of five species in Mediterranean forests, we compare three TLS methods (*LiDAR Pulse*, *2D Intensity Image* and *Voxel-Based*) to derive PAI and compare with co-located DHP. We then separate leaf and wood in individual tree point clouds to calculate wood to total plant area (α), a metric to correct for non-photosynthetic material in LAI estimates. We use individual tree TLS point clouds to estimate how α varies with species, tree height and stand density.

We find the *LiDAR Pulse* method agrees most closely with DHP, but is limited to single scan data so cannot determine individual tree α. The *Voxel-Based* method shows promise for ecological studies as it can be applied to individual tree point clouds. Using the *Voxel-Based* method, we show that species explain some variation in α, however, height and density were ~~stronger~~ better predictors.

Our findings highlight the value of TLS data to improve fundamental understanding of tree form and function, but also the importance of rigorous testing of TLS data processing methods at a time when new approaches are being rapidly developed. New algorithms need to be compared against traditional methods, and existing algorithms, using common reference data. Whilst promising, our results show that metrics derived from TLS data are not yet reliably calibrated and validated to the extent they are ready to replace traditional approaches for large scale monitoring of PAI and LAI.

1 Introduction

Terrestrial Laser Scanning (TLS) generates high-resolution 3D measurements of whole forests and individual trees (Burt et al., 2018; Disney, 2018), leading to the development of completely new monitoring approaches to understand the structure and function of ecosystems (Lines et al., 2022). Unlike traditional passive sensors, TLS can estimate plant, wood and leaf area indices (PAI; WAI; LAI) for both whole plots and individual tree point clouds (Calders et al., 2018), and is unaffected by illumination conditions. This has led to the development of several methods for processing TLS data to extract the key metrics PAI, WAI and LAI (e.g. Hosoi and Omasa, 2006; Jupp et al., 2008; Zheng et al., 2013). However, intercomparison of algorithms and processing approaches to derive the same metrics from different TLS methods are lacking.

Leaf Area Index (LAI), defined as half the amount of green leaf area per unit ground area (Chen and Black, 1992), determines global evapotranspiration, phenological patterns and canopy photosynthesis, and is therefore an essential climate variable (ECV), as well as a key input in dynamic global vegetation models (Sea et al., 2011; Weiss et al., 2004). Accurate measurements of LAI, WAI and PAI have historically been derived from labour intensive destructive sampling (Baret et al., 2013; Jonckheere et al., 2004), so over large spatial or temporal scales these can only be measured indirectly, typically with remote sensing. Large-scale remote sensing, using spaceborne and airborne instruments, has been widely used to estimate LAI over large areas (Pfeifer et al., 2012), but requires calibration and validation using in situ measurements to constrain information retrieval (Calders et al., 2018). Non-destructive in situ vegetation index estimates have historically been made by measuring light transmission below the canopy and using simplifying assumptions about canopy structure to estimate the amount of intercepting material (e.g. Beer-Lambert law; Monsi and Saeki, 1953). The most common method, Digital Hemispherical hotography (DHP; Figure 1a), requires both model assumptions and subjective user choices during data acquisition and processing in order to estimate both PAI and LAI (Breda, 2003). DHP images are processed by separating sky from canopy, but not photosynthetic from non-photosynthetic vegetative material, so additional assumptions are needed to calculate either LAI or WAI (Jonckheere et al., 2004; Pfeifer et al., 2012). Separation of LAI from PAI can be achieved by removing or masking branches and stems from hemispherical images (e.g. Sea et al., 2011; Woodgate et al., 2016), but is not reliable when leaves are occluded by woody components (Hardwick et al., 2015). An alternative approach is to take separate DHP measurements in both leaf on and leaf off conditions, and derive empirical wood to plant ratios (WAI/PAI, α) (Leblanc and Chen, 2001), but this is not always practical, for example in evergreen forests. The difficulty of separation means that studies often omit correcting for the effect of WAI on optical PAI measurements altogether (Woodgate et al., 2016), but since woody components in the forest canopy can account for more than 30% of PAI (Ma et al., 2016) this can introduce overestimation. Further, although DHP estimates of LAI or PAI are valuable both for ecosystem monitoring and developing satellite LAI products (Hardwick et al., 2015; Pfeifer et al., 2012), they are limited to sampling only at a neighbourhood or plot level , Weiss et al., 2004), and cannot be used to measure individual tree LAI except for open grown trees (Béland et al., 2014).

The ratio of wood to total plant area, α, is known to be dynamic, changing in response to abiotic and biotic conditions. For example, the Huber value (sapwood to leaf area ratio, a related measure to α) may vary according to water availability (Carter and White 2009). Leaf area may therefore be indicative of the drought tolerance level of a tree, with more drought tolerant species displaying a lower leaf area, reducing the hydraulic conductance of the whole tree and therefore increasing its drought tolerance (Niinemets and Valladares, 2006). α has been hypothesised to increase with the size of a tree in response to the increased hydraulic demand associated with greater hydraulic resistance of tall trees (Magnani et al., 2000) and higher transpiration rates of larger LAI (Battaglia et al., 1998; Phillips et al., 2003). Stand density may also impact α (Long and Smith, 1988; Whitehead, 1978), as increased stand level water use scales linearly with LAI (Battaglia et al., 1998; Specht and Specht, 1989), reducing water availability to individual trees competing for the same resources (Jump et al., 2017). Large scale quantification of α or Huber value, however, is difficult as studies usually rely on a small number of destructively sampled trees (e.g. Carter and White, 2009; Magnani et al., 2000), litterfall traps (e.g. Phillips et al., 2003) or masking hemispherical images (e.g. Sea et al., 2011; Woodgate et al., 2016). These approaches are only applicable on a small to medium scale, and in the case of image masking, cannot differentiate between individuals. Variation in α, for example by species and or stand structure, is therefore largely unknown.

1.2 TLS methods for calculating PAI, LAI and WAI

TLS methods for extracting PAI, LAI and WAI can be broadly categorised into two types: (1) LiDAR return counting, using single scan data (e.g., the *LiDAR Pulse* method; Jupp et al., 2008, and *2D Intensity Image* method; Zheng et al., 2013) and (2) point cloud voxelisation, usually using co-registered scans (e.g., the *Voxel-Based* method; Hosoi and Omasa, 2006).

The *LiDAR Pulse* method (Jupp et al., 2008; Figure 1b) estimates gap fraction (~~*Pgap*~~P_{gap}) using single scan data, as a function of the total number of outgoing LiDAR pulses from the sensor and the number of pulses that are intercepted by the canopy. This method, which eliminates illumination impacts associated with the use of DHP (Calders et al., 2014), has been implemented in the python module, *PyLidar* (www.pylidar.org) and the R package, *rTLS* (Guzman, et al. 2021). Using the *LiDAR Pulse* method, Calders et al. (2018) compared ~~TLS PAI~~ PAI estimates from two ground-based passive sensors (LiCOR LAI-2000 and DHP) with TLS data collected with a RIEGL VZ-400 TLS in a deciduous woodland, and found the two passive sensors underestimated PAI values compared to TLS, with differences dependent on DHP processing and leaf on/off conditions.

The *2D Intensity Image* method (Zheng et al., 2013; Figure 1c), also uses raw single scan TLS point clouds, but unlike the *LiDAR Pulse* method, this approach converts LiDAR returns into 2D panoramas where pixel values represent intensity. PAI is estimated by classifying pixels as sky or vegetation, based on their intensity value, to estimate P_{gap}~~*Pgap*~~, and then applying Beer-Lambert's law. As for the *LiDAR Pulse* method, this approach has been shown to generate higher PAI estimates than DHP (Calders et al., 2018; Woodgate et al., 2015; Grotti et al., 2020), with differences attributed to the greater pixel resolution and viewing distance of TLS resolving more small canopy details (Grotti et al., 2020).

The *Voxel-Based* method (Figure 1d) estimates PAI by segmenting a point cloud into voxels and either simulating radiative transfer within each cube (Béland et al., 2014; Kamoske et al., 2019), or classifying voxels as either containing vegetation or not, and dividing vegetation voxels by the total number of voxels (Hosoi and Omasa, 2006; Itakura and Hosoi, 2019; Li et al., 2017). Crucially, this method may be applied to multiple co-registered scan point clouds and so can be used to calculate PAI for both whole plots and individual, segmented TLS trees. However, PAI estimates derived using the voxel method are highly dependent on voxel size (Calders et al., 2020). Using a radiative transfer approach, Béland et al., (2014) demonstrated that voxel size is dependent on canopy

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clumping, radiative transfer model assumptions and occlusion effects, making a single, fixed choice of voxel size within methods for all datasets impossible. To test various approaches to selecting voxel size using a voxel classification approach, ~~(~~Li et al., (2016) matched voxel size to point cloud resolution, individual tree leaf size, and minimum beam distance and tested against destructive samples, finding that voxel size matched to point cloud resolution had the closest PAI values to destructive samples.

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The *LiDAR Pulse* method and *2D Intensity Image* method both use single scan data. However, to generate robust estimates of canopy properties that avoid errors from occlusion effects, multiple co-registered scans taken from different locations are likely needed (Wilkes et al., 2017). Further, both these methods require raw unfiltered data to accurately measure the ratio of pulses emitted from the scanner and number of pulses that are intercepted by vegetation. This means “noisy” points caused by backscattered pulses (Wilkes et al., 2017) are included in analyses, potentially leading to higher PAI estimates. However, the *LiDAR Pulse* and *2D Intensity Image* methods may introduce fewer estimation errors compared DHP, which is influenced by differences in sky illumination conditions and camera exposure (Weiss et al., 2004).

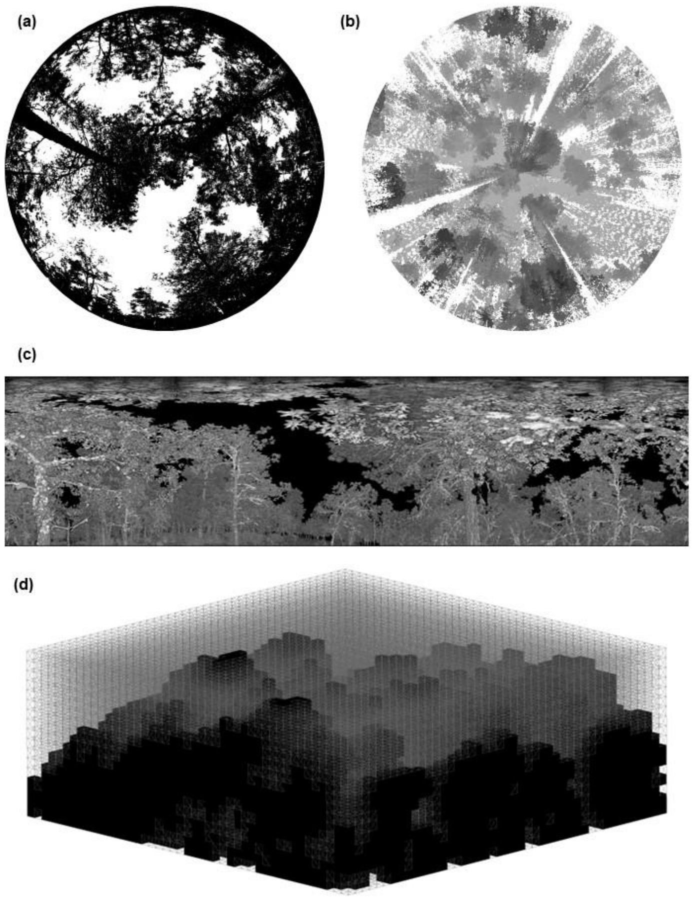

Figure 1: Methods for PAI estimation applied in this study: (a) a binarised digital hemispherical photograph (DHP), (b) TLS raw single scan point cloud, used within the LiDAR Pulse method (Jupp et al., 2008)**. Image shows a top-down view of raw point cloud and greyscale represents low (grey) and high (black) Z values, (c) TLS 2D intensity image for the 2D Intensity Image method** (Zheng et al., 2013)**, (d) Voxelised co-registered whole plot point cloud for the Voxel-Based method** (Hosoi and Omasa, 2006)**, showing a representative schematic of cube voxels with edge length of 1m, voxelised using the *R* package *VoxR*** (Lecigne et al., 2018)**. Solid black voxels are classified as containing vegetation (filled) and voxels outlined with grey lines are voxels classified as empty.**

1.3 Scope and aims

The aims of this study are twofold: the first aim is to compare three TLS methods for estimating PAI with traditional DHP. The second aim of this study is to use TLS to drivers of individual tree α variation.

In this study we use a dataset of 528 co-located DHP and high-resolution TLS scans from 33 forest plots to compare DHP derived PAI (PAI_{DHP}) with estimates from three methods to estimate PAI from TLS data (PAI_{TLS}): the *LiDAR Pulse* method; the *2D Intensity Image* method and the *Voxel-Based* method (Figure 1). We use a dataset collected from a network of pine/oak forest plots in Spain (Owen et al., 2021) and ask **(1)** are the three TLS methods able to reproduce ~~DHP PAI~~PAI_{DHP} estimates at single scan and whole plot level? **(2)** does α, calculated from the *Voxel-Based* method on individual tree point clouds, vary with species and tolerance to drought; and **(3)** does α scale with height and stand density?

2. Methods

2.1 Study site

We collected TLS and DHP data from 29 plots in Alto Tajo Natural Park (40°41′N 02°03′W; FunDIV (Functional Diversity) plots; see Baeten et al., (2013) for detailed description of plots) and four plots in Cuellar (41°23′N 4°21′W) in June - July 2018 (see Owen et al., (2021) for full details) (Figure B1). Plots contained two oak species: semi-deciduous *Q. faginea* and evergreen *Q. ilex,* and three pine species: *P. nigra*, *P. pinaster* and *P. sylvestris*. *P. sylvestris* is the least drought tolerant species, followed by *P. nigra*, *Q. faginea*, *Q. ilex*; shade tolerance follows the same ranking (Niinemets and Valladares, 2006; Owen et al., 2021). Although not quantitatively ranked, *P. pinaster* has been shown to be very drought tolerant, appearing in drier areas than the other species (Madrigal-González et al., 2017). The area is characterised by a Mediterranean climate (altitudinal ~~gradient~~ range 840 – 1400 m.a.s.l.) (Jucker et al., 2014; Madrigal-González et al., 2017). In addition to the five main canopy tree species, plots contained an understory of *Juniperus thurifera* and *Buxus sempervirens* (Kuusk et al., 2018).

2.2 Field protocol

In each of the 33 30 x 30 m plots we collected TLS scans on a 10 m grid, making 16 scan locations following Wilkes et al., (2017) to minimise occlusion effects associated with insufficient scans. We used a Leica HDS6200 TLS set to super high resolution (3.1 x 3.1mm resolution at 10 m with a beam divergence of ≤ 5 mm at 50 m; scan time 6m 44 s; see Owen et al., (2021)). At each of the 528 scan locations and following the protocol in Pfeifer et al., (2012), we captured co-located DHP images with three exposure settings (automatic and ± one stop exposure compensation), levelling a Canon EOS 6D full frame DSLR sensor with a Sigma EX DG F3.5 fisheye lens, mounted on a Vanguard Alta Pro 263AT tripod.

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2.3 Calculation of single scan and whole plot PAI using DHP data

For each of the red-green-blue (RGB) DHP images we extracted the blue band for image thresholding, as this best represents sky/vegetation contrast (Pfeifer et al., 2012). For each plot, we picked the exposure setting that best represented sky/ vegetation difference based on pixel brightness histograms of four sample locations indicative of the plot. We carried out automatic image thresholding using the Ridler and Calvard method (1978), to create a binary image of sky and vegetation, avoiding subjective user pixel classification (Jonckheere et al., 2005). We calculated PAI from the binary image, limiting the field of view to a 5º band centred on the hinge angle of 57.5º (55º – 60º). The hinge angle has a path length through the canopy twice the canopy height, so the band around it is an area of significant spatial averaging taken as representative of canopy structure of the area (Calders et al., 2018; Jupp et al., 2008). From the binarised hinge angle band we calculated ~~gap fraction~~P_{gap} as the number of sky pixels divided by the total number of pixels and PAI using an inverse Beer-Lambert law equation (Monsi and Saeki, 1953). We calculated whole plot PAI as the arithmetic mean within plot scan location PAI. As this value does not correct for canopy clumping, it is better described as effective PAI, rather than true PAI (Woodgate et al., 2015). However, as the TLS and DHP methods we apply here account for canopy clumping differently, we compared effective values and here-on refer to effective PAI as PAI (Calders et al., 2018).

2.4 Calculation of single scan and whole plot PAI from TLS data

To calculate PAI using the *LiDAR Pulse* method (Jupp et al., 2008), we calculated the ~~gap fraction (~~P_{gap}~~)~~ for a single scan (Figure 1b) by summing all returned laser pulses and dividing by the number of total outgoing pulses, following Lovell et al. (2011; see Eq. 7 in that study), and then estimated PAI following Jupp et al. (2008; see Eq. 18 in that study), setting the sensor range to 5º around the hinge angle as before (55º – 60º). Single scan PAI was taken as the cumulative sum of PAI values estimated by vertically dividing the hinge region into 25 cm intervals (Calders et al., 2014). We implemented the *LiDAR Pulse* method using the open-source *R* (R Core Team, 2020) package, *rTLS* (Guzmán and Hernandez, 2021).

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To calculate PAI using the *2D Intensity Image* method (Zheng et al., 2013), we converted 3D TLS point cloud data from all 528 scan locations into polar coordinates, ~~and~~ scaled intensity values to cover the full 0-255 range (Figure 1c) and rasterised into a 2D intensity image using the open-source *R* package, *raster* (Hijmans, 2022). We cut the 2D intensity image to a 5º band around the hinge angle (55º – 60º) and classified sky and vegetation pixels in each image using the Ridler and Calvard method (1978). We calculated P_{gap} as the number of pixels classified as sky divided by the total number of pixels and derived PAI with an inverse Beer-Lambert law equation (Monsi and Saeki, 1953).

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Following the same approach as applied to our DHP data, we calculated whole plot PAI for the *LiDAR Pulse* and *2D Intensity Image* methods as the arithmetic mean of within plot single scan PAI estimates.

To calculate PAI using the *Voxel-Based* method, we followed a voxel classification approach (Hosoi and Omasa, 2006), downsampling the point cloud to 0.05 m to aid computation time and matching the voxel size to the resolution of the point cloud ~~(0.05 m)~~, following ~~(~~Li et al., (2016), who showed that matching the voxel size to the point cloud point to point minimum distance (resolution) increases accuracy as small canopy gaps are not included in voxels classified as vegetation. We chose a voxel classification approach as this method is widely applicable to a range of TLS systems and levels of processing as well as providing explicit guidance on voxel size selection, which is known to impact derived PAI estimates (Li et al., 2016). We re-combined individually segmented trees, filtered for noise using a height-dependent statistical filter (see Owen et al., 2021) back into whole plot point clouds and voxelised them using the open source *R* package, *VoxR* (Lecigne et al., 2018), with a full grid covering the minimum to maximum XYZ ranges of the plot. We classified any voxel containing > 0 points as vegetation ("filled"), and empty voxels as gaps. We then split the voxelised point cloud into slices one voxel high. Within each slice, the contact frequency is calculated as the fraction of filled to total number of voxels. We then multiplied the contact frequency by a correction factor for leaf inclination, set at 1.1 (Li et al., 2017), and whole plot PAI was calculated as the sum of all slices' contact frequencies.

2.5 Calculation of individual tree PAI, WAI and α using the voxel-based method

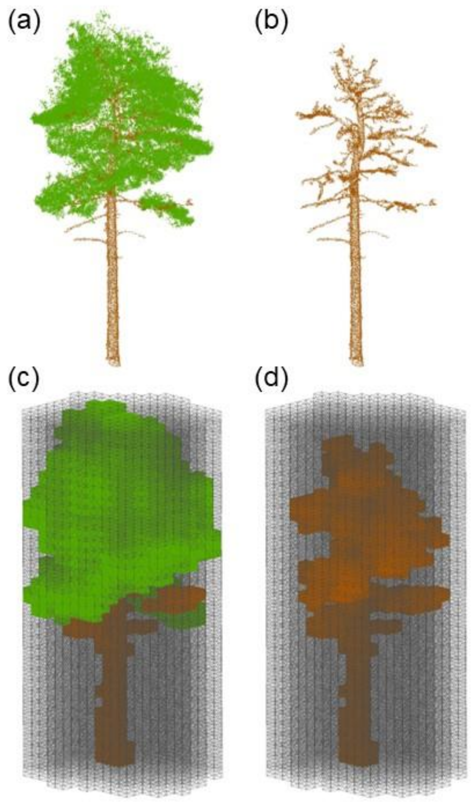

Figure 2: Visualisation of the workflow for applying the Voxel-Based method to estimate individual-tree PAI, WAI and α. (a) Individual tree point cloud; (b) separated leaf off (wood) individual tree point cloud; (c) voxelised individual tree point cloud; (d) voxelised wood cloud. ~~Solid black~~ Coloured voxels (green represents leaf and brown represents wood) are filled voxels and grey lines are empty voxels. Empty voxels occupy the space within the projected crown area of the tree. Image shows schematic of point cloud voxelised with cube voxels with edge length of 0.5 m. Panels a and b show ~~W~~wood and leaf separation of an example *P. sylvestris*, ~~was~~ carried out using *TLSeparation* (Vicari et al., 2019)**. Point cloud voxelisation was carried out using modified functions from *R* package *VoxR*** (Lecigne et al., 2018)**.**

As the only method using multiple co-registered scans, the *Voxel-Based* method is only method compared in this study ~~we found~~ capable of deriving PAI, WAI and LAI of segmented individual tree point clouds ~~estimating individual tree leaf and wood properties~~. We estimated PAI and WAI for 2472 individual trees segmented from co-registered point clouds following a similar method to the whole plot point cloud. We used individual tree point clouds downsampled to 0.05 m, to aid computation time, and ~~extracted~~ segmented ~~individual trees~~ using the automated tree segmentation program *treeseg* (Burt et al., 2019), implemented in C++, ~~see~~ by Owen et al., (2021) for that study. ~~full details, and~~ Individual segmented tree data are available in Owen et al., (2022). ~~for individual segmented tree data.~~

To estimate PAI, WAI and α for each tree, we ~~first separated leaf from wood points in~~ used individual tree point clouds wood – leaf separated by ~~(~~Owen et al., (2021) using the open source Python library *TLSeparation* (Vicari et al., 2019), and then used the separated wood ~~only~~ point clouds to calculate WAI. *TLSeparation* ~~classifies~~ assigns points ~~as~~ as either leaf or wood, iteratively looking at a predetermined number of nearest neighbours (*knn*). The *knn* of each iteration is directly dependent on point cloud density, since high density point clouds will require higher a *knn* (Vicari et al., 2019). ~~We used t~~The utility package in *TLSeparation* was used to automatically detect the optimum *knn* for each tree point cloud.

To voxelise individual tree complete (Figure 2a) and wood only (Figure 2b) point clouds, we used a modified approach based on Lecigne et al., (2018), voxelising within the projected crown area of the whole tree point cloud (Figure 2c) to calculate PAI. In the same way as for PAI, w~~W~~e calculated WAI using the separated wood point cloud within the projected crown area of the whole tree (Figure 2d; using the whole crown and not just the wood point cloud), and derived α for each tree as $^{WAI}/_{PAI}$. To allow a comparison with existing literature estimating α, (Sea et al., 2011; Woodgate et al., 2016) we focused on α values.

2.6 Statistical Analyses

We tested the relationships between ~~TLS PAI~~PAI_{TLS} and ~~DHP PAI~~PAI_{DHP} estimates using Standardised Major Axis (SMA) using the open source *R* (R Core Team, 2020) package, *smatr* (Warton et al., 2012). SMA is an approach to estimating a line of best fit where we are not able to predict one variable from another (Warton et al., 2006); we chose SMA because we do not have a 'true' validation dataset, so avoid assuming either DHP or any of the TLS methods produces the most accurate results. For each TLS method, we assessed the relationship with DHP using the coefficient of determination and RMSE. We chose to compare PAI values rather than WAI or LAI as each method corrects for non-photosynthetic elements in different ways and would introduce bias, limiting the ability to directly compare metrics. To further understand observed drivers of variance in PAI, we tested the relationship between PAI and TLS estimated whole plot crown area index, CAI, calculated as the sum of projected crown area~~,~~ divided by the plot area (Owen et al., 2021), ~~and indicative~~ and a proxy measure of stand density and local competition (Caspersen et al., 2011; Coomes et al., 2012), using SMA.

To test if α differs by species, we used linear mixed models (LMMs) in the *R* package, *lme4* (Bates et al., 2015). We included an intercept only random plot effect to account for local effects on α:

$$\alpha_{i,sj} = a_s + Plot_j \qquad (1)$$

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here, α_i is α of an individual of species *s*, in plot *j*, and a_s is the parameter to be fit. To test the effect of stand structure and tree height on α, we fit relationships separately for each species, again including a random plot effect:

$$\alpha_{i,sj} = a_s + b_s H_i + c_s CAI_j + Plot_{sj} \quad (2)$$

here H_i is the height of the tree, CAI_j is the crown area index for the plot, with other parameters as before.

For each species' model (equation 2), we calculated the intra-class correlation coefficient (ICC). The ICC, similar to coefficient of determination, quantifies the amount of variance explained by the random effect in a linear mixed model (Nakagawa et al., 2017).

3. Results

3.1 Comparison of plant area index estimated by DHP and single scan TLS

Of the two single scan TLS methods tested (*LiDAR Pulse* method and *2D Intensity Image* method), we found that the relationship between PAI estimated using the *LiDAR Pulse* method and ~~more strongly agreed with DHP PAI~~PAI$_{DHP}$, ~~but there was also significant correlation for~~ had a higher R^2 than the *2D Intensity Image* method (SMA; *LiDAR Pulse* method R^2 = 0.50, slope = 0.73, p<0.001, RMSE = 0.14, and *2D Intensity Image* method R^2 = 0.22, slope = 0.38, p<0.001, RMSE = 0.39, respectively, Figure 3a). At larger PAI values, relative to DHP, both TLS methods underestimated PAI ~~compared with DHP~~ (Figure 3b). We found statistically significant negative correlations between residuals and DHP for both methods (SMA; *2D Intensity Image* method residuals R^2 = 0.85, slope = -0.88, p<0.01; *LiDAR Pulse* method residuals R^2 = 0.47, slope = -0.70, p<0.01; Figure 3b). The *2D Intensity Image* method showed larger underestimation at higher ~~DHP PAI~~PAI$_{DHP}$ values, suggesting this method may saturate sooner than both DHP and the *LiDAR Pulse* method at higher PAI values (Figure 3b).

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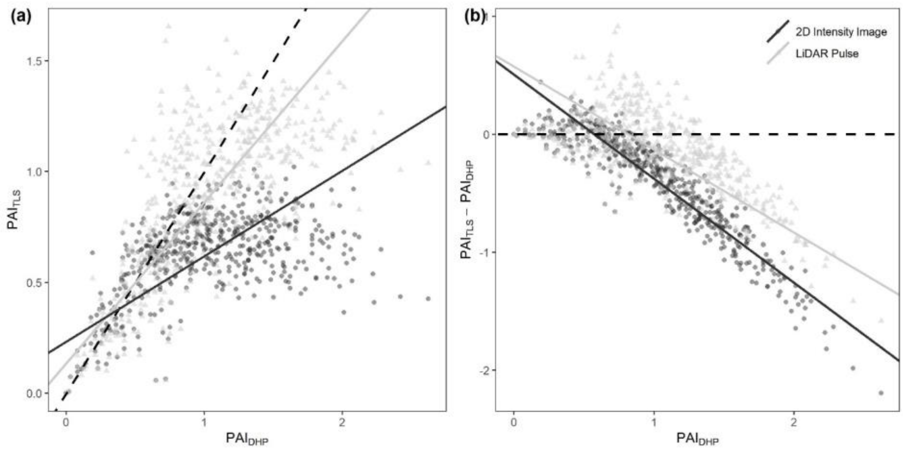

Figure 3: Comparison of single scan ~~TLS PAI~~PAI_{TLS} and ~~DHP PAI~~PAI_{DHP} estimates, for all 528 scan locations (16 per plot). (a) The correlation between DHP derived PAI with PAI derived using the 2D Intensity Image method R^2 = 0.22, slope = 0.38, p<0.001, RMSE = 0.39 (circles), and LiDAR Pulse method R^2 = 0.50, slope = 0.73, p<0.001, RMSE = 0.14 (triangles). Dashed line in panel a represents 1:1 relationship. (b) The difference between ~~TLS~~ PAI_{TLS} and ~~DHP PAI~~PAI_{DHP} estimates for the 2D Intensity Image method, and LiDAR Pulse method (dashed line ~~at~~ in panel b represents 0). Lines show statistically significant relationships fitted using SMA (p<0.01).

3.2 Comparison of whole plot plant area index estimated using TLS and DHP and the effect of plot structure on PAI

We found statistically significant correlations between whole plot ~~TLS whole plot~~ PAI_{TLS} values and ~~DHP PAI~~PAI_{DHP} for all three TLS methods. As for single scans ~~(Figure 3)~~, the *LiDAR Pulse* method showed the closest agreement to ~~DHP PAI~~PAI_{DHP}, here compared to both the *Voxel-Based* and *2D Intensity Image* methods (SMA; *LiDAR Pulse* method R^2 = 0.66, slope = 0.82, p<0.01, RMSE = 0.14; *Voxel-Based* method R^2 = 0.39, slope = 2.76, p<0.01, RMSE = 0.88; *2D Intensity Image* method R^2 = 0.35, slope = 0.36, p<0.01, RMSE = 0.39, respectively; Figure 4a). The *2D Intensity Image* method and *LiDAR Pulse* method consistently underestimated PAI compared to DHP, whilst the *Voxel-Based* method underestimated in plots with lower ~~DHP PAI~~PAI_{DHP} and overestimated in plots with higher ~~DHP PAI~~PAI_{DHP}. The *Voxel-Based* method's high PAI values compared to other methods is likely due to its use of multiple co-registered scans reducing occlusion effects prevalent in single scan data.

To assess the effect of plot structure on variation in TLS derived PAI, we compared ~~TLS PAI~~PAI_{TLS} estimates to TLS estimated crown area index (CAI, m^2 projected crown area per m^2 ground area, Figure 4b). We found a significant positive relationship between CAI and PAI estimated using each of the *LiDAR Pulse* method, the *Voxel-Based* method, and DHP (SMA*; LiDAR Pulse* method R^2 = 0.79, slope = 1.69, p<0.01; *Voxel-Based* method R^2 = 0.76, slope = 5.72, p<0.01; *2D Intensity Image* method R2 = 0.15, slope = 0.76, p<0.05; DHP R^2 = 0.46, slope = 2.07, p<0.01, respectively; Figure 4b), where the *2D Intensity Image* method appears to saturate at medium CAI values (Figure 4b).

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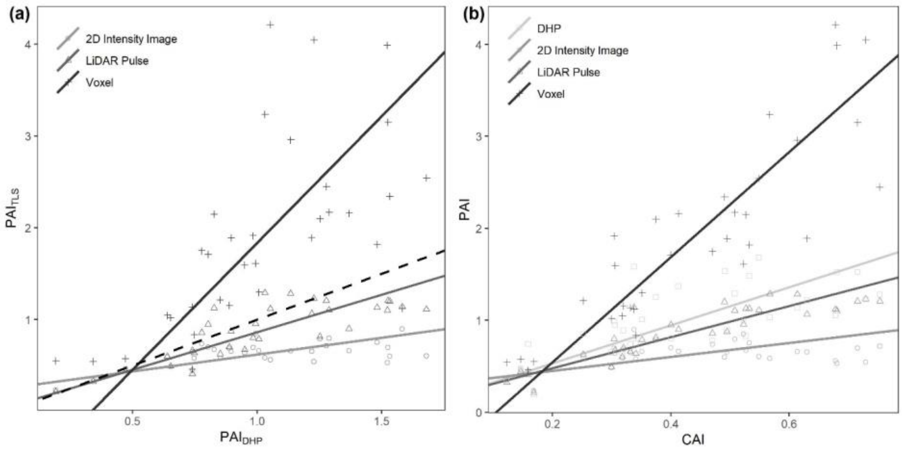

Figure 4: Comparison of plot level ~~TLS PAI~~ PAI_{TLS} and ~~DHP PAI~~ PAI_{DHP}, and CAI vs PAI estimates for all 33 plots. (a) The correlation between DHP derived PAI and PAI derived using 2D Intensity Image $R^2 = 0.35$, slope = 0.36, $p<0.01$, RMSE = 0.39 (circle), LiDAR Pulse $R^2 = 0.66$, slope = 0.82, $p<0.01$, RMSE = 0.14 (triangle) and Voxel-Based $R^2 = 0.39$, slope = 2.76, $p<0.01$, RMSE = 0.88 (cross) methods (b) The correlation between TLS derived CAI and PAI derived using DHP $R^2 = 0.46$, slope = 2.07, $p<0.01$ (square), 2D Intensity Image $R^2 = 0.15$, slope = 0.76, $p<0.05$ (circle) LiDAR Pulse $R^2 = 0.79$, slope = 1.69, $p<0.01$ (triangle) and Voxel-Based $R^2 = 0.76$, slope = 5.72, $p<0.01$ (cross) methods. Lines show statistically significant relationships fitted using SMA ($p<0.01$). Dashed line in panel a represents 1:1 relationship.

3.4 Influence of species, tree height and CAI on α

To understand drivers of variance in α, we used individual tree PAI and WAI, calculated using the *Voxel-Based* method to test the relationship between species and α, and height/ CAI and α. We found that more drought tolerant species generally had higher α values than less drought tolerant species (Table A1; Figure 5), however, confidence intervals were wide and overlapping, suggesting that species is not a strong predictor of variation in α. We found a statistically significant negative effect of height ($p<0.001$; Table A2; Figure 6a) and positive effect of CAI ($p<0.01$ – 0.05; Table A2; Figure 6b) on α for all species apart from *P. sylvestris*. α decreased more rapidly with height and increased less rapidly with CAI for oaks than pines. Statistically significant ICC values were higher for *P. nigra* (ICC = 0.211; Table A2) than *P. pinaster*, *Q. faginea* and *Q. ilex* (ICC = 0.036; 0.060; 0.070, respectively), showing that more α variation is explained by the random plot effect in *P. nigra* than the other species. *P. pinaster* has a wider confidence interval (Figure 5), possibly explained by its lower sample size. To

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understand drivers of variance in WAI we carried out additional analysis to test the relationship between WAI and species, height, CAI and PAI, and presented these results in Appendix C.

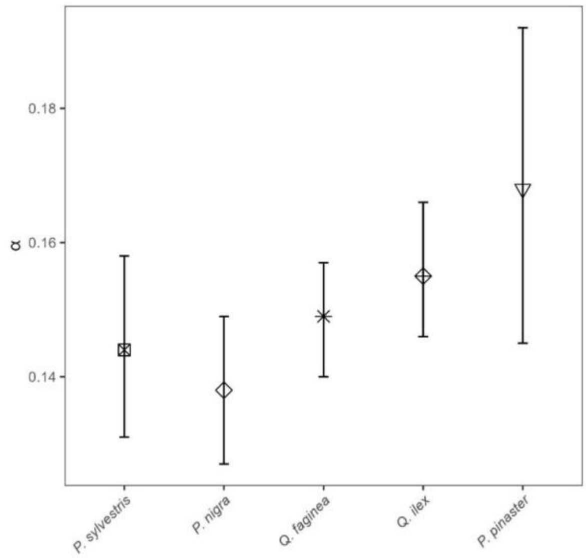

Figure 5: Linear mixed model derived α values (a, equation 1) for all 2472 individual trees of species *P. sylvestris, P. nigra, Q. faginea, Q. ilex* and *P. pinaster*. Error bars represent 95% confidence intervals. Species are listed from low – high drought tolerance, with the exception of *P. pinaster*, for which drought tolerance index has not been calculated in the literature. Drought tolerance rankings are taken from ~~(~~Niinemets and Valladares, (2006)

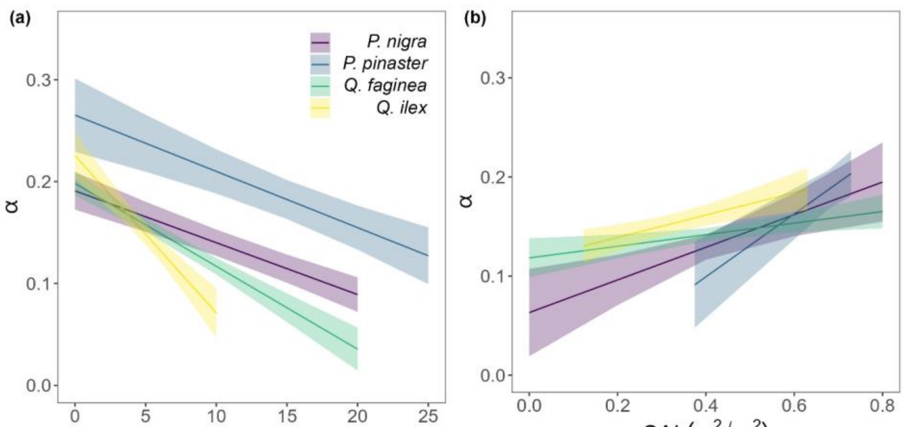

Figure 6: Variation in α for each species: *Pinus nigra, P. pinaster, Q. faginea* and *Q. ilex* with (a) height and (b) plot CAI. Lines represent statistically significant linear mixed models (equation 2; $p < 0.001$ – $p < 0.05$). Ribbons represent 95% confidence intervals. The model for *P. sylvestris* was not statistically significant.

4. Discussion

4.1 Comparison of approaches to deriving PAI from remote sensed data

We found substantial differences in PAI values estimated from TLS and DHP and from different TLS processing methods (Figures 3 and 4). Further, differences between TLS methods varied across plot structure (CAI), with the greatest differences between methods in plots with high CAI, and therefore high canopy density. Although previous studies have presented TLS as an improvement over DHP due to its independence of illumination and sky conditions during the data acquisition phase, and ability to resolve fine-scale canopy elements and gaps (Calders et al., 2018; Grotti et al., 2020; Zhu et al., 2018), we have shown that there is large variability between TLS processing methods in Mediterranean forests. Rigorous intercomparison of approaches, ideally using standard benchmarking TLS datasets, and destructive sampling, would improve trust and reliability of TLS algorithms.

~~4.2 The *LiDAR Pulse* and *2D Intensity Image* method derived PAI estimates were lower than those derived from DHP and the *Voxel-Based* method~~

We found the *LiDAR Pulse* method (Jupp et al., 2008) to have the best agreement with DHP for both whole plot and single scan PAI estimates. In contrast to previous studies comparing PAI_{TLS} with– PAI_{DHP} ~~comparisons~~ (Calders et al., 2018; Grotti et al., 2020; Woodgate et al., 2015), we found that the *LiDAR Pulse* and *2D Intensity Image* methods underestimated PAI compared to DHP, except at very low PAI values ($PAI_{TLS} < 0.5$). Quantification of PAI from DHP may introduce additional sources of error, for example, its relatively lower resolution compared to TLS could lead to mixed pixels that have a greater chance of misclassification of sky as vegetation (Jonckheere et al., 2004). This effect could be enhanced in a Mediterranean forest as trees in drier climates tend to have smaller leaves (Peppe et al., 2011), leading to more small canopy gaps that TLS may resolve where DHP cannot. Further, although we took steps to reduce the error introduced at DHP data acquisition and processing steps, including using automatic thresholding and collecting images with multiple exposures, DHP processing requires both model and user assumptions that can impact results. For example, ~~DHP PAI~~PAI_{DHP} estimates are highly sensitive to camera exposure; increasing one stop of exposure can result in 3 – 28% difference in PAI and use of automatic exposure can result in up to 70% error (Zhang et al., 2005).

We found the *Voxel-Based* method overestimated PAI values compared to the other methods at the whole plot level. This is likely due to the method's use of co-registered scans, rather than averaged single scan PAI values, since co-registered scans will reduce occlusion effects prevalent in single scan data that could to lead to an underestimation of PAI (Wilkes et al., 2017). The *Voxel-Based* method is, however, sensitive to voxel size (Li et al., 2016), and larger voxels lead to larger PAI estimates as they fill small canopy gaps; we chose a voxel size of 0.05 m to match the minimum distance between points in our downsampled dataset. However, the *Voxel-Based* method is a memory intensive approach to calculating PAI, and smaller voxels have higher memory requirements. We picked this data resolution, and therefore voxel size, to balance the need to capture fine-scale canopy details against memory requirements for running many large plots. Voxel size could have been chosen based on estimates' match to DHP, but this would assume (1) that DHP estimates are most accurate, and (2) that DHP data are always available, limiting the wider applicability of our findings. Understanding which method is over or underestimating would require a destructively sampled dataset for validation, which was not possible for this

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study (or most ecosystems). However, other studies using voxel approaches have found that although these produce high LAI values for individual trees, these are underestimates compared with destructive samples (Li et al., 2016). Regardless, PAI and LAI estimates using a *Voxel-Based* approach are highly dependent on voxel size ~~(Béland et al., 2014)~~ (Li et al., 2016), and future work should test the influence of voxel size on PAI estimates, using destructive samples in a range of environments.

~~4.3 Relationship between PAI and CAI varied according to method and sensor~~

The relationship between the *LiDAR Pulse* method ~~had the strongest relationship (defined as highest R^2) with~~ and TLS derived CAI had the highest R^2, demonstrating that the method is well suited to measuring PAI across the range of plot CAI values used in this study. Although the *2D Intensity Image* method can tackle the significant challenges presented by edge effects and partial beam interceptions, particularly present in phase-shift systems (Grotti et al., 2020), our results suggest this method has a lower performance ability, with saturation occurring sooner than all other methods in dense forests (Figures 3 and 4). The *2D Intensity Image* method uses the same raw single scan data as the *LiDAR Pulse* method, so the better performance from the latter is likely due to the method's use of vertically resolved gap fraction; both the *LiDAR Pulse* method and *Voxel-Based* method account for the vertical structure of the canopy by summing vertical slices through the canopy.

4.4 α variation between species and plot

We used the *Voxel-Based* method to investigate individual tree α variation between species and across structure, as this was the only approach we compared~~identified~~ that could be applied to single tree point clouds. We found α values obtained were within the range of values obtained from destructive approaches (0.1 – 0.6, Gower et al., 1997). The drought and shade intolerant *P. nigra* showed stronger variability in α across plots (higher ICC value, Table A2) than other species, suggesting its wood – leaf ratio may be more sensitive to site factors. However, as the plots measured in this study vary in both abiotic conditions (altitude, aspect, slope, wetness) as well as species composition, stem density and canopy cover, there may be other drivers of variation in α values.

We found some evidence that species with higher drought tolerance had higher α values (Figure 5; Table A1), however, confidence intervals were wide, suggesting a weak relationship. There is evidence that trees that tolerate water limited environments have a lower leaf area (Battaglia et al., 1998; Mencuccini and Grace, 1995), so higher α values may reflect maintenance of homeostasis of leaf water use through adjustment of wood to leaf area ratio (Carter and White, 2009; Gazal et al., 2006). The potential for a tree to lose water is mostly regulated through leaf traits including stomatal conductance and leaf area, and both stand (Battaglia et al., 1998; Specht and Specht, 1989) and individual tree (Mencuccini, 2003) water use have been found to scale linearly with LAI, with drought often mitigated through leaf shedding (López et al., 2021).

4.5 Tree stature and stand density drives α variation

Although species had a weak relationship with~~explain some variation in~~ α, tree height and plot CAI ~~were stronger predictors~~had a statistically significant relationship with α ($p<0.001$ – $p<0.05$) for all species, showing the importance of local stand structure on leaf and woody allocation. We found that α scaled negatively with height for all species apart from *P. sylvestris*, suggesting that in this environment, taller trees generally have a lower proportion of wood to plant area index than shorter ones. *P. sylvestris*, which is at the edge of its geographical range and physiological limits (Castro-Díez et al., 1997; Owen et al., 2021), showed no significant relationship between height and α. We found that α scaled positively with plot level CAI for all species apart from *P. sylvestris*, that is, trees growing in denser plots have a higher α. This supports theory that trees growing in dense forests are competing for resources, reducing individual tree leaf area (Jump et al., 2017). The negative height – α and positive CAI – α relationships in our model suggest that trees may initially invest in vertical growth to reach the canopy level, and once there invest in lateral growth, with more leaf area, to increase light capture. This supports theory that trees grow to outcompete neighbouring individuals for light capture (Purves and Pacala, 2008) and evidence that both lateral growth and LAI are reduced beneath closed canopies (Beaudet and Messier, 1998; Canham, 1988).

Wood may be harder to accurately classify than leaves in TLS data (Vicari et al., 2019), resulting in a higher occurrence of false positives in wood clouds, potentially leading to an overestimation in WAI, and therefore underestimation of α, especially in trees with small leaves which are prevalent in dry, Mediterranean environments (Peppe et al., 2011). The problem of misclassification will increase in taller trees due to TLS beam divergence, occlusion and larger beam footprint at further distances (Vicari et al., 2019), suggesting that WAI overestimation could be more pronounced in tall trees. Although our dense scanning strategy (Owen et al., 2021) was designed to mitigate some of these effects, it is possible our findings could underestimate the slope of the negative relationship between α and tree height.

4.6 Correcting for non-photosynthetic elements in LAI estimates using TLS

The value of TLS data to estimate individual tree PAI, WAI and subsequently α, demonstrates their potential to corrective factors for non-photosynthetic components in ground based remote sensing measurements of LAI. Properly correcting for WAI in LAI estimates is of global importance as small errors in ground based measurements propagate through to large scale satellite observations generating large errors in global vegetation models (Calders et al., 2018). The work presented here provides a foundation for future work combining multi-source and multi-scale remote sensing datasets to correct large-scale LAI products. Our results echo others' in finding that the prevalence of woody material in the tree canopy, and therefore α, is dynamic and varies by species as well as senescence, crown health and, in the case of deciduous forests, leaf phenology (Gower et al., 1999). The use of single α value in a plot or region (Olivas et al., 2013; Woodgate et al., 2016), invariant of species, size and forest structure, to convert PAI to LAI is therefore problematic (Niu et al., 2021). Our study demonstrates the importance of taking species mix and structural variation into account when correcting for non-photosynthetic material in ground-based LAI estimates.

5. Conclusions

We tested three methods for estimating PAI using Terrestrial Laser Scanning data and compared these against traditional DHP measurements. We found large variation between PAI values estimated from each TLS method and DHP, demonstrating that care should be taken when deriving PAI from ground based remote sensing methods. Although the *LiDAR Pulse* method was found to have the best agreement with both single scan and whole plot PAI values measured by DHP, the *Voxel-Based* method allowed separate analysis of the key metric used to correct for the effect of WAI in LAI measurements, α, in individual trees. We recommend the *LiDAR Pulse* method as a fast and effective method for PAI estimation independent of illumination conditions. Whilst the *Voxel-Based* method may be used to analyse individual tree α and determine ecological drivers of variation, work remains to determine the validity of these approaches, in particular correct voxel size choice. We found that α varies by species, height and stand density, showing the importance of accurately correcting for WAI on the individual tree level and the utility of TLS to do so.

The variation in our results for the different methods used to derive PAI from TLS data show that there is some way to go before TLS derived vegetation indices can be interpreted as robust and reliable. Validation using destructive samples and further intercomparison studies of methods are needed to demonstrate the advantages of TLS, and use of benchmarking datasets should be standard. DHP is a faster, cheaper and more widely accessible method for PAI estimation, and while TLS promises to alleviate potential bias in DHP estimates, results are highly methods dependent. Our results demonstrate the challenges that stand in the way of large scale adoption of TLS for vegetation indices monitoring.

6. Code availability

See https://github.com/will-flynn/tls_dhp_pai.git for all processing and modelling code.

7. Data availability

See Owen et al., (2022) for individual segmented tree data.

8. Author contribution

All authors designed the study. HJFO and WRMF collected and processed TLS and DHP data; WRMF performed formal analysis with guidance from all authors. WRMF led the writing with input from all authors. All authors contributed critically to drafts and gave final approval for publication.

9. Competing interests

The authors declare that they have no conflict of interest.

7. Acknowledgements

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Appendix A

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Table 1: species – α linear mixed model (equation 1) showing relationship between tree species and α for all 2472 individual trees. Species are listed from low – high drought tolerance, with the exception of *P. pinaster*, for which drought tolerance index has not been calculated in the literature.

Species	***α* (eq. 1)**	**95% CI**
P. sylvestris	0.144	0.131, 0.158
P. nigra	0.138	0.127, 0.149
Q. faginea	0.149	0.140, 0.157
Q. ilex	0.155	0.146, 0.166
P. pinaster	0.168	0.145, 0.192

Table 2: height – α linear mixed models for each species (equation 2) showing relationship between tree height and plot CAI and α for all 2472 individual trees. Species are listed from low – high estimated α. Significance codes: p < 0.001 '*'; p < 0.01 '**'; p < 0.05 '*'; not significant '^{ns}'**

Species	***b* (eq. 2) (95% CI)**	***c* (eq. 2) (95% CI)**	**ICC**
P. sylvestris	-0.002^{ns} (-0.004, 0.000)	0.134^{ns} (0.010 0.259)	0.151
P. nigra	-0.005*** (-0.006, -0.004)	0.164** (0.063, 0.263)	0.211
Q. faginea	-0.008*** (-0.010, -0.007)	0.058* (0.016, 0.101)	0.060
Q. ilex	-0.015*** (-0.020, -0.011)	0.113** (0.050, 0.179)	0.070
P. pinaster	-0.006*** (-0.008, -0.004)	0.317* (0.177, 0.453)	0.036

Appendix B

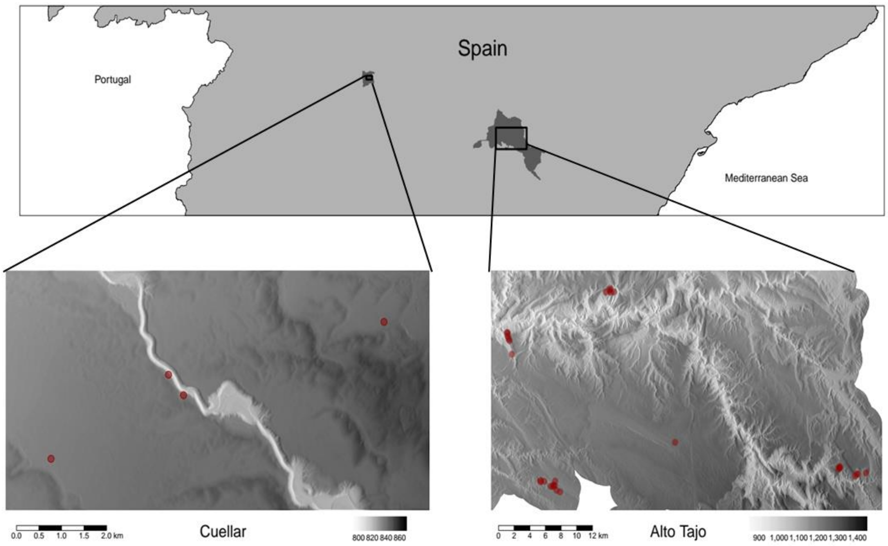

Figure 1: Map of plot locations within two field sites in central Spain (Cuellar, left and Alto Tajo, right). Red points show plot locations on high-resolution digital terrain models enhanced with hillshading shown in greyscale.

Appendix C

$WAI = m_{species} + b$ (1)

$WAI = m_{height} + b$ (2)

$WAI = m_{CAI} + b$ (3)

$WAI = m_{PAI} + b$ (4)

Where WAI is the wood area index, *species, height, CAI* and PAI are the tree species, tree height, crown area index of the plot in which the tree is growing and tree plant area index respectively and *m* and *b* are parameters to be fit.

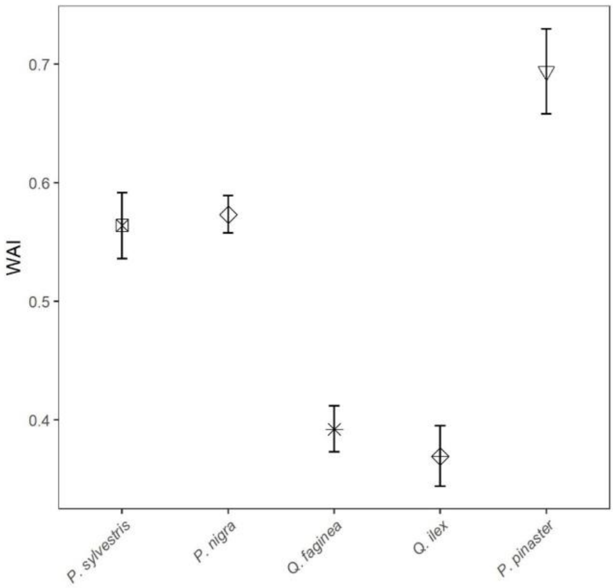

Figure 2: Linear model derived WAI values (m, equation C1) for all 2472 individual trees of species *P. sylvestris, P. nigra, Q. faginea, Q. ilex* and *P. pinaster*. Error bars represent 95% confidence intervals. Species are listed from low – high drought tolerance, with the exception of *P. pinaster*, for which drought tolerance index has not been calculated in the literature.

Table 3: Linear model (equation C1) showing relationship between tree species and WAI for all 2471 individual trees. Significance codes: p < 0.001 '*'; p < 0.01 '**'; p < 0.05 '*'; not significant 'ns'**

Species	*m* (eq. 1)	Std. Error	P value
P.nigra	0.57	0.008	***
P. pinaster	0.69	0.018	
P. sylvestris	0.56	0.014	
Q. faginea	0.39	0.010	***
Q. ilex	0.37	0.013	***

Table 4: Linear models (equations C2, C3, C4) predicting WAI as a function of tree height, CAI (density) and PAI Significance codes: p < 0.001 '*'; p < 0.01 '**'; p < 0.05 '*'; not significant 'ns'**

	m (eq. 2, 3, 4)	R^2	P value
Tree Height	0.02	0.27	***
CAI	0.39	0.78	***
PAI	0.11	0.35	***