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Geopolitics of bitterness: Deciphering the history and cultural biogeography of *Quassia amara* L

Guillaume Odonne [a,*], Marc-Alexandre Tareau [a], Tinde van Andel [b]

[a] LEEISA (Laboratoire Ecologie, Evolution, Interactions des Systèmes Amazoniens), CNRS, Université de Guyane, IFREMER, 97300, Cayenne, French Guiana
[b] Naturalis Biodiversity Center, Leiden, the Netherlands

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ABSTRACT

Ethnopharmacological relevance: *Quassia amara* L. recently came into the spotlight in French Guiana, when it became the object of a biopiracy claim. Due to the numerous use records throughout the Guiana shield, at least since the 18th century, a thorough investigation of its origin seemed relevant and timely. In the light of the Convention on Biological Diversity (CBD) and the Nagoya protocol, questions about the origin of local knowledge are important to debate.

Aim of the study: Defining cultural biogeography as the dynamics through space and time of biocultural complexes, we used this theoretical framework to shed light on the complex biogeographical and cultural history of *Q. amara*. We explored in particular the possible transfer of medicinal knowledge on an Old World species to a botanically related New World one by enslaved Africans in Suriname.

Materials and methods: Historical and contemporary literature research was performed by means of digitized manuscripts, archives and databases from the 17th to the 21st century. We retrieved data from digitized herbarium vouchers in herbaria of the Botanic Garden Meise (Belgium); Naturalis Biodiversity Center (the Netherlands); Missouri Botanical Garden, the Smithsonian National Museum of Natural History, the Field Museum (USA); Royal Botanic Gardens Kew (UK); the IRD Herbarium, French Guiana and the Museum National d'Histoire Naturelle (France). Vernacular names were retrieved from literature and herbarium specimens and compared to verify the origin of *Quassia amara* and its uses.

Results: Our exploration of digitized herbarium vouchers resulted in 1287 records, of which 661 were *Q. amara* and 636 were *Q. africana*. We observed that the destiny of this species, over at least 300 years, interweaves politics, economy, culture and medicine in a very complex way. *Quassia amara*'s uses are difficult to attribute to specific cultural groups: the species is widely distributed in Central and South America, where it is popular among many ethnic groups. The species spread from Central to South America during the early 18th century due to political and economic reasons. This migration possibly resulted from simultaneous migration by religious orders (Jesuits) from Central America to northern South America and by Carib-speaking Amerindians (from northern South America to Suriname). Subsequently, through colonial trade networks, *Q. amara* spread to the rest of the world. The absence of African-derived local names in the Guiana shield suggests that *Q. africana* was not sufficiently familiar to enslaved Africans in the region that they preserved its names and transferred the associated medicinal knowledge to *Q. amara*.

Conclusions: Cultural biogeography has proven an interesting concept to reconstruct the dynamics of biocultural interactions through space and time, while herbarium databases have shown to be useful to decipher evolution of local plant knowledge. Tracing the origin of a knowledge is nevertheless a complex adventure that deserves time and interdisciplinary studies.

1. Introduction

Historical ethnobotany seeks to decipher the complex coevolution of people and plants through time, and is a truly interdisciplinary field. Although the convergence between historical and biological sciences is facing epistemological difficulties (Heinrich et al., 2006), the study of

* Corresponding author.
E-mail address: guillaume.odonne@cnrs.fr (G. Odonne).

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historical texts and archives is highly valuable to understand the dynamics of the relations between humans and plants from a diachronic perspective (Medeiros, 2016), and particularly regarding medicinal uses (Lardos, 2015). This has been successfully applied to the description of the evolution of phytotherapeutical practices and of medicinal floras, and numerous examples from Europe (Lardos and Heinrich, 2013; Leonti et al., 2010), Latin-America (Brandão et al., 2012, 2008), the Caribbean (Soelberg et al., 2016), Asia (Sathasivampillai et al., 2017) or Africa (El-Gharbaoui et al., 2017; Soelberg et al., 2015) help to understand the dynamics underpinning medicinal plant knowledge and transmission. Beside these historical studies, considering cultural exchanges of plants at a geographical level in the contemporary era is another important field of ethnobiology, particularly developed with regards to the South American and Caribbean diaspora in urban areas in Europe and the US (Ceuterick et al., 2011; 2008; Pieroni and Vandebroek, 2007). Plant transfers have had particular biocultural repercussions in the case of historic migrations, such as the transatlantic slave trade, a subject that has been the focus of recent anthropological and ethnobotanical research (van Andel et al., 2014; 2016; Voeks and Rashford, 2012). Nevertheless, disentangling such processes at both a historical and a geographical level is an ambitious goal, as some started before the Colombian encounter, others were enhanced by the transatlantic trade, and some accelerated through colonial and preindustrial times.

A few years ago, one particular plant species (*Quassia amara* L.) entered the spotlight in French Guiana, when it became the object of a biopiracy claim. In 2016, the *France Libertés* Foundation filed a patent opposition to the European Office on the legitimacy of two patents deposited by the *Institut pour la Recherche et le Développement* (IRD) on Simalikalactone E, a pharmacologically active compound against malaria and cancer, present in the leaves of *Q. amara*. This event became known afterwards in France as the "kwasi affair" (*l'affaire kwachi*), after the local name of the plant in the region (Bourdy et al., 2017; Burelli, 2019; Collomb, 2018; Thomas, 2018). Steering clear from the political aspects of this debate, in substance as well as in form, we were interested to shed light on the complex biogeographical and cultural history of this species. We observed that the destiny of this plant, since at least 300 years, interweaves politics, economy, culture and medicine in a very complex way, shaking up thoughts on the definition of traditional knowledge and the dynamics behind it. In the framework of the Convention on Biological Diversity (CBD) and the Nagoya protocol, such controversial points related to origin and ownership of knowledge are to be debated carefully, being the center of political claims (Eimer, 2020; Pedrollo and Kinupp, 2015).

Q. amara is a shrubby tree (2–8 m high) in the Simaroubaceae family, with imparipinnate leaves (5–7 leaflets) and a conspicuously winged rachis. Inflorescences are racemose, flowers are bisexual and bright red. The fruits are apocarpous, and consist of multiple drupes (Woodson et al., 1973). Although the species is said to be native to Central America (Woodson et al., 1973), the first mention of *Q. amara*, as well as the type specimen, come from Suriname (Pulle et al., 1979). Both its local and its scientific name refer to Kwasi, an enslaved African who was born in Guinea (Fermin, 1769; Dragtenstein, 2004), who possibly discovered its antimalarial properties, and certainly made this species famous in Paramaribo (Price, 1979).

The 'scientific history' of *Q. amara* reflects complex historical events of trade and exchange in plants and knowledge, and may also testify of the transfer of medicinal knowledge from an Old World species to a botanically related New World one by enslaved Africans in Suriname. Indeed, the cultural connection with Africa is even more important, as shown by recent ethnobotanical studies. Enslaved Africans contributed to the addition of contemporary American medicinal flora by recognizing in the Neotropical flora a number of taxa that they knew as useful in their countries of origin in western Africa. They often transposed vernacular names and uses of Old World plants to the related New World species (Bilby, 2000; Carney and Rosomoff, 2011; van Andel, 2016; van Andel et al., 2014).

Our objective is to elucidate and trace back the complex "cultural biogeography" of *Q. amara* in colonial times by using historical written sources and herbarium vouchers. Despite an increasing use of data from herbarium collections by ecologists to reveal phenological trends related to climate change (Calinger et al., 2013; Hart et al., 2014; Willis et al., 2017), or to investigate phytogeography by means of DNA (Roullier et al., 2013a), such material has been little explored regarding geographical similarities and differences in medicinal uses of plants. Exceptions include a recent study on the 'evolution' of Traditional Chinese Medicine by using the Economic Botany collections in Kew (Brand et al., 2017) and a comparison of Surinamese phytotherapy over 250 years (van Andel et al., 2012a).

Cultural biogeography is defined here as the dynamics through space and time of biocultural complexes. In the present paper, we explain how *Q. amara* spread from Central to South America and the rest of the world, and verify if (and why) its use as a febrifuge was discovered far from its origin, and whether traditional uses of the botanically related African species *Quassia africana* (Baill.) Baill. May help explain this key event.

2. Material and methods

2.1. Historical and contemporary literature research

Following recent research in historical ethnobotany (Lardos, 2015), we traced back the history of *Q. amara*'s uses by consulting compilations and original historic sources, in the form of books (hardcopy or eBooks) retrieved on Biblioteca Nacional de Colombia (2020), Google books (2020), Gallica (2020), Botanicus (2020) and journal articles. We reviewed the (ethno-) botanical literature of northern South America and Central America, such as floras and ethnobotanical compilations, for *Q. amara* and related species, and the Central and West African literature for *Q. africana* and related species to record past and contemporary uses.

2.2. Data mining from digitized herbarium vouchers

Herbarium voucher labels are an important source of ecological and (ethno-) botanical information, as they often include data on geographic localities, surrounding ecosystems, vernacular names, ethnic groups, medicinal or other uses that help to reconstruct the (ancient) habitats, biogeography or cultural knowledge of a species. Since herbarium collections are increasingly digitalized and published online, access to label information is easier and allows for a greater diffusion of knowledge. Some vouchers date back to the 17th century, and contain information that was once confined to museums (Boulangeat, 2014; Chupin, 2018; van Andel et al., 2012c). From March to June 2020, we explored herbarium databases and digitized vouchers to gather information related to contemporary or ancient distribution, ecology or uses of *Q. amara* and *Q. africana*, mostly from online resources: the Botanic Garden Meise (2020), Belgium (BR); Naturalis Biodiversity Center (2020), Leiden, the Netherlands (L); Missouri Botanical Garden (2020), (MO); the Smithsonian National Museum of Natural History (2020), (US); and the Field Museum (2020), (F) in the US; Royal Botanic Gardens Kew (2020), UK (K); the French Guiana IRD Herbarium, 2020 in Cayenne (CAY); and the Museum National d'Histoire Naturelle (2020), in Paris, France (P). Brazilian vouchers from other institutions were also checked through the website Reflora (2020). When data originated from a herbarium specimen, we cited it with the herbarium abbreviation, the name of the first collector and the specimen number (e.g., MO-Smith 15,674).

2.3. Linguistic comparison of folk names

The study of local plant names is a useful way to decipher biocultural history, as local names often travel with the plants and are exchanged among different cultural groups (Balée, 2003; Balée and Moore, 1991; Grenand, 1995; van Andel et al., 2014). In order to have a clear insight

into *Q. amara*'s travel through the Americas, and to verify the trans-atlantic hypothesis of African plant knowledge applied to the flora of the Americas, local names from both *Q. amara* and *Q. africana* were collected from literature, herbarium labels and databases and compared. According to methods previously published (van Andel et al., 2014) our comparison was based on phonological, morphosyntactic, and semantic similarities between all American names for *Q. amara* (from Amerindian, European or Afro-American languages) as well as for names for *Q. africana* in African languages. A strong correspondence in sound, structure, and semantics between vernacular names in different languages was considered as evidence for a shared origin. We paid attention not to cite redundant information and refer to primary sources as much as possible.

3. Results and discussion

3.1. Herbarium data mining

Exploration of digitized herbarium vouchers and labels resulted in 1287 records, of which 661 were *Q. amara* and 636 were *Q. africana*, or labelled as such, because a few of them were misidentified. For our analysis, we used virtual specimens from L (102), P (157), US (135), BR (30), F (26), CAY (23), K (1), and labels from MO (187). For *Q. africana*, virtual specimens were analyzed from BR (436), L (184), US (13) and K (3). All specimen information directly cited in our analysis is listed in Appendix A.

3.2. A rapid history of Quassia's name and fame

The febrifugal and stomachic properties are said to have been discovered by an enslaved African in Suriname, known as Kwasi or Quassie van Nieuw Timotibo (Dragtenstein, 2004). Born between 1692 and 1697 in 'Guinea', Kwasi was enslaved before 1712 and put to work around 1727 on the plantation Nieuw Timotibo in the former Dutch colony (Dragtenstein, 2004; Stedman, 1796). As Kwasi is an Akan 'day' name for a male person born on Sunday, he may have been born in Ghana, but it is also possible that he received this name in Suriname. Around 1727, he started working as a scout for the colonial authorities and headed expeditions against Maroon villages, descendants of escaped slaves who settled in the interior forests. For his services, Kwasi was freed in 1755, though he was already honored as "*faithful to the Whites*" in 1730, which gave him the nickname 'Kwasimukamba' (Kwasi the white man) among the Maroons (Dragtenstein, 2004; Price, 1979). As an outspoken and controversial person, he was both feared and renowned as a traditional healer, illegal trader in enslaved Amerindians, and as a sorcerer, renowned for his protective amulets. Kwasi served as the official healer of the governor of the Dutch colony and eventually became a plantation owner himself (Dragtenstein, 2004; Price, 1979). Kwasi became famous after he (supposedly) discovered the healing properties of *Q. amara* around 1730, when he had frequent interactions with Amerindians, and his successful treatments of both enslaved Africans and Europeans suffering from fever (Dragtenstein, 2004).

On December 20, 1755, the Swedish biologist Daniel Rolander, sent to Suriname to collect specimens for the famous botanist Carolus Linnaeus, wrote in his diary: "*A man skilled in plants and their uses is viewed in this region as both enviable and dangerous. I myself conversed with Quassi on a couple of occasions. He was quite guarded with his wisdom; he said he would reveal nothing until receiving a considerable sum of money*" (Rolander, 2008). Although the wood of *Q. amara*, known as *lignum quassiae*, was already exported in large quantities to Europe in 1755, Rolander was the first to provide a (Latin) description of the flowering and fruiting parts of this plant, but Linnaeus never got hold of his specimens (van Andel et al., 2012a). Kwasi is said to have sold his secret knowledge regarding *Q. amara* to Carl Gustav Dahlberg, the Swedish owner of the plantation Nieuw Timotibo and Rolander's mentor (Davis, 2016). In 1761, Dahlberg brought a specimen of the plant to Linnaeus, who dedicated its scientific name to Kwasi and the bitter taste of the wood (Blom, 1763; Linné, 1762).

The Belgian physician Phillipe Fermin challenged Kwasi's discovery of *Q. amara*: "*This does not seem quite probable to me, since it had already been known, for nearly forty years, to almost all the inhabitants of Surinam, who made use of the flowers brought by this tree, and who regarded them as very stomachic; and this when I arrived in 1754*" (Fermin, 1769). Fermin's remarks suggest that around 1714 this remedy for stomach pain was already well-known. However, *Q. amara* is absent from the first herbarium collections from Suriname, dating from 1687 and representing 48 useful species (van Andel et al., 2012c). The species neither appears in the plant drawings of Maria Sybilla Merian, who portrayed 60, mostly cultivated plant species in Suriname around 1699 (Merian, 1705). Kwasi was invited to travel to the Dutch Republic in 1776 and fêted by Willem V, Prince of Orange (Price, 1979; Voeks and Greene, 2018), a rather uncommon treatment for a former enslaved African at that time. During this visit, he complained that Dahlberg had earned a fortune with the export of the bitter wood, for which he had received very little (Dragtenstein, 2004).

3.3. Quassia amara's long journey southeast

According to Woodson et al. (1973), Grandtner and Chevrette (2013) and herbarium specimens in GBIF (2020a), the present distribution of *Quassia amara* ranges from Michoacan (Mexico) to the northeast Brazil, with the highest density between northern Panama and southern Nicaragua (Fig. 1). This distribution may reflect a collection bias, and GBIF data include herbarium specimens from cultivated individuals. However, despite the assumption of Woodson et al. (1973) that its exact origin is impossible to determine because of its frequent cultivation in the last centuries, *Q. amara* is unambiguously considered as native to tropical America (Fig. 1). It is observed wild in Panama in 'monsoon' forest and in evergreen seasonal forests up to 1000 m (D'Arcy, 1987; Woodson et al., 1973), and in evergreen moist forest in Costa Rica (Díaz et al., 2006). According to Pulle et al. (1979) and the herbarium labels consulted, the species has an affinity for wetlands, flooded forests or riverbanks. It is nowadays commonly found naturalized along rivers in Suriname (F-Maguire 23,851, van Andel personal observation) and on former plantations in French Guiana (CAY-Feuillet 2859 and CAY-Houël 1). It is also frequently cultivated in gardens in the coastal areas of Guyana, Suriname and French Guiana. The map of *Q. amara* distribution shows a relatively standard pattern, with a high density of specimens collected at a central position, indicating the putative center of origin, and a decreasing occurrence towards the periphery of its range.

Q. amara supposedly arrived in French Guiana in 1772 (Barbier, 1824), where it gained its local name "*quinquina de Cayenne*", referring to the Andean quinine bark (*Cinchona* spp., Rubiaceae), subsequently leading to several confusions. The first herbarium specimen from Cayenne was collected in 1788 (P-Stoupy s. n.), and the second in 1792 (P-Leblond s. n.). The fact that *Q. amara* does not appear in the inventories of Barrère (1743, 1749) or Aublet (1775) supports this time of introduction, despite the difficulty to correspond the 18th century names and identifications to modern ones if no specimens exist. In 1896, the species was collected growing spontaneously close to Cayenne (P-Soubirou s. n.). Circulation of knowledge in French Guiana mainly occurs (today and in the past) within the coastal area and along the main rivers, such as the Maroni and the Oyapock (Tareau, 2019; Tareau et al., 2019). The fact that the species is unknown among the Wayãpi, Wayana and Teko indigenous groups currently living in the remote South of French Guiana, whose only links to the coast are these rivers, also support this coastal way of introduction (Grenand et al., 2004; Odonne & Davy, unpublished results).

In Colombia, *Q. amara* was first collected along the Rio Viejo (close to the Magdalena River) in 1801 (P-Bonpland 1536), the voucher being dated after Sprague (1926). Although we were unable to determine the context of this collection, it's local name (*cruzette*) is similar to what it is

Fig. 1. Approximate range of *Q. amara* in Central and South America from herbarium collection localities recorded in GBIF.

called two centuries later. The Spanish physician and botanist José Celestino Mutis imported the plant to Colombia around 1775 (Mutis, 1778), in spite of its probable natural occurrence in the northeastern parts of the country, which was probably unknown to Mutis as one of the first botanists exploring the country. At the Missouri herbarium (MO), there are eight Colombian specimens (mostly from the northwest of the country), of which three were collected from the wild in disturbed forest.

Although Berry (2005) ambiguously considers *Q. amara* as "native to the Venezuelan Guayana, the Guianas and Northern Brazil", based on only one collection from a wild individual in secondary forest, the absence of specimens from Eastern Colombia and Venezuela is striking (Fig. 1). As far as we know, the plant is very little used in Venezuela today, as it is absent from medicinal market surveys held in Caracas (Giraldo et al., 2009) and not cited among the medicinal species recorded in the Trujillo state (Bermúdez and Velázquez, 2002; Carrillo-Rosario and Moreno, 2006), nor in the Aragua state (Jaramillo et al., 2014). The only Venezuelan specimen with a local name (MO-Trujillo 21,360) was collected in 1988 in a fairly isolated community of Carib-speaking Akawaio Amerindians, who live close to the border with Guyana.

The plant is notably absent from the earliest extensive natural history description from Brazil, the Historia Naturalis Brasiliae (Alcantara-Rodriguez et al., 2019). It is also lacking in the early 19th century floristic inventories by C.F.P. von Martius and A. de Saint-Hilaire, and neither listed by European botanists in Brazil in the 19th century (Brandão et al., 2012; 2008; Breitbach et al., 2013). Its first collection was made in 1841 and is labelled "woods maranham" (K-Gardner 5982), suggesting a possible collection in a forest from the Maranhão (called Maranham in the 19th century). The harbor of Saõ Luis (Maranhão's capital) was an important colonial trade hub, and might have been the entry point of this species. According to the previous references, we consider its native status in Brazil very unlikely and this specimen might have been collected in a secondary forest, as observed in Suriname or French Guiana. The second most ancient specimen was collected in 1873, cultivated in Barreiras (lower Amazon) (K-Traill 102), then in 1918 in the Rio de Janeiro botanical garden (F-Whitford 21), while the few other early 20th century specimens (e.g. F-Dahlgreen 49) are from the Para state, which is close to French Guiana.

Q. amara does not appear in the comprehensive list by Rios et al. (2007) of 1191 useful species in Ecuador, based on specimens in the Herbarium da Pontificia Universidad Católica del Ecuador (QCA), and likewise in Peru, as it is not cited in the Peruvian Checklist from the Missouri Botanical Garden website (2020). The species was collected in the wild in Nicaragua in 1853 (P-Wright s. n.), and several wild specimens were found in the southeastern part of Mexico, with the first record from the state of Colima in 1891 (US-Palmer 1338).

Regarding the Caribbean, the first collections come from the French West Indies, probably introduced there from French Guiana. In 1820, a sample was collected from a cultivated plant in Martinique known as "*quinquina du pays*" and used against fevers, and said to come from French Guiana (P-Plée s. n.), while the first specimen collected in Guadeloupe dates from 1808 and was cultivated as well (P-L'Herminier s. n.). In 1895, the plant was present in Trinidad (L-Hart 4492), and maybe even earlier, as a specimen from the A.L. de Jussieu herbarium (P-Riedlé s. n.) was thought to be collected on this island around 1798, as well as a specimen from 1828 (P-Brongniart s. n.). In the US Virgin Islands, one specimen supposedly comes "*ad habitat naturalis*" from Saint-Thomas in 1887 (P-Eggers 155), but the specimen collected in Saint-Croix in 1896 was cultivated (P-Ricksecker s. n.).

Just like the fate of many other useful plants after the Columbian encounter (Boumediene, 2016; Voeks and Greene, 2018), *Q. amara* experienced a rapid fame in colonial territories in the Old World, and spread as far as Saigon (sent from Suriname) in 1874 (P-Pierre 3864; P-Poli s. n.), Bangkok in 1899 (US-Zimmermann 67), Manila and Batavia in 1903 (US-Merril 3434; L-Backer 82), Guinea in 1905 (P-Chevalier 13, 043), Ambon (Indonesia) in 1913 (US-Robinson 1765), and the Congo in 1922 (P-Goossens 3076). It arrived in Hawaii in 1931 from Singapore (L-Shearard et al. 27), and in Micronesia in 1949 (US-Glassman 2562).

3.4. Geopolitics of bitterness

The typical distribution of *Q. amara* and the fact it has been rarely found outside gardens and former plantation areas in the Guiana shield, suggest that it is probably not native in the southeastern part of its range. The species probably originates from the area between Nicaragua, Costa

Rica and Panama (Woodson et al., 1973), and has been introduced northwest to Mexico and southeast by travelers towards northern Brazil between the early 18th and the 19th century.

The absence from Southern Colombia and Ecuador is striking: a species that can thrive in such a wide area and survives in secondary forests would have been able to spread further southeast, at least following human introduction. Ecuador was part of the *Virreinato del Perú* until 1720, whereupon it became part of the *Virreinato de Nueva Granada* (currently Colombia). This area (southern Colombia, Ecuador and northern Peru) is the natural home of the quina trees (*Cinchona* spp., Rubiaceae), which were at that time the main source of bitter antimalarials and the most sought-after medicinal plant species. Mutis, who organized in 1783 the "*Real Expedición Botánica del Nuevo Reino de Granada*" (Jaramillo-Arango, 1952), wrote an influential text on the study of quina bark (Mutis and de Gregorio, 1828). However, an unpublished manuscript by Mutis, dating from 1778 (Fig. 2), is of particular interest for our story: the "*informe presentado al virrey sobre muestras de quina de la Guayana*". In this text, Mutis, after having analyzed some samples from (most probably) *Q. amara* "*affirms […] that the so-called quina de la Guyana not only lacks all the characters of the real quina or* Cinchona officinal*, but not even […] enters as a subordinate species of this genus, in the concept of the botanists"* (Mutis, 1778).

This short text, indirectly speaking of the increasing fame of *Q. amara*, helps us to grasp one of the great stakes of that time. *Cinchona* bark was at the very core of intense politico-economical battles and finding alternative sources (or other species with similar properties) was essential for the colonial nations that competed with Spain (Crawford, 2016). This aspect is confirmed by Leblond (1789), when he states "I set out for the Oyapock River with much food, trade goods, and twenty-four men with the intention of reaching the sources of that river […] to search for [*Cinchona*], […] but there was none of that."

The spread of *Q. amara* far from its natural range may be related to religious discords, notably between orders. Around the mid-18th century, the Jesuits were famous for their interest in South-American *materia medica* (Boumediene, 2020), natural substances with potential value for European pharmacies (Anagnostou, 2005). While seeking these medicinal plants, they published some interesting descriptions of natural history. The "*Orinoco ilustrado y defendido*" (Gumilla, 1745) is one of the important works on uses and customs in the area covered by Jesuit's missions, notably along the Orinoco River. The only very bitter plant described in this book was identified as *Crotalaria stipularia* Desv. by del Rey Fajardo (2017), from which we may interpret that they were unfamiliar with *Q. amara*. However, the eventuality that the Jesuits would have spread this yet undescribed plant eastward is not impossible, although it is not the most likely hypothesis. The Orinoco was roughly the eastern limit of the Jesuit settlements (Tarble and Scaramelli, 2004) and can thus be considered as a cultural biogeographical limit for the use of *Q. amara*, which is more frequent east of this river in the Guiana shield. Considering that the Jesuits were ruling the trade in *Cinchona*, widely known by the name of Jesuit's bark (Boumediene, 2020), we speculate that the appearance of *Q. amara* in the few territories where the Jesuits were absent could be related to some kind of disinterest from this order over the concurrent species of *Cinchona*. Even if *Q. amara* was already famous in Suriname at this time, the Jesuit's expulsion from Spanish territories in 1767 may have contributed to free its way to Europe and other South American colonies. Jesuit's networks and the commercial exploitation of *Cinchona* bark likely explains the absence of *Q. amara* from southern Colombia to Peru, while the influence of other religious and political organizations could be a possible explanation of its 'sudden appearance' in a Dutch colony.

3.5. *Quassia amara's linguistic legacy*

The greater the variety of local names for a plant species in a specific region, the higher the probability that plant is native from that area (Brown et al., 2013a; Shepard Jr and Ramirez, 2011; Westengen et al., 2014). Our review of the vernacular names of *Q. amara* (Table 1) confirms that the species is native to Central America, given its higher number of (indigenous) names compared to the Guiana Shield and Brazil, where most names are derived from post-Colombian names, such as *kwasi* or *quinine/quina* or *Cayenne*. Moreover, in Brazil nearly 25 species of febrifugal plants share the name of *quina* (Pio Corrêa, 1926; 1969; 1978). It is interesting that the Kali'na and Palikur indigenous peoples in French Guiana name this species *kuwasi* or *kwasβan*, names also derivated from *kwasi*.

Amerindians in Suriname, and particularly Carib-speaking groups, are the only people in the Guiana shield to have their own specific vernacular names that are not derived from *kwasi* (Table 1). The single Venezuelan unique vernacular name is also from Carib-speaking Amerindians. The diversity of names in Carib languages for *Q. amara* may be a sign of a long-standing associated knowledge of this group, which originally comes from northern South America (Antczak et al., 2017; Davis and Goodwin, 1990). However, the limited number of specimens, indigenous names and uses recorded in Venezuela (from where the Carib groups originate) makes the hypothesis of a strictly Carib-based discovery and diffusion unlikely. Some names, such as *peunpe*, from the Carib-speaking Wayana, also refer to other species, notably the other bitter Simaroubaceae tree *Simarouba amara* Aubl.

A possible explanatory hypothesis would be that the plant was spread by European colonists during the early 18th century, without leaving written traces, from Central America to Northern South America (current Venezuela), from where Carib-speaking groups have transported it through the Guiana shield down to Suriname, where Kwasi made it famous. Then, from Suriname, the species was subsequently brought to French Guiana and Brazil by European, Afro-American and/or and Amerindian groups. The unfamiliarity with this species among the southernmost indigenous groups of French Guiana (Grenand et al., 2004; Odonne and Davy, unpublished results), combined with the lack

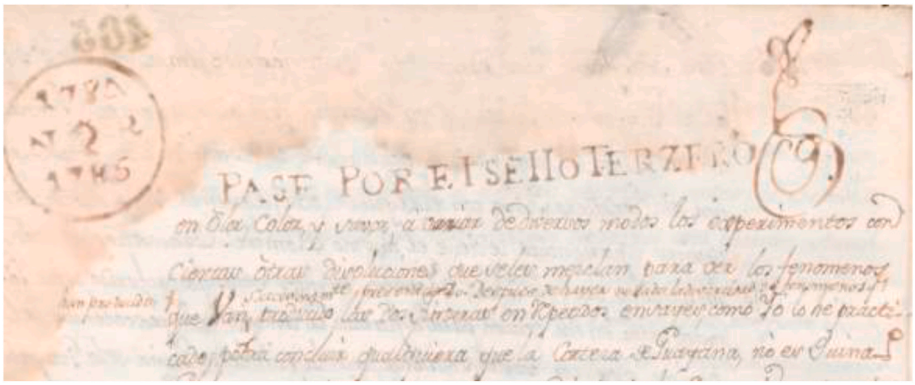

Fig. 2. Excerpt of Mutis (1778) stating that "in repeated trials as I have practiced, will be able to conclude that whatever the bark of Guiana is, it is not Quina".

Table 1
Local names of *Q. amara* in the Neotropics mention in literature and on herbarium labels.

Country (North to South)	Cultural group	Language	Name	References
Mexico	?	Spanish	quina	US-Hinton 15,865
Mexico	?	Spanish	quina roja	MO-Hinton 16,221
Mexico	?	Spanish	cuasia	MO-Breen 1077
Nicaragua	?	Spanish	hombre grande	F-Proctor 26,929
Nicaragua	?	?	wama baka	MO-Grijalva et al., 6044
Nicaragua	Garifuna	Arawak	wéwe gífi	Coe and Anderson (1996)
Nicaragua	Rama	Chibchan (name in English Creole)	bitta wood	Coe (2008)
Nicaragua	Ulwa (Sumu)	Misumalpan	batakka dî basta	Coe and Anderson (1999)
Costa Rica	?	?	bakonki	Fournier and García 1998 in Díaz et al. (2006)
Costa Rica	?	Spanish	cuasia	Fournier and García 1998 in Díaz et al. (2006)
Costa Rica	?	Spanish	hombre grande	MO-Mertinez 280; Pittier (1908)
Costa Rica	?	?	guabo	Pittier (1908)
Costa Rica	?	Spanish	hombrón	Fournier and García 1998 in Díaz et al. (2006)
Costa Rica	?	?	kläklö	Fournier and García 1998 in Díaz et al. (2006)
Costa Rica	?	?	pito kicha	Fournier and García 1998 in Díaz et al. (2006)
Costa Rica	?	?	quini	Fournier and García 1998 in Díaz et al. (2006)
Costa Rica	?	?	webblakló	Fournier and García 1998 in Díaz et al. (2006)
Panama	?	Spanish	crucete	MO-Sharp 1962; Mo-Standley 27,417
Panama	?	Spanish	guabo amargo	MO-Howell 8
Panama	?	Spanish	guavita amarga	MO-Sharp 1962
Panama	?	Spanish	guavito	MO-Kluge 36, Sexton 114
Panama	Chocó	Chocó (name in Spanish)	hombre grande	MO-Duke & Kirkbride 14,074; Duke (1970)
Panama	?	Spanish	juavita amarga	MO-Smith et al., 3280
Panama	Kuna (Bayano)	Chibchan	udut pulu	MO-Duke 14,471
Colombia	?	Spanish	contra-cruceta	US-Romero Castaneda 604
Colombia	?	Spanish	cruceto morado	F-Dugand et al. 367
Colombia	?	French (name derived from Spanish)	cruzette	P-Bonpland 1536
Colombia	?	Spanish	cuásia	US-Dugand et al., 4105
Venezuela	?	Spanish	bejuco barbasco	Berry (2005)
Venezuela	Akawaio	Carib	maipa	MO-Trujillo 21,360
Venezuela	?	Spanish	salsa hueca	F-Steyermark 60,962
Venezuela	?	Spanish	palo isidoro	F-Aristeguieta 2110, US-Pittier 10,970
Venezuela	?	Spanish	mamoncillo	F-Steyermark 86,595
Guyana	All Guyanese	Creole	quashi bitter; quassy bitters	F-Dahlgreen et al. sn., van Andel (2000)
Guyana	All Guyanese	Creole	bitter wood	Lindeman et al. (1963)
Suriname	All Surinamese	Dutch Creole	kwasibita	van Andel and Ruysschaert (2014)
Suriname	All Surinamese	Dutch	bitterhout	van Andel and Ruysschaert (2014)
Suriname	Wayana	Carib	peunpe	van Andel and Ruysschaert (2014)
Suriname	Arawaks	Arawak	kareudan	van Andel and Ruysschaert (2014)
Suriname	Kali'na	Carib	apekyi/ apekïi, (a) pekeï	van't Klooster et al. (2003)
Suriname	Kali'na	Carib	këripu/ k'eripu	van't Klooster et al. (2003)
French Guiana	Kali'na	Carib	kuwasi	Grenand pers. com.
French Guiana	Palikur	Amerindian	kwasβan	Grenand et al. (2004)
French Guiana	Créoles	French Creole	kwachi/ couachi	Grenand et al. (2004) and P-Benoist s.n.
Brazil	?	Portuguese	amargo	Lorenzi and Matos (2008)
Brazil	?	Portuguese	quássia (amarga)	Lorenzi and Matos (2008)
Brazil	?	Portuguese	quássia-de-caiena	Lorenzi and Matos (2008)
Brazil	?	Portuguese	quina	Lorenzi and Matos (2008) & F-Archer 7543
Brazil	?	Portuguese	quinarana	Lorenzi and Matos (2008)
Brazil	?	Portuguese	pau-quássia	Lorenzi and Matos (2008)
Brazil	?	Portuguese	murubá, murupá	Pio Corrêa (1978)
Martinique	?	French Creole	quinquina de Cayenne	US-Stehlé 5872
Martinique	?	French Creole	quina pays	P-Bélanger s.n.
Guadeloupe	?	French Creole	quinine caraïbe	P-Stehlé 8038

of herbarium specimens outside the coastal area, support the latter part of this hypothesis. Still, the possibility of a transatlantic knowledge transfer remains to be analyzed.

3.6. Medicinal uses of Q. amara in the Neotropics

To complete the diffusion and subsequent biogeography of *Q. amara*, we reviewed its uses in South and Central America. Throughout the Neotropics, it is used for a wide range of affections such as fever, snakebites (US-de Bruijn 1042; US-Romero Castaneda 604), diarrhea, urinary infections, diabetes and stomach pain (Coe and Anderson, 1996; Girón et al., 1991; House et al., 1995). According to Pittier (1908), the plant was one of the most commonly used remedies by the native communities in Costa Rica, where it was employed to heal cold sores and as an aperitive, and Duke (2008) also reported its use against hangovers. It was found as a remedy against fevers in Panama in 1924 (US-Kluge 36), and against malaria in Nicaragua in 1946 by natives of the Isla Zapatero and in 1990 in the Rio San Juan area (MO-Grijalva, 1946; MO-Salick 7832). In Mexico, it was found in a herbalist store in the Monterrey area and sold to stimulate drainage of the gall bladder (MO-Breen 1077). Few uses were registered in Venezuela, but it was used in 1944 in Tumeremo (Bolivar) to treat fevers and hemorrhages (F-Steyermark 60,962) and in 1954 in Perija (Zulia) against "*calenturas*", probably also referring to fever (F-Aristeguieta et al., 2110).

In Suriname, it is widely found on the markets of Paramaribo and Albina (van Andel et al., 2007), where carved wooden cups called *kwasi bita bekers* are sold to be filled with water or rum (Fig. 3). The content is drunk as a bitter tonic, stomachic or remedy against fevers (Odonne et al., 2007). The wood is also a frequent ingredient of bitter aphrodisiac bottles (van Andel et al., 2012b) (Fig. 3). These cups allow the Saamaka Maroons to perpetuate their great ability in wood carving, an undeniable African heritage (Price et al., 2005).

This practice of shaping goblets was also current in Guyana in 1934, as retrieved from a specimen label (US-Archer 2615), stating that bitter cups shaped like wine glasses were filled with cane juice distillate and the extract used as a substitute for quinine, which was confirmed by another specimen label from 1955 (US-Little 16,700).

In French Guiana, the wood of *Q. amara* was once thought to be mainly a Creole remedy (Grenand et al., 2004), but it recently emerged as the fifth most cited medicinal species, among 12 of the 16 cultural groups interviewed by Tareau (2019). The bitter wood was even cited by recent Haitian migrants in Cayenne, showing the adaptation of these cultures to the medicinal flora of their new host country. *Q. amara* was also the most cited species in Saint-Georges de l'Oyapock, located at the border between French Guiana and Brazil, as a general medicinal plant (Tareau et al., 2019).

In the upper Amazonia, the plant is infused or macerated as a febrifuge (Castner et al., 1998), used to treat hepatitis in Peru (Brack, 1999) and to combat malaria, vesicular colic, intestinal gases and dyspepsia in Brazil (Gupta, 1995; Lorenzi and Matos, 2008). In brief, *Q. amara* has two main domains of uses: gastro-intestinal complaints and fevers.

3.7. Colonial and industrial uses (and the rise of taxonomical confusion)

Soon acclaimed in the 19th century European medical treaties (Gänger, 2015; Heckel, 1897; Mérat and de Lens, 1837; Reclu, 1889; Roques, 1837), *Q. amara* became popular in Europe for diverse medicinal applications. It also was employed as a bitter ingredient in beer (Heckel, 1897), which might explain its confusing names *bois d'absynthe* [absynth wood] and *bois de frêne* [ash wood] on a specimen's label from 1894 collected on Guadeloupe (US-Duss 2977). In 1869, Suriname exported 245 tons of *Q. amara* wood to Europe (Price, 1983). *Quassia* is cited in the 1820 version of the US Pharmacopeia (Hershenson, 1964), but with the species name *Q. excelsa*, which may refer to another Simaroubaceae (*Picrasma excelsa* Planch.) with which *Q. amara* was often mistaken or adulterated in the 19th century (Ocampo and Mora, 2011). This confusion is also observed in the Brazilian Pharmacopeia from 1926 (Brandão et al., 2013), as well as in products sold in other places of the world (Fig. 4) and acknowledged by Duke (2008).

Around the middle of the 19th century (Crookes, 1860), "tonic cups", "tonic goblets" or "*Quassia* cups" where sold against both

Fig. 3. Carved medicinal cup made from *Q. amara* wood and an aphrodisiac bottle containing pieces of wood from the same species. Picture: G. Odonne.

Fig. 4. 19th century box of "*Quassia*" chips with two different scientific names (© The Field Museum of Natural History - Botany Department - Catalog Number: 1,970,701. CC BY-NC).

gastro-intestinal complaints and fevers in drugstores in the US, Canada and UK (Fig. 5). However, defining the species used for each of these wooden cups is difficult. They are unlikely to be all made from *Q. amara* wood, as they differ in size, color and wood structure (Odonne et al., 2007). One of the most challenging issues in historical (ethno-)pharmacology is to ensure the correct identification of plants in plant-based remedies. The world history of plant trade and pharmacy is a story of drug adulteration and frauds, associated to the carelessness of some plant providers. Many mismatches between names also originate from the use of different languages. Possibly, the current local uses of *Q. amara* have been influenced by these 19th/20th century uses, in a kind of retroactive knowledge hybridization, although this is difficult to prove.

3.8. Related species in the Neotropics

Several other species in the Simaroubaceae family are used as medicinal plants in tropical America, occasionally sharing folk names, uses, morphological or chemical properties, in what Bye et al. (1995) call a "medicinal plant complex". The most salient species, due to its frequent confusion with *Q. amara* for centuries, is *Picrasma excelsa* (*Jamaican quassia*, Figs. 4 and 5), which is still a popular medicinal plant in Jamaica today (Ocampo and Mora, 2011; Picking et al., 2015). In the Guiana shield, *Simarouba amara* Aubl. is a tree up to 40 m, with similar white and bitter wood that is used against malaria in French Guiana (Gentry, 1996; Grenand et al., 2004). *Picrolemma sprucei* Hook. f. is a shrub or small tree (1–10 m) with orange fruits (Berry, 2005), of which the wood is used against diabetes and fever in Amazonia (Grenand et al., 2004), and sometimes replaces *Q. amara* in French Guiana. *Picramnia pentandra* Sw. is a shrub or small tree (1.5–8 m) named *bwa mondong* ("wood of the African Mandingo cultural group") in Martinique, where it grows in xerophytic forests on basaltic substrate (Fournet, 1978). This name explicitly refers to its use by enslaved Africans, and both in Martinique (Nossin, 2019) and Cuba (Cabrera, 1993), this species is a popular ritual plant among people of African descent. In Cuba, it is also used against fevers (Cabrera, 1993).

3.9. Out of Africa?

Several Neotropical plant species have been named by enslaved Africans after botanically related species in Africa (van Andel et al., 2014). This recognition of New World medicinal species by analogy with related Old World species is a perfect illustration of a cultural hybridization process (Stockhammer, 2012), and it could be a plausible scenario that enslaved Africans recognized *Q. amara* in Suriname because they knew the properties of a related African species: *Quassia africana*. This would be concurrent with what Chevalier and Russell (1936) wrote on this topic with an intuition whose accuracy was perhaps underestimated at the time: "*Isn't it a noteworthy fact that the use of the bitter wood provided by the Simaroubaceae among the primitive peoples* [sic] *of both Tropical America and Black Africa?*" The American *Q. amara* was only recently introduced in Africa, and nearly all the specimens are cultivated (e.g. from Ivory Coast: L-Leeuwenberg 3829) or clearly stated as imported, such as the Ghanaian specimen from 1972 that was introduced from Brazil (L-Cudjoe 588).

Q. africana is mainly distributed in Central Africa: the Democratic Republic of Congo, the Republic of Congo, Gabon, Cameroon and Equatorial Guinea (GBIF, 2020b). There, it is used as an antimalarial (Mbatchi et al., 2006), febrifuge (Musuyu Muganza et al., 2012), and against diarrhea, worms, stomach pains and as a tonic (Longanga Otshudi et al., 2000; Bajin ba Ndob et al., 2016). This corresponds to current uses of *Q. amara* in the Guiana shield (Grenand et al., 2004; Odonne et al., 2007; Tareau, 2019), which makes the hypothesis that enslaved Africans (instead of Amerindians) discovered its medicinal uses more credible.

However, the most salient uses of *Q. africana* that emerges from herbarium voucher labels are to treat lice (quoted 10 times), digestive disorders (7), worms (4), fever (3), poisoning (3), sexually transmitted diseases (2), and other ailments (3). Given the diverse uses of *Q. africana* and its occurrence in a region where many slave traders were purchasing their captives (Warner-Lewis, 2003), it is surprising that none of the Central African names for *Q. africana* were transferred to *Q. amara* in the Americas. The transfer from Africa to America is eventuality possible explanation for gastrointestinal-related disorders only, which are in both places the most frequently treated disorders with these species. Our hypothesis, however, is nevertheless not supported by the absence of any local American names for *Q. amara* (Table 1) to the hundred names reported for *Q. africana* (Appendix B). However, most local names for *Q. africana* are from Central Africa and the Bantu linguistic family. As Kwasi probably had an Akan-speaking (West African) origin, he or fellow Akan-speakers may not have recognized this Central African species.

The discrepancy between the few early 20th century specimens mentioning African uses of *Quassia* against fevers, and the many contemporary references that claim it, suggest a possible cultural transfer from *Q. amara* to *Q. africana*, i.e. from America to Africa. Did the colonial trade of *Q. amara* bitters stimulate the use of the botanically related African species? The massive worldwide use of bitter *Cinchona* barks from the 17th to the 19th century, and the subsequent use of its isolated bitter component quinine from the mid-19th onwards as a treatment against malaria, may have shaped a post-colonial cognitive relationship between malaria treatment and bitterness. Such a relation is observed every day in field interviews when speaking about malaria and its herbal remedies, for which bitterness is often sought after. The connection between bitterness and malaria may have a historical base (Cosenza et al., 2013).

3.10. Perspectives for cultural biogeography

"Cultural biogeography" is an interesting concept to reconstruct the dynamics of biocultural interactions through space and time. In this particular case, relying on herbarium databases helps to decipher the "evolution" of medicinal plant use, particularly for the last few

Fig. 5. Early 20th century tonic cup, probably from *Picrasma excelsa* (© The Field Museum of Natural History - Botany Department - Catalog Number: 271,505. CC BY-NC).

centuries, and to understand the ecological niches (primary or secondary forests) and domestication status of plants (cultivated, escaped from gardens, etc.). Some major limitations of herbarium labels, however, is the scarce ethnobotanical information provided, the bias of the botanical collector and the fact that the recorded plant use is often based on the knowledge of a single person. Historic specimens often come without detailed locality data, local names or uses, but valuable information emerges when huge quantities of specimens are reviewed.

A next step in tracing the details of the origin and spread of *Q. amara* would be to perform DNA analyses on herbarium specimens, as genetic tools now allow to precise the ancient geographical origin of useful species and trace pre- and postcolonial exchange networks and other long-time movements of plants and people (Clement et al., 2017; Moreira et al., 2017; Przelomska et al., 2020; Rossetto et al., 2017; Roullier et al., 2013b). The field of Historical genomics (Brousseau et al., 2020) can decipher long-term migrations of plants, and indicate domestication events or strong biocultural interactions (van Andel et al., 2016). Molecular studies on herbarium samples would shed more light on the genetic distance between *Q. amara* samples from the Guiana Shield and Central America, which can reveal historic migration routes. In our case, DNA barcoding could also help to identify the wooden objects in museums labelled as "*Quassia*".

Linguistics, and particularly paleobiolinguistics, is a useful tool to study cultural biogeography, but so far is only applied to trace back the origins of food crops (Brown et al., 2013a; 2013b; Westengen et al., 2014). Interdisciplinary studies are needed more than ever to unravel complex itineraries of plants and people (Perrier et al., 2011), as represented in the archaeobotany of both physical remains and pictorial representations (Hather, 2010), and in the study of ancient DNA (Brown et al., 2015; Przelomska et al., 2020) or in anthracology (Bodin et al., 2020).

4. Conclusion

Our research points out that *Quassia amara*'s uses are difficult to attribute to a particular cultural group: the species is widely distributed in Central and South America, where it is popular among many indigenous and non-indigenous groups. Based on our results, we conclude that *Q. amara* was spread during the early 18th century due to political and economic reasons. This spread is possibly the result of simultaneous actions by European colonists from Central America to northern South America and by Carib-speaking Amerindians from northern South America to Suriname, where Kwasi increased its fame as an antimalarial around 1730. From there, it spread southeast towards French Guiana (in 1772) and Brazil in the 19th century (maybe via São Luis or Belem, the main harbors on the North), and in the beginning of the 19th century, to the rest of the world. The presence of *Cinchona* spp. in Southern Colombia, Ecuador and Peru may have caused little interest in *Q. amara*, and prevented a successful introduction in that region. Today, the species is cultivated throughout the tropics, both for domestic medicine and for pharmaceutical applications.

The absence of African-derived local names in the Guiana shield suggests that enslaved Africans in the Guiana shield were not familiar with *Q. africana* to have preserved its name and transferred this to *Q. amara*. The "discovery" of the medicinal properties of *Q. amara* in Suriname seems, thus, to be a knowledge transfer to a West African by

Carib-speaking Amerindians, who may have imported the species for medicinal reasons. However, no documented traces remain of this event.

Cultural biogeography had proven an interesting concept to reconstruct the dynamics of biocultural interactions through space and time. Herbarium databases have proved useful to decipher evolution of local knowledge in our research. Nevertheless, given the current threats to ethnobotanical (and ethnoecological) knowledge, it is time to react with an inclusive approach fostering the preservation of biocultural diversity more broadly. Explaining the species, their uses, and their associated knowledge as global biocultural heritage, and engaging efforts toward a better comprehension of their history, may help avoid counterproductive political standstill.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jep.2020.113546.

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