

**Biogeography, evolution and systematics of *Casearia*
Jacq. (Salicaceae) in the Neotropics**

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Declaration

I, Astrid de Mestier, certified that the entire work of this thesis have been carried on by myself and that all assistance received as been fully acknowledged.

*“L’arbre est un organisme tellement généreux qu’il offre son ombre à ceux qui viennent
l’abattre.”*

Francis Hallé

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Summary

Casearia is a pantropical genus of circa 240 species of the Salicaceae family, and the most species rich genus of the tribe Samydeae. The Neotropics harbours half of all *Casearia* species, which are present in every biome of the New World. Despite its abundance in tropical biomes, *Casearia* has been poorly studied, mostly because of the complexity of identification at the species level. This thesis presents the first well-resolved phylogenetic study of the genus *Casearia*. The objectives were to test its monophyly and to elucidate its relationships to other taxa of the Samydeae tribe, as well as to study the biogeography of the genus. Furthermore, species boundaries of some Neotropical taxa were investigated, using an integrative taxonomy approach. Finally, the last objective was to elaborate a reliable World checklist of every currently accepted *Casearia* species, a tool most needed for taxonomy, conservation and biodiversity management.

A molecular dataset of 103 accessions from four plastid regions (*petD*, *rpl16*, *rps4/trnLF* and *trnK/matK*) and on nuclear region (ITS) was generated, corresponding to 54 species, of which 42 belong to *Casearia*. The study focuses on Neotropical species and the dataset included five Samydeae genera: *Euceraea*, *Lunania*, *Neoptychocarpus*, *Ryania* and *Tetrathylacium*, to understand the relationship between *Casearia* and the Samydeae tribe. Phylogenetic relationships were inferred using Bayesian inference, maximum likelihood and parsimony analysis. The origin of *Casearia* in the Caribbean and its biogeographical relationships to species from the South American mainland was investigated. Therefore, divergence time and ancestral area were estimated. Seven key morphological characters were studied, in order to retrieve synapomorphies for the genus, using BayesTraits. The results of the phylogenetic reconstruction showed a well-supported Samydeae clade and a well-supported *Casearia* clade, as sister to the other Samydeae. The genus *Casearia* was identified as not monophyletic, because the included species of the two Neotropical genera *Euceraea* and *Neoptychocarpus* were found nested with good support within the *Casearia* clade. Several major clades were retrieved, mostly constituted of entirely Neotropical species, one of which being consisted of only species from the Caribbean. A clade of all Paleotropical species was found nested in the clade with the New World *Casearia* taxa.

Two morphological characters that work well to delimitate a monophyletic genus concept were identified. First, a branched inflorescence (fasciculate, glomerulous or cymous) and second a single row of stamen. In addition, some traits previously used as diagnostic for

the genus, have been identified as homoplastic. For example, the presence of pellucid dots or lines on the leaves, that appeared earlier within Samydeae and were lost in *Ryania* and *Tetrathylacium*, a dioecious reproduction system, used to diagnose *Neoptychocarpus*, or a higher number of stamen, used to diagnose *Laetia* and *Zuelania*.

The time estimation analysis of the present study showed that the Samydeae clade originated in South America during the Cretaceous, 102 Ma, which corresponds to the rapid radiation of the Malpighiales. The *Casearia* clade is of South American origin and begins to diversify in the Eocene, 90 Ma. The Paleotropical clade of *Casearia* was found to have originated later than the Neotropical one, therefore from New World ancestors, in the Oligocene/Miocene boundary, 40 Ma and that it was divided into two clades, an African and an Asian one. More sampling from Old World taxa would be needed, in order to identify the origin of this Paleotropical clade. The results show that *Casearia* migrated multiple times to the Caribbean, and gave rise to a clade of Caribbean endemics in the late Miocene, 9 Ma, most likely of South American origin. In addition, the species limits of five Neotropical taxa were investigated. Those taxa were retrieved as nested singletons, which are taxa with a single or few accessions of an accepted species, nested within a clade of another accepted species. Here, an integrative taxonomy approach was applied as a successful way to study the taxonomical status of those taxa, to evaluate whether the singletons may be considered as a synonym, or if they constitute an emerging species, using both morphological and ecological analysis. To that aim, morphological and ecological differentiations were calculated, or on the contrary the absence of differentiation, between those nested singleton and the taxa in which it is nested. Phenotypic differentiation was analysed using morphometry based on the characters that are used as diagnostic characters of the taxa. For the ecological analysis, the niche space differentiation was evaluated and ecological niche equivalency and similarity tests were performed. Furthermore, the distribution range of those species was mapped. One species, *C. grandiflora*, is recovered nested within a *C. arborea* clade. However, the analyses showed that it presents some degree of differentiation, both morphological and ecological. Therefore, the results suggest that they are indeed two species and *C. grandiflora* is most likely a recent emerging lineage. Two other cases of nested singleton were found, *C. selloana* and *C. zizyphoides*, retrieved within the *C. sylvestris* clade. The results show that they present little to no morphological and ecological differentiation and a narrower distribution range as the widely distributed *C. sylvestris*. Therefore, it suggests that they most likely represent a subspecies of *C. sylvestris*. Another nested singleton of *C. mariquitensis* is retrieved within a

C. mollis clade and they are most likely synonyms, given the absence of morphological or ecological differentiation.

Finally, an up-to-date checklist of all currently accepted *Casearia* species is presented, which includes both Neotropical and Paleotropical taxa. The database was created using information from floristic treatments, monographs, regional checklists and taxonomic treatments at species level. For each taxon, the complete information on protologue, types and synonyms has been provided. Our aim was to give the genus a taxonomic backbone that can serve as a basis for further research in taxonomy, ecology and species conservation. The EDIT platform for Cybertaxonomy was used; it is an open-source platform that presents all the tools necessary to establish a taxonomic checklist. It provides the user with a taxonomic editor where every relevant taxonomic information can be entered and an online data portal. Here, the most complete checklist of *Casearia* species to date at a global scale is presented. 708 names, 222 accepted species, 464 synonyms and 22 unresolved names were included, combining information from taxonomical revision, floristic treatments and regional checklists.

Zusammenfassung

Casearia ist eine pantropische Pflanzengattung aus der Familie Salicaceae mit einem Umfang von etwa 240 Arten und die artenreichste Gattung der Tribus Samydeae. Die Neotropis beherbergt etwa die Hälfte aller *Casearia*-Arten, welche in jedem Biom der Neuen Welt präsent sind. Trotz ihres sehr abundanten Vorkommens im tropischen Biom wurde die Gattung bisher nur wenig gründlich untersucht, was hauptsächlich den Schwierigkeiten bei der Identifizierung auf Artenebene geschuldet ist. Hauptziel der vorliegenden Studie war es, die Monophylie der Gattung zu prüfen und ihre Relation zu anderen Taxa des Tribus Samydeae aufzuklären und ebenso einen tieferen Einblick in die Biogeographie und Entstehungsgeschichte der Gattung zu geben. Die Arbeit präsentiert die erste gut aufgelöste phylogenetische Studie der Gattung *Casearia*. Darüber hinaus wurden die Artengrenzen einiger neotropischer *Casearia*-Taxa mit einem integrativen Ansatz taxonomisch untersucht und die erste weltweite Checkliste aller derzeit akzeptierten *Casearia*-Arten erstellt, welche als Instrument für die Taxonomie, den Schutz und das Biodiversitätsmanagement der Gattung dringend benötigt wird.

Es wurde ein molekularer Datensatz von 103 Akzessionen von vier Plastidenregionen (*petD*, *rpl16*, *rps4/trnLF* und *trnK/matK*) und der Kernregion (ITS) generiert, welcher 54 Arten entspricht, von denen 42 zu *Casearia* gehören. Die Studie konzentrierte sich auf neotropische Arten der Gattung und der Datensatz umfasste die fünf Samydeae-Gattungen *Euceraea*, *Lunania*, *Neoptychocarpus*, *Ryania* und *Tetrathylacium*, um auch die Beziehung zwischen *Casearia* und dem Tribus Samydeae besser zu verstehen. Phylogenetische Beziehungen wurden mittels Bayes'scher Inferenz-, Maximum Likelihood- und Parsimonie-Analysen rekonstruiert. Der Ursprung der Gattung *Casearia* in der Karibik und ihre biogeographischen Beziehungen zu Arten vom südamerikanischen Festland wurden untersucht. Daher wurden die Divergenzzeit und das ancestrale Verbreitungsgebiet ermittelt. Sieben morphologische Schlüsselmerkmale wurden untersucht, um mithilfe von BayesTraits Synapomorphien für die Gattung zu ermitteln.

Das Ergebnis der phylogenetischen Analyse wies fünf neotropische Taxa als „nested singletons“ aus. Hierbei handelt es sich um Taxa mit einem einzelnen oder wenigen Exemplaren einer akzeptierten Art, die inmitten einer Klade einer anderen akzeptierten Art auftreten. Im Zuge der vorliegenden Studie wurde mittels Nutzung eines integrativen Ansatzes ein erfolgreicher Weg zur Untersuchung des taxonomischen Status dieser Taxa auf

Basis morphologischer und ökologischer Analysen entwickelt, um bewerten zu können, ob ein „singleton“ als Synonym angesehen werden kann oder ob es sich um den Vertreter einer sich in Entwicklung begriffenen neuen Art handelt. Zu diesem Zweck wurden morphologische und ökologische Differenzierungen oder im Gegenteil das Fehlen einer Differenzierung zwischen diesen „nested singletons“ und den umliegenden Taxa näher untersucht. Die phänotypische Differenzierung wurde morphometrisch analysiert, wobei die hier einbezogenen Merkmale die diagnostisch verwendeten Merkmale der Taxa darstellten. Im Rahmen der ökologischen Analysen wurde die Nischenraumdifferenzierung bewertet und es wurden ökologische Nischenäquivalenz- und Nischenähnlichkeitstests durchgeführt. Darüber hinaus wurde das Verbreitungsgebiet dieser Arten kartiert.

Schließlich wird eine aktuelle Checkliste aller derzeit akzeptierten *Casearia*-Arten vorgestellt, welche sowohl Taxa aus den Neotropen als auch aus den Paläotropen beinhaltet. Die Datenbank wurde mit der EDIT-Plattform erstellt unter Verwendung von Informationen aus taxonomischen Revisionen, regionalen und lokalen Floren sowie wissenschaftlichen Publikationen. Für jedes Taxon wurden hier Informationen zu Protolog, Typen und Synonymen bereitgestellt. Unser Ziel war es, der Gattung ein taxonomisches Rückgrat zu geben, das als Grundlage für weitere Forschungen in Taxonomie, Ökologie und Artenschutz dienen kann.

Die Ergebnisse der phylogenetischen Rekonstruktion zeigten eine Samydeae-Klade und eine *Casearia*-Klade als Schwester der Samydeae mit guter statistischer Unterstützung. Die Gattung *Casearia* wurde als nicht monophyletisch identifiziert, da die einbezogenen Arten der zwei neotropischen Gattungen *Euceraea* und *Neoptychocarpus* mit guter Unterstützung innerhalb der *Casearia*-Klade erschienen. Es wurden mehrere große Kladen gefunden, die größtenteils vollständig neotropische Arten beinhalten, von denen eine ausschließlich aus Arten bestand, die nur in der Karibik vorkommen. Eine Klade aus allen paläotropischen Arten ist in die Klade mit den neuweltlichen *Casearia*-Arten eingebettet. Im Zuge der morphologischen Analysen wurden zwei Merkmale identifiziert, die gut geeignet sind, um ein monophyletisches Gattungskonzept abzugrenzen. Erstens, ein verzweigter Blütenstand (faszikuliert, glomerulös oder zymös) und zweitens eine einreihige Staubblattreihe. Außerdem wurden einige Merkmale, welche zuvor als diagnostische Merkmale für die Gattung verwendet wurden, als homoplastisch identifiziert, wie zum Beispiel das Vorhandensein von durchscheinenden Punkten oder Linien auf den Blättern, welche bereits bei Samydeae-Arten auftreten und in *Ryania* und *Tetrathylacium* verloren gingen, sowie ein zweihäusiges Reproduktionssystem, das zur Diagnose von

Neoptychocarpus verwendet wurde, oder der größeren Anzahl von Staubblättern, die bei der Diagnose von *Laetia* und *Zuelania* angewandt wurden.

Die als Teil der vorliegenden Studie durchgeführten Zeitabschätzungen ergaben, dass die Samydeae-Klade in Südamerika während der Kreidezeit vor etwa 102 Mio. Jahren entstanden ist, was mit der schnellen Radiation der Malpighiales korrespondiert. Die *Casearia*-Klade ist südamerikanischen Ursprungs und begann sich im Eozän, vor etwa 90 Mio. Jahren, zu diversifizieren. Es wurde festgestellt, dass sich die paläotropische Klade von *Casearia* aus neotropischen Vorfahren im Oligozän / Miozän-Grenze, vor etwa 40 Mio. Jahren entwickelte und dass sie sich in eine afrikanische und eine asiatische Klade unterteilen lässt. Die Ergebnisse zeigen, dass *Casearia* mehrfach in die Karibik migrierte und im späten Miozän, etwa vor 9 Mio. Jahren, eine Gruppe karibischer Endemiten hervorbrachte, die wahrscheinlich südamerikanischen Ursprungs waren.

Die Analyse zu den Artengrenzen unter Einbezug morphologischer, ökologischer und verbreitungsbiologischer Daten von fünf neotropischen *Casearia*-Taxa, welche als „nested singletons“ in den phylogenetischen Untersuchungen erschienen, ergab die folgenden Ergebnisse: *C. grandiflora*, die inmitten der *C. arborea*-Klade erschien, wies ein gewisses Maß an Differenzierung auf. Die Ergebnisse legen daher nahe, dass es sich tatsächlich um zwei Arten handelt und *C. grandiflora* höchstwahrscheinlich eine erst kürzlich entstandene Abstammungslinie ist. In zwei weiteren „singleton“-Fällen, *C. selloana* und *C. zizyphoides*, die innerhalb von *C. sylvestris* gefunden wurden, legen die Ergebnisse nahe, dass es sich höchstwahrscheinlich um eine oder zwei Unterarten von *C. sylvestris* handelt. Im Falle von *C. mariquitensis*, welche innerhalb einer *C. mollis*-Klade auftauchte, handelt es sich höchstwahrscheinlich um eine synonyme Art, da hier keine morphologische oder ökologische Differenzierung ermittelt werden konnte.

Die vorliegende Studie stellt die bisher vollständigste und erste weltweite Checkliste für die Gattung *Casearia* bereit: 708 Namen, 222 akzeptierte Arten, 464 Synonyme und 22 ungelöste Namen wurden aufgenommen, wobei Informationen aus taxonomischen Revisionen, Floren und wissenschaftlichen Veröffentlichungen kombiniert wurden.

Table of contents

Acknowledgments	iv
Summary	vi
Zusammenfassung	ix
Chapter 1: General introduction	1
1.1 The origin of the Neotropical biodiversity	1
1.2 Biogeography of the Neotropics and the Caribbean	3
1.2.1 General concepts in Neotropical biogeography	3
1.2.2 General concepts in Caribbean biogeography	4
1.3 The use of integrative taxonomy in recognizing and describing species	6
1.3.1 Species delimitation in flowering plants	6
1.3.2 The rise of integrative taxonomy	7
1.3.3 The need for comprehensive taxonomic backbones	8
1.4 Salicaceae and systematics of <i>Casearia</i>	9
1.4.1 The family Salicaceae	9
1.4.1.1 Taxonomic history of the family	9
1.4.1.2 Molecular studies and taxonomic conclusions	10
1.4.2 The genus <i>Casearia</i> - taxonomy and morphology	11
1.4.2.1 Taxonomic history of <i>Casearia</i>	11
1.4.2.2 Morphological characteristics of <i>Casearia</i>	13
1.5 Overview of the dissertation	15
Chapter 2: Character evolution and biogeography of <i>Casearia</i>	17
2.1 Summary	17
2.2 Introduction	18
2.3 Materials and methods	25
2.3.1 Taxon sampling	25
2.3.2 DNA Isolation, Sequencing, Alignment and indel coding	26
2.3.3 Phylogenetic analyses	27
2.3.4 Assessment of morphological characters and ancestral character state reconstruction	29
2.3.5 Estimation of divergence time	30
2.3.6 Ancestral area reconstruction	31

2.4 Results	31
2.4.1 Phylogenetic analyses	31
2.4.2 Phylogenetic relationships inferred from the plastid genome.....	34
2.4.3 Phylogenetic relationships inferred from ITS	35
2.4.4 Ancestral character states	37
2.4.5 Divergence time estimates	40
2.4.6 Ancestral areas	42
2.5 Discussion.....	44
2.5.1 Phylogenetic relationships of <i>Samydeae</i>	44
2.5.2 Phylogenetic relationships of <i>Casearia</i>	45
2.5.3 Evolution of morphological characters and the circumscription of <i>Casearia</i>	46
2.5.4. Biogeography of the pantropical genus <i>Casearia</i> at a continental level	48
2.5.5 Biogeographic relations between the Caribbean islands and adjacent mainland	49
2.5.6 Implications for species delimitation	52
2.7 Conclusion	53
Chapter 3: Nested singletons in species-level phylogenetic trees of <i>Casearia</i>	54
3.1 Summary.....	54
3.2 Introduction	55
3.3. Material & Methods.....	60
3.3.1 Taxon sampling and phylogenetic reconstruction	60
3.3.2 Target taxa	61
3.3.3 Locality data.....	61
3.3.4 Morphological analyses	62
3.3.5 Environmental niche space analysis	63
3.3.6 Distribution maps.....	64
3.3.7 Decision between emerging species or singleton	64
3.4 Results	65
3.4.1 Phylogenetic reconstruction.....	65
3.4.2 Phylogenetic relationship of nested singletons	67
3.4.3 Morphological analyses	70
3.4.4 Environmental niche space analysis	74
3.4.5 Distribution	76
3.5 Discussion.....	78

3.6 Conclusion	81
Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of <i>Casearia</i>	83
4.1 Summary.....	83
4.2 Introduction	83
4.3 Material and methods	86
4.4 Results	88
4.5 Discussion.....	94
4.5 Specific outlook.....	95
Chapter 5: General conclusions.....	97
5.1 Phylogeny of <i>Casearia</i> and its taxonomic implications	97
5.2 Biogeography of <i>Casearia</i>	98
5.3 Integrative taxonomy as a tool to solve the case of nested singletons in phylogenetic studies	99
5.5 A worldwide checklist of <i>Casearia</i> as a taxonomic backbone for the genus.....	100
References	101
List of manuscripts	126
Appendices	127

Chapter 1: General introduction

1.1 The origin of the Neotropical biodiversity

The Neotropical region extends from Central Mexico to Southern Brazil, covering all of Central America and the Caribbean. It is one of the most biodiverse areas of the planet, harbouring 37% of the World's species, with 90 000 to 110 000 seeds plants (Antonelli & Sanmartín, 2011) and six of the 25 World's biodiversity hotspots (Myers & al., 2000). It consists in a wide variety of biomes, from mid-elevation montane forests to high elevation grasslands, as well as seasonally dry forests, tropical rainforests, savannas and deserts (Hughes & al., 2013; Morrone, 2014). Despite this outstanding variety, the processes leading to such a high biodiversity are still debated. Ecological diversity together with a complex geological history, are factors that play a key role in the species diversification of the Neotropics. Recently, the development of molecular technics and dated molecular phylogenies marked an important step in testing several hypothesis regarding the origin and evolution of the Neotropical biota (Antonelli & Sanmartín, 2011).

Traditionally, two models are proposed to explain the origin of the high Neotropical biodiversity. First, the “museum model” hypothesised that a constant speciation rate, together with a low extinction rate, allowed the accumulation of species (Antonelli & Sanmartín, 2011). Indeed, South America was isolated from other continents 100 Ma, in the mid-cretaceous, until the creation of the Isthmus of Panama in the Miocenetherefore being “an island continent”. During that period, it experienced a stable climate, and thus, time together with climate stability and isolation, led to a low extinction rate, that allowed the accumulation of species (Mittelbach & al., 2007). Recently, phylogenetic studies in many groups, such as in the Lecythidaceae (Vargas & Dick, 2020), in Annonaceae (Couvreur & al., 2011b), in Menispermaceae (Wang & al., 2012) or in Arecaceae (Couvreur & al., 2011a) found a steady diversification rate over time, therefore supporting the museum theory of diversification.

Another hypothesis is the “evolutionary cradle” model, which postulates that the high biodiversity of the Neotropics is due to rapid and recent speciation via high speciation rates. Those high speciation rates would have occurred during the Pleistocene, that harboured climatic changes and geological events, which are likely to have triggered speciation (Haffer,

Chapter 1: General introduction

1969; Prance, 1982). New phylogenetic studies carried on in a variety of groups, such as *Inga* Mill. (Richardson & al., 2001) and Meliaceae (Koenen & al., 2015), suggest a much younger age for the diversification of the Neotropical Flora than what was previously thought, thus supporting the “cradle model” hypothesis. It is now commonly accepted that both theories are not mutually exclusive and that they are both at the origin of such a high biodiversity in the Neotropics (Mittelbach & al., 2007; Antonelli & Sanmartín, 2011; Canal & al., 2018)(Mittelbach & al., 2007; Antonelli & Sanmartín, 2011; Canal & al., 2019).

There are many factors, both abiotic and biotic, that are put forward to explain the origin of the Neotropical biodiversity (Antonelli & Sanmartín, 2011; Rull, 2011, 2020). First, climate change played an important part in shaping the diversity of the Neotropics, especially from the Pleistocene on. The “refuge theory” received a lot of attention in the 70’s. It considers that the Pleistocene was the theatre of around 20 major glacial events (Haffer, 1969) and that those climatic changes would have led to the fragmentation of the lowland forest of Amazonia in the coldest periods, as well as served as a refuge for a number of species, favouring allopatric speciation (Prance, 1982; Antonelli & Sanmartín, 2011). However, new data challenged this hypothesis, Colinvaux & al. (2000) showed that there was a continuity of the Amazonian lowland rainforest during the Late Glacial Maximum (LGM), thus refuting the forest fragmentation process of the refuge theory. There is nowadays still a debate as to whether or not the refuge theory should be taken into account (Rull, 2020). Nevertheless, other hypotheses were developed that involved processes leading to a rapid diversification in the Pleistocene, such as the dispersal-vicariance hypothesis. It postulates that the species composition of the forest would have changed due to migrations, especially montane forests taxa going down due to environmental changes such as cooling that would have enhance speciation (Rull, 2020).

Geological changes are also potential drivers of diversity in the Neotropics with the creation of geographical barriers, favouring allopatric speciation (Antonelli & al., 2009). The orogenesis of the Andes is at the origin of a rapid radiation in many groups. For examples, a study in Andean Cymbidieae and Pleurothallinideae showed that radiations in Orchids are correlated with the Andean uplift (Pérez-Escobar & al., 2017). Similar results were found in other taxa such as Andean bellflowers (Lagomarsino & al., 2016), *Brownea* Jacq. (Schley & al., 2018), Espeletiinae (Diazgranados & Barber, 2017), Iriarteeae palms (Bacon & al., 2018) and *Philodendron* Schott (Canal & al., 2019). The mountain uplift triggered diversification as it favoured allopatric speciation, separating taxa previously occurring in the same area, such as in two tribes of the Rubiaceae, Cinchoneae and Isertieae (Manns & al., 2012) or *Brunfelsia* L.

(Filipowicz & Renner, 2012). Additionally, the uplift of the Western Cordilleras is at the origin of a North-South corridor, connecting the Northern and Central Andes, therefore creating a new migration route that allows species dispersion and drove species diversification (Antonelli & Sanmartín, 2011). The Miocene uplift of the Andes also caused hydrological changes in Amazonia and Patagonia, leading to the humidification of those regions, by modifying the course of the Amazon, therefore changing the gene-flow in the area (Gregory-Wodzicki, 2000; Luebert & Weigend, 2014; Antonelli & al., 2018b; Rahbek & al., 2019).

On the side of biotic factors, one can first cite the adaptation of species to different soils (Antonelli & Sanmartín, 2011). Fine & al. (2005) studied the distribution pattern of 35 western Amazonian species of Burseraceae and found that 26 were associated with only one soil type among the three occurring in the Amazonian region, showing a strong soil adaptation pattern. Studies focusing on the Amazonian rainforest found that there is a correlation between soil composition and biodiversity and the richer the soil, the higher number of species it harbours (Steege & al., 2006; Tuomisto & al., 2014).

Another biotic factor that drove species diversification in the Neotropics is the interaction between taxa, such as herbivory, interaction between plant and pollinators or seed dispersal (Fine & al., 2005). Studies in the genus *Inga* showed a strong selection for traits that are related to defence against herbivory (Kursar & al., 2009). Another study in Neotropical *Costus* L. demonstrates that one fifth of the speciation events occurring in the genus are due to a shift in pollinator (Kay & Schemske, 2008). Finally, dispersion of seed is fundamental.

1.2 Biogeography of the Neotropics and the Caribbean

1.2.1 General concepts in Neotropical biogeography

Biogeography is the science that investigates the distribution pattern of taxa across space and time and identifies its drivers (Brown & Lomolino, 1998). Biogeographical studies are crucial to understand the process of species diversification and they considerably developed with the use of dated molecular phylogenies (Magallón, 2004; Posadas & al., 2006; Hoorn & al., 2010). There are two main mechanisms used to explain the distribution patterns of organisms: vicariance, which postulates speciation by allopatry (Pennington & Dick, 2010; Nogueira & al., 2011), and dispersal (Särkinen & al., 2007). Nevertheless, it is now widely

accepted that the two processes are not exclusive and both contribute to the actual patterns of biodiversity in the New World (Antonelli & al., 2018a; Maestri & al., 2020).

Neotropical biomes harbour a wide variety of species and it is crucial to understand the process behind the differentiation of biodiversity among biomes to understand patterns of plant evolution in the New World (Hughes & al., 2013). Niche conservatism postulates that species cannot easily adapt to a change in the environment and thus mostly migrate to new areas that present similar environmental conditions (Wiens, 2004; Donoghue & Edwards, 2014). A study by Crisp & al. (2009) showed that biome shifts were responsible for only 3.6% of the 11 000 evolutionary divergence events detected by the authors in the Southern Hemisphere, and that transoceanic colonization almost never occurred. Indeed, adapting to new environmental characteristics is a struggle and finding an appropriate environment enhances the possibility of colonisation of a new area by a species (Wiens, 2004). Nevertheless, studies in several taxa of the Neotropics challenged that theory. In Proteaceae, it was shown that interaction between different environments was at the origin of a new group in the family (Onstein & al., 2016). Similar results have been found in the Neotropics, in Caesalpinoideae (Fabaceae) in the Brazilian Cerrado (Souza-Neto & al., 2016) or in Bignoniaceae (Lohmann & al., 2013). In 2018, Antonelli and colleagues performed a large study on Neotropical taxa and confirmed that interaction and dispersal events among various biomes in the New World occurred much more than previously thought (Antonelli & al., 2018b). Following those results, a meta-analysis, showed that migration between biomes, followed by in situ speciation is a driver for the Neotropical biodiversity. Furthermore, the Amazonian rainforest is the first source of the Neotropical biodiversity as the most dispersion events occurred in the area and more than 2 800 lineages were supplied to other biomes of the Neotropics (Antonelli & al., 2018b; Zizka, 2019).

1.2.2 General concepts in Caribbean biogeography

One of the seven biodiversity hotspots of the Neotropics is the Caribbean. Despite its relatively small area, it harbours 12 000 plant species, accounting for 2.3% of the plant species worldwide (Acevedo-Rodríguez & Strong, 2008). Like in other parts of the Neotropics, plant diversity in that region is strongly correlated with geological events, such as tectonic movements, volcanism, formation and submersion of islands, as well as its interaction with adjacent biomes. Indeed, the adjacent landmasses of Mexico, Meso-America and South America possess an exceptionally rich flora that could have colonised the islands

through time (Santiago-Valentin & Olmstead, 2004). Traditionally, to explain the origin of the Caribbean flora four hypotheses are put forward (Roncal & al., 2020).

First, the vicariance hypothesis states that the proto-Antillean islands would have drifted from a lower Central American archipelago, which nowadays is Central America towards its actual isolated position, during the Late Mesozoic, early Cenozoic. The biota of the Caribbean would have evolved from there by allopatric speciation (Rosen, 1975). This hypothesis is supported by several molecular clock analyses of animals groups (Hedges, 2006).

The second hypothesis was made by Iturralde-Vinent, the Greater Antilles Aves Ridges (GAARlandia) hypothesis (Iturralde-Vinent, 1999). GAARlandia is a land bridge that would have connected South America to the Caribbean between 35 and 33 Ma, several studies in *Copernicia* Mart. ex Endl. (Bacon & al., 2012) or *Croton* L. (Van Ee & al., 2008) and *Styrax* L. (Fritsch, 2003) agree with this hypothesis. However, it is a controversial theory and Ali (2012) warned against it, as there is no geological data available to support the actual existence of such a bridge. Furthermore, phylogenetic studies of some plant groups also did not support that hypothesis and a recent supertree-analysis by Nieto-Blázquez and colleagues, surveying 625 seed plant genera of which 32 are endemic to the Caribbean based on published sequence data showed that only five of them have a South American origin. From those five genera, two were retrieved with a mean stem age too young and one too old, for GAARlandia to have played a role as a colonization route (Nieto-Blázquez & al., 2017).

A third, more widely accepted hypothesis, assumes dispersal from adjacent mainlands towards the islands (Hedges & al., 1992; Vargas & al., 2015), allowing the colonisation of new areas by species from adjacent landmass. This long distance dispersal would also be favored by the many hurricanes happening in the region, allowing the transportation of propagules, as well as by transportation by birds or fishes (Hedges, 2001). Other studies in Acalyphoideae (Euphorbiaceae) (Cervantes & al., 2016), *Adiantum* L. (Pteridaceae) (Regalado & al., 2018), Coryphoideae (Arecaceae) (Cano & al., 2018) and in animal groups such as *Pholidoscelis* Fitzinger (Tucker & al., 2017) also agree with a colonization of the islands through overwater dispersion.

Finally, the fourth hypothesis states that in situ speciation within islands is a key process for the diversification of the Caribbean. In the Caribbean lizards, *Anolis* Daudin, it was found that within islands speciation played a more important role than overwater dispersal (Losos & Schluter, 2000). Indeed, islands are isolated from the mainland and this isolation is a driver of species radiation, therefore the Caribbean islands often present a high level of

endemism (Warren & al., 2010). Furthermore, colonisation within archipelagos and the “island progression rule” states that old islands constitute a reservoir of species that colonise the younger islands (Whittaker & al., 2017).

The timing of the closure of the Isthmus of Panama was also a key factor in Caribbean biogeography. South America was isolated from other continents and when the closure occurred it allowed Meso-American taxa to reach the Caribbean through overwater dispersion, thus influencing the diversification of the Caribbean flora through South American ancestors (Leigh & al., 2014).

1.3 The use of integrative taxonomy in recognizing and describing species

1.3.1 Species delimitation in flowering plants

Recognizing and formally describing species is a major issue in systematic biology. This is because the species is the unit for analysis in biogeography, ecology, conservation assessment and delimitation of protected areas and correct species delimitation are needed in order to establish accurate biodiversity management measures (Stanton & al., 2019). One example that illustrates well why species limits should be carefully studied and discussed is with *Otatea* (McClure & E.W. Sm.) Calderón & Soderstr. (Poaceae). It was observed that for one species, *Otatea fimbriata* Soderstr., distributed from Mexico to Colombia, the boundaries were not accurately established. The authors of the study found that the specimens occurring in Colombia were actually different morphologically than the specimen occurring in Central America, therefore justifying the description of a new species. This new species exists only in a restricted area of Colombia, that is a non-protected area, which would imply its classification as “critically endangered”, therefore advocating for the classification of those areas as protected (Ruiz-Sanchez & Londoño, 2017).

However, defining the limits of a species is a complicated task and many species concepts have been proposed, following various principles such as biological, ecological or morphological (Mayr, 1942; Simpson, 1951; Van Valen, 1976). This plurality of concepts has a negative impact on taxonomy since depending on the method used, the inferred species limits might be different and as a consequence also the obtained taxon concept at species level (Agapow & al., 2004). Historically, plant species have been described just on the basis of

differing morphological characters, therefore based on a morpho-species concept (Stuessy, 2009). The rise of molecular phylogenetics is at the origin of a great change in the way taxonomists delimitate species (Borsch & al., 2015). Nowadays, DNA is a widely used tool to diagnosed species on the basis of shared molecular characters (González Gutiérrez & al., 2013). Moreover, in many groups, molecular studies revealed the presence of cryptic species, meaning two species retrieved as sisters in the phylogenetic tree, although they were not differentiated under a morpho-species concept, which implies that they share no obvious morphological differences (Bickford & al., 2007). Therefore, the use of molecular phylogenies did mark a turn in systematic studies, however phylogenetic relationships cannot always be accurately inferred (Wiens, 2007; Leavitt & al., 2016).

Naciri & Linder (2015) identified no less than seven processes that can lower the phylogenetic signal, such as intergenomic transfers, when nuclear and plastid DNA is being exchanged. This can lead to relationships that do not reflect the actual evolutionary history of the lineages. Another process is hybridization events that can result in horizontal gene transfer. The process of incomplete lineage sorting can also occur when multiple copies of the same gene coexist in the ancestral population, which can lead to discordance between gene and species trees. Furthermore, whole genome duplication events can modify the genome organisation. Other factor such as demography, selection and phylogeographic structure can influence the phylogenetic signals as well and make the identifications of species through the use of phylogenetic tree only complicated and inaccurate.

1.3.2 The rise of integrative taxonomy

A common problem faced during phylogenetic reconstruction studies is the presence of paraphyletic species. When a species is retrieved nested within another species clade, they could either be considered as potential synonyms, or they could be showing signal of a recent speciation event, implying that if sufficient time is given, the two species would each be retrieved as monophyletic (Hörandl & Stuessy, 2010). In Gesneriaceae, *Columnnea kucyniakii* Raymond was retrieved paraphyletic with respect to a clade of *Columnnea strigosa* Benth. Nevertheless, the authors of the study advocate for the recognition of both species, arguing for incipient speciation (Smith & al., 2018).

In the last decades, a new approach has been developed, that aims at identifying the boundaries in lineages through the use of multiple methods (Benoît, 2005; Padial & al., 2010). This integrative taxonomic approach has two major goals. First, it aims at resolving taxonomic

uncertainties and, second, it intends to be more reliable as a species delimitation method, by taking into account multiple lines of evidences (Padial & al., 2010). Most authors now agree on the use of an integrative taxonomy method that yields better and more reliable results (Will & al., 2005; Schlick-Steiner & al., 2010; Pante & al., 2015; Thomson & al., 2018). Rissler & Apodaca (2007) suggested that in the case of unresolved lineages, for example at a molecular level, the study of their ecological niches can help to make a decision and the lineage could be actually circumscribed with respect to the formally described taxon. If two species possess a distinct ecological niche and present no overlap in their distributions, it could be argued that gene flow is prevented. Therefore, the lineages would indeed be distinct from one another, even if it is not retrieved on the molecular phylogenetic tree.

The use of an integrative taxonomy approach has already resolved taxonomical uncertainties in many groups. For example, in the black salamander, a mitochondrial phylogeny revealed cryptic species that are associated to differentiation in the environment of the taxa. Thus, environmental data actually confirmed the relationships found with molecular data (Rissler & Apodaca, 2007). In *Rhodiola* section *trifida* (Crassulaceae), phylogenetic, morphological and ecological analysis revealed that the number of species in the section was actually over estimated, lowering the number from seven to three (Li & al., 2019b). It also allowed the revelation of a new species in the *Stenocereus griseus* (Haw.) Buxb. species complex (Cactaceae), in a study that combined genetical, ecological and morphological data, revealing one new species (Alvarado-Sizzo & al., 2018). Finally, it seems that integrative taxonomy approaches are increasingly used and many authors argue that it is the future of taxonomy (Benoît, 2005; Padial & al., 2010; Schlick-Steiner & al., 2010; Daglio & Dawson, 2019).

1.3.3 The need for comprehensive taxonomic backbones

Taxonomy is the basis to understand biodiversity and protect it, therefore the availability of trustworthy taxonomic information is crucial (Mace, 2004). Taxonomic data can be found in taxonomical revision, local or regional Flora and independent research papers. Although those publications are indispensable to the establishment of a curated taxonomic knowledge, it has to be made available in a synthesised manner, in order to provide a credible inventory of the world's plant diversity that can be used in a variety of fields, from biogeography to conservation and biodiversity management (Costello & al., 2014; Borsch &

al., 2020). Checklists are a basis for such studies as they bring together taxonomic information from various sources. They provide an updated list of scientific names, useful for further investigation in taxonomy, as well as for biodiversity management efforts (Funk, 2006). Developing checklists at a global scale are a necessary task and such initiative are developing. For example the World Flora Online Portal is an important step toward a scientifically verified biodiversity database on plants (Borsch & al., 2020). It aims at providing verified checklists of plants species worldwide, that are developed by experts and therefore at providing a taxonomic backbone for various taxa. Nevertheless, such a taxonomic backbone at the genus level is still missing for *Casearia*.

1.4 Salicaceae and systematics of Casearia

1.4.1 The family Salicaceae

1.4.1.1 Taxonomic history of the family

Flacourtiaceae is a complicated family with a complex history and no clear morphological characters and even the botanist Gentry stated in his field guide “if you don’t have any idea what the family is, try Flacourtiaceae” (Gentry, 1996). Clos (1855 and 1857), was the first botanist to reunite the species together, under the name “Flacourtianées” (Clos, 1855, 1857). His treatment was followed by Bentham in 1862 who put most of the Flacourtiaceae within the Bixinae and later by Hooker (1867) who placed the taxa with a hypanthium in Samydaceae as part of the Passiflorales (Bentham & Hooker, 1862). Baillon reunited the Bixanae and Samydaceae together, under the super family Bixaceae, subdivided in ten tribes. He reunited in one tribe both the Flacourtiaceae of Clos and the Samydaceae of Hooker and separated the Lacistemataceae in another tribe (Baillon, 1873). Eichler in 1871 kept the concept of Baillon, reuniting the Flacourtiaceae with the Samydaceae under Bixaceae but separated the Lacistemataceae in its own family (Eichler, 1871). The first modern treatment of the Flacourtiaceae was later realised by Warburg in 1894, who divided the family into 11 tribes (Warburg, 1895). Hutchinson mostly kept the family’s concept of Warburg in his own revision of the family, however changing the number of tribe from 11 to 10 with a new tribe, Alzateae constituted of the single genus *Alzatea* Ruiz & Pav. (Hutchinson, 1967). The last synopsis of the family was made by Lemke in 1988 (Lemke, 1988). He kept the

Samydaceae within the Flacourtiaceae as the Samydeae tribe. Finally, Chase & al. (2002) used molecular techniques on the whole Flacourtiaceae family, revealing its paraphyly. Following those results, all Flacourtiaceae species were placed within the two existing family Salicaceae and Achariaceae (Chase & al., 2002; Bremer & al., 2003).

1.4.1.2 Molecular studies and taxonomic conclusions

Salicaceae sensu lato is a medium sized family of 54 genera and 1200 species. It is found on every continent, apart from Antarctica, and possesses emblematic and widely studied taxa such as *Salix* L. and *Populus* L (Stevens, 2017). It was considerably extended in terms of number of genera following the molecular study of Chase & al. (2002). The authors investigated the relationships of the Flacourtiaceae family with *rbcL* sequence data from the plastid genome and demonstrated the polyphyly of the family as some of its species were retrieved nested in different clades of the Malpighiales. In their study, Chase & al. proposed taxonomical changes, and no longer accepted Flacourtiaceae as a family. The genera that used to belong to it were transferred to two existing families Achariaceae and Salicaceae. For the latter, Chase recognised nine tribes, one of the most controversial being the Samydeae, defined by axillary inflorescence, bisexual and apetalous flowers and the stamens that are disposed in one to three series, alternating with staminodes. The Samydeae tribe consists of nine genera, *Casearia* Jacq., *Euceraea* Mart., *Lunania* Hook, *Neoptychocarpus* Buch., *Ophiobotrys* Gilg., *Osmelia* Thwaites, *Pseudosmelia* Sleumer, *Ryania* Vahl and *Tetrathylacium* Poepp. & Endl. (Chase & al., 2002; Alford, 2005; Samarakoon & Alford, 2019). The taxonomical status of the tribe is debated and some authors argue that it should be raised at the family level. Indeed, Mac Alford in 2005 performed a phylogenetic study of the Flacourtiaceae, using both morphological and sequence data from chloroplast DNA (*trnL-F*). In order to account for the morphological differences and the molecular results that he retrieved, he chose to raise the Samydeae tribe at the family level (Alford, 2005). Thus, he resurrected the Samydaceae family with the addition of the genus *Trichostephanus* Gilg, which was placed by Chase in its own tribe, Trichostephanae. However, the molecular results itself do not present enough support to justify such changes and the Samydeae phylogenetic tree remains mostly unresolved.

Casearia is the most species rich genus of the Samydeae tribe and a key taxon in biogeographical studies. Indeed, the genus is pantropical, with 240 species, of which around 100 are found in the New World (Sleumer, 1980; Samarakoon & Alford, 2019). Its presence is reported in every biome of the Neotropics, such as the Amazonian rainforests and the Brazilian cerrados (Sleumer, 1980; Gutiérrez, 2000; Marquete & Mansano, 2012), the savannas (Devecchi & al., 2020) and the Caribbean (Sleumer, 1980; Correll & Correll, 1982; Howard, 1989; Liogier, 1994; Gutiérrez, 2000). It is among the most species rich genera of Neotropical dry forest (DRYFLOR; Banda-R. & al., 2016) and some of its species are hyper dominant for example in Western Amazonia (Steege & al., 2013). Despite its abundance in tropical biomes, the genus is still poorly studied, perhaps because it presents only few commercial uses and is complicated to identify properly at the species level. Samarakoon investigated in 2015 the phylogeny of *Casearia* and retrieved it as paraphyletic to *Hecatostemon* S.F. Blake, *Laetia* Loef. ex L, *Samyda* Jacq. and *Zuelania* A. Rich. Unfortunately, the relationships within the genus are still not well-resolved as the molecular results are not well-supported at the species level (Samarakoon, 2015).

1.4.2 The genus *Casearia* - taxonomy and morphology

1.4.2.1 Taxonomic history of *Casearia*

Casearia was first described by Jacquin in 1760 (Jacquin, 1760). Clos in his first concept of the “Flacourtianées” do not mention the genus (Clos, 1855, 1857) and it is Bentham & Hooker that placed *Casearia* in the Samydaceae, within the Caseariae tribe, defined with four to five calyx lobes, no petals and six to thirty stamens. The tribe consisted of three other genera, *Euceraea* Mart., *Lunania* Hook. and *Osmelia* Thwaites (Bentham & Hooker, 1862). Warburg kept *Casearia* in the Caseariaea tribe, within the Flacourtiaceae family and added new genera to it, namely, *Laetia*, *Patrisia* J. St.-Hil. (*syn. Ryania* Vahl.), *Samyda*, *Tetrathylacium* Poepp., and *Zuelania* (Warburg, 1895). He defined the tribe as having no petals and perigynous flowers, leaves that present pellucid dots and/or lines and twice or more stamens than sepals, apart from *Tetrathylacium* that possesses both in the same number. Furthermore, all members of the Caseariae tribe have staminodes. Warburg divided *Casearia* into five sections, of which only one present species from the Old World, along with taxa from the Neotropics. A later revision of the Flacourtiaceae by Hutchinson in 1967 recognised 10 tribes, and added genera to the Caseariaea Benth tribe, namely *Abatia* Ruiz & Pav., *Aphaerema* Miers, *Bivinia* Jaub. ex Tul., *Gossypiospermum* Urb., *Hecatostemon*,

Chapter 1: General introduction

Neoptychocarpus Buch., *Ophiobotrys* Gilg and *Pseudosmelia* Sleumer (Hutchinson, 1967). He did not conserve the division in section for the genus *Casearia*. In 1980, Sleumer studied the Flacourtiaceae in the Neotropics and chose to not use the division into tribes, as established by Hutchinson (Sleumer, 1980). He divided *Casearia* into five sections, mostly following Warburg's concept. The five section of *Casearia* according to Sleumer were *Casearia*, subdivided into six groups, *Crateria* Benth., *Endoglossum* Sleumer, *Gossypiospermum* Griseb., *Guidonia* (DC.) Eichler, and *Piparea* (Aubl.) Benth in Hook. In a later study of Lemke, the division of the Flacourtiaceae into tribe was resurrected and Lemke placed *Casearia* within the Casearieae tribe (Lemke, 1988). Finally, Chase placed *Casearia* in the Salicaceae family and within the Samydeae tribe, as he explained that the name Casearieae was not validly published according to Art. 32.1 (b) of the code (Chase & al., 2002). A historical history of the genus is presented in Table 1.1

	Bentham & Hooker (1862)	Warburg (1895)	Hutchinson (1967)	Lemke (1988)	Chase (2002)
Family	Samydeceae	Flacourtiaceae	Flacourtiaceae	Flacourtiaceae	Salicaceae
Tribe	Caseariae	Caseariae	Caseariae	Caseariae	Samydeae
Species	<i>Casearia</i>	<i>Casearia</i>	<i>Casearia</i>	<i>Casearia</i>	<i>Casearia</i>
	<i>Osmelia</i>	<i>Osmelia</i>	<i>Osmelia</i>	<i>Osmelia</i>	<i>Osmelia</i>
	<i>Euceraea</i>	<i>Euceraea</i>	<i>Euceraea</i>	<i>Euceraea</i>	<i>Euceraea</i>
	<i>Lunania</i>	<i>Lunania</i>	<i>Lunania</i>	<i>Lunania</i>	<i>Lunania</i>
		<i>Laetia</i>	<i>Laetia</i>	<i>Laetia</i>	<i>Laetia</i>
		<i>Patrisia</i>	<i>Patrisia</i>	<i>Patrisia</i>	<i>Patrisia</i>
		<i>Samyda</i>	<i>Samyda</i>	<i>Samyda</i>	<i>Samyda</i>
		<i>Tetrathylacium</i>	<i>Tetrathylacium</i>	<i>Tetrathylacium</i>	<i>Tetrathylacium</i>
		<i>Zuelania</i>	<i>Zuelania</i>	<i>Zuelania</i>	<i>Zuelania</i>
		<i>Neoptychocarpus</i>	<i>Neoptychocarpus</i>	<i>Neoptychocarpus</i>	<i>Neoptychocarpus</i>
		<i>Ophiobotrys</i>	<i>Ophiobotrys</i>	<i>Ophiobotrys</i>	<i>Ophiobotrys</i>
		<i>Pseudosmelia</i>	<i>Pseudosmelia</i>	<i>Pseudosmelia</i>	<i>Pseudosmelia</i>
		<i>Hecatostemon</i>	<i>Hecatostemon</i>	<i>Hecatostemon</i>	<i>Hecatostemon</i>
		<i>Bivinia</i>	<i>Bivinia</i>	<i>Bivinia</i>	
		<i>Gossypiospermum</i>			
		<i>Abatia</i>			
		<i>Aphaerema</i>			

Table 1.1: Taxonomic history of the genus *Casearia* with the name of the family and tribe. All genera of the tribe are indicated.

The latest taxonomical revision of the genus for the New World was made by Sleumer in 1980, where 11 genera are included within *Casearia*: *Anavinga* Adans, *Antigona* Vell., *Athenaea* Schreb., *Bigelovia* Spreng., *Chaetocrater* Ruiz & Pav., *Crateria* Pers., *Gossypiospermum* (Griseb.) Urb., *Iroucana* Aubl., *Pitumba* Aubl., *Synandrina* Standl. & L.O. Williams and *Valentinia* Sw (Sleumer, 1980). Within the *Casearia* genus concept are also the Old World *Bedusia* Raf., *Clasta* Comm. ex Vent., *Melistaureum* J. R. Forst. & G. Forst., *Tardiella* Gagnep and *Vareca* Gaertn. In 2019, four genera belonging to the Samydeae tribe were merged within *Casearia* on the basis of morphological characters *Hecatostemon*, *Laetia*, *Samyda* and *Zuelania* (Samarakoon & Alford, 2019). In that same study, Samarakoon & Alford raised the *Piparea* section at the genus level, therefore resurrecting the Neotropical genus *Piparea* (Aubl.) Benth.

1.4.2.2 Morphological characteristics of *Casearia*

Casearia species are trees or shrubs mostly unarmed; they possess alternate, crenate or serrate leaves with a petiole. The limb presents characteristics pellucid dots and lines. The inflorescence is axillary, few to many flowered, usually pedicellate and sometimes with an articulate pedicel. The flowers are apetalous, monoecious and mostly arranged in fascicules or glomerules. They possess uniseriate free stamens, usually twice as many as the sepals, imbricated and usually free above and present staminodes, alternating with the stamen. *Casearia* species possesses a free unilocular superior ovary with one style, which can be entire or three branched. The fruit is in most cases a capsule, mostly fleshy but that can be dry and that can contain many arillate seeds (Warburg, 1895; Hutchinson, 1967; Sleumer, 1980; Samarakoon & Alford, 2019) (Fig. 1.1). Unfortunately, the ecological interactions of *Casearia* species are poorly known. Nevertheless, it has been reported for one species, *Casearia grandiflora* Cambess., the presence of flies, as a potential pollinator, as well as bees and butterflies (Machado & Oliveira, 2000). In several species of the genus, a dispersion of the fruit by birds (Howe & Primack, 1975) and monkeys (Gautier-Hion, A., & al., 1985) has also been observed.



A



B



C



D

Figure 1.1: Illustration representing *Casearia*. A: *C. aculeata* Jacq., Colombia, *C. Martinez & al.* 2928 (UNO). B: Flowering branch of *C. aculeata* Jacq., Colombia, *C. Martinez & al.* 2935 (UNO). C: Fruits of *C. corymbosa* Kunth, Colombia. D: Flowers of *C. spinescens* (Sw.) Griseb. Cuba, *T. Borsch & al.* 5942 (B, HAJB). Image copyright C © *Francisco Fajardo* and image copyright D © *Thomas Borsch*

1.5 Overview of the dissertation

This doctoral project is carried out in the framework of the Colombian-German research program “Integrated Biodiversity Management in exemplar regions of Colombia” of the BMBF-funded project “Kooperation mit dem Botanischen Garten Bogotá und der Universidad del Norte Barranquilla” (ColBioDiv, BMBF, FK 01DN17006) and contributes to the Work Package 1 “Biodiversity Assessment and Analysis”. The ColBioDiv project aims to study biodiversity management at a landscape level with a transdisciplinary approach, in two model regions of Barranquilla and Bogotá in Colombia.

The main goal of the present PhD study is to investigate the diversity and the evolutionary history of *Casearia* and to give insights into the biogeography and taxonomy of the most species rich genus of the Samydeae tribe. The objectives are (1) to resolve the phylogeny of *Casearia* and test its monophyly (2) to reconstruct the evolution of morphological characters to find synapomorphies for the group (3) to resolve the biogeography of the genus and observe where and when *Casearia* originated (4) to study the species delimitation of unclear taxa, in particular species occurring in the Colombian Caribbean, with an integrative taxonomy approach that combines molecular, morphological and ecological data (5) to compile the first expert-revised world checklist of the genus using the EDIT platform for cybertaxonomy.

The thesis is divided in five chapters.

Chapter 1 is a general introduction for the study.

In **Chapter 2**, the historical biogeography of *Casearia* and some relative genera from the tribe Samydeae were investigated, with a focus on the Neotropics and the Caribbean. Sequences of the chloroplast and nuclear genome were generated to reconstruct a phylogenetic tree and infer ancestral state of selected morphological characters in order to retrieve synapomorphies for the genus *Casearia*. Divergence time estimation was performed on the obtained tree, and ancestral areas were retrieved, in order to investigate where and when the genus originated and how it diversified in time and space.

In **Chapter 3**, an integrative taxonomy approach was developed to study species limits of taxa that are represented by only one or a few specimens in a phylogeny, referred here as “nested singletons”. A framework that combined morphological, ecological and distributional data was used to clarify if those nested singletons stand for a taxon that should in fact be regarded as a synonym of the more widespread species (and accepted name) or could rather be considered an emerging species, to which the widespread accepted species would be

Chapter 1: General introduction

paraphyletic. Several lineages and taxa were selected as exemplars among Neotropical species of *Casearia* based on results from chapter 2.

Chapter 4 presents a taxonomic backbone including all available validly published names in *Casearia* as circumscribed as a monophylum (using evidence from chapter 2). Accepted names of *Casearia* (corresponding to species currently recognized based on the available data from this study and published literature) should be presented with full synonymy and thereby resolving as many names as possible. It includes for each name protologue and type information and can serve as a basis for further work to be done in the genus.

Finally, **Chapter 5** presents the general findings of this study and a general conclusion.

Chapter 2: Character evolution and biogeography of *Casearia*

Evidence for the South American origin of a pantropical genus and for multiple migrations to the Caribbean islands

2.1 Summary

Casearia (Salicaceae) is a pantropical genus of circa 200 species, around half of which dwell in the Neotropics. Despite the availability of phylogenetic studies, which suggest that *Casearia* sensu Sleumer (1980) is not monophyletic, a strong phylogenetic framework was still lacking for this genus. We tested the monophyly of *Casearia* and examined the relationship of its species to other taxa of the tribe Samydeae including *Laetia*, *Samyda* and *Zuelania*, which recently have been sunk in *Casearia*, as well as *Euceraea*, *Lunania*, *Neoptychocarpus*, *Ryania* and *Tetrathylacium*. We further put a focus on the Neotropical taxa since *Casearia* and allies are speciose both on the Caribbean islands and adjacent mainlands, thus providing an interesting group to address the origin of the Caribbean and Cuban flora. Our phylogenetic analyses based on four combined rapidly evolving plastid regions (*petD*, *rpl16*, *rps4-trnT-L-F*, *trnK-matK-psbA*) as well as nuclear ITS revealed *Casearia* as monophyletic with high support, including not only the former members of *Laetia*, *Samyda* and *Zuelania* but also *Euceraea* and *Neoptychocarpus*. *Casearia* is constituted by several major clades, mostly being entirely neotropical, one of which exclusively comprises species endemic to the Caribbean islands (clade B5). Another clade that includes all Paleotropical species (clade B6) is nested among neotropical lineages. Our divergence date estimates using the plastid data set and fossil calibration points in Salicaceae indicate that the *Casearia* crown group started to diversify during the late Eocene approx. 39 Ma. The stem of the Old-World clade diverged from Neotropical ancestors around 27. Ma in the Oligocene. We used BayesTraits to reconstruct the evolution of seven characters commonly used to define *Casearia* and allied genera. We found morphological characters, such as branched inflorescences (fasciculate, glomerulous, cymous) or uniseriate stamen series work well to circumscribe the genus, whereas dioecy that was used to diagnose *Neoptychocarpus* or higher stamen numbers (>12) found in *Laetia* and *Zuelania* are homoplastic in Salicaceae and

Chapter 2: Character evolution and biogeography of *Casearia*

derived within *Casearia* from ancestors with 7-12 stamens. Pellucid dots appear to have evolved earlier than the divergence of the *Casearia* clade in Samydeae, and were lost in *Ryania* and *Tetrathylacium*, and thus are no synapomorphy for *Casearia*. Our reconstruction of ancestral areas using BioGeoBears indicates that South America is the ancestral area of *Casearia*. From there, multiple migrations occurred to Mesoamerica and the Caribbean islands. The Caribbean clade B5 that comprises nearly all Caribbean endemics started to diversify around 9.5 Ma. Our trees depict *C. corymbosa*, which exhibits significant infraspecific phylogenetic structure for the sampled Mexican and Colombian individuals, as the sister to the Caribbean clade. The other clade with Cuban endemics (*C. ternstroemioides*, clade B5) but also Mesoamerican and South American taxa is not sufficiently resolved internally, to allow biogeographic conclusions. The Old World clade of *Casearia* provides another example for a late Laurasian migration starting in the Neotropics.

2.2 Introduction

The genus *Casearia* Jacq. (Salicaceae) is pantropical with approximately 200 species (Sleumer, 1980), among which ca. 90 are found in the Neotropics (Gentry, 1996). Formerly, the genus formed part of the widely polyphyletic family Flacourtiaceae Rich. ex DC. (Warburg, 1895; Sleumer, 1980; Lemke, 1988). Phylogenetic studies by Chase & al. (2002) revealed the Flacourtiaceae to consist of different clades located in distant positions within Malpighiales, which were then recognized as the families Achariaceae Harms and Salicaceae Mirb. (Bremer & al., 2003; Chase & al., 2016). The latter includes *Casearia*. Based on *rbcl* sequences the authors inferred *Casearia sylvestris* Sw. as sister to all remaining Salicaceae (Chase & al., 2002), followed by *Scyphostegia* Stapf. This topology was confirmed by subsequent studies using 82 plastid genes (Xi & al., 2012) and 17 genes from all three genomic compartments (Soltis & al., 2011). Whereas the Salicaceae as a whole and its first two branches were well supported, all these studies were limited in taxon sampling. Alford (2005) carried out a phylogenetic analysis of the former Flacourtiaceae, with a much better representation of taxa, in particular of the tropical members of the Salicaceae clade sensu lato (Chase & al., 2002). Using plastid *trnLF* and *ndhF* sequence data and a comprehensive morphological dataset the resulting trees provided good support for three clades within Salicaceae s.l.. He recognized these three clades at family level, namely as Samydeaceae Vent. (including *Casearia*), Scyphostegiaceae Hutch. and Salicaceae (Alford, 2005) to account for

Chapter 2: Character evolution and biogeography of *Casearia*

their morphological differences. However, the plastid trees alone did not show *Samydeaceae* as a clade but indicated a clade comprising *Casearia* and allied genera (see Alford, 2005: Fig. 2.7).

The species of *Casearia* are trees or shrubs with pellucid dots or striations on the leaves, which in most cases have serrate margins (Hutchinson, 1967; Gentry, 1996). The flowers are axillary and apetalous, with twice as many (or more) stamens than sepals (Fig. 2.1). The stamens are more or less perigynous, uniseriate and the ovary is unilocular with three parietal multi-ovulate placentas (Warburg, 1895). Identification of *Casearia* species is generally difficult, particularly in the field, as the commonly used diagnostic characters are mainly floral features no bigger than a few millimetres (Sleumer, 1980). The first comprehensive treatment of *Casearia* and relatives can be attributed to Warburg (1895) who dealt with the genus in the context of the whole *Flacourtiaceae*. He divided the family into 11 tribes, one of which was the *Casearieae* Benth., including *Casearia*, *Euceraea* Mart., *Laetia* Loef. ex L., *Lunania* Hook., *Osmelia* Thwaites, *Patrisia* J. St.-Hil. (*syn. Ryania* Vahl.), *Samyda* Jacq., *Tetrathylacium* Poepp. and *Zuelania* A. Rich. He defined the tribe as having no petals and perigynous flowers. The leaves present pellucid dots and there are twice or more stamens than sepals, apart from *Tetrathylacium* that possesses both in equal numbers. Plus, all members of the *Casearieae* tribe have staminodes. He then presented the genus *Casearia* with the following diagnostic characters: 4 to 6 persistent sepals, 6 to 15 uniseriate stamens and the same number of staminodia alternating with them, being free or merged at the base, punctate leaves and a simple or 3-4 parted style (Warburg, 1895). The pellucid dots and striation of *Casearia* leaves are ducts and cavities present in the limb. They are often secretory structures that play a role in the chemical defence of the plant (Roupert, 1926; Evert, 2006). In the case of *Casearia*, their structure has been studied but their function remains unknown (Ferreira Fernandes & al., 2018). Hutchinson (1967) largely adopted Warburg's classification but added new genera to the tribe *Casearieae* Benth., namely *Neoptychocarpus* Buch., *Ophiobotrys* Gilg. and *Pseudosmelia* Sleumer. Chase & al. (2002) then pointed out that the name *Casearieae* is not validly published according to Art. 31(1)b of the ICBN, so that *Samydeae* has to be used. The *Casearieae* was considered as a well-defined natural group in the classification system of Lemke (1988), who defined 10 tribes of *Flacourtiaceae* by a set of morphological, wood anatomical and secondary compound characters (Lemke, 1988). The tribe *Casearieae* was characterised to have small or obsolete floral bracts, lacking petals and vessels without spiral thickenings and simple perforation plates (Lemke, 1988). Lemke also described the tribe to have a half inferior ovary, which probably is a confusion as *Casearia*

Chapter 2: Character evolution and biogeography of Casearia

possess a superior ovary (Warburg, 1895; Alford, 2005). His circumscription corresponded to the Casearieae of Hutchinson (1976) but additionally included *Bivinia* Jaub. ex Tul. (later transferred to Homalieae; Chase & al., 2002) and *Synandrina* Standl. & Steyerl. (now synonym of *Casearia*).

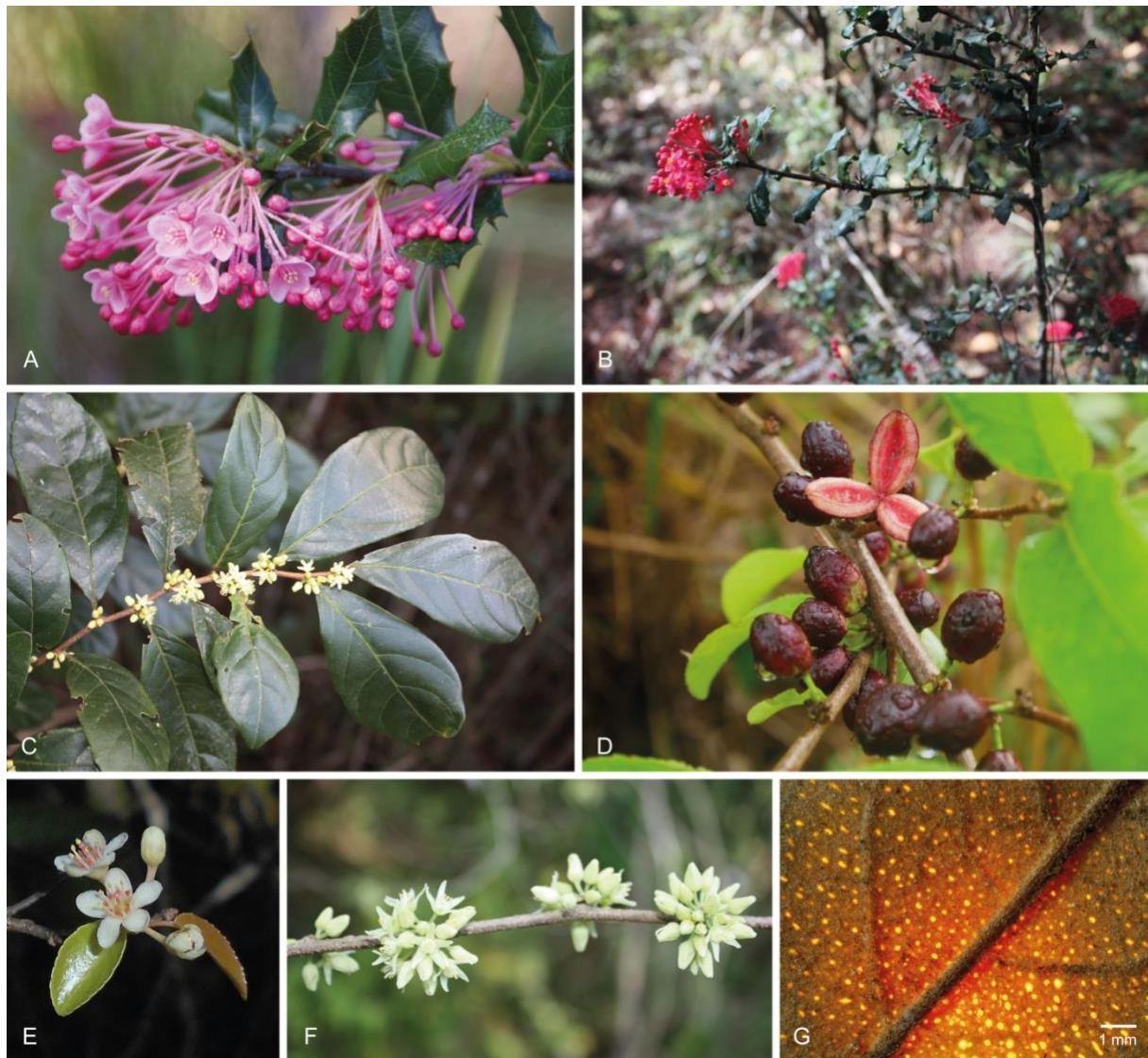


Fig. 2.1: Morphology and species diversity of *Casearia*. A: Inflorescence of *C. bissei* from Cuba, Guantanamo (Borsch & al. 4428 [B, HAJB; SAL012]) photo M. Ackermann; B: flowering branch with coriaceous leaves of *C. crassinervis* from Cuba, Holguin (Borsch & al. 4056 [B, HAJB; SAL002]); C: axillary flowers of *C. aculeata* from Cuba, Villa Clara (Borsch & al. 5243 [B, HAJB; SAL014]); D: Fruits of *C. aculeata* Jacq. From Colombia, photo: O. Rojas-Zamora; E: flowers of *C. nitida*, Cuba, photo: J.-L. Gomez; F: flowers in glomerules on branch of *C. mollis* from Cuba (Borsch & al. 5138 [B, HAJB; SAL013]); G: pellucid dots and lines of *C. arborea*, Cuba, (Borsch & al. 4845 [B, HAJB]).

Chapter 2: Character evolution and biogeography of *Casearia*

Phylogenetic studies by Samarakoon (2015) focused on the Samydeae (there classified as Samydaceae on family level) and provided better resolved trees based on combined plastid *ndhF* + *matK* and nuclear *EMB2765* + *GBSSI* sequence data (Samarakoon, 2015). The author included 21 species of *Casearia*, most of which appeared in a core clade called *Samydeae*, whereas *C. commersoniana* Cambess. and *C. javitensis* Kunth together with *Ryania* and *Trichostephanus* were depicted as the sister clade, and called *Ryanieae*. Those two species were part of the section *Piparea* (Aubl.) Benth. in Hook. Recently, the members of this tribe were put into the genus *Piparea* Aubl. on the basis of those phylogenetic results (Samarakoon & Alford, 2019). Within the narrowly defined Samydeae, the core of *Casearia* appeared paraphyletic to the small segregated genera *Hecatostemon*, *Laetia*, *Samyda* and *Zuelania*, which were merged with *Casearia* (Samarakoon & Alford, 2019). Warburg (1895) recognized five sections of *Casearia*, of which only one possesses species from the Old World, together with species from the New World. Sleumer (1980) also recognized six sections of *Casearia*. First is the section *Guidonia* (DC.) Eichler with three species, which is characterised by an undivided style, formed by the upper part of the ovary and staminodes fused to the corona. The type species of this section is *C. spinescens* (Sw.) Griseb. Second is the section *Endoglossum* Sleumer containing only *C. tremula* (Griseb.) Griseb. ex C. Wright, characterised by an undivided style and free staminodia that are disposed in a distinct row as the row of stamen. Third is the section *Casearia*, which is the largest of all sections, comprising all species of the Old World, around 100, together with about 60 species from the New World. This section was divided into six informal groups including the group *Ilicifoliae*, with species endemic to the Caribbean islands Cuba and Hispaniola. Similar to the section *Endoglossum* it is distinguished by having an undivided style, but the free staminodes are arranged in the same row as the stamens, and alternating with them. Fourth is the section *Gossypiospermum* Griseb. with around three species characterised by hairy seeds, a trifid style and free staminodes. The type is *C. praecox* Griseb. The fifth section is *Crateria* Benth. in Hook., with around three species, and defined in having a trifid style and staminodes alternating with the stamen. The type is *C. carpinifolia* Benth. (= *C. sylvestris* var. *lingua* (Camb.) Eichler as currently accepted name). Finally, he recognized the section *Piparea*, the species of which also have a trifid style but staminodes placed in the same row as the stamens with *C. commersoniana* as the type species. However, this section was recently excluded from *Casearia* by Samarakoon (Samarakoon & Alford, 2019) who resurrected the genus *Piparea*. According to the same study (Samarakoon & Alford, 2019), *Casearia* now includes further nine species formerly known as *Samyda*, characterised by perigynous stamens, lacking

Chapter 2: Character evolution and biogeography of *Casearia*

staminodes and sepals fused into a tube. The authors also merged the eight species of the genus *Laetia* with *Casearia* (which are also characterised by perigynous, albeit free stamens and the absence of staminodes). Furthermore, they merged the monotypic genera *Hecatostemon* that was originally diagnosed as distinct because of numerous (90-100) stamens and *Zuelania*, characterised by numerous stamens and an absent style.

Most of the species diversity of the pantropical genus *Casearia* is centred in the Neotropics. In the circumscription of Samarakoon & Alford (2019) the genus comprises some 220 species including the four above-mentioned segregate genera that only occur in the Americas, totalling to about 110 species in the Americas. Asia and Oceania comprise about 100 species, whereas Africa only has some 15-30 species, depending on their circumscription (Breteler, 2008; African Plant Database (version 3.4.0), 2020). From the 110 American species, about 70 are found in continental South America and 50 are restricted to that area (70%) based on Sleumer (1980) and later described species (Marquete & Mansano, 2010, 2012, 2013; Alford, 2015; Nepomuceno & Alves, 2017), whereas Mesoamerica and Mexico possess around 30 species, of which 15 are endemics (50%), based on Sleumer (1980) and later described species (Castillo-Campos & Medina Abreo, 2003; Linares & Angulo F., 2005). The Caribbean islands harbour about 30 species, of which 15 to 20 are endemic (50%; including many of the former genus *Laetia*), based on Sleumer (1980) and later described taxa (Gutiérrez, 1980). There are also two taxa endemic to Cuba which are recognized subspecies of widely distributed species: *C. arborea* subsp. *occidentalis* J.E. Gut. and *C. sylvestris* subsp. *myricoides* (Griseb.) J.E. Gut.

Although less pronounced than in other genera, *Casearia* belongs to those neotropical lineages with significant species diversity and endemism in the Caribbean in relation to adjacent mainland, like *Acalypha* and other Acalyphoideae, Euphorbiaceae (Cervantes & al., 2016); *Brunfelsia* L., Solanaceae (Filipowicz & Renner, 2012); the tribe Miconeae, Melastomataceae (Michelangeli & al., 2008); *Phyllanthus* L., Phyllanthaceae (Falcón & al., 2020); or *Rondeletia* L., Rubiaceae (Torres-Montúfar & al., 2020). In addition to species with ranges restricted to either the islands or the mainland, there are eight species in *Casearia* with a distribution shared between the Colombian mainland and the Caribbean islands.

Casearia species grow in Neotropical dry forests, in humid rain forests and savanna habitats. They mostly occur at low elevations but can go up as far as 2000 m (Sleumer, 1980). Another interesting feature is that the genus comprises some widely distributed species occurring in a broad range of habitats, whereas others show more restricted distribution or ecological niches (Gutiérrez, 2000; Gonzalez, 2007; Breteler, 2008). *Casearia* is therefore an interesting model

Chapter 2: Character evolution and biogeography of Casearia

to study both the origin of Neotropical taxa in the context of the evolution of a pantropical genus as well as biogeographic relationships and species diversification in northern South America adjacent to the Caribbean and on the islands themselves.

Biogeographic relations between the Caribbean islands and adjacent mainland have been the subject of several recent studies. The evolution of plant diversity in the Caribbean was strongly influenced by a complex geological history (tectonic movements, volcanism, formation and submersion of islands), as well as the proximity of continental land masses with an exceptionally rich flora, as a source for plants to colonise the islands through time (Santiago-Valentin & Olmstead, 2004). There are three major geological scenarios hypothesised that potentially have influenced the distribution patterns of the flora.

First, the Greater Antilles Aves Ridge (GAARlandia) (Iturralde-Vinent, 1999), thought to have connected the islands with Mesoamerica in the Eocene from 35-32 Ma., has been put forward to explain some diversification patterns such as in *Copernicia* Mart. ex Endl. (Bacon & al., 2012). The respective lineages were supposed to have colonized the Caribbean from Northern parts of South America via GAARlandia bridge, as in other genera such as *Croton* L. and *Styrax* L. (Fritsch, 2003; Van Ee & al., 2008) and also animals (Dávalos, 2004; Deler-Hernández & al., 2018). However, this hypothesis remains controversial and some authors doubt that it played a major role to support plant migrations to the Caribbean islands. Cervantes & al. (2016) analysed the speciose subfamily Acalyphoideae (Euphorbiaceae) and found repeated arrivals of the ancestors of Caribbean island endemic lineages only since the Miocene (approx. 9 Ma and younger), many of which came from Central America and Mexico, thus not being compatible with the GAARlandia hypothesis. Nieto-Blázquez & al. (2017) looked at divergence times of 32 Caribbean endemic genera using published sequence data, indicating younger stem and crown nodes than the GAARlandia time frame in 22 of these, albeit not all lineages were appropriately sampled taxonomically. More recently, Roncal & al. (2020) reviewed so far published phylogenetic studies, what essentially confirmed the picture envisaged by Cervantes & al. (2016) in that Central and South America are important ancestral areas of Caribbean endemic lineages most of which diversified after the Eocene. Ali (2012) even questioned its existence from a geological point of view.

The second important geological event is the closure of the Panama Isthmus that connects South America to Mesoamerica, and was fundamental for the migration of animals and plants between the Americas, including South American ancestors of Mesoamerican and Mexican species, that later reached Cuba and other islands over a near sea distance from the West. However, the exact timing is still debated. The latest review of all available data

Chapter 2: Character evolution and biogeography of *Casearia*

(geological, paleontological and molecular record) concluded a closure in the Late Pliocene (O’Dea & al., 2016), although Bacon & al. (2015) had suggested from a macroecological study and reviewing biogeographic data from both plants and animals, that the exchange between South and Mesoamerica started as early as the Oligocene - Miocene boundary.

The third complex of geological and palaeoenvironmental factors are major sea level changes shaping intra-archipelagic connectivity (Caribbean islands) and thus, speciation through vicariance (Weigelt & al., 2016; Heads, 2018). Sea level changes also affect the outline of islands. They could cause the extinction of plant populations that can no longer function as the source for radiations, for example when an area of distribution became submerged (Alonso & al., 2012). According to Iturralde-Vinent (1999), the sea level raised considerably in the Caribbean at 30 Ma, thus reducing the surface of land available for plants and creating barriers. However, sea level changes and their impact on land plants are still poorly studied in the Caribbean, and this includes the much more recent Pliocene fluctuations that included lower sea levels and potentially increased connectivity in periods of glaciation. On the other hand, overwater dispersion is also proposed to explain how plants migrated in the wider Caribbean, such as in Acalyphoideae (Cervantes & al., 2016) or palms of the tribes Cryosophyleae and Sabaleae (Cano & al., 2018). Such dispersal is supposed to be facilitated by hurricanes, that happen repeatedly in the region (Lugo & al., 2000; Hedges, 2001; Andraca-Gómez & al., 2015). The more recent investigation of species-rich lineages such as *Phyllanthus* or the Acalyphoideae (Euphorbiaceae) with a distribution on all adjacent mainland (South America, Mesoamerica and Mexico) as well as the islands even suggested more frequent migrations between Mesoamerica and Mexico and the Caribbean islands, with continuous arrivals since the Miocene, often followed by speciation on the islands (Cervantes & al., 2016; Falcón, 2020).

Well-resolved and dated molecular phylogenies are crucial to understand the origins and diversification of the Caribbean flora. However, a thorough analysis of these patterns also requires extensive knowledge of species-level taxonomy. Currently, detailed revisions or monographs covering both the islands and adjacent mainland are rare, as are species-level phylogenetic analyses with such a geographic coverage.

This study has therefore two major objectives: the first is to provide a phylogenetic framework for *Casearia* and relatives in order to better understand the phylogenetic position of Neotropical taxa in this pantropical genus, which includes an evaluation of the evolution of key morphological characters for a monophyletic circumscription of the genus. We therefore sampled five of the nine genera belonging to the tribe Samydeae of the Salicaceae. The

Chapter 2: Character evolution and biogeography of *Casearia*

phylogenetic analysis of Samarakoon (2015) provided important insights towards a monophyletic circumscription of the genus *Casearia*. However, the relationships between *Casearia* and allied genera remained still uncertain due to the limited resolution and node support in her molecular trees, and also, contrary to Asian species, Neotropical taxa were only sparsely sampled. Based on our phylogenetic hypothesis of *Casearia* and relatives, which provides the first well-supported molecular trees for this group of plants, our second major objective is to unravel the origin of the species of *Casearia* in the Caribbean and in particular to test for biogeographic relationships with entities occurring in the adjacent South American mainland. We therefore estimated divergence times and ancestral areas of the *Casearia* clade in order to provide a first picture of its divergence in time and space.

2.3 Materials and methods

2.3.1 Taxon sampling

In this study 103 samples corresponding to 54 species were included, of which 42 belong to *Casearia* in the circumscription of Samarakoon & Alford (2019) including the segregate genera *Laetia*, *Samyda* and *Zuelania* (Voucher information in Appendix 2.1). From the Samydeae we further sampled *Euceraea*, *Lunania*, *Neoptychocarpus*, *Piparea*, *Ryania*, and *Tetrathylacium*. Seven genera served to represent other lineages of Salicaceae and *Lacistema* (Lacistemataceae) as outgroup, considering the topology of Malpighiales published by Xi & al. (2012). Plant material was collected in the Colombian departments Atlántico, La Guajira, Magdalena and Bolívar between 2017 and 2019 (32 accessions) as well as in Cuba and the Dominican Republic between 2010 and 2017 (29 accessions). We further sampled herbarium specimens from B, BR, and P from other parts of the Neotropics, Africa and Asia (8 accessions). Field-collected plant tissue was silica-dried and corresponding vouchers were deposited in the herbaria B, HAJB, and UNO. Information about localities, collectors etc. can be found in Appendix 2.1. Recently, plastid genomes of *Casearia decandra* Jacq. and *Casearia velutina* Blume were published (Li & al., 2019), so we also included the respective genomic regions from these sequences in our analyses. It is to be noted that for them the vouchers are not available, but we were able to confirm their identification with barcode sequences available in Genbank for the same species.

Chapter 2: Character evolution and biogeography of *Casearia*

2.3.2 DNA Isolation, Sequencing, Alignment and indel coding

Genomic DNA was extracted from herbarium specimens following the modified CTAB protocol (with triple extraction) from Borsch (Borsch & al., 2003). After a chloroform extraction step, the DNA was precipitated with isopropanol, resuspended in TE and purified by ammonium acetate and sodium acetate washing steps followed by ethanol precipitation. Extraction of genomic DNA from silica-dried leaf material was achieved using the NucleoSpin Plant II Kit (Macherey-Nagel, Düren, Germany). Four plastid genomic regions (*petD*, *rpl16*, *rps4-trnT-L-F*, *trnK-matK-psbA*) and one nuclear region (nrITS) were selected based on their utility to resolve relationships at the genus and species levels (Borsch & Quandt, 2009). Universal primers were used to amplify these regions as much as possible, but also new internal primers were designed in this study (Table S1) for more fragmented DNAs from herbarium specimens. The larger *rps4-trnT-L-F* and *trnK-matK-psbA* regions were generally amplified in two overlapping halves. Most primers were also used for sequencing (Table S1). Amplifications were made with a peqStart Thermocycler (peqLab Biotechnologie GmbH, Erlangen, Germany). Each tube contained 4 µL of DNA with a concentration of 25 ng/µL, 19.2 µL water, 0.3 µL DNA polymerase Hot start (PeqLab, Erlangen Germany), 5 µL Taq Buffer S, 2.5 µL MgCl₂, 10 µL dNTP, 5 µL betaine and 2 µL forward and 2 µL reverse primers. In some cases an enhancer was added, enhancer solution P (PeqLab, Erlangen Germany). Most of the regions were amplified using a program with initial denaturation (1'30 min at 95°C), 34 cycles of denaturation (0'30 min at 95°C), annealing (1 min at 52°C), extension (1 min at 72°C) and a final extension step (10 min at 72°C). For the amplification of *rpl16*, we used a program with initial denaturation (1'30 min at 95°C), 34 cycles of denaturation (0'30 min at 95°C), annealing (1 min at 55°C), extension (1 min at 72°C) and a final extension step (10 min at 72°C). And for ITS, we used a program with 35 cycles of denaturation (1 min at 96°C), annealing (1 min at 48°C), extension (1'45 min at 60°C) and a final extension step (7 min at 72°C). PCR products were stained with 100x SYBR Green nucleic acid stain and electrophoresed on a 1.5% NEEO agarose gel (Carl Roth, Germany) running for 2 hours at 100 volts. When excised from the gel the products were purified using the GEL/PCR DNA Fragment Extraction Kit (AveGene Life Science), or PCR products were cleaned directly using the Stratec Kit (Germany). After a concentration adjustment all PCR products were sent to Macrogen Europe (Amsterdam, the Netherlands) and sequenced on an ABI 3730 XL capillary sequencer using the KB3730-Pop7-BDTv3 dye set.

Contigs were assembled in PhyDE after prior inspection of pherograms for erroneous base calls. A motif-based approach (Löhne & Borsch, 2005) was used align the sequences

Chapter 2: Character evolution and biogeography of *Casearia*

using PhyDE v. 09971 (Müller & al., 2010) after initial pre-alignment with the MUSCLE plug in. Short regions of uncertain homology (hotspots) were excluded from the analyses. Gaps were coded using the simple indel coding method (Simmons & Ochoterena, 2000) as implemented in SeqState version 1.4.1 (Müller, 2005). Consensus DNA sequences were submitted to ENA (European Nucleotide archive) (www.ebi.ac.uk/ena/) using the software tool *annonex2embl* (Gruenstaeudl, 2020).

2.3.3 Phylogenetic analyses

Parsimony analysis (MP) was performed in PAUP* v.4.0b10 (Swofford, 2008) using the commands obtained from the parsimony ratchet (Nixon, 1999) as implemented in PRAP (Müller, 2004). The files generated by PRAP included all characters with equal weight and treated the gaps as missing characters. Ratchet settings included 200 iterations, unweighting 25% of the positions randomly (weight=2) and 100 random additional cycles. Jack-Knife (JK) support was obtained by a single heuristic search in PAUP within each of 10,000 JK pseudo-replicates, TBR branch swapping, and 36.79% of characters being deleted in each replicate. Bayesian Inference (BI) was performed in MrBayes v.3.2.7.a (Ronquist & al., 2011) using the CIPRES portal (Miller & al., 2011). We chose the optimal nucleotide substitution models for our matrices using jModelTest v.2.1.7 (Darriba & al., 2012) under the Akaike's Information Criterion (AIC). Matrices were obtained from partitions corresponding to individual genomic regions (Table 2.1), also for the best fit models). Regarding the indels, we used the model proposed by Ronquist (2011), which is the F81 like model. We realized four runs each with four chains performed for 50 million generations, for the plastid dataset and 20 million for the nuclear dataset, sampling every ten thousandth generation. We verified the convergence of the runs using the average standard deviation of split frequencies and post burn-in sampling size (ESS). The first 10% of trees were discarded as *burn-in* and the remaining trees were used to construct a 50% majority-rule consensus tree.

Chapter 2: Character evolution and biogeography of Casearia

	rps4-trnLF	trnK-matK	rpl16	petD	combined plastid	ITS
Number of taxa	103	103	103	103	103	66
Aligned length (bp)	2133	3138	1128	1333	7732	761
Parsimony-informative characters	356	529	237	265	1036	236
Consistency index (CI)	0.813	0.789	0.768	0.812	0.689	0.567
Retention index (RI)	0.897	0.901	0.866	0.933	0.828	0.767
Tree length	889	1376	604	532	3923	993
Partition	spacer rps - trnTexon	trnK intron	rpl16 intron	spacer petD - petDexon	petDintron	
	spacer trnT trnL - trnL exon	matK				
	trnL intron - spacer trnL trnF - trnF	trnKintron 2-trnKexon 2-spacer - psbA				
Substitution model	GTR+G	GTR+G	GTR+G	GTR+I	partitioned	GTR+I+G
	GTR+G	GTR+G		GTR+G		
	GTR+G	GTR+G				

Table 2.1: Summary of character statistics, evolutionary models and tree statistics for each dataset under parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI)

Maximum Likelihood (ML) analyses were performed using RAxML v. 8.2.12 in CIPRES. Rapid bootstrap support (BS) was estimated based on the majority-rule consensus tree from 1000 pseudo-replicates with 200 searches. The models *general time-reversible (GTR) + I* and *binary (BIN) + I* were used for the nucleotide and indel partitions, respectively.

The 50% majority-rule consensus tree obtained in MrBayes was processed in TreeGraph v.2.14.0-771 (Stöver & al., 2010). The add support values function was used to add support values from MP and ML analyses.

2.3.4 Assessment of morphological characters and ancestral character state reconstruction

Morphological characters were selected that have been used to diagnose genera and sections in the Samydeae. The characters and their states were the following: (1) sexual system (0 = bisexual, 1 = dioecious) and (2) calyx lobes fused into a tube (0 = absent, 1 = present). Characters 1 and 2 were used to diagnose *Neoptychocarpus* (Buchheim, 1959; Sleumer, 1980; Gentry, 1996). We also assessed diagnostic characters for the genus *Casearia*, which were (3) presence of pellucid dots on the leaves (0 = absent, 1 = present; see Fig. 2.1.G), (4) the number of stamens (1 = 1-6, 2 = 7-12, 3 >12), as the number of stamens was used to distinguish *Casearia* species with usually 7 to 12 stamens, whereas species of *Laetia*, *Samyda* and *Zuelania* possess more (Sleumer, 1980) and (5) the presence of staminodes (0 = absent, 1 = present) (Warburg, 1895; Hutchinson, 1967; Sleumer, 1980). We also looked at (6) the arrangement of the stamen (0 = spiral, 1 = uniseriate) and (7) the inflorescence type (0 = panicle, 1 = catkin, 2 = raceme/corymb, 3 = fascicle/glomerule, 4 = cyme, 5 = solitary). In order to limit the number of states that can be handled by BayesTraits (Pagel & Meade, 2006), we grouped together the states “raceme” and “corymb” because a corymb can be understood as a specialized raceme. We also combined “fascicle” and “glomerule” since both are very similar and differ solely in the presence (fascicle) or absence of peduncles (glomerule) (Beentje, 2016). The information on characters and states was obtained from the literature (Warburg, 1895; Hutchinson, 1967; Sleumer, 1980; Gutiérrez, 2000; Marquete & Mansano, 2012), herbarium vouchers and protologues. The resulting morphological character matrix can be found in Table S2.

For the reconstruction of ancestral character states a reduced plastid matrix with one sample per species was employed. From the post *burn-in* trees inferred with MrBayes, using the above stated specifications, a maximum credibility tree was generated with Mesquite V3.6 (Maddison & Maddison, 2018) and a population of 1000 trees from the MrBayes analysis were randomly selected to consider topological variation. Probabilities for ancestral states were estimated in BayesTraits V2.0.2 (Pagel & Meade, 2006). Therefore we generated a command file in TreeGraph v.2.14.0-771 (Stöver & Müller, 2010) using the function AddNodes including all relevant nodes for the analysis. We then used a reverse jump Markov chain Monte Carlo (rjMCMC) approach to consider both the phylogenetic uncertainty and the ancestral state uncertainty. An exponential hyperprior with the mean on a uniform interval [0-100] was employed for each rjMCMC run in order to reduce the problem of assigning arbitral

Chapter 2: Character evolution and biogeography of *Casearia*

values to the parameters of the prior distribution. We then visualized the results using the Import BayesTraits data option in TreeGraph v.2.14.0-771.

2.3.5 Estimation of divergence time

Divergence time was estimated using BEAST v.2.6.1, setting up the input file with BEAUTi (Drummond & al., 2012). We used a log normal, uncorrelated relaxed clock (UCLN) model with three calibration points (Drummond & al., 2006) and applied a GTR+G model to the plastid matrix. The first calibration point was applied to the *Salix-Idesia* clade using a fossil of *Pseudosalix*, which was found in the USA and dated 48 Ma (Boucher & al., 2003). The second calibration point was applied to the *Casearia* clade, as defined above, including *Euceraea* and *Neoptychocarpus* using a fossil of *Casearia*. It is a pollen fossil found in Panama and dated 37 Ma (Graham, 1985). The pollen of *Casearia* has been studied by Keating (Keating, 1973) and this particular pollen was already used in other studies (Davis & al., 2005; Xi & al., 2012). As it cannot be identified at the species level, we assigned it to the crown node of our *Casearia* clade. Indeed, it seems that this fossil could be attributed with certainty to the *Casearia* genus and it is most similar to *C. sylvestris* Sw. Attributing it to the crown group of *Casearia* allows to not underestimate the age of the crown group. Fossil calibrations are used as a minimum age and we selected a lognormal distribution, which gives higher probabilities to older ages. We respectively selected 37 Ma and 48 Ma as the minimum age (*Casearia* and *Pseudosalix* fossil) and used the age of the Eocene, where the fossil was dated as a maximum age. Details of fossil calibration points are found in Table S3. We also gave a maximum age to the root of the tree, using the 92.78 Ma crown group age of the Malpighiales (Foster & al., 2017). The effect of the Yule speciation model versus the Birth-Death model as speciation priors was tested using a steppingstone sampling (SSS), with 150 path steps, each with a chain length of one million iterations. The other parameters were set by default in BEAST v2.6.0. We then calculated the log-Bayes factor (BFs; Table S4) and found that the Yule model fitted best.

We used BEAST v.2.6.1 under the relaxed clock normal and Yule model with 50 million (logging parameters every 10,000 generations). We used Tracer v.1.7.1 (Rambaut & al., 2018) to check for convergence using the effective sample size (ESS). The first 10% of the Markov chain Monte Carlo (MCMC) generations were removed as a *burn-in* and the post *burn-in* MCMC runs were summarised using TreeAnnotator v. 2.6.0 (Drummond & Rambaut,

Chapter 2: Character evolution and biogeography of *Casearia*

2007) to generate a maximum clade credibility tree visualized in FigTree v.1.4.4 (Rambaut, 2010).

2.3.6 Ancestral area reconstruction

Areas were scored following Cervantes & al. (2016) as (A) Mexico, (B) Mesoamerica, (C) South America, (D) Caribbean Islands and (E) Africa. The only difference in our area definitions used here is that (F) stands for Asia and a separate area is defined for New Caledonia (G). As species limits in *Casearia* are in many cases not fully understood and distribution areas depend on currently accepted names with which specimens are identified, we preferred to code all samples by their respective areas from which they were collected. Thus, we were able to test for phylogeographic patterns in presumably widespread taxa and to properly code samples in the case currently accepted species were not resolved as monophyletic. This was particularly relevant for our goal to analyse species diversification between the Caribbean islands and adjacent mainlands. Consequently, the area of occurrence of each individual was coded rather than the area of distribution of the respective species corresponding to the currently applied taxon concept. The ML tree from the analysis of the plastid dataset was used in BioGeoBears implemented in Rasp v.4 (Yu & al., 2020). BioGeoBears estimates the ranges of the areas taking into account processes such as dispersal, extinction, founder-event speciation and vicariance. We evaluated the models Bayarealike, DIVA and DEC and compared the AIC values and likelihood ratio tests (LRTs).

2.4 Results

2.4.1 Phylogenetic analyses

For this study we generated 344 new sequences from four plastid genomic regions. The concatenated multiple sequence alignment of the four plastid genomic regions had 8228 positions, of which *rps4-trnT-L-F* contributed 2316, *trnK-matK-psbA* 3260, *petD* 1395 and *rpl16* 1257 positions. The matrix used for tree inference had 7732 positions, after exclusion of hotspots (for *rps4-trnLF*: three poly-A microsatellites in alignment positions 434-443, 651-663, 1392-1403; one poly-AT microsatellite in 864-879; seven hotspots of other AT-rich

Chapter 2: Character evolution and biogeography of *Casearia*

sequence elements of unclear homology in 980-1000, 1055-1063, 1160-1172, 1609-1627, 1873-1881, 1923-1958, 2220-2234; one poly-T microsatellite in 2039-2047; for *trnK-matK*: five poly-A microsatellites in 2565-2578, 2661-2666, 2908-2919, 4910-4921, 5311-5325, two poly-T microsatellites in 2785-2793, 2891-2894, one poly-AT microsatellite in 3102-3125, one hotspots of other AT-rich sequence elements of unclear homology in 5110-5136, ; for *petD*: one poly-A microsatellite in 5881-5888, three poly-T microsatellites in 6038-6047, 6223-6236, 6528-6538, and one hotspot of other AT-rich sequence elements of unclear homology in 6366-6384 and for *rpl16*: three poly-A microsatellites in 7057-7067, 7271-7274, 7364-7372 two hotspots of other AT-rich sequence elements of unclear homology in 7804-7819, 7925-7981, one poly-AT microsatellite in 8063-7981. In addition, 381 indels were coded. Sequence statistics, models of sequence evolution, and tree statistics for the individual genomic regions and concatenated matrices are presented in Table 2.1. The plastid trees obtained with BI, ML and MP are mostly congruent and the ML and MP trees are presented in Appendix 2.2 and Appendix 2.3. On average most nodes received significant support, with PPs > 0.95, and BS as well as JK values > 75 % (Fig. 2.2).

Chapter 2: Character evolution and biogeography of Casearia

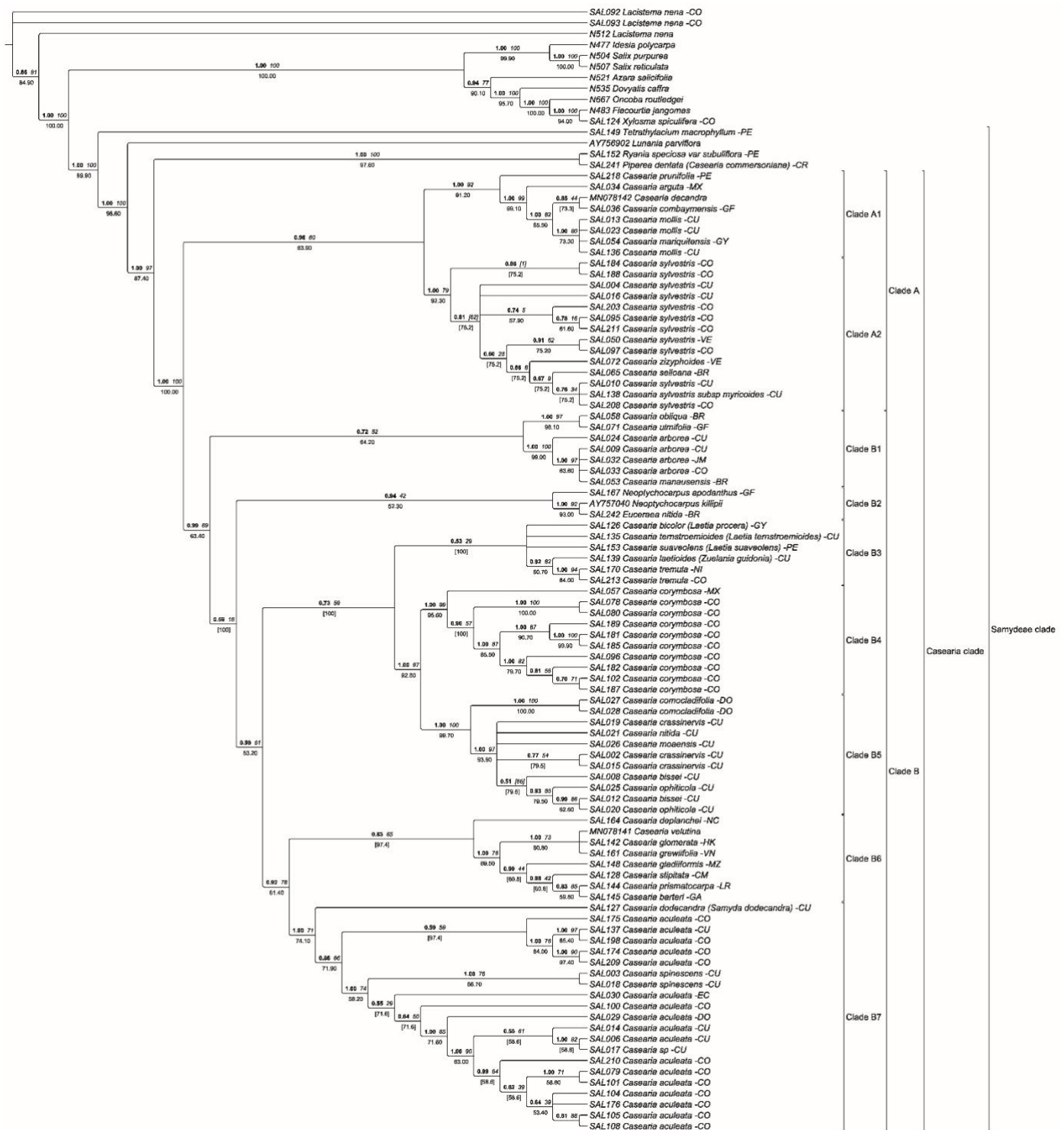


Fig. 2.2: Bayesian 50% majority rule consensus tree of *Casearia* based on four plastid markers (*rps4/trnLF*, *trnK/matK*, *rpl16* and *petD*). Values above the node indicate posterior probability (PP), bootstrap support values are in italic and Jackknife support is indicated below the node. Square bracket values indicate conflicted topologies between Bayesian analysis and maximum likelihood (italic) or parsimony (below the node). At the tip of the node is the DNA number followed by the species name and the country code from where the individual was collected (see Appendix 2.1 for more information)

2.4.2 Phylogenetic relationships inferred from the plastid genome

Plastid sequences revealed a well-supported clade of Samydeae (BI-PP: 1.00, ML-BS: 100, MP-JK: 99.90), including *Tetrathylacium* as well as a *Lunania* and a *Ryania* and *Piparea* lineage, as successive sisters to a *Casearia* clade (PP: 1.0, BS: 100, JK: 100), that includes the genera *Laetia*, *Samyda*, and *Zuelania* (Fig. 2.2, clades B2 & B6), which recently were merged into *Casearia*. One species of *Euceraea* and two species of *Neoptychocarpus* were found as nested well inside the *Casearia* clade (Fig. 2.2, clade B2). The other genera of Salicaceae appear in an also well supported sister-clade to the Samydeae.

Within the *Casearia* clade we found two well supported clades (Clades A and B, Fig. 2.2). **Clade A** (PP: 0.98, BS: 60, JK: 63.9) includes species from South America, Mexico and the Caribbean islands. Two subclades, **Clade A1** (PP: 1.00, BS: 92, JK: 91.2) and **Clade A2** (PP: 1.00, BS: 79, JK: 92.3) were revealed, the latter of which comprises the samples of *C. sylvestris* with the different subspecies from Colombia, Cuba and Venezuela, which constitute a paraphyletic group since this clade also includes *C. zizyphoides* Kunth and *C. selloana* Eichler. **Clade B** (PP: 0.99, BS: 69, JK: 63.4) comprises species both from the New and the Old World. Seven subclades can be distinguished which are well-supported: **Clade B1** (PP: 0.72, BS: 52, JK: 64.2) with all *C. arborea* (Rich.) Urb. samples from Colombia, Cuba and Jamaica as well as *C. manausensis* Sleumer as one lineage (PP: 1, BS: 97, JK: 63.6) that is sister to *C. obliqua* Spreng. plus *C. ulmifolia* Vahl ex. Vent. (PP: 1, BS: 97, JK: 98.1). **Clade B2** (PP: 0.94, BS: 42, JK: 52.3) comprises the largely Amazonian *Euceraea nitida* and two species of the Neotropical genus *Neoptychocarpus*. **Clade B3** (PP: 0.53, BS: 29, JK: [100]) consists of *C. tremula* together with species that formerly were part of the genera *Laetia* and *Zuelania*. **Clade B4** (PP: 1, BS: 99; JK: 95.6) harbours all individuals of *C. corymbosa* Kunth. from the Colombian Caribbean as sister to a sample from Mexico. **Clade B5** (PP: 1.00, BS: 100; JK: 99.7) comprises species from the Caribbean islands, *C. comocladifolia* Vent. from Hispaniola and *C. nitida* Jacq., *C. crassinervis* Urb., *C. moaensis* Vict., *C. ophiticola* Vict. and *C. bissei* J.E. Gut. from Cuba. **Clade B6** (PP: 0.83, BS: 65; JK: [97.4]) includes *C. deplanchei* Sleumer from New Caledonia together with species from the Old World, in two well supported lineages. One (PP: 1.00, BS: 73, JK: 60.8) includes three species from Asia and the other (PP: 0.99, BS: 44, JK: [60.8]) one four species from Africa. Finally, **Clade B7** (PP: 1, BS: 7.15, JK: 74.1) comprises taxa from Colombia, Ecuador, Dominican Republic and Cuba. *Casearia dodecandra* (Jacq.) T. Samar. & M.H. Alford (formerly *Samyda*) is sister to a

Chapter 2: Character evolution and biogeography of *Casearia*

broadly paraphyletic assemblage of individuals from *C. aculeata* Jacq. that includes individuals currently identified as *C. spinescens* from Cuba.

2.4.3 Phylogenetic relationships inferred from ITS

The ITS dataset focuses on the Samydeae clade with *Xylosma* G. Forst as outgroup. This was due to the strongly deviant ITS sequences in the other lineages of Salicaceae and Lacistemataceae that were not reliably alignable. The multiple sequence alignment of ITS resulted in 902 positions (Table 2.1) and 66 ITS sequences were newly generated in this study. The matrix had 761 positions, after exclusions of hotspots (alignment positions 128-148, 162-174, 296-305, 350-359, 385-410, 589-601, 606-621). In addition, 140 indels were coded. Sequence statistics and models of sequence evolution are presented in Table 2.1.

The trees obtained with BI, ML and MP are mostly congruent presented in Appendix 2.4 and Appendix 2.5. The Bayesian majority rule consensus tree, based on the ITS dataset is shown in Fig. 2.3. All three tree inference methods resolved a *Casearia* clade (PP: 1, BS: 66, JK: 80). We found the same nine subclades as in the plastid phylogeny, however, with a lower resolution of the early branching in the *Casearia* clade (Fig. 2.3). *Euceraea nitida* is retrieved together with *Neoptychocarpus* with good support (PP: 1, BS: 97, JK: 90.6) and within the *Casearia* clade, like in the plastid tree. However, this lineage, which appears within clade B in the plastid trees, is here depicted in a polytomy with other subclades of clade B and a weakly supported clade A. In the ITS tree all samples of *C. aculeata* appear in a clade with within *C. spinescens* as sister. Compared to the plastid dataset, the ITS tree presents four major sublineages of clade B, namely Clades B1, Clades B2, B3 and Clades B3, B4, B5, B7, respectively, in a polytomy. *Casearia bicolor* (formerly *Laetia procera* (Poepp.) Eichler) is found as sister of *C. suaveolens* (formerly *L. suaveolens* (Poepp.) Benth.) in a polytomy with clade A and clade B of the ITS tree, and *C. ternstroemioides* (= *L. ternstroemioides*) is part of Clade B6 in ITS (Fig. 2.3) along with taxa from the Old World.

Chapter 2: Character evolution and biogeography of *Casearia*

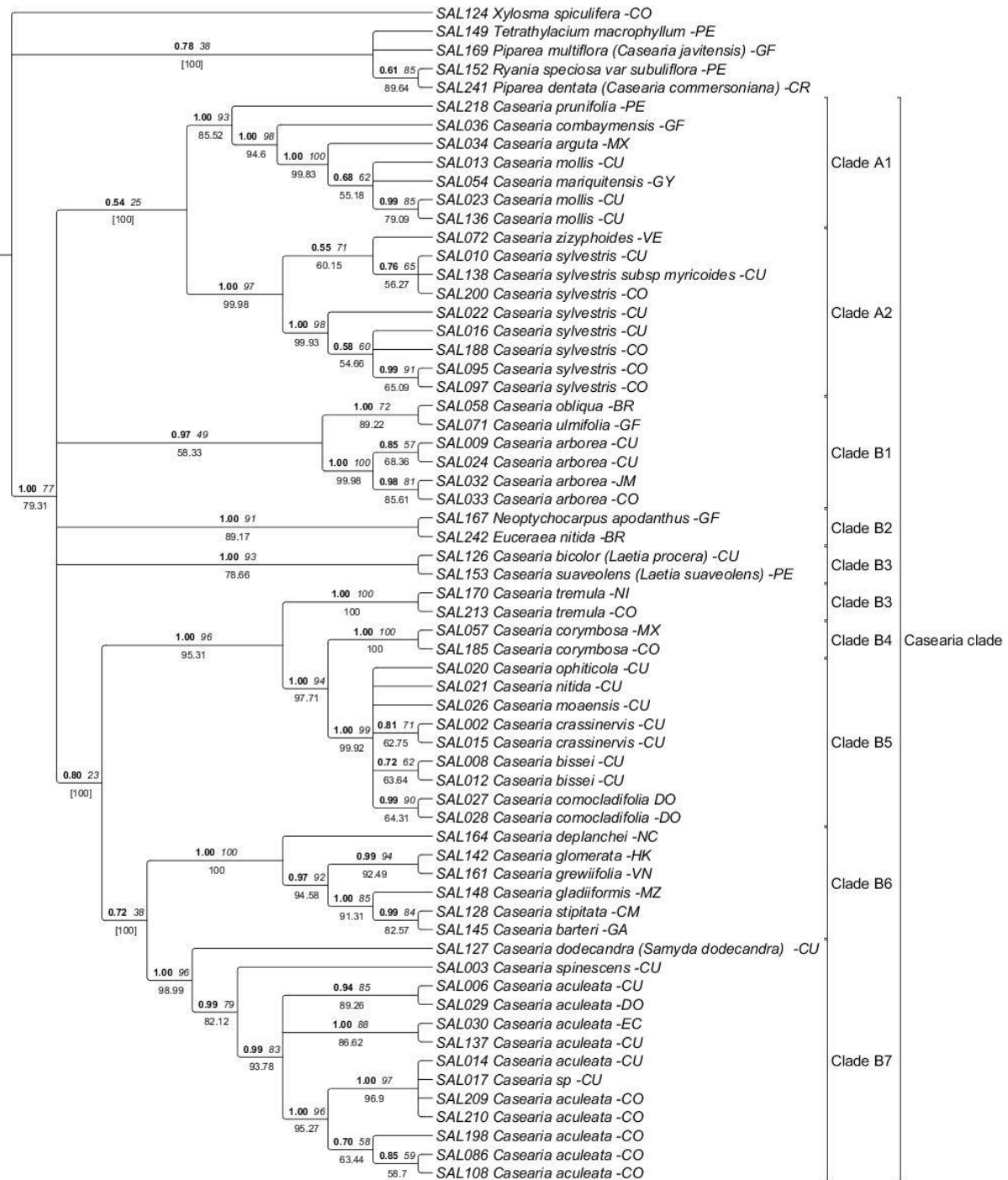


Fig. 2.3. (previous page): Bayesian 50% majority rule consensus tree of *Casearia* based on the nuclear marker *ITS*. Values above the node indicate posterior probability (PP), bootstrap support values are in italic and Jackknife support is indicated below the node. Square bracket values indicate conflicted topologies between Bayesian analysis and maximum likelihood (italic) or parsimony (below the node). At the tip of the node is the DNA number followed by the species name and the country code from where the individual was collected (see Appendix 2.1 for more information)

Chapter 2: Character evolution and biogeography of *Casearia*

2.4.4 Ancestral character states

The matrix of morphological characters is provided in Table S2. The ancestral character states are visualized as pie charts in Fig. 2.4 & 2.5 and the exact posterior probabilities calculated with Bayes Traits for each node can be found in Appendix 2.6. The reconstructions in Fig. 2.4 & 2.5 show that the a number of stamens between seven and 12, the presence of staminode, one series of stamen and the fasciculate/glomerate inflorescence are ancestral characters of *Casearia* with high probability (respectively BPP = 1, BPP = 1, BPP = 1 and BPP = 0.98 see Appendix 2.6). However, clade B3 with old Neotropical *Laetia* and *C. tremula* seemed to have gained an important number of stamens, as it has more than 12,. The analyses indicate that a plesiomorphic character for the clade is the presence of staminodes, but they are lost in some species of *Casearia* (formerly *Laetia*) and *Neoptychocarpus*. The fasciculate/glomerate state is also plesiomorphic for the genus, although *Euceraea* presents a paniculate inflorescence. The analyses indicate that more strongly ramified inflorescences are gained in this lineage and also in clade B4. The presence of pellucid dots on the leaves has been considered as a key character in the identification of *Casearia* species. However, our ancestral character state reconstruction (Fig. 2.4) shows the presence of pellucid dots not only in *Casearia* but also in *Lunania* and *Piparea*, indicating that it arose earlier than the divergence of the actual *Casearia* clade but was lost again in *Ryania*. Interestingly, the vast majority of *Casearia* species and all other species of the Samydeae are bisexual. However, the lineage of *Neoptychocarpus* evolved dioecy, and *Euceraea*, which also belongs to this lineage, has an unknown sexual system but it is suspected to be dioecious or androdioecious (Berry & Oslon, 1998). Contrary to the Samydeae, the other Salicaceae are largely dioecious, and dioecy apparently has originated early on (Fig. 2.4).

Chapter 2: Character evolution and biogeography of Casearia

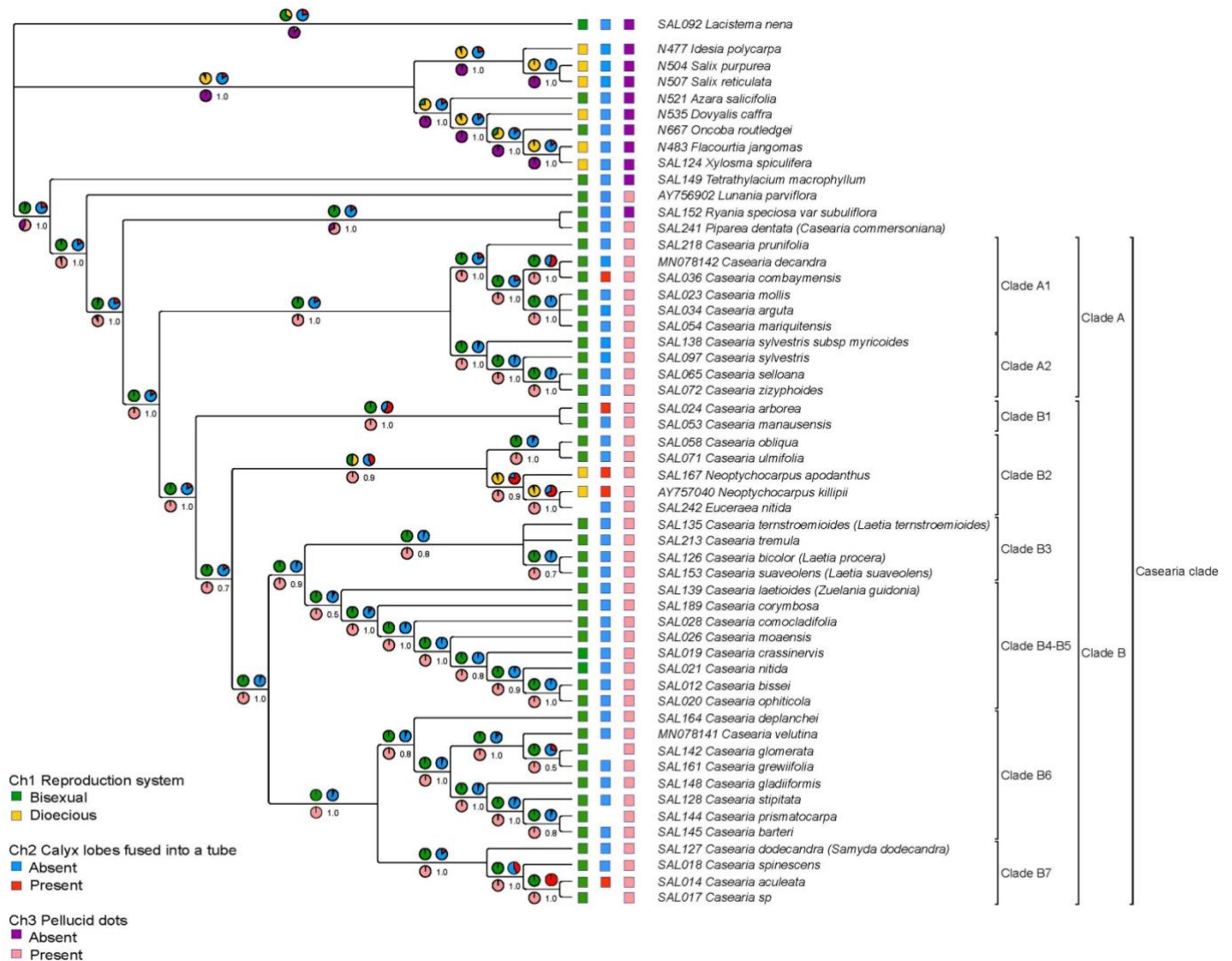


Fig. 2.4. Bayesian inference of ancestral state reconstruction of three morphological characters plotted on the Bayesian majority rule consensus tree. Reconstructed ancestral character state is represented as pie charts at the stem node. The legend indicates the state of each character. Squares indicate the state of character for each species, white squares represent missing data.

Chapter 2: Character evolution and biogeography of Casearia

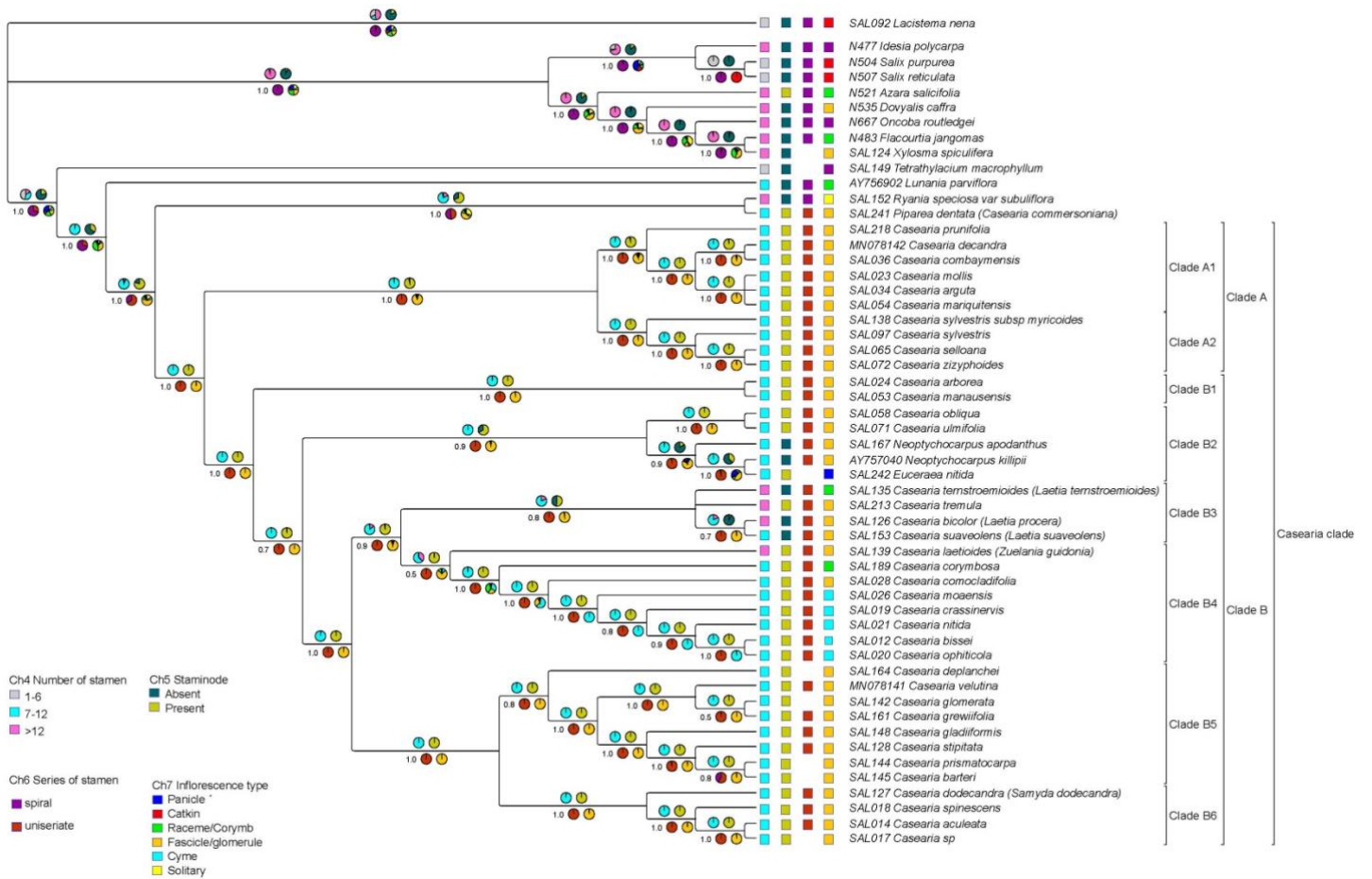


Fig. 2.5. Bayesian inference of ancestral state reconstruction of four morphological characters plotted on the Bayesian majority rule consensus tree. Reconstructed ancestral character state is represented as pie charts at the stem node. The legend indicates the state of each character. Squares indicate the state of character for each species, white squares represent missing data.

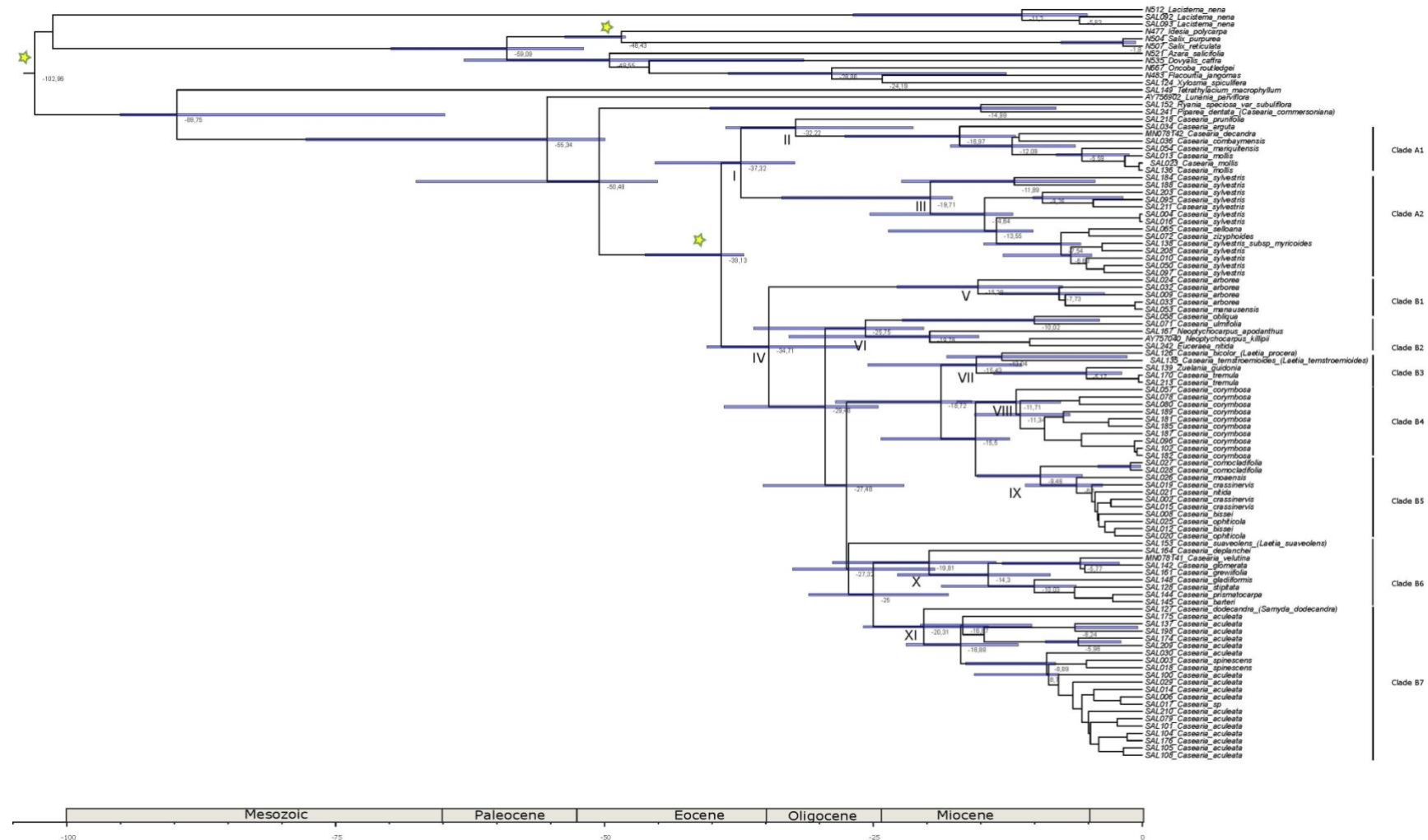
Chapter 2: Character evolution and biogeography of *Casearia*

2.4.5 Divergence time estimates

The crown group of the *Casearia* clade has an Eocene age of 39. Ma (95% HPD: 37.04 - 46.22), whereas the stem dates back to the Paleocene 50 Ma (95% Highest Posterior Density (HPD): 45.09 - 67.52; Fig. 2.6). The African/Asian clade (Clade B6) started to diverge from Neotropical ancestors in the Oligocene (25 Ma; 95% HPD: 18.01 - 31.01) and the crown age of the group is Miocene (20 Ma; 95% HPD: 13.6 -28.79, node XI). The crown group of Clade A (37 Ma 95% HPD: 32.32-45.29) is slightly older than that of clade B 34 Ma (95% HPD: 26.3-40.47). The most complex Caribbean clade (Clade B5) originated around 15 Ma (95% HPD: 12.32-24.28) from South American ancestors and its crown group started to diversify around 9 Ma (95% HPD: 5.57-15.35). The other Caribbean lineages are all younger. The precise ages estimated for all nodes can be found in Table S5.

Fig. 2.6. (next page): Maximum Clade Credibility (MCC) chronogram obtained in BEAST based on four plastid markers (*rps4-trnLF*, *trnK/matK*, *rpl16* and *petD*) with age estimate using three calibration points. Time interval is indicated in the scale in millions of years ago, yellow stars correspond to the calibration points. Grey bars represent 95% HPD intervals of the divergence times and the number above each node represents the median age of the Most Recent Common Ancestor (MRCA)

Chapter 2: Character evolution and biogeography of Casearia



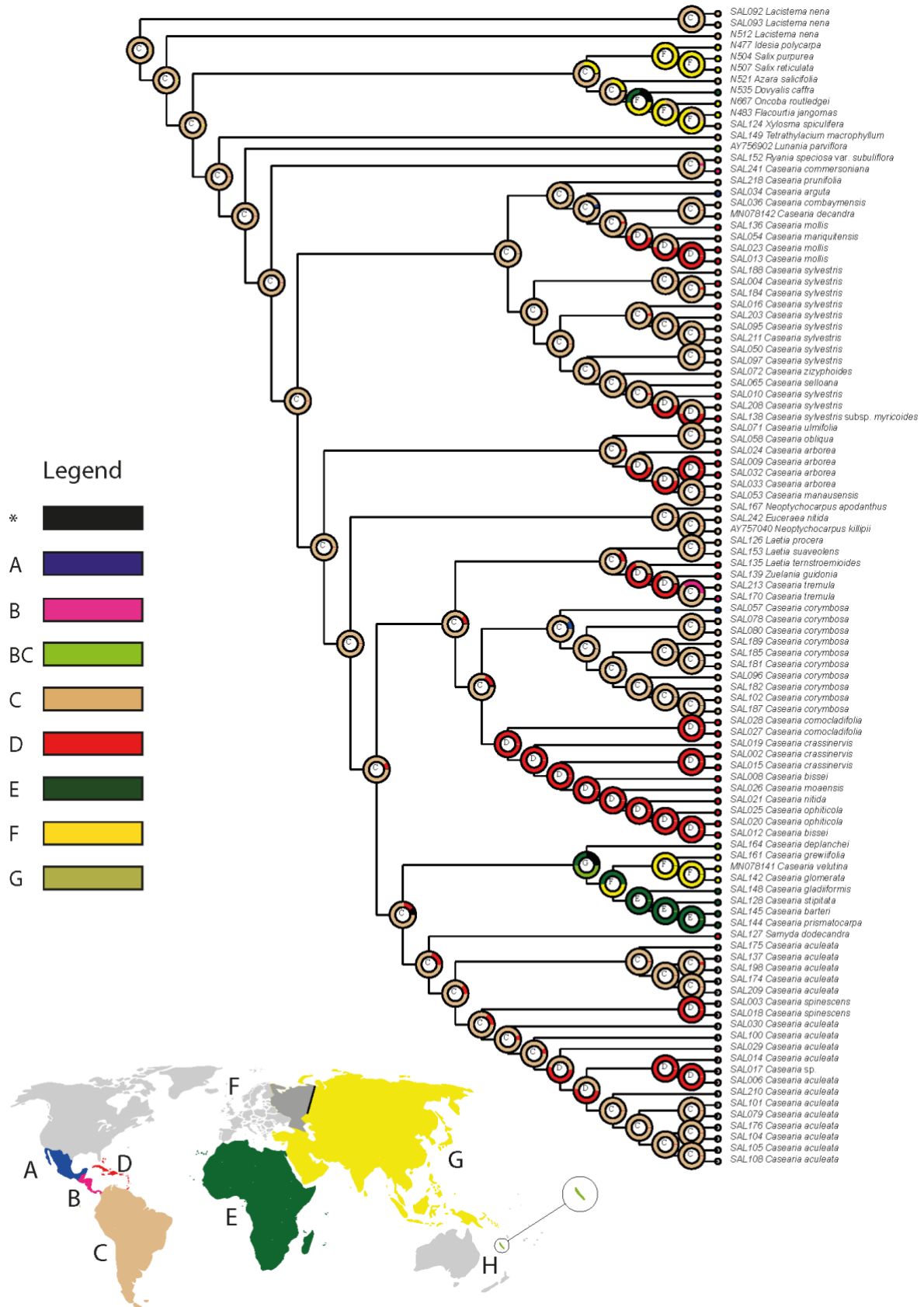
2.4.6 Ancestral areas

We found the BayArea model with founder speciation event (BAYAREALIKE+J) to be the most accurate model to reconstruct the ancestral areas of *Casearia* and its relatives. Table S6 shows the log-likelihood (LnL) values and likelihood ratio test (LRT) results across all tested models. The Samydeae including the *Casearia* clade originated in South America with multiple migrations to the Caribbean Islands and one towards the Old World (Fig. 2.7). The most comprehensive Caribbean clade (Clade B5) is sister to a lineage (Clade B4) composed of Colombian and Mexican samples of *C. corymbosa*, and these two clades are sister to a mixed Mesoamerican, Caribbean, South American (Colombia and GY) clade B3. Notably, the ancestral areas reconstructed (Fig. 2.7) are always in South America, indicating that the most recent common ancestors of species in the Caribbean islands came from there. Subclade B4 further shows *C. comocladifolia* from the Dominican Republic as sister to a lineage with endemic taxa from Cuba such as *C. bissei* or *C. ophiticola*, thus suggesting a single common ancestor for the Cuban species and an early split in *Casearia* diversification on different Caribbean islands soon after a Miocene (crown group age of 9 Ma of Clade B5) arrival. The Old World clade clearly has South American ancestors (Fig. 2.7) that apparently split into an African and into an Asian lineage at the beginning of their crown group diversification. The obtained probabilities for the respective ancestral areas in each node of the tree are provided in Table S7.

Fig. 2.7. (next page) Result of the Bayesian Binary Method (BBM) analysis for the ancestral area reconstruction obtained with RASP. The pie chart at each node gives insight into the ancestral geographic range at the different nodes, black represents other ancestral ranges.

Chapter 2: Character evolution and biogeography of Casearia

BAYAREALIKE+J results



2.5 Discussion

2.5.1 Phylogenetic relationships of *Samydeae*

With this investigation we were able to recover a well-supported *Samydeae* clade (PP: 1.00, BS: 100, JK: 99.9). This clade includes *Tetrathylacium*, *Lunania*, *Ryania*, *Piparea* and a more inclusive also well supported *Casearia* clade (Figs. 2.2 & 2.3). Our molecular trees therefore considerably advance the previously existing knowledge (Alford, 2005; Samarakoon, 2015) about phylogenetic relationships in this part of the Salicaceae. The *Casearia* clade includes not only the genera *Samyda*, *Laetia* and *Zuelania* that were recently merged into *Casearia* (Samarakoon & Alford, 2019) but also the neotropical genera *Euceraea* and *Neoptychocarpus*. The *Samydeae* are retrieved as sister to a well-supported clade (Fig. 2.2) comprising all other sampled genera of the Salicaceae with *Idesia* Maxim. and *Salix* L. in one subclade and *Azara* Ruiz & Pav., *Flacourtia* Comm. ex L'Hér., *Oncoba* Forssk and *Xylosma* in another. These findings are in line with the results of Chase & al. (2002), and Xi & al. (2012) depicting two major lineages within Salicaceae, although we did not sample *Scyphostegia* that appeared as sister to them. More recently, Li & al. (2019) inferred a lineage of *C. decandra* and *C. velutina* as sister to other Salicaceae in their maximum likelihood analysis of 63 plastid gene sequences, where other taxa of *Samydeae* were not included (Li & al., 2019). We retrieved *Tetrathylacium macrophyllum* Poepp. as sister to all other *Samydeae* with high support based on our combined plastid matrix and with all three inference methods (Fig. 2.2). This topology was also shown by Alford (2005) after combining *trnLF* and *ndhF* sequence data with his morphological matrix and *Lunania parviflora* Spruce ex Benth alone forming the second branch (Alford, 2005; his Fig. 2.8). Also *Ryania speciosa* Vahl and *Piparea dentata* Aubl. are here inferred as sisters, as third branch in *Samydeae* (Fig. 2.2) The *Casearia* clade, retrieved in our plastid tree with high support (PP: 1, BS: 100, JK: 100; Fig. 2.2), was also found in the combined morphological analysis by Alford (2005) with a JK value of 100%, although the internal relationships of the *Casearia* clade remained largely unresolved in his study. Now, we found *Samyda dodecandra* Jacq. as first branch of the well-supported subclade B7 of the *Casearia* clade in our plastid and ITS trees (Figs. 2.2 & 2.3). The segregate genus *Laetia* is monophyletic within the *Casearia* clade, with *L. ternstroemioides*, *L. procera* and *L. suaveolens* retrieved together, however in a low supported subclade B3, along with *Zuelania guidonia* (Sw.) Britton & Millsp. and *C. tremula* (Fig. 2.2). Thus, our results support the recent nomenclatural changes made by Samarakoon & Alford.

Chapter 2: Character evolution and biogeography of *Casearia*

(2019). However, *Casearia* still appears paraphyletic to *Euceraea* and *Neoptychocarpus*, which was retrieved with good support within the *Casearia* clade, in both the plastid and the nuclear trees (Figs. 2.2 & 2.3).

2.5.2 Phylogenetic relationships of *Casearia*

With the results of this study (Figs. 2.2 & 2.3) we present the most comprehensive species-level phylogeny of *Casearia* to date, sampling 37 currently accepted taxa. Within the monophyletic genus *Casearia* (including *Euceraea* and *Neoptychocarpus*), nine subclades are retrieved that are mostly consistent in composition when the plastid (Fig. 2.2) and ITS trees (Fig. 2.3) are compared. Relationships between these subclades are better resolved in the plastid trees than with ITS, probably caused by considerable homoplasy and even alignment uncertainty due to predominant indels in ITS at larger distances as also observed in other datasets (Fuentes-Bazan & al., 2012; Falcón & al., 2020). Subclades A1 and A2 are consistently supported as sister by plastid and ITS data, both comprising South American, Mexican and Caribbean Island taxa. The Palearctic species were retrieved together in a well-supported clade (subclade B6) nested among New World *Casearia*. Direct sister is subclade B7 including all samples of *C. aculeata* as well as *C. spinescens* from Cuba and *C. dodecandra* (formerly *Samyda dodecandra*) branching first. The subclade B5 with species from the Caribbean islands is sister to *C. corymbosa*, a species very common in the Caribbean part of Colombia but also distributed in Meso- and South America. Subclade B5 is constituted of species that were informally called the Ilicifoliae group defined by Sleumer (Sleumer, 1980) together with one new species from Cuba, *C. bissei* that are morphologically different from other *Casearia* species by forming thick coriaceous and mostly spiny leaves and pink or white flowers (Fig. 2.1). The Ilicifoliae group is endemic to Hispaniola and Cuba with *C. comocladifolia* occurring on the coast of Cuba and Hispaniola (Gutiérrez, 2000) as sister to a lineage of Cuban serpentine endemics (*C. bissei*, *C. crassinervis*, *C. moaensis* and *C. ophiticola*). Although *C. nitida* is not in the Ilicifoliae group sensu Sleumer, Gutiérrez (1998) already suggested its affinity with it, which is confirmed by the molecular results. The well supported serpentine clade is in line with what has been found in other flowering plant genera such as *Buxus* (Gonzalez Gutierrez, 2014) or *Phyllanthus* (Falcón & al., 2020). In these cases the serpentine adapted species often also differ by coriaceous and smaller leaves from their next relatives growing on limestone (Brady & al., 2005; Anacker, 2014). The typical section

Chapter 2: Character evolution and biogeography of *Casearia*

Casearia with *C. nitida* as type species is paraphyletic to the former segregate genera *Laetia*, *Samyda* and *Zuelania* and also to *Euceraea* and *Neoptychocarpus*. The section *Guidonia* with the type species *C. spinescens* appears to be very closely related to *C. aculeata* and is nested within the *Casearia* section, as is the monotypic sect. *Endoglossum* with *C. tremula*. Also, subclade A1 with *C. mollis* Kunth, *C. prunifolia* Kunth and relatives belongs to sect. *Casearia*, as currently classified, so that sect. *Crateria* with *C. sylvestris* and relatives becomes deeply nested in sect. *Casearia*. Thus, the currently used sectional classification (Sleumer, 1980) is highly artificial.

Some reticulation or incomplete lineage sorting becomes evident by comparing plastid and nuclear ITS topologies. Apparently, this only applies to individual taxa or samples within terminal subclades such as *C. spinescens* from Cuba, nested among samples of *C. aculeata* in the plastid tree (B7, Fig. 2.2), whereas it is sister to *C. aculeata* in ITS (Fig. 2.3). At this level speciation is still ongoing with some probability that our dichotomous trees do not fully describe evolutionary relationships, but also that an even more complete sampling of individuals and populations across the range of species will yield further insights.

2.5.3 Evolution of morphological characters and the circumscription of *Casearia*

The ancestral character state reconstruction showed that the crown group of the *Casearia* clade (including the segregate genera *Euceraea*, *Laetia*, *Neoptychocarpus*, *Samyda* and *Zuelania*) is marked by a number of character state transitions. Several of the states are almost unique or completely unique to the members of this clade and thus support the corresponding monophyletic circumscription of *Casearia*. The pellucid dots on the leaves (Fig. 2.4) is a useful character to recognize *Casearia* in the field. However, the results of our analysis show that it is not a synapomorphy for the genus. Pellucid dots already evolved before the divergence of *Lunania* although they were lost in *Ryania* (Fig. 2.4). Fasciculate and glomerate inflorescences are almost a synapomorphy of the *Casearia* clade within the *Samydeae*, although corymbs and cymose inflorescences respectively present in *C. corymbosa* and Cuban endemic species are derived from a fasciculate state. The first independently gained in *Casearia corymbosa* and *C. (= Laetia) ternstroemioides*, and the cymes within the Caribbean subclade B4 (Fig. 2.5). The presence of one series of stamens is also almost a

Chapter 2: Character evolution and biogeography of *Casearia*

synapomorphy for the *Casearia* clade, although it got lost again in the *Neoptychocarpus* sublineage. *Laetia* and *Samyda* were recognized as distinct from *Casearia* and long accepted as separate genera on the basis of a few characters such as the absence of staminodes and a higher stamen number (Warburg, 1895; Sleumer, 1980; Samarakoon, 2015). However, our ancestral character state reconstruction shows that the presence of staminodes is homoplastic as they were lost two times, both in *Neoptychocarpus* and in *Laetia* (Fig. 2.5; the species *C. bicolor* (= *L. procera*), *C. (=L.) suaveolens* and *C. (=L.) ternstroemioides* in clade B3). The position of *C. tremula* in clade B3 is not resolved so that no conclusion is possible whether staminodes were re-gained in *C. tremula* or lost after its divergence. Furthermore, the stamen number is also homoplastic as it increased independently in subclade B3 (*C. tremula*, *C. bicolor* (= *L. procera*) and *C. (=L.) ternstroemioides* and in *C. laetioides* (= *Z. guidonia*) which are deeply nested in *Casearia*. The genus *Zuelania* can therefore not be distinguished from *Casearia* based on a higher number of stamens (de la Sagra, 1845; Sleumer, 1980). *Neoptychocarpus* is a South American genus with three species. It was first described by Buchheim (1959) and separated from *Casearia* for being dioecious, having the calyx lobes fused into a tube in addition to lacking staminodes, however, the transition from bisexual flowers to a dioecious arrangement of unisexual flowers is frequent in flowering plants (Renner & Ricklefs, 1995). Within Neotropical Samydeae, dioecy is only present in *Neoptychocarpus* and is also suspected to occur in the genus *Euceraea*, although its mode of reproduction remains unclear (Berry & al., 1998). Two Old World Samydeae, *Osmelia* and *Pseudosmelia* also are dioecious (Sleumer, 1956; Alford, 2005) The transition from free to fused calyx lobes happened multiple times in the evolution of the *Casearia* clade, so apart from *Neoptychocarpus* in *C. arborea*, *C. combaymensis* Tul. and the *C. aculeata*-*C. spinescens* lineage. Finally, some *Casearia* species (formerly *Laetia*) also lack staminodes but this is a secondary loss (Fig. 2.5). Therefore, both morphology and the molecular phylogeny support the inclusion of *Neoptychocarpus* into *Casearia*. *Euceraea* is a South American genus of three species, first described by Martius (1831) and separated from *Casearia* for having a paniculate inflorescence, four perianth parts and a sessile stigma (Sleumer, 1980; Berry & Olson, 1998). However, like *Casearia* it possesses pellucid dots on the leaves, has eight stamen and staminodes. Individuals of *Casearia* can present four sepals, the paniculate inflorescence has been independently gained in the taxon and other species also present a sessile stigma such as *C. laetioides* (= *Z. guidonia*). Therefore, both morphology and the molecular phylogeny support the inclusion of *Euceraea* into *Casearia*. The taxonomical changes will be made in a coming publication.

2.5.4. Biogeography of the pantropical genus *Casearia* at a continental level

The Salicaceae and the Samydeae are part of the rapid radiation of the Malpighiales that started in the Cretaceous (Davis & al., 2005). The origin of the Samydeae here estimated as 102 Ma (95% HPD: 86.05-102.08 stem) and 90 Ma (95% HPD: 64.86-95.04, crown) falls into a time when the breakup of Gondwana could still have resulted in vicariant biogeographic patterns. The Samydeae clade is unambiguously South American in origin (Fig. 2.7). Our ancestral area reconstruction infers this even for the Salicaceae, although additional taxon sampling will be necessary to better understand the diversification in the other tribes of Salicaceae. Apparently, there was no migration into or out of South America within the Samydeae at Gondwanan times. The *Casearia* clade started to diversify during the Eocene (40 Ma, 95% HPD: 37.04-46.22, crown group age), and from the perspective of the diversification of the pantropical genus *Casearia* it is noteworthy that there is a sole Old World subclade (B6, labelled as node X) that diverged from Neotropical ancestors at the Oligocene/Miocene boundary (stem age 25 Ma, 95% HPD: 18.01-31.01). In our trees the crown group of the Old World subclade is split into an African and Asian lineage at 14 Ma (95% HPD: 8.55-22.76). Although our estimation of the crown group age may be slightly too young, considering that a denser sampling of species from this subclade may break down the rather long stem, it can be considered as Miocene with confidence (Fig. 2.7).

Casearia therefore shows a clear pattern of a South American ancestral area, from where migration or dispersal must have occurred towards Africa and Asia. There are two main hypotheses. One is migration across Laurasia via a series of connections that may have acted as a huge bridge (the “North Atlantic Land Bridge”) for plant migrations, at a time with Eocene paratropical climates (Tiffney, 1985), considering that the breakup of Gondwana started in the Southern hemisphere. Such as scenario was assumed for Malpighiaceae by Davis & al. (2002), supported by fossils found in North America and Europe. Our case of the late Oligocene/early Miocene stem age (25, 18-31 HPD) of the Old World clade (B6) of *Casearia* is at the verge of supporting a scenario of Laurasian migration or being too young. The split into an African and an Asian sublineage of the Old World subclade of *Casearia* could be consistent with ancestors having migrated eastwards, first reaching Africa and then Asia. However, considering that the so far sampled African and Asian species of *Casearia* are resolved into two sister clades, any further conclusions on the directionality based on the sampling of this investigation are limited. It is noteworthy that the New Caledonian *C.*

Chapter 2: Character evolution and biogeography of *Casearia*

deplanchei is sister to the African plus Asian clade (Figs. 2.2, 2.3) and has diverged already in the early Miocene (stem age of 19.8 Ma, Fig. 2.6), whereas the African-Asian split of the crown group occurred much later (14.3 Ma). It is therefore questionable whether *C. deplanchei* represents a “Gondwanan relic” or an arrival from other continents after the breakup of Gondwana, additional sampling in particular of SE-Asian species of *Casearia* would be required, considering that New Caledonian biota have debated origins (Pillon, 2012).

There are other plant groups for which South America is the ancestral area, such as the Solanaceae (Dupin & al., 2017). In that case, many dispersal events from South America to other continents were dated to have occurred well after the breakup of Gondwana, starting at the end or later than the Oligocene, mostly into Central and North America. While the authors do not reject a migration through Beringian (Dupin & al., 2017), they favour a transoceanic long distance dispersal due to the variety of fruits from dry to fleshy that can easily be transported through currents or migrating animals. Contrary to the Solanaceae that include a large number of taxa growing in temperate climates, a migration of *Casearia* via the Beringia land bridge does not seem to be likely in *Casearia* which is exclusively constituted by tropical shrubs and trees, for which the climate probably was too cold. There are other cases in which plants from the Neotropics migrated to the Old World, through long-distance dispersal as in the African *Tragia/Tragiella* lineage, (Euphorbiaceae) (Cervantes & al., 2016) or the *Cissus trianae* clade (Vitaceae) (Rodrigues & al., 2014). Long distance dispersal is also considered to explain the relatively recent origin of Neotropical Acanthaceae from Old World ancestors (Tripp & McDade, 2014) and it is another hypothesis for *Smilax* and Solanaceae (Zhao & al., 2013; Dupin & al., 2017) or *Phyllanthus procerus* and relatives (Falcón & al., 2020). *Casearia* fruits are small and fleshy, their dispersal by birds is therefore a possible dispersal mechanism given the colourful arils (Howe & al., 1977; Howe & Primack, 1975).

2.5.5 Biogeographic relations between the Caribbean islands and adjacent mainland

The largest Caribbean subclade with mostly Cuban endemics (e.g., *C. crassinervis*, *C. ophiticola*) and the Dominican *C. comocladifolia* started to diversify during the late Miocene (9 Ma, 95% HPD: 5.57-15.35, Figs. 2.6 & 2.7). Studies on other genera, which comprise endemic Caribbean subclades, also found similar divergence times of their crown groups

Chapter 2: Character evolution and biogeography of *Casearia*

(Appelhans & al., 2012; Filipowicz & Renner, 2012; Cervantes & al., 2016; Machado & al., 2018). Indeed, during the late Miocene-Pliocene, the islands were separating from each other, which very likely triggered speciation (Alonso & al., 2012). Whereas Santiago-Valentín & Olmstead (2004) summarized that most of the mainland areas adjacent to the Caribbean islands could have been places of origin for the ancestors of island taxa, some better resolved and supported phylogenetic trees point to South American origins as in *Brunfelsia* (Filipowicz & Renner, 2012), which has not reached Mesoamerica, and *Philodendron* (Canal & al., 2019). However, Cervantes & al. (2016) showed through their biogeographic analysis of the subfamily Acalyphoideae (Euphorbiaceae), a speciose group of flowering plants on the Caribbean islands and as well on all adjacent mainland, that multiple colonization events from Mexico and Mesoamerica to the islands occurred since the Miocene

In the case of *Casearia*, our results depict multiple migrations of the genus towards the Caribbean from South America, followed by speciation within the islands, especially Cuba and Hispaniola. The Caribbean clade is sister to *C. corymbosa*, here represented by several samples from Colombia and one from Mexico (Fig. 2.2). Due to the current sampling, the origin of the Caribbean *Casearia* clade is inferred as South American with the only Mexican individual appearing as sister to a Colombian clade. Our divergence time estimate indicates that stem nodes relevant for the split of Caribbean island lineages are not older than 12 to 15 Ma (Fig. 2.6). This also the case for the shallow clade with *C. mollis* from Cuba and *C. mariquitensis* Kunth from Guyana, that are sister to the *C. arguta* from Mexico (Figs. 2.2 & 2.3, clade A1). Further sampling of individuals within widespread species and Mesoamerican-Mexican taxa will be needed to test if the ancestor of the Cuban-Hispaniolan *Casearia* clade B5 in the Miocene really arrived from the South American continent and to better resolve relationships in clade A1.

On the other hand, the stem and crown of the Caribbean subclade B5 are far too young to assume a migration via a GAARlandia land bridge, that was advocated to have existed in the early Eocene ca. 40 Ma (Iturralde-Vinent, 1999). The debate if such a land bridge existed and if it facilitated the direct migration of plants to the Caribbean islands from South America is still ongoing (Nieto-Blázquez & al., 2017; Roncal & al., 2020), and our results add further evidence of Caribbean plant migrations that do not support the GAARlandia hypothesis.

Contrary to earlier ideas, the closure of the isthmus of Panama is often reported as early as Miocene (Bacon & al., 2015; Cervantes & al., 2016; Sosa & al., 2018) and could have facilitated the subsequent crossing of relatively short marine distances.

Chapter 2: Character evolution and biogeography of *Casearia*

The timing and extent of this American Biotic Interchange is therefore relevant for Caribbean *Casearia* as a potential migration route rather than arrivals on Caribbean islands directly from South America. About 24% of *Casearia* species occur in Mesoamerica and Mexico, with eight species occurring only in that area (e.g., *C. bartletii* Lundell, *C. elegans* Standl., *C. williamsiana* Sleumer). However, these are still underrepresented in our taxon sampling. Looking at widespread species, there is more taxa shared only between South America and the Caribbean islands than taxa shared only between Mesoamerica and the Caribbean. Our analysis includes two widely distributed species of *Casearia*, namely *C. aculeata* and *C. sylvestris*, which occur on most of the Caribbean Islands, in southern Mexico, Mesoamerica and large parts of South America (GBIF.org, 2020). The split into the respective lineages containing these species was inferred to have occurred 20 Ma (95% HPD: 14.28-25.95, stem age, Fig. 2.6) and 37 Ma (95% HPD: 32.32-45.29, stem age, Fig. 2.6), respectively.

Our current ancestral area reconstruction (Fig. 2.7) identifies South American ancestors for the sampled Caribbean plants. Whereas the existence of multiple migrations between mainland and Caribbean islands is suggested by our data, further analyses are required to understand the precise patterns, also because the currently applied species concepts appear to be very wide, with multiple heterotypic synonyms in both of these species (Sleumer, 1980; WFO, 2021).

Our gene trees do not entirely correspond to current species circumscriptions, which may indicate incomplete lineage sorting and reticulate speciation. Another explanation may be that the currently accepted taxa based on few deviating morphological characters (alpha-taxonomy) do not reflect meaningful biological entities. Interestingly, Cuba has a morphologically well-defined endemic subspecies *C. sylvestris* subsp. *myricoides*, found on serpentine soil (Gutiérrez, 2000), which appears nested within the *C. sylvestris* subclade, although it is distant from Cuban samples of *C. sylvestris* subsp. *sylvestris*. Interestingly, the individual of *C. arborea* from Jamaica is found sister to the plant from Colombia in our ITS tree (Fig. 2.3) but further sampling of this widespread species also from the lesser Antilles and Mesoamerica as well as phylogeographic methods applied to species complexes within *Casearia* will be needed to illuminate their biogeographic history, which is likely to include more recent dispersals in addition to migration events in the Miocene. Considering that the majority of endemic Caribbean species belongs to more widespread and not endemic genera, further detailed analyses of such bigger genera will be instrumental to obtain a full picture of the evolution and diversification of Caribbean plants in time and space.

2.5.6 Implications for species delimitation

Our molecular phylogenetic results reveal the need to clarify species limits within *Casearia*, as some species were retrieved paraphyletic to other species currently accepted. This regards to the widespread *C. sylvestris* in subclade A2 that is one of the most common species of the New World in the currently accepted species classification, ranging from Argentina and Uruguay to Mexico and to all Caribbean islands. *C. sylvestris* is retrieved paraphyletic to two South American taxa: *Casearia selloana*, the type of which is from Bahia, Brazil, and which was already considered to be a possible variant of *C. sylvestris* in very dry habitats (Sleumer, 1980).

The second taxon is *Casearia zizyphoides* that was originally described from Venezuela (where our sample is from) but was also reported from Trinidad and Tobago and was considered a dry adapted relative of *C. sylvestris* (Sleumer, 1980). It can be morphologically distinguished by the mucronate leaves and the simple style (branched in *C. sylvestris*). It should be examined in more detail if the individuals morphologically matching *C. zizyphoides* are closely related to the populations of *C. sylvestris* subsp. *myricoides* that occur as xerophytic shrubs over serpentine in Cuba (Gutiérrez, 2000), given that they appear closely related in our ITS trees, albeit without statistical support.

Another species retrieved as paraphyletic is *Casearia arborea*, a widely distributed species from Mexico to Northern Argentina, including the Caribbean islands. It is retrieved together with *C. manausensis*, described in 1980 and so far only reported from Manaus, Brazil (Sleumer, 1980). It appears in the same group of *C. arborea* and is morphologically very similar. Its leaves differ in being hirsutulous beneath at the midrib and lateral nerves and *C. arborea* leaves are reported to be entirely glabrous. We also retrieved a *C. aculeata* clade including *C. spinescens* in the plastid trees (Fig. 2.2), whereas *C. spinescens*, a widespread species here represented by two Cuban samples, appears as sister to all other samples from *C. aculeata* (Caribbean islands, Colombia and Ecuador) in the ITS trees (Fig. 2.3). The topological differences between plastid and nuclear trees may indicate plastid capture in *C. spinescens* and warrant the addition of further material matching the morphotype of *C. spinescens* to test if this evolved once or if the less numerous flowers in the inflorescences of *C. spinescens*, the smaller fruits compared to *C. aculeata* and a different distribution of spines on the plant (Gutiérrez, 2000; Sleumer, 1980) are more an adaptive homoplastic trait. *Casearia aculeata* is a widespread species that has more than 20 synonyms and was first

Chapter 2: Character evolution and biogeography of *Casearia*

described by Jacquin (1760) from a plant collected in Haiti. No authentic specimen is known for this species and a lectotype was later designated by Sleumer (Sleumer, 1980) as an illustration from Plumier (Plumier, Pl. Am. ed. Burman, p. 138, t. 147, f. l. 1757).

2.7 Conclusion

We presented here the most comprehensive study to date of the tribe Samydeae and more precisely of *Casearia*, based on five molecular markers from plastid and nuclear DNA. Samydeae was retrieved as a well-supported clade as was a *Casearia* clade with nine subclades and *Neoptychocarpus*. The combination of rapidly evolving plastid genomic regions with high levels of hierarchical phylogenetic signal resulted in an overall well resolved and supported phylogenetic tree of the Samydeae. Considering that the topology is largely consistent with the trees inferred from nuclear ITS, our study provides the first picture on the evolution of *Casearia* and relatives through time and space. Our study unravelled that some of the currently accepted taxon concepts at species level are in conflict with a more evolutionary based delimitation of these species, in particular of the taxa considered to be more widespread with ranges shared between the Caribbean islands and Mesoamerica, Mexico and South America. Further work is needed that uses a geographically representative sampling within these taxa, and employs further molecular markers to increase resolution within shallow terminal clades and also network analyses. Our inference of ancestral areas underscores the importance of both a dense taxon sampling and a thorough knowledge of species-level taxonomy to illuminate the origin of the Caribbean flora and its biogeographic relationships. We have used an approach where the geographic origin of each specimen included in the molecular trees was coded, and thus were able to avoid bias that could have been introduced by extrapolating distributions of taxa without prior clarification of species limits. Our study shows once again that migrations between the Caribbean islands and adjacent mainland have been frequent within genera since the Miocene, and that including or not including of some species may be fundamental to correctly infer to geographic origin of the Caribbean flora.

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

evidence for synonymy or emerging lineages?

3.1 Summary

Using molecular phylogenetic data of the genus *Casearia*, the potential status of so-called nested singletons was investigated. Nested singletons are single or few specimens corresponding to species currently accepted based on deviating morphological features but appearing as nested within clades of individuals of a related species. It is assumed that incomplete lineage sorting could have led to a nested placement. In that case the taxon represented by a singleton should exhibit a limited distribution range relative to the species depicted as paraphyletic and a significant degree of phenotypic and/or ecological differentiation. If these criteria are not fulfilled, the name of nested singleton should be considered a synonym.

To that end, the nested and the including taxa were compared in terms of phenotypic distinctiveness, ecological differentiation, and distribution ranges. A reference phylogeny was established, based on the *trnK/matK* and *rps4/trnLF* regions and reconstructed by means maximum likelihood, based on 124 accessions, representing 65 species. The present study focuses on the following cases of nested singletons: *C. grandiflora* and *C. manausensis* nested within *C. arborea*; *C. mariquitensis* vs. *C. mollis* and *C. selloana* and *C. zizyphoides* nested within *C. sylvestris*. For these species, voucher specimens were selected, following established taxonomic concepts, including those sequenced when accessible. For a total of 200 specimens, PCA and cluster analysis were performed to analyse phenotype differentiation, based on a morphomatrix of 10 characters traditionally used as diagnostic characters in taxonomic treatments. Niche space differentiation was calculated based on bioclim variables and using specimen geocoordinates, by means of cluster analyses and niche equivalency and similarity tests. Finally, the distribution ranges were mapped.

The potential statuses of five cases of nested singletons were resolved, including a range of possible outcomes. *Casearia grandiflora* appears to be a recently emerging species

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia

nested within *C. arborea*, with some degree of morphological and ecological differentiation. A very recently emerging lineage appears to be *C. manausensis*, nested within *C. arborea*, also with some level of morphological and ecological differentiation, but in both cases quite narrow, reflected by the narrow range within the broad area of *C. arborea*; in this case, *C. manausensis* is perhaps best recognized at subspecies level. While *C. selloana* and *C. zizyphoides*, both nested within *C. sylvestris*, also exhibit a narrow range compared to the latter, they exhibit little morphological and ecological differentiation relative to the latter and may represent synonyms or at best be recognized at the level of variety. In one case, the absence of discernable morphological, ecological, and biogeographical differentiation, suggest potential synonymy, namely *C. mariquitensis* with *C. mollis*.

3.2 Introduction

Delimiting plant species is a challenging task, both in practical terms regarding a sufficient sampling of characters and individuals and with respect to considering the different kinds of species concepts that range from a morpho-species concept to concepts reflecting complex speciation mechanisms in plants (Comes, 2004; Naciri & Linder, 2015). In general, speciation can be allopatric through geographical isolation (vicariance) or sympatric through ecological differentiation (Van Valen, 1976; Colinvaux & al., 2000; Rundle & Nosil, 2005). Allopatric speciation has been reported to occur in many plants groups, like in *Carex* L. (Cyperaceae) (Maguilla & al., 2017), *Iberodes* M. Serrano, R. Carbajal & S. Ortiz (Boraginaceae) (Otero & al., 2019), *Piofontia* Cuatrec. (Asteraceae) (Vargas & Simpson, 2019), Primulaceae (Boucher & al., 2016) and *Ranunculus* L. (Ranunculaceae) (Tomasello & al., 2020), among others. On the other hand, sympatric isolation is rare in plants and only few cases have been reported. On Lord Howe Island, sympatric speciation has been shown to have occurred in the palm genus *Howea* Hook. f., where two species formed through genetic isolation in sympatry (Savolainen & al., 2006; Babik & al., 2009). The same phenomenon was observed in other plant groups on the same island (Papadopulos & al., 2014). Sympatric speciation in plants is often reported in cases where it is driven by allopolyploidy (Rieseberg & Willis 2007, Weiss-Schneeweiss & al. 2013), like in cryptic species of the aquatic angiosperm *Najas* L. (Les & al., 2015), or the genus *Androsace* L. (Primulaceae, Dixon & al.,

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

2009). The process of speciation in flowering plants frequently involves incomplete lineage sorting, when not all alleles of the gene or haplotypes of organellar genomes occur consistently throughout the genomes of all individuals of a species (Avice, 2000). In that case, the respective differing genotypes are usually concentrated in certain parts of the geographical range of a species and may also lead to different morphological or physiological traits that affect the fitness of the respective individuals (Montalvo & Ellstrand, 2001; Bucharova & al., 2017). Moreover, hybridization and introgression may occur between different species or also genotypes, when isolation barriers such as geographical isolation or reproductive isolation through different flowering times breaks down, e.g. as a consequence of plant migrations or shifts in climatic and other environmental factors. Hybridization and introgression involve a transfer of genetic material between different species. In plants, the resulting offspring may exhibit different levels of fertility. Depending on the parent species involved, the hybrids may possess reduced fertility or not, and hybrids may possess altered or new traits, sometimes being more competitive than their parents (Rieseberg & Willis, 2007). In some cases, this may lead to hybrid speciation without any change in ploidy level (Abbott & al., 2010; Nieto Feliner & al., 2017), or unreduced gametes form fertile allopolyploids. In real data sets, incomplete lineage sorting is not easy to distinguish from introgression and hybridization (Holland & al., 2008; Joly & al., 2015), in particular if molecular phylogenetic trees are incompletely resolved and/or only few loci were sequenced or sequence data are just available for single genomic compartments, thus posing challenges to illuminating species limits.

Historically, plant species have been defined on the basis of the phenotype, particularly using diagnostic morphological characters shared among the individuals presumed to belong to a so-defined species. Such an alpha-taxonomic approach applies a morpho-species concept (Stuessy, 2009), and has been implemented by the taxonomic community since the raise of formal species descriptions and naming with binomials in the mid of the 18th century (Linnaeus, 1753). Later on, since the 1960ies discrete quantitative and qualitative characters were measured and observed and entered into matrices that were subjected to analyses with multivariate statistics in order to obtain entities that could be classified as species based on a more representative set of characters (Sneath & Sokal, 1962, 1973). However, such an alpha-taxonomic approach still faces challenges, as often the number of characters that can actually be used is limited (Scotland & al., 2003), and the frequent convergent evolution of characters and states is hard to detect. Following the advent of phylogenetic systematics (Hennig, 1950, 1966), which provided a method to infer ancestor-

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

descendant relationships and thus to reconstruct the history of species diversifications, DNA sequence information became a widely used tool to delimitate species with evolutionary methods (Hillis, 1987). An undeniable advantage of molecular methods is that they allowed the study of an ever increased number of characters, thus greatly improving the resolution when investigating species limits. It boosted the application of biological and phylogenetic species concepts that have to be tested for by methods of molecular phylogenetic and evolutionary biology, as a basis for the development of a genealogy-based classification.

Nowadays, plant taxonomy is in a transition phase from alpha-taxonomy to evolutionary approaches, in which species are formally classified and named subsequent to inferring the corresponding distinct biological entity, usually including molecular methods (Borsch & al., 2015). This transition phase is also evident in mixture of taxa in current classification systems, at the genus and even more so at species level, for which a morpho-species concept still forms the basis of many of the currently used taxa. In an ongoing process, species limits and the corresponding taxon concept at species level are tested and eventually adjusted, which frequently leads to accepted names becoming synonyms, species merged as synonyms becoming resurrected, or even species new to science being described upon a proper assignment of the known individuals to biologically sound taxon concepts at species level (Berendsohn, 1995b).

DNA sequencing has in many cases challenged hitherto-used taxon concepts at species level, either unveiling that molecular phylogenies do not agree with the morphology-based classification as evident by terminal clades with samples identified with one species name contain also samples identified with other currently accepted names. Alternatively, the use of DNA can unravel instances of cryptic speciation, when entities that share the same morphological character states are found to be phylogenetically distinct (Simpson, 1951; Fišer & al., 2018).

In order to reconcile molecular-based phylogenies with phenotype characters integrative taxonomy has recently emerged as a principal approach, considering also ecological data (Benoît, 2005; Will & al., 2005; Padial & al., 2010; Pante & al., 2015; Schlick-Steiner & al., 2010). The need to include morphological, cytological and ecological data into the analysis of species limits is further underscored by the fact that species of even the same genus may considerably differ in their infraspecific phylogenetic structure, which becomes more and more evident when multiple individuals from different populations throughout their geographic range are included into phylogenetic analyses (Borsch & al.,

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia

2018). A fundamental principle is to generate specimen-based character data (Kilian & al., 2015) that can allow precise testing of the placement of individuals (individual specimens) as subjected to different inference methods. Recent examples where an integrative taxonomic approach led to new insights into species limits, and subsequently to altered taxon concepts at species level include the genus *Rhodiola* Lour. (Crassulaceae), where the use of combined phylogenetic, morphometric and ecological niche data led to a reduction in the number of species from seven to three (Li & al., 2019b). In the *Stenocereus griseus* (Haw.) Buxb. species complex (Cactaceae), the use of genetic, ecological and morphological data revealed one new species (Alvarado-Sizzo & al., 2018). However, such approaches are still few.

A particular, but often encountered challenge for species delimitation resulting from molecular phylogenetic trees is the nested placement of individuals from hitherto accepted species within clades composed by individuals of another species, defying the concept of reciprocal monophyly. Indeed, the occurrence of paraphyletic species, often connected to still incompletely sorted out lineages of the ancestral species, and thus giving rise to a nested species is now widely accepted (Crisp & Chandler, 1996; Hörandl & Stuessy, 2010; Carnicero & al., 2019; Kato & al., 2019). However, in real examples of phylogenetic trees including singletons, i.e. species represented by a single terminal, these appear within shallow terminal subclades with limited internal resolution, so that also the possible paraphyly of the more widespread species needs to be further tested, such as with *Bouteloua vaneedenii* Pilg. (Poaceae) a singleton retrieved within the *B. curtispindula* (Michx.) Torr. lineage (Siqueiros-Delgado & al., 2013), or in the case of *Metaxya rostrata* (Kunth) C. Presl. (Metaxyaceae) (Cárdenas & al., 2016), as well as in *Piresia* (Poaceae) (Carvalho & al., 2021). Once a dense sampling of individuals has revealed such cases, a sufficient character base, both molecular and morphological, will be needed to yield well resolved trees and to properly assess species limits.

However, trees obtained as a result of phylogenetic and taxonomic research often include singletons, either due to rarity of the corresponding taxon or due to difficult access to suitable material. Also, the needed phylogenetic or phylogenomic analyses to fully explore species limits are in many cases not easy to implement, due to limitations in time, capacities and resources, and this often would require even higher quality material. On the other hand, for conserving and managing species diversity, there is the need to arrive at the best quality taxonomic treatment at the earliest point in time (Vogel Ely & al., 2017; Supple & Shapiro, 2018; Stanton & al., 2019), and overcome the phylogeny to classification gap (Mayo & al.,

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

2008; Hinchliff & al., 2015). Nevertheless, in some cases, taxonomic conclusions are made straightforwardly, such as in *Astragalus* L. (Leguminosae), where *Astragalus sciureus* var. *subsessilis* Bornm. was retrieved nested within *Astragalus kohrudicus* Bunge and the two were therefore synonymised, as morphology also support such a change (Bagheri & al., 2016). Another possibility to assess the status of those nested singletons is to apply an integrative taxonomy approach in extending the sequence data set by further samples from other geographic areas, thus broadening the sampling of hitherto not yet sequenced material that was identified using morphology, and by adding new morphological, ecological and distributional data.

In the approach developed here to investigate the taxonomic status of nested singletons, it was assumed that recently diverging species may show a lack of genetic differentiation compared to phenotypic and/or ecological differentiation, particularly in the markers used to reconstruct the underlying phylogeny (Lexer & Widmer, 2008; Ravinet & al., 2017). In lieu of additional sequenced specimens, the potential status of nested singletons can therefore be assessed using four criteria: emerging branch length (Pons & al., 2006); phenotypic differentiation; ecological differentiation; and distribution range (Thompson & al., 2005). For a nested singleton to represent a separate species, one would then postulate that at least one of four criteria apply: (1) a longer branch length than the terminals of the including species, (2) some level of phenotypic and/or (3) ecological differentiation (assessed based on additional specimens corresponding to the underlying taxonomic concept), and/or (4) that the nested species either has a narrow distribution range or a different distribution compared to the including species, i.e., allopatry, parapatry or peripatry.

Here, these assumptions are tested based on nested singletons detected in the phylogeny of the genus *Casearia* Jacq. established in the previous chapter of this thesis (Chapter 2). *Casearia* is a pantropical genus that comprises around 220 species of shrubs or trees, half of which are found in the Neotropics (Sleumer, 1980). It is the largest genus within a broadly defined Salicaceae, including the tribe Samydeae, which is sometimes classified at the rank of the family Samydaceae (Alford, 2005). *Casearia* forms with alternate, serrate leaves that present pellucid dots or striations, and with axillary and usually fasciculate inflorescences. The flowers are apetalous with five sepals and they present staminodes, alternating with the stamen or sometimes inserted outside of the row of stamen (Warburg, 1895; Sleumer, 1980). Most species are widely distributed and found across various biomes in the Neotropics, including Amazonian rainforests, Brazilian cerrados (Sleumer, 1980;

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

Gutiérrez, 2000; Marquete & Mansano, 2012), dry forest (DRYFLOR; Banda-R. & al., 2016), savannas (Devecchi & al., 2020) and the Caribbean (Sleumer, 1980; Correll & Correll, 1982; Howard, 1989; Liogier, 1994; Gutiérrez, 2000), whereas others are considered range restricted (Breteler, 2008) or endemic (Marquete & Mansano, 2010; Applequist & Gates, 2020).

Sleumer (1980) provided the most complete revision of the genus in the Neotropics, but some species remain unclear. Gentry (1996) noted that Neotropical *Casearia* are “generally rather nondescript”. In the previous chapter of the thesis presented here, a comprehensive phylogeny of the genus was provided and several cases of nested singletons were detected, particularly within the presumably widespread and common taxa *C. arborea* (Rich.) Urb., *C. mollis* Kunth and *C. sylvestris* Sw. The specific objectives of this study were to investigate the status of these nested singletons using an extended molecular phylogeny and by adding morphological, ecological and distributional data in an integrative taxonomic approach.

3.3. Material & Methods

3.3.1 Taxon sampling and phylogenetic reconstruction

The phylogenetic reference tree was based on the data set of the previous chapter. For the present study, the sampling was increased by adding 31 sequences from Genbank (voucher information in Appendix 3.1). The updated phylogeny was based on *matK* and *trnLF*, to avoid too many missing data. The dataset consisted of 125 accessions, representing 64 species, 46 from the ingroup and 18 from the outgroup. In total, 10 species were added to the previous phylogeny, six belonging to *Casearia*.

The alignment of the previous chapter was used to incorporate the further sequences implementing a motif-alignment approach (see Löhne & Borsch 2005) in PhyDE (Müller & al., 2010). Short regions of uncertain homology (hotspots) were excluded from the analyses and gaps were coded using the simple indel coding method (Simmons & Ochoterena, 2000) as implemented in SeqState version 1.4.1. Maximum Likelihood (ML) analyses were performed using RAxML v. 8.2.12 in CIPRES. Rapid bootstrap support (BS) was estimated based on the majority-rule consensus tree from 1000 pseudo-replicates with 200 searches. The models

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

general time-reversible (GTR) + τ and *binary (BIN) + τ* , respectively, were used in nucleotide and indel partitioning. All those analyses were realised through the CIPRES portal (Miller & al., 2011). The 50% majority-rule consensus tree obtained was processed in FigTree v1.4.4 (Rambaut, 2010). This phylogenetic tree allowed to further identify taxa with unclear species limits and nested singletons that will be studied here. In order to verify the congruence between gene tree and species tree, individual gene tree were realised (Appendix 3.2&3.3).

Sequence identity matrices were calculated, between the nested singleton and the clade in which it is nested in, for each case of nested singleton using the software BioEdit v7.2.5 (Hall, 1999). A sequence identity matrix provides the proportion of identical nucleotide between sequences. It was used here to quantify the branch length pattern that was observed in the phylogram.

3.3.2 Target taxa

The following cases of nested singletons were selected for this study. *C. grandiflora* Cambess and *C. manausensis* Sleumer nested within *C. arborea* (Rich.) Urb.; *C. selloana* Eichler and *C. zizyphoides* Kunth nested within *C. sylvestris* Sw., and *C. mariquitensis* Kunth vs. *C. mollis* Kunth. In the previous chapter, *C. spinescens* was also retrieved nested within *C. aculeata*, however, given the incongruence between plastid and nuclear trees, where *C. spinescens* is retrieved as sister to *C. aculeata*, it was chosen to not further analyse it here.

3.3.3 Locality data

Using a set of specimens corresponding taxonomically to the above taxa following the taxon concept at species level sensu Sleumer (1980), occurrence data from different herbaria B, COL, FMB, HEUS, HUA, JAUM, JBGP, MEDEL, MEXU, NY, UNO, UTMC and GBIF (<https://www.gbif.org/>) were compiled. Recently, the development of herbarium digitalisation (James & al., 2018; Rønsted & al., 2020), providing data such as morphological and distributional, added to the extension of the worldwide database GBIF regarding distributional data (Robertson & al., 2014) allow to explore a wide variety of specimen through online photos and considerably improve the data collection. GBIF data were filtered for specimen-based occurrences only. Only specimen records identified by specialists in the group were

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

considered, or those with digital voucher images where the identification could be verified. Coordinates were manually checked, to verify that they matched with the corresponding localities. When the coordinates were missing but locality data precise enough to allow for reliable georeferentiation, the specimens were georeferenced. For Colombian samples centroid coordinates of either municipality, veredas, Natural Park or reserve was used, following the administrative divisions of Colombia (DANE, 2017). For the remaining samples, Google Earth (GoogleInc., 2020) was used. Duplicate accessions were then deleted, filtering the data by coordinates and localities using R v4.0.3 (RCoreTeam, 2013).

3.3.4 Morphological analyses

Based on directly inspected vouchers or digital specimens from the herbaria of B, K, NY, P and Jstor Global Plant, 200 vouchers were examined and scored for up to 10 morphological characters (Table 3.1). For all specimens, the length and the width of the leaf were examined, as well as the length of the petiole. Further characters were specifically studied for each pair of nested vs. the corresponding paraphyletic taxon, indicated as being diagnostic in taxonomic treatments (Sleumer, 1980; Olson & al., 1999; Nepomuceno & Alves, 2020). Quantitative measurements were performed using the digital image analyses software ImageJ 1.53a (Schneider & al., 2012). Descriptive statistics for all quantitative variables (mean, standard deviation) were computed. For categorical variables, the “fastdummies” package (Kaplan, 2020) was used in R v.4.0.3 (RCoreTeam, 2013), which transforms the variables into binary variables, recoding states as presence/absence variables. Principal Component Analysis (PCA) and cluster analysis were employed using the Ward.D2 method with the NbClust package (Charrad, M. & al. 2014) to analyse the character matrices for nested vs. corresponding paraphyletic species pairs in multivariate fashion. All information regarding the specimens and the respective measurements can be found in Table S1.

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia

	<i>C. arborea</i>	<i>C. grandiflora</i>	<i>C. manausensis</i>	<i>C. mariquitensis</i>	<i>C. mollis</i>	<i>C. selloana</i>	<i>C. sylvestris</i>	<i>C. zizyphoides</i>
Leaves margins	serrulate	crenulate to serrate	subserrate to crenate	serrate	serrate	entire to serrate	subentire to serrate	subentire
Leaves pilosity	glabrous	tomentellous beneath	hirsutous	glabrous	tomentellous beneath	glabrous	glabrous	glabrous
Leaves color when dry	brown	brown	light brown	brown	-	-	-	-
Discolorous	presence	presence	absence	absence	absence	absence	absence	absence
Inflorescence	pedicellate	sessile	subsessile	pedicellate	pedicellate	pedicellate	pedicellate	pedicellate
Flower number	up to 15	up to 15	6 to 10	10 to 15	more than 15	many	many	10 to 15
Leaves punctuation	presence	presence	presence	presence	presence	impunctate with age	densely punctate and lineate	presence
Mucron	absence	absence	absence	absence	absence	absence	absence	presence
Tip of the leave	acuminate, acute	acuminate	acute	subcaudate to acuminate	acuminate	acuminate	acuminate to acute	
Style	entire	entire		entire	entire	3-parted	3-parted	Entire
Source	Sleumer, 1980; protologue, type	Sleumer, 1980; protologue, type	Sleumer, 1980; protologue, type	Sleumer, 1980; Olsen, 1995	Sleumer, 1980; Olsen, 1995	Sleumer, 1980	Sleumer, 1980	Sleumer, 1980

Table 3.1: Morphological diagnostical characters for each pairs of species. Flowering characters are presented for general information but are not used in the analyses.

3.3.5 Environmental niche space analysis

In order to test divergence in environmental niche space between nested vs. including species, 19 climatic layers from WorldClim at 1 km² resolution were obtained (<http://www.worldclim.org/bioclim>). A shape layer was generated by cropping the grid data to the area of the Neotropics using R v.4.0.3 (RCoreTeam, 2013). Furthermore, to reduce complexity and avoid overparametrization, a collinearity test was carried out, using the Pearson correlation coefficient from the “remove Collinearity” function of the “VirtualSpecies” package (Leroy, B., & al. 2016), with a cutoff value that we set at 0.75. One variable for each group of correlated environmental variables was selected, usually the variable representing the annual trend (mean). This reduced the dataset to nine climatic layers (Table S2).

Based on the georeferenced locality data for specimens representing each taxon, PCA analyses were realised to visualize potential differences in the ecology between pairs of

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia

species. To assess niche equivalency and similarity, the “Ecospat” package (Di Cola & al., 2017) was used. First, the Schoener’s D statistic was computed, to quantify niche overlap between pairs of species, ranging between 0 for no overlap in environmental space and 1 for identical environmental space. Given that in the case of allopatric species, geographical differences might lead to differences in the environmental conditions available, a niche similarity test was conducted, which used the model of one species to predict the occurrence of the second species (Warren, D.L. & al. 2010). Information regarding the specimen used for the analyses can be found in Table S3.

3.3.6 Distribution maps

Distribution maps were generated with the geographic information software QGIS 3.10 (QGIS association, 2020), using the locality data of specimen with verified identification and locality data from local flora when no specimen were available with reliable coordinates. These were drawn by nested vs. including species pairs in order to observe potential geographic differentiation.

3.3.7 Decision between emerging species or singleton

It was assumed that if the singleton exhibit a limited distribution range relative to the species depicted as paraphyletic and a significant degree of phenotypic and/or ecological differentiation, then it might actually constitute an emerging species and that the nested placement of this singleton could be explained by incomplete lineage sorting. On the contrary, if the nested singleton does not present a significant degree of phenotypic of ecological differentiation, then it should be considered as a synonym of the taxon it is nested in.

3.4 Results

3.4.1 Phylogenetic reconstruction

The concatenated multiple sequence alignment of the two plastid genomic regions had 5610 positions, of which *rps4-trnT-L-F* contributed 2164 and *trnK-matK* 3142. The final matrix consisted of 5553 positions with 247 indels, after exclusion of hotspots (Table 3.2). On average most nodes received significant support, with BS > 75 % (Fig. 3.1).

	rps4-trnLF	trnK-matK	combined
Number of taxa	128	128	128
Aligned length (bp)	2312	3243	5555
Parsimony-informative characters	385	541	926
Parsimony-uninformative characters	282	405	687
Consistency index (CI)	0.784	0.791	0.763
Retention index (RI)	0.888	0.906	0.884
Tree length	914	1371	2359
Partitions	spacer rps - trnT exon spacer trnT-trnL - trnL exon trnL intron - spacer trnL trnF - trnF	trnK intron matK trnK intron 2-trnK- exon 2-spacer - psbA	

Table 3.2: Summary of character statistics, evolutionary models and trees statistics for the dataset

Fig. 3.1 (next page): Phylogram from a RAxML analysis of *Casearia* with two plastid markers (*rps4/trnLF* and *trnK/matK*). Values above the node indicate bootstrap support. At the tip of the node is the species name followed by the labcode DNA number and country code of where the individual was collected. The highlighted clades are: red, *C. mollis* clade; green, *C. sylvestris* clade; blue, *C. arborea* clade

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia



3.4.2 Phylogenetic relationship of nested singletons

Casearia mariquitensis from Guyana was found with good support in the *C. mollis* clade, appearing in red in the tree (Fig. 3.1), as a nested singleton within two samples of *C. mollis* from Cuba (BS: 91). Furthermore, *C. mariquitensis* is retrieved on a short branch.

Casearia selloana from Brazil and *C. zizyphoides* from Venezuela were retrieved in the *C. sylvestris* clade in green in the tree (BS: 36) within *C. sylvestris* samples from the Caribbean, Central and South America, and the terminal branch of the specimens considered as a singleton are short. In the well-supported *C. arborea* subclade (BS: 98), with samples from the Caribbean and South America, one sample of *C. grandiflora* from Venezuela was retrieved, the terminal branch of this singleton is a long branch relatively to the other internal branches of the subclade containing the singleton. *Casearia manausensis*, from Brazil also appears as a nested singleton within *C. arborea*, although on a short branch.

The sequence identity matrix was retrieved, in order to quantify the molecular differences between the nested taxa and the lineage in which it is nested. Results can be found in Table 3.3. The sequence identity matrix gives the proportion of homologous sites in the alignment, by calculating the number of nucleotide difference.

For the *C. arborea* clade, it was observed that in general each *C. arborea* between them share a higher number of homologous sites than with *C. grandiflora*, at the exception of *C. grandiflora* and *C. arborea* SAL033, where a proportion of 0.74 of the nucleotides were identical. For *C. manausensis*, the results show that there is no difference between *C. manausensis* and *C. arborea*, than in between accessions of *C. arborea*.

For the *C. mariquitensis* and *C. mollis* clade, it was retrieved the two sequences of *C. mollis* with a proportion of 0.99 of the nucleotides and *C. mariquitensis* 0.17.

Finally, regarding the *C. sylvestris* clade, it was found no difference between the accession of *C. selloana* and the accessions of *C. sylvestris*, as well as with *C. zizyphoides* and the rest of accessions of *C. sylvestris*.

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia

Table 3.3: Sequence identity matrix for the different clades: (a) *C. arborea*, *C. grandiflora*, *C. manausensis* (b) *C. mariquitensis*, *C. mollis* and their sister clade, (c) *C. selloana*, *C. sylvestris*, *C. zizyphoide*, *C. sy.* stands for *C. sylvestris*, *C. sy_my* stands for *C. sylvestris* subsp. *myricoides* and *C. sy_sy* stands for *C. sylvestris* subsp. *sylvestris*.

	<i>C.</i> <i>arborea_MK797141_JQ589106</i>	<i>C. arborea_SAL009</i>	<i>C. arborea_SAL024</i>	<i>C.</i> <i>arborea_SAL032</i>	<i>C.</i> <i>arborea_SAL033</i>	<i>C.</i> <i>grandiflora_AY756894</i>	<i>C.</i> <i>manausensis_SAL053</i>
<i>C. arborea_MK797141_JQ589106</i>	ID	0.58	0.30	0.42	0.32	0.28	0.35
<i>C. arborea_SAL009</i>	0.58	ID	0.50	0.32	0.22	0.17	0.46
<i>C. arborea_SAL024</i>	0.30	0.50	ID	0.30	0.11	0.09	0.61
<i>C. arborea_SAL032</i>	0.42	0.32	0.30	ID	0.36	0.28	0.34
<i>C. arborea_SAL033</i>	0.32	0.22	0.11	0.36	ID	0.74	0.18
<i>C. grandiflora_AY756894</i>	0.28	0.17	0.09	0.28	0.74	ID	0.15
<i>C. manausensis_SAL053</i>	0.35	0.46	0.61	0.34	0.18	0.15	ID

3.A

	<i>C. mariquitensis_SAL054</i>	<i>C. mollis_SAL013</i>	<i>C. mollis_SAL136</i>
<i>C. mariquitensis_SAL054</i>	ID	0.17	0.17
<i>C. mollis_SAL013</i>	0.17	ID	0.99
<i>C. mollis_SAL136</i>	0.17	0.99	ID

3.B

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia

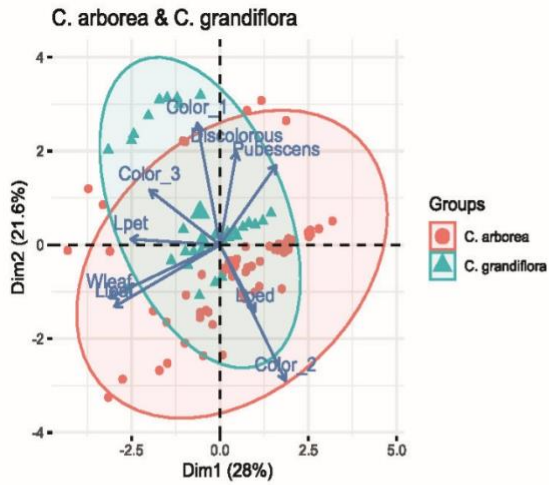
	<i>C.</i> <i>selloana</i> _SAL06 5	<i>C.</i> <i>sy. my_</i> SAL010	<i>C.</i> <i>sy. AY</i> 757012	<i>C.</i> <i>sy. GQ</i> 981954	<i>C.</i> <i>sy. HM</i> 446664	<i>C.</i> <i>sy. JQ</i> 589115	<i>C.</i> <i>sy. S</i> AL01 6	<i>C.</i> <i>sy. S</i> AL05 0	<i>C.</i> <i>sy. S</i> AL09 5	<i>C.</i> <i>sy. S</i> AL09 7	<i>C.</i> <i>sy. S</i> AL18 4	<i>C.</i> <i>sy. S</i> AL18 8	<i>C.</i> <i>sy. S</i> AL20 3	<i>C.</i> <i>sy. S</i> AL21 1	<i>C.</i> <i>sy. my_</i> SAL138	<i>C.</i> <i>sy. sy_</i> SAL00 4	<i>C.</i> <i>zizyphoide</i> s_SAL072
<i>C.</i> <i>selloana</i> _SAL06 5	ID	0.16	<.001	0.05	0.09	0.09	0.51	0.47	0.14	0.52	0.50	0.49	0.14	0.28	0.47	0.18	0.60
<i>C.</i> <i>sy. subsp myri</i> <i>coides</i> _SAL010	0.16	ID	0.18	0.00	0.00	0.00	0.26	0.26	0.67	0.29	0.25	0.08	0.67	0.35	0.28	0.63	0.24
<i>C.</i> <i>sy. AY</i> 757012	<.001	0.18	ID	0.00	0.00	0.00	0.06	0.00	0.14	0.07	0.06	0.08	0.14	0.08	0.06	0.28	0.08
<i>C.</i> <i>sy. GQ</i> 981954	0.05	0.00	0.00	ID	0.65	0.65	0.09	0.07	0.00	0.11	0.09	0.13	0.00	0.13	0.10	0.00	0.14
<i>C.</i> <i>sy. HM</i> 446664	0.09	0.00	0.00	0.65	ID	0.86	0.14	0.07	0.00	0.16	0.14	0.21	0.00	0.17	0.15	0.00	0.22
<i>C.</i> <i>sy. JQ</i> 589115	0.09	0.00	0.00	0.65	0.86	ID	0.14	0.09	0.00	0.16	0.14	0.21	0.00	0.19	0.15	0.00	0.22
<i>C.</i> <i>sy. SAL016</i>	0.51	0.26	0.06	0.09	0.14	0.14	ID	0.25	0.36	0.86	0.97	0.63	0.36	0.70	0.92	0.17	0.60
<i>C.</i> <i>sy. SAL050</i>	0.47	0.26	0.00	0.07	0.07	0.09	0.25	ID	0.21	0.24	0.25	0.18	0.21	0.35	0.27	0.32	0.39
<i>C.</i> <i>sy. SAL095</i>	0.14	0.67	0.14	0.00	0.00	0.00	0.36	0.21	ID	0.42	0.36	0.07	1.00	0.50	0.39	0.45	0.21
<i>C.</i> <i>sy. SAL097</i>	0.52	0.29	0.07	0.11	0.16	0.16	0.86	0.24	0.42	ID	0.86	0.53	0.41	0.59	0.80	0.20	0.61
<i>C.</i> <i>sy. SAL184</i>	0.50	0.25	0.06	0.09	0.14	0.14	0.97	0.25	0.36	0.86	ID	0.65	0.36	0.69	0.90	0.17	0.60
<i>C.</i> <i>sy. SAL188</i>	0.49	0.08	0.08	0.13	0.21	0.21	0.63	0.18	0.07	0.53	0.65	ID	0.07	0.37	0.56	0.09	0.61
<i>C.</i> <i>sy. SAL203</i>	0.14	0.67	0.14	0.00	0.00	0.00	0.36	0.21	1.00	0.41	0.36	0.07	ID	0.50	0.39	0.45	0.21
<i>C.</i> <i>sy. SAL211</i>	0.28	0.35	0.08	0.13	0.17	0.19	0.70	0.35	0.50	0.59	0.69	0.37	0.50	ID	0.75	0.24	0.47
<i>C.</i> <i>sy. subsp myric</i> <i>oides</i> _SAL138	0.47	0.28	0.06	0.10	0.15	0.15	0.92	0.27	0.39	0.80	0.90	0.56	0.39	0.75	ID	0.18	0.54
<i>C.</i> <i>sy. subsp sylves</i> <i>tris</i> _SAL004	0.18	0.63	0.28	0.00	0.00	0.00	0.17	0.32	0.45	0.20	0.17	0.09	0.45	0.24	0.18	ID	0.27
<i>C.</i> <i>zizyphoides</i> _SA L072	0.60	0.24	0.08	0.14	0.22	0.22	0.60	0.39	0.21	0.61	0.60	0.61	0.21	0.47	0.54	0.27	ID

3C

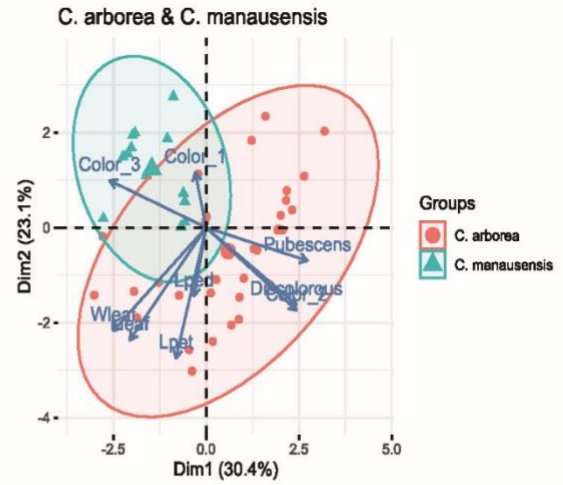
3.4.3 Morphological analyses

A total of 200 vouchers were analysed for the morphometric analyses, 60 vouchers of *C. arborea*, 36 vouchers of *C. grandiflora*, 13 vouchers of *C. manausensis*, 15 vouchers of *C. mariquitensis*, 22 vouchers of *C. mollis*, 10 vouchers of *C. selloana*, 34 vouchers of *C. sylvestris* and 10 vouchers of *C. zizyphoides*. The PCA analysis of *C. grandiflora* vs. *C. arborea* showed considerable morphological overlap, but a strong tendency of differentiation along the two perpendicular axes (Fig. 3.2a), whereas cluster analysis revealed four distinct groups that did not coincide with the two species (Fig. 3.3a). In this case, distribution of individuals between the main clusters was rather homogeneous. The morphological overlap between *C. manausensis* vs. *C. arborea* was less pronounced than in the previous two cases of *C. grandiflora* and *C. mariquitensis* (Fig. 3.2b) and cluster analysis indicated a nested structure, with most specimens of *C. manausensis* placed in one of the groups but mixed with specimens of *C. arborea* (Fig. 3.3b). For *C. mariquitensis* vs. *C. mollis*, PCA showed a complete morphological overlap (Fig. 3.2c) and the cluster analysis supported no distinction. Cluster 1 contained 71% *C. mariquitensis* and 29% *C. mollis*, whereas cluster 2 consisted of 75% *C. mollis* and 25% *C. mariquitensis* and cluster 3 of 80% *C. mollis* and 20% *C. mariquitensis* (Fig. 3.3c). A different pattern was found for *C. selloana* vs. *C. sylvestris*, with little overlap in the PCA analysis (Fig. 3.2d), although this distinction was less obvious in the cluster analysis (Fig. 3.3d). *Casearia selloana* thereby seemed to present longer petioles with entire margins and an acute tip. For *C. zizyphoides* vs. *C. sylvestris*, PCA also showed limited overlap (Fig. 3.2e), whereas in the cluster analysis, two clusters were retrieved that did not correspond to the two taxa (Fig. 3e).

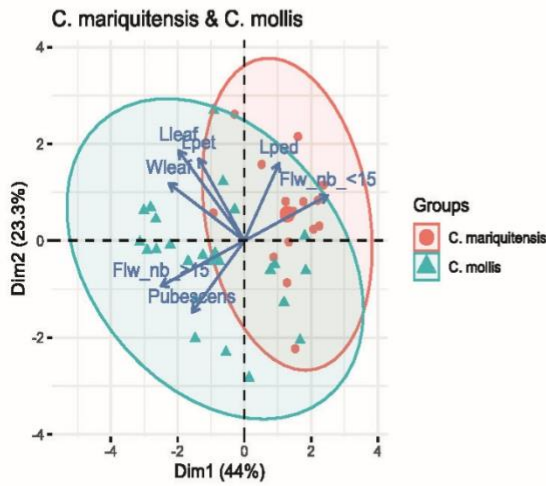
Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia



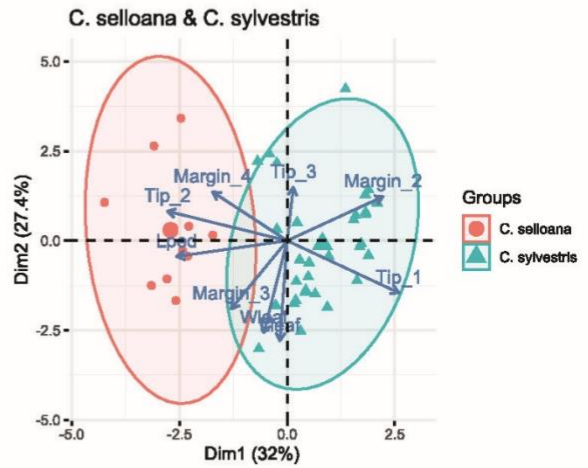
2.a



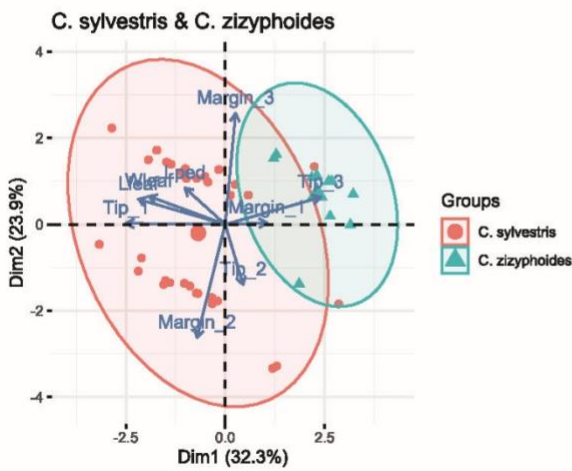
2.b



2.c



2.d



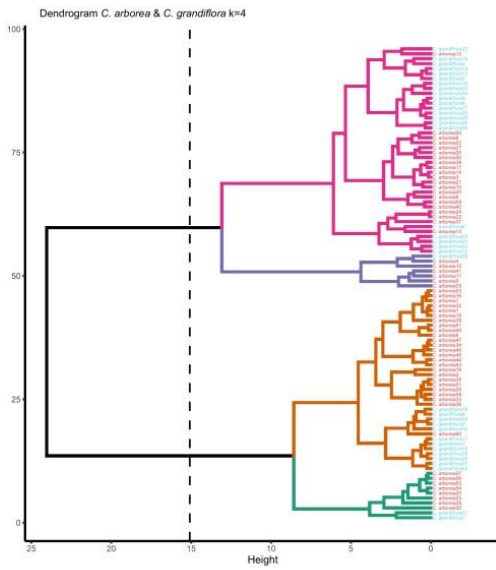
2.e

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia

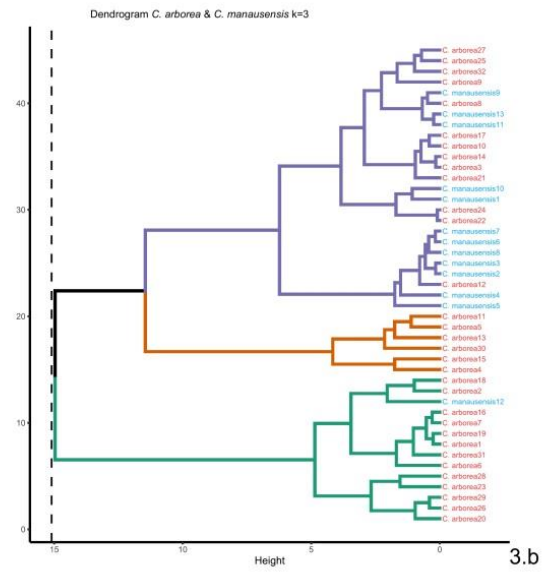
Fig. 3.2 (previous page): PCA plot based on selected morphological characters for pairs of species: (2.a) *C. arborea*/*C. grandiflora*, (2.b) *C. arborea*/*C. manausensis*, (2.c) *C. mariquitensis*/*C. mollis*, (2.d) *C. selloana*/*C. sylvestris*, (2.e) *C. sylvestris*/*C. zizyphoides*. Points represent individuals, arrows individual parameters. Lleaf: Limb length, Wleaf: limb width, Lpet: petiole length, Lped: pedicelle length (or presence/absence for 2a), margin 1/2/3/4: margins crenate/subentire/serrate/entire (presence/absence), color 1/2/3: leaf color when dry, green/brown/light brown (presence/absence), discholorous: superior side of the limb darker than the inferior side (presence/absence), pubescens: presence of pubescens on the limb (presence/absence), Flw nb 0-15: up to 15 flowers (presence/absence), Flw nb 15-30: between 15 and 30 flowers (presence/absence), Tip 1/2/3: tip shape, acuminate/acute/mucronate (presence/absence)

Fig. 3.3 (next page): Dendrograms plots for pair of species (a) *C. arborea* (blue) and *C. grandiflora* (red), (b) *C. arborea* (red) and *C. manausensis* (blue), (c) *C. mariquitensis* (red) and *C. mollis* (blue), (d) *C. selloana* (red) and *C. sylvestris* (blue), (e) *C. sylvestris* (red) and *C. zizyphoides* (blue) on morphological characters

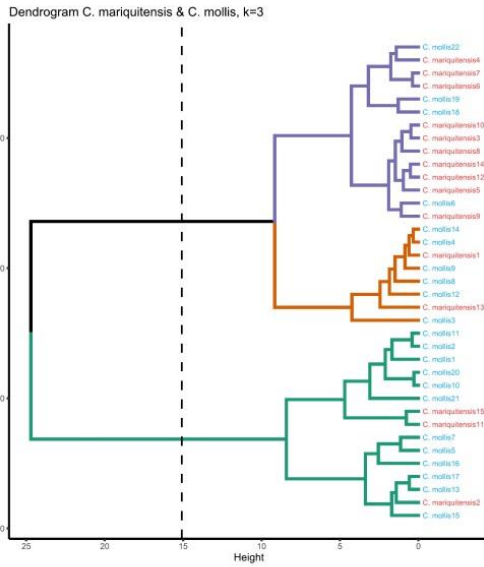
Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia



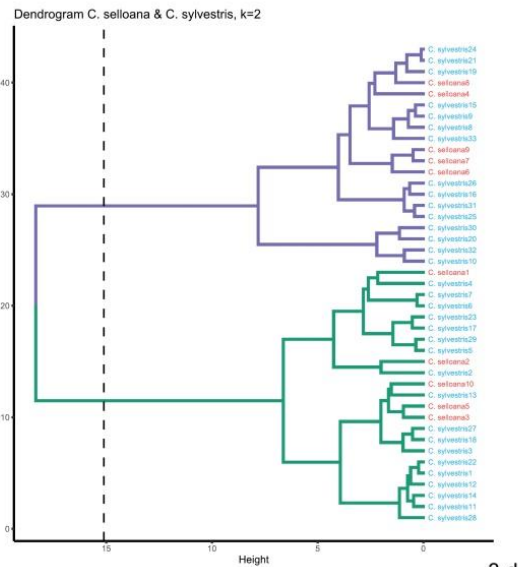
3.a



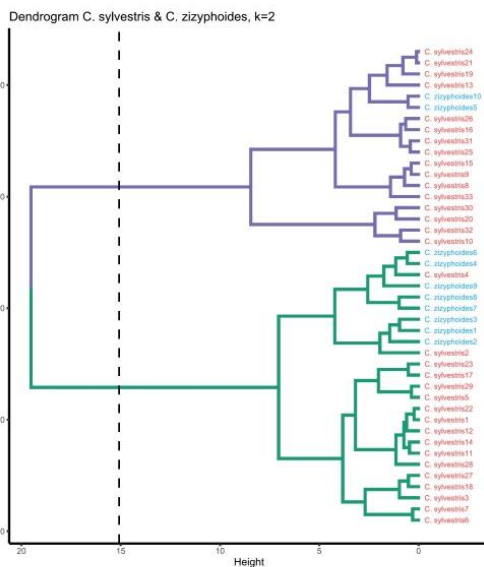
3.b



3.c



3.d



3.e

3.f
73

3.4.4 Environmental niche space analysis

For the environmental niche space analyses coordinates data for 921 occurrences were retrieved, 219 occurrences of *C. arborea*, 168 occurrences of *C. grandiflora*, 12 occurrences of *C. manausensis*, 89 occurrences of *C. mariquitensis*, 33 occurrences of *C. mollis*, 39 occurrences of *C. selloana*, 327 occurrences of *C. sylvestris* and 33 occurrences of *C. zizyphoides*. Ecological differentiation were analysed by performing PCA analysis. Results for *C. grandiflora* and *C. arborea* showed considerable ecological overlap which did not show ecological differentiation (Fig. 3.4a). In the case of *C. manausensis* vs. *C. arborea*, the PCA analysis showed a nested structure with individuals from *C. manausensis* being nested within *C. arborea*, i.e. with a much narrower ecological niche (Fig. 3.4b). For *C. mariquitensis* and *C. mollis* a high ecological overlap was also retrieved in the PCA analysis (Fig. 3.4c). *Casearia selloana* and *C. sylvestris* also presented no discernible ecological differentiation (Fig. 3.4d), and the same pattern was found for *C. sylvestris* and *C. zizyphoides* (Fig. 3.4e).

Niche similarity tests resulted significant for all cases of paired species, therefore the niche similarity was always higher than expected by chance (Table 3.4). Highest niche overlap was 0.74 for *C. mariquitensis* vs. *C. mollis* with a significant level of niche equivalence (Table 3.4). For the remaining pairs, niche equivalence was not significant and niche overlap was lower, ranging from 0.43 in *C. grandiflora* vs. *C. arborea* to as low as 0.02 in *C. manausensis* vs. *C. arborea*, with *C. selloana* vs. *C. sylvestris* (0.26) and *C. zizyphoides* vs. *C. sylvestris* (0.20) inbetween (Table 3.4).

Chapter 3: Nested singletons in species-level phylogenetic trees of Casearia

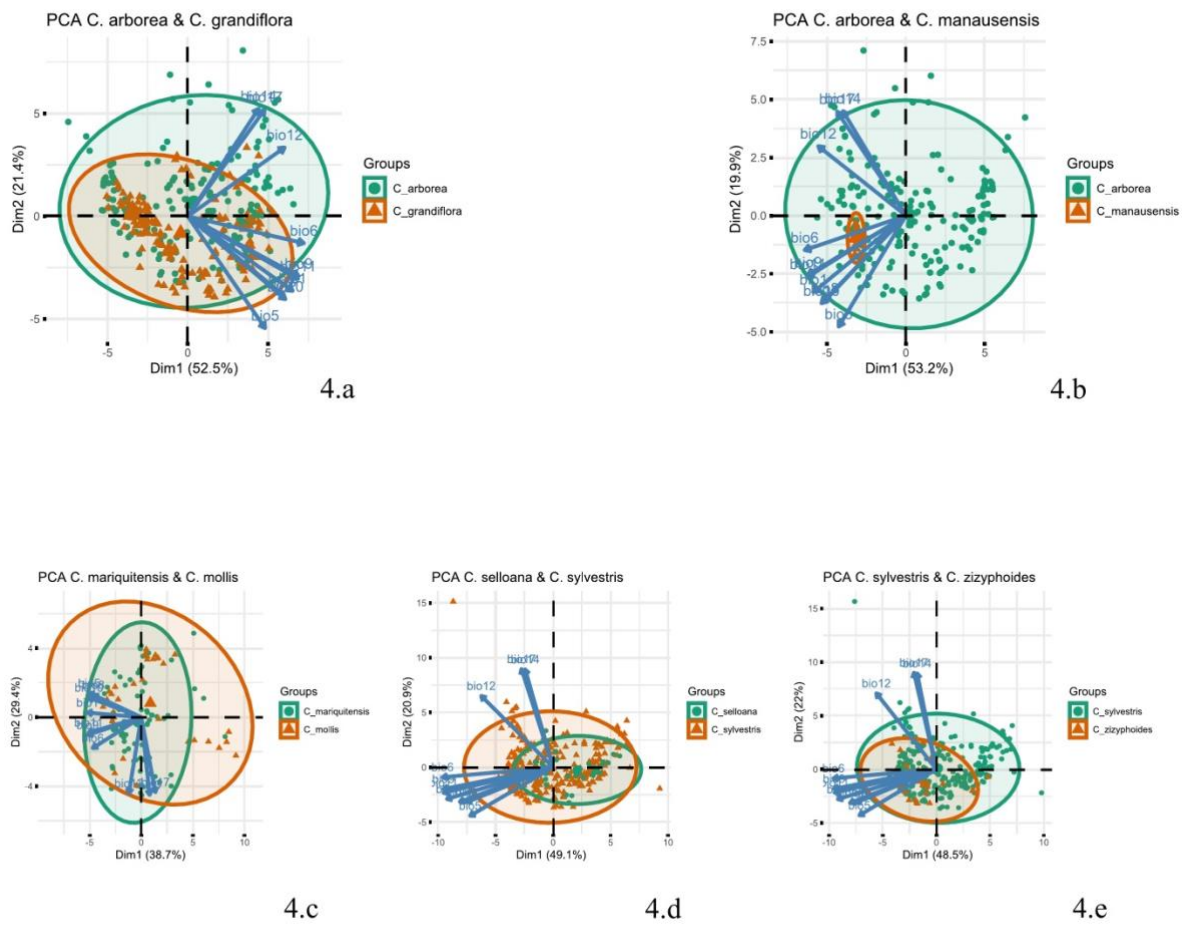


Fig. 3.4: PCA plot based on selected ecological variables from WorldClim for pairs of species: (a) *C. arborea* and *C. grandiflora*, (b) *C. arborea* and *C. manausensis*, (c) *C. mariquitensis* and *C. mollis*, (d) *C. selloana* and *C. sylvestris*, (e) *C. sylvestris* and *C. zizyphoides*. Points represent individuals, arrows individual parameters.

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

Species		Niche overlap (D)	Niche similarity		Niche equivalency
a	b		greater	lower	
<i>C. arborea</i>	<i>C. grandiflora</i>	0.44	p= 0.06	p=0.92	ns
<i>C. arborea</i>	<i>C. manausensis</i>	0.04	p= 0.003	p= 1	ns
<i>C. mariquitensis</i>	<i>C. mollis</i>	0.71	p= 0.002	p= 1	p= 0.04
<i>C. sylvestris</i>	<i>C. selloana</i>	0.3	p= 0.001	p= 1	ns
<i>C. sylvestris</i>	<i>C. zizyphoides</i>	0.47	p= 0.001	p= 1	ns

Table 3.4: Results of the ecological niche analysis

3.4.5 Distribution

Distribution maps for the selected species are shown in Fig. 3.5. *Casearia arborea* and *C. grandiflora* are both widely distributed. Whereas *C. arborea* is concentrated in the mountainous regions of the Northern Andes, Central America, the Caribbean and the Brazilian Atlantic forest, *C. grandiflora* is mostly found in the broader Amazon region in wet and dry forests (Fig. 3.5b). *Casearia manausensis* has a narrow distribution within the broad range of *C. arborea*, reported only from a small area in the central Amazon, around Manaus (Fig. 3.5b). *Casearia mariquitensis* and *C. mollis* are, broadly overlapping in northern South America, but with *C. mollis* also present in Cuba, whereas *C. mariquitensis* extends further south in South America (Fig. 3.5c). *Casearia sylvestris* is the most broadly distributed species in this study, being found across the entire Neotropics; in contrast, *C. selloana* is restricted to the Brazilian Atlantic forest and *C. zizyphoides* is only found in northern South America (Fig. 3.5d).

Fig. 3.5 (next page): Distribution maps: (a) *C. arborea*, *C. grandiflora* and *C. manausensis*, (b) *C. mariquitensis* and *C. mollis*, (c) *C. selloana*, *C. sylvestris* and *C. zizyphoides*.

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*



3.5 Discussion

Discussing species boundaries on solely phylogenetic data can be impeded by low genetic variation, especially in recent diverging lineages, and the rate of molecular evolution do not always follow the rate of morphological changes (Bromham & al., 2002). Therefore, an integrative taxonomy approach with addition to other type of data to an unresolved phylogeny has shown useful in providing insights into the assessment of species limits. Such an approach has been used in a variety of groups like *Cyrtorchis* (Orchidaceae), in a phylogenetically unresolved complex, where species limits could be assessed by morphometric analyses (Azandi & al., 2021), in *Otatea* (Poaceae), that presented a mostly unresolved phylogenetic tree but strong morphological differentiation (Ruiz-Sanchez & Londoño, 2017) and in *Pagamea* Aubl. (Rubiaceae) (Prata & al., 2018). In the present study, a multiple line of evidences approach is proposed, that takes into account, morphological and ecological variations, as well as information regarding the distribution, in order to fully investigate the case of nested taxa in a phylogeny. In particular we focused on nested singleton, one or few taxa, nested in a phylogenetic tree. Indeed, species delimitation is crucial for ecological studies, as well as conservation (Agapow & al., 2004; Rojas-Soto & al., 2010) and biodiversity monitoring can be impeded by the unavailability of taxonomical data. In the present study, the use of integrative data, here molecular, morphological and ecological help resolve issues in species delimitation, which would not be solved with one single type of data alone. In the approach presented here, no formal conclusion is made on species boundaries but rather an insight is proposed into the study of species limits and especially in the case of nested singletons.

For the selected cases of nested singletons, only the *Casearia grandiflora* singleton, nested within *C. arborea*, emerged on a longer branch, indicating genetical differentiation between the singleton and the clade it is nested in. This is confirmed by the sequence identity matrix, which shows the proportion of identical nucleotide in the alignment, as *C. grandiflora* is found to have more difference with other samples of *C. arborea* than *C. arborea* samples among them. This needs to be tested by sequencing further individuals. If the longer branch corresponds to divergence time, the possibility of phenotype differentiation and subsequent range expansion is higher in this case, so it

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

would be expected differences in morphology towards *C. arborea*, going along with a broader overlap in range. Indeed, both patterns are apparent in the data: range overlap is indeed comparatively broad, whereas morphology shows some degree of differentiation along the two perpendicular axes. Even if represented by a single sequenced terminal, based on the data from non-sequenced specimens, it is considered that *C. grandiflora* is supported as a separate species, reflecting a relatively recent speciation event followed by possibly fast expansion. *Casearia grandiflora* is distinguished from *C. arborea* in always having sessile flowers, whereas *C. arborea* presents pedicellate flowers. Although both are pubescent beneath, *C. grandiflora* presents a very dense indumentum whereas *C. arborea* shows a fine grey pubescence. Furthermore, *C. grandiflora* has linear-lanceolate stipules and *C. arborea* presents narrowly ovate stipules and an ellipsoid-subglobose capsule with two to six seeds, whereas, *C. grandiflora* possesses an ovoid-ellipsoid capsule and three to four seeds (Sleumer, 1980; Olson & al., 1999). Those morphological characters allow a clear differentiation of fertile material and support the distinction of the two species. In contrast to *C. grandiflora*, the remaining cases all emerged on short branches, indicating very recent divergences or speciation in process.

Casearia manausensis was found as a nested singleton within *C. arborea* on a short branch, with one sample from Brazil. The morphological analysis resolved *C. manausensis* individuals in one small cluster, within the much broader variational range of *C. arborea*. The same pattern was detected with respect to the ecological analysis, which also indicated some ecological differentiation in the niche equivalency test. *Casearia arborea* is widely distributed in the Neotropics, from Central America to Southern Brazil and into the Caribbean, whereas *C. manausensis* is restricted to a small area in the Amazon, within the range of *C. arborea*. *Casearia manausensis* is usually characterised as hirsutulous beneath on the main and lateral nerves, whereas *C. arborea* is tomentellous to puberulous all over the undersurface, becoming glabrous with age. *Casearia manausensis* presents sessile inflorescences with only six to ten flowers, whereas *C. arborea* has shortly pedunculate inflorescences with a higher number of flowers (10-25). Thus, morphological and ecological results support the hypothesis that *C. manausensis* is a recently emerging lineage, with a clearly defined, narrow range, nested within *C. arborea*, in which case one could also defend its formal recognition as a subspecies or variety of the latter.

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

A single sample of *Casearia mariquitensis*, from Guyana, was nested on a short branch within two samples of *Casearia mollis* from Cuba in the analysis. Both morphological and ecological analyses revealed a considerable overlap. Their distribution ranges broadly overlap in South America, although *C. mollis* is present in the Caribbean (Cuba). *C. mariquitensis* and *C. mollis* were both describe in the same work by Kunth (Humboldt & al., 1815) and these results suggest that *C. mollis* might be a synonym of *Casearia mariquitensis*. The latter possesses five synonyms, reflecting a high morphological variation within the species. It is usually characterized in having an acute base of the leaf, whereas *C. mollis* presents a rotund base, although it has been described as obtuse-angulate in some Cuban specimens (Gutiérrez, 2000). The leaves of *C. mariquitensis* are glabrous whereas the leaves of *C. mollis* are tomentellous beneath, but they can turn glabrous with age (Gutiérrez, 2000). *Casearia mariquitensis* has 10 to 15 flowers, whereas *C. mollis* presents more than 15 flowers; however, Sleumer (1980) reported that *C. mariquitensis* occasionally can have up to 30 flowers. Also here, there seems to be some confusion in the delimitation of the two species, already noted by Sleumer (1980) and by Olson & al. (1999), who stated that *C. mariquitensis* and *C. mollis*, along with three other species, formed a poorly understood complex. Our results are thus in line with the consideration of *C. mariquitensis* and *C. mollis* being synonyms, in which case a decision is required which of the two names should be used.

The result retrieved one accession of *Casearia selloana*, from Brazil, as a nested singleton on a short branch within *C. sylvestris*. PCA and cluster analysis on morphological characters showed little differentiation, and the environmental analysis showed high overlap, although the niches of the two species were not fully equivalent. *Casearia selloana* has a restricted distribution in the Brazilian Atlantic forest, overlapping with *C. sylvestris*, although the latter possesses a much wider distribution range, throughout the Neotropics, a pattern similar to what was seen in *C. manausensis* vs. *C. arborea*. According to taxonomic treatments, *C. selloana* differs from *C. sylvestris* by being practically impunctate and having coriaceous leaves, whereas *C. sylvestris* is densely pellucid-punctate and its leaves vary in texture. Furthermore, *C. selloana* possesses entire leaf margins, whereas *C. sylvestris* presents subentire margins. Sepals are pubescent in *C. sylvestris* and glabrous to tomentose in *C. selloana* (Nepomuceno & Alves, 2019). The tip of the leaf is acute to acuminate in *C. selloana* vs. acuminate to subcaudate in *C. sylvestris*. Notably, *Casearia sylvestris* encompasses two varieties, var.

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

sylvestris and var. *lingua* (Cambess.) Eichler, the latter restricted to the Brazilian Atlantic forest, which raises the question as to the differences of var. *lingua* with *C. selloana*. Indeed, Sleumer (1980) suggested that *C. selloana* might be a variant of *C. sylvestris* in very dry habitats. *Casearia sylvestris* var. *sylvestris* has over 20 synonyms, reflecting the high morphological variability of the species. Our results overall resolved *C. selloana* vs. *C. sylvestris* as a case somewhat similar to *C. manausensis* vs. *C. arborea*, i.e. possible recognition at infraspecies level, although less clear.

The last singleton, *Casearia zizyphoides*, from Venezuela, was resolved as a nested singleton also within *C. sylvestris*. Again, PCA showed no discernable morphological differentiation and both taxa had a high ecological overlap. Like *C. selloana*, *C. zizyphoides* was nested within the wide distribution range of *C. sylvestris*, albeit in this case in northern South America. Based on taxonomic treatments, *C. zizyphoides* presents a characteristic mucronate tip of the leaves, inter-staminal staminodes, and a faintly 3-lobed stigma, whereas *C. sylvestris* presents long acuminate to subcaudate leaf tips, intra-staminal staminodes, and a trifid stylum. In the Flora of the Venezuelan Guyana, the authors already noticed the morphological similarities between the two species (Olson & al., 1999). Although taxonomic treatments seem to distinguish the two taxa rather well, our quantitative analysis of specimens identified as either *C. zizyphoides* or *C. sylvestris* showed that the morphological differentiation is rather unclear, also raising the possibility of synonymy or *C. zizyphoides* at best representing an infraspecific taxon of *C. sylvestris*.

3.6 Conclusion

The approach presented here shows that quantitative evaluation of non-sequenced specimens that were identified based on morphological characters and using existing pre-phylogenetic treatments can be successful in evaluating the status of so-called nested singletons that were found in phylogenetic analyses. In the present study, the entire range of possible outcomes in such cases were resolve, from recently emerging species that already show some degree of morphological, ecological and/or biogeographical differentiation (*C. grandiflora* vs. *C. arborea*), to very recently emerging lineages perhaps best recognized at subspecies or variety level (*C. manausensis* vs. *C. arborea*; perhaps

Chapter 3: Nested singletons in species-level phylogenetic trees of *Casearia*

also *C. selloana* and *C. zizyphoides* vs. *C. sylvestris*), to cases where synonymy is likely (*C. mariquitensis* vs. *C. mollis*). Under normal circumstances, one would target several specimens of a species complex to address species delimitation, then also ideally combining molecular, morphological, ecological, and distributional data in an integrative approach. However, singletons are usually the result of non-targeted sampling, i.e. such taxa have not been specifically targeted and they are included as singletons in phylogenetic analysis either because the overarching question is at a different taxonomic level (e.g. genus delimitation or genus placement) or because they represent opportunistic sampling within a larger clade. In such cases, the strategy presented here offers an effective approach: (1) initial hypothesis of potential synonymy due to nested phylogenetic placement, (2) initial testing using quantitative morphology, ecology and distribution of numerous non-sequenced samples taxonomically identified as a given species, and (3) subsequent targeted sampling for further molecular studies. The approach is therefore not only useful to identify taxa of interest for targeted sampling for further species delimitation approaches but can also serve to make an initial decision about the taxonomic status of taxa in case further sampling is logistically challenging but taxonomic data and decisions are needed in a timely manner such as for completing checklists and Flora treatments and the evaluation of the conservation status.

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

4.1 Summary

Since 1980, no update of the taxonomical revision of Sleumer for Neotropical *Casearia* has been published. Regarding the Old World, a checklist of all currently accepted *Casearia* species is still missing. Such work is crucial for taxonomical studies and for conservation or biodiversity management. The present study compiled a worldwide up-to-date checklist of all currently accepted *Casearia* species in the current monophyletic circumscription of the genus and their synonyms using the EDIT Platform for Cybertaxonomy based on a taxonomic revision and literature. Further relevant information for each species, such as protologues and types are included as well. The results of the checklist presented here are compared with the Plants of the World (POWO), The Plant List (TPL) and the World Checklist of Vascular Plants (WCVP). The present study includes a total of 708 names, 222 accepted species names, 464 synonyms and 22 unresolved names.

4.2 Introduction

Biodiversity studies rely on the availability of taxonomical knowledge, synthesised in checklists, databases, floras and monographs (Funk, 2006; Marhold & al., 2013). The accuracy of those datasets is crucial as they serve as a basis to study the biodiversity as well as to develop tools to manage it and to establish solid conservation or restoration

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

measures (Patterson & al., 2010; Borsch & al., 2015; Ulloa, Ulloa & al., 2017; Thomson & al., 2018).

Single country endemics represent 46 to 62% of the world flora (Pitman & Jørgensen, 2002) and taxonomic studies are usually carried out at a local or regional scale. A global perspective is often missing which can lead to inaccuracy in the definition of species boundaries. For example, the same species could be described twice from two different areas, therefore creating synonyms (Wortley & Scotland, 2004). Ultimately, it can hamper the establishment of effective biodiversity management measures, and be detrimental to conservation, as already shown in various groups (Bernardo, 2011; Zachos, 2013; Gippoliti & al., 2018; Thomson & al., 2018; Simkins & al., 2020). Only taxonomic work at a global scale allows researchers to apprehend the morphological variation in a given group and to reliably establish species limits (Thomas, 1999), especially when combined with ecological or molecular data. Furthermore, such a checklist can guide further inventories and conservation status assessments (Garnett & Christidis, 2017; Thomson & al., 2018).

Accordingly, comprehensive global checklists that include all members of a taxon (ie a comprehensive taxonomic backbone in the terminology of World Flora Online) in a given group are a most needed tool and especially, large scale checklist are essential, as they allow the compilation of regional and national flora into a single database (Borsch & al., 2020), thus helping taxonomic revisions, molecular studies and the establishment of correct biodiversity management and conservation measures (Ulloa, Ulloa & al., 2017). Lately, the development of online databases such as the Plant List (Plant List, 2013), Plants of the Worlds Online (POWO, 2021), Tropicos (tropicos.org), or the World Flora Online (WFO, 2021) partially fulfilled those needs.

The EDIT Platform for Cybertaxonomy is a digital tool to facilitate the taxonomic workflow (Ciardelli & al., 2009; Berendsohn, 2010). The platform covers all aspects of taxonomic work, including online publication. It is open source, easily accessible and therefore a key tool in the construction of a dynamic taxonomic backbone by allowing to compile, process and publish the data as well as to modify them (Berendsohn & al., 2018).

The genus *Casearia* is pantropical and consists of more than 200 species, which makes it the most species rich genus of the Samydeae tribe, in the Salicaceae family. It is described as having pellucid dots on the leaves, dentate or serrate leaf margins, axillary

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

apetalous flowers with four to six sepals, one series of staminodes often alternating with the stamens, a three to four-parted style and an unilocular ovary (Warburg, 1895; Hutchinson, 1967; Gentry, 1996). The genus *Casearia* was first described by Jacquin (1760), with three species, *C. nitida* Jacq., *C. aculeata* Jacq. and *C. decandra* Jacq., based on Caribbean specimens. Currently, the IUCN Redlist compiled information on 72 of its species. It has reported 46 *Casearia* species in the category “least concerned”, five are treated as “near threatened”, eight as “vulnerable”, eight as “endangered”, four as “critically endangered” and two species, *C. tinifolia* Vent. and *C. quinduensis* Tul. are reported to be extinct (IUCN, 2021).

The first comprehensive treatment of the genus was made by Warburg (1895) who revised the whole Flacourtiaceae family. Bentham (1861) had noted how probably many species had been described twice under different names. Later, Woodson & al. (1968) highlighted that the genus is still in need of a comprehensive monography. Finally, Sleumer (1980) provided the first and still only taxonomic revision of all the Neotropical *Casearia* species, thus considerably increasing the knowledge of the group’s New World species. Although Sleumer also wrote treatments for the African, Australian and Malesian species (Sleumer, 1954, 1971, 1982), a work including all species from the Paleotropics is still missing. Species limits in the genus are still controversial and recently, a taxonomic study by Samarakoon & Alford (2019) resulted in the transfer of four genera, *Hecatostemon*, *Laetia*, *Samyda* and *Zuelania*, before part of the Samydeae tribe, into *Casearia*. The first phylogenetic study of *Casearia* (chapter 2 of this thesis) included three of those genera, confirmed their inclusion in *Casearia* and points out problems in the delimitation of some taxa.

Specifically, the objectives of this study were to provide an updated checklist of the Neotropical species of *Casearia* since the last revision by Sleumer (1980) and to present all currently accepted species from the Paleotropics using the EDIT platform for Cybertaxonomy. This checklist is the first comprehensive taxonomic backbone of the genus, at a global scale, as types and synonyms information on all species were collected in order to trace the taxonomic background behind the accepted names. Data from various sources of information such as monographs, floras and other publication were compiled, to provide an up-to-date worldwide checklist of *Casearia* species that can be used as a basis for further taxonomical or molecular studies in the genus.

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

4.3 Material and methods

The EDIT platform for Cybertaxonomy (Berendsohn, 1995a; Ciardelli & al., 2009) provides the features needed to edit and manage taxonomic information and allows the creation of an open source database that can be accessed and modified online. It permits the association of a name with its protologue reference, types, synonyms (both homotypic and heterotypic), and the currently accepted nomenclatural status. The work presented here constitutes the first World checklist of *Casearia* to present the “secundum” (“sec.”) function, which is particularly useful for taxonomic revisions as it permits the specification of the source of a given species concept. It can be either the author of the species, or the author of a later revision, that synonymised other names to this taxon (Berendsohn, 1995a). Other features of the platform are the indication of distributional data and further factual data with references.

This checklist specifies synonyms both heterotypic and homotypic, for each species, with author names, publications details and information regarding the type. The platform can also provide a text file with all information, already compiled. Using this user-friendly tool, we were able to provide a strong framework for the taxonomy of *Casearia*.

A list of 617 *Casearia* names, including their references was obtained from the World Checklist of Vascular Plants (WCVP, 2019), additional names from the literature were entered manually. Those names were resolved in their current taxonomical status, either as accepted names, synonyms or unresolved names, and their protologue were studied in order to retrieve the types.

For the circumscription of the species, relevant taxonomic treatments or monographs were favoured, as well as regional Floras.

For the New World, the most important works used were the Flora Neotropica, that constitutes the last taxonomic revision of the whole genus for the Neotropics (Sleumer, 1980), as well as the recent taxonomic treatment by Samarakoon & Alford (2019), which merged four *Samydeae* genera within *Casearia*. Different regional Floras were used, such as the Flora of the Bahamas (Correll & Correll, 1982), the Flora de Cuba (Gutiérrez, 2000), the Manual de Plantas de Costa Rica (Gonzalez, 2007), the Flora the Lesser Antilles (Howard, 1989), the Flora de Nicaragua (Pool, 2001), the Flora de Panama

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

(Woodson & al., 1968), the Flora de Puerto Rico (Liogier, 1994) and the Flora of the Venezuelan Guyana (Olson & al., 1999), among others.

Regarding the Old World species, for which no taxonomic revision for the whole region is available for the genus, the approach consisted in investigating every revision in local floras or from independent publications. The principal source of information were regional Floras, mainly the Flora of Australia (Sleumer, 1982), Flora of British India (Clarke, 1879) and the Flora of India (Mitra, 1993), Flora of China (Qiner & Zmarzty, 2007), Co's Digital Flora (Pelser & al., 2019), Flora of Tropical East Africa (Sleumer, 1975), the Flora Malesiana (Sleumer, 1954), the Flora of Thailand (Harwood, 2015), the Flora of Vietnam (Ho, 1999) and the revision of Breteler for West and Central African *Casearia* species (Breteler, 2008). If there is a disagreement between an already existing database and a regional Flora, the treatment of the Flora was followed as it presents a published work, based on investigation of specimen's vouchers.

In order to investigate the species diversity in both the Neotropics and the Paleotropics, distribution for each species was implemented from the World Checklist of Vascular Plants (WCVP, 2019). The data was verified and changed, if necessary, by comparing with local and regional flora, as well as taxonomic revisions. The regions were divided according to the World Geographical Scheme for Recording Plant Distributions (TDWG, level 3) (Brummit, 2001). For the New World, the defined regions are Brazil, the Caribbean, Central America, Mexico, Northern South America, Southern South America and Western South America. For the Old World, in Asia the regions were divided with the level 2 or 3 of TDWG, depending of if they harbour a high diversity of species. Therefore, Asia was divided into Asia temperate (TDWG level 2), and since the diversity is more important in Asia tropical, that area was divided into Indian subcontinent, Indo-China, Malesia and Papuasia (TDWG level 3). Regarding Oceania, the regions were divided into Australasia and Pacific (TDWG level 2). Africa was divided according to TDWG into East Tropical Africa, North-East Tropical Africa, Southern Africa, South Tropical Africa, and West Central Tropical Africa, Western Indian Ocean and West Tropical Africa (TDWG level 3).

As there is no *Casearia* species shared between the Neotropics and the Paleotropics, the database is composed of two sections, one including New World taxa and one including Old World taxa. The genera *Hecatostemon*, *Laetia*, *Samyda* and

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

Zuelania that were recently merged within the genus *Casearia* based on both morphological and molecular data, were also included in the checklist, under their currently accepted names (Samarakoon & Alford, 2019).

Information was compiled and verified regarding authorship, synonyms and protologues. For each species, the taxonomical status was also verified and modified if necessary, adding the reference with the secundum function. Type information of each taxon were researched with protologues and through a search in online herbaria and included into the database, as well as information such as collector number and name, area and year of collection, when available. Other information such as morphology, keys or type specimen scans are not yet included.

The checklist is presented here as an Appendix (Appendix 1).

4.4 Results

The database compiled includes 222 currently accepted species of *Casearia*, five subspecies and 12 varieties. It consists of three parts, one with 103 species from the New World, one with 119 species from the Old World and 22 excluded names. In total, it includes 708 names and 464 synonyms.

Results were compared between three databases, the Plant List; Plants of the World Online and World Checklist of Vascular Plants, and the checklist realised in the present study in terms of numbers of species. Results are presented in Table 4.1. The Plant List retrieved 185 fewer names than the checklist presented here, but it is comparable in term of accepted species and synonyms, respectively 235 and 473, whereas the checklist presented here retrieved 222 accepted species and 464 synonyms. The World Checklist of Vascular Plants also retrieved a lower number of names and synonyms, 617 and 374 which is 91 fewer names than the checklist and 90 fewer synonyms; however it contains nine more accepted species. Finally, Plants of the World Online contains the same number of names with 708 names but a higher number of accepted species 235 (POWO, 2021).

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of Casearia

	Total	Accepted	Synonyms	Unresolved	Subspecies	Varieties
EDIT	708	222	464	22	5	12
Plant List	523	216	281	26	1	8
POWO	708	235	473	-	3	4
WCVP	617	231	374	12	3	5

Table 4.1: Comparison between Plant of the World Online, the Plant List and the checklist presented here, in term of number of accepted species, synonyms and unresolved taxa.

A comparison between this checklist and the previous revision of Sleumer (1980) is found in Table 4.2. Regarding the Neotropical species, the present database includes 28 more taxa compared to Sleumer's revision that contained 75 accepted species and 176 synonyms.

	Total	Accepted species	Synonyms
Sleumer, 1980	251	75	176
EDIT New World	422	103	319

Table 4.2: Comparison of the checklist for the New World species and Flora Neotropica (Sleumer, 1980)

The species with the most synonyms are found in Table 4.3. It is the New World *C. aculeata* Jacq. with 37 synonyms. In contrast, the species with more synonyms for the Old World possess half less than the one in the New World. It is *C. grewiiifolia* var. *gelonioides* (Blume) Sleumer with 17 synonyms.

Species with most synonyms	Geography	EDIT	Sleumer's revision
<i>C. aculeata</i> Jacq.	New World	37	35
<i>C. sylvestris</i> Sw.	New World	33	38
<i>C. arborea</i> Kunth	New World	25	26
<i>C. grewiiifolia</i> var. <i>gelonioides</i> (Blume) Sleumer	Old World	17	-
<i>C. tomentosa</i> var. <i>tomentosa</i> Roxb.	Old World	15	-

Table 4.3: Taxa retrieved with highest number of synonyms

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

The approach here was to compile existing information and thus, it is no taxonomical revision of *Casearia*, as species delimitation need to be further investigated. However, it provides the necessary information to conduct such investigations in the genus.

Casearia grewiifolia var. *gelonioides* is here presented at the variety level, following Flora of India (Mitra, 1993) and Flora Malesiana (Sleumer, 1954). However, it is to be noted that Harwood & Tathana (2011) strongly suspect that the taxa should actually be raised at the species level, based on morphological data.

Some inconsistencies were found between the WCVF and our checklist. In the Old World taxa, some species had incomplete distribution information, such as *C. calva* Craib, that was synonymised by Sleumer with *C. grewiifolia* var. *gelonioides* (Blumer) Sleumer in the Flora of Thailand (Sleumer, 1985). It was later accepted as a species by Harwood (Harwood & Tathana, 2011) who first reported it from Thailand and later also reported it from Peninsular Malaysia and Indonesia, in the Flora of Thailand (Harwood, 2015). Likewise, *C. halmaherensis* Slooten is endemic to Indonesia (Slooten, 1925).

For the New World taxa, some species were wrongly reported from some areas, such as *C. maynacarpa* Liesner & P. Jorg., reported from Bolivia, Brazil, North Colombia, Peru, and Bangladesh, which is most likely a mistake. Indeed, no *Casearia* species have been found to be shared between the Neotropics and the Paleotropics. Another inconsistency was with *C. nitida* Jacq. This species is Caribbean and the phylogenetic study of the previous chapter (Chapter 2) retrieved it with good support within the Caribbean clade. It was described from Jamaica, although the author did not collect any authentic material. Sleumer (1980) reported it from Cuba, the Bahamas, Hispaniola and Jamaica. However, it was wrongly reported from Mexico. It seems that *C. nitida* is often confused with *C. corymbosa* Kunth, a solely continental taxon, as one of the original drawing attributed to *C. nitida* was actually from Cartagena in Colombia and most likely a *C. corymbosa* (Sleumer, 1980). Thus, its distribution was modified in the checklist.

Number of species in each region is presented in Fig. 4.1 and level of endemism in Fig. 4.2. In the Neotropics, the region Brazil (TDWG) harbours the highest number of species with 52 taxa, 21 being endemics (40%), followed by Western South America with

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

44 species, 9 endemics (20%) and Northern South America with 31 species and only one endemic (3%). The Caribbean presents the highest level of endemic species 33 species and 19 endemics (58%). Central America harbours 27 species and nine endemics (33%). Finally, Mexico possesses 18 species with three endemic (17%) and Southern South America seven species with none being endemics.

In the Palearctic, the Pacific has the highest number of species, 51, with 50 being endemic (98%), it is followed by Malesia with 40 species and 32 endemic (80 %) and Indo-China that harbours 15 taxa, three endemic (20%). The regions Asia temperate, Australasia and Indian Subcontinent possess the same number of species, seven, with respectively, one (0.1%), four (57%) and two (29%) endemics. For Africa, Western Tropical Africa harbours the highest number of species with five taxa, three being endemic (60%), followed by Western Central Tropical Africa and Eastern Tropical Africa with both four species and one endemic. South Africa and Southern Tropical Africa harbour both two species of *Casearia*, South Africa with one endemic species, whereas Southern Tropical Africa does not present any endemic taxa. Finally, Northern Tropical Africa only presents one species of *Casearia*, *C. barteri* Mast., which is not endemic to the region.

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of Casearia

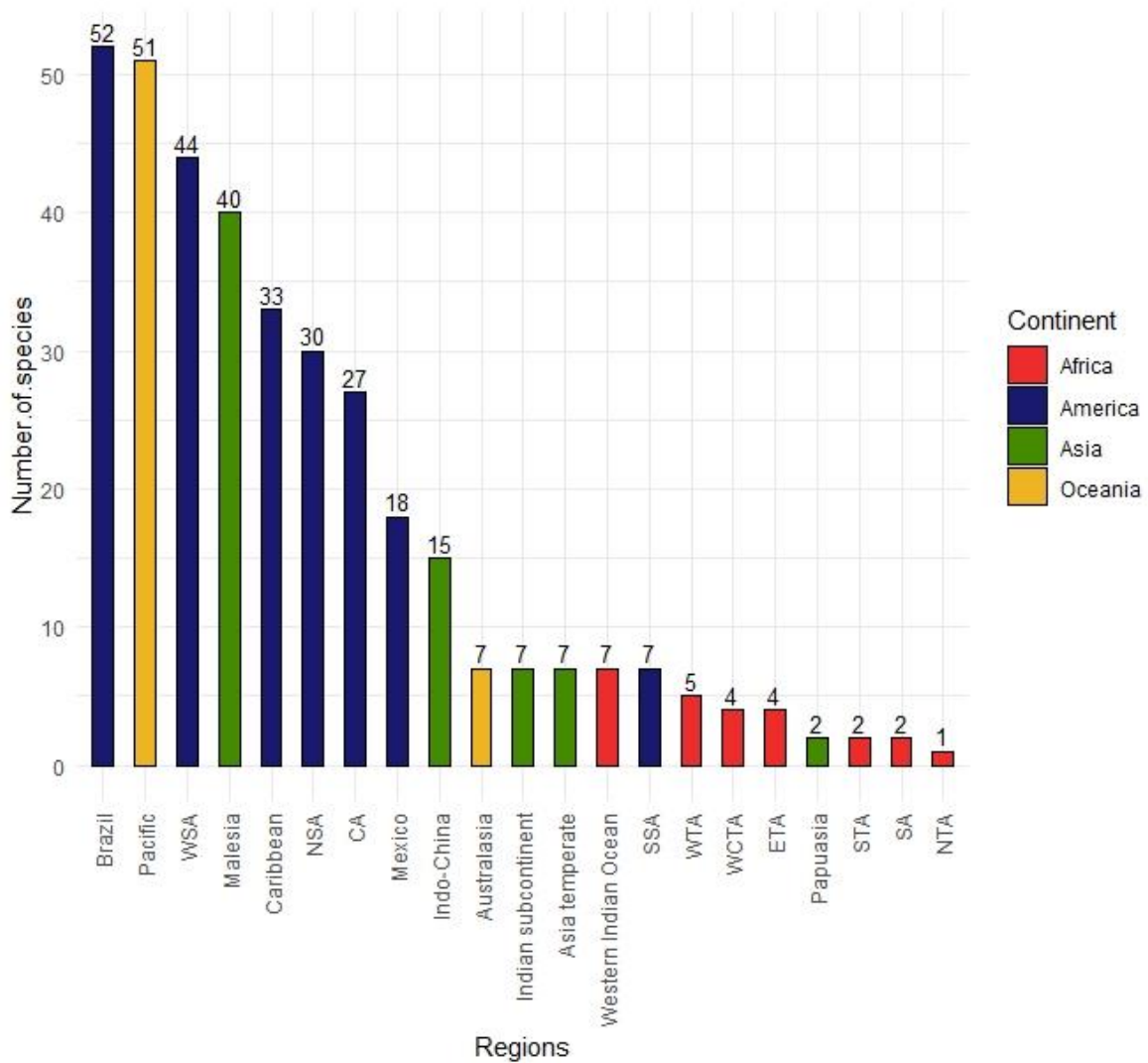


Fig. 4.1: Number of species per region (CA: Central America, WSA: Western South America, NSA: Northern South America, SSA: Southern South America, WTA: Western Tropical Africa, NTA: Northeast Tropical Africa, WCTA: Western Central Tropical Africa, ETA: Eastern Tropical Africa, STA: Southern Tropical Africa, SA: Southern Africa).

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of Casearia

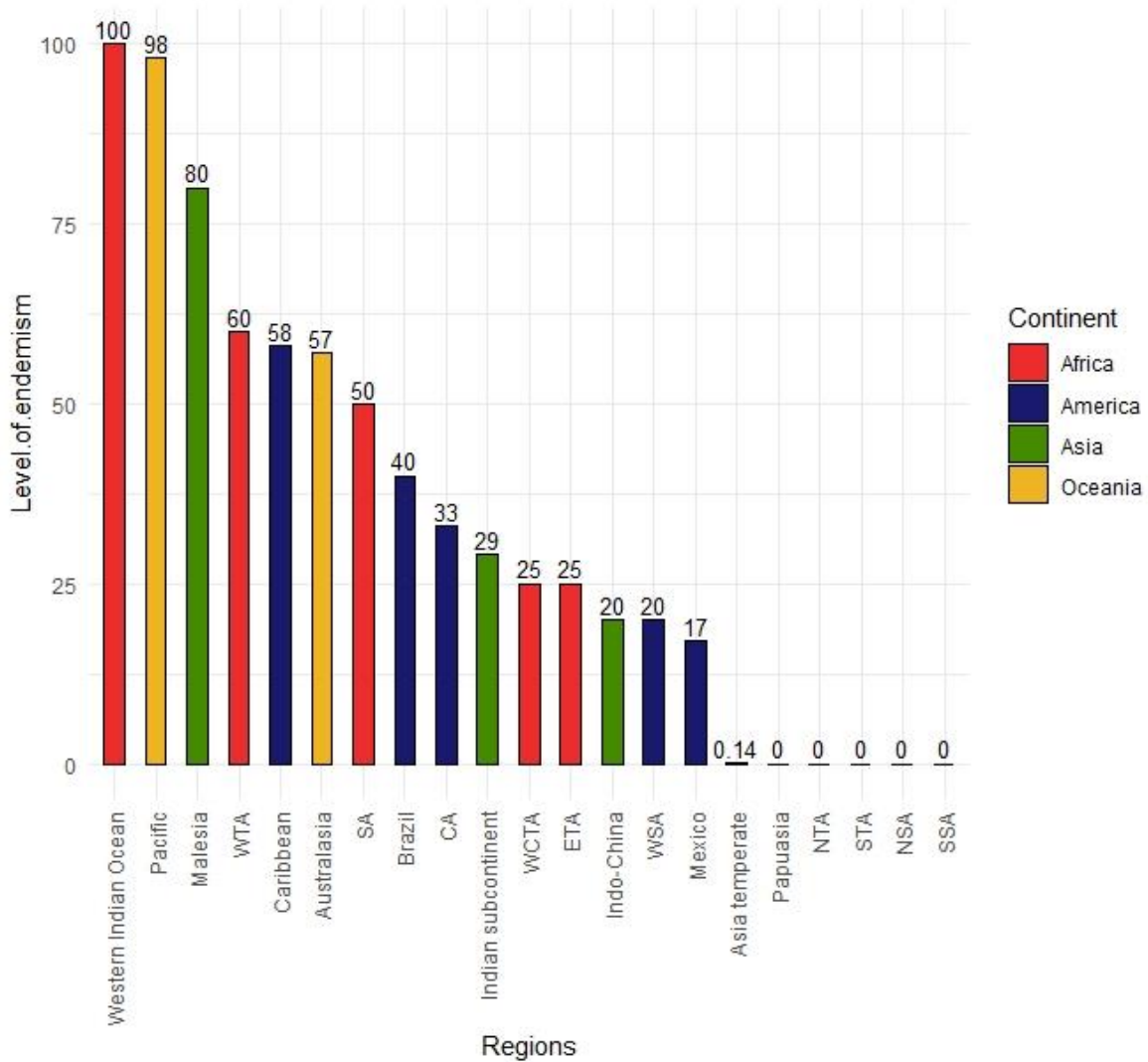


Fig. 4.2: Level of endemism per region (CA: Central America, WSA: Western South America, NSA: Northern South America, SSA: Southern South America, WTA: Western Tropical Africa, NTA: Northeast Tropical Africa, WCTA: Western Central Tropical Africa, ETA: Eastern Tropical Africa, STA: Southern Tropical Africa, SA: Southern Africa).

Overall, the New World regions harbour the highest number of species, as three of the five regions with more species belong to the Neotropics. It is followed by Oceania and Asia (Fig.4.1). Nevertheless, highest levels of endemism are retrieved in the Old World, with four of the five regions with higher endemism level belonging to the Paletropics (Fig.4.2).

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

4.5 Discussion

The work presented here is a global view on the diversity of *Casearia* in its current monophyletic circumscription. It has the objective to create a synthesis of the genus at a global scale and to unite all validly published names coming from various sources, from taxonomic revisions to regional and local floras. It is an expert-revised taxonomic backbone that includes the best possible knowledge on the circumscription of species, and provides clear references as to which names are accepted as species names and which are treated as synonyms. It is an online portal that will constitute an up-to-date dynamic taxonomic backbone. The novelty is that it contains all information and reference, crucial for further taxonomic work in the genus. Furthermore, all currently accepted 119 Old World species are compiled in the same database. It is also an updated checklist of the Neotropics, since the last revision of Sleumer (1980).

This checklist presents 28 new taxa for the New World, that were not mentioned in Sleumer's revision of *Casearia*, because they were published later or because they have changed name recently and in general it contains more names than the already existing databases. The first database, The Plant List presents 180 fewer names. The second, the Plants of the World Online database retrieves the same amount of names. Nevertheless, POWO contains more accepted species than the checklist presented here, mostly because POWO accepts taxa that are treated here as unresolved, given the scarce amount of taxonomic information available. For example, *C. astyla* Turcz. was treated as unresolved in the present checklist, since no further mention of the species was found in the studied Flora, however, it was accepted in POWO. Finally, the third database, the World Checklist of Vascular Plants also contains fewer names. Therefore, this work constitutes the most complete and cured database on the genus to this date, with references for each species.

Casearia is a species-rich genus of great morphological variability (Warburg, 1895; Hutchinson, 1967; Sleumer, 1980) and many taxa possess a lot of synonyms. The amount of synonyms retrieved for the New World, 319, is more than twice the number of synonyms of the Old World, 145. This is in part due to Sleumer's revision in 1980, that considerably reduced the number of species, as he synonymised many taxa (Sleumer, 1980). Second, there is no taxonomical revision made for the whole Paleotropics yet. It is likely one of the reason for such a gap in synonyms number between the two regions.

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of *Casearia*

Indeed, synonyms are often established when revising a genus at a global scale (Wortley & Scotland, 2004). Nonetheless, the checklist retrieved 143 more synonyms for the Neotropics than Sleumer's revision, mostly because four genera, *Hecatostemon*, *Laetia*, *Samyda* and *Zuelania*, that were considered as different from *Casearia* by Sleumer were merged together with the genus by Samarakoon in 2019 (Sleumer, 1980; Samarakoon & Alford, 2019).

Endemism level is crucial to establish conservation policies, as they are dependent on the correct definition of an area but also on the establishment of precise taxonomic treatments (Daru & al., 2020). The results presented here show that in the Neotropics, Brazil harbours the highest number of species, 52, whereas the highest level of endemism is retrieved in the Caribbean with 58% of the species being endemic.

There is an extremely high level of endemism in the Old World, with six of the 14 regions defined harbouring more than 50% of endemic species. The Western Indian Ocean and the Pacific present respectively 100% and 98% of their species being endemic. One of a possible reason for such a difference in endemism level between the New World and the Old world is that a global revision is still missing at the scale of the whole Old World. Species are described and studied in regional flora and species can be described multiple times under different names. Therefore, the establishment of a world checklist containing relevant information and including distribution data is crucial for taxonomical work, as it will allow the elaboration of clear species concepts. Taxonomical work will also be facilitated by the *secundum* function, allowing to give a reference to the circumscription of the taxa.

4.5 Specific outlook

The present chapter is an updated global checklist of all *Casearia* species, compiled with taxonomic information. The objective of such an investigation is that it can be used as a basis for conservation, ecology and taxonomic driven research.

The checklist of *Casearia* presented here has the advantage, compared to other existing database to compile crucial taxonomic information in the genus, such as type,

Chapter 4: Using the EDIT Platform for Cybertaxonomy to compile a comprehensive global taxonomic backbone of Casearia

synonyms and author of the species concept, which will considerably facilitate any later taxonomical work in the genus.

Chapter 5: General conclusions

5.1 Phylogeny of *Casearia* and its taxonomic implications

This PhD study presents the first well-resolved phylogenetic study of the genus *Casearia*, with plastid and nuclear markers, using Bayesian inference, maximum likelihood and parsimony analyses. The analyses retrieved all Samydeae in a monophyletic clade, including *Lunania*, *Ryania* and *Piparea* as successive sister to *Casearia*. However, the genus *Casearia* was not found to be monophyletic. Indeed, the two Neotropical genera *Euceraea* and *Neoptychocarpus* were retrieved nested within the genus with good support. Therefore, those two genera most likely belong to *Casearia* and in a coming publication, the taxonomical changes will be proposed. *Euceraea* and *Neoptychocarpus* will then be merged with *Casearia*, therefore establishing a monophyletic genus concept of *Casearia*. Within *Casearia*, nine major clade were identified that do not correspond to the sections described by Sleumer (Sleumer, 1980). The results retrieved a monophyletic Caribbean clade constituted of Caribbean endemic and an Old World clade, recovered within the New World taxa of *Casearia*. The old Samydeae genera *Laetia*, *Samyda* and *Zuelania*, that were recently merged within *Casearia* (Samarakoon & Alford, 2019) were also retrieved within the *Casearia* clade, therefore justifying the previous taxonomical changes established by Samarakoon & Alford.

Morphological characters, traditionally used to circumscribe *Casearia*, were studied using BayesTraits in order to find synapomorphies for the genus and two synapomorphic characters were retrieved, that can be used to delineate the genus. The first one is the character state of a branched inflorescence, either fasciculate, glomerulous or cymous and the second one is an uniseriate stamen series. On the contrary, the other characters studied; traditionally used as diagnostic characters for the genus were retrieved as homoplastic.

5.2 Biogeography of *Casearia*

The present PhD study investigated the evolutionary history of *Casearia*. Divergence time estimate and ancestral range were inferred using a Bayesian approach. The results show that the Samydeae clade originated in South America during the Cretaceous, 102 Ma. In the Eocene, approximately 90 Ma, the *Casearia* clade started to diversify. The analyses retrieved that the genus originated in South America and the Old World clade originated later during the Oligocene/Miocene boundary, 40 Ma, from New World ancestors. This Paleotropical clade was divided into an African and an Asia clade. However, the sampling of Old World species of the present study is not representative enough of the diversity of *Casearia* in the Paleotropics and further studies are needed to identify the origin of this Paleotropical clade. Two hypotheses can be made regarding the migration from the Neotropics toward the Paleotropics. The first hypothesis is that a migration occurred across Laurasia via the North Atlantic Land Bridge, a scenario already assumed for Malpighiaceae (Davis & al., 2002). The other hypothesis would be transoceanic dispersal events, as suggested in Solanaceae (Dupin & al., 2017).

The results show that *Casearia* migrated multiple times to the Caribbean, and gave rise to a clade of Caribbean endemics during the late Miocene, 9 Ma, therefore the relatively young age of the Caribbean clade reject the hypothesis of a GAARlandian route between South America and the Antille. This period correspond to the separation of the Caribbean islands from each other, which is expected to have triggered speciation in the area (Santiago-Valentin & Olmstead, 2004). The analyses indicate that this Caribbean clade is likely to be of South American origin. However, the sampling of Central American taxa does not allow to identify the migration routes from there toward the islands and it might be hypothesised that plants migrated first from South America towards Central America and from there towards the Caribbean islands, facilitated by short marine distance, as reported in many groups (Cervantes & al., 2016; Sosa & al., 2018; Roncal & al., 2020).

5.3 Integrative taxonomy as a tool to solve the case of nested singletons in phylogenetic studies

The present PhD study investigated the species limits of five Neotropical *Casearia* species. The phylogenetic analysis retrieved some nested singleton which are a single or a few specimen of an accepted species, nested within a clade of another accepted species. In the present study, a successful way to investigate the taxonomical status of those nested singletons is proposed with an integrative taxonomy approach, which studies morphology, ecology and distribution. If there is some phenotypical or ecological differentiation between the singleton and the taxon it is nested in, the nested placement of the specimen could be due to incomplete lineage sorting and the singleton might actually be a recently diverged species. On the contrary, if no morphological or ecological differentiation is retrieved between the two taxa, they could be considerate as a synonym. In the present study, the phenotypical differences were investigated by performing morphometric analyses, on character traditionally used to diagnose the species. Furthermore, the ecological difference between the two taxa was analysed by calculating niche space differentiation and performing ecological niche similarity and equivalence tests.

One species, *C. grandiflora*, was retrieved nested within the *C. arborea* clade. It presented some degree of morphological and ecological differentiation with *C. arborea*, suggesting that they are indeed two species and that *C. grandiflora* is most likely a recent emerging lineage. *C. manausensis* was also retrieved with good support within the *C. arborea* clade. The results of the morphological and ecological analyses show little differentiation with *C. arborea*, therefore suggesting that *C. manausensis* might be a subspecies of *C. arborea*. Two species, *C. selloana* and *C. zizyphoides*, were retrieved as nested singleton within the *C. sylvestris* clade. As for *C. manausensis*, the results of morphological and ecological analyses presented some little differentiation, indicating that the nested singleton likely represent a subspecies of *C. sylvestris*. Finally, *C. mariquitensis* was retrieved as a nested singleton within the *C. mollis* clade. The result of the morphological and ecological analyses shows an absence of differentiation, which suggest that the two species are synonyms.

5.5 A worldwide checklist of *Casearia* as a taxonomic backbone for the genus

This PhD study presents an up-to-date and curated checklist of all currently accepted *Casearia* species, for the first time at a global scale. Here, information from taxonomical revision, local flora and independent studies were combined, and a total of 708 names, 222 accepted species, 464 synonyms and 22 unresolved names were included, therefore presenting the most complete database of *Casearia* to date. The checklist is constituted of two parts, the first one includes all species of the New World and the second part compiles all species of the Old World. Since the last revision of Sleumer for the Neotropical *Casearia* (Sleumer, 1980), no checklist has been made regarding the species of the New World. Here, Sleumer's revision is updated by adding or correcting taxa. In the Paleotropics, no checklist has ever been drawn for the genus at the scale of the whole region. In the work presented in this study, information from different sources was compiled, in order to establish a reliable source of information, as to which species is present in the region. Therefore, this checklist is the first compilation of *Casearia* species from the whole Paleotropics into the same database. For each name, necessary taxonomical information was provided such as the protologue where the species was first published; complete type citation; synonyms and distributional data, in order to facilitate later work in the genus. The objective is to provide a dynamic taxonomic backbone, which can serve as a basis for any taxonomical research and to the establishment of efficient conservation and biodiversity management measures.

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List of manuscripts

Chapter 2 and 3 of the thesis serves as the basis for manuscript submitted or in preparation for submission to peer-reviewed journals.

- **de Mestier, A.; Brokamp, G.; Celis, M., Falcón Hidalgo; B.; Gutiérrez, J.; Borsch, T.** Character evolution and biogeography of *Casearia* (Salicaceae): evidence for the South American origin of a pantropical genus and for multiple migrations to the Caribbean islands (submitted to *Taxon*, 2021)

Own contribution:

Fieldwork, data acquisition and analyses, writing of the manuscript.

- **de Mestier, A.; Lücking, R.; Gutiérrez, J.; Borsch, T.** (in preparation) Nested singleton in phylogenetic analyses: do they indicate taxonomic synonymy or emerging lineage? **Nested singletons in species-level phylogenetic trees of *Casearia* (Salicaceae): evidence for synonymy or emerging lineages?**

Own contribution:

Fieldwork, data acquisition and analyses, writing of the manuscript.

Appendices

Supporting information to Chapter 2

Appendix 2.1 Taxa used for molecular data (Name and author, Labnumber, DNA bank number, locality, collector and collector number, herbarium voucher and NCBI accession number for rps4/trnLF, trnK/matK, rpl16, petD and ITS, respectively). Herbaria acronyms for voucher locations follow Index Herbariorum (Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/>). Species names are used following Sleumer (1980). Accessions are listed in alphabetic order. Abbreviations: s.n. = sine numero (without number). ¹Korotkova & al. (2009), ²Li & al. (2019), ³Alford (2005)

Outgroups: *Azara salicifolia* Griseb., N521, Bolivia, *G. Torrico & C. Peca* 204 (LPB), FM178041¹; *Dovyalis caffra* (Hook. f. & Harv.) Warb., BG Bochum, *T. Borsch* (B), FM178039¹; *Flacourtia jangomas* (Lour.) Raeusch., BG Bonn 12841, *N. Korotkova* 59 (BONN), FM1780421¹; *Idesia polycarpa* Maxim., BG Bonn 15364, *N. Korotkova* 12 (BONN), FM178040¹; *Lacistema nena* J. F. Macbr., SAL092, Colombia: La Guajira, *M.C. Martinez-Habibe & al.* 2552 (UNO), HG997980, HG997900, HG998084, FR990812; *Lacistema nena* J. F. Macbr., SAL093, Colombia: La Guajira, *M.C. Martinez-Habibe & al.* 2553 (UNO), HG997981, HG997901, HG998085, FR990813; *Lacistema nena* J. F. Macbr., N512, Bolivia, *P. Espinoza* 3 (B, LPB), FM178032¹; *Ryania speciosa* var. *subuliflora* (Sand.) Monach., SAL152, DB 44793, Peru, *M. Rimachi* Y. 8081 (BR), HG998004, HG997922, HG998104, FR990829; *Salix purpurea* L., BG Bonn 17982, *A. Worberg* 30 (BONN), FM178037¹; *Salix reticulata* L., Germany: Bavaria, *T. Borsch* 3825 (B), FM178038¹; *Tetratylacium macrophyllum* Poepp., SAL149, DB 44790, Peru: Loreto, *M. Rimachi* Y. 8224 (BR), HG997921, HG998103, FR990828; *Xylosma spiculifera* (Tul.) Triana & Planch., SAL124, Colombia: Cundinamarca, *Mariasole Calbi & al.* 205 (JBB), HG997991, HG998094, FR990817

Ingroups: *Casearia aculeata* Jacq., SAL006, DB 44708, Cuba: Guantanamo, *T. Borsch* 4284 (HAJB, B), HG997945, HG997867, FR990780; *Casearia aculeata* Jacq., SAL014, DB 44716, Cuba: Villa Clara, *T. Borsch* 5243, (HAJB, B), HG997951, HG997871, HG998057, FR990786; *Casearia aculeata* Jacq., SAL029, DB 27861, Dominica: Pedernales, *W. Greuter* 26587 (B), HG997964, HG997884, HG998070, FR990798; *Casearia aculeata* Jacq., SAL030, DB 27862, Ecuador: Guayas, *E. Asplund* 15213 (B), HG997965, HG997885, HG998071, FR990799; *Casearia aculeata* Jacq., SAL079, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2510 (UNO), HG997978, HG997898,

HG998082; *Casearia aculeata* Jacq., SAL086, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2538 (UNO), FR990811; *Casearia aculeata* Jacq., SAL100, Colombia: La Guajira, *M.C. Martinez-Habibe & al.* 2591 (UNO), HG997985, HG997905, HG998088; *Casearia aculeata* Jacq., SAL101, Colombia: La Guajira, *M.C. Martinez-Habibe & al.* 2593 (UNO), HG997986, HG997906, HG998089; *Casearia aculeata* Jacq., SAL104, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2605 (UNO), HG997988, HG997908, HG998091; *Casearia aculeata* Jacq., SAL105, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2606 (UNO), HG997989, HG997909, HG998092; *Casearia aculeata* Jacq., SAL108, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2611 (UNO), HG997990, HG997910, HG998093, FR990816; *Casearia aculeata* Jacq., SAL137, DB 44778, Cuba: Artemisa, *S. Fuentes & al.* 1977 (HAJB, B), HG997997, HG997916, HG998098, FR990823; *Casearia aculeata* Jacq., SAL174, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2929 (UNO), HG998009, HG998109; *Casearia aculeata* Jacq., SAL175, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2938 (UNO), HG998010, HG997928, HG998110; *Casearia aculeata* Jacq., SAL176, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2940 (UNO), HG998011, HG998111; *Casearia aculeata* Jacq., SAL198, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 3000 (UNO), HG998019, HG997935, HG998119, FR990838; *Casearia aculeata* Jacq., SAL209, Colombia: La Guajira, *M.C. Martinez-Habibe & al.* 2745 (UNO), HG998021, HG997937, HG998121, FR990840; *Casearia aculeata* Jacq., SAL210, Colombia: La Guajira, *M.C. Martinez-Habibe & al.* 2756 (UNO), HG998022, HG997938, HG998122, FR990841; *Casearia arborea* (Rich.) Urb., SAL009, DB 44711, Cuba: Guantanamo, *T. Borsch & al.* 4845 (HAJB, B), HG997947, HG998055, FR990782; *Casearia arborea* (Rich.) Urb., SAL024, DB 44726, Cuba: Holguin, *S. Fuentes & al.* 1370 (HAJB, B), HG997959, HG997880, HG998065, FR990794; *Casearia arborea* (Rich.) Urb., SAL032, DB 27864, Jamaica: Parish of Clarendon, *E. Köhler* 231 (HAJB, B), HG997966, HG997886, HG998072, FR990800; *Casearia arborea* (Rich.) Urb., SAL033, DB27865, Colombia: Antioquia, *R. Fonnegra* 6711 (B), HG997967, FR990801; *Casearia arguta* Kunth, SAL034, DB27866, Mexico: Chiapas, *E. Martinez* M-26281 (B), HG997968, HG997887, HG998073, FR990802; *Casearia barteri* Mast., SAL145, DB 44786, Gabon: Moyen-Ogooué, *F. J. Breteler* 13106 (BR), HG998001, HG997919, HG998102, FR990826; *Casearia bicolor* Urb., SAL126, DB33090, Guyana: Rupununi, *M. J. Jansen-Jacobs* 2495 (B), HG997992, HG997911, FR990818; *Casearia bissei* J.E. Gut., SAL008, DB 44710, Cuba: Guantanamo, *M. Ackerman* 862 (HAJB, B), HG997946, HG997868, HG998054, FR990781; *Casearia bissei* J.E. Gut., SAL012, DB 44714, Cuba: Guantanamo, *T. Borsch & al.* 4428 (HAJB, B), HG997949, HG997869, HG998056, FR990784; *Casearia combaymensis* Tul., SAL036, DB27868, French Guyana, *J.J. de Granville* 13157 (B), HG997969, HG997888, HG998074, FR990803; *Casearia comocladifolia* Vent., SAL027, DB 44729, Cuba: Independancia, *S. Fuentes & al.* 1164 (HAJB, B), HG997962, HG997882, HG998068, FR990796; *Casearia comocladifolia* Vent., SAL028, DB 44730, Cuba: Barahona, *S. Fuentes & al.* 1212 (HAJB, B), HG997963, HG997883, HG998069, FR990797; *Casearia commersoniana* Cambess., SAL241, Costa Rica, *Salaza* 2638 (BH); *Casearia corymbosa* Kunth, SAL057, DB27889, Mexico: Oaxaca, *Misael Elorsa* C. 478 (B), HG997973, HG997892, HG998077, FR990805; *Casearia corymbosa* Kunth, SAL078, Colombia:

Bolivar, *M.C. Martinez-Habibe & al.* 2502 (UNO), HG997897, HG998081; *Casearia corymbosa* Kunth, SAL080, Colombia: Bolivar, *M.C. Martinez-Habibe & al.* 2512 (UNO), HG997979, HG997899, HG998083; *Casearia corymbosa* Kunth, SAL096, Colombia: La Guajira, *M.C. Martinez-Habibe & al.* 2572 (UNO), HG997983, HG997903, HG998086; *Casearia corymbosa* Kunth, SAL102, Colombia: La Guajira, *M.C. Martinez-Habibe & al.* 2598 (UNO), HG997987, HG997907, HG998090; *Casearia corymbosa* Kunth, SAL181, Colombia: Magdalena, *M.C. Martinez-Habibe & al.* 2973 (UNO), HG998012, HG997929, HG998112; *Casearia corymbosa* Kunth, SAL182, Colombia: Magdalena, *M.C. Martinez-Habibe & al.* 2976 (UNO), HG998013, HG997930, HG998113; *Casearia corymbosa* Sw., SAL185, Colombia: Magdalena, *M.C. Martinez-Habibe & al.* 2982 (UNO), HG998015, HG997932, HG998115, FR990836; *Casearia corymbosa* Kunth, SAL187, Colombia: Magdalena, *M.C. Martinez-Habibe & al.* 2986 (UNO), HG998016, HG997933, HG998116; *Casearia corymbosa* Kunth, SAL189, Colombia: Magdalena, *M.C. Martinez-Habibe & al.* 2988 (UNO), HG998018, HG997934, HG998118; *Casearia crassinervis* Urb., SAL002, DB 44704, Cuba: Holguin, *T. Borsch & al.* 4056 (HAJB, B), HG997942, HG998052, FR990778; *Casearia crassinervis* Urb., SAL015, DB 44717, Cuba: Holguin, *N. Köster & al.* 2724 (HAJB, B), HG997952, HG997872, HG998058, FR990787; *Casearia crassinervis* Urb., SAL019, DB 44721, Cuba: Holguin, *S. Fuentes & al.* 453 (HAJB, B), HG997956, HG997876, HG998062; *Casearia decandra* Jacq., MN078142² (complete genome); *Casearia deplanchei* Sleumer, SAL164, DB 44875, New Caledonia, *G. Dagostini* 783, P 04819071, HG998006, HG997925, HG998106, FR990832; *Casearia dodecandra* (Jacq.) T. Samar. & M.H. Alford, SAL127, DB 33091, Dominica: Pedernales, *W. Greuter* 26585 (B), HG997993, HG997912, HG998095, FR990819; *Casearia gladiiformis* Mast., SAL148, DB 44789, Mozambique, *P. C. M. Jansen* 7670, BR 0000015960818, HG998003, HG997920, FR990827; *Casearia glomerata* Roxb., SAL142, DB 44783, Hong Kong, *L. Tsuen* 12687 (BR), HG998000, HG997918, HG998101, FR990825; *Casearia grewiifolia* Vent., SAL161, DB 44874, Vietnam, *U. Swenson* 1541 (P), HG997924, HG998105, FR990831; *Casearia sp.*, SAL017, DB 44719, Cuba: Holguin, *S. Fuentes & al.* 442 (HAJB, B), HG997954, HG997874, HG998060, FR990789; *Casearia javitensis* Kunth, SAL169, DB 44877, French Guyana, *J. J. de Granville* 17165 (P), FR990834; *Casearia laetioides* (A. Rich.) Northr., SAL139, DB 44780, Cuba: Pinar del Rio, *T. Borsch & al.* 5954 (B), HG997999, HG998100; *Casearia manausensis* Sleumer, SAL053, DB27885, Brasil: Amazonas, *J. L. Santos* 855 (B), HG997971, HG997890, HG998076; *Casearia mariquitensis* Kunth, SAL054, DB27886, Guyana: Rupununi, *M. J. Jansen-Jacobs* 4348 (B), HG997972, HG997891; *Casearia moaensis* Vict., SAL026, DB 44728, Cuba: Holguin, *S. Fuentes & al.* 1689 (HAJB, B), HG997961, HG998067, FR990795; *Casearia mollis* Kunth, SAL013, DB 44715, Cuba: Villa Clara, *T. Borsch & al.* 5138 (HAJB, B), HG997950, HG997870, FR990785; *Casearia mollis* Kunth, SAL023, DB 44725, Cuba: Matanzas, *T. Borsch & al.* 5611 (HAJB, B), HG997879, HG998064, FR990793; *Casearia mollis* Kunth, SAL136, DB 44777, Cuba: Artemisia, *S. Fuentes & al.* 1976 (HAJB, B), HG997996, HG997915, HG998097, FR990822; *Casearia nitida* Jacq., SAL021, DB 44723, Cuba: Las Tunas, *S. Fuentes & al.* 841 (HAJB, B), HG997958, HG997878, FR990791; *Casearia obliqua* Sprengel, SAL058, DB27890, Brasil: Parana, *R. Kummrow*

3000 (B), HG997974, HG997893, FR990806; *Casearia ophiticola* Vict., SAL020, DB 44722, Cuba: Holguin, S. Fuentes & al. 656 (HAJB, B), HG997957, HG997877, HG998063, FR990790; *Casearia ophiticola* Vict., SAL025, DB 44727, Cuba: Holguin, S. Fuentes & al. 1645 (HAJB, B), HG997960, HG997881, HG998066; *Casearia prismatocarpa* Mast., SAL144, Liberia, C. C. H. Jongkind 9804 (BR); *Casearia prunifolia* Kunth, SAL218, DB 44851, Peru: Loreto, A. Gentry 29158 (JBGP), HG998025, HG997941, FR990843; *Casearia selloana* Eichler, SAL065, DB27897, Brasil: Paraiba do Sul, Schwacke 3215 (B), HG997975, HG997894, HG998078; *Casearia spinescens* (Sw.) Griseb., SAL003, DB 44705, Cuba: Holguin, T. Borsch & al. 4115 (HAJB, B), HG997943, HG997866, HG998053, FR990779; *Casearia spinescens* (Sw.) Griseb., SAL018, DB 44720, Cuba: Holguin, S. Fuentes & al. 445 (HAJB, B), HG997955, HG997875, HG998061; *Casearia stipitata* Mast., SAL128, DB33096, Cameroon, A J. M. Leeuwenberg 9884 (B), HG997994, HG997913, HG998096, FR990820; *Casaria suaveolens* (Poepp.) T. Samar. & M.H. Alford, SAL 153, Peru, M. Rimachi Y. 7666 (BR), HG998005, HG997923, FR990830; *Casearia sylvestris* Sw., SAL016, DB 44718, Cuba: Holguin, SF 441 (HAJB, B), HG997953, HG997873, HG998059, FR990788; *Casearia sylvestris* Sw., SAL050, DB27882, Venezuela: Guericco, H. & E. Walter 236 (B), HG997970, HG998075; *Casearia sylvestris* Sw., SAL095, Colombia: La Guajira, M.C. Martinez-Habibe & al. 2569 (UNO), HG997982, HG997902, FR990814; *Casearia sylvestris* Sw., SAL097, Colombia: La Guajira, M.C. Martinez-Habibe & al. 2581 (UNO), HG997984, HG997904, HG998087, FR990815; *Casearia sylvestris* Sw., SAL184, Colombia: Magdalena, M.C. Martinez-Habibe & al. 2981 (UNO), HG998014, HG997931, HG998114; *Casearia sylvestris* Sw., SAL188, Colombia: Magdalena, M.C. Martinez-Habibe & al. 2987 (UNO), HG998017, HG998117, FR990837; *Casearia sylvestris* Sw., SAL200, Colombia: Bolivar, M.C. Martinez-Habibe & al. 3002 (UNO), FR990839; *Casearia sylvestris* Sw., SAL203, Colombia: Bolivar, M.C. Martinez-Habibe & al. 3005 (UNO), HG998020, HG997936, HG998120; *Casearia sylvestris* Sw., SAL211, Colombia: La Guajira, M.C. Martinez-Habibe & al. 2764 (UNO), HG998023, HG997939, HG998123; *Casearia sylvestris* Sw., SAL022, DB 44724, Cuba: Pinar del Rio, T. Borsch & al. 5784 (HAJB, B), FR990792; *Casearia sylvestris* subsp. *myricoides* (Griseb.) J.E. Gut., SAL010, DB 44712, Cuba: Guantanamo, T. Borsch & al. 4901 (HAJB, B), HG997948, FR990783; *Casearia sylvestris* subsp. *myricoides* (Griseb.) J.E. Gut., SAL138, DB 44779, Cuba: Sancti Spiritu, S. Fuentes & al. 1727 (HAJB, B), HG997998, HG997917, HG998099, FR990824; *Casearia ternstroemiodes* (Griseb.) T. Samar. & M.H. Alford, SAL 135, DB 44776, Cuba: Guantanamo, T. Borsch & al. 4425 (HAJB, B), HG997995, HG997914, FR990821; *Casearia tremula* (Griseb.) Griseb. ex C. Wright, SAL 170, DB, Nicaragua: Boaco, J. B. Quezada 242 (P), HG998008, HG997927, HG998108, FR990835; *Casearia tremula* (Griseb.) Griseb. ex C. Wright, SAL 213, DB 44846, Colombia: Bolivar, V. Londono 408 (JBGP), HG998024, HG997940, HG998124, FR990842; *Casearia ulmifolia* Vahl ex Vent., SAL071, DB27903, French Guyana, S. Mori 21177 (B), HG997976, HG997895, HG998079, FR990807; *Casearia velutina* MN078141² (complete genome); *Casearia zizyphoides* Kunth, SAL072, DB27904, Venezuela: Bolivar, J. A. Steyermark 88293 (B), HG997977, HG997896, HG998080, FR990808; ; *Euceraea nitida* Mart., SAL242, Brazil, G. Hobbes 213 (BH);

Neoptychocarpus apodanthus (Kuhl.) Buch., SAL167, DB 44802, French Guyana, *O. Lachenaud* 2143 (P), HG998007, HG997926, HG998107, FR990833; *Neoptychocarpus killipii* (Monach.) Buch., *Alford & Grandez* 3119, AY757040³

Table S1: Primers used for amplification and sequencing reactions

Primer	Sequence	Authors
trnTc	CGA AAT CGG TAG ACG CTA CG	Taberlet et al. (1991)
trnTf	ATT TGA ACT GGT GAC ACG AG	Taberlet et al. (1991)
trnL110R	GAT TTG GCT CAG GAT TGC CC	Borsch et al. (2003)
trnL460F	GAG AAT AAA GAT AGA GTC C	Worberg et al. (2007)
rps4-5R	AGG CCC TCG GTA ACG SG	Sauquet et al. (2003)
trnTd	GGGGATAGAGGGACTTGAAC	Taberlet et al. (1991)
trnT48R	CTTAGCTCAGAGGTTAGAGC	
MPmatK502F	CTTCGYTACTGGGTGAAAG	
MPmatK470F	TACCTTAYCCCATCCATCT	
SALmatK645R	AYTCGTATTCATATACATG	
SALmatK740F	CTTGTCTCAAGTAAATCGAG	
SALmatK830R	CTCCCGAAAGATAAGTGG	
SALmatK1960R	CCGAGAAATCAGCCCAGG	
SALmatK1800F	GTGGTACGGAGTCAAATGC	
psbA5'R	AACCATCCAATGTAAAGACGGTTT	Shaw et al. 2005
trnK-F-M13F	GTAAAACGACGGCCAGTGGGTTGCTAACTCAATGGTAGAG	Wicke & Quandt (2009)
rpl16R	TCTTCCTCTATGTTGTTTACG	Campagna & Downie (1998)
rpl16F	CTATGCTTAGTGTGTGACTC	Campagna & Downie (1998)
SALrpl16-570F	GCGATGGGAACGATGGAAC	
SALrpl16-710R	CTTCATTTGTGGGGTTAATC	
SALrpl16-653R	AATAACATAAAAACCTTCGC	

SALrp116-580F	GCGAAACTAACTAACCAAGAC	
PlpetB1365F	TTGACYCGTTTTTATAGTTTAC	Löhne&Borsch (2002)
CApetD324R	ATCCCYTGTTTCACTCCGATAG	Schäferhoff B. et al. 2009
PlpetD738R	AATTTAGCYCTTAATACAGG	Löhne &Borsch (2002)
CApetD194F	CAGGCTCCGTAARATCCAG	Schäferhoff B. et al. 2009
SALpetD-170F	ATGATCAGACCCAATCATG	
SALpetD-214R	AATAGAATATGAATTCTACC	
ITS4	TCCTCCGCTTATTGATATGC	White et al. (1990)
ITS5	GGAAGTAAAAGTCGTAACAAGG	White et al. (1990)
ITS2-SR	CTTAAACTCAGCGGGTAGTCCC	
ITS3	GCATCGATGAAGAACGCAGC	White et al. (1990)
ITS5-M13F	GTAAAACGACGGCCAGTGGAAAGTAAAAGTCGTAACAAGG	
SAL-ITS5	CGTAACAAGGTTCCGTAGGTG	
SAL-5-8S-R	CGGGATTCTGCAATTCACACC	

Table S2: Matrix of coded of morphological characters (Ch stands for characters)

Code_Species	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Source
<i>N512_Lacistema_nena</i>	0	0	0	1	0	0	1	Sleumer (1980), Macbride (1941)
<i>N521_Azara_salicifolia</i>	0	0	0	3	1	0	2	Sleumer (1980), Mac Alford (2015)
<i>N535_Dovyalis_caffra</i>	1	0	0	3	0	0	3	Protologue, herbarium specimen
<i>N483_Flacourtia_jangomas</i>	1	0	0	3	0	0	2	Sleumer (1955), Mac Alford (2015)
<i>N477_Idesia_polycarpa</i>	1	0	0	3	0	0	0	Yang (2007)
<i>N667_Oncoba_routledgei</i>	0	0	0	3	0	0	5	Type, herbarium voucher
<i>AY756902_Lunania_parviflora</i>	0	0	1	2	0	0	2	Sleumer (1980)
<i>AY757040_Neoptychocarpus_killipii</i>	1	1	1	2	0	1	3	Sleumer (1980), protologue, Mac Alford (2015)
<i>SAL124_Xylosma_spiculifera</i>	1	0	0	3	0	-	3	Sleumer (1980)
<i>SAL149_Tetrathylacium_macrophyllum</i>	0	0	0	1	0	-	0	Sleumer (1980), Mac Alford (2015)
<i>SAL152_Ryania_speciosa_var_subuliflora</i>	0	0	0	3	0	0	5	Sleumer (1980), Mac Alford (2015)
<i>N504_Salix_purpurea</i>	1	0	0	1	0	0	1	Argus (1986), herbarium specimen
<i>N507_Salix_reticulata</i>	1	0	0	1	0	0	1	Argus (2003), herbarium specimen
<i>MN078142_Casearia_decandra</i>	0	0	1	2	1	1	3	Sleumer (1980)
<i>MN078141_Casearia_velutina</i>	0	0	1	2	1	1	3	Sleumer (1955), Yang (2007)
<i>SAL019_Casearia_crassinervis</i>	0	0	1	2	1	1	4	Gutierrez (2000), herbarium voucher
<i>SAL018_Casearia_spinescens</i>	0	0	1	2	1	1	3	Gutierrez (2000)
<i>SAL012_Casearia_bissei</i>	0	0	1	2	1	1	4	Gutierrez (2000)
<i>SAL017_Casearia_sp</i>	0	-	1	2	1	-	3	Herbarium voucher
<i>SAL020_Casearia_ophitica</i>	0	0	1	2	1	1	4	Gutierrez (2000)
<i>SAL021_Casearia_nitida</i>	0	0	1	2	1	1	4	Gutierrez (2000), herbarium voucher
<i>SAL023_Casearia_mollis</i>	0	0	1	2	1	1	3	Sleumer (1980)
<i>SAL024_Casearia_arborea</i>	0	1	1	2	1	1	3	Sleumer (1980), herbarium voucher
<i>SAL026_Casearia_moaensis</i>	0	0	1	2	1	1	4	Gutierrez (2000), herbarium voucher
<i>SAL028_Casearia_comocladifolia</i>	0	0	1	2	1	1	3	Gutierrez (2000)
<i>SAL034_Casearia_arguta</i>	0	0	1	2	1	1	3	Sleumer (1980), herbarium voucher
<i>SAL036_Casearia_combaymensis</i>	0	1	1	2	1	1	3	Sleumer (1980)
<i>SAL053_Casearia_manausensis</i>	0	0	1	2	1	1	3	Sleumer (1980), herbarium voucher
<i>SAL054_Casearia_mariquitensis</i>	0	0	1	2	1	1	3	Sleumer (1980)
<i>SAL058_Casearia_obliqua</i>	0	0	1	2	1	1	3	Sleumer (1980)
<i>SAL065_Casearia_selloana</i>	0	0	1	2	1	1	3	Sleumer (1980)
<i>SAL071_Casearia_ulmifolia</i>	0	0	1	2	1	1	3	Sleumer (1980), Marquete (2012)
<i>SAL072_Casearia_zizyphoides</i>	0	0	1	2	1	1	3	Sleumer (1980), herbarium voucher
<i>SAL189_Casearia_corymbosa</i>	0	0	1	2	1	1	2	Sleumer (1980)
<i>SAL097_Casearia_sylvestris</i>	0	0	1	2	1	1	3	Sleumer (1980), herbarium voucher, Mac Alford (2015)
<i>SAL126_Casearia_bicolor_(Laetia_procera)</i>	0	0	1	3	0	1	3	Sleumer (1980), herbarium voucher
<i>SAL127_Casearia_dodecandra_(Samyda_dodecandra)</i>	0	0	1	2	1	1	3	Gutierrez (2000)
<i>SAL128_Casearia_stipitata</i>	0	0	1	2	1	1	3	Sleumer (1971), Breteler (2008)
<i>SAL135_Casearia_ternstroemioides_(Laetia_ternstroemioides)</i>	0	0	1	3	0	1	2	Sleumer (1980)
<i>SAL138_Casearia_sylvestris_subsp_myricoides</i>	0	0	1	2	1	1	3	Gutierrez (2000), herbarium voucher
<i>SAL139_Casearia_laetioides_(Zuelania_guidonia)</i>	0	0	1	3	1	1	3	Sleumer (1980), Gutierrez (2000)
<i>SAL142_Casearia_glomerata</i>	0	-	1	2	1	-	3	Yang (2007)

<i>SAL144_Casearia_prismatocarpa</i>	0	-	1	2	1	-	3	Breteler (2008)
<i>SAL145_Casearia_barteri</i>	0	0	1	2	1	-	3	Sleumer (1971), Breteler (2008)
<i>SAL148_Casearia_gladiiformis</i>	0	0	1	2	1	1	3	Sleumer (1971), Mac Alford (2015)
<i>SAL153_Casearia_suaveolens_(Laetia_suaveolens)</i>	0	0	1	2	0	1	3	Sleumer (1980)
<i>SAL161_Casearia_grewiaefolia</i>	0	-	1	2	1	1	3	Sleumer (1955)
<i>SAL167_Neoptychocarpus_apodanthus</i>	1	1	1	2	0	1	3	Sleumer (1980)
<i>SAL213_Casearia_tremula</i>	0	0	1	3	1	1	3	Sleumer (1980), Gutierrez (2000), Mac Alford (2015), herbarium voucher
<i>SAL218_Casearia_prunifolia</i>	0	0	1	2	1	1	3	Sleumer (1980)
<i>SAL164_Casearia_deplanchei</i>	0	0	1	2	1	-	3	Sleumer (1974), Lescot (1980)
<i>SAL014_Casearia_aculeata</i>	0	1	1	2	1	1	3	Sleumer (1980), Gutierrez (2000), herbarium voucher
<i>SAL241_Euceraea_nitida</i>	-	0	1	2	1	-	0	Sleumer (1980), Mac Alford (2015)
<i>SAL242_Casearia_commersoniana</i>	0	0	1	2	1	1	3	Sleumer (1980)

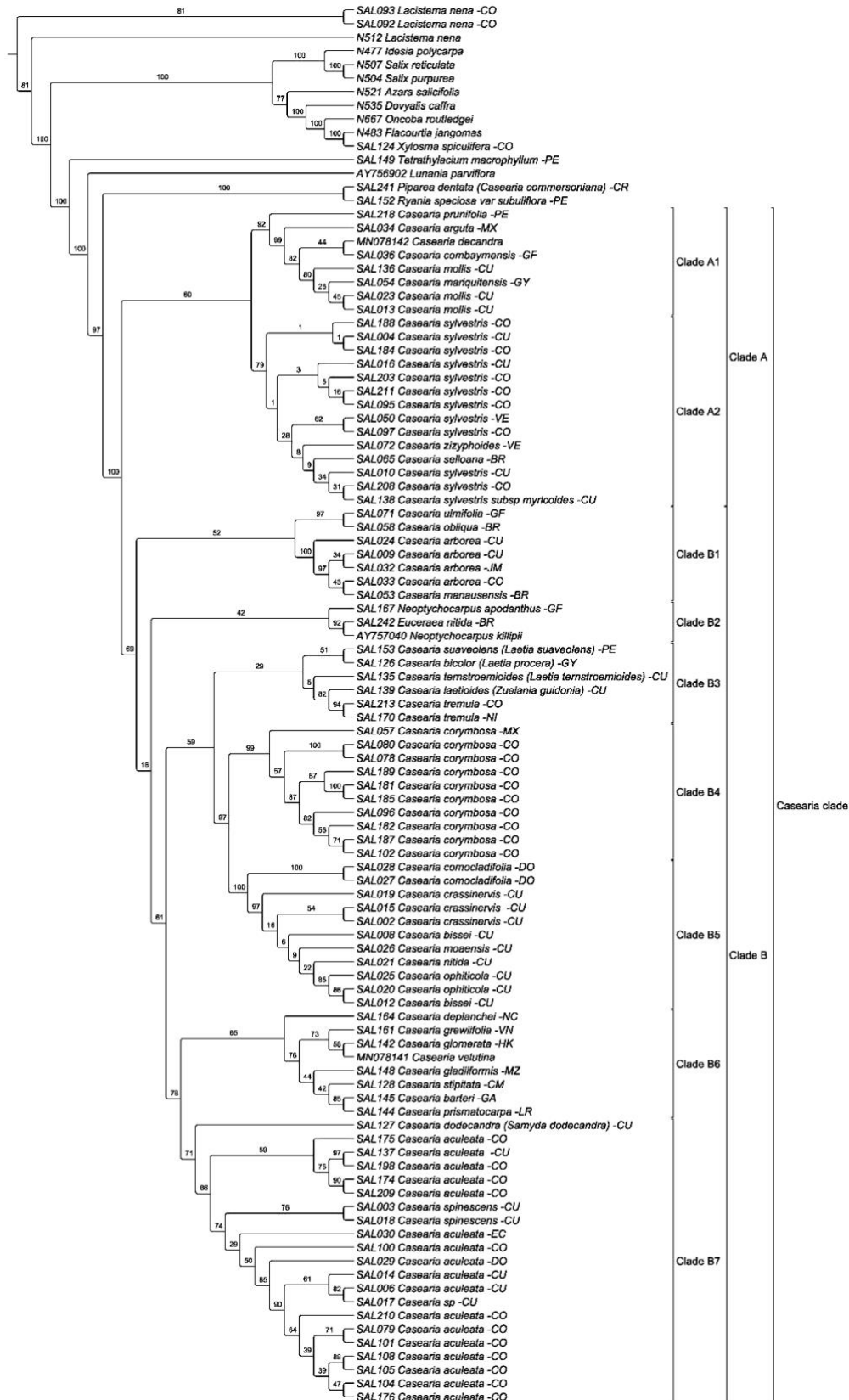
Table S3: Setting of fossils and secondary calibration points in the molecular analyses

	<i>Casearia</i>	<i>Pseudosalix</i>	Malpighiales
Prior distribution	lognormal	lognormal	normal
Offset	37	48	-
Mean	1	1	92.78
Standard deviation	1.2	1.2	4.6
Median age	39.7	50.7	92.9
Lower and upper boundary (5% and 95%) (Ma)	37.4-56.6	48.4-67.6	83.9-100

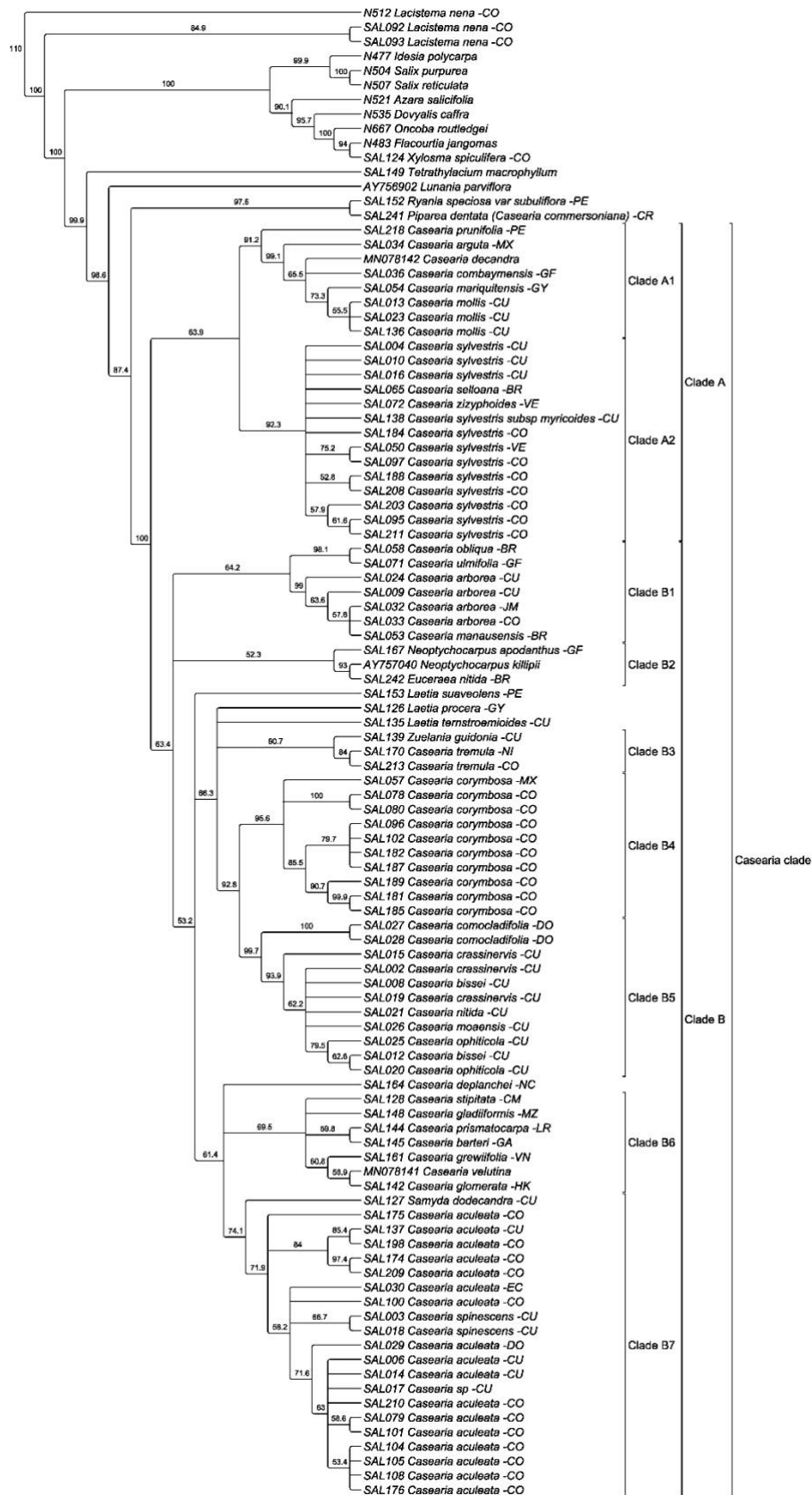
Table S4: Values of the marginal likelihood estimation and Bayes factor analyses using stepping-stone sampling with 150 path steps. In bold is the chosen model

Speciation prior (under UCLN)	ESS	MLE	BF
Birth-death model	110.52	-32418.39	349.34
Yule model	85.86	-32069.05	-

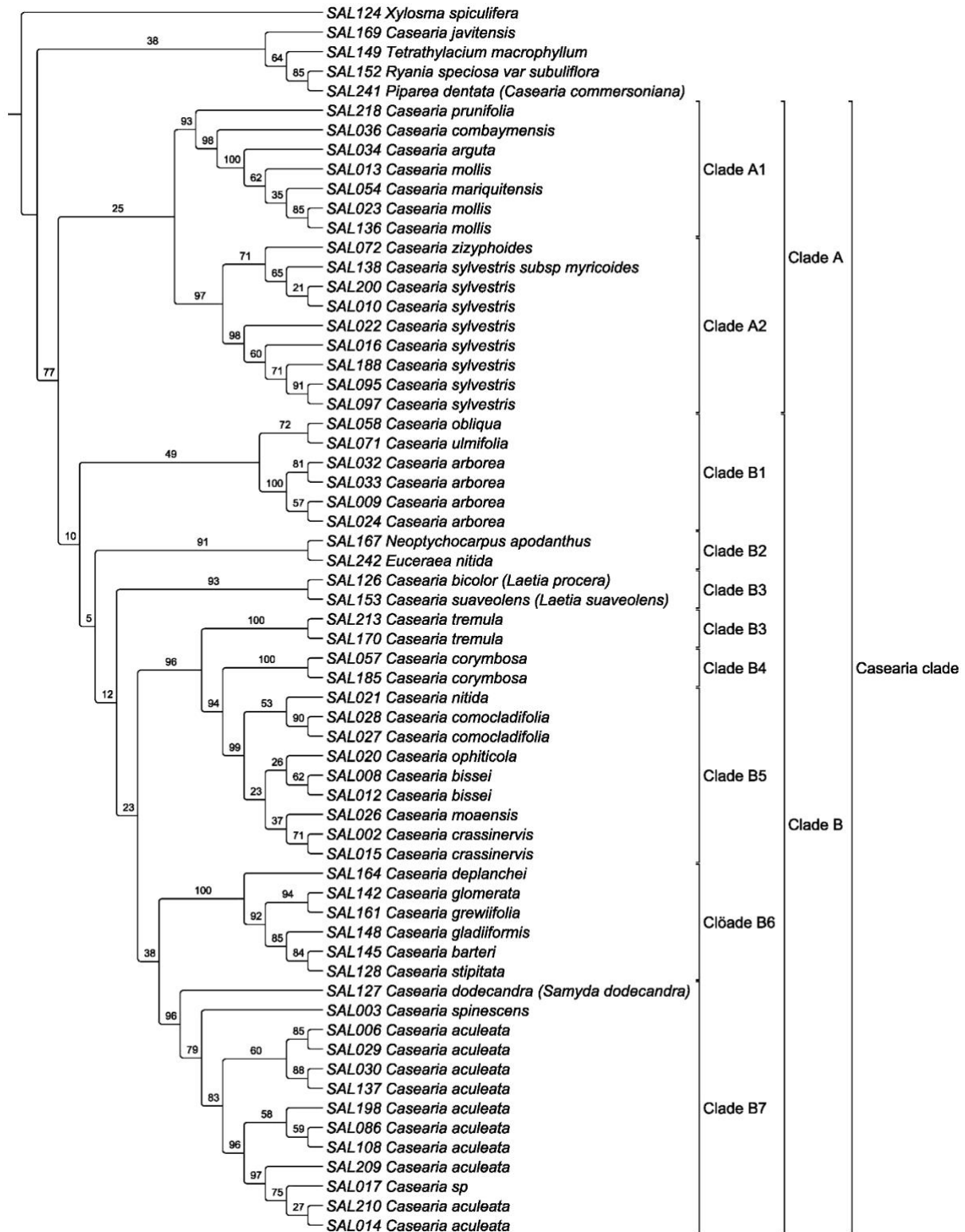
Appendix 2.2: Tree inferred with Maximum Likelihood, bootstrap support values are above the node for the chloroplastic dataset. At the tip of the node is the DNA number followed by the species name and the country code of where the individual was collected (see table 1 for more informations)



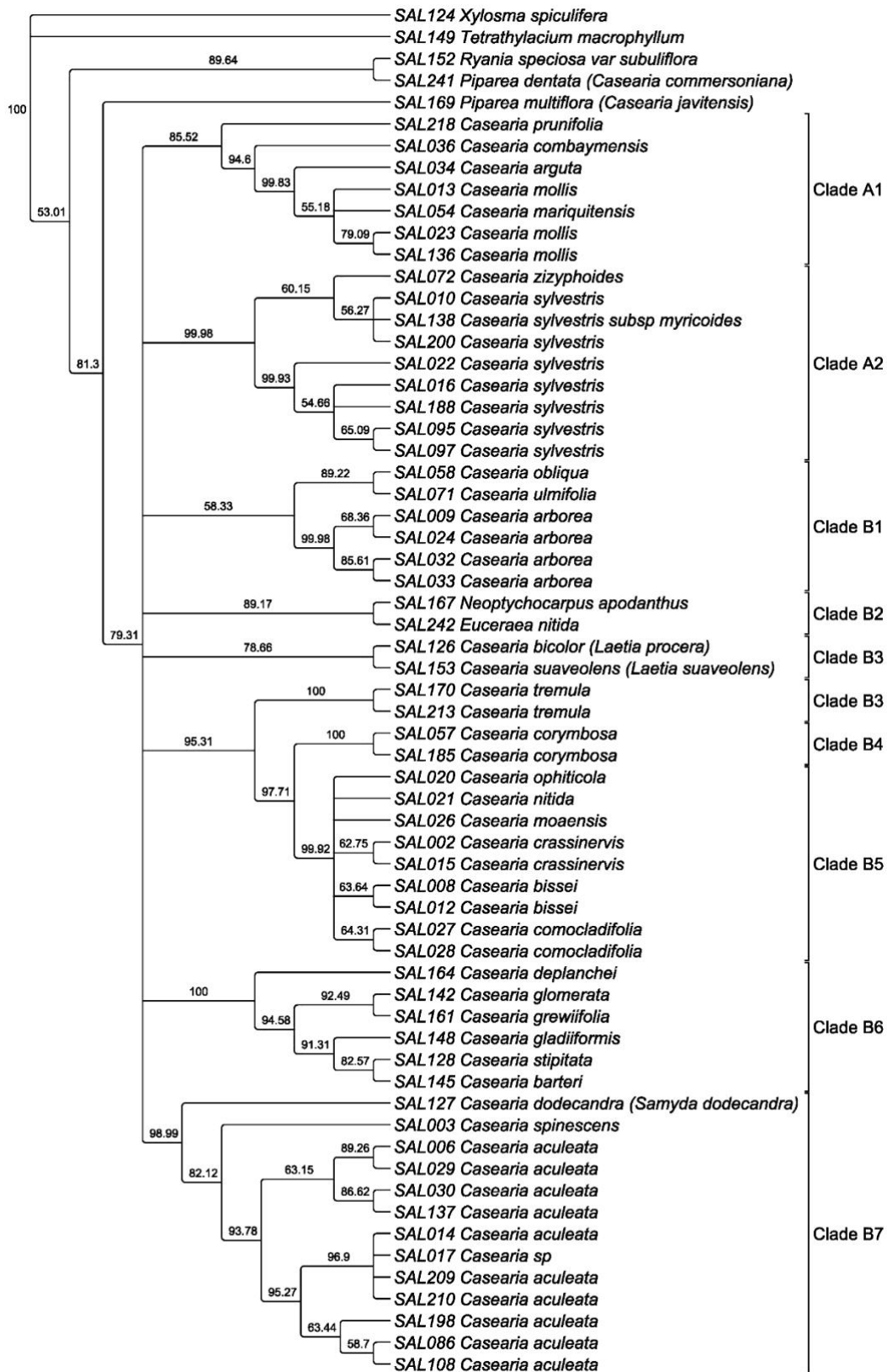
Appendix 2.3: Tree inferred with parsimony, Jackknife support values are above the node for the chloroplast dataset. At the tip of the node is the DNA number followed by the species name and the country code of where the individual was collected (see table 1 for more informations)



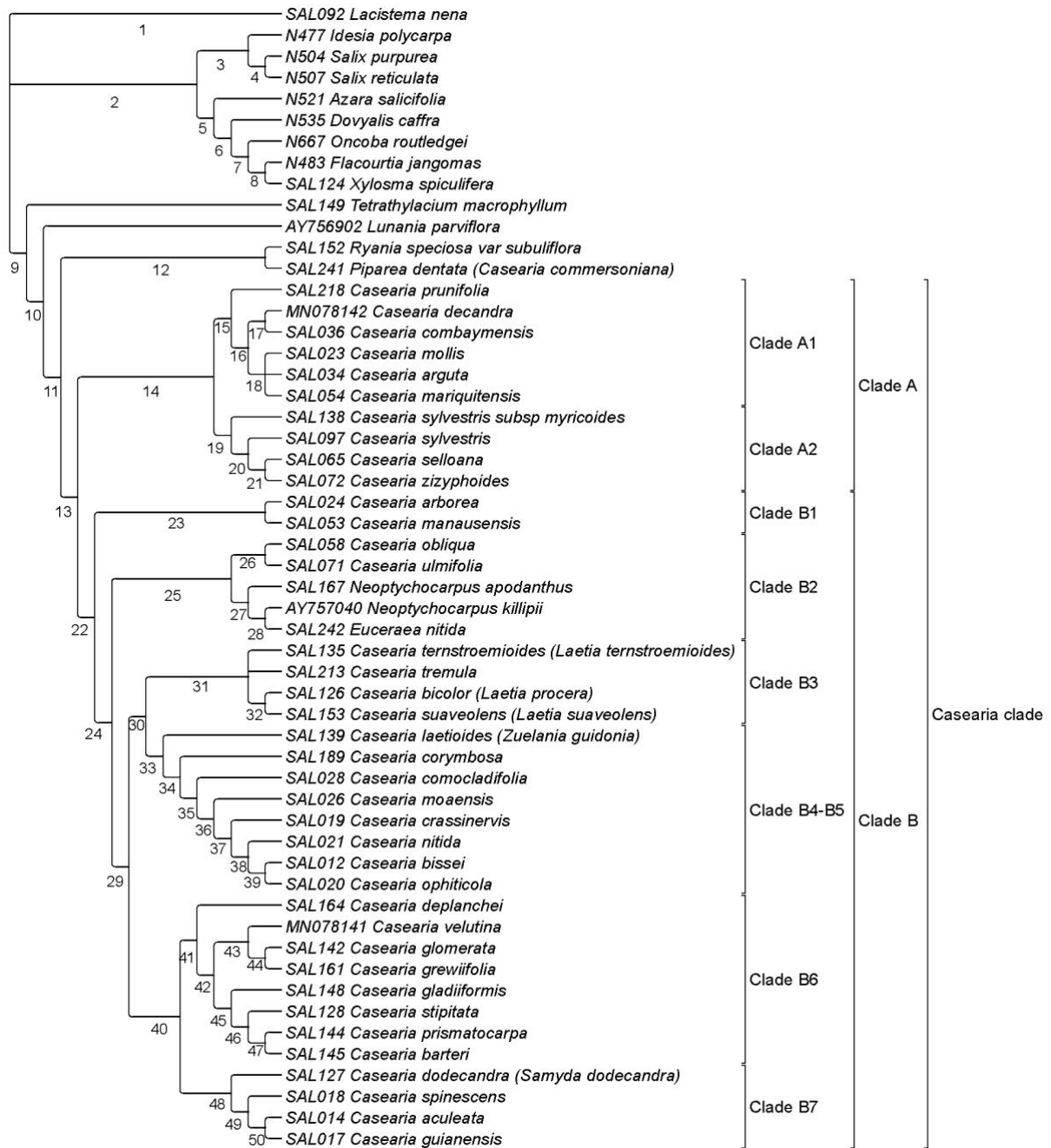
Appendix 2.4: Tree inferred with Maximum Likelihood, bootstrap support values are above the node, for the ITS dataset. At the tip of the node is the DNA number followed by the species name and the country code of where the individual was collected (see table 1 for more informations)



Appendix 2.5: Tree inferred with parsimony, Jackknife support values are above the node, for the ITS dataset. At the tip of the node is the DNA number followed by the species name and the country code of where the individual was collected (see table 1 for more informations)



Appendix 2.6: BayesTraits Posterior Probabilities (BPP) of the ancestral character state reconstruction analysis for each node and for seven morphological characters.



Appendices

Node	Ch1: Reproduction system		Ch2: Calyx lobes fused into a tube		Ch3: Pellucids dots		Ch4: Number of stamen			Ch5: Staminodes		Ch6: Series of stamen		Ch7: Type of inflorescence					
	B	D	0	1	0	1	1-6	7-12	>12	0	1	S	U	P	C	R/C	F/G	C	S
1	0.66	0.34	0.78	0.22	0.89	0.11	0.33	0.18	0.49	0.84	0.16	0.94	0.06	0.22	0.12	0.21	0.21	0.11	0.13
2	0.07	0.93	0.84	0.16	1.00	0.00	0.04	0.01	0.95	0.94	0.06	1.00	0.00	0.19	0.07	0.26	0.24	0.08	0.16
3	0.06	0.94	0.78	0.22	0.98	0.02	0.25	0.04	0.71	0.87	0.13	0.98	0.02	0.46	0.19	0.11	0.04	0.09	0.10
4	0.00	1.00	0.99	0.01	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
5	0.26	0.74	0.84	0.16	1.00	0.00	0.01	0.01	0.98	0.86	0.14	1.00	0.00	0.06	0.04	0.27	0.40	0.06	0.17
6	0.09	0.91	0.86	0.14	1.00	0.00	0.01	0.01	0.99	0.97	0.03	1.00	0.00	0.05	0.03	0.18	0.45	0.06	0.22
7	0.33	0.67	0.87	0.13	1.00	0.00	0.00	0.01	0.99	0.98	0.02	0.99	0.01	0.05	0.03	0.29	0.17	0.06	0.39
8	0.02	0.98	0.84	0.16	0.99	0.01	0.01	0.02	0.97	0.95	0.05	0.96	0.04	0.05	0.03	0.38	0.42	0.05	0.06
9	0.94	0.06	0.78	0.22	0.42	0.58	0.48	0.35	0.17	0.78	0.22	0.71	0.29	0.28	0.07	0.22	0.21	0.10	0.11
10	0.98	0.02	0.84	0.16	0.04	0.96	0.01	0.98	0.01	0.66	0.34	0.73	0.27	0.05	0.03	0.42	0.36	0.06	0.08
11	0.95	0.05	0.79	0.21	0.09	0.91	0.03	0.92	0.06	0.20	0.80	0.35	0.65	0.07	0.05	0.10	0.55	0.08	0.15
12	0.98	0.02	0.86	0.14	0.31	0.69	0.03	0.79	0.18	0.32	0.68	0.51	0.49	0.06	0.04	0.10	0.43	0.07	0.29
13	1.00	0.00	0.85	0.15	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.98	0.00	0.00
14	0.99	0.01	0.83	0.17	0.00	1.00	0.01	0.99	0.01	0.03	0.97	0.00	1.00	0.02	0.02	0.03	0.89	0.02	0.02
15	0.98	0.02	0.81	0.19	0.01	0.99	0.01	0.98	0.01	0.05	0.95	0.01	0.99	0.03	0.02	0.03	0.86	0.03	0.03
16	1.00	0.00	0.80	0.20	0.00	1.00	0.00	1.00	0.00	0.01	0.99	0.00	1.00	0.01	0.00	0.01	0.97	0.01	0.01
17	0.99	0.01	0.45	0.55	0.00	1.00	0.00	0.99	0.00	0.02	0.98	0.00	1.00	0.01	0.01	0.01	0.94	0.01	0.01
18	1.00	0.00	0.98	0.02	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
19	1.00	0.00	0.94	0.06	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.98	0.00	0.00
20	1.00	0.00	0.96	0.04	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00
21	1.00	0.00	0.96	0.04	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00
22	0.99	0.01	0.83	0.17	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00
23	1.00	0.00	0.40	0.60	0.00	1.00	0.00	1.00	0.00	0.01	0.99	0.00	1.00	0.00	0.00	0.00	0.98	0.00	0.00
24	0.98	0.02	0.86	0.14	0.00	1.00	0.00	1.00	0.00	0.01	0.99	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00
25	0.49	0.51	0.57	0.43	0.00	1.00	0.00	1.00	0.00	0.33	0.67	0.00	1.00	0.02	0.01	0.01	0.94	0.01	0.01
26	1.00	0.00	0.93	0.07	0.00	1.00	0.00	1.00	0.00	0.01	0.99	0.00	1.00	0.00	0.00	0.01	0.97	0.01	0.01
27	0.05	0.95	0.20	0.80	0.00	1.00	0.00	0.99	0.00	0.84	0.16	0.01	0.99	0.10	0.02	0.04	0.75	0.04	0.04
28	0.05	0.95	0.34	0.66	0.00	1.00	0.00	0.99	0.00	0.62	0.38	0.03	0.97	0.30	0.04	0.08	0.45	0.06	0.06
29	1.00	0.00	0.95	0.05	0.00	1.00	0.00	0.98	0.02	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00
30	1.00	0.00	0.94	0.06	0.00	1.00	0.00	0.85	0.15	0.02	0.98	0.00	1.00	0.01	0.00	0.04	0.90	0.04	0.01
31	1.00	0.00	0.96	0.04	0.00	1.00	0.00	0.81	0.19	0.48	0.52	0.00	1.00	0.00	0.00	0.02	0.97	0.01	0.00
32	1.00	0.00	0.96	0.04	0.00	1.00	0.00	0.82	0.18	0.94	0.06	0.00	1.00	0.00	0.00	0.01	0.98	0.01	0.00
33	1.00	0.00	0.93	0.07	0.00	1.00	0.01	0.62	0.37	0.01	0.99	0.00	1.00	0.01	0.01	0.11	0.74	0.11	0.02
34	1.00	0.00	0.91	0.09	0.00	1.00	0.00	1.00	0.00	0.01	0.99	0.00	1.00	0.03	0.02	0.36	0.24	0.30	0.04
35	1.00	0.00	0.97	0.03	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.02	0.01	0.04	0.29	0.61	0.02
36	1.00	0.00	0.99	0.01	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00
37	1.00	0.00	0.99	0.01	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00
38	1.00	0.00	0.98	0.02	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00
39	1.00	0.00	0.99	0.01	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00
40	1.00	0.00	0.94	0.06	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
41	1.00	0.00	0.95	0.05	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.01	0.99	0.00	0.00	0.00	0.99	0.00	0.00
42	1.00	0.00	0.96	0.04	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
43	1.00	0.00	0.90	0.10	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00

44	1.00	0.00	0.72	0.28	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.01	0.99	0.00	0.00	0.00	1.00	0.00	0.00
45	1.00	0.00	0.95	0.05	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.99	0.00	0.00
46	1.00	0.00	0.95	0.05	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.02	0.98	0.00	0.00	0.00	0.99	0.00	0.00
47	1.00	0.00	0.94	0.06	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.41	0.59	0.00	0.00	0.00	0.99	0.00	0.00
48	1.00	0.00	0.85	0.15	0.00	1.00	0.00	1.00	0.00	0.01	0.99	0.00	1.00	0.00	0.00	0.01	0.97	0.01	0.01
49	1.00	0.00	0.57	0.43	0.00	1.00	0.00	1.00	0.00	0.01	0.99	0.00	1.00	0.00	0.00	0.00	0.98	0.00	0.00
50	1.00	0.00	0.02	0.98	0.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00

Table S5: Values of branch supports and divergence time estimation using BEAST (PP: Posterior Probabilities, HPD: 95% intervals, C: Crown node, S: stem node)

Clade	Node	BEAST-PP	Mean	HPD
Clade A	I s	0.99	39.13	37.04-46.22
	I c	0.76	37.32	32.32-45.29
Clade A1	II s	0.76	37.32	32.32-45.29
	II c	0.99	32.22	21.3-38.71
Clade A2	III s	0.76	37.32	32.32-45.29
	III c	1	19.71	17.64-33.52
Clade B	IV s	0.99	39.13	37.04-46.22
	IV c	0.98	34.71	26.3-40.47
Clade B1	V s	0.98	34.71	26.3-40.47
	V c	0.98	15.29	7.41-22.79
Clade B2	VI s	0.98	29.48	26.3-40.47
	VI c	0.63	25.75	20.32-36.12
Clade B3	VII s	0.76	18.72	15.85-28.51
	VII c	0.67	15.43	11.22-25.52
Clade B4	VIII s	1	15.5	12.32-24.28
	VIII c	1	11.71	7.58-17.23
Clade B5	IX s	1	15.5	12.32-24.28
	IX c	1	9.46	5.57-15.35
Clade B6	X s	0.71	25	18.01-31.01
	X c	0.56	19.81	13.6-28.79
Clade B7	XI s	0.71	25	18.01-31.01
	XI c	0.99	20.31	14.28-25.95

Table S6: Models evaluated in BioGeoBears with Akaike Information Criterion (AIC) values

	LnL	numparams	d	e	j	AICc	AICc_wt
DEC	-154.9	2	3.75	3.03	0	314	4.80E-13
DEC+J	-131.8	3	2.81	2.92	0.023	269.8	0.0019
DIVALIKE	-166.9	2	3.84	4.1	0	337.9	3.00E-18
DIVALIKE+J	-133	3	2.62	4.31	0.025	272.2	0.0006
BAYAREALIKE	-454.8	2	0.076	0.28	0	913.7	2.90E-143
BAYAREALIKE+J	-125.5	3	0.19	1.00E-07	0.03	257.3	1

Table S7: Ancestral area reconstruction for key nodes. Nodes referred to the one in Fig. 7 and fig. 7. The letters referred to the biogeographical area: (A) Meso America, (B) Central America, (C) South America, (D) the Caribbean, (E) Africa, (F) Asia and (G) New Caledonia

Clades	Node	Probabilities for nodal reconstruction BBM (above 0.1)								
		A	B	C	D	E	F	G	AC	*(other ancestral range)
Casearia clade		0	0	1	0	0	0	0	0	0
Clade A	I	0	0	1	0	0	0	0	0	0
Clade A1	II	0	0	1	0	0	0	0	0	0
Clade A2	III	0	0	1	0	0	0	0	0	0
Clade B	IV	0	0	1	0	0	0	0	0	0
Clade B1	V	0	0	0.98	0	0	0	0	0	0
Clade B2	VI	0	0	1	0	0	0	0	0	0
Clade B3	VII	0	0	0.89	0.11	0	0	0	0	0
Clade B4	VIII	0	0	0.9	0.1	0	0	0	0	0
Clade B5	IX	0	0	0	1	0	0	0	0	0
Clade B6	X	0	0	0	0	0.25	0.25	0.5	0	0
Clade B6	XI	0	0	0	0	0.5	0.5	0	0	0
Clade B7	XII	0	0	0.79	0.2	0	0	0	0	0

Supporting information to Chapter 3

Appendix 3.1: Taxa used for molecular data (Name and author, Labnumber, DNA bank number, tissue bank number, locality, collector and collector number, herbarium voucher and NCBI accession number for rps4/trnLF, trnK/matK, rpl16, petD and ITS, respectively). Herbaria acronyms for voucher locations follow Index Herbariorum (Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/>). Species names are used following Sleumer (1980). Accessions are listed in alphabetic order. Abbreviations: s.n. = sine numero (without number).

Outgroups: *Azara salicifolia* Griseb., N521, Bolivia, G. Torrico & C. Peca 204 (LPB), FM178041; *Bivinia jalbertii* Tul., Phillipson & al. 3183 (K) AY757004; *Dovyalis caffra* (Hook. f. & Harv.) Warb., BG Bochum, T. Borsch (B), FM178039; *Flacourtia jangomas* (Lour.) Raeusch., BG Bonn 12841, N. Korotkova 59 (BONN), FM178042; *Idesia polycarpa* Maxim., BG Bonn 15364, N. Korotkova 12 (BONN), FM178040; *Lacistema nena* J. F. Macbr., SAL092, DB 44868, BGT0020382, Colombia: La Guajira, CM 2552 (UNO), HG997980, HG997900, HG998084, FR990812; *Lacistema nena* J. F. Macbr., SAL093, DB 44746, BGT0020383, Colombia: La Guajira, CM 2553 (UNO), HG997981, HG997901, HG998085, FR990813; *Lacistema nena* J. F. Macbr., N512, DB ---, Bolivia, P. Espinoza 3 (B, LPB), FM178032; *Lunania parviflora* Spruce ex Benth., Alford & Grandez 3114 (BH) AY756902, EF135561; *Osmelia philippina* Fern.-Vill, Singapore: Bukit Timah, Lum, S., KJ709026; *Ryania speciosa* Vahl, Alford & Grandez 3118 (BH) AY757061, AY756904; *Ryania speciosa* var. *subuliflora* (Sand.) Monach., SAL152, DB 44793, Peru, M. Rimachi Y. 8081 (BR), HG998004, HG997922, HG998104, FR990829; *Salix purpurea* L., BG Bonn 17982, A. Worberg 30 (BONN), FM178037; *Salix reticulata* L., Germany: Bavaria, T. Borsch 3825 (B), FM178038; *Tetratylacium johansenii* Standl., Panama, GQ982110; *Tetratylacium macrophyllum* Poepp., SAL149, DB 44790, Peru: Loreto, M. Rimachi Y. 8224 (BR), HG997921, HG998103, FR990828; *Trichostephanus gabonensis* Breteler; Wieringa & Haegens 2571 (WAG) AY757076; *Xylosma spiculifera* (Tul.) Triana & Planch., SAL124, DB 44775, Colombia: Cundinamarca, MSC 205 (JBB), HG997991, HG998094, FR990817

Ingroups: *Casearia aculeata* Jacq., SAL006, DB 44708, Cuba: Guantanamo, T. Borsch 4284, B 1003823633, HG997945, HG997867, FR990780; *Casearia aculeata* Jacq., SAL014, DB 44716, Cuba: Villa Clara, T. Borsch 5243, (B), HG997951, HG997871,

HG998057, FR990786; *Casearia aculeata* Jacq., SAL029, DB 27861, Dominica: Pedernales, W. Greuter 26587, B 100412779, HG997964, HG997884, HG998070, FR990798; *Casearia aculeata* Jacq., SAL030, DB 27862, Ecuador: Guayas, E. Asplund 15213, B 100517879, HG997965, HG997885, HG998071, FR990799; *Casearia aculeata* Jacq., SAL074, DB 44732, Cuba: Pinar del Rio, T. Borsch 5848 (B), FR990809; *Casearia aculeata* Jacq., SAL079, DB 44866, BGT0020260, Colombia: Bolivar, CM 2510 (UNO), HG997978, HG997898, HG998082; *Casearia aculeata* Jacq., SAL086, DB 44740, BGT0020039, Colombia: Bolivar, CM 2538 (UNO), FR990811; *Casearia aculeata* Jacq., SAL100, DB 44753, BGT0020339, Colombia: La Guajira, CM 2591 (UNO), HG997985, HG997905, HG998088; *Casearia aculeata* Jacq., SAL101, DB 44754, BGT0020340, Colombia: La Guajira, CM 2593 (UNO), HG997986, HG997906, HG998089; *Casearia aculeata* Jacq., SAL104, DB 44757, BGT0020025, Colombia: Bolivar, CM 2605 (UNO), HG997988, HG997908, HG998091; *Casearia aculeata* Jacq., SAL105, DB 44758, BGT0020026, Colombia: Bolivar, CM 2606 (UNO), HG997989, HG997909, HG998092; *Casearia aculeata* Jacq., SAL108, DB 44761, BGT0020293, Colombia: Bolivar, CM2611 (UNO), HG997990, HG997910, HG998093, FR990816; *Casearia aculeata* Jacq., SAL137, DB 44778, Cuba: Artemisa, S. Fuentes 1977 (B), HG997997, HG997916, HG998098, FR990823; *Casearia aculeata* Jacq., SAL174, DB 44807, Colombia: Bolivar, CM 2929 (UNO), HG998009, HG998109; CM 2611 (UNO); *Casearia aculeata* Jacq., SAL175, DB 44808, Colombia: Bolivar, CM 2938 (UNO), HG998010, HG997928, HG998110; *Casearia aculeata* Jacq., SAL176, DB 44809, Colombia: Bolivar, CM 2940 (UNO), HG998011, HG998111; *Casearia aculeata* Jacq., SAL198, DB 44831, BGT0020368, Colombia: Bolivar, CM 3000 (UNO), HG998019, HG997935, HG998119, FR990838; *Casearia aculeata* Jacq., SAL209, DB 44842, Colombia: La Guajira, CM 2745 (UNO), HG998021, HG997937, HG998121, FR990840; *Casearia aculeata* Jacq., SAL210, DB 44843, Colombia: La Guajira, CM 2756 (UNO), HG998022, HG997938, HG998122, FR990841; *Casearia arborea* (Rich.) Urb., Costa Rica, area de conservacion Guanacaste, sector Pitilla, La Cuestona, Pitilla, Roberto Espinosa, JQ589106; *Casearia arborea* (Rich.) Urb., OT2637, MK797141; *Casearia arborea* (Rich.) Urb., SAL009, DB 44711, Cuba: Guantanamo, T. Borsch 4845, B 100416441, HG997947, HG998055, FR990782; *Casearia arborea* (Rich.) Urb., SAL024, DB 44726, Cuba: Holguin, S. Fuentes 1370, B 100670063, HG997959, HG997880, HG998065, FR990794; *Casearia arborea* (Rich.) Urb., SAL032, DB 27864, Jamaica: Parish of Clarendon, E. Köhler 231, B 100411336, HG997966, HG997886, HG998072, FR990800; *Casearia arborea* (Rich.)

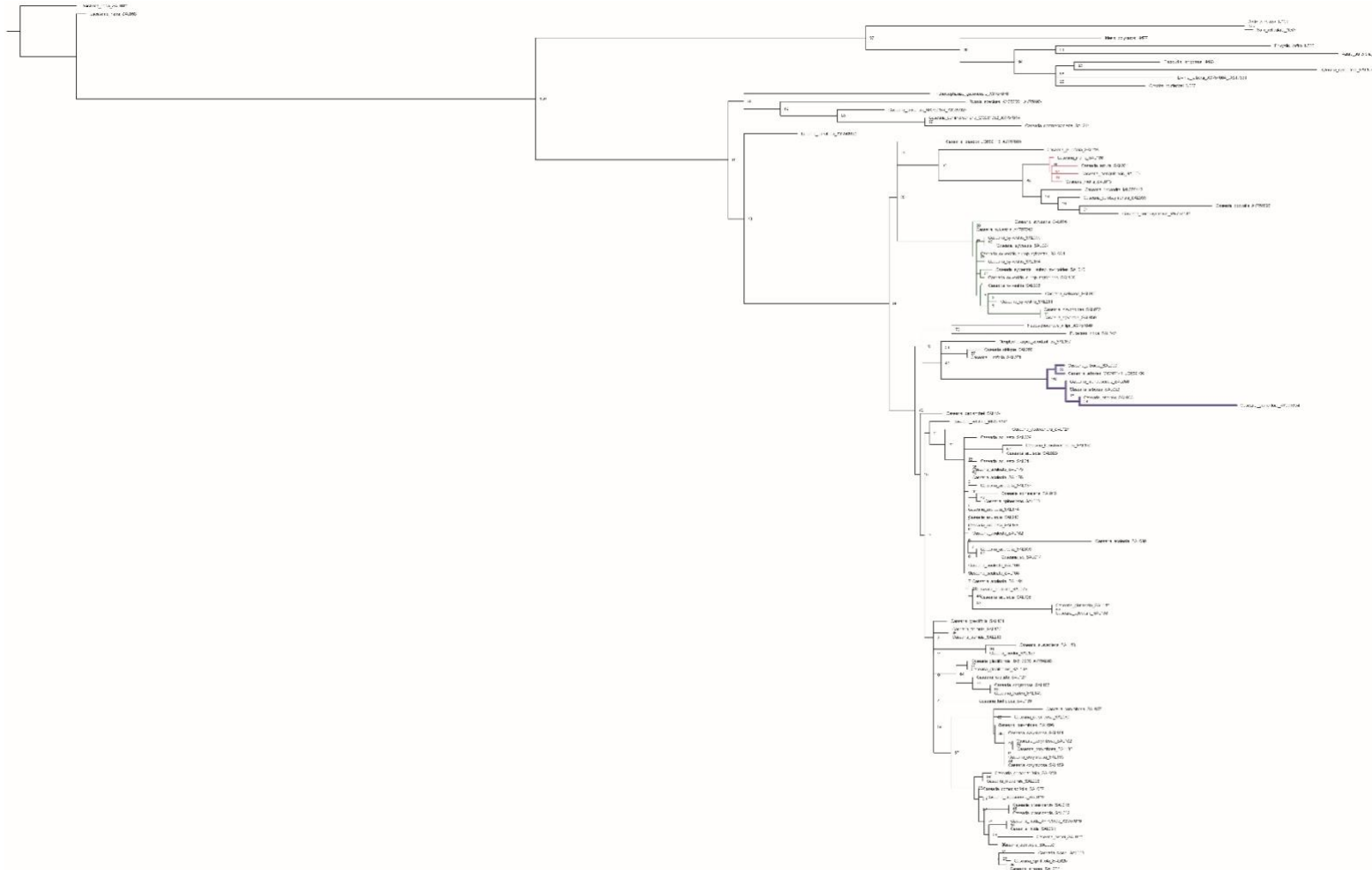
Urb., SAL033, DB27865, Colombia: Antioquia, *R. Fonnegra 6711*, B 100408900, HG997967, FR990801; *Casearia arguta* Kunth, SAL034, DB27866, Mexico: Chiapas, *E. Martinez M-26281*, B 100517881, HG997968, HG997887, HG998073, FR990802; *Casearia barteri* Mast., Cameroon: Korup, Parc National de Korup, CTFS, forest dynamic plot, close to Chimpanzee camp, 19 km from Mundemba village, Parmentier Ingrid & Mambo Peter, KC627849; *Casearia barteri* Mast., SAL145, DB 44786, Gabon: Moyen-Ogooué, *F. J. Breteler 13106*, BR 0000015348678, HG998001, HG997919, HG998102, FR990826; *Casearia bicolor* Urb., SAL126, DB33090, Guyana: Rupununi, *M. J. Jansen-Jacobs 2495*, B 101015449, HG997992, HG997911, FR990818; *Casearia bissei* J.E. Gut., SAL008, DB 44710, Cuba: Guantanamo, *M. Ackerman 862* (B), HG997946, HG997868, HG998054, FR990781 ; *Casearia bissei* J.E. Gut., SAL012, DB 44714, Cuba: Guantanamo, *T. Borsch 4428* (B), HG997949, HG997869, HG998056, FR990784; *Casearia combaymensis* Tul., OT2207, MK797142; *Casearia combaymensis* Tul., SAL036, DB27868, French Guyana, *J.J. de Granville 13157*, B 100517882, HG997969, HG997888, HG998074, FR990803; *Casearia comocladifolia* Vent., SAL027, DB 44729, Cuba: Independancia, *S. Fuentes 1164* (B), HG997962, HG997882, HG998068, FR990796; *Casearia comocladifolia* Vent., SAL028, DB 44730, Cuba: Barahona, *S. Fuentes 1212* (B), HG997963, HG997883, HG998069, FR990797; *Casearia commersoniana* Cambess., SAL241, DB----, Costa Rica, *Salazar 2638* (BH); *Casearia coronata* Standl. & L.O. Williams, Costa Rica: area de conservacion Guanacaste, sector Cacao, camino a Cacao, 2 km al norte de la entrada principal de Gongora, Adrian Guadamuz, JQ589110; *Casearia corymbosa* Kunth, SAL057, DB27889, Mexico: Oaxaca, *Misael Elorsa C. 478*, B 100517815, HG997973, HG997892, HG998077, FR990805; *Casearia corymbosa* Kunth, SAL078, DB 44865, BGT0020258, Colombia: Bolivar, *CM 2502* (UNO), HG997897, HG998081; *Casearia corymbosa* Kunth, SAL080, DB 44867, BGT0020267, Colombia: Bolivar, *CM 2512* (UNO), HG997979, HG997899, HG998083; *Casearia corymbosa* Kunth, SAL096, DB 44749, BGT0020207, Colombia: La Guajira, *CM 2572* (UNO), HG997983, HG997903, HG998086; *Casearia corymbosa* Kunth, SAL102, DB 44755, BGT0020346, Colombia: La Guajira, *CM 2598* (UNO), HG997987, HG997907, HG998090; *Casearia corymbosa* Kunth, SAL181, DB 44814, BGT0020116, Colombia: Magdalena, *CM 2973* (UNO), HG998012, HG997929, HG998112; *Casearia corymbosa* Kunth, SAL182, DB 44815, BGT0020134, Colombia: Magdalena, *CM 2976* (UNO), HG998013, HG997930, HG998113; *Casearia corymbosa* Sw., SAL185, DB 44818, BGT0020129, Colombia: Magdalena, *CM 2982* (UNO), HG998015, HG997932,

HG998115, FR990836; *Casearia corymbosa* Kunth, SAL187, DB 44820, BGT0020133, Colombia: Magdalena, *CM* 2986 (UNO), HG998016, HG997933, HG998116; *Casearia corymbosa* Kunth, SAL189, DB 44822, BGT0020143, Colombia: Magdalena, *CM* 2988 (UNO), HG998018, HG997934, HG998118; *Casearia crassinervis* Urb., SAL002, DB 44704, Cuba: Holguin, T. Borsch 4056 (B), HG997942, HG998052, FR990778; *Casearia crassinervis* Urb., SAL015, DB 44717, Cuba: Holguin, N. Köster 2724, B 100480617, HG997952, HG997872, HG998058, FR990787; *Casearia crassinervis* Urb., SAL019, DB 44721, Cuba: Holguin, S. Fuentes 453, B 100532054, HG997956, HG997876, HG998062; *Casearia decandra* Jacq., MN078142 (complete genome); *Casearia deplanchei* Sleumer, SAL164, DB 44875, New Caledonia, G. Dagostini 783, P 04819071, HG998006, HG997925, HG998106, FR990832; *Casearia dodecandra* (Jacq.) T. Samar. & M.H. Alford, SAL127, DB 33091, Dominica: Pedernales, W. Greuter 26585, B 100412781, HG997993, HG997912, HG998095, FR990819; *Casearia gladiiformis* Mast., Robertson 7500 (K) AY756893; *Casearia gladiiformis* Mast., Mozambique: Sofala, Catapu/Gorongosa, next to the James white saw mill, 0.7 km SSE from M'Phingwe camp site, Olivier Maurin, Michelle van der Bank, Meg Coates-Palgrave, JX517926; *Casearia gladiiformis* Mast., SAL148, DB 44789, Mozambique, P. C. M. Jansen 7670, BR 0000015960818, HG998003, HG997920, FR990827; *Casearia glomerata* Roxb., SAL142, DB 44783, Hong Kong, L. Tsuen 12687 (BR), HG998000, HG997918, HG998101, FR990825; *Casearia gossypiosperma* Briq., Brazil: parcela permanente 10.24ha, estacao ecologica de Caetetus, Galia county, Sao Paulo State, R.A.F. Lima & I. Marechaux, MG718929; *Casearia grandiflora* Cambess., Michelangeli & Alford 692 (BH) AY756894; *Casearia grewiifolia* Vent., SAL161, DB 44874, Vietnam, U. Swenson 1541, P 00955203, HG997924, HG998105, FR990831; *Casearia guianensis* (Aubl.) Urb., SAL017, DB 44719, Cuba: Holguin, S. Fuentes 442, B 100454590, HG997954, HG997874, HG998060, FR990789; *Casearia javitensis* Kunth, Ecuador, M. Alford 3098 (BH) AY935927; *Casearia javitensis* Kunth, NH200627, MK797144; *Casearia javitensis* Kunth, SAL169, DB 44877, French Guyana, J. J. de Granville 17165, P 05499467, FR990834; *Casearia laetioides* (A. Rich.) Northr., SAL139, DB 44780, Cuba: Pinar del Rio, T. Borsch 5954 (B), HG997999, HG998100; *Casearia manausensis* Sleumer, SAL053, DB27885, Brasil: Amazonas, J. L. Santos 855, B 100517811, HG997971, HG997890, HG998076; *Casearia mariquitensis* Kunth, SAL054, DB27886, Guyana: Rupununi, M. J. Jansen-Jacobs 4348, B 100517812, HG997972, HG997891; *Casearia membranacea* Hance, Taiwan: Lienhuachih Forest Dynamics Polt, KJ687490; *Casearia*

moaensis Vict., SAL026, DB 44728, Cuba: Holguin, *S. Fuentes* 1689, B 100594169, HG997961, HG998067, FR990795; *Casearia mollis* Kunth, SAL013, DB 44715, Cuba: Villa Clara, *T. Borsch* 5138 (B), HG997950, HG997870, FR990785; *Casearia mollis* Kunth, SAL023, DB 44725, Cuba: Matanzas, *T. Borsch* 5611 (B), HG997879, HG998064, FR990793; *Casearia mollis* Kunth, SAL136, DB 44777, Cuba: Artemisia, *S. Fuentes* 1976 (B), HG997996, HG997915, HG998097, FR990822; *Casearia multinervosa* C. T. White & Sleumer, *G. Smyrell* (129308787), KM894433; *Casearia nitida* Jacq., Alford & Lewis 3029 (BH) AY756895, AY757010; *Casearia nitida* Jacq., Costa Rica, area de conservacion Guanacaste, Sector Santa Rosa, bosque San Emilio, Adrian Guadamuz, JQ589111; *Casearia nitida* Jacq., SAL021, DB 44723, Cuba: Las Tunas, *S. Fuentes* 841, B 100531804, HG997958, HG997878, FR990791; *Casearia obliqua* Sprengel, SAL058, DB27890, Brasil: Parana, *R. Kummrow* 3000, B 100517816, HG997974, HG997893, FR990806; *Casearia obovalis* Poepp. ex. Griseb., Alford 3102 (BH) AY756896; *Casearia ophiticola* Vict., SAL020, DB 44722, Cuba: Holguin, *S. Fuentes* 656, B 100473899, HG997957, HG997877, HG998063, FR990790; *Casearia ophiticola* Vict., SAL025, DB 44727, Cuba: Holguin, *S. Fuentes* 1645, B 100646880, HG997960, HG997881, HG998066; *Casearia prismatocarpa* Mast., SAL144, DB ---, Liberia, *C. C. H. Jongkind* 9804, BR 0000016836853; *Casearia prunifolia* Kunth, SAL218, DB 44851, Peru: Loreto, *A. Gentry* 29158 (JBGP), HG998025, HG997941, FR990843; *Casearia selloana* Eichler, SAL065, DB27897, Brasil: Paraiba do Sul, *Schwacke* 3215, B 100517820, HG997975, HG997894, HG998078; *Casearia spinescens* (Sw.) Griseb., SAL003, DB 44705, Cuba: Holguin, *T. Borsch* 4115 B 100382453, HG997943, HG997866, HG998053, FR990779; *Casearia spinescens* (Sw.) Griseb., SAL018, DB 44720, Cuba: Holguin, *S. Fuentes* 445 B 100454572, HG997955, HG997875, HG998061; *Casearia spinescens* (Sw.) Griseb., SAL076, DB 44734, Cuba: Pinar del Rio, *T. Borsch* 5942 (B), FR990810; *Casearia stipitata* Mast., SAL128, DB33096, Cameroon, *A J. M. Leeuwenberg* 9884, B 100046568, HG997994, HG997913, HG998096, FR990820; *Casaria suaveolens* (Poepp.) T. Samar. & M.H. Alford, SAL 153, DB ---, Peru, *M. Rimachi* Y. 7666 (BR), HG998005, HG997923, FR990830; *Casearia sylvestris* Sw., Michelangeli & Alford 625 (BH) AY757012; *Casearia sylvestris* Sw., Panama, GQ981954; *Casearia sylvestris* Sw., Puerto Rico, N.Swensen, HM446664; *Casearia sylvestris* Sw., Costa Rica, area de conservacion Guanacaste, sector Santa Rosa, Bosque San Emilio, Roberto Espinoza & Adrian Guadamuz, JQ589115; *Casearia sylvestris* Sw., SAL016, DB 44718, Cuba: Holguin, *SF* 441, B 100454589, HG997953, HG997873, HG998059, FR990788; *Casearia sylvestris*

Sw., SAL050, DB27882, Venezuela: Guericco, *H. & E. Walter* 236, B 100517808, HG997970, HG998075; *Casearia sylvestris* Sw., SAL095, DB 44748, BGT0020288, Colombia: La Guajira, *CM 2569* (UNO), HG997982, HG997902, FR990814; *Casearia sylvestris* Sw., SAL097, DB 44750, BGT0020214, Colombia: La Guajira, *CM 2581* (UNO), HG997984, HG997904, HG998087, FR990815; *Casearia sylvestris* Sw., SAL184, DB 44817, BGT0020130, Colombia: Magdalena, *CM 2981* (UNO), HG998014, HG997931, HG998114; *Casearia sylvestris* Sw., SAL188, DB 44821, BGT0020145, Colombia: Magdalena, *CM 2987* (UNO), HG998017, HG998117, FR990837; *Casearia sylvestris* Sw., SAL200, DB 44833, BGT0020367, Colombia: Bolivar, *CM 3002* (UNO), FR990839; *Casearia sylvestris* Sw., SAL203, DB 44836, BGT0020003, Colombia: Bolivar, *CM 3005* (UNO), HG998020, HG997936, HG998120; *Casearia sylvestris* Sw., SAL211, DB 44844, Colombia: La Guajira, *CM 2764* (UNO), HG998023, HG997939, HG998123; *Casearia sylvestris* Sw., SAL022, DB 44724, BGT0020367, Cuba: Pinar del Rio, *T. Borsch* 5784 (B), FR990792; *Casearia sylvestris* subsp. *myricoides* (Griseb.) J.E. Gut., SAL010, DB 44712, Cuba: Guantanamo, *T. Borsch* 4901, B 100416559, HG997948, FR990783; *Casearia sylvestris* subsp. *myricoides* (Griseb.) J.E. Gut., SAL138, DB 44779, Cuba: Sancti Spiritu, *S. Fuentes* 1727 (B), HG997998, HG997917, HG998099, FR990824; *Casearia ternstroemiodes* (Griseb.) T. Samar. & M.H. Alford, SAL 135, DB 44776, Cuba: Guantanamo, *T. Borsch* 4425 (B), HG997995, HG997914, FR990821; *Casearia tremula* (Griseb.) Griseb. ex C. Wright, Costa Rica, area de conservacion Guanacaste, Sector Santa Rosa, Llano Los Cebollines, Roberto Espinosa, JQ587936; *Casearia tremula* (Griseb.) Griseb. ex C. Wright, SAL 170, DB, Nicaragua: Boaco, *J. B. Quezada* 242, P 00955196, HG998008, HG997927, HG998108, FR990835; *Casearia tremula* (Griseb.) Griseb. ex C. Wright, SAL 213, DB 44846, Colombia: Bolivar, *V. Londono* 408 (JBGP), HG998024, HG997940, HG998124, FR990842; *Casearia ulmifolia* Vahl ex Vent., SAL071, DB27903, French Guyana, *S. Mori* 21177, B 100210714, HG997976, HG997895, HG998079, FR990807; *Casearia velutina* MN078141 (complete genome); *Casearia zizyphoides* Kunth, SAL072, DB27904, Venezuela: Bolivar, *J. A. Steyermark* 88293, B 100517825, HG997977, HG997896, HG998080, FR990808; ; *Euceraea nitida* Mart., SAL242, DB---, Brazil, *G. Hobbes* 213 (BH); *Neoptychocarpus apodanthus* (Kuhlm.) Buch., SAL167, DB 44802, French Guyana, *O. Lachenaud* 2143, P00979039, HG998007, HG997926, HG998107, FR990833; *Neoptychocarpus killipii* (Monach.) Buch., *Alford & Grandez* 3119, AY757040

Appendix 3.2: Phylogram from a RAxML analysis of *Casearia* with one plastid markers (*rps4/trnLF*). Values above the node indicate bootstrap support. At the tip of the node is the species name followed by the labcode DNA number.



Appendix 3.3: Phylogram from a RAxML analysis of *Casearia* with one plastid markers (*trnK/matK*). Values above the node indicate bootstrap support. At the tip of the node is the species name followed by the labcode DNA number.

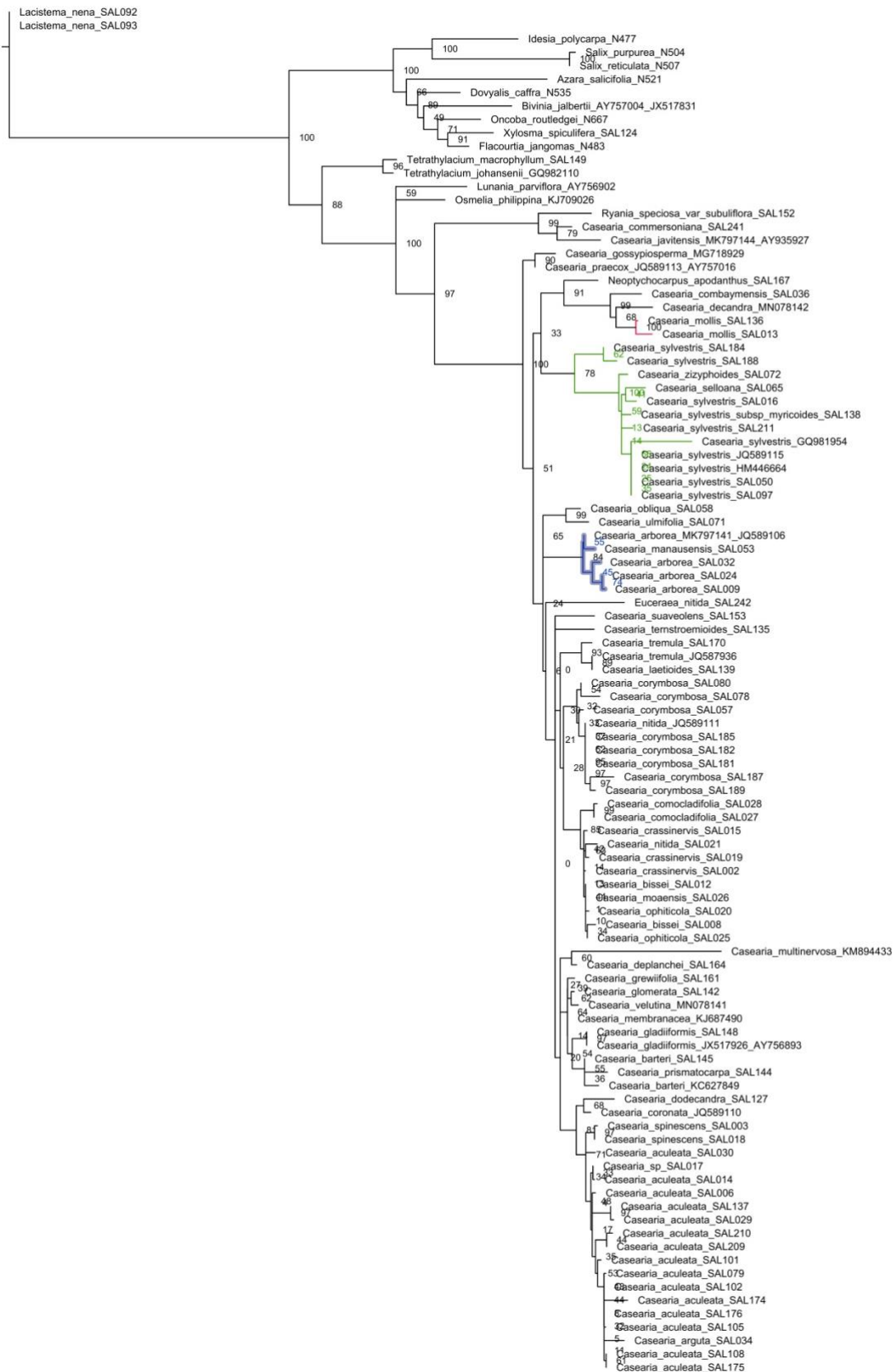


Table S1: List of the studied morphometric characters (and their abbreviations), of selected *Casearia* species, with a link to their digital image when available. All measurements (mean, standard deviation) are in cm, only the mean are included in the Principal Component Analysis (PCA) and the clustering analysis. For the following characters: leaves margins, ped_flw (pedicel of the flower), discholorous leaves (the face superior and inferior of the leaves are of different colors), leaves pubescens, leaves pilosity and mucron, 0 means absence and 1 presence. For the following character: leaves color, 1 means green and 2 means brown.

Individual	Herbarium	Voucher nb	Country	Link to digitized specimen	Lleaf	Wleaf	Lpet	Lped	Margins	Color	Discolorous	Pubescens	Flw_nb	Tip
C. arborea1	B		CU		6.64	1.73	0.28	1		2	1	1		
C. arborea2	B		JM		5.42	1.48	0.24	1		1	1	1		
C. arborea3	COL	COL000232564	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/7824/	8.52	2.99	0.42	1		2	1	1		
C. arborea4	COL	COL000232580	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/17247/	13.57	3.54	0.38	1		2	1	1		
C. arborea5	COL	COL000232532	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/20155/	11.47	3.22	0.34	1		2	1	1		
C. arborea6	COL	COL000232556	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/33021/	7.11	3.02	0.35	1		2	1	1		
C. arborea7	COL	COL000232544	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/129634/	6.96	1.66	0.22	1		2	1	1		
C. arborea8	COL	COL000232552	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/179042/	8.36	2.47	0.20	1		2	0	0		
C. arborea9	COL	COL000232538	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/204765/	9.60	3.22	0.38	1		2	0	0		
C. arborea10	COL	COL000232562	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/244363/	8.84	2.52	0.23	1		2	1	1		
C. arborea11	COL	COL000232528	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/257731/	11.20	3.62	0.26	1		2	0	1		
C. arborea12	COL	COL000232576	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/258383/	7.63	2.99	0.38	1		3	0	0		
C. arborea13	COL	COL000232536	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/331567/	11.30	3.30	0.48	1		3	1	1		
C. arborea14	COL	COL000369200	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/554384/	8.49	2.89	0.32	1		2	1	1		
C. arborea15	COL	COL000455315	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/692453/	13.80	3.45	0.30	1		3	1	0		
C. arborea16	NY	NY01020682	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1112322	6.88	1.90	0.20	1		2	1	1		
C. arborea17	NY	NY01020675	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1112305	8.46	2.40	0.26	1		2	1	1		
C. arborea18	NY	NY01087686	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1196450	6.36	1.80	0.23	1		1	1	1		
C. arborea19	NY	NY01386442	DO	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654629	6.53	1.90	0.25	1		2	1	1		
C. arborea20	NY	NY01386485	HT	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654672	4.99	1.38	0.22	1		2	1	1		
C. arborea21	NY	NY01026496	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1112514	9.32	2.67	0.26	1		2	1	1		
C. arborea22	NY	NY01026490	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1112529	9.51	2.74	0.30	1		1	1	1		
C. arborea23	NY	NY01020676	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1112307	3.67	0.98	0.22	1		2	1	1		

C. arborea24	NY	NY01026494	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1112517	9.48	2.81	0.27	1	1	1	1
C. arborea25	NY	NY01386505	JM	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654692	9.05	2.28	0.31	1	2	1	0
C. arborea26	NY	NY01386496	JM	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654683	5.63	1.52	0.29	1	2	1	1
C. arborea27	NY	NY01386432	JM	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654619	8.41	2.57	0.35	1	2	1	0
C. arborea28	P	P00371634	GF	https://science.mnhn.fr/institution/mnhn/collection/p/item/p00371634	3.91	2.50	0.27	1	2	1	1
C. arborea29	P	BM000624363	PE	https://data.nhm.ac.uk/dataset/collection-specimens/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb?filters=collectionCode%3AAbot%7CcatalogNumber%3Abm000624363	12.65	3.94	0.42	1	2	0	0
C. arborea30	P	BM000624351	Leeward Islands	https://data.nhm.ac.uk/dataset/collection-specimens/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/4985610	3.23	0.81	0.26	1	1	0	1
C. arborea31	P	P00689741	PR	https://science.mnhn.fr/institution/mnhn/collection/p/item/p00689741	6.04	1.44	0.27	1	2	1	1
C. arborea32	K	K00471187	JM	http://apps.kew.org/herbcat/getImage.do?imageBarcode=K000471187	6.52	1.73	0.33	1	2	1	1
C. arborea33	U	U0002158	SU		5.90	1.80	0.28	1	2	1	1
C. arborea34	M	M0113034	BR		6.61	2.04	0.38	1	2	0	1
C. arborea35	L	L0010559	BR		6.01	1.59	0.27	1	2	1	1
C. arborea36	L	L0010561	PE		5.60	2.20	0.19	1	2	1	1
C. arborea37	NY	NY00097928	BO	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=490619	10.79	3.72	0.38	1	1	1	0
C. arborea38	NY	G00355576	PR	https://www.ville-ge.ch/musinfo/bd/cjb/chg/result.php?type_search=simple&lang=en&criteria=G00355576&mode=tout	8.36	2.62	0.33	1	2	1	1
C. arborea39	G	G00355581	BR	https://www.ville-ge.ch/musinfo/bd/cjb/chg/result.php?type_search=simple&lang=en&criteria=G00355581&mode=tout	7.48	1.51	0.45	1	2	1	1
C. arborea40	P	P00790000	GF	https://science.mnhn.fr/institution/mnhn/collection/p/item/p00790000	9.38	2.95	0.43	1	2	1	0
C. arborea41			SU		11.22	3.32	0.50	1	2	0	0
C. arborea42	B		BR		9.82	2.90	0.28	1	2	0	1
C. arborea43	B				5.97	1.82	0.36	1	2	0	1
C. arborea44	B		PR		6.20	1.78	0.23	1	2	0	1
C. arborea45	B		MX		9.47	2.20	0.30	1	2	0	0
C. arborea46	B		BR		6.78	1.90	0.33	1	2	0	1
C. arborea47	B		GY		6.73	2.05	0.38	1	2	0	1
C. arborea48	B		GF		6.66	2.35	0.33	1	2	0	1
C. arborea49	B		GF		7.23	2.41	0.24	1	2	1	1
C. arborea50	B		GY		8.57	3.13	0.40	1	2	0	0
C. arborea51	B		BR		7.26	2.38	0.38	1	2	1	1

C. arborea52	B		VE		8.38	2.60	0.43	1	2	0	1
C. arborea53	B		BR		6.76	1.83	0.27	1	2	1	1
C. arborea54	B	B 10 0361357	CU		4.91	1.58	0.20	1	2	1	1
C. arborea55	B	B 10 0361424	CU		4.66	1.41	0.24	1	2	1	1
C. arborea56	B	B 10 0385965	CU		4.41	1.35	0.25	1	2	1	1
C. arborea57	B	B 10 0411338	CU		4.52	1.20	0.22	1	2	1	1
C. arborea58	B	B 10 0411340	CU		6.23	1.92	0.20	1	2	1	1
C. arborea59	B	B 10 0535392	VE		9.59	2.62	0.40	1	2	0	1
C. arborea60	B	B 10 0670063	CU		6.50	1.77	0.20	0	2	1	0
C. grandiflora1	NY	NY897071	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=970998	7.19	2.35	0.37	0	2	1	1
C. grandiflora2	NY	NY2149994	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304442	5.99	2.38	0.33	0	2	1	1
C. grandiflora3	NY	NY2423032	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2679976	8.61	3.20	0.39	0	1	1	1
C. grandiflora4	NY	NY02698818	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2979344	6.29	1.83	0.29	0	2	1	1
C. grandiflora5	NY	NY1039371	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1485629	7.75	2.71	0.34	0	1	1	1
C. grandiflora6	NY	NY00897070	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=970994	10.15	2.80	0.42	0	3	1	1
C. grandiflora7	NY	NY00897217	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=972001	5.50	3.42	0.40	0	3	1	1
C. grandiflora8	COL	COL000232835	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/11651/	8.58	2.40	0.45	0	2	1	1
C. grandiflora9	COL	COL000232828	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/20161/	8.40	2.45	0.32	0	2	1	1
C. grandiflora10	COL	COL000232830	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/23021/	8.74	3.08	0.37	0	2	1	1
C. grandiflora11	COL	COL000232822	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/131511/	6.95	2.33	0.34	0	2	1	1
C. grandiflora12	COL	COL000232814	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/245314/	10.33	3.30	0.30	0	2	1	1
C. grandiflora13	COL	COL000376282	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/563012/	7.73	2.34	0.41	0	1	1	1
C. grandiflora14	COL	COL000402936	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/636045/	7.60	2.11	0.32	0	1	1	1
C. grandiflora15	NY	NY00897175	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=971787	8.75	2.15	0.49	0	1	1	1
C. grandiflora16	NY	NY897149	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=971543	8.36	3.15	0.34	0	2	1	1
C. grandiflora17	NY	NY00897150	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=971545	8.56	2.04	0.42	0	2	1	1
C. grandiflora18	NY	NY00897153	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=971561	6.95	2.42	0.62	0	2	1	1
C. grandiflora19	NY	NY02149955	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304395	6.65	1.87	0.35	0	2	1	1
C. grandiflora20	NY	NY2149978	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304423	6.68	2.68	0.29	0	2	1	1
C. grandiflora21	NY	NY2149986	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304431	9.43	2.86	0.42	0	2	1	1

C. grandiflora22	NY	NY02149987	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304435	9.77	3.32	0.42	0	2	1	1
C. grandiflora23	NY	NY2149990	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304438	8.13	2.87	0.38	0	3	1	1
C. grandiflora24	NY	NY2149993	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304441	9.92	2.21	0.38	0	2	1	1
C. grandiflora25	NY	NY2150002	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304450	7.47	2.48	0.33	0	2	1	1
C. grandiflora26	NY	NY2150004	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304452	8.97	2.50	0.39	0	2	1	1
C. grandiflora27	NY	NY2150009	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304457	7.71	2.44	0.32	0	2	1	1
C. grandiflora28	NY	NY02150014	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304466	14.01	3.73	0.41	0	2	1	1
C. grandiflora29	NY	NY2150015	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304468	6.85	2.60	0.38	0	2	1	1
C. grandiflora30	NY	NY02150020	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304474	5.98	2.18	0.29	0	2	1	1
C. grandiflora31	P	P00506593	BR	https://science.mnhn.fr/institution/mnhn/collection/p/item/p00506593	4.75	1.40	0.56	0	3	1	1
C. grandiflora32	NY	NY00097940	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=52819	5.55	1.58	0.32	0	2	1	1
C. grandiflora33	B	B 10 0413404	BR	https://www.jacq.org/detail.php?ID=1678724	8.89	2.20	0.45	0	2	1	1
C. grandiflora34	B	B 10 0573017	VE	https://www.jacq.org/detail.php?ID=1678676	8.63	3.14	0.30	0	2	0	1
C. grandiflora35	B	B 10 0615150	VE	https://www.jacq.org/detail.php?ID=1678674	7.79	2.25	0.35	0	2	0	1
C. grandiflora36	B		BR		7.97	2.54	0.33	0	2	0	1
C. manausensis1	NY	NY02150228	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304895	9.25	2.37	0.29	0.23	1	1	0
C. manausensis2	NY	NY02150229	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304896	7.34	2.40	0.26	0.20	3	0	0
C. manausensis3	NY	NY02150232	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304899	7.45	2.48	0.25	0.29	3	0	0
C. manausensis4	NY	NY097949	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=539120	8.72	2.84	0.38	0.28	3	0	0
C. manausensis5	NY	NY02150227	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304894	6.92	2.52	0.24	0.20	3	0	1
C. manausensis6	NY	NY02150235	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304902	7.80	2.29	0.24	0.30	3	0	0
C. manausensis7	NY	NY02150226	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304893	7.63	2.27	0.21	0.28	3	0	0
C. manausensis8	NY	NY02150225	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304879	7.83	2.63	0.23	0.30	3	0	0
C. manausensis9	NY	NY02150231	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304898	8.61	2.85	0.22	0.33	2	0	0
C. manausensis10	NY	NY02150233	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304900	9.02	2.67	0.26	0.30	1	0	0
C. manausensis11	NY	K001216365	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=802382&pageCode=1&presentPage=1&queryId=1&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K001216365	8.09	2.77	0.28	0.25	2	0	0
C. manausensis12	NY	K001216370	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=802398&pageCode=1&presentPage=1&queryId=2&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K001216370	6.42	2.56	0.18	0.20	1	0	0
C. manausensis13	NY	K001216366	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=802386&pageCode=1&presentPage=1&queryId=3&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K001216366	8.03	2.98	0.24	0.18	2	0	0

C. mariquitensis1	NY	NY476217	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=733439	6.41	2.90	0.49	0.28	1	<15
C. mariquitensis2	NY	NY2150244	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2304944	11.45	3.97	0.55	0.36	0	>15
C. mariquitensis3	NY	NY00897133	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=971384	8.70	3.63	0.43	0.38	0	<15
C. mariquitensis4	K	K000471241	COL	http://apps.kew.org/herbcat/detailsQuery.do?imageId=740981&pageCode=1&presentPage=1&queryId=4&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K000471241	7.60	3.81	0.50	0.30	1	<15
C. mariquitensis5	K	K001216593	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=804347&pageCode=1&presentPage=1&queryId=6&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K001216593	9.40	4.06	0.49	0.30	0	<15
C. mariquitensis6	K	K001216592	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=804346&pageCode=1&presentPage=1&queryId=7&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K001216592	7.61	2.75	0.48	0.43	0	<15
C. mariquitensis7	K	K001216595	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=804349&pageCode=1&presentPage=1&queryId=8&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K001216595	7.54	3.10	0.39	0.35	0	<15
C. mariquitensis8	K	K001216601	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=804355&pageCode=1&presentPage=1&queryId=9&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K001216601	9.00	2.60	0.40	0.50	0	<15
C. mariquitensis9	K	K001216599	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=804353&pageCode=1&presentPage=1&queryId=10&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K001216599	9.59	2.87	0.41	0.40	1	<15
C. mariquitensis10	K	K000471243	EC	http://apps.kew.org/herbcat/detailsQuery.do?imageId=169534&pageCode=1&presentPage=1&queryId=11&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K000471243	8.53	3.21	0.27	0.40	0	<15
C. mariquitensis11	U	U0002169	SU		14.09	4.06	0.54	0.28	0	<15
C. mariquitensis12	K	K000471243	EC	http://apps.kew.org/herbcat/detailsQuery.do?imageId=169534&pageCode=1&presentPage=1&queryId=11&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K000471243	9.53	3.46	0.46	0.30	0	<15
C. mariquitensis13	G	G00236798	EC		4.70	3.90	0.19	0.20	1	<15
C. mariquitensis14	K	K000471244	PE	http://apps.kew.org/herbcat/detailsQuery.do?imageId=169535&pageCode=1&presentPage=1&queryId=12&sessionId=B7CD1C94FFA8426E2287456AEB71E810&barcode=K000471244	9.50	3.05	0.70	0.48	0	<15
C. mariquitensis15	B		BR		14.12	4.77	0.85	0.26	0	<15
C. mollis1	NY	NY1386734	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654980	14.12	6.99	0.69	0.44	1	<15
C. mollis2	NY	NY1386725	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654971	14.20	6.85	0.59	0.30	1	>15
C. mollis3	NY	NY1386767	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1655013	3.85	1.27	0.46	0.27	1	>15
C. mollis4	NY	NY1386747	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654993	6.65	3.25	0.41	0.50	1	<15
C. mollis5	NY	NY1386729	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654975	11.64	5.75	0.70	0.28	1	<15
C. mollis6	NY	NY1386751	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654997	9.48	3.95	0.36	0.27	1	<15
C. mollis7	NY	NY1386733	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654979	12.66	5.30	0.50	0.27	1	<15
C. mollis8	NY	NY1386742	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654988	5.82	2.34	0.30	0.20	1	<15
C. mollis9	NY	NY1386758	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1655004	6.15	3.62	0.58	0.28	1	<15
C. mollis10	NY	NY1386766	CU	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1655012	13.15	6.10	0.51	0.25	1	>15
C. mollis11	NY	NY1386721		http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654967	14.57	6.85	0.43	0.35	1	>15

C. mollis12	NY	NY1386736		http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654982	6.16	3.03	0.38	0.27		1	>15
C. mollis13	NY	NY1386749		http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654995	11.76	4.46	0.48	0.34		1	>15
C. mollis14	NY	NY1386720		http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1654966	6.84	3.29	0.38	0.23		1	<15
C. mollis15	P	P00679652	VE	https://science.mnhn.fr/institution/mnhn/collection/p/item/p00679652	10.47	3.59	0.55	0.40		1	>15
C. mollis16	US	US00114881	VE		10.57	6.09	0.85	0.30		1	>15
C. mollis17	B	B 10 0069474	CU		11.38	4.85	0.67	0.29		1	>15
C. mollis18	B	B 10 0434845	VE		7.76	3.74	0.63	0.25		1	>15
C. mollis19	B	B 10 0487234	CU		8.98	4.07	0.40	0.18		1	>15
C. mollis20	B	B 10 1103790	CU		13.42	6.15	0.57	0.20		1	>15
C. mollis21	B	B 10 0480831	CU		16.25	6.85	0.40	0.22		1	>15
C. mollis22	B				6.70	4.15	0.25	0.24		0	<15
C. selloana1	M	M0113065	BR		7.27	1.69	0.68		4		2
C. selloana2	F	F0093243F	BR		3.78	2.06	0.41	0.23	4		2
C. selloana3	MAC	MAC0050542	BR		7.66	3.63	0.63	0.2	3		2
C. selloana4	HUFU	HUFU00022879	BR		9.94	3.05	1.11	0.4	4		2
C. selloana5	MAC	MAC0011263	BR		6.79	3.49	0.33		3		2
C. selloana6	HUEFS	HUEFS150905	BR		10.48	4.95	0.62		3		2
C. selloana7	MAC	MAC0034797	BR		9.6	4.35	0.9	0.35	3		2
C. selloana8	ESA	ESA80490	BR		9.65	3.07	0.59		3		2
C. selloana9	HUEFS	HUEFS150949	BR		9.15	4.34	0.74		3		2
C. selloana10	MAC	MAC0014945	BR		7.84	2.34	0.62	0.2	3		2
C. sylvestris1	COL	COL000233228	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/6290/	7.3	2.6	0.3		2		1
C. sylvestris2	COL	COL000233080	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/6292/	4.4	1.3	0.2		2		3
C. sylvestris3	COL	COL000233146	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/23739/	6.7	2.3	0.2		3		1
C. sylvestris4	COL	COL000233086	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/23760/	6	1.8	0.5		3		3
C. sylvestris5	COL	COL000233090	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/33024/	1	3.1	0.3		3		1
C. sylvestris6	COL	COL000233224	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/61752/	5.9	2.1	0.3		2		1
C. sylvestris7	COL	COL000233078	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/77111/	6	1.5	0.7		3		1
C. sylvestris8	COL	COL000233074	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/98592/	5.8	1.4	0.5		3		1
C. sylvestris9	COL	COL000233122	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/127773/	10.8	3.2	0.4		3		1

C. sylvestris10	COL	COL000233132	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/144028/	10.2	3.3	0.2		3	1
C. sylvestris11	COL	COL000233138	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/208116/	12.7	4	0.3		3	1
C. sylvestris12	COL	COL000233116	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/216720/	7.8	2.5	0.3		2	1
C. sylvestris13	COL	COL000233144	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/222181/	7	2.3	0.2		2	1
C. sylvestris14	COL	COL000233120	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/232360/	8.2	3.4	0.4		3	1
C. sylvestris15	COL	COL000233174	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/287575/	7.6	2.1	0.2		2	1
C. sylvestris16	COL	COL000233170	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/304343/	10.3	3.6	0.4		3	1
C. sylvestris17	COL	COL000233126	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/310901/	9.3	3.3	0.3		2	1
C. sylvestris18	COL	COL000070414	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/348684/	6.3	2.3	0.3		2	2
C. sylvestris19	COL	COL000362926	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/555151/	7.6	2.8	0.3		3	1
C. sylvestris20	COL	COL000351591	BO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/596809/	9.2	2.8	0.3		3	1
C. sylvestris21	COL	COL000355723	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/598846/	12.4	3.8	0.3		2	1
C. sylvestris22	COL	COL000404742	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/644885/	9.6	3.4	0.3		3	1
C. sylvestris23	COL	COL000419034	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/660425/	7.5	2.6	0.4		2	1
C. sylvestris24	COL	COL000420623	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/673770/	6.2	1.8	0.4		2	2
C. sylvestris25	COL	COL000161315	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/609748/	9.6	3.3	0.3		3	1
C. sylvestris26	COL	COL000450444	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/688656/	8.8	3.7	0.3		2	1
C. sylvestris27	COL	COL000461541	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/701585/	9.7	3.8	0.2		2	1
C. sylvestris28	COL	COL000466983	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/708667/	7.1	2.8	0.4		3	1
C. sylvestris29	COL	COL000466985	CO	http://www.biovirtual.unal.edu.co/es/colecciones/detail/708669/	6.9	3.1	0.4		2	1
C. sylvestris30	NY	NY2154211	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2307985	6.25	2.16	0.33	0.12	2	1
C. sylvestris31	NY	NY01026343	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1113229	12.57	4.89	0.55	0.3	2	1
C. sylvestris32	NY	NY676574	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=561765	9.06	3.82	0.61	0.2	2	1
C. sylvestris33	NY	NY01026523	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=1112825	13.47	4.23	0.71	0.3	3	1
C. sylvestris34	NY	NY02681771	PR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2944026	11.49	3	0.61	0.26	3	1
C. zizyphoides1	NY	NY2154288	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2308209	4.83	2.22	0.28	0.10	3	3
C. zizyphoides2	NY	NY685867	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=822329	3.60	2.47	0.28	0.15	3	3
C. zizyphoides3	NY	NY2154286	BR	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=2308207	4.46	1.34	0.21	0.15	3	3
C. zizyphoides4	NY	NY04192543	VE	http://sweetgum.nybg.org/science/vh/specimen-details/?irn=4513604	5.56	2.49	0.30	0.20	3	3
C. zizyphoides5	NY	K001216583	BR	http://apps.kew.org/herbcat/detailsQuery.do?imageId=804337&pageCode=1&presentPage=1&queryId=1&sessionId=3684B6FF31F9CFC1FF98	8.66	3.52	0.31	0.20	3	3

			497D6DF30707&barcode=K001216583						
C. zizyphoides6	B	GY		5.89	2.95	0.20	0.17	3	3
C. zizyphoides7	B	GY		6.39	2.26	0.33	0.23	3	1
C. zizyphoides8	B	GY		6.93	3.08	0.34	0.18	3	1
C. zizyphoides9	B	GY		5.65	2.53	0.30	0.20	3	2
C. zizyphoides10	B	GY		8.57	3.02	0.44	0.20	3	3

Table S2: List of environmental variables from the WorldClim database. In bold are the nine variables selected after collinearity test and used in the ecological niche similarity and equivalence analyses

Name	Variable
bio1	Annual Mean Temperature
bio2	Mean Diurnal Temperature Range
bio3	Isothermality
bio4	Temperature Seasonality
bio5	Maximum Temperature Warmest month
bio6	Minimum Temperature Coldest Month
bio7	Temperature Annual Range
bio8	Mean Temperature Wettest Quarter
bio9	Mean Temperature Driest Quarter
bio10	Mean Temperature Warmest Quarter
bio11	Mean Temperature Coldest Quarter
bio12	Annual Precipitation
bio13	Precipitation Wettest Month
bio14	Precipitation Driest Month
bio15	Precipitation Seasonality
bio16	Precipitation Wettest Quarter
bio17	Precipitation Driest Quarter
bio18	Precipitation Coldest Quarter
bio19	Precipitation Warmest Quarter

Supporting information to Chapter 4

Appendix 1: Checklist realized with EDIT, including all currently accepted species of *Casearia* with information regarding the types

Casearia s.l. New World taxa. Sec. de Mestier (2020)***Casearia aculeata* Jacq., Enum. Syst. Pl.: 21. 1760, not defined. Sec. de Mestier (2020)**

Type statement(s): Hispaniola, Jacquin, no authentic specimen collected - Lectotype. illustration Plumier, Pl. Am. ed., p. 138, t. 147, f.l. 1757.

- = *Samyda spinosa* L., Sp. Pl., ed. 2: 557. 1762, nom. illeg. syn. sec. De Mestier (2020) ≡ *Casearia spinosa* Willd., Sp. Pl., ed. 4, 2: 626. 1799, nom. illeg. syn. sec. De Mestier (2020) Type statement(s): nom. illeg. superfl. based on *C. aculeata* Jacq. (Kiger, 1983); nom. illeg. superfl. based on *S. spinosa* L. (Kiger, 1984).
- = *Samyda tomentosa* Sw., Prodr. Veg. Ind. Occ.: 68. 1788 syn. sec. De Mestier (2020) ≡ *Casearia hirta* Sw., Fl. Ind. Occid. 2: 756. 1800 syn. sec. De Mestier (2020) ≡ *Chaetocrater hirtum* (Sw.) Raf., Sylva Tellur.: 149. 1838 syn. sec. De Mestier (2020) ≡ *Guidonia hirta* (Sw.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 64. 1889 syn. sec. De Mestier (2020) Type: Jamaica, Swartz s n. (holotype: S S-R-5563; isotype: BM BM000938978).
- = *Samyda multiflora* Cav., Icon. 1: 48. 1791 syn. sec. De Mestier (2020) Type: Cavanilles Ic. 1: 48, t. 67. (iconotype:).
- = *Casearia dentata* DC., Prodr. 2: 51. 1825 syn. sec. Mcvaugh (2001) ≡ *Casearia obovata* Schldtl. in Linnaea 13: 434-436. 1839 syn. sec. De Mestier (2020) ≡ *Samyda enneandria* Sessé & Moc., Pl. Nov. Hisp.: 71. 1888 syn. sec. De Mestier (2020) ≡ *Samyda spinosa* Sessé & Moc., Fl. Mexic., ed. 2: 112. 1894 syn. sec. De Mestier (2020) ≡ *Samyda tomentosa* Sessé & Moc., Fl. Mexic., ed. 2. 1894, nom. illeg. syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Nueva Espana, Sessé & Mocino s n. (lectotype: G G00355985); Mexico, United Mexican States, Vera Cruz, in sylvis prope la Hacienda de la Orduna, 17 Aug 1829, Schiede & Deppe s n. (holotype: HAL HAL0041943; isotypes: BR BR0000005104321, F phot F0BN013684, L L0010720); Mexico, United Mexican States, Veracruz, Cordoba, 1793, Sessé & Moc. 1234. (holotype: MA phot F; isotype: G G00355933); Mexico, United Mexican States, Veracruz, Cordoba, Sessé & Mocino 1233. (original materials: BM BM000624330, G G00355965).
- = *Casearia hirsuta* var. *glabrata* DC., Prodr. 2: 50. 1825 syn. sec. De Mestier (2020) ≡ *Guidonia hirsuta* var. *glabrata* (DC.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 94. 1889 syn. sec. De Mestier (2020) Type: Puerto Rico, Bertero s n. (holotype: G).
- = *Samyda affinis* Spreng., Syst. Veg. 2: 354. 1825 syn. sec. De Mestier (2020) Type statement(s): Hispaniola, date and collector unknown (B, lost).
- = *Casearia odorata* Macfad., Fl. Jamaica 1: 216. 1837 syn. sec. De Mestier (2020) Type: Jamaica, Macfayden 1921. (holotype: K K000471184).
- = *Casearia alba* A.Rich. in Hist. Fis. Cuba, Bot. 10: 368. 1845 syn. sec. De Mestier (2020) ≡ *Guidonia alba* (A.Rich.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 64. 1889 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Oriente, Guanabo, de la Sagra s n. (holotype: P P00789810).
- = *Casearia prunifolia* Tul. in Ann. Sci. Nat., Bot., sér. 3, 7: 363. 1847, nom. illeg. syn. sec. De Mestier (2020) Type statement(s): Colombia, Tolima, Iguanima, près de Piedras, Goudot s n.
- = *Casearia berteroana* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31(I): 461. 1858 syn. sec. De Mestier (2020) ≡ *Casearia microphylla* Bertero ex Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31(I): 461. 1858 syn. sec. De Mestier (2020) Type: Puerto Rico, 1820, Bertero s n. (holotype: NY NY01020696; isotype: MO).
- = *Casearia rufidula* Triana & Planch. in Ann. Sci. Nat., Bot., sér. 4, 17: 107. 1862 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Guataqui, Ophia, sur le Magdalena, 1851–1857, Triana s n. (syntypes: BM BM00064353, COL COL000002917, F F0060187, FI FI005275, G G00355573, K K000471232, K000471233, K000471234 & K000471235, L L0010540, L0010541 & L0010542, NY NY00107366, P P04761021, US US00114898); Colombia, Republic of, Tolima, Mariquita, entre Opia et Ambelema, 1851–1857, Triana s n. (lectotype: P P04760961).

- = *Casearia avellana* Miq. ex Eichler, Fl. Bras. 13(1): 463. 1871 syn. sec. De Mestier (2020) Type: Suriname, Republic of, Kappler 1374. (holotype: U U0002153; isotypes: FI FI004321, G G00355574 & G00355579, MO MO279834, P P00789811 & P04760955, S S04-528).
- = *Casearia spinosa* var. *tafallana* Eichler, Fl. Bras. 13(1): 464. 1871 syn. sec. De Mestier (2020) ≡ *Casearia aculeata* var. *tafallana* (Eichler) J.F.Macbr. in Publ. Field Columb. Mus., Bot. Ser. 13(4): 40. 1941 syn. sec. De Mestier (2020) Type: Ecuador, Republic of, Guayas, Guayaquil, 1778, Ruiz & Pavon s n. (holotype: F0BN013711; isotypes: BM BM000624344, F F0060194F & F0060195F, G G00236796 & G00236795, L L0010544).
- = *Guidonia hirta* var. *glabriora* M.Gómez in Anales Soc. Esp. Hist. Nat. 23: 55. 1894 syn. sec. De Mestier (2020)
- = *Casearia riparia* S.Moore in Trans. Linn. Soc. London, Bot. 4: 363. 1895 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Mato Grosso, ad ripas flum, 1891, S.Moore 509. (holotype: BM BM000624371; isotype: F F0BN013689).
- = *Casearia boliviana* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 69. 1898 syn. sec. De Mestier (2020) ≡ *Casearia obtusifolia* Rusby in Bull. New York Bot. Gard. 4: 362. 1907 syn. sec. De Mestier (2020) Type: Bolivia, Plurinational State of, La Paz, Coroico, 1894, Bang 2421. (isotypes: BM BM000611044, E E00570052, G G00355577 & G00355575, GH GH00066478, K K000471236, M M0113032, MICH MICH1111066, US US00114887, WU WU0023807); Bolivia, Plurinational State of, La Paz, Coroico, 1894, Bang 2421. (holotype: NY NY00107361).
- = *Casearia spinosa* var. *coriacifolia* Kuntze, Revis. Gen. Pl. 3(2): 100. 1898 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Mato Grosso, Corumba, 1892, Kuntze. (holotype: NY NY00107368 & NY00107369; isotype: F F0060193F).
- = *Xylosma turrialbana* Donn.Sm. in Bot. Gaz. 31: 109. 1901 syn. sec. De Mestier (2020) Type: Costa Rica, Republic of, Cartago, Turrialba, 1899, Pittier 13217. (holotype: US US00114786; isotypes: GH GH00066970, K K000471141).
- = *Casearia hassleri* Briq. in Bull. Herb. Boissier, sér. 2, 7: 671. 1907 syn. sec. De Mestier (2020) Type: Paraguay, Republic of, Prope Concepcion, 1902, Hassler 7612. (holotype: G G00008415; isotypes: A A00066468, BM BM000526883 not designated, F F0BN013674, G G00008416, G00008387, G00008389 & G00008388, K K000471148 & K000471149, MICH MICH1210009, MO MO279835, MPU MPU011164, NY NY00097945, P P04760394, S S04547, UC UC941434).
- = *Casearia nicoyensis* Donn.Sm. in Bot. Gaz. 49: 454. 1910 syn. sec. De Mestier (2020) Type: Costa Rica, Republic of, Puntarenas, Nicoya, 1900, Tonduz 13901. (holotype: US US00114883; isotypes: GH GH00066428, K K000471143 & K000471142, NY NY00097880, US US00956139 & US00956140).
- = *Casearia urbaniana* Gand. in Bull. Soc. Bot. France 65: 27. 1918 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Pinar del Rio, 1904, Wilson & Baker 1199. (holotype: LY; isotypes: F, GH, US01086186).
- = *Casearia berberoidea* Rusby in Mem. New York Bot. Gard. 7: 307. 1927 syn. sec. De Mestier (2020) Type: Bolivia, Plurinational State of, Beni, Rosario Havienda, pampas near Lake Roguaga, 1921, Rusby 1652. (holotype: NY NY00097931; isotypes: GH GH00066462, MICH MICH1111056, NY NY00097932, US US00114840).
- = *Casearia sericea* L.O.Williams & A.R.Molina in Fieldiana, Bot. 29: 360. 1961 syn. sec. De Mestier (2020) Type: Honduras, Republic of, Morazan, Rio Jalan, 3 km North of Guaimaca, 1950, Molina 3085. (holotype: F F0060130F; isotype: EAP EAP58049).
- = *Casearia guianensis* var. *rafflesioides* Croat in Ann. Missouri Bot. Gard. 62: 484. 1975 syn. sec. De Mestier (2020) Type: Panama, Republic of, Canal zone, Barro Colorado Island, Armour Trail 685, 1971, Croat 14057. (holotype: MO MO1387267; isotypes: DUKE DUKE10000444, F F0060119F, K K000471237, MO MO1387268, NY NY00097874, PMA PMA1153, VEN VEN112088).

Distribution (areas). – Argentina Northeast (present); Belize (present); Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present); Cayman Is. (present); Colombia (present); Costa Rica (present); Cuba (present); Dominican Republic (present); Ecuador (present); El Salvador (present); French Guiana (present); Guatemala (present); Guyana (present); Haiti (present); Honduras (present); Jamaica (present); Mexico Central (present); Mexico Gulf (present); Mexico Northeast (present); Mexico Northwest (present); Mexico Southeast (present); Mexico Southwest (present); Nicaragua (present); Panamá (present); Paraguay (present); Peru (present); Puerto Rico (present); Suriname (present); Venezuela (present)

***Casearia acuminata* DC., Prodr. 2: 50. 1825. Sec. Sleumer (1980)**

Type: French Guiana, Cayenne, Martin anno 1819. (holotype: F phot F7014; isotypes: K K000471192, L L0010545).

= *Casearia martinii* Benoist in Bull. Mus. Natl. Hist. Nat. 26: 352. 1920 syn. sec. De Mestier (2020) Type: French Guiana, 1824, Poiteau s n. (syntypes: K K000471193 & K000471194, L L0010546 & L0010547, P P00789994 & P00789995, U U0158390); French Guiana, 1842, Melinon 290. (syntype: P P00789987, P00789988 & P00789989); French Guiana, Cayenne, 1819, Martin anno 1819. (lectotype: P P00789990; isolectotypes: L L0010545, P P00789991, P00789992 & P00789993).

Distribution (areas). – Brazil North (present); Ecuador (present); French Guiana (present); Guyana (doubtfully present); Suriname (present)

***Casearia altiplanensis* Sleumer, Fl. Neotrop. Monogr. 22: 319. 1980.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Fed. Distr., summit of Chapada da Contagem, ca 10 km E of Brasilia, 1965, Irwin, Souza & Reis dos Santos 8256. (holotype: IAN IAN129395; isotypes: F F0060141F, L L0010550, NY NY00097923, RB RB00538545, US US00114824); Brazil, Federative Republic of, Goiás, Locally common. Campo, ca. 8 km. N.W. of Veadeiros, road to Cavalcante., Irwin, Souza & Reis dos Santos 9472. (paratypes: F, GH, IAN IAN129509, K K001216359, L, MO, NY NY896927, UB, UB).

Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present); Brazil West-Central (present)

***Casearia americana* (L.) T. Samar. & M.H. Alford in Novon 27: 68. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Laetia americana* L., Syst. Nat., ed. 10, 2: 1074. 1759 syn. sec. De Mestier (2020). Type: Colombia, Republic of, Bolivar, Cartagena, Jacquin s n. (neotype: BM).

= *Laetia apetala* Jacq. in Select. Stirp. Amer. Hist.: 167. 1763 syn. sec. De Mestier (2020) ≡ *Guidonia apetala* (Jacq.) Kuntze, Revis. Gen. Pl. 1: 44. 1891 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Bolivar, Cartagena, Jacquin s n. (holotype: BM BM000624031).

= *Azara umbellata* C.Presl, Reliq. Haenk. 2: 92. 1835 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, 1791, Haenke s n. (holotype: HAL0041991).

= *Laetia acuminata* Bonpl. ex Triana & Planch. in Ann. Sci. Nat., Bot., sér. 4, 17: 104. 1862 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Tolima, Quindio, Bonpland s n. (holotype: P P02442054; isotypes: B B-W10127-01 0, F F0BN013637).

= *Laetia apetala* var. *pubescens* Eichler, Fl. Bras. 13(1): 452. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Mato Grosso, Cuiaba, Riedel s n. (holotype: LE).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); Ecuador (present); Paraguay (present); Peru (present); Venezuela (present)

***Casearia aquifolia* C.Wright in Anales Acad. Ci. Méd. Habana 5: 201. 1868.** Sec. Sleumer (1980)

≡ *Valentia coriacea* Griseb., Cat. Pl. Cub.: 9. 1866 syn. sec. De Mestier (2020) ≡ *Casearia coriacea* (Griseb.) Eichler, Fl. Bras. 13(1): 436. 1871, nom. illeg. syn. sec. De Mestier (2020). Type: Cuba, Republic of, Oriente, cuchillas de Baracoa, Wright 12. (holotype: GOET GOET003787; isotypes: BM, GH GH00066436, K K000471190, MO MO-2049503, S S04-529).

= *Casearia grisebachii* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 62. 1898, nom. illeg. syn. sec. De Mestier (2020)

Distribution (areas). – Cuba (present)

***Casearia arborea* (Rich.) Urb., Symb. Antill. 4: 421. 1910.** Sec. de Mestier (2020)

***Casearia arborea* subsp. *arborea*.** Sec. de Mestier (2020)

≡ *Samyda arborea* Rich. in Actes Soc. Hist. Nat. Paris 1: 109. 1792 syn. sec. De Mestier (2020) ≡ *Casearia stipularis* Vent., Choix Pl.: t. 46. 1808, nom. superfl. syn. sec. De Mestier (2020) ≡ *Samyda stipularis* Poir., Encycl., Suppl. 5: 32. 1817, nom. superfl. syn. sec. De Mestier (2020) ≡ *Casearia stipularis* Cambess., Fl. Bras. Merid. 2: 169. 1830 syn. sec. De Mestier (2020) ≡ *Guidonia stipularis* M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 54. 1889, nom. illeg. syn. sec. De Mestier (2020). Type: French Guiana, Cayenne, 1792, Leblond. (holotypes: P P00371634, P P00371634; isotypes: B -W 08355 -01 0, B -W 08355 -01 0, G G00355989, G G00355989).

= *Samyda viridiflora* Aubl., Hist. Pl. Guiane 2(Suppl.): 402. 1775 syn. sec. Kiger (1984) Type: French Guiana, Aublet s n. (holotype: BM BM000624374).

= *Chaetocrater capitatus* Pers., Syst. Veg. Fl. Peruv. Chil. 1: 108. 1798 syn. sec. De Mestier (2020) ≡ *Casearia capitata* (Ruiz & Pav.) Pers., Syn. Pl. 1: 485. 1805, not defined syn. sec. De Mestier (2020) Type: Peru, Republic of, Huanuco, in nermoribus Cuchero, Chinchao et Pozuzo, Ruiz & Pavon s n. (holotype: MA; isotypes: BM BM000624363, F F0041353F & F0041354F, G G00355578, HAL, P P04762912).

- = *Casearia serrulata* Sw., Fl. Ind. Occid. 2: 754. 1800 syn. sec. Kiger (1984) ≡ *Samyda niviana* Poir., Encycl. 6: 493. 1805 syn. sec. De Mestier (2020) ≡ *Guidonia stipularis* var. *serrulata* (Sw.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 54. 1889 syn. sec. De Mestier (2020) Type: West Indies, Leeward Islands, Saint Kitt and Nevis, 1780, Masson s n. (holotype: BM BM000624351; isotype: S S-R-943).
- = *Casearia incana* Bertero ex Spreng., Syst. Veg. 2: 355. 1825 syn. sec. De Mestier (2020) Type: Puerto Rico, Bertero s n. (holotype: B lost; isotype: P P00689741 & P00689742).
- = *Casearia serrata* Macfad., Fl. Jamaica 1: 215. 1837 syn. sec. De Mestier (2020) Type: Jamaica, Macfayden s n. (holotype: K K000471185, K00471187 & K000471186).
- = *Casearia lanceolata* Miq. in Linnaea 18: 753. 1844 syn. sec. De Mestier (2020) ≡ *Casearia hostmanniana* Steud. ex Griseb., Fl. Brit. W. I.: 23. 1859 syn. sec. De Mestier (2020) Type: Suriname, Republic of, Paramaribo, Hostmann 1104. (holotype: U U0002158; isotypes: BM BM000525953, P P04761381 & P02442215); Suriname, Republic of, Paramaribo, Kappler 1618 (=Hostmann 1104). (Nametype:G G00355601; isotypes: M, MO MO279833, S S04-550 & S04-551).
- = *Casearia brasiliensis* Eichler, Fl. Bras. 13(1): 477. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, 1840, Claussen 129. (syntype: BR BR0000013346461); Brazil, Federative Republic of, Ackermann s n. (syntype: BR BR0000013346454); Brazil, Federative Republic of, Bahia, Caeteeté, Martius s n. (lectotype: M M0113034 & M0113037); Brazil, Federative Republic of, Blanchet 3430. (syntypes: BR BR0000013346331, BR0000013346355 & BR0000013346348, HAL HAL0041948); Brazil, Federative Republic of, Glaziou 2562. (syntype: BR & BR0000013346379, BR0000013346386 & BR0000013346393); Brazil, Federative Republic of, Glaziou 845. (syntypes: BR BR0000013346430 & BR0000013346423, HBG HBG515755); Brazil, Federative Republic of, Glaziou 848. (Nametype:BR BR0000013346409 & BR0000013346416).
- = *Casearia cambessedesii* var. *angustifolia* Eichler, Fl. Bras. 13(1): 476. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Sello s n. (holotype: B lost).
- = *Casearia cambessedesii* var. *parvifolia* Eichler, Fl. Bras. 13(1): 476. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Rio de Janeiro, Beyrich s n. (holotype: B lost).
- = *Casearia oligantha* Eichler, Fl. Bras. 13(1): 476. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Bahia, inter campos et Victoria, Sello 290. (lectotype: B lost; isolectotype: F FOBN013685); Brazil, Federative Republic of, Rio de Janeiro, Brattasewitz s n. (syntype: W); Brazil, Federative Republic of, Rio de Janeiro, Ponta Negra, Schott 5969. (syntypes: L L0010559, W); Brazil, Federative Republic of, Sello 218. (syntype: B lost; isosyntypes: L L0010558, P P00689743); Brazil, Federative Republic of, Sello 372. (syntype: B lost).
- = *Casearia poeppigii* Eichler, Fl. Bras. 13(1): 475. 1871 syn. sec. De Mestier (2020) Type: Peru, Republic of, Loreto, Maynas, Poeppig 3100. (holotype: L L0010560; isotypes: BM BM000624364, F F0041349F & FOBN013687, G G00355596 & G00355580, HAL HAL0041954, L L0010561, P P004762911).
- = *Casearia bangii* Rusby in Mem. Torrey Bot. Club 3(3): 34. 1893 syn. sec. De Mestier (2020) Type: Bolivia, Plurinational State of, La Paz, Yungas, Songo, 1890, Bang 845. (holotype: NY NY00097928; isotypes: BM BM000624354, BR BR0000005103980, E E00570053, G G00355582 & G00355583, GH GH0006646, K K000471231, L L0010563 & L0010564, M M0113030, MIN MIN1000519, MO MO279832, NY NY00097929 & NY00097930, PH PH00001266, US US00930921 & US00114839, WIS WIS0255857, WU WU0069446, Z Z000019920).
- = *Samyda virgata* Sessé & Moc., Fl. Mexic., ed. 2: 113. 1894 syn. sec. Kiger (1984) Type: Puerto Rico, 1787, Sessé y Lacasta & J.M.Mocino 1238. (lectotype: MA MA0100602955; isolectotype: F phot F43766); Puerto Rico, Sessé y Lacasta & J.M.Mocino 1231. (syntypes: F phot F43757, FI FI004305, G G00355576, MA MA602955).
- = *Casearia glaziovii* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 72. 1898 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Rio de Janeiro, Guanabara, Nova Friburgo, Alto Macahé, 1881, Glaziou 13404. (holotype: G G00355581; isotypes: BR BR0000006410995, K K000471160, P P04762914 & P04762915, R R000010186).
- = *Casearia umbellifera* Benoist in Bull. Mus. Natl. Hist. Nat. 26: 353. 1920 syn. sec. De Mestier (2020) Type: French Guiana, St Jean du Maroni, Benoist 873. (syntypes: L0010562, P P00789999 & P00790000).
- = *Casearia glaberrima* Uittien in Recueil Trav. Bot. Néerl. 22: 371. 1925 syn. sec. De Mestier (2020) Type: Suriname, Republic of, Zaandam 6665. (holotype: U0002154, U0002155, U0002156 & U0002157; isotypes: BR BR0000006411282 & BR0000006411107, C C10012558, IAN IAN049416, RB RB00283377).
- Distribution (areas). – Belize (present); Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); Costa Rica (present); Cuba (present); Dominican Republic (present); Ecuador (present); French Guiana (present); Guatemala (present); Guyana (present); Haiti (present); Jamaica (present); Mexico Gulf (present); Mexico Southeast (present); Mexico Southwest (present); Nicaragua (present); Panamá (present); Peru (present); Puerto Rico (present); Suriname (present); Trinidad-Tobago (present); Venezuela (present)

***Casearia arborea* subsp. *occidentalis* J.E.Gut. in Revista Jard. Bot. Nac. Univ. Habana 11: 11. 1990.** Sec. J.E.Gut. (1990)

Type: Cuba, Republic of, Cuba occidental, Pinar del Rio, 1857, Wright 16. (holotype: HAC; isotype: BR BR0000013478209 & BR0000013478216).

Distribution (areas). – Cuba (present)

***Casearia arguta* Kunth, Nov. Gen. Sp. 5: 363. 1823.** Sec. Sleumer (1980)

Type: Mexico, United Mexican States, Guerrero, Bonpland 3895. (holotype: P00679651; isotype: F phot F0BN013659).

Distribution (areas). – Belize (present); Bolivia (present); Colombia (present); Costa Rica (present); Ecuador (present); El Salvador (present); Guatemala (present); Honduras (present); Mexico Central (present); Mexico Gulf (present); Mexico Northeast (present); Mexico Northwest (present); Mexico Southeast (present); Mexico Southwest (present); Nicaragua (present); Panamá (present); Peru (present); Venezuela (present)

***Casearia atlantica* Sleumer, Fl. Neotrop. Monogr. 22: 303. 1980.** Sec. Sleumer (1980)

Type: Panama, Republic of, 25 Feb 1975, S. Mori 6671. (paratypes: L, MO); Panama, Republic of, S. Mori & J. Kallunki 3238. (Nametype:L; paratype: MO); Panama, Republic of, S. Mori & J. Kallunki 3945. (paratypes: L, MO); Panama, Republic of, S. Mori & al. 3853. (paratype: MO); Panama, Republic of, Veraguas, NW of Sta. Fé, 8.8 km from Escuela Agricola Alto de Piedra, on road to Calovebora, 25 Feb 1975, S. Mori & J. Kallunki 4846. (holotype: L L0010567; isotypes: MO MO194715, PMA PMA1155).

Distribution (areas). – Panamá (present)

***Casearia bahiensis* Sleumer, Fl. Neotrop. Monogr. 22: 362. 1980.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Bahia, Bondar 2291. (paratypes: F, US); Brazil, Federative Republic of, Bahia, Itabuna, km 80 between Betanha and Canavieiros, 13 Jul 1964, N. Silva 58418. (holotype: NY00097927; isotypes: F F0060143F, K K001097599, L L0010569, S S04-531, US US00114838); Brazil, Federative Republic of, Pernambuco: Sao Miguel dos Campos, Paiva 3324. (paratype: US).

Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present)

***Casearia bartlettii* Lundell in Lloydia 2: 104. 1939.** Sec. Sleumer (1980)

≡ *Samyda bartlettii* (Lundell) Lundell in Wrightia 2: 56. 1960 syn. sec. De Mestier (2020). Type: Guatemala, Republic of, Peten, Uaxactun, 1931, Bartlett 12558. (holotype: MICH MICH1111054; isotypes: A A00066420, CAS CAS0001448, L L0010574, LL LL00372010, MO MO-194720, NY NY00097868 & NY00468419, TEX TEX00372011).

Distribution (areas). – Belize (present); Guatemala (present); Mexico Southeast (present); Mexico Southwest (present).

***Casearia bicolor* Urb., Symb. Antill. 1: 372. 1899.** Sec. T. Samar. & M.H. Alford (2019)

Type: Puerto Rico, prope Utado, in monte Santa Isabella, 1887, Sintenis 6181. (holotype: B lost; lectotype: P P02442049; isolectotypes: BM BM000582578, F F0060137F & F0060138F, G G00364258, G00364261 & G00364269, GH GH00066874, HBG HBG515669, L L0011075 & L2470579, M M0113019, NY NY00688928, P P02442048, S S04-533, US US00114841, WU WU0097175, Z Z000017504).

= *Samyda procera* Poepp., Nov. Gen. Sp. Pl. 3: 67. 1845 syn. sec. De Mestier (2020) ≡ *Casinga procera* (Poepp.) Griseb., Fl. Brit. W. I.: 710. 1864 syn. sec. De Mestier (2020) ≡ *Laetia procera* (Poepp.) Eichler, Fl. Bras. 13(1): 453. 1871 syn. sec. De Mestier (2020) ≡ *Guidonia procera* (Poepp.) Kuntze, Revis. Gen. Pl. 1: 44. 1891 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Amazonas, Ega, Poeppig 2853. (holotype: W W0048642; isotypes: F F0060290F & F0060291F, G G00364250 & G00364264, GH GH00066937, P P02442217, W W0048643).

= *Laetia casearioides* Sagot ex Benth. in J. Proc. Linn. Soc., Bot. 5(Suppl. 2): 85. 1861 syn. sec. De Mestier (2020) Type: French Guiana, Karouany, Sagot 1137. (holotype: K K000471403 & K000471402; isotypes: B B10 0243751, BM BM000582582 & BM000582583, BR BR0000005104215, G G00364251, GOET GOET003815, S S04-521, U U0002191).

= *Casearia belizensis* Standl. in Publ. Field Columb. Mus., Bot. Ser. 12: 412. 1936 syn. sec. De Mestier (2020) Type: Belize, Toledo, Temash River, 1935, Schipp 1314. (holotype: F0060114F; isotypes: A A00066421, BM BM000624032, CAS CAS0001449, G G00364273, K K000471409, L L0011074, MICH MICH1111055, NY NY00097869, S S04-532).

Distribution (areas). – Belize (present); Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil West-Central (present); Colombia (present); Costa Rica (present); Dominican Republic (present); Ecuador (present); French Guiana (present); Guatemala (present); Guyana (present); Haiti (present); Nicaragua (present); Panamá (present); Peru (present); Puerto Rico (present); Suriname (present); Trinidad-Tobago (present); Venezuela (present)

***Casearia bissei* J.E.Gut. in Revista Jard. Bot. Nac. Univ. Habana 1: 104. 1981 ["1980"].** Sec. J.E.Gut. (1981)

Type: Cuba, Republic of, Prov. Oriente, Baracoa, carreterade Quibijan, 3.1.1960, Alain & lopez Figueiras 7259. (holotype: HAJBG000313).

Distribution (areas). – Cuba (present)

***Casearia cajambrensis* Cuatrec. in Fieldiana, Bot. 27: 103. 1950.** Sec. Sleumer (1980)

Type: Colombia, Republic of, Valle, Costa del Pacifico, Rio Cajambre, Quebrada de Guapecito, 1944, Cuatrecasas 17717. (holotype: F F0060148F; isotypes: COL COL000002907 & COL000002908, F F0060147F, L L0010580).

Distribution (areas). – Colombia (present); Panamá (present); Venezuela (present)

***Casearia catharinensis* Sleumer, Fl. Neotrop. Monogr. 22: 376. 1980.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Santa Catarina, Rio do Sul, Serra do Matador, 2 Aug 1958, Reitz & Klein 6931. (holotype: L; isotypes: B 10 0243770 & B 10 0243771, GH GH00066464, K K001097598, NY NY00074321, US US00114847, WIS WISv0255858WIS); Brazil, Federative Republic of, Sta. Catarina, Klein 2986. (paratype: L); Brazil, Federative Republic of, Sta. Catarina, Reitz & Klein 11396. (paratype: L); Brazil, Federative Republic of, Sta. Catarina, Reitz & Klein 1963. (paratypes: HBR, L); Brazil, Federative Republic of, Sta. Catarina, Reitz & Klein 6868. (paratypes: L, S); Brazil, Federative Republic of, Sta. Catarina, Reitz & Klein 7324. (paratypes: L, S).

Distribution (areas). – Brazil South (present)

***Casearia combaymensis* Tul. in Ann. Sci. Nat., Bot., sér. 3, 7: 362. 1847.** Sec. Sleumer (1980)

Type: Colombia, Republic of, Tolima, near Ibaguè along the River Combayma, Goudot 106. (holotype: P00116733; isotypes: FI FI004303 & FI004304, P P00116734).

= *Casearia subopaca* Planch. & Triana in Ann. Sci. Nat., Bot., sér. 4, 17: 110. 1862 syn. sec. De Mestier (2020)

Type: Colombia, Republic of, Antioquia, Cordillera Central, Triana s n. (lectotype: P00790001; isolectotypes: BM BM000624365, L L0010591); Colombia, Republic of, Norte de Santander, Ocana, 1853, Schlim 586. (syntypes: F F0060197F, G G00364151, G00364160 & G00364161, K K000471228).

= *Casearia singularis* Eichler, Fl. Bras. 13(1): 473. 1871 syn. sec. De Mestier (2020) Type: Suriname, Republic of, Hostmann & Kappler 1158. (holotype: W; isotypes: BM BM000624375, C C10012556, F F0060192F, G G00364162 & G00364169, K K000471171, K000471172 & K000471173, L L0010592, MO MO-279824, S S04-570, U U0002159).

= *Casearia bracteifera* Sagot in Ann. Sci. Nat., Bot., sér. 6, 13: 285. 1882 syn. sec. De Mestier (2020) Type: French Guiana, Acarouany, 1857, Sagot s n. (lectotype: P00116736; isolectotypes: K K000471170, L L0010593, P P00116737, P00790003 & P00116736); French Guiana, Melinon 118. (Nametype:K000471169; syntypes: K000471169, P P00116739, P00116740 & P00790018).

= *Casearia membranacea* Britton in Bull. Torrey Bot. Club 17: 214. 1890, nom. illeg. syn. sec. De Mestier (2020) Type: Bolivia, Plurinational State of, Beni, junction of the River Beni and Madre de Dios, 1886, Rusby 2074. (holotype: NY00107351; isotypes: BM BM000624355, E E00570048, G G00364155, GH GH00066472, K K000471229, MICH MICH1111063, NY NY00107352, PH PH00001273, US US00930920 & US00114877, WIS WISv0255860WIS).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); Ecuador (present); French Guiana (present); Guyana (present); Peru (present); Suriname (present); Venezuela (present)

***Casearia comocladifolia* Vent., Choix Pl.: t. 44. 1808.** Sec. Sleumer (1980)

≡ *Anavinga comocladifolia* (Vent.) Raf., Sylva Tellur.: 149. 1838 syn. sec. De Mestier (2020). Type: Dominican Republic, aux environs de Monte Cristi, Turpin anno 1807. (holotype: P P00678804; isotype: G G00364174).

= *Casearia guantanamoensis* Vict. in Contr. Inst. Bot. Univ. Montréal 49: 42, f. 8. 1944 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Oriente, United States Naval Station, Guantanamo Bay, 1909, Britton 2096. (lectotype: US US00114862; isolectotypes: BM BM000624352, F F0060139F, NY NY00097914).

Distribution (areas). – Cuba (present); Dominican Republic (present); Haiti (present).

***Casearia completa* (Jacq.) T. Samar. & M.H. Alford in Novon 27. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Laetia completa* Jacq., Enum. Syst. Pl.: 24. 1760 syn. sec. De Mestier (2020) ≡ *Hecatostemon completus* (Jacq.) Sleumer in Blumea 24. 1978 syn. sec. De Mestier (2020). Type: Colombia, Republic of, Bolivar, Cartagena, Jacquin s n. (neotype: BM).

= *Laetia guazumifolia* Kunth, Nov. Gen. Sp. 5: 356. 1823 syn. sec. De Mestier (2020) Type: Venezuela, Bolivarian Republic of, Sucre, Bordones, near Cumana, Humboldt 358. (holotype: P P00679640; isotype: F F0BN013635).

= *Laetia hirtella* Kunth, Nov. Gen. Sp. 5: 355. 1823 syn. sec. De Mestier (2020) Type: Venezuela, Bolivarian Republic of, Sucre, Cumana, Humboldt & Bonpland s n. (holotype: P P00679639; isotypes: F F0060245F, L L0011068).

= *Laetia guazumifolia* var. *tomentosa* Triana & Planch. in Ann. Sci. Nat., Bot., sér. 4, 17: 103. 1862 syn. sec. De Mestier (2020) ≡ *Hecatostemon guazumifolius* (Kunth) Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 12: 55. 1934 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Bolivar, Cartagena, 1844, Triana s n. (lectotype: P P00679640; isolectotype: BM); Colombia, Republic of, Magdalena, Cerro de San Antonio, 1844, Goudot. (syntypes: F, P).

= *Hecatostemon dasygynus* S.F.Blake in Contr. Gray Herb. 53: 43. 1918 syn. sec. De Mestier (2020) Type: Venezuela, Bolivarian Republic of, Miranda, Rio Limon, 1917, Haman 807. (holotype: GH GH00066713; isotypes: NY NY00107428, US US00114916 & US00114917).

Distribution (areas). – Brazil North (present); Colombia (present); Guyana (present); Peru (present); Venezuela (present)

***Casearia coronata* Standl. & L.O.Williams in Fieldiana, Bot. 29: 548. 1963.** Sec. Sleumer (1980)

Type: Costa Rica, Republic of, Limon, 6 miles inland from mouth of Estrella River, 21.4.1952, Stork 4616. (holotype: F F0060115F & F0060116F; isotypes: L L0010605, UC UC1239803 & UC1254051).

Distribution (areas). – Colombia (present); Costa Rica (present); El Salvador (present); Panamá (present)

***Casearia corymbosa* Kunth, Nov. Gen. Sp. 5: 366. 1823.** Sec. Sleumer (1980)

Type: Colombia, Republic of, Bolivar, prope Mompox, Bonpland. (syntype: P P04699625 & P04699626); Colombia, Republic of, Tolima, Honda, Bonpland. (lectotype: P P00679653; isolectotypes: F F0060155F, P P0469961, P04699618 & P04699620).

= *Casearia dubia* Moc. & Sessé ex DC., Prodr. 2: 51. 1825 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Calques, Sessé y Lacasta & J.M.Mocino s n. (holotype: G; isotype: F phot F30573).

= *Casearia salicifolia* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31(I): 460. 1858 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Funk, N. & Schlim, L. s n. (syntype: KW KW001001120).

= *Casearia lindeni* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 67. 1898 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Tabasco, Rio Teapa, 1840, Linden 621. (holotype: NY NY00097877; isotypes: BR BR0000005104819, F F0060121F, FI FI004295, G G00355935, G00355960, G00355961 & G00355975, K K000471097, P P00790021).

= *Casearia orizabana* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 67. 1898 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, 1855, Sumichrast 1061. (syntype: G G00355964); Mexico, United Mexican States, Veracruz, Orizaba, 1855, Botteri 1061. (lectotype: G G00355962 & G00355963; isolectotypes: BM BM000624331, F F0060125F, K K000471098).

= *Casearia pringlei* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 65. 1898 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Jalisco, Guadalajara, 1889, Pringle 2551. (holotype: A A00066430; isotypes: B B100243769, BM BM000624332, BR BR0000008719560 & BR0000006411077, CAS CAS0001439, CM CM1462, F F0060127F, G G00355930 & G00355936, K K000471095, MEL MEL2474905, MEXU MEXU00026510, NY NY00097881 & NY00097882, P P00790022, U U0002161, US US00114893, VT UVMVT053139 & UVMVT024592, YU YU069982).

= *Casearia banquitana* E.H.L.Krause in Beih. Bot. Centralbl. 32(2): 345. 1914 syn. sec. De Mestier (2020) Type: Nicaragua, Republic of, Banquito, Borntraeger s n. (holotype: B lost; isotypes: F F0BN013660, NY NY00097867).

= *Casearia dolichophylla* Standl. in Contr. U.S. Natl. Herb. 23: 846. 1923 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Oaxaca, Picacho, 1914, Purpus 7447. (holotype: US US00114857; isotypes: GH GH00066423, MO MO194805 & MO194806, NY NY00097872).

- = *Casearia laevis* Standl. in Contr. U.S. Natl. Herb. 23: 845. 1923 syn. sec. De Mestier (2020) ≡ *Casearia banquitana* var. *laevis* (Standl.) I.M.Johnst. in Sargentia 8: 211. 1949 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Sinaloa, Mazatlan, 1910, Rose, Standley & Russell 14154. (holotype: US US00114866; isotypes: F F0060120F, GH GH00066425, NY NY00097876).
- = *Casearia mollifolia* Standl. in Publ. Field Columb. Mus., Bot. Ser. 9: 311. 1940 syn. sec. De Mestier (2020) Type: Honduras, Republic of, Yoro, Aguan river valley, Medina, 1938, Yuncker & al. (holotype: F F0060124F; isotypes: BM BM000624346, G G00364175, GH GH00066426, K K00471144, MICH MICH1111064, MO MO194717, NY NY00097878 & NY00097879, S S04-563, US US00114880).
- = *Casearia phegocarpa* Standl. in Publ. Field Columb. Mus., Bot. Ser. 9: 312. 1940 syn. sec. De Mestier (2020) Type: Honduras, Republic of, Atlantida, Tela, Lancetilla Valley, 1927, Standley 55212. (holotype: F0060126F; isotypes: A A00066429, US US01199222).
- = *Casearia gentlei* Lundell, Field & Lab. 13: 9. 1945 syn. sec. De Mestier (2020) Type: Belize, Toledo, Bolo camp, upper reach of Golden Stream, 1944, Gentle 4489. (LL LL00372012; isotypes: F F0060118F, K K000471145, LL LL00208161, MO MO194718, TEX TEX00372013, UC UC1179402, US US00114860).

Distribution (areas). – Belize (present); Colombia (present); Costa Rica (present); El Salvador (present); Guatemala (present); Honduras (present); Mexico Central (present); Mexico Gulf (present); Mexico Northeast (present); Mexico Northwest (present); Mexico Southeast (present); Mexico Southwest (present); Nicaragua (present); Panamá (present); Venezuela (present)

***Casearia corymbulosa* (Spruce ex Benth.) T. Samar. & M.H. Alford in Novon 27: 68. 2019.** Sec. T. Samar. & M.H. Alford (2019)

- ≡ *Laetia corymbulosa* Spruce ex Benth. in J. Proc. Linn. Soc., Bot. 5(Suppl. 2): 83. 1861 syn. sec. De Mestier (2020) ≡ *Guidonia corymbulosa* (Spruce ex Benth.) Kuntze, Revis. Gen. Pl. 1: 44. 1891 syn. sec. De Mestier (2020). Type: Brazil, Federative Republic of, Amazonas: ad oram meridionalem flum. Amazonum adosium flum. Solimoes., 1851, Spruce 1599. (holotype: K K000471407; isotypes: BM BM000624043, FI FI005745, K K000471406, L L0011070 & L0011071, M M0113005, P P04793631, W W1889-0163017).
- = *Laetia floribunda* Spruce in J. Proc. Linn. Soc., Bot. 5(Suppl. 2): 83. 1861 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Amazonas, Managuirí near the confluence of Rio Solimoes and Rio Negro, Jun 1851, Spruce 1580. (holotype: K K000471404; isotypes: BM BM000624041, E E00296673, F F0060244F, FI FI005746, G G00364247 & G00364248, K K000471405, M M0113004, NY NY00107486, P P04793629, W W1889-0163018).
- = *Laetia corymbulosa* var. *floribunda* (Spruce ex Benth.) Eichler, Fl. Bras. 13(1): 453. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Amazonas, ad oram meridionalem flum. Amazonum ad ostium flum, Solimoes, Spruce 1599. (holotype: K K000471407; isotypes: BM BM000624043, FI FI005745, K K000471406, L L0011071, M M0113005).

Distribution (areas). – Brazil North (present); Colombia (present); Peru (present)

***Casearia cotticensis* Uittien in Recueil Trav. Bot. Néerl. 22: 369. 1925.** Sec. Marquete (2012)

Type: Suriname, Republic of, Cottica river, 21 Jun 1921, Gonggrijp BW. 5332. (holotype: U U0002179; isotypes: K K000471158, RB RB00081575, U U0002180).

- = *Casearia reginae* J.F.Macbr. ex Ll.Williams in Publ. Field Columb. Mus., Bot. Ser. 15: 356. 1936 syn. sec. De Mestier (2020) Type: Peru, Republic of, Loreto, La Victoria, Williams 2758. (holotype: F F0041350F; isotype: G G00364185 & G00364186).

Distribution (areas). – Brazil North (present); Colombia (present); Guyana (present); Peru (present); Suriname (present)

***Casearia crassinervis* Urb. in Repert. Spec. Nov. Regni Veg. 19: 118. 1923.** Sec. Sleumer (1980)

Type: Cuba, Republic of, Oriente, Pinar Mayari Abajo, Wright 12a. (holotype: B lost; isotypes: GH GH00066438, K K000471191, L L0010607, NY NY00097905, NY00097906 & NY00097907, S S04-536, US US00114844).

Distribution (areas). – Cuba (present)

***Casearia decandra* Jacq., Enum. Syst. Pl.: 21. 1760.** Sec. de Mestier (2020)

Type: Martinique, West Indies, Martinique, in montibus sylvaticis circa vicum Case Pilote, 1755, Jacquin. (holotype: BM BM000611040; isotype: MO MO279830).

- = *Samyda parviflora* Loefl., Iter Hispan.: 260. 1758, nom. illeg. syn. sec. Steyermark & al. (1995–2005)

- = *Casearia parviflora* Jacq. in Select. Stirp. Amer. Hist.: 65. 1780, nom. superfl. syn. sec. De Mestier (2020) Type statement(s): based on *C. decandra* Jacq.
- = *Casearia parvifolia* Willd., Sp. Pl., ed. 4, 2: 628. 1799, nom. superfl. syn. sec. De Mestier (2020) ≡ *Guidonia parvifolia* M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 93. 1889, nom. superfl. syn. sec. De Mestier (2020) Type statement(s): based on *C. decandra* Jacq.
- = *Samyda parvifolia* Poir., Encycl. 6: 492. 1805 syn. sec. De Mestier (2020) Type statement(s): based on *C. decandra* Jacq.
- = *Anavinga parvifolia* Lam., Tabl. Encycl. 2: 484. 1819 syn. sec. De Mestier (2020) Type: Lamarck, t. 355, f. 2, 1797. (holotype:).
- = *Casearia adamantium* Cambess., Fl. Bras. Merid. 2: 230. 1830 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Minas Gerais, St Hilaire 2017. (holotype: P P02442213; isotypes: F F0076295F, MPU MPU011173, P P02442214).
- = *Casearia adstringens* Mart., Syst. Mat. Med. Bras.: 51. 1843 syn. sec. De Mestier (2020) ≡ *Guidonia adstringens* (Mast.) Baill. in Traité Bot. Méd. Phan. 2: 827. 1884 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Amazonas, in ripa canalis Massari prope ostium flum. Madeira in Amazonum, Martius 2739. (holotype: M M0113023, M0113025 & M0113028; isotypes: FI FI004281, L, P P).
- = *Casearia nitida* Sieber ex Griseb., Fl. Brit. W. I.: 23. 1859 syn. sec. De Mestier (2020)
- = *Casearia parvifolia* var. *microcarpa* Eggers in Smithsonian Misc. Collect. 23(3): 26. 1879 syn. sec. De Mestier (2020) Type: US Virgin Islands, St. Croix, Eggers anno 1874. (holotype: C).
- = *Samyda lancifolia* Sessé & Moc., Fl. Mexic., ed. 2: 113. 1894 syn. sec. De Mestier (2020) Type: Puerto Rico, Sessé y Lacasta & J.M.Mocino 1239. (holotype: MA MA602980).
- = *Casearia floribunda* Briq. in Bull. Herb. Boissier, sér. 2, 7: 672. 1907 syn. sec. De Mestier (2020) Type: Paraguay, Republic of, in regiones cursus super. flum, 1901, Hassler 7706. (holotype: G G00008420; isotypes: A A00066466, BM BM000526891 & BM000526894, CAS CAS0001435, F F0076420F & F0076296F, F F0BN013671, G G00008421, G00008422, G00008393 & G00008394, MICH MICH1111059, MO MO279830, MPU MPU011169 & MPU011168, NY NY00097936 & NY00097937, P P02442241 & P02442242, S S04544, UC UC941437).
- = *Casearia parvifolia* var. *paraguariensis* Briq. in Bull. Herb. Boissier, sér. 2, 7: 672. 1907 syn. sec. De Mestier (2020) Type: Paraguay, Republic of, Tayi, 1898–1899, Hassler 4374. (holotype: G G00008413; isotypes: A A00066479, BM BM000526893, F F0060176F, G G00008413, G00008390, G00008391 & G00008392, MPU MPU011160, NY NY00107364, P P02442240, S S04-566, UC UC950145).
- = *Casearia albicaulis* Rusby in Mem. New York Bot. Gard. 7: 307. 1927 syn. sec. De Mestier (2020) Type: Bolivia, Plurinational State of, Beni, pampas near Lake Ragagua, 1921, Rusby 1366. (holotype: NY NY00097922; isotypes: K K000471238, MICH MICH1111053, NY NY00097921, US US00114823).
- = *Casearia pavoniana* Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 958. 1934 syn. sec. De Mestier (2020) Type: Peru, Republic of, Junin, Vitoc, 1792, Ruiz & Pavon 27. (holotype: MA MA813540; isotypes: F F0041345F & F0041344F, FI FI004280, L0010615).
- = *Casearia reflexa* Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 959. 1934 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Rio Grande do Sul, Neu-Württemberg, 1905, Bornmüller 549. (holotype: B lost; isotypes: CAS CAS0001441, F F0060182F, G G00236797, GH GH00066481, HBG HBG515747, L L0010616, U U0002162).
- = *Chaetocrater reflexus* Ruiz & Pav. in Anales Inst. Bot. Cavanilles 15: 130. 1957 syn. sec. De Mestier (2020) Type: Peru, Republic of, Junin, Vitoc, Ruiz & Pavon s n. (holotype: MA; isotypes: BM, F, G).
- *Casearia parvifolia* var. *genuina* Briq. in Bull. Herb. Boissier, sér. 2, 7: 672. 1907, nom. inval. syn. sec. De Mestier (2020)
- *Casearia serrulata* Sieber, nom. inval. syn. sec. De Mestier (2020)

Distribution (areas). – Argentina Northeast (present); Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); Dominican Republic (present); Ecuador (present); French Guiana (present); Haiti (present); Honduras (present); Leeward Is. (present); Panamá (present); Paraguay (present); Peru (present); Puerto Rico (present); Suriname (present); Trinidad-Tobago (present); Uruguay (present); Venezuela (present); Windward Is. (present)

***Casearia dodecandra* (Jacq.) T. Samar. & M.H. Alford in Novon 27: 21. 2019.** Sec. T. Samar. & M.H. Alford (2019)

- ≡ *Samyda dodecandra* Jacq., Enum. Syst. Pl. 1760 syn. sec. De Mestier (2020) ≡ *Samyda serrulata* L., Sp. Pl., ed. 2: 558. 1762, nom. illeg. syn. sec. De Mestier (2020) ≡ *Samyda denticulata* Poir., Dict. Sci. Nat., ed. 2, 47: 159. 1827, nom. illeg. syn. sec. De Mestier (2020). Type statement(s): Lectotype. Illustration. Pl. Amer. t. 146, f.2. 1757.

- = *Samyda oligostemon* Urb. in Ark. Bot. 17(7): 43. 1921 syn. sec. De Mestier (2020) Type: Haiti, Republic of, morne de la Hotte, 11.6.1917, Ekman 155. (holotype: S S04-520; isotype: F F0BN005791).
- = *Samyda campanulata* Borhidi & O. Muñiz in Acta Bot. Acad. Sci. Hung. 22: 313. 1977 ["1976"] syn. sec. De Mestier (2020) Type: Cuba, Republic of, prov. Oriente, Rente, Santiago de Cuba, 8.1951, Chrysogone 1982. (holotype: HAC; isotype: GH GH00066933).
- = *Samyda subintegra* Borhidi & O. Muñiz in Acta Bot. Acad. Sci. Hung. 22: 314. 1977 ["1976"] syn. sec. De Mestier (2020) Type: Cuba, Republic of, Prov. Camaguey, Pastelillo, Nuevitas, 7.1948, Leon 23385. (holotype: HAC; isotype: GH GH00066936).
- = *Samyda decandra* Jacq., Enum. Syst. Pl.: 21. 1760 syn. sec. Liogier (1972–1978) Type: St. Martin (French part), Fr. Arnoldo 3397. (neotype: U); St. Martin (French part), Jacquin anno 1755-57. (holotype: not preserved).
- = *Samyda rosea* Sims in Bot. Mag. 16: t. 550. 1802 syn. sec. De Mestier (2020) Type: Bot. Mag. t. 550. (lectotype:). Type statement(s): Cultivated, probably introduced from St. Vincent, no authentic specimen.
- = *Samyda rubra* DC., Prodr. 2: 48. 1825 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, apparently from Puerto Rico, Sessé & Mocino. (no authentic specimen); de Candolle Calq. Fl. Mexic. Icon. Ined. 182. (lectotype: G).
- = *Samyda velutina* DC., Prodr. 2: 48. 1825 syn. sec. De Mestier (2020) Type: Haiti, Republic of, Poiteau anno 1802. (holotype: G DC; isotypes: FI FI004329, G G00364204 & G00364205).
- = *Samyda tenuifolia* Urb., Symb. Antill. 7: 289. 1912 syn. sec. De Mestier (2020) Type: Dominican Republic, Barahona Province, 1911, Fuertes 898. (holotypes: B lost, F phot F0BN005792; isotypes: NY NY00000046, US US00114811).

Distribution (areas). – Cuba (present); Dominican Republic (present); Haiti (present); Jamaica (present); Leeward Is. (present); Netherlands Antilles (present); Puerto Rico (present); Trinidad-Tobago (present); Windward Is. (present)

***Casearia dolichanthera* T. Samar. & M.H. Alford in Novon 27: 67. 2019.** Sec. T. Samar. & M.H. Alford (2019)

- ≡ *Samyda grandiflora* Griseb., Cat. Pl. Cub.: 11. 1866, nom. illeg. syn. sec. De Mestier (2020) ≡ *Samyda macrantha* P. Wilson in Torreyia 30. 1930 syn. sec. De Mestier (2020). Type: Cuba, Republic of, Matanzas, Rugel 313. (syntype: L L0011223); Cuba, Republic of, Matanzas, in savannis Guamacaro (Limonar) & La Palma Sola, Wright 1158 (=1897). (lectotype: GOET GOET003906; isolectotypes: B 10 0243738, BM BM000611064, G G00364206 & G00364209, GH GH00066935, GOET GOET003907, GOET003908 & GOET003909, K K000471278, MO MO-2049502, NY NY108158 & NY108159, P P00790010, S S04-517 & S12-23089, US US00114808 & US00114809); Cuba, Republic of, Matanzas, in savannis Guamacaro (Limonar) and La Palma Sola, Wright 1897. (lectotype: GOET GOET003906; isolectotypes: B 10 0243738, BM BM000611064, G G00364206 & G00364209, GH GH00066935, GOET GOET003907, GOET003908 & GOET003909, K K000471278, MO MO-2049502, S S04-517 & S12-23089).

Distribution (areas). – Cuba (present)

***Casearia draganae* M.H. Alford in J. Bot. Res. Inst. Texas 9: 325. 2015.** Sec. M.H. Alford (2015)

Type: Colombia, Republic of, Valle del Cauca: Bajo Calima, concesion Pulpapel/Buenaventura, bosque pluvial tropical, 3°55'N, 77°00'W, 100m, 23.11.1984, M. Monsalve B. 541. (holotype: COL).

Distribution (areas). – Colombia (present); Ecuador (present)

***Casearia duckeana* Sleumer, Fl. Neotrop. Monogr. 22: 349. 1980.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Amazonas, Albuquerque & Elias 67-46. (paratype: INPA); Brazil, Federative Republic of, Amazonas, B. Krukoff 6854. (paratypes: A, B 10 0243768, BM, BR, F, G, IAN, K K001216533, MICH, MO, NY NY2149967, S, U, US); Brazil, Federative Republic of, Amazonas, F. Chagas & Dionisio s n. (paratypes: IAN, INPA 3242); Brazil, Federative Republic of, Amazonas, F. Chagas s n. (paratypes: INPA 110, MG 21083); Brazil, Federative Republic of, Amazonas, Francisco s n. (paratypes: INPA 2066, MG 21096); Brazil, Federative Republic of, Amazonas, Lima & al. s n. (paratype: INPA); Brazil, Federative Republic of, Amazonas, Manaus, Reserva Florestal Ducke proximo a estrada, 4 Sep 1968, J. Aluisio 145. (holotypes: INPA, L L0010620); Brazil, Federative Republic of, Amazonas, O. Monteiro & Ramos 50. (paratype: INPA); Brazil, Federative Republic of, Amazonas, Schultes & W. Rodrigues 21121 A. (paratype: INPA); Brazil, Federative Republic of, Amazonas, W. Rodrigues & D. Coelho 8295. (paratype: INPA); Brazil, Federative Republic of, Amazonas, W. Rodrigues & Loureiro 5761. (paratype: INPA); Brazil, Federative Republic of, Rondonia, G. Prance & al. 8541. (paratypes: F, GH, INPA, L, MG, NY, U, US).

Distribution (areas). – Bolivia (present); Brazil North (present); Venezuela (present)

***Casearia eichleriana* Sleumer, Fl. Neotrop. Monogr. 22: 313. 1980.** Sec. Sleumer (1980)

≡ *Casearia microphylla* Eichler, Fl. Bras. 13(1): 474. 1871, nom. illeg. syn. sec. De Mestier (2020). Type: Brazil, Federative Republic of, Bahia, Blanchet 3371. (paratypes: BM, G, K); Brazil, Federative Republic of, Bahia, Harley & al. 15480. (paratypes: K, L); Brazil, Federative Republic of, Bahia, Harley & al. 16691. (paratypes: K, L); Brazil, Federative Republic of, Bahia, Harley & al. 16995. (paratypes: K, L); Brazil, Federative Republic of, Bahia, Irwin & al. 32608. (paratypes: IAN, L, MICH, NY NY375231, U, US); Brazil, Federative Republic of, Bahia, Irwin & al. 32617. (paratypes: C, K, L, NY NY375230, US US2709366); Brazil, Federative Republic of, Bahia, Ule 7212. (paratype: K); Brazil, Federative Republic of, Minas Gerais, Anderson & al. 35100. (paratypes: K, L, NY NY897056, US US01887927); Brazil, Federative Republic of, Minas Gerais, Anderson 8350. (paratypes: C, NY NY897055, US US2755042); Brazil, Federative Republic of, Minas Gerais, Glaziou 18853. (paratypes: K, P, R); Brazil, Federative Republic of, Minas Gerais, Irwin & al. 22905. (paratypes: K, L, NY NY897052, US US01887933); Brazil, Federative Republic of, Minas Gerais, Irwin & al. 23314. (paratypes: K, L, NY NY897053, US); Brazil, Federative Republic of, Minas Gerais, Serra da Lapa, Riedel s n. (holotype: LE; isotypes: F F0060172F, G G00355993, GH GH00066473, K K000471162, L L0010621, NY NY107355).

Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present)

***Casearia elegans* Standl. in Publ. Field Columb. Mus., Bot. Ser. 9: 311. 1940.** Sec. Sleumer (1980)

Type: Honduras, Republic of, Atlantida, foothills back of Ceiba, 4 Aug 1938, Yuncker & al. 8804. (holotype: F F0060117F; isotypes: BM BM000546838, G G00355974, GH GH00066424, K K000471138, L L0010623, MICH MICH1111058, MO MO-194719, NY NY00097873, S S04-540, US US00114858).

= *Casearia hintonii* Lundell in Wrightia 3: 122. 1965 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Michoacan, Coalcoman, Aquila, 7 Aug 1941, Hinton 15694. (holotype: LL LL00372015; isotypes: GBH GBH015964, L L0010624, MICH MICH1111061, NY NY97875, S S10-12205).

= *Casearia mayana* Lundell in Wrightia 5: 165. 1975 syn. sec. De Mestier (2020) Type: Guatemala, Republic of, Izabal, El Estor, bordering Rio Sarco, on Rancho El Melagro, 21 May 1975, Lundell & Contreras 19325. (holotype: LL LL00372018; isotypes: BM BM000624334, CAS CAS0001436, DUKE DUKE10000448, F F0060122F, K K000471139, L L0010622, S S10-15151 & S04-562).

Distribution (areas). – Guatemala (present); Honduras (present); Mexico Southeast (present); Mexico Southwest (present)

***Casearia emarginata* C.Wright ex Griseb., Cat. Pl. Cub.: 10. 1866.** Sec. Sleumer (1980)

Type: Cuba, Republic of, Oriente, prope Quemado, 1860, Wright 1894. (holotype: GOET GOET003804; isotypes: B 10 0277748, BM BM000611041, G G00364180 & G00356000, GH GH00057202, K K000471181, L L0010629, MO MO-279838, NY NY00097909, P P00790026, YU YU069984).

= *Casearia ehrenbergiana* Urb., Symb. Antill. 1: 373. 1899 syn. sec. De Mestier (2020) Type: Haiti, Republic of, Port-au-Prince, 1828, Ehrenberg s n. (holotypes: B lost, F phot F0BN005793; isotypes: HAL HAL0041971, L L0010627).

= *Casearia randioides* Lundell, Contr. Univ. Michigan Herb. 6: 48. 1941 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Yucatan, km 20 Merida-Progreso road, 1938, Lundell & Lundell 7982. (holotype: MICH MICH1111067; isotypes: A A00066432, CAS CAS0001440 & CAS0026242, DUKE DUKE10000449, F F0060129F, K K000471140, L L0010626, LL LL00372019, NY NY00097883, TEX TEX00372020, US US00114895).

Distribution (areas). – Cuba (present); Haiti (present); Mexico Southeast (present)

***Casearia espiritosantensis* R.Marquete & Mansano in Novon 20: 179. 2010.** Sec. R.Marquete & Mansano (2010)

Type: Brazil, Federative Republic of, Espirito Santo: Santa Teresa, Reserva Biol. Augusto Ruschi, estrada principal, proximo a sede, 2 Sep 2003, J. Rossini, E. Bausen & W. Pizziolo 527. (holotype: RB RB00608924; isotype: RB RB00609137).

Distribution (areas). – Brazil North (present)

***Casearia fasciculata* (Ruiz & Pav.) Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 955. 1934.** Sec. Sleumer (1980)

- ≡ *Chaetocrater fasciculatus* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil.: 107. 1798 syn. sec. De Mestier (2020) ≡ *Crateria fasciculata* (Ruiz & Pav.) Pers., Syn. Pl. 1: 485. 1805 syn. sec. De Mestier (2020) ≡ *Casearia punctata* Spreng., Syst. Veg. 2: 355. 1825, nom. illeg. syn. sec. De Mestier (2020). Type: Peru, Republic of, Huanuco, in Chinchao nemoribus circa Hualqui praedium, Ruiz & Pavon s n. (holotype: MA MA813536; isotypes: F F0041355F & F0041356F, FI FI004294, L L0010633 & L0010634).
- = *Casearia petiolaris* Poepp. ex Eichler, Fl. Bras. 13(1): 471. 1871 syn. sec. De Mestier (2020) Type: Peru, Republic of, Loreto, Yurimaguas, Poeppig 2482. (holotype: W; isotypes: F F0041346F & F0041347F, F F0041348F, G G00364110, HAL HAL0077029, L L0010632).
- = *Casearia maculata* Pilg. in Verh. Bot. Vereins Prov. Brandenburg 47: 161. 1905 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Amazonas, Rio Jurua, Jurua-Miry, Ule 5566. (holotype: B lost; isotypes: F phot F0BN013680, G G00355991, HBG HBG515745, L L0010635, MG MG005507).
- Distribution (areas). – Bolivia (present); Brazil North (present); Colombia (present); Ecuador (present); Peru (present); Venezuela (present)

***Casearia gossypiosperma* Briq. in Bull. Herb. Boissier 7(App. 1): 55. 1899. Sec. Sleumer (1980)**

- ≡ *Gossypiospermum paraguayense* Rehder, Trop. Woods 32: 7. 1932, nom. nov. syn. sec. De Mestier (2020). Type: Paraguay, Republic of, San Bernardino near Concepcion, 1885–1895, Hassler 1107. (holotype: G G00008423, G00008424 & G00008425; isotypes: BM BM000526898, NY NY00097939, P P00371637 & P00371638).
- = *Casearia lanosperma* Diogo in Bol. Mus. Nac. Rio de Janeiro 1: 263. 1924 syn. sec. De Mestier (2020) ≡ *Gossypiospermum lanospermum* (Diogo) Pickel in Ark. Bot., a.s., 3: 195. 1958 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Mato Grosso, Bonfim, Canal da lagoa Mondioré., 8.1908, Diogo 219. (holotype: R R000004969; isotype: RB RB00538546).

Distribution (areas). – Argentina Northeast (present); Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present); Paraguay (present); Peru (present); Uruguay (present)

***Casearia grandiflora* Cambess., Fl. Bras. Merid. 2: 232. 1830. Sec. Sleumer (1980)**

Type: Brazil, Federative Republic of, Province de Minas Gerais, St Hilaire 472. (holotype: P P00506593 & P00506594).

- = *Casearia hypoleuca* Mart. in Flora 20(2 Beibl.): 128. 1837 syn. sec. De Mestier (2020) ≡ *Casearia grandiflora* var. *hypoleuca* (Mart.) Eichler, Fl. Bras. 13(1): 479. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Mato Grosso, Da Silva Manso. (holotype: M M0113038; isotypes: BR BR0000005104338, E E00296670, F F0060162F, FI FI004293, G G00355998 & G00355990, K K000471168, L L0010645, NY NY00097947).
- = *Casearia grandiflora* var. *obtusifolia* Eichler, Fl. Bras. 13(1): 479. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Minas Gerais, inter Diamantina et Rio Paranyhyba, Verava-legitima to Rio das Vehlas, 1834, Burchell 5810. (syntypes: BR BR0000005105465, K K000471166, P P04760611); Brazil, Federative Republic of, Sao Paulo, in campis inter Rio das Vehlas et Sta. Anna, Riedel s n. (lectotypes: B lost, F F0BN013673; isolectotypes: BM BM000624361, FI FI005273, G G00355999, GH GH00066467, K K000471164, L L0010647, NY NY00097940); Brazil, Federative Republic of, Sao Paulo, in campos ad Sta. Anna, Lund s n. (syntype: P P047).
- = *Casearia grandiflora* var. *pauciflora* Eichler, Fl. Bras. 13(1): 479. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Goiaz, Serra dos Cristais, Pohl 850. (holotype: W; isotype: L L0010646).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); French Guiana (present); Guyana (present); Panamá (present); Suriname (present); Venezuela (present)

***Casearia guevarana* Cast.-Campos & M.E.Medina in Novon 13: 30. 2003. Sec. Cast.-Campos & M.E.Medina (2003)**

Type: Mexico, United Mexican States, Reserva Natural de La Mancha, G. Castillo C. 19238. (paratype: XAL XAL0081599, XAL0081600 & XAL0081602); Mexico, United Mexican States, Veracruz: Nature Reserve "El Morro de la Mancha", mun. Actopan, approx. 10 m, 24.5.2001, G. Castillo C. 20801. (holotype: XAL XAL0081598; isotypes: ENCB, MEXU, MO MO-335465, XAL XAL0082947).

Distribution (areas). – Mexico Gulf (present); Mexico Southeast (present)

***Casearia guianensis* (Aubl.) Urb., Symb. Antill. 3: 322. 1902. Sec. Sleumer (1980)**

- ≡ *Iroucana guianensis* Aubl., Hist. Pl. Guiane 1: 329. 1775 syn. sec. De Mestier (2020) ≡ *Athenaea guianensis* (J.F.Gmel.) Aubl., Syst. Nat. ed. 13[bis] : 700. 1791: 629 syn. sec. De Mestier (2020) ≡ *Samyda iroucana* Rich. in Actes Soc. Hist. Nat. Paris 1: 109. 1792, nom. illeg. syn. sec. De Mestier (2020) ≡ *Casearia athenaea* (Aubl.) Schreb. ex Forsyth f. in Bot. Nomencl.: 257. 1794 syn. sec. De Mestier (2020). Type: France, French Republic, Aublet s n. (BM BM000624378; isotype: P P00689737); French Guiana, Prope maris littora Caiennae et Guianae, Aublet s n. (holotype: BM BM000624378; isotype: P P00689737). Type statement(s): Aubl. pl. guj. I, p.328, t. 127; Based on *Iroucana guianensis*.
- = *Casearia ramiflora* Vahl in Symb. Bot. 2: 50. 1791, nom. illeg. syn. sec. De Mestier (2020) ≡ *Guidonia ramiflora* (Vahl) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 64. 1889 syn. sec. De Mestier (2020) Type: US Virgin Islands, West Indies, Leeward Islands, St Croix. (holotype: C; isotype: L L0010666).
- = *Casearia fallax* Miq. in Linnaea 19: 128. 1847 syn. sec. De Mestier (2020) Type: Suriname, Republic of, Jodensavanna, 1844, Kappler 1672. (holotype: U U0002167; isotypes: G G00355997, L L0010665, MO MO1541376, S S04-543).
- = *Guidonia ramiflora* var. *spinosa* M.Gómez in Anales Soc. Esp. Hist. Nat. 23: 55. 1894 syn. sec. De Mestier (2020)
- = *Samyda octandra* Sessé & Moc., Fl. Mexic., ed. 2: 113. 1894 syn. sec. De Mestier (2020) Type: Puerto Rico, Sessé y Lacasta & J.M.Mocino 1236. (lectotype: MA MA0100602961; isolectotypes: G G00355996, MA MA0100602959 & MA0100602960).

Distribution (areas). – Brazil North (present); Brazil Northeast (present); Brazil Southeast (present); Cayman Is. (present); Colombia (present); Costa Rica (present); Cuba (present); Dominican Republic (present); French Guiana (present); Guyana (present); Haiti (present); Jamaica (present); Leeward Is. (present); Mexico Gulf (present); Mexico Southeast (present); Panamá (present); Puerto Rico (present); Suriname (present); Trinidad-Tobago (present); Venezuela (present); Venezuelan Antilles (present); Windward Is. (present)

***Casearia hirsuta* Sw., Fl. Ind. Occid. 2: 755. 1800. Sec. Sleumer (1980)**

Type: Jamaica, Swartz s n. (holotype: S S-R-942).

- = *Samyda pubescens* L., Sp. Pl., ed. 2: 758. 1762 syn. sec. De Mestier (2020) Type: Jamaica, P.Browne s n. (lectotype: LINN LINN558.2; isolectotype: LINN 558.1).
- = *Samyda hirsuta* (Sw.) Poir., Encycl. 6: 493. 1805 syn. sec. De Mestier (2020) ≡ *Guidonia hirsuta* (Sw.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 94. 1889 syn. sec. De Mestier (2020) Type: West Indies, Swartz s n. (lectotype: S-R-942).
- = *Casearia rufinervis* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31(I): 462. 1858 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Oriente, Monte Libano, 1844, Linden 1795. (holotype: KW KW001001119; isotypes: BM BM000624341, FI FI004290, G G00355931 & G00364739, K K000471183, P P00789806 & P04762639).

Distribution (areas). – Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Cayman Is. (present); Colombia (present); Costa Rica (present); Cuba (present); Haiti (present); Jamaica (present); Venezuela (present)

***Casearia ilicifolia* Vent., Choix Pl.: t. 44. 1808. Sec. Sleumer (1980)**

Type: Dominican Republic, near Monter Cristi, Turpin s n. (holotype: G G00364382); Haiti, Republic of, Maribarou, non procul a mari solo saxoso, Swartz s n. (holotype: S S-R-6324; isotypes: BM BM000611039, LD LD1253957).

Distribution (areas). – Dominican Republic (present); Haiti (present)

***Casearia itzana* Lundell in *Wrightia* 6: 10. 1978. Sec. Lundell (1978)**

Type: Guatemala, Republic of, Peten, La Cumbre, in zapotal, west of km 141-142 of the Peten-Izabal road, 1 Mar 1975, Lundell & Contreras 19082. (holotype: LL LL00372016; isotypes: LL LL00372017, S S04-549).

Distribution (areas). – Guatemala (present)

***Casearia kigeri* T. Samar. & M.H. Alford in *Novon* 27: 68. 2019. Sec. T. Samar. & M.H. Alford (2019)**

≡ *Samyda glabrata* Sw., Prodr. Veg. Ind. Occ. 1788 syn. sec. De Mestier (2020). Type: Jamaica, Mtns. of the southern part, Swartz s n. (holotype: S S-R-5561; isotypes: BM BM000624404, M M0113022, SBT SBT12510).

= *Samyda acuminata* Urb., Symb. Antill. 5: 441. 1908 syn. sec. De Mestier (2020) Type: Jamaica, old England, Harris 5176. (holotype: B lost; isotypes: BM BM000624403, F phot F0BN005790).

Distribution (areas). – Jamaica (present)

***Casearia laetioides* (A.Rich.) Northr., Mem. Torrey Bot. Club: 12:55. 1902.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Zuelania laetioides* A.Rich., Hist. Phys. Cuba, Pl. Vasc.: 89. 1845 syn. sec. De Mestier (2020) ≡ *Thiodia laetioides* (A.Rich.) Griseb., Fl. Brit. W. I.: 22. 1859 syn. sec. De Mestier (2020) ≡ *Guidonia laetioides* (A.Rich.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 55. 1889 syn. sec. De Mestier (2020). Type: Cuba, Republic of, 1859, Wright 1111. (PH PH00029981); Cuba, Republic of, Ramon de la Sagra s n. (lectotype: P P00789605; isolectotype: P P00789606).

= *Laetia guidonia* Sw., Prodr. Veg. Ind. Occ.: 83. 1788 syn. sec. De Mestier (2020) ≡ *Samyda icosandra* Sw., Fl. Ind. Occid. 3: 1962. 1806 syn. sec. De Mestier (2020) ≡ *Zuelania icosandra* (Sw.) Clos in Ann. Sci. Nat., Bot., sér. 4, 8: 242. 1857 syn. sec. De Mestier (2020) ≡ *Casearia icosandra* Planch. & Triana ex Hemsl. in Biol. Cent.-Amer., Bot. 1: 469. 1880, nom. illeg. syn. sec. De Mestier (2020) ≡ *Guidonia icosandra* Kuntze, Revis. Gen. Pl. 1: 44. 1891 syn. sec. De Mestier (2020) ≡ *Zuelania guidonia* (Sw.) Britton & Millsp., Bahama Fl.: 285. 1920 syn. sec. De Mestier (2020) ≡ *Casearia guidonia* (Sw.) Lundell in Wrightia 5: 41. 1974, nom. illeg. syn. sec. De Mestier (2020) Type: Jamaica, Swartz s n. (lectotype: S S10-15229; isolectotypes: BM BM000624397, SBT SBT12507).

= *Laetia crenata* A.Rich., Hist. Phys. Cuba, Pl. Vasc.: 87. 1845 syn. sec. De Mestier (2020) ≡ *Zuelania crenata* (A.Rich.) Griseb., Cat. Pl. Cub.: 9. 1866 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Ramon de la Sagra s n. (holotype: P P02442056).

= *Laetia longifolia* A.Rich., Hist. Phys. Cuba, Pl. Vasc.: 85. 1845 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Ramon de la Sagra s n. (holotype: P P02442051).

= *Zuelania roussoviae* Pittier in Contr. U.S. Natl. Herb. 18: 163. 1916 syn. sec. De Mestier (2020) Type: Panama, Republic of, hills, between Rio Grande and Pedro Vidal, canal zone on road to Arraijan, 1911, Pittier 2710. (holotype: US US00114833; isotypes: BM BM000611057, F F0060323F, GH GH00245568, MO MO-1164543, NY NY00108224, S S04-27).

Distribution (areas). – Bahamas (present); Belize (present); Cayman Is. (present); Colombia (present); Costa Rica (present); Cuba (present); Guatemala (present); Haiti (present); Jamaica (present); Mexico Central (present); Mexico Gulf (present); Mexico Northeast (present); Mexico Southeast (present); Mexico Southwest (present); Nicaragua (present); Panamá (present); Trinidad-Tobago (present); Venezuela (present)

***Casearia lasiophylla* Eichler, Fl. Bras. 13(1): 468. 1871.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, 1843, Stephan s n. (syntype: BR BR0000013346508); Brazil, Federative Republic of, Caldas, 1864, Regnell III-392. (syntypes: BR BR0000013346492, K K000187408, S S04-553, US US00114868); Brazil, Federative Republic of, Minas Gerais, 1842, Gardner 4494. (syntype: K K000187406; isosyntypes: BM BM000611052, G G00355988); Brazil, Federative Republic of, Minas Gerais, Caldas, Regnell III-393. (syntypes: FI FI004285, P P00371632, S S04-555, S04-556, S10-15149 & S10-15150); Brazil, Federative Republic of, Minas Gerais, Claussen 624. (syntype: BR BR0000013346485); Brazil, Federative Republic of, Riedel s n. (syntype: K K000187407); Brazil, Federative Republic of, ex numero probably from Sao Paulo, Itapeva-Sorocaba-Ipanema, Sello 5237. (lectotype: B lost; isolectotypes: FI FI004288, M M0113052, P P00371629 & P00371630).

= *Antigona serrata* Vell., Fl. Flumin. 4: 187. 1829 syn. sec. Sleumer (1980)

Distribution (areas). – Argentina Northeast (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present)

***Casearia lemkeana* T. Samar. & M.H. Alford in Novon 27: 67. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Samyda cubensis* P.Wilson in Torreyia 30: 1930 syn. sec. De Mestier (2020). Type: Cuba, Republic of, Wright 1896. (holotype: NY NY00108155; isotypes: NY NY00108156, S S04-516, US US00114807).

= *Samyda lunana* P.Wilson in Torreyia 30: 72. 1930 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Las Villas, Lomas de Banao, 1920, Luna 859. (holotype: NY NY00108160).

Distribution (areas). – Cuba (present)

***Casearia littoralis* T. Samar. & M.H. Alford in Novon 27: 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Samyda microphylla* Urb. in Repert. Spec. Nov. Regni Veg. 20: 307. 1924 syn. sec. De Mestier (2020). Type: Cuba, Republic of, Oriente: Nipe Bay, near Antilla, 1916, Ekman 7323. (holotype: S S04-518; isotype: NY NY00108161).

= *Casearia ramosissima* C.Wright ex Griseb., Cat. Pl. Cub.: 10. 1866 syn. sec. De Mestier (2020) ≡ *Samyda ramosissima* (C.Wright ex Griseb.) J.E.Gut. in Revista Jard. Bot. Nac. Univ. Habana 4(1): 13. 1983 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Oriente, prope Quemado, 1860-1861, Wright 1893. (holotype: GOET GOET003838; isotypes: B 10 0277749 & B 10 0277750, BM BM000624340, G G00364177, G00364178 & G00364181, GH GH00057201, GOET GOET003839 & GOET003805, K K000471182, L L0010628, MO MO-2049498, S S10-14318, YU YU069989).

= *Samyda minutifolia* Urb. in Repert. Spec. Nov. Regni Veg. 22: 90. 1925 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Oriente, near Holguin, Aguas Claras, 28.8.1916, Ekman 7658. (lectotype: S S04-519; isolectotype: NY NY00108162).

Distribution (areas). – Cuba (present)

***Casearia lopeziana* Sleumer, Fl. Neotrop. Monogr. 22: 369. 1980. Sec. Sleumer (1980)**

Type: Colombia, Republic of, Norte de Santander, between Chinacota and La Esmeralda, Killip & Smith 20895. (paratypes: A, GH, NY, US US03026308); Venezuela, Bolivarian Republic of, Aragua: Tovar, Fendler 762. (paratypes: GH, NY); Venezuela, Bolivarian Republic of, Biscaina, Fendler 766. (paratype: GH); Venezuela, Bolivarian Republic of, La Mesa de Ejido, Ehrendorfer 6400-42. (paratypes: L, WU); Venezuela, Bolivarian Republic of, La Mesa de Ejido, S. Lopez-Palacios & al. 4309. (paratypes: B 10 0243767, L, MERF, NY, S, U); Venezuela, Bolivarian Republic of, La Mesa de Ejido, S. Lopez-Palacios 1212. (paratype: MERF); Venezuela, Bolivarian Republic of, La Mesa de Ejido, S. Lopez-Palacios 2147. (paratype: MERF); Venezuela, Bolivarian Republic of, Merida, La Mesa de Ejido La Enfadosa, 6 Sep 1977, S. Lopez-Palacios, L. Ruiz-Teran & Sleumer 4307. (holotype: L L0010683; isotypes: BM BM000624388, L L0010684, MO MO-279916, US US00114872, VEN VEN178277); Venezuela, Bolivarian Republic of, Mérida: La Capilla, abajo de Ejido, Bautista s n. (paratypes: L, MER); Venezuela, Bolivarian Republic of, between S. Juan de los Morros y Uberito, Pittier 11334. (paratypes: A, G, GH, K K000471195 & K000471196, M, NY, P, US US03026309).

Distribution (areas). – Colombia (present); Venezuela (present)

***Casearia luetzelburgii* Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 955. 1934. Sec. Sleumer (1980)**

Type: Brazil, Federative Republic of, Paraíba do Norte, Serra Chabitaca, Nov 1920, von Luetzlburg 12352. (holotype: B lost; isotype: L L0010686).

= *Gossypiospermum crimeanum* Pickel in Ark. Bot., a.s., 3: 195. 1958 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Pernambuco, Nazaré de Mata, 22 Dec 1954, J. Coelho de Moraes 1278. (holotype: SP SP000738; isotype: L L0010685).

Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present)

***Casearia manausensis* Sleumer, Fl. Neotrop. Monogr. 22: 321. 1980. Sec. Sleumer (1980)**

Type: Brazil, Federative Republic of, Amazonas, B.A.M., margem do Igarapé do Bindá, terreno firme, argiloso (amarelo) mata virgem, D. Coelho 3201. (paratype: IAN IAN092245); Brazil, Federative Republic of, Amazonas, Manaus-Igarapé Leao road, 5 km from Manaus-Caracarai, 21.1.1971, G. Prance, Ramos, Steward & Pinheiro 11416. (holotype: INPA; isotypes: F F0060168F, K K000471159, L L0010688, MG MG042455, NY NY00097949, S S04-559, U U0002168, US US00114875, WAG WAG0248103); Brazil, Federative Republic of, Amazonas. Manaus-Itacoatiara Highway, Km 64; forest on terra firme, 3.1967, G. Prance & B. Pena 4709. (paratype: MG MG034924); Brazil, Federative Republic of, Amazonas. Manaus. Estrada Tarumã. Near to Ponta Negra; forest on terra firme, 1.1967, G. Prance & B. Pena 3924. (paratype: MG MG034368); Brazil, Federative Republic of, Amazonas. Manaus. Km 10 da BR-17; terra firme, 12.1954, J. Chagas s n. (paratype: MG MG021081); Brazil, Federative Republic of, Amazonas. Manaus. Mata das terras altas além de Flores, 1.1943, Ducke 1176. (paratypes: IAN IAN010132, MG MG018753); Brazil, Federative Republic of, Amazonas: Manaus - Itacoatiara Highway, Km. 64, 27.3.1967, G. Prance, B. Pena, Forero, Ramos & O. Monteiro 4709. (paratype: S S04-561); Brazil, Federative Republic of, Manaus, Estrada Tarumã, near to Ponta Negra, forest on terra firme, 10.1.1967, G. Prance, Ramos & Forero 3924. (paratypes: B 10 0243766, S S04-560).

Distribution (areas). – Brazil North (present)

***Casearia mariquitensis* Kunth, Nov. Gen. Sp. 5: 363. 1823. Sec. Sleumer (1980)**

Type: Colombia, Republic of, Tolima, Mariquita, Cerro de la Copa, Bonpland s n. (holotype: P P00307128; isotypes: F F0041339F, L L0010691).

= *Casearia fockeana* Miq. in Ann. Sci. Nat., Bot., sér. 3, 1: 39. 1844 syn. sec. De Mestier (2020) Type: Suriname, Republic of, Paramaribo, Focke 746. (lectotype: U0002169); Suriname, Republic of, prope Paramaribo in silva vidente ad Kwatta, Focke 837. (syntype: U0142511).

- = *Casearia pubiflora* Benth. in Bot. Voy. Sulphur: 66. 1844 syn. sec. De Mestier (2020) Type: Ecuador, Republic of, Guayas, Guayaquil, Sinclair anno 1841. (holotype: K K000471243not designated).
- = *Casearia platyphylla* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 68. 1898 syn. sec. Jorgensen & Leon-Yanez (1999) Type: Ecuador, Republic of, Guayas, Guayaquil, 1800, Pavon 796. (holotype: G G00236798; isotypes: F phot F24110, G G00236799).
- = *Casearia camporum* Sprague in Trans. & Proc. Bot. Soc. Edinburgh 22: 427. 1900 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Meta, Cabuyaro on Rio Meta, Sprague 167. (holotype: K K000471241 & K000471242 parts).
- = *Casearia tarapotina* Pilg. in Verh. Bot. Vereins Prov. Brandenburg 47: 161. 1905 syn. sec. De Mestier (2020) Type: Peru, Republic of, San Martin, Tarapoto, 1902, Ule 6936. (holotype: B lost, phot F0BN013691; isotypes: F F0041351F, G G00355995, HBG HBG515748, K K000471244, L L0010690, MG MG006491).
- Distribution (areas). – Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); Ecuador (present); French Guiana (present); Guyana (present); Peru (present); Suriname (present); Trinidad-Tobago (present); Venezuela (present)

***Casearia marqueti* Nepom. & M.Alves in Phytotaxa 311(3): 297. 2017.** Sec. Nepom. & M.Alves (2017)

Type: Brazil, Federative Republic of, Paraiba: João Pessoa, Jardim Botânico Benjamim Maranhão, Mata do Buraquinho, 7°08'17"S, 34°50'53"W, 50 m elev., 7.11.2016, F. Nepomuceno 288. (holotype: UFP; isotype: RB).

Distribution (areas). – Brazil Northeast (present)

***Casearia maynacarpa* Liesner & P.Jørg. in Novon 22: 422. 2013.** Sec. Liesner & P.Jørg. (2013)

≡ *Carpotroche parvifolia* J.F.Macbr. in Candollea 5: 390. 1934 syn. sec. De Mestier (2020) ≡ *Mayna parvifolia* (J.F.Macbr.) Sleumer in Repert. Spec. Nov. Regni Veg. 45: 12. 1938 syn. sec. De Mestier (2020). Type: Peru, Republic of, Loreto: Puerto Arturo, Yurimaguas, 20.11.1929, Williams 5260. (holotype: F F0041335F; isotypes: G G00364232 & G00364243, L L0011142, US US00114653).

Distribution (areas). – Bangladesh (present); Bolivia (present); Brazil North (present); Colombia (present); Peru (present)

***Casearia megacarpa* Cuatrec. in Fieldiana, Bot. 27: 99. 1950.** Sec. Sleumer (1980)

Type: Colombia, Republic of, Valle, Hoya del Rio Sanquini, La Laguna, 10 Dec 1943, Cuatrecasas 15408. (holotype: F F0060170F & F0060171F; isotypes: COL COL000002913 & COL000002914, G G00355954, U U0002171, US US00114876, WIS WIS00000763MAD).

= *Casearia cordillerana* Cuatrec. in Fieldiana, Bot. 27: 102. 1950 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Valle, extremo N filo de la Cordillera Occidental sobre Las Brisas, Monte El Tabor, 22 Oct 1946, Cuatrecasas 22419. (holotype: F F0060153F & F0060154F; isotypes: COL COL000002910 & COL000002911, L L0010693).

Distribution (areas). – Colombia (present)

***Casearia melliodora* Eichler, Fl. Bras. 13(1): 469. 1871.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Rio de Janeiro, Corcovado, Riedel s n. (lectotype: B lost; isolectotypes: BM BM000624372, F phot F0BN013681, GH GH00066471, K K000187401, L L0010695, NY NY00097950, P P00371626 & P00371627).

Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present)

***Casearia mestrensis* Sleumer, Fl. Neotrop. Monogr. 22: 320. 1980.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Bahia, Anderson & al. 36769. (paratypes: L, NY NY375586, US US01888230); Brazil, Federative Republic of, Bahia, Anderson & al. 36774. (paratypes: K K001097602, L, NY NY375587, US US01888229); Brazil, Federative Republic of, Bahia, Espigao Mestre, Serra 34 km W of Barreiras, 2 Mar 1972, Anderson, Stieber & Kirkbride Jr. 36463. (holotype: NY NY00107353; isotypes: B 10 0243765, BR BR0000006913335, E E00296668, K K001097602, L L0010696, MO MO-279829).

Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present)

***Casearia mexiae* Sandwith, Kew Bull. 4: 494. 1950 ["1949"].** Sec. Sleumer (1980)

Type: Ecuador, Republic of, Pichincha, Quito, in remnant wood on crest to right of road from Nono to Gualea, 13 Sep 1935, Mexia 7674. (holotype: K K000471239; isotypes: K K000471240, L L0010697, MO MO-279828, NY NY00107354, S S10-14342, UC UC686860).

Distribution (areas). – Ecuador (present)

***Casearia mexicana* (Rose) T. Samar. & M.H. Alford in Novon 27: 67. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Samyda mexicana* Rose in Contr. U.S. Natl. Herb. 5. 1897 syn. sec. De Mestier (2020). Type: Mexico, United Mexican States, Guerrero: Acapulco, 10.1894-3.1895, E. Palmer 81. (holotype: US US00114810; isotypes: BM BM000617448, CAS CAS0004426, F F0060283F & F0060284F, GH GH00066932, K K000471277, MICH MICH1111076, MO MO-194809, NY NY00108154, UC UC140730).

Distribution (areas). – Mexico Southwest (present)

***Casearia moaensis* Vict. in Contr. Inst. Bot. Univ. Montréal 49: 51. 1944.** Sec. Sleumer (1980)

Type: Cuba, Republic of, Oriente, Moa, entre le Rio Cabanas et Rio Yagrumaje, Victorin & Clemente 21714. (holotype: MT MT00113236 & MT00117703; isotype: HAC).

Distribution (areas). – Cuba (present)

***Casearia mollis* Kunth, Nov. Gen. Sp. 5: 362. 1823.** Sec. Sleumer (1980)

Type: Venezuela, Bolivarian Republic of, Aragua, in convallibus umbrosis Araguensium, Humboldt & Bonpland s n. (holotype: P00679652; isotype: F F0BN013682).

= *Casearia mollipila* Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 956. 1934 syn. sec. De Mestier (2020)
Type: Venezuela, Bolivarian Republic of, Aragua, La Trinidad de Maracay, 1913, Pittier 5781. (holotype: B lost; isotypes: L L0010701, P P00789800, US US00114881).

Distribution (areas). – Colombia (present); Cuba (present); Venezuela (present)

***Casearia murceana* R.Marquete & Mansano in Novon 22: 199. 2012.** Sec. R.Marquete & Mansano (2012)

Type: Brazil, Federative Republic of, Para: Santarem, 5.3.1923, Ducke s n. (holotype: RB RB00081569; isotype: RB RB00724932 & RB00724933).

Distribution (areas). – Brazil North (present); Brazil West-Central (present)

***Casearia neblinae* Sleumer, Fl. Neotrop. Monogr. 22: 322. 1980.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Amazonas, Rio Cauaburi, Rio Maturaca, Serra Pirapucu, Comisao de Limites Marker BR-1, 26.1.1966, N. Silva & Brazao 60882. (holotype: IAN IAN158072; isotypes: IAN IAN142157, L L0010704, NY NY00107357 & NY00107358).

Distribution (areas). – Brazil North (present)

***Casearia negrensis* Eichler, Fl. Bras. 13(1): 466. 1871.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Amazonas, ad flum. Rio Negro, 1.12.1851, Spruce 1986. (holotype: P P00506595 & P00506596; isotypes: F F0060174F, K K000471150, L L0010705).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil West-Central (present); Colombia (present); French Guiana (present); Peru (present); Suriname (present)

***Casearia nigricans* Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 956. 1934.** Sec. Sleumer (1980)

Type: Peru, Republic of, Loreto, mountains E. of Moyobamba, Weberbauer 4727. (holotype: B lost); Peru, Republic of, San Martin, Zepelacio near Moyomamba, 3.1934, Klug 3560. (neotype: S S04-564; isoneotypes: CAS CAS0001437, G G00364104, GH GH00066475, K K000471245, LIL LIL000934, MO MO-279827, NY NY00107359, US US00114884, WIS WISv0255861WIS).

Distribution (areas). – Colombia (present); Ecuador (present); Panamá (present); Peru (present)

***Casearia nigricolor* Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 957. 1934.** Sec. Sleumer (1980)

Type: Peru, Republic of, Libertad, valley system of Rio Mixiollo, 1909, Weberbauer 7051. (holotype: F F0041340F; isotypes: G G00364105, GH GH00066476, L L0010713, MOL MOL00002808, US US00114885).

Distribution (areas). – Bolivia (present); Peru (present)

***Casearia nitida* Jacq., Enum. Syst. Pl.: 21. 1760.** Sec. Sleumer (1980)

≡ *Samyda nitida* L., Syst. Nat., ed. 10, 2: 1025. 1759 syn. sec. De Mestier (2020) ≡ *Guidonia nitida* (Jacq.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 28. 1889 syn. sec. De Mestier (2020). Type statement(s): Lectotype: P. Browne. Civ. Nat. Hist. Jamaica, t.23, f.3, 1756; Lectotype: P. Browne. Civ. Nat. Hist. Jamaica, t.23, f.3, 1756.

= *Samyda crenata* Poir., Encycl. 6: 491. 1805, nom. superfl. syn. sec. De Mestier (2020) Type statement(s): based on *C. nitida* Jacq.

= *Casearia bahamensis* Urb., Symb. Antill. 3: 322. 1902 syn. sec. De Mestier (2020) Type: Bahamas, Commonwealth of the, Andros, Nicols Town, 26 Mar 1890, Northr. & Northr. 384. (holotype: B lost; lectotype: NY NY00097903; isolectotypes: A A00066437, F F0060135F & F0060136F, GH GH00245571, K K000471188 & K000471189, NY NY00097904).

Distribution (areas). – Bahamas (present); Cuba (present); Dominican Republic (present); Florida (introduced); Haiti (present); Jamaica (introduced); Mexico Central (present); Mexico Gulf (present); Mexico Northeast (present); Mexico Northwest (present); Mexico Southeast (present); Mexico Southwest (present)

***Casearia obliqua* Spreng., Syst. Veg. 2: 355. 1825.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Sello s n. (holotype: B lost; isotypes: B 10 0243761, B 10 0243762, B 10 0243763 & B 10 0243764, BM BM000624382, F phot F13683, FI FI004286 & FI004289, K K000187402, L L0010716, NY NY00107360, P P00371625).

= *Bigelovia brasiliensis* Spreng. in Neue Entdeck. Pflanzenk. 2: 150. 1821 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Sello s n. (holotype: B lost; isotype: M M0113070).

= *Samyda selloi* Spreng., Syst. Veg. 2: 354. 1825 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Sellow s n. (holotype: B lost; isotype: M).

= *Casearia inaequilatera* Cambess., Fl. Bras. Merid. 2: 237. 1830 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Sao Paulo, bois vieux près Tagsahy, 1816-1821, St Hilaire Cat. D, nr. 810. (holotype: P P02442160, P02442161 & P02442162; isotypes: F F0060163F, MPU MPU011163).

= *Casearia montana* Gardner in London J. Bot. 2: 335. 1843 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Rio de Janeiro/Guanabara, Serra dos Orgaos, 1837-1838, Gardner 335. (lectotype: K K000187403; isolectotypes: BM BM000624390 & BM000624391, E E00570040, G G00364106, GH GH00066474); Brazil, Federative Republic of, Rio de Janeiro/Guanabara, Serra dos Orgaos, 1837-1838, Gardner 336. (syntype: K K000471200; isosyntypes: BM BM000611053, E E00570042 & E00570043, F F0060173F, FI FI004287, G G00364728 & G00364730, K K000471201, NY NY00107356, US US00114879).

Distribution (areas). – Argentina Northeast (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present)

***Casearia oblongifolia* Cambess., Fl. Bras. Merid. 2: 234. 1830.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Rio de Janeiro/Guanabara, "nascitur prope Sebastianopolim", St Hilaire s n. (holotype: P P00371623; isotypes: F F0092810F, MPU MPU011161, P P00371624).

= *Casearia clausseniana* Miq. in Linnaea 19: 441. 1847 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, 1842, Claussen 2088. (holotype: U U0002172; isotypes: F F0BN013666, FI FI004282, FR FR0036180, G G00364108 & G00364109, HBG HBG515734, L L0010717, US US00114851).

Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present); Brazil West-Central (present)

***Casearia obovalis* Poepp. ex Griseb. in Abh. Königl. Ges. Wiss. Göttingen 9: 27. 1860.** Sec. Sleumer (1980)

≡ *Casearia obovata* Poepp. ex Eichler, Fl. Bras. 13(1): 472. 1871, nom. illeg. syn. sec. De Mestier (2020) ≡ *Casearia commutata* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 765. 1898 syn. sec. De Mestier (2020). Type: Peru, Republic of, Loreto, Yurimaguas, Poeppig 2438. (holotype: B 10 0243760; isotypes: A A00066477, B 10 0243759, BM BM000624383, F F0041341F & F0041342F, G G00364107, G00364148 & G00364149, HAL HAL0077066, L L0010718 & L0010719).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil West-Central (present); Colombia (present); Ecuador (present); Peru (present).

***Casearia ophiticola* Vict. in Contr. Inst. Bot. Univ. Montréal 49: 47. 1944.** Sec. J.E.Gut. (2000)

Type: Cuba, Republic of, Oriente, Moa entre le Rio Cabanas et Rio Yagrumaje, Victorin & Clemente 21698. (holotype: MT MT00113245 & MT00117704; isotype: HAC).

= *Casearia pseudophyticola* J.E.Gut. in Revista Jard. Bot. Nac. Univ. Habana 1: 102. 1981 ["1980"] syn. sec. De Mestier (2020) Type: Cuba, Republic of, prov. Holguin, Sagua de Tanamo, Ioma 5 km al suroeste de Naranjo Agrio, 9.5.1980, Bisse & al. 43005. (holotype: HAJB; isotypes: B 10 0385067, HAC, JE JE00019575 & JE00019576).

Distribution (areas). – Cuba (present)

***Casearia panamensis* T. Samar. & M.H. Alford in Novon 27: 68. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Laetia micrantha* A.Robyns in Ann. Missouri Bot. Gard. 54: 190. 1967 syn. sec. De Mestier (2020). Type: Panama, Republic of, Darien, vicinity of Cana, 24.6.1959, Stern & al. 513. (holotype: MO MO-1164544; isotypes: GH GH00245569, L L0011073, US US00114813).

Distribution (areas). – Panamá (present)

***Casearia paranaensis* Sleumer, Fl. Neotrop. Monogr. 22: 365. 1980.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Parana, Min. S. Jose de Pinhaes, usina Chamina, 13 Jul 1973, G. Hatschbach 32235. (holotype: L L0010727; isotypes: BHC BHC000162, CTES CTES0001811, MO MO-279826, MU MU000000219, NY NY00107363, S S04-565, UC UC1485383, US US00114888); Brazil, Federative Republic of, Parana: S. José de Pinhaes, Col. S. Andrade, Hatschbach 14589. (paratypes: C, L, MBM, NY NY375640, P P04761117, US US01888332); Brazil, Federative Republic of, Parana: S. José de Pinhaes, Col. S. Andrade, Hatschbach 16877. (paratypes: MBM, MO, US US01888330 & US01888331).

Distribution (areas). – Brazil South (present); Brazil Southeast (present)

***Casearia pauciflora* Cambess., Fl. Bras. Merid. 2: 235. 1830.** Sec. Sleumer (1980)

Type: Brazil, Federative Republic of, Minas Gerais, St Hilaire s n. (holotype: P P00371622; isotype: F F0092811F).

Distribution (areas). – Brazil Northeast (present); Brazil South (present); Brazil Southeast (present)

***Casearia pitumba* Sleumer in Blumea 24: 118. 1978.** Sec. Sleumer (1980)

≡ *Pitumba guianensis* Aubl., Hist. Pl. Guiane, Suppl.: 29. 1775 syn. sec. De Mestier (2020) ≡ *Samyda pitumba* Poir., Encycl. 6: 492. 1805, nom. superfl. syn. sec. De Mestier (2020). Type: French Guiana, Aublet s n. (holotype: BM BM000611049).

= *Casearia macrophylla* Vahl in Eclog. Amer. 2: 32. 1798, nom. superfl. syn. sec. De Mestier (2020) Type: France, French Republic, Cayenne, von Rohr 137. (holotype: C C10012557; isotypes: BM BM000611049, F phot F21323).

= *Casearia microphylla* Dennst., Nomencl. Bot. ed. 1: 94. 1810, nom. illeg. syn. sec. Sleumer (1980)

= *Casearia macrophylla* var. *barbatula* J.F.Macbr. in Publ. Field Columb. Mus., Bot. Ser. 13(4): 45. 1941 syn. sec. De Mestier (2020) Type: Peru, Republic of, Loreto, Iquitos, Aug 1929, Killip & Smith 26977. (holotype: F F0041338F; isotypes: G G00364111, US US00114874).

– *Pitumba edulis* Rich. ex Eichler, Fl. Bras. 13(1): 470. 1871, nom. inval. syn. sec. De Mestier (2020)

– *Casearia timbuchi* J.F.Macbr. ex Ll. Williams in Publ. Field Columb. Mus., Bot. Ser. 15: 358. 1936, nom. inval. syn. sec. De Mestier (2020) Type: Peru, Republic of, Loreto, Timbuchi, Upper Nanay, 26 Jun 1926, Williams 995. (holotype: F F0041352F).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil West-Central (present); Colombia (present); Ecuador (present); French Guiana (present); Guyana (present); Peru (present); Suriname (present); Venezuela (present)

***Casearia povedae* (N.Zamora, Aguilar & D.Santam.) T. Samar. & M.H. Alford in Novon 27: 68. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Laetia povedae* N.Zamora, Aguilar & D.Santam., Phytoneuron 2015-15. 2015 syn. sec. De Mestier (2020). Type: Costa Rica, Republic of, Alajuela: Canton de San Carlos, Pital, Llanura de San Carlos, ca. 13 km NE de Boca Tapada, Finca Aserradero, San Jorge, 10°44'54"N, 84°10'7"W, 20.6.1996, B. Hammel, A. Rodriguez & N. Zamora 20240. (holotype: CR; isotypes: INB, MO).

Distribution (areas). – Costa Rica (present); Nicaragua (present); Panamá (present)

***Casearia praecox* Griseb., Cat. Pl. Cub.: 10. 1866.** Sec. Sleumer (1980)

- = *Gossypiospermum praecox* (Griseb.) P.Wilson in *Torreyia* 30: 72. 1930 syn. sec. De Mestier (2020). Type: Cuba, Republic of, 1863, Wright 953. (holotype: B100277752; isotypes: G G00364117 & G00364116, GH GH00066453, GOET, K K000471179, MO MO772463 & MO772465, YU YU069988).
- = *Casearia eriophora* C.Wright ex Griseb., *Cat. Pl. Cub.*: 11. 1866 syn. sec. De Mestier (2020) = *Gossypiospermum eriophorum* (C.Wright ex Griseb.) Urb. in *Repert. Spec. Nov. Regni Veg.* 19: 7. 1923 syn. sec. De Mestier (2020) = *Guidonia eriophora* (Wright ex Griseb.) Maza, *Anales Soc. Esp. Hist. Nat.*: 23: 56 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Rugel 664. (syntype: NY NY00097912); Cuba, Republic of, Rugel 801. (syntype:); Cuba, Republic of, Wright 1895. (lectotype: GOET; isolectotypes: BM BM000624350, CAS CAS0001446, G G00364112, G00364113 & G00364115, GH GH00066439, L L0010728, MO MO772463, NY NY00097910 & NY00097911, P P04760876, S S04-542, US US00114859, YU YU069985).
- = *Guidonia rosauriana* M.Gómez in *Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos*: 11. 1889, nom. illeg. syn. sec. De Mestier (2020) Type statement(s): Based on *C. eriophora*.
- = *Ampelocera crenulata* Urb. in *Repert. Spec. Nov. Regni Veg.* 15: 399. 1919 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Ramon de la Sagra 413. (holotype: B lost; isotype: G00355932).
- Distribution (areas). – Colombia (present); Costa Rica (present); Cuba (present); Honduras (present); Nicaragua (present); Venezuela (present)

***Casearia prunifolia* Kunth, *Nov. Gen. Sp.* 5: 362. 1823. Sec. Sleumer (1980)**

- Type: Peru, Republic of, Cajamarca, near Jaen, Bonpland 3625. (holotype: P P00679650; isotype: L L0010730 & L0010731).
- = *Casearia mathewsii* Turcz. in *Bull. Soc. Imp. Naturalistes Moscou* 36(I): 608. 1863 syn. sec. De Mestier (2020) Type: Peru, Republic of, Amazonas, Yambrasbamba, Mathews 1649. (holotype: KW KW001001117; isotypes: E E00296666, L L0010729).
- Distribution (areas). – Colombia (present); Ecuador (present); Peru (present); Venezuela (present)

***Casearia quinduensis* Tul. in *Ann. Sci. Nat., Bot., sér.* 3, 7: 360. 1847. Sec. Sleumer (1980)**

- Type: Colombia, Republic of, Tolima, Mariquita, Quindiu Mts., 2.1840, Linden 1126. (syntype: P P04760921 & P04760938; isosyntypes: BM BM000624349 & BM000624359, F F0060180F & F0060181F, G G00364118 & G00364159, K K000471197, L L0010735); Colombia, Republic of, Tolima, Quindiu Mts., La Palmilla, Rancheria de la Cueva, Goudot s n. (lectotype: P P04760922, P04760923 & P04760924).
- Distribution (areas). – Colombia (present); Ecuador (present)

***Casearia resinifera* Spruce ex Eichler, *Fl. Bras.* 13(1): 466. 1871. Sec. Sleumer (1980)**

- Type: Brazil, Federative Republic of, Amazonas, Upper Rio Negro, prope Panuré ad Rio Vaupes, 1852-1853, Spruce 2685. (holotype: W W1889-0006951; isotypes: B 10 0277751, BM BM000624392, BR BR0000005104017, C C10012560, F F0060183F, F0060184F & F0060185F, F phot F0BN013688, G G00364119 & G00364120, GH GH00066482, GOET GOET003807, K K000471151, K000471152 & K000471153, L L0010736, MG MG019626, NY NY00107365, S S04-567, TCD TCD0005426).
- Distribution (areas). – Brazil North (present); Brazil Northeast (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); French Guiana (present); Peru (present)

***Casearia rufescens* Cambess., *Fl. Bras. Merid.* 2: 231. 1830. Sec. Sleumer (1980)**

- Type: Brazil, Federative Republic of, Minas Gerais, in campis porpe pagum Sao Joao, St Hilaire s n. (holotype: P P00506597 & P00506598; isotypes: F F0060186F, MPU MPU011159).
- = *Casearia pohliana* Eichler, *Fl. Bras.* 13(1): 474. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Minas Gerais, Fanado, Pohl s n. (syntypes: F phot F32156, W; isosyntypes: F F0060179F, L L0010740, M M0113044); Brazil, Federative Republic of, Minas Gerais, inter Estrema et Viera do Matto, Pohl 3130. (lectotype: W; isolectotype: F F0060178F).
- = *Casearia ferruginea* Briq. in *Annuaire Conserv. Jard. Bot. Genève* 2: 70. 1898 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Minas Gerais, entre Sitio et Barbacena, 1883, Glaziou 13529. (holotype: G G00364121; isotypes: BR BR0000005104345, F F0060159F, K K001097600 & K001097601, LIL LIL000935, P P00506599, P00506874 & P00506875, R R000010176).
- *Casearia ferruginea* Briq. ex Glaz. in *Mém. Soc. Bot. France* 3: 307. 1909, nom. inval. syn. sec. De Mestier (2020)
- Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present)

***Casearia rupestris* Eichler, Fl. Bras. 13(1): 468. 1871. Sec. Sleumer (1980)**

Type: Brazil, Federative Republic of, Minas Gerais, Claussen s n. (syntypes: L L0010747, P P04762365, P04762366 & P04762367); Brazil, Federative Republic of, Minas Gerais, Lagao Santa, 8 Feb 1865, Warming anno 1865. (lectotype: C C10012561; isolectotype: F F0060188F); Brazil, Federative Republic of, Minas Gerais, Uberava, 1848, Regnell III-1546. (syntypes: BR BR0000006913595, K K000471198, L L0010746, S S10-15170, S04-568 & S10-8251).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil Southeast (present); Brazil West-Central (present)

***Casearia rusbyana* Briq. in *Annuaire Conserv. Jard. Bot. Genève* 2: 73. 1898. Sec. Sleumer (1980)**

Type: Venezuela, Bolivarian Republic of, Terr. Delta Amacuro, (Sta.) Catalina, on lower Orinoco, 1896, Rusby & Squires 156. (holotype: G G00007865; isotypes: A A00066483, BM BM000624369, CAS CAS0001442, F F0060189F, F0060190F & F0060191F, G G00007866, K K000471230, L L0010748, M M0113066, MICH MICH1111068, MIN MIN1000520 & MIN1002848, MO MO279825, NY NY00107367, US US00731234, US00731235 & US00114899).

Distribution (areas). – Brazil North (present); French Guiana (present); Guyana (present); Suriname (present); Venezuela (present)

***Casearia sanchezii* J.Linares & Angulo in *Revista Mex. Biodivers.* 76: 3. 2005. Sec. J.Linares & Angulo (2005)**

Type: El Salvador, Republic of, Chalatenango: Municipio San Ignacio. Loc. Fca. El Malcotal (Propiedad de Salvador Sánchez) estribaciones del cerro El Pital, alt. 2100 m, 28 Apr 2002, J. Linares & Angulo 5937. (holotype: MEXU MEXU01173313; isotypes: EAP, MEXU MEXU01173309).

Distribution (areas). – El Salvador (present); Mexico Southeast (present)

***Casearia selloana* Eichler, Fl. Bras. 13(1): 483. 1871. Sec. Sleumer (1980)**

Type: Brazil, Federative Republic of, Bahia, Ilheus, 1834, Blanchet 1857. (syntypes: BM BM000624393, F F0093243F); Brazil, Federative Republic of, Bahia, between Bahia and Vitoria, Sello s n. (lectotype: B lost; isolectotypes: L L0010749 & L0010750, M M0113065, P P00371621).

Distribution (areas). – Brazil Northeast (present); Brazil Southeast (present)

***Casearia sessiliflora* Cambess., Fl. Bras. Merid. 2: 231. 1830. Sec. Sleumer (1980)**

Type: Brazil, Federative Republic of, Rio de Janeiro/Guanabara, Barra do Furado, Sitio do Pires, St Hilaire Cat. B 2, nr.218 s. (holotype: P P00371619; isotypes: F F0092812F, MPU MPU012022, P P00371620).

Distribution (areas). – Brazil Southeast (absent)

***Casearia souzae* R.Marquete & Mansano in *J. Syst. Evol.* 51: 228. 2013. Sec. R.Marquete & Mansano (2013)**

Type: Brazil, Federative Republic of, Espírito Santo: Águia Branca, Comunidade São Pedro, propriedade Sr. João Ferreira, Pedra da Bandeira, 17.1.2008, Souza, M. Saavedra, R. Monteiro & C. Fraga 610. (holotype: RB RB462219; isotypes: IAC, IBGE, SPF).

Distribution (areas). – Brazil Southeast (present)

***Casearia spinescens* (Sw.) Griseb., Cat. Pl. Cub.: 10. 1866. Sec. Sleumer (1980)**

≡ *Samyda spinescens* Sw., Prodr. Veg. Ind. Occ.: 68. 1788 syn. sec. De Mestier (2020) ≡ *Guidonia spinescens* (Sw.) Griseb., Fl. Brit. W. I.: 24. 1859 syn. sec. De Mestier (2020). Type: Haiti, Republic of, Swartz s n. (holotype: S S-R-5562).

= *Casearia brevipes* Benth. in *J. Bot. (Hooker)* 4: 110. 1842 syn. sec. De Mestier (2020) Type: Guyana, Republic of, Pirara, Schomburgk 773. (holotype: K K000471174; isotypes: BM BM000624379, K K000471175, L L0010577).

= *Casearia guidonia* Benth. in *J. Proc. Linn. Soc., Bot.* 5(Suppl. 2): 89. 1861, nom. illeg. syn. sec. De Mestier (2020)

= *Casearia cubensis* Urb. in *Repert. Spec. Nov. Regni Veg.* 22: 91. 1925 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Oriente, near Santiago de Cuba, 1918, Ekman 9216. (holotype: S04-537; isotypes: NY NY00097908, S S04-538).

Distribution (areas). – Bahamas (present); Brazil North (present); Cuba (present); Guyana (present); Haiti (present); Nicaragua (present); Panamá (present); Southwest Caribbean (present); Trinidad-Tobago (present); Venezuela (present)

***Casearia spinulosa* (Vent.) T. Samar. & M.H. Alford in Novon 27: 67. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Samyda spinulosa* Vent., Choix Pl.: t. 43. 1808 syn. sec. De Mestier (2020). Type: US Virgin Islands, St. Thomas, 1797, Riedlé s n. (holotype: G G00364207; isotype: P P04676899).

= *Samyda macrocarpa* Sessé & Moc. ex DC., Prodr. 2: 48. 1825 syn. sec. T. Samar. & M.H. Alford (2019) Type: Mexico, United Mexican States, Fl. Mex. Icon. 183, Sessé & Mocino. (lectotype: G).

= *Guayabilla odorata* Sessé & Moc., Fl. Mexic., ed. 2: 113. 1894, nom. illeg. syn. sec. T. Samar. & M.H. Alford (2019)

Distribution (areas). – Leeward Is. (present); Puerto Rico (present)

***Casearia staffordiae* Proctor, Fl. Cayman Islands: 316. 2012.** Sec. Proctor (2012)

Type: Cayman Islands, Along the Mastic trail, 9.1.2005, Proctor s n. (holotype: IJ).

Distribution (areas). – Cayman Is. (present)

***Casearia standleyana* Sleumer, Fl. Neotrop. Monogr. 22: 297. 1980.** Sec. Sleumer (1980)

Type: Costa Rica, Republic of, Cartago, Guayacan, ca 20 km NNE of Turrialba, 3 Aug 1974, P. Maas 1103. (holotype: L L0010759; isotypes: F F0060131F, NY NY00097884, U U0002173); Costa Rica, Republic of, Limon: La Palma, Sixaola valley, Dunlop 466. (paratypes: A, F, US); Costa Rica, Republic of, Suerre y Dos Bocas, drenajes de los Rios Parisimina y Reventazon, Shank & Molina 4278. (paratypes: F, GH, US).

Distribution (areas). – Costa Rica (present)

***Casearia stjohnii* I.M.Johnst. in Sargentia 8: 213. 1949.** Sec. Hammel & al. (2010)

≡ *Casearia guianensis* var. *stjohnii* (I.M.Johnst.) Croat in Ann. Missouri Bot. Gard. 62: 487. 1975 syn. sec. De Mestier (2020). Type: Panama, Republic of, Panama, San Jose island, 26 Jun 1945, Erlanson 369. (holotype: US US00114904; isotypes: GH GH00066433, NY NY00097885, US US00131059).

Distribution (areas). – Costa Rica (present); El Salvador (present); Panamá (present)

***Casearia suaveolens* (Poepp.) T. Samar. & M.H. Alford in Novon 27: 68. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Samyda suaveolens* Poepp., Nov. Gen. Sp. Pl. 3x: 66. 1845 syn. sec. De Mestier (2020) ≡ *Casinga suaveolens* (Poepp.) Griseb. in Abh. Königl. Ges. Wiss. Göttingen 9: 27. 1861 syn. sec. De Mestier (2020) ≡ *Laetia suaveolens* (Poepp.) Benth. in J. Proc. Linn. Soc., Bot. 5(Suppl. 2): 85. 1861 syn. sec. De Mestier (2020) ≡ *Guidonia suaveolens* (Poepp.) Kuntze, Revis. Gen. Pl. 1: 44. 1891 syn. sec. De Mestier (2020). Type: Brazil, Federative Republic of, Amazonas: Ega, Poeppig 2912. (holotype: W W18890111296; isotypes: F F0060292F & F0BN013636, P P02442216, W W18890045575).

= *Laetia calophylla* Eichler, Fl. Bras. 13(1): 454. 1871 syn. sec. De Mestier (2020) Type: Venezuela, Bolivarian Republic of, Terr. Amazonas, ad flum. Casiquiari, Vasiva et Pacimoni, Spruce 3451. (holotype: Wnot designated; isotypes: BM BM000582584, BR BR0000005058006, E E00296672, K BM000582584, NY NY107485, P P04793717 & P04793624).

– *Samyda petiolaris* Spruce ex Eichler, Fl. Bras. 13(1): 454. 1871, nom. inval. syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Province Rio Negro, May 1851, Spruce 1507. (syntypes: FI FI005747, K K001219606 & K001219607, NY NY2060514, P P04793720, TCD TCD0005438).

Distribution (areas). – Bolivia (present); Brazil North (present); Colombia (present); Ecuador (present); Guyana (present); Peru (present); Venezuela (present)

***Casearia sylvestris* Sw., Fl. Ind. Occid. 2: 752. 1800.** Sec. de Mestier (2020)

***Casearia sylvestris* subsp. *myricoides* (Griseb.) J.E.Gut. in Fl. Rep. Cuba, ser. A, 5(1): 52. 2000.** Sec. J.E.Gut. (2000)

- ≡ *Casearia sylvestris* var. *myricoides* Griseb., Cat. Pl. Cub.: 9. 1866 syn. sec. De Mestier (2020) ≡ *Guidonia sylvestris* var. *myricoides* (Griseb.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 96. 1889 syn. sec. De Mestier (2020). Type: Cuba, Republic of, 1860, Wright 1891. (lectotype: GOET; isolectotypes: B B100243756, BM BM000624342, G G00364128 & G00364154, GH GH00066456 & GH00066457, NY NY00097919, P P00789599); Cuba, Republic of, 1860, Wright 1892. (syntypes: BM BM000611042, G G00364130 & G00364153, K K000471178, P P00789600, YU YU069991).
- = *Casearia formosa* Urb. in Repert. Spec. Nov. Regni Veg. 22: 91. 1925 syn. sec. De Mestier (2020) Type: Cuba, Republic of, Las Villas, Ekman 18890. (lectotype: S S04-545; isotypes: A, NY NY00097913).
- Distribution (areas). – Cuba (present)

***Casearia sylvestris* subsp. *sylvestris*. Sec. De Mestier (2020)**

- ≡ *Samyda sylvestris* (Sw.) Poir., Encycl. 6: 492. 1805 syn. sec. De Mestier (2020) ≡ *Guidonia sylvestris* (Sw.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 95. 1889 syn. sec. De Mestier (2020). Type: Jamaica, Swartz. (holotype: S S10-15273; isotypes: BM BM000624362, LD LD1254017); Jamaica, Wright s n. (syntypes: BM BM000810880, NY NY00097918); West Indies, Swartz. (syntype: S S-R-944).
- = *Casearia lindeniana* Urb. in Repert. Spec. Nov. Regni Veg. 22: 92. 1925 syn. sec. De Mestier (2020) – *Casearia ekmanii* Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 954. 1934, nom. provis. syn. sec. De Mestier (2020) Type: Cuba, Republic of, Oriente, 1844, Linden 1961. (holotype: B lost; isotypes: BR BR0000005104819, G G00236800).
- = *Casearia sylvestris* var. *angustifolia* Uittien in Recueil Trav. Bot. Néerl. 22: 373. 1926 syn. sec. De Mestier (2020) Type: Suriname, Republic of, 1827, Weigelt. (syntypes: BR BR0000005105472, HBG HBG515733); Suriname, Republic of, 1910. (lectotype: U U0120553 & U0120554).
- = *Casearia sylvestris* var. *paraensis* Uittien in Recueil Trav. Bot. Néerl. 22: 373. 1926 syn. sec. De Mestier (2020) Type: Suriname, Republic of, 1916, B.W. 2428. (lectotype: U U0229303 & U0231715).
- = *Casearia schulziana* O.C.Schmidt in Repert. Spec. Nov. Regni Veg. 32: 87. 1933 syn. sec. De Mestier (2020) Type: Dominican Republic, Peninsula Samana, slope of Pan de Azucar, 1930, Ekman 14870. (holotype: S S04-569; isotypes: CAS CAS0001443, G G00364127, GH GH00066454, K K000471177, NY NY00097917, US US00114900, WIS WISv025862WIS).
- = *Casearia ovoidea* Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 11: 958. 1934 syn. sec. De Mestier (2020) Type: Peru, Republic of, Junin, La Merced, 1923, Macbride 5260. (holotype: F F0041343F).
- = *Casearia sylvestris* var. *martinicensis* Macbride ex Williams, L., Publ. Field Mus. Nat. Hist., Bot. 13: 357. 1936 syn. sec. De Mestier (2020) Type: Peru, Republic of, San Martin, Tarapoto, Williams 6831. (holotype: F).
- = *Casearia subsessiliflora* Lundell, Contr. Univ. Michigan Herb. 6: 50. 1941 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Quintana Roo, Coba, 1938, Lundell & Lundell 7824. (holotype: MICH1111069; isotypes: F F0060133F, K K000471136, LL LL00372021, TEX TEX00372022, US US00114906).
- = *Samyda parviflora* L., Syst. Veg. 10(2): 1025. 1759, nom. illeg. syn. sec. De Mestier (2020) ≡ *Casearia parviflora* J.F.Gmel., Syst. Nat. ed. 13[bis]: 700. 1791, nom. illeg. syn. sec. De Mestier (2020) Type: Jamaica, P.Browne s n. (holotype: LINN 558.1).
- = *Casearia parviflora* Willd., Sp. Pl., ed. 4, 2: 627. 1799, nom. illeg. syn. sec. De Mestier (2020)
- = *Anavinga samyda* C.F.Gaertn., Suppl. Carp. 3: 240. 1807 syn. sec. De Mestier (2020) ≡ *Casearia samyda* (C.F.Gaertn.) DC., Prodr. 2: 51. 1825 syn. sec. De Mestier (2020) Type: Puerto Rico, Riedlé s n. (holotype: TUB).
- = *Casearia punctata* Spreng. in Neue Entdeck. Pflanzenk. 2: 154. 1821 syn. sec. De Mestier (2020) Type: Puerto Rico, Bertero s n. (syntype: B lost); Puerto Rico, Perrin s n. (syntype: B lost).
- = *Casearia integrifolia* Vahl ex DC., Prodr. 2: 49. 1825 syn. sec. De Mestier (2020)
- = *Casearia sylvestris* var. *platyphylla* DC., Prodr. 2: 49. 1825 syn. sec. De Mestier (2020) ≡ *Guidonia sylvestris* var. *platyphylla* (DC.) M.Gómez in Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenos: 95. 1889 syn. sec. De Mestier (2020) Type: US Virgin Islands, St. Thomas, Bertero s n. (holotype: G).
- = *Casearia parviflora* var. *microphylla* Schtdl. in Linnaea 4: 90. 1829 syn. sec. De Mestier (2020) Type: America, Anon. (syntype: B -W08350-01 0, B -W08350-02 0 & B -W08350-03 0).
- = *Casearia affinis* Gardner in London J. Bot. 1: 529. 1842 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Rio de Janeiro, 1836, Gardner 160. (holotype: K K000471206; isotypes: BM BM000611055, BM000611056 & BM000624386, E E0057044 & E00570045, FI FI004327, G G00364124 & G00364139, GH GH00066458, NY NY00097920, P P02442172 & P01479062).
- = *Casearia benthamiana* Miq. in Ann. Sci. Nat., Bot., sér. 3, 1: 38. 1844 syn. sec. De Mestier (2020) ≡ *Casearia sylvestris* var. *benthamiana* (Miq.) Uittien in Recueil Trav. Bot. Néerl. 22: 372. 1926 syn. sec. De Mestier (2020) Type: Suriname, Republic of, Paramaribo, 1842, Focke 764. (holotype: U U0002174).

- = *Samyda parviflora* Sessé & Moc., Fl. Mexic., ed. 2: 122. 1894, nom. illeg. syn. sec. De Mestier (2020) Type: Puerto Rico, Sessé & Moc. 1237. (lectotype: MA; isolectotype: F F0060286F & F0060285F); Sessé & Mocino 1230. (syntypes: F, MA).
- = *Casearia attenuata* Rusby in Mem. Torrey Bot. Club 6: 40. 1895 syn. sec. De Mestier (2020) Type: Bolivia, Plurinational State of, La Paz, Bang 1529. (holotype: NY NY00097924; isotypes: A A00066460, BM BM000624370, BM000938979 & BM000624383, CAS CAS0001447, CORD CORD00003360, E E00570046, F F0060142F, G G00364140 & G00364147, K K000471249, L L0010762, M M0113058, NY NY00097925 & NY00097926, S S04-530, US US00930923, US00114831 & US00114837).
- = *Casearia sylvestris* var. *tomentella* Rusby in Mem. Torrey Bot. Club 6: 41. 1896 syn. sec. De Mestier (2020) Type: Bolivia, Plurinational State of, La Paz, 1892, Bang 1592. (holotype: NY NY00107372; isotypes: CAS CAS0001445, E E00570047, G G00364126, GH GH00364141 & GH00066484, K K000471250, M M0113059, NY NY00107373, US US00114907).
- = *Casearia sylvestris* var. *wydleri* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 74. 1898 syn. sec. De Mestier (2020) Type: Puerto Rico, 1827, Wydler 191. (holotype: G G00364143; isotypes: FI FI004326, G G00364143, G00364144, G00364145 & G00364146, K K000370542, P P00789611).
- = *Casearia sylvestris* var. *eichleri* Briq. in Bull. Herb. Boissier, sér. 2, 7: 672. 1907 syn. sec. De Mestier (2020)
- = *Casearia chlorophoroidea* Rusby in Descr. S. Amer. Pl.: 63. 1920 syn. sec. De Mestier (2020) ≡ *Casearia sylvestris* var. *chlorophoroidea* (Rusby) Sleumer, Fl. Suriname 3: 298. 1935 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Magdalena, Santa Marta, near Calacasa, 1898, Smith 800. (holotype: NY NY00097935; isotypes: CM CM1460, F F0060152F, GH GH00066465, K K000471247, MICH MICH1111057, US US00114850).
- = *Casearia herbert-smithii* Rusby in Descr. S. Amer. Pl.: 63. 1920 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Magdalena, Santa Marta, near Minca, 1898, Smith 1768. (holotype: NY NY00097946; isotypes: A A00066470, BM BM000624360, BR BR0000005105144, CM CM1461, DAO DAO000455228, F F0060160F, G G00364114 & G00364192, GH GH00066469, K K000471248, LL LL00372014, MA MA251459, MICH MICH1111060, MO MO279823, P P00789603 & P00789604, PH PH00001271, S S04-548, US US00114863, WIS WISv0255859WIS).
- = *Casearia onacaensis* Rusby in Descr. S. Amer. Pl.: 62. 1920 syn. sec. De Mestier (2020) Type: Colombia, Republic of, Magdalena, Santa Marta, probably from Onaca, 1898, Smith 906. (holotype: NY NY00107362; isotype: K K000471246).
- = *Casearia caudata* Uittien in Recueil Trav. Bot. Néerl. 22: 373. 1925 syn. sec. De Mestier (2020) Type: Suriname, Republic of, 1912, Anon 232. (holotype: U0123405; isotype: NY NY00097934).
- Distribution (areas). – Argentina Northeast (present); Argentina Northwest (present); Belize (present); Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present); Cayman Is. (present); Colombia (present); Costa Rica (present); Cuba (present); Dominican Republic (present); Ecuador (present); El Salvador (present); French Guiana (present); Guatemala (present); Guyana (present); Haiti (present); Honduras (present); Jamaica (present); Leeward Is. (present); Mexico Central (present); Mexico Gulf (present); Mexico Northeast (present); Mexico Northwest (present); Mexico Southeast (present); Mexico Southwest (present); Nicaragua (present); Panamá (present); Paraguay (present); Peru (present); Puerto Rico (present); Suriname (present); Trinidad-Tobago (present); Uruguay (present); Venezuela (present); Windward Is. (present)

***Casearia sylvestris* var. *lingua* (Cambess.) Eichler, Fl. Bras. 13(1): 482. 1871. Sec. Sleumer (1980)**

- ≡ *Casearia lingua* Cambess., Fl. Bras. Merid. 2: 236. 1830 syn. sec. De Mestier (2020) ≡ *Casearia sylvestris* subvar. *campestris* Eichler, Fl. Bras. 13(1): 482. 1871 syn. sec. De Mestier (2020). Type: Brazil, Federative Republic of, Minas Gerais, près contendas, 1796, St Hilaire B 1796 4. (holotype: P P02442174; isotype: P P00789602).
- = *Casearia carpinifolia* Benth. in J. Bot. (Hooker) 4: 112. 1842 syn. sec. De Mestier (2020) ≡ *Casearia sylvestris* var. *carpinifolia* (Benth.) Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 74. 1898 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Piauí, Oeiras, 1838, Gardner 1528. (syntypes: BM BM000624384, FI FI004325, K K000471202, K000471209 & K000471211); Guyana, Republic of, 1836, Schomburgk 103. (lectotype: BM BM000624389; isolectotypes: G G00364131 & G00364150, K K000471207, K000471176 & K000471210, P P00789602, U U0123403, US US00114845, US0114846 & US00902054); Guyana, Republic of, 1837, Schomburgk 263. (syntypes: BM BM000611050, FI FI004345, G G00364152 & G00364193, K K000471202 & K000472104, L L0010763 & L0010764, P P06688328, U U0008433, US US00902055).
- = *Casearia sylvestris* subvar. *pedicellaris* Eichler, Fl. Bras. 13(1): 482. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Sao Paulo, Mogi-Merim, Burchell 5111. (holotype: BR0000006411015; isotype: K K001216940).

Distribution (areas). – Argentina Northeast (present); Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil South (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); French Guiana (present); Guyana (present); Suriname (present); Venezuela (present)

***Casearia tacanensis* Lundell in *Lloydia* 4: 54. 1941. Sec. Sleumer (1980)**

Type: Mexico, United Mexican States, Chiapas, Volcan de Tacana, 8.1938, Matuda 2441. (holotype: MICH MICH1111070; isotypes: A A00066435, F F0060134F, K K000471137, L L0010765, LL LL00372023, MEXU MEXU00087982, NA NA0026261, NY NY00097902).

Distribution (areas). – Belize (present); Costa Rica (present); Guatemala (present); Honduras (present); Mexico Gulf (present); Mexico Southeast (present); Mexico Southwest (present); Nicaragua (present); Panamá (present)

***Casearia tachirensis* Steyererm. in *Fieldiana, Bot.* 28: 406. 1952. Sec. Sleumer (1980)**

Type: Venezuela, Bolivarian Republic of, Tachira, Betania, base of Paramo de Tama, 14.7.1944, Steyermark 57276. (holotype: F F0060198F; isotypes: L L0010766, NY NY00107374).

Distribution (areas). – Colombia (present); Venezuela (present)

***Casearia tenuipilosa* Sleumer, *Fl. Neotrop. Monogr.* 22: 368. 1980. Sec. Sleumer (1980)**

Type: Brazil, Federative Republic of, Amazonas, Basin of Rio Negro, 10 km above mouth of Rio Curicuriari, 3 Nov 1971, G. Prance & al. 16050. (holotype: INPA; isotypes: C C10012564, F F0060199F, K K001097597, L L0010768, MG MG044590, MICH MICH1111071, NY NY00107375, S S04-572, U U0002176, US US00114908); Brazil, Federative Republic of, Amazonas, E. Oliveira 2289. (paratype: IAN); Brazil, Federative Republic of, Amazonas, G. Black 48-2829. (paratypes: IAN, K, L, P); Brazil, Federative Republic of, Amazonas, J. Pires 769. (paratype: IAN); Brazil, Federative Republic of, Amazonas, M. Silva & D. Coelho 29. (paratype: INPA); Brazil, Federative Republic of, Amazonas, Mello & Mota s n. (paratype: INPA 57929); Brazil, Federative Republic of, Amazonas, Mello & Mota s n. (paratype: INPA 58068); Brazil, Federative Republic of, Amazonas, N. Silva & Brazao 60757. (paratypes: L, NY); Brazil, Federative Republic of, Amazonas, R. Froes 12378-138. (paratypes: A, F, NY NY2154258); Brazil, Federative Republic of, Amazonas, R. Froes 22162. (paratypes: IAN, U); Brazil, Federative Republic of, Amazonas, Spruce anno 1852. (paratypes: B, BM, C, G, GOET, K, NY, P, RB); Brazil, Federative Republic of, Amazonas, W. Rodrigues & D. Coelho 4772. (paratype: INPA); Brazil, Federative Republic of, Para, G. Black & P. Ledoux 50-10041. (paratype: IAN); Brazil, Federative Republic of, Para, G. Black 48-3193. (paratype: IAN).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil West-Central (present); Ecuador (present)

***Casearia ternstroemioides* (Griseb.) T. Samar. & M.H. Alford, *Pl. Wright.* 1: 156. 1860. Sec. T. Samar. & M.H. Alford (2019)**

≡ *Laetia ternstroemioides* Griseb., *Pl. Wright.* 1: 156. 1860 syn. sec. T. Samar. & M.H. Alford (2019) ≡ *Guidonia ternstroemioides* (Griseb.) Kuntze, *Revis. Gen. Pl.* 1: 4. 1891 syn. sec. De Mestier (2020) ≡ *Thamnia ternstroemioides* (Griseb.) M.Gómez in *Bol. Secr. Agric. Comerc. Trab., Cuba* 22: 69. 1914 syn. sec. De Mestier (2020). Type: Cuba, Republic of, Oriente, Monteverde, 1859, C.Wright 1107. (holotype: GOET GOET003816; isotypes: B 10 0243750, BR BR0000005104543 & BR0000005104567, F F0060242F, G G00364260, GH GH00066875 & GH00245575, K K000471408, MO MO-1164542, NY NY00107484, PH PH00016675, S S04-10, UC UC936821, YU YU069996).

Distribution (areas). – Cuba (present).

***Casearia thamnia* (L.) T. Samar. & M.H. Alford in *Novon* 27: 69. 2019. Sec. T. Samar. & M.H. Alford (2019)**

≡ *Laetia thamnia* L., *Pl. Jamaic. Pug.*: 31. 1759 syn. sec. De Mestier (2020) ≡ *Guidonia thamnia* Kuntze, *Revis. Gen. Pl.* 1: 44. 1891 syn. sec. De Mestier (2020). Type: Jamaica, red hills above the Angels, P.Browne s n. (holotype: LINN 680.1).

= *Laetia thamnia* Sw., *Prodr. Veg. Ind. Occ.*: 83. 1788, nom. illeg. syn. sec. T. Samar. & M.H. Alford (2019)

= *Thamnia swartzii* Hitchc., *Rep. (Annual) Missouri Bot. Gard.* 4: 59. 1893 syn. sec. T. Samar. & M.H. Alford (2019)

= *Casearia contracta* Urb., *Symb. Antill.* 6: 19. 1909 syn. sec. De Mestier (2020) Type: Jamaica, Troy, 8.1904, Harris 8756. (holotype: B lost; isotype: BM BM000582580).

Distribution (areas). – Belize (present); Colombia (present); Costa Rica (present); Cuba (present); Dominican Republic (present); Guatemala (present); Jamaica (present); Mexico Gulf (present); Mexico Southeast (present); Nicaragua (present); Panamá (present); Windward Is. (present)

***Casearia tremula* (Griseb.) Griseb. ex C.Wright in Anales Acad. Ci. Méd. Habana 5: 201. 1868.** Sec. Sleumer (1980)

- ≡ *Zuelania tremula* Griseb., Cat. Pl. Cub.: 9. 1866 syn. sec. De Mestier (2020) ≡ *Guidonia tremula* (Griseb.) M.Gómez in Anales Soc. Esp. Hist. Nat. 23: 56. 1894 syn. sec. De Mestier (2020). Type: Cuba, Republic of, Wright 2640. (lectotype: GOET; isolectotypes: BM BM000611043, G G00364135, GH GH00067018, MO MO279837, NY NY00108225, YU YU069992).
- = *Casearia spiralis* J.R.Johnst. in Proc. Amer. Acad. Arts 40: 691. 1905 syn. sec. De Mestier (2020) Type: Venezuela, Bolivarian Republic of, Nueva Espana, Margarita Island, El Valle, 1903, Johnston 283. (holotype: GH GH00066455; isotype: US US00114902).
- = *Casearia bonairensis* Bold., Fl. Dutch W. Ind. Is. 5: 68. 1914 syn. sec. De Mestier (2020) Type: Curacao, hills to the E of Westpunt, Boldingh 4942. (holotype: U; isotype: NY).
- = *Laetia glabra* Brandege in Univ. Calif. Publ. Bot. 6: 369. 1917 syn. sec. De Mestier (2020) Type: Mexico, United Mexican States, Oaxaca, San Geronimo, Purpus 7531. (holotype: UC UC187791).
- = *Zuelania belizensis* Lundell in Wrightia 1: 58. 1945 syn. sec. De Mestier (2020) Type: Belize, Toledo, Bolo Camp, upper reach of Golden stream, 1944, Gentle 4537. (holotype: LL LL00372035; isotype: LL LL00208030).

Distribution (areas). – Aruba (present); Belize (present); Colombia (present); Costa Rica (present); Cuba (present); El Salvador (present); Guatemala (present); Honduras (present); Mexico Central (present); Mexico Northwest (present); Mexico Southeast (present); Mexico Southwest (present); Netherlands Antilles (present); Nicaragua (present); Trinidad-Tobago (present); Venezuela (present); Windward Is. (present)

***Casearia uleana* Sleumer, Fl. Neotrop. Monogr. 22: 378. 1980.** Sec. Sleumer (1980)

Type: Bolivia, Plurinational State of, Beni, Meyer 175. (paratype: U); Brazil, Federative Republic of, Amazonas, B. Krukoff 5158. (paratypes: A, BM, BM, F, G, K, MICH, MO, NY, NY, U, US); Brazil, Federative Republic of, Madre de Dios, Ule 9624. (paratypes: G, K, L, MG, MG, U); Peru, Republic of, Lleras & al. P 16924. (paratypes: INPA, L, NY, S, US); Peru, Republic of, Loreto, Croat 18843. (paratypes: C, MO, NY); Peru, Republic of, Loreto, McDaniel & al. ANDCO2646. (paratype: US); Peru, Republic of, Loreto, McDaniel 13641. (paratypes: F, MO); Peru, Republic of, Loreto, Plowman & al. 7014. (paratype: GH); Peru, Republic of, Loreto, Tessmann 3569. (paratypes: G, NY); Peru, Republic of, Loreto, Tessmann 5249. (paratype: NY); Peru, Republic of, Madre de Dios, Seringal Auristella on the Peruvian border of Rio Acre, Jun 1911, Ule 9625. (holotype: L L0010775; isotypes: G G00364136, U U0002178, US US00114909); Peru, Republic of, Mathias & Taylor 5511. (paratype: US); Peru, Republic of, N. Silva 3504. (paratype: IAN).

Distribution (areas). – Bolivia (present); Brazil North (present); Colombia (present); Peru (present)

***Casearia ulmifolia* Vahl ex Vent., Choix Pl.: t. 46 verso. 1808.** Sec. Marquete (2012)

- ≡ *Guidonia ulmifolia* (Vahl ex Vent.) Baill. in Traité Bot. Méd. Phan. 2: 827. 1884 syn. sec. De Mestier (2020). Type: Trinidad and Tobago, Republic of, Ryan s n. (holotype: C; isotypes: B B-W08351-01 0, BM BM000624343, BR BR0000005104826, C C10012570, C10012571, C10012567, C10012565 & C10012568, L L0010781, P P00678826).
- = *Casearia celtidifolia* Kunth, Nov. Gen. Sp. 5: 362. 1823 syn. sec. De Mestier (2020) Type: Venezuela, Bolivarian Republic of, Terr. Fed. Amazonas, prope Angostura et Carichana, ad ripum flum, Orinoco, Humboldt & Bonpland s n. (holotype: P00679649).
- = *Casearia ulmifolia* Cambess., Fl. Bras. Merid. 2: 169. 1830, nom. illeg. syn. sec. De Mestier (2020)
- = *Casearia petraea* Benth. in J. Bot. (Hooker) 4: 111. 1842 syn. sec. De Mestier (2020) Type: Guyana, Republic of, Pirara, stony savannahs, 1839, Schomburgk 718. (holotype: K K000471157; isotypes: BM BM000611051, F F0060177F, FI FI004323, G G00364188 & G00364187, GH GH00066480, K K000471156, L L0010780, P P04677484, US US00114891).
- = *Casearia blanchetiana* Miq. in Linnaea 22: 801. 1849 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Bahia, forêts des marais d'Othos, 1840, Blanchet 3119. (holotype: U U0002182; isotypes: BM BM000624395 & BM000624396, BR BR0000005104741 & BR0000005105151, F F0BN013661, F0060144F, F0060145F & F0060146F, FI FI004322, G G00364156, G00364184 & G00364190, K K000471154, L L0010779, NY NY00097933, P P04677436, P04677437 & P04677438, U U0002181).
- = *Casearia cambessedesii* Eichler, Fl. Bras. 13(1): 475. 1871 syn. sec. De Mestier (2020) Type: Brazil, Federative Republic of, Minas Gerais, sur les bords du Piracicaba, St Hilaire B 1, nr. 608. (holotype: P P02442175; isotypes: F F0060149F, L L0010776).

= *Casearia tremifolia* J.F.Macbr. in Candollea 8: 23. 1940 syn. sec. De Mestier (2020) ≡ *Casearia celtidifolia* Poepp. ex Eichler, Fl. Bras. 13(1): 477. 1871 syn. sec. De Mestier (2020) Type: Peru, Republic of, Loreto, Maynas, 1831, Poeppig 2263. (holotype: L L0010777; isotypes: F F0041336F, L L0010778, P P04677476).

Distribution (areas). – Bolivia (present); Brazil North (present); Brazil Northeast (present); Brazil Southeast (present); Brazil West-Central (present); Colombia (present); Ecuador (present); French Guiana (present); Guyana (present); Peru (present); Suriname (present); Trinidad-Tobago (present); Venezuela (present)

***Casearia villosa* (Sw.) T. Samar. & M.H. Alford in Novon 27: 68. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Samyda villosa* Sw., Prodr. Veg. Ind. Occ.: 68. 1788 syn. sec. De Mestier (2020) ≡ *Sadymia villosa* (Sw.) Griseb., Fl. Brit. W. I.: 25. 1859 syn. sec. De Mestier (2020). Type: Jamaica, In the mtns, Swartz s n. (lectotype: S S-R-5564; isotype: G -DC; isolectotypes: C C10012584, GOET, LD, LD LD1254077, S S10-15226 & S10-15228, SBT SBT12509).

Distribution (areas). – Jamaica (present).

***Casearia williamsiana* Sleumer, Fl. Neotrop. Monogr. 22: 285. 1980.** Sec. Sleumer (1980)

≡ *Synandrina riparia* Standl. & L.O.Williams in Ceiba 3: 75. 1952 syn. sec. De Mestier (2020). Type: Honduras, Republic of, Morazan, rio de la Orilla, faldas del Cerro Majicaran, W of El Zamorano, 23.3.1950, Molina 2711. (holotype: US US00114912; isotype: GH GH00066949 & GH00066950).

Distribution (areas). – Honduras (present); Nicaragua (present)

***Casearia yucatanensis* (Standl.) T. Samar. & M.H. Alford in Novon 27: 68. 2019.** Sec. T. Samar. & M.H. Alford (2019)

≡ *Samyda yucatanensis* Standl. in Contr. U.S. Natl. Herb. 23: 842. 1923 syn. sec. De Mestier (2020). Type: Mexico, United Mexican States, Yucatan: Merida, 1865, Schott 603. (holotype: US US00114812; isotypes: F F0060287F, F0060288F & F0060289F, MO MO-194810 & MO-194811).

Distribution (areas). – Mexico Southeast (present)

***Casearia zahlbruckneri* Szyszyl., Diss. Cl. Math.-Phys. Acad. Litt. Cracov., ser. 2, 29: 226. 1894.** Sec. Sleumer (1980)

Type: Peru, Republic of, Cajamarca, Tambillo between Chota and Cutervo, Jelski 347. (holotype: KRA; isotypes: L L0010795, US US00114910).

Distribution (areas). – Bolivia (present); Colombia (present); Ecuador (present); Peru (present)

***Casearia zizyphoides* Kunth, Nov. Gen. Sp. 5: 362. 1823.** Sec. Sleumer (1980)

Type: Venezuela, Bolivarian Republic of, Anzoategui, prope Nova Barcelona, Bonpland 1087. (holotype: P P00307129; isotype: F F0BN013693).

= *Casearia celastroides* Klotzsch ex Sleum. in Notizbl. Bot. Gart. Berlin-Dahlem 12: 53. 1934 syn. sec. De Mestier (2020) Type: Guyana, Republic of, Pirara, 1843, Schomburgk 1112. (holotype: B lost; isotype: F phot F0BN013664).

Distribution (areas). – Brazil North (present); Colombia (present); French Guiana (present); Guyana (present); Trinidad-Tobago (present); Venezuela (present); Venezuelan Antilles (present)

***Casearia* s.l. Old World taxa. Sec. De Mestier (2020)**

***Casearia adiantoides* Sleumer in Bull. Bernice P. Bishop Mus. 141: 98. 1936.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, southern slopes of Mt: Seatura, Mbua province, Vanua Levu, 27 Apr 1934+, Smith 1682. (holotype: BISH BISH1001803; isotypes: GH GH00066637, K K000591498, L L0010548, NY NY00107380, S S-G-1191, US US00114835).

Distribution (areas). – Fiji (present)

***Casearia albicans* Wall. ex C.B.Clarke, Fl. Brit. India 2: 593. 1879.** Sec. Sleumer (1955)

Type: Malaysia, Penang, Wallich 7197. (syntypes: K K001126889, K001126890 & K001126891, L L0010549).

Distribution (areas). – Malaya (present)

***Casearia amplexans* Sleumer in Blumea 7: 484. 1954, not defined.** Sec. Sleumer (1955)

Type: Papua New Guinea, 4 km SW of Bernhard Camp, Idenburg river, rainforest undergrowth, 850 m, Mar 1939, Brass 15470. (holotype: L L0010551; isotype: A A00066537).

Distribution (areas). – New Guinea (present)

***Casearia andamanica* King in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 67: 16. 1898.** Sec. Pham Hoang Ho

Type: India, Republic of, Andaman Islands, 1884, King's collectors s n. (holotype: CAL; isotypes: BM BM000948323, CAL, K K000591436).

Distribution (areas). – Andaman Is. (present); Myanmar (present); Vietnam (present)

***Casearia angiensis* Sleumer in Blumea 7: 484. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, Manokwari Distr., Angi Gita Lake, in moist forest, 1800 m, Oct 1948, Kostermans 2116. (holotype: L L0010552; isotypes: A A00066538, BO, BRI BRI-AQ0209570, L L0010553, SING SING0054135).

Distribution (areas). – New Guinea (present)

***Casearia angustifolia* A.C.Sm. in Sargentia 1: 63. 1942.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, on the southern slope of Mt. Mariko, Thakaundrove Province, Vanua Levu, 14 Nov 1933, Smith 411. (holotype: GH GH00066635; isotypes: BISH BISH1001804, K K000591499, L L0010554, S S-G-1192, US US00114825).

Distribution (areas). – Fiji (present)

***Casearia anisophylla* Gilg in Bot. Jahrb. Syst. 55: 289. 1918.** Sec. Sleumer (1955)

Type: Papua New Guinea, Nordöstl. Neu-Guinea: Etappenberg im Speikgebiet, im dichten, bis 25 m hohen Höhenwald, 850 m ü.M., Oct 1912, Ledermann 9522. (syntypes: K K000591473, L L0010555).

Distribution (areas). – New Guinea (present)

***Casearia annamensis* (Gagnep.) Lescot & Sleumer in Adansonia, n.s., 10: 290. 1970.** Sec. Pham Hoang Ho

≡ *Tardiella annamensis* Gagnep., Notul. Syst. (Paris) 15: 32. 1955 syn. sec. De Mestier (2020). Type: Viet Nam, Socialist Republic of, prov. de Tuyen Duc: Pn. Sapoum, sud de la station agricole de Blao, Poilane 23714. (holotype: P; isotype: L L0010556).

Distribution (areas). – Cambodia (present); Vietnam (present)

***Casearia anosyensis* Appleq. & Gates, M.T., Novon: 28 (4). 2020.** Sec. de Mestier (2020)

Type: Madagascar, Anosy [Toliara]: Comb. Iabakoho, fkt. Ambanihazo, village le plus proche, Andranomavo, savane boisée, alt. 9 m, 24°38'19"S, 47°12'37"E, 20 Nov 2011, Rakotonirina & al. 667. (holotype: MO MO-6588535; isotypes: P, TAN).

***Casearia archboldiana* Sleumer in Blumea 7: 485. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, W. New Guinea, 15 km SW of Bernhard Camp, Idenburg Riv., mossy forest, 1800 m, 1939, Brass 12098. (holotype: L L0010565; isotypes: A A00066539, BM BM000611032, BRI BRI-AQ0342715).

Distribution (areas). – New Guinea (present)

***Casearia arfakensis* Sleumer in Blumea 7: 485. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, NW. New Guinea, Arfak Mts., near Putat, 1872, Beccari 333. (holotype: FI FI007991; isotype: L L0010568).

Distribution (areas). – New Guinea (present)

***Casearia auriculata* Sleumer in Blumea 7: 486. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, N.W. New Guinea, Ramoi, Beccari 333. (holotype: FI FI007991; isotype: L L0010568).

Distribution (areas). – New Guinea (present)

***Casearia austroafricana* A.E.van Wyk, R.G.C.Boon & Retief in Phytotaxa 383: 275. 2018.** Sec. African Plant Database. 2012

Type: South Africa, Republic of, KwaZulu-Natal: Ndwedwe District, Itafamana Mission, on TMS cliffs, 2500 ft (850 m), 16 Jul 1966, Moll 3290. (holotype: PRE; isotype: NU).

Distribution (areas). – Cape Provinces (present); KwaZulu-Natal (present)

***Casearia barteri* Mast., Fl. Trop. Afr. 2: 494. 1871.** Sec. de Mestier (2020)

Type: Nigeria, Federal Republic of, Onitsha, Barter 1635. (lectotype: K K000231401).

= *Casearia mannii* Mast., Fl. Trop. Afr. 2: 494. 1871 syn. sec. De Mestier (2020) Type: Sao Tome and Principe, Democratic Republic of, 1861, Mann 1134. (lectotype: K K000231396, K000231397 & K000231398; isolectotypes: L L0010689, P P00412990).

= *Casearia bule* Gilg in Bot. Jbuleahrb. Syst. 40: 513. 1908 syn. sec. De Mestier (2020) Type: Cameroon, United Republic of, Bpipindi im Urwald, Zenker 2201. (syntype: K K000231394; isosyntypes: G G00355937 & G00013799, HBG HBG515753, WAG WAG0003880); Cameroon, United Republic of, bei Bipindi im Urwald, 1904, Zenker 3218. (syntypes: BM BM000624315, K K000231395not designated); Cameroon, United Republic of, bei Bipindi im Urwald, Zenker 1666. (lectotype: B lost; isolectotypes: B 10 0160051, B 10 0160052 & B 10 0160053, BM BM000624317, BR BR0000006422349, LECB LECB0001753, P P00412984); Cameroon, United Republic of, bei Bipindi im Urwald, Zenker 3035. (syntypes: B 10 0160054, BR BR0000006421656, G G00355938, GOET GOET003791, K K000231391 & K000231393); Cameroon, United Republic of, im Urwald bei Johann Albrechtshöhe, Staudt 799. (syntypes: EA EA000002079, K K000231402); Cameroon, United Republic of, im botanischer Garten in Victoria, Winkler 1166. (syntype: PRE PRE0594536-0).

= *Casearia thonneri* De Wild., Études Fl. Bangala & Ubangi: 240. 1911 syn. sec. De Mestier (2020) Type: Congo, Democratic Republic of, 7 Feb 1909, Thonner 157. (holotypes: BR BR0000008900265 & BR0000008900890, L L0010573; isotype: K K000231388).

= *Casearia runssorica* Gilg in Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot. 2: 570. 1913 syn. sec. De Mestier (2020) Type: Congo, Democratic Republic of, Masisi-Walikale, 1957, Michelson 986. (neotype: BR BR0000006877095 & BR0000006876760); Congo, Democratic Republic of, Ruwenzori, 1908, Mildbraed 2676. (holotype: B lost).

= *Casearia klaineana* Pierre ex A. Chev., Veg. Utiles Afrique Trop. Franc. 9: 55. 1917 syn. sec. De Mestier (2020) Type: Gabon, Gabonese Republic, 1896, Klaine 618. (holotype: P P017842, P017843 & P017844).

= *Casearia noldei* A.Fern. & Diniz, Bol. Soc. Brot., sér. 2.: 32: 79. 1958 syn. sec. De Mestier (2020) Type: Angola, Republic of, Quela, May 1968, Nolde 748. (holotype: BM BM000838997; isotype: L L0010581).

Distribution (areas). – Burundi (present); Cabinda (present); Cameroon (present); Central African Republic (present); Congo (present); Gabon (present); Ghana (present); Gulf of Guinea Is. (present); Ivory Coast (present); Liberia (present); Nigeria (present); Rwanda (present); Sierra Leone (present); Sudan (present); Tanzania (present); Uganda (present); Zaire (present)

***Casearia battiscombei* R.E.Fr. in Notizbl. Bot. Gart. Berlin-Dahlem 9: 326. 1925.** Sec. Sleumer (1971)

Type: Kenya, Republic of, Mt. Aberdare orient, 13 Mar 1922, Fries 2289. (paratype: K K000231387; isoparatype: L L0010575); Kenya, Republic of, Mt. Kenya, Embu District, Kiye R., Fries 2012. (holotype: UPS; isotype: K K000231386).

= *Rinorea cafassii* Chiov. in Racc. Bot.: 6. 1935 syn. sec. Sleumer (1971) Type: Kenya, Republic of, Balbo 162. (TO).

– *Casearia chirindensis* Engl., Veg. Erde 3: II. 1921, nom. nud. syn. sec. De Mestier (2020)

Distribution (areas). – Kenya (present); Malawi (present); Mozambique (present); Tanzania (present); Uganda (present); Zimbabwe (present)

***Casearia brassii* Sleumer in Blumea 7: 486. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, Papua, W. Div., upper Wassi Kussa Riv., left branch, in rainforest fringing river, 1937, Brass 8626. (holotype: A A00066540; isotypes: BM BM000624280, BO, BRI BRI-AQ0342717, L L0010576).

Distribution (areas). – New Guinea (present)

***Casearia brideliifolia* Sleumer in Blumea 7: 487. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, Dalman, Nabire, in Agathis forest, 400 m, Mar 1940, Kanchira & Hatusima 12272. (paratype:); Papua New Guinea, N. W. New Guinea, Geelvink Bay, Sennen, 10 km inward Nabire, rainforest, 400 m, Mar 1940, Kanchira & Hatusima 12512. (holotype: A A00066541; isotypes: BO, L L0010578).
Distribution (areas). – New Guinea (present)

***Casearia brunneostriata* Gilg in Bot. Jahrb. Syst. 55: 291. 1918.** Sec. Sleumer (1955)

Type: (B lost). (holotype: B lost).
Distribution (areas). – New Guinea (present)

***Casearia buelowii* Whistler, Rainforest Trees Samoa: 187. 2004.** Sec. Whistler (2004)

Type: Tonga, Kingdom of, Vava'u Group, Vava'u Island, top of Mt Talau, 9 Jul 1978, G. Buelow 1445. (holotype: BISH BISH1001805).
Distribution (areas). – Tonga (present)

***Casearia calva* Craib in Bull. Misc. Inform. Kew 1930: 405. 1930.** Sec. Co's Digital Flora of the Philippines. 2011

Type: Thailand, Kingdom of, 1921, Kerr 5365. (syntypes: BK, BM BM000624271, K K000591398).

***Casearia capitellata* Blume in Mus. Bot. 1: 254. 1851.** Sec. Harwood (2015)

Type: Indonesia, Republic of, Borneo, Khortals s n. (syntypes: K K000591445, L L0010582 & L0010583, S S-G-1193).

= *Casearia latifolia* Ridl. in J. Straits Branch Roy. Asiat. Soc. 75: 34. 1917 syn. sec. De Mestier (2020)
= *Casearia borneensis* Merr. in J. Straits Branch Roy. Asiat. Soc. 86: 333. 1922 syn. sec. De Mestier (2020)
Type: Indonesia, Republic of, British North Borneo, near Sandakan, 20 Oct 1920, Wood 961. (syntypes: A A00066533, K K000591443, US US00114842); Indonesia, Republic of, British North Borneo, near Sandakan, Clemens 9499. (paratype:); Indonesia, Republic of, British North Borneo, near Sandakan, Ramos 1167. (paratype:).

Distribution (areas). – Borneo (present); Malaya (present); Sumatera (present); Thailand (present)

***Casearia carrii* Sleumer in Blumea 7: 487. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, Centr. Div. Isuarava, secondary forest, 4000 ft, Carr 15476. (holotype: BM BM000624289; isotypes: A A00066542, K K000591471, L L0538554, L0010584 & L0010585, SING SING0054137 & SING0054138).

Distribution (areas). – New Guinea (present)

***Casearia cauliflora* Volkens in Bot. Jahrb. Syst. 31: 469. 1901.** Sec. Costion (2012)

Type: Micronesia, Federated States of, Palau islands: Yap, Volkens 225. (syntypes: L L0010588, SING SING0054136, US US00114848 & US00114849).

Distribution (areas). – Caroline Is. (present)

***Casearia championii* Thwaites, Enum. Pl. Zeyl.: 19. 1858.** Sec. Mitra (1993)

Type: Sri Lanka, Democratic Socialist Republic of, Prov. cent. Alt. 3000-4000, Thwaites 2608. (holotype: PDA; isotypes: BM BM000948412, FR FR0036171, GH GH00066489, K K000591421, L L0010797).

= *Casearia bourdillonii* Mukh. in Bull. Bot. Soc. Bengal 19: 109. 1967 syn. sec. De Mestier (2020)

Distribution (areas). – Myanmar (present).

***Casearia clarkei* King in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 67. 1898.** Sec. Sleumer (1955)

***Casearia clarkei* var. *clarkei*.** Sec. Sleumer (1955)

Type: Malaysia, Malacca, Maingay 660. (holotype: K; isotypes: A A00518005, L L0010589); Singapore, Republic of, Ridley 6334. (paratype:).

Distribution (areas). – Malaya (present)

***Casearia clarkei* var. *kunstleri* (King) Ridl., Fl. Malay Penins. 1: 833. 1922.** Sec. Sleumer (1955)

≡ *Casearia kunstleri* King in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 67: 17. 1898 syn. sec. De Mestier (2020). Type: Malaysia, Perak, King's collectors 3694. (syntype: K K000591409); Malaysia, Perak, King's collectors 6936. (syntypes: A A00518003 & A00518004, SING SING0184416); Malaysia, Perak, King's collectors 7118. (syntype:); Malaysia, Perak, Wray 3752. (syntype: SING SING0184417 & SING0184418).

Distribution (areas). – Malaya (present)

***Casearia clutiifolia* Blume in Mus. Bot. 1: 255. 1851.** Sec. Sleumer (1955)

Type: Indonesia, Republic of, New Guinea, Irian Jaya, Nov. Guinea, Zippelius 217. (unknown type category: L L0010590, MEL MEL2474907).

= *Casearia mollis* K.Schum., Fl. Kais. Wilh. Land: 50. 1889, nom. illeg. syn. sec. De Mestier (2020)

– *Corizospermum clutiifolium* Zipp. ex Blume in Mus. Bot. 1: 255. 1851, nom. inval. syn. sec. De Mestier (2020)

Distribution (areas). – Maluku (present); New Guinea (present); Solomon Is. (present)

***Casearia congensis* Gilg in Bot. Jahrb. Syst. 40: 513. 1908.** Sec. Breteler (2008)

Type: Congo, Democratic Republic of, Bolobo-Lukolela, Dec 1896, Dewere 734. (lectotype: BR BR0000008803412; isolectotype: BR BR0000008803733 & BR0000008803085).

= *Casearia schlechteri* Gilg in Bot. Jahrb. Syst. 40: 512. 1908 syn. sec. De Mestier (2020) Type: Cameroon, United Republic of, Moloundou, Dja R., 24 Nov 1910, Mildbraed 3923. (neotype: HBG HBG515749; isoneotype: HBG HBG515750).

Distribution (areas). – Cameroon (present); Central African Republic (present); Congo (present); Zaire (present)

***Casearia coriacea* Vent., Choix Pl.: t. 45. 1808.** Sec. Sleumer (1971)

≡ *Samyda coriacea* (Vent.) Poir., Encycl., Suppl. 5: 32. 1817 syn. sec. De Mestier (2020). Type: Mauritius, 1797, Rich. s n. (holotype: G G00355987; isotype: L L0010603).

= *Casearia fragilis* Vent., Choix Pl.: t. 47 verso. 1808 syn. sec. De Mestier (2020) ≡ *Clasta fragilis* Comm. ex Vent., Choix Pl.: sub t.47. 1808 syn. sec. Sleumer (1971) ≡ *Samyda fragilis* (Vent.) Poir., Encycl., Suppl. 5: 32. 1817 syn. sec. De Mestier (2020) ≡ *Guidonia fragilis* (Vent.) Cordem., Fl. Réunion: 357. 1895 syn. sec. De Mestier (2020) Type: Mascareignes, Riche s n. (holotype: G G00355987).

= *Guidonia gelonioides* Baill. in Bull. Mens. Soc. Linn. Paris 1: 567. 1886 syn. sec. De Mestier (2020) ≡ *Casearia gelonioides* (Baill.) Warb., Nat. Pflanzenfam. 3(6a): 51. 1893 syn. sec. De Mestier (2020) Type: Reunion, Commerson s n. (syntype: P P00077469 & P00077470).

– *Casearia fasciculata* Bojer, Hortus Maurit.: 71. 1837, nom. nud. syn. sec. De Mestier (2020)

Distribution (areas). – Mauritius (present); Réunion (present)

***Casearia coriifolia* Lescot & Sleumer in Blumea 22: 138. 1974.** Sec. Lescot (1980)

Type: New Caledonia, Mt. Do, plateau sommital, 800-1000 m, 26 Jan 1972, Mackee 24910. (paratype:); New Caledonia, Mt. Do, plateau sommital, 800-1000 m, 28 Nov 1966, Mackee 15966. (paratype: P P05564184); New Caledonia, Mt. Do. Plateau sommital. 950-1020 m, 28 Oct 1969, Mackee 19. (holotype: P P00641365; isotypes: L L0010604, NOU NOU005960, P P00641366 & P00641367); New Caledonia, en foret dense Aruacaria-Nothofagus, sur terrain serpentineux, 28 Oct 1969, Veillon 2050. (paratype: P P05496115).

Distribution (areas). – New Caledonia (present)

***Casearia costulata* Jessup, Fl. Australia 8: 385. 1982.** Sec. Jessup (1982)

Type: Australia, Commonwealth of, Davies Creek, Qld, 1964, Webb & Tracey 6406. (holotype: BRI BRI-AQ0337235; isotypes: A A00066646, CANB CANB338699, CNS QRS75475, L L0010606, MEL MEL626088, MO MO-2267135, NSW NSW830676).

Distribution (areas). – Queensland (present)

***Casearia crassipes* A.C.Sm., Fl. Vit. Nova 2: 655. 1981.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, in hills between the Vatukawa and Wainio Rivers, Ndrekeniwai Valley, Thakaundrove Province, Vanua Levu, 24 Nov 1933, Smith 586. (holotype: BISH BISH1001789).

Distribution (areas). – Fiji (present)

***Casearia cuspidata* Blume in Mus. Bot. 1: 255. 1851. Sec. Sleumer (1955)**

Type: Indonesia, Republic of, Sumatra, Korthals s n. (unknown type categorys: K K000591394, L L0010608 & L0010609, MEL MEL2455094, S S-G-1195).

= *Casearia turbinata* Blume in Mus. Bot. 1: 225. 1850 syn. sec. De Mestier (2020) Type: Indonesia, Republic of, Sumatra, Sumatera Selatan, Palembang, Res. Palembang, Praetorius s n. (holotype: L L0010612).

= *Casearia grandifolia* Miq., Fl. Ned. Ind. 1(1): 712. 1856 syn. sec. De Mestier (2020)

= *Casearia forbesii* Baker f. in J. Bot. 62(Suppl.): 43. 1924 syn. sec. De Mestier (2020) Type: Indonesia, Republic of, Forbes 2454. (syntypes: BM BM000624284, L L0010610 & L0010611).

Distribution (areas). – Sumatera (present)

***Casearia dallachyi* F.Muell., Fragm. 5: 107. 1866. Sec. Jessup (1982)**

Type: Australia, Commonwealth of, Rockingham Bay, Qld, Dallachy s n. (syntype: MEL).

Distribution (areas). – Queensland (present)

***Casearia deplanchei* Sleumer in Blumea 22: 139. 1974. Sec. Lescot (1980)**

Type: New Caledonia, Koumac, crete calcaire rocheuse au Nord du Ruisseau Grande Foret, 250 m, 1 Dec 1972, Mackee 26007. (paratype:); New Caledonia, Mt. Boulinda, Jaffré 1003. (paratype:); New Caledonia, Mt. Boulinda, Jaffré 970. (paratype:); New Caledonia, Tanlé, 1861, Deplanche 427. (holotype: P P00641359; isotypes: G G00355986, K K000591487, L L0010617 & L0010618, P P00641360 & P00641361).

Distribution (areas). – New Caledonia (present)

***Casearia engleri* Gilg in Bot. Jahrb. Syst. 40: 511. 1908. Sec. African Plant Database. 2012**

Type: Tanzania, United Republic of, Lushoto District, Mbalu, Engler 1446. (holotype: B lost).

Distribution (areas). – Tanzania (present)

***Casearia erythrocarpa* Sleumer in Blumea 7: 488. 1954. Sec. Sleumer (1955)**

Type: Papua New Guinea, Papua, West. Div., Fly riv., 528 mile camp, rainforest undergrowth, 80 m, May 1936, Brass 6692. (holotype: A A00066544; isotypes: BRI BRI-AQ0342719, L L0010630).

Distribution (areas). – New Guinea (present)

***Casearia euphlebica* Merr. in Philipp. J. Sci., C 13: 34. 1918. Sec. Co's Digital Flora of the Philippines. 2011**

Type: Philippines, Republic of the, 3 Jun 1915, Wenzel 1502. (syntypes: A A00066560, CAS CAS0032663, L L0010631).

Distribution (areas). – Philippines (present)

***Casearia fissistipula* A.C.Sm., Fl. Vit. Nova 2: 655. 1981. Sec. Smith (1981)**

Type: Fiji, Republic of Fiji, Nayacini, Naitasiri province, Viti Levu, 11 May 1939, Parham 1151. (holotype: BISH BISH1001806; isotype: SUVA).

Distribution (areas). – Fiji (present)

***Casearia flavovirens* Blume in Mus. Bot. 1: 254. 1851. Sec. de Mestier (2020)**

Type: Indonesia, Republic of, Java, Hasselt s n. (unknown type categorys: L L0010637, MEL MEL2368479, S S-G-1199).

= *Casearia odorata* Teijsm. & Binn. in Ned. Kruidk. Arch. 3: 408. 1855 syn. sec. De Mestier (2020) Type: Indonesia, Republic of, Java, unknown s n. (holotype: L L0010638).

= *Casearia condorensis* Pierre ex Gagnep., Notul. Syst. (Paris) 3: 244. 1916 syn. sec. De Mestier (2020) Type: Viet Nam, Socialist Republic of, Ba Ria Vung Tau, Con Son, Cochinchina: Poula Condor, 1876, Harmand 751. (holotype: P P04022257; isotype: L L0010636).

= *Casearia pallida* Craib in Bull. Misc. Inform. Kew 1930: 406. 1930 syn. sec. De Mestier (2020) Type: Thailand, Kingdom of, 19 Jul 1928, Kerr 15855. (syntypes: BK BK257904, BM BM000624285, K K000591401, TCD TCD0016966).

Distribution (areas). – Jawa (present); Lesser Sunda Is. (present); Malaya (present); Sumatera (present); Thailand (present); Vietnam (present)

***Casearia flexicaulis* K.Schum., Fl. Schutzgeb. Südsee, Nachtr.: 320. 1905. Sec. Sleumer (1955)**

Distribution (areas). – New Guinea (present)

***Casearia flexula* Ridl., Fl. Malay Penins. 1. 1922.** Sec. Sleumer (1955)

≡ *Casearia flexuosa* Ridl. in J. Fed. Malay States Mus. 7: 41. 1916, nom. inval. syn. sec. Sleumer (1955). Type: Malaysia, Kedah Peak, 1893, Ridley 5218. (syntype: SING SING0054142); Malaysia, Kedah Peak, 1915, Robinson & Kloss 6025. (syntype: K000591405); Malaysia, Kedah peak, 1893, Ridley 5364. (syntype: SING0184126); Malaysia, Penang, 1886, Curtis 1019. (syntype: SING0184121).

***Casearia flexuosa* Craib in Bull. Misc. Inform. Kew 1911. 1911.** Sec. de Mestier (2020)

Type: Thailand, Kingdom of, 20 Jun 1909, Kerr 694. (syntypes: BM BM000624262, BM BM000624263, K K000591402 & K000591403, TCD TCD0016974).

= *Casearia harmandiana* Pierre ex Gagnep., Notul. Syst. (Paris) 3: 245. 1916 syn. sec. De Mestier (2020) Type: Lao People's Democratic Republic, Plateau d'Attopeu, Harmand 1263. (syntype:); Lao People's Democratic Republic, Plateau d'Attopeu, Harmand 1167. (syntypes: L L0010639, P P04022260, P P04022261).

= *Casearia yunnanensis* F.C.How & W.C.Ko in Acta Bot. Sin. 8: 28. 1959 syn. sec. De Mestier (2020) Type: China, People's Republic of, Yunnan: Tawei Shan, Chinchuping, 800 m, 5 Apr 1940, Wang, Ko & S. Lau 100387. (holotype:).

Distribution (areas). – Borneo (present); China South-Central (present); Laos (present); Malaya (present); Maluku (present); Thailand (present); Vietnam (present)

***Casearia fuliginosa* (Blanco) Blanco, Fl. Filip., ed. 2: 262. 1845.** Sec. de Mestier (2020)

≡ *Anavinga fuliginosa* Blanco, Fl. Filip.: 372. 1837 syn. sec. De Mestier (2020)

= *Casearia densifolia* Elmer in Leafl. Philipp. Bot. 4: 1516. 1912 syn. sec. De Mestier (2020) Type: Philippines, Republic of the, Magallanes (Mt. Giting-giting), Province of Capiz, Island of Sibuyan, Apr 1910, Elmer 12217. (isotype: A A00066559; syntypes: CAS CAS0032662, FI FI014614, HBG HBG515746, K K000591453, L L0010640, MO MO-279821, NY NY00107382, US US00114855).

= *Casearia glauciramea* Elmer in Leafl. Philipp. Bot. 4: 1517. 1912 syn. sec. De Mestier (2020) Type: Philippines, Republic of the, Magallanes (Mt. Giting-giting), Province de Capiz, Island of Sibuyan, Apr 1910, Elmer 12216. (syntypes: BM BM000624290, FI FI014615, HBG HBG515744, K K000591451, L L0010641, NY NY00107386, US US00114861).

= *Casearia nitens* Merr. in Philipp. J. Sci. 30: 412. 1926 syn. sec. De Mestier (2020) Type: Philippines, Republic of the, 1924, Ramos & Edano 44116. (unknown type categorys: A A00066571, BM BM000611035, K K000591452, NY NY00107392, UC UC257293).

Distribution (areas). – Philippines (present)

***Casearia gallifera* Tathana in Thai Forest Bull., Bot. 39: 25. 2011.** Sec. Harwood (2015)

Type: Thailand, Kingdom of, Harwood 2085. (holotype: BKF).

Distribution (areas). – Thailand (present)

***Casearia gambiana* Breteler in Kew Bull. 73(4)-46: 1. 2018.** Sec. African Plant Database. 2012

Type: Gambia, Republic of the, Kendingsaibel (Keninding Saibali on Google Earth), 13°17.08'N, 16°47.05'W, 22 Apr 2016, Dijkstra 3. (holotype: WAG WAG0392359 & WAG0392360).

Distribution (areas). – Gambia, The (present)

***Casearia gigantifolia* Slooten in Bull. Jard. Bot. Buitenzorg, sér. 3, 7: 399. 1925.** Sec. Sleumer (1955)

Type: Indonesia, Republic of, Sumatra. Res Atjèh and Dependencies: P. Simaloer, Aug 1918, Achmad 573. (syntype:); Indonesia, Republic of, Sumatra. Res. Atjèh and Dependencies: P. Simaloer, Apr 1919, Achmad 1043. (syntype:); Indonesia, Republic of, Sumatra. Res. Atjèh and Dependencies: P. Simaloer, May 1919, Achmad 1150. (syntype:); Indonesia, Republic of, Sumatra. Res. Atjèh and Dependencies: P. Simaloer, Oct 1918, Achmad 656. (syntype:).

Distribution (areas). – Sumatera (present)

***Casearia glabra* Roxb., Hort. Beng. 33: 421. 1814.** Sec. Sleumer (1955)

Type: Indonesia, Republic of, Moluccas, Maluku, Ambon, Ambonia. (unknown type category: S S-G-1202).

= *Casearia moluccana* Blume in Mus. Bot. 1: 255. 1851 syn. sec. De Mestier (2020) Type: Indonesia, Republic of, Moluccas, Maluku, Ambon, Ambonia. (isotypes: MEL MEL2368478, S S-G-1202; unknown type category: L L0043248).

Distribution (areas). – Maluku (present)

***Casearia gladiiformis* Mast., Fl. Trop. Afr. 2: 493. 1871.** Sec. Sleumer (1971)

Type: Mozambique, People's Republic of, Shupanga, 1859, Kirk s n. (holotype: K K000231383).

= *Casearia junodii* Schinz, Mém. Herb. Boissier 10: 52. 1900 syn. sec. De Mestier (2020) Type: Mozambique, People's Republic of, Delagoa Bay, 1893, Junod 351. (unknown type category: BR BR0000006244620, G G00013775 & G00013800, K K000231384, L L0010642, NY NY00107379, US US00901820, Z).

= *Casearia holtzii* Gilg in Bot. Jahrb. Syst. 40: 510. 1908 syn. sec. De Mestier (2020) Type: Tanzania, United Republic of, Uzaramo District, Pongu Hills, Holz 659. (syntype: B lost); Tanzania, United Republic of, Uzaramo District, Pugu Hills, Holz 649. (syntype: B lost).

= *Casearia macrodendron* Gilg in Bot. Jahrb. Syst. 40: 510. 1908 syn. sec. De Mestier (2020) Type: Tanzania, United Republic of, Uluguru Mts., Tawa, Stuhlmann 8924. (syntype: B lost); Tanzania, United Republic of, Uzaramo, Stuhlmann 8599. (syntype: B lost).

Distribution (areas). – Cape Provinces (present); Kenya (present); KwaZulu-Natal (present); Malawi (present); Mozambique (present); Tanzania (present)

***Casearia globifera* Gilg in Bot. Jahrb. Syst. 55: 289. 1918.** Sec. Sleumer (1955)

Type: Papua New Guinea, In den Wäldern am Djamu, 300 m ü. M, Schlechter 16890. (holotype: L L0010643).

Distribution (areas). – New Guinea (present)

***Casearia glomerata* Roxb., Fl. Ind. 2: 419. 1832.** Sec. de Mestier (2020)

≡ *Guidonia glomerata* (Roxb.) Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46: 92. 1877 syn. sec. De Mestier (2020). Type: India, Republic of, Roxb. drawing 2250. (iconotype:).

= *Casearia merrillii* Hayata in Icon. Pl. Formosan. 3: 30. 1913 syn. sec. Yang Qiner (2007)

= *Casearia sikkimensis* N.Mukh. in J. Bombay Nat. Hist. Soc. 69: 392. 1972 syn. sec. Mitra (1993) ≡ *Casearia glomerata* var. *sikkimensis* (N.Mukh.) R.C.Srivast., Fl. Sikkim: 128. 1998 syn. sec. Chakrabarty (2010) Type: India, Republic of, Dhobijhua ad Kurseong mense, Apr 1882, J. Gamble. (holotype: CAL).

= *Casearia glomerata* f. *pubinervis* How & Ko, Acta Bot. Sin.: 8(1): 31. 1959 syn. sec. Yang Qiner (2007) Type: China, People's Republic of, Kwangtung: Fangchen, 11 Dec 1929, Wu 69. (holotype:).

– *Casearia membranacea* f. *nigrescens* S.S.Lia, Cat. Type Spec. China, Suppl. 1: 87. 1999, comb. inval. syn. sec. Yang Qiner (2007)

Distribution (areas). – Assam (present); Bangladesh (present); China Southeast (present); East Himalaya (present); India (doubtfully present); Myanmar (present); Taiwan (present); Vietnam (present)

***Casearia graveolens* Dalzell in Hooker's J. Bot. Kew Gard. Misc. 4: 107. 1852.** Sec. de Mestier (2020)

= *Casearia ovata* (Lam.) Willd., Sp. Pl., ed. 4, 2: 629. 1799 syn. sec. De Mestier (2020) ≡ *Guidonia ovata* (Lam.) Baill. in Traité Bot. Méd. Phan. 2: 827. 1884 syn. sec. De Mestier (2020) – *Anavinga ovata* Lam., Encycl. 1: 148. 1783, nom. rej. syn. sec. Samarakoon (2015)

= *Samyda glabra* Buch.-Ham. in Trans. Linn. Soc. London 17: 227. 1835 syn. sec. Kiger (1984) Type: India, Republic of, Mangga, 4 Jan 1811, Hamilton s n. (holotype: K).

= *Casearia macrogyna* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31(I): 463. 1858 syn. sec. Fl. Brit. India 2: 592. 1879 Type: India, Republic of, Prope urbem Mangalor in terra Canara Indiae orientalis, Hohenacker 105. (holotype: K KW001000605).

= *Casearia graveolens* var. *lintsangensis* S.Y.Bao in Acta Bot. Yunnan. 5: 378. 1983 syn. sec. Yang Qiner (2007)

– *Casearia hamiltonii* Wall., Numer. List: 7195. 1832, nom. nud. syn. sec. Fl. Brit. India 2: 592. 1879

Distribution (areas). – Bangladesh (present); China South-Central (present); East Himalaya (present); India (present); Laos (present); Myanmar (present); Nepal (present); Pakistan (present); Sri Lanka (present); Thailand (present); Vietnam (present); West Himalaya (present)

***Casearia grayi* Jessup, Fl. Australia 8: 385. 1982.** Sec. Jessup (1982)

Type: Australia, Commonwealth of, State Forest Reserve 194, adjacent to Portion 69, Herberton, Qld, 28 Nov 1978, Gray 1154. (holotype: BRI BRI-AQ0337237; isotypes: A A00268166, BISH BISH1001807, CANB CANB590536, CNS QRS54102 & QRS54103, K K000912642 & K000591479, L L0700327).
Distribution (areas). – Queensland (present)

***Casearia grewiifolia* Vent., Choix Pl.: t. 48. 1808.** Sec. de Mestier (2020)

***Casearia grewiifolia* var. *cinerea* (Turcz.) Sleumer, Fl. Males. 5: 95. 1954.** Sec. Co's Digital Flora of the Philippines. 2011

≡ *Casearia cinerea* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31(I): 462. 1858 syn. sec. De Mestier (2020).
Type: Philippines, Republic of the, Luzon. Prov. Pangasanan, 1841, Cuming 1011. (holotype: KW KW001001115; isotypes: FI FI004291, G G00355979, G00355980 & G00355981, K K000591463 & K000591464, L L0043249 & L0043250, MEL MEL2368494 & MEL2368495).

= *Samyda serrulata* Blanco, Fl. Filip.: 374. 1837, nom. illeg. syn. sec. Co's Digital Flora of the Philippines. 2011

= *Samyda pubescens* Blanco, Fl. Filip., ed. 2: 263. 1845, nom. illeg. syn. sec. De Mestier (2020)

= *Casearia pilosissima* Quisumb. & Merr. in Philipp. J. Sci. 37: 171. 1928 syn. sec. De Mestier (2020) Type: Philippines, Republic of the, 1927, Ramos & Edano 48874. (syntypes: K K000591462, NY NY00107394, UC UC329920).

Distribution (areas). – Laos (present); Philippines (present)

***Casearia grewiifolia* var. *gelonioides* (Blume) Sleumer, Fl. Males. 6: 944. 1972.** Sec. de Mestier (2020)

≡ *Casearia hexagona* var. *gelonioides* Blume in Mus. Bot. 1. 1850 syn. sec. Sleumer (1955)

= *Casearia hexagona* Decne. in Ann. Mus. Natl. Hist. Nat. 3: 429. 1804 syn. sec. Sleumer (1955) ≡ *Casearia grewiifolia* var. *hexagona* (Decne.) Govaerts, World Checkl. Seed Pl. 3(1): 13. 1999 syn. sec. Co's Digital Flora of the Philippines. 2011

= *Casearia uniflora* Decne. in Nouv. Ann. Mus. Hist. Nat. 3: 428. 1834 syn. sec. Sleumer (1955)

= *Laurus serrata* Blanco, Fl. Filip.: 319. 1837 syn. sec. Sleumer (1955)

= *Casearia glabrata* Blume in Mus. Bot. 1: 253. 1851 syn. sec. Sleumer (1955)

= *Casearia laurina* Blume in Mus. Bot. 1: 253. 1851 syn. sec. Sleumer (1955) Type: Indonesia, Republic of, Borneo, Khortals s n. (unknown type categories: L L0010658 & L0010659, MEL MEL2368395, S S-G-1200).

= *Casearia salacioides* Blume in Mus. Bot. 1: 252. 1851 syn. sec. Sleumer (1955)

= *Casearia truncata* Blume in Mus. Bot. 1: 252. 1851 syn. sec. De Mestier (2020)

= *Casearia angustata* Teijsm. & Binn. in Ned. Kruidk. Arch. 3: 409. 1855 syn. sec. Sleumer (1955)

= *Casearia gonocarpa* Miq., Fl. Ned. Ind. 1(1): 1093. 1858 syn. sec. Sleumer (1955) Type: Indonesia, Republic of, Sumatra, in Priaman, Diepenhorst 2145. (unknown type categories: L L0010653, U U0002164).

= *Casearia leucolepis* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31(I): 463. 1858 syn. sec. Sleumer (1955) Type: Singapore, Republic of, 1848, Lobb. 468. (syntypes: BM BM000624295, FI FI004292, G G00165538 & G00165539, K K000591494 & K000591461, KW KW001000607, LE LE00015362).

= *Casearia grewiifolia* var. *deglabrata* Koord. & Valetton, Bijdr. Boomsort. Java 1: 174. 1894 syn. sec. Sleumer (1955)

= *Casearia crenata* Merr. in Philipp. J. Sci. 1(Suppl.): 99. 1906 syn. sec. Sleumer (1955) Type: Philippines, Republic of the, Jul 1904, Ahorn 1504. (syntype: BM BM000624308); Philippines, Republic of the, Mar 1905, Whitford 1150. (syntypes: K K000591457, NY NY00107385, US US00114853); Philippines, Republic of the, Mar 1905, Whitford 1210. (syntype:).

= *Casearia polyantha* Merr. in Philipp. J. Sci. 1(Suppl.): 99. 1906 syn. sec. Sleumer (1955) Type: Philippines, Republic of the, Antopolo. Province of Rizal, Jun 1905, Ahorn 3143. (US US00664136; isotypes: K K000591458, NY NY00107395, SING SING0054148); Philippines, Republic of the, May 1905, Borden 3039. (syntype: NY NY00107396); Philippines, Republic of the, Merrill 138. (syntype:).

= *Casearia subcordata* Merr. in Philipp. J. Sci., C 9: 328. 1914 syn. sec. Sleumer (1955) Type: Philippines, Republic of the, Mindanao, Bukidnon Subprovince, Aug 1912, Fénix 15698. (syntypes: A A00066632, BM BM000624303, K K000591460, US US00114905).

= *Casearia luteocarpa* Elmer in Leafl. Philipp. Bot. 9: 3189. 1934 syn. sec. Sleumer (1955) Type: Philippines, Republic of the, Mt. Pinatuba Zambales Mountains, Province of Pampanga, Luzon, May 1927, Elmer 22309. (isotype: B 10 0277744; syntypes: A A00066569, BM BM000624311, GH GH00066568, HBG HBG515739, K K000591459, L L0010661, MICH MICH1111062, MO MO-279820, NY NY00107387, SING SING0054145).

Distribution (areas). – Andaman Is. (present); Bismarck Archipelago (present); Borneo (present); Jawa (present); Malaya (present); Maluku (present); New Guinea (present); Nicobar Is. (present); Philippines (present); Solomon Is. (present); Sulawesi (present); Sumatera (present); Thailand (present); Vietnam (present)

***Casearia grewiifolia* var. *grewiifolia*. Sec. de Mestier (2020)**

- ≡ *Samyda grewiifolia* (Vent.) Poir., *Encycl., Suppl.* 5: 32. 1817 syn. sec. Sleumer (1955). Type: Indonesia, Republic of, Java, Lahaye s n. (holotype: G G00364738; isotype: G G00364691).
- = *Casearia variabilis* Blume in *Mus. Bot.* 1: 252. 1851 syn. sec. Sleumer (1955)
- = *Casearia contermina* Miq., *Fl. Ned. Ind.* 1(1): 707. 1856 syn. sec. Sleumer (1955)
- = *Casearia subcuneata* Miq., *Fl. Ned. Ind.* 1(1): 706. 1856 syn. sec. Sleumer (1955) Type: Indonesia, Republic of, Java, Horsfield s n. (holotype: U U0002166).
- = *Casearia microdon* Miq., *Fl. Ned. Ind., Eerste Bijv.*: 333. 1861 syn. sec. Sleumer (1955) Type: Indonesia, Republic of, Sumatra austr. in prov. Lampong prope Natar, Teijsm. (unknown type categorys: L L0010649, U U0002165).
- = *Casearia kerrii* Craib in *Bull. Misc. Inform. Kew* 1911: 55. 1911 syn. sec. Harwood (2015) Type: Thailand, Kingdom of, Chiangmai in deciduous eng jungle, 300 m, Kerr 580. (holotype: K K000591400).
- = *Casearia agusanensis* Elmer in *Leafl. Philipp. Bot.* 7: 2652. 1915 syn. sec. Co's Digital Flora of the Philippines. 2011 Type: Philippines, Republic of the, Cabadbaran (Mt. Urdaneta), Province of Agusan, Mindanao, Sep 1912, Elmer 13650. (syntypes: CAS CAS0032661, FI FI014616, GH GH00066556, L L0010650).
- = *Casearia confertiflora* Merr. in *Philipp. J. Sci., C* 13: 34. 1918 syn. sec. Co's Digital Flora of the Philippines. 2011 Type: Philippines, Republic of the, Luzon, Ilocos Norte Province, Bangui, Ramos 27442. (syntypes: A A00066558, K K000591454, US US00114852).
- = *Casearia sogerensis* Baker f. in *J. Bot.* 61(Suppl.): 22. 1923 syn. sec. Sleumer (1955) Type: Papua New Guinea, Forbes 377. (syntypes: A A00066555, BRI BRI-AQ0342731, E E00296671, FI FI007992, K K000591474, L L0010651, MEL MEL569156 & MEL569158, SING SING0083789).
- = *Casearia oblonga* Craib in *Bull. Misc. Inform. Kew* 1930: 405. 1930 syn. sec. Harwood (2015) Type: Thailand, Kingdom of, Chumpawn, Siep Yuan, 1928, Kerr 16246. (syntypes: BK BK257903, BM BM000624265, K K000591399, TCD TCD0016967).

Distribution (areas). – Borneo (present); Cambodia (present); Jawa (present); Laos (present); Lesser Sunda Is. (present); Malaya (present); Maluku (present); New Guinea (present); Philippines (present); Queensland (present); Sulawesi (present); Sumatera (present); Thailand (present); Vietnam (present)

***Casearia grewiifolia* var. *insularis* (Vasudeva Rao & Chakrab.) Chakrab. & M.Gangop. in *J. Econ. Taxon. Bot.* 16: 717. 1992. Sec. Chakrab. & M.Gangop. (1992)**

- ≡ *Casearia insularis* Vasudeva Rao & Chakrab. in *J. Econ. Taxon. Bot.* 5: 991. 1984 syn. sec. De Mestier (2020). Type: India, Republic of, Andaman Island, Balakrishnan 5389. (holotype: A; isotype: PBL); India, Republic of, Audaman Nicobar Islands, Balakrishnan 5375. (paratype: PBL); India, Republic of, Audaman Nicobar Islands, Balakrishnan 5425. (paratype:).

Distribution (areas). – Andaman Is. (present)

***Casearia halmaherensis* Slooten in *Bull. Jard. Bot. Buitenzorg, sér.* 3, 7. 1925. Sec. Slooten (1925)**

Type: Indonesia, Republic of, Galéla, 150 m, Sep 1921, Beguin 1783. (syntype:); Indonesia, Republic of, Ternate and Dependancies. Halmahéra, Soatobaro near Galéla, 60 m, Jun 1922, Beguin 2006. (syntype: L L0010667); Indonesia, Republic of, Ternate: Lagoena, 350 m, Apr 1920, Beguin 1. (syntype:).

***Casearia hirtella* Hosok. in *Trans. Nat. Hist. Soc. Formosa* 28: 63. 1938. Sec. Hosok. (1938)**

Type: Palau, 1937, Hosokawa 9084. (unknown type categorys: A A00055052, L L0010668, US US00114864).

Distribution (areas). – Caroline Is. (present)

***Casearia hosei* Merr. in *Philipp. J. Sci., C* 11: 93. 1916. Sec. Sleumer (1955)**

Type: Philippines, Republic of the, Baram District, Long Lama, Oct 1894, Hose 483. (syntypes: BM BM000624296 & BM000624309, G G00355978, L L0010671, L0010672 & L0010673, SING SING0054143, US US00114865); Philippines, Republic of the, Mount Murud, 6 Dec 1914, Native collector 2932. (paratype:).

= *Casearia moultonii* Ridl. in Bull. Misc. Inform. Kew 1938: 111. 1938 syn. sec. De Mestier (2020) Type: Malaysia, Sarawak, 1914, Moulton 188. (paratype: K K000591389); Malaysia, Sarawak. Near Kuching, 1893, Haviland 3096. (syntypes: BM BM000624297, K K000591388, L L0010669 & L0010670, SING SING0054144).

Distribution (areas). – Borneo (present); Sulawesi (present)

***Casearia impressinervia* Merr. in Philipp. J. Sci., C 11: 96. 1916.** Sec. Sleumer (1955)

Type: Philippines, Republic of the, Sarawak, Native collector 1731. (syntypes: A A00066536, K K000591390, L L0010674, US US00604199).

Distribution (areas). – Borneo (present)

***Casearia inaequalis* Hutch. & Dalziel, Fl. W. Trop. Afr. 1: 168. 1927.** Sec. Breteler (2008)

Type: Sierra Leone, Republic of, Bandajuma, May 1914, Aylmer 73. (holotype: K K000041152; isotype: L L0010579).

Distribution (areas). – Ivory Coast (present); Liberia (present); Nigeria (present); Sierra Leone (present)

***Casearia kaalaensis* Lescot & Sleumer in Blumea 22: 138. 1974.** Sec. Lescot (1980)

Type: New Caledonia, Mt. Kaala, pente Sud, 20-200 m, maquis sur terrain rocheux serpentineux, 10 Oct 1965, Mackee 13547. (holotype: P P00641368; isotype: L L0010675).

Distribution (areas). – New Caledonia (present)

***Casearia kostermansii* Sleumer in Blumea 7: 488. 1954.** Sec. Sleumer (1955)

Type: Malaysia, Borneo, S. E., Borneo, Sampit Distr., Sg. Panjakuan (N. of Sampit), dry land, 10 m, Mar 1948, Kostermans 4722. (holotype: BO; isotypes: K K000591442, L L0010676); Malaysia, Sg. Wain region, N. of Balikpapan, low ridge, 40 m, Nov 1950, Kostermans 4330. (paratype:).

Distribution (areas). – Borneo (present)

***Casearia kurzii* C.B. Clarke, Fl. Brit. India 2: 594. 1879.** Sec. Yang Qiner (2007)

***Casearia kurzii* var. *gracilis* S.Y. Bao in Acta Bot. Yunnan. 5. 1983.** Sec. Yang Qiner (2007)

Type: China, People's Republic of, Yunnan expedition 9507. (holotype: KUN).

***Casearia kurzii* var. *kurzii*.** Sec. Yang Qiner (2007)

Distribution (areas). – Bangladesh (present); China South-Central (present); East Himalaya (present); Myanmar (present)

***Casearia ledermannii* Gilg in Bot. Jahrb. Syst. 55: 286. 1918.** Sec. Sleumer (1955)

Type: Papua New Guinea, Nordöstl. Neu Guinea: Kamelsrücken, Westspitze, im knorrigen, bemoosten Gebirgswald, 1150 m ü. M., Ledermann 8858. (syntypes: K K000591476, L L0010679, SING SING0083821); Papua New Guinea, Nordöstl. Neu-Guinea: Lordberg, Ledermann 10320. (syntype: K K000591477); Papua New Guinea, Nordöstl. Neu-Guinea: Lordberg, Ledermann 9990. (syntype:).

Distribution (areas). – New Guinea (present)

***Casearia lifuana* Däniker, Vierteljahrsschr. Naturf. Ges. Zürich 79(Beibl. 19): 275. 1933.** Sec. Lescot (1980)

Type: New Caledonia, Däniker 2300. (holotype: Z; isotype: L L0010680).

Distribution (areas). – New Caledonia (present)

***Casearia lobbiana* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31(I): 463. 1858.** Sec. Sleumer (1955)

Type: Indonesia, Republic of, 1846, Lobb. 416. (syntypes: BM BM000624299 & BM000624300, FI FI004283, G G00165540 & G00355977, K K000591415, KW KW001000606, LE LE00015363).

Distribution (areas). – Malaya (present); Myanmar (present); Sumatera (present)

***Casearia loheri* Merr. in Philipp. J. Sci., C 9: 327. 1914.** Sec. Co's Digital Flora of the Philippines. 2011

Type: Philippines, Republic of the, Loher 6215. (syntype: M M0113051); Philippines, Republic of the, Luzon, province of Rizal, San Isidro, Ramos 13525. (syntypes: BM BM000624301, L L0010681, US US00114870).

= *Casearia elliptifolia* Merr. in Philipp. J. Sci., C 11: 92. 1916 syn. sec. De Mestier (2020) Type: Philippines, Republic of the, Sarawak, Baram district, Miri River, Jan 1895, Hose 528. (syntypes: BM BM000624283, K K000591441, L L0010625).

= *Casearia paucinervia* Merr. & Quisumb. in Philipp. J. Sci. 83: 331. 1954 syn. sec. De Mestier (2020) Type: Philippines, Republic of the, Samar, Apr–May 1948, Sulit 6445. (holotype: A A00066573).

Distribution (areas). – Borneo (present); Philippines (present)

***Casearia longifolia* A.C.Sm. in Sargentia 1: 64. 1942.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, Viti Levu: Ra: Vatundamu, vicinity of Rewasa, near Vaileka, alt. 50-200 m, 2 Jun 1941, Degener 15390. (holotype: A).

Distribution (areas). – Fiji (present)

***Casearia macrantha* Gilg in Bot. Jahrb. Syst. 55: 290. 1918.** Sec. Sleumer (1955)

Type: Papua New Guinea, Etappenberg im Sepikgebiet, in dichtem, bis 25 m hohen Höhenwald, 850 m ü. M., Ledermann 9501. (syntype: K K001040284); Papua New Guinea, Etappenberg im Sepikgebiet, in dichtem, bis 25 m hohen Höhenwald, 850 m ü. M., Ledermann 8953. (syntype: K K001040283); Papua New Guinea, Nordöstl. Neu-Guinea: in den Wäldern des Maboro, Schlechter 19510. (syntype:); Papua New Guinea, in den Wäldern des Kani-Gebirges, 1000 m ü. M., Schlechter 17757. (syntypes: BR BR0000013346515, K K000591470).

Distribution (areas). – New Guinea (present)

***Casearia macrocarpa* C.B.Clarke, Fl. Brit. India 2: 593. 1879.** Sec. Sleumer (1955)

Type: Malaysia, Pinano, Maingay 660/2. (syntypes: A A00518002, GH GH00518001, K K000591407 & K000591408, L L0010687).

Distribution (areas). – Malaya (present)

***Casearia mauritiana* Bosser in Adansonia, n.s., 19: 337. 1980.** Sec. Sleumer (1980)

Type: Mauritius, Montagne Cocotte, 11 Mar 1978, Friedmann 3364. (holotype: P P00077472; isotype: P P00077473 & P00077474).

Distribution (areas). – Mauritius (present)

***Casearia megalophylla* Gilg in J. Arnold Arbor. 10: 81. 1929.** Sec. Sleumer (1955)

Type: Papua New Guinea, Kerema, Gulf Division, rainforest, 24 Mar 1926, Brass 1211. (syntypes: A A00066546 not designated, BRI BRI-AQ0342721, L L0010694).

Distribution (areas). – New Guinea (present).

***Casearia membranacea* Hance in J. Bot. 6: 113. 1868.** Sec. Yang Qiner (2007)

Type: China, People's Republic of, prope Kieng-chau, metropolin ins. Hae-nan, 18 Nov 1866, Sampson 13669. (holotype: BM BM000624259).

= *Casearia aequilateralis* Merr. in Lingnan Sci. J. 14: 38. 1935 syn. sec. De Mestier (2020) Type: China, People's Republic of, 8 Jun 1932, S. Lau 39. (syntypes: A A00066485, K K001070736, NY NY00107376).

Distribution (areas). – China Southeast (present); Hainan (present); Vietnam (present)

***Casearia michelsonii* Breteler in Kew Bull. 63: 107. 2008.** Sec. African Plant Database. 2012

Type: Congo, Democratic Republic of, foret de Mushwere, montagne Ouest de Walungu, Oct 1943–Jan 1944, Michelson 530. (holotype: BR BR0000006877484 & BR0000006877156).

Distribution (areas). – Zaire (present)

***Casearia microcarpa* Sleumer in Blumea 7: 489. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, Mc Cluer Gulf, Jakati, near Babo, 50 m, May 1941, Aet (Exp. Lundquist) 144. (paratype:); Papua New Guinea, N. W. New Guinea, Geelvink Bay, Chaban, Nabire, 1940, Kanchira &

Hatusima 11858. (holotype: A A00066548; isotype: L L0010699); Papua New Guinea, N.E. New Guinea, Sepik Distr., August Riv., Sep 1949, Womerstey N. G. F. 3846. (paratype:).
Distribution (areas). – New Guinea (present)

***Casearia mindanaensis* Merr. in Philipp. J. Sci. 20: 410. 1922.** Sec. Co's Digital Flora of the Philippines. 2011

Type: Philippines, Republic of the, Mindanao, Zamboanga District, Mount Tubuan, Ramos & Edano 36567. (syntypes: A A00066570, K K000591465, L L0010698, US US00114878).
Distribution (areas). – Philippines (present)

***Casearia minutiflora* Ridl. in J. Bot. 62: 297. 1924.** Sec. Sleumer (1955)

Type: Malaysia, State of Pahang Fraser Hill, upon the selangor border, 16 Sep 1922, Burhill & Holtuum 8581. (holotype: K K000591406; isotypes: L L0010700, SING SING0054146).
Distribution (areas). – Malaya (present)

***Casearia monticola* Sleumer in Blumea 7: 489. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, Boridi, forest, 5000 ft., Sep 1935, Carr 13400. (paratype:); Papua New Guinea, Papua, Centr. Div. Isuarava, forest, 4500 ft, Carr 15522. (holotype: BM BM000624302; isotypes: A A00066549, K K000591475, L L0010702 & L0010703, SING SING0054147).
Distribution (areas). – New Guinea (present)

***Casearia montigena* Appleq. & Gates, M.T., Novon: 28 (4). 2020.** Sec. de Mestier (2020)

Type: Madagascar, SAVA [Antsiranana]: Marojejy RNI, Maroambihy, Sambava, au sommet de Marojejy, env. 13 km NW de Maroambihy, env. 9,35 km NW du Fkt. de Mandena, alt. 2132 m, 14°26'50"S, 49°43'57"E, 23–24 Mar 1995, Rasoavimbahoaka 532. (holotype: MO MO-6084925; isotypes: P, TAN).

***Casearia multinervosa* C.T.White & Sleumer in Notizbl. Bot. Gart. Berlin-Dahlem 12: 474. 1935.** Sec. Jessup (1982)

Type: Australia, Commonwealth of, Sandiland Ranges, N. S. W., Nov 1904, Boorman. (holotype: B; isotypes: K K000591478, NSW NSW59044).
Distribution (areas). – New South Wales (present); Queensland (present)

***Casearia myrsinoides* Sleumer in Bull. Bernice P. Bishop Mus. 141: 98. 1936.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, Mt. Kasi, Yanawai River region, Thakaundrove Province, Vanua Levu, 1934, Smith 1772. (holotype: BISH BISH1001809; isotypes: GH GH00066640, K K000591488, NY NY00107391, P P00646346, US US00114882).
Distribution (areas). – Fiji (present)

***Casearia nigrescens* Tul. in Ann. Sci. Nat., Bot., sér. 5, 9: 326. 1868.** Sec. Sleumer (1971)

***Casearia nigrescens* var. *lucida* (Tul.) Sleumer in Bull. Jard. Bot. Natl. Belg. 41: 415. 1971.** Sec. Sleumer (1971)

≡ *Casearia lucida* Tul. in Ann. Sci. Nat., Bot., sér. 5, 9: 325. 1868 syn. sec. De Mestier (2020) ≡ *Guidonia lucida* (Tul.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 567. 1886 syn. sec. De Mestier (2020). Type: Madagascar, Hab. Vicinis circa urbem Tananarivon metropol provin. Emirn. Ins Madag., Bojer s n. (syntypes: G G00018511, K K000231379, L L0010711, M M0109493 & M0109494, P P00077475, TUB TUB002836).

= *Casearia parvifolia* Tul. in Ann. Sci. Nat., Bot., ser. 5, 9: 328. 1868, nom. illeg. syn. sec. De Mestier (2020)
Type: Madagascar, Baie de Rigny, in monte praec. Tananarivo, Dec 1848, Boivin 2565. (holotype: P P00077477; isotypes: G G00018969, L L0010710, P P00077476).

= *Guidonia tulasneana* Baill. in Bull. Mens. Soc. Linn. Paris 1: 567. 1886 syn. sec. De Mestier (2020) ≡ *Casearia tulasneana* (Baill.) Warb., Nat. Pflanzenfam. 3(6a): 51. 1893 syn. sec. De Mestier (2020)

Distribution (areas). – Madagascar (present)

***Casearia nigrescens* var. *nigrescens*.** Sec. Sleumer (1971)

≡ *Guidonia nigrescens* (Tul.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 567. 1886 syn. sec. De Mestier (2020).
Type: Madagascar, Foulpointe, Chapelier 19. (holotype: P00077478; isotype: L L0043254).

- = *Casearia amplissima* Tul. in Ann. Sci. Nat., Bot., sér. 5, 9: 327. 1868 syn. sec. African Plant Database. 2012 ≡ *Guidonia amplissima* (Tul.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 567. 1886 syn. sec. De Mestier (2020) Type: Madagascar, Antongio, Richard. (holotype: P P00077487).
- = *Casearia elliptica* Tul. in Ann. Sci. Nat., Bot., sér. 5, 9: 329. 1868, nom. illeg. syn. sec. African Plant Database. 2012 ≡ *Guidonia elliptica* (Tul.) Baill. in Bull. Mens. Soc. Linn. Paris 1: 567. 1886 syn. sec. De Mestier (2020) Type: Madagascar, Bernier 307. (holotype: P P00077486).
- = *Casearia elliptica* f. *elongata* H. Perrier, Mem. Mus. Natl. Hist. Nat. 13. 1940 syn. sec. De Mestier (2020) Type: Madagascar, Est foret orientale, sur le Bamarivo près de Sambava, Perrier de la Bathie 18575. (holotype: P P00077483).
- = *Casearia elliptica* var. *macrocarpa* H. Perrier, Mem. Mus. Natl. Hist. Nat. 13. 1940 syn. sec. De Mestier (2020) Type: Madagascar, Centre Massif d'Andringitra, vers 1200 m, Perrier de la Bathie 14439. (holotype: P P00077484; isotypes: L L0010707, P P00077485).
- = *Casearia nigrescens* var. *onivensis* H. Perrier, Mem. Mus. Natl. Hist. Nat. 13. 1940 syn. sec. De Mestier (2020) Type: Madagascar, Centre: Foret d'Andasibe sur l'Onive, vers 900 m d'alt., 1925, Perrier de la Bathie 17050. (syntypes: L L0010708, P P00077479).
- = *Casearia nigrescens* var. *ovata* H. Perrier, Mem. Mus. Natl. Hist. Nat. 13. 1940 syn. sec. De Mestier (2020) Type: Madagascar, Foret d'Analamazoatra, 800 m, Feb 1903, Perrier de la Bathie 4453. (syntypes: L L0010706, P P00077481).
- = *Casearia nigrescens* var. *subtrinervia* H. Perrier, Mem. Mus. Natl. Hist. Nat. 13. 1940 syn. sec. De Mestier (2020) Type: Madagascar, Est (centre): foret d'Analamazoatra, 900 m, foret des cimes, Perrier de la Bathie 4653. (syntypes: L L0010709, P P00077482 not designated).

Distribution (areas). – Madagascar (present)

***Casearia novoguineensis* Valetton in Bull. Dép. Agric. Indes Néerl. 10: 35. 1907. Sec. Sleumer (1955)**

Type: Papua New Guinea, Atasrip 68. (unknown type category: L L0010714 & L0010715).

Distribution (areas). – New Guinea (present)

***Casearia olivacea* Sleumer in Blumea 7: 490. 1954. Sec. Sleumer (1955)**

Type: Papua New Guinea, Central Div., Sogeri region, Forbes Pl. Papuan 415. (paratype:); Papua New Guinea, Fly Riv., 528 miles camp, on low ridge, 80 m, May 1936, Brass 6814. (paratype:); Papua New Guinea, Fly Riv., d'Albertis anno 1877. (paratype: FD); Papua New Guinea, Lake Daviumbu, Middle Fly river, 1936, Brass 7783. (holotype: A A00066550; isotypes: BRI BRI-AQ0342723, L L0010721 & L0010722); Papua New Guinea, Pamer Riv. 2 miles below junction Black Riv., 100 m, Jun 1936, Brass 6931. (paratype:).

Distribution (areas). – New Guinea (present)

***Casearia oreogenes* Sleumer in Blumea 7: 490. 1954. Sec. Sleumer (1955)**

Type: Papua New Guinea, N. E. New Guinea, Morobe Distr., Sattelberg to Wareo, hill woods, 2000-3000 ft, Feb 1936, Clemens 1724. (holotype: L L0010723 & L0010724).

Distribution (areas). – New Guinea (present)

***Casearia pachyphylla* Gilg in Bot. Jahrb. Syst. 55: 288. 1918. Sec. Sleumer (1955)**

Type: Papua New Guinea, Nordöstl. Neu-guinea: Sepikgebiet, Schraderberg, im 15-20 m hohen bemoosten Gebirgswald, 2070 m ü. M., Ledermann 11903. (syntype:); Papua New Guinea, Nordöstl. Neu-guinea: Sepikgebiet, Schraderberg, im 15-20 m hohen bemoosten Gebirgswald, 2070 m ü. M., Ledermann 12213. (syntype:).

Distribution (areas). – New Guinea (present)

***Casearia papuana* Sleumer in Blumea 7: 491. 1954. Sec. Sleumer (1955)**

Type: Papua New Guinea, Dalman, in Agathis forest, 500 m, Kanchira & Hatusima 12100. (paratype:); Papua New Guinea, N. W. New Guinea, Nabire, Bivouac Prao, 30 km inward of Nabire, rainforest, 100 m, Mar 1940, Kanchira & Hatusima 12795. (paratype:); Papua New Guinea, ibid., Ayeryat, in fringing forest on rocky slope, 300 m, Kanchira & Hatusima 12614. (holotypes: A A00066551, BO; isotype: L L0010725); Papua New Guinea, rainforest, 300 m, Kanchira & Hatusima 12732. (paratype:).

Distribution (areas). – New Guinea (present)

***Casearia parhamii* A.C.Sm. in J. Arnold Arbor. 31: 317. 1950. Sec. Smith (1981)**

Type: Fiji, Republic of Fiji, Viti Levu: Tailevu: Waindina Falls, Jun 1936, Parham 25. (holotype: A A00066641).

Distribution (areas). – Fiji (present)

***Casearia parvistipula* Tathana in Thai Forest Bull., Bot. 39: 26. 2011.** Sec. Harwood (2015)

Type: Thailand, Kingdom of, Harwood 2087. (holotype: BKF).

Distribution (areas). – Thailand (present)

***Casearia phanerophlebia* Merr. in Philipp. J. Sci., C 10: 277. 1915.** Sec. Co's Digital Flora of the Philippines. 2011

Type: Philippines, Republic of the, Leyte, Buenavista, near Jaro. In forests, altitude about 500 meters, 30 Jul 1914, Wenzel 979. (syntypes: A A00066574, L L0010726, NY NY00107393).

= *Casearia wenzelii* Merr. & Quisumb. in Philipp. J. Sci. 76(3): 54, 210. 1944 syn. sec. De Mestier (2020) Type: Philippines, Republic of the, 9 Aug 1927, Wenzel 3026. (syntypes: A A00066634, CAS CAS0032666, K K000591466, M M0113078 & M0113079, NY NY00107398).

Distribution (areas). – Philippines (present)

***Casearia philippinensis* Merr. in Philipp. J. Sci., C 10: 329. 1915.** Sec. Co's Digital Flora of the Philippines. 2011

Type: Philippines, Republic of the, Luzon, province of Cagayan, Claveria, Mar 1909, Ramos 7364. (holotype:).

Distribution (areas). – Philippines (present)

***Casearia prismatocarpa* Mast., Fl. Trop. Afr. 2: 494. 1871.** Sec. Breteler (2008)

Type: Equatorial Guinea, Republic of, Rio Muni, Aug 1862, Mann 1750. (lectotype: K K000231390 & K000252710; isolectotypes: L L0010572, P P00493520).

= *Casearia dinklagei* Gilg in Bot. Jahrb. Syst. 40: 511. 1908 syn. sec. De Mestier (2020) Type: Liberia, Republic of, Fishtown, May 1898, Dinklage 1909. (holotype: B lost; isotypes: B 10 0160055, L L0010571).

= *Casearia hexagona* Pierre ex A. Chev., Veg. Utiles Afrique Trop. Franc. 9: 55. 1917 syn. sec. De Mestier (2020) Type: Gabon, Gabonese Republic, Libreville, 1895, Klaine 279. (holotype: P P017839).

= *Casearia calodendron* Gilg ex Engl. in Veg. Erde 3: 590. 1921 syn. sec. De Mestier (2020) Type: Togo, Togolese Republic, Lomé, 1900–1902, Warnecke 452. (holotype: B lost; lectotype: K K000041148).

Distribution (areas). – Angola (present); Benin (present); Cameroon (present); Central African Republic (present); Congo (present); Gabon (present); Ghana (present); Guinea (present); Ivory Coast (present); Liberia (present); Nigeria (present); Sierra Leone (present); Togo (present); Zaire (present)

***Casearia procera* A.C.Sm. in J. Arnold Arbor. 31: 318. 1950.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, Viti Levu: Mba: Western slopes of Mt. Tomanivi (Mt. Victoria), alt. 850-1000 m, 7 Jul 1947, Smith 5119. (holotype: A A00066642; isotypes: BISH BISH1001810, BRI BRI-AQ0342725, K K000591493, NY NY00107400, S S-G-1203, US US00114894).

Distribution (areas). – Fiji (present)

***Casearia pseudoglomerata* Sleumer in Blumea 30: 248. 1985.** Sec. Harwood (2015)

Type: Thailand, Kingdom of, Phuket, Khao Chiang Khrod and Khao Khu Thalang, in wet evergreen forest, to 200 m alt., 7 May 1968, Van Beusekom & Phengklai 609. (holotype: L L0010732; isotypes: C C10012559, K K000591396).

Distribution (areas). – Thailand (present)

***Casearia puberula* Guillaumin in Bull. Mus. Natl. Hist. Nat., sér. 2, 4: 694. 1932.** Sec. Lescot (1980)

Type: New Caledonia, 1908, Le Rat 201. (holotype: P P00641371; isotypes: L L0010733 & L0010734, P P00641372 & P00641373).

Distribution (areas). – New Caledonia (present)

***Casearia pubipes* A.C.Sm. in Pacific Sci. 25: 492. 1971.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, near Navakathuru, Yathata Island (Northern Lau Group), 2 Apr 1968, DA 15553. (holotype: BISH BISH1001811; isotypes: CHR 213522, K K000591501, MASS, SUVA).
Distribution (areas). – Fiji (present)

***Casearia rhynchophylla* Gilg in J. Arnold Arbor. 10: 81. 1929.** Sec. Sleumer (1955)

Type: Papua New Guinea, Ihu, Vailala River, rain forest, 13 Feb 1926, Brass 965. (syntypes: A A00066552, BRI BRI-AQ0342727, L L0010737).
Distribution (areas). – New Guinea (present)

***Casearia richii* A.Gray, U.S. Expl. Exped., Phan. 1: 82. 1854.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, Ovalau, 1840, U. S. Expl. Exped. 47730. (syntypes: GH GH00066643, US00114897).

= *Casearia disticha* A.Gray, U.S. Expl. Exped., Phan. 1. 1854 syn. sec. De Mestier (2020) Type: Fiji, Republic of Fiji, 1840, Wilkes Explor. Exped. s n. (holotype: US US00114856).

= *Alsodeia storckii* Seem. in J. Bot. 2: 75. 1864 syn. sec. De Mestier (2020) ≡ *Rinorea storckii* (Seem.) Melch., Nat. Pflanzenfam., ed. 2, 21: 352. 1925 syn. sec. De Mestier (2020) Type: Fiji, Republic of Fiji, 1860, Stork 867. (syntypes: BM BM000611036, K K000591496).

= *Casearia seemanni* Briq. in Annuaire Conserv. Jard. Bot. Genève 2. 1898 syn. sec. De Mestier (2020) Type: Fiji, Republic of Fiji, Seemann 11. (holotype: L L0010619; isotype: L L2458957).

Distribution (areas). – Fiji (present).

***Casearia rinorcoides* Sleumer in Blumea 7: 491. 1954.** Sec. Sleumer (1954)

Type: Papua New Guinea, Geelvink Bay, Paterna, 40 km inward of Nabire, rare, 300 m, R. Kanehira & S. Hatusima 11955. (holotype: A 00066553; isotype: BO).

Distribution (areas). – New Guinea (present)

***Casearia ripicola* Sleumer in Blumea 7: 492. 1954.** Sec. Sleumer (1955)

Type: Papua New Guinea, 9 km N. E. Habbema Lake, second growth forest on moist soil, 2700 m, Sep 1933, Brass 4911. (paratype:); Papua New Guinea, N. W. New Guinea, Bele Riv., 18 km NE of Habbema Lake, 2200 m camp, 1938, Brass 11544. (holotype: L L0010739; isotypes: A A00066554, BO, BRI BRI-AQ0342729); Papua New Guinea, N. W. New Guinea. Bele Riv., 18 km N. E. of Habbema Lake 2200 m camp, common in second growth rainforest, Nov 1983, Brass 11356. (paratype:).

Distribution (areas). – New Guinea (present)

***Casearia rubescens* Dalzell in Hooker's J. Bot. Kew Gard. Misc. 4: 108. 1852.** Sec. Mitra (1993)

Type: India, Republic of, Mumbai, Maharashtra Bombay, Dalzell s n. (holotype: K K000591430).

= *Casearia rubescens* var. *gamblei* N.Mukh. in J. Bombay Nat. Hist. Soc. 69: 393. 1972 syn. sec. De Mestier (2020) Type: India, Republic of, South India, evergreen forest of Pirmed 3500', Bourdillon 181. (holotype: CAL).

Distribution (areas). – India (present)

***Casearia rugulosa* Blume in Mus. Bot. 1: 255. 1851.** Sec. Sleumer (1955)

Type: Indonesia, Republic of, Borneo, unknown s n. (holotype: L L0010741).

= *Casearia minutidens* Merr. in Philipp. J. Sci., C 11: 94. 1916 syn. sec. De Mestier (2020) Type: Malaysia, 8 Nov 1894, Hose 407. (syntypes: BM BM000624327, K K000912643, L L0010742 & L0010743).

= *Casearia pubescens* Merr. in Philipp. J. Sci., C 11: 95. 1916 syn. sec. De Mestier (2020) Type: Malaysia, Nov 1894, Hose 454. (syntypes: BM BM000624304, G G00355929, K K000591395, L L0010911, L0010744 & L0010745).

Distribution (areas). – Borneo (present)

***Casearia samoensis* Whistler, Rainforest Trees Samoa: 189. 2004.** Sec. Whistler (2004)

Distribution (areas). – Samoa (present)

***Casearia silvana* Schltr. in Bot. Jahrb. Syst. 39: 198. 1906.** Sec. Lescot (1980)

Type: New Caledonia, 1902, Schlechter 15114. (holotype: FI FI014618; isotypes: BR BR0000006912031, E E00279753, HBG HBG515737, K K000591485, P P00641364, S S-G-1204); New Caledonia, Schlechter 15076. (syntypes: BM BM000624325, K K000591484, L L0010752, P00641362); New Caledonia, Schlechter 15370. (syntypes: BR BR0000006913205, G G00355968); Papua New Guinea, 1902, Schlechter 15375. (syntype: K K000591486).

= *Melistorum distichum* J.R.Forst. & G.Forst., Char. Gen. Pl.: 144. 1776 syn. sec. De Mestier (2020) Type: New Caledonia, Forster 10. (holotype: S S06-3724).

= *Samyda polyandra* Willd., Sp. Pl., ed. 4, 2: 626. 1799, nom. superfl. syn. sec. De Mestier (2020)

= *Casearia melistorum* Spreng., Syst. Veg. 2: 354. 1825, nom. superfl. syn. sec. De Mestier (2020)

= *Casearia melistorum* var. *germainii* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 64. 1898 syn. sec. De Mestier (2020) Type: New Caledonia, Ile du Pin, Germain 16. (holotype: G G00355944; isotypes: L L0010754, P P00641374).

= *Casearia melistorum* var. *minor* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 64. 1898 syn. sec. De Mestier (2020) Type: New Caledonia, 1867, Deplanche 35. (syntype: G G00355943); New Caledonia, Gatope, 1861, Vieillard 339. (syntypes: BM BM000624326, G G00355952, MEL MEL2475548, P P00641375 & P00641376); New Caledonia, Vieillard 1168. (syntype: P P05114142, P05114143, P04819082 & P04819083); New Caledonia, Vieillard 1169. (syntypes: BR BR0000006912543, P P05114139, P05114140, P05114141, P05114144, P05114145, P05114146, P051141347 & P04819058); New Caledonia, Vieillard 1170. (syntype: P P05114148, P05114149, P05114150 & P04819084).

= *Casearia silvana* var. *oubatchensis* Schltr. in Bot. Jahrb. Syst. 39: 198. 1906 syn. sec. De Mestier (2020) Type: New Caledonia, Nord-Bezirk: in den Wäldern der Berge bei Oubatche, 600 m ü. M., Dec 1902, Schlechter 15520. (isotypes: BM BM000624322, E E00279751, G G00355946 & G00355976, HBG HBG515738, K K000591483, L L0010753, M M0113073, P P00641369; unknown type categorys: BR BR0000006911782, S S-G-1205).

= *Casearia comptonii* Baker f. in J. Linn. Soc., Bot. 45: 319. 1921 syn. sec. De Mestier (2020) Type: New Caledonia, 1 Dec 1914, Compton 2290. (holotype: BM BM000624319; isotypes: L L0010755, P P00641381).

Distribution (areas). – New Caledonia (present)

***Casearia* sp.** Sec. De Mestier (2020)

= *Casearia brevipes* Merr. in Philipp. J. Sci., C 9: 326. 1914, nom. illeg. syn. sec. De Mestier (2020) Type: Philippines, Republic of the, along streams, 31 Aug 1912, Reillo 16113. (.)

Notes. – Type specimen not seen.

Distribution (areas). – Philippines (present)

***Casearia stapfiana* Ridl. in Bull. Misc. Inform. Kew 1938: 110. 1938.** Sec. Sleumer (1955)

Type: Malaysia, Sarawak, Haviland & Hose 3581. (paratype:); Malaysia, Sarawak, Kuching, 1892, Haviland 1669. (syntypes: K000591393, L L0010760).

Distribution (areas). – Borneo (present)

***Casearia stenophylla* A.C.Sm. in J. Arnold Arbor. 31: 318. 1950.** Sec. Smith (1981)

Type: Fiji, Republic of Fiji, Vanua Levu: Mathuata: Seanggangga Plateau in drainage of Korovuli River, vicinity of Natua, alt. 100-200 m, 28 Nov 1947, Smith 6701. (holotype: A A00066644; isotype: US US00114903).

Distribution (areas). – Fiji (present)

***Casearia stipitata* Mast., Fl. Trop. Afr. 2: 493. 1871.** Sec. African Plant Database. 2012

Type: Nigeria, Federal Republic of, Aboh, Barter 322. (holotype: K K000231403).

= *Casearia zenkeri* Gilg in Bot. Jahrb. Syst. 40: 512. 1908 syn. sec. De Mestier (2020) Type: Cameroon, United Republic of, Süd Kamerun: am Lokundjeufer, ein Baum mit überhängenden Zeigen, Zenker 2028. (holotype: B lost; isotypes: B 10 0160036, BM BM000624312, G G00013781 & G00013792, GOET GOET003810, HBG HBG515732, K K000231399, L L0010761, M M0113075, P P00412991, P00412992 & P00412993, S S10-12137, WAG WAG0003879).

Distribution (areas). – Benin (present); Cameroon (present); Central African Republic (present); Congo (present); Gabon (present); Ivory Coast (present); Nigeria (present); Zaire (present)

***Casearia tardieuae* Lescot & Sleumer in Adansonia, n.s., 10: 293. 1970.** Sec. Yang Qiner (2007)

Type: Viet Nam, Socialist Republic of, (Sud), prov. dee Khank Hoa: ile de Tre, près de Nba Trang, Poilane 3098. (holotype: P; isotype: L L0010767).

= *Casearia calciphila* C.Y.Wu & Y.C.Huang ex S.Y.Bao in Acta Bot. Yunnan. 5: 375. 1983 syn. sec. De Mestier (2020)

Distribution (areas). – China South-Central (present); China Southeast (present); Laos (present); Vietnam (present)

***Casearia thwaitesii* Briq. in Annuaire Conserv. Jard. Bot. Genève 2: 62. 1898.** Sec. Mitra (1993)

≡ *Casearia coriacea* Thwaites, Enum. Pl. Zeyl.: 20. 1858, nom. illeg. syn. sec. De Mestier (2020). Type: Sri Lanka, Democratic Socialist Republic of, Ceylon, Thwaites 465. (isotypes: BM BM000948322, MEL MEL2474912; syntypes: FR FR0036170, L L0010769; unknown type category: BR BR0000005103676).

= *Casearia varians* var. *obovata* Thwaites, Enum. Pl. Zeyl.: 20. 1858 syn. sec. De Mestier (2020) Type: Sri Lanka, Democratic Socialist Republic of, Ceylon, Thwaites C. P. 1247. (syntype:); Sri Lanka, Democratic Socialist Republic of, Ceylon, Thwaites C.P. 1217. (syntypes: BR BR0000005104000, FR FR0036169, GH GH00066494, L L0010770, MEL MEL2475524).

Distribution (areas). – Sri Lanka (present)

***Casearia tinifolia* Vent., Choix Pl.: t. 47. 1808.** Sec. Sleumer (1980)

≡ *Samyda tinifolia* (Vent.) Poir., Encycl., Suppl. 5: 32. 1817 syn. sec. De Mestier (2020) ≡ *Chetocrater tinifolia* (Vent.) Raf., Sylva Tellur.: 149. 1838 syn. sec. De Mestier (2020). Type: Mauritius, Delahaye anno 1797. (holotype: G G00165542; isotypes: K K000231382, L L0010771).

Distribution (areas). – Mauritius (native: formerly native)

***Casearia tomentosa* Roxb., Fl. Ind. 2: 421. 1832.** Sec. de Mestier (2020)

***Casearia tomentosa* subsp. *reducta* Verdc., Revis. Handb. Fl. Ceylon 10: 234. 1996.** Sec. De Mestier (2020)

Distribution (areas). – Sri Lanka (present)

***Casearia tomentosa* var. *tomentosa*.** Sec. De Mestier (2020)

≡ *Guidonia tomentosa* (Roxb.) Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46: 92. 1877 syn. sec. De Mestier (2020)

= *Anavinga lanceolata* Lam., Encycl. 1: 148. 1783 syn. sec. Mitra (1993)

= *Casearia elliptica* Willd., Sp. Pl., ed. 4, 2: 628. 1799, nom. superfl. syn. sec. Mitra (1993)

= *Bedousia malabarica* Dennst., Schlüssel Hortus Malab.: 31. 1818 syn. sec. De Mestier (2020)

= *Casearia ovata* Roxb., Fl. Ind. 2: 420. 1832, nom. illeg. syn. sec. De Mestier (2020)

= *Casearia cheela* Royle in Ill. Bot. Himal. Mts.: 170. 1835 syn. sec. De Mestier (2020)

= *Casearia pauciflora* Royle in Ill. Bot. Himal. Mts.: 170. 1835 syn. sec. De Mestier (2020)

= *Casearia piscidia* Buch.-Ham. ex Royle in Ill. Bot. Himal. Mts.: 170. 1835 syn. sec. De Mestier (2020)

= *Samyda canziala* Buch.-Ham. in Trans. Linn. Soc. London 17: 225. 1835 syn. sec. De Mestier (2020) ≡ *Guidonia canziala* (Buch.-Ham.) Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46: 92. 1877 syn. sec. De Mestier (2020) – *Casearia canziala* (Buch.-Ham.) Wall. in Rep. Calcutta Bot. Gard.: 31. 1840, nom. nud. syn. sec. De Mestier (2020) Type: India, Republic of, Habora, 21 Mar 1803, Hamilton s n. (holotype: K).

= *Bedousia aromatica* Raf., Sylva Tellur.: 11. 1838 syn. sec. De Mestier (2020)

= *Casearia anavinga* Dalzell & A.Gibson, Bombay Fl.: 11. 1861 syn. sec. De Mestier (2020)

– *Samyda bazanica* Buch.-Ham. ex Wall., Numer. List: 7192 C. 1832, nom. inval. syn. sec. De Mestier (2020) Type: India, Republic of, Goyalpara, Jul 1808, Hamilton s n. (holotype: K).

– *Samyda piscidia* Buch.-Ham. ex Wall., Numer. List: 7193 D. 1832, nom. inval. syn. sec. De Mestier (2020) Type: India, Republic of, Karik Kal, 10 Apr 1811, Hamilton s n. (lectotype: K); India, Republic of, Sukanazar, 24 Mar 1810, Hamilton s n. (syntype: K).

Distribution (areas). – Bangladesh (present); India (present); Myanmar (present)

***Casearia trivalvis* (Blanco) Merr., Sp. Blancoan.: 275. 1918.** Sec. Sleumer (1955)

≡ *Samyda trivalvis* Blanco, Fl. Filip.: 374. 1837 syn. sec. Co's Digital Flora of the Philippines. 2011. Type: Philippines, Republic of the, Exposed places, 100 m, Los Banos, Laguna Prov., Luzon, 25 Mar 1915, Mabesa 2. (neotype: US).

- = *Casearia solida* Merr. in Publ. Bur. Sci. Gov. Lab. 35: 46. 1906 ["1905"] syn. sec. Sleumer (1955) Type: Philippines, Republic of the, Luzon, Province of Bataan, Mount Mariveles, Mar 1905, Meyer 2810. (syntypes: NY NY00107397, SING SING0054149, US US00114901).
- = *Casearia zschokkei* Elmer in Leafl. Philipp. Bot. 8: 3083. 1919 syn. sec. Sleumer (1955) Type: Philippines, Republic of the, Los Banos (Mt. Maquiling), Province of Laguna, Luzon, Sep 1919, Mabesa 555. (syntype: NY NY00107399).
- = *Gelonium pinatubense* Elmer in Leafl. Philipp. Bot. 9: 3186. 1934 syn. sec. De Mestier (2020) ≡ *Suregada pinatubensis* (Elmer) Croizat, Bull. Jard. Bot. Buitenzorg, sér. 3., 17: 216. 1942 syn. sec. Sleumer (1955) Type: Philippines, Republic of the, Mt. Pinatubo, Zambales Mountains, Province of Pampanga, Luzon, May 1927, Elmer 21966. (syntype: G G00441603); Philippines, Republic of the, Mt. Pinatubo, Zambales Mountains, Province of Pampanga, Luzon, May 1927, Elmer 22032. (syntype: L L0010772).

Distribution (areas). – Philippines (present)

***Casearia tuberculata* Blume in Mus. Bot. 1: 254. 1851.** Sec. Co's Digital Flora of the Philippines. 2011

= *Casearia hydnocarpoides* Quisumb. in Philipp. J. Sci. 76(3): 54. 1944 syn. sec. De Mestier (2020)

Distribution (areas). – Jawa (present); Malaya (present); Philippines (present); Sumatera (present); Thailand (present)

***Casearia urophylla* Gilg in Bot. Jahrb. Syst. 55: 287. 1918.** Sec. Sleumer (1955)

Type: Papua New Guinea, Nordöstl. Neu-Guinea: beim Standlager am Aprilfluß, in gut gangbarem Urwald mit viel Baumfarn, 60 m ü. M., Ledermann 8836. (syntypes: K K000591666, SING SING0083822).

Distribution (areas). – New Guinea (present)

***Casearia vareca* Roxb., Fl. Ind. 2: 418. 1832.** Sec. Mitra (1993)

≡ *Guidonia vareca* (Roxb.) Baill. ex Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46: 92. 1877 syn. sec. De Mestier (2020)

Distribution (areas). – Assam (present); Bangladesh (present); East Himalaya (present); Myanmar (present)

***Casearia velutina* Blume in Mus. Bot. 1: 253. 1851.** Sec. de Mestier (2020)

Type: Indonesia, Republic of, Java, unknown s n. (unknown type categorys: K K000591392, L L0010784, L L0010786 & L0010787, MEL MEL2458694, S S-G-1206).

= *Casearia propinqua* Blume in Mus. Bot. 1: 253. 1851 syn. sec. De Mestier (2020)

= *Casearia balansae* Gagnep., Notul. Syst. (Paris) 3: 243. 1916 syn. sec. Yang Qiner (2007) Type: Viet Nam, Socialist Republic of, Tonkin: environ de Tu-phap, Balansa 3332. (syntype: G G00165536 & G00165534).

= *Casearia balansae* var. *cuneifolia* Gagnep., Notul. Syst. (Paris) 3: 244. 1916 syn. sec. Yang Qiner (2007) Type: Viet Nam, Socialist Republic of, Tonkin: environs de Tu-phap, Balansa 3331. (syntype: G G00165535 & G00165537).

= *Casearia villilimba* Merr. in Philipp. J. Sci. 23: 254. 1923 syn. sec. De Mestier (2020)

= *Casearia multipunctata* Merr., Pap. Michigan Acad. Sci. 19: 174. 1934 ["1933"] syn. sec. De Mestier (2020)

= *Casearia petelotii* Merr. in J. Arnold Arbor. 19: 57. 1938 syn. sec. Yang Qiner (2007) Type: Viet Nam, Socialist Republic of, IndoChina: Tonkin, Chapa, Apr 1936, Petelot 5930. (syntypes: A A00066491, L L0010783, NY NY00107377, US US00114890).

= *Casearia balansae* var. *subglabra* S.Y.Bao in Acta Bot. Yunnan. 5: 377. 1983 syn. sec. Yang Qiner (2007)

Distribution (areas). – China South-Central (present); Hainan (present); Jawa (present); Laos (present); Malaya (present); Sumatera (present); Thailand (present); Vietnam (present)

***Casearia velutinoso* Ridl. in J. Straits Branch Roy. Asiat. Soc. 75: 34. 1917.** Sec. Sleumer (1955)

Type: Malaysia, Peninsular Malaysia Perak, 1896, Ridley 7972. (syntypes: K K000591417, SING SING0054331); Malaysia, Perak. Gunnong Keledang, 1898, Ridley 9529. (lectotype: K K000591416; isolectotypes: L L0010791, SING SING0054150).

Distribution (areas). – Borneo (present); Malaya (present)

***Casearia virescens* Pierre ex Gagnep., Notul. Syst. (Paris) 3: 245. 1916.** Sec. Pham Hoang Ho

Type: Viet Nam, Socialist Republic of, Tonkin: vallée de Lankok (mont Bavi), Balansa 4200. (syntypes: K K000591397, L L0010792 & L0010793).

Distribution (areas). – Vietnam (present)

***Casearia wynadensis* Bedd. in Icon. Pl. Ind. Or. 1: 34. 1869.** Sec. Mitra (1993)
Distribution (areas). – India (present)

***Casearia yatesii* Sleumer in Blumea 7: 492. 1954.** Sec. Sleumer (1955)
Type: Indonesia, Republic of, Sumatra. Eastcoast, Asahan, Gurach Batu, Yates 2116. (holotype: L L0010794; isotype: BRI BRI-AQ0209137).
Distribution (areas). – Sumatera (present)

***Casearia zeylanica* (Gaertn.) Thwaites, Enum. Pl. Zeyl.: 19. 1858.** Sec. de Mestier (2020)
≡ *Vareca zeylanica* Gaertn., Fruct. Sem. Pl. 1: 290, t. 60. 1788 syn. sec. De Mestier (2020). Type: Sri Lanka, Democratic Socialist Republic of, Thwaites c. p. 415. (syntypes: BR BR0000013479619, FR FR0036174, L L0793718).
= *Casearia esculenta* Roxb., Fl. Ind. 2: 422. 1832 syn. sec. De Mestier (2020) ≡ *Guidonia esculenta* (Roxb.) Baill. in Traité Bot. Méd. Phan. 2: 827. 1884 syn. sec. De Mestier (2020)
= *Casearia laevigata* Dalzell in Hooker's J. Bot. Kew Gard. Misc. 4: 108. 1852 syn. sec. De Mestier (2020)
= *Casearia varians* var. *minor* Thwaites, Enum. Pl. Zeyl.: 19. 1858 syn. sec. De Mestier (2020) ≡ *Casearia ovata* var. *minor* (Thwaites) N.Mukh. in Bull. Bot. Surv. India 14: 184. 1975 ["1972"] syn. sec. De Mestier (2020) Type: Sri Lanka, Democratic Socialist Republic of, Thwaites C. P. 3365. (syntypes: BM BM000948264, BR BR0000005105489, FR FR0036172, GH GH00066493, L L0010799, MEL MEL2475525).
= *Casearia varians* var. *ovata* Thwaites, Enum. Pl. Zeyl.: 19. 1858 syn. sec. De Mestier (2020) Type: Sri Lanka, Democratic Socialist Republic of, Thwaites C. P. 2604. (syntypes: BM BM000948268, K K000591419 & K000591420, L L0010796); Sri Lanka, Democratic Socialist Republic of, Thwaites C. P. 2657. (syntypes: BR BR0000013346584 & BM000948263, FR FR0036173, GH GH00066492, K K000591422, MEL MEL2475523).
= *Casearia esculenta* var. *angusta* C.B.Clarke, Fl. Brit. India 2: 592. 1879 syn. sec. De Mestier (2020) Type: Sri Lanka, Democratic Socialist Republic of, Ceylon, Thwaites 2603. (holotype: PDA; isotypes: BM BM000948262, L L0010798).
Distribution (areas). – India (present); Myanmar (present); Sri Lanka (present)

Unresolved. Sec. De Mestier (2020)

***Samyda viridiflora* Poir., Encycl. 6: 493. 1805, nom. illeg.** Sec. de Mestier (2020)

***Casearia anavinga* Pers., Syn. Pl. 1: 485. 1805, nom. illeg.** Sec. De Mestier (2020)
syn: *C. graveolens* (sec. Kew) but no further references

***Casearia astyla* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 36(II): 608. 1863.** Sec. De Mestier (2020)
Flora of British India 2:595. 1879
Type: India, Republic of, Roxburgh. (unspecified: KW KW001000608).
No further mention

***Casearia guidonia* (L.) Benth. in J. Proc. Linn. Soc., Bot. 5(Suppl. 2): 89. 1861.** Sec. De Mestier (2020)
Same as *C. guidonia* Benth., synonym of *C. spinescens*? Excluded by Sleumer (1980)

***Casearia guineensis* G.Don, Gen. Hist. 2: 53. 1832.** Sec. De Mestier (2020)
Sleumer, 1971. Probably not *Casearia*.

***Casearia impunctata* Hook. & Arn. in Bot. Beechey Voy.: 61. 1832.** Sec. De Mestier (2020)
Probably not *Casearia*, lack the pellucid dots

***Casearia micrantha* G.Don, Gen. Hist. 2: 52. 1832.** Sec. De Mestier (2020)
No further mention. No type.

***Casearia ramiflora* Seem. in Bot. Voy. Herald: 98. 1853.** Sec. De Mestier (2020)
protologue cite it as *C. ramiflora* Vahl

***Casearia viridiflora* Lam.** Sec. De Mestier (2020)
No further mention

***Crateria capitata* Pers., Syn. Pl. 1: 485. 1805.** Sec. De Mestier (2020)
No further mention

***Laetia parviflora* Spreng., Syst. Veg. 2: 609. 1825.** Sec. De Mestier (2020)
application of the name enigmatic (no specimen)
Notes. – Unresolved species: no further mention in Flora do Brasil, or Sleumer, or Samarakoon.

***Laetia scabra* Spreng., Syst. Veg. 2: 609. 1825.** Sec. De Mestier (2020)
Doubtful species (sec. Liogier, 1981)
Distribution (areas). – Dominican Republic (present)

***Laetia serrulata* Ruiz & Pav. ex Pritz. in Icon. Bot. Index: 615. 1855.** Sec. De Mestier (2020)
Unresolved, no mention in Flora, Sleumer or Samarakoon
Notes. – Unresolved, no mention of it in Flora, Samarakoon or Sleumer.

***Laetia serrulata* Ruiz & Pav. in Anales Inst. Bot. Cavanilles 17(1): 398. 1959.** Sec. De Mestier (2020)
Unresolved, no mention in Flora, Sleumer or Samarakoon
Notes. – Unresolved, no mention of it in Flora, Samarakoon or Sleumer.

***Lindleya mollis* Kunth, Nov. Gen. Sp. 5. 1823.** Sec. De Mestier (2020)
Protologue do not mention that species.

***Melistaureum arboreum* Hasselt ex Blume in Mus. Bot. 1. 1850.** Sec. De Mestier (2020)
No protologue

***Samyda comocladifolia* (Vent.) Poir., Encycl., Suppl. 5: 32. 1817.** Sec. De Mestier (2020)
Not cited in the protologue

***Samyda decurrens* Spreng., Syst. Veg. 2: 354. 1825, not defined.** Sec. De Mestier (2020)
Sprengel's diagnosis suggests that this name surely does not represent a true *Samyda*. The application of the name must remain enigmatic.
Notes. – Application of the name enigmatic (specimen unknown). sec. Kiger, 1984.
Distribution (areas). – Brazil South (present)

***Samyda grandiflora* Spreng., Syst. Veg. 2: 354. 1825.** Sec. De Mestier (2020)
Unresolved, no specimen (sec. Kiger, 1984)
Notes. – Application of the name enigmatic (specimen unknown). sec. Kiger, 1984.

***Samyda lucida* Steud. in Nomencl. Bot., ed. 2, 2: 509. 1841.** Sec. De Mestier (2020)
Unresolved, no specimen (sec. Kiger, 1984)
Notes. – Application of the name enigmatic (specimen unknown). sec. Kiger, 1984.

***Samyda macrophylla* Willd., Sp. Pl., ed. 4, 2: 625. 1799.** Sec. De Mestier (2020)
Synonym of *Pisonia grandis*, sec. Kiger, 1984

Type: India, Republic of, Klein sn. (B -W 08340 -01 0).

Samyda nobilis W.Bull, Nursery Cat. (William Bull) 60: 30. 1871. Sec. De Mestier (2020)

Unknwown. No mention anywhere.

Distribution (areas). – Brazil South (present)

Index to scientific names

- Alsodeia storckii* Seem. 201
Ampelocera crenulata Urb. 179
Anavinga comocladifolia (Vent.) Raf. 165
Anavinga fuliginosa Blanco 192
Anavinga lanceolata Lam. 203
Anavinga ovata Lam. 193
Anavinga parvifolia Lam. 168
Anavinga samyda C.F.Gaertn. 182
Antigona serrata Vell. 173
Athenaea guianensis (J.F.Gmel.) Aubl. 172
Azara umbellata C.Presl 162
Bedousia aromatica Raf. 203
Bedousia malabarica Dennst. 203
Bigelovia brasiliensis Spreng. 177
Carpotroche parvifolia J.F.Macbr. 175
Casearia aculeata 160
Casearia aculeata Jacq. 160
Casearia aculeata var. *tafallana* (Eichler) J.F.Macbr. 161
Casearia acuminata DC. 161
Casearia adamantium Cambess. 168
Casearia adiantoides Sleumer 186
Casearia adstringens Mart. 168
Casearia aequilateralis Merr. 197
Casearia affinis Gardner 182
Casearia agusanensis Elmer 195
Casearia alba A.Rich. 160
Casearia albicans Wall. ex C.B.Clarke 186
Casearia albicaulis Rusby 168
Casearia altiplanensis Sleumer 162
Casearia americana (L.) T. Samar. & M.H. Alford 162
Casearia amplexans Sleumer 187
Casearia amplissima Tul. 199
Casearia anavinga Dalzell & A.Gibson 203
Casearia anavinga Pers. 205
Casearia andamanica King 187
Casearia angiensis Sleumer 187
Casearia angustata Teijsm. & Binn. 194
Casearia angustifolia A.C.Sm. 187
Casearia anisophylla Gilg 187
Casearia annamensis (Gagnep.) Lescot & Sleumer 187
Casearia anosyensis Appleq. & Gates, M.T. 187
Casearia aquifolia C.Wright 162
Casearia arborea (Rich.) Urb. 162
Casearia arborea subsp. *arborea* 162
Casearia arborea subsp. *occidentalis* J.E.Gut. 164
Casearia archboldiana Sleumer 187
Casearia arfakensis Sleumer 187
Casearia arguta Kunth 164
Casearia astyla Turcz. 205
Casearia athenaea (Aubl.) Schreb. ex Forsyth f. 172
Casearia atlantica Sleumer 164
Casearia attenuata Rusby 183
Casearia auriculata Sleumer 187
Casearia austroafricana A.E.van Wyk, R.G.C.Boon & Retief 188
Casearia avellana Miq. ex Eichler 161
Casearia bahamensis Urb. 177
Casearia bahiensis Sleumer 164
Casearia balansae Gagnep. 204
Casearia balansae var. *cuneifolia* Gagnep. 204
Casearia balansae var. *subglabra* S.Y.Bao 204
Casearia bangii Rusby 163
Casearia banquitana E.H.L.Krause 166
Casearia banquitana var. *laevis* (Standl.) I.M.Johnst. 167
Casearia barberi Mast. 188
Casearia bartlettii Lundell 164
Casearia battiscombei R.E.Fr. 188
Casearia belizensis Standl. 164
Casearia benthamiana Miq. 182
Casearia berberoidea Rusby 161
Casearia berteriana Turcz. 160
Casearia bicolor Urb. 164
Casearia bissei J.E.Gut. 165
Casearia blanchetiana Miq. 185
Casearia boliviana Briq. 161
Casearia bonairensis Bold. 185
Casearia borneensis Merr. 189
Casearia bourdillonii Mukh. 189
Casearia bracteifera Sagot 165
Casearia brasiliensis Eichler 163
Casearia brassii Sleumer 188
Casearia brevipes Benth. 180
Casearia brevipes Merr. 202
Casearia brideliifolia Sleumer 188
Casearia brunneostriata Gilg 189
Casearia buelowii Whistler 189
Casearia bule Gilg 188
Casearia cajambrensis Cuatrec. 165

- Casearia calciphila* C.Y.Wu & Y.C.Huang ex S.Y.Bao 203
Casearia calodendron Gilg ex Engl. 200
Casearia calva Craib 189
Casearia cambessedesii Eichler 185
Casearia cambessedesii var. *angustifolia* Eichler 163
Casearia cambessedesii var. *parvifolia* Eichler 163
Casearia camporum Sprague 175
Casearia canziana (Buch.-Ham.) Wall. 203
Casearia capitata (Ruiz & Pav.) Pers. 162
Casearia capitellata Blume 189
Casearia carpinifolia Benth. 183
Casearia carrii Sleumer 189
Casearia catharinensis Sleumer 165
Casearia caudata Uittien 183
Casearia cauliflora Volkens 189
Casearia celastroides Klotzsch ex Sleum. 186
Casearia celtidifolia Kunth 185
Casearia celtidifolia Poepp. ex Eichler 186
Casearia championii Thwaites 189
Casearia cheela Royle 203
Casearia chirindensis Engl. 188
Casearia chlorophoroidea Rusby 183
Casearia cinerea Turcz. 194
Casearia clarkei King 189
Casearia clarkei var. *clarkei* 189
Casearia clarkei var. *kunstleri* (King) Ridl. 189
Casearia clausseniana Miq. 177
Casearia clutiifolia Blume 190
Casearia combaymensis Tul. 165
Casearia commutata Briq. 177
Casearia comocladifolia Vent. 165
Casearia completa (Jacq.) T. Samar. & M.H. Alford 166
Casearia comptonii Baker f. 202
Casearia condorensis Pierre ex Gagnep. 191
Casearia confertiflora Merr. 195
Casearia congensis Gilg 190
Casearia contermina Miq. 195
Casearia contracta Urb. 184
Casearia cordillerana Cuatrec. 175
Casearia coriacea (Griseb.) Eichler 162
Casearia coriacea Thwaites 203
Casearia coriacea Vent. 190
Casearia coriifolia Lescot & Sleumer 190
Casearia coronata Standl. & L.O.Williams 166
Casearia corymbosa Kunth 166
Casearia corymbulosa (Spruce ex Benth.) T. Samar. & M.H. Alford 167
Casearia costulata Jessup 190
Casearia cotticensis Uittien 167
Casearia crassinervis Urb. 167
Casearia crassipes A.C.Sm. 190
Casearia crenata Merr. 194
Casearia cubensis Urb. 180
Casearia cuspidata Blume 190
Casearia dallachyi F.Muell. 191
Casearia decandra Jacq. 167
Casearia densifolia Elmer 192
Casearia dentata DC. 160
Casearia deplanchei Sleumer 191
Casearia dinklagei Gilg 200
Casearia disticha A.Gray 201
Casearia dodecandra (Jacq.) T. Samar. & M.H. Alford 168
Casearia dolichanthera T. Samar. & M.H. Alford 169
Casearia dolichophylla Standl. 166
Casearia draganae M.H.Alford 169
Casearia dubia Moc. & Sessé ex DC. 166
Casearia duckeana Sleumer 169
Casearia ehrenbergiana Urb. 170
Casearia eichleriana Sleumer 170
Casearia ekmanii Sleumer 182
Casearia elegans Standl. 170
Casearia elliptica f. *elongata* H. Perrier 199
Casearia elliptica Tul. 199
Casearia elliptica var. *macrocarpa* H. Perrier 199
Casearia elliptica Willd. 203
Casearia elliptifolia Merr. 197
Casearia emarginata C.Wright ex Griseb. 170
Casearia engleri Gilg 191
Casearia eriophora C.Wright ex Griseb. 179
Casearia erythrocarpa Sleumer 191
Casearia esculenta Roxb. 205
Casearia esculenta var. *angusta* C.B.Clarke 205
Casearia espiritosantensis R.Marquete & Mansano 170
Casearia euphlebia Merr. 191
Casearia fallax Miq. 172
Casearia fasciculata (Ruiz & Pav.) Sleumer 170
Casearia fasciculata Bojer 190
Casearia ferruginea Briq. 179
Casearia ferruginea Briq. ex Glaz. 179
Casearia fissistipula A.C.Sm. 191
Casearia flavovirens Blume 191
Casearia flexicaulis K.Schum. 191
Casearia flexula Ridl. 192
Casearia flexuosa Craib 192
Casearia flexuosa Ridl. 192
Casearia floribunda Briq. 168
Casearia fockeana Miq. 174
Casearia forbesii Baker f. 191
Casearia formosa Urb. 182
Casearia fragilis Vent. 190
Casearia fuliginosa (Blanco) Blanco 192
Casearia gallifera Tathana 192
Casearia gambiana Breteler 192
Casearia gelonioides (Baill.) Warb. 190
Casearia gentlei Lundell 167
Casearia gigantifolia Slooten 192
Casearia glaberrima Uittien 163
Casearia glabra Roxb. 192
Casearia glabrata Blume 194
Casearia gladiiformis Mast. 193
Casearia glauciramea Elmer 192
Casearia glaziovii Briq. 163
Casearia globifera Gilg 193
Casearia glomerata f. *pubinervis* How & Ko 193

- Casearia glomerata* Roxb. 193
Casearia glomerata var. *sikkimensis* (N.Mukh.) R.C.Srivast. 193
Casearia gonocarpa Miq. 194
Casearia gossypiosperma Briq. 171
Casearia grandiflora Cambess. 171
Casearia grandiflora var. *hypoleuca* (Mart.) Eichler 171
Casearia grandiflora var. *obtusifolia* Eichler 171
Casearia grandiflora var. *pauciflora* Eichler 171
Casearia grandifolia Miq. 191
Casearia graveolens Dalzell 193
Casearia graveolens var. *lintsangensis* S.Y.Bao 193
Casearia grayi Jessup 193
Casearia grewiiifolia var. *cinerea* (Turcz.) Sleumer 194
Casearia grewiiifolia var. *deglabrata* Koord. & Valeton 194
Casearia grewiiifolia var. *gelonioides* (Blume) Sleumer 194
Casearia grewiiifolia var. *grewiiifolia* 195
Casearia grewiiifolia var. *hexagona* (Decne.) Govaerts 194
Casearia grewiiifolia var. *insularis* (Vasudeva Rao & Chakrab.) Chakrab. & M.Gangop. 195
Casearia grewiiifolia Vent. 194
Casearia grisebachii Briq. 162
Casearia guantanamensis Vict. 165
Casearia guevarana Cast.-Campos & M.E.Medina 171
Casearia guianensis (Aubl.) Urb. 171
Casearia guianensis var. *rafflesioides* Croat 161
Casearia guianensis var. *stjohnii* (I.M.Johnst.) Croat 181
Casearia guidonia (L.) Benth. 205
Casearia guidonia (Sw.) Lundell 173
Casearia guidonia Benth. 180
Casearia guineensis G.Don 205
Casearia halmaherensis Slooten 195
Casearia hamiltonii Wall. 193
Casearia harmadiana Pierre ex Gagnep. 192
Casearia hassleri Briq. 161
Casearia herbert-smithii Rusby 183
Casearia hexagona Decne. 194
Casearia hexagona Pierre ex A. Chev. 200
Casearia hexagona var. *gelonioides* Blume 194
Casearia hintonii Lundell 170
Casearia hirsuta Sw. 172
Casearia hirsuta var. *glabrata* DC. 160
Casearia hirta Sw. 160
Casearia hirtella Hosok. 195
Casearia holtzii Gilg 193
Casearia hosei Merr. 195
Casearia hostmanniana Steud. ex Griseb. 163
Casearia hydnocarpoides Quisumb. 204
Casearia hypoleuca Mart. 171
Casearia icosandra Planch. & Triana ex Hemsl. 173
Casearia ilicifolia Vent. 172
Casearia impressinervia Merr. 196
Casearia impunctata Hook. & Arn. 205
Casearia inaequalis Hutch. & Dalziel 196
Casearia inaequilatera Cambess. 177
Casearia incana Bertero ex Spreng. 163
Casearia insularis Vasudeva Rao & Chakrab. 195
Casearia integrifolia Vahl ex DC. 182
Casearia itzana Lundell 172
Casearia junodii Schinz 193
Casearia kaalaensis Lescot & Sleumer 196
Casearia kerrii Craib 195
Casearia kigeri T. Samar. & M.H. Alford 172
Casearia klaineana Pierre ex A. Chev. 188
Casearia kostermansii Sleumer 196
Casearia kunstleri King 190
Casearia kurzii C.B.Clarke 196
Casearia kurzii var. *gracilis* S.Y.Bao 196
Casearia kurzii var. *kurzii* 196
Casearia laetioides (A.Rich.) Northr. 173
Casearia laevigata Dalzell 205
Casearia laevis Standl. 167
Casearia lanceolata Miq. 163
Casearia lanosperma Diogo 171
Casearia lasiophylla Eichler 173
Casearia latifolia Ridl. 189
Casearia laurina Blume 194
Casearia ledermannii Gilg 196
Casearia lemkeana T. Samar. & M.H. Alford 173
Casearia leucolepis Turcz. 194
Casearia lifuana Däniker 196
Casearia lindeniana Briq. 166
Casearia lindeniana Urb. 182
Casearia lingua Cambess. 183
Casearia littoralis T. Samar. & M.H. Alford 173
Casearia lobbiana Turcz. 196
Casearia loheri Merr. 196
Casearia longifolia A.C.Sm. 197
Casearia lopeziana Sleumer 174
Casearia lucida Tul. 198
Casearia luetzelburgii Sleumer 174
Casearia luteocarpa Elmer 194
Casearia macrantha Gilg 197
Casearia macrocarpa C.B.Clarke 197
Casearia macrodendron Gilg 193
Casearia macrogyna Turcz. 193
Casearia macrophylla Vahl 178
Casearia macrophylla var. *barbatula* J.F.Macbr. 178
Casearia maculata Pilg. 171
Casearia manausensis Sleumer 174
Casearia mannii Mast. 188
Casearia mariquitensis Kunth 174
Casearia marquettei Nepom. & M.Alves 175
Casearia martinii Benoist 162
Casearia mathewsii Turcz. 179
Casearia mauritiana Bosser 197
Casearia mayana Lundell 170
Casearia maynacarpa Liesner & P.Jørg. 175
Casearia megacarpa Cuatrec. 175
Casearia megalophylla Gilg 197

- Casearia melistaurum* Spreng. 202
Casearia melistaurum var. *germainii* Briq. 202
Casearia melistaurum var. *minor* Briq. 202
Casearia melliodora Eichler 175
Casearia membranacea Britton 165
Casearia membranacea f. *nigrescens* S.S.Lia 193
Casearia membranacea Hance 197
Casearia merrillii Hayata 193
Casearia mestrensis Sleumer 175
Casearia mexiae Sandwith 175
Casearia mexicana (Rose) T. Samar. & M.H. Alford 176
Casearia michelsonii Breteler 197
Casearia micrantha G.Don 205
Casearia microcarpa Sleumer 197
Casearia microdon Miq. 195
Casearia microphylla Bertero ex Turcz. 160
Casearia microphylla Dennst. 178
Casearia microphylla Eichler 170
Casearia mindanaensis Merr. 198
Casearia minutidens Merr. 201
Casearia minutiflora Ridl. 198
Casearia moaensis Vict. 176
Casearia mollifolia Standl. 167
Casearia mollipila Sleumer 176
Casearia mollis K.Schum. 190
Casearia mollis Kunth 176
Casearia moluccana Blume 193
Casearia montana Gardner 177
Casearia monticola Sleumer 198
Casearia montigena Appleg. & Gates, M.T. 198
Casearia moultonii Ridl. 196
Casearia multinervosa C.T.White & Sleumer 198
Casearia multipunctata Merr. 204
Casearia murceana R.Marquete & Mansano 176
Casearia myrsinoides Sleumer 198
Casearia neblinae Sleumer 176
Casearia negrensis Eichler 176
Casearia nicoyensis Donn.Sm. 161
Casearia nigrescens Tul. 198
Casearia nigrescens var. *lucida* (Tul.) Sleumer 198
Casearia nigrescens var. *nigrescens* 198
Casearia nigrescens var. *onivensis* H. Perrier 199
Casearia nigrescens var. *ovata* H. Perrier 199
Casearia nigrescens var. *subtrinervia* H. Perrier 199
Casearia nigricans Sleumer 176
Casearia nigricolor Sleumer 176
Casearia nitens Merr. 192
Casearia nitida Jacq. 177
Casearia nitida Sieber ex Griseb. 168
Casearia noldei A.Fern. & Diniz 188
Casearia novoguineensis Valetton 199
Casearia obliqua Spreng. 177
Casearia oblonga Craib 195
Casearia oblongifolia Cambess. 177
Casearia obovalis Poepp. ex Griseb. 177
Casearia obovata Poepp. ex Eichler 177
Casearia obovata Schldtl. 160
Casearia obtusifolia Rusby 161
Casearia odorata Macfad. 160
Casearia odorata Teijsm. & Binn. 191
Casearia oligantha Eichler 163
Casearia olivacea Sleumer 199
Casearia onacaensis Rusby 183
Casearia ophiticola Vict. 177
Casearia oreogenes Sleumer 199
Casearia orizabana Briq. 166
Casearia ovata (Lam.) Willd. 193
Casearia ovata Roxb. 203
Casearia ovata var. *minor* (Thwaites) N.Mukh. 205
Casearia ovoidea Sleumer 182
Casearia pachyphylla Gilg 199
Casearia pallida Craib 191
Casearia panamensis T. Samar. & M.H. Alford 178
Casearia papuana Sleumer 199
Casearia paranaensis Sleumer 178
Casearia parhamii A.C.Sm. 199
Casearia parviflora J.F.Gmel. 182
Casearia parviflora Jacq. 168
Casearia parviflora var. *microphylla* Schldtl. 182
Casearia parviflora Willd. 182
Casearia parvifolia Tul. 198
Casearia parvifolia var. *genuina* Briq. 168
Casearia parvifolia var. *microcarpa* Eggers 168
Casearia parvifolia var. *paraguariensis* Briq. 168
Casearia parvifolia Willd. 168
Casearia parvistipula Tathana 200
Casearia pauciflora Cambess. 178
Casearia pauciflora Royle 203
Casearia paucinervia Merr. & Quisumb. 197
Casearia pavoniana Sleumer 168
Casearia petelotii Merr. 204
Casearia petiolaris Poepp. ex Eichler 171
Casearia petraea Benth. 185
Casearia phanerophlebia Merr. 200
Casearia phegocarpa Standl. 167
Casearia philippinensis Merr. 200
Casearia pilosissima Quisumb. & Merr. 194
Casearia piscidia Buch.-Ham. ex Royle 203
Casearia pitumba Sleumer 178
Casearia platyphylla Briq. 175
Casearia poeppigii Eichler 163
Casearia pohliana Eichler 179
Casearia polyantha Merr. 194
Casearia povedae (N.Zamora, Aguilar & D.Santam.) T. Samar. & M.H. Alford 178
Casearia praecox Griseb. 178
Casearia pringlei Briq. 166
Casearia prismatocarpa Mast. 200
Casearia procera A.C.Sm. 200
Casearia propinqua Blume 204
Casearia prunifolia Kunth 179
Casearia prunifolia Tul. 160
Casearia pseudoglomerata Sleumer 200
Casearia pseudophiticola J.E.Gut. 178
Casearia puberula Guillaumin 200
Casearia pubescens Merr. 201

- Casearia pubiflora* Benth. 175
Casearia pubipes A.C.Sm. 200
Casearia punctata Spreng. 171, 182
Casearia quinduensis Tul. 179
Casearia ramiflora Seem. 205
Casearia ramiflora Vahl 172
Casearia ramosissima C.Wright ex Griseb. 174
Casearia randioides Lundell 170
Casearia reflexa Sleumer 168
Casearia reginae J.F.Macbr. ex Ll.Williams 167
Casearia resinifera Spruce ex Eichler 179
Casearia rhynchophylla Gilg 201
Casearia richii A.Gray 201
Casearia rinorcooides Sleumer 201
Casearia riparia S.Moore 161
Casearia ripicola Sleumer 201
Casearia rubescens Dalzell 201
Casearia rubescens var. *gamblei* N.Mukh. 201
Casearia rufescens Cambess. 179
Casearia rufidula Triana & Planch. 160
Casearia rufinervis Turcz. 172
Casearia rugulosa Blume 201
Casearia runsorica Gilg 188
Casearia rupestris Eichler 180
Casearia rusbyana Briq. 180
Casearia s.l. New World taxa 160
Casearia s.l. Old World taxa Old World 186
Casearia salacioides Blume 194
Casearia salicifolia Turcz. 166
Casearia samoensis Whistler 201
Casearia samyda (C.F.Gaertn.) DC. 182
Casearia sanchezii J.Linares & Angulo 180
Casearia schlechteri Gilg 190
Casearia schulziana O.C.Schmidt 182
Casearia seemanni Briq. 201
Casearia selloana Eichler 180
Casearia sericea L.O.Williams & A.R.Molina 161
Casearia serrata Macfad. 163
Casearia serrulata Sieber 168
Casearia serrulata Sw. 163
Casearia sessiliflora Cambess. 180
Casearia sikkimensis N.Mukh. 193
Casearia silvana Schltr. 201
Casearia silvana var. *oubatchensis* Schltr. 202
Casearia singularis Eichler 165
Casearia sogerensis Baker f. 195
Casearia solida Merr. 203
Casearia souzae R.Marquete & Mansano 180
Casearia sp. 202
Casearia spinescens (Sw.) Griseb. 180
Casearia spinosa var. *coriacifolia* Kuntze 161
Casearia spinosa var. *tafallana* Eichler 161
Casearia spinosa Willd. 160
Casearia spinulosa (Vent.) T. Samar. & M.H. Alford 181
Casearia spiralis J.R.Johnst. 185
Casearia staffordiae Proctor 181
Casearia standleyana Sleumer 181
Casearia stapfiana Ridl. 202
Casearia stenophylla A.C.Sm. 202
Casearia stipitata Mast. 202
Casearia stipularis Cambess. 162
Casearia stipularis Vent. 162
Casearia stjohnii I.M.Johnst. 181
Casearia suaveolens (Poepp.) T. Samar. & M.H. Alford 181
Casearia subcordata Merr. 194
Casearia subcuneata Miq. 195
Casearia subopaca Planch. & Triana 165
Casearia subsessiliflora Lundell 182
Casearia sylvestris subsp. *myricoides* (Griseb.) J.E.Gut. 181
Casearia sylvestris subsp. *sylvestris* 182
Casearia sylvestris subvar. *campestris* Eichler 183
Casearia sylvestris subvar. *pedicellaris* Eichler 183
Casearia sylvestris Sw. 181
Casearia sylvestris var. *angustifolia* Uittien 182
Casearia sylvestris var. *benthamiana* (Miq.) Uittien 182
Casearia sylvestris var. *carpinifolia* (Benth.) Briq. 183
Casearia sylvestris var. *chlorophoroidea* (Rusby) Sleumer 183
Casearia sylvestris var. *eichleri* Briq. 183
Casearia sylvestris var. *lingua* (Cambess.) Eichler 183
Casearia sylvestris var. *martinicensis* Macbride ex Williams, L. 182
Casearia sylvestris var. *myricoides* Griseb. 182
Casearia sylvestris var. *paraensis* Uittien 182
Casearia sylvestris var. *platyphylla* DC. 182
Casearia sylvestris var. *tomentella* Rusby 183
Casearia sylvestris var. *wydleri* Briq. 183
Casearia tacanensis Lundell 184
Casearia tachirensis Steyerm. 184
Casearia tarapotina Pilg. 175
Casearia tardieuae Lescot & Sleumer 202
Casearia tenuipilosa Sleumer 184
Casearia ternstroemioides (Griseb.) T. Samar. & M.H. Alford 184
Casearia thamnina (L.) T. Samar. & M.H. Alford 184
Casearia thonneri De Wild. 188
Casearia thwaitesii Briq. 203
Casearia timbuchi J.F.Macbr. ex Ll.Williams 178
Casearia tinifolia Vent. 203
Casearia tomentosa Roxb. 203
Casearia tomentosa subsp. *reducta* Verdc. 203
Casearia tomentosa var. *tomentosa* 203
Casearia tremifolia J.F.Macbr. 186
Casearia tremula (Griseb.) Griseb. ex C.Wright 185
Casearia trivalvis (Blanco) Merr. 203
Casearia truncata Blume 194
Casearia tuberculata Blume 204
Casearia tulasneana (Baill.) Warb. 198
Casearia turbinata Blume 191
Casearia uleana Sleumer 185
Casearia ulmifolia Cambess. 185

- Casearia ulmifolia* Vahl ex Vent. 185
Casearia umbellifera Benoist 163
Casearia uniflora Decne. 194
Casearia urbaniana Gand. 161
Casearia urophylla Gilg 204
Casearia vareca Roxb. 204
Casearia variabilis Blume 195
Casearia varians var. *minor* Thwaites 205
Casearia varians var. *obovata* Thwaites 203
Casearia varians var. *ovata* Thwaites 205
Casearia velutina Blume 204
Casearia velutinoso Ridl. 204
Casearia villilimba Merr. 204
Casearia villosa (Sw.) T. Samar. & M.H. Alford 186
Casearia virescens Pierre ex Gagnep. 204
Casearia viridiflora Lam. 206
Casearia wenzelii Merr. & Quisumb. 200
Casearia williamsiana Sleumer 186
Casearia wynadensis Bedd. 204
Casearia yatesii Sleumer 205
Casearia yucatanensis (Standl.) T. Samar. & M.H. Alford 186
Casearia yunnanensis F.C.How & W.C.Ko 192
Casearia zahlbruckneri Szyszyl. 186
Casearia zenkeri Gilg 202
Casearia zeylanica (Gaertn.) Thwaites 205
Casearia zizyphoides Kunth 186
Casearia zschokkei Elmer 204
Casinga procera (Poepp.) Griseb. 164
Casinga suaveolens (Poepp.) Griseb. 181
Chaetocrater capitatus Pers. 162
Chaetocrater fasciculatus Ruiz & Pav. 171
Chaetocrater hirtum (Sw.) Raf. 160
Chaetocrater reflexus Ruiz & Pav. 168
Chaetocrater tinifolia (Vent.) Raf. 203
Clasta fragilis Comm. ex Vent. 190
Corizospermum clutiiifolium Zipp. ex Blume 190
Crateria capitata Pers. 206
Crateria fasciculata (Ruiz & Pav.) Pers. 171
Gelonium pinatubense Elmer 204
Gossypiospermum crimeanum Pickel 174
Gossypiospermum eriophorum (C.Wright ex Griseb.) Urb. 179
Gossypiospermum lanospermum (Diogo) Pickel 171
Gossypiospermum paraguariense Rehder 171
Gossypiospermum praecox (Griseb.) P.Wilson 179
Guayabilla odorata Sessé & Moc. 181
Guidonia adstringens (Mast.) Baill. 168
Guidonia alba (A.Rich.) M.Gómez 160
Guidonia amplissima (Tul.) Baill. 199
Guidonia apetala (Jacq.) Kuntze 162
Guidonia canziana (Buch.-Ham.) Kurz 203
Guidonia corymbulosa (Spruce ex Benth.) Kuntze 167
Guidonia elliptica (Tul.) Baill. 199
Guidonia eriophora (Wright ex Griseb.) Maza 179
Guidonia esculenta (Roxb.) Baill. 205
Guidonia fragilis (Vent.) Cordem. 190
Guidonia gelonioides Baill. 190
Guidonia glomerata (Roxb.) Kurz 193
Guidonia hirsuta (Sw.) M.Gómez 172
Guidonia hirsuta var. *glabrata* (DC.) M.Gómez 160
Guidonia hirta (Sw.) M.Gómez 160
Guidonia hirta var. *glabriora* M.Gómez 161
Guidonia icosandra Kuntze 173
Guidonia laetioides (A.Rich.) M.Gómez 173
Guidonia lucida (Tul.) Baill. 198
Guidonia nigrescens (Tul.) Baill. 198
Guidonia nitida (Jacq.) M.Gómez 177
Guidonia ovata (Lam.) Baill. 193
Guidonia parvifolia M.Gómez 168
Guidonia procera (Poepp.) Kuntze 164
Guidonia ramiflora (Vahl) M.Gómez 172
Guidonia ramiflora var. *spinosa* M.Gómez 172
Guidonia rosauriana M.Gómez 179
Guidonia spinescens (Sw.) Griseb. 180
Guidonia stipularis M.Gómez 162
Guidonia stipularis var. *serrulata* (Sw.) M.Gómez 163
Guidonia suaveolens (Poepp.) Kuntze 181
Guidonia sylvestris (Sw.) M.Gómez 182
Guidonia sylvestris var. *myricoides* (Griseb.) M.Gómez 182
Guidonia sylvestris var. *platyphylla* (DC.) M.Gómez 182
Guidonia ternstroemiodes (Griseb.) Kuntze 184
Guidonia thammia Kuntze 184
Guidonia tomentosa (Roxb.) Kurz 203
Guidonia tremula (Griseb.) M.Gómez 185
Guidonia tulasneana Baill. 198
Guidonia ulmifolia (Vahl ex Vent.) Baill. 185
Guidonia vareca (Roxb.) Baill. ex Kurz 204
Hecatostemon completus (Jacq.) Sleumer 166
Hecatostemon dasygynus S.F.Blake 166
Hecatostemon guazumifolius (Kunth) Sleumer 166
Iroucana guianensis Aubl. 172
Laetia acuminata Bonpl. ex Triana & Planch. 162
Laetia americana L. 162
Laetia apetala Jacq. 162
Laetia apetala var. *pubescens* Eichler 162
Laetia calophylla Eichler 181
Laetia casearioides Sagot ex Benth. 164
Laetia completa Jacq. 166
Laetia corymbulosa Spruce ex Benth. 167
Laetia corymbulosa var. *floribunda* (Spruce ex Benth.) Eichler 167
Laetia crenata A.Rich. 173
Laetia floribunda Spruce 167
Laetia glabra Brandegees 185
Laetia guazumifolia Kunth 166
Laetia guazumifolia var. *tomentosa* Triana & Planch. 166
Laetia guidonia Sw. 173
Laetia hirtella Kunth 166
Laetia longifolia A.Rich. 173
Laetia micrantha A.Robyns 178
Laetia parviflora Spreng. 206

- Laetia povedae* N.Zamora, Aguilar & D.Santam. 178
Laetia procera (Poepp.) Eichler 164
Laetia scabra Spreng. 206
Laetia serrulata Ruiz & Pav. 206
Laetia serrulata Ruiz & Pav. ex Pritz. 206
Laetia suaveolens (Poepp.) Benth. 181
Laetia ternstroemioides Griseb. 184
Laetia thammia L. 184
Laetia thammia Sw. 184
Laurus serrata Blanco 194
Lindleya mollis Kunth 206
Mayna parvifolia (J.F.Macbr.) Sleumer 175
Melistaurum arboreum Hasselt ex Blume 206
Melistaurum distichum J.R.Forst. & G.Forst. 202
Pitumba edulis Rich. ex Eichler 178
Pitumba guianensis Aubl. 178
Rinorea cafassii Chiov. 188
Rinorea storkii (Seem.) Melch. 201
Sadymia villosa (Sw.) Griseb. 186
Samyda acuminata Urb. 172
Samyda affinis Spreng. 160
Samyda arborea Rich. 162
Samyda bartlettii (Lundell) Lundell 164
Samyda bazanica Buch.-Ham. ex Wall. 203
Samyda campanulata Borhidi & O.Muñiz 169
Samyda canzuala Buch.-Ham. 203
Samyda comocladifolia (Vent.) Poir. 206
Samyda coriacea (Vent.) Poir. 190
Samyda crenata Poir. 177
Samyda cubensis P.Wilson 173
Samyda decandra Jacq. 169
Samyda decurrens Spreng. 206
Samyda denticulata Poir. 168
Samyda dodecandra Jacq. 168
Samyda enneandria Sessé & Moc. 160
Samyda fragilis (Vent.) Poir. 190
Samyda glabra Buch.-Ham. 193
Samyda glabrata Sw. 172
Samyda grandiflora Griseb. 169
Samyda grandiflora Spreng. 206
Samyda grewiifolia (Vent.) Poir. 195
Samyda hirsuta (Sw.) Poir. 172
Samyda icosandra Sw. 173
Samyda iroucana Rich. 172
Samyda lancifolia Sessé & Moc. 168
Samyda lucida Steud. 206
Samyda lunana P.Wilson 173
Samyda macrantha P.Wilson 169
Samyda macrocarpa Sessé & Moc. ex DC. 181
Samyda macrophylla Willd. 206
Samyda mexicana Rose 176
Samyda microphylla Urb. 173
Samyda minutifolia Urb. 174
Samyda multiflora Cav. 160
Samyda nitida L. 177
Samyda niviana Poir. 163
Samyda nobilis W.Bull 206
Samyda octandra Sessé & Moc. 172
Samyda oligostemon Urb. 169
Samyda parviflora L. 182
Samyda parviflora Loefl. 167
Samyda parviflora Sessé & Moc. 183
Samyda parvifolia Poir. 168
Samyda petiolaris Spruce ex Eichler 181
Samyda piscidia Buch.-Ham. ex Wall. 203
Samyda pitumba Poir. 178
Samyda polyandra Willd. 202
Samyda procera Poepp. 164
Samyda pubescens Blanco 194
Samyda pubescens L. 172
Samyda ramosissima (C.Wright ex Griseb.) J.E.Gut. 174
Samyda rosea Sims 169
Samyda rubra DC. 169
Samyda selloi Spreng. 177
Samyda serrulata Blanco 194
Samyda serrulata L. 168
Samyda spinescens Sw. 180
Samyda spinosa L. 160
Samyda spinosa Sessé & Moc. 160
Samyda spinulosa Vent. 181
Samyda stipularis Poir. 162
Samyda suaveolens Poepp. 181
Samyda subintegra Borhidi & O.Muñiz 169
Samyda sylvestris (Sw.) Poir. 182
Samyda tenuifolia Urb. 169
Samyda tinifolia (Vent.) Poir. 203
Samyda tomentosa Sessé & Moc. 160
Samyda tomentosa Sw. 160
Samyda trivalvis Blanco 203
Samyda velutina DC. 169
Samyda villosa Sw. 186
Samyda virgata Sessé & Moc. 163
Samyda viridiflora Aubl. 162
Samyda viridiflora Poir. 205
Samyda yucatanensis Standl. 186
Suregada pinatubensis (Elmer) Croizat 204
Synandrina riparia Standl. & L.O.Williams 186
Tardiella annamensis Gagnep. 187
Thammia swartzii Hitchc. 184
Thammia ternstroemioides (Griseb.) M.Gómez 184
Thiodia laetioides (A.Rich.) Griseb. 173
Unresolved 205, 206
Valentia coriacea Griseb. 162
Vareca zeylanica Gaertn. 205
Xylosma turrialbana Donn.Sm. 161
Zuelania belizensis Lundell 185
Zuelania crenata (A.Rich.) Griseb. 173
Zuelania guidonia (Sw.) Britton & Millsp. 173
Zuelania icosandra (Sw.) Clos 173
Zuelania laetioides A.Rich. 173
Zuelania roussoviae Pittier 173
Zuelania tremula Griseb. 185