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Cryptic species and phylogeographical structure in the tree *Cedrela odorata* L. throughout the Neotropics

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Running head: Cryptic species and phylogeographical structure in *Cedrela*

ABSTRACT

Aim The origins of much Neotropical biodiversity remain a topic of debate, with both palaeogeographical and more recent climatic drivers playing a role in diversification both among and within species. Here we use a combination of molecular data to assess genetic variation within and among species in the Neotropical tree genus *Cedrela*, with a focus on *Cedrela odorata*, to test hypotheses on the drivers of diversification, to place known ecotypic variation in context and to detect intraspecific phylogeographical structure.

Location Central and South America, Cuba, Cayman Islands, Trinidad and Guadeloupe.

Methods Samples were collected from the field, existing collections and herbaria from across the geographical range, including a total of 528 individuals from 72 sites. A phylogenetic framework was constructed using internal transcribed spacer (ITS) sequence data (intergenic spacers plus flanking 18S and 26S regions), and genetic structure was analysed using a combination of chloroplast DNA sequences (*trn*C–*ycf*6, *trn*H–*psb*A) and chloroplast and nuclear microsatellite (single sequence repeat, SSR) loci. Phylogenetic reconstruction was undertaken using a combination of Bayesian and parsimony-based approaches; divergence times were estimated for major nodes. Geographical structure in chloroplast SSR data was analysed using SAMOVA, while that in nuclear SSR data was assessed using a combination of Bayesian clustering and principal coordinates analysis.

Results ITS sequence data supported phylogenetic distinctiveness of four morphologically cryptic species within *C. odorata*. Chloroplast sequence and microsatellite data showed geographical structuring both among and within species, suggesting the influence of climatic and geographical drivers. Intraspecific genetic divergence was also present in nuclear microsatellite data, suggesting contemporary gene flow limitation across sea and mountain

barriers.

Main conclusions The data support diversification of the genus *Cedrela* in South America with subsequent recolonization into Central America prior to the formation of the Isthmus of Panama. At least four morphologically cryptic taxa were evident within *C. odorata* and within-species phylogeographical divergence across the Andes and within Central America were present, the latter suggestive of Pleistocene climatic influence. Previously recognized ecotypes in Central America should be elevated to species level. The new molecular data support the recent reclassification and will support the monitoring of exploitation in the genus.

Keywords:

Conservation genetics, cryptic species, dispersal, diversification, Meliaceae, Neogene, phylogeography, Pleistocene, Spanish cedar, vicariance.

INTRODUCTION

The origins of Neotropical biodiversity are a topic of ongoing debate (Pennington & Dick, 2004; Pennington *et al.*, 2004; Zink *et al.*, 2004; Rull, 2008, 2011a,b; Hoorn *et al.*, 2010; Corlett, 2011; Graham, 2011a). For example, the once widely supported Pleistocene refuge theory (Hooghiemstra & van der Hammen, 1998), which suggested that many species originated in response to dramatic vegetation shifts mediated by Quaternary (< 2.5 Ma) climatic cycles, has now been modified by models suggesting much older, Neogene (23–2.5 Ma) origins for diversity at the species level and below (Albert *et al.*, 2006; Zarza *et al.*, 2008; Castoe *et al.*, 2009; Palma-Silva *et al.*, 2009). The consequence of this shift in perspective is that palaeogeographical drivers such as Andean uplift, Amazonian marine incursions and the formation of the Isthmus of Panama may have played an equal or stronger role in driving diversification than Pleistocene climate fluctuations (Rull, 2011a,b). The improved evolutionary resolution that has shifted the debate has come in particular from the use of dated molecular phylogenies, incorporating fossil evidence and new statistical dating approaches. However, for many Neotropical species, taxonomic treatment remains imperfect and deep intraspecific divergence or cryptic species – where evolutionary divergence in the genome is not reflected in the phenotype (Wagner, 2005) – have frequently been uncovered in molecular studies of apparently widespread species, e.g. *Carapa guianensis* (Scotti-Saintagne *et al.*, 2012a), *Jacaranda copaia* (Scotti-Saintagne *et al.*, 2012b), *Vriesia gigantea* (Palma-Silva *et al.*, 2009) and *Cedrela* (Muellner *et al.*, 2009, 2010). If the main drivers of Neotropical diversity are to be identified – knowledge vital for its effective conservation – a much wider sampling within species, of geographical range and of type and number of genetic loci, is needed to improve phylogenetic resolution and to place taxa in a robust evolutionary framework.

The situation is acute for Neotropical tree species, many of which are currently described as widespread and/or habitat generalists. Although wide ranges offer the potential to test hypotheses of dispersal or vicariance by comparing the timing of diversification among distributed populations relative to dated palaeogeographical events, the taxonomic treatment of

widespread or apparently generalist species may disguise levels of diversification not apparent from morphological phenotypes alone or from thinly sampled molecular analyses (e.g. Silvera *et al.*, 2003). Successful identification of the drivers of divergence needs careful application of data from multiple sources, including distributional analysis, morphometrics, fossil data and molecular data. When applied to broad collections, such an approach can resolve cryptic species, deep intraspecific divergences or phylogeographical structure due to more recent restrictions of gene flow.

The contemporary geography of the Neotropics was largely completed with the final formation of the Amazon river system (*c.* 7 Ma), the development of the northern Andean cordilleras to modern heights (4–3 Ma, Graham, 2011b) and the final closure of the Isthmus of Panama [3.5–3.1 Ma (Coates & Obando, 1996); new estimates place this as early as 22 Ma (Farris *et al.*, 2011)]. The long development of the latter probably involved the formation and gradual linkage of an island chain, across which many early dispersers successfully colonized. In the Caribbean, the Greater Antilles formed and were present above sea level from around 45 Ma (Graham, 2011b) with the Lesser Antilles probably attaining their present form since the Pliocene (Iturralde-Vinent & MacPhee, 1999). Latterly, during the Pleistocene (> 2.5 Ma), climatic cycles have caused repeated vegetation range shifts across this landmass, driving phases of contraction, fragmentation and expansion of species distributions (Graham, 2011b). The ways in which these processes affected a species depend on its evolutionary age and ecology. For example, older species such as *Symphonia globulifera* (> 10 Ma) show clear signatures of having developed intraspecific diversity as a consequence of early and long-distance dispersal and the uplift of the Andean cordilleras (Dick *et al.*, 2003; Dick & Heuertz, 2008), while the majority of species within the highly diverse genus *Inga* have speciated in South America subsequent to 2 Ma (Richardson *et al.*, 2001).

The genus *Cedrela* (Meliaceae; Cedreleae) includes timber tree species of global economic importance. Consequently, significant research effort has been directed at resolving taxonomic relationships within the genus and a recent revision has increased the number of

121 extant species from about 8 to 17 (Pennington & Muellner, 2010). The most recent common
122 ancestor (MRCA) of Cedreleae dates back to the early Eocene and was distributed in the
123 Northern Hemisphere (Muellner *et al*., 2010; Pennington & Muellner, 2010). From Europe,
124 *Cedrela* moved westwards on a boreotropical dispersal path and occurs in North American fossil
125 records from 51 Ma until 15–13 Ma (51 Ma, Wind River Creek, Wyoming; 15-14 Ma, Succor
126 Creek, Oregon; 13.8 Ma, Trout Creek, Oregon; Graham, 2011b), finally retreating south in the
127 mid-Miocene as a result of declining northern temperatures. The mid-Miocene cooling that
128 precipitated this distributional change was coupled with the onset of a drier, seasonal climate
129 that is likely to have benefited species adapted to these conditions (Graham, 2011b), as the
130 ancestral *Cedrela* seems likely to have been (Pennington & Muellner, 2010). The start of
131 diversification in *Cedrela* is estimated at between 33 and 22 Ma (Muellner *et al.*, 2010), when
132 separate Central and South American clades formed, indicating that dispersal from North to
133 South America was complete well before the final formation of the Isthmus of Panama, a pattern
134 that has been seen in other Neotropical genera (e.g. Pennington *et al.*, 2004; Erkens *et al.*, 2009).
135 Of all the *Cedrela* species, perhaps the best known is *Cedrela odorata* L. (Spanish cedar),
136 until recently described as a widespread but highly variable species (Cavers *et al*., 2003;
137 Pennington *et al.*, 1981). It has been heavily exploited for timber throughout much of its range,
138 exhausting sources of old-growth trees in many places and resulting in CITES listing for some
139 populations. Previous marker-based and trial-based studies of genetic variation within the
140 species in Central America (Gillies *et al.*, 1997; Navarro *et al.*, 2002, 2004; Cavers *et al.*, 2003a,b)
141 have demonstrated genetic differentiation between northern types (north-western Costa Rica to
142 Mexico), which are adapted to dry, seasonal conditions, and those from southern Central
143 America (eastern and south-western Costa Rica to Panama), where more rainfall is experienced.
144 However, chloroplast data showed strong phylogeographical structure within the northern
145 group. Recent revision, based on molecular data, now indicates the presence of at least three
146 genetic lineages within *C. odorata* that merit recognition as species in their own right (Muellner
147 *et al.*, 2010). These were: *C. odorata sensu stricto* (s.s.), including the type specimen from

148 Jamaica and samples from El Salvador and Belize; a clade including specimens from Ecuador and
149 French Guiana; and a clade including specimens from Brazil and Venezuela. Muellner *et al.*
150 (2010) suggest that *C. odorata* s.s. most probably recolonized Central America from South
151 America at around the time of the formation of the Isthmus of Panama. Given the value and long
152 history of exploitation of *Cedrela* species, there is an urgent need to improve taxonomic
153 resolution in the genus to develop the means to monitor and control trade in its timber, and
154 produce informed strategies for seed-sourcing for restoration planting (Broadhurst *et al.*, 2008).
155 At the same time, wider sampling and analysis would help to answer questions about the
156 distributions of morphologically cryptic species, and about drivers of diversity in this important
157 genus.

158 In this study, we aimed to assess genetic variation at multiple markers across the range
159 of *C. odorata*. We use a combination of molecular loci – nuclear and organellar sequences and
160 hypervariable markers. With the objective of establishing the geographical distribution of
161 lineages within *C. odorata* and of genetically distinctive units within them, we addressed the
162 following questions: (1) Have Neogene biogeographical drivers played a more prominent role in
163 diversification within *Cedrela* than Pleistocene climatic fluctuations? (2) Is the previously
164 documented ecotypic differentiation within *C. odorata* a species-level divergence? (3) Does
165 northern Central American *C. odorata* show any intraspecific phylogeographical structure?
166

MATERIALS AND METHODS

Study species

The group of morphologically similar species described by Pennington *et al.* (1981) as *C. odorata* comprises large, fast growing and long lived trees with paripinnate leaves. The trees occur in Pacific and Atlantic Central America and the Antilles, and in South America both east and west of the Andes, in central and eastern coastal Brazil and northern Argentina (Pennington & Muellner, 2010). In general, they grow below 800 m, but there are some records of occurrence above 1500 m in Ecuador. Although found in both evergreen rain forest and drier forest, they have adaptations to dry environments including a deciduous habit, buds protected by scale leaves and fruit maturation largely timed to coincide with the dry season. The trees are monoecious, pollinated by small insects and have small, wind-dispersed seeds.

Sampling and DNA extraction

Samples were collected from 72 locations across Central and South America and the Caribbean, including new and existing collections and herbarium specimens (see Tables S1–S2 & Fig. S1 in Appendix S1 of the Supporting Information). Where possible, voucher specimens were either prepared (new collections) or sampled (herbaria), however this was not possible for all sampled regions. DNA extraction and polymerase chain reaction (PCR) methods for sequence [internal transcribed spacer (ITS) plus flanking 18S and 26S regions, and chloroplast *trn*C–*ycf*6, *trn*H–*psb*A], chloroplast and nuclear microsatellites (single sequence repeats, SSR) are given in Appendix S2.

Data analysis

Sequence data

Sequence alignments were assembled using CODONCODE ALIGNER 3.5.4 (CodonCode Corporation, Centreville, MA, USA) and checked manually. Finalized sequences were lodged with GenBank under the accession numbers JN112854–JN112898 (Appendix S1: Table S3). For analysis,

chloroplast sequences were appended to form one 708-bp sequence, including binary codes denoting presence or absence of insertions/deletions (indels).

ITS sequence data was used to check for monophyly of the Cedreleae and order clades within Cedreleae following Muellner *et al.* (2010). Homologous ITS sequences for other species of *Toona* and *Cedrela* were obtained from GenBank and incorporated into the phylogenetic analysis and subsequent divergence-time estimations. Parsimony-based analyses were performed using PAUP* 4.0b10 (Swofford, 2000) using heuristic searches with 1000 random addition replicates, tree bisection–reconnection (TBR) branch swapping and MulTrees option on. A strict consensus tree was computed from the resulting equally parsimonious trees. Support for the clades was assessed by bootstrap analysis using a faststep heuristic search strategy with 10,000 replicates. Bayesian inference was performed in MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). MRMODELTEST 2.3 (Nylander, 2004) identified HKY+G+I as the model of sequence evolution that best fitted the data, and the topology of the resulting majority-rule consensus tree was compared to that of the strict consensus tree produced by maximum parsimony. Four Markov chain Monte Carlo (MCMC) simulations (three heated, one cold) were run with sampling every 100 generations for 5,000,000 generations with the first 10% discarded as burn-in after convergence was reached, after testing for minimum burn in period. Trees remaining after burn-in were used to calculate posterior probabilities for nodes in the majority-rule consensus tree.

Divergence timing

Divergence times among branches of the phylogenetic tree were estimated using Bayesian MCMC analyses of the ITS sequences, using BEAST 1.6.1 (Drummond & Rambaut, 2007). A speciation model with a Yule tree prior and an uncorrelated lognormal relaxed clock was used in combination with the HKY+G+I model. Four independent runs of 10 million generations were performed, each with a burn-in of 1000 generations. The four runs were combined in TRACER 1.5 (Drummond & Rambaut, 2007) to analyse effective sample size (ESS) values and frequency

plots.

Most recent common ancestor (MRCA) ages which serve as calibration points were derived from fossil data (Muellner *et al.*, 2010). Priors provide information regarding the age and distribution of an individual node calibration. Lognormal and exponential prior age distributions are appropriate when modelling fossil calibration (Ho, 2007), and were tested here in addition to a normal prior age distribution. The normal mean age of the MRCA of *Cedrela* was set to 33.62 Ma (95% confidence interval (CI): 31.66–35.58 Ma) and the MRCA of *Cedrela* and *Toona* was set to 48.60 Ma (95% CI: 46.84–50.56 Ma) based on Muellner *et al*. (2010). An exponential prior age distribution was used with a minimum age of 31.66 Ma (one standard deviation from the mean age used Muellner *et al*., 2010) and a mean age of 33.62 Ma for the MRCA of *Cedrela*, and a minimum age of 46.64 Ma with a mean age of 48.60 Ma for the MRCA of *Cedrela* and *Toona*. The lognormal mean age of the MRCA of *Cedrela* was set to 33.62 Ma with a minimum age of 31.66 Ma (95% CI: 31.96–46.82 Ma), with the mean age of the MRCA of *Cedrela* and *Toona* set to 48.60 Ma with a minimum age of 46.64 Ma (95% CI: 46.97–63.35 Ma). Standard deviations of 1.0 and 0.5 were tested. Average ages for nodes were taken over the four independent runs for each prior type (Table 1).

A median-joining network of unique chloroplast haplotypes was constructed using NETWORK 4.6 (Fluxus Technology, Clare, England) using the greedy algorithm, epsilon set at 40 and with differential weighting across mutations (indels, 40; transversions, 15; transitions, 5).

cpSSRs

A network of chloroplast single sequence repeat (cpSSR) haplotypes was constructed using the minimum evolution method in NETWORK 4.6 (Fluxus Technology). Spatial structuring of cpSSR haplotypes was analysed by spatial analysis of molecular variance (SAMOVA) using SAMOVA 1.0 (Dupanloup *et al.*, 2002). One hundred simulated annealing processes were used for values of *K* from 2 to 10. Basic diversity statistics, for the data set as a whole and for groups detected by SAMOVA were calculated using GENALEX 6.4 (Peakall & Smouse, 2006). Analysis of molecular

variance (AMOVA) was conducted, with data partitioned by population only and by major SAMOVA group.

nSSRs

The entire collection was tested for population structure by analysis of nuclear SSR (nSSR) data using Bayesian clustering (STRUCTURE 2.3.3; Pritchard *et al.*, 2000). Initially the full data set was tested for structure with no prior assumptions and with population location as a prior (LOCPRIOR on); subsequently a subset of the data, for which both ITS and nSSR data had been obtained, were tested for structure, with no prior assumptions, and then using ITS clade identity as a prior. In addition, the full data set was regionally subdivided to check for levels of structure below the optimal level found for the full data set. In all analyses, a series of initial simulations were conducted to optimize the burn-in period and then 20 replicate simulations for each value of K were performed with a 10,000-cycle burn-in followed by 100,000 iterations; values of K between 1 and 10 were tested. For all other settings, default values were used. The optimal value of K was determined by the method of Evanno *et al.* (2005).

To assess among-population differences, principal coordinates analysis (PCoA) of a pairwise F_{ST} matrix was carried out. The adjusted pairwise F_{ST} matrix was produced using the software FREENA (Chapuis & Estoup, 2007) and then PCoA was carried out using GENALEX 6.4. Hierarchical partitioning of variation in the data set was determined using AMOVA (GENALEX 6.4), with the data set partitioned into populations and then spatially using the geographical regions Central America + Cuba, South America (west of Andes), South America (east of Andes).

RESULTS

ITS sequence data

Muellner *et al.* (2010) indicated that ITS resolves the major taxa within *Cedrela*; the primary resolution of relationships within our collection was therefore based on ITS sequence data. Because our topology broadly matched that obtained previously, we use the same clade nomenclature. For the ITS data set, a total of 152 samples were sequenced; 428 bp of sequence were obtained, yielding 28 SNPs and 6 indels, and characterizing 22 haplotypes (Fig. 1, Appendix S1: Tables S3 & S4). As reported previously (Muellner *et al.*, 2010), there was strong support for the monophyly of *Cedrela* (82%, Fig. 2), and published sequences of the Central American species *Cedrela tonduzii* C.DC., *Cedrela salvadorensis* Standl., *C. oaxacensis* C.DC. & Rose, *Cedrela dugesii* S.Watson and *Cedrela monroensis* T.D. Penn. were internal and basal to the generic clade (Central America clade 2, Muellner *et al.*, 2010).

The main collection formed five clades. Of these, the most strongly supported (98%) was a monophyletic clade including nine haplotypes (H6–H14) and previously published sequences from Belize, El Salvador and Antigua (Central America clade 1, '*C. odorata* s.s.; Muellner *et al.*, 2010). This included the widespread haplotype H12 that occurred in 90/152 samples and was found in the Greater and Lesser Antilles, Central America (apart from Panama and southern and eastern Costa Rica), Ecuador and Peru (Table S4). The eight other haplotypes in this group were confined to Cuba and Central America north of Nicaragua. The other clades were less well supported but were broadly stable under repeated iterations of phylogenetic analysis. All samples from the Cayman Islands (Fig. 2, haplotypes H15, H16 and H17) grouped together consistently and sister to a clade containing samples and previously published sequences from South America ('South America clade 1'; Muellner *et al.*, 2010). The latter was further divided into two clades: the first included previously published sequences for *Cedrela saltensis* M.A.Zapater & del Castillo (Peru/Bolivia), *Cedrela nebulosa* T.D.Penn. & Daza (Ecuador/Peru), *Cedrela weberbaueri* Harms (Peru) and haplotypes H1 and H2, from southern and eastern Costa Rica, Panama and Manabi, Ecuador, plus two previously published sequences,

nominally *C. odorata*, from the Dominican Republic and French Guiana; the second included *Cedrela fissilis* Vell., *Cedrela balansae* C.DC. and haplotypes H3 and H4, which we found only in Boca do Acre, Brazil, and previously published sequences from Brazil and Venezuela. All remaining haplotypes – H5 and H18–H22 – were from Ecuador: H5 occurred only in the southern population Loja and, with H22, grouped with previously published sequences for *Cedrela angustifolia* Moc. & Sessé ex DC. (previously *Cedrela lilloi*) and *Cedrela montana* Turcz., while H19–H22 were all represented in Pichincha, but also found in Esmeraldas and in herbarium samples from Ecuador.

Divergence time estimation

Estimates based on normal and two lognormal (standard deviations of 1 and 0.5) age distribution models were similar within confidence limits; those based on an exponential model were consistently older. For most nodes (Fig. 2), ages were in broad agreement with those obtained previously, but our estimate for the divergence time of Central America clade 1 was substantially older. These suggest divergence of the South American clade 1 (node 3, Fig. 2) at around 17–19 Ma, with South American clade 2 (node 4, Fig. 2) diverging later, at 14 Ma. Central American clade 2 (node 5, Fig. 2) began diverging at 9.5 Ma, with Central American clade 1 (*C. odorata* s.s., node 6, Fig. 2) following from 8 Ma. Divergence of the Cayman Islands haplotypes (node 7, Fig. 2) are estimated at around 5–6 Ma, and divergence of *C. angustifolia* and *C. montana* (node 8) was latest at 3–4 Ma.

Chloroplast sequence data

The two concatenated chloroplast fragments produced 723 bp of sequence, yielding 17 SNPs and 6 indels and characterizing 17 haplotypes (Appendix S1: Table S5). Haplotype network analysis (Fig. 3, Appendix S1: Table S6) showed some geographical organization of haplotypes: haplotypes H1 and H2 were found exclusively in Central American populations north of Nicaragua and in Cuba, apart from one individual in Jimenez, Costa Rica (Fig. 3, Table S6), were

323 together and distant from other haplotypes. Haplotype H3 was found exclusively in Nicaragua
324 and Honduras apart from one individual in Upala, Costa Rica, whilst haplotype H4 was found in
325 Costa Rica, Panama and the Cayman Islands. Haplotypes H13 and H14 segregated in populations
326 in Ecuador (H13 in Manabi and herbarium specimens; H14 in Pichincha). Haplotypes H5–H10,
327 H16 and H17 were together in the same part of the network and were found in South America
328 and Guadeloupe; the latter had two unique haplotypes (H5, H6). Haplotype H7 was found in
329 both French Guiana and Amazonian Ecuador. Haplotype H8 was exclusive to Brazil's Boca do
330 Acre, H9 was found in Peru, Amazonian Ecuador, and in Boca do Acre and Para, Brazil.
331 Haplotypes H10, H16 and H17 were confined to Amazonian Ecuador. In different parts of the
332 network, haplotype H11 was unique to the Amazonian Ecuadorian population Orellana,
333 haplotype H15 was unique to the southern Ecuadorian population Loja, while haplotype H12
334 was confined to Ecuador but found on both sides of the Andes (albeit to the east in only a single
335 occurrence at Napo). In general, this means that 11 of the 17 haplotypes occurred in Ecuador, 8
336 of them exclusively –only one haplotype (H12) was found on both sides of the Andes.
337
338 **cpSSRs**
339 The loci *ccmp2*, *ccmp5* and *ccmp6* were polymorphic and were screened throughout the whole
340 collection. At these loci, 2, 2 and 6 variants were found, respectively, characterizing 13
341 haplotypes (Fig. 4, Appendix S1: Tables S7–S8). Of these, seven were private haplotypes: H8
342 (Peten, Guatemala), H10 (Sagua, Moa, Cuba), H7 (Esmereldas, Ecuador), H11 (Manabi, Ecuador),
343 H12 (Napo, Ecuador), H13 (French Guiana) and H1 (French Guiana). Haplotype H9 occurred
344 exclusively in Cuba and Central America north of Honduras. Haplotype H6 was largely confined
345 to Honduras and Nicaragua, although also present as single occurrences in Ecuador, Brazil and
346 Guyana. Haplotypes H2–H5 were confined to Central America south of Nicaragua, South America
347 and Guadeloupe; the widespread haplotypes H2 and H5 were not present in Ecuador west of the
348 Andes. Ecuador as a whole had high haplotype diversity with 8 of the 13 haplotypes present in
349 the country.

SAMOVA identified $K = 3$ as the optimal clustering of populations. At $K = 2$, populations were grouped into Cuba and Central America north of Honduras versus southern Central America, South America and Guadeloupe. At *K*-values of 3–5, French Guiana, Najasa (Cuba), and Nicaragua and Honduras were successively separated out as distinctive groupings, reflecting the occurence of private haplotypes.

With populations ungrouped, 72% of the variation was partitioned among populations ($\Phi_{PT} = 0.72$, $P > 0.01$). Grouping the data according to the two principal SAMOVA groups ($K = 2$), mean within-population diversity in the northern group (Cuba and Central America north of Honduras) was 0.01, and number of alleles (N_a)/effective number of alleles (N_e) were 1.50/1.01, while in the southern group (Southern Central America, South America and Guadeloupe), diversity (h) was 0.11 and N_a/N_e were 3.67/1.28. Partitioned this way, 82% of variation was among groups ($\Phi_{PT} = 0.82$, $P > 0.01$); partitioning according to $K = 3$ made little difference ($\Phi_{PT} = 0.81$, $P > 0.01$). Below this level – within the major SAMOVA groupings ($K = 2$) – the vast majority of variation was partitioned within populations (Φ_{PT} (northern group) = 0, $P > 0.01$; Φ_{PT} (southern group) = 0.11, $P > 0.01$).

nSSRs

Amplification success was variable across the collection, most likely due to variable sample quality – the collection comprised a range of tissue ages from decades-old herbarium material to weeks-old leaf. There were no clear regional patterns of amplification failure, although locus *ced61a* failed to amplify in most samples from South America. Deviations from Hardy–Weinberg equilibrium (HWE) were tested for at the population level in all populations with sufficient sample sizes. Significant deviations were common, although it was notable that populations from Costa Rica and mainland Central America tended to show no deviation across loci. It was from this region that the samples used for microsatellite development were obtained, which suggests some ascertainment bias.

The optimal clustering of the whole data set, both with and without using prior

information about population locations, was $K = 2$ (Appendix S1: Fig. S3a). With local exceptions, including single populations in Honduras and Colombia, this divides the collection into two geographical groupings within which populations have majority assignment to one group, of: (1) northern Central America + Cuba; and (2) southern Central America, South America and Lesser Antilles. Considering only those individuals for which ITS data were available, and using 'ITS clade' (Fig. 2) as a prior with four clades represented, also returned $K = 2$ as optimal (Fig. S3b). At $K = 4$ individuals did not follow clade assignments; rather, they broadly followed geographical location. Indeed, using population location as a prior with the same data set returned $K = 3$ as optimal (Fig. S3c), with populations in groups from Cuba, Central America and South America.

When subdividing the whole data set, structuring at lower hierarchical levels was present within regions. For example, considering Central American populations alone, $K = 3$ was the optimal clustering value and recovered geographical groups of Mexico/Guatemala; Honduras/Nicaragua/north-west Costa Rica; south-east Costa Rica/Panama. Considering western South American populations alone recovered $K = 3$, with the Ecuadorian populations Pichincha/Esmeraldas and the Peruvian population Loreto as two distinct groups, and Manabi (west Ecuador)/Napo and Orellana (Amazonian Ecuador)/Boca do Acre (Brazil) as a separate cross-Andean group. Analysing Cuba together with Central American populations always recovered Cuba as a separate group – the easternmost Cuban population of Viñales showed the most admixture with mainland Central American populations, but this was the minor component in most individuals.

Null alleles were present in all populations at frequencies of 7–30%; the data set was therefore adjusted using FREENA to produce a matrix of pairwise F_{ST} values. Among-population divergences were represented by a plot of the first three principal axes of a PCoA, which cumulatively summarized 76.07% of the total variance in the data set (Appendix S1: Fig. S4). In this plot, Cuban and Central American populations form relatively tight but distinct groups in similar parts of the plot space. Populations from Guadeloupe and Peru (Loreto) were distinct

404 but both removed from the main group; populations Pichincha and Esmeraldas from Ecuador
405 were removed from the main Ecuador cluster, the former extremely so. Brazilian samples
406 grouped near those from the main Ecuadorian group along with samples from French Guiana
407 and population San Francisco from Panama (Central America).
408 Partitioning the data according to geographical regions, namely Central America +
409 Cuba, South America (west of Andes), South America (east of Andes), AMOVA found the majority
410 of variation was within populations (56%; Table 2) but significant proportions were found
411 among populations and among regions (22% each).
412
413

DISCUSSION

In its previous wide circumscription, *C. odorata* was a geographically widespread species encompassing a range of phenotypic and genetic variation (Pennington *et al.*, 1981). Recent morphological and molecular treatments (Muellner *et al.*, 2009, 2010, 2011) have identified at least three genetically distinct cryptic species within *C. odorata* and formal subdivision is now under way (Pennington & Muellner, 2010), although all taxa are morphologically highly similar and hard to distinguish in the field. In this study, using a combination of nuclear and organellar DNA sequences and molecular markers, it was possible to clearly detect the recently identified taxa and to document their geographical ranges in more detail. In addition, potential further new taxa were detected and it was possible to identify phylogeographical structure within *Cedrela odorata* s.s. From the distribution of variation in ITS sequences and divergence time estimates, our data support previous studies that indicated that dispersal across barriers such as the ocean between North and South America prior to the formation of the Isthmus of Panama, and the Andes, has been possible in the past, and it appears to have occurred even within contemporary species. However, analysis of data from nuclear microsatellites indicated some clear genetic disjunctions within taxa, such as between Cuban and mainland Central American populations, which suggested that, despite a long-term capability for cross-sea dispersal (from phylogenetic evidence), recent gene flow among populations separated by geographical barriers is limited. The data build on the recent revision of *C. odorata*, and identify some of the major influences involved in diversification among and within species.

Phylogenetic relationships, biogeography and cryptic species

Analysis of phylogenetic relationships based on ITS data supported recent revisions to taxonomic relationships within *Cedrela* (Muellner *et al.*, 2009, 2010, 2011; Pennington & Muellner, 2010), and estimates for the timings of divergence points were generally similar to previous ones. This suggests that the genus entered South America from North America during the mid-Oligocene (*c.* 25 Ma), potentially making use of islands present in formations on the

441 Chortís (Honduras, Nicaragua) and Chorotega (Costa Rica, Panama) blocks. Hence, dispersal of a
442 *Cedrela* ancestor must have involved transoceanic migration from the region of contemporary
443 southern Mexico to northern South America. In the mid-Oligocene, climatic conditions were
444 warm enough to support the presence of subtropical vegetation as far north as Oregon, and the
445 continuing presence of *Cedrela* in the pollen record in North America until the mid-Miocene
446 (Graham, 2011b) suggests that several Central American taxa (including *C. dugesii*, *C. oxacensis*,
447 *C. tonduzii*, *C. salvadorensis* and *C. monroensis;* Central America clade 2 in Fig. 2) are likely to
448 have developed from an ancestral population that remained here.
449 Meanwhile, diversification proceeded in the South American branch of *Cedrela* and,
450 from here, recolonization of Central America and the Antilles occurred, probably before the
451 formation of the Isthmus of Panama. Today, this has resulted in three distinct clades, which
452 include morphologically distinctive species. Building on the identification of three new taxa
453 within *C. odorata* (Muellner *et al.*, 2010), we found firstly that the new species previously
454 represented by samples from Brazil and Venezuela contains additional nuclear and chloroplast
455 diversity present only in Brazil. Secondly, the new species from Ecuador and French Guiana
456 extends to Panama and Costa Rica, generally in regions with moist forest habitat; in Ecuador, it
457 was restricted to sites on the Pacific side of the Andes. Chloroplast haplotypes suggest Costa
458 Rican and Panamanian populations of this lineage share close relationships with Ecuadorian
459 populations; those in Guyana share different haplotypes with populations from Ecuador while
460 samples from French Guiana had unique types. This pattern – a common phylogenetic lineage
461 with geographically structured organellar haplotypes – suggests the effect of vicariance or long-
462 distance dispersal across the Andes, with an originally widespread ancestral population
463 becoming subdivided as the mountains formed. Thirdly and finally, *C. odorata* s.s., previously
464 recognized from Belize, El Salvador and Jamaica, was found throughout northern Central
465 America from Guanacaste in Costa Rica to the Yucatán and Cuba. This includes a widespread ITS
466 haplotype (H12) found across these locations, but also in Ecuador, Peru and Guadeloupe,
467 suggesting retention of ancestral South American variation during northward migration or

468 return colonization back to South America. However, distinct chloroplast haplotypes within the
469 lineage suggest a long period of isolation. Previously, it was suggested that, due to the depth of
470 organellar differentiation between lineages in Central America, multiple waves of northward
471 colonization may have occurred (Cavers *et al.*, 2003a), with an initial migration prior to the final
472 formation of the land bridge. The current ITS data support the latter event, at around 8 Ma, but
473 the placement of *C. odorata* s.s. as internal to South American clade 2 suggests that the entire
474 northern lineage entered Central America from the south and that the internal structure is
475 therefore likely to have arisen due to later drivers such as Pleistocene climatic fluctuations.
476 Re-examining previous studies in the light of the new data, ecotypes of *C. odorata*
477 within Costa Rica should probably be recognized as species. Phylogenetic analysis indicates
478 substantial evolutionary divergence between ecotypes, matching previous estimates of
479 substantial molecular differentiation (based on RAPDs, Gillies *et al.*, 1997; RFLPs, Cavers *et al.*,
480 2003a; AFLPs, Cavers *et al.*, 2003b) and quantitative trait divergence (Newton *et al.*, 1995;
481 Navarro *et al.*, 2002, 2004, 2005). This suggests that previous results may require re-
482 interpretation – for example, the combined analysis of ecotypes within single experimental trials
483 should probably be re-examined with the ecotypes separated as species. It may be worth
484 considering the analogy of the related genus *Swietenia* in this region, where moist-forest forms
485 are recognized as *Swietenia macrophylla* and dry-forest forms as *Swietenia humilis*, although
486 these are also morphologically distinct. On current results, this moist-forest form of *C. odorata*
487 appears to be distributed from Costa Rica through Panama to Ecuador and across northern
488 South America to French Guiana; the distinctiveness of haplotypes from French Guiana suggests
489 they have experienced isolation.
490 A distinct new clade, most closely grouped with *C. odorata* s.s., comprises samples from
491 the Cayman Islands, including three haplotypes. The Cayman Islands are only likely to have been
492 above sea level since the Miocene (*c.* 10 Ma; Jones & Hunter, 1990; Brunt & Davies, 1994).
493 Several distinct species have evolved in the Caymanian flora and fauna and, because the islands
494 have never been linked to the mainland, immigrant species must have arrived by transoceanic

dispersal. Chloroplast haplotypes shared with populations in Costa Rica and Panama suggest that this was the origin of the dispersal event, although this is not the closest point to the islands geographically. In several Central American species, it appears that phylogeographical structure originates from distribution across the proto-Central American island chain (e.g. Poelchau *et al.*, 2012); lineage sharing between Costa Rica and the Cayman Islands may also reflect this biogeographical history. The populations of *C. odorata* on both Grand Cayman and Cayman Brac merit morphological investigation to establish their distinctiveness.

In Ecuador, a number of haplotypes (H5, H18–H22) were identified that were found nowhere else and formed a clade including the montane species *C. montana* (largely restricted to the northern Andes) and *C. angustifolia*. Despite a close affinity with these montane species, most of our specimens were obtained from lowland sites, from trees showing clear *C. odorata* morphology. The exceptions were samples obtained at Pichincha and Loja; in both cases, unique haplotypes (3 and 1, respectively) were identified and some specimens shared morphological characteristics with *C. montana*. In the case of Pichincha, one ITS haplotype was shared with trees from the lowland Pacific site of Esmeraldas. The extent to which such sharing results from hybridization (the species co-occur between 1500 and 1900 m) or retained ancestral variation is unclear. In very few instances were common haplotypes found in populations on both sides of the mountains; the apparent sharing of cpSSR haplotypes may therefore be due to homoplasy. Assuming that microsatellite mutation occurs more frequently than the indel events or single nucleotide polymorphisms in the sequence data (Provan *et al.*, 1999), the differences between eastern and western populations are entirely accounted for by single base steps, and similarities therefore seem likely to be examples of convergent molecular evolution rather than evidence of migration. Dispersal across the mountains therefore appears rare.

Phylogeography and population genetics

Within *C. odorata* s.s., phylogeographical structure at organellar loci was evident in the differentiation between Honduran and Nicaraguan populations and those from further north

522 and in Cuba. Although clearly within the *C. odorata* s.s. lineage, differentiation of these
523 populations at chloroplast loci was found (at both sequence and cpSSR markers) and had been
524 previously noted at RFLP loci (Cavers *et al.*, 2003a). As phylogenetic analysis suggests
525 colonization before the formation of the Isthmus of Panama, it seems likely that this structure
526 has developed as a result of vegetation movements during the Pleistocene. In Central America,
527 forest vegetation may have been restricted to refugial populations as dry habitats expanded in
528 some areas (Pennington *et al*., 2000). The uplands of the Chortís block (Honduras and north-
529 eastern Nicaragua) may have presented a significant barrier to forest species during these times
530 and may account for the divergence between northern and southern populations within
531 *C. odorata* s.s.

532 In South America, a cross-Andean division was evident in the organellar data with
533 association between trees from Costa Rica/Panama and Pacific Ecuador, in contrast to those
534 from Amazonian Ecuador, which were associated with populations in northern South America.
535 As all of these samples were part of a single ITS clade, this suggests that the structure in
536 organellar data has developed by vicariance, with the development of the northern Andes (6–
537 3 Ma) causing ultimate disruption of gene flow. The apparent existence of a distinct South
538 American gene pool east of the Andes tends to support the idea that mountain formation has
539 played a significant role in genetic subdivision. The fact that some populations were only
540 differentiated at microsatellite loci suggested that this population structure has developed later,
541 as suggested in other studies (De La Torre *et al.*, 2008).

542 In general, it was possible to distinguish population structure below the species level.
543 Using ITS-based classification as a prior did not result in optimal clustering of nuclear
544 microsatellite genotypes into species. Rather, clustering below this level was predominant and
545 tended to reflect geographical location (although AMOVA indicated a substantial among-
546 population component, even taking regional structure into account). In particular, a group
547 containing only Cuban populations was consistently recovered at all clustering levels, despite
548 some admixture in the westernmost Cuban populations with populations from the Mexican

549 Yucatán. Thus, despite evidence for historical transoceanic dispersal, contemporary oceanic
550 barriers have restricted gene flow on shorter time-scales.
551
552 **CONCLUSIONS**
553 The study has supported and built upon the recent revision of *C. odorata*, although it is clear that
554 further refinement of the current taxonomy is needed (and see Garcia *et al*., 2011). The results
555 have shown the complexity of evolutionary history in the Neotropics, in northern South America
556 and Central America in particular, where the influence of both long time-scale
557 palaeogeographical processes, such as geological movements and more recent climate-mediated
558 vegetation dynamics, are detectable. The revision of the former widespread *C. odorata* has
559 dramatically altered the framework for conservation and monitoring of these still important
560 tropical timber species (Muellner *et al.*, 2011). As a number of more localized cryptic species
561 have now been recognized, their conservation status urgently needs to be assessed and
562 guidance for monitoring exploitation of these species will have to be updated. Given the
563 difficulty of morphological identification, it would also be valuable to develop a practical, DNA-
564 based system for identification and tracking of timber shipments. It seems likely that as more
565 Neotropical tree species are studied in detail across their ranges, further examples of cryptic
566 species will emerge, which highlights the extent to which a taxonomic deficit continues to
567 hamper effective conservation of many tropical tree species.
568
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580 **REFERENCES**

581 Albert, J.S., Lovejoy, N.R. & Crampton, W.G.R. (2006) Miocene tectonism and the separation of
582 cis- and trans-Andean river basins: evidence from Neotropical fishes. *Journal of South*
583 *American Earth Sciences*, **21,** 14–27.

584 Broadhurst, L.M., Lowe, A., Coates, D.J., Cunningham, S.A., McDonald, M., Vesk, P.A. & Yates, C.
585 (2008) Seed supply for broadscale restoration: maximizing evolutionary potential.
586 *Evolutionary Applications*, **1,** 587–597.

587 Brunt, M.A. & Davies, J.E. (1994) *The Cayman Islands: natural history and biogeography*. Kluwer
588 Academic Publishers, Dordrecht.

589 Castoe, T.A., Daza, J.M., Smith, E.N., Sasa, M.M., Kuch, U., Campbell, J.A., Chippindale, P.T. &
590 Parkinson, C.L. (2009) Comparative phylogeography of pitvipers suggests a consensus of
591 ancient Middle American highland biogeography. *Journal of Biogeography*, **36,** 88–103.

592 Cavers, S., Navarro, C. & Lowe, A.J. (2003a) Chloroplast DNA phylogeography reveals
593 colonization history of a Neotropical tree, *Cedrela odorata* L., in Mesoamerica. *Molecular*
594 *Ecology*, **12,** 1451–1460.

595 Cavers, S., Navarro, C. & Lowe, A.J. (2003b) A combination of molecular markers identifies
596 evolutionarily significant units in *Cedrela odorata* L. (Meliaceae) in Costa Rica.
597 *Conservation Genetics*, **4,** 571–580.

598 Chapuis, M.-P. & Estoup, A. (2007) Microsatellite null alleles and estimation of population
599 differentiation. *Molecular Biology and Evolution*, **24,** 621–631.

600 Coates, A.G. & Obando, J.A. (1996) The geologic evolution of the Central American isthmus.
601 *Evolution and environment in tropical America* (ed. by J.B.C. Jackson, A.F. Budd and A.G.
602 Coates), pp. 21–56. University of Chicago Press, Chicago.

603 Corlett, R.T. (2011) Impacts of warming on tropical lowland rainforests. *Trends in Ecology and*
604 *Evolution*, **26,** 606–613.

605 Dick, C.W. & Heuertz, M. (2008) The complex biogeographic history of a widespread tropical
606 tree species. *Evolution*, **62,** 2760–2774.

607 Dick, C.W., Abdul-Salim, K. & Bermingham, E. (2003) Molecular systematic analysis reveals
608 cryptic Tertiary diversification of a widespread tropical rain forest tree. *The American*
609 *Naturalist*, **162,** 691–703.

610 Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees.
611 *BMC Evolutionary Biology*, **7,** 214.

612 Dupanloup, I., Schneider, S. & Excoffier, L. (2002) A simulated annealing approach to define the
613 genetic structure of populations. *Molecular Ecology*, **11,** 2571–2581.

614 Erkens, R.H.J., Maas, J.W. & Couvreur, T.L.P. (2009) From Africa via Europe to South America:
615 migrational route of a species-rich genus of Neotropical lowland rain forest trees
616 (*Guatteria*, Annonaceae). *Journal of Biogeography*, **36,** 2338–2352.

617 Evanno, G., Regnaut, S. & Goudet, J. (2005) Detecting the number of clusters of individuals using
618 the software STRUCTURE: a simulation study. *Molecular Ecology*, **14,** 2611–2620.

619 Farris, D.W., Jaramillo, C., Bayona, G., Restrepo-Moreno, S.A., Montes, C., Cardona, A., Mora, A.,
620 Speakman, R.J., Glascock, M.D. & Valencia, V. (2011) Fracturing of the Panamanian
621 Isthmus during initial collision with South America. *Geology*, **39,** 1007–1010.

622 Garcia, M.G., Silva, R.S., Carniello, M.A., Veldman, J.W., Rossi, A.A.B. & de Oliveira, L.O. (2011)
623 Molecular evidence of cryptic speciation, historical range expansion, and recent
624 intraspecific hybridization in the Neotropical seasonal forest tree *Cedrela fissilis*
625 (Meliaceae). *Molecular Phylogenetics and Evolution*, **61,** 639–649.

626 Gillies, A.C.M., Cornelius, J.P., Newton, A.C., Navarro, C., Hernández, M. & Wilson, J. (1997)
627 Genetic variation in Costa Rican populations of the tropical timber species *Cedrela*
628 *odorata* L., assessed using RAPDs. *Molecular Ecology*, **6,** 1133–1145.

629 Graham, A. (2011a) The age and diversification of terrestrial New World ecosystems through
630 Cretaceous and Cenozoic time. *American Journal of Botany*, **98,** 336–351.

631 Graham, A. (2011b) *A natural history of the New World: the ecology and evolution of plants in the*
632 *Americas*. University of Chicago Press, Chicago.

633 Ho, S.Y.M. (2007) Calibrating molecular estimates of substitution rates and divergence times in
634 birds. *Journal of Avian Biology*, **38,** 409–414.

635 Hooghiemstra, H. & van der Hammen, T. (1998) Neogene and Quaternary development of the
636 neotropical rain forest: the forest refugia hypothesis, and a literature overview. *Earth-*
637 *Science Reviews*, **44,** 147–183.

638 Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I.,
639 Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R.,
640 Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T. & Antonelli, A. (2010) Amazonia
641 through time: Andean uplift, climate change, landscape evolution, and biodiversity.
642 *Science*, **330,** 927–931.

643 Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees.
644 *Bioinformatics*, **17,** 754–755.

645 Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Palaeogeography of the Caribbean region:
646 implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural*
647 *History*, **238,** 1–95.

648 Jones, B. & Hunter, I.G. (1990) Pleistocene paleogeography and sea levels on the Cayman
649 Islands, British West Indies. *Coral Reefs*, **9,** 81–91.

650 Muellner, A.N., Pennington, T.D. & Chase, M.W. (2009) Molecular phylogenetics of Neotropical
651 Cedreleae (mahogany family, Meliaceae) based on nuclear and plastid DNA sequences
652 reveal multiple origins of "*Cedrela odorata*". *Molecular Phylogenetics and Evolution*, **52,**
653 461–469.

654 Muellner, A.N., Pennington, T.D., Koecke, A.V. & Renner, S.S. (2010) Biogeography of *Cedrela*
655 (Meliaceae, Sapindales) in Central and South America. *American Journal of Botany*, **97,**
656 511–518.

657 Muellner, A.N., Schaefer, H. & Lahaye, R. (2011) Evaluation of candidate DNA barcoding loci for
658 economically important timber species of the mahogany family (Meliaceae). *Molecular*

Ecology Resources, **11,** 450–460.

Navarro, C., Ward, S. & Hernandez, M. (2002) The tree *Cedrela odorata* (Meliaceae): a morphologically subdivided species in Costa Rica. *Revista de Biologia Tropical*, **50,** 21–29.

Navarro, C., Montagnini, F. & Hernández, G. (2004) Genetic variability of *Cedrela odorata* Linnaeus: results of early performance of provenances and families from Mesoamerica grown in association with coffee. *Forest Ecology and Management*, **192,** 217–227.

Navarro, C., Cavers, S., Pappinen, A., Tigerstedt, P., Lowe, A. & Merilä, J. (2005) Contrasting quantitative traits and neutral genetic markers for genetic resource assessment of Mesoamerican *Cedrela odorata*. *Silvae Genetica*, **54,** 281–292.

Newton, A.C., Cornelius, J.P., Mesén, J.F. & Leakey, R.R.B. (1995) Genetic variation in apical dominance of *Cedrela odorata* seedlings in response to decapitation. *Silvae Genetica*, **44,** 146–150.

Nylander, J.A.A. (2004) *MrModeltest v2.* Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Palma-Silva, C., Lexer, C., Paggi, G.M., Barbará, T., Bered, F. & Bodanese-Zanettini, M.H. (2009) Range-wide patterns of nuclear and chloroplast DNA diversity in *Vriesea gigantea* (Bromeliaceae), a neotropical forest species. *Heredity*, **103,** 503–512.

Peakall, R. & Smouse, P.E. (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, **6,** 288–295.

Pennington, R.T. & Dick, C.W. (2004) The role of immigrants in the assembly of the South American rainforest tree flora. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359,** 1611–1622.

Pennington, T.D. & Muellner, A.N. (2010) *A monograph of* Cedrela *(Meliaceae)*. DH Books, Milborne Port, UK.

Pennington, T.D., Styles, B.T. & Taylor, D.A.H. (1981) *A monograph of the Neotropical Meliaceae*. New York Botanical Gardens, New York.

Pennington, R.T., Prado, D.E. & Pendry, C.A. (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, **27,** 261–273.Pennington, R.T., Lavin, M., Prado, D.E., Pendry, C.A., Pell, S.K. & Butterworth, C.A. (2004) Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359,** 515–537.Poelchau, M.F. & Hamrick, J.L. (2012) Comparative phylogeography of three common Neotropical tree species. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2011.02599.x.

Pritchard, J.K., Stephens, M. & Donnelly, P. (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155,** 945–959.

Provan, J., Soranzo, N., Wilson, N.J., Goldstein, D.B. & Powell, W. (1999) A low mutation rate for chloroplast microsatellites. *Genetics*, **153,** 943–947.

698 Rambaut, A. (2009) *Figtree, a tree figure drawing tool.* University of Edinburgh. Available from:
699 http://tree.bio.ed.ac.uk/software/figtree/.

700 Richardson, J.E., Pennington, R.T., Pennington, T.D. & Hollingsworth, P.M. (2001) Rapid
701 diversification of a species-rich genus of Neotropical rain forest trees. *Science*, **293,**
702 2242–2245.

703 Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under
704 mixed models. *Bioinformatics*, **19,** 1572–1574.

705 Rull, V. (2008) Speciation timing and neotropical biodiversity: the Tertiary–Quaternary debate
706 in the light of molecular phylogenetic evidence. *Molecular Ecology*, **17,** 2722–2729.

707 Rull, V. (2011a) Neotropical biodiversity: timing and potential drivers. *Trends in Ecology and*
708 *Evolution*, **26,** 508–513.

709 Rull, V. (2011b) Origins of biodiversity. *Science*, **331,** 398–399.

710 Scotti-Saintagne, C., Dick, C.W., Caron, H., Vendramin, G.G., Guichoux, E., Buonamici, A., Duret, C.,
711 Sire, P., Valencia, R., Lemes, M.R., Gribel, R. & Scotti, I. (2012a) Phylogeography of a
712 species complex of lowland Neotropical rain forest trees (*Carapa*, Meliaceae). *Journal of*
713 *Biogeography*, doi:10.1111/j.1365-2699.2011.02678.x.

714 Scotti-Saintagne, C., Dick, C.W., Caron, H., Vendramin, G.G., Troispoux, V., Sire, P., Casalis, M.,
715 Buonamici, A., Valencia, R., Lemes, M.R., Gribel, R. & Scotti, I. (2012b) Amazon
716 diversification and cross-Andean dispersal of the widespread Neotropical tree species
717 *Jacaranda copaia* (Bignoniaceae). *Journal of Biogeography*, doi:10.1111/j.1365-
718 2699.2012.02797.x.

719 Silvera, K., Skillman, J.B. & Dalling, J.W. (2003) Seed germination, seedling growth and habitat
720 partitioning in two morphotypes of the tropical pioneer tree *Trema micrantha* in a
721 seasonal forest in Panama. *Journal of Tropical Ecology*, **19,** 27–34.

722 Swofford, D.L. (2000) *PAUP*: phylogenetic analysis using parsimony (*and other methods).*
723 Version 4.0b10. Sinauer Associates, Sunderland, MA.

724 de la Torre, A., López, C., Yglesias, E. & Cornelius, J.P. (2008) Genetic (AFLP) diversity of nine
725 *Cedrela odorata* populations in Madre de Dios, southern Peruvian Amazon. *Forest*
726 *Ecology and Management*, **255,** 334–339.

727 Wagner, A. (2005) *Robustness and evolvability in living systems*. Princeton University Press,
728 Princeton, NJ.

729 Zarza, E., Reynoso, V.H. & Emerson, B.C. (2008) Diversification in the northern neotropics:
730 mitochondrial and nuclear DNA phylogeography of the iguana *Ctenosaura pectinata* and
731 related species. *Molecular Ecology*, **17,** 3259–3275.

732 Zink, R.M., Klicka, J. & Barber, B.R. (2004) The tempo of avian diversification during the
733 Quaternary. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359,**
734 215–220.

735

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supporting tables and figures.

Appendix S2 Details of amplification protocols for molecular laboratory work.

BIOSKETCH

Stephen Cavers is a population geneticist interested in genetic diversity, gene flow and adaptation, primarily in trees. The research team involved in the study came together as part of the SEEDSOURCE consortium and the members have broad interests in the taxonomy, population genetics, evolution and ecology of trees.

Author contributions: S.C., R.V., C.N., A.J.L. and G.G.V, designed the sampling and analysis; S.C., C.N., F.A.C., R.V. and C.N., collected the samples; S.C., F.A.C., A.T., A.B. and G.G.V performed molecular and statistical analyses; S.C. wrote the paper; and all authors read and approved the manuscript.

Editor: James Richardson

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760 **TABLES**
761
762
763 **Table 1** Age estimates for principal branching events within the tribe Cedreleae, obtained by
764 Bayesian Markov chain Monte Carlo (MCMC) analyses of internal transcribed spacer (ITS)
765 sequences using BEAST 1.6.1. See text for details of analyses. Node labelling follows that in Fig. 2.
766
767

		Age distribution model				Estimates from Muellner *et al.* (2010)*	
Node	Description	Normal	Exponential	Lognormal SD1	Lognormal SD0.5	ITS data only	ITS and chloroplast
1	Root	48.43	54.71	48.33	48.89	48.5	48.4
2	*Cedrela*	33.75	44.50	34.30	35.08	33.6	33.8
3	South American clade 1	19.40	23.13	17.81	19.11	16.6	15.7
4	South American clade 2	14.00	17.85	14.48	14.59	n/a	n/a
5	Central American clade 2	9.32	12.04	9.73	9.81	10.3	12.1
6	Central American clade 1	8.09	10.40	8.33	8.54	2.8	3.2
7	Cayman Islands	5.49	6.92	5.66	5.70	n/a	n/a
8	*Cedrela montana / Cedrela angustifolia*	4.05	4.14	3.36	3.44	3.3	6.9

768
769 *Based on normal age distribution model
770
771

772 **Table 2** Hierarchical AMOVA based on nuclear simple sequence repeat (nSSR) data for the
773 *Cedrela odorata* species complex, structured as population and geographical region. Regions
774 were Central America + Cuba, South America (west of Andes) and South America (east of
775 Andes). (d.f. – degrees of freedom, SS – sum of squares, MS – mean square)
776

Source	d.f.	SS	MS	Variance	Percentage
Among regions	2	628.354	314.177	1.906	22%
Among populations	21	841.131	40.054	1.916	22%
Within populations	439	2148.787	4.895	4.895	56%
Total	462	3618.272		8.717	100%

777
778

779 **FIGURE LEGENDS**
780
781 **Figure 1** Geographical distribution of all 22 internal transcribed spacer (ITS) haplotypes
782 identified in the study for the *Cedrela odorata* species complex in the Neotropics. Apart from the
783 widespread haplotype, H12 (shown as black), colours reflect phylogenetic structure as shown in
784 Fig. 2, with shades of one colour used for groups of phylogenetically closely related haplotypes.
785 The map was produced using ARCMAP in ARCGIS 9.2 (ESRI, Redlands, CA).
786
787 **Figure 2** Bayesian 50% majority-rule consensus phylogram of ITS sequences from the *Cedrela*
788 *odorata* species complex in the Neotropics generated in FIGTREE 1.3.1. Support for branches is
789 indicated by posterior probability (above) and bootstrap (below) values. Asterisks (*) indicate
790 where clades are not supported by maximum parsimony strict consensus tree. Clades are
791 labelled following Muellner *et al*. (2010) for discussion. Taxa given with GenBank accession
792 numbers are sequences obtained from the database. Where samples of *C. odorata* are shown,
793 location of samples is given (DR, Dominican Republic; EC, Ecuador; AN, Antigua; FG, French
794 Guiana; BR, Brazil; BE, Belize; ES, El Salvador; VE, Venezuela). Haplotypes obtained in this study
795 are labelled H*x*, where *x* = 1–22, with representative location. Numbered nodes correspond with
796 those for which divergence time estimates are given in Table 1. The scale bar indicates the
797 average number of substitutions per site.
798
799 **Figure 3** Geographical distribution of the 17 chloroplast haplotypes identified by the study for
800 the *Cedrela odorata* species complex in the Neotropics. Colouring follows inset. Inset: median-
801 joining network of chloroplast sequence haplotypes, constructed in NETWORK 4.6. Colouring of
802 haplotype nodes reflects that in main figure. The map was produced using ARCMAP in ARCGIS 9.2
803 (ESRI, Redlands, CA).
804
805 **Figure 4** Distribution of chloroplast SSR haplotypes for the *Cedrela odorata* species complex in
806 the Neotropics; colours match location in network. Inset: chloroplast SSR haplotype network.
807 Construction followed minimum evolution model (NETWORK 4.6); grey shading indicates
808 haplotypes found in Ecuador; dotted oval indicates haplotypes found exclusively in Honduras,
809 Guatemala, Mexico and Cuba. Mutational steps among haplotypes are indicated by scores on
810 lines (1–2 steps) or by the figure in a box (> 2 steps). The map was produced using ARCMAP in
811 ARCGIS 9.2 (ESRI, Redlands, CA).

Figure 1

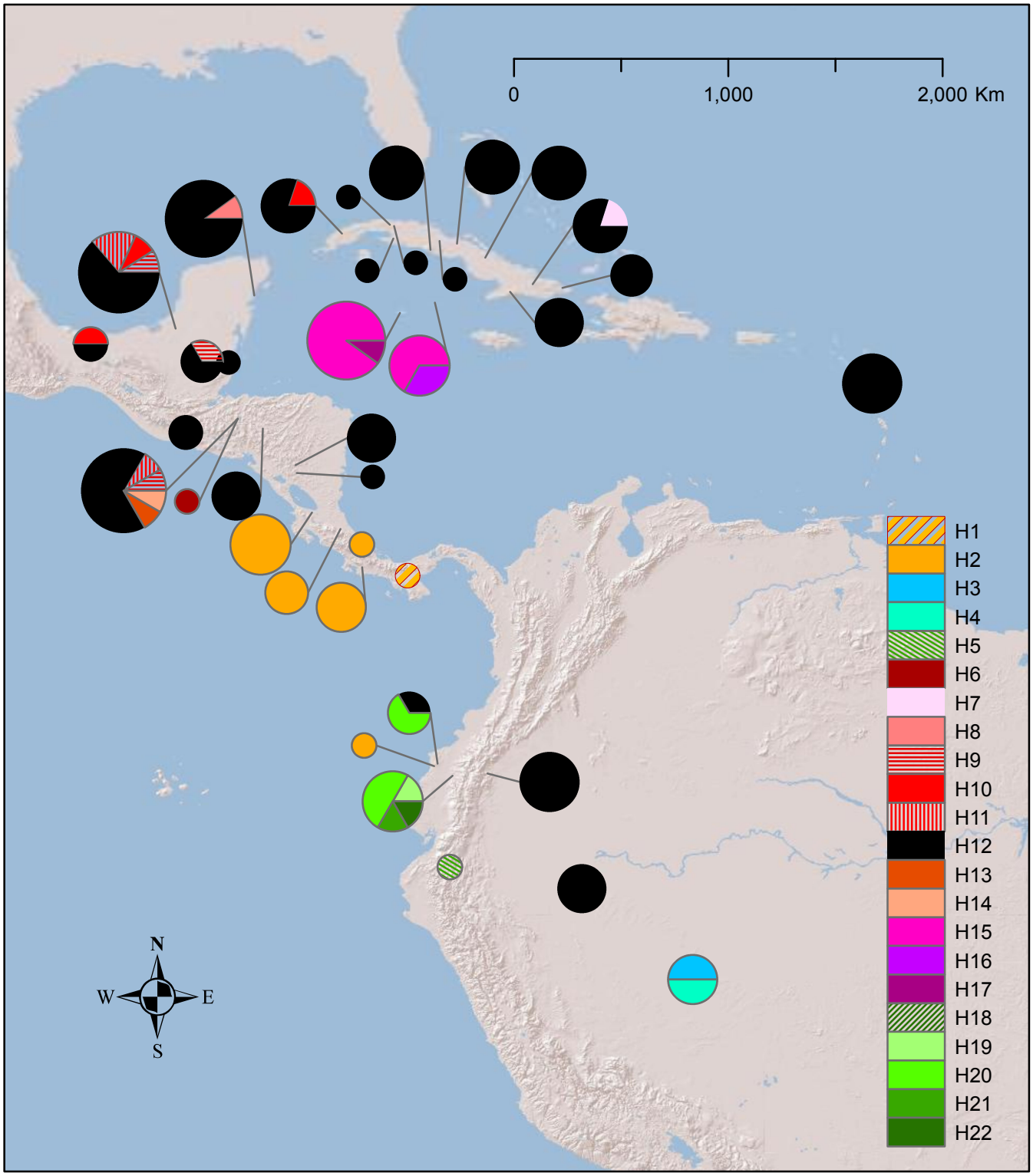

0
1,000
2,000 Km
N
W
E
S
H1
H2
H3
H4
H5
H6
H7
H8
H9
H10
H11
H12
H13
H14
H15
H16
H17
H18
H19
H20
H21
H22

Figure 2

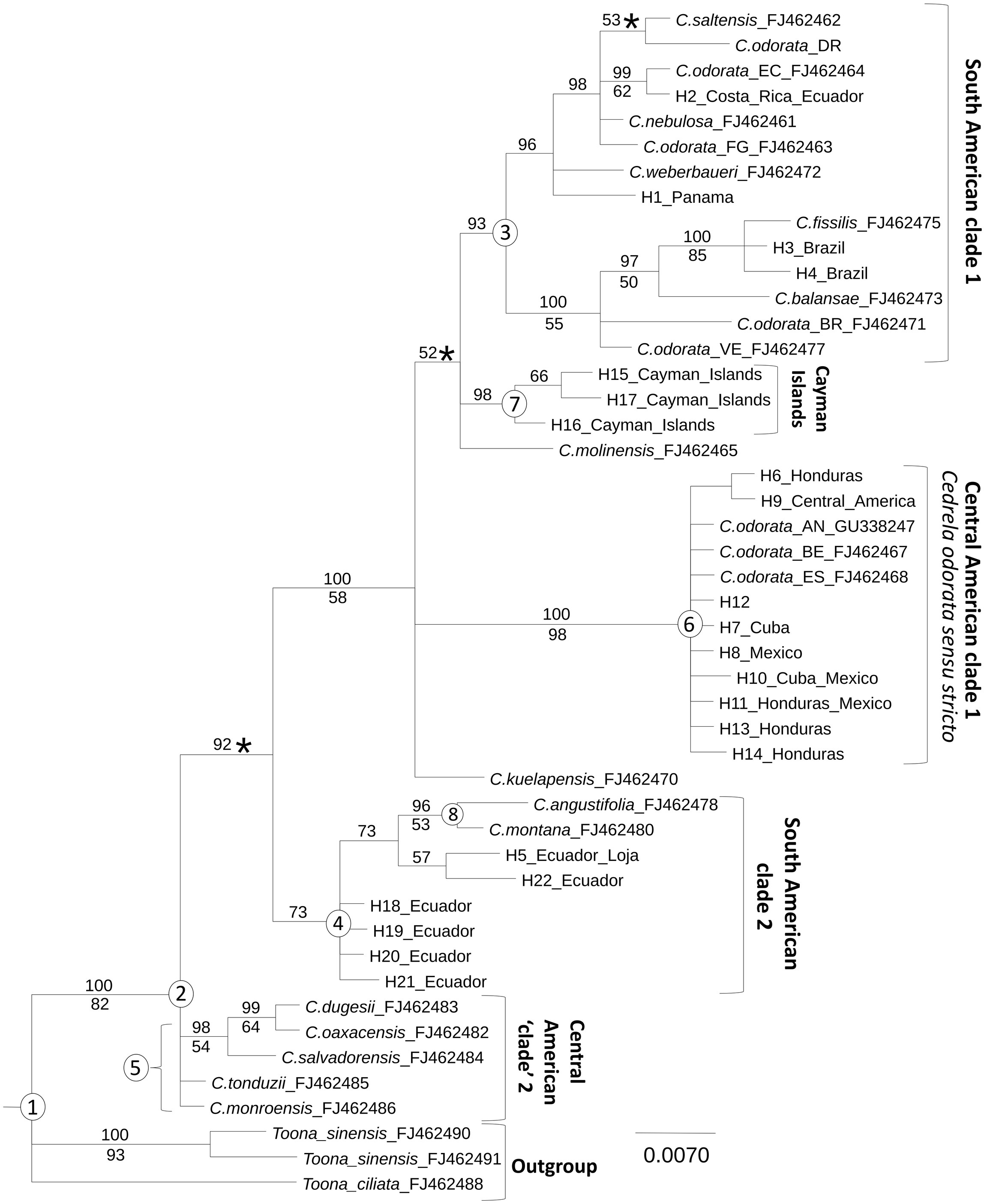
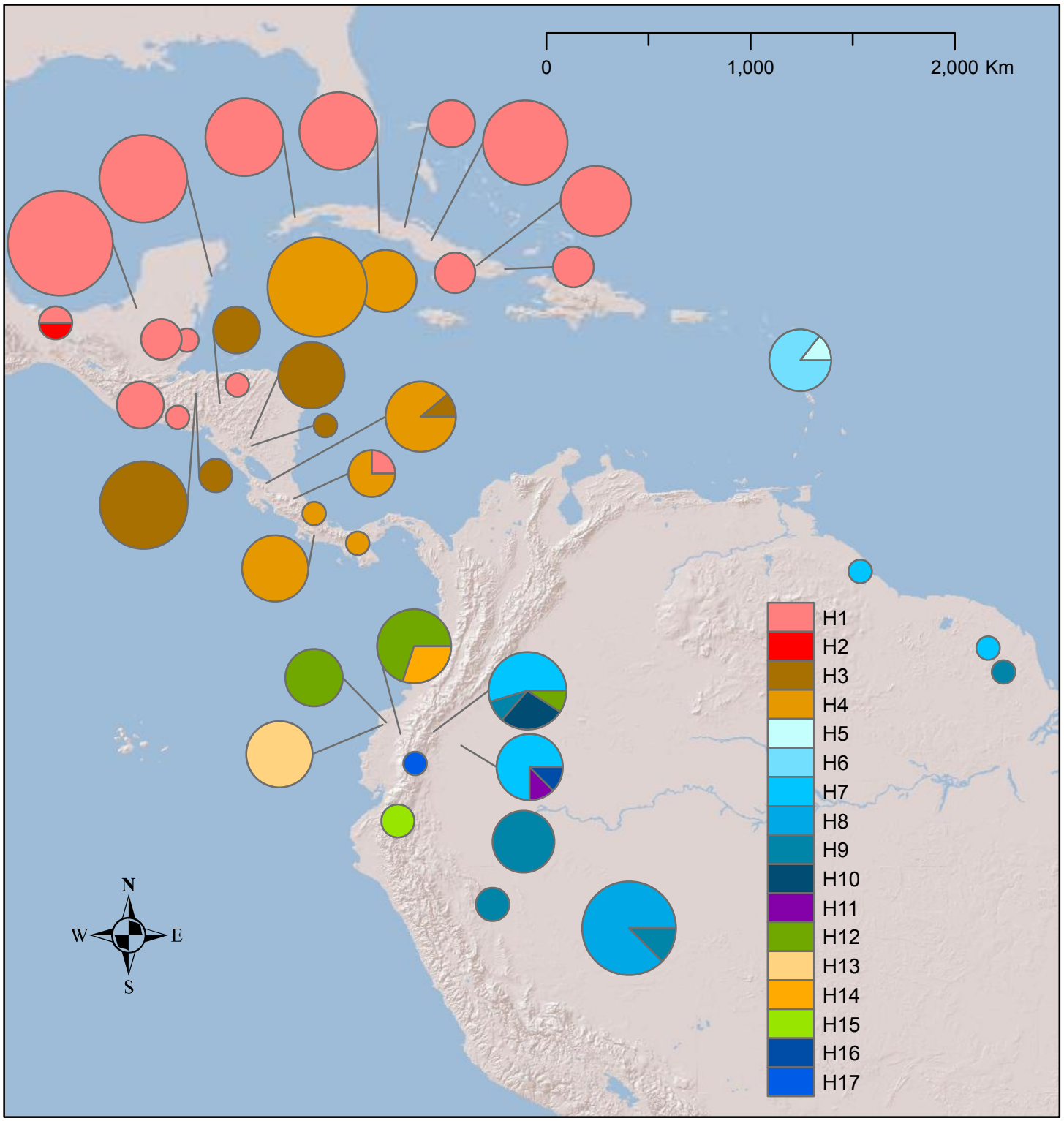

53
C.saltensis_FJ462462
C.odorata_DR
99
62
C.odorata_EC_FJ462464
H2_Costa_Rica_Ecuador
98
C.nebulosa_FJ462461
96
C.odorata_FG_FJ462463
C.weberbaueri_FJ462472
H1_Panama
93
3
C.fissilis_FJ462475
100
85
H3_Brazil
97
50
H4_Brazil
C.balansae_FJ462473
100
55
C.odorata_BR_FJ462471
C.odorata_VE_FJ462477
52
66
H15_Cayman_Islands
98
7
H17_Cayman_Islands
H16_Cayman_Islands
C.molinensis_FJ462465
H6_Honduras
H9_Central_America
C.odorata_AN_GU338247
C.odorata_BE_FJ462467
C.odorata_ES_FJ462468
H12
100
58
100
98
6
H7_Cuba
H8_Mexico
H10_Cuba_Mexico
H11_Honduras_Mexico
H13_Honduras
H14_Honduras
92
C.kuelapensis_FJ462470
96
53
8
C.angustifolia_FJ462478
C.montana_FJ462480
73
57
H5_Ecuador_Loja
H22_Ecuador
73
4
H18_Ecuador
H19_Ecuador
H20_Ecuador
H21_Ecuador
100
82
2
99
64
C.dugesii_FJ462483
98
54
C.oaxacensis_FJ462482
C.salvadorensis_FJ462484
5
C.tonduzii_FJ462485
C.monroensis_FJ462486
1
100
93
Toona_sinensis_FJ462490
Toona_sinensis_FJ462491
Toona_ciliata_FJ462488
South American clade 1
Cayman Islands
Central American clade 1
Cedrela odorata sensu stricto
South American clade 2
Central American 'clade' 2
Outgroup
0.0070

Figure 3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1,000
2,000 Km
N
W
E
S
H1
H2
H3
H4
H5
H6
H7
H8
H9
H10
H11
H12
H13
H14
H15
H16
H17

Figure 3 Inset

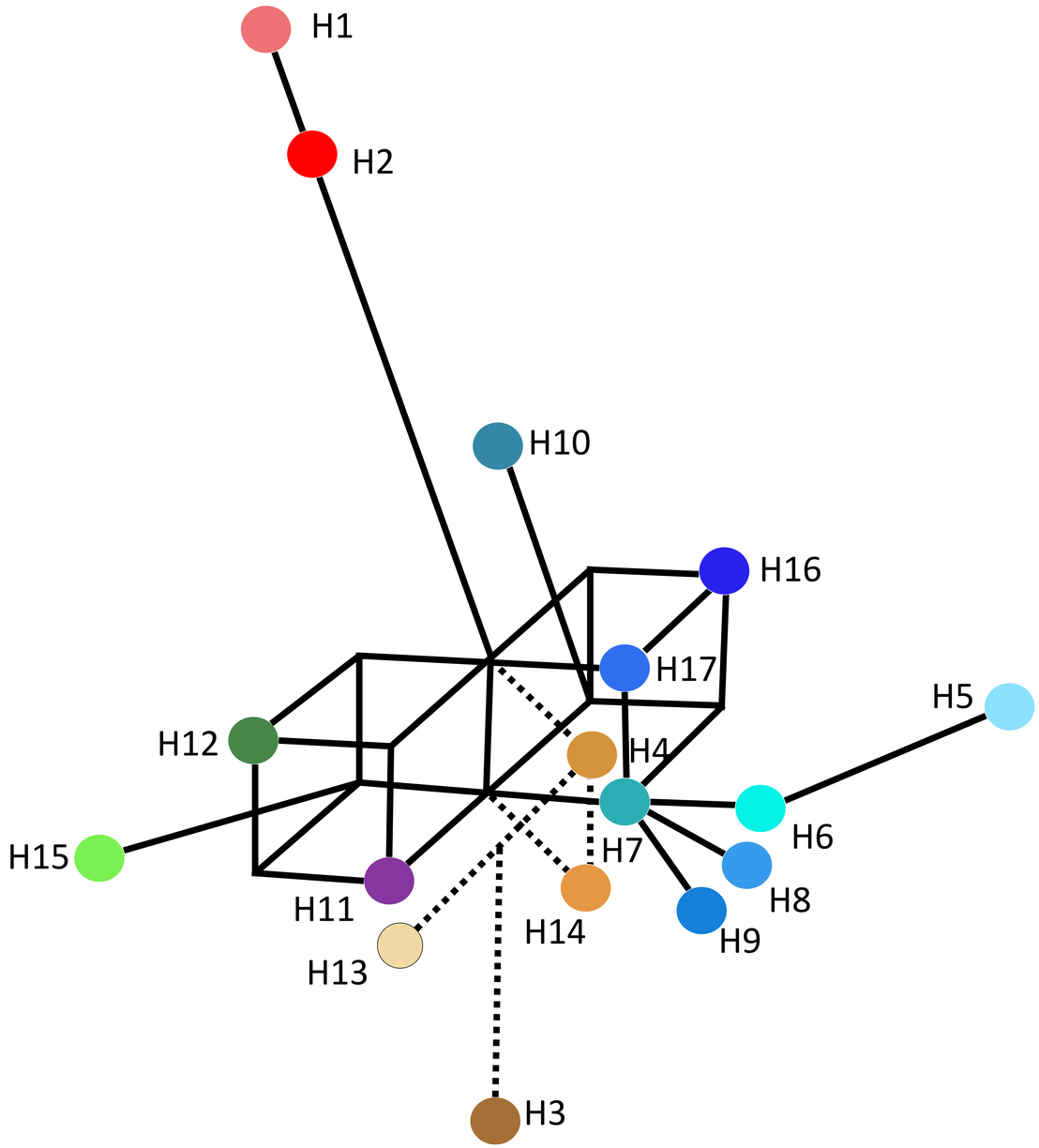


Figure 4

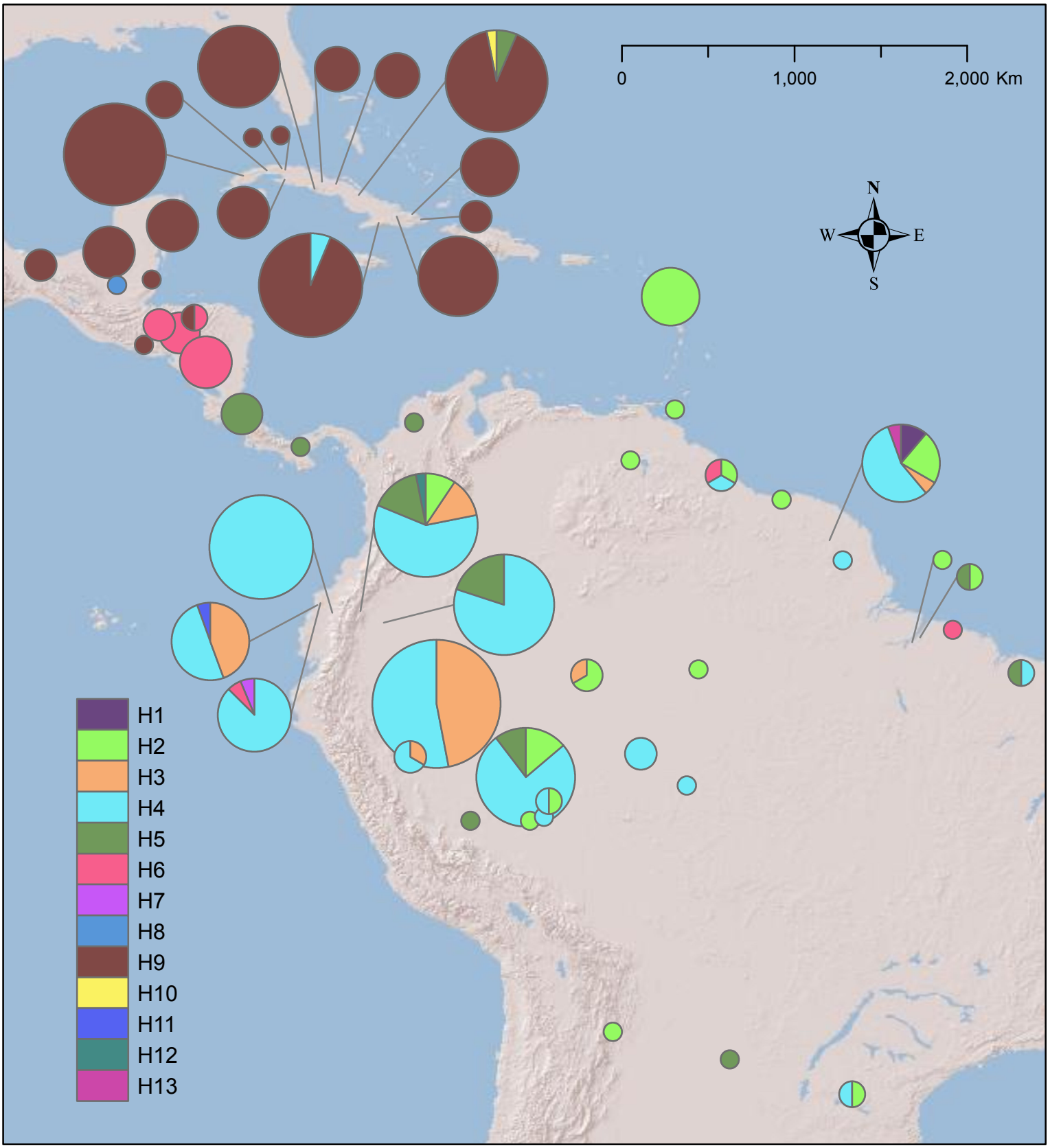
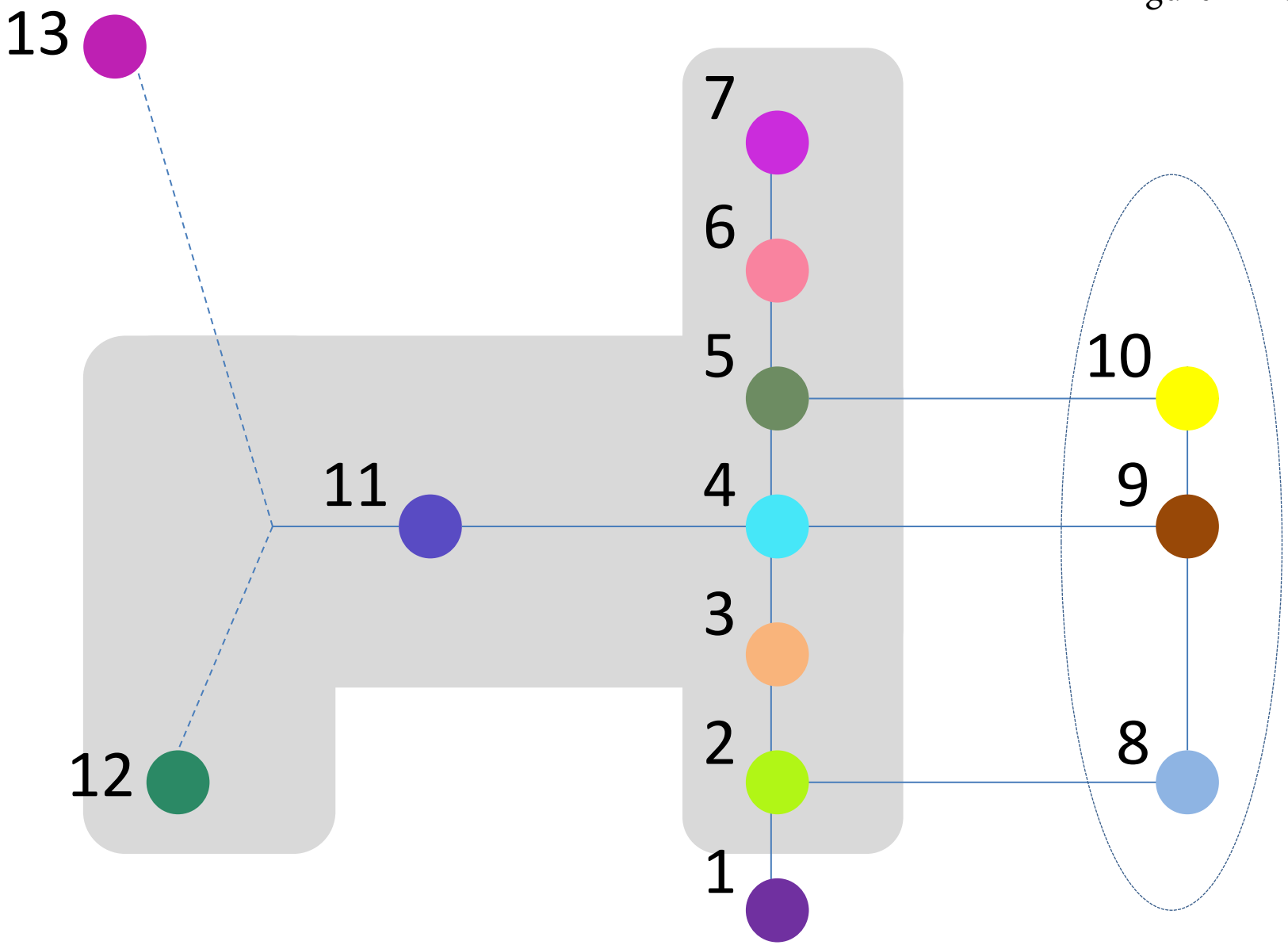


Figure 4 Inset



SUPPORTING INFORMATION

Cryptic species and phylogeographical structure in the tree *Cedrela odorata* L. throughout the Neotropics

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Journal of Biogeography

Contents

Appendix S1 Supporting tables and figures

Table S1 Geographical origin of all samples of the *Cedrela odorata* species complex collected for the study, columns indicate where genetic data was obtained and for how many samples.

Country	Population	Latitude	Longitude	Sample number, *n*			
				ITS	cpSEQ	cpSSR	nSSR
Belize	Belize	17.195	−88.494	**1**	**1**	1	1
Bolivia	Arce, Tarija	−22.000	−64.483	—	—	1	1
Bolivia	Ballivian, Beni	−9.167	−60.633	—	—	1	—
Bolivia	Manuripi,Pando	−10.800	−68.067	—	—	1	—
Brazil	Abaetetuba, PA	−1.700	−48.900	—	—	1	1
Brazil	Amazonas	−3.424	−65.841	—	—	3	2
Brazil	Belém, PA	−1.450	−48.480	—	—	2	1
Brazil	Boca de Acre	−22.000	−64.483	4	16	29	21
Brazil	Brasiléia, AC	−11.000	−68.800	—	—	1	—
Brazil	Braganca*	−1.051	−46.784	—	—	1	—
Brazil	Huimaita*	−7.511	−63.026	—	—	3	—
Brazil	Manaus, AM	−3.113	−60.025	—	—	1	2
Brazil	Maranhao	−3.300	−43.217	—	—	2	1
Brazil	Para	2.567	−52.517	—	1	1	1
Brazil	Paraná	−25.249	−52.022	—	—	2	1
Brazil	Rio Branco, AC	−9.978	−67.812	—	—	2	1
Cayman Islands	Grand Cayman	19.275	−81.291	10	18	—	—
Cayman Islands	Cayman Brac	19.711	−79.834	6	7	—	—
Colombia	Jambrano Bolivar	9.750	−74.833	—	—	1	5
Costa Rica	Jimenez	10.200	−83.794	3	4	5	—
Costa Rica	Costa Rica	10.893	−84.999	—	—	—	1
Costa Rica	Horizontes	10.715	−85.596	—	—	—	16
Costa Rica	Pacifico Sur	8.588	−82.886	4	8	—	3
Costa Rica	Talamanca	9.551	−82.891	1	1	—	11
Costa Rica	Upala	10.893	−84.989	6	9	—	6
Cuba	Baracoa	20.330	74.480	3	3	3	3
Cuba	Bayate-Mayarí	20.480	75.730	5	9	19	19
Cuba	Ceiba-mocha	22.980	−81.722	1	—	1	1
Cuba	Chambas	22.180	78.900	5	4	6	6
Cuba	Cidra	22.922	−81.539	1	—	1	1
Cuba	Ciénaga de Zapata	22.400	81.570	1	—	8	8
Cuba	Escambray	21.930	80.020	5	11	20	20
Cuba	Guisa	20.160	76.680	4	3	32	32
Cuba	Ariguanabo	22.880	82.500	—	—	4	4
Cuba	Moa-Sagua	20.610	74.930	—	—	10	10
Cuba	Najasa	21.600	77.720	5	13	31	31
Cuba	Placetas	22.300	79.630	1	—	6	6
Cuba	Viñales	22.610	83.730	5	11	31	31
Ecuador	Quito herbarium *	−4.000	−78.200	3	6	1	—
Ecuador	Loja	−4.000	−79.200	1	2	—	—
Ecuador	Esmeraldas	0.334	−79.714	3	6	16	14
Ecuador	Manabí	0.233	−79.863	1	8	18	19
Ecuador	Napo	−0.069	−77.620	6	11	32	32
Ecuador	Orellana	−0.678	−76.406	—	8	30	29
Ecuador	Pichincha	−0.168	−79.087	6	10	32	32
Ecuador	Tungurahua	−1.467	−78.442	—	1	—	—
El Salvador	El Salvador	13.793	−88.898	—	1	1	1
French Guiana	FG	3.617	−53.200	—	1	18	7
Guadalupe	Guadalupe	16.307	−61.474	6	7	10	10
Guatemala	Los Esclavos	14.250	−90.283	2	4	—	13
Guatemala	Peten	16.915	−90.298	—	—	1	1

Country	Population	Latitude	Longitude	Sample number, *n*			
				ITS	cpSEQ	cpSSR	nSSR
Guatemala	Tikal	17.226	−89.617	3	3	—	11
Guyana	Barima-Waini	7.367	−59.700	—	—	3	1
Guyana	Guyana	7.000	−58.833	—	1	—	2
Honduras	Honduras	15.213	−86.269	—	1	2	1
Honduras	Comayagua	14.417	−87.050	4	4	5	—
Honduras	Taulabe	14.833	−88.100	1	2	3	—
Honduras	Meambar	14.833	−88.100	12	14	—	13
Mexico	Escarcega	18.617	−90.717	11	20	8	12
Mexico	Mexico	17.950	−94.278	2	2	3	2
Mexico	Zona Maya	20.010	−87.407	10	14	8	12
Nicaragua	Nicaragua	12.545	−85.630	1	1	3	4
Nicaragua	Wabule	12.885	−85.676	4	8	8	—
Panama	Panama*	8.480	−80.745	—	—	1	1
Panama	San Francisco	8.236	−80.971	1	1	—	11
Paraguay	Paraguay*	−23.437	−58.395	—	—	1	—
Peru	Loreto	−4.914	−73.667	4	7	49	49
Peru	Manu	−11.000	−71.900	—	—	1	—
Peru	Peru	−7.679	−75.030	—	2	3	2
Suriname	Suriname	5.732	−55.700	—	—	1	1
Trinidad and Tobago	Trinidad*	10.429	−61.251	—	—	1	—
Venezuela	Bolivar	7.774	−63.573	—	—	1	1
			Totals	152	264	490	528

* Coordinates are placeholders – none supplied with voucher specimen. Sample(s) not used in spatial analysis.

Table S2 List of herbarium samples of the *Cedrela odorata* species complex used in the study. Codes follow Index Herbariorum: QCA, Pontificia Universidad Católica del Ecuador; INPA, Instituto Nacional de Pesquisas da Amazônia; IAN, Embrapa Amazônia Oriental; CAY, Institut de Recherche pour le Developpement (IRD) Cayenne; MO, Missouri Botanical Garden; U(L), Utrecht University Herbarium, transferred to National Herbarium of the Netherlands, Leiden.

								Haplotype		
Original collection number	Additional code	Country	Population	Herbarium	Collector name	Latitude	Longitude	cpSSR	cpSEQ	ITS
1992		Belize	Cayo	MO	Balick	17.500	−88.500	9	1	12
142359		Bolivia	Arce, Tarija	INPA		−22.000	−64.483	2	—	—
85970		Bolivia	Ballivian, Beni	INPA		−9.167	−60.633	4	—	—
86086		Bolivia	Manuripi, Pando	INPA		−10.800	−68.067	4	—	—
86085		Bolivia	Nicolas Suares, Pando	INPA		−11.333	−68.500	—	—	—
157615		Brazil	Abaetetuba, PA	IAN	Kanashiro	−1.700	−48.900	2	—	—
158569		Brazil	Almeirim, PA	IAN		−9.167	−60.633	—	—	—
203280		Brazil	Amazonas	INPA		−5.000	−63.000	3	—	—
62825		Brazil	Amazonas	INPA		−5.000	−63.000	2	—	—
40668		Brazil	Amazonas	INPA		−5.000	−63.000	—	—	—
63635		Brazil	Amazonas	INPA		−5.000	−63.000	2	—	—
79134		Brazil	Aripuanã, MT	INPA		−9.167	−60.633	—	—	—
29314		Brazil	Belém, PA	IAN		−1.450	−48.480	2	—	—
168999		Brazil	Belém, PA	IAN	Cordeiro	−1.450	−48.480	5	—	—
18419		Brazil	Braganca	U(L)		−1.051	−46.784	6	—	—
173844		Brazil	Brasiléia, AC	INPA		−11.000	−68.800	2	—	—
35446		Brazil	Huimaita	U(L)		−7.511	−63.026	4	—	—
161417		Brazil	Manaus, AM	INPA		−3.113	−60.025	—	—	—
58597		Brazil	Manaus, AM	INPA		−9.167	−60.633	—	—	—
143039		Brazil	Manaus, AM	INPA		−3.113	−60.025	2	—	—
100079		Brazil	Maranhao	U(L)		−3.300	−43.217	4	—	—
116465		Brazil	Maranhão	INPA		−4.000	−44.667	5	—	—
48438		Brazil	Para	U(L)		2.567	−52.517	4	9	—
106329		Brazil	Paraná	INPA		−24.000	−51.000	4	—	—
125609		Brazil	Paraná	INPA		−24.000	−51.000	2	—	—
168881		Brazil	Rio Branco, AC	INPA		−9.978	−67.812	4	—	—
160135		Brazil	Rio Branco, AC	INPA		−9.978	−67.812	2	—	—
006-IC-FLO-DNBAPVS/MA	SDAP09-8	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.363	−79.717	6	12	20
006-IC-FLO-DNBAPVS/MA	SDAP09-2	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.336	−79.734	3	12	—
006-IC-FLO-DNBAPVS/MA	SDAP09-7	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.358	−79.716	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP09-4	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.337	−79.709	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP09-5	Ecuador	Esmeraldas	QCA	A.J. Pérez 2893	0.334	−79.714	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP09-6	Ecuador	Esmeraldas	QCA	A.J. Pérez 2893	0.329	−79.718	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP08-5	Ecuador	Esmeraldas	QCA	A.J. Pérez 2893	0.336	−79.707	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP09	Ecuador	Esmeraldas	QCA	A.J. Pérez 2893	0.336	−79.708	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP08-3	Ecuador	Esmeraldas	QCA	A.J. Pérez 2893	0.338	−79.708	4	—	—

Original collection number	Additional code	Country	Population	Herbarium	Collector name	Latitude	Longitude	Haplotype		
								cpSSR	cpSEQ	ITS
006-IC-FLO-DNBAPVS/MA	SDAP08-2	Ecuador	Esmeraldas	QCA	A.J. Pérez 2893	0.338	−79.708	4	12	—
006-IC-FLO-DNBAPVS/MA	SDAP08	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.336	−79.734	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP08-4	Ecuador	Esmeraldas	QCA	A.J. Pérez 2893	0.337	−79.707	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP09-3	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.337	−79.709	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP08-1	Ecuador	Esmeraldas	QCA	A.J. Pérez 2893	0.358	−79.712	4	12	—
006-IC-FLO-DNBAPVS/MA	SDAP09-1	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.336	−79.734	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP08-6	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.336	−79.733	4	12	20
006-IC-FLO-DNBAPVS/MA	SDAP08-7	Ecuador	Esmeraldas	QCA	A.J. Pérez 2891	0.336	−79.734	7	12	12
006-IC-FLO-DNBAPVS/MA	SDAP11-4	Ecuador	Manabí	QCA	A.J. Pérez 3176	0.217	−79.819	3	—	—
006-IC-FLO-DNBAPVS/MA	SDAP12-5	Ecuador	Manabí	QCA	A.J. Pérez 3181	0.233	−79.863	3	—	—
006-IC-FLO-DNBAPVS/MA	SDAP12-4	Ecuador	Manabí	QCA	A.J. Pérez 3181	0.236	−79.855	3	13	2
006-IC-FLO-DNBAPVS/MA	SDAP14-1	Ecuador	Manabí	QCA	A.J. Pérez 3182	0.216	−79.857	3	13	—
006-IC-FLO-DNBAPVS/MA	SDAP14-3	Ecuador	Manabí	QCA	A.J. Pérez 3186	0.221	−79.865	—	—	—
006-IC-FLO-DNBAPVS/MA	SDAP14-4	Ecuador	Manabí	QCA	A.J. Pérez 3186	0.228	−79.873	3	13	—
006-IC-FLO-DNBAPVS/MA	SDAP14-2	Ecuador	Manabí	QCA	A.J. Pérez 3182	0.218	−79.859	—	13	—
006-IC-FLO-DNBAPVS/MA	SDAP12-6	Ecuador	Manabí	QCA	A.J. Pérez 3181	0.233	−79.861	3	13	—
006-IC-FLO-DNBAPVS/MA	SDAP12-2	Ecuador	Manabí	QCA	A.J. Pérez 3181	0.234	−79.846	3	13	—
006-IC-FLO-DNBAPVS/MA	SDAP11-1	Ecuador	Manabí	QCA	A.J. Pérez 3176	0.205	−79.809	4	13	—
006-IC-FLO-DNBAPVS/MA	SDAP11-3	Ecuador	Manabí	QCA	A.J. Pérez 3176	0.211	−79.815	4	13	—
006-IC-FLO-DNBAPVS/MA	SDAP11-5	Ecuador	Manabí	QCA	A.J. Pérez 3176	0.235	−79.828	11	—	—
006-IC-FLO-DNBAPVS/MA	SDAP12-1	Ecuador	Manabí	QCA	A.J. Pérez 3181	0.234	−79.845	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP11-2	Ecuador	Manabí	QCA	A.J. Pérez 3176	0.211	−79.813	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-34	Ecuador	Manabí	QCA	A.J. Pérez 3182	0.211	−79.852	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP11	Ecuador	Manabí	QCA	A.J. Pérez 3176	0.234	−79.853	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP12	Ecuador	Manabí	QCA	A.J. Pérez 3181	0.236	−79.854	4	—	—
134-006-1L-FLO-DNBAPUS/MA	134-006-1L-FLO-DNBAPUS/MA	Ecuador	Manabí	QCA	Pérez / Iglesias	0.234	−79.842	4	—	—
143-006-1L-FLO-DNBAPUS/MA	143-006-1L-FLO-DNBAPUS/MA	Ecuador	Manabí	QCA	Pérez / Iglesias	0.236	−79.869	4	—	—
371		Ecuador	Morona-Santiago	MO	Cerna	0.000	−79.815	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB10-2	Ecuador	Napo	QCA	Herbario QCA 2060	1.046	77.739	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB10-3	Ecuador	Napo	QCA	Herbario QCA 2060	1.054	77.694	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB05	Ecuador	Napo	QCA	Herbario QCA 2161	−0.954	−77.745	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB03	Ecuador	Napo	QCA	Herbario QCA 2059	1.042	77.726	4	7	—
006-IC-FLO-DNBAPVS/MA	SDGB10-1	Ecuador	Napo	QCA	Herbario QCA 2060	−1.052	−77.703	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB08	Ecuador	Napo	QCA	Herbario QCA 2056	−1.067	−77.621	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP16-1	Ecuador	Napo	QCA	A.J. Pérez 2771	−1.066	−77.634	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-3	Ecuador	Napo	QCA	A.J. Pérez 2754	−0.069	−77.620	4	7	—
006-IC-FLO-DNBAPVS/MA	SDAP16-2	Ecuador	Napo	QCA	A.J. Pérez 2771	−1.066	−77.635	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB06	Ecuador	Napo	QCA	Herbario QCA 2052	−1.061	−77.599	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP16	Ecuador	Napo	QCA	A.J. Pérez 2771	−1.066	−77.632	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB10-4	Ecuador	Napo	QCA	Herbario QCA 2161	−0.953	−79.750	4	—	—

Original collection number	Additional code	Country	Population	Herbarium	Collector name	Latitude	Longitude	Haplotype		
								cpSSR	cpSEQ	ITS
006-IC-FLO-DNBAPVS/MA	SDGB10-5	Ecuador	Napo	QCA	Herbario QCA 2161	−0.949	−79.754	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB10-6	Ecuador	Napo	QCA	Herbario QCA 2161	−0.943	−79.755	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-2	Ecuador	Napo	QCA	Herbario QCA 2185	−0.937	−79.764	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB09-4	Ecuador	Napo	QCA	Herbario QCA 2052	−1.049	−77.671	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15	Ecuador	Napo	QCA	A.J. Pérez 2754	−1.069	−77.620	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB09-1	Ecuador	Napo	QCA	Herbario QCA 2054	−1.066	−77.643	2	—	—
006-IC-FLO-DNBAPVS/MA	SDGB04	Ecuador	Napo	QCA	Herbario QCA 2058	−1.042	−77.726	2	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-1	Ecuador	Napo	QCA	A.J. Pérez 2754	−1.071	−77.616	5	7	—
006-IC-FLO-DNBAPVS/MA	SDGB08-1	Ecuador	Napo	QCA	Herbario QCA 2056	−1.068	−77.625	5	—	—
006-IC-FLO-DNBAPVS/MA	SDGB07	Ecuador	Napo	QCA	Herbario QCA 2056	−1.065	−77.612	3	10	12
006-IC-FLO-DNBAPVS/MA	SDGB13-1	Ecuador	Napo	QCA	Herbario QCA 2185	−0.937	−77.758	5	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-2	Ecuador	Napo	QCA	A.J. Pérez 2754	−1.066	−77.614	3	10	—
006-IC-FLO-DNBAPVS/MA	SDGB09	Ecuador	Napo	QCA	Herbario QCA 2054	−1.066	−77.630	5	—	—
006-IC-FLO-DNBAPVS/MA	SDGB11	Ecuador	Napo	QCA	Herbario QCA 2057	−0.956	−77.751	3	—	—
006-IC-FLO-DNBAPVS/MA	SDGB09-3	Ecuador	Napo	QCA	Herbario QCA 2052	−1.062	−77.658	4	9	12
006-IC-FLO-DNBAPVS/MA	SDGB12	Ecuador	Napo	QCA	Herbario QCA 2051	−0.961	−77.747	12	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13	Ecuador	Napo	QCA	Herbario QCA 2185	−0.936	−77.756	5	7	12
006-IC-FLO-DNBAPVS/MA	SDGB11-1	Ecuador	Napo	QCA	Herbario QCA 2051	−0.960	−77.749	4	7	12
006-IC-FLO-DNBAPVS/MA	SDGB10	Ecuador	Napo	QCA	Pérez / Iglesias	−1.054	−77.694	2	7	12
006-IC-FLO-DNBAPVS/MA	SDGB09-9	Ecuador	Napo	QCA	Pérez / Iglesias	−1.049	−77.671	3	10	12
006-IC-FLO-DNBAPVS/MA	SDAP15-27	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.683	−76.378	5	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-23	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.691	−76.385	5	7	—
006-IC-FLO-DNBAPVS/MA	SDAP15-25	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.692	−76.385	4	7	—
006-IC-FLO-DNBAPVS/MA	SDAP15-24	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.692	−76.384	5	7	—
006-IC-FLO-DNBAPVS/MA	SDGB13-3	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.678	−76.395	5	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-32	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.683	−76.385	5	7	—
006-IC-FLO-DNBAPVS/MA	SDAP15-31	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.690	−76.378	5	7	—
006-IC-FLO-DNBAPVS/MA	SDAP15-30	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.688	−76.378	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-29	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.686	−76.378	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-7	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.672	−76.405	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-16	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.681	−76.384	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-20	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.684	−76.381	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-19	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.684	−76.381	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-5	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.673	−76.398	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-6	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.667	−76.403	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-18	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.684	−76.384	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-17	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.684	−76.383	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-15	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.681	−76.384	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-4	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.681	−76.393	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-10	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.676	−76.408	4	11	—
006-IC-FLO-DNBAPVS/MA	SDAP15-12	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.678	−76.406	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-14	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.677	−76.401	4	—	—

Original collection number	Additional code	Country	Population	Herbarium	Collector name	Latitude	Longitude	Haplotype		
								cpSSR	cpSEQ	ITS
006-IC-FLO-DNBAPVS/MA	SDAP15-26	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.692	−76.386	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-11	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.677	−76.408	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-28	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.684	−76.378	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-8	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.674	−76.398	4	7	—
006-IC-FLO-DNBAPVS/MA	SDAP15-9	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.674	−76.408	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-13	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.676	−76.402	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-21	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.688	−76.382	4	—	—
006-IC-FLO-DNBAPVS/MA	SDAP15-22	Ecuador	Orellana	QCA	A.J. Pérez 3065	−0.688	−76.383	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-19	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.170	−79.007	3	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-18	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.173	−79.011	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-25	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.096	−79.003	4	12	—
006-IC-FLO-DNBAPVS/MA	SDGB13-23	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.142	−78.997	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-20	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.161	−79.004	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-10	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.179	−79.027	4	12	20
006-IC-FLO-DNBAPVS/MA	SDGB13-17	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.168	−79.087	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-24	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.128	−78.997	4	12	21
006-IC-FLO-DNBAPVS/MA	SDGB13-9	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.180	−79.031	4	—	20
006-IC-FLO-DNBAPVS/MA	SDGB13-7	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.175	−79.034	4	12	19
006-IC-FLO-DNBAPVS/MA	SDGB13-13	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.181	−79.025	4	12	20
006-IC-FLO-DNBAPVS/MA	SDGB13-11	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.179	−79.028	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-8	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.177	−79.032	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-15	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.178	−79.018	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-16	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.178	−79.016	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-21	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.152	−79.000	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-22	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.148	−78.997	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-14	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.181	−79.022	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-6	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.170	−79.046	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-5	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.170	−79.044	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-32	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.162	−79.086	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB72-12	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.180	−79.028	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-30	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.166	−79.067	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-28	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.168	−79.052	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-31	Ecuador	Pichincha	QCA	A.J. Pérez 3255	−0.164	−79.080	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-26	Ecuador	Pichincha	QCA	A.J. Pérez 3255	0.148	−78.996	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-27	Ecuador	Pichincha	QCA	A.J. Pérez 3255	0.168	−79.049	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-33	Ecuador	Pichincha	QCA	A.J. Pérez 3255	0.145	−78.996	4	—	—
006-IC-FLO-DNBAPVS/MA	SDGB13-29	Ecuador	Pichincha	QCA	A.J. Pérez 3255	0.166	−79.064	4	—	—
36		Ecuador	Pichincha	QCA		−0.173	−79.011	—	14	22
1855		Ecuador	Pichincha	QCA		−0.173	−79.011	—	14	—
C66		Ecuador	Pichincha	QCA		−0.173	−79.011	—	14	—
451		El Salvador	Ahuachapan	MO	Sandoval E.	13.667	−89.167	9	1	—
HB132		French Guiana		CAY		3.750	−53.033	2	—	—

Original collection number	Additional code	Country	Population	Herbarium	Collector name	Latitude	Longitude	Haplotype		
								cpSSR	cpSEQ	ITS
HB135	25060	French Guiana	French Guiana	CAY	Mori	3.750	−53.033	4	—	—
HB138	719	French Guiana	French Guiana	CAY	VieillesCazes	4.033	−52.700	—	—	—
HB139	1521	French Guiana	French Guiana	CAY	Sabatier	4.050	−52.700	4	—	—
HB133	N19208	French Guiana	French Guiana	CAY	Mori	3.617	−53.200	4	—	—
HB134	6037	French Guiana	French Guiana	CAY	Amshoff	3.750	−53.033	—	—	—
HB136	103	French Guiana	French Guiana	CAY	Stahel	3.750	−53.033	4	—	—
HB137	2691	French Guiana	French Guiana	CAY	Villiers	3.750	−53.033	4	7	—
HB140	59N	French Guiana	French Guiana	CAY	Nolland Lion	3.750	−53.033	3	—	—
HB141	1434	French Guiana	French Guiana	CAY	Grenand	3.750	−53.033	4	—	—
108039		Guatemala	Peten	INPA		16.915	−90.298	8	—	—
U 0088192		Guyana	Barima-Waini	U(L)		7.367	−59.700	6	—	—
U 0214762		Guyana	Guyana	U(L)		7.367	−59.700	4	7	—
U 0214763		Guyana	Pomeroon-Supenaam	U(L)		7.000	−58.833	2	—	—
106		Honduras	Francisco-Morazan	MO	Sanchez J.	14.100	−87.217	9	1	—
35515		Honduras	Yoro	MO	Davidse	14.100	−87.217	6	—	—
4851		Mexico	Oaxaca	MO	Wendt	19.000	−90.717	9	—	—
1868		Mexico	Oaxaca	MO	Hernandez	19.000	−90.717	9	2	10
9398		Mexico	Quintana Roo	MO	Alvarez	19.000	−90.717	9	1	12
16432		Nicaragua	Madriz	MO	Stevens	12.885	−85.676	6	—	—
1961		Nicaragua	Rivas	MO	Robleto	12.885	−85.676	—	—	—
28188		Nicaragua	Rivas	MO	Nee	12.885	−85.676	6	—	—
49025		Panama	Panama	INPA		8.480	−80.745	5	—	—
18510		Paraguay	Central	MO	Zardini	−23.437	−58.395	5	—	—
2512		Peru	Loreto	MO	Diaz	−4.914	−73.667	4	—	—
2496		Peru	Loreto	MO	Diaz	−4.914	−73.667	3	—	—
19056		Peru	Loreto	MO	Croat	−4.914	−73.667	4	—	—
169420		Peru	Manu, Madre de Dios	INPA		−11.000	−71.900	5	—	—
1663		Peru	Pasco	MO	Diaz	−4.914	−73.667	—	—	—
U0183255	12625	Suriname	Suriname	U(L)		5.732	−55.700	2	—	—
U0214764	617	Suriname	Suriname	U(L)		5.732	−55.700			
5321		Trinidad	Trinidad	U(L)		10.429	−61.251	2	—	—
97206		Venezuela	Bolivar (Venezuela)	INPA		7.774	−63.573	2	—	—
66524		Ecuador	Loja	QCA		−4.000	−79.200	—	15	5
75372		Ecuador	Loja	QCA		−4.000	−79.200	—	15	—
16139		Ecuador	Napo	QCA		−1.052	−77.703	—	12	—
2494		Ecuador	Orellana	QCA		−0.667	−76.403	—	16	—
1365		Ecuador	Pichincha	QCA		−0.173	−79.011	—	12	—
8146		Ecuador	Pichincha	QCA		−0.173	−79.011	—	12	—
2691		Ecuador	Tungurahua	QCA		−1.467	−78.442	—	17	—
GB-72-CO189-1		Ecuador	Ecuador	QCA		0.000	−79.815	—	12	18
GB-72-CO189-2		Ecuador	Ecuador	QCA		0.000	−79.815	—	13	—
GB-72-CO189-3		Ecuador	Ecuador	QCA		0.000	−79.815	—	12	20

								Haplotype		
Original collection number	Additional code	Country	Population	Herbarium	Collector name	Latitude	Longitude	cpSSR	cpSEQ	ITS
GB-72-CO189-4		Ecuador	Ecuador	QCA		0.000	−79.815	—	13	2
GB-73-CO190/SDGB4-1		Ecuador	Ecuador	QCA		0.000	−79.815	—	—	—
GB-73-CO190/SDGB4-2		Ecuador	Ecuador	QCA		0.000	−79.815	—	—	—
GB-80-CO259/SDGB7-1		Ecuador	Ecuador	QCA		0.000	−79.815	—	13	—
GB-80-CO259/SDGB7-2		Ecuador	Ecuador	QCA		0.000	−79.815	—	—	—
GB-80-CO259/SDGB7-3		Ecuador	Ecuador	QCA		0.000	−79.815	—	13	—

Table S3 Details of the polymorphic positions (single nucleotide polymorphisms, SNPs, and insertion/deletion mutations, indels (—)) in ITS sequences and the multilocus haplotypes of the *Cedrela odorata* species complex identified for the collection (H1–H22). Consensus sequence given, identical nucleotides indicated (.)

	GenBank accession number	60	65	94	95	96	101	102	105	106	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	130	136	149	162	163	169	178	179	207	221	248	262	266	273	287	289	475
		G	A	C	G	G	G	C	G	G	G	C	G	C	G	C	G	G	C	G	C	G	C	G	A	C	G	C	C	A	T	G	T	T	–	C	C	A	C	T	G	T	T
H1	JN112854	C	.	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.	.	C	.	A	.	.	.	.	.	.	.
H2	JN112855	C	.	G	.	.	.	.	.	.	.	.	.	.	T	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	–	.	.	.	.	.	.	.
H3	JN112856	.	A	.	.	.	.	–	A	A	.	.	.	.	T	C	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	A	C	.	–	.	.	.	.	.	A	.
H4	JN112857	.	A	.	.	.	.	–	A	A	.	.	.	.	T	C	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	A	C	.	–	G	.	.	.	.	A	.
H5	JN112858	.	A	.	–	–	.	.	.	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.	A	.	.	G	.	.	.	.	–	.	.	G	T	.	.	.
H6	JN112859	.	.	.	.	R	R	K	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	T	.	.	.	.	.	–	.	T	.	.	.	A	C
H7	JN112860	.	.	.	.	R	A	T	.	T	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	T	.	.	.	.	.	–	.	Y	.	.	.	A	C
H8	JN112861	.	.	.	.	R	A	T	.	T	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	T	.	.	.	.	.	–	.	T	.	.	.	A	C
H9	JN112862	.	.	.	.	A	R	K	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	T	.	.	.	.	.	–	.	T	.	.	.	A	C
H10	JN112863	.	.	.	.	A	A	T	.	T	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	.	.	.	.	–	.	T	.	.	.	A	C
H11	JN112864	.	.	.	.	A	A	T	.	T	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	T	.	.	.	.	.	–	.	Y	.	.	.	A	C
H12	JN112865	.	.	.	.	A	A	T	.	T	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	T	.	.	.	.	.	–	.	T	.	.	.	A	C
H13	JN112866	.	.	.	.	.	R	K	.	T	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	T	T	.	.	.	.	.	–	.	T	.	.	.	A	C
H14	JN112867	.	.	.	.	.	A	T	.	T	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	T	.	.	.	.	.	–	.	T	.	.	.	A	C
H15	JN112868	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	–	.	.	.	.	C	.	.
H16	JN112869	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	–	.	.	.	.	.	.	.
H17	JN112870	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	–	.	.	.	.	C	.	.
H18	JN112871	.	T	.	.	A	.	.	.	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.	A	.	.	G	.	.	Y	.	–	.	.	C	T	.	.	.
H19	JN112872	.	T	.	.	A	.	.	.	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.	A	.	.	G	.	.	C	.	–	.	.	C	T	.	.	.
H20	JN112873	.	T	.	.	A	.	.	.	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.	A	.	.	G	.	.	.	.	–	.	.	C	T	.	.	.
H21	JN112874	.	T	.	.	.	.	.	.	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.	A	.	.	G	.	.	C	.	–	.	.	C	T	.	.	.
H22	JN112875	.	T	.	–	–	.	.	.	.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.	A	.	.	T	.	.	C	.	–	.	.	G	T	.	.	.

Table S4 Distribution of the 22 ITS haplotypes of the *Cedrela odorata* species complex identified (Table S3) in populations across Central and South America and the Caribbean.

		ITS haplotype																						
Country	Row labels	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
Cuba	Baracoa												3											3
Cuba	Bayate-Mayarí							1					4											5
Cuba	Ceiba-mocha												1											1
Cuba	Chambas												5											5
Cuba	Cidra												1											1
Cuba	Cienaga d.Z.												1											1
Cuba	Escambray												5											5
Cuba	Guisa												4											4
Cuba	Najasa												5											5
Cuba	Placetas												1											1
Cuba	Viñales										1		4											5
Belize	Belize												1											1
Mexico	Escarcega									1	1	2	7											11
Mexico	Mexico										1		1											2
Mexico	Zona Maya								1				9											10
Guatemala	Los Esclavos												2											2
Guatemala	Tikal									1			2											3
Honduras	Comayagua												4											4
Honduras	Meambar									1		1	8	1	1									12
Honduras	Taulabe						1																	1
Nicaragua	Nicaragua												1											1
Nicaragua	Wabule												4											4
Costa Rica	Jimenez		3																					3
Costa Rica	Pacifico Sur		4																					4
Costa Rica	Talamanca		1																					1
Costa Rica	Upala		6																					6
Panama	San Francisco	1																						1
Cayman Islands	Cayman Brac															4	2							6
Cayman Islands	Grand Cayman															9		1						10
Guadeloupe	Guadalupe												6											6
Ecuador	Ecuador		1																1		1			3
Ecuador	Esmeraldas												1								2			3
Ecuador	Loja					1																		1
Ecuador	Manabí		1																					1
Ecuador	Napo												6											6
Ecuador	Pichincha																			1	3	1	1	6
Brazil	Boca de Acre			2	2																			4
Peru	Loreto												4											4
	Total	1	16	2	2	1	1	1	1	3	3	3	90	1	1	13	2	1	1	1	6	1	1	152

Table S5 Details of the polymorphic positions (single nucleotide polymorphisms, SNPs and insertion/deletion mutations, indels) in chloroplast sequences (reported here as concatenated trnC–*ycf*6 and *trn*H–*psb*A) and the multilocus haplotypes of the *Cedrela odorata* species complex identified for the collection (H1–H17). Consensus sequence given, identical nucleotides indicated with a dot. Hap, haplotype.

							Mutation number / position / consensus sequence																
	Indels						1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Hap	292	352	439–500		505	701	83	104	169	189	270	336	365	413	428	463	527	570	577	595	636	641	665
							G	T	A	T	T	T	G	A	T	A	A	T	A	C	G	A	C
H1	1	0	0	1	0	1	.	.	.	.	.	G	.	.	.	.	.	C	T	.	A	T	.
H2	1	0	0	1	0	1	.	.	.	.	.	.	.	.	.	.	.	C	T	.	A	T	.
H3	0	0	1	1	0	0	.	.	.	.	.	.	.	.	.	C	.	C	.	.	.	.	A
H4	0	0	0	1	0	0	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.
H5	0	1	1	0	0	1	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
H6	0	1	0	1	0	1	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
H7	0	0	0	1	0	1	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
H8	0	0	0	1	0	1	.	.	C	.	.	.	.	.	.	.	C	.	.	.	.	.	.
H9	0	0	0	1	0	1	.	.	C	.	.	.	.	T	.	.	.	.	.	.	.	.	.
H10	0	0	0	1	0	1	.	.	.	G	G	.	T	.	.	.	.	.	.	.	.	.	.
H11	0	0	0	1	0	1	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
H12	0	0	0	1	0	1	A	.	.	.	.	.	.	.	G	.	.	C	.	.	.	.	.
H13	0	0	0	1	0	0	.	G	.	.	.	.	.	.	.	C	.	C	.	.	.	.	.
H14	0	0	0	1	0	0	.	.	?	.	.	?	?	?	?	?	?	?	?	?	.	.	.
H15	0	0	0	1	1	1	.	.	?	.	.	.	.	.	G	.	.	C	.	A	.	.	.
H16	0	0	0	1	0	1	.	.	C	G	.	.	.	.	.	.	.	.	.	.	.	.	.
H17	0	0	0	1	0	1	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table S6 Distribution of 17 chloroplast sequence haplotypes of the *Cedrela odorata* species complex identified (Table S5) in populations across Central America, South America and the Caribbean.

		Chloroplast sequence haplotype																	
Country	Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
Cuba	Baracoa	3																	3
Cuba	Bayate-Mayarí	9																	9
Cuba	Chambas	4																	4
Cuba	Escambray	11																	11
Cuba	Guisa	3																	3
Cuba	Najasa	13																	13
Cuba	Viñales	11																	11
Belize	Belize	1																	1
Mexico	Escarcega	20																	20
Mexico	Mexico	1	1																2
Mexico	Zona Maya	14																	14
El Salvador	El Salvador	1																	1
Guatemala	Los Esclavos	4																	4
Guatemala	Tikal	3																	3
Honduras	Honduras	1																	1
Honduras	Comayagua			4															4
Honduras	Meambar			14															14
Honduras	Taulabe			2															2
Nicaragua	Nicaragua			1															1
Nicaragua	Wabule			8															8
Costa Rica	Upala			1	8														9
Costa Rica	Jimenez	1			3														4
Costa Rica	Pacifico Sur				8														8
Costa Rica	Talamanca				1														1
Panama	San Francisco				1														1
Cayman Islands	Cayman Brac				7														7
Cayman Islands	Grand Cayman				18														18
Guadeloupe	Guadalupe					1	6												7
French Guiana	French Guiana							1											1
Guyana	Guyana							1											1
Ecuador	Esmeraldas												6						6
Ecuador	Manabí													8					8
Ecuador	Ecuador												2	4					6
Ecuador	Pichincha												7		3				10
Ecuador	Loja															2			2
Ecuador	Tungurahua																	1	1
Ecuador	Napo							6		1	3		1						11
Ecuador	Orellana							6				1					1		8
Peru	Loreto									7									7
Peru	Peru									2									2
Brazil	Boca de Acre								14	2									16
Brazil	Para									1									1
	Total	100	1	30	46	1	6	14	14	13	3	1	16	12	3	2	1	1	264

Table S7 Description of 13 chloroplast microsatellite haplotypes of the *Cedrela odorata* species complex characterized at five cpSSR loci and frequency of occurrence (*n*) in total collection screened.

Haplotype	*ccmp2*	*ccmp3*	*ccmp4*	*ccmp6*	*ccmp10*	*n*
H1	202	122	92	117	110	2
H2	202	122	92	118	110	35
H3	202	122	92	119	110	38
H4	202	122	92	120	110	170
H5	202	122	92	121	110	27
H6	202	122	92	122	110	23
H7	202	122	92	123	110	1
H8	202	122	98	118	110	1
H9	202	122	98	120	110	189
H10	202	122	98	121	110	1
H11	206	122	92	120	110	1
H12	210	123	89	124	110	1
H13	235	122	94	108	113	1
					Total	490

Table S8 Distribution of the 13 chloroplast microsatellite haplotypes of the *Cedrela odorata* species complex identified (Table S7) in populations across Central America, South America and the Caribbean.

		Chloroplast SSR haplotype													
Country	**Population**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**Total**
Cuba	Baracoa									3					3
Cuba	Bayate-Mayarí									19					19
Cuba	Ceiba-mocha									1					1
Cuba	Chambas									6					6
Cuba	Cidra									1					1
Cuba	Ciénaga de Zapata									8					8
Cuba	Escambray									20					20
Cuba	Guisa				2					30					32
Cuba	Ariguanabo									4					4
Cuba	Moa-Sagua									10					10
Cuba	Najasa					2				28	1				31
Cuba	Placetas									6					6
Cuba	Viñales									31					31
Belize	Belize									1					1
El Salvador	El Salvador									1					1
Mexico	Escarcega									8					8
Mexico	Mexico									3					3
Mexico	Zona Maya									8					8
Guatemala	Peten								1						1
Honduras	Comayagua						5								5
Honduras	Honduras						1			1					2
Honduras	Taulabe						3								3
Nicaragua	Nicaragua						3								3
Nicaragua	Wabule						8								8
Costa Rica	Jimenez					5									5
Panama	Panama					1									1
Colombia	Jambrano Bolivar					1									1
Venezuela	Venezuela		1												1
Ecuador	Ecuador				1										1
Ecuador	Esmereldas				14		1	1							16
Ecuador	Manabí			8	9							1			18
Ecuador	Napo		3	4	19	5							1		32
Ecuador	Orellana				24	6									30
Ecuador	Pichincha				32										32
Peru	Loreto			23	26										49
Peru	Manu					1									1
Peru	Peru			1	2										3
Brazil	Abaetetuba, PA		1												1
Brazil	Amazonas		2	1											3
Brazil	Belém, PA		1			1									2
Brazil	Boca de Acre		4		22	3									29
Brazil	Brasiléia, AC		1												1
Brazil	Braganca*						1								1
Brazil	Huimaita*				3										3
Brazil	Manaus, AM		1												1
Brazil	Maranhão				1	1									2
Brazil	Para				1										1
Brazil	Paraná		1		1										2
Brazil	Rio Branco, AC		1		1										2
French Guiana	F. Guiana	2	4	1	10									1	18
Guadeloupe	Guadalupe		10												10
Guyana	Guyana		1		1		1								3
Surinam	Suriname		1												1
Trinidad and Tobago	Trinidad		1												1
Bolivia	Arce, Tarija		1												1
Bolivia	Ballivian, Beni				1										1
Bolivia	Manuripi,Pando				1										1
Paraguay	Paraguay					1									1
														Total	490

Figure S1 Map of sampling locations included in this study.

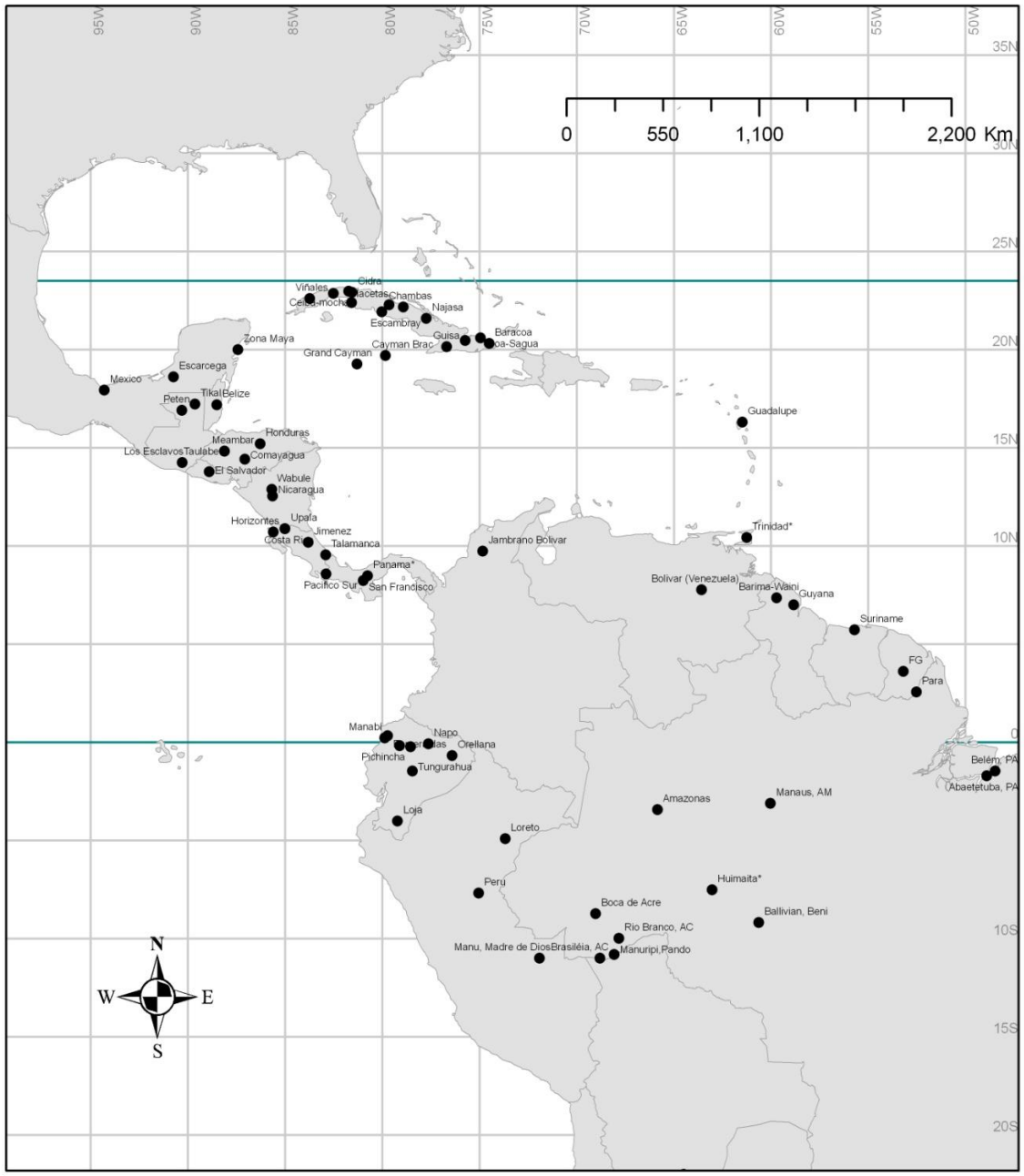


Figure S2a Clustering of all individuals of the *Cedrela odorata* species complex in collection based on multilocus genotypes obtained from six nuclear microsatellite loci. Clustering was estimated using STRUCTURE 2.3.3, using default settings apart from LOCISPRIOR (on). Using the maximum deceleration approach, $K = 2$ was the optimal value; $K = 3$ and 4 are shown to illustrate lower hierarchical levels of structure in the dataset. In this figure, samples are ordered approximately by country and with latitude, starting in Cuba. Selected populations are identified to illustrate the nature of groupings at $K = 4$. Figures are produced from mean values across replicate runs, determined using CLUMPP 1.1.1 (Jakobsson & Rosenberg, 2007) using the greedy algorithm with random input order and 10,000 permutations. Output plots were produced using DISTRUCT 1.1 (Rosenberg, 2004).

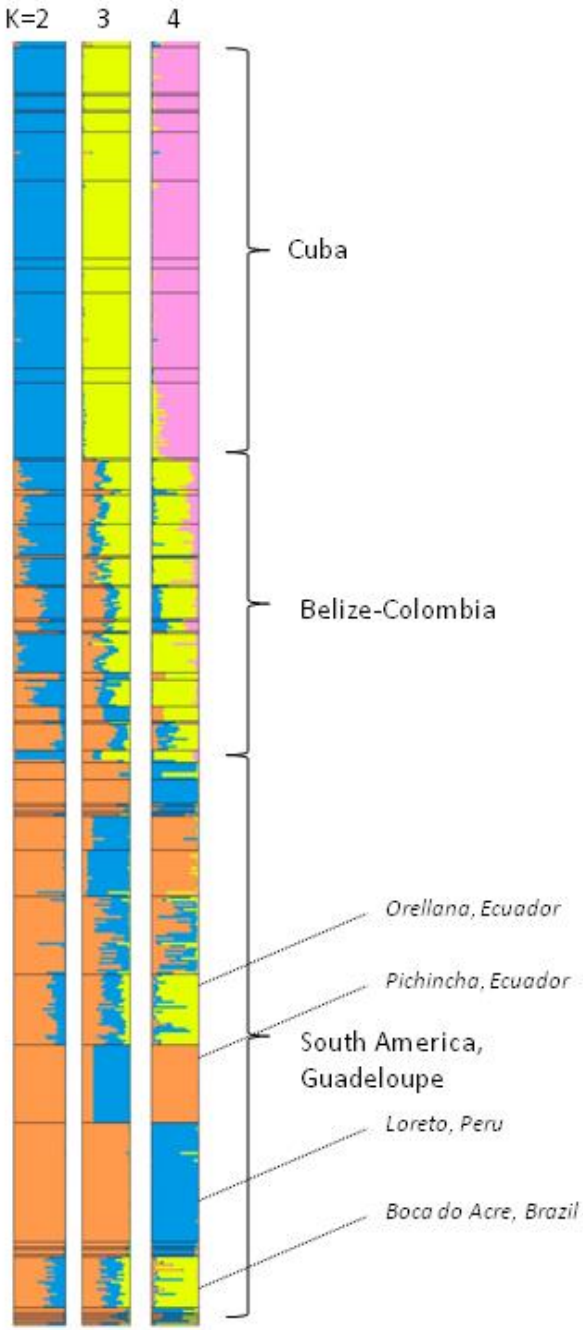


Figure S2b Clustering of all individuals of the *Cedrela odorata* species complex for which ITS data was also available, based on multilocus genotypes obtained from six nuclear microsatellite loci. Individuals were *a priori* assigned to clades following the ITS phylogenetic analysis (Fig. 2) and ITS clade was then used as a prior for cluster analysis. Clustering was estimated using STRUCTURE 2.3.3, using default settings. Optimal value of *K* was estimated as 2.

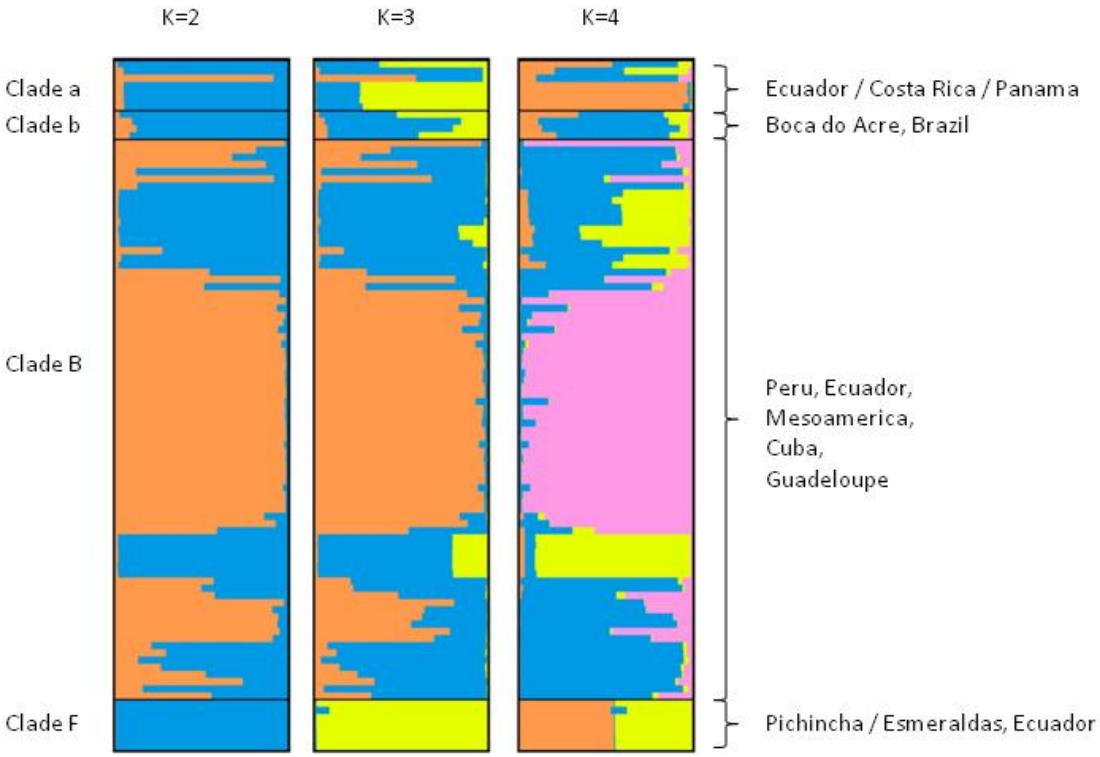


Figure S2c Clustering of all individuals of the *Cedrela odorata* species complex for which ITS data was also available, based on multilocus genotypes obtained from six nuclear microsatellite loci. Clustering was estimated using STRUCTURE 2.3.3, using default settings apart from LOCISPRIOR (on). Optimal value of *K* was estimated to be 3.

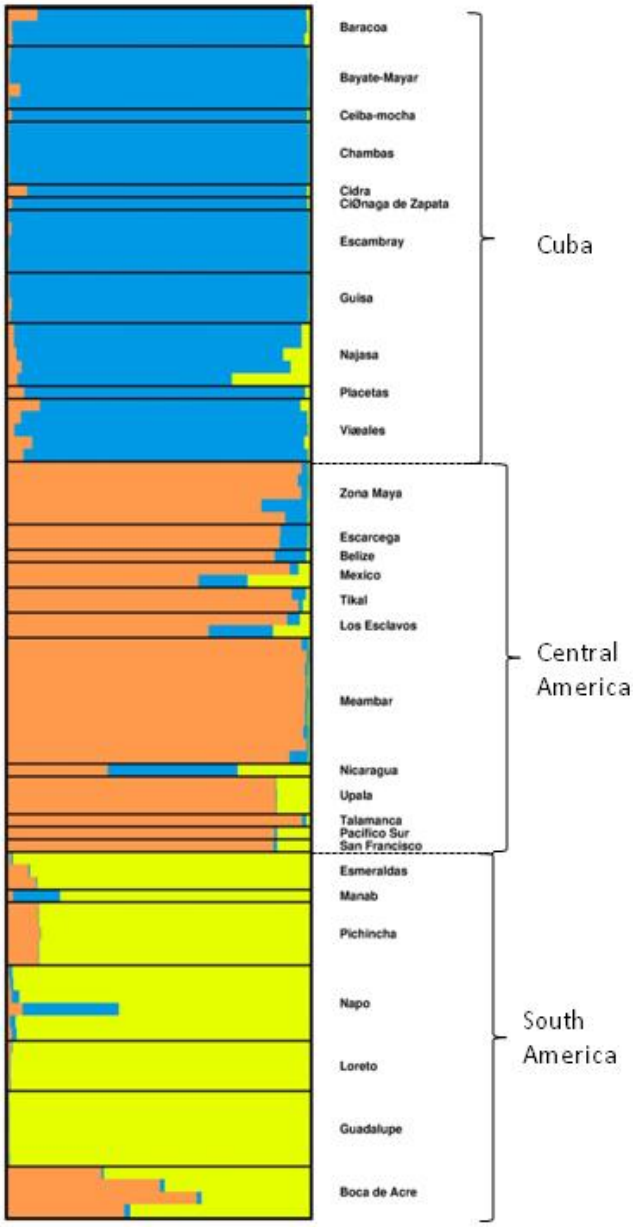
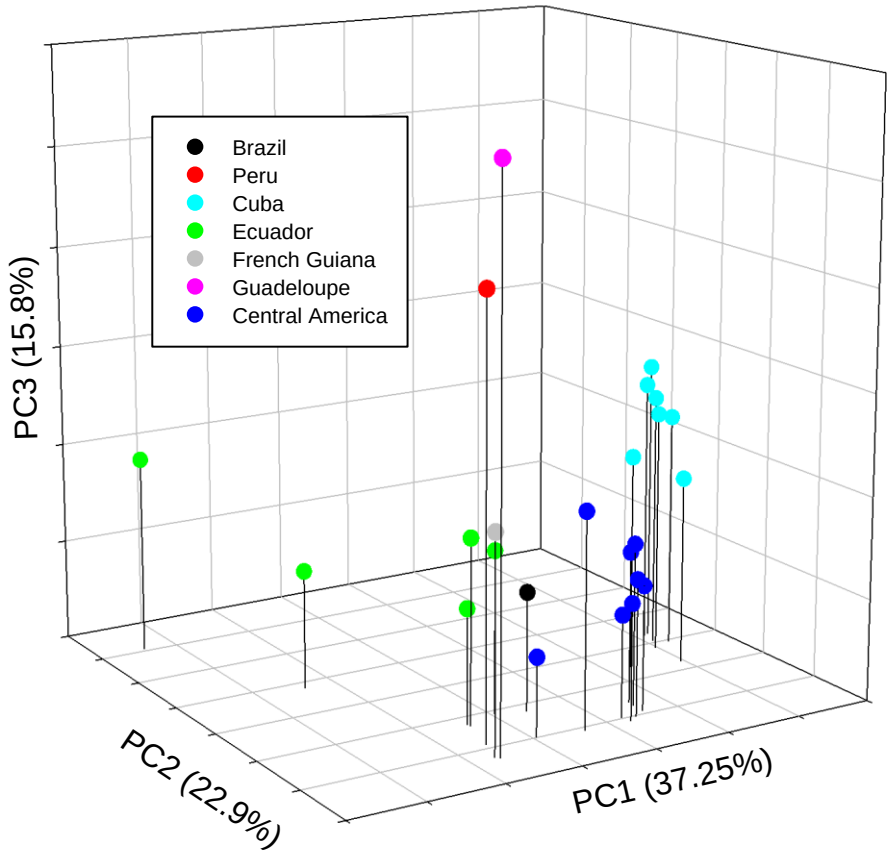


Figure S3 Plot of the first three axes of a principal coordinates analysis of pairwise F_{ST} among populations of the *Cedrela odorata* species complex, derived from nuclear microsatellite genotypes. F_{ST} values were adjusted for the presence of null alleles using the software FREENA (Chapuis & Estoup, 2007). The three axes shown account for a total of 75.95% of the total variation.



Appendix S2 Details of amplification protocols for molecular laboratory work.

DNA extraction

DNA was extracted from all samples of the *Cedrela odorata* species complex using the Qiagen DNeasy 96 Plant kit (Qiagen, Crawley, UK) following the manufacturer's 'frozen plant tissue' protocol.

Marker amplification

ITS and cp sequences

For amplification of both ITS (ITS plus flanking 18S and 26S regions) and chloroplast (*trn*C–*ycf*6, *trn*H–*psb*A) loci, polymerase chain reactions (PCRs) were performed in 25 μL volumes containing 2.5 μL 10× ThermoPol reaction buffer (New England Biolabs, Hitchin, UK), 200 μM each dNTP, 1.6% v/v bovine serum albumin (BSA) for chloroplast regions or 5% dimethyl sulfoxide (DMSO) for ITS, 0.2 μM each primer, 1 U Taq DNA polymerase (New England Biolabs, Hitchin, UK) and 5 ng template DNA. Reactions were performed in Thermo Hybaid thermal cyclers using the following protocols: to amplify the intergenic transcribed spacer (using primers F1-ITS–R1-ITS; Muellner *et al.*, 2005), 94 °C initial denaturation for 3 min, 36 cycles of denaturation at 94 °C for 1 min, 57 °C annealing for 1 min, and an extension of 72 °C for 1 min; to amplify chloroplast region *trn*C–*ycf*6 (Demesure *et al.*, 1995; Shaw *et al.*, 2005), 3 min at 94 °C, 40 cycles of 94 °C, 55 °C and 72 °C each for 1 min. A standard protocol was followed for *trn*H–*psb*A (Tate & Simpson, 2003; Shaw *et al.*, 2005). All amplification protocols finished with a final extension of 72 °C for 10 min. PCR products were purified with a Sap-Exo enzyme treatment, and sent for sequencing at NERC Biomolecular Analysis Facility (NBAF) at the University of Edinburgh.

cpSSRs

Universal primers for chloroplast microsatellite (cpSSR) loci were used to screen for variation in a subset of the sample collection (*ccmp1*–*ccmp7* and *ccmp10*, amplified according to Weising & Gardner, 1999). Amplified products were run on a MegaBace 96 capillary automatic sequencer (GE Healthcare, Little Chalfont, UK), following (Heuertz *et al.*, 2006). Loci *ccmp2*, *ccmp5* & *ccmp6* were found to be polymorphic and were screened through the whole collection.

nSSRs

A set of six nuclear SSR loci (*ced44*, *ced41*, *ced61a*, *ced65*, *ced95* and *ced131*, following Hernández *et al.*, 2008) were used to genotype 490 individual samples. Amplification protocols followed (Hernández *et al.*, 2008) with reactions carried out on Thermo Hybaid thermal cyclers (Thermo Scientific, Epsom, UK) and visualized by electrophoresis on 6% denaturing acrylamide gel on a Licor 4200

IR2 sequencer (Licor Biosciences, Lincoln, NE, USA). Alleles were scored by comparison to size standards using SAGA software (Licor Biosciences, Lincoln, NE, USA). For reasons discussed below, amplification success was variable across the collection and missing data were frequent although rarely localized within population samples. Therefore, prior to analysis, the final data set was sorted to remove any individuals with more than three missing loci.

REFERENCES

Demesure, B., Sodzi, N. & Petit, R.J. (1995) A set of universal primers for amplification of polymorphic non-coding regions of mitochondrial and chloroplast DNA in plants. *Molecular Ecology*, **4,** 129–131.

Hernández, G., Buonamici, A., Walker, K., Vendramin, G.G., Navarro, C. & Cavers, S. (2008) Isolation and characterization of microsatellite markers for *Cedrela odorata* L. (Meliaceae), a high value neotropical tree. *Conservation Genetics*, **9,** 457–459.

Heuertz, M., De Paoli, E., Källman, T., Larsson, H., Jurman, I., Morgante, M., Lascoux, M. & Gyllenstrand, N. (2006) Multilocus patterns of nucleotide diversity, linkage disequilibrium and demographic history of Norway spruce [*Picea abies* (L.) Karst]. *Genetics*, **174,** 2095–2105.

Jakobsson, M. & Rosenberg, N.A. (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, **23,** 1801–1806.

Muellner, A.N., Samuel, R., Chase, M.W., Pannell, C.M. & Greger, H. (2005) *Aglaia* (Meliaceae): an evaluation of taxonomic concepts based on DNA data and secondary metabolites. *American Journal of Botany*, **92,** 534–543.

Rosenberg, N.A. (2004) DISTRUCT: a program for the graphical display of population structure. *Molecular Ecology Notes*, **4,** 137–138.

Shaw, J., Lickey, E.B., Beck, J.T., Farmer, S.B., Liu, W., Miller, J., Siripun, K.C., Winder, C.T., Schilling, E.E. & Small, R.L. (2005) The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany*, **92,** 142–166.

Tate, J.A. & Simpson, B.B. (2003) Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploid species. *Systematic Botany*, **28,** 723–737.