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Clay and soil organic matter drive wood multi-elemental composition of a tropical tree species: Implications for timber tracing

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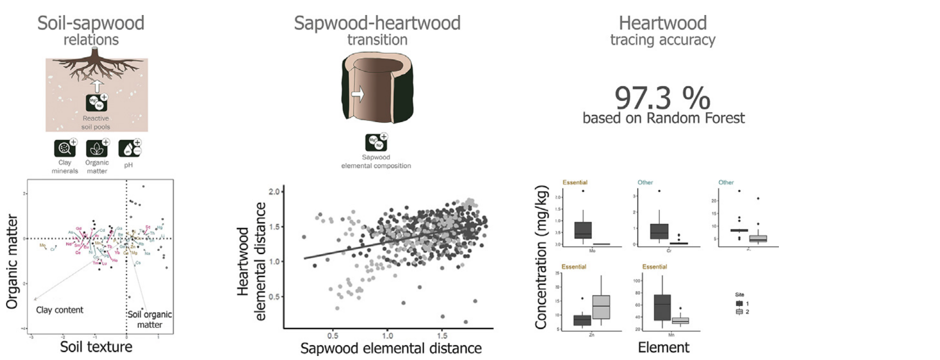
HIGHLIGHTS

- Multi-elemental composition can provide a chemical fingerprint for timber tracing.
- Insight into what drives elemental variation is needed to apply the method in wood.
- Our results show variation in soil clay content and organic matter are important.
- Heartwood formation further affects individual elements but not composition.
- Elemental tracing accuracy was 97.3 % for our study species at two sites in Cameroon.

GRAPHICAL ABSTRACT



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ABSTRACT

Forensic methods to independently trace timber origin are essential to combat illegal timber trade. Tracing product origin by analysing their multi-element composition has been successfully applied in several commodities, but its potential for timber is not yet known. To evaluate this potential the drivers of wood multi-elemental composition need to be studied. Here we report on the first study relating wood multi-elemental composition of forest trees to soil chemical and physical properties.

We studied the reactive soil element pools and the multi-elemental composition in sapwood and heartwood for 37 Azobé (*Lophira alata*) trees at two forest sites in Cameroon. A total of 46 elements were measured using ICP-MS. We also measured three potential drivers of soil and wood elemental composition: clay content, soil organic matter and pH. We tested associations between soil and wood using multiple regressions and multivariate analyses (Mantel test, db-RDA). Finally, we performed a Random Forest analysis of heartwood elemental composition to check site assignment accuracy.

We found elemental compositions of soil, sapwood and heartwood to be significantly associated. Soil clay content and organic matter positively influenced individual element concentrations (for 13 and 9 elements out of 46 respectively) as well as the multi-elemental composition in wood. However, associations between wood and topsoil elemental concentrations were only significant for one element. We found close associations between element concentrations and composition in sapwood and heartwood. Lastly, the Random Forest assignment success was 97.3 %.

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Our findings indicate that wood elemental composition is associated with that in the topsoil and its variation is related to soil clay and organic matter content. These associations suggests that the multi-elemental composition of wood can yield chemical fingerprints obtained from sites that differ in soil properties. This finding in addition to the high assignment accuracy shows potential of multi-element analysis for tracing wood origin.

1. Introduction

Illegal timber trade is widespread, causing harm to the environment and the economies of exporting countries as well as fostering social inequality. To stop this, increased transparency in the timber supply chain is needed, in particular for tropical timbers (Hoare, 2015; Nellemann, 2012). Major forms of fraud in the sector are the false reporting of origin and mixing legally and illegally sourced timber (Kleinschmit, 2016; Brancalion, 2018). At present, these types of fraud are hard to detect, because methods to independently verify timber origin are limited and are fully depended on external documents and tags (Bisschop, 2012; Lowe et al., 2016). Therefore, a variety of tracing methods is under development to trace timber origin based on intrinsic wood properties, such as techniques using DNA (Vlam et al., 2018), stable isotopes (Gori et al., 2018) and metabolic profiles (Deklerck et al., 2020). They reduce the dependency on external documents and tags which are currently used to track origin (Dormontt et al., 2015; Gasson et al., 2021). All of these methods rely on natural variation in wood characteristics within a species range. This variation determines the discrimination power as well as the spatial accuracy of the method (Vlam et al., 2018).

Methods based on the chemical analysis of the multi-elemental composition are already successfully applied for tracing the geographical origin of a wide variety of commodities (Drivelos and Georgiou, 2012), but not yet for wood. Wine origin for example was distinguished on a scale of 100 km (Gonzálvez et al., 2009) and green tea at an even finer scale of 10 km (Ma et al., 2016). The method relies on the quantification of a large set of elements after digestion of the organic material, measured simultaneously by analytical techniques like Inductively Coupled Plasma Mass Spectrometry (ICP-MS). This chemical profile then provides a specific 'fingerprint' per area to enable verification of the geographical origin. However, additional challenges arise when applying the method to wood. As wood is the product of a continuous growing process of trees over many years, inter-annual fluctuations in physiological processes within the tree trunk can lead to variation in its elemental composition (Hietz et al., 2015). Additionally, further element allocation processes in the trunk and the proportion of different cell types can affect the elemental composition of the heartwood, the traded part of the tree (Hietz et al., 2015). These processes may reduce differences in elemental composition between trees and thus obscure possible individual or site-specific elemental fingerprints in wood. So far, the drivers of spatial variation in wood elemental composition remain poorly understood: earlier studies showed a lack of longitudinal or latitudinal patterns in wood chemical composition (Kagawa, 2007), while others showed associations with bedrock type (Durand et al., 1999).

To assess the potential of wood multi-elemental analysis for tracing timber, it is important to understand what drives wood elemental composition. Yet, little is known about the underlying mechanisms that drive the uptake and allocation of many elements found in wood, especially so for many non-essential elements such as metals and rare earth elements (Watanabe et al., 2007; Brun et al., 2010). Such knowledge is essential, for instance because non-essential elements are not actively attracted by roots. Therefore their concentration and composition in wood may reflect soil conditions and thus provide a site-specific chemical fingerprint. Their composition is likely to be affected by physical-chemical soil properties that affect the binding of elements in soil, such as pH, clay content and soil organic matter (Hevia et al., 2017; Tyler and Olsson, 2001) These properties may then provide a first indication for the potential of using elemental composition for tracing wood. This is aided by the increasing availability and quality of global soil maps (Poggio et al., 2021).

To address this knowledge gap and improve our understanding of how physical and chemical soil properties (clay content, soil organic matter, pH) as well as tree physiological processes (heartwood formation) drive variation in wood elemental composition, we applied a five step approach: 1) we evaluated associations of individual element concentrations in sapwood with their concentration in soil and these three soil properties, 2) we tested the associations of sapwood elemental composition with soil elemental composition and these soil properties, 3) we evaluated changes in wood elemental composition from sapwood to heartwood, 4) we tested the assignment success of heartwood based on the multi-elemental composition and 5) we visualised the spatial variation in relevant soil properties within the distributional range of our study species. Steps 1–3 yield an understanding of the associations between soil and wood elemental composition, and thus the mechanism by which chemical tracing may operate. Steps 4–5 aimed to provide a first proof of principle of elemental timber tracing. We conducted the study on Azobé, *Lophira alata* (*L. alata*), a major African timber species.

The first two steps aim to investigate the relationships between soil and wood elemental composition in two ways. For step 1, we analysed the concentrations of each element by itself in soil and wood, hereafter called the individual element concentrations. For step 2, we assessed all the occurring elements simultaneously, hereafter referred to as elemental composition in soil and wood. This step addresses element stoichiometry: it shows whether elemental composition in wood and soil co-varies across trees (Scharnweber et al., 2016).

We tested the following hypotheses, illustrated in Fig. 1. Soil organic matter and clay minerals are expected to provide a buffer function in the soil as they retain cations at their reactive surfaces, preventing such cations from leaching (Fig. 1a) (Rieuwerts, 2007; Soong, 2020; Antoniadis et al., 2017). Both soil constituents are thus hypothesised to have a positive effect on the geochemically reactive soil cations pools, from which trees can potentially take up the associated cations. The binding of cations to these reactive soil particles also depends on soil pH (Bukata and Kyser, 2008). However, since the variation in pH of very acidic tropical soils is usually small, no strong effect of soil pH on the wood element concentrations is expected here (Rieuwerts, 2007; DeWalle et al., 1991). From the reactive soil pools, the elements are then taken up by the roots and transported through the sapwood so we hypothesize that sapwood elemental composition primarily reflects the reactive soil pools (Vitousek, 1984). This association with soil elemental composition was also observed in other commodities (Wang, 2020; Baroni et al., 2015; Pilgrim et al., 2010) as well as in wood (Lira-Martins et al., 2019; Heineman et al., 2016; Buras et al., 2020; DeWalle et al., 1991). Yet, trees are not just passive monitors of the reactive soil pools: soil properties and environmental factors can shift the association between soil and plant elemental compositions (Martin et al., 2006; Wyttenbach et al., 1995; Hevia et al., 2017; Russell et al., 2017; Bukata and Kyser, 2008). We therefore test for their effect on wood elemental composition.

After uptake, within-tree differences in wood elemental composition are expected due to the transition from sapwood to heartwood (Fig. 1b) (Hillis, 1999; Colin-Belgrand et al., 1996; Amais et al., 2021). During this process, physiologically relevant elements can be relocated through selective recycling from the inner sapwood, which is transformed to heartwood, to the outer sapwood (Smith et al., 2014). This relocation results in higher concentrations of essential elements in sapwood compared to heartwood (Meerts, 2002; Hevia et al., 2017). For the non-essential elements an opposite pattern is expected: concentrations will be higher closer to the centre of the tree because the wood cation binding capacity decreases from the pith

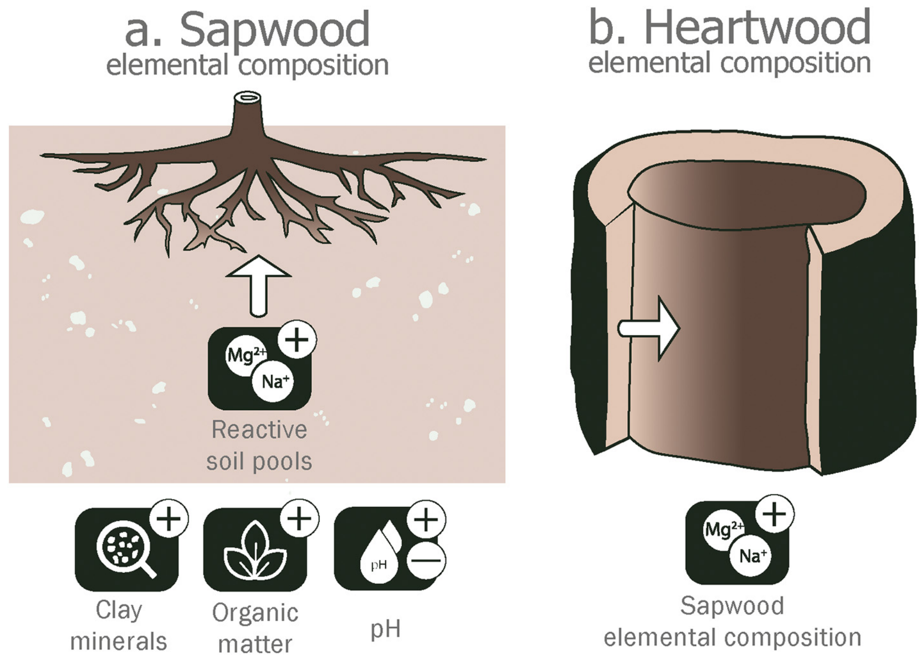

Fig. 1. Schematic overview of processes driving sapwood (a) and heartwood (b) elemental composition of tropical trees. Hypothesised direction of the effects is indicated (positive + or no strong effect expected +/−). a) Sapwood elemental composition is expected to be a function of the reactive soil pools, which are driven by clay content, organic matter content and pH. For elements that occur predominantly as anions, such as P and As, soil organic matter and clay play a smaller role in buffering reactive element pools than for cationic elements. From the reactive soil pools, elements (both cations and anions) are taken up by the roots and transported and incorporated into the sapwood. b) Elemental composition in the heartwood is affected by translocation of elements from sapwood to heartwood during heartwood formation.

to the outer wood (Herbauts et al., 2002; Momoshima and Bondietti, 1990; Amais et al., 2021).

2. Materials and methods

2.1. Study species and sample collection

The study was conducted on the commercial Central African timber species Azobé (*Lophira alata*, Ochnaceae). It occurs in evergreen and moist deciduous forests from Guinea to the Democratic Republic of Congo (GBIF.org, 2021), mostly on Ferrasols and Acrisols. Both soil types are characterised by low nutrient reserves and acidity. The species produces mainly superficially spreading roots and forms associations with arbuscular mycorrhyzae (Doumenge and Sene, 2012). Mineral crystals are found in its parenchyma cells, which are potentially important storage locations for trace elements (Doumenge and Sene, 2012).

Sampling was conducted in two logging concessions in southern Cameroon in September and October 2019. The concessions are approximately 100 km apart and experience similar climatic conditions (locations in Table 1). Average annual rainfall is 2250 mm and annual average temperature is 25 °C.

We sampled heartwood and sapwood from 20 Azobé trees at each concession (so 40 in total), as well as the corresponding topsoil. Trees within each concession were between 100 m and 5 km apart. They were of at least 30 cm diameter breast height (DBH) and were either standing or recently felled. Sapwood and heartwood samples were collected as increment cores (Haglöf Increment borer 350 mm × 5,15 mm; $n = 18$), wood chunks ($n = 12$) or wood powder samples gained with an electrical drill ($n = 10$). All samples were taken at least 20 cm into the tree. Additionally, topsoil was sampled within 1 m from each tree trunk. Because L. *alata* roots are expected to grow mainly superficially, topsoil was assumed to be the most important for element acquisition by roots. Three soil subsamples of 20 cm deep were dug, which were then mixed and manually cleaned of large roots and leaves. The resulting soil samples were air-dried in the field.

2.2. Wood processing and chemical analysis

For the chemical analysis a subsample of heartwood and sapwood was cut from every increment core and wood chunk, spanning at least 3–5 cm of wood to ensure the samples include wood formed during multiple years (estimated at 5 years or more). *L. alata* shows a clear colour difference between sapwood and heartwood, allowing for easy distinction. The resulting samples were analysed using an adapted protocol for large element screening (SOP-A-1120). For this purpose, 1.0 g of wood was digested using a microwave technique (CEM Mars 6), using 3 mL of 70 % HNO_3 and 5 mL of ultrapure Milli-Q H_2O. The remaining solutions contained no traces of organic constituents.

Element concentrations in the digests were determined by ICP-MS (NexION 350D, PerkinElmer). Two multi-element solutions (1.0 mg/L) and a Hg solution (10 mg/L) were used to prepare calibration standards, including 60 elements: Ag, Al, As, Ba, Be, Bi, Ca, Cd, Ce, Co, Cr, Cs, Cu, Dy, Er, Eu, Fe, Ga, Gd, Ge, Hf, Ho, K, La, Li, Lu, Mg, Mn, Mo, Na, Nb, Nd, Ni, P, Pb, Pr, Rb, Re, Sb, Sc, Se, Si, Sm, Sn, Sr, Ta, Tb, Te, Th, Ti, Tl, Tm, U, V, W, Y, Yb, Zn, Zr and Hg. Spiked and non-spiked certified reference material BCR 482 Lichen were used to guarantee the accuracy of the measurements. Rh was used as internal standard. The detection limit was determined per element per measurement cycle, calculated as three times the intensity of that element in a blank standard. Only elements

Table 1
Site topsoil properties (mean ± sd); basement rock (from Gazel, 1956), pH, organic matter content (OM) and clay content.

	Latitude	Longitude	Basement rock	pH-$CaCl_2$	OM (g/kg)	Clay (g/kg)
Site 1	2.796°	11.071°	Gneiss	3.75 ± 0.26	91.64 ± 20.31	418.05 ± 110.97
Site 2	2.981°	10.265°	Granite	3.63 ± 0.24	97.39 ± 23.48	245.59 ± 92.35

measured at a concentration above their detection limit in more than half of the wood samples were included in further data analyses. Two elements (Fe, essential element and Al, 'other element') were measured but results were considered to be unreliable due to the high occurrence of inferences in the ICP-MS measurements. Consequently, we have no quantitative information on the occurrence of Fe- and Al-(hydr)oxides in our soil samples, which are responsible for the binding of oxyanions in tropical soils (Mendez et al., 2022). For three trees the internal standard was not sufficiently high in the sapwood or heartwood measurement, therefore the final dataset contained 37 trees.

2.3. Topsoil processing and analysis

Soil samples were dried for at least 24 h at 40 °C upon arrival in the laboratory, after which they were sieved to grain size <2 mm. In every soil sample, pH was measured in a settling suspension after shaking the samples in a 0.01 M $CaCl_2$ solution at a solution-to-soil ratio of 10 L/kg for two hours at 20 °C (Houba et al., 2000). Soil organic matter and clay mineral contents were determined according to standard analytical procedures (Houba, 1995). Soil organic matter content was measured by loss-on-ignition in a muffle furnace at 550 °C. Clay mineral content was determined using the sieve and pipette method. To measure the reactive elemental pool in topsoil, we used the 0.43 M HNO_3 extraction method, following Groenenberg et al. (2017). The soil samples were shaken for four hours in a 0.43 M HNO_3 solution at 20 °C using a solution-to-soil ratio of 10 L/kg. After centrifuging and filtration, element concentrations were measured by ICP-MS as described above for the wood samples.

2.4. Statistical analysis

2.4.1. Associations between individual element concentrations in soil and sapwood

All statistical analyses were performed in R version 4.1.0 (R Core Team, 2020). For step 1, individual concentrations of elements in topsoil and sapwood were correlated using Spearman rank correlations. Additionally, the effect of soil properties on the sapwood concentration was tested per element by modelling sapwood element concentration as a function of clay content, soil organic matter, pH and the soil concentration of the respective element in multiple linear regressions. Interactions between clay content, soil organic matter, pH and soil element concentration were also included in the full model. Site was not included as factor in these models, because we had no interest in distinguishing sites. All variables except for pH were log-transformed prior to analysis. A small number (10^{-12} mg/kg for all elemental concentrations and 10^{-12} g/kg for soil organic matter and clay content) was added in order to shift all values to above zero as some element concentrations that fell below their detection limit were recorded as zero. Then all variables were centred and scaled to zero mean and one standard deviation. Each full model was dredged to generate a list of candidate models ranked by AICc. Full model averaging was performed using candidate models within the top two ΔAICc units (Burnham and Anderson, 2002). All interactions were tested but only 'clay content x organic matter' occurred in the candidate models. Model dredging and averaging were conducted with the MuMIn package (Barton, 2020).

2.4.2. Multivariate analysis of elemental composition

To test the associations between topsoil and sapwood elemental composition (step 2), we calculated distance matrices for all sapwood and topsoil samples based on scaled element concentrations. Distance matrices were calculated using Chord distances:

$$CD_{i,h} = \sqrt{\sum_{j=1}^{p}\left(\left(\frac{a_{i,j}}{\Sigma_{j=1}^{p} a_{i,j}^2}\right) - \left(\frac{a_{h,j}}{\Sigma_{j=1}^{p} a_{h,j}^2}\right)\right)^2}$$

where $CD_{i,h}$ is the Chord distance between sample i and h. The data matrix has p element columns and $CD_{i,h}$ includes the differences in all p elements: $a_{i,j}$ (the concentration of element j in sample i) minus $a_{h,j}$ (the concentration of element j in sample h), both standardized to the summed concentration of all measured elements within the sample.In this equation, differences in total concentration among samples are removed and this thus provides a measure of relative element concentrations within a sample (McCune and Grace, 2002). The resulting distance matrices (for topsoil and sapwood) were correlated by Mantel tests (9999 iterations) based on Spearman correlations.

To test whether any soil properties (clay content, soil organic matter, pH) significantly explained the relative elemental composition in the sapwood, we conducted a distance based Redundance Analysis (db-RDA). This calculates the variance explained by the three soil properties. Mantel tests and db-RDA were conducted using the vegan package (mantel and capscale) (Oksanen, 2020).

2.4.3. Correlating element concentrations and elemental composition in sapwood and heartwood

To address step 3, the associations of elemental concentrations in sapwood vs. heartwood were tested using Spearman rank correlations. Additionally, Mantel tests were used to correlate elemental compositions of sapwood and heartwood. As in the analysis of topsoil and sapwood correlations, this was calculated based on Chord distances. Lastly, we tested whether elemental concentrations were higher in sapwood or heartwood, by calculating radial discrepancy (RD (%) = (sapwood - heartwood)/sapwood * 100, Heineman et al. (2016)).

2.4.4. Potential for timber tracing: site assignment and modelling of soil properties within the species range

In step 4 we aimed to verify whether elemental composition can be used to assign wood to its respective origin in these two study sites using a Random Forest classification model. In this analysis, we assigned heartwood samples to their most likely origin based on the 46 measured elements . Furthermore, the elements that were most important to distinguish between the two sites were identified based on variable importance in the Random Forest analysis. This was done using the randomForest package (Liaw, 2018).

As 5th and final step, clay and soil organic matter – two soil variables that turned out to be important in determining wood elemental composition – were plotted within the species range of *L. alata*. This was done in order to show the variation in these two soil properties and thus potential for tracing within the range of *L. alata*. The species distribution range was modelled using Maxent (Phillips et al., 2006), based on GBIF occurrence data (GBIF.org, 2021) and 19 bioclimatic variables from worldclim.org (Fick and Hijmans, 2017). Clay content and soil organic carbon (SOC), were obtained from Soilgrids within this range (Poggio et al., 2021). We divided SOC by 0.58 to obtain soil organic matter values, to compare it to the soil organic matter measured in this study (Pribyl, 2010). Species distribution modelling was conducted with the dismo package (Hijmans, 2020), maps were plotted with the raster package (Hijmans, 2021).

3. Results

3.1. Soil and wood properties

Soils at the study sites were acid, which is typical for the region (pH between 3.06 and 4.38; Table 1). Clay content showed the largest variation of the three soil properties (125.38–543.49 g/kg). It was higher on average in site 1 (S1) but still overlapped across the two sites. The average in soil organic matter content was similar at both sites, ranging from 45.70 to 139.90 g/kg.

Single element concentrations varied by four orders of magnitude, from 0.12 μg/kg for Dy to almost 1 g/kg for K. Out of the 60 measured elements, 46 were detected in over half of the heartwood and sapwood samples of *L. alata*. All of these elements were also detected in the corresponding soil samples. We categorized them in three categories: 1) 10 essential elements (K, Mg, Ca, Mn, Ni, Cu, Zn, Mo, Si and P); 2) 16 rare earth elements (Sc, Y, La, Ce, Pr, Nd, Sm, Eu, Gd, Tb, Dy, Ho, Er, Tm, Yb and Lu) and 3) 20 'other elements' (Li, Na, Rb, Cs, Be, Sr, Ba, Ti, Cr, Co, Zr, Cd, Hg, Ga, Sn, Pb, Ge, As, Th and U). Twelve elements were omitted from the analyses because they fell below the detection limit in >50 % of the samples (all 'other elements'): Ag, Bi, Hf, Nb, Re, Sb, Se, Ta, Te, Tl, V, W.

3.2. Soil to sapwood regression models

Step 1 of our five-step approach yielded multiple regressions of sapwood element concentration as a function of soil properties. The regressions contained a significant explanatory variable in only 16 out of 46 elements (Fig. 2). Among the regression variables included in the models, clay content was significant in most of the models (13 of 46 elements), followed by soil organic matter (9 of 46) and pH (2 of 46). The effect of clay on sapwood element concentration was mostly positive (11 of 13 elements). For soil organic matter, the effect was positive for 6 of the 9 elements where it was significant (alkali metals and lanthanides). The observed minor effect of pH is likely due to its very limited variability in this acidic range where the pH-dependent solubility of most major and trace elements is relatively high. An effect of the reactive element concentration in the topsoil on elemental concentration in sapwood was only found in one multiple regression model (Zr, 'other element' class).

In addition to the regression models, we also checked for associations between soil and wood elemental concentrations using Spearman correlations. These showed somewhat contrasting patterns to the regression models: 14 out of 46 correlations between element concentrations in topsoil and sapwood were significant (Fig. S1). Of those correlations, 13 were positive and one negative.

In the regression models, the effect of soil properties on sapwood elemental concentrations was different for the three predefined elements groups. Within the category of essential elements we did not find a strong pattern in the effect of the soil properties. Clay content and organic matter had a strong effect on the sapwood concentration of only two essential elements, Mo and Mn (Fig. 2). In contrast, we found more consistent significant effects of soil properties on the sapwood concentrations of the rare earth elements. For half of the rare earth elements, clay content or the combination of clay content and organic matter had a strong positive effect on the sapwood element concentrations. Among the drivers of sapwood concentrations, clay content turned out to be most important as it was included in all significant models for rare earth elements. Within the category of 'other elements', model results were quite variable. We found no consistent effect of soil properties on sapwood elemental composition there, neither when grouped based on atomic mass or element type in the periodic system.

3.3. Elemental composition in topsoil and sapwood

Step 2 involved conducting multivariate analyses in order to assess drivers of wood elemental composition. We found significant correlations of Chord distances of topsoil and sapwood elemental concentrations, i.e.

Fig. 2. Multiple regression models of sapwood element concentrations as a function of soil element concentration, soil properties and their interactions (step 1). Elements are grouped and colour-coded by category, and within category ordered by type and weight in the periodic system. Explanatory variables are concentration of the respective element in topsoil (soil conc, mg/kg), pH, organic matter content (g/kg), clay content (g/kg) and interaction of clay and organic matter. Coefficient plots include slope estimates (mean and 95 CI), averaged across top-ranked models. The CI of the red and green circles does not overlap with zero and therewith denotes a strong and large effect, green for a positive and red for a negative effect. The grey circles were included in the top models but their CI overlaps with zero, therefore they do not indicate a strong effect on the response variable. Numbers in the panels represent averaged adjusted R^2 of the best models.

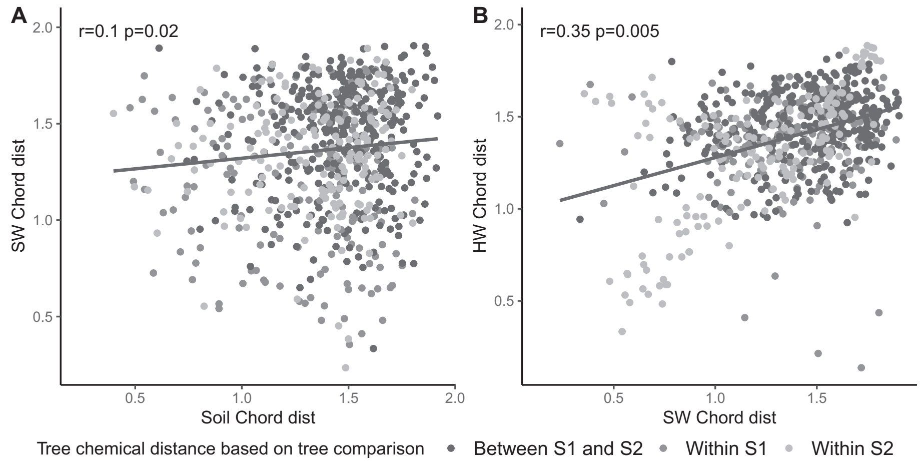

Fig. 3. Associations between chemical composition in soil, sapwood (SW) and heartwood (HW), based on Mantel tests (results shown per panel). Soil and sapwood (A; step 2) and sapwood and heartwood (B; step 3) distances based on Chord distance. Grey shades of symbols indicate whether trees were from different sites (dark grey), both from S1 (medium dark grey) or both from site 2 (S2) (light grey). Grey lines show significant relations.

when element concentrations were standardized to the total element concentration per sample (Fig. 3A; multivariate scaling shown in Fig. S2A and B).

Our db-RDA analysis of the soil properties showed that clay content and soil organic matter together explained 22.34 % of the variation in sapwood elemental composition, while pH was not significant (Fig. 4). Most variation (19.6 %) was explained by the first axis. Consistent with results for the element concentrations, clay content was also the most important driving variable explaining variation in sapwood elemental composition: it defined most of the first RDA axis.

3.4. Elemental composition in sapwood and heartwood

In step 3 we found significant associations of elemental composition in sapwood and heartwood (Fig. 3B; multivariate scaling shown in Fig. S2B and C). This indicates that elemental composition in the sapwood was largely conserved after heartwood formation. This association was also reflected by the large share of positive correlations (35 out of 46) between sapwood and heartwood concentrations of individual elements (Fig. S3).

Comparisons of concentration differences between sapwood and heartwood, expressed as the radial discrepancy, revealed that concentrations

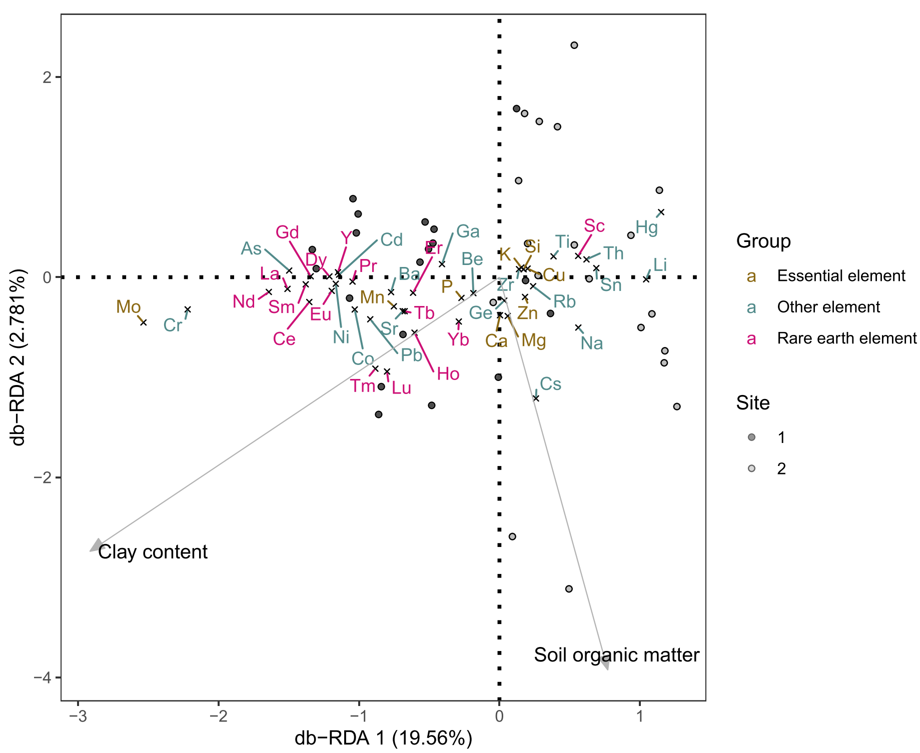

Fig. 4. Distance based Redundancy Analysis (db-RDA) of sapwood elemental composition (step 2). Relative position of trees (dots) is based on Chord distances of square root transformed element concentrations, coloured by site. Weight and direction of the element concentrations in the sapwood is indicated as crosses, element categories colour-coded as in Fig. 2. Vectors indicate the weight and the direction of the two significant important soil properties. Percentages in axis labels denote the percentage of total variance explained.

were higher in sapwood for three of the 10 major essential elements (Cu, K and P, Fig. 5). Two elements from the 'other elements' category (Rb and Cs), known to be similar to K in terms of plant uptake and chemical behaviour (Zhu and Smolders, 2000), were also more abundant in the sapwood. In the rare earth element category, over half of the elements was more abundant in the heartwood (9/16 elements) and the rest did not differ between the two wood compartments (7/16).

3.5. Tracing potential: origin assignment and spatial variation within the distributional range of L. alata

Step 4 then provided a first evaluation of the assignment success of elemental tracing at our two study sites. The Random Forest classification was very successful: 36 of the 37 trees were correctly assigned (success rate of 97.3 %). The five most important elements in the Random Forest analysis were in the essential element category (Mo, Zn, Mn) and 'other element' category (Cr, Sr; concentrations shown in Fig. 6). The highest ranking rare earth element in terms of importance was La, at place number nine.

In step 5, we further evaluated the potential of chemical tracing for our study species beyond the two study sites, by mapping the spatial variation of the two most important drivers of wood chemical composition (clay content and soil organic matter). We found soil clay content to differ five-fold within the distributional range of *L. alata*, with large differences at small scales such as in southern Cameroon (Fig. 7A). Regional differences in soil organic carbon were also found although not as pronounced as for clay content (Fig. 7B), except for one region in Ghana.

4. Discussion

We found that wood element concentrations and composition of a tropical tree species were associated with soil clay content and organic matter but the individual element concentrations were not directly linked with element concentrations in the topsoil. We also found that relative elemental composition was retained across topsoil, sapwood and heartwood. Furthermore, we observed shifts in individual element concentrations from sapwood to heartwood. Finally, we could correctly assign heartwood to one of the two study sites with 97.3 % accuracy.

4.1. Elemental composition of soil is reflected in wood

We hypothesised that wood elemental composition would be driven by soil composition for elements taken up by the roots. In our study, the relative elemental composition of the topsoil was indeed retained in the sapwood as well as the heartwood (step 2, Fig. 3). This is in line with findings on other commodities such as bananas and honey, for which the elemental composition of the commodities was also linked to soil element composition including multiple elements (Wang, 2020; Baroni et al., 2015).

In contrast, individual topsoil element concentrations, as extracted by 0.43 M HNO_3 (Groenenberg et al., 2017), were not a good single predictor for the sapwood concentrations in our regression and correlation models (step 1, Figs. 2 and S1 respectively). This is consistent with results from previous studies on nutrients in soil and wood (Bukata and Kyser, 2008; Johnson et al., 2001; Russell et al., 2017), although contrasting findings have also been reported (Heineman et al., 2016; Lira-Martins et al., 2019). A possible explanation is that the studies reporting significant associations between soil and wood concentrations included a wide range of soil element concentrations or studied multiple tree species (Heineman et al., 2016; Lira-Martins et al., 2019). In our study, concentration differences were relatively small and between-site distance was <100 km. Therefore, research of these relations across larger soil gradients is needed to provide further insights into the influence of soil elemental concentrations on wood chemistry.

4.2. Clay content and soil organic matter drive wood element concentrations and elemental composition

Individual wood element concentrations were found to be associated more with chemical and physical soil properties than with the individual element concentrations in the soil (step 1, Fig. 2). This is consistent with other studies indicating the importance of soil properties for wood elemental composition (Soong, 2020; Hevia et al., 2017). Among the 18 regression

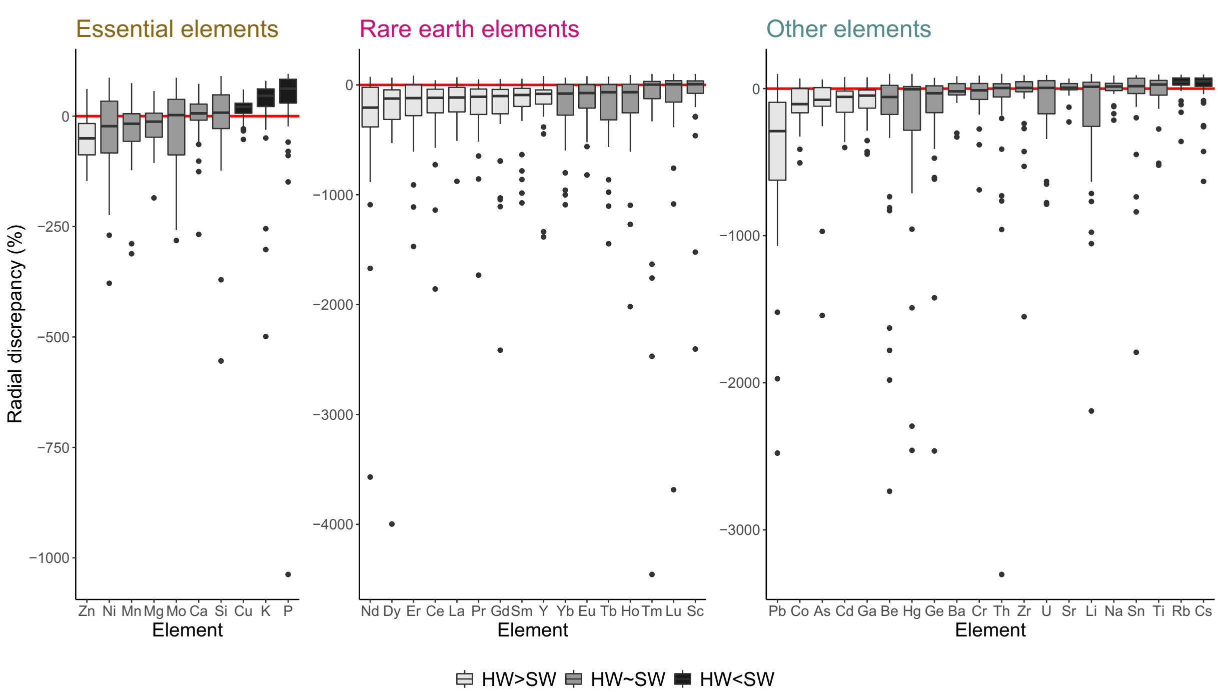

Fig. 5. Radial discrepancy plot of element concentrations in heartwood (HW) compared to sapwood (SW; step 3). Grey shades indicate whether 3 of the 4 quantiles fell above, around or below zero. Values below zero indicate higher concentrations in the heartwood (lightest grey), whereas values above zero indicate higher concentrations in the sapwood (darkest grey). Values around zero indicate similar sapwood and heartwood concentrations (medium dark grey).

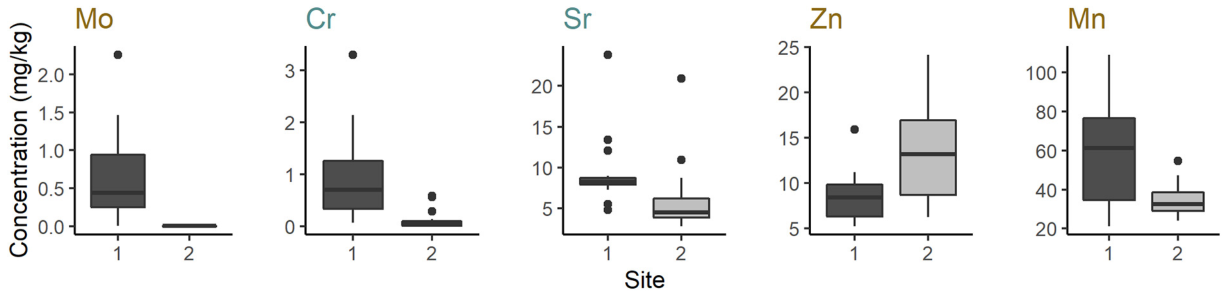

Fig. 6. Element concentrations (mg/kg) of the five most important elements of the Random Forest analysis, in decreasing order of importance (Random Forest assignment accuracy of 97.3 %; step 4). Elements are colour-coded per category as in Fig. 2.

models of wood element concentration with significant explanatory variables, clay content and soil organic matter were most commonly included as explanatory variable. That effect was mostly positive for both soil properties, in line with our hypothesised framework (Fig. 1). The effect of clay content and soil organic matter was also found in the relative concentrations of these elements across soil and wood: variation in the relative elemental composition, was explained by clay content and soil organic matter (step 3, Fig. 4).

This positive effect of clay content and soil organic matter on wood element concentrations contrasts that of similar research on annual crops, where it is often found that clay content and soil organic matter decrease cation mobility and thus uptake by plants (Antoniadis et al., 2017). This discrepancy is likely explained by the longevity of trees. On time scales of days to weeks, relevant to annual crops, a high number of cation exchange sites in the soil results in decelerated cation mobility and thus cation availability (Römkens et al., 2009; Antoniadis et al., 2017; Kabata-Pendias, 2011). For trees however, those fixed cations can also be taken up from less directly available pools as they gradually become available through weathering or by active displacement of cations from soil exchange sites over the period of multiple years or decades (Russell et al., 2017). Thus, at longer time scales, a larger number of cation binding sites may prevent short-term leaching of cations and then a higher concentration of clay minerals and soil organic matter may act as a long-term reservoir of elements (Rieuwerts, 2007; Soong, 2020). Even though the applied HNO_3-extraction method has been developed to represent these longer-term available element pools (Groenenberg et al., 2017), we did not find a direct relationship between soil and wood concentrations (Fig. 2). This may be caused by the limited gradients in availability controlling soil properties (i.e., pH, soil organic matter, clay minerals) in this study.

Even though we found an effect of some soil properties on wood concentrations, there were also 28 of 46 individual element models where we found no effect of any of our tested soil properties (step 1, Fig. 2). Testing these relations across larger gradients of clay content, organic matter and pH is needed to verify whether this absence of soil effects on wood element concentrations is rigorous. However, finding such a gradient in a single tree species may be challenging, as soil conditions are a major driver of species occurrence. Further studies should also include analyses of clay mineralogy as this can potentially affect the availability of trace elements in tropical soils through weathering of clay minerals (Antoniadis et al., 2017; Rieuwerts, 2007). Furthermore, we recommend addressing the role of Fe- and Al-(hydr)oxides in future studies as they are especially important for elements forming oxyanions like phosphate and arsenic (Mendez et al., 2022). Together, these recommendations will generate a more complete understanding of the links between soil and wood chemistry for tropical trees.

4.3. Heartwood and sapwood: elemental composition is retained, but individual elements differ

In addition to soil chemistry, elemental composition in the heartwood is also determined by stem physiological processes such as the transition from sapwood to heartwood. We found that individual concentrations of three essential (Cu, K, P) as well as two non-essential elements that are similar in uptake and behaviour to K (Rb, Cs) were consistently higher in sapwood compared to heartwood (step 3, Fig. 5). These higher sapwood concentrations are commonly found in tree species, and likely result from the active translocation of nutrients during heartwood formation (Hietz et al., 2015; Andrews et al., 1999; Meerts, 2002).

Furthermore, many rare earth elements followed the hypothesised pattern of higher concentrations in the heartwood. This is unlikely caused by active translocation, but may be explained by the increasing amounts of pectates in a gradient from bark to pith, which bind cations (Amais et al., 2021). In spite of the substantial shifts in some individual element concentrations from sapwood to heartwood, the relative elemental composition of the sapwood was retained in the heartwood. This indicates that the stoichiometric relations among elements are largely retained in the radial direction of the tree trunk, even after the transition from sapwood to heartwood. Yet, it is unclear whether this also holds for wood along the

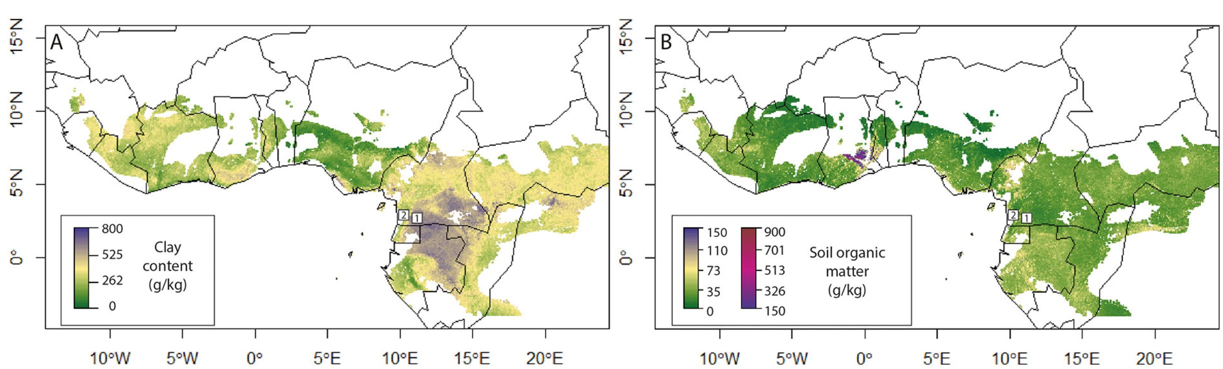

Fig. 7. Variation in clay content (A; g/kg) and soil organic matter (B; g/kg) within the predicted distributional range of *L. alata* (step 5). Predicted range was based on Maxent modelling using observation data from GBIF and 19 bioclimatic variables. Note the two colour scales for soil organic matter, to better show variation across most of the species range (values above 150 g/kg are only found in one region in Ghana). Numbers indicate the research sites.

height of trunks (Scharnweber et al., 2016). This needs to be verified to ascertain that wood originating from different heights along the trunk has similar elemental composition.

4.4. Implications for timber tracing based on multi-element analysis

Our findings help to evaluate the potential of multi-element analysis for tracing of *L. alata*. The results of steps 1–3 suggest potential for elemental tracing of timber in areas where soil chemical composition varies spatially. Even though we did not find strong associations for individual element concentrations, we did find that the reactive elemental composition in the topsoil was reflected in sapwood and heartwood. We also found wood chemical composition to be associated with chemical and physical soil properties. The soil property in which our two sites differed most was clay content, although it was not significantly different (Table 1). Thus, our results suggest that the elemental fingerprint of wood in our study species reflects that in the topsoil and is associated with general soil properties.

Our proof of principle to use elemental composition to assign samples to sites (step 4) showed a high assignment accuracy: 97.3 %. This value is comparable to that obtained using elemental tracing in other commodities (Gonzálvez et al., 2009; Ma et al., 2016). We found three essential elements to be important in distinguishing our two study sites (Mo, Zn, Mn; Fig. 6). In contrast with findings of elemental tracing for other commodities, rare earth elements were not included in the top elements in the Random Forest analysis (Drivelos and Georgiou, 2012). Clearly, these findings are based on only one species, sampled at just two sites. Thus, the accuracy obtained for this first evaluation should be interpreted cautiously and cannot be extrapolated to larger areas or other species. Nevertheless, this high accuracy value – in combination with the soil-wood associations of elemental composition – does suggest that elemental tracing of tropical timber has a high potential to reach required accuracy levels for forensic tracing, and doing so at relatively short distances (100 km). To further evaluate the potential and prepare this technique for practical forensic application, we recommend testing soil-wood chemical associations and assignment tests in larger areas and for other tree species. Based on our finding that wood elemental composition is most strongly related to soil clay content and soil organic matter, regions with high variation in these soil properties, e.g. southern Cameroon, are particularly suitable for such next steps (step 5, Fig. 7).

If the associations between soil and wood elemental composition found here are similar for other traded timbers in the region, this would allow pooling reference data from various species for tracing studies. Pooling samples would generate an advantage of this method over other tracing methods that require species-specific databases, e.g. genetic tracers or metabolites (Vlam et al., 2018; Deklerck et al., 2020), as it would greatly reduce the effort to collect reference data.

CRediT authorship contribution statement

Laura E. Boeschoten: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Ute Sass-Klaassen:** Conceptualization, Methodology, Writing – review & editing. **Mart Vlam:** Funding acquisition, Conceptualization, Methodology, Writing – review & editing. **Rob N.J. Comans:** Methodology, Writing – review & editing. **Gerwin F. Koopmans:** Methodology, Writing – review & editing. **Barbara Rocha Venâncio Meyer-Sand:** Investigation, Writing – review & editing. **Steve N. Tassiamba:** Investigation. **Martin T. Tchamba:** Investigation. **Herman T. Zanguim:** Investigation. **Pascaline T. Zemtsa:** Investigation. **Pieter A. Zuidema:** Funding acquisition, Conceptualization, Investigation, Methodology, Writing – review & editing.

Data availability

Data will be made available on request.

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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Data availability statement

The data of this study are available from the corresponding author upon reasonable request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157877.

References

Amais, Renata S., et al., 2021. Trace elements distribution in tropical tree rings through high-resolution imaging using LA-ICP-MS analysis. J. Trace Elem Med. Biol. 68 (July). https://doi.org/10.1016/j.jtemb.2021.126872.

Andrews, Jeffrey A., Siccama, Thomas G., Vogt, Kristiina A., 1999. The effect of soil nutrient availability on retranslocation of ca, mg and K from senescing sapwood in Atlantic white cedar. Plant Soil 208 (1), 117–123. https://doi.org/10.1023/A:1004512317397.

Antoniadis, Vasileios, et al., 2017. Trace elements in the soil-plant interface: phytoavailability, translocation, and phytoremediation–a review. Earth Sci. Rev. 171, 621–645. https://doi.org/10.1016/j.earscirev.2017.06.005.

Baroni, María V., et al., 2015. Linking soil, water, and honey composition to assess the geographical origin of argentinean honey by multielemental and isotopic analyses. J. Agric. Food Chem. 63 (18), 4638–4645. https://doi.org/10.1021/jf5060112.

Barton, Kamil, 2020. MuMIn: Multi-Model Inference. R Package Version 1.43.17.

Bisschop, Lieselot, 2012. Out of the woods: the illegal trade in tropical timber and a european trade hub. Glob. Crime 13 (3), 191–212. https://doi.org/10.1080/17440572.2012.701836.

Brancalion, Pedro H.S., 2018. Fake legal logging in the Brazilian Amazon. Sci. Adv. 4 (8), eaat1192. https://doi.org/10.1126/sciadv.aat1192.

Brun, Christian B., et al., 2010. Spatial distribution of major, trace and ultra trace elements in three Norway spruce (Picea abies) stands in boreal forests, forsmark, Sweden. Geoderma 159 (3-4), 252–261. https://doi.org/10.1016/j.geoderma.2010.07.018.

Bukata, Andrew R., Kyser, T.Kurtis, 2008. Tree-ring elemental concentrations in oak do not necessarily passively record changes in bioavailability. Sci. Total Environ. 390 (1), 275–286. https://doi.org/10.1016/j.scitotenv.2007.09.005.

Buras, Allan, et al., 2020. Reduced above-ground growth and wood density but increased wood chemical concentrations of Scots pine on relict charcoal hearths. Sci. Total Environ. 717, 137189. https://doi.org/10.1016/j.scitotenv.2020.137189.

Burnham, Kenneth P., Anderson, David R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd ed. Springer New York, New York.

Colin-Belgrand, Micheline, Ranger, Jacques, Bouchon, Jean, 1996. Internal nutrient translocation in chestnut tree stemwood: III. Dynamics across an age series of Castanea sativa (Miller). Ann. Bot. 78 (6), 729–740. https://doi.org/10.1006/anbo.1996.0183.

Deklerck, Victor, et al., 2020. Chemical fingerprinting of wood sampled along a pith-to-bark gradient for individual comparison and provenance identification. Forests 11 (1), 1–13. https://doi.org/10.3390/f11010107.

DeWalle, David R., et al., 1991. Spatial variations of sapwood chemistry with soil acidity in appalachian forests. J. Environ. Qual. 20 (2), 486–491. https://doi.org/10.2134/jeq1991. 00472425002000020024x.

Dormontt, Eleanor E., et al., 2015. Forensic timber identification: it's time to integrate disciplines to combat illegal logging. Biol. Conserv. 191, 790–798. https://doi.org/10.1016/j.biocon.2015. 06.038.

Doumenge, C., Sene, V.O., 2012. In: Lemmens, R.H.M.J., Louppe, D., Oteng-Amoako, A.A. (Eds.), Lophira alata Banks ex C.F.Gaertn Wageningen, the Netherlands.

Drivelos, Spiros A., Georgiou, Constantinos A., 2012. Multi-element and multi-isotope-ratio analysis to determine the geographical origin of foods in the European Union. TrAC Trends Anal. Chem. 40, 38–51. https://doi.org/10.1016/j.trac.2012.08.003.

Durand, Stephen R., et al., 1999. Trees, chemistry, and prehistory in the american southwest. J. Archaeol. Sci. 26 (2), 185–203. https://doi.org/10.1006/jasc.1998.0315.

Fick, Stephen E., Hijmans, Robert J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/JOC.5086.

Gasson, Peter E., et al., 2021. World Forest ID: addressing the need for standardized wood reference collections to support authentication analysis technologies; a way forward for checking the origin and identity of traded timber. Plants, People, Planet 3 (2), 130–141. https://doi.org/10.1002/ppp3. 10164.

Gazel, J., 1956. Carte geologique a 1:1 000 000 du Cameroun. Planche 1-A nord.

GBIF.org, 2021. GBIF Occurrence Download. https://doi.org/10.15468/dl.wpwm8v Date accessed: 202111-25.

González, A., et al., 2009. Elemental fingerprint of wines from the protected designation of origin Valencia. Food Chem. 112 (1), 26–34. https://doi.org/10.1016/j.foodchem.2008.05.043.

Gori, Yuri, Stradiotti, Ana, Camin, Federica, 2018. Timber isoscapes. A case study in a mountain area in the Italian Alps. PLOS ONE 13 (2), e0192970. https://doi.org/10.1371/journal.pone.0192970 Ed. by Berthold Heinze.

Groenenberg, Jan E., et al., 2017. Evaluation of the single dilute (0.43 M) nitric acid extraction to determine geochemically reactive elements in soil. Environ. Sci. Technol. 51 (4), 2246–2253. https://doi.org/10.1021/acs.est.6b05151.

Heineman, Katherine D., Turner, Benjamin L., Dalling, James W., 2016. Variation in wood nutrients along a tropical soil fertility gradient. New Phytol. 211 (2), 440–454. https://doi.org/10.1111/nph.13904.

Herbauts, J., et al., 2002. Radial variations in cation exchange capacity and base saturation rate in the wood of pedunculate oak and european beech. Can. J. For. Res. 32 (10), 1829–1837. https://doi.org/10.1139/x02-097.

Hevia, Andrea, et al., 2017. Towards a better understanding of long-term wood-chemistry variations in old-growth forests: a case study on ancient Pinus uncinata trees from the Pyrenees. Sci. Total Environ. 625, 220–232. https://doi.org/10.1016/j.scitotenv.2017.12.229.

Hietz, Peter, et al., 2015. High-resolution densitometry and elemental analysis of tropical wood. Trees 29 (2), 487–497. https://doi.org/10.1007/s00468-014-1126-7.

Hijmans, Robert J., 2020. dismo: Species Distribution Modeling. R Package Version 1.3-5.

Hijmans, Robert J., 2021. raster: Geographic Data Analysis and Modeling. R Package Version 3.5-9.

Hillis, W.E., 1999. The formation of heartwood and its extractives. Phytochemicals in Human Health Protection, Nutrition, and Plant Defense. Springer, Boston, MA, pp. 215–253 https://doi.org/10.1007/978-1-4615-4689-4{_}9.

Hoare, Alison, 2015. Tackling Illegal Logging and the Related Trade: What Progress and Where Next? https://doi.org/10.1016/S0966-3274(00)00025-3

Houba, V.J.G., 1995. Part5B: soil analysis procedures. Soil and Plant Analysis. Agricultural University Wageningen, Wageningen.

Houba, V.J.G., et al., 2000. Soil analysis procedures using 0.01 M calcium chloride as extraction reagent. Commun. Soil Sci. Plant Anal. 31 (9–10), 1299–1396. https://doi.org/10.1080/00103620009370514.

Johnson, Christine M., et al., 2001. Carbon and nutrient storage in primary and secondary forests in eastern Amazônia. For. Ecol. Manag. 147 (2–3), 245–252. https://doi.org/10.1016/S03781127(00)00466-7.

Kabata-Pendias, Alina, 2011. Trace Elements in Soils and Plants. 4thed. CRCPress isbn: 9781420093681.

Kagawa, Akira, 2007. Stable isotopes and inorganic elements as potential indicators of geographic origin of Southeast Asian timber. Proceedings of the International Symposium on Development of Improved Methods to Identify Shorea Species Wood and its Origin, pp. 39–44.

Kleinschmit, Daniela, 2016. Illegal Logging and Related Timber Trade – Dimensions, Drivers, Impacts and Responses. A Global Scientific Rapid Response Assessment Report. IUFRO World SeriesVolume 35. International Union of Forest Research Organizations (IUFRO), p. 148 Date accessed: 202111-25.

Liaw, Wiener, 2018. randomForest: Breiman and Cutler's Random Forests for Classification and Regression Version 4.6-14.

Lira-Martins, Demetrius, et al., 2019. Tropical tree branch-leaf nutrient scaling relationships vary with sampling location. Front. Plant Sci. 10 (July). https://doi.org/10.3389/fpls.2019.00877.

Lowe, Andrew J., et al., 2016. Opportunities for improved transparency in the timber trade through scientific verification. Bioscience 66 (11), 990–998. https://doi.org/10.1093/biosci/biw129.

Ma, Guicen, et al., 2016. Determining the geographical origin of chinese green tea by linear discriminant analysis of trace metals and rare earth elements: taking dongting biluochun as an example. Food Control 59, 714–720. https://doi.org/10.1016/j.foodcont.2015.06.037.

Martin, Ronald R., et al., 2006. High variability of the metal content of tree growth rings as measured by synchrotron micro x-ray fluorescence spectrometry. X-Ray Spectrom. 35 (1), 57–62. https://doi.org/10.1002/xrs.817.

McCune, B., Grace, J.B., 2002. Chapter 6: distance measures. Analysis of Ecological Communities. Mjm Software Design.

Meerts, Pierre, 2002. Mineral nutrient concentrations in sapwood and heartwood: a literature review. Ann. For. Sci. 59 (7), 713–722. https://doi.org/10.1051/forest:2002059.

Mendez, Juan C., et al., 2022. Surface reactivity of the natural metal (hydr)oxides in weathered tropical soils. Geoderma 406, 115517. https://doi.org/10.1016/j.geoderma.2021.115517.

Momoshima, N., Bondietti, E.A., 1990. Cation binding in wood: applications to understanding historical changes in divalent cation availability to red spruce. Can. J. For. Res. 20 (12), 1840–1849. https://doi.org/10.1139/x90-247.

Nellemann, Christian, 2012. Green Carbon, Black Trade: Illegal logging, tax fraud and laundering in the world's tropical forests. A Rapid Response Assessment. United Nations Environment Programme, GRID- Arendal. INTERPOL Environmental Crime Programme , p. 72 isbn: 9788277011028 www.grida.no.

Oksanen, Jari, 2020. vegan: Community Ecology Package. R Package Version 2.5-7.

Phillips, Steven J., Anderson, Robert P., Schapire, Robert E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190 (3–4), 231–259. https://doi.org/10.1016/j. ecolmodel.2005.03.026.

Pilgrim, Tamara S., John Watling, R., Grice, Kliti, 2010. Application of trace element and stable isotope signatures to determine the provenance of tea (Camellia sinensis) samples. Food Chem. 118 (4), 921–926. https://doi.org/10.1016/j.foodchem.2008.08.077.

Poggio, Laura, et al., 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. Soil 7 (1), 217–240. https://doi.org/10.5194/soil-7-217-2021.

Pribyl, Douglas W., 2010. A Critical Review of the Conventional SOC to SOM Conversion Factor. https://doi.org/10.1016/j.geoderma.2010.02.003.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Rieuwerts, John S., 2007. The mobility and bioavailability of trace metals in tropical soils: a review. Chem. Speciat. Bioavailab. 19 (2), 75–85. https://doi.org/10.3184/095422907X211918.

Römkens, P.F.A.M., et al., 2009. Prediction of cadmium uptake by brown rice and derivation of soil-plant transfer models to improve soil protection guidelines. Environ. Pollut. 157 (8-9), 2435–2444. https://doi.org/10.1016/j.envpol.2009.03.009.

Russell, Ann E., Hall, Steven J., Raich, James W., 2017. Tropical tree species traits drive soil cation dynamics via effects on pH: a proposed conceptual framework. Ecol. Monogr. 87 (4), 685–701. https://doi.org/10.1002/ecm.1274.

Scharnweber, Tobias, et al., 2016. Common trends in elements? Within- and between-tree variations of wood-chemistry measured by X-ray fluorescence — a dendrochemical study. Sci. Total Environ. 566–567, 1245–1253. https://doi.org/10.1016/j.scitotenv.2016.05.182.

Smith, Kevin T., et al., 2014. Dendrochemical patterns of calcium, zinc, and potassium related to internal factors detected by energy dispersive X-ray fluorescence (EDXRF). Chemosphere 95, 58–62. https://doi.org/10.1016/j.chemosphere.2013.08.017.

Soong, Jennifer L., 2020. Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests. Sci. Rep. 10 (1). https://doi.org/10.1038/s41598-020-58913-8 isbn:9781420093681.

Tyler, Germund, Olsson, Tommy, 2001. Plant uptake of major and minor mineral elements as influenced by soil acidity and liming. Plant Soil 230 (2), 307–321. https://doi.org/10.1023/A: 1010314400976.

Vitousek, Peter M., 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65 (1), 285–298. https://doi.org/10.2307/1939481.

Vlam, Mart, et al., 2018. Developing forensic tools for an african timber: regional origin is revealed by genetic characteristics, but not by isotopic signature. Biol. Conserv. 220 (February), 262–271. https://doi.org/10.1016/j.biocon.2018.01.031.

Wang, Zhijun, 2020. Linking growing conditions to stable isotope ratios and elemental compositions of Costa Rican bananas (Musa spp.). Foodserv. Res. Int., 129 https://doi.org/10.1016/j.foodres.2019.108882.

Watanabe, Toshihiro, et al., 2007. Evolutionary control of leaf element composition in plants: rapid report. New Phytol. 174 (3), 516–523. https://doi.org/10.1111/j.1469-8137.2007.02078.x.

Wyttenbach, A., Furrer, V., Tobler, L., 1995. The concentration ratios plant to soil for the stable elements cs, rb and K. Sci. Total Environ. 173–174, 361–367. https://doi.org/10.1016/0048-9697(95)04737-9.

Zhu, Y.G., Smolders, E., 2000. Plant uptake of radiocaesium:a review of mechanisms, regulation and application. J. Exp. Bot. 51 (351), 1635–1645. https://doi.org/10.1093/jexbot/51.351.1635.