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Article

Evidence of Hybrid Origin for Domesticated *Spondias* (Anacardiaceae) Taxa from Northeastern Brazil: A Picture of Ongoing Domestication of Fruit Species

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Abstract

Hybridization is considered an important process in plant evolution, especially in the origin domesticated plant taxa, with many crop species being the result of interspecific hybridization events. There are several unidentified lineages of *Spondias* in the Northeastern region of Brazil known only by vernacular names such as 'cajaguela', 'umbu-cajá', and 'umbuguela'. These taxa are often regarded as being of hybrid origin, based on supposedly intermediate morphological features. However, the morphology-based hypotheses of hybrid origin and parentage of these *Spondias* taxa remains largely untested experimentally. We collected 355 accessions of *Spondias* including the putative hybrid taxa and both native and introduced species. We then reconstructed phylogenies of plastid and nuclear markers, and also haplotype networks in order to ascertain the genetic affinities between putative hybrids and other *Spondias* species. All taxa with intermediate morphology were confirmed as hybrids between their putative parental species. All hybrids involving *S. purpurea* (native to Mexico) appear to be F1 generation. The recently described *Spondias bahiensis* is shown to have originated from hybridization between *S. tuberosa* and *S. venulosa*. The other 'umbu-cajá' taxon found in Northeastern of Brazil is revealed to be the result of hybridization between *S. mombin* and *S. tuberosa*. Both the northern 'umbu-cajá' taxon and *S. bahiensis* appear to be well-established hybrid lineages and not early generation hybrids. Additionally, some introgression and backcrossing processes between *S. bahiensis* and one of the parents was also observed. Our findings confirm the hybrid origins of the domesticated *Spondias* taxa found in Northeastern Brazil.

Keywords: *Spondias*; hibridization; domestication; Northeastern Brazil; Caatinga

1. Introduction

Hybridization is considered an important process in shaping the evolutionary trajectory of angiosperm evolution, to the point that a majority of all plant species have been suggested as derived from past hybridization events (e.g., [1–8]). Hybridization is of particular importance in the creation of domesticated plant taxa, with a number of staple foods, such as wheat [9], being of hybrid origin. Interspecific hybridization is also at the origin of many tree crop species [10] and has been a powerful force in the evolution of domesticated perennials. Examples of hybrid tree crops range from apples (*Malus domestica* Borkh.; [11–13]), bananas and plantains (*Musa paradisiaca* L.; [14–16], kiwi fruit (*Actinidia deliciosa* (A.Chev.) C.F.Liang & A.R.Ferguson; [17–19]), and various *Citrus* L. crops such as grapefruit (*C. paradisi* Macfad.), lemon (*C. limon* (L.) Osbeck), Mexican lime (*C. aurantiifolia* (Christm.) Swingle), sweet orange (*C. sinensis* (L.) Osbeck), sour orange (*C. aurantium* L.), and willowleaf mandarin (*C. deliciosa* Ten.) ([20–23]). Further examples are listed in Table 2 of [10].

Spondias L. (Anacardiaceae) comprises ca. 18 species native to tropical areas of the Americas, Asia, and Madagascar [24]. All *Spondias* species possess edible fruits, and some of the species are highly valued for the very agreeable taste of their fruits; these species are therefore widely cultivated both on a regional scale (e.g. *S. pinnata*, *S. tuberosa*) and pantropically (*S. dulcis*, *S. mombin*, *S. purpurea*). Eleven *Spondias* species are found in Brazil: three are introduced and cultivated and eight are native to the country, of which three are Brazilian endemics (Table 1). Hybridization in *Spondias* has so far only been documented between *S. mombin* and *S. purpurea* [25,26], with the hybrid product of this cross described as *Spondias* × *robe* [27].

Table 1. *Spondias* species found in Brazil. Species marked with a plus sign (+) are introduced. Species marked with an asterisk (*) are Brazilian endemics restricted to the Eastern regions of the country.

mark	Species	Distribution
*	<i>Spondias admirabilis</i> J.D. Mitch. & Daly	Atlantic Forest of Rio de Janeiro, Brazil (Mitchell & Daly 2015) [149] Originally from Society Islands (Kostermans 1991 [150]), Polynesia (Campbell & Sauls 1994 [151]), widely cultivated pantropically.
+	<i>Spondias dulcis</i> Parkinson	Atlantic Forest of Espírito Santo and Minas Gerais, Brazil (Mitchell & Daly 2015) [149]
*	<i>Spondias expeditionaria</i> J.D. Mitch. & Daly	W Amazonia; outlier in Zulia, Venezuela (Mitchell & Daly 2015) [149]
+	<i>Spondias pinnata</i> (L.f.) Kurtz	Originally from India to Myanmar and Thailand (Kostermans 1991) [150], sporadically cultivated elsewhere, in Brazil found in a few collections.
+	<i>Spondias purpurea</i> L.	Originally from Mexico and Central America (Miller & Schaal 2005) [25], widely cultivated pantropically. Brazil, found in humid forests in southern Bahia, Espírito Santo, southeastern Minas Gerais and Rio de Janeiro states.
*	<i>Spondias macrocarpa</i> Engl.	Widely distributed in the neotropics, naturalized in parts of Africa (Duvall 2006) [152], widely cultivated pantropically.
	<i>Spondias mombin</i> L.	Restricted to a small area in Bolivia (Pando), Brazil (Acre), and Peru (Huanuco, Ucayali) (Mitchell & Daly 1998) [153].
	<i>Spondias testudinis</i> J.D.Mitch. & Daly	Brazil, found in most states of Northeastern Brazil and in the northern region of Minas Gerais state, growing in the Caatinga seasonally dry woodlands; sporadically cultivated elsewhere.
*	<i>Spondias tuberosa</i> Arruda	Brazil, occurring in semi-deciduous forests in Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro states.
*	<i>Spondias venulosa</i> (Engl.) Engl.	

In the Northeastern region of Brazil area some taxa of *Spondias* which are known only by vernacular names such as ‘cajaguela’, ‘umbu-cajá’, and ‘umbuguela’. These plants appear to occur exclusively in cultivation, being actively maintained and propagated by man, and can thus be considered as domesticated [28]. These taxa are often regarded as being of hybrid origin, with basis on seemingly intermediate morphological features displayed by these plants; the vernacular names applied to these plants clearly reflect this hence ‘cajaguela’ is regarded as a hybrid between ‘cajá’ (*S. mombin*) and ‘ciriguela’ (*S. purpurea*), ‘umbu-cajá’ a hybrid between ‘cajá’ (*S. mombin*) and ‘umbu’ (*S. tuberosa*), and ‘umbuguela’ a hybrid between ‘ciriguela’ (*S. purpurea*) and ‘umbu’ (*S. tuberosa*). However, two distinct taxa share the vernacular name ‘umbu-cajá’ [28,29]: a northern ‘umbu-cajá’ taxon whose center of diversity lies within the states of Ceará, Paraíba, Piauí, and Rio Grande do Norte, and a southern ‘umbu-cajá’ taxon whose center of diversity lies within the state of Bahia. The northern ‘umbu-cajá’ taxon is also found in Alagoas, Pernambuco, Maranhão, and Sergipe states, as the result of introduction and cultivation by man; likewise, the Bahian taxon is also found in northern Minas Gerais, Pernambuco and Sergipe (Figure 1). The two taxa differ considerably in gross morphology, including the dimensions of the plants, leaf size, number and morphology of leaflets, and morphology of inflorescence and fruits. Due to the fact that both taxa possess the same vernacular name, there is much confusion in the literature, with authors investigating one taxon often citing studies where the other taxon has been investigated instead. The southern ‘umbu-cajá’ taxon from Bahia was discovered to be more closely related to *S. venulosa* and described as *Spondias bahiensis* [28]. This taxon, in a karyological study, displays exclusive band in relation to both putative parents [30], which was considered an evidence for the recognition in specific status.

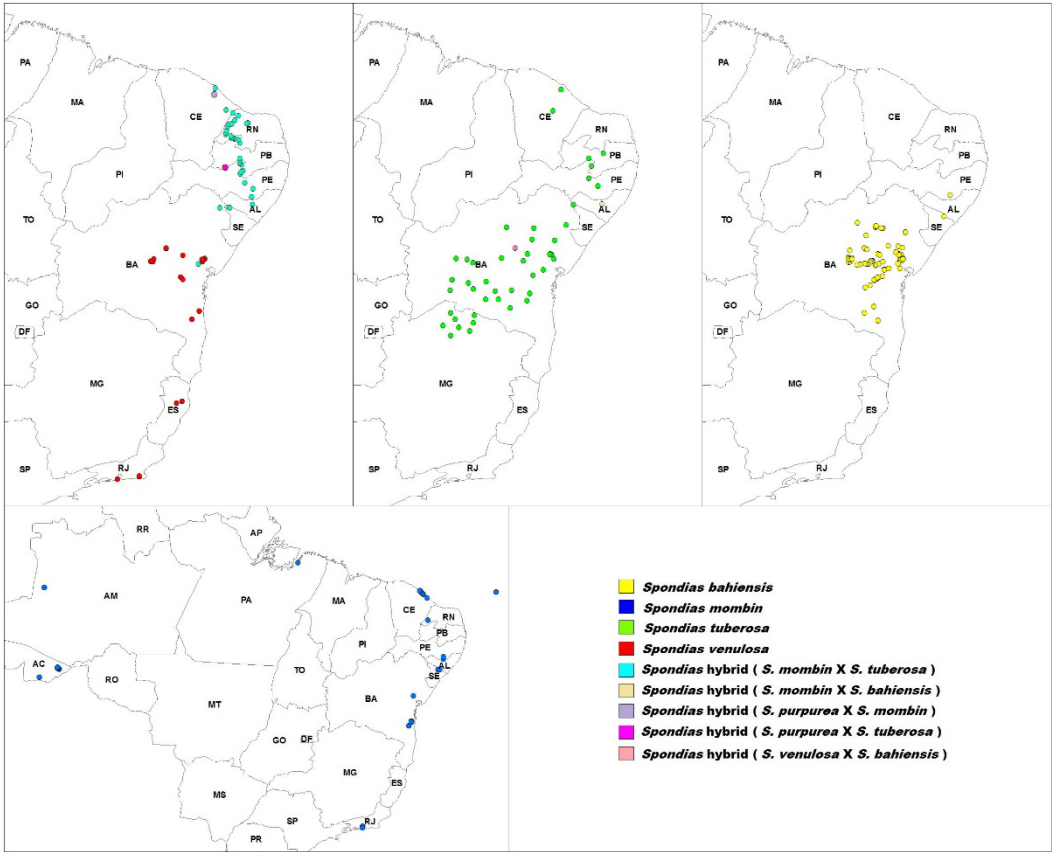


Figure 1. Maps of distribution of the *Spondias* taxa collected for this study. States contours are shown in black, and state acronyms are: AC. Acre; AL. Alagoas; AM. Amazonas; AP. Amapá; BA. Bahia; CE. Ceará; DF. Distrito Federal; ES. Espírito Santo; GO. Goiás; MA. Maranhão; MG. Minas Gerais; MS. Mato Grosso do Sul; MT. Mato Grosso. PA. Pará; PB. Paraíba; PE. Pernambuco; PI. Piauí; PR. Paraná; RJ. Rio de Janeiro; RN. Rio Grande do Norte; RO. Rondônia; RR. Roraima; SE. Sergipe; SP. São Paulo; TO. Tocantins. See Table S1 for locality and voucher information.

These putative hybrid taxa are maintained in cultivation because of their desirable features, such as thick, juicy mesocarp, lower acidity, and distinct aroma and flavor. The fruits are consumed locally and also marketed both locally and regionally. Fruits are eaten fresh, and also used to make juices, jams and other products. The growing interest in these plants as commercial crops have encouraged initiatives aimed at characterizing and implementing germplasm collections with the purpose of propagating and preserving the existing genetic diversity, and also to promote the cultivation of these taxa [31–40]. In this context, the establishment of the origins and affinities of the putative hybrid taxa can not only contribute insights into their evolution but also ways for improving these crops, by suggesting what pathways could be taken for breeding superior *Spondias* varieties with enhanced characteristics such as larger, juicier, less acid, quicker maturing fruits, and increased appeal due to higher variation in fruit shape, color, aroma and flavor. Therefore, in this study we employ molecular analyses of plastid cpDNA and nuclear ribosomal nrDNA regions to test the morphology-based hypotheses of hybrid origin and parentage of the *Spondias* spp. taxa found in Northeastern Brazil.

2. Results

In the phylogenies reconstructed without the inclusion of 'taxon genetic classes' TGCs (see materials and methods) from any putative hybrid taxa, both cpDNA and ETS data reveal strongly supported clades corresponding to the grouping of TGCs of each of the recognized species, and no significant differences are observed in the topologies between the cpDNA and ETS datasets (data not shown). Figure 2 shows the resulting cpDNA and ETS consensus trees including all TGCs. Statistics of the matrices and parsimony analyses of the full combined cpDNA and ETS datasets are summarized in Table 2. For all recognized species, every TGC belonging to the species was placed in a well-supported but usually non-exclusive clade that also included TGCs belonging to putative hybrid taxa. None of the putative hybrids had their TGCs resolved in a well-supported clade. In both cpDNA and ETS datasets, no TGCs belonging to one of the recognized species were placed in clades composed of TGCs belonging to a different species. A high degree of incongruence between datasets was observed for the putative hybrid taxa: TGCs belonging to a putative hybrid which were resolved in a clade of one species in the cpDNA dataset, were often resolved in the clade of a different species in the ETS dataset (Figure 2).

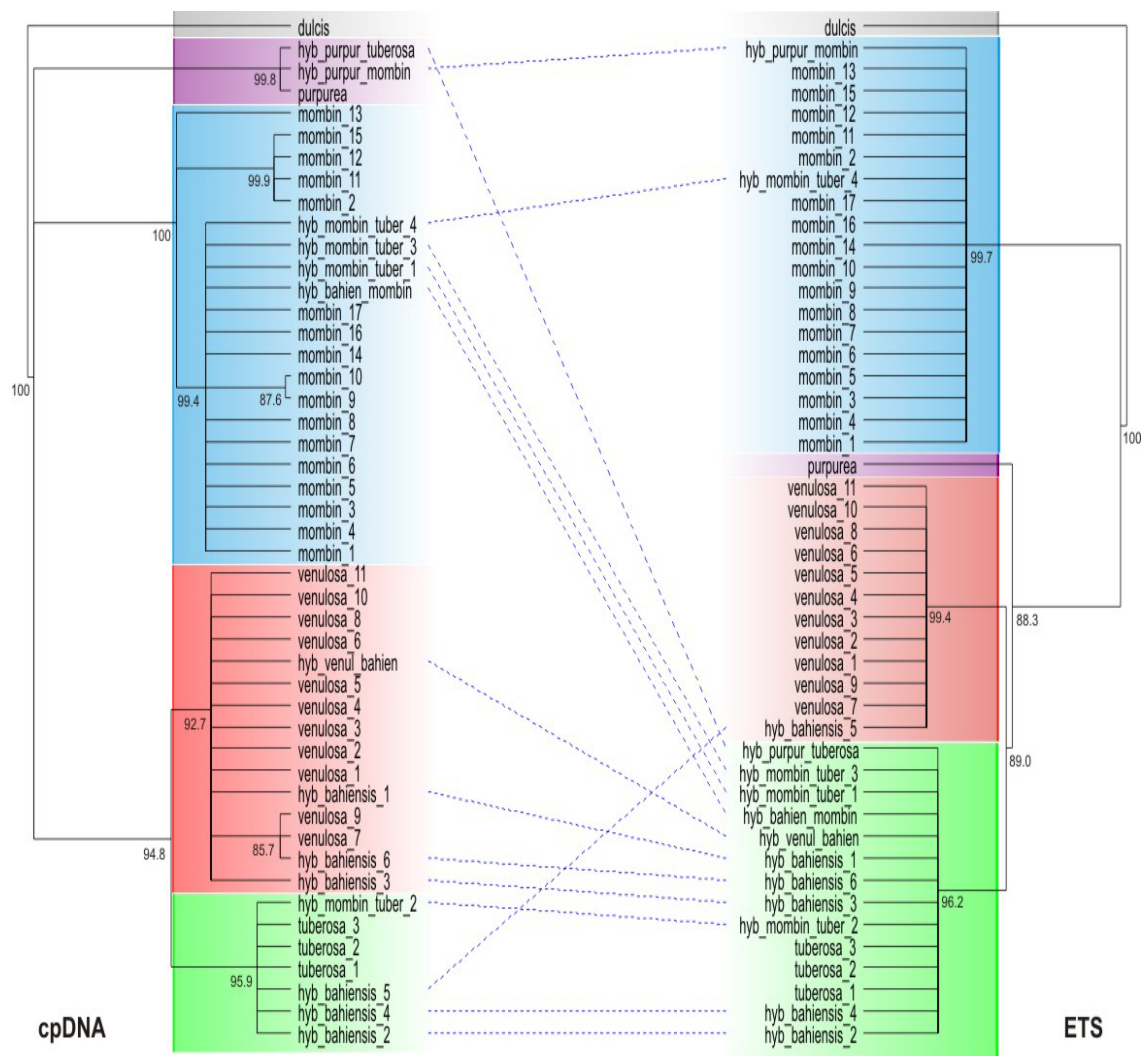


Figure 2. Majority rule consensus bootstrap trees from the parsimony analyses of the cpDNA (left) and ETS (right) datasets using taxon genetic classes (TGCs) as terminals. Bootstrap support values above 80% are displayed below the branches. Different colors are given to clades consisting of TGCs belonging to one species and associated hybrid taxa (identified by the prefix “hyb_”). Blue dotted lines connect TGCs from each hybrid taxon from one tree to the corresponding TGCs in the other tree.

Table 2. Statistics of the parsimony analyses of the cpDNA and ETS datasets.

	cpDNA dataset	ETS
Total number of characters	1590	371
Number of constant characters	1509	331
Number of substitutions	81	40
Number of parsimony-uninformative characters	22	13
Number of parsimony-informative characters	59	27
Number of indels	32	4
Size range of indels	1–96	2–3
Number of trees retained in heuristic search	11	2

Tree length	89	49
Consistency index (CI)	0.9438	0.8776
CI excluding uninformative characters	0.9254	0.8286
Retention index (RI)	0.9926	0.9855

Figure 3 depicts the haplotype networks reconstructed from the cpDNA and ETS matrices, both with and without the inclusion of accessions belonging to the putatively hybrid *Spondias* spp. taxa. The cpDNA and ETS haplotypes identified for each accession are listed in Supplementary Table S1. In the haplotype networks reconstructed excluding the putative hybrid taxa (Figures 3A,C), each of the recognized species possessed a distinct set of haplotypes – no haplotypes were found which were shared between distinct species. In the cpDNA network (Figure 3A), *S. dulcis* is represented by one haplotype, *S. mombin* by eight haplotypes, *S. purpurea* by one haplotype, *S. tuberosa* by two haplotypes, and *S. venulosa* by six haplotypes. In the ETS network (Figure 3C), *S. dulcis* is represented by one haplotype, *S. mombin* by six haplotypes, *S. purpurea* by one haplotype, *S. tuberosa* by one haplotype, and *S. venulosa* by two haplotypes. In the haplotype networks reconstructed including all accessions (Figures 3B,D), all the putative hybrid taxa share haplotypes with the recognized species, and there are no haplotypes exclusive to the putative hybrid taxa except for haplotypes H_19 and H_20 in the cpDNA network (Figure 3B), which are exclusive to *S. bahiensis*.

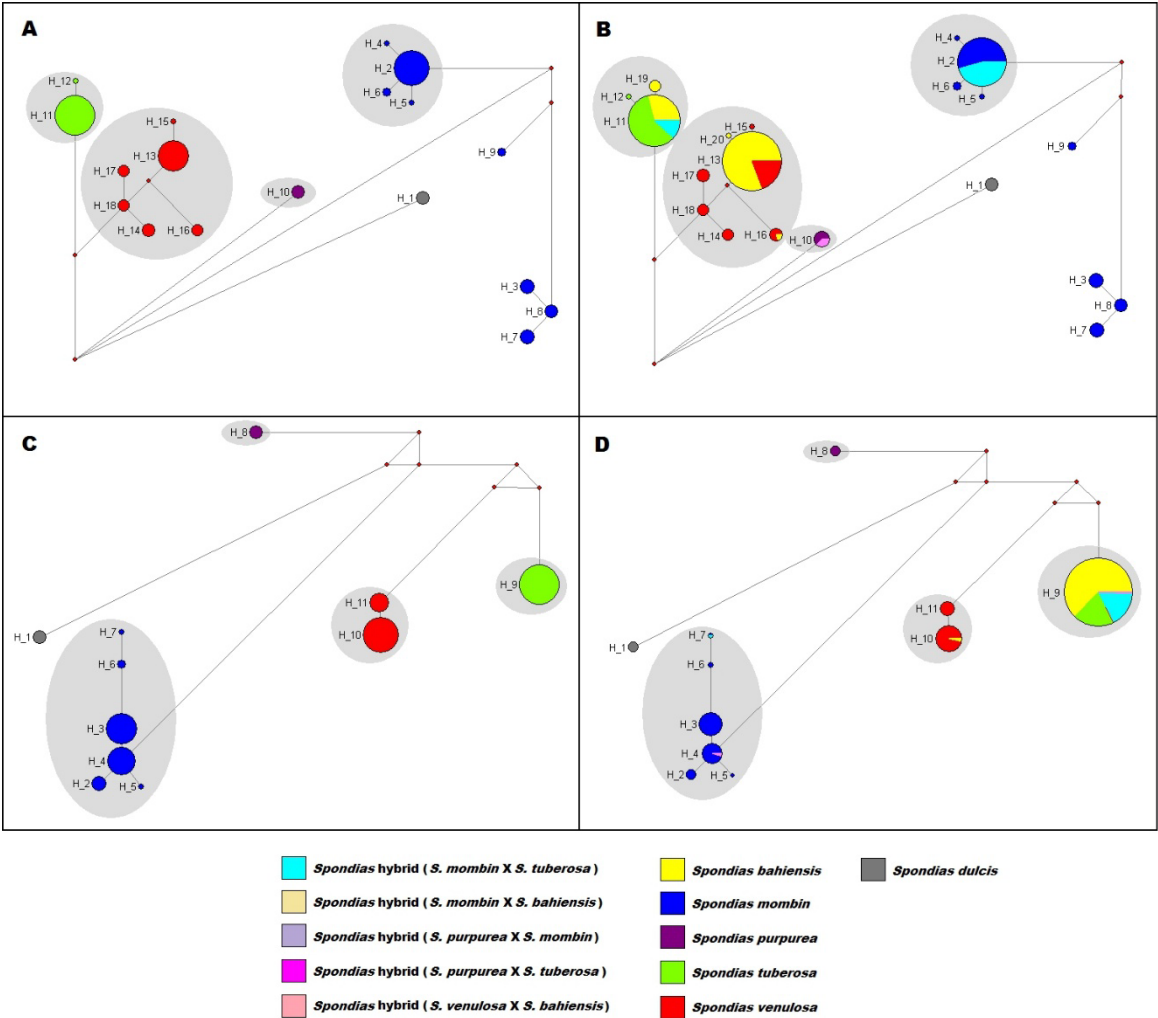


Figure 3. Haplotype networks reconstructed from cpDNA (A and B) and nuclear ETS (C and D) sequences obtained from the sampled taxa. A and C. Haplotype networks reconstructed using only the accessions belonging to recognized species (*S. dulcis*, *S. mombin*, *S. purpurea*, *S. tuberosa*, *S. venulosa*). B and D. Haplotype

networks reconstructed using all accessions – including accessions from the putatively hybrid *Spondias* spp. taxa. Shading is applied to show the groups of haplotypes belonging to a species which are shared with the putative hybrid taxa.

The majority of the individuals sampled for *Spondias bahiensis* (123 accessions) shared cpDNA haplotypes with *S. venulosa* (Figures 3B and 4A) and ETS haplotypes with *S. tuberosa* (Figures 3D and 4A). Of these accessions, 121 possessed the most common cpDNA haplotype of *S. venulosa* (H_13) and the most common ETS haplotype of *S. tuberosa* (H_09). One accession of *S. bahiensis* (Spo.bahie_2437.03) shared with *S. venulosa* a different cpDNA haplotype (H_16), but shared the same ETS haplotype with *S. tuberosa* (H_09) as the other accessions. A single accession of *S. bahiensis* (Spo.bahie_2263.23) possessed an exclusive cpDNA haplotype, H_20, which is linked by one mutational step to the most common cpDNA haplotype found in *S. venulosa* (H_13); the ETS haplotype of this accession was also the most common ETS haplotype found in *S. tuberosa* (H_09).

A total of 25 accessions of *S. bahiensis* shared both cpDNA and ETS haplotypes with *S. tuberosa*; of these, 23 accessions shared with *S. tuberosa* the most common haplotypes found in this species in both the cpDNA (H_11) and ETS (H_09) datasets. Four accessions of *S. bahiensis* possessed an exclusive cpDNA haplotype, H_20, which is linked by one mutational step to the most common haplotype found in *S. tuberosa* (H_11); three of these accessions shared the ETS haplotype H_09 with *S. tuberosa*, while one accession (Spo.bahie_2394.05) shared the ETS haplotype H_10 with *S. venulosa* (the most common ETS haplotype in this species).

The majority of the individuals sampled for the northern ‘umbu-cajá’ taxon (29 accessions) shared haplotype with the most common cpDNA haplotype of *S. mombin* (H_02; Figures 3B and 4A) and the ETS haplotype with the most common ETS haplotype of *S. tuberosa* (H_09; Figures 3D and 4A). Nine accessions of the northern ‘umbu-cajá’ taxon possess the most common haplotypes of *S. tuberosa* both in the cpDNA (H_11) and ETS (H_09) datasets. One accession (Spo.xmotu_2446.03) shared both cpDNA and ETS haplotypes with *S. mombin*: its cpDNA haplotype was the most common found in *S. mombin* (H_02) while its ETS haplotype was a rare haplotype found in *S. mombin* (H_07).

The putative hybrids involving *S. purpurea* (‘cajaguela’ and ‘umbuguela’) shared the cpDNA haplotype of *S. purpurea*, with ‘cajaguela’ sharing with *S. mombin* the ETS haplotype H_04, and ‘umbuguela’ sharing with *S. tuberosa* the most common ETS haplotype found in this species (H_09). The putative hybrid between *S. venulosa* and *S. bahiensis* possesses the most common cpDNA haplotype of *S. venulosa* (H_13) and the most common ETS haplotype of *S. tuberosa* (H_09). The putative hybrid between *S. mombin* and *S. bahiensis* possess the most common cpDNA haplotype of *S. mombin* (H_02) and the most common ETS haplotype of *S. tuberosa* (H_09). Figure 4 summarizes with which of the recognized species each accession of the putative hybrid taxa share haplotypes in both the cpDNA and ETS networks.

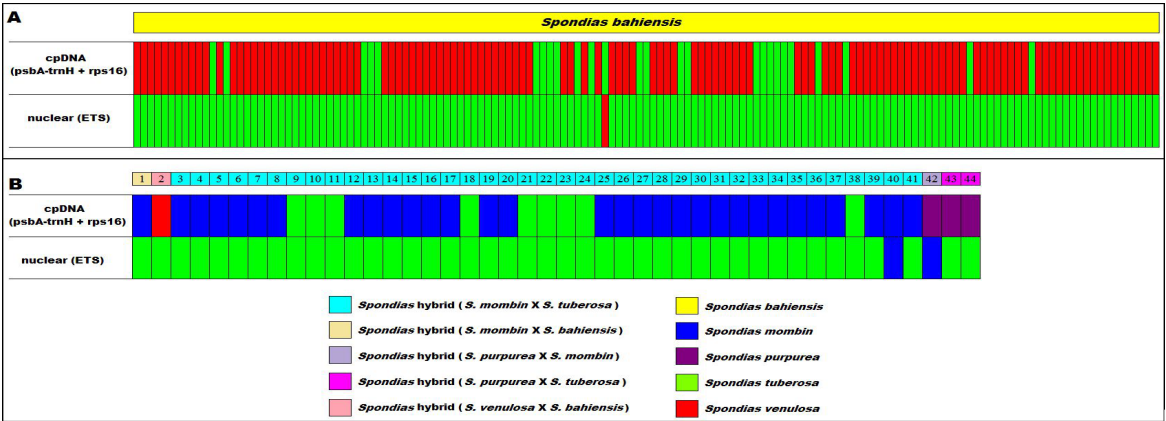


Figure 4. Accessions of the putative hybrid taxa and with which of the recognized species each accession share haplotypes in both the cpDNA and ETS networks.

3. Discussion

3.1. Hybrid Origins of *Spondias* Taxa Found in Northeastern Brazil

Interspecific hybrids are most commonly identified by topological discordance between phylogenies reconstructed from sequences of nuclear and plastid regions, with relationships to different species recovered for the phylogenies from each data partition, denoting distinct parental contributions to the hybrid genome. Such cytonuclear incongruence is generally taken as evidence confirming morphology-based hypotheses of hybrid origin [41–56]. Nuclear alleles are biparentally inherited, whereas plastids are typically inherited from the female (seed) parent in most families of angiosperms [57–59]. Due to the biparental mode of inheritance of nuclear regions, newly formed hybrids potentially possess copies from both parental species and thus their DNA sequences are expected to display an additive pattern, creating polymorphic sites where the two parental species differ in their sequences [53,60]. No polymorphic sites were found in the ETS sequences from the putative hybrid taxa, what is probably the result of homogenization to one parental ETS type due to widely reported mechanisms of concerted evolution [60]. Homogenization by concerted evolution normally take a period of many generations to complete, but it can also occur rather quickly [61,62], with nuclear sequences of one parent becoming fixed [53,60].

Topological discordance between the cpDNA and ETS phylogenies was found for most TGCs of the putative hybrid *Spondias* taxa, with TGCs placed in one clade with one of the recognized species in the cpDNA phylogeny, but clustered with a different species in the ETS phylogeny (Figure 2). Moreover, two of the putative hybrid taxa (the northern umbu-cajá taxon and *S. bahiensis*) displayed TGCs distributed in different clades (and therefore associated to different species) in both the cpDNA and ETS phylogenies (Figure 2), indicating multiple origins for the individuals assigned to these taxa. The haplotype networks (Figure 3) also show that the distribution of haplotypes between the different partitions of the genome is markedly incongruent among the accessions of the putative hybrid *Spondias* taxa. Individuals belonging to the hybrid taxa usually shared haplotypes with one of the recognized species in one dataset, then with a different species in the other dataset (Figure 3). It is noteworthy that there is no sharing of haplotypes nor topological discordance between the recognized species when the putative hybrid taxa are removed from the analyses (Figure 3A,C). These results lend support to the hypothesis, inferred from the morphological features of these taxa, that they originated from events of hybridization between the recognized species.

Maternal inheritance of cpDNA occurs in about 80% of angiosperms [57–59] and *Spondias* species are assumed to follow this pattern. This assumption is confirmed by the patterns involving *Spondias purpurea*. In natural populations of this species, the individuals as dioecious with a predominance of male trees and sexual reproduction, whereas in cultivation all trees are female and exclusively vegetatively propagated, with fruits produced via parthenocarpy [10,63,64]. Hybrids involving

cultivated *S. purpurea* are therefore expected to always have this species as the seed parent. If maternal cpDNA inheritance occurs in *Spondias* then all hybrids involving *S. purpurea* should possess the cpDNA haplotypes of this species. This pattern has been confirmed in the present study for both putative hybrids ‘cajagueta’ and ‘umbugueta’ (Figure 4B, accessions 42–44) share the cpDNA haplotype with *S. purpurea*, and the nuclear ETS haplotype with *S. mombin* (“cajagueta”, which is thus the same taxon as *S. × robe* Urban) and *S. tuberosa* (“umbugueta”). As a result, the putative male parents of these hybrids with basis on morphology have also been confirmed.

The majority of *Spondias bahiensis* accessions (82.55%) displayed cpDNA haplotypes of *S. venulosa* and ETS haplotypes coming from *S. tuberosa*, and nearly all of these accessions share the most frequent haplotypes of *S. venulosa* and *S. tuberosa* in the cpDNA and ETS networks respectively (Figures 3B,D and 4A). This could be indicative of a single origin for this group of *S. bahiensis* accessions, or it could simply be the result of recurring hybridization events between the most common lineages of the parental species, related to aspects of their pollination mechanism which require further study. There is evidence for the latter pattern, since two accessions of *S. bahiensis* did not share the most common cpDNA haplotype of *S. venulosa*. One of these accessions, which was collected in the southern region of the state of Bahia, had the haplotype found in *S. venulosa* accessions which were also collected in the same region. The other *S. bahiensis* accession possesses an exclusive haplotype that is linked by a single mutation to the most common *S. venulosa* haplotype; it could mean that this *S. bahiensis* lineage is old enough to have accumulated this mutation, a pattern also compatible with some exclusive bands found in its karyotype [30] or simply mean that it has a rare haplotype of *S. venulosa* that failed to be sampled in the accessions of that latter species included in our study.

Interestingly, 16.78% of the *S. bahiensis* accessions possess both cpDNA and ETS haplotypes coming from *S. tuberosa*, and most of these accessions share the most frequent haplotypes of *S. tuberosa* in the cpDNA and ETS networks. The morphology displayed by these accessions does not differ from the majority of *S. bahiensis* accessions, and also does not support the idea that these accessions could represent pure *S. tuberosa*. These accessions could represent instances of *S. bahiensis* originated from the reversed parental combination observed in the majority of accessions (that is, having *S. tuberosa* as the seed parent and *S. venulosa* as the pollen parent), and homogenization of ETS sequences biased towards the *S. tuberosa* type. Alternatively, it is possible that these accessions could be the result of introgressive backcrosses between *S. bahiensis* and *S. tuberosa* with the latter as the female parent.

Three *S. bahiensis* accessions have an exclusive cpDNA haplotype that is linked by a single mutation to the most common *S. tuberosa* haplotype; the most likely explanation is that these *S. bahiensis* accessions possess a rare haplotype of *S. tuberosa* that was not sampled for the species in this study. Since the population size of *S. tuberosa* is very large, this haplotype would occur at very low frequency in the species, but because the population size of *S. bahiensis* is much smaller than that of *S. tuberosa*, the frequency of the haplotype would be higher in *S. bahiensis*, with increased probability that the haplotype would be sampled in this taxon than in *S. tuberosa*. Alternatively, this exclusive haplotype could mean that this *S. bahiensis* lineage has diverged long enough from *S. tuberosa* for a mutation to have occurred and become fixed in the cpDNA regions analyzed. Only a single *S. bahiensis* accession was found to possess the pattern of cpDNA haplotype coming from *S. tuberosa* and ETS haplotype coming from *S. venulosa*. This could represent an instance of hybridization between *S. tuberosa* and *S. venulosa* where the former was the seed parent and the latter the pollen parent. However, this accession possesses the cpDNA haplotype which was found exclusively in *S. bahiensis*; therefore, it is more likely that it represents an instance of introgression between *S. bahiensis* and *S. venulosa* with the former as the seed parent.

The majority (74.36%) of the accessions of the northern ‘umbu-cajá’ taxon have cpDNA haplotypes shared with *S. mombin* and ETS haplotypes shared with *S. tuberosa*, the haplotypes being the most frequent ones of the respective species (Figure 4B, accessions 3–8, 12–17, 19, 20, 25–37, 39, 41). This result lends support to the hypothesized hybrid origin of this taxon from crosses between *S.*

mombin and *S. tuberosa*. A smaller number of accessions (23.08%) of the northern ‘umbu-cajá’ taxon share the most frequent haplotypes from *S. tuberosa* in both cpDNA and ETS datasets (Figure 4B, accessions 9–11, 18, 21–24, 38). As with *S. bahiensis*, these ‘all tuberosa’ accessions could represent instances of hybrids originated by crossings having *S. tuberosa* as the seed parent and *S. mombin* as the pollen parent, with later homogenization of ETS sequences biased towards the *S. tuberosa* type. The alternative explanation is that these accessions are the result of introgressive hybridization between individuals of the northern umbu-cajá taxon and *S. tuberosa*, the latter being the female parent. A single accession of the northern ‘umbu-cajá’ taxon have both cpDNA and ETS haplotypes associated with *S. mombin*, which may indicate introgression in *S. mombin* or that there was homogenization of ETS sequences biased towards the *S. mombin* type (Figure 4B, accession 40).

During fieldwork carried out to collect samples for this study, we found a *Spondias* specimen whose morphological characteristics point out to a putative hybrid between *S. bahiensis* and *S. mombin*. In our data, this individual presented the most frequent cpDNA haplotype of *S. mombin* and the most frequent ETS haplotype of *S. tuberosa* (Figure 4B, accession 1). Although the results clearly indicated the hybrid origin of this taxon, they are inconclusive to determine the pollen parent of this hybrid since *S. bahiensis* has ETS haplotypes from *S. tuberosa*; however, given the morphology of the hybrid, it is assumed that the paternal parent is indeed *S. bahiensis*.

A second specimen found in the field possesses morphological features very similar to *Spondias venulosa*, however a diagnostic character of *S. venulosa* – the base of leaflets with margins distinctly revolute towards the abaxial surface and possessing a tuft of flexuous trichomes to 0.6mm long – was not present in this specimen, even though this character was present in two other specimens of *S. venulosa* growing at the locality. This locality also presented cultivated individuals of *S. bahiensis*. This suggested that the aberrant ‘venulosa-like’ specimen could actually represent a hybrid between *S. bahiensis* and *S. venulosa*. The analyses have shown that the aberrant specimen has the most frequent cpDNA haplotype of *S. venulosa* and the most frequent ETS haplotype of *S. tuberosa* (Figure 4B, accession 2). This result supports the hypothesis that the aberrant specimen could be a backcrossed hybrid between *S. bahiensis* and *S. venulosa*, since *S. bahiensis* has ETS haplotypes from *S. tuberosa*.

3.2. Mode and Time of Origin of the *Spondias* Hybrids from Northeastern Brazil

The *Spondias* hybrids found in Northeastern Brazil are spontaneous – they did not arise from intentional crosses between the species. However, we cannot discard that they could be triggered by cultivation of one or more parental species, that brings more contact between pairs of species than the original distribution in the wild. But why is Northeastern Brazil a ‘melting pot’ of hybridization in *Spondias*? Species can be found co-occurring in other regions of the country – for example, *S. mombin* and *S. purpurea* in areas of Central-Western and Northern Brazil. Why are there so many different hybrids in Northeastern Brazil? The most plausible explanation is that, due the more strict climatic conditions in with a narrow rain reason found in the region, there is more overlap in flowering periods of the different species [65], allowing interspecific crosses to take place when two or more species are grown at the same place or in close proximity. Species growing in their natural environments are recorded as having different flowering periods, which may relate to the climatic conditions found where the plants occur: flowering of *Spondias* species generally take place during the dry season [65], which vary from place to place. For example, *S. mombin* has a flowering peak in August and September in Pará [66,67] whereas *S. tuberosa* has a flowering peak in November and December in Pernambuco and Paraíba [68–70].

The question of when the hybrids originated is easier to answer for the hybrids derived from *S. purpurea*, since the introduction of the species in Brazil is rather recent, only about two centuries ago [71,72], and it did not become widely cultivated in the Northeastern region until at least one century later [73]. It is unclear when exactly *S. purpurea* was introduced in Brazil. It is possible that it was brought to the country sometime in the period 1809-1817, when French Guiana was occupied by Portugal. In this period many plants were transferred to Brazil from the botanical garden La Gabrielle in Cayenne, French Guiana, which possessed plants from a number of French colonies [74,75].

Spondias purpurea was potentially one of the many tree species grown in the La Gabrielle botanical garden since it was also grown in the French West Indies [76,77] and other areas of the Antilles [78]. The plants brought from French Guiana to Brazil were first cultivated at the Botanical Garden of Belém, Pará, in the Amazon region. Incidentally, [79] (p. 138) observed cultivated plants that could be either *S. mombin* or *S. purpurea* in Belém, Pará in 1826. D'Orbigny recorded the plants as *Spondias myrobalanus*, a name that has been applied to both *S. purpurea* and *S. mombin*; he also employed the vernacular name 'Mombin', which is again inconclusive since both species can be referred to by this name.

More mentions to *S. purpurea* started to appear in the literature in the second half of the 19th century: [72] (pp. 373–374) cited a herbarium specimen, *Riedel 103*, of a plant of *S. purpurea* cultivated in Brazil; [80] (p. 18) recommended using *S. purpurea* as a shade tree in coffee plantations; [71] (p. 237) listed *S. purpurea* and wrote: “it is a Brazilian tree that grows in the Amazon. Its fruit is red, and is known in that region as 'Mombin' and 'Spanish plum'”; [81] (p. 103–104) also mentioned *S. purpurea*, although this author made some confusion with *S. tuberosa* since he listed the vernacular names of the latter as well as the ways in which it is used. Botanist Adolpho Ducke collected *S. purpurea* in Tefé, Amazonas in 1912 (the specimen is deposited in Rio de Janeiro Botanical Garden Herbarium under number *RB20625*), and the specimen is annotated as probably being an introduction from Eastern Peru. These references to *S. purpurea* indicate that by the end of the 19th century the species was already cultivated in Brazil, but until the second half of the 20th century the species was probably not widely grown. For instance, [73,82] reported that “... its introduction in Ceará is recent, and even more so in São Paulo, where the first seeds were planted in June 1938 in the Genetic Section of the Agronomic Institute of Campinas”. *Spondias purpurea* is recorded as being cultivated in Fortaleza, Ceará around 1920 [83]. Therefore, it is safe to assume that the few known hybrids involving *S. purpurea* are either primary (F1) or early generation hybrids.

The timescale for the origin of *S. bahiensis* and the northern ‘umbu-cajá’ taxon might be slightly more complex to establish. *Spondias bahiensis* exhibits high levels of phenotypic [29,35,91–3684c] variability among different accessions [29, 35, 36 84–91] as well as considerable genetic diversity [88, 89 92–94], and kary [29,35,91–3684]typic differences in relation to both progenitor species [30]. The same applies to the northern ‘umbu-cajá’ taxon, which also display morphological [95–102] and genetic [98,103] variability. If hybridization is recent in these taxa, then it must be recurrent and widespread, and some of the variability might be the result of introgression with the parental species. Alternatively, both taxa might represent lineages created by older hybridization events.

A common statement in the literature is that these hybrids are difficult to propagate sexually because most endocarps lack viable seeds [84,86,87,89,90,93,94,96,97,101,104–109]. Some authors do not cite references [104,105,107,108] whereas the remaining authors cite the works of Souza and collaborators [31,110]. Although the majority of the studies mentioned above were carried out in *S. bahiensis*, the studies by Souza and collaborators were based on the northern ‘umbu-cajá’ taxon, evidencing the confusion stemming from both taxa having the same vernacular names. Unlike the northern ‘umbu-cajá’, *Spondias bahiensis* produces a high percentage of viable seeds [35] which germinate readily (first author, personal observation). Although plants with more desirable features are often vegetatively propagated, volunteer seedlings are tolerated in cultivation gardens and allowed to grow. Given the levels of both genetic and morphological diversity observed in *S. bahiensis* and the northern ‘umbu-cajá’ taxon, these taxa seem to represent hybrid lineages rather than primary (F1) hybrids. If this is the case then the key question is whether these hybrids arose through natural contact between the parental species or because humans intentionally or unintentionally brought them together enabling gene flow to occur between hitherto geographical or ecologically isolated species.

The parental species of *S. bahiensis* and the northern ‘umbu-cajá’ taxon are *S. mombin*, *S. tuberosa* and *S. venulosa*, with the northern ‘umbu-cajá’ taxon the result of hybridization between the former two species and *S. bahiensis* the result of hybridization between the latter two species. *Spondias mombin*, *S. tuberosa* and *S. venulosa* are ecologically confined to different habitats where they normally

do not occur in sympatry under natural conditions. *Spondias mombin* is adapted to more humid conditions and is widely distributed in the Amazon and Atlantic forests of Brazil; *S. tuberosa* is restricted to the semiarid region which encompasses all states in Northeastern Brazil and also the Northern region of Minas Gerais, occurring within the xerophytic vegetation known as Caatinga; *S. venulosa* occurs in semi-deciduous forests and its distribution encompasses the states of Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro. However, the species could have come in contact in periods of past climatic changes [111–114] during which the alternation of dry and humid periods caused the vegetation adapted to either more xeric or more mesic habitats to expand and contract.

The probable area of origin for *S. bahiensis* is the eastern region of Bahia, east of the Chapada Diamantina (a mountain range in the middle of the state); this is the only region where *S. tuberosa* and *S. venulosa* could have come into contact in the past. In Bahia, *S. venulosa* occurs in semi-deciduous forests in the eastern slopes of the Chapada Diamantina and also nearer the coast in a strip of semi-deciduous forest that constitute a transitional zone between the Caatinga vegetation and more humid phases of the coastal Atlantic forest. *Spondias mombin* also occurs in the Atlantic forest of Bahia but remains ecologically isolated from *S. tuberosa*. Incidentally, *S. bahiensis* is most diverse and abundant in Bahia, and its introduction to Minas Gerais and other states in Northeastern Brazil must be somewhat recent. The probable area of origin of the northern ‘umbu-cajá’ taxon is more difficult to determine, but likely areas of prior contact between *S. mombin* and *S. tuberosa* are near the coast in Maranhão, Piauí and Ceará, where the Caatinga vegetation where *S. tuberosa* occurs comes very close to the coastal areas where *S. mombin* is normally found. The central areas of Brazil are covered by fire-prone, savanna vegetation that harbors no *Spondias* species.

An alternative scenario for the origin of *S. bahiensis* and the northern ‘umbu-cajá’ taxon is that they arose as a product of humans activities – there is archaeobotanical evidence that the indigenous people consumed fruits of *Spondias* species. An investigation of archaeological plant remains at two sites in northern Minas Gerais revealed that *S. tuberosa* was gathered continuously from 150–4250 BP [115–117]; investigations at a number of sites in Pernambuco revealed that *S. tuberosa* was intermittently gathered from 888–9150 BP [118–121]. It is conceivable that the indigenous human populations would not only consume fruits in-situ but also transport them as they move from place to place. These human-mediated plant movements could have promoted the contact between hitherto isolated species via the collection of fruits of a species in its original habitat and later discard of the seeds in environments where other species occurred. Contact between species may also have occurred more recently, post-colonization of Brazil by the Portuguese; some (unintentional?) cultivation of *S. tuberosa* is recorded as early as 1587 by [122] (p. 172), who wrote that “these trees already occur in the farms of the Portuguese, born from seeds”. If the Portuguese settlers discarded seeds of one species in habitats where other species occur; these seeds could germinate and produce volunteer seedlings that upon growing to maturity could potentially cross with the other species, since flowering in *Spondias* is dictated by water availability [65] and when growing in the same environment the different species usually have synchronous or overlapping flowering [65]. This kind of process whereby hybrids are serendipitously created via plants established in backyard dumps is well-documented for the genus *Leucaena* in Mexico [123], and could also be the case in *Spondias*.

Hybridization is a frequent outcome in various contexts when otherwise isolated plant species were brought into sympatry [123–127]. However, it remains uncertain if the hybridization events that created *S. bahiensis* and the ‘northern umbu-cajá’ taxon preceded or were precipitated by human activities. References to both taxa are very scant in the literature prior to about 1980, and there are also very few botanical collections in herbaria. Perhaps the earliest mention to these taxa is by [128] (p. 83), who realized that the ‘northern umbu-cajá’ taxon was something different from *S. tuberosa*; they wrote that “certainly one other variety [of *S. tuberosa*] exist, since besides the common type found in the Caatinga of Bahia, there is another type, larger and with bigger canopy, that has pubescent leaves and is rather common in Piauí”. The earliest collection of *S. bahiensis* is by Inacio de Menezes in 1940 (the specimen is deposited in Rio de Janeiro Botanical Garden Herbarium under number RB42811), and there is a mention to *S. bahiensis* in a 1949 article about fruit-flies [129]. The lack of

earlier records makes it impossible to establish for how long these plants have been known by man, what could give clues to how old these hybrid lineages are.

The other hybrids investigated – the hybrid between *S. bahiensis* and *S. mombin* and the hybrid between *S. bahiensis* and *S. venulosa* – are further examples that show how novel combinations between *Spondias* taxa are continuously being created in Northeastern Brazil; they demonstrate that the evolution of the hybrid *Spondias* taxa from Northeastern Brazil is rather complex one and is by no means finished.

4. Materials and Methods

4.1. Taxon Sampling

For the molecular analysis we sampled 355 accessions of *Spondias* (Supplementary Table S1), including *S. bahiensis* (149 accessions), *S. dulcis* (five accessions), *S. mombin* (60 accessions), *S. purpurea* (five accessions), *S. tuberosa* (46 accessions), *S. venulosa* (46 accessions), and the putative hybrid taxa ‘umbuguela’ (two accessions), ‘cajaguela’ (one accession), the northern ‘umbu-cajá’ taxon (39 accessions), a hybrid between *S. venulosa* and *S. bahiensis* (one accession), and a hybrid between *S. mombin* and *S. bahiensis* (one accession). All samples were collected in the field, and for those taxa with a large geographical distribution we tried to collect samples from thorough their distribution in Brazil. Collection localities, voucher information, and GenBank accession numbers are given in Supplementary Table S1.

All the samples used in this study were collected by the senior author and his colleagues or cooperators, and no special permissions were required for collection. Samples were collected either from public or privately owned land, and in the latter case we had the permission of the landowners to collect the samples. No collections were made in protected areas, and the field studies do not involve endangered or protected species.

4.2. DNA Extraction, Amplification and Sequencing

Genomic DNA was extracted from fresh or silica gel dried leaf tissue using a modified cetyltrimethylammonium bromide (CTAB) 2× protocol [130] modified for CTAB gel sample storage [131]. For the genetic analyses we amplified the *psbA-trnH* intergenic spacer [45] and the *rps16* intron [132] from the cpDNA genome, and the external transcribed spacer (ETS) region from the nuclear encoded small subunit ribosomal DNA (SSU rDNA) using the primers ETS1F [133] and 18S-IGS [134]. We used TopTaq Master Mix Kit (Qiagen) to amplify both regions. Polymerase chain reaction (PCR) was performed in a total volume of 10 µL containing 1 µL (ca. 30 ng) of template DNA, 0.2 µL each of forward and reverse primers at 15 µM concentration, 6 µL TopTaq mix, 2 µL TBT [135] and 0.4 µL of water. The thermal profile for amplifying the cpDNA regions consisted of an initial denaturing step of 80°C for 5 min; followed by 35 cycles of 95°C for 1 min, 52°C for 1 min, and 65°C for 5 min; and a final extension of 65°C for 5 min. The thermal profile for amplifying the ETS region was that described by [134]. To check amplification success, 1.5 µL of each PCR product were quantified in ethidium bromide-stained 2% agarose gels. Prior to sequencing, the PCR products were cleaned using the polyethylene glycol (PEG)-NaCl 11% precipitation [136]. DNA sequencing was performed with Big Dye Terminator Cycle 3.1 Sequencing Kit (Applied Biosystems, São Paulo, Brazil) with the same primers used for the PCR reactions. The cycle sequencing reaction followed a program of 25 cycles of denaturation at 96°C for 10 s, annealing at 50°C for 5s, and extension at 60°C for 4 min. Products were then sequenced using an ABI 3130XL genetic analyzer (Applied Biosystems). The amplified ETS sequences did not exhibit sequence heterogeneity and thus cloning was not performed for any of the putative hybrid taxa.

4.3. Sequence Edition, Alignment and Analysis

Electropherograms were edited and assembled using the Staden Package [137]. Sequences were manually aligned using Seaview 4.2.6 [138,139]. Both ends of the aligned matrices were cropped so that all accessions possessed the same sequence length. The matrices were then saved in FASTA format.

Phylogenetic analyses were performed on a reduced dataset consisting of “taxon genetic classes”, hereinafter TGCs (unique combinations of taxa and DNA sequences). In order to identify the TGCs, all DNA regions were manually combined into a single FASTA file (sequences of the *psbA-trnH*, *rps16* and ETS regions were concatenated for each accession). The resulting matrix was entered in DnaSP 5.10 [140], where haplotype data was generated in Nexus format with the option of including sites containing gaps in the analysis. The haplotype identified for each accession (Table S1, column “Combined haplotype”) was then compared to the taxon to which each accession is assigned, and unique combinations of taxa and haplotypes were given a name (Table S1, column “Taxon genetic class”). Accessions assigned to a TGC possess identical DNA sequences. A total of 48 TGCs were identified, and these were used as terminals for the phylogenetic analyses. Two matrices were prepared, one consisting of ETS sequences from each TGC, and a second matrix consisting of the combined *psbA-trnH* and *rps16* intron sequences from each TGC. The two cpDNA regions were combined in tree reconstructions since the entire chloroplast genome is regarded as being a single linkage group and thus all cpDNA regions are expected to exhibit the same phylogenetic pattern [141].

Phylogenies were reconstructed both including and excluding TGCs from the putative hybrid taxa in order to assess their influence in tree topologies. The cpDNA and ETS datasets were analyzed using maximum parsimony as optimality criterion, because we were interested in detecting discrete mutation patterns in the taxa, using PAUP* 4.0b10 [142]. The single TGC for the introduced species *Spondias dulcis* was used to root the tree. Parsimony analysis was performed using a heuristic search to generate 1,000 replicates of random taxon addition using equal (Fitch) weights and TBR, 10 trees held at each step, MulTrees off, saving only the shortest trees or the shortest from each replicate. The resulting trees were used as starting points in another round of TBR with MulTrees on. In the analyses presented here, gaps were treated as missing data, poly repeats were included, and branches with a minimum length of zero were collapsed. Support for tree topology was evaluated with 1,000 bootstrap (BS) replicates in PAUP* 4.0b10 (TBR, 10 trees held at each step, MulTrees on). From the bootstrap analyses of the cpDNA and ETS datasets we collapsed branches with less than 80% support in the majority rule consensus trees. The trees were plotted facing each other in R version 3.1.1 [143,144] using the function cophyloplot of the package APE version 3.1-4 [145]. The resulting graphic image was saved as a PDF file containing the image in vector format and then edited using Inkscape 0.48.4 [146].

In order to visualize the distribution of haplotypes from the putative hybrid taxa relative to the distribution of haplotypes from the parental species, we prepared cpDNA and ETS matrices containing all accessions of the species (without the putative hybrids), and cpDNA and ETS matrices with all accessions included. The resulting matrices were input to DnaSP 5.10 [140], where haplotype data were generated in Roehl Data Format (.rdf) with the option of removing from analysis sites containing gaps. The .rdf files were then input to Network 4.6.1.1. [147] to calculate and draw median-joining networks [148]. The haplotype networks were then assembled and edited in Inkscape 0.48.4 [146]. We also prepared a graphic image contrasting cpDNA and ETS haplotypes found for the accessions of the putative hybrid taxa. Haplotypes shared between putative hybrids and recognized species were colored with the color assigned to the corresponding species.

Supplementary Materials: The following supporting information can be downloaded at: Preprints.org, Table S1: List of accessions collected for this study, haplotype list, provenance and genbank numbers.

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C.v.d.B.; writing—original draft preparation, M.C.M.; writing—review and editing, C.v.d.B. and A.S-S.; supervision, C.v.d.B. and A.S-S.; project administration, C.v.d.B.; funding acquisition, C.v.d.B. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: All the sequences generated for this study are deposited in Genbank (see Supplementary Table S1 for accession numbers). Vouchers are deposited at HUEFS.

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