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An Integrated Similarity Analysis of Anatomical and Physical Wood Properties of Tropical Species from India, Mozambique, and East Timor

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Abstract: Tropical species are highly valued timber sources showing a large diversity of wood characteristics. Since there are major concerns regarding the sustainability of these tropical species in many tropical regions, knowledge of the variability in wood properties is therefore a valuable tool to design targeted exploitation and to enlarge the wood resources base, namely by identifying alternatives for CITES-listed species. In this study, 98 tropical wood species belonging to 73 genera from India, Mozambique, and East Timor were investigated regarding wood anatomy and physical properties. Numerical taxonomy, by means of cluster analysis and principal component analysis grouped species with anatomical and physical similarities from different geographical origins. In addition to wood density, ray and vessel characteristics as well as wood moisture and wood shrinkage properties explained the main variability of these species. The contribution of wood color patterns was highlighted as consistently separating the Mozambique woods. A distinct geographical pattern was not observed, reinforcing that species from India, Mozambique, and East Timor show similar anatomical and physical wood properties, which could be useful to increase timber trade diversity. The multivariate analysis showed that species from Mozambique, such as *Morus mesozygia*, and *Millettia stuhlmannii* and *Swartzia madagascariensis*, could be alternatives for the CITES-listed species *Cedrela odorata* and *Dalbergia melanoxylon*, respectively.

Keywords: tropical species; wood anatomy; wood density; wood color; multivariate analysis; species diversity

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1. Introduction

Tropical species play an important role in world forest diversity as well as in timber trade. The sustainability of tropical forests is a matter of global concern, and international conventions have been crucial in controlling illegal wood trade. Wood identification and the characterization of tropical species are increasingly considered tools for trade monitoring (e.g., [1–4]). Most commercial tropical woods are mainly appreciated for their high wood density and aesthetic properties, such as wood color, although a high natural species variability is found. In fact, wood density varies within species and/or genera, ranging, for example, from 100 kg/m^3 in *Ochroma* sp. (balsa) and 380 kg/m^3 in *Triplochiton scleroxylon* K. Schum. (obeche) to over 1000 kg/m^3 in *Diospyros* sp. (ebony), *Tamarindus indica* L. (tamarind), and *Lophira alata* Banks ex Gaertn. (azobé) [5,6]. Wood color variability ranges from yellowish white in *Triplochiton scleroxylon* and *Turraenthus africana* Harms (avodire) to reddish brown in *Pterocarpus soyauxii* Taub. (padauk) and black in *Diospyrus crassiflora* Hiern and *Dalbergia melanoxylon* Guill. and Perr. (ebony) [7]. Even if there is this species diversity and wood properties variability, there are global concerns regarding the sustainability of the tropical forests for which the contribution of international conventions has been crucial

by increasing the interest in wood identification and wood characterization of the tropical species as a tool to control illegal trade.

The anatomical wood characteristics and their interactions across different taxa (genera, families, and species) and climatic and ecological gradients have been extensively analyzed and are of great interest for phylogenetic, taxonomic, and wood identification purposes (e.g., [8–14]). However, tropical species represent important challenges due to their large diversity and the similarity of anatomical wood patterns in many genera and species (e.g., [15,16]. Therefore, genetic and chemical data are also being successfully studied to discriminate between tropical species (e.g., [4,17,18]).

Wood density is of high interest for taxonomic and phylogenetic studies since it is greatly controlled by genetic factors [19,20]. Thus, the genetic and/or geographical provenance effects on wood density are often studied for the most valued woods due to their practical implications for tree breeding and conservation programs (e.g., [21–25]).

The species characterization of the anatomical (e.g., tissue composition, cellular dimension and arrangement) and physical wood properties (e.g., wood density) is essential to analyze the specific wood quality and product suitability [26]. Given the within-species variability regarding wood properties, interactions across different geographical locations and ecological gradients are often studied to analyze the potential for wood production and/or species conservation [27–30].

Compared to temperate forests, less studies are found on the variability in the anatomical and physical wood properties from different tropical species across different geographical regions. Therefore, the systematic wood characterization of different tropical wood species is challenging and may allow their better sustainable use, i.e., by highlighting the importance of valuable secondary species that may increase the number of available timber species, thereby mitigating the tropical deforestation and species over-exploitation that are expressed by the endangered timber species listed in the Convention on International Trade of Endangered Species in Wild Fauna and Flora (CITES). About 25% of the traded timber in industrial countries in the northern hemisphere comes from tropical forests, namely from the Asia–Pacific region, followed by South America and Africa [31]. Some of the most valuable tropical woods, such as *Spirostachys africana* Sond. (tamboti, African sandalwood) and *Dalbergia melanoxylon,* are found in Mozambique; *Santalum album* L. (sandalwood) is found in East Timor; and *Tectona grandis* L. (teak) is found in India and East Timor. However, in these regions, other lesser-known wood species, such as *Pseudolachnostylis maprounaefolia* Pax, *Pericopsis angolensis* Meeuwen, *Sterculia appendiculata* K. Schum., and *Sterculia quinqueloba* K. Schum. or lesser-known provenances, for instance, of *Tectona grandis,* may reveal promising end uses [21,32,33].

In this study, the anatomical and physical wood characteristics from 98 tropical species from India, Mozambique, and East Timor were analyzed and compared by means of a multivariate analysis. The overarching goal of this research was to contribute to the better use of tropical wood resources by obtaining and adding knowledge on these tropical wood species based on the anatomical and physical wood characterization. The specific aims were to obtain the species classifications and analyze the similarities in the anatomical and physical properties of wood between species from different origins.

2. Materials and Methods

2.1. Collections

The data included in this paper are based on original observations of wood samples and published results [34–38]. The studied samples were selected from wood collections of the Forest Research Center of the School of Agriculture (Portugal LISFLw xylarium) and the Tropical Botanical Garden (Portugal LISJCw xylarium), both from the University of Lisbon (UL) in Portugal and from the University of Eduardo Mondlane (UEM) in Maputo, Mozambique. The wood samples were obtained from mature trees and correspond to mature wood. Biometric data and the ages of the trees were often not recorded. A total of 98 wood samples from tropical species were studied: 17 from India (I), corresponding to

the former "Portuguese India" (Goa); 33 from East Timor (T); and 48 from Mozambique (M—from the UL or N—from the UEM), as described in Table 1.

Table 1. List of the 98 studied tropical species by code according to each geographical provenance: India (I), Mozambique (M or N), and East Timor (T). The species with more than one geographical provenance and the genera with more than one species are marked in bold. Species marked with an asterisk are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix II.

Code	Species	Code	Species
I1	***Acacia*** *catechu* Willd.	T1	***Albizia*** *lebbeckoides* (DC) Benth.
I2	*Aegle marmelos* Corrêa	T2	*Aleurites moluccana* Willd.
I3	***Albizia*** *lebbeck* Benth.	T3	*Alstonia scholaris* (L.) R. Br.
I4	***Artocarpus integrifolia*L.**	T4	***Artocarpus integrifolia* L.**
I5	***Bombax*** *malabaricum* DC.	T5	*Bischofia javanica* Blume
I6	*Careya arborea* Roxb.	T6	*Calophyllum inophyllum* L.
I7 *	***Dalbergia*** *sissoo* Roxb.	T7	*Canarium commune* L.
I8	*Eugenia jambolana* Lam.	T8	*Cassia fistula* L.
I9	***Ficus*** *indica* Roxb.	T9	*Casuarina junghuhniana* Miq.
I10	*Lagerstroemia parviflora* Roxb.	T10 *	***Cedrela*** *toona* var *australis* Roxb. C. DC.
I11	*Mangifera indica* L.	T11	*Decaspermum paniculatum* Kurz
I12	*Polyalthia fragans* Benth. and Hook	T12	*Elaeocarpus sphaericus* K. Schum.
I13	***Tectona grandis*L.**	T13	***Ficus*** *macrophylla* Roxb.
I14	***Terminalia*** *bellirica* Roxb.	T14	*Ganophyllum falcatum* Blume
I15	***Terminalia*** *paniculata* Roth	T15	*Hibiscus tiliaceus* L.
I16	***Terminalia*** *tomentosa* W. et Arn.	T16	*Homalium tomentosum* Benth.
I17	***Xylia*** *dolabriformis* Benth.	T17	*Intsia bijuga* O. K.
M1	*Adina microcephala* (del.) Hiern	T18	*Macaranga tanarius* Muell.
M2	*Afrormosia angolensis* (Bak.) Harms	T19	***Melaleuca leucadendron* L.**
M3	*Afzelia quanzensis* Welw.	T20	*Pometia pinnata* Forst.
M4	***Albizia*** *adianthifolia* W. F. Wight	T21	***Pterocarpus*** *indicus* Willd.
M5	***Albizia*** *versicolor* Welw. ex Oliv.als	T22	*Pterospermum acerifolium* Will.
M6	***Amblygonocarpus*** *obtusangulus* Harms	T23	*Pygeum* sp.
M7	*Androstachys johnsonii* Prain	T24	*Santalum album* L.
M8	***Bombax*** *rhodognaphalon* K. Schum. ex. Engl.	T25	*Sarcocephalus cordatus* Miq.
M9	*Burkea africana* Hook.	T26	*Schleichera oleosa* Merr.
M10	***Celtis*** *durandii* Engl.	T27	***Sterculia*** *foetida* L.
M11	***Celtis*** *kraussiana* Bernh.	T28	*Tamarindus indica* L.
M12	*Chlorophora excelsa* (*Milicia excelsa)* (Welw.) Benth. Hook	T29	***Tectona grandis* L.**
M13	*Colophospermum mopane* Kirk.	T30	***Terminalia catappa* L.**
M14	***Combretum*** *imberbe* Wawra	T31	*Thespesia populnea* Soland, ex Corrêa
M15	*Cordyla africana* Lour.	T32	*Timonius rumphii* DC.
M16 *	***Dalbergia*** *melanoxylon* Guill. and Perr	T33	*Vitex pubescens* Vahl
M17	*Dialium schlechteri* Harms	N1	***Acacia*** *robusta* Burch

Table 1. *Cont.*

Code	Species	Code	Species
M18	*Diospyros mespiliformis* Hochst. ex A. DC.	N2	***Amblygonocarpus*** *andongensis* (Welw. ex Oliv.) Excell and Torre
M19	***Erythrophleum*** *africanum* (Benth.) Harms	N3	*Berchemia discolor* (Klotzsch) Hemsl.
M20	***Erythrophleum*** *guineense* Don	N4 *	***Cedrela*** *odorata* L.
M21	*Khaya* sp.	N5	*Cleistanthus schlechteri* (Pax) Hutch.
M22	*Khaya* sp.	N6	***Combretum*** *zeyheri* Sond.
M23	*Millettia stuhlmannii* Taub.	N7	*Diplorhynchus condylocarpon* (Mull. Arg.) Pichon
M24	***Morus*** *lactea* Mildbr. (*Celtis lactea* Sim.)	N8	***Melaleuca leucadendron*****(L.) L.**
M25	*Ostryoderris stuhlmannii* Dunn ex Baker f.	N9	***Morus*** *mesozygia* Stapf
M26	*Piliostigma thonningii* (Schumach.) Milne-Redhead	N10	***Pterocarpus*** *antunesii* (Tab.) Harms
M27	*Piptadenia buchananii* Bak. (*Newtonia buchananii*)	N11	*Rhodognaphalon schumannianum* A. Robyns
M28	*Pteleopsis myrtifolia* (Lawson) Engl. and Diels	N12	*Schrebera trichoclada* Welw.
M29	***Pterocarpus*** *angolensis* DC.	N13	*Syncarpia glomulifera* (Sm.) Wield.
M30	*Ricinodendron rautanenii* (Schinz) Radcl-Sm	N14	*Syringa vulgaris* L.
M31	*Spirostachys africana* Sond.	N15	***Xylia*** *torreana* Brenan
M32	***Sterculia*** *quinqueloba* (Garcke) K. Schum.		
M33	*Swartzia madagascariensis* Desv.		

* According Palacio et al. [14], since 2017, all species of the genus *Dalbergia* have been listed in CITES Appendix II, except *D. nigra*, which has been listed in Appendix I since 1992; *Cedrela* P. Browne comprises 18 species, all of them listed in CITES Appendix II.

2.2. Wood Characterization

2.2.1. Anatomical Characterization

Microscopic slides were prepared from wood samples following the usual methods of softening, sectioning, staining, and mounting. The wood samples were softened in boiling water or in a 50/50 glycerin solution. Sections of 17–20 µm thickness were cut with a sliding microtome, stained with safranin, and mounted with Euparal. Macerations were prepared using Jeffrey's solution and stained with 1% gentian violet. Macro- and microphotographs were taken for each wood section of each species. Samples were observed by light microscopy (Leitz Dialux 20EB), and 40 measurements, at least, per feature were performed using image analysis software (Leica Qwin Standard). The fiber dimensions were measured in individualized cells (maceration); the vessel diameters were measured in transverse sections as well as the vessel frequency and the vessel wall thickness; the vessel element lengths and vessel pits were measured in tangential sections; the ray widths and ray lengths were measured in tangential sections; the ray frequency was measured in the tangential; and uniseriate, biseriate, and multiseriate rays were counted as one ray each. The anatomical descriptions followed the recommendations of the IAWA Committee [39].

2.2.2. Physical Properties Determination

The wood density, moisture content (MC), and wood shrinkage values were determined according to the following methods. Cubic samples with 30 mm of edge and faces corresponding to the transverse, tangential, and radial sections were prepared. Volumes and weights were measured for each sample. Samples were saturated, air-dried, and oven-dried, first at 60 °C and then at 103 ± 2 °C to a constant weight for the determination of wood basic density, referred to here as wood density, calculated on the basis of oven dry

weight. Moisture content and wood shrinkage determinations were made according to the Portuguese standards (NP-614 and NP-615), i.e., samples were at 60% relative humidity and 20 °C until they reached a constant mass, and wood density was also assessed.

2.2.3. Color Measurements

Wood color was measured directly on the tangential surface of the standard wood samples after a fine sanding of the surface to represent the natural wood color. The CIELab chromatic system from the Commission Internationale d'Eclairage (CIE) was used to measure lightness (L*), ranging from 0 (black) to 100 (white); redness (a*), from +a*(red) to –a* (green); and yellowness degree (b*), from +b* (yellow) to –b* (blue), from 0 to 60. Four measurements were performed per each tangential face using a Minolta CM–3630 Spectrophotometer, and data were analyzed by Papercontrol v. 2. A color intensity qualitative character ranging from 1 (light) to 27 (black), was conceived using a scale of 33 different wood species and wood textures with an expert-based classification taking into account the visual observation and comparative analysis.

2.3. Character Selection

A total of 29 variables related to 13 anatomical and 16 physical (including 4 colorimetric) characteristics were selected and are compiled in Table 2. The mean value for each wood species was used in the different analyses.

Table 2. Descriptions and codes of the anatomical and physical wood variables.

Code	Character Description (Units)	Code	Character Description (Units)
V1	Mean number (Nr) of vessels/mm^2	FIS1	Wood density, 12% MC (g/cm^3)
V4	Mean vessel pit diameter (µm)	FIS2	Oven-dry wood density (g/cm^3)
V5	Mean vessel wall thickness (µm)	FIS3	MC, dry basis (%)
V6	Mean vessel element length (µm)	FIS4	MC, wet basis (%)
V7	Mean vessel diameter (µm)	FIS5	Volumetric shrinkage (%)
R1	Mean Nr of rays/mm	FIS6	Tangential shrinkage (%)
R3	Ray height in cell numbers (#)	FIS7	Radial shrinkage (%)
R5	Mean ray height (µm)	FIS8	Axial shrinkage (%)
R7	Ray width in cell numbers (#)	FIS9	Coefficient of volumetric shrinkage (%)
R8	Mean ray width (µm)	FIS10	Coefficient of tangential shrinkage (%)
F1	Mean fiber wall thickness (µm)	FIS11	Coefficient of radial shrinkage (%)
F2	Mean fiber length (µm)	FIS12	Coefficient of axial shrinkage (%)
F4	Mean fiber width (µm)	C4	L* polished sample/natural wood
		C5	a* polished sample/natural wood
		C6	b* polished sample/natural wood
		C7	Color intensity

2.4. Data Analysis

The similarity of the anatomical and physical wood characteristics of the different tropical wood species was quantified by means of cluster analysis (CA) and principal component analysis (PCA), generating classification systems accordingly [40,41]. The CA was performed using the UPGMA method (unweighted pair-group average) to express the relationships existing between taxa based on their pairwise similarities. The distortion degree of the generated dendrogram was given by the cophenetic correlation coefficient (c) to measure how faithfully the pairwise distances between the original unmodeled data points were preserved.

The PCA was conducted to identify directions along which the variance in the data was maximal. Eigenvalues, eigenvectors, and principal component (PC) axis scores were produced for the datasets. PCs were plotted against one another to reveal clustering or structure in the dataset due to similarities between the wood species. The overlapping of PCA projections with MST (minimum spanning tree), also known as the SCN (shortest connection network) method, resulted in a network of connections between the

different tropical woods, detecting pairs that, even if they were close within the PC1 and PC2 plan, were in fact distant, taking into consideration the plan of PC1 and PC3. The principal component axis scores of PCs 1 vs. 2 and PCs 1 vs. 3 were plotted to identify clustering patterns.

The number of tropical wood species and the variables included in each analysis are shown in Table 3. Some species and variables were excluded from the analysis to avoid biased results, namely species with missing values or highly correlated variables (e.g., ratios between variables and standard deviation values), while the variables were set as equally important, as required by the multivariate analysis criteria.

Table 3. Number and list of the tropical wood species (codes as in Table 1) and variables (codes as in Table 2) included in each analysis.

Species (#)	Tropical Species Code	Variable Code
81	I1 to I17, M1 to M33, T1 to T17, T20 to T33	V1, V4, V5, V6, V7, R1, R3, R5, R7, R8, F1, F2, F4, C4, C5, C6, C7, FIS1, FIS3, FIS5
87	I1 to I17, M1 to M6, M8 to M21, M23 to M29, M31, M33, T2 to T23, T25, T26, T28 to T33, N2 to N9, N11 to N13	V1, V4, V5, V6, V7, R1, R3, R5, R7, R8, F1, F2, F4
54	I1 to I17, M1 to M6, M8 to M30, M33, T9, T10, T17, T20, T21, T25, T28	FIS1, FIS4 to FIS12, C4, C5, C6, C7

The statistical analysis was performed using the NTSYSpc (v.2.1, New York, NY, USA) software program.

3. Results

3.1. Species Variability Based on Anatomical and Physical Wood Characteristics

A high variability was found for the anatomical and physical wood properties, as observed in the range of values shown in Table 4. For the main anatomical variables, such as vessel frequency, ray and fiber tissues, wood density, and wood color, the following were found: the highest vessel frequency was 193 vessels per mm^2 in *Androstachys jobnsonii* (M7), and the lowest was in *Bombax malabaricum* (I5); the tallest and largest rays were 1500 µm × 215 µm in *Sterculia quinqueloba* (M32), and the shortest rays were 101 µm in *Dalbergia sissoo* (I7); the longest fibers measured 3780 µm in *Syringa vulgaris,* and the widest were 46 µm in *Ricinodendron rautanenii* (M30); and the highest value of wood density was 1400 kg/m^3 for *Tamarindus indica* (T28), while the lowest was 230 kg/m^3 for *Ricinodendron rautanenii* (M30). The wood color varied from the lightest-colored wood in *Aleurites moluccana* (T2) to the reddest in *Pterocarpus indicus* (T21), the yellowest in *Morus lactea* (M24), and the darkest wood in *Dalbergia melanoxylon* (M16). The mean values are summarized in Table S1.

Table 4. Minimum and maximum values found for each of the studied anatomical or physical variables and the scientific names and codes of the corresponding species. For code characters and abbreviations see Table 2.

Character (Units)	Min–Max Values/Species Name/Species Code
V1 (Nr vessels/mm^2)	1–193/*Bombax malabaricum–Androstachys jobnsonii*/I5–M7
V4 (µm)	1.16–15.85/*Cleistanthus schlechteri–Ricinodendron rautanenii*/N5–M30
V5 (µm)	3.1–15.6/*Khaya–Xylia torreana*/M21–N15
V6 (µm)	150–850/*Dalbergia sissoo–Aleurites moluccana*/I7–T2
V7 (µm)	45–285/*A. jobnsonii–R. rautanenii*/M7–M30
V8 (µm)	5–85/*Schrebera trichoclata–Sterculia quinqueloba*/N12–M32
R1 (Nr of rays/mm)	2–23/*Acacia robusta–Pterocarpus antunesii*/N1–N10
R3 (#)	5–67/*Calophyllum inophyllum–A. robusta*/T6–N1

Table 4. *Cont.*

Character (Units)	Min–Max Values/Species Name/Species Code
R5 (μm)	101–1500/*Dalbergia sissoo–S. quinqueloba*/I7–M32
R7 (#)	1–11/*Lagerstromia parviflora–S. quinqueloba*/I10–M32
R8 (μm)	13–215/*Ganophyllum falcatum–Albizia lebbeckoides*/T14–T1
F1 (μm)	2.4–7.2/*Elaeocarpus sphaericus–O. stuhlmannii*/T12–M25
F2 (μm)	700–3780/*Dalbergia melanoxylon–Syringa vulgaris*/M16–N14
F4 (μm)	12–46/*Colophospermum mopane–R. rautanenii*/M13–M30
C4	25.91–85.11/*D. melanoxylon–A. moluccana*/M16 –T2
C5	1.86–20.29/*D. melanoxylon–P. indicus*/M16–T21
C6	0.97–34.89/*D. melanoxylon–Morus lactea*/M16–M24
C7	1–27/*Diospyros mespiliformis–D. melanoxylon*/M18–T2
FIS1 (g/cm^3)	0.23–1.37/*R. rautanenii–Tamarindus indica*/M30–T28
FIS2 (g/cm^3)	0.21–1.31/*R. rautanenii–T. indica*/M30–T28
FIS3 (%)	10.0–16.9/*P. indicus–Bischofia javanica*/T21–T5
FIS4 (%)	9.1–31.0/*P. indicus–Ficus indica*/T21–I9
FIS5 (%)	3.50–14.33/*Cordyla africana–Terminalia tomentosa*/M15–I16
FIS6 (%)	1.6–9.17/*Cordyla africana–Aegle marmelos*/M15–I2
FIS7 (%)	1.20–5.17/*Albizia adianthifolia–Terminalia tomentosa*/M4–I16
FIS8 (%)	0.01–0.65/*Aegle marmelos–Terminalia bellirica*/I2–I14
FIS9 (%)	0.26–0.77/*R. rautanenii–Casuarina junghuniana*/M30–T9
FIS10 (%)	0.14–0.50/*R. rautanenii–C. junghuniana*/M30–T9
FIS11(%)	0.09–0.30/*R. rautanenii–T. indica*/M30–T28
FIS12 (%)	0.00–0.04/*Eugenia jambolana–P. indicus*/I8–T21

The dendrogram based on 13 anatomical and 7 physical wood characteristics of 81 tropical species (listed in Tables 1 and 3) originated several groups and showed that *Androstachys johnsonii* (M7) and three groups of species (T5 and T1; M30, T2, and T12; and I5, M32, and T27) were clearly different from all other sets (Figure 1).

Cumulatively, PCs 1–3 accounted for 49.6% of the total amount of variance in the overall dataset of 81 species (Tables 5 and S2). From PC axis score plots, the clustering of wood species was apparent, showing its relative importance (Figure 2a). PC1 explained 23.0% of the variation, and the highest loadings were found for eight anatomical (vessel element length, V6; vessel diameter, V7; number of rays/mm, R1; ray height, R5 and R7; ray width, R8; fiber length, F2; and fiber width, F4) and two physical (b* parameter, C6, and wood density, FIS1) variables. Along PC1, the species showing the highest wood density (FIS1), shortest vessel elements (V6), thinner fibers (F4), and lowest values of the b* parameter (C6) were grouped in the right-hand region: *Casuarina junghuhniana* (T9), *Colophospermum mopane* (M13), *Dialium schlechteri* (M17), *Dalbergia sissoo* (I7), *Tamarindus indica* (T28), and *Dalbergia melanoxylon* (M16) (Figure 2b). In the left-hand region, the wood species from India and Mozambique and some from East Timor were grouped, showing the taller and wider rays (R5, R7, and R8), the yellower colored wood (high values for the b* parameter) (C6), the longer (F2) and larger (F4) fibers, and the longer (V6) and wider (V7) vessels. PC2 explained 15.4% of the residual variation, and three color (L* parameter, C4; a* parameter, C5; and qualitative designation, C7) and two anatomical (ray height, R3, and fiber wall thickness, F1) variables showed the highest loadings. The lighter woods (with the highest values for the L* parameter) (C4) were grouped in the upper region, composed of *Aleurites moluccana* (T2), *Alstonia scholaris* (T3), *Elaeocarpus sphaericus* (T12), and *Ficus macrophylla* (T13) from East Timor as well as *Ricinodendron rautanenii* (M30) from Mozambique. In the opposite region, the woods correlated with high values for the cell number of ray height (R3), fiber wall thickness (F1), and color intensity (C7) were grouped, corresponding to species from Mozambique (darker woods). The remaining variation (11.2%) was explained by PC3, grouping the species showing high vessel frequency (V1), in opposition to species showing high values for mean vessel pit diameter (V4), vessel wall thickness (V5), high moisture content (FIS3), and volumetric shrinkage (FIS5), corresponding to a high number of species from East Timor (Figure S1).

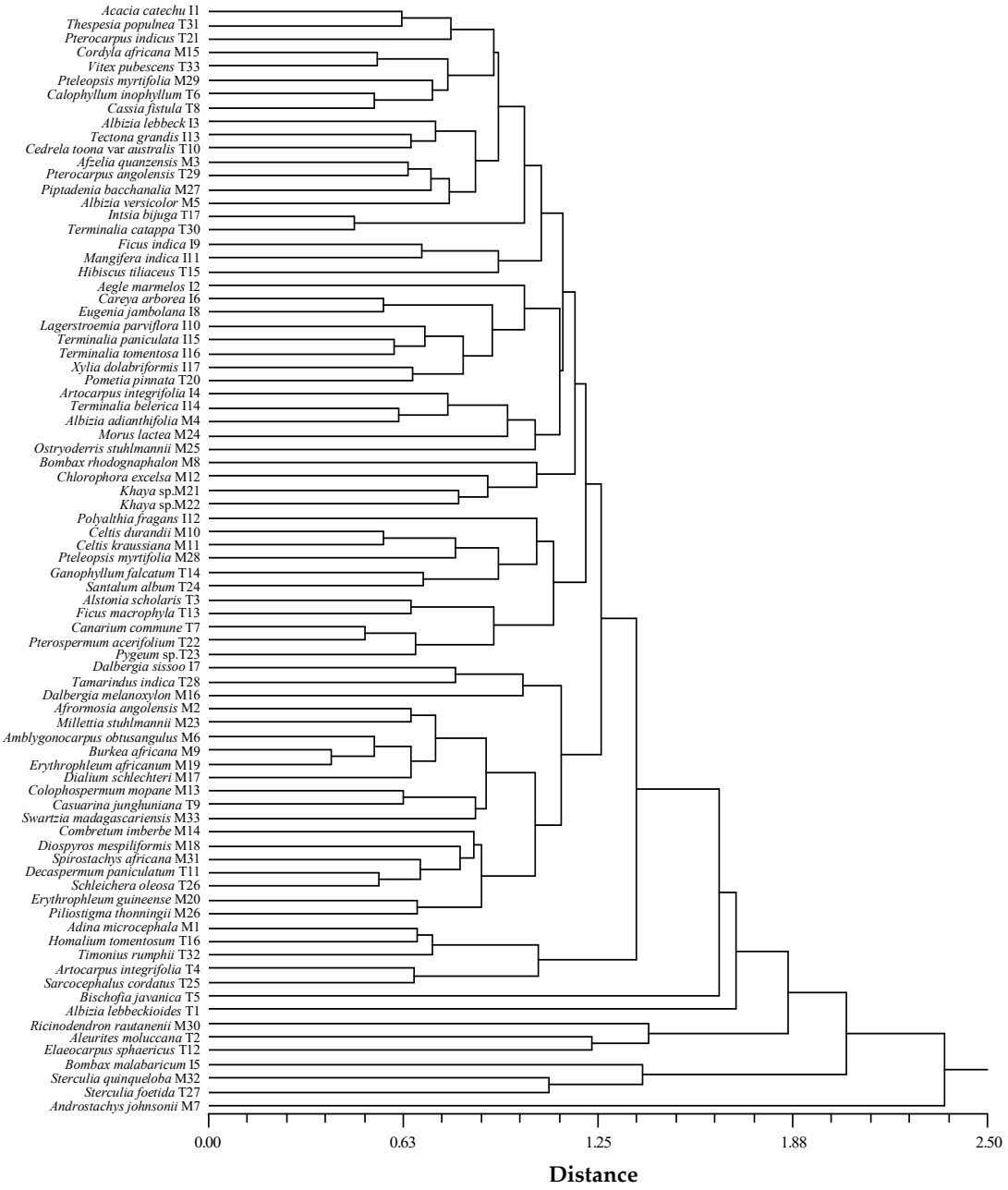


Figure 1. Classification of 81 tropical species (listed in Tables 1 and 3) based on 13 anatomical and 7 physical wood characteristics (coded in Table 2), obtained by the UPGMA clustering method (c = 0.798).

Table 5. Statistics of the principal component analyses (PCA) for the anatomical and physical wood characteristics (coded in Table 2) of the tropical species sets (as described in Tables 1 and 3). The contributions of components 1–3 to the wood species variation (eigenvalue (E.V.), proportion explained (P.E.), and cumulative proportion (C.P.).

	81 Species			**87 Species**			**54 Species**		
Variable	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
E.V.	4.606	3.079	2.240	3.433	2.217	2.065	4.213	3.925	1.992
P.E. (%)	23.0	15.4	11.2	26.7	17.1	15.9	30.1	28.0	14.2
C.P. (%)	23.0	38.4	49.6	26.7	43.8	59.7	30.1	58.1	72.3

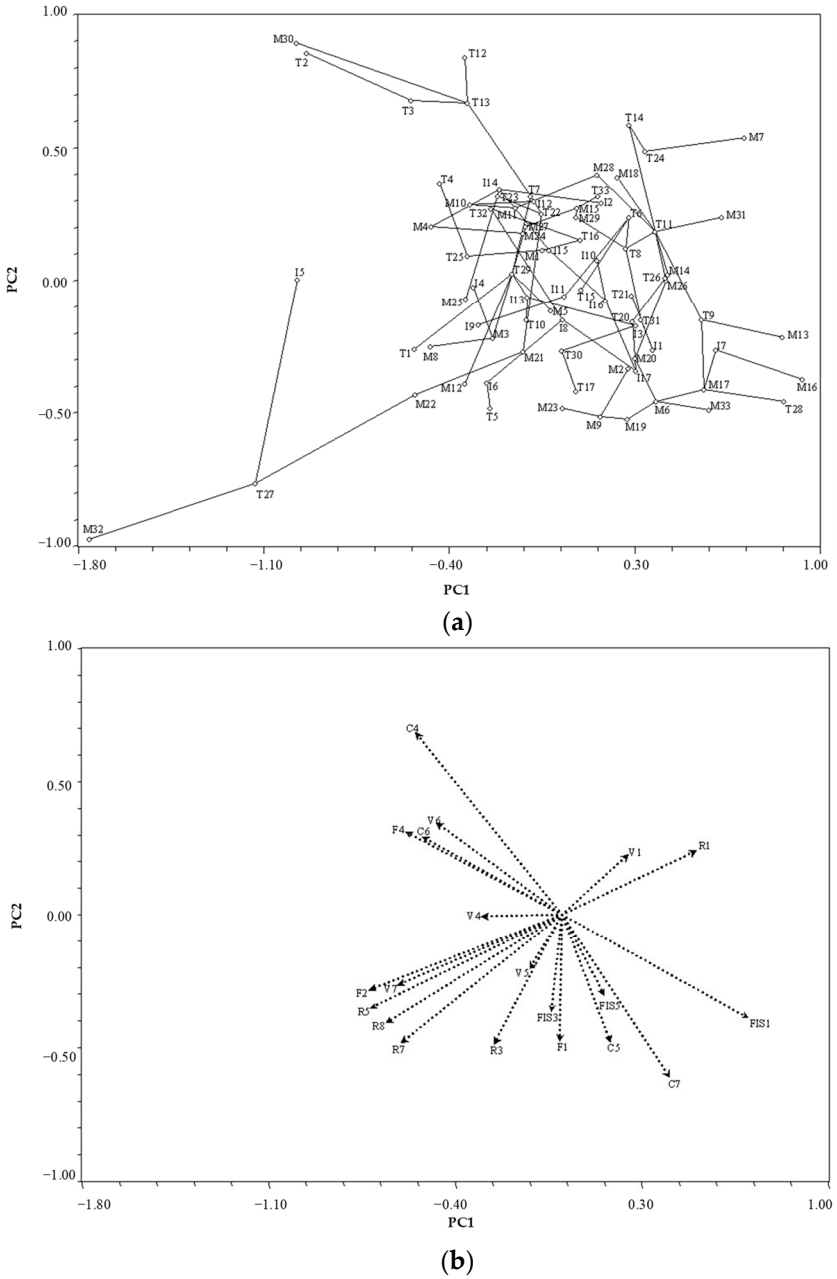


Figure 2. (**a**) PC1 and PC2 projection plots of the 81 tropical species (as listed in Tables 1 and 3) based on 20 anatomical and physical wood characteristics (coded in Table 2), overlapped by the MST method (similarity coefficient of 0.87). (**b**) The indication of the correlation degree between the variables based on the position of the vector.

As shown in Figure 2a, the most different wood species formed one group composed of M30, T2, T3, T12, and T13 (at the top) and a second group of M22, M32, T1, T27, and I5 (on the bottom of the left side), while *Androstachys johnsonii* (M7) was kept separate from all sets in accordance with Figure 1.

3.2. Species Variability Based on Anatomical Characteristics

The cluster analysis of the correlation matrix of 87 species (as listed in Tables 1 and 3) based on 13 anatomical quantitative characteristics showed a low similarity coefficient (r = 0.695), i.e., the dendrogram was not a good representation of the original distances (Figure S2).

The PCA revealed that PCs 1–3 accounted for 59.7% of the total variation of 87 wood species (Table 5). PC1 explained 26.7% of the variation, and the variables with the highest loadings were ray frequency (R1), ray height (R3), ray width (R7 and R8), and fiber length (F2). The variables with the highest loadings for PC2 were the vessel frequency (V1), ray height (R5), and fiber wall thickness (F1), in opposition to the vessel wall thickness (V5) and vessel diameter (V7). Along PC2, the wood species with high vessel frequency (V1), taller rays (R5), and thicker fibers (F1) are found in the upper region, in opposition to wood species with vessels with thicker walls (V5) and wider vessels (V7) (Figure 3). A group of wood species composed of *Bombax malabaricum* (I5), *Bombax rhodognaphalon* (M8), *Chlorophora excelsa* (*Milicia excelsa*) (M12), *Afzelia quanzensis* (M3), *Careya arborea* (I6), and *Ficus indica* (I9) is found in the left-hand region and is quite different from all other sets, in opposition to a group composed of *Decaspermum paniculatum* (T11), *Homalium tomentosum* (T16), *Casuarina junghuhniana* (T9), *Pteleopsis myrtifolia* (M28), *Spirostachys africana* (M31) *Ganophyllum falcatum* (T14), *Schleichera oleosa* (T26), and *Melaleuca leucadendron* (T19). The variables with the highest loadings for PC3 were vessel pit diameter (V4), vessel element length (V6), and fiber width (F4), forming two groups of wood species of East Timor, one comprising *Aleurites moluccana* (T2), *Bischofia javanica* (T5), *Artocarpus integrifolia* (T4), *Sarcocephalus cordatus* (T25), and *Timonius rumphii* (T32) and the other comprising *Macaranga tanarius* (T18), *Elaeocarpus sphaericus* (T12), and *Alstonia scholaris* (T3), which were considered different from all other sets (Figure S3).

A tendency to group tropical wood species from either East Timor or Mozambique was observed, while wood species from India were found to be more dispersed.

3.3. Species Variability Based on Physical Characteristics

The dendrogram based on 14 physical characteristics of 54 species (listed in Tables 1 and 3) showed two groups composed of 29 species mostly from Mozambique and a third group of 13 species from India, all of them forming subgroups (Figure 4).

Cumulatively, PCs 1–3 explained 72.3% of the total variance of 54 wood species (Table 5). PC1 explained 30.1% of the variation, and the variable with the highest loadings was the axial shrinkage coefficient (FIS12), in opposition to the other shrinkage characters (volumetric shrinkage, FIS5; tangential shrinkage, FIS6; radial shrinkage, FIS7; the volumetric shrinkage coefficient, FIS9; the tangential shrinkage coefficient, FIS10; and the axial shrinkage coefficient, FIS11). Along PC1, in the top left-hand quadrant, a group composed mainly of the species from India (I17, I16, I6, I8, I10, I13, I11, I15, I9, I4, I5, I12, and I2) is shown to be clearly different from all other sets, showing high values of moisture content (FIS4) and volumetric, tangential, and axial shrinkage (FIS5, FIS6, and FIS7) while showing lower axial shrinkage coefficients (FIS12) (Figure 5). *Albizia versicolor* (M5), *Pterocarpus angolensis* (M29), *Cordyla africana* (M15), and *Ricinodendron rautanenii* (M30) are found on the right-hand side, showing lower values for those characteristics. The second component explained 28.0% of the variation, and the variables of the lightness of the wood (L*, C4) and the moisture content (FIS4) showed high loadings, in opposition to the wood redness (C5) and wood density (FIS1). Along PC2, one group of species from India (I8, I10, I11, I15, I9, I4, I12, I5, and I2) showing high values for those characteristics was formed, while the redder (higher value of a*, C5) species from Mozambique (M1, M6, M16, M33, M13, M9, M19, M20, and M2) and some from East Timor (T28, T9, and T21) showing high wood density (FIS1) were grouped on the bottom side. The species from India showed a mean wood density of 650 kg/m^3, 24.9 % MC, and 10.7 % wood (volumetric) shrinkage, in opposition to 770 kg/m^3, 11.3% MC, and 5.9 % mean values obtained for the species from Mozambique. In the third component, 14.2% of the remaining variation was explained by the yellowness (C6) and axial shrinkage (FIS8), in opposition to the color intensity (C7). Along PC3, the wood species *Cedrela toona* var *australis* (T10), *Ostryoderris stuhlmannii* (M25), and *Terminalia bellirica* (I14), with yellower woods (high values of b*, C6) and high axial shrinkage (FIS8) are found in the upper region, in opposition to the darker woods of *Dalbergia melanoxylon*

(M16), *Ficus indica* (I9), and *Mangifera indica* (I11), which showed the highest color intensity values (C7) (Figure S4).

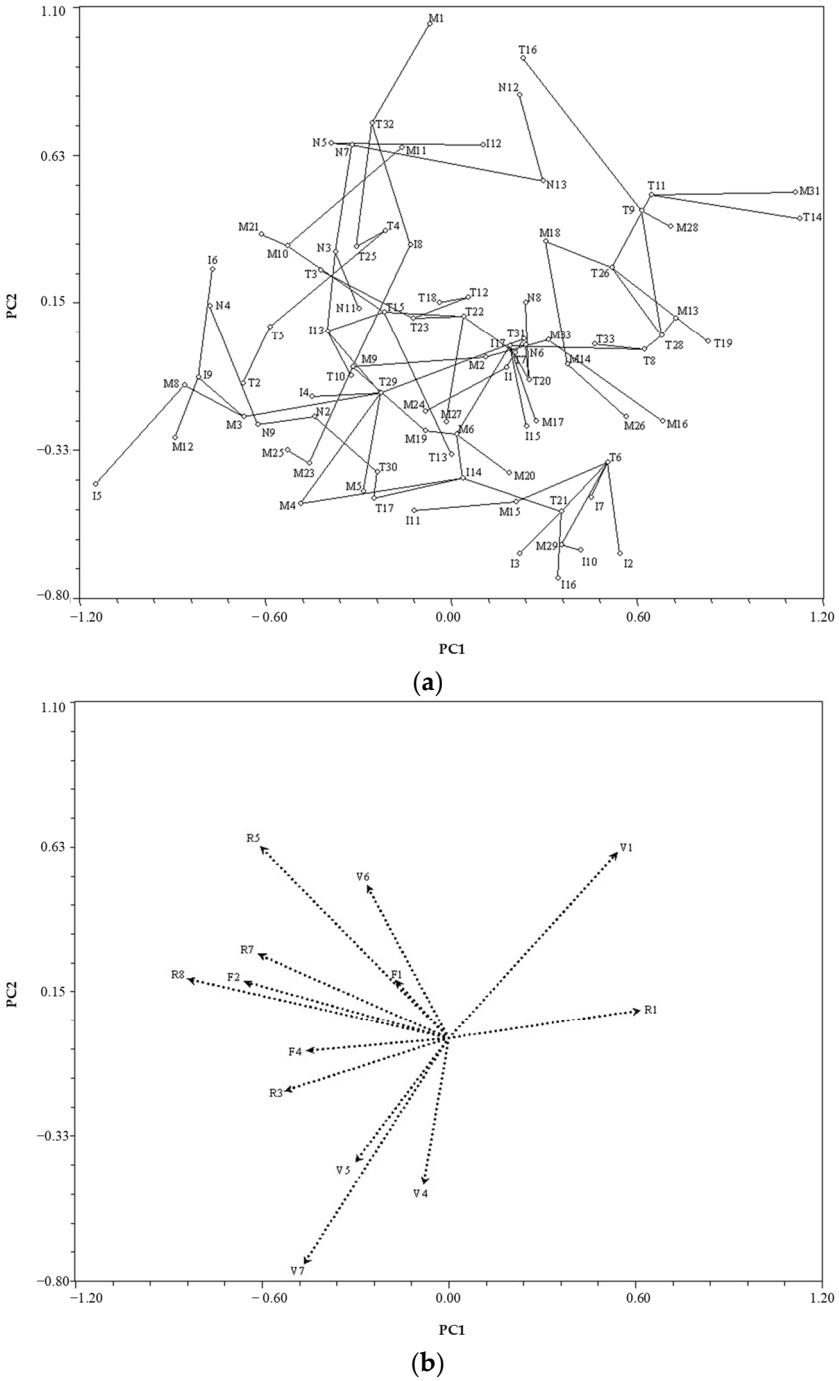


Figure 3. (**a**) PC 1 and PC 2 projection plots of the 87 tropical species (listed in Tables 1 and 3) based on anatomical wood characteristics (coded in Table 2), overlapped with the MST method (c = 0.87). (**b**) The correlation degree between the variables based on the position of the vector.

3.4. Similarity within Species and Genus

3.4.1. Similarity Based on Both Anatomical and Physical Wood Characteristics

Similarity based on both anatomical and physical properties within species (specimens showing more than one geographical provenance) was only observed for *Tectona grandis* from India (I13) and East Timor (T29). Four other weaker connections were found for *Tectona grandis* from East Timor (T29) with *Albizia lebbeckoides* (T1), *Chlorophora excelsea*

(M12), *Albizia versicolor* (M5), and *Afzelia quanzensis* (M3), while *Tectona grandis* from India (I13) was only connected to one more species, *Terminalia catappa* (T30) (Figures 2a and S5).

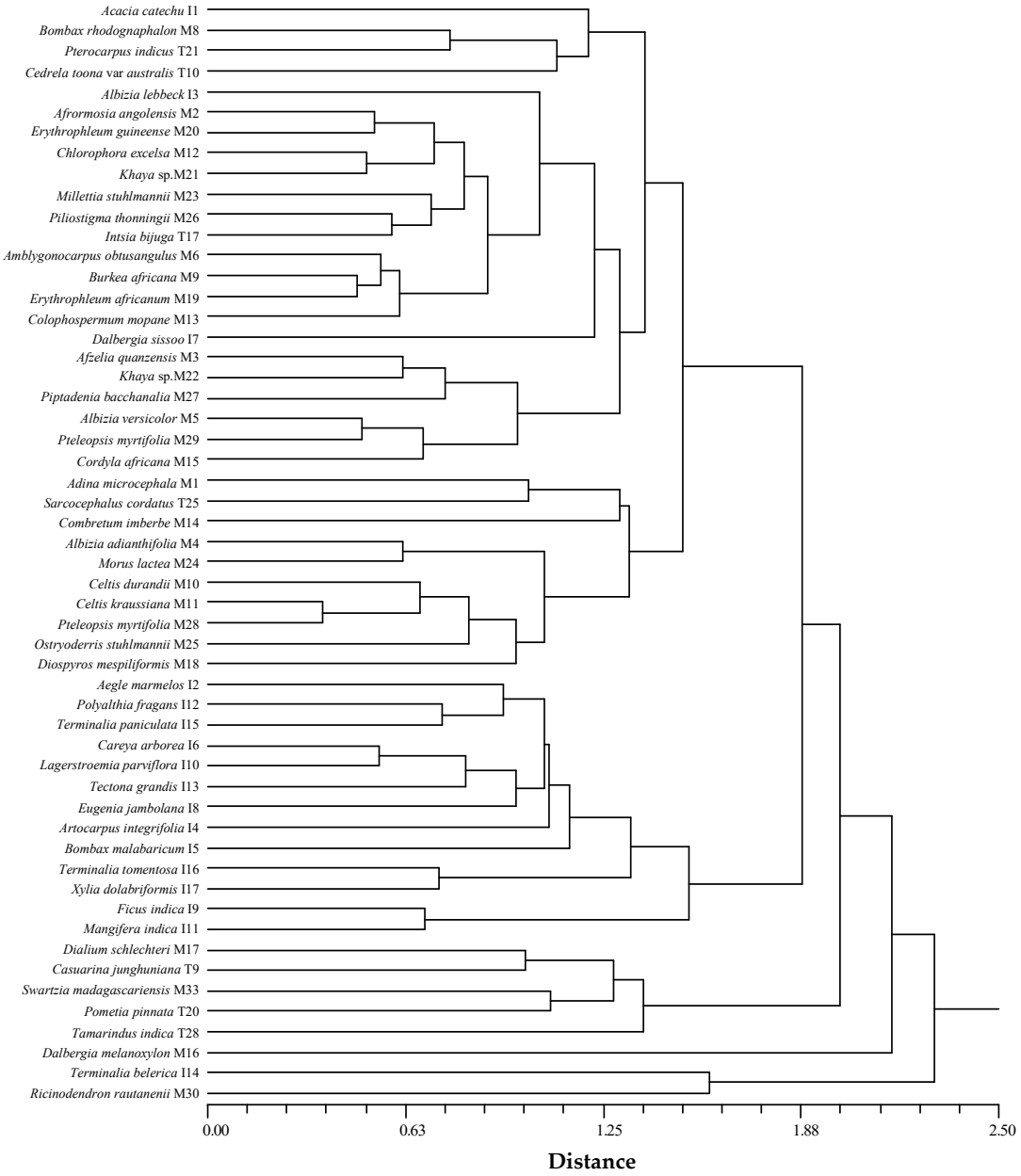
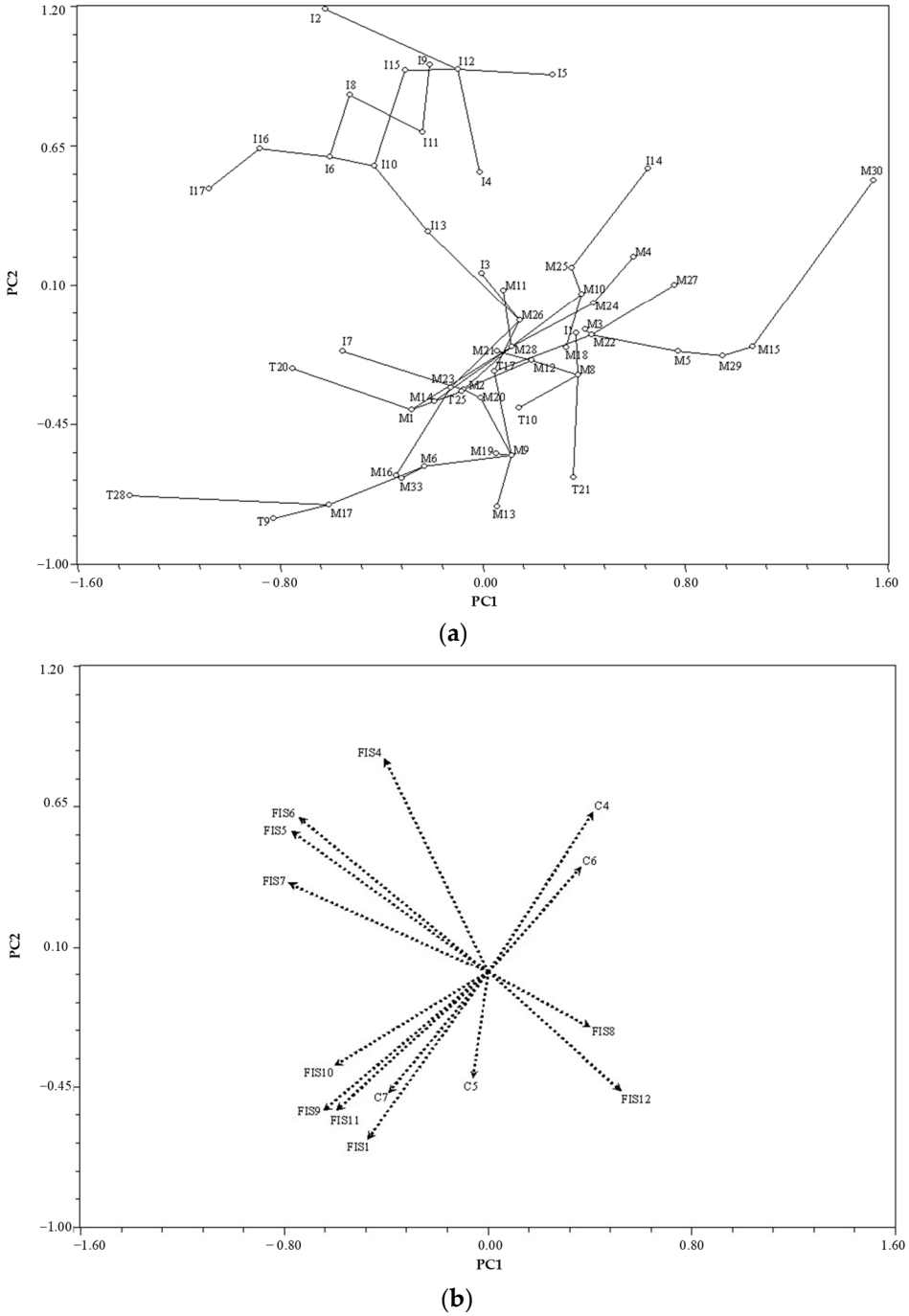


Figure 4. Classification of 54 tropical species (listed in Tables 1 and 3) based on 14 physical wood characteristics (coded in Table 2), obtained by the UPGMA clustering method (c = 0.720).

The *Artocarpus integrifolia* from India (I4) and East Timor (T4) were found to be connected to species from different genera: *Tectona grandis* (T29) and *Sarcocephalus cordatus* (T25), respectively.

Within the genus, i.e., from the genera showing more than one species (*Acacia* spp., *Albizia* spp., *Ambylognocarpus* spp., *Bombax* spp., *Cedrela* spp., *Celtis* spp., *Combretum* spp., *Dalbergia* spp., *Erythroplhleum* spp., *Ficus* spp., *Morus* spp., *Pterocarpus* spp., *Sterculia* spp., *Terminalia* spp., and *Xylia* spp.), four connections were found: *Dalbergia melanoxylon* (M16) with *Dalbergia sissoo* (I7) and *Celtis durandii* (M10) with *Celtis kraussiana* (M11), both from Mozambique, *Sterculia quinqueloba* (M32) with *Sterculia foetida* (T27), *Terminalia bellirica* (I14) with *Terminalia paniculate* (I15), and *Terminalia tomentosa* (I16) with *Terminalia paniculate* (I15), even if a long Euclidean distance was observed that highlighted their differences.



(**a**)

(**b**)

Figure 5. (**a**) PC 1 and PC 2 projection plots of the 54 tropical species (listed in Tables 1 and 3) based on physical wood characteristics (coded in Table 2), overlapped by the MST method (c = 0.92). (**b**) The correlation degree between the variables based on the position of the vector.

Stronger similarities were found between different genera compared to the previously mentioned cases, such as *Tectona grandis* (I13) and *Cedrela toona* (T10), *Careya arborea* (I6) and *Bischofia javanica* (T5), *Elaeocarpus sphaericus* (T12) and *Ficus macrophylla* (T13), *Millettia stuhlmannii* (M23) and *Burkea africana* (M9), *Erythrophleum africanum* (M19) and *Burkea africana* (M9), *Amblygonocarpus obtusangulus* (M6) and *Erythrophleum africanum* (M19), *Dalbergia sissoo* (I7) and *Dialium schlechteri* (M17), *Ganophyllum falcatum* (T14) and *Santalum album* (T24), *Cordyla africana* (M15) and *Pterocarpus angolensis* (M29), and *Pterospermum acerifolium* (T22) and *Canarium commune* (T7).

The CITES-listed species *Dalbergia melanoxylon* (M16) from Mozambique showed both anatomical and physical similarity to the CITES-listed species *Dalbergia sissoo* from India (I7).

3.4.2. Similarity Based on Anatomical Characteristics

Within the three cases of species showing more than one geographical origin, only *Tectona grandis* from India (I13) and from East Timor (T29) were connected, while *Artocarpus integrifolia* from East Timor (I4) was connected to *T. grandis* (T29), *Melaleuca leucadendron* from East Timor (T19) was connected to *Schleichera oleosa* (T26), and *M. leucadendron* from Mozambique (N8) was connected to *Pometia pinnata* (T20) (Figures 3a and S6).

Within the genus (a total of 15 different genera), i.e., from *Acacia* spp., *Albizia* spp., *Ambylognocarpus* spp., *Bombax* spp., *Cedrela* spp., *Celtis* spp., *Combretum* spp., *Dalbergia* spp., *Erythroplhleum* spp., *Ficus* spp., *Morus* spp., *Pterocarpus* spp., *Sterculia* spp., *Terminalia* spp., and *Xylia* spp.), only *Celtis durandii* (M10) and *Celtis kraussiana* (M11), both from Mozambique, were shown to be connected, even if a long Euclidean distance was observed, thereby highlighting their differences.

In fact, stronger similarities compared to the previously mentioned cases were found, such as *Tectona grandis* (I13) and *Hibiscus tiliaceus* (T15), *Tectona grandis* (I13) and *Cedrela toona* (T10), *Tectona grandis* (T29) and *Artocarpus integrifolia* (I4), *Melaleuca leucadendron* (T19) and *Schleichera oleosa* (T26), *Terminalia catappa* (T30) and *Intsia bijuga* (T17), and *Combretum imberbe* (M14) and *Piliostigma thonningii* (M26).

Anatomical similarity was also observed for other species from the set, such as *Acacia catechu* (I1) and *Thespesia populnea* (T31), *Amblygonocarpus obtusangulus* (M6) and *Terminalia bellirica* (I14) as well as *Xylia dolabriformis* (I17), *Xylia dolabriformis* (I17) and *Pometia pinnata* (T20), *Melaleuca leucadendron* (N8) and *Pometia pinnata* (T20), *Canarium commune* (T7) and *Pterospermum acerifolium* (T22), *Afrormosia angolensis* (M2) and *Sterculia quinqueloba* (M32) as well as *Burkea africana* (M9), *Ficus indica* (I9) and *Afzelia quanzensis* (M3), and *Ostryoderris stuhlmannii* (M25) and *Millettia stuhlmannii* (M23).

The CITES-listed species *Cedrela odorata* (N4) and *Dalbergia melanoxylon* (M16) showed similarity to non-CITES species *Morus mesozygia* (N9) and *Swartzia madagascariensis* (M33), respectively.

3.4.3. Similarity Based on Physical Characteristics

No similarity was observed within the genus, i.e., none of *Albizia* spp. (M4, M5, and I3), *Bombax* spp. (I5 and M8), *Celtis* spp. (M10 and M11), *Dalbergia* spp. (M16 and I7), *Erythrophleum* spp. (M19 and M20), *Pterocarpus* spp. (M29 and T21), or *Terminalia* spp. (I14, I15, and I16) were connected between themselves (other species were not analyzed due to missing physical data) (Figures 5a and S7).

The species with stronger similarities were: *Pteleopsis myrtifolia* (M28) and *Celtis kraussiana* (M11), *Burkea africana* (M9) and *Erythrophleum africanum* (M19), and *Albizia versicolor* (M5) and *Pterocarpus angolensis* (M29). More distant connections were found between the species: *Burkea africana* (M9) and *Colophospermum mopane* (M13), *Erythrophleum guineense* (M20) and *Burkea africana* (M9), *Burkea Africana* (M9) and *Amblygonocarpus obtusangulus* (M6), and *Afrormosia angolensis* (M2) and *Erythrophleum guineense* (M20).

Concerning the CITES-listed species found in the set, physical similarity was observed for *D. melanoxylon* (M16) and the non-CITES species *Millettia stuhlmannii* (M23).

4. Discussion

4.1. Species Clustering

The grouping of species by their geographical location (i.e., India, East Timor, and Mozambique) based on both anatomical and physical characteristics was more evident for the 81 species set, with a stronger tendency to group species from Mozambique. The most dispersed species were *Ricinodendron rautanenii* (M30), *Aleurites moluccana* (T2), *Alstonia scholaris* (T3), *Elaeocarpus sphaericus* (T12), *Ficus macrophylla* (T13), *Khaya* sp. (M22), *Sterculia quinqueloba* (M32), *Albizia lebbeckoides* (T1), *Sterculia foetida* (T27), *Bombax malabaricum* (I5),

and *Androstachys johnsonii* (M7). In fact, different geographical distribution trends were found when separately analyzing the anatomical and physical characteristics, i.e., anatomical similarity grouped species from East Timor and Mozambique, and dispersed species from India, while the physical similarity aggregated species from India. The analyses showed large clusters of species from India, Mozambique, and East Timor, which reflects their wood properties similarity. The CA clustering was, in general, confirmed by the PCA results. Thus, wood properties were, in general, of limited value in the delimitation of the geographical origin of wood species, and specific features should be considered according to specific species and each region. In fact, numerical taxonomy methods have been very useful in many comparative and phylogenetic studies within different taxa and/or across different ecological gradients, even if they have been mostly based on qualitative anatomical characters [11,42–46].

4.2. Variability and Interaction of Wood Properties

4.2.1. Both Anatomical and Physical Properties

The diagnostic value of the different wood characters was confirmed by PCA, showing that the variability of the tropical species, based on both anatomical and physical characteristics, was mostly explained by wood density (FIS1), ray (height, R5, and width, R7 and R8), and fiber (length, F2, and width, F4) (Figure 2). Color characteristics (lightness, C4; redness, C5; and intensity, C7) accounted for the species variability. The diagnostic value of vessel-related features was less consistent, with the highest values for the vessel element length (V6) and vessel diameter (V7). Wood density (FIS1) was crucial to grouping wood species. Those showing high wood density were grouped in opposition to wood species showing narrow fibers (F4) and longer vessel elements (V6). Other studies highlighted the relationship between high wood density and longer and thinner fibers in *Eucalyptus* spp. in Brazil [47]. Moreover, the wood (twigs) density variation of different tropical species was more controlled by the wood (fiber and parenchyma) tissues surrounding vessels rather than the vessel lumen proportion, although ambiguous ecological patterns for fiber–parenchyma tissues were found [29,48]. However, studies have usually focused on specific anatomical features, and wood density variability, explained as a function of multiple anatomical traits, is still not well-understood.

Another relatively consistent distribution pattern was found based on wood color (C4, C5, and C7), and it was interesting to note the importance of the lightness of the wood (C4) to forming geographical groups, i.e., the darker woods were mainly from Mozambique (*Afrormosia angolensis* (M2), *Amblygonocarpus obtusangulus* (M6), *Burkea africana* (M9), *Erythrophleum africanum* (M19), *Millettia stuhlmannii* (M23), and *Swartzia madagascariensis* (M33)), while the lighter woods were mainly from East Timor (*Aleurites moluccana* (T2), *Alstonia scholaris* (T3), *Elaeocarpus sphaericus* (T12), and *Ficus macrophylla* (T13)). The formation of wood color is associated with several factors, among others, wood density, wood structure (e.g., growth rings), and anatomy as well as chemical features, namely the content and composition of extractives [19]. Since edaphoclimatic conditions may influence all these wood features [19], it is possible to find a wood color range within the same species. This is certainly a matter where more studies are needed.

The distribution pattern related to vessel features was also observed in wood species showing wider vessels (V7) in opposition to high vessel frequency (V1). Within the present study, the explained variance between the two sets was different, and the lowest vessel frequency (V1) was found for *Bombax malabaricum* (I5) from India (one vessel per mm^2), showing a vessel diameter of 264 μm. This type of distribution is more studied due to the importance of the safety and efficiency of the conductive system that is being reported as habitat and geographically related. The values reported here agree with the literature values. Species from tropical Africa and America, Southeast Asia, and India show 5 to 20 vessels per mm^2 and diameters over 100 μm, in contrast with species from Europe, North America, and Temperate Asia that show narrow vessels and more than 40 vessels per mm^2 [10,49–52]. In fact, tropical species showing a low frequency of vessels

and wider vessels are considered safer and more efficient [49,53]. For example, vessel frequency and vessel diameter as well as wood density were effective for the identification and delimiting *Pterocarpus santalinus* L.f. within the genus, including species from different geographical origins [46]. Moreover, *Dalbergia cearensis* Ducke could be separated from *D. nigra* on the basis of vessel frequency, showing the highest vessel frequency (over 10 vessels per mm^2) [11]. Vessel diameter was found to be relevant to differentiating the wood from the species of the Araucaria Forest in Brazil [54]. Other anatomical characters, such as the number of rays per mm^2 (R1), vessel pit diameter (V4), and fiber wall thickness (F1), contributed less to the set variability (PC3).

4.2.2. Quantitative Wood Anatomy

The variability exclusively explained by the quantitative wood anatomy was mainly due to the ray frequency (R1), height (R3), and width (R7 and R8) and the fiber length (F2). The vessel frequency (V1), vessel wall thickness (V5), vessel diameter (V7), and fiber wall thickness (F1) were also important, while the vessel pit diameter (V4), vessel element length (V6), and fiber width (F4) accounted less for the species set variation. The contributions of vessel frequency, diameter, and element length are consistent with the analysis discussed above. Species showing longer vessel elements (V6) and high values for vessel pit diameter (V4) only explained part of the residual variation (PC3) but made it possible to distinguish some species from East Timor: *Aleurites moluccana* (T2), *Bischofia javanica* (T5), *Artocarpus integrifolia* (T4), *Sarcocephalus cordatus* (T25), *Timonius rumphii* (T32), *Macaranga tanarius* (T18), *Elaeocarpus sphaericus* (T12), and *Alstonia scholaris* (T3). The vessel pitting of Lauraceae species allowed their distinction between other families in Brazilian forests [54]. In fact, the variability in vessel pits is also gaining more interest to explain species distribution [12,50,51,55,56]. With regards to the fiber-related geographical pattern, it has been reported that half of the species from tropical and South Africa show fibers with extremely thick walls [10], while very thin-walled fibers are more prevalent at higher latitudes and in more humid environments and milder temperatures [8]. In this study, *Elaeocarpus sphaericus* (T12) from East Timor showed the thinnest fibres (2.4 µm), in opposition to *Ostryoderris stuhlmannii* (M25) (7.2 µm) from Mozambique and Southeast Africa.

Theoretically there is a compromise between mechanical resistance (fiber thickness) and conductive efficiency (wide vessels) and safety (narrow vessels) [57]. However, most genera present thinner to thicker fibers as well as all the vessel diameter ranges [10]. The fiber–parenchyma variation of several species from Australia was poorly correlated with vessel features and with the climate at different sites [48]. In the present analysis, the fiber thickness (V4) was less relevant compared to the vessel diameter (V6) for explaining the species variability, as it was observed in previous analyses, including physical properties. Ray characters accounted for most of the anatomical variability (PC1) but are considered to be ecologically or geographically related [8,10]. For instance, uniseriate rays were correlated with lower latitudes, rays two cells wide were found more often in warmer environments, and rays three cells wide tended to be found in higher latitudes, but they did not indicate ecological trends related to ray composition [10]. In contrast, quantitative ray features such as the number of rays per mm and ray height are established variables in systematic wood anatomy [39], which might suggest their diagnostic function overlap. For example, ray frequency was distinct between *Dalbergia miscolobium* Benth. and *Dalbergia nigra* [11]. The long and wide rays of *Citronella paniculata* (Mart.) R. A. Howard and *Myrsine coriacea* (Sw.) R.Br. ex Roem. and Schult. allowed their anatomical wood discrimination [54]. With regards to wood potential, for example, quantitative ray characters were also important to select *Dalbergia nigra* as a tropical wood species showing good quality for musical instruments [58].

The lack of distinct anatomical geographical patterns, as found here, might be related to the fact that external (e.g., climate and edaphic) and internal (e.g., age and stem sampling location) factors that account for wood variability within species were not included in the

analyses. Those influences may overlap the taxonomic value of some anatomical quantitative features of wood [13,43,59]. In addition, the qualitative anatomical features, such as the type of growth ring porosity, vessel grouping and arrangement, vessel perforation plates, and parenchyma were also not included and vary by geographic region [8,10,11].

4.2.3. Physical Properties

Despite the wood density (FIS1) importance, the wood shrinkage and wood color, contributions were highlighted for the species distribution based on physical properties. In fact, wood density is greatly controlled by genetic factors [19], allowing the study of the effects of geographical provenance on wood density for a higher number of species from temperate to tropical regions due to their practical implications for tree improvement programs (e.g., [22–25,60]). In neotropical species, for example, wood density was found to be highly phylogenetically conserved [20]. Opposite results showing a small wood density variation (500 kg/m^3 to 800 kg/m^3) with no distinct geographical pattern were found for tropical species from Asia (Malaysia, Sri Lanka, and the east of India), America (Brazil, Venezuela, Guyana, and Surinam), and Africa (Cameroon and Gabon) [61]. In fact, factors other than the climate of origin, such as soil fertility, should also be determinant for the genetic patterns [30]. For example, the wood density variation of *T. grandis* was high among different provenances [23], and the wood density of tropical species from Costa Rica, Panama, and Peru was found to be inversely correlated with site fertility [62].

Due to the stronger genetic control of wood density, wood shrinkage is generally estimated based on wood density, and a positive and strong correlation is generally accepted [19]. However, shrinkage genetic control in *Calycophyllum spruceanum* Benth. has suggested its potential to improve wood quality [63]. Other wood properties are also of interest to explain wood shrinkage, such as the high extractives content in *Bagassa guianensis* Aubl. (from Africa and French Guinea), even if it is strongly controlled by the wood density in heartwood [64] and the high resistance of vessel walls in *Eucalyptus resinifera* Sm. [65].

The geographical wood color pattern found here, i.e., showing Mozambican species with darker woods and Asian species with lighter woods, could also be explained by the genetic effects on the lightness of the wood (L*). For instance, the stronger genetic control on wood lightness (L*) compared to the redness (a*) and yellowness (b*) was reported for African and Peruvian tropical species [66,67]. Moreover, the climatic conditions explain more of the color variation compared to the edaphic conditions for *T. grandis* in Costa Rica [68] and in African species, for instance, in Mali [67]. The ranges of values were in agreement with other species from Africa (30.5–72.3) and Asia (48.1–55.1) that are expected to be lower when compared to the temperate woods (e.g., Europe and North America), which are known to be lighter (51.1–84.5) [69]. In fact, this color variation is also explained due to extractives formation during the heartwood development, which is higher in tropical woods when compared to temperate species [19].

However, there are few multispecies datasets, and analyses and comparisons are complex due to different wood density determination methods and unaccounted internal (genetic, phylogenetic, or ontogenetic) or external (climatic) effects [20,70]. Moreover, internal and external factors, as discussed above, were not included, and their influence was not accounted for in the species distribution based on the physical characteristics.

4.3. Similarity within Species and Genus

Tectona grandis from India (I13) and from East Timor (T29) showed anatomical and physical similarity, which is in accordance with previous wood anatomy (macroscopic and microscopic) and physical descriptions mentioning similar vessel, ray, and fiber characteristics as well as wood density [36,37]. However, tree growth (measured as ring width) shows considerable variation between regions, even if found comparable between teak from India and East Timor [71,72]. Moreover, the ring structure, namely the proportion of fibers and parenchyma cells have been related to have more effects on the wood quality of teak in India, being influenced by geographical conditions [71]. These aspects were not

studied here, and a careful interpretation is needed. Moreover, the wood density of teak is considered to show strong genetic control [23], and it could not be compared here due to missing values.

The species *Albizia adianthifolia* (M4), *Albizia versicolor* (M5), *Albizia lebbeck* (I3), and *Albizia lebbeckoides* (T1), from the same geographical origin, did not show any similarity, while the species from the genus *Cedrela* (N4 and T10), *Sterculia* (T27 and M32), *Dalbergia* (M16 and I7), and *Terminalia* (I14, I15, and I16) showed similarity on 13 anatomical and 7 physical characteristics. In fact, for the *Albizia* genus, several attempts have been made to distinguish species based in their anatomical characteristics, such as the seriation of rays and the presence of septa in fibers, for species in India [73]. Even quantitative characteristics such as fiber and vessel diameter have shown taxonomic significance in Nigeria species [74]. This high anatomical wood variability might be related to the wide natural distribution in different continents, such as in the *Albizia* genus, or due to wide world plantation for other species, such as *Cedrela*. Thus, besides the diagnostic value, within the genus, of the different anatomical characteristics, the physical characteristics such as the color parameters, wood density, moisture content, and volumetric shrinkage could be also considered, for example, for wood identification and discrimination analysis.

The species *Pterocarpus antunesii* (N10), *Terminalia paniculata* (I15), and *Sterculia quinqueloba* (M32) were found to be clearly different from all studied wood species. Few anatomical comparative studies are found for these species. In fact, due to the general morphological character variability and overlap in some species such as in *Terminalia* spp., other methods have also been applied to species identification [75]. Moreover, the superficial similarity between species may generate confusion, as seen in the example of *S. quinqueloba* and *Sterculia appendiculata* K. Schum, with the former known essentially for bark uses and the latter for its soft wood. Nevertheless, species classification based on anatomical characteristics was found to be reasonable for the CITES-listed species such as *P. santalinus* [46]. Descriptions of specific anatomical characters such as chambered prismatic crystals have also shown value for distinguishing *Sterculia comorensis* Baill. and *Sterculia appendiculata* K.Schum. in Mozambique [33].

The similarity of *Cedrela odorata* (N4) and *Dalbergia melanoxylon* (M16), as CITES-listed species, to non-CITES species is of particular interest. The commercial substitution of high-value CITES-listed species with alternative species certainly requires a full wood characterization, including mechanical properties, chemical features, and durability performance. In the present study, we were restricted to the available information and to nondestructive measurements of the xylarium samples. Wood density and wood shrinkage were chosen in this study to be indicative of wood quality. Therefore, the proposal made for the commercial introduction of alternative species into the timber market should be considered as indicative and as a first step requiring further characterization, including postharvest processing, namely drying and sawing performance. The similarity found for *Cedrela odorata* (N4) and non-CITES *Morus mesozygia* (N9) was interesting, even if *M. mesozygia* (N9) showed longer fibers (F2) and narrower and shorter vessels (V6 and V7) compared to *Cedrela odorata* [76,77]. Nevertheless, *M. mesozygia* (N9) is also recommended for sliced veneer, furniture, flooring, decorative artefacts, and toys [76–79]. For *Dalbergia melanoxylon* (M16), the anatomical similarity was found to be discreet for non-CITES *Swartzia madagascariensis* (M33), while the physical similarity was more evident for non-CITES *Millettia stuhlmannii* (M23), even if the physical similarity with *Millettia stuhlmannii* (M23) was not observed in the dendrogram, which showed a weaker representation of the original distances (0.720 vs. 0.920). However, the anatomical similarity between the *Dalbergia* and *Swartzia* genera is also considered for other CITES-listed species such as *Dalbergia nigra* and both *Swartzia leiocalycina* Benth. (Guiana and Suriname) and *Swartzia benthamiana* Miq. (Brasil and Colombia), with the latter two *Swartzia* species frequently being mistaken in commerce [80]. This genus similarity is confirmed here. Specifically, *Swartzia madagascariensis* (M33) showed similarity to *Dalbergia melanoxylon* regarding its wood color, wood density, and wood moisture content, as non-CITES *Swartzia madagascariensis* (M33) is also

endemic to Mozambique, which could increase species diversity. The physical similarity of *Dalbergia melanoxylon* and *Millettia stuhlmannii* (M23) was also interesting, even if *Dalbergia melanoxylon* is denser (1250 kg/cm^3 vs. 868 kg/m^3), being used for wood carving, while *Millettia stuhlmannii* is used for construction, ship and boat building, railway sleepers, flooring, and furniture [7,32,34,38].

Different results were obtained with regards to species similarity, suggesting that anatomical or physical characteristics may be chosen to be analyzed depending on the purpose of the study or diagnosis. Thus, the identification of characters with the maximum variability between different species by PCA might be very useful for wood selection. However, the cumulative variance found here was not high, and similarities within species and genera might have been compromised by the constraints discussed above for the lack of distinct geographical patterns.

5. Conclusions

This was the first insight into an integrated analysis of anatomical and physical wood characteristics and the potential geographical patterns of tropical species from India, Mozambique, and East Timor. The anatomical and physical wood characteristics revealed to be independent, generating different species distributions. No geographical distribution was found, i.e., species from different origins showed similar wood properties, and therefore different wood origins may be considered to increase the diversity in the tropical timber trade. The wood potential of species, such as *Millettia stuhlmannii* and *Swartzia madagascariensis* from Mozambique, as alternatives for the CITES-listed species *Dalbergia melanoxylon* were highlighted as well as *Morus mesozygia* as an alternative for the CITES-listed *Cedrela odorata*. The multivariate analyses by PCA may be applied for wood identification if combined with comparative wood anatomy as well as for the control and management of sustainable wood production and legal timber trade.

However, this study is a general overview, and information should be taken carefully, considering the response of a single species to different climatic conditions and its use.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13101675/s1, Table S1: Mean values for each of the studied anatomical or physical wood variables and scientific names and codes of the corresponding species (as listed in Table 1). For code characters and abbreviations, see Table 2; Table S2: Statistics of the principal component analyses (PCA) for the anatomical and physical wood characteristics (coded in Table 2) of the tropical species sets (as described in Tables 1 and 3). Loadings of the anatomical and physical variables to principal components (PC) 1–3 of variation; Figure S1: (a) PC1 and PC3 projection plots of the 81 tropical species (as listed in Tables 1 and 3) based on both anatomical and physical wood characteristics (coded in Table 2), overlapped by the MST method. (b) The indication of the correlation degree between the variables based on the position of the vector; Figure S2: Classification of 87 tropical species (listed in Tables 1 and 3) based on 13 anatomical wood characteristics (coded in Table 2), obtained by the UPGMA clustering method (c = 0.695); Figure S3: (a) PC1 and PC3 projection plots of the 87 tropical species (as listed in Tables 1 and 3) based on anatomical wood characteristics (coded in Table 2), overlapped by the MST method. (b) The indication of the correlation degree between the variables based on the position of the vector; Figure S4: (a) PC1 and PC3 projection plots of the 54 tropical species (as listed in Tables 1 and 3) based on physical wood characteristics (coded in Table 2), overlapped by the MST method. (b) The indication of the correlation degree between the variables based on the position of the vector; Figure S5: The minimum spanning tree (MST), also known as SCN (shortest connection network), showing the connections of the 81 tropical species set (distances are not to scale); Figure S6: The minimum spanning tree (MST), also known as SCN (shortest connection network), showing the connections of the 87 tropical species set (distances are not to scale); Figure S7: The minimum spanning tree (MST), also known as SCN (shortest connection network), showing the connections of the 54 tropical species set (distances are not to scale).

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