Effects of stem and pith eccentricity on the accuracy of basal area increment estimations.

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Abstract

Accurate tree growth quantification is crucial in ecology to assess tree growth. Basal area increment (BAI) is typically calculated from tree rings on increment cores, assuming trees are perfect circles with centered piths. However, trees often have pith offset and stem out-of-roundness, leading to estimation errors. Yet, we do not know how much estimation error results from these eccentricities. Using geometric principles that hold across all tree sizes, we quantified the effects of these eccentricities on BAI accuracy by comparing estimates from four calculation methods and varying core numbers (one to four) against true BAIs taken from cross-section scans.

Analysis of 109 cross-sections from 25 temperate species showed that with one core, pith eccentricity accounts for 21% of the error in BAI estimation, and stem eccentricity for 8%. Taking multiple cores, especially two-opposite cores, significantly reduces these errors, with four cores fully accounting for both eccentricities.

We recommend using multiple cores to minimize error, with two-opposite cores—taken uphill and downhill—being the most effective approach. We also provide methods for quantifying and reporting pith and stem eccentricity in the field, offering practical guidance for practitioners to calculate estimation errors based on their methods.

1. Introduction

The rate of tree growth is an essential variable in forestry, ecology, and tree-ring science as it quantifies the performance and health of individual trees, populations, and the forest community (Grissino-Mayer, 2003; Pirie, Fowler, & Triggs, 2015). Forestry is a major economic engine for many countries, making assessment of tree growth rate of economic relevance. Thus, accurate estimations of tree growth are key to both the economy and to the environmental sustainability of all the countries with large forestry industry sectors and national forestry inventory programs.

A common way to estimate the growth rate of a tree is to calculate basal area increment (BAI; Biging & Wensel, 1988). BAI is the difference in cross-sectional area of a tree at breast height (1.3m above ground) between two time points (Shi et al., 2015). BAI can be measured on live trees in two ways, either from differences in the diameter at breast height (DBH) measured at two time points, or from the difference in estimated areas between two rings sampled from cores or from cross-sections. Taking tree cross-sections is the most accurate method as it allows one to calculate the exact BAI and allows us to measure the age, pith location, shape of the tree stem and other ring irregularities, but since this method kills the tree, it is not possible for most applications. Repeated measurements of tree diameter using a diameter tape is a common alternative, but it requires multiple visits to the site, which is often not possible. Taking increment cores is often the method of choice when trees cannot be killed or when multiple visits to a site are not possible.

Current BAI calculations from cores calculate basal area from the radii using the equation for the area of a circle ($A = \pi r^2$) which assumes that trees have a perfectly circular stem with centred piths (Biging & Wensel, 1988; Johnson & Abrams, 2009; Fig. 1). However, tree cross-sections tend to deviate from a perfect circle and other studies have shown that this eccentricity leads to error (Biging & Wensel 1988, Bakker 2005, Fallah *et al.* 2012, Visser *et al.* 2023). Yet, to our knowledge the error in BAI estimation arising from eccentricity has not been quantified, and we do not know whether we can correct for this error. Recently, increment core data has been incorporated into forest monitoring programs (Evans et al. 2022) as well as in simulation models of forest growth (Giebink et al. 2022; Shi et al., 2023), such that improving our understanding of BAI estimation error from increment cores is timely.

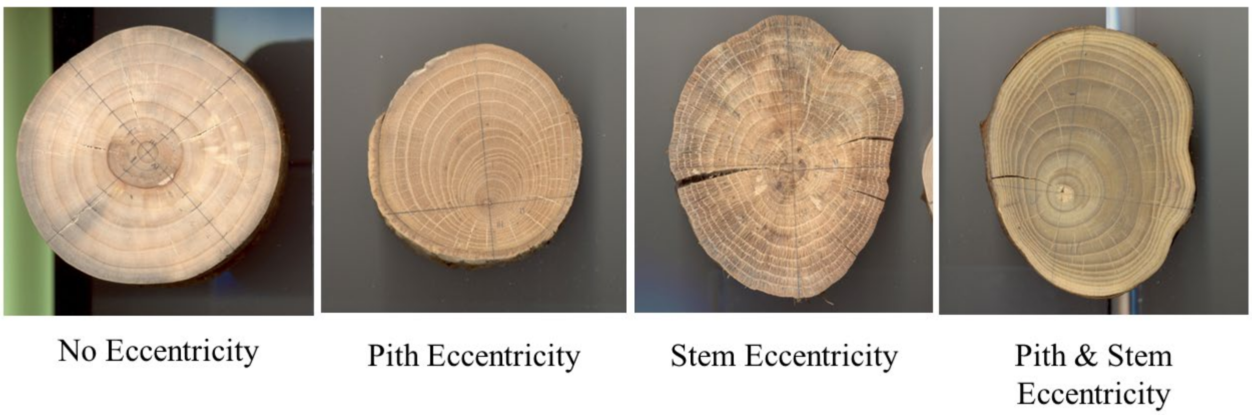

Figure 1. Tree eccentricity on stem cross-sections. Tree stems can exhibit differing levels and combinations of pith and stem eccentricity, such as no eccentricity (first image on the left), only pith or only stem eccentricity (second and third images respectively), or both pith and stem eccentricity (image on right). The type and degree of the eccentricity depends on tree growth conditions, such as growing on an incline (Biging & Wensel, 1988).

Here, we assess how much estimation error arise from two forms of tree eccentricities; pith eccentricity (pith offset from the centre - POC) and stem eccentricity (stem out-of-roundness - OOR; Fig. 1) and explore whether we can correct for this error using different area estimation methods, or by taking multiple cores per individual. These questions are relevant to sampling methods that sample the pith (called ‘inside-out’ in some dendrochronology software; Bunn 2008), such that radii can be calculated, but not to methods where radii are missing, and diameters must instead be used for area calculation (then called ‘outside-in’). The effects of other factors on area estimation error - such as increment cores lacking the pith, lobbing of the stem, missing or partly missing rings and false rings - is beyond the scope of this work, but see Buras & Wilmking (2014) and Visser (2023) for a treatment of these issues.

Specifically, this study addresses three research questions: (Q1) How much BAI estimation error results from pith and stem eccentricities, (Q2) How does the number of cores sampled affect this estimation error, and (Q3) Do some area calculation methods produce less estimation errors with eccentric cross-sections?

2. Materials & Methods

Sample Selection

Stem cross-sections were obtained from saplings of 25 different temperate hardwood species from Mont Saint-Hilaire (45°33′8″N, 73°9′3″W), a natural reserve located in Quebec, Canada. The saplings were from the subcanopy (shorter than two-thirds of the canopy height) and had a diameter at breast height ranging from 1 – 5 cm. The cross-sections were taken from the base and had an average diameter ranging from 1.5 – 7.5 cm. Using tree cross-sections of smaller size was necessary to get full scans and to measure their true BAI. Four to five saplings per species were studied for a total of 109 cross-sections. From a set of 380 cross-section samples, a subset of 109 cross-sections with clearly visible growth rings was selected to cover the available range of pith and stem eccentricity. The samples rings did not show ‘lobing’ or other significant departures from circular growth (see Buras & Wilmking 2014). POC metrics can theoretically range from 0 to 1 and our sample’s POC values range from 0 to 0.6. Similarly, OOR metrics can theoretically range from 0 to 1 and our sample’s OOR values range from 0 to 0.4. Although the diameter of our samples is smaller than the typical trees of interest in ecology, dendrochronology and forestry, this does not restrict the applicability of the results because they span the biologically realistic ranges of eccentricities in forest trees. Indeed, this work explores the effects geometry on area estimation error, properties that hold irrespective of the size of the shapes studied. Thus, findings from this study should apply to populations of samples ranging in OOR from 0 to 0.4 and in POC from 0 to 0.6. Each selected cross-section was sanded with increasingly fine sandpaper, up to 600 grit (Cook & Kairiukstis, 2013).

MEASUREMENTS AND CALCULATIONS

Area and Radii Measurements. The cross-sections were scanned at 1200 dpi resolution and the images were measured with Fiji and ImageJ software using the ObjectJ plugin (Schindelin *et al.* 2012; Rueden *et al.* 2017). For each cross-section, the longest diameter was identified, from which 4 perpendicular radii were then drawn (Fig. 2A). We then selected a single clear and complete focal ring on each tree scan on which to measure the true and estimated BAIs. The following measurements were then taken on the focal ring: true basal areas of the cross-sections corresponding to the inner and outer edges of the focal ring, > radii corresponding to the inner and outer edge of the focal ring in the four directions (r_{1in} to r_{4in} and r_{1out} to r_{4out}), shortest (r_{short}) and longest radii (r_{long}) on the longest diameter, and the diameter of the largest circle that could be inscribed within the cross-section (required to measure stem out-of-roundness; Koch, 1990; Fig. 2A). We measured the true area of the outer and inner rings of interest (Fig. 2B) with ImageJ by tracing the outline of the outer and inner rings to form polygons for which the areas were calculated (Fig. 2, yellow and pink polygons). The true BAI of the focal ring was then measured by subtracting the inner ring area from the outer ring area (Shi et al., 2015). The lengths of the radii were measured from the pith to the ring boundary along the 4 lines drawn on the sample (Fig. 2B). To avoid bias when labelling cores 1 through 4 in a cross-section, core number 1 was assigned randomly when the sample had circular symmetry (henceforth ‘symmetrical’). For asymmetrical cross-sections the shortest radius was assigned as radius number one.

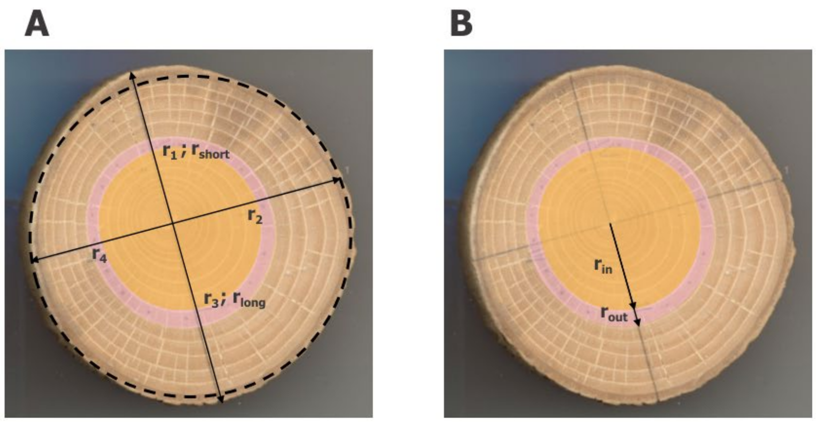

Figure 2. Diagram of the measurements taken on the stem cross sections. (A) The true BAI of the focal ring is shown with the pink polygon. The inner area is represented by the orange polygon. The dashed circle represents the largest circle that can be fully inscribed in the cross-section and is used in the OOR calculation. The black arrows show the four full radii of the sample. Core number 1 was assigned randomly as the sample is symmetrical. r_1 and r_3 correspond to the r_{short} and r_{long} radii, respectively, on the longest diameter of the cross section. For legibility, “IN” and “OUT” subscripts are omitted. **(B)** Inner (r_{in}) and outer (r_{out}) radii on one of the 4 cores. For clarity, measurements along a single core (i.e. r_{2IN}, r_{2OUT}) are shown.

Area Calculation Methods. To reproduce the estimated BAI that would be obtained from increment cores, we estimated BAI from the stem radii. To determine which BAI estimation method can best account for eccentricity, we obtained BAI estimates using four different area calculation methods. Three BAI estimation methods use the area of a circle but calculate the mean radius differently: using the arithmetic (Eqn. 1), geometric (Eqn. 2), and quadratic means (Eqn. 3). The fourth estimation method uses the area of an ellipse, which requires two or more perpendicular radii. Eqn. 4a below gives the equation for the case with 4 radii and 4b the for the case with 2 perpendicular radii. In the case of one radius, the equation becomes the same as Eqn. 1. In equations 1-4, *n* is the number of radii.

$$A_{arith} = \pi \bar{r}^2, where\ \bar{r} = \frac{r_1 + r_2 + \cdots + r_n}{n} \quad \text{Eqn. 1}$$

$$A_{geom} = \pi \bar{r}^2, where\ \bar{r} = \sqrt[n]{r_1 \times r_2 \times \ldots \times r_n} \quad \text{Eqn. 2}$$

$$A_{quad} = \pi \bar{r}^2, where\ \bar{r} = \sqrt{\frac{{r_1}^2 + {r_2}^2 + \cdots + {r_n}^2}{n}} \quad \text{Eqn. 3}$$

$$A_{ellipse,\ 4\,radii} = \frac{r_1 \times r_2 \times \pi}{4} + \frac{r_2 \times r_3 \times \pi}{4} + \frac{r_3 \times r_4 \times \pi}{4} + \frac{r_4 \times r_1 \times \pi}{4} \quad \text{Eqn.4a}$$

$$A_{ellipse,\ 2\,perpendicular\,radii} = r_1 \times r_2 \times \pi \quad \text{Eqn.4b}$$

Number of cores used. To assess how the number and location of the cores on the stem might affect BAI estimation accuracy, for each of these methods we estimated BAI using a mean radius $\bar{r}$, calculated with one to four radii. Given that the equation for an ellipse requires pairs of perpendicular radii, we calculated $A_{ellipse}$ with 2 perpendicular and four radii.

For one to three radii on asymmetrical cross-sections, the choice of which cores among the four possible ones are used in basal area estimation affects the estimated BAI. For trees with eccentric cross sections, we assumed the tree was growing on a slope resulting in the ratio of longest and shortest radius being less than 1. Thus, for n=1 to n=3, we selected the radii based on how cores are usually sampled in the field due to practical restrictions. When a single core is taken in the field, it is typically taken from uphill, as it facilitates the coring procedure (Speer, 2010). This corresponds to r_{short} in these angiosperm samples which form tension wood, which would also be considered r_1. For BAI estimates calculated from one radius, the uphill radius was used on asymmetrical cross-sections and was taken at random on symmetrical cross-sections

(Fig. 2). For BAI estimates calculated from the mean of two radii, we tested two alternative radii positions: opposite and perpendicular. For 2-opposite, we selected the uphill (r_1) and downhill (r_3) radii. For 2-perpendicular, we selected two radii perpendicular to each other: the first uphill (r_1) and the second chosen randomly between r_2 or r_4. For area calculations made from the mean of three radii, the uphill (r_1) and downhill (r_3) radii were selected, plus one perpendicular chosen at random. Last, for visibly circular cross-section, r_1 was assigned randomly and the identity of cores r_2 to r_4 were then assigned in a clockwise manner, without the r_{short} or r_{long} designations.

Pith and Stem Eccentricity. Methods described in the literature were used to calculate pith and stem eccentricity. We calculated stem eccentricity using the out-of-roundness index (OOR) method described in Koch *et al.* (1990). This index calculates stem eccentricity using the ratio of the minor diameter (diameter of the largest circle that can be fully inscribed within the stem cross-section; e.g. dashed circle in Fig. 2A) over the major diameter (the maximum diameter on the cross-section). Koch's OOR can theoretically range from 0 to 1, with a value of 1 describing a perfect circle. For clarity, increasing values of OOR should reflect increasing eccentricity. Thus, here we report OOR values as 1 - Koch's OOR, such that values of 0 describe a perfect circle. The OOR of our samples ranged from 0 to 0.3 (see third and fourth images of Fig 1 for samples with OOR values of 0.3 and 0.2). Pith eccentricity (a.k.a. pith offset) was calculated using the 'pith off-centre' (POC) index (Singleton *et al.* 2003), which is the ratio of the difference between the shortest and average radii along the longest diameter, over the average of those two radii [Eqn. 5]. POC can theoretically range from 0 to 1, with values increasing as the pith gets closer to the edge. The POC of our samples ranged from 0 to 0.6 (see second and fourth images of Fig 1 for samples with POC values of 0.6 and 0.3).

$$POC = \frac{r_{avg} - r_{short}}{r_{avg}}, where\ r_{avg} = \frac{r_{short} + r_{long}}{2} \quad \text{Eqn. 5}$$

Response Variables. BAI estimation accuracy was assessed as both percent error (%Error) and its absolute value (|% Error|). Percent error was calculated as the estimated BAI (calculated from radii) minus the true BAI (measured from polygons), divided by the true BAI and multiplied by 100. The absolute value of the percent error (|% Error|) was also calculated as an error estimate that does not consider whether the area is under- or overestimated. We assessed the relationship between the response variables and the four predictor variables: POC, OOR, number of cores, and area calculation method. Since results with both response variables were largely similar, and since to the best of our knowledge, over- or underestimation of BAI are not driven by different biological or geometric mechanisms, in the main text we only report results for |%Error| unless both results differ. All results with %Error are given in Supplementary Materials.

STATISTICAL ANALYSES

All statistics were performed in R version 2022.07.1 (R core team, 2022). To examine how the four factors of interest (area calculation method, pith and stem eccentricity and number of radii) interact to affect estimation accuracy, we built a general linear mixed model predicting |%Error| and %Error from the four above variables and their 2- and 3-way interactions as fixed effects, and with the sample identity as random effect. We built linear mixed effects regressions with the lmer() function from the lme4{} package (Bates *et al.* 2015). This full model was simplified with car{} (Fox & Weisberg, 2019) by removing non-significant variables, starting with three- then two- way interactions. To avoid collinearity, we also verified that all remaining variables had a variance inflation factor (vif) smaller than five. We checked all the GLMM model assumptions using diagnostic plots as described in Zuur & Ieno (2016). To address heteroscedasticity in the data set, we $\log_{10}$ transformed the response variable (|%Error|), following recommendations from

Zuur *et al.* (2007). For %Error, we reduced the heteroscedasticity by adding a squared predictor term (OOR^2 and POC^2) to the model, as prescribed by Zuur *et al.* (2007). Outliers were identified using boxplots (data not shown). To make the figures readable, they were removed after verifying that the results of the GLMM were qualitatively identical with and without the outliers.

In addition to building a GLMM model, we performed targeted statistical tests addressing each research question. In all of these tests sample identity was used as a random effect. First, to answer how much BAI estimation error results from tree eccentricity, we regressed the error metrics against each of pith and stem eccentricity (POC and OOR). We used BAI estimates calculated with the quadratic method (Eqn. 3) since it was the best performing method (based on a one-way ANOVA with Tukey post-hoc test, when BAI was estimated from four cores). We ran these regressions both with BAI estimated with one core, which is the worst-case scenario with a minimal sampling effort, and with 4 cores which is the best-case scenario where a large sampling effort is possible. Second, to assess how the number of cores affects estimation error arising from pith and stem eccentricity (POC and OOR), we performed ANCOVAs of the error metrics against each number and position of cores. This question was addressed using BAI estimated with the Quadratic method (Eqn. 3) and Sample ID was used as a random effect. Third, to address which area calculation method best accounts for error arising from pith and stem eccentricity (POC and OOR), we performed ANCOVAs of error metrics against estimation method. To address this question, we used BAI estimated from 2-perpendicular cores, which is the second worst case scenario. The worst-case scenario, one core only, was inadequate to address this question because one core results in identical area estimates across methods. Here we chose to use BAI estimates with the least amount of information possible to detect how the different methods perform with biased data.

3. Results

General Linear Mixed Models

The simplified GLMM model retained both measures of eccentricity, BAI calculation method and number of cores, as well as all the two-way interaction terms as significant predictors of estimation error (Table S2). The multiple regression revealed a significant and large negative interaction between the two eccentricities. This indicates that the effect of POC on error decreases with increasing OOR and that the effect of OOR on error decreases with increasing POC. The total variance explained by the model's fixed effects (i.e., the marginal R^2) was 34%. Since the results from the multiple regression were consistent with the targeted tests associated with each of the research questions, below we discuss the results of the targeted analyses. This allows us to use the test statistics to answer our specific research questions, which is not possible with the test statistics in multivariate regressions.

In order to determine which method of area estimation to use in the analyses answering the first two research questions, we first assessed which area estimation method produces the least error in our samples, irrespectively of eccentricity. On average, the Geometric method produced a significantly higher |%Error| than the other three methods, irrespective of eccentricity (5.37% versus 3.39%, respectively; ANOVA, $p = 1.28E-07$; Table S8 & S9; Fig. S1). The Arithmetic, Ellipse and Quadratic methods performed similarly (ANOVA, $p > 0.05$). To standardize the BAI estimation method in subsequent analyses, we chose to use the Quadratic method because it produces fewer and smaller outliers, because it did not tend to overestimate %

Error (Fig S2; distribution centered on 0), and because it can be used with all coring possibilities, which is not the case for the Ellipse methods (Fig. S1).

How much BAI estimation error arises from pith and stem eccentricity?

For both POC and OOR, the effect of eccentricity on |%Error| depends on the number of cores taken. We therefore present results with the highest and lowest number of cores. When using four cores, POC did not significantly affect the |%Error|, which remains low (6%) across all values of POC (Adj R^2 = 0.006, F = 1.603, DF = 107, p = 0.208; Fig. 3A; Table S4). However, when using only one core POC has a large impact on |%Error|: with a POC value of zero, one core gives on average 13% error, while a POC value of 0.6 gives on average 88% error (Adj R^2 = 0.21, F = 28.6, DF = 105, p = 5.24E-07; Fig. 3B; Table S5). Additionally, analyses on percent error with BAI estimated from one core show that increased POC leads to an underestimation of BAI (Fig. S3B).

Similarly, with 4 cores the effect of OOR on |%Error| was negligible: it predicts approximately 3% of the error with marginal significance (Adj R^2 = 0.018, F = 2.948, p = 0.089; Fig. 3C; Table S6). However, with one core, OOR has a consequential effect on |%Error|. With an OOR value of zero, one core gives on average 13% error, while a OOR value of 0.4 gives on average 79% error (Adj R^2 = 0.084, F = 10.77, DF = 105, p = 0.0014; Fig. 3D; Table S7). Further, analyses on percent error with BAI estimated from one core show that increased OOR leads to an underestimation of BAI (Fig. S4B).

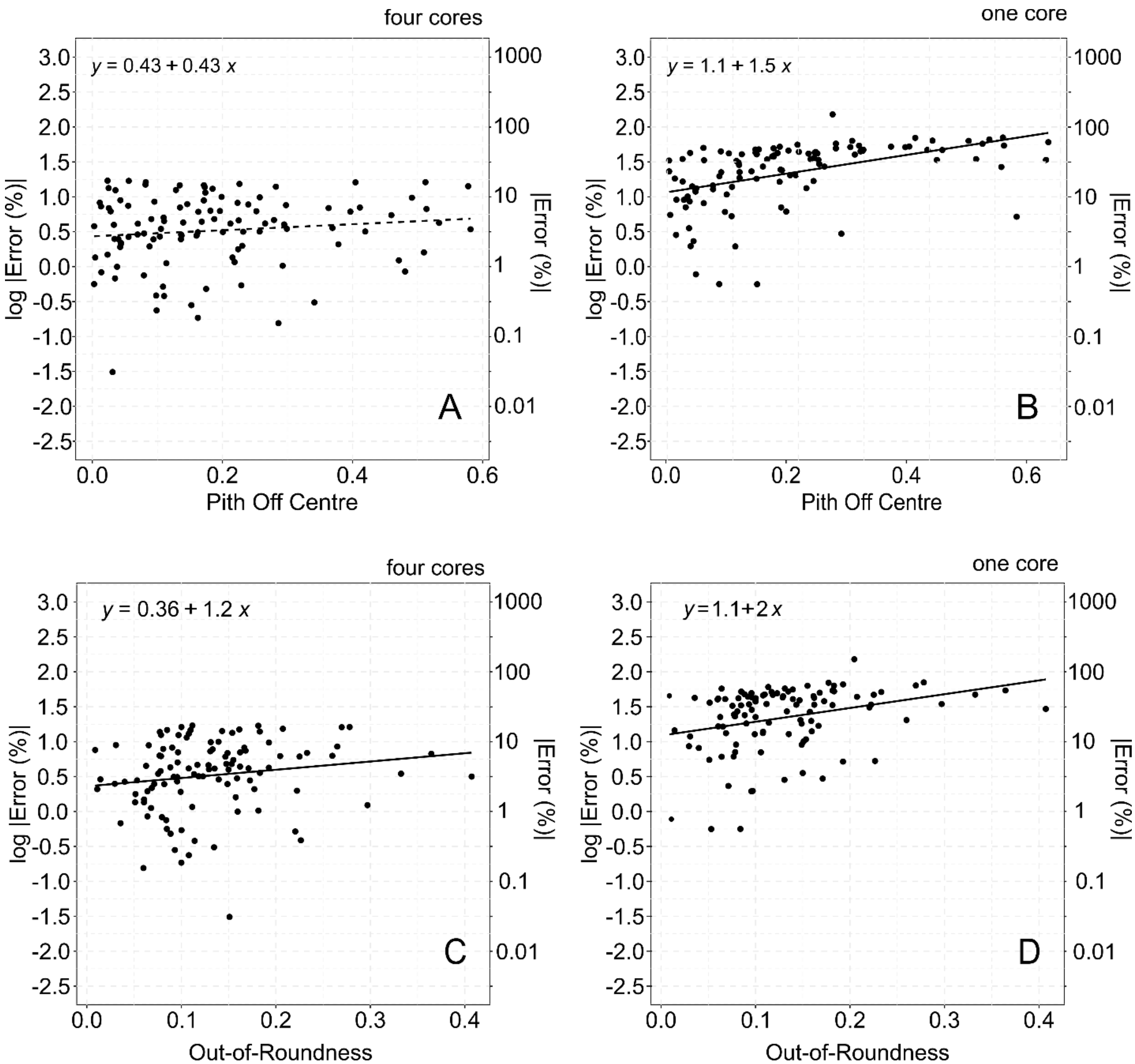

Figure 3. Effect of Pith off centre (POC) and stem out-of-roundness (OOR) on log(|%Error|) using the quadratic method, with 1 and 4 cores. For ease of interpretation, |%Error| is shown on the right as a second y axis. Panel A. Effect of four cores on POC with |%Error|. Panel B. Effect of one core on POC with |%Error|. Panel C. Effect of four cores on OOR. Panel D. Effect of one core on OOR. Non-significant slopes are shown as dotted and significant slopes are shown as solid.

How does the number and position of cores affect estimation accuracy in eccentric trees?

For all degrees of eccentricity, the height of the intercept is inversely proportional to the number of cores. This indicates that increasing the number of cores taken significantly decreases BAI estimation error (POC Table S10, $p = 3.68E-09$; OOR Table S11, $p = 1.20E-4$; Fig. 4A & B). With increasing eccentricity, it is overall better to take two opposite cores, instead of two cores perpendicular to each other (Fig. 4). For both types of eccentricity, the two coring positions have similar intercept, which reflects the amount of error resulting from this coring approach in non-eccentric samples (Table S10 & S11). However, the slopes of 2-perpendicular are steeper than the slopes of 2-opposite, indicating that higher eccentricity leads to more error when two cores are taken perpendicularly.

POC eccentricity does not increase estimation error when 2-opposite, 3 or 4 cores are taken, as the regression slope estimates are not different from 0. However, with one or 2-perpendicular cores, POC eccentricity leads to significant |%Error| (Fig. 4B; Table S10). Combining the effects of higher intercept and significant slopes, taking a single core overall gives the worst outcome, resulting in up to 102% error with POC values of 0.6, (Fig. 4B; Table S4).

The effect of OOR eccentricity on estimation error was marginally significant with one, 2-opposite, three and four cores, all of which have similar slopes (Table S11). It increased error at a significantly faster rate with 2-perpendicular cores (Fig 4A; Table S11). Note that due to the significantly higher slope for 2-perpenducular, this method produces the same error as the 2-opposite coring positions when samples have low OOR, but the same error as one core when samples exhibit high OOR (Fig 4A; Table S11). For example, for a sample with an OOR value of 0.4, taking one core would give 76% error on average and two perpendicular cores would give an average of 71% error on average (Fig. 4A). In comparison, for this OOR value taking two cores opposite and three cores would give 25% an 18% error on average, respectively.

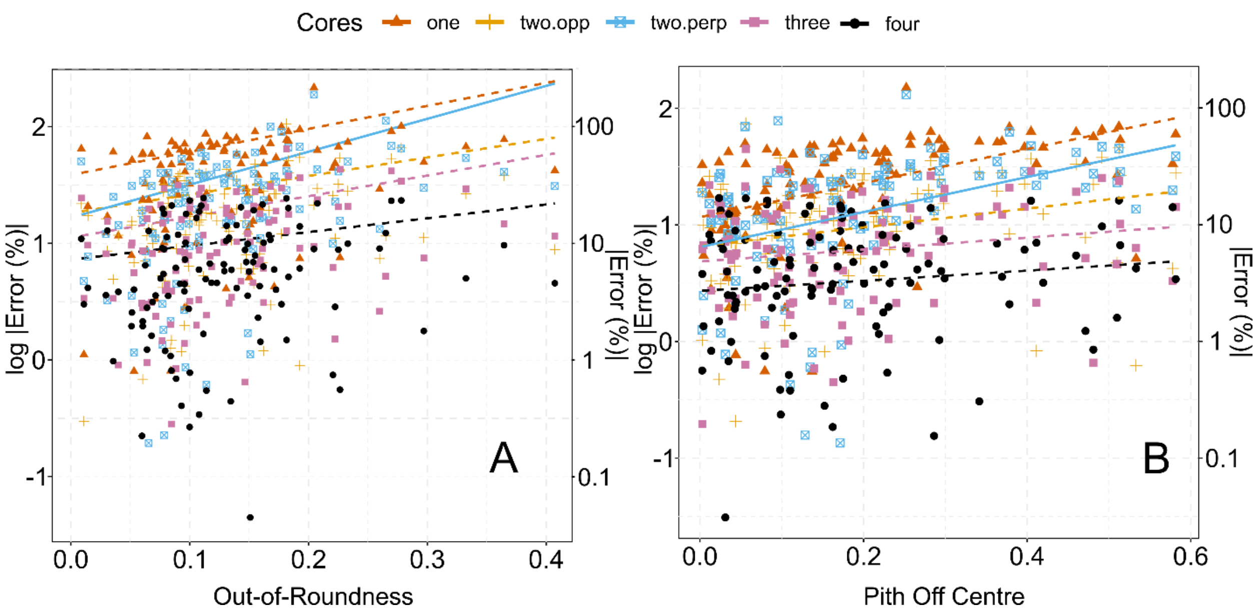

Figure 4. Effect of eccentricity on BAI estimation error, as a function of the number and placement of cores sampled. Panel A. Effect of stem out-of-roundness (OOR) on |%Error|. Increasing OOR increases estimation error but increasing the number of cores sampled can correct for this. Taking 2-opposite cores is better than 2-perpendicular. OOR regressions: With 4 cores, log(|%Error|) = 0.36 + 1.18*OOR. With 3 cores, log(|%Error) = 0.55 + 1.77*OOR. With 2-opposite cores, log(|%Error|) = 0.76 + 1.59*OOR. With 2-perpendicular cores, log(|%Error|) = 0.72 + 2.82*OOR. With one core, log(|%Error|) = 1.09 + 1.97*OOR (Table S9). Panel B. Effect of pith off centre on |%Error|. Increasing POC increases estimation error but increasing the number of cores sampled can correct for this. Taking 2-opposite cores is better than 2-perpendicular. POC regressions: with 4 cores, log(|%Error|) = 0.43 + 0.43*POC. With 3 cores, log(|%Error|) = 0.68 + 0.51*POC. With 2-opposite cores, log(|%Error|) = 0.81 + 0.80*POC. With 2-perpendicular cores, log(|%Error|) = 0.81 + 1.5*POC. With one core, log(|%Error|) = 1.07 + 1.44*POC (Table S10). Dotted lines have non-significant slopes and solid lines have significant slopes.

WHICH METHOD OF BAI ESTIMATION BEST ACCOUNTS FOR ERROR DUE TO ECCENTRICITY?

With two perpendicular cores, we found differences in the ability of different area calculation methods to account for POC, but not for OOR (Fig. 5; Table S1, S12 & S13). The effect of POC on BAI estimation error only varied slightly with0. the method used. For this type of eccentricity, the Ellipse and Geometric methods performed identically as each other and differently from Arithmetic and Quadratic methods, with significantly higher intercepts and lower slopes (Table S13, Fig. 5B). At low POC values, their higher intercept led to 8% more error (estimates = 0.92 vs. 0.82, p = 0.02), but as POC values increase, Ellipse and Geometric methods out-performed Arithmetic and Quadratic, due to their lower slope (estimates 0.71 v. 1.35, p = 0.001). For example, stems with POC of 0.6 led to an error of 22% on average with the Geometric and Ellipse methods and of 43% on average for the Arithmetic and Quadratic methods.

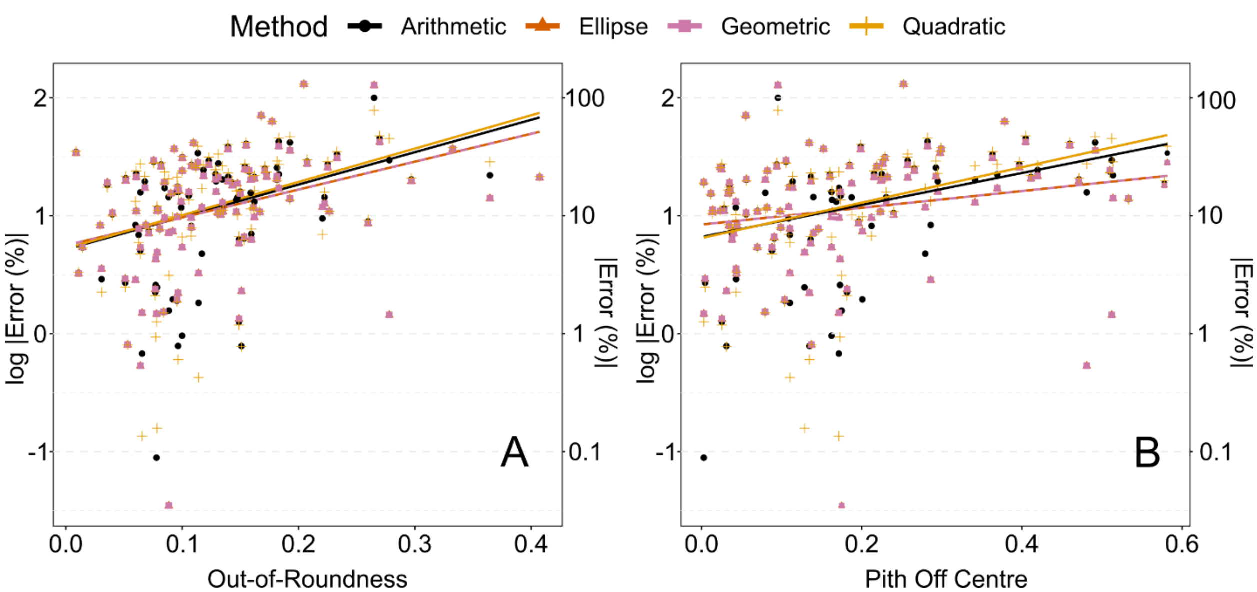

Figure 5. Effect of eccentricity on BAI estimation error, as a function the method. Since Ellipse and geometric overlap each other, the Ellipse is shown as a dotted line. Panel A. Effect of out-of-roundness (OOR) on |% Error|. None of the four methods explored can correct for the increasing in estimation error due to OOR. OOR Regressions: With Arithmetic, log(|%Error|) = 0.71 + 2.75*OOR. With Ellipse and Geometric, log(|%Error|) = 0.74 + 2.37*OOR. With Quadratic, log(|%Error|) = 0.72 + 2.83*OOR. Panel B. Effect of pith off-centre (POC) on |% Error|. None of the explored methods can account for the increases in estimation error due to POC. The Ellipse and Geometric methods preform significantly better than the other two methods (p = 0.02). POC Regressions: With Arithmetic, log(|%Error|) = 0.82 + 1.35*POC. With Ellipse and Geometric, log(|%Error|) = 0.92 + 0.71*POC. With Quadratic, log(|%Error|) = 0.81 + 1.5*POC. Solid lines show significant regressions.

4. Discussion

Accurate BAI estimations are essential for ecology and forestry to obtain accurate estimations of tree growth, population dynamics and lumber yields. Current BAI estimation methods assume that trees are perfect circles, yet trees commonly exhibit eccentricity, both in pith location and stem shape. Current estimation methods may therefore introduce bias by not accounting for this eccentricity. Indeed, in this dataset, eccentricity was common with a median pith off-centre eccentricity (POC) of 0.162, with values ranging from 0 to 0.6, and a median out-of-roundness eccentricity (OOR) of 0.114, with values ranging from 0 to 0.4. BAI estimated single cores on samples with no eccentricity, produced error of 10% on average (Fig. 4). Overall, our study found two key takeaways: (1) tree eccentricity does affect BAI estimation accuracy, with both POC and OOR having comparable effects and, (2) the number and location of cores taken impacts estimation accuracy.

The data shows that POC and OOR can significantly impact estimation accuracy when few cores are taken (Fig. 3). Hence, accounting for both POC and OOR can considerably improve BAI estimations in eccentric trees, which was commonly observed in our dataset. Likewise, we found that increasing the number of cores taken (up to 4 cores) significantly improves BAI estimation accuracy on eccentric trees. Indeed, increasing the number of cores taken can account for both types of eccentricity, with 4 cores being able to fully account for the error associated with eccentricity (Fig. 4). Our finding that eccentricity impacts BAI estimations accuracy is consistent with the literature, which found that OOR (Biging & Wensel, 1988; Fallah *et al.* 2012; Visser *et al.* 2023) and POC (Fallah *et al.* 2012; Pirie, Fowler, & Triggs, 2015; Visser *et al.*, 2023) were important factors to consider when estimating BAI. Our results corroborate findings by Visser *et al*. (2023) who suggested taking four cores to obtain ‘reasonably good’ BAI estimates. Our results are also in line with Buras & Wilmking (2014) who found that in shrubs, taking four radial measurements per stem disc provides a good representation of the average stem disk growth. Here, we find that taking fewer than four cores reduces but does not fully correct for eccentricity (Fig. 4B). Thus, when sampling one to three cores, we should also quantify, and report estimation error induced by OOR and POC. Note that the findings from Visser *et al.* (2023) were based on simulations of tree growth following different models, and the work from Buras & Wilmking (2014) were based on plants of shrubby growth forms. The conclusion that the error arising from eccentricity is reduced with increasing core numbers is becoming robust, as it is supported by work using different methods and study systems.

Our results also show that the position of the cores taken relative to each other also impact BAI estimation. We found that when stems are eccentric, sampling two cores opposite from each other better captures both POC and OOR than sampling the cores perpendicular from each other (Fig. 4). Further, this core placement allows us to quantify the pith eccentricity of the sample.

Pith and stem eccentricities are not the only possible sources of error when estimating BAI from cores. Indeed, here the glmm model found that 34% of the variance in error was associated with the four factors studied here: the two eccentricities, the area calculation method and the number of cores sampled. The fact that two thirds of the error is unexplained suggests that much of the error in BAI estimation comes from other sources, including geometric irregularities not captured by our two-eccentricity metrics (see Visser et al. 2023).

Further, other sources of errors that were not present in our samples but that are common to increment core samples or cross-sections could interact with the error due to pith and stem eccentricities. For example, it is common for the pith to be missing and for the samples to containing missing, partly missing, or false rings (Buras & Wilmking 2014, Visser 2023). On cores with missing piths, the area is typically calculated using diameter measurements instead of radii. Calculating area from diameters assumes that the pith is centered, which is bound to lead to an error of unknown magnitude when it is not. To our knowledge, no research has been done on the interaction between eccentricities and other sources of error. Future research examining how errors from eccentricity and other sources interact would therefore be valuable to improve BAI estimations. Given that we have no data on how these various sources of error might interact, if samples are known to have error from multiple sources, statistical best practices advise to add these errors (Taylor. 1997). While not optimal, this approach provides the most conservative error estimates.

RECOMMENDATIONS

Method: Our findings show that while eccentricity leads to error, field sampling strategies can help minimize it. When deciding on a calculation method to estimate BAI, we recommend not using geometric method because it performs significantly worse than other methods. The other three methods examined performed similarly. In this study, the quadratic method produced fewer and smaller outliers and did not systematically over or under-estimate error. If our data are representative of other populations, it may be beneficial to calculate the area using the area of a circle and a mean radius calculated from a quadratic mean (Fig. 5). We note that our results on the best method to use differ from Visser *et al*. (2023) who found that the ellipse approach, which multiplies adjacent radii, yielded a smaller error. This difference could be due to differences in methods. Visser *et al.* (2023) estimated BAI from 'outside in' (i.e. when the position of the pith on the sample was unknown and diameter measurements were used instead of radii measurements). In contrast, our study used the ‘inside-out’ approach, where the true position of the pith is known, and radii are used to calculate area.

Number and location of cores: Further, as discussed above, 3 or 4 cores should ideally be taken, as multiple cores can effectively account for both stem and pith eccentricity and will therefore provide the most accurate estimations of BAI from tree cores. However, this recommendation is not practical in the field, as getting even one good core that samples the pith in an eccentric stem often requires multiple coring attempts. Fortunately, taking two opposite cores provides drastic improvements over taking a single core, we thus recommend taking two cores opposite from each other (180˚) to minimize the error introduced by POC. Pith eccentricity is often associated with terrain inclination, such that the pith will be located uphill of the geometric centre in gymnosperms (compression wood formation) and downhill of the geometric centre in angiosperms (tension wood formation). Thus, taking the two oppose cores uphill and downhill of the slope is likely to sample the longest and shortest diameters on the stem. As these two measurements are also required to calculate POC, a second benefit of taking the two cores opposite to each other is that it allows us to quantify pith eccentricity and thus to report confidence intervals around the BAI estimates.

Unfortunately, this sampling recommendation that will minimize estimation error is counter to the current best practices for quantitative wood anatomy measurements – where taking cores uphill or downhill is avoided to avoid sampling reaction wood (compression or tension wood). It may thus not be possible to take core samples on eccentric trees that are adequate for both wood anatomy measurements and accurate growth estimations.

Estimating eccentricity: Since with a single core, in some samples we found BAI estimation error arising from eccentricity upwards of 700% (data not shown), we strongly recommend taking more than one core. However, this may not be possible for logistical reasons. As a single core can give widely wrong estimates and taking a second core is time consuming, we recommend estimating POC of the sampled tree in the field after taking a first core in order to determine if sampling a second core is needed. This decision can be based on a pre-determined threshold of acceptable error. First, the radius of a circle being the circumference divided by 2π, the average radius used in the POC calculation (Eqn. 5) can be calculated on trees with circular boles as the DBH measurement divided by two. Second, if a core that hits the pith is taken perpendicular to the circumference, then the observed radius on the core is the shortest radius. Eqn. 5 then becomes $|r_{EXPECTED} - r_{OBSERVED}| / r_{EXPECTED}$, with $r_{EXPECTED}$ being the radius calculated from the diameter tape and $r_{OBSERVED}$ being the radius observed on the core. For example, if one aims to maintain the error in BAI estimation arising from POC under 30%, based on the equations provided in Table S1, any POC value higher than 0.2 would warrant taking a second opposite core (Fig. 4B). OOR can also be estimated in the field based on two simple measurements. OOR is the ratio of the diameter of the smallest circle inscribed within the cross-section over its largest diameter. On stems without concavities or lobes, the largest diameter can be found in the field by placing a tree caliper horizontally around the stem at breast height and rotating it until the largest diameter is found. The diameter perpendicular to this largest diameter approximates the diameter of the largest circle inscribed within the cross section. The ratio of these two diameters then gives an estimate of OOR. These diameters will include the thickness of the bark and will include some degree of error if bark thickness or flexibility is not even at the two points of measurement. If so desired, practitioners can remove this error by measuring bark thickness with a bark gauge at the 4 points of diameter measurements and subtracting it to obtain the diameters of the xylem.

The supplementary materials provide examples of how to extract the relevant formula from the glmm coefficients in order to calculate |%Error| from POC and OOR based on the area calculation method used and the number of cores taken. We also show how one can then calculate for each cross-section the BAI estimation error arising from its POC and OOR values. When possible, practitioners can parametrize these equations based on their specific study system, which may have different ranges of POCs and OORs from the dataset used here.

In summary, irrespective of the number of cores one can collect, we recommend as a best practice that, using the method described above, ecologists and foresters report confidence intervals around the BAI estimation arising from both POC and OOR.

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Supplementary Materials

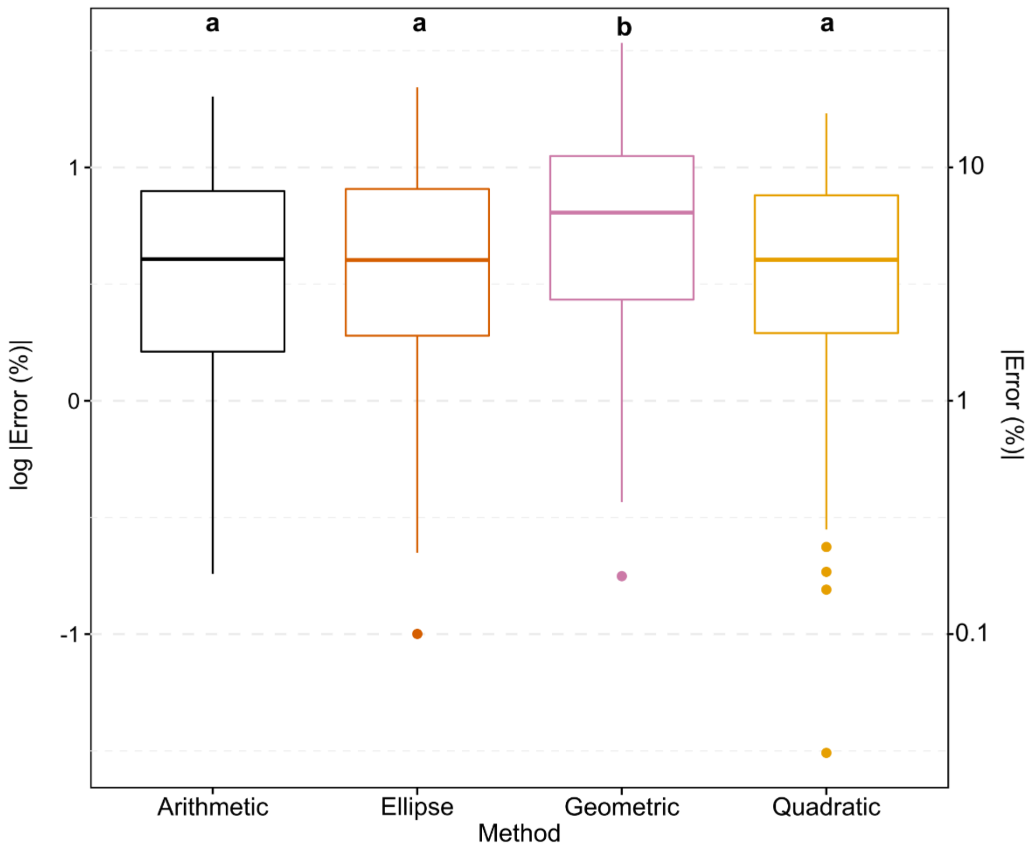

Figure S1. Effect of BAI Estimation Method on |%Error|. Estimating the mean radius using the geometric mean produces a significantly worse estimate of BAI, than the other three methods, but the other three methods are not significantly different from each other (ANOVA: p = 1.282E-07, Table S7 & S8).

Results with |%Error|

Table S1. Full General Linear Mixed Model (GLMM) with All Variables and log(|%Error|). The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. Bolded terms are statistically significant. Default method of the intercept is arithmetic and default number of cores is four. Bolded terms are statistically significant at a threshold of alpha = 0.05.

Predictor	Parameter Estimate	Confidence Interval	P-value	
(Intercept) [Four cores; Arithmetic]	**0.19**	**0.00 : 0.39**	**0.049**	*
OOR	**1.72**	**0.30 : 3.14**	**0.019**	*
POC	**1.59**	**0.80 : 2.38**	**1.13E-4**	***
Method [Ellipse]	0.04	-0.11 : 0.19	0.595	
Method [Geometric]	**0.19**	**0.05 : 0.33**	**0.007**	**
Method [Quadratic]	-0.08	-0.22 : 0.05	0.234	
Cores [one]	**0.64**	**0.49 : 0.78**	**<2.00E-16**	***
Cores [three]	**0.25**	**0.09 : 0.40**	**0.002**	**
Cores [two opp]	**0.32**	**0.17 : 0.48**	**3.28E-05**	***
Cores [two perp]	**0.33**	**0.18 : 0.47**	**1.05E-05**	***
OOR * Method [Ellipse]	0.04	-0.85 : 0.93	0.931	
OOR * Method [Geometric]	0.05	-0.68 : 0.79	0.885	
OOR * Method [Quadratic]	0.35	-0.39 : 1.08	0.355	
Method [Ellipse] * Cores [one]	-0.03	-0.18 : 0.12	0.680	
Method [Geometric] * Cores [one]	**-0.20**	**-0.35 : -0.05**	**0.008**	**
Method [Quadratic] * Cores [one]	0.01	-0.14 : 0.16	0.872	
Method [Geometric] * Cores [three]	**-0.16**	**-0.31 : -0.01**	**0.032**	*
Method [Quadratic] * Cores [three]	0.06	-0.09 : 0.21	0.432	
Method [Geometric] * Cores [two opp]	**-0.26**	**-0.41 : -0.11**	**0.001**	***
Method [Quadratic] * Cores [two opp]	0.11	-0.03 : 0.26	0.132	
Method [Ellipse] * Cores [two perp]	-0.05	-0.20 : 0.10	0.531	
Method [Geometric] * Cores [two perp]	**-0.22**	**-0.37 : -0.07**	**0.004**	*
Method [Quadratic] * Cores [two perp]	0.03	-0.12 : 0.18	0.696	

OOR * Cores [one]	0.57	-0.27 : 1.40	0.182	
OOR * Cores [three]	0.60	-0.31 : 1.50	0.195	
OOR * Cores [two opp]	**0.93**	**0.02 : 1.83**	**0.044**	*
OOR * Cores [two perp]	**1.73**	**0.92 : 2.55**	**3.31E-05**	***
POC * Method [Ellipse]	-0.08	-0.51 : 0.36	0.733	
POC * Method [Geometric]	0.03	-0.33 : 0.39	0.884	
POC * Method [Quadratic]	0.14	-0.22 : 0.50	0.446	
POC * Cores [one]	**0.57**	**0.16 : 0.98**	**0.006**	**
POC * Cores [three]	**-0.63**	**-1.07 : -0.18**	**0.006**	**
POC * Cores [two opp]	**-0.56**	**-1.01 : -0.12**	**0.013**	*
POC * Cores [two perp]	-0.04	-0.44 : 0.36	0.845	
OOR * POC	**-6.52**	**-10.79 : -2.24**	**0.003**	*
Random Effect (Sample ID)				
σ^2	0.16			
$\tau_{00\ SampleID}$	0.05			
ICC	0.24			
$N_{SampleID}$	109			
Observations	1954			
Marginal R^2 / Conditional R^2	0.339 / 0.499			
Significance codes	‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05; ‘.’ 0.1			

Table S2. Simplified General Linear Mixed Model with log(|%Error|). Backwards model selection was performed to simplify the GLMM shown in Table S1. The terms dropped from the full model are OOR*Method and POC*Methods. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. The default method of the model is arithmetic and default number of cores is four. The terms for quadratic method are in purple and those for one core are in blue to illustrate the calculation example below. Bolded terms are statistically significant at a threshold of alpha = 0.05.

Predictor	Parameter Estimate	Confidence Interval	P-values	
(Intercept) [Four cores; Arithmetic]	0.18	-0.01 : 0.36	0.063	
OOR	**1.83**	**0.49 : 3.17**	**0.008**	**
POC	**1.62**	**0.86 : 2.37**	**4.90E-05**	***
Method [Ellipse]	0.03	-0.07 : 0.14	0.554	
Method [Geometric]	**0.20**	**0.10 : 0.31**	**1.53E-04**	***
Method [Quadratic]	-0.01	-0.12 : 0.09	0.822	
Cores [one]	**0.64**	**0.49 : 0.78**	**<2.00E-16**	***
Cores [three]	**0.24**	**0.09 : 0.39**	**0.002**	**
Cores [two opp]	**0.31**	**0.16 : 0.46**	**4.39E-05**	***
Cores [two perp]	**0.33**	**0.18 : 0.47**	**1.03E-05**	***
Method [Ellipse] * Cores [one]	-0.03	-0.18 : 0.12	0.677	
Method [Geometric] * Cores [one]	**-0.20**	**-0.35 : -0.05**	**0.008**	**
Method [Quadratic] * Cores [one]	0.01	-0.14 : 0.16	0.874	
Method [Geometric] * Cores [three]	**-0.16**	**-0.31 : -0.01**	**0.032**	*
Method [Quadratic] * Cores [three]	0.06	-0.09 : 0.21	0.432	
Method [Geometric] * Cores [two opp]	**-0.26**	**-0.41 : -0.11**	**6.44E-04**	***
Method [Quadratic] * Cores [two opp]	0.11	-0.03 : 0.26	0.132	
Method [Ellipse] * Cores [two perp]	-0.05	-0.20 : 0.10	0.531	
Method [Geometric] * Cores [two perp]	**-0.22**	**-0.37 : -0.07**	**0.004**	**
Method [Quadratic] * Cores [two perp]	0.03	-0.12 : 0.18	0.696	
OOR * Cores [one]	0.57	-0.27 : 1.40	0.182	
OOR * Cores [three]	0.62	-0.26 : 1.50	0.167	
OOR * Cores [two opp]	**0.95**	**0.07 : 1.83**	**0.035**	*
OOR * Cores [two perp]	**1.73**	**0.92 : 2.55**	**3.27E-05**	***

POC * Cores [one]	**0.57**	**0.16 : 0.98**	**0.006**	**
POC * Cores [three]	**-0.59**	**-1.03 : -0.16**	**0.007**	**
POC * Cores [two opp]	**-0.53**	**-0.97 : -0.10**	**0.016**	*
POC * Cores [two perp]	-0.04	-0.44 : 0.36	0.845	
OOR * POC	**-6.52**	**-10.79 : -2.24**	**0.003**	**
Random Effect (Sample ID)				
σ^2	0.16			
τ_{00} SampleID	0.05			
ICC	0.24			
N SampleID	109			
Observations	1954			
Marginal R^2 / Conditional R^2	0.339 / 0.499			
Significance codes	'***' 0.001; '**' 0.01; '*' 0.05, '.' 0.1			

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Extracting the relevant formula from coefficients in Table S2

Practitioners can extract from the glmm table S2 the appropriate equation to use based on their sampling design. The formula is of the general shape:

$\log(|\%Error|) = \alpha_{ij} + \beta_{1ij}OOR + \beta_{2ij}POC + \beta_{3}OOR{:}POC + \varepsilon$ [Eqn. S1]

where α is the intercept, β are the slopes, ε is the error associated with the equation and follows the form $\varepsilon \sim N(0, \sigma^2 = 0.0499)$, i refers to the specific area calculation method used, and j refers to the specific number and position of cores used. The parameter estimates of the two categorical variables (Methods i [Ellipse, Geometric or Quadratic] and Cores j [one, three, two opp and two perp] and of their interaction (Methods * Cores)) are added as needed to modify the intercept parameter α_{ij} in Eqn. S1. The parameter estimates of the interaction terms between categorical and continuous variables (OOR*Cores and POC*Cores) are added as needed to modify the respective slopes β_{1ij} and β_{2ij} in Eqn. S1 (Zuur & Ieno 2016). Thus, if one is indeed using the formula's default levels of the categorical variables (four cores, is estimating basal area assuming the area of a circle and calculating the mean radius using the arithmetic mean) the formula is:

Method: Arithmetic; Cores: Four

$\log(|\%Error|) = 0.18 + 1.83*OOR + 1.62*POC - 6.52*OOR{:}POC$ [Eqn. S2]

We recommend using the quadratic method, as it produced fewer and smaller outliers in our dataset. Below we report the equations associated with each of the 5 combinations of quadratic methods and the 5 alternative coring positions and number.

Method: Quadratic; Cores: Four

$\log(|\%Error|) = 0.17 + 1.83*OOR + 1.62*POC - 6.52*OOR{:}POC$ [Eqn. S3]

Method: Quadratic; Cores: Three

$\log(|\%Error|) = 0.47 + 2.45*OOR + 1.03*POC - 6.52*OOR{:}POC$ [Eqn. S4]

Method: Quadratic; Cores: Two-Opposite

$\log(|\%Error|) = 0.59 + 2.78*OOR + 1.09*POC - 6.52*OOR{:}POC$ [Eqn. S5]

Method: Quadratic; Cores: Two-Perpendicular

$\log(|\%Error|) = 0.53 + 3.56*OOR + 1.58*POC - 6.52*OOR{:}POC$ [Eqn. S6]

Method: Quadratic; Cores: One

$\log(|\%Error|) = 0.82 + 2.4*OOR + 2.19*POC - 6.52*OOR{:}POC$ [Eqn. S7]

Below we provide an example of how we derived these parameters, for the quadratic method and 1 core. Applying all the modifiers associated with these two factors, the equation becomes:

$$\log(|\%Error|) = 0.18-0.01+0.64+0.01 +(1.83+0.57)*OOR +(1.62 + 0.57)*POC -6.52*OOR{:}POC$$
$$= 0.82 + 2.4*OOR + 2.19*POC - 6.52*OOR{:}POC$$

Calculating BAI estimation error with the equations.

If one had a cross-section with the median POC of our samples (0.3) and the median OOR of our samples (0.2) and a single core, they could calculate their specific BAI estimation error using equation S7 as:

$$\log(|\%Error|) = 0.82 + 2.4*OOR + 2.19*POC - 6.52*OOR{:}POC$$
$$= 0.82 + (2.4*0.2) + (2.19*0.3) - (6.52*0.2*0.3)$$
$$= 0.82 + 0.48 + 0.657 - 0.3912$$
$$= 1.5658$$

For this sample, the error associated with the measurement due to eccentricities is:

$$\log_{10}(|\%Error|) = 1.5658$$
$$|\%Error| = 10^{1.5658}$$
$$Error = \pm 37\ \%$$

An estimated BAI of $500 cm^2$ could then be reported as BAI = $500 \pm 185\ cm^2$

Table S3. %error associated with the quadratic method of calculating the mean radius of a circle, and each of the five possible coring number and placement for a cross-section of median OOR (0.2) and median POC (0.3)

Core number and position	% Error
1	37%
2-perpendicular	21%
2-opposite	12%
3	8%
4	4%

Table S4. Linear regression to determine the impact of four cores on pith eccentricity using log(|%Error|). The intercept gives results from a linear regression using the Quadratic method and four cores. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. Bolded terms are statistically significant at a threshold of alpha = 0.05

Predictors	Estimates	CI	p	
(Intercept) [Quadratic, four cores]	**0.43**	**0.27 : 0.60**	**4.60E-07**	***
POC	0.43	-0.24 : 1.11	0.208	
Observations	109			
Residual standard error: 0.520 on 107 degrees of freedom, Multiple R^2: 0.0148, Adjusted R^2: 0.00555, F-statistic: 1.603 on 1 and 107 DF, p-value: 0.208				

Table S5. Linear regression to determine the impact of one core on pith eccentricity using (log)|%Error|. The intercept gives results from a linear regression using the Quadratic method and one core. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. Bolded terms are statistically significant at a threshold of alpha = 0.05

Predictors	Estimates	CI	p	
(Intercept) [Quadratic, one core]	**1.07**	**0.94 : 1.20**	**<2.00E-16**	***
POC	**1.46**	**0.92 : 2.00**	**5.24E-07**	***
Observations	107			
Residual standard error: 0.413 on 105 degrees of freedom, Multiple R^2: 0.214, Adjusted R^2: 0.207, F-statistic: 28.6 on 1 and 105 DF, p-value: 5.242E-07				

Table S6. Linear regression to determine the impact of four cores on stem eccentricity using (log)|%Error|. The intercept gives results from a linear regression using the Quadratic method and four cores. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. Bolded terms are statistically significant at a threshold of alpha = 0.05

Predictors	Estimates	CI	p	
(Intercept) [Quadratic, four cores]	**0.36**	**0.16 : 0.56**	**0.001**	***
OOR	1.18	-0.18 :2.55	0.089	.
Observations	109			
Residual standard error: 0.517 on 107 degrees of freedom, Multiple R^2: 0.0268, Adjusted R^2: 0.0178, F-statistic: 2.948 on 1 and 107 DF, p-value: 0.0889				

Table S7. Linear regression to determine the impact of one core on stem eccentricity using log(|%Error|). The intercept gives results from a linear regression using the Quadratic method and one core. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. Bolded terms are statistically significant at a threshold of alpha = 0.05

Predictors	Estimates	CI	p	
(Intercept) [Quadratic, one core]	**1.09**	**0.91 : 1.26**	**<2.00E-16**	***
OOR	**1.97**	**0.78 : 3.17**	**0.001**	***
Observations	107			
Residual standard error: 0.444 on 105 degrees of freedom, Multiple R^2: 0.0930, Adjusted R^2: 0.084, F-statistic: 10.77 on 1 and 105 DF, p-value: 0.0014				

Table S8. 1-way ANOVA to determine the effect of area estimation method on BAI |% error|, irrespective of number of cores and eccentricity (Fig. S1). The intercept gives results from an ANOVA using the Arithmetic method. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. Bolded terms are statistically significant at a threshold of alpha = 0.05

Fixed Effects	Estimate	Std.Error	df	t value	Pr (>|t|)
(Intercept) [Arithmetic]	**0.528**	**0.0463**	**201.10**	**11.403**	**<2.00E-16**
Method [Ellipse]	0.0317	0.0404	324	0.784	0.434
Method [Geometric]	**0.203**	**0.0404**	**324**	**5.029**	**8.19E-07**
Method [Quadratic]	-0.012	0.0404	324	-0.299	0.765
Sum Sq = 3.275, Mean. Sq = 1.0917, NumDF = 3, DenDF = 324, F = 12.261, p = 1.28E-07 R^2 marginal = 0.0312, R^2 conditional = 0.631					

Table S9. Post-hoc Tukey Test for the 1-way ANOVA to determine the effect of area estimation method on BAI |% error|, irrespective of number of cores. Bolded terms are statistically significant at a threshold of alpha = 0.05

	Estimate	Std.Error	z value	Pr (>|z|)	
Ellipse-Arithmetic	0.032	0.040	0.784	0.866	
Geometric-Arithmetic	**0.203**	**0.040**	**5.029**	**2.47E-06**	***
Quadratic-Arithmetic	-0.012	0.040	-0.299	0.866	
Geometric-Ellipse	**0.172**	**0.040**	**4.245**	**8.75E-05**	***
Quadratic-Ellipse	-0.044	0.040	-1.083	0.837	
Quadratic-Geometric	**-0.215**	**0.040**	**-5.328**	**5.97E-07**	***
Signifiance codes: ‘***” 0.001; ‘**’ 0.01; ‘*’ 0.05, ‘.’ 0.1					

Table S10. ANCOVA of |%Error| as a function of pith off centre (POC) and number of cores (Fig 4B). The intercept gives results from an ANCOVA using four cores. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. The column 'meaning' explains how to use the estimates for each parameter to obtain the equations associated with each method. Bolded terms are statistically significant at a threshold of alpha = 0.05

Meaning	Predictors	Estimates	CI	p	
Baseline intercept	**(Intercept) [four cores]**	**0.43**	**0.29 : 0.58**	**3.68E-09**	***
Baseline Slope	(Slope) POC	0.43	-0.17 : 1.03	0.156	
Intercept modifiers	**Cores [three]**	**0.25**	**0.08 : 0.43**	**0.005**	**
	Cores [two opp]	**0.38**	**0.21 : 0.56**	**2.07E-05**	***
	Cores [two perp]	**0.38**	**0.20 : 0.55**	**3.13E-05**	***
	Cores [one]	**0.64**	**0.46 : 0.82**	**5.20E-12**	***
Slope modifiers	POC * Cores [three]	0.08	-0.66 : 0.82	0.835	
	POC * Cores [two opp]	0.37	-0.37 : 1.11	0.325	
	POC * Cores [two perp]	**1.07**	**0.33 : 1.81**	**0.005**	**
	POC * Cores [one]	**1.01**	**0.27 : 1.75**	**0.008**	**
Random Effects					
σ2		0.16			
τ00 SampleID		0.05			
ICC		0.24			
N SampleID		109			
Observations		543			
Marginal R^2 / Conditional R^2		0.321 / 0.483			

Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Equations of the regression lines
4 cores, log(|%Error|) = 0.43 + 0.43*POC
3 cores, log(|%Error|) = 0.68 + 0.51*POC
2-opposite cores, log(|%Error|) = 0.81 + 0.80*POC
2-perpendicular cores, log(|%Error|) = 0.81 + 1.5*POC
1 core, log(|%Error|) = 1.07 + 1.44*POC

Table S11. ANCOVA of log (|%Error|) as a function of out-of-roundness (OOR) and number of cores (Fig. 4A). The intercept gives results from an ANCOVA using four cores. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. The column 'meaning' explains how to use the estimates for each parameter to obtain the equations associated with each method. Bolded terms are statistically significant at a threshold of alpha = 0.05

Meaning	Predictors	Estimates	CI	p	
Baseline intercept	**(Intercept) [four cores]**	**0.36**	**0.18 : 0.54**	**1.21E-4**	***
Baseline Slope	(Slope) OOR	1.18	-0.04 : 2.41	0.058	.
Intercept modifiers	Cores [three]	0.19	-0.04 :0.41	0.101	
	Cores [two perp]	**0.36**	**0.13 : 0.59**	**0.002**	**
	Cores [two opp]	**0.40**	**0.17 : 0.63**	**0.001**	***
	Cores [one]	**0.73**	**0.50 : 0.95**	**7.57E-10**	***
Slope modifiers	OOR * Cores [three]	0.59	-0.92 : 2.11	0.443	
	OOR * Cores [two opp]	0.41	-1.11 : 1.92	0.598	
	OOR * Cores [two perp]	**1.64**	**0.13 : 3.16**	**0.034**	*
	OOR * Cores [one]	0.79	0.74 : 2.32	0.309	
	Random Effects				
σ2		0.17			
τ00 SampleID		0.05			
ICC		0.24			
N SampleID		109			
Observations		543			
Marginal R^2 / Conditional R^2		0.308 / 0.471			

Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Equations of the regression lines
4 cores, log(|%Error|) = 0.36 + 1.18*OOR
3 cores, log(|%Error|) = 0.55 + 1.77*OOR
2-opposite cores, log(|%Error|) = 0.76 + 1.59*OOR
2-perpendicular cores, log(|%Error|) = 0.72 + 2.82*OOR
1 core, log(|%Error|) = 1.09 + 1.97*OOR

Table S12. ANCOVA of (log|%Error|) as a function of out-of-roundness (OOR) and area estimation method. The intercept gives results from an ANCOVA using 2-perpendicular cores and the arithmetic method. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects (Fig. 7B). The column 'meaning' explains how to use the estimates for each parameter to obtain the equations associated with each method. Bolded terms are statistically significant at a threshold of alpha = 0.05.

Meaning	Predictors	Estimates	CI	p	
Baseline intercept	**(Intercept) [Arithmetic, 2-perp cores]**	**0.71**	**0.52 : 0.90**	**8.99E-12**	***
Baseline Slope	**OOR**	**2.75**	**1.48 : 4.01**	**3.64E-05**	***
Intercept modifiers	Method [Ellipse]	0.03	-0.08 : 0.15	0.569	
	Method [Geometric]	0.03	-0.08 : 0.15	0.569	
	Method [Quadratic]	0.01	-0.11 : 0.12	0.902	
Slope modifiers	OOR * Method [Ellipse]	-0.38	-1.17 : 0.41	0.342	
	OOR * Method [Geometric]	-0.38	-1.17 : 0.41	0.342	
	OOR * Method [Quadratic]	0.08	-0.71 : 0.86	0.846	
	Random Effects				
σ^2		0.05			
$\tau_{00\ SampleID}$		0.19			
ICC		0.81			
$N_{SampleID}$		109			
Observations		436			
Marginal R^2 / Conditional R^2		0.129 / 0.832			
Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1					

Equations of the regression lines

Arithmetic, log(|%Error)| = 0.71 + 2.75*OOR

Ellipse, log(|%Error)| = 0.74 + 2.37*OOR

Geometric, log(|%Error)| = 0.74 + 2.37*OOR

Quadratic, log(|%Error)| = 0.72 + 2.83*OOR

Table S13. ANCOVA of (log)|%Error| as a function of pith off centre (POC) and area estimation method. The intercept gives results from an ANCOVA using 2-perpendicular cores and the arithmetic method. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects (Fig. 7A). The default method used in the model is Arithmetic. The column 'meaning' explains how to use the estimates for each parameter to obtain the equations associated with each method. Bolded terms are statistically significant at a threshold of alpha = 0.05

Meaning	Predictors	Estimates	CI	p	
Baseline intercept	**(Intercept) [Arithmetic, 2-perp cores]**	**0.82**	**0.67 : 0.97**	**<2.00E-16**	***
Baseline Slope	**(slope) POC**	**1.35**	**0.72 : 1.99**	**4.72E-05**	***
Intercept modifiers	**Method [Ellipse]**	**0.10**	**0.02 : 0.19**	**0.020**	*
	Method [Geometric]	**0.10**	**0.02 : 0.19**	**0.020**	*
	Method [Quadratic]	-0.01	-0.10 : 0.08	0.823	
Slope modifiers	**POC * Method [Ellipse]**	**-0.64**	**-1.02 : -0.27**	**0.001**	***
	POC * Method [Geometric]	**-0.64**	**-1.02 : -0.27**	**0.001**	***
	POC * Method [Quadratic]	0.15	-0.22 : 0.52	0.437	
	Random Effects				
σ^2		12.95			
$\tau_{00\ SampleID}$		329.63			
ICC		0.96			
$N_{SampleID}$		109			
Observations		436			
Marginal R^2 / Conditional R^2		0.102 / 0.845			
Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1					

<u>*Equations of the regression lines*</u>
Arithmetic, log(|%Error)| = 0.82 + 1.35*POC
Ellipse, log(|%Error)| = 0.92 + 0.71*POC
Geometric, log(|%Error)| = 0.92 + 0.71*POC
Quadratic, log(|%Error)| = 0.81 + 1.5*POC

Results with %Error

Does one method produce less error than the others?

Our results with |%Error| are corroborated by our results with %Error, where the geometric method also produces significantly more error than the other three methods (Table S13). Further, with %Error the Arithmetic and Ellipse methods performed similarly to each other ($p > 0.05$; Table S13; Fig. S2) and are also overestimating %Error. However, similar to %Error, there are fewer and less outliers with the Quadratic method, compared to the other three BAI estimation methods (Fig. S2).

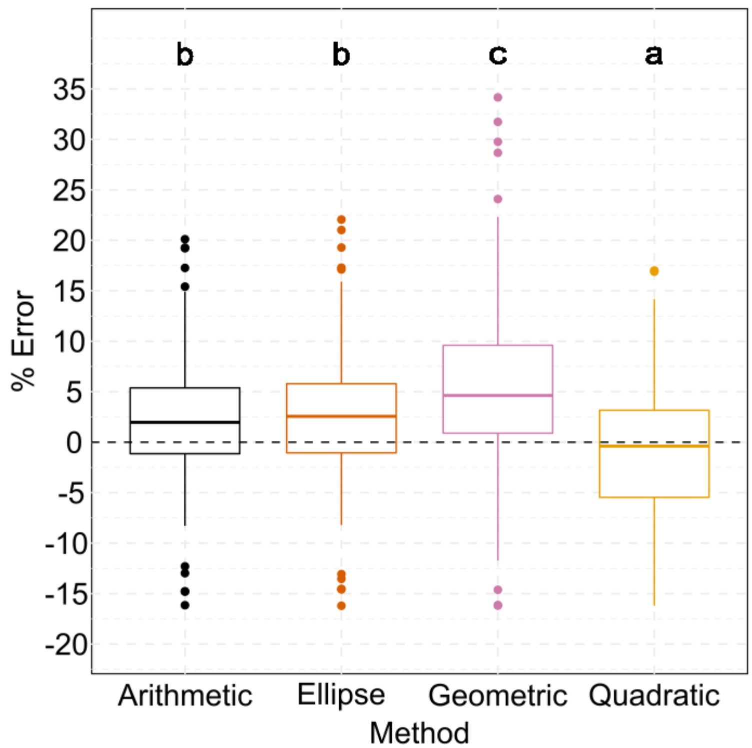

Figure S2. Effect of BAI Estimation Method on % Error.
Estimating the mean radius using the geometric mean produces a significantly worse estimate of BAI (See Kruskal-Wallis test, Table S14).

How much BAI estimation error results from eccentricity?

When considering % error instead of |% error|, we observe a similar trend, however it reveals that the large impact of POC on percent error is an underestimation of BAI (Fig. S3A): with a POC value of 0, one core gives on average -2.2% error, while a POC value of 0.6 gives on average -59.8% error (p = <2.2E-16; S = 333; rho = -0.630; Adj R^2 = 0.176; Table S14). Increasing underestimation of the basal area with increasing pith offset is expected when taking only 1 core, as this core and is the short radius of the long axis.

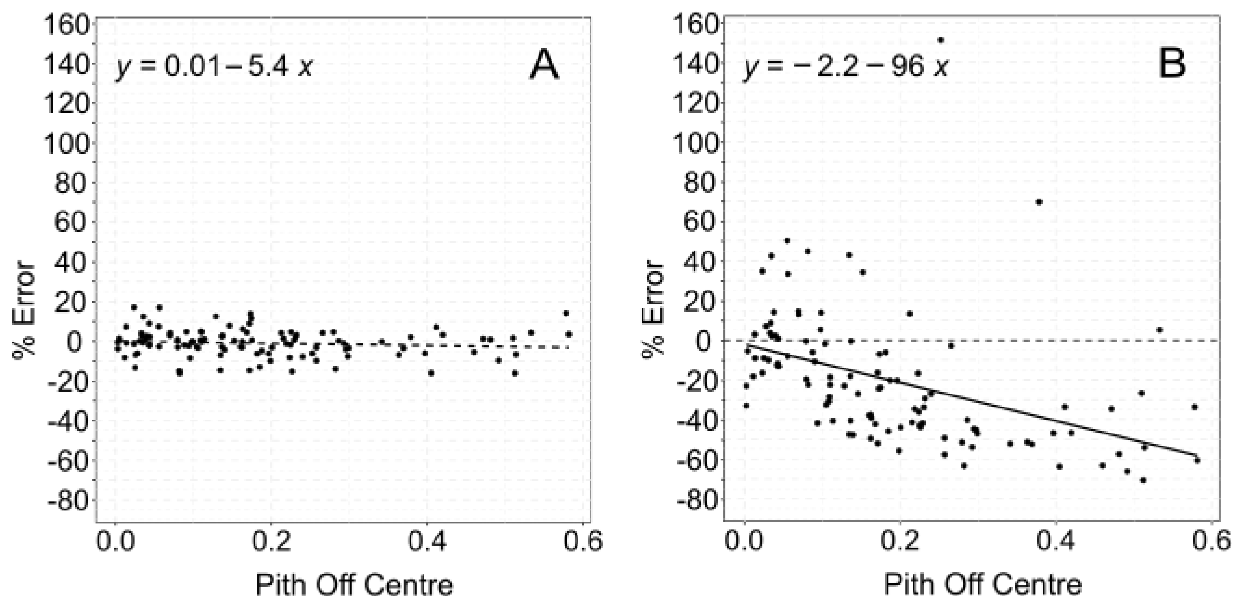

Figure S3. Effect of Pith off centre (POC) on % Error using the quadratic method, with 1 and 4 cores. Panel A. Effect of four cores on POC with % Error. Effect of POC on percent error is not significant (p = 0.193). Panel B. Effect of one core on POC with % Error. Effect of POC on percent error is significant ($p < 0.05$, Adj R^2 = 0.176; Table S14).

Similar results to POC are seen with OOR, where there is also an underestimation of BAI (Fig. S4; Table S14). However, in contrast to POC, the effect of OOR on percent error is significantly worse when taking both four cores (p = 0.044; Table 13; Fig. S3) and just one core (p = 0.024; Table 13; Fig. S3).

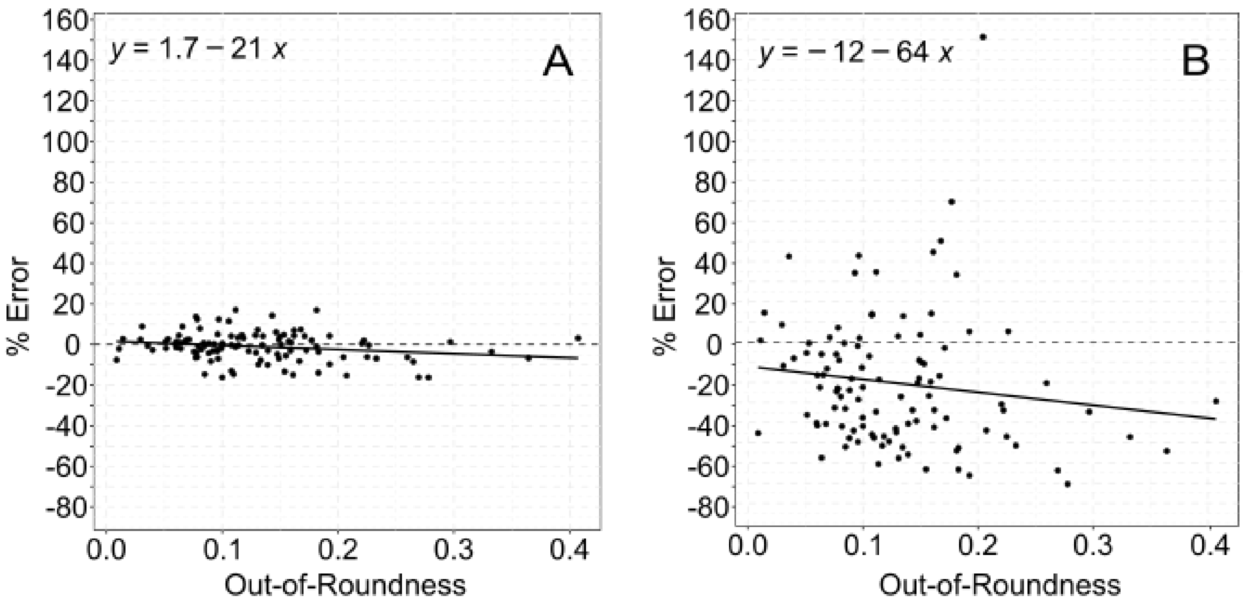

Figure S4. Effect of out-of-roundness (OOR) on % Error using the quadratic method, with 1 and 4 cores. Panel A. Effect of four cores on OOR with % Error. Effect of POC on percent error is significant with four cores (p = 0.044; Table S14). Panel B. Effect of one core on OOR with % Error. Effect of POC on percent error is significant with one core (p = 0.024; Table S14).

Which method of BAI estimation best accounts for error due to eccentricity?

Similar to |%Error|, increasing the number of cores taken decreases BAI estimation error (Table S15 & S16; Fig S5). However, with OOR there is no significant differences between the different coring methods (Table S16). With POC on the other hand, one core (p = 6.87E-11) and two cores perpendicular (p = 6.57E-06) preform worse than four cores, especially when the pith is more out of centre (i.e. higher POC values; Table S15; Fig. S5). With increasing eccentricity, it is overall better to take two opposite cores, as opposed to two cores perpendicular to each other (Fig. S5).

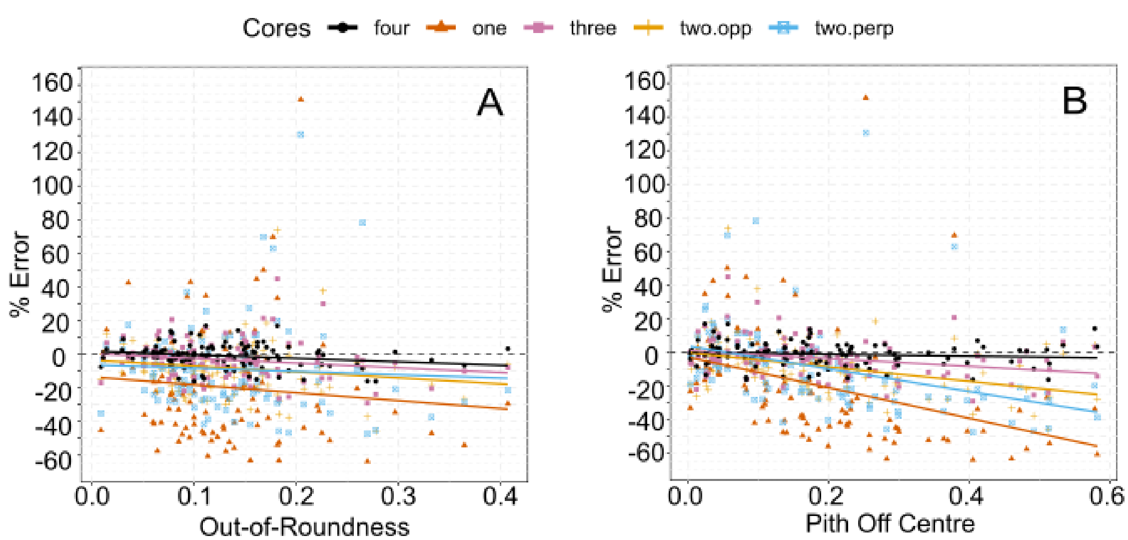

Figure S5. Effect of eccentricity on BAI estimation error, as a function of the number and placement of cores sampled. Panel A. Effect of stem out-of-roundness on % Error. Increasing OOR increases estimation error but increasing the number of cores sampled can correct for this. Taking 2-opposite cores is better than 2-perpendicular. OOR regressions: With 4 cores, (%Error) = 1.69 – 20.65*OOR. With 3 cores, (%Error) = 0.34 – 28.15*OOR. With 2-opposite cores, (%Error) = -3.52 – 20.65*OOR. With 2-perpendicular cores, (%Error) = -6.34 – 35.32*OOR. With 1 core, (%Error) = -12.52 – 59.58*OOR. Panel D. Effect of pith off centre on % Error. Increasing POC increases estimation error but increasing the number of cores sampled can correct for this. Taking 2-opposite cores is better than 2-perpendicular. POC regressions: With 4 cores, (%Error) = 0.01 – 5.44*POC. With 3 cores, (%Error) = 0.99 – 23.15*POC. With 2-opposite cores, (%Error) = -0.15 – 42.69*POC. With 2-perpendicular cores, (%Error) = 3.72 – 67.52*POC. With 1 core, (%Error) = -1.97 – 96.85*POC.

How does the number of cores used affect estimation accuracy in eccentric trees?

With two perpendicular cores, we found differences in the ability of different methods to account for POC, but not OOR (Fig. S6; Table S17 & S18). Similar to |%Error|, the effect of POC on BAI estimation error does vary slightly depending on the method used. At low POC values, Ellipse and Geometric methods perform identically, and slightly, but not significantly worse than Arithmetic and Quadratic (Table S17, Fig. S6B). As POC values increase, the Ellipse and Geometric methods perform slightly better, with significantly lower slopes than Arithmetic (Table S17). For example, for stems with POC of 0.6 this leads to an error of -25% with the Geometric and Ellipse methods and -32% for the Arithmetic method.

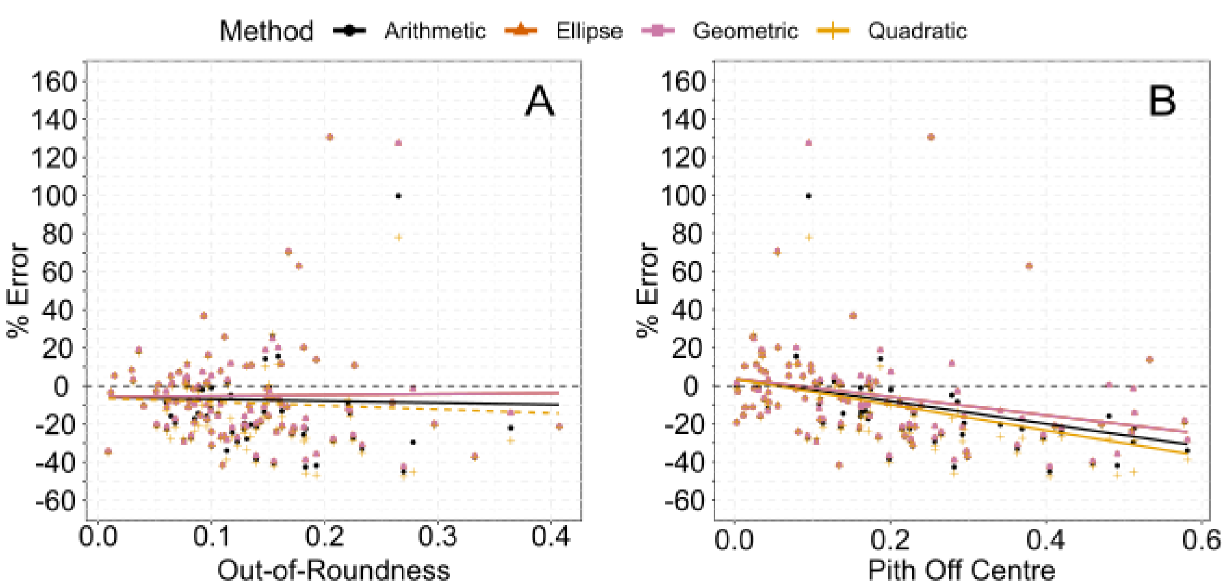

Figure S6. Effect of eccentricity on BAI estimation error, as a function the method. Ellipse and geometric overlap each other such that only geometric is visible here. Panel A. Effect of out-of-roundness (OOR) on %Error. None of the four methods explored can considerably correct for the increasing in estimation error due to OOR. The Ellipse and Geometric methods preform significantly better than the other two methods ($p = 0.04$). OOR Regressions: With Arithmetic, (%Error) = -5.92 – 9.56*OOR. With Ellipse, (%Error) = -5.7 + 5.1*OOR. With Geometric, (%Error) = -5.7 -9.56*OOR. With Quadratic, (%Error) = -6.33 + 5.1*OOR. Panel B. Effect of pith off centre (POC) on % Error. None of the explored methods can considerably account for the increases in estimation error due to POC. The Ellipse and Geometric methods preform significantly better than the other two methods ($p = 0.02$). POC Regressions: With Arithmetic, (%Error) = 3.94 – 59.43*POC. Ellipse, (%Error) = 4.02 – 48.4*POC. Geometric, (%Error) = 4.02 – 48.4*POC. Quadratic, (%Error) = 3.71 – 67.52*POC.

Table S14. Kruskal-Wallis test determine the effect of area estimation method on BAI error, irrespective of number of cores. Pairwise comparisons were done using the Wilcoxon rank sum test with continuity correction. Bolded terms are statistically significant at a threshold of alpha = 0.05. See Figure S2.

Kruskal-Wallis chi-squared	**df**	**p**	
36.582	3	5.64E-08	
Pairwise comparisons			
	Arithmetic (*p*)	Ellipse (*p*)	Geometric (*p*)
Ellipse	0.668		
Geometric	**0.007**	**0.021**	
Quadratic	**8.80E-04**	**3.30E-04**	**8.90E-08**

Table S15. Spearman ranked correlation to determine the impact of one or four cores on pith eccentricity or stem eccentricity using %Error. Bolded terms are statistically significant at a threshold of alpha = 0.05.

Eccentricity	**Number of Cores**	**S value**	**rho**	**p**	
POC	**1**	**333**	**-0.63**	**< 2.2E-16**	***
	4	243	-0.1257	0.193	
OOR	**1**	**249**	**-0.219**	**0.024**	*
	4	**258**	**-0.194**	**0.044**	*
Signifiance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1					

Table S16. Table S9. ANCOVA of %Error as a function of pith off centre (POC) and number of cores. The intercept gives results from an ANCOVA using four cores. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. As prescribed by Zuur *et al.* (2007), we reduced the heteroscedasticity by adding to the model a squared predictor term for the continuous variable. Bolded terms are statistically significant at a threshold of alpha = 0.05.

Predictors	Estimates	CI	p	
(Intercept) [four cores]	3.51	-3.83 : 10.84	0.348	
POC	-50.76	-112.86 : 11.34	0.109	
Cores [one]	-1.97	-8.37 : 4.43	0.546	
Cores [three]	0.98	-5.36 : 7.32	0.761	
Cores [two opp]	-0.16	-6.50 : 6.18	0.960	
Cores [two perp]	3.71	-2.63 : 10.04	0.251	
POC^2	88.43	-22.71 : 199.56	0.119	
POC * Cores [one]	**-91.45**	**-118.29 : -64.61**	**6.87E-11**	***
POC * Cores [three]	-17.71	-44.43 : 9.01	0.194	
POC * Cores [two opp]	**-37.25**	**-63.97 : -10.53**	**0.006**	**
POC * Cores [two perp]	**-62.08**	**-88.80 : -35.36**	**6.57E-06**	***
Random Effects				
σ^2	214.94			
$\tau_{00\ SampleID}$	153.79			
ICC	0.42			
$N_{SampleID}$	109			
Observations	543			
Marginal R^2 / Conditional R^2	0.242 / 0.558			
Signifiance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1				

Table S17. ANCOVA of %Error as a function of out-of-roundness (OOR) and number of cores. The intercept gives results from an ANCOVA using four cores. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. As prescribed by Zuur *et al.* (2007), we reduced the heteroscedasticity by adding to the model a squared predictor term for the continuous variable. Bolded terms are statistically significant at a threshold of alpha = 0.05.

Predictors	Estimates	CI	p	
(Intercept) [four cores]	-0.50	-12.03 : 11.04	0.933	
OOR	12.19	-121.72 : 146.09	0.858	
Cores [one]	**-14.21**	**-22.84 : -5.58**	**0.001**	***
Cores [three]	-1.35	-9.94 : 7.24	0.758	
Cores [two opp]	-5.21	-13.80 : 3.38	0.234	
Cores [two perp]	-8.03	-16.62 : 0.57	0.067	.
OOR ^2	-94.54	-446.44 : 257.37	0.598	
OOR * Cores [one]	-38.92	-97.09 : 19.25	0.189	
OOR * Cores [three]	-7.50	-65.08 : 50.08	0.798	
OOR * Cores [two opp]	-14.67	-72.25 : 42.91	0.617	
OOR * Cores [two perp]	0.95	-56.63 : 58.53	0.974	
Random Effects				
σ^2	242.00			
$\tau_{00\ SampleID}$	194.23			
ICC	0.45			
$N_{SampleID}$	109			
Observations	543			
Marginal R^2 / Conditional R^2	0.105 / 0.503			
Signifiance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1				

Table S18. ANCOVA of %Error as a function of pith off centre (POC) and area estimation method. The intercept gives results from an ANCOVA using 2-perpendicular cores and the arithmetic method. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. As prescribed by Zuur *et al.* (2007), we reduced the heteroscedasticity by adding to the model a squared predictor term for the continuous variable. Bolded terms are statistically significant at a threshold of alpha = 0.05.

Predictors	Estimates	CI	p	
(Intercept) [Arithmetic, 2-perp. cores]	7.60	-3.32 : 18.52	0.172	
POC	**-106.82**	**-212.69 : -0.95**	**0.048**	*
Method [Ellipse]	0.08	-1.52 : 1.68	0.922	
Method [Geometric]	0.08	-1.52 : 1.68	0.922	
Method [Quadratic]	-0.23	-1.83 : 1.37	0.779	
POC^2	92.48	-104.26 : 289.22	0.356	
POC * Method [Ellipse]	**11.03**	**4.28 : 17.77**	**0.001**	***
POC * Method [Geometric]	**11.03**	**4.28 : 17.77**	**0.001**	***
POC * Method [Quadratic]	**-8.09**	**-14.83 : -1.34**	**0.019**	*
Random Effects				
σ^2	13.68			
$\tau_{00\ SampleID}$	612.99			
ICC	0.98			
$N_{SampleID}$	109			
Observations	436			
Marginal R^2 / Conditional R^2	0.108 / 0.981			
Signifiance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1				

Table S19. ANCOVA of %Error as a function of out-of-roundness (OOR) and area estimation method. The intercept gives results from an ANCOVA using 2-perpendicular cores and the arithmetic method. The Sample ID was used as a random effect. Marginal R^2 gives the amount of variance explained only by the fixed effects, and the conditional R^2 gives the amount of variance explained by the fixed and random effects. As prescribed by Zuur *et al.* (2007), we reduced the heteroscedasticity by adding to the model a squared predictor term for the continuous variable. Bolded terms are statistically significant at a threshold of alpha = 0.05.

Predictors	Estimates	CI	p	
(Intercept) [Arithmetic, 2-perp. Cores]	-11.35	-28.50 : 5.81	0.194	
OOR	71.85	-145.09 : 288.78	0.515	
Method [Ellipse]	0.22	-1.90 : 2.35	0.836	
Method [Geometric]	0.22	-1.90 : 2.35	0.836	
Method [Quadratic]	-0.41	-2.54 : 1.71	0.701	
OOR ^2	-234.35	-826.29 : 357.59	0.437	
OOR * Method [Ellipse]	**14.66**	**0.42 : 28.90**	**0.044**	*
OOR * Method [Geometric]	**14.66**	**0.42 : 28.90**	**0.044**	*
OOR * Method [Quadratic]	-10.14	-24.38 : 4.10	0.162	
Random Effects				
σ^2	14.78			
$\tau_{00\ SampleID}$	682.23			
ICC	0.98			
$N_{SampleID}$	109			
Observations	436			
Marginal R^2 / Conditional R^2	0.010 / 0.979			
Signifiance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1				

References

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