

Evaluating the potential of oxygen isoscapes for tropical timber tracing

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ABSTRACT

Independent verification of timber origin is needed to enforce legislation aimed at combatting illegal tropical timber trade. A potential technique is tracing back the stable isotope signal preserved in wood samples, but the scarcity of reference data currently hampers its operationalization. This can be overcome by creating isoscapes. Here we develop continental isoscapes (at 0.5° resolution) for five tropical timbers based on wood $\delta^{18}\text{O}$ ratios and assess their potential for timber tracing. We compiled a pantropical database of $\delta^{18}\text{O}$ measurements from 712 trees in 20 countries. We tested effects of $\delta^{18}\text{O}$ in rainfall, potential evapotranspiration (PET), temperature and precipitation on wood $\delta^{18}\text{O}$ and used these to develop isoscapes based on quantile regression forests. A first indication of the tracing potential of these isoscapes was tested in leave one out cross validation (LOOCV) analyses. Across the five isoscapes, ranges in wood $\delta^{18}\text{O}$ values (10th–90th percentile) averaged 3.9 ‰ and $\delta^{18}\text{O}$ differences increased with distance. Yet local variability in wood $\delta^{18}\text{O}$ was substantial compared to large-scale variability. The LOOCV analysis showed that the actual origin was included in the probable origin for 59–79 % of the cases. The area of probable origin was large, however, suggesting a low spatial precision of assignment. This study finds limited support for a potential to use wood oxygen isoscapes for tropical timber tracing within continents. Necessary future steps in timber isotope tracing include improving regional representation, conducting similar analyses for other isotopes, rigorous testing of species differences and conducting blind sample tests.

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1. Introduction

An estimated 50–90 % of the traded volume of timber from major producing tropical countries is illegally sourced (Hoare, 2015), causing substantial environmental and socio-economic damage. To combat illegal timber trade, legislation has been implemented that prohibits the production, selling and import of illegally sourced timber. Enforcement of this legislation is based on the verification of required permits along the timber value chain, but this paper trail is sensitive to fraud (Wiedenhoeft et al., 2019). Forensic techniques that allow verifying the origin of tropical timber are therefore needed as an independent control mechanism (Dormontt et al., 2015; Low et al., 2022). Forensic tracing tools for tropical timber are in high demand by authorities, but also increasingly by timber producers, timber traders and certification schemes (Boekhout van Solinge et al., 2016; Gasson et al., 2021).

Two main types of fraud in tropical timber trade exist: false reporting of traded species and false reporting of geographic origin. Forensic techniques to detect species fraud are well-developed and widely applied in enforcement (Gasson, 2011; Low et al., 2022). In contrast, forensic techniques to detect false claims of geographic origin of tropical timber – based on chemical or genetic wood characteristics – are upcoming but still under development (Gasson et al., 2021). One of the promising techniques is the measurement of stable isotope ratios in wood tissue (Watkinson et al., 2020; Boeschoten et al., 2023). Relative abundance of stable isotopes of ^{13}C , ^{18}O , ^2H , ^{15}N , ^{34}S and ^{87}Sr in wood of tropical trees are associated with climatic, edaphic or other environmental conditions experienced by trees (van der Sleen et al., 2017; Watkinson et al., 2020; van der Sleen et al., 2022). As a result, these isotopic signatures may contain information on the geographic origin of traded timber and can thus assist in verifying the claimed origin of timber (English et al., 2001; Gori et al., 2018; Watkinson et al., 2022). We focus on $\delta^{18}\text{O}$ here, since $\delta^{18}\text{O}$ tracing has been successfully used to verify the geographic origin of plant-based commodities produced in temperate, e.g. wine (West et al., 2007), and tropical climate zones, e.g. cocaine, coffee and bananas (Ehleringer et al., 2000; Driscoll et al., 2020; Wang et al., 2020). It has also been applied to wood from temperate (Horacek et al., 2009; Kagawa and Leavitt, 2010; Gori et al., 2018; Watkinson et al., 2020) and tropical trees (Vlam et al., 2018; Watkinson et al., 2022). Overall, these results suggest a potential for isotopic timber tracing at coarse spatial scales. Our main question is whether wood $\delta^{18}\text{O}$ values can be used to trace back the origin of tropical timber at a within-continent scale.

So far isotopic tracing of tropical timber was strongly limited by the scarcity of reference data and limited geographic coverage of existing datasets (Gasson et al., 2021). The availability of global data products with variables on environmental conditions, such as precipitation, drought indices and ^{18}O in rainfall, which are known to influence isotopic fractionation in wood, may overcome the scarcity of reference data. Using this data, it is possible to create spatial models of isotopic signatures: isoscapes.

Here we use a unique database of $\delta^{18}\text{O}$ isotopic measurements on 712 tropical trees from 27 species in 20 countries across three continents. We link $\delta^{18}\text{O}$ values to global data products, to evaluate the potential of isotopic tracing for major tropical timbers. First, we tested if wood $\delta^{18}\text{O}$ is determined by the isotopic signature of rainfall (root uptake), total rainfall (“amount effect”) and drought (evapotranspiration). This is based on physiological insights into the main determinants of $\delta^{18}\text{O}$ in wood of tropical trees (Fig. 1; Barbour, 2007): ^{18}O in source water and ^{18}O enrichment through transpiration in leaves. During water uptake by roots no fractionation of oxygen isotopes occurs, thus water in the xylem has the same $\delta^{18}\text{O}$ as the soil water surrounding the roots, i.e. as source water (Dawson and Ehleringer, 1991). The $^{18}\text{O}/^{16}\text{O}$ ratio in source water is thus an essential determinant of wood $^{18}\text{O}/^{16}\text{O}$ ratio (Epstein et al., 1977). Leaf water $\delta^{18}\text{O}$ is controlled by the isotopic composition of the vapor outside the leaf, the air humidity and the ratio of water vapor pressure outside the leaf to saturated water vapor

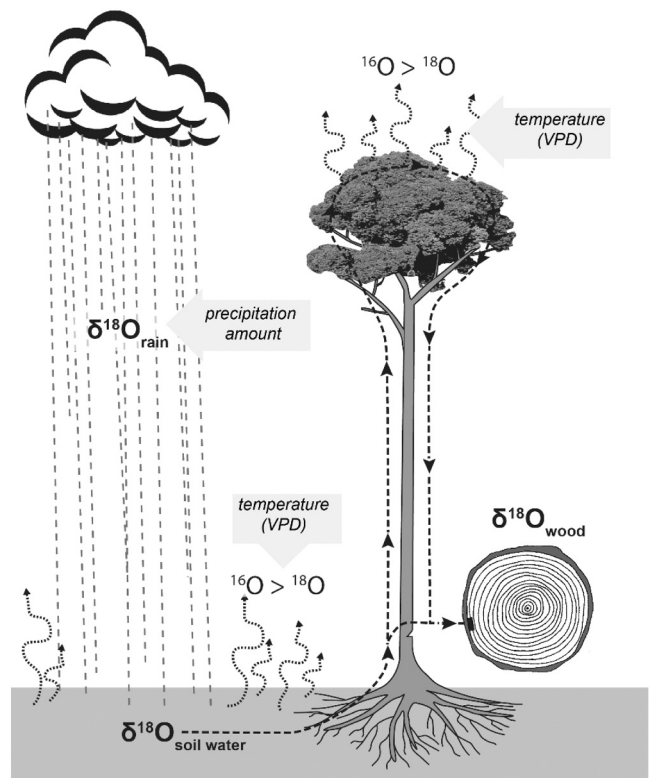


Fig. 1. Schematic representation of main processes and environmental drivers of $\delta^{18}\text{O}$ signature in wood of tropical trees. The first process is the uptake of soil water by trees, with the $\delta^{18}\text{O}$ signature of xylem water being mainly determined by the $\delta^{18}\text{O}$ signature of rainwater (the latter related to precipitation amount in the tropics). The second process is transpiration, which enriches leaf water with ^{18}O . Environmental conditions that increase leaf evapotranspiration (e.g. high temperature and VPD) can thus increase wood $\delta^{18}\text{O}$ values.

pressure in the leaf intercellular space (Zhang et al., 2020). The $\delta^{18}\text{O}$ signature of leaf assimilates is thus shaped by source water $\delta^{18}\text{O}$ values and enriched with ^{18}O through factors driving transpiration: potential evapotranspiration (PET), temperature and soil water availability. It is therefore expected that PET and temperature have a positive, and water availability a negative effect on tree-ring $\delta^{18}\text{O}$ values (Rodén and Ehleringer, 2000; Cernusak et al., 2016).

As a second step, we created genus-specific $\delta^{18}\text{O}$ isoscapes, for five tropical tree genera commonly traded for timber: *Cedrela* (Americas), *Entandrophragma*, *Erythrophleum* and *Lophira* (Africa) and *Shorea* (Southeast Asia). These isoscapes predict and map the ranges of wood $\delta^{18}\text{O}$ -isotopic values within the genus-specific distributional areas. Finally, we used these $\delta^{18}\text{O}$ isoscapes to evaluate the spatial scale at which $\delta^{18}\text{O}$ -isotopic tracing is expected to differentiate wood samples within genera by application of leave one out cross validation (LOOCV).

2. Methods

2.1. Data collection

To set up a database of $\delta^{18}\text{O}$ measurements in tropical timber species we collected wood samples from two sources: (1) live trees in natural old-growth forests (wood chunks or cores) and (2) xylarium and herbarium specimens (Tervuren Xylarium of the Royal Museum for Central Africa and Nationaal Herbarium Nederland). The largest share of samples (>90 %) were obtained from live trees, most of which have been included in earlier studies using standardized sampling protocols, sample preparation and isotopic measurements at the same facility (van der Sleen, 2014; van der Sleen et al., 2015; Paredes-Villanueva et al., 2022,

Boeschoten et al., 2023). We did not add published wood isotope data collected from other sources, because differences in sample preparation, e.g. cellulose extraction, prohibit direct comparison. Our database consisted of $\delta^{18}\text{O}$ measurements obtained from 712 trees, belonging to 27 species and 10 genera (Table 1). The timber of all these species is traded internationally, including major timbers such as Azobé (*Lophira alata* Banks ex Gaertn.f.), Tali (*Erythrophleum* spp.) and Meranti (*Shorea* spp., section *Rubroshorea* spp.). Our aim has been to cover a large number of traded timber species across tropical forests from all continents and not sample species at equal proportions. The eventual five genus-specific isoscapes were based on 677 out of the 712 trees: 179 Tropical Cedar (*Cedrela* spp.) trees, 22 trees for *Entandrophragma* spp., 272 Tali (*Erythrophleum ivorense* and *Erythrophleum suaveolens*) trees, 144 Azobé (*Lophira alata*) trees and 60 Meranti (*Shorea* spp.) trees (Table 1).

2.2. Isotope measurements

The majority of measurements (>80 %) were based on wood bulk samples and included multiple growth years. In species where identifiable growth rings were present (e.g. *Cedrela* spp.; ~25 % of samples), at least 10 growth years were included. When growth rings were indistinct, heartwood samples were collected along at least 3 cm in the radial direction (~50 % of the samples), as described by Boeschoten et al. (2023), likely representing > 10 growth years. A smaller proportion of measurements (<20 %; *Erythrophleum* spp.) was based on small (< 5 cm³) sapwood samples including possibly one to a few growth years, as described by Vlam et al. (2018). In all cases about 25 mg of wood was obtained using a sharp knife and measurements per tree were at least duplicated to reduce the potential effect of outliers. Next, cellulose extraction was performed following a modified version of the Jayme-Wise protocol (Wieloch et al., 2011). We deliberately chose to measure the $\delta^{18}\text{O}$ in cellulose instead of whole wood, even though isotopic composition between the two is assumed to be correlated. Whole-wood measurements include more wood constituents such as lignin, extractives and resin, which have different isotopic signatures (Szymbczak et al., 2011). As a result, the isotopic signal in whole wood is also affected by differences in wood composition such as higher lignin content. Cellulose, on the other hand, has a more stable isotopic signal as variation due to different biosynthetic pathways of wood constituents has been removed. This is especially relevant when aiming to identify origin in areas with low isotope variability. If measurements would be done on whole wood, a low signal of natural variability could then be masked by differences in wood composition and complicate tracing. Furthermore, measuring cellulose rather than whole wood reduces differences between species as a result of wood composition, therefore facilitating a better species comparison. Crude cellulose samples were collected from the glass funnels using a pipette and mixed by pipetting and homogenized by vortexing the watery samples for five seconds. The samples were oven-dried for three days at 55 °C. Per sample ~0.3 mg of cellulose was subsequently weighed into each of 4 mm × 3.2 mm silver cups ($\delta^{18}\text{O}$). For further detail on cellulose extraction procedure and

Table 2

Results of leave one out cross validation (LOOCV) for five tropical tree genera. The column '% correctly assigned' indicates the percentage of cases in which the area of probable origin included the actual location of origin of the test sample. The column 'Distributional area assigned' shows the average area of the probable origins, expressed as a percentage of the total distributional area of the genus.

Genus	Correctly assigned	Distributional area assigned
<i>Cedrela</i>	59 %	91 %
<i>Entandrophragma</i>	79 %	73 %
<i>Erythrophleum</i>	76 %	85 %
<i>Lophira</i>	73 %	79 %
<i>Shorea</i>	73 %	95 %
Total mean	72 %	85 %

isotopic composition determination, see Vlam et al. (2018), Parades-Villanueva et al. (2022) and Boeschoten et al. (2023).

2.3. Temporal and spatial variation in $\delta^{18}\text{O}$ wood values

Two sources of variability may induce uncertainty and noise in large-scale wood $\delta^{18}\text{O}$ patterns: inter-annual variation and spatial variation. To assess their potential influence, we quantified both types of variability.

First, inter-annual variation in wood $\delta^{18}\text{O}$ values can be substantial (van der Sleen et al., 2017) and may create uncertainty in spatial patterns of $\delta^{18}\text{O}$ wood values. Our database contains annual $\delta^{18}\text{O}$ measurements over several decades for 5–7 trees belonging to three species spread across continents (Tables S1; van der Sleen, 2014, van der Sleen et al., 2015) and allows estimating the possible implications of temporal variation in $\delta^{18}\text{O}$. The effect of temporal variation on the uncertainty in $\delta^{18}\text{O}$ values decreases with the number of years included in wood samples. To assess the effect of the number of years included, we calculated the 10th-to-90th quantile range of wood $\delta^{18}\text{O}$ values per tree when those values were averaged over 5, 10 or 20 years. We used this range as a proxy for uncertainty in wood $\delta^{18}\text{O}$ values.

Second, local versus global spatial variation may induce uncertainty and noise in large-scale wood $\delta^{18}\text{O}$ patterns. To assess its potential influence, we quantified this variability. Within site variation could be assessed based on $\delta^{18}\text{O}$ values from 6 to 34 sites. For each timber we calculated the range of wood $\delta^{18}\text{O}$ values across all sites. Similar analyses were done for within continent variation (3 continents) and global variation. These analyses can be used to evaluate local vs global spatial variability.

2.4. Quantile regression forests: wood $\delta^{18}\text{O}$ isoscape

We identified relevant environmental co-variables from stable isotope theory and prior studies and obtained those variables at the growth locations of all trees. We subsequently modelled the relationship between wood isotopic composition and mean annual $\delta^{18}\text{O}$ in

Table 1

Summary of the database of tropical wood $\delta^{18}\text{O}$ values used in this study. Columns show the number of countries from which trees were included, the number of unique trees, total number of wood samples taken across all trees, the numbers of species, and minimum and maximum latitudes are shown. The last two columns show median isoscape $\delta^{18}\text{O}$ value and median inter-quantile range (10th-90th percentile).

Genus	Timber	Continent	N Countries	N Trees	N Species	Latitudinal range (°)	Isoscape median $\delta^{18}\text{O}$ value	Median 10–90 % $\delta^{18}\text{O}$ IQR
<i>Cedrela</i>	Tropical cedar	Americas	11	179	6	–21.06 25.67	23.5	5.4
<i>Entandrophragma</i>	Sapele, Sipo, Kosipo, Tiama	Africa	5	22	4	0.76 7.61	28.2	2.2
<i>Erythrophleum</i>	Tali	Africa	5	272	2	–3.74 7.00	27.9	3.0
<i>Lophira</i>	Azobé	Africa	4	144	1	–2.18 5.38	28.0	2.7
<i>Shorea</i>	Meranti	Asia	1	60	unknown	–1.52 2.05	22.1	3.7
Other	-	-	8	35	10	–15.76 15.64	-	-
Total	-	-	20	712	27	–21.06 25.67	-	-

precipitation (GNIP), elevation, CRU TS3.21 mean 2001–2010 annual maximum temperature, precipitation, PET (Harris et al., 2020) and 19 bioclimatic variables (Fick and Hijmans, 2017). To do this we used quantile regression forests. Therefore, a total of 24 environmental variables and species and genus were added as explanatory variables to test for a species and/or genus effect. The final timber isoscapes were based on the information from the environmental variables only. Random Forest Regression, the underlying method for this analysis, is not influenced by co-linearity and non-normal data distributions and has been successfully applied for other isoscapes (Hengl et al., 2018; Brlík et al., 2023). The confidence interval around the predicted median was quantified based on all individual prediction trees, from which the inter-quantile range (10th–90th percentile) was calculated. This provided an estimation of prediction uncertainty. Based on these quantile regression forests, we predicted the spatial distribution of wood $\delta^{18}\text{O}$ in the study area by applying them to gridded layers of all covariables. To verify and visualize relations between the four most important variables in the quantile regression forest and wood $\delta^{18}\text{O}$, we constructed a multiple regression model with these explanatory variables and report its R^2 value.

2.5. Creating genus-specific isoscapes

Using the output of quantile regression forest, we created five genus-specific wood $\delta^{18}\text{O}$ isoscapes that cover the distributional range of each genus. We only included those five genera because each was represented by > 20 trees in the dataset (22–272 trees, with a mean of 135 trees per genus). We first established distribution models using occurrence records (<https://www.gbif.org/>; GBIF Secretariat, 2021) and species distribution modelling (Maxent; Phillips et al., 2006). We checked the geographic range of occurrence records and cropped these based on locations that were improbable climatically or most likely represented records outside natural forests (e.g., plantations or arboreta). Next, to reduce the effect of spatial bias due to local high density of observations, we selected only one record per 0.5° grid cell (the spatial resolution of our isoscape). Species distribution models (Maxent) used 19 bioclimatic variables (Worldclim; downloaded at 5-minute resolution) to identify climatic determinants of species occurrences. Next, all grid cells with a probability of occurrence > 0.2 were retained to get a genus distribution map. A relatively low threshold was chosen, because we did not want uncertainty in species range models to restrict the distributional area and hence provide the impression of a limited potential for isotopic tracing. All the species distribution maps within a genus were added together to get a genus level distribution area. Finally, the genus level distribution area was overlaid with the genus-specific quantile regression forest model to create a genus-specific isoscape. Because each of these genera is confined to a single continent (i.e., Americas, Africa, Asia-Oceania), the resulting isoscapes are continent-specific. These analyses were conducted in R, using the *dismo* and *terra* packages (Hijmans et al., 2020; Hijmans, 2021).

2.6. Using wood $\delta^{18}\text{O}$ isoscapes to evaluate the potential for tracing

To evaluate the potential of $\delta^{18}\text{O}$ for tracing of tropical timbers, we performed leave out cross validation (LOOCV) tests to determine tracing accuracy. This method was chosen because of the lack of blind samples in this study. Each tree in the dataset was once treated as a test sample by leaving it out of the reference dataset and subsequently performing the quantile regression forest and produce the isoscape based on $n-1$. Then for each cell in the isoscape the minimum and maximum wood $\delta^{18}\text{O}$ value was calculated based inter-quantile range. If the predicted $\delta^{18}\text{O}$ value of the test sample was within the inter-quantile range, the cell was considered a probable origin; if outside the inter-quantile range it was not considered a probable origin. Next, we verified whether actual origin of the test sample fell within the area of probable origin, in which case the assignment was considered correct. If it fell outside the

predicted area the assignment was considered incorrect. This analysis was repeated for each sampled tree in the five genera and the percentage correct assignments was calculated. For *Cedrela*, 35 % (64) of the samples were obtained from locations outside the predicted distribution area (based on MaxEnt modelling). These 64 samples were omitted from the LOOCV.

As a second step a measure of the spatial scale of correct assignments was obtained by expressing the area of probable origin as a percentage of the total isoscape area. This was calculated for each test tree and averaged to get a genus-specific value. A low percentage indicates a high spatial precision of the isoscape. Together the percentages for correct assignments and spatial scale provide an indication for expected performance of the $\delta^{18}\text{O}$ tracing for the tested genera. A high percentage correct assignment combined with a small percentage of the total distributional area as a probable origin indicates a high spatial precision. Yet, a high level of correct assignment combined with a large percentage of the total distributional area as a probable origin indicates a low spatial precision.

3. Results

3.1. Temporal and local spatial variation in wood $\delta^{18}\text{O}$

The wood $\delta^{18}\text{O}$ values in our database varied between 14.7 ‰ and 32.6 ‰, with a mean of 26.2 ‰, a standard deviation of 2.2 ‰ and a 10th-to-90th quantile range of 5.5 ‰ (23.0–28.5 ‰). This inter-quantile range is large compared to the measurement errors of the mass spectrometer used, which are in the order of 0.2 ‰.

Our analyses on the implication of interannual variability revealed that estimates of wood $\delta^{18}\text{O}$ from samples including few years can be quite uncertain (Fig S1). For instance, the 10th-to-90th quantile range of temporal variability in two of the three tested species may be close to 2 ‰ (*Cariniana ianeirensis* and *Toona ciliata*). Yet, these ranges drop strongly, to values around 0.5 ‰ when 20-year bulk samples are taken (Fig S1). To quantify local variability in wood $\delta^{18}\text{O}$ for each genus the variation both within and among sites was analysed (Fig. 2). Results show that across genera, the inter-quantile range (10th–90th percentile) of local spatial variability in wood $\delta^{18}\text{O}$ is typically around 1.0 ‰ but can be as small as 0.5 ‰ (*Entandrophragma*) or as large as 3.0 ‰ (*Shorea*). Within continent variability was higher, around 4 ‰ and among continent variability higher still: 7 ‰. These analyses show that local variability in wood $\delta^{18}\text{O}$ can be substantial compared to large-scale variability, but also that variation increases with spatial scale.

3.2. Determinants of pantropical variation in wood $\delta^{18}\text{O}$

Using quantile regression forest, we first developed a single pantropical isoscape predicting wood $\delta^{18}\text{O}$ values. The four most important environmental predictors in this model were mean $\delta^{18}\text{O}$ in precipitation, mean potential evapotranspiration (PET) and mean temperature of wettest and warmest quarters (bio8 and bio10; Fig S2A). When species and genus were included as variables in the quantile regression forest, genus was the fourth most important variable in the model indicating a genus effect in wood $\delta^{18}\text{O}$ values (Fig S2A).

We also compared the sign and magnitude of the effect of these three environmental variables in a multiple regression model and found that these were significant for precipitation $\delta^{18}\text{O}$ and PET, but not for mean temperature, explaining 67 % of variance (Fig. 3). For mean temperature of wettest quarter (bioclim variable bio8) and mean temperature of warmest quarter (bio10) the relation was not significant.

3.3. Genus-level $\delta^{18}\text{O}$ isoscapes

The genus effect in the quantile regression forest did not support the creation of a single isoscape that includes all species and genera. We therefore produced five genus-level isoscapes for well-represented

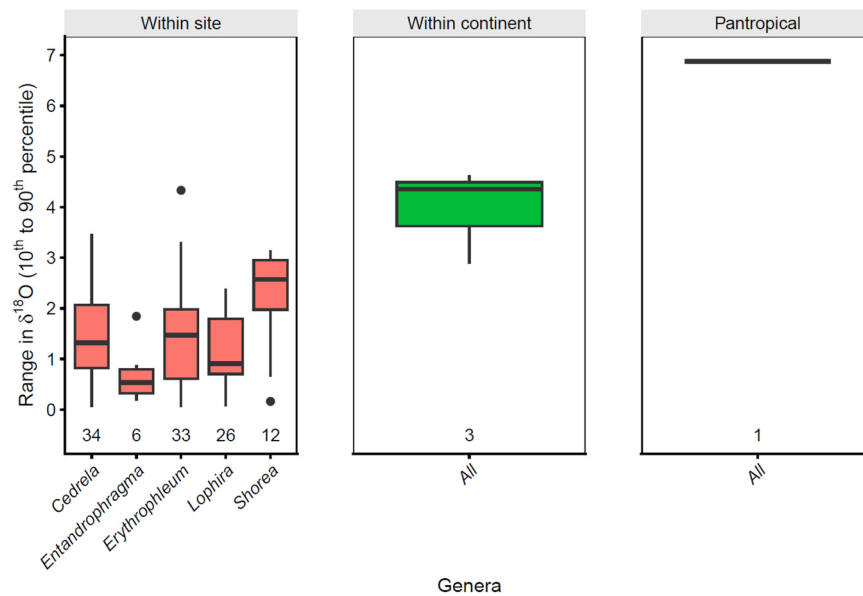


Fig. 2. Shifts in the ranges of tropical wood $\delta^{18}\text{O}$ values at different spatial scales. (A) An estimate of the local variability in wood $\delta^{18}\text{O}$. Shown is the distribution of wood $\delta^{18}\text{O}$ ranges (max-min) for trees belonging to the same genus and sampled within a site. (B) Estimate of the within continent variability and (C) the among continent variability. Number above the x-axis shows the number of sites (A) and continents (B) included.

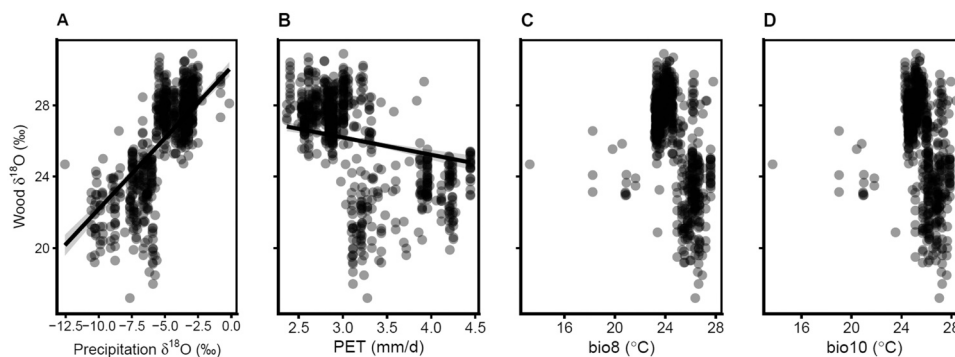


Fig. 3. Determinants of pantropical variation in wood $\delta^{18}\text{O}$. Wood $\delta^{18}\text{O}$ values are shown as a function of four variables with the highest importance in the quantile regression forest: $\delta^{18}\text{O}$ in rainwater (A), potential evapotranspiration (PET; B), mean temperature of wettest quarter (bio8; C) and mean temperature of warmest quarter (bio10; D). The black lines represent significant relationships in the multiple regression model and grey area 95 % confidence interval.

genera. The isoscape for *Cedrela* (Americas) had a mean $\delta^{18}\text{O}$ value of 23.6 ‰ and a mean inter-quantile range of 5.7 ‰ (Table 1; Figure S3). A continental-scale gradient in wood isotopic values was observed, with more ^{18}O -depletion in wood of trees growing in the west of the continent compared to the east (Fig. 4A). This continental gradient mimics that of $\delta^{18}\text{O}$ in precipitation, supported by the highest importance of $\delta^{18}\text{O}$ in rainfall for the *Cedrela* quantile regression forest (Fig S2B).

For the three African genera, no clear subcontinental-scale shift in isotopic signature was found, only a slight shift to higher $\delta^{18}\text{O}$ values for central Africa compared to West Africa. The absolute $\delta^{18}\text{O}$ values for *Lophira*, *Entandrophragma* and *Erythrophleum* (Africa), however, were quite distinct from those of *Cedrela* (Americas) and *Shorea* (Asia; Table 1, Fig. 4). With mean isoscapes $\delta^{18}\text{O}$ values between 27.8 and 28.2 ‰ for the African genera (Fig S3) and inter-quantile ranges between 2.2 and 2.9 ‰. For *Shorea*, mean $\delta^{18}\text{O}$ value was 22.1 ‰ (Fig S3) with a mean inter-quantile range of 3.7 ‰ (Table 1), which showed no clear gradient across its distributional range.

3.4. LOOCV results

For each tree in the dataset, the location of origin was predicted based on the genus-specific isoscape and leaving a specific sample out:

the LOOCV. This generally led to 72 % correct assignment of the test samples, i.e. where the actual origin was included in the probable origin based on the isoscape (for an example see Fig S4). Note, however, that the area of origin was generally large (Table S2): on average the area of probable origin included 85 % of the total distributional area for the genus, with a range of 73–95 %.

4. Discussion

Here we present the first pantropical analysis of environmental drivers for tropical wood $\delta^{18}\text{O}$ and the first set of genus-level $\delta^{18}\text{O}$ isoscapes. At the pantropical level, we find significant effects of $\delta^{18}\text{O}$ in rainfall and PET explaining spatial variability in wood $\delta^{18}\text{O}$ ratios. The five genus-specific isoscapes reveal high local variability (inter-quantile ranges), suggesting high uncertainty. This high local variability led to a low spatial precision in the LOOCV tests. On average (across 5 genera) the area of probable origin of test samples in the LOOCV analyses covered 85 % of the distributional area.

4.1. Temporal and spatial variability in wood $\delta^{18}\text{O}$

Ranges in values of wood $\delta^{18}\text{O}$ generally increase with spatial scales,

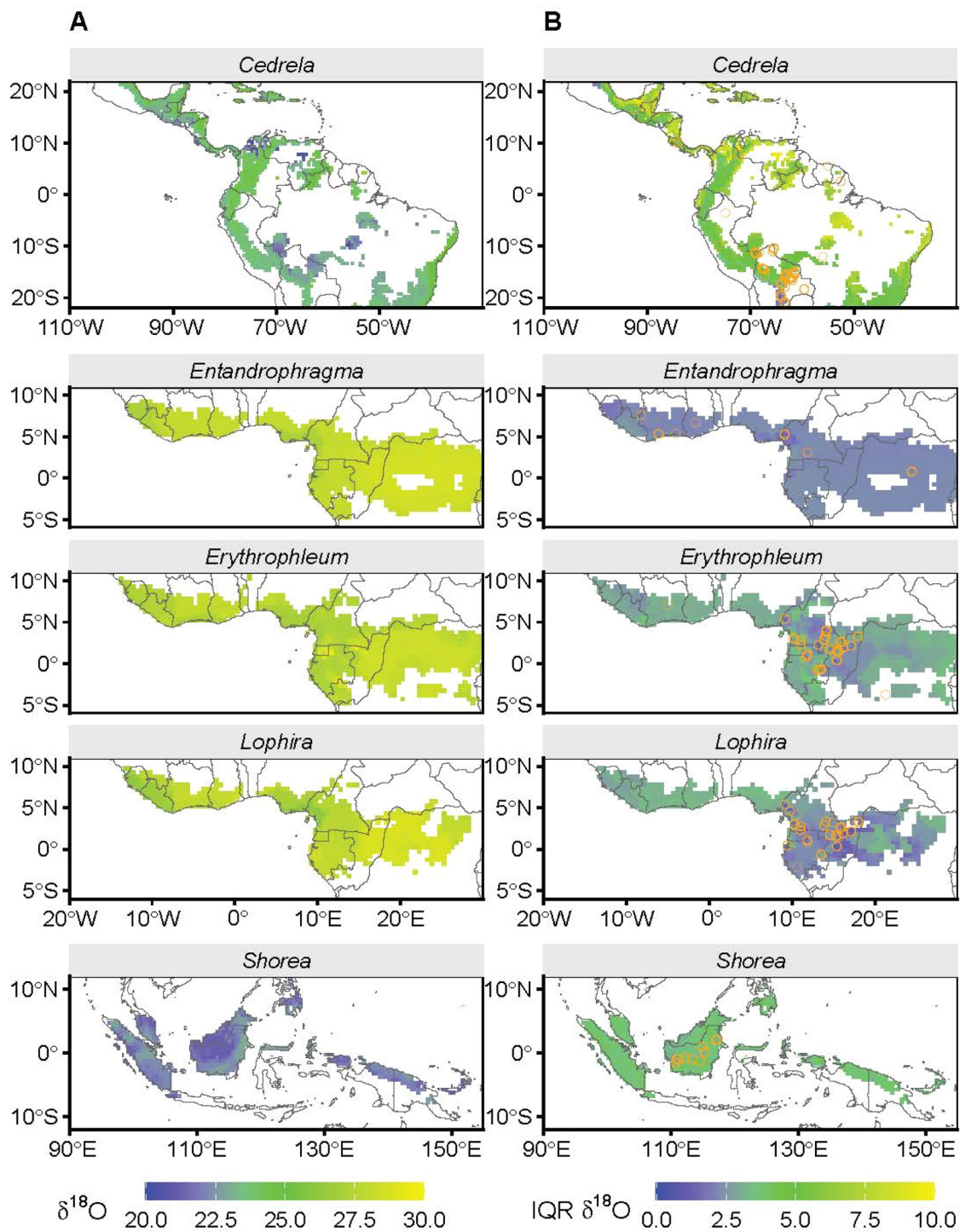


Fig. 4. Genus-specific wood $\delta^{18}\text{O}$ isoscapes for *Cedrela*, *Lophira*, *Entandrophragma*, *Erythrophleum* and *Shorea*. (A) Median wood $\delta^{18}\text{O}$ values in ‰ predicted by quantile regression forest. (B) Inter-quantile range (10th–90th percentile) of wood $\delta^{18}\text{O}$ isoscapes in ‰, predicted by quantile regression forest. Isoscapes are confined to distributional areas of the genera. The red circles indicate sampling locations.

which – in principle – provides a good basis for the application in tracing. The within-site variability, however, was relatively high compared to within-continent variability (Fig. 2). The $\delta^{18}\text{O}$ measurements for all genera (Fig. 2A) showed substantial among site variability compared to among continent variability (Fig. 2B). This induces uncertainty in estimating genus-level $\delta^{18}\text{O}$ values and creating isoscapes, thereby limiting the potential to differentiate timber based on wood $\delta^{18}\text{O}$ values alone.

Firstly, our annual $\delta^{18}\text{O}$ measurements for three species (Fig S1)

showed strong temporal variability which may induce substantial uncertainty in estimating tree-level $\delta^{18}\text{O}$ values and creating isoscapes. This is consistent with results from previous studies, which reported inter-annual variability in $\delta^{18}\text{O}$ as high as 5 ‰ (Brienen et al., 2012). The main driver of this variation is the $\delta^{18}\text{O}$ signature of source water, determined by the “amount effect” and recycling of rainfall (Fig. 1; Kurita et al., 2009; Brienen et al., 2012). The uncertainty in tree-level $\delta^{18}\text{O}$ induced by temporal variability can be strongly reduced by taking samples of wood formed during > 20 years and in any case > 10

years. For species with average radial growth rates (1.5 mm/y; Locosselli et al., 2020) this translates to samples measuring at least 3 cm in radial direction (3 mm annual diameter growth); for faster growing species we advise samples of 5 cm in radial direction. In addition, we advise taking and mixing 2–3 wood samples per tree to get a more robust tree-level estimate.

There are several other potential causes for high local variation in wood $\delta^{18}\text{O}$ values. Firstly, gradual changes in wood $\delta^{18}\text{O}$ over time may be caused by increasing rooting depth or shifting transpiration with tree size (van der Sleen et al., 2017). To minimize this uncertainty, we advise taking reference samples from recently formed wood and large individuals. Secondly, to account for changes in $\delta^{18}\text{O}$ of precipitation over time we recommend recording data on wood collection date and tree size, to potentially include this in future analyses. Thirdly, uncertainty in large-scale wood $\delta^{18}\text{O}$ isoscapes may be caused by local spatial variation within a population of trees of one species (Fig. 2). Such variation can be caused by differences in rooting depth, water availability and crown size of trees (van der Sleen et al., 2017), or – at scales of 10 s of km – by steep gradients in isotopic signature of rainfall (Förstel et al., 2011). When taking reference samples, the impact of local variation can be reduced by sampling multiple (5–10) individuals from a location and averaging $\delta^{18}\text{O}$ values.

4.2. Environmental drivers of pantropical variation in wood $\delta^{18}\text{O}$

The quantile regression forest analysis on the pantropical dataset identified three major drivers of variation in wood $\delta^{18}\text{O}$: $\delta^{18}\text{O}$ in precipitation, PET and mean temperature. Among these drivers, $\delta^{18}\text{O}$ in precipitation and PET were confirmed to significantly drive wood $\delta^{18}\text{O}$ in a multiple regression analysis. The positive effect of $\delta^{18}\text{O}$ in precipitation was expected because of the strong signature of source water $\delta^{18}\text{O}$ on wood $\delta^{18}\text{O}$ (van der Sleen et al., 2017) and is consistent with studies on spatial variation in $\delta^{18}\text{O}$ in oak wood (Watkinson et al., 2020), larch wood (Horacek et al., 2009) and coffee beans (Driscoll et al., 2020). These results are also in accordance with the strong effect of fluctuations in $\delta^{18}\text{O}$ in precipitation on temporal variation in wood $\delta^{18}\text{O}$ of tropical tree species (Brienen et al., 2012; Baker et al., 2015).

The importance of temperature annual range as an explanatory variable may be explained by two large groups of samples in this database. The first group consists of ‘continental samples’ – i.e. *Cedrela* spp. samples from Bolivia – being collected at larger distances from the oceanic source of rainfall. The other group of samples – the samples collected in Africa – being collected closer to the coast. Both higher elevations and longer distance to the sea are generally associated with lower $\delta^{18}\text{O}$ values in precipitation (IAEA/WMO, 2020) which is reflected by lower $\delta^{18}\text{O}$ values in wood.

The negative effect of potential evapotranspiration (PET) on wood $\delta^{18}\text{O}$ is rather puzzling. The opposite effect was expected, because higher PET is often associated with higher actual transpiration, causing stronger ^{18}O enrichment of leaf water and thus increasing wood $\delta^{18}\text{O}$ values. Explaining the negative association between PET and wood $\delta^{18}\text{O}$ is further complicated because the calculation of PET (Penman–Monteith equation; Harris et al., 2020) includes multiple climatic variables. In addition, the relation between PET and wood $\delta^{18}\text{O}$ within a species may be quite different from that across species, due to inter-specific differences in transpiration responses to atmospheric conditions.

4.3. Genus differences

The $\delta^{18}\text{O}$ signature of tropical tree genera growing in the same area can vary quite strongly, due to interspecific differences in $\delta^{18}\text{O}$ values of water sources, e.g. caused by rooting depth, leaf phenology and transpiration (Watkinson et al., 2022). Genus differences in wood $\delta^{18}\text{O}$ became apparent in the pantropical quantile regression forest analysis, in which genus was the fourth most important variable in explaining

among-tree variation. This result prompted us to create genus-specific isoscapes.

A better quantification of genus and/or species effects on tropical wood $\delta^{18}\text{O}$ is needed and can be obtained by sampling multiple genera/species with sufficient spatial replication (at least 10 sites per genus/species) and across large climatic gradients. The genus-level isoscapes presented here will be helpful in deciding where sampling efforts should be focused to better quantify genus/species differences and in designing sampling strategies for reference sampling initiatives such as World Forest ID (Gasson et al., 2021).

4.4. Using global gridded data to establish isoscapes: opportunities and limitations

In spite of recent initiatives to collect large amounts of samples from tropical timber species (Gasson et al., 2021) and unite references databases (Global Timber Tracking Network; <https://globaltimbertrackingnetwork.org/products/reference-database/>), it is very unlikely that in the near future isotopic reference databases will have a sufficient resolution and coverage to produce species-specific isoscapes based on reference samples only. The establishment of statistical relations between isotopic measurements and environmental variables, such as climate and soil, combined with the availability of gridded data for such variables, offers the opportunity to reduce the “burden of proof” on reference samples. This allows for making well-informed – yet cautious – inferences on expected isotopic signatures for regions not included in the reference database. That approach has been applied previously in studies on the provenance of various commodities, including coffee (Driscoll et al., 2020) and wood from temperate forests (Gori et al., 2018; Watkinson et al., 2020).

The creation of isoscapes based on statistical relations with environmental information is greatly facilitated by the increasing availability, spatial resolution and quality of gridded data products for climatic drivers of wood isotopic values. Yet, there are also some limitations to this approach. First, the reliability of the generated isoscapes strongly depends on the quality, spatial resolution and uncertainty of the gridded data, which may vary strongly among gridded data products. Cautious and critical use of these products is therefore required. Ideally, uncertainty of the gridded data would be propagated to the resulting isoscape, but techniques to do so have not been developed until now, as far as we are aware. Second, the low spatial flexibility (i.e., coarse spatial structure) of some of the gridded data products may reduce the association with isotopic data in case these vary strongly at local scales. Thus, the spatial stiffness of gridded data may reduce the spatial resolution of the isoscape, even if the map has a high resolution, and hamper reliable predictions of fine spatial structure, but see also Gori et al. (2018). Finally, it may not always be beneficial or necessary to establish isoscapes based on gridded data. For instance, if the reference dataset is large or covers the regions of interest, simple statistical comparisons and assignment tests may suffice (Horacek et al., 2009). Such direct comparisons may also be an appropriate approach if isotopic variation is poorly explained by gridded climate data in statistical models or there is reason to assume that the isoscape does not represent local isotopic variation.

4.5. What is the potential for tropical timber tracing based on wood $\delta^{18}\text{O}$?

Assessing the potential of wood $\delta^{18}\text{O}$ measurements for tropical timber tracing based on this study is difficult, because we have not conducted a blind sample test. Still, the leave one out cross validation (LOOCV) provides an indication and shows that within-continent tracing potential is limited. The general percentage of correct assignment is low (on average 72 %) and total area assigned in case of correct assignment covers a large proportion (on average 85 %) of the distributional area of the genus. In our view, these two results of the LOOCV limit the potential practicality of wood $\delta^{18}\text{O}$ for timber tracing within

continents. Yet, when considering differences among continents, we did find clear differences in isotope ratios. For example, African wood samples have clearly distinct wood $\delta^{18}\text{O}$ values compared to American and Asian samples, reflected in different values in the isoscapes. Thus, ^{18}O signatures may still be used for tracing at cross-continental scales, if reference databases contain samples of the same tree genus from different continents.

There are also possibilities to increase the spatial resolution of within continent isotopic tracing by combining $\delta^{18}\text{O}$ isoscapes with isoscapes based on other stable isotopes such as $\delta^{13}\text{C}$, $\delta^2\text{H}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$. Combining wood stable isotope ratios will increase predictive power and improve tracing potential and reliability (Watkinson et al., 2020). Additionally, adding samples that cover the entire isotopic range of a species or continent will improve the quantile regression forest models and thus the predictions of $\delta^{18}\text{O}$. To be able to do so on a large scale, it is essential that data acquisition is done in a comparable way across laboratories in order to build a shared database. Currently, collation of data is complicated by differences in sample preparation and measurement protocols. Though Barbour et al. (2001) showed that oxygen stable isotope ratios in whole wood, cellulose and lignin show a high degree of coherence, providing a basis for merging timber stable isotope databases using different sample preparation.

5. Conclusions

Our genus-level analyses of the wood $\delta^{18}\text{O}$ isoscape can be used to provide some cautious clues on species characteristics that may increase the potential for wood $\delta^{18}\text{O}$ tracing. First, genera (and species) occurring in regions with a large isotopic variation such as the West-East $\delta^{18}\text{O}$ gradient in South America likely are more suitable than those growing in Africa or Asia. Second, species with a large distributional range or from which timber is derived across tropical continents likely have a higher potential. Third, tropical timbers obtained from both natural forests and plantations can be separated based on wood $\delta^{18}\text{O}$ if plantations are located on a different continent than the species' native range natural. This latter option may be beneficial for timbers, such as teak, for which exploitation in natural forests is strongly restricted or prohibited because of the conservation status of the species. But we conclude that solely using timber oxygen isoscapes has limited potential for tropical timber tracing. This potential may increase when multiple wood stable isotope ratios, other wood chemical traits or timber genetic signatures are combined.

CRediT authorship contribution statement

Tassiamba Steve: Resources, Investigation. **Siregar Iskandar:** Writing – review & editing, Resources, Investigation. **Toumba-Paka Bijoux:** Investigation. **Tchamba Martin:** Investigation. **Paredes Kathelyn:** Writing – review & editing, Resources, Methodology, Investigation, Formal analysis, Data curation. **Rocha Venâncio Meyer-Sand Barbara:** Writing – review & editing, Resources, Methodology, Investigation, Data curation, Conceptualization. **Rahman Mohamad:** Resources, Investigation. **Moundounga Cynel:** Resources, Investigation, Data curation. **Mbika Dieu-merci:** Resources. **Ndiade Bouroubou Dyana:** Resources, Investigation. **Ndangani Rita:** Resources, Investigation. **Engone Obiang Nestor:** Resources, Investigation. **Kuzee Tijs:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Loumeto Joël:** Resources. **Guieshon-Engongoro Mesly:** Resources, Investigation. **Ciliane-Madikou Jannici:** Writing – review & editing, Resources. **Bouka Gaël:** Writing – review & editing, Resources. **Boom Arnold:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Zemtsa Pascaline:** Investigation. **Boeschoten Laura:** Writing – review & editing, Visualization, Formal analysis. **Zanguim Herman:** Writing – review & editing, Resources, Methodology. **Vlam Mart:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation,

Funding acquisition, Formal analysis, Data curation, Conceptualization. **Adzkie Ulf:** Writing – review & editing, Resources, Investigation. **Zuidema Pieter:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **van der Sleen Peter:** Writing – review & editing, Methodology, Investigation, Formal analysis.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122757.

Data availability

Data will be made available on request.

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