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Phylogenetic, Morphometric, and Biogeographic Investigations of Trema micrantha (Cannabaceae)

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PHYLOGENETIC, MORPHOMETRIC, AND BIOGEOGRAPHIC INVESTIGATIONS OF TREMA MICRANTHA (CANNABACEAE)

by

Breanna Faye Whitley

B.S., Southern Illinois University, 2019

A Thesis
Submitted in Partial Fulfillment of the Requirements for the
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Approved by:

Kurt Neubig, Chair

Nancy Garwood

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Graduate School
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MAJOR PROFESSOR: Dr. Kurt Neubig

Trema micrantha L. Blume (Cannabaceae) is a pioneer tree species that is broadly distributed across the Neotropics. Taxonomic circumscriptions of this group have long been debated and problematic due to its morphological variation and broad geographic range. Delimitation of lineages within *T. micrantha* has remained unclear as molecular phylogenies with limited character and taxon sampling have not resolved the polyphyly of this group. To evaluate relationships within *T. micrantha,* I utilized phylogenetic, morphometric, and biogeographic methods. Using various DNA datasets, including ETS only, 5 DNA loci, plastome and whole nuclear ribosomal datasets, the recognition of 9 clades within *T. micrantha* was supported. Leaf shape morphometrics determined that several of these clades are morphologically diagnosable, but with some overlap in leaf shape, while ecological niche models elucidated ecological tolerance differences between clades. I thus evaluated these data across three species concepts (phylogenetic, morphological, and ecological) for future taxonomic revisions. The clades supported include *T. micrantha* A, *T. micrantha* C, and *T. micrantha* D. Within *T. micrantha* group B, 6 clades satisfy at least two species concepts and thus deserve recognition as distinct species, including *T. micrantha* B1a, B1b, B2, B3, B4, and B5.

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DEDICATION

This work is dedicated to Bonnie Faye Tedder, Rhonda Faye Whitley, Renee Sue Laird, Ravyn Karlene Laird, and Alexis Jewel Laird. For everything I am, is because of these women. For everything I do, is for these women. For their love and friendship, I am forever grateful.

I'd also like to dedicate this to Drs. Kurt Neubig and Nancy Garwood, the best advisors in all of academia. I could never thank you enough for your support.

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CHAPTER 1

INTRODUCTION

Cannabaceae *sensu* APG IV (Chase et al. 2016) is an economically and ecologically significant plant family with a cosmopolitan distribution (Zhang et al. 2018). An important member of Cannabaceae is *Trema* Lour., a pantropical genus composed entirely of pioneer tree species that occupy a broad range of habitats (Yesson et al. 2004). In these habitats, *Trema* species often serve as important components of successional vegetation following various disturbances (Yesson et al. 2004). Being ecological pioneers, representatives of *Trema* also present significant implications for habitat restoration (Stolarski et al. 2018; Garcia-Orth & Martinez-Ramos 2011; Vazguez-Yanes 1998).

Several species of *Trema* are also of economic importance. For centuries, *T. micrantha* (L.) Blume has been utilized for paper production by the Otomi people of Mexico (Peters et al. 1987). Paleotropical (also known as "Old World") members of *Trema* have demonstrated potential medical efficacy with antibacterial (Nasir Uddin et al. 2008), antimicrobial, and antiplasmodial properties (Oyebola et al. 2017). Additionally, recent study also indicates that *T. orientalis* (L.) Blume leaf extracts may offer treatment against carcinoma cells with its apoptosis induction property and cytotoxicity (Kabir et al. 2019).

Trema is widely distributed across the global tropics, with Neotropical members inhabiting various habitat in Florida, the Caribbean, as well as Central and South America, and Paleotropical members in Africa, Madagascar, India, Asia, Australia, and Polynesia (Yesson et al. 2004). Despite being a unique group of pantropical pioneer tree species, there is significant disparity in taxonomic knowledge. Currently, there are 20 recognized species and 2 accepted varieties, with 66 synonyms and 10 ambiguous names (World Flora Online 2022). In the

Neotropics, four species are typically recognized (Figure 1). *Trema cubensis* Urb. And *T. lamarckiana* (Roem. & Schult.) Blume are both small-leaved species restricted to the Caribbean (Acevedo-Rodriguez & Strong 2012). *Trema domingensis* Urb., the only Neotropical species with entire leaf margins, is distributed across Central and South American, but rare in the Caribbean (Garwood et al. 2018). *Trema micrantha* is the most widely distributed and morphologically variable Neotropical species with a distribution ranging from Florida, throughout the Caribbean, Central America, and South America. There is no global monograph of *Trema*, therefore species concepts vary widely across regional floras and variability of taxonomic treatments is especially problematic for *T. micrantha.*

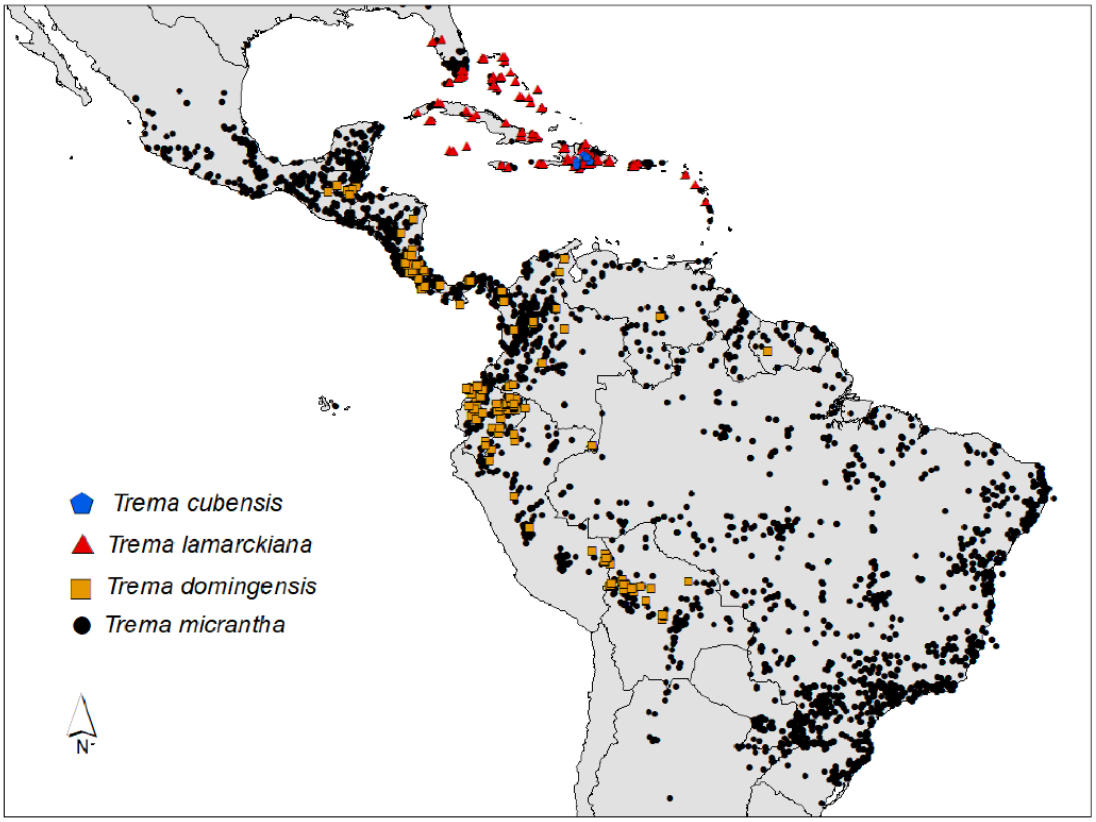


Figure 1. Distribution of Neotropical *Trema* species. Occurrence data derived from GBIF.org.

Authors of many local floras across the Neotropics have noted the morphological variation within *T. micrantha.* Some treatments recognize *T. micrantha* as a highly variable species (Torres and Luca 2005; Philcox 1982; Legaard & Balslev 2014; MacBride 1937), while others divide it into varieties (i.e., var. *floridana* (Britton ex Small) Stand. & Steyerm.*,* var. *strigillosa* (Lundell) Stand. & Steyerm.) or as distinct species (*T. micrantha, T. floridana* Britton ex Small*, T. strigillosa* Lundell*, T. mollis* (Hum. & Bonpl. Ex Willd) Blume) (Nee 2015; Machado et al. 2019; Adams 1972; Britton 1908; Lundell 1939).

To address this taxonomic uncertainty, Yesson et. al (2004), employed the first phylogenetic study of *Trema* (36 specimens) using the nuclear ribosomal internal transcribed spacer (ITS) and the plastid DNA region *trnL-F*. They recovered a moderately supported New World clade (BP = 79%), with unresolved relationships within the clade, including the polyphyly of *T. micrantha*, (Yesson et al. 2004). They found two groups within *T. micrantha. Trema micrantha* **I** contained all specimens with brown endocarps and formed a well-supported clade (BP = 99%) (Yesson et al. 2004). *Trema micrantha* **II** included all specimens with black endocarps, but did not form a monophyletic group, because specimens of *T. integerrima* (Beurl.) Standl. (now *T. domingensis*) were nested within the group (Yesson et al. 2004). Furthermore, there is evidence that these putative lineages may inhabit different ecological niches (Silvera et al. 2003). In Panama, at least two morphotypes have been identified, which correspond with lineages *T. micrantha* **I** and *T. micrantha* **II.** Within the Barro Colorado Nature Monument in Panama, *T. micrantha* **I** was found almost exclusively on landslides along the shoreline, while *T. micrantha* **II** was only found growing in treefall gaps of secondary forests (Silvera et al. 2003).

More recently, Garwood et al. (2018) presented a taxonomic reassessment of the Neotropical *Trema* species with entire leaf margins - *T. integerrima* (Beurl.) Standl., *T.*

domingensis Urb., and *T. laxiflora* Lundell (now all *T. domingensis*) using a five DNA region phylogeny (Figure 2). The plastid DNA regions *trnL-F*, *rbcL*, and *trnH-psbA* along with the nuclear ribosomal ITS and external transcribed spacer (ETS), provided better resolution for *T. micrantha*. Four well-supported clades within *T. micrantha* were recovered: *T. micrantha* A, C, B1, and B2, with *T. domingensis* sister to the *T. micrantha* B clades (Garwood et al. 2018). *Trema domingensis*, while sister to *T. micrantha* (B1+B2), is morphologically distinct with an entire leaf margin and unique trichome morphology (Garwood et al. 2018).

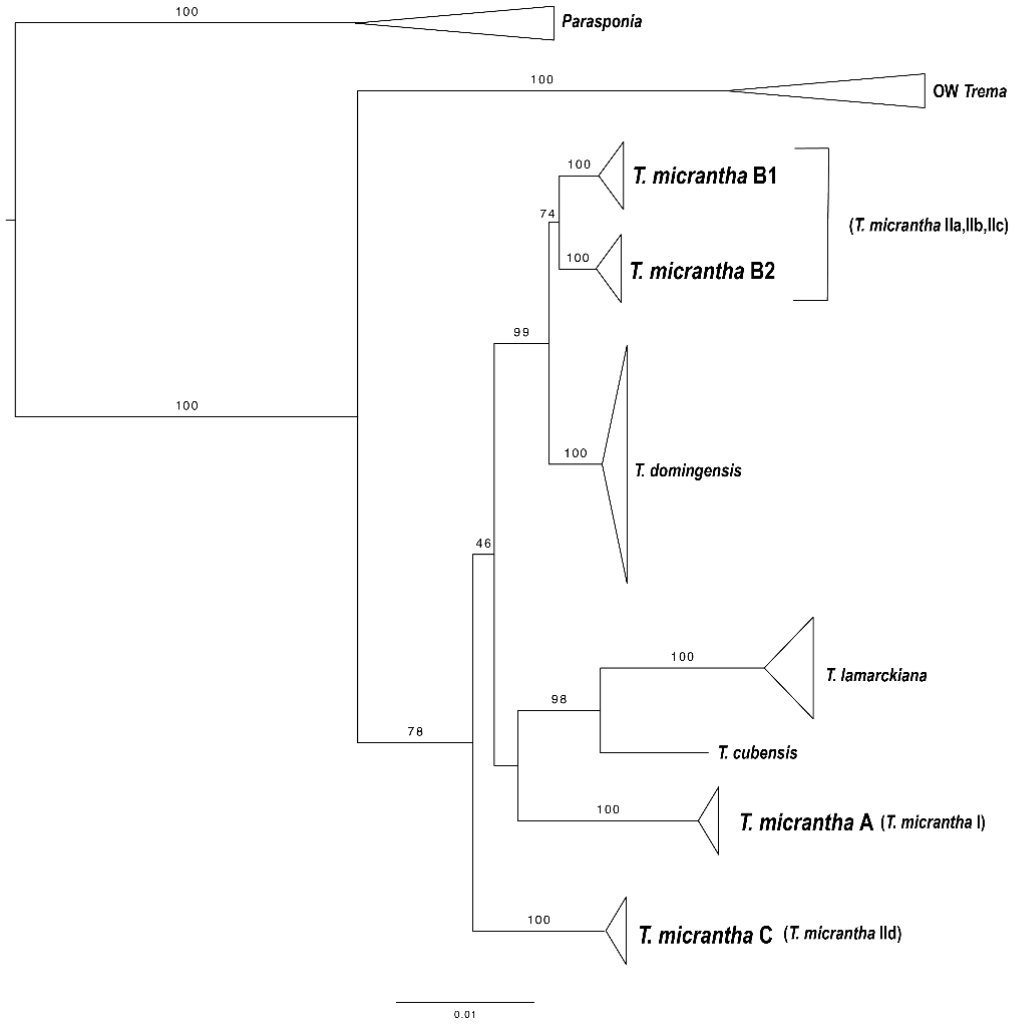


Figure 2. Maximum likelihood phylogeny of 5 DNA loci adapted from Garwood et al. (2018) with clade assignments from Yesson et al. (2014) in parentheses.

These earlier phylogenetic studies indicate that *Trema micrantha* is a poorly circumscribed species. *Trema micrantha* is polyphyletic, representing several lineages, widely distributed throughout the Neotropics, and morphologically variable. Current lack of monophyly for *T. micrantha* presents the need for additional investigation into its lineages. *Trema micrantha* A (= *T. micrantha* **I**) has the synapomorphy of brown endocarps and *T. micrantha* C (= *T. micrantha* **IId**) has a distinct montane distribution and unique leaf morphology. *Trema micrantha* B (= *T. micrantha* **IIa, IIb, IIc**) however, is not well-supported as a clade. Instead, there are several subclades (Garwood et al. 2018) that are morphologically variable.

Thus far, taxonomic knowledge of *T. micrantha* is limited by local descriptions, inadequate sampling across a broad geographic range, and minimal molecular characters. The purpose of this study is to address the taxonomic and biological complexity of this group (specifically *T. micrantha* group B), through a multi-faceted approach that draws together information regarding phylogenetic relationships, morphological characters, and ecological preferences. Therefore, to disentangle the putative lineages of *T. micrantha* B, I have employed phylogenetic, morphometric, and biogeographic analyses with a broad taxon sampling (Table 1).

Phylogeny

Using several molecular datasets and robust phylogenetic methods, I sought to answer the following questions: **How many lineages are present within *T. micrantha* (with a focus on *T. micrantha* group B) and is there strong phylogenetic support of those lineages?** Unpublished data with limited taxon sampling suggests that genome skimming generated data for the plastome and nuclear ribosomal cistron (NRC) provide greater resolution of relationships within Neotropical *Trema* than the 5-gene approach of Garwood et al. (2018). The NRC is organized in abundant, tandemly repeated transcription units (Kim et al. 2015), that have remained

homogenous through concerted genome evolution given their role in ribosome assembly and nucleolus formation (Kim et al. 2015). The NRC is highly repeated and contains an external transcribed spacer (ETS), the small-subunit rDNA gene (18S), internal transcribed spacer 1 (ITS1), the 5.8S rDNA gene, internal transcribed spacer 2 (ITS2), the large-subunit (26S), and an intergenic spacer (IGS) (Kim et al. 2015; Li et al. 2016). While the ribosomal genes are conserved, making them good molecular markers for phylogenetic analyses at or above the species-level (Li et al. 2016), the ETS and the ITS regions are highly variable and useful for phylogenetic analysis at and below species level (Li et al. 2016). Plastomes are haploid, maternally inherited, circular, organellar genomes, with a conserved gene number and gene arrangement (Wang et al. 2019). Genome scale analyses have shown utility in resolving phylogenetic uncertainties across various taxonomic levels (Cascales et al. 2017; He et al. 2019; Wang et al. 2019; Nauheimer et al. 2019). Thus far, understanding relationships within *T. micrantha* has been limited by taxon sampling and data of limited phylogenetic utility. Using high-throughput Illumina sequencing, I have vastly increased character sampling compared to previous phylogenetic studies to increase support for nodes in the phylogeny. Additionally, I have increased taxon sampling (Table 1) for *T. micrantha* across a broad geographic distribution by employing Sanger sequencing of five DNA loci to better understand morphological and geographic variation of each lineage. Lastly, to further increase the sample size of *T. micrantha* lineages identified by the genome-skimming and five-loci datasets, I sampled over three hundred *Trema* specimens by targeting the nuclear external transcribed spacer (ETS). Unpublished data indicated that ETS data were sufficient to genotype a specimen for clade assignment and to identify hybrids.

Morphology

It is important to evaluate discriminative morphological characters between lineages. Thus, with the utility of leaf shape analyses, I plan to address the question: **Do the phylogenetically divergent lineages within *T. micrantha* B have distinct leaf shape morphology and thus make them morphologically diagnosable?**

One of the major challenges in addressing the taxonomy of *Trema* is the difficulty in finding reliable morphological characters to distinguish species (Yesson et al. 2004). *Trema* has small, uniform flowers across species, so fruit and leaf characters are often used to distinguish species (Nee 2015). In a numerical taxonomic study of 158 specimens identified broadly as *T. guineensis* from Togo, West Africa, St. Laurent et al. (2000) assessed the discriminatory utility of 44 leaf morphology characters. Three leaves were sampled per specimen including the longest, shortest, and a randomly chosen one. Morphological characters measured include leaf length, leaf width, apex length, apex width, teeth density, vestiture type, etc. (St. Laurent et al. 2000). Statistical cluster methods and canonical discriminant analyses supported the recognition of three different species (St. Laurent et al. 2000). Investigations into leaf characters in Neotropical *Trema* have also shown informative results (Garwood et al. 2018). Increased sampling and more statistical tests are required to evaluate if there are adequate leaf shape characters to define phylogenetic lineages within *T. micrantha*. Here I present multivariate and univariate statistical analyses of leaf shape for specimens with molecular data to aid in morphological distinction of *T. micrantha* B lineages.

Biogeography & Ecology

Trema micrantha is a prevalent pioneer species in tropical and subtropical areas and authors have noted morphological intermediacy across ecological and geographic gradients (i.e.,

Nee 2015). The biogeographic question I aim to answer is: given the known geographic occurrence through herbarium specimen localities, **what ecological niche does each lineage of *T. micrantha* B occupy?**

The spatial distributions of organismal diversity, both within and between species results from complex evolutionary, geological, and ecological processes (Rosauer et al. 2015). Thus, when species limits are poorly resolved, interpretation of biogeographic ranges and diversification patterns may likely be confounded. Once *T. micrantha* lineages were phylogenetically evaluated across various datasets, I sought to characterize the geographic distributions and environmental preferences of each lineage using locality information available on labels of specimens with molecular data. Construction of species ranges, and their environmental tolerances are predominately achieved using Ecological Niche Modeling (ENM) (also commonly known as Species Distribution Modeling, SDM). Through ENM, one can predict habitat, or niche, suitability by assessing correlations between species' occurrence data and environmental variables (Elith & Leathwick 2009). These correlations allow for the inference of the fundamental niche of a species and so provide critical information about the abiotic preferences of a species (Alvarado-Serrano & Knowles 2014).

CHAPTER 2

MATERIALS & METHODS

Sampling, DNA Extraction, and Sequencing

Taxon sampling was directed to address relationships within Neotropical *Trema*, with a specific emphasis on sampling *T. micrantha* across its broad geographic range (Table 1). To root the phylogeny, accessions representing Paleotropical taxa were included. Tissue samples were taken with permission from herbarium specimens from the institutions (Table 1). Collections preserved in silica from field collections were also utilized. Genomic DNA was extracted using a modified CTAB method (Doyle & Doyle 1987), with a 1 mL volume reaction and approximately 10 mg of dried, ground tissue. Samples were incubated in 1 mL of CTAB 2x buffer and 10 µl proteinase-K for at least two hours at 55°C, with occasional mixing. To remove secondary compounds, a 24:1 chloroform/isoamyl alcohol solution was added, then the supernatant was purified on silica columns (Neubig et al. 2014). For some samples, DNA was precipitated by adding 3 M sodium acetate and isopropanol to the supernatant, then centrifuged until a DNA pellet was formed (Neubig et al. 2014). Select DNA samples were used for sequencing on an Illumina HiSeqX or NovSeq for the purpose of genome skimming, while a broader sampling was used for Sanger sequencing of five loci (*trnL-F*, *rbcL*, *trnH-psbA,* ITS, and ETS) or ETS alone.

For Sanger sequencing, we amplified via polymerase chain reaction (PCR) the plastid loci *rbcL*, *trnH-psbA* intergenic spacer, and the *trnL-F* intron and intergenic spacer, as well as the nuclear ribosomal internal transcribed spacer (ITS) and external transcribed spacer (ETS). Amplifications were carried out using a SimpliAmp thermal cycler (Life Technologies, Carlsbad, CA). Phusion New England Biolabs (Ipswich, MA) brand reagents were used for *trnH-psb*A and

GoTaq Promega brand reagents (Madison, WI) were used for *rbcL*, *trnL-F*, ITS, and ETS in 25 µl volumes.

For *trnH-psbA* PCR components included 2 µl of template DNA, 14.5 µl of water, 5 µl 5x HF buffer, 2 µl of 25 mM $MgCl_2$, 0.5 µl of 10 µM dNTPs, 0.5 µl of 10 µM primer (Table 2), and 0.2 µl of Phusion polymerase. For *rbcL*, *trnL-F*, ITS, and ETS, PCR components included 1 µl of template DNA, 16.5 µl water, 5 µl of GoTaq buffer, 1.5 µl of 25 mM $MgCl_2$, 0.5 µl of 10 µM dNTPs, 0.5 µl of each 10 µM primer (Table 2), and 0.15 µl of Taq polymerase. PCR conditions for the nuclear loci (ITS, ETS) were at 98°C, 1 minute, then 35 rounds of 95°C for 15 seconds, 55°C for 15 seconds, and 72°C for 1 minute, followed by 1 minute at 98°C for the final time with primer combinations A+B (Abbott 2009), or as two amplicons A+C and B+D (Abbott 2009) in low quality samples for ITS and the primers ETSF + 18SR (Garwood et al. 2018) for ETS. For *trnH-psbA,* PCR conditions were set for 98°C, 2 minutes, 36 rounds of 98°C for ten seconds, 55°C for 15 seconds, and 72°C for 1.5 minutes, ending with 72°C for three minutes with primer combinations F + R (Xu et al. 2000). For *trnL-F,* PCR conditions were 94°C for 2 minutes, 33 rounds of 94°C for 30 seconds, 56°C for 30 seconds, and 72°C for 1 minute, then 72°C for 3 minutes with the primer combinations C+F (Taberlet et al. 1991), or as two amplicons C+D and E+F (Taberlet et al. 1991) for low quality samples. For *rbcL*, PCR conditions were 95°C for 1 minute, 35 rounds at 95°C for 15 seconds, 55°C for 15 seconds and 72°C for 1 minute, ending with 72°C for 3 minutes with the primer combinations rbcLZ1 + rbcL3' (Clayton et al. 2007), or rbcLaF + rbcLaR (Kress et al. 2012) for low quality samples. PCR products were assessed on a 1% agarose gel for quality and concentration. PCR products were sequenced at Eurofins Genomics (Louisville, Kentucky) on an ABI3730xl. Additional specimens were targeted using the same approach for ETS genotyping to assign accessions to clades and identify hybrids.

For genome skimming, extracted DNA was quantified by a QuBit 3.0 Fluorometer before quality assessment on an agarose gel to examine DNA degradation. Satisfactory samples were sent to Rapid Genomics LLC (Gainesville, Florida) for library preparation, barcoding, and shotgun sequencing on an Illumina HiSeqX or NovaSeq of unenriched samples to produce between three and thirteen million paired-end, 100-250 base paired-end reads.

Sanger Sequence Editing

Raw Sanger sequence data were viewed and edited in Geneious R10.2.4 (Kearse et al. 2012; www.geneious.com). Forward and reverse sequences were assembled, then poor quality ends and primer sequences were trimmed. Sequences were manually checked for erroneous base calls and polymorphisms. Each locus (*rbcL*, *trnH-psbA*, *trnL-F*, ITS, and ETS) was aligned in Geneious using the default MUSCLE parameters (Edgar 2004). All data matrices were concatenated in Geneious to produce a 5-loci data matrix. Additionally, the aligned ETS matrix was examined further to identify unique genotypes among specimens as well as identify hybrids between genotypes based on polymorphisms. Any accessions with polymorphisms representing hybridization between putative lineages were removed to prevent ambiguity in phylogenetic analyses.

Genome Skimming Data Editing & Assembly

Paired reads of high throughput Illumina data consisted of three to thirteen million sequences per sample. Adapters and low-quality bases were removed using Trimmomatic 0.36 (Bolger et al. 2014) with the following options: LEADING and TRAILING = 20 (quality cutoff of the start and end of a read and MINLEN = 30 (minimum length of reads). Trimmed, paired reads were then assembled using the GetOrganelle toolkit (Jin et al. 2020) and the script "get_organelle_from_reads.py." This script performs the main workflow of GetOrganelle, using

Bowtie2 (Langmead & Salzberg 2012), BLAST (Camacho et al. 2009), SPAdes (Bankevich et al. 2012), and Python libraries (Jin et al. 2020). GetOrganelle first uses an iterative approach to map sequence reads to a reference, then a *de novo* assembly to produce all possible configurations of a circular genome (Jin et al. 2020). *Trema orientalis* (MH118126) was used as the reference, with all other parameters set as the default. When the plastomes were assembled, a final reference assembly using the raw reads was employed to verify the final sequence. A 10x minimum coverage with a consensus threshold of 75% was used for the final plastome reference assembly. Regions with missing data were denoted with "NNNNNNNNN" to indicate inadequate coverage.

When GetOrganelle could not recover the complete plastome, sequence reads were initially assembled to a reference (*Trema orientalis*: MH118126), allowing 25% mismatch in Geneious 10.2.4. The used reads from the initial reference assembly were then assembled using a *de novo* assembly to produce contigs of various lengths. Contigs were manually inspected for quality and length and consensus sequences were produced. The used reads were assembled to the consensus sequences iteratively 5 to 10 times. Contigs from this step were assembled *de novo* to form the majority of the plastome. This method only captures one of the two inverted repeats; thus, the "find repeats" plug-in" in Geneious 10.2.4 was used to locate the beginning of each inverted repeat. The entire repeat region was extracted, reverse complemented, and substituted for the fragments of the missing inverted repeat. After each plastome was manually assembled, a final reference assembly with the raw reads was used to confirm sequence composition.

To assemble the NRC from the trimmed, paired reads, accessions were initially assembled to a *Trema* NRC reference that included ETS-18S-ITS1-5.8S-ITS2-26S with 5 iterations and 10-15% mismatch. The used reads for the initial assembly were then assembled *de*

novo to produce multiple contigs, then a consensus sequence was produced from the contigs to form a continuous sequence, and the trimmed, raw reads were reference assembled with 5 iterations to the consensus sequence to confirm sequence identity and produce the entire NRC. To detect polymorphisms, a consensus threshold of 75% was used with a minimum coverage depth of 30x reads. This approach produced sequences of 8,000-10,000 base pairs, which were subsequently used as references for accessions of closely related taxa.

Final sequences for both the plastome and NRC dataset were aligned using MAFFT v. 7.427 under the default parameters (Katoh 2013). Hybrid/polymorphic accessions identified in the ETS matrix were excluded from all datasets to prevent phylogenetic ambiguity. The resulting alignments were visually inspected for irregularities and re-assembled from the raw reads, if necessary.

Nuclear ribosomal cistrons were annotated using the *Trema* NRC reference allowing 30% mismatch. To confirm annotations, ETS and ITS loci from GenBank (Garwood et al. 2018) were also referenced. Annotations for one reference *Trema* plastome were created using GeSeq of CHLOROBOX (Tillich et al. 2017), to annotate ribosomal RNAs, transfer RNA exons and introns, and coding sequence (CDS) exons and introns, and intergenic spacers. CHLOROBOX cannot annotate alignments, thus the reference *Trema* plastome was imported into Geneious and the aligned plastomes matrix was annotated using the "Annotate by Database" function in Geneious with 10% mismatch. Annotations were then manually checked in Geneious noting start and stop codons. The second inverted repeat was not included in phylogenetic analyses to exclude redundant data. Additionally, portions of the intergenic spacer (IGS) of the NRC were also excluded in phylogenetic analyses.

Phylogenetic Analyses

To adequately select substitution rate models and rate heterogeneity across sites, likelihood model selections for the ETS, 5-loci, NRC, and plastome datasets were conducted using ModelFinder (Kalyaanamoorthy et al. 2017) within IQ-TREE v. 1.6.12 (Nguyen et al. 2015) with the command "-m TEST." Maximum likelihood (ML) analyses with ultrafast bootstrapping (100,000 replicates) were conducted in IQ-TREE v. 1.6.12 (Nguyen et al. 2015). Bayesian inference (BI) analyses using the Markov chain Monte-Carlo (MCMC) algorithm were conducted in Mr. Bayes 3.2.7a (Ronquist et al. 2012) for 1,000,000 generations at a sampling frequency of 1000 to ensure that the average standard deviation of split frequencies fell below 0.01. The BI analyses ran with four chains and two simultaneous runs. Phylogenetic trees were visualized in FigTree v1.4.3 (Rambaut 2007) and edited in Adobe Illustrator.

To identify genotype clusters in the ETS dataset, an Unweighted Pair Group Method with Arithmetic Mean (UPGMA) analysis was conducted in PAUP* v. 4.0a (Swofford 2003) under the HKY-85 model of nucleotide substitution.

Morphological Data Collection and Morphometric Analyses

Neotropical *Trema* species are typically differentiated by leaf shape characters (Garwood et al. 2018), thus I measured eight leaf shape characters (Figure 3) to determine if leaf shape differs between the *T. micrantha* B lineages. For each specimen (n=150), I sampled three mature leaves, the smallest, largest, and one intermediate-sized and measured blade length (BL), blade width (BW), distance from the base of the blade to the widest point (BD), basal indentation (BI), apex length (AL), apex width (AW), petiole length (PL), and teeth density (number of teeth/cm; TD). All measurements were taken using a millimeter ruler. For specimens where only images were available, measurements were recorded using ImageJ (Rasband 1997-2016). Only

specimens with DNA sequence data to support clade assignment were used in morphological analyses. The mean across the three leaves was calculated for each variable in Microsoft Excel. A principal component analysis (PCA) was conducted on the mean dataset for all eight variables, with clade (lineage assignment) as the factor to measure variance of leaf characters across lineages. Results from the PCA were also used to reduce the number of variables for subsequent analyses. Lineages with $n < 5$ specimens (the number of variables retained after reduction by the PCA), were excluded from the analysis. To determine which lineages were different across each leaf character, one-way analyses of variance (ANOVA) for each variable were conducted and followed by post-hoc Tukey's Honest Significant Difference (HSD) tests to identify pairwise differences among lineages. All statistical analyses were carried out in R Software (R Core Team 2018).

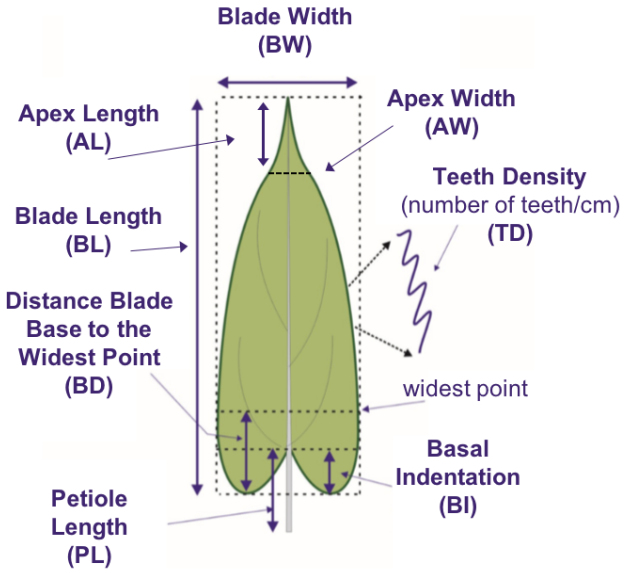


Figure 3. Eight leaf characters measured for leaf morphometric analyses.

Ecological Niche Modeling

Coordinates for *T. micrantha* lineages were obtained from locality information on herbarium specimen labels. When exact coordinates were not included on the labels, locality information was interpreted by N.C. Garwood using Google Earth. Ecological Niche Models (ENMs) were modeled using MaxEnt (Phillips et al. 2006) and parameterized in SDMToolbox (Brown 2014), a python-based, GIS compatible toolbox. Coordinates for each lineage were recorded in CSV files, then converted to shapefiles in the WGS84 datum format in ArcMap (ESRI 2011). Two sets of environmental variables used in the analyses: a) 19 standard CHELSA bioclimatic variables (Karger et al. 2017), which summarize precipitation and temperature patterns, and b) 10 soil variables (Hengl et al. 2014) at 5 cm soil depth at a 1-kilometer (30 arc-second) resolution. Because variables contributing most to each model were compared across lineages, co-correlated environmental variables ($r > 0.80$) were removed. To adequately account for climate heterogeneity across *T. micrantha* lineage distributions, climate heterogeneity was calculated using the "Climate Heterogeneity" tool in SDMtoolbox. This then allows for spatial rarefication of occurrence data at several distances. In this case, localities were rarefied at 5,15, and 25 km^2 to filter spatial clusters according to high, medium, and low environmental heterogeneity. Spatial rarefication is important for model calibration and evaluation and minimizes potential spatial biases and spatial autocorrelation (Brown 2014). As with the morphological analyses, only accessions with molecular data were included in ENM. Bias files were created for each lineage from the rarefied occurrence data using a minimum convex polygon with a buffer size of 1500 km in SDMToolbox (Brown et al. 2017). Bias files control where background points are sampled, and aid in avoiding habitats that are outside a species' known range (Brown et al. 2017). Five feature classes (linear; linear and quadratic; hinge; linear,

quadratic and hinge; and linear, quadratic, hinge and product) and eight regularization multipliers (0.5,1.0,1.5,2.0,2.5,3.0,4.0,5.0) were evaluated to determine model performance with the "Spatial Jackknifing" tool in SDMToolbox. For lineages with 15 or more occurrence points geographically structured k-fold cross-validation was used to test and evaluate spatially segregated localities (Brown et al. 2017). This tool splits the landscape into 3 regions based on Voronoi polygons and spatial clustering of occurrence data (Brown et al. 2017). Then, models are calibrated with all permutations of the spatial groups using occurrence data and background points from *n-1* spatial groups and evaluated against the withheld group (Brown et al. 2017). For lineages with less than 15 occurrence points, models were calibrated with subsampling, 5 replicates, and 20 percent random test points. The best models were chosen based on the omission error rate (OER) and the area under the curve (AUC). Along with a final ENM, response curves, and jackknifing of environmental variables were produced. Geographic distributions, derived from herbarium locality information, were mapped in ArcMap (ESRI 2011). Elevation derived from herbarium specimens, was also used in a One-Way ANOVA to determine if elevation was significantly different between clades.

Species Concepts

With the methods applied here, I have sought to evaluate three species concepts. The phylogenetic analyses evaluated the phylogenetic species concept *sensu* Mishler and Theriot (Wheeler and Meier 2000), where a species is the least inclusive taxon and organisms are grouped by monophyly. The morphological species concept (Mayr 1992) was evaluated using traditional leaf shape morphometrics to determine if lineages are diagnosable by morphological characters. Lastly, ecological niche models were utilized to examine the ecological species concept (Grant 1992).

CHAPTER 3

RESULTS

Phylogenetic analysis of 5-loci dataset

The 5-loci (*rbcL*, *trnH-psbA*, *trnL-F*, ITS, ETS) maximum likelihood (ML) (Figure 4a) and Bayesian Inference (BI) (Figure 4b) trees based on 226 specimens recovered a strongly supported Neotropical clade of *Trema* (Bootstrap (BS) and Posterior Probability (PP) = 100%), with a polyphyletic *T. micrantha.* Within *T. micrantha,* groups A, C, and D were monophyletic with high support (BS & PP = 100%) in both the ML and BI trees. *Trema micrantha* group B was sister to *T. domingensis* and demonstrated the most sequence variability with several clades within the group. The 5-loci maximum likelihood (ML) tree strongly supported (BS ≥ 89%) monophyly of 3 *T. micrantha* B groups - B1a, B2, and B4. *Trema micrantha* B3 had a bootstrap value of 81% in the ML tree. The inclusion of *Dalling 54* reduced bootstrap support for B1b (59%) and was placed sister to the rest of the clade. Without *Dalling 54*, bootstrap support for B1b was recovered as 98%. The BI tree strongly supported (PP ≥ 97%) the monophyly of B1a, B1b, B2, B3, and B4. Both the ML and BI trees identified B1a + B1b and B2 + B4 as sister taxa, with B3 sister to these clades.

Phylogenetic analysis of plastome and nuclear ribosomal cistron (NRC) datasets

The plastome ML Figure 5a and BI trees Figure 5b recovered a strongly supported Neotropical *Trema* clade (BS & PP = 100%), with the inclusion of two specimens of *T. orientalis* sister to *T. domingensis* + *T. micrantha* group B. *Trema micrantha* A, C, and D were highly supported as clades (BS & PP = 100%). Within *T. micrantha* group B, B2, B3, and B4 were monophyletic groups with strong support in ML and BI tree (BS & PP = 100%). *Trema micrantha* B1b did not form a distinct clade, instead it was paraphyletic relative to B1a, with

strong support of the whole group together (BS & PP = 100%). *Trema domingensis* was sister to B1 (B1a + B1b) + B3. In contrast to the 5 DNA loci phylogeny, *Dalling 54* was included in B1a with high support.

In the NRC ML tree (Figure 6a) Neotropical *Trema* was well supported as a clade (BS = 97%). As with the plastome and 5-loci phylogenies, *T. micrantha* A, C, and D were well-supported clades (BS = 100%). Within *T. micrantha* group B, B2 and B4 were strongly supported clades (BS = 97%, 99% respectively). While B1b was monophyletic and well supported (BS = 100%), it is nested within the B3 group. Group B3 + B1b is moderately supported (BS = 70%). Group B1a was recovered as sister to B2 + B4 in the NRC phylogeny and was moderately supported (BS = 61%), with the inclusion of *Dalling 54.* Group B1a was well-supported (BS =100%) without *Dalling 54.* The NRC BI tree (Figure 6b) also recovered strong support for the Neotropical *Trema* clade (PP = 100%). The same relationships as demonstrated by the ML were also recovered in the BI tree, but all clades were well-supported (PP ≥ 94%).

Phylogenetic analysis of the ETS data set and genotype clusters

The ETS ML phylogeny (Figure 7a) strongly supported (BS > 80%) B1 (B1a + B1b), B2, B3, and B5. Group B4 was monophyletic with moderate support (BS = 74%). B1b was well-supported (BS = 94%) but was paraphyletic with B1a. The ETS UPGMA dendrogram (Figure 7b) (n=268) identified 6 genotype clusters within *T. micrantha* B group, denoted as *T. micrantha* – B1a, B1b, B2, B3, B4, and B5. (Figure 7b). The ETS dataset also revealed hybrids between lineages (Table 3) as well as admixture within lineages. The B5 genotype recovered in the UPGMA dendrogram and Maximum Likelihood phylogeny was not sampled in the three other phylogenies.

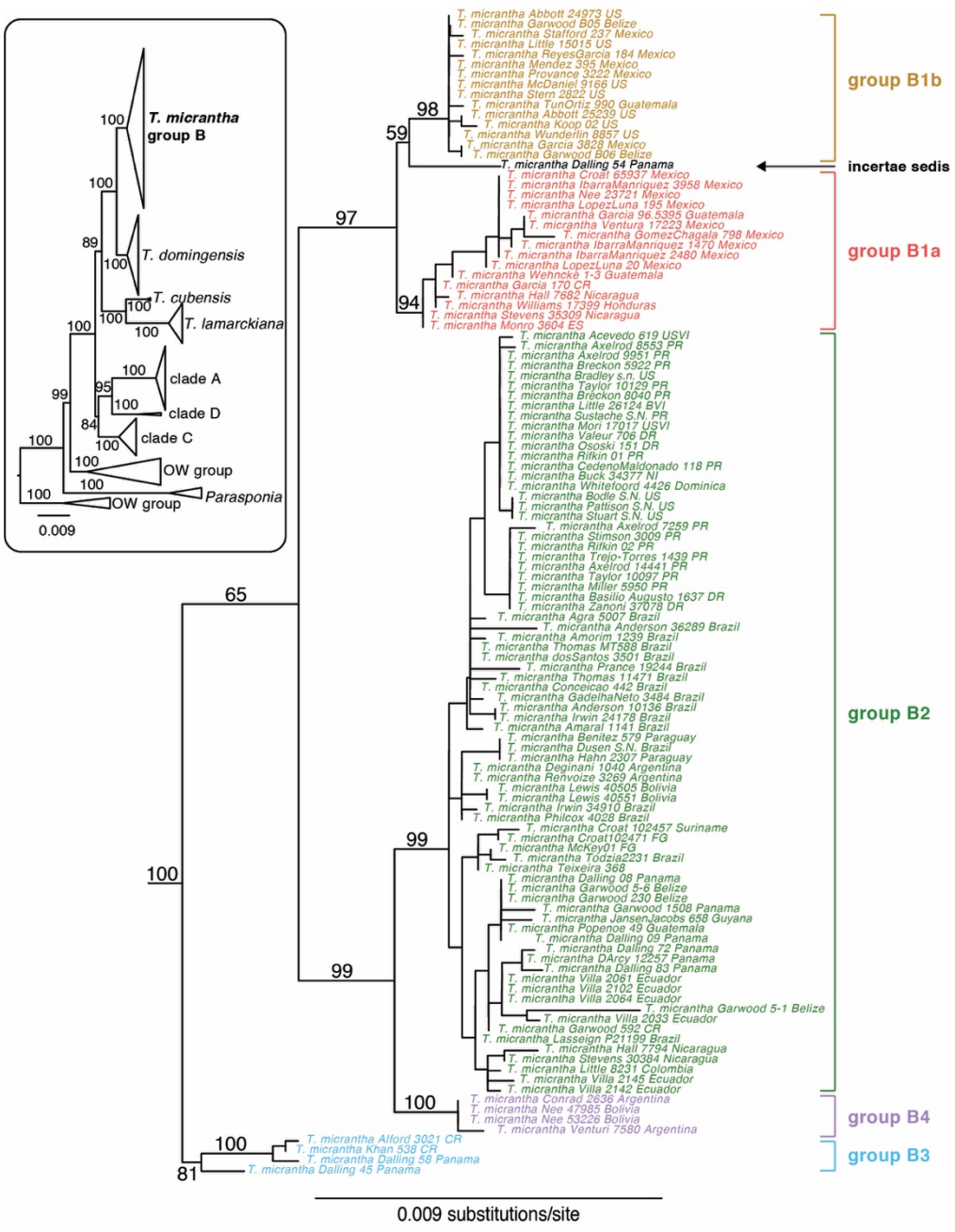


Figure 4a. Maximum likelihood phylogeny of 5 DNA loci for *Trema* with clades outside of *T. micrantha* group B simplified. Lineages within *T. micrantha* group B are denoted with different colors. Bootstrap values within clades were removed for clarity, except for major lineages. *Dalling 54* is noted as "incertae sedis," due to its unclear phylogenetic placement. Accessions in this and following trees are labeled by first collector, collection number, and country of origin. Abbreviations for countries: CR = Costa Rica, PR = Puerto Rico, US = United States (Florida), FG = French Guiana, DR = Dominican Republic, USVI = United States Virgin Islands, ES = El Salvador

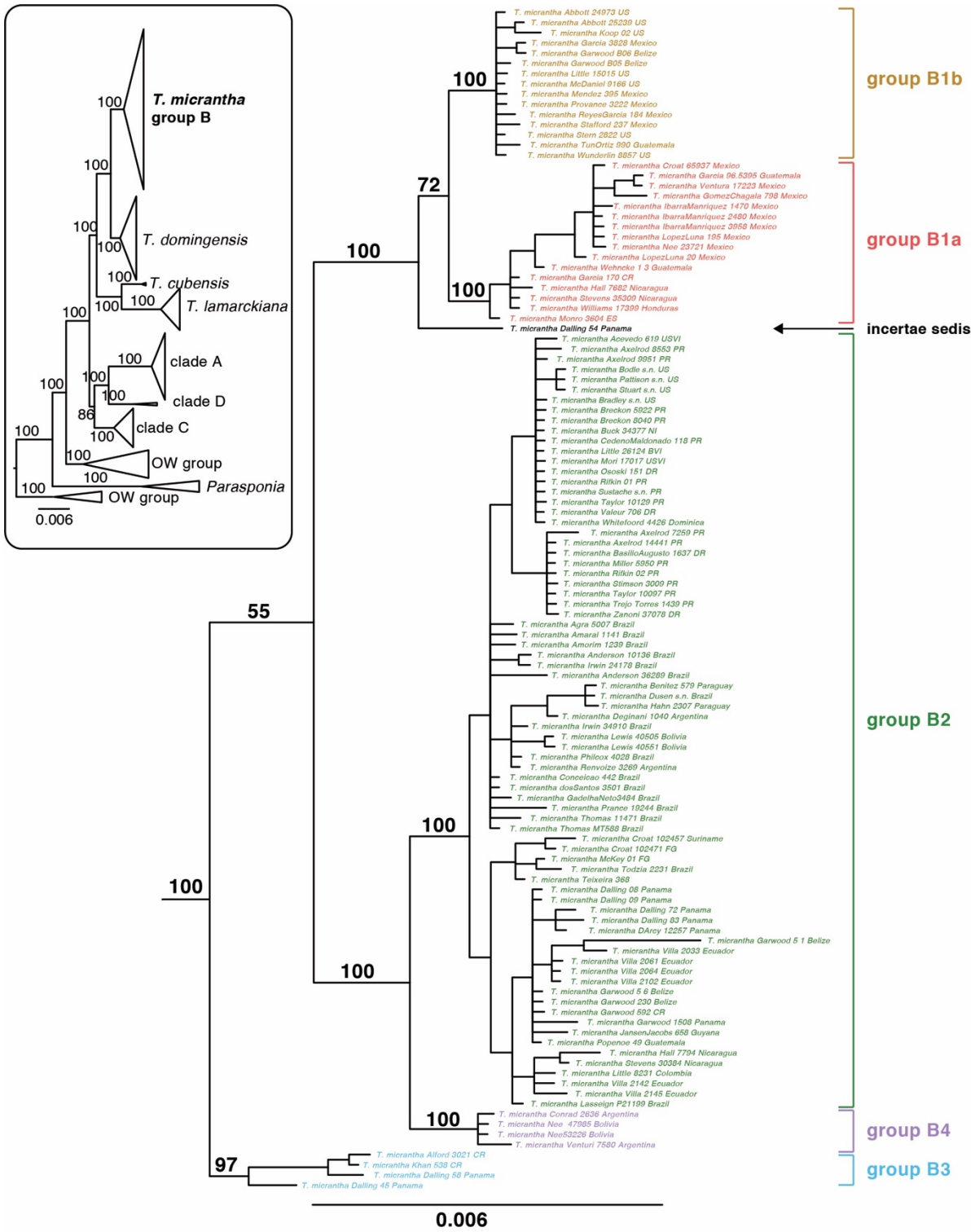


Figure 4b. Bayesian inference phylogeny of 5 DNA loci for *Trema* with clades outside of *T. micrantha* group B simplified. Lineages within *T. micrantha* group B are denoted with different colors. Bootstrap values within clades were removed for clarity, except for major lineages. *Dalling 54* is noted as "incertae sedis," due to its unclear phylogenetic placement.

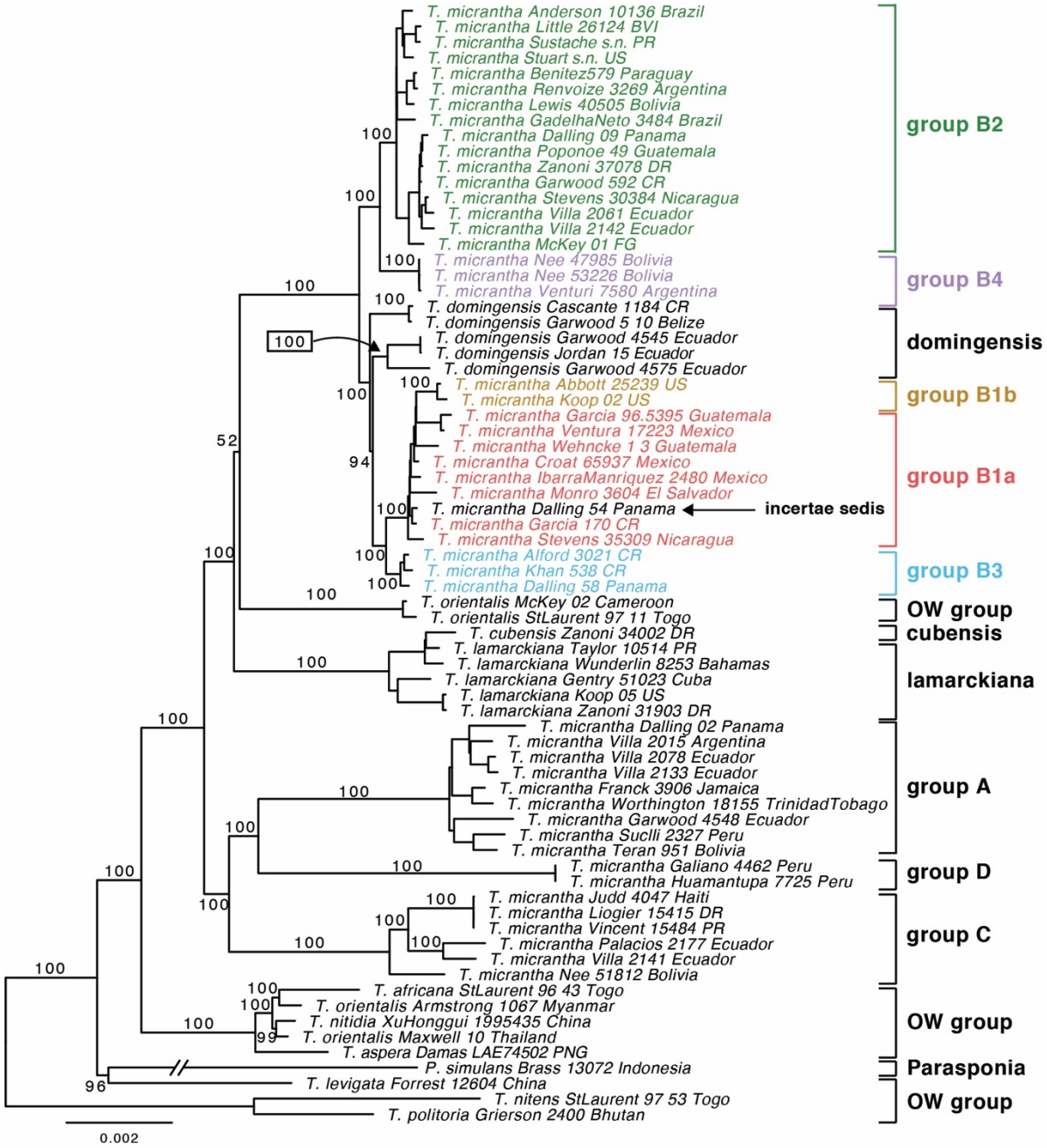


Figure 5a. Maximum likelihood phylogeny of plastome data for *Trema.* Lineages within *T. micrantha* group B are denoted with different colors. Bootstrap values within clades were removed for clarity, except for major lineages. *Dalling 54* is noted as "incertae sedis," due to its unclear phylogenetic placement.

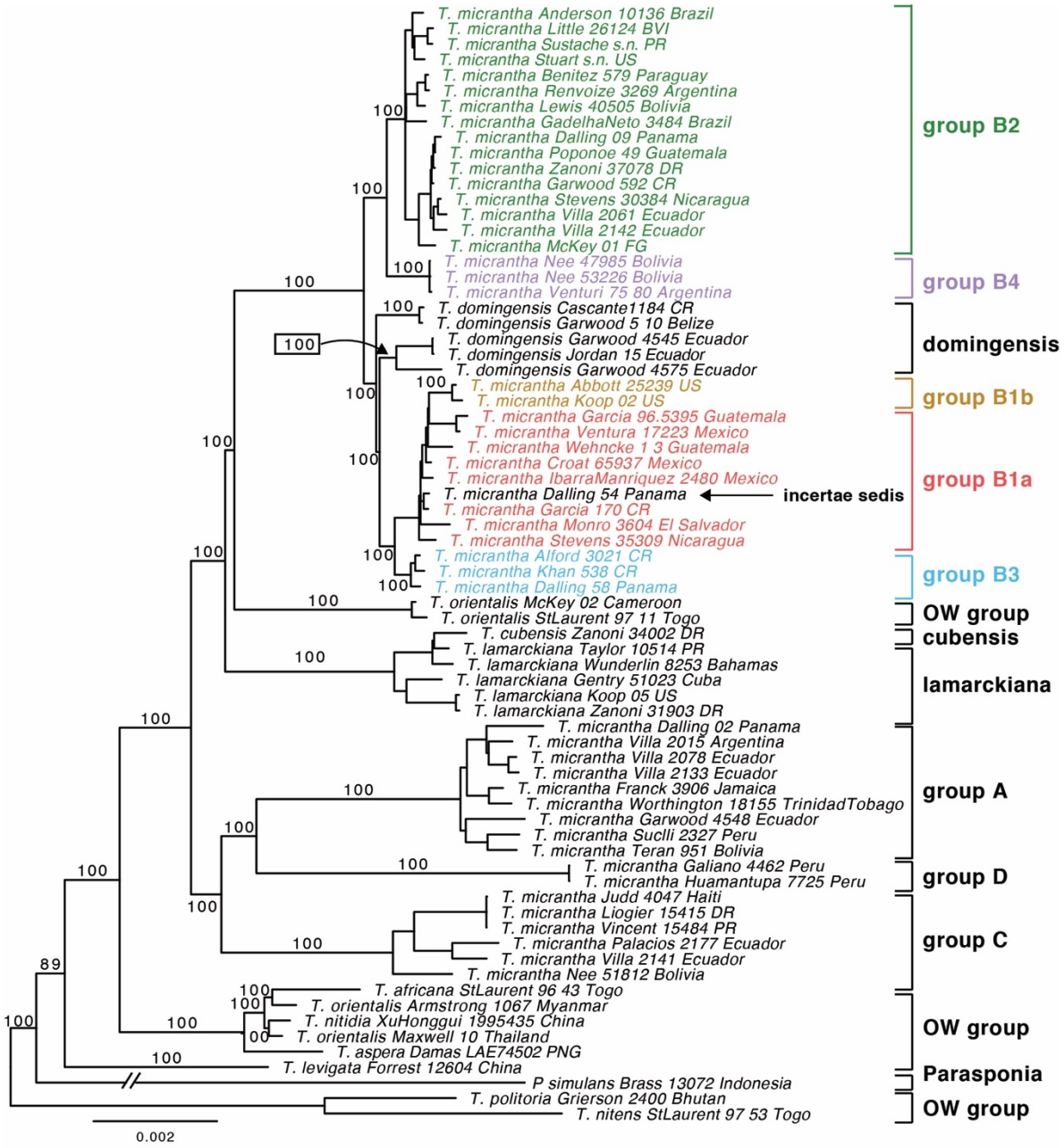


Figure 5b. Bayesian inference phylogeny of plastome data for *Trema.* Lineages within *T. micrantha* group B are denoted with different colors. Bootstrap values within clades were removed for clarity, except for major lineages. *Dalling 54* is noted as "incertae sedis," due to its unclear phylogenetic placement.

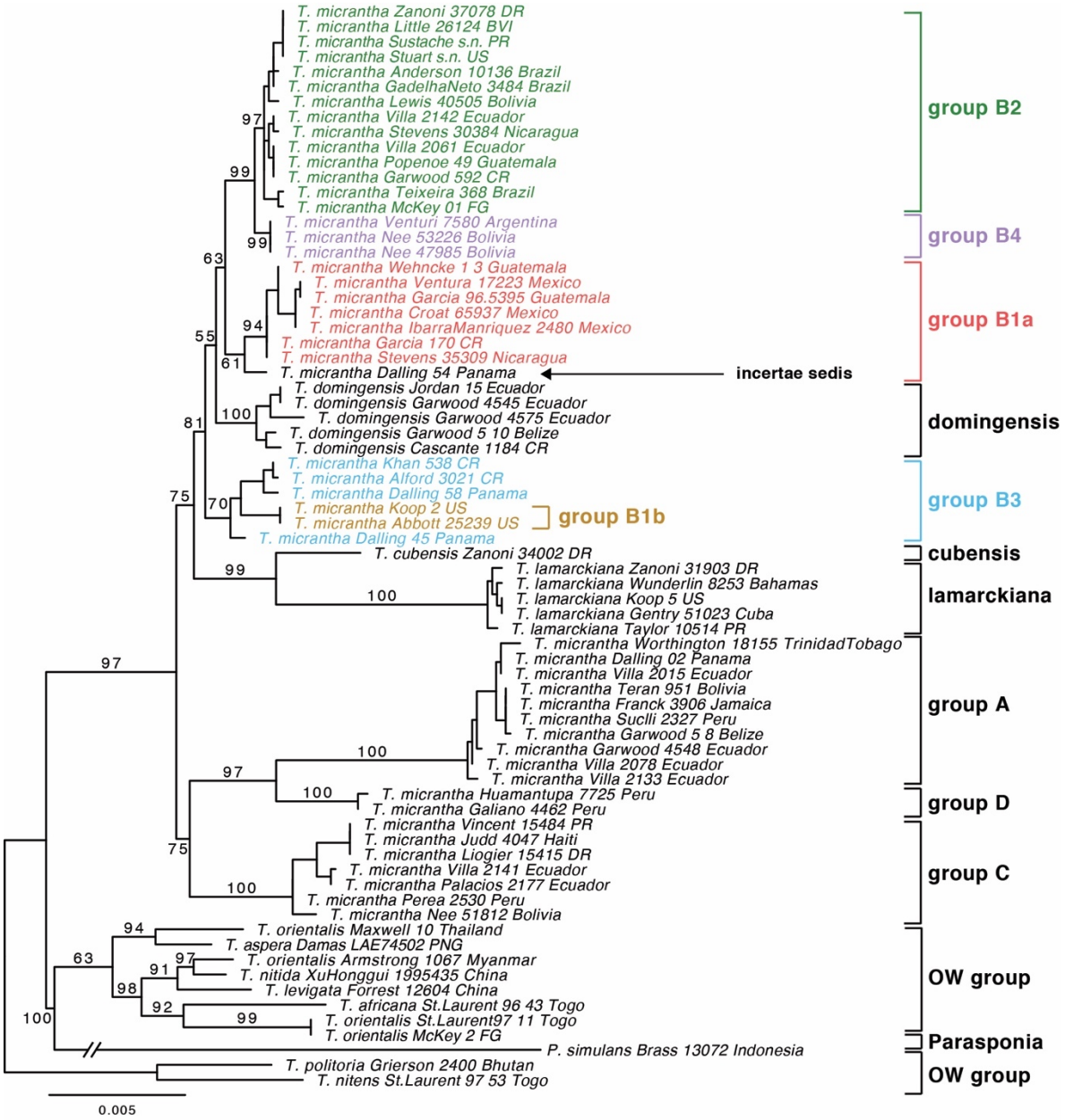


Figure 6a. Maximum likelihood phylogeny of nuclear ribosomal cistron data for *Trema.* Lineages within *T. micrantha* group B are denoted with different colors. Bootstrap values within clades were removed for clarity, except for major lineages. *Dalling 54* is noted as "incertae sedis," due to its unclear phylogenetic placement.

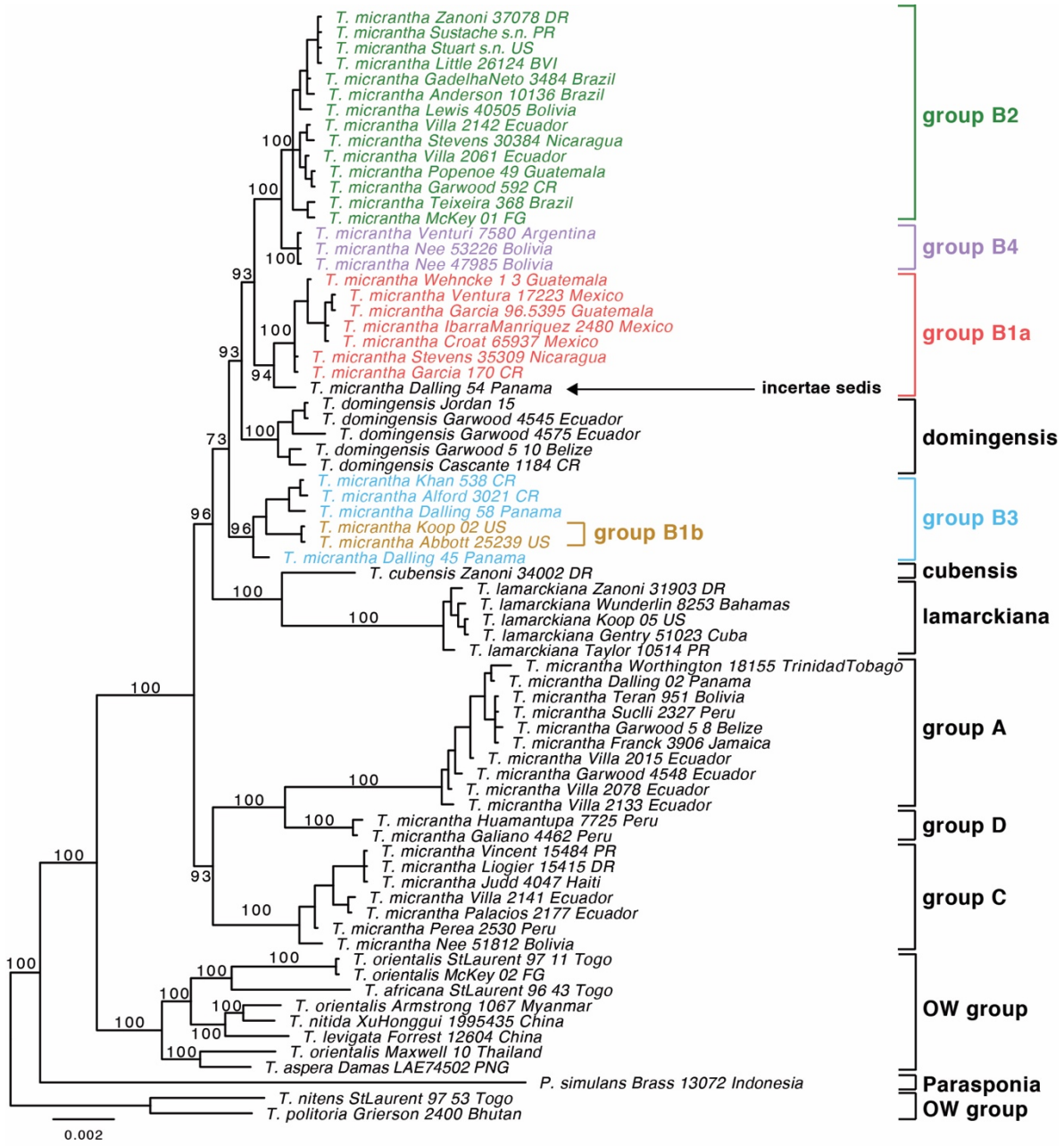


Figure 6b. Bayesian inference phylogeny of nuclear ribosomal cistron data for *Trema.* Lineages within *T. micrantha* group B are denoted with different colors. Bootstrap values within clades were removed for clarity, except for major lineages. *Dalling 54* is noted as "incertae sedis," due to its unclear phylogenetic placement.

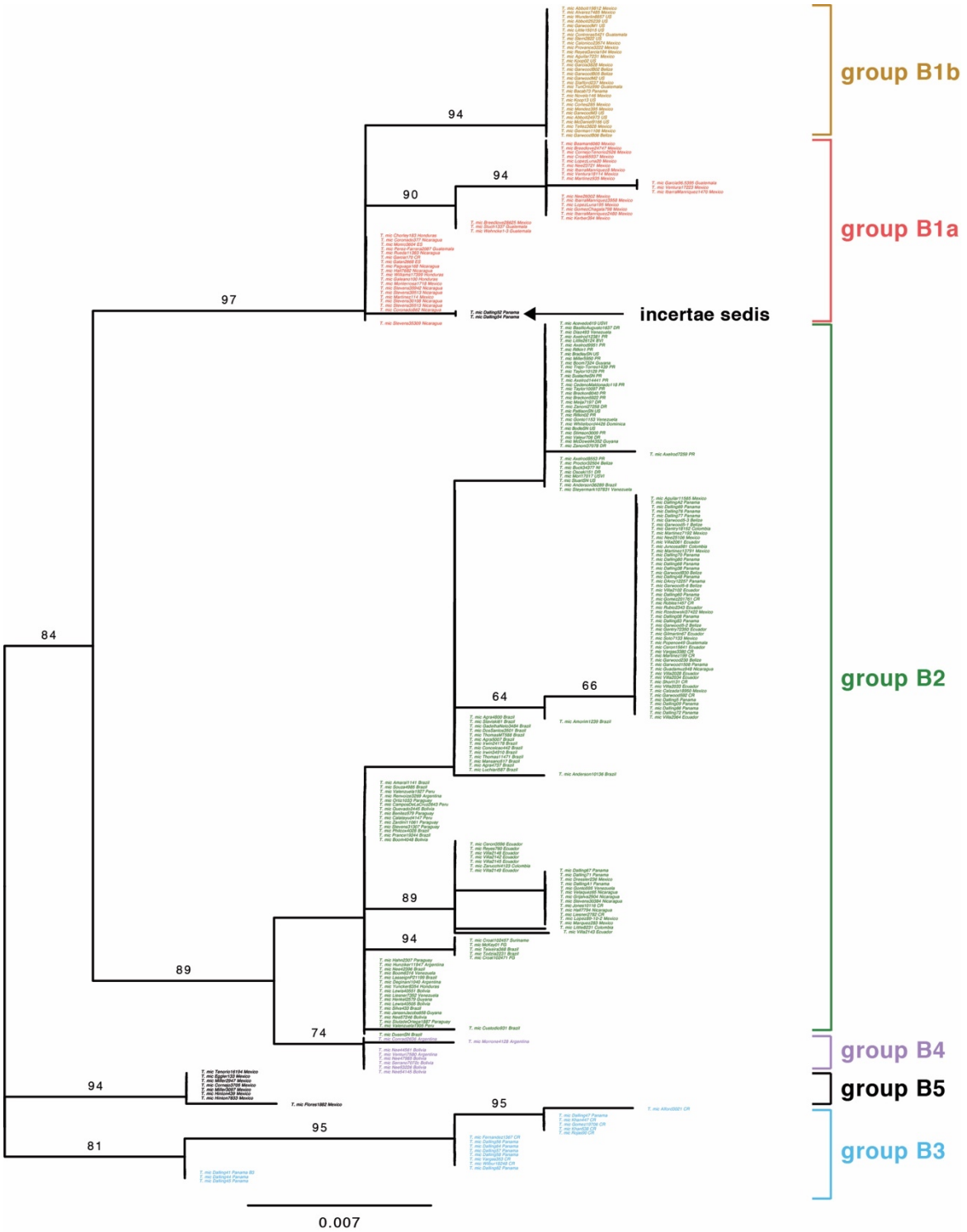


Figure 7a. Maximum likelihood phylogeny of ETS data for *Trema micrantha* group B. Lineages within *T. micrantha* group B are denoted with different colors. Bootstrap values within clades were removed for clarity along with bootstrap values less than 50%. *Dalling 54* and *Dalling 52* are noted as "incertae sedis," due to its unclear phylogenetic placement. Old world *Trema* was used to root the tree.

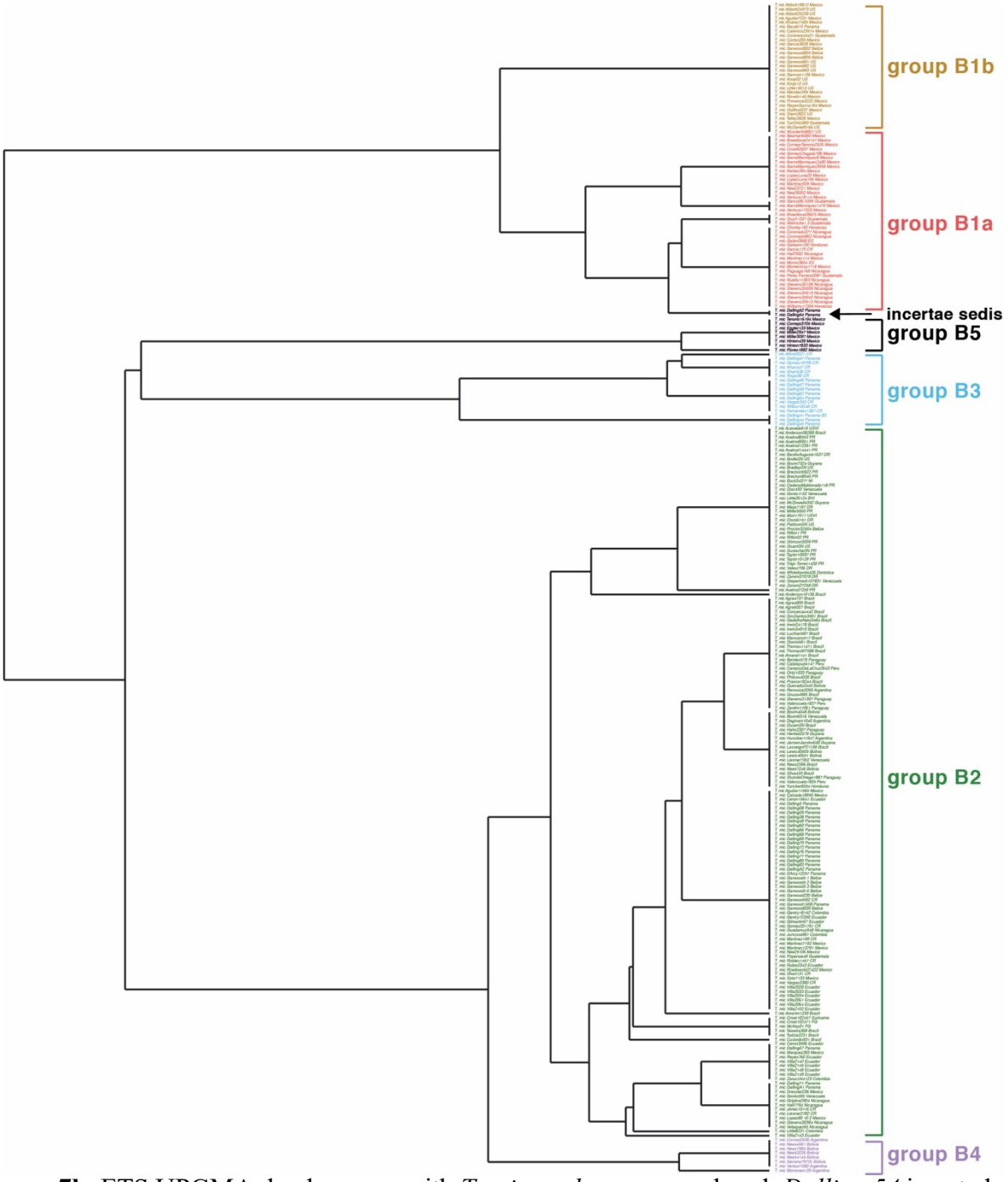


Figure 7b. ETS UPGMA dendrogram, with *T. micrantha* groups colored. *Dalling 54* is noted as incertae sedis due to its uncertain phylogenetic placement.

Morphometrics

The PCA (Figure 8) was carried out on 150 specimens representing all B lineages identified in the phylogenetic analyses. This included B1a (n=19), B1b (n=20), B2 (n=85), B3 (n=15), B4 (n=7), and B5 (n=4). Principal Component 1 (PC1) explains 84.75% of the variance, and Principal Component 2 (PC2) explains 8.89%. Blade length defines most of the variance of PC1 with a loading factor with the absolute value of 0.91 (Table 4). Principal Component 2 (PC2) is a contrast between blade width (BW) which has a loading factor of 0.54 and apex length (AL) (-0.77) and apex width (AW) (-0.26). Graphically, groups B1a, B1b, and B5 occupy morphological space distinct from B2 + B4, with PC2 separating these groups. Group B3 overlaps significantly with B2 while also falling in the same morphological space as B1a and B1b. Both clades B4 and B5 have small sample sizes (n=7, n=4, respectively), making it difficult to separate these lineages in the PCA.

Results from the PCA were also used to identify leaf character variables that are most effective in discriminating *T. micrantha* B lineages. Petiole length (PL), basal indentation (BI), and teeth density (TD) had eigenvectors (factor loadings) with absolute values < 0.20 and were excluded in subsequent analyses. One-way ANOVAs were conducted on the 5 remaining, informative variables (BL, BW, BD, AL, AW), all of which had factor loadings ≥ 0.20 for either PC1 or PC2. Clades B1a, B1b, B2, B3, and B4 had an adequate sample size (n > 5) for statistical analysis. Morphological comparisons with Tukey's HSD are illustrated by boxplots with letters indicating statistically, significantly ($p < 0.05$) different groups (Figure 9). Apex length (AL) was significantly different ($p < 0.05$) between B1a – B2 and B3, B1b – B2 and B3. Apex width (AW) was highly significantly different between B1a and B2 ($p < 0.01$) and significantly different ($p < 0.05$) between B1b and B2. Distance from the base of the blade to widest point (BD) was a

character that significantly differentiated B1a from all other groups and was highly significantly different ($p < 0.01$) between B1a and B1b as well as B1a and B4. Groups B2 and B4 were also significantly different ($p < 0.05$) for BD. Blade length (BL) was highly significantly different ($p < 0.01$) between B1a and B1b, as well as B1b and B2. Blade length was significantly different ($p < 0.05$) B1a and B4. Blade width (BW) was highly significantly different ($p < 0.01$) between B1b and B4, and significantly different ($p < 0.05$) between B1a and B4.

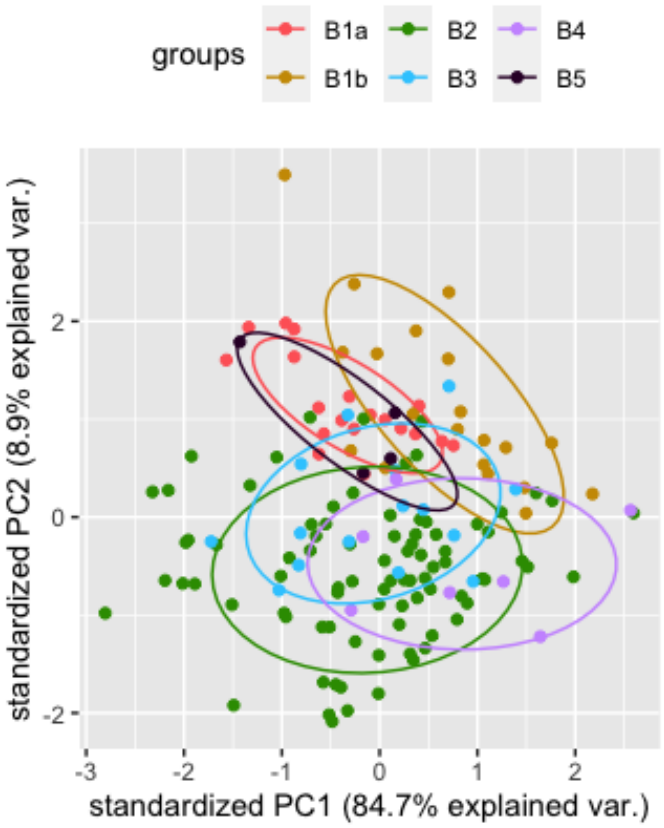


Figure 8. Principal Component Analysis of leaf shape for *T. micrantha* group B. Ellipses are shown with 95% confidence intervals.

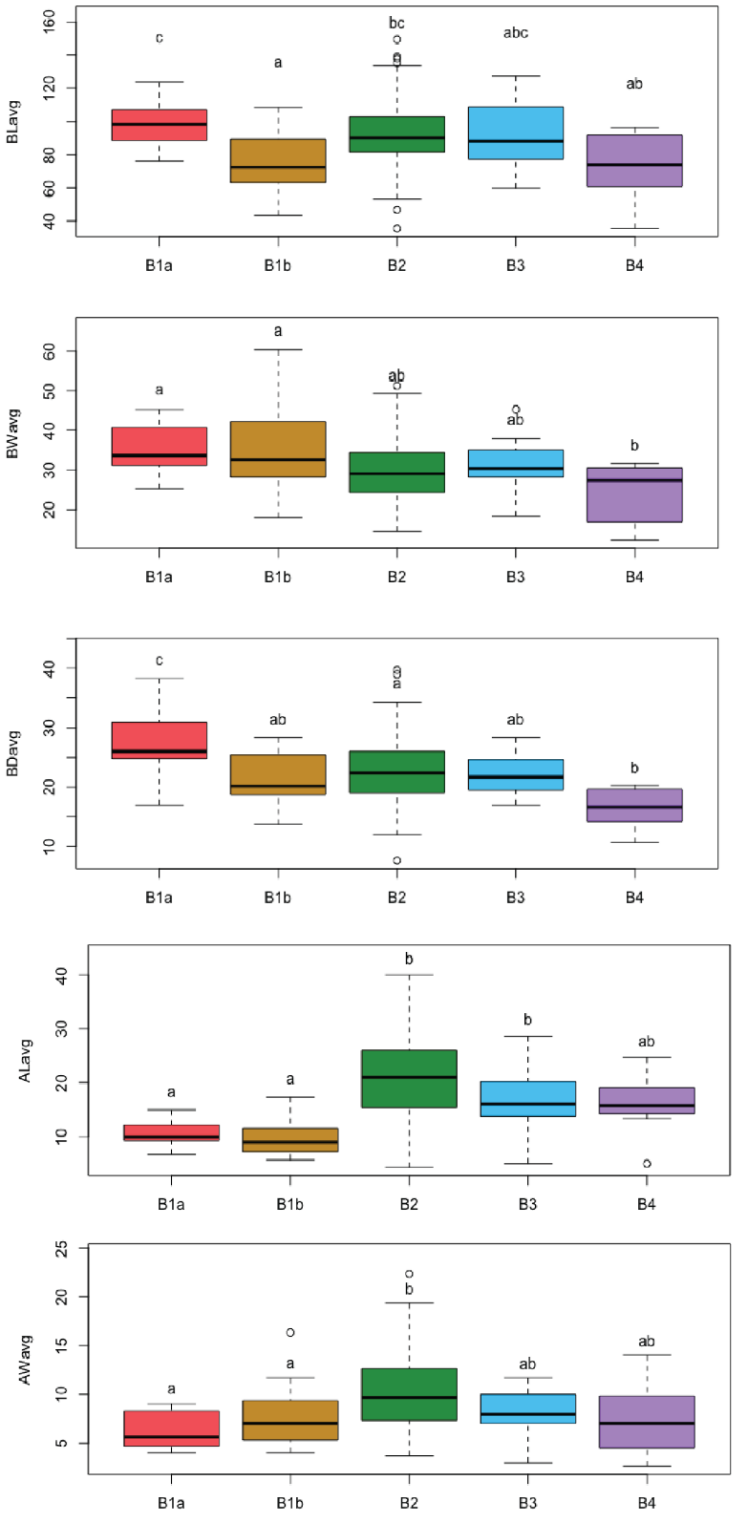


Figure 9. Boxplots of 5 leaf shape characters. Black bars represent medians, with 75% quartiles above and 25% quartiles below. Dotted lines above and below each box represent 95% confidence intervals. Circles represent outliers. Letters indicate statistically significantly different groups ($p < 0.05$) using Tukey's HSD test.

Biogeography & Ecological Niche Modeling

The geographic distributions of the *T. micrantha* B lineages are derived from specimen locality information are shown in Figure 10; only specimens with molecular evidence for clade assignment were used. *Trema micrantha* B2 was the most widely distributed clade found throughout lowland areas in the Neotropics. Only 7% of B2 specimens had elevations recorded at ≥ 1000 meters (m) and 84% of specimens have elevations ≤ 500 m (Figure 10b, Supplementary Table 1) Geographically, Group B2 overlapped with B1a, B1b, B5, and B3. B1b was also found to be a lowland lineage (only 2 specimens had elevations > 1000 m) (Figure 10b, Supplementary Table 1) distributed throughout Central America and Florida. Group B1a was distributed throughout Central America, where it occurs in moderate to high elevation areas (Figure 10b). For group B1a, 85% of the specimens had elevations recorded at elevations ≥ 500 m and 56% at elevations ≥ 1000 m (Supplementary Table 1). Group B3 was narrowly distributed in Costa Rica and Panama, where it was found in both the lowlands and higher elevations (Figure 10b; Supplementary Table 1). Groups B4 and B5 were both higher elevation groups (Figure 10b) with distributions in Bolivia and Argentina (B4) and Mexico (B5). The ETS dataset revealed that where these lineages (B1a× B1b, B1× B2, and B1×B3) overlap in Central America, there is significant hybridization. The localities of hybrids that were identified with high confidence (Table 3) are shown in Figure 11.

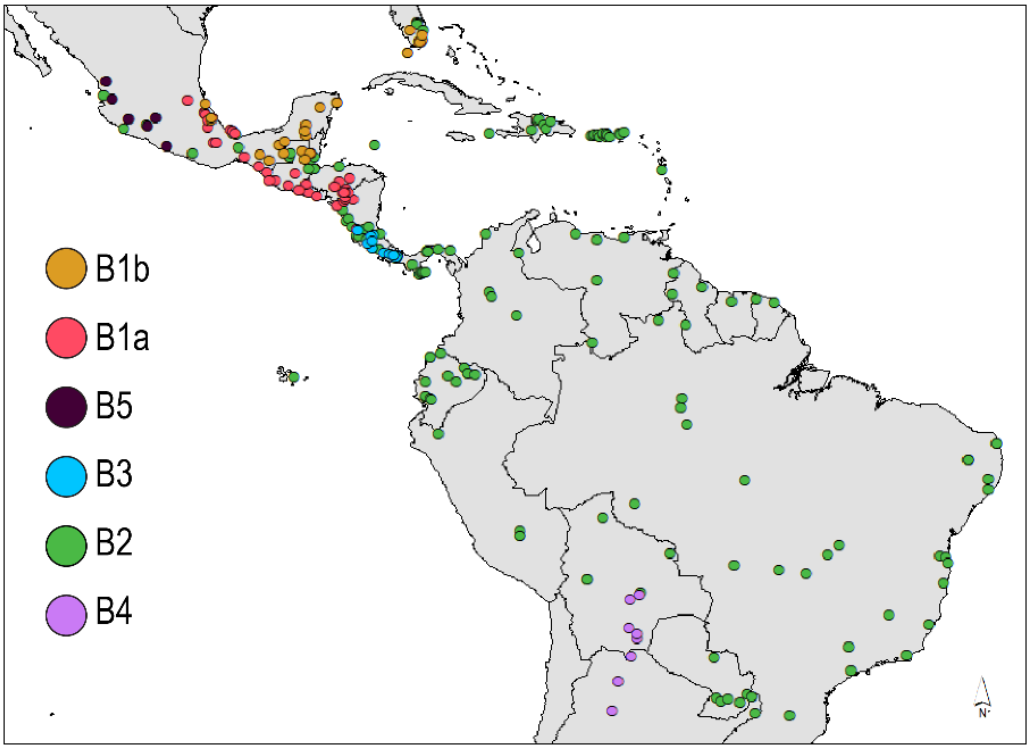


Figure 10a. The geographic distribution of *T. micrantha* group B lineages from specimens with molecular evidence for clade assignment and subsequently used for ecological niche modeling.

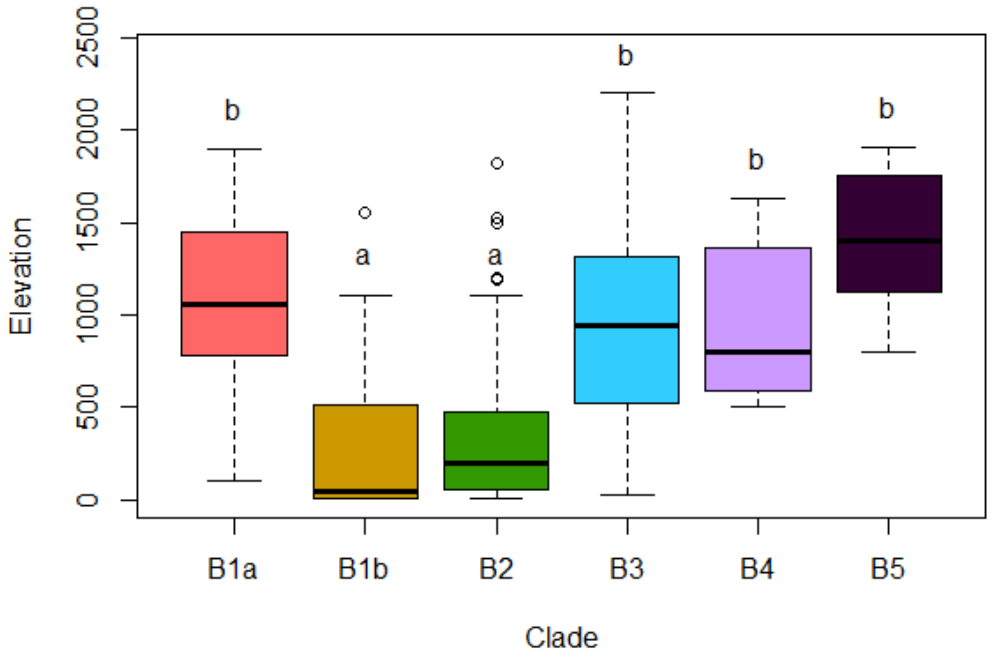


Figure 10b. Boxplots of elevation for each *T. micrantha* lineage, based on the same occurrence data from Fig. 10a. Black bars represent medians, with 75% quartiles above and 25% quartiles below. Dotted lines above and below each box represent 95% confidence intervals. Circles represent outliers. Letters indicate statistically significantly different groups ($p < 0.05$) using Tukey's HSD test.

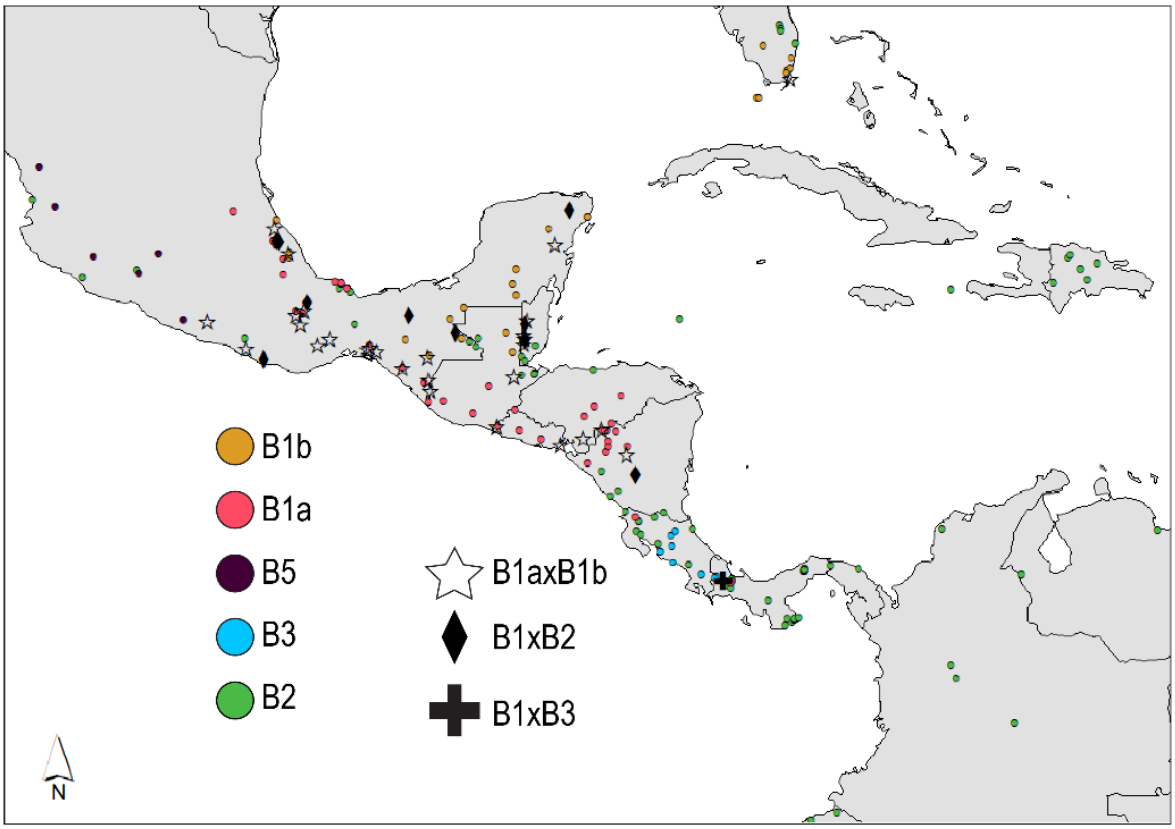


Figure 11. Distribution of *T. micrantha* group B hybrids.

Ten of the 19 bioclimatic variables were retained for ecological niche modeling after removing co-correlated variables ≥ 0.80 (Table 5). No soil variables were co-correlated and therefore retained.

Omission Error Rates (OER) and Area Under the Curve (AUC) values obtained for each of the *T. micrantha* B group models indicated that the models performed well and adequately characterized suitable habitat. Omission error rates for all clade models were < 0.2 and the AUC values were > 0.8 (Table 6). Percent contributions of each variable used in the ecological niche models were used to examine potential niche differentiation between clades and Table 7 shows variables with percent contributions > 10% for each model.

Trema micrantha B1a (Figure 12) occurrence records were found throughout southern Mexico, southern Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.

Habitat suitability was highest primarily along the western coast of Mexico and north Central America, from which I had many specimens. Some sites in the Caribbean were also identified as suitable, but I do not have specimens from those locales. Throughout the modeled distribution, temperature seasonality (21.7%) and soil pH (17.3%) were the most important environmental variables affecting habitat suitability (Table 7).

Trema micrantha B1b (Figure 13) was found in Florida, Mexico along the eastern coast and on the Yucatan peninsula, northern Guatemala, and Belize. The largest areas of highly suitable habitat were in Mexico (especially the Yucatan Peninsula) and northeastern Central America, continuing into Cuba and southern Florida. I examined many specimens from these areas, but none from Cuba (which are poorly represented in herbaria). Isolated areas of suitable habitat also occur in the Andes, Costa-Rica, and other areas in the Caribbean, but no specimens of B1b have been found from these areas. Temperature seasonality was the highest contributing variable (53%), with depth to bedrock contributing 33.1% and mean diurnal air temperature range 12.5% (Table 7).

Trema micrantha B2 (Figure 14) was the most broadly distributed of the B lineages, with a distribution in Florida, throughout the Caribbean islands, Mexico, Guatemala, Belize, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Paraguay, Bolivia, Peru, and Ecuador. Areas of high modeled habitat suitability were found through most of Central America and southern Mexico, northern South America and down the eastern flanks of the Andes The most important variables contributing to the ENM were mean diurnal air temperature range (27.5%), soil organic carbon content (22.8%), temperature seasonality (14.9%), and soil pH (13.1%) (Table 7).

Trema micrantha B3 (Figure 15) had a narrow distribution in Costa Rica and Panama. The most important variables for the ENM were mean monthly precipitation amount of the coldest quarter (43.1%), isothermality (15.6%), and mean annual air temperature (10.7%) (Table 7).

Trema micrantha B4 (Figure 16) had a range restricted to Bolivia and Argentina on the eastern portion of the Andes. The most suitable modeled habitats encompass this area, but also western Ecuador and eastern Brazil, both area in which this lineage have not been found. The most important environmental variables for the modeled distribution were mean monthly precipitation amount of the warmest quarter (42.4%), precipitation seasonality (23.4%), volumetric percentage of coarse fragments (20.5%), and temperature seasonality (10.7%) (Table 7).

Trema micrantha B5 (Figure 17) has only been detected in western Mexico. Precipitation seasonality had the highest importance to the model (50.6%), pH index (19.9%) and temperature seasonality (19.3%) also moderately contributed.

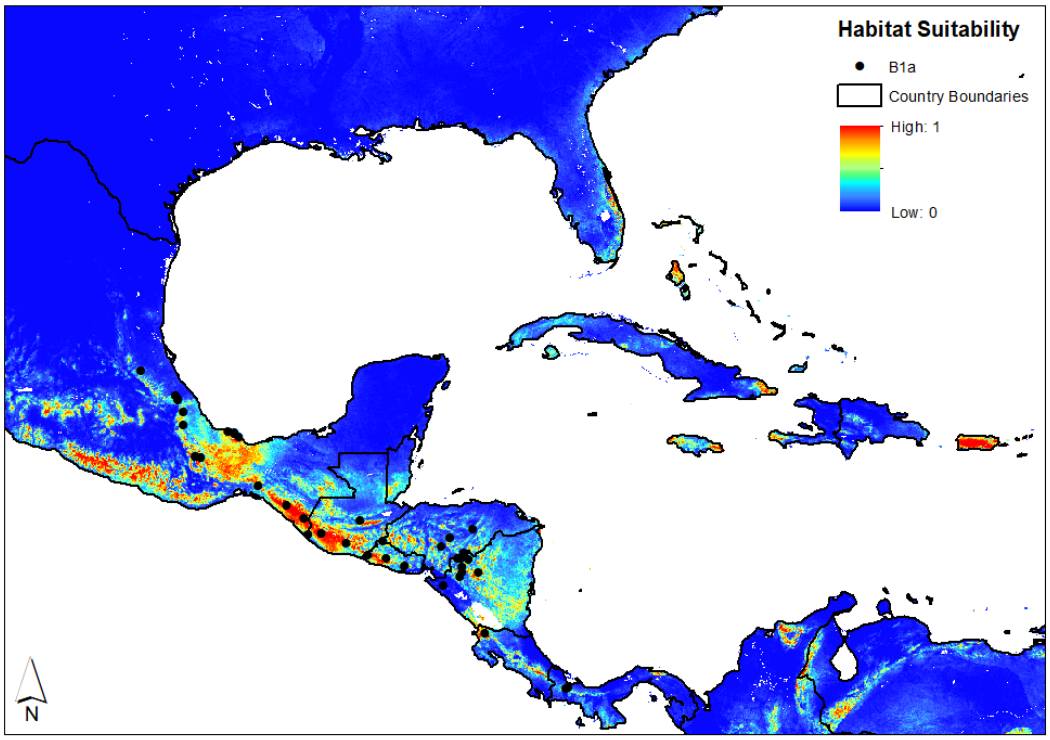


Figure 12. Ecological Niche Model for *T. micrantha* group B1a.

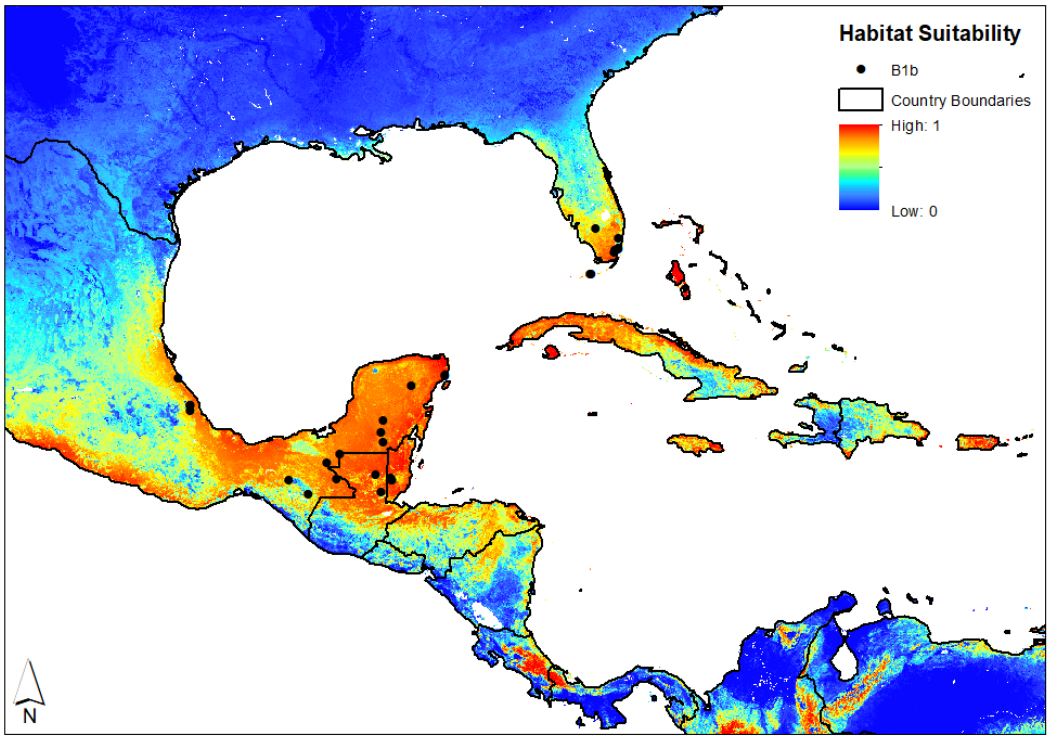


Figure 13. Ecological Niche Model for *T. micrantha* group B1b

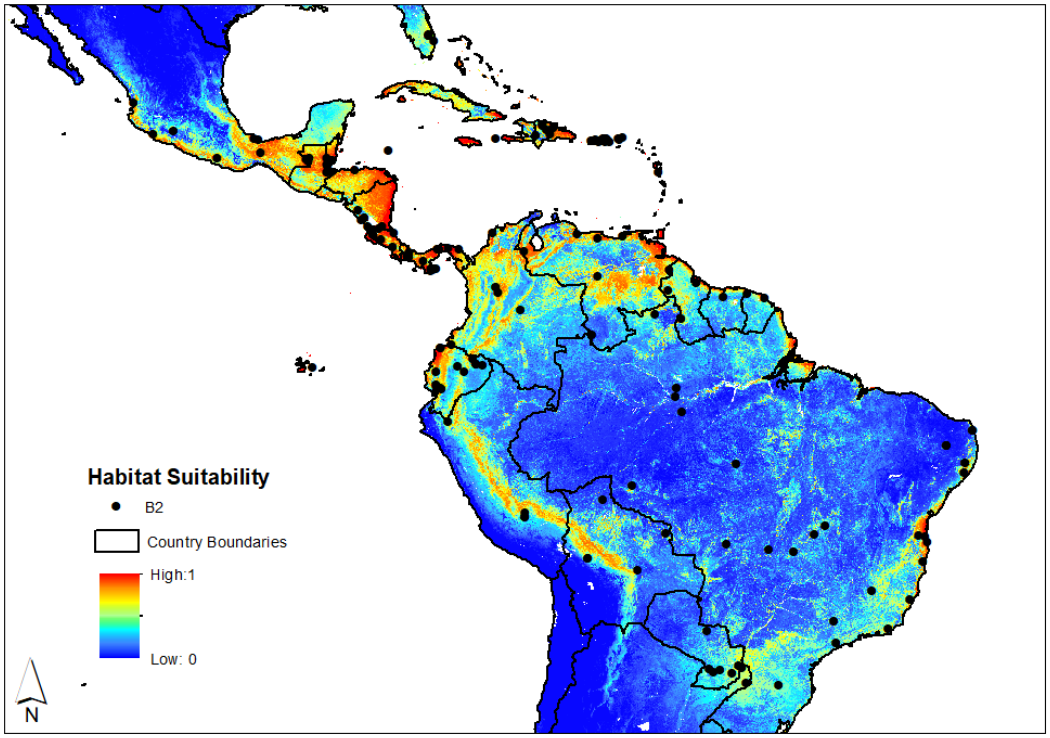


Figure 14. Ecological Niche Model for *T. micrantha* group B2.

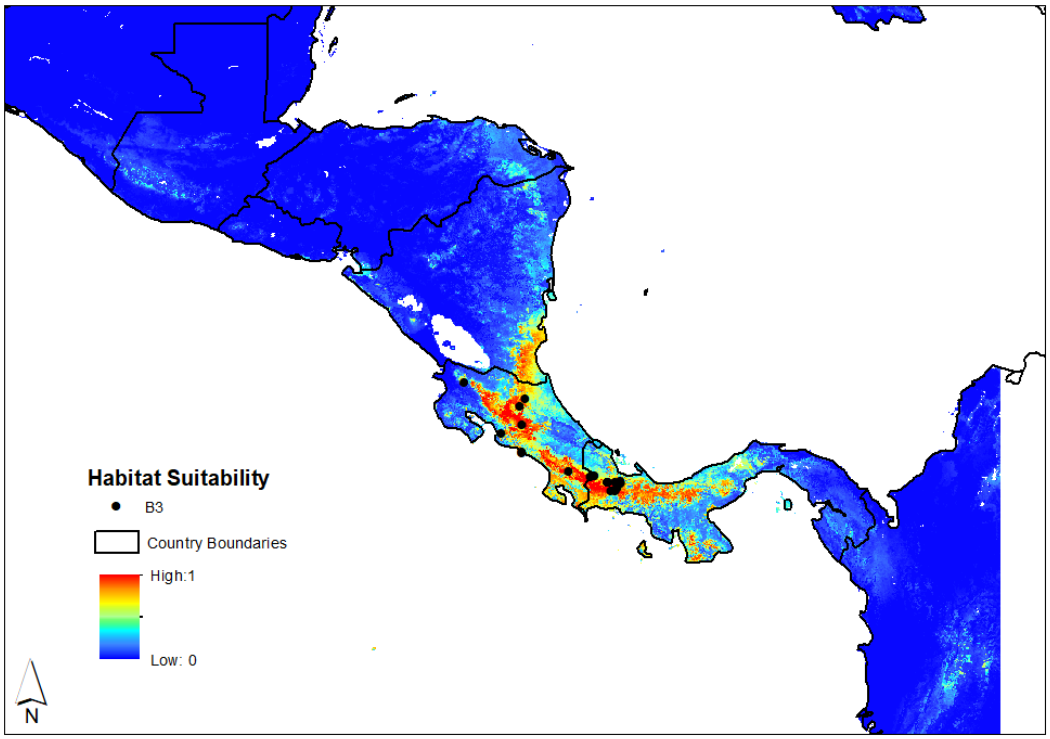


Figure 15. Ecological Niche Model for *T. micrantha* group B3.

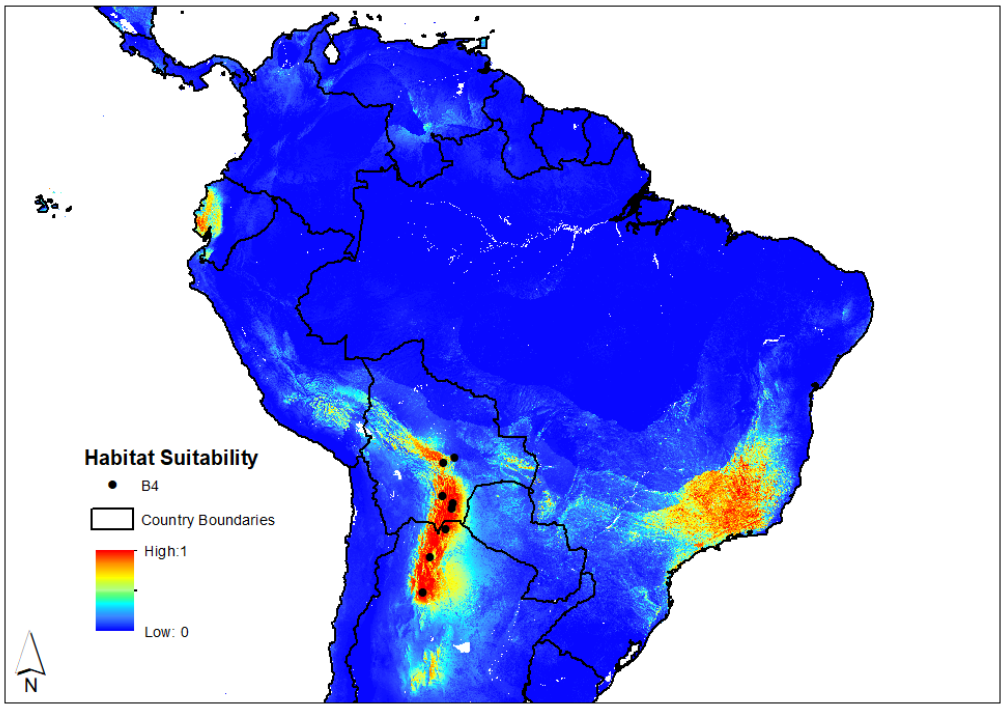


Figure 16. Ecological Niche Model for *T. micrantha* group B4.

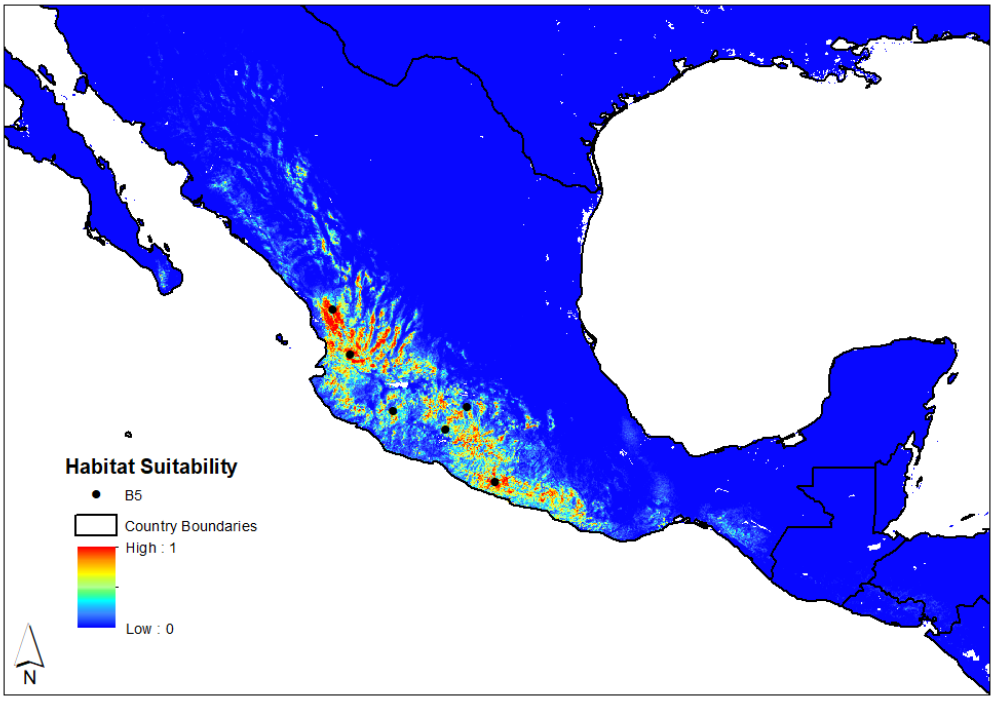


Figure 17. Ecological Niche Model for *T. micrantha* group B5.

CHAPTER 4

DISCUSSION

The major objective of this work was to evaluate relationships within *Trema micrantha.* To date, no other studies have investigated this species with a sampling broad enough to capture the molecular and morphological variation of *T. micrantha* across its vast geographic distribution. Here, I present six major lineages within *T. micrantha* group B that satisfy phylogenetic, morphological, and/or ecological species concepts. If a group met the conditions of at least two species concepts, it is presented here as meriting recognition as a distinct species. Additionally, the results of this study provide the framework for a taxonomic revision of *T. micrantha* that would delimit several species within the group.

Phylogenetic relationships within *T. micrantha* – Major lineages & hybridization

The molecular phylogenies presented here provide resolution of several species within *T. micrantha*. In all phylogenetic analyses, three *T. micrantha* clades (A, C and D) for a clade and were recovered as sister to all the other Neotropical lineages (*T. micrantha* group B, *T. domingensis, T. lamarckiana*, and *T. cubensis*). Previous work noted two of these lineages as *T. micrantha* A (= *T. micrantha* **I**) and *T. micrantha* C (= *T. micrantha* **IId**) (Garwood et al. 2018; Yesson et al. 2004, Figure 1). Increased sampling in this study also recovered a clade sister to *T. micrantha* A, which I preliminarily denoted as *T. micrantha* D, which is currently only known from montane areas near Cuzco, Peru. These clades have strong support and consistent relationships across all phylogenies (i.e., 5-loci, nuclear ribosomal cistron, and plastome datasets) and should be recognized as distinct species. However, further taxon sampling for *T. micrantha* D is required to discern the full scope of this lineage.

In the 5-DNA loci phylogeny, *T. domingensis* was sister to *T. micrantha* group B, but in the genomic datasets (NRC and plastome) *T. domingensis* was embedded within group B. The plastome and nuclear ribosomal cistron phylogenies reveal that the evolutionary relationships between *T. domingensis* and *T. micrantha* group B are complex and should be further explored. Morphologically, *T. domingensis* is easily distinguishable from *T. micrantha* by its entire leaf margins and distinct pubescence (Garwood et al. 2018).

Within *T. micrantha* group B, clades B2 and B4 were always sister taxa and well-supported across the phylogenetic analyses of the four molecular datasets. Group B3 was well-supported in the 5-loci and plastome phylogenies but formed a clade with B1b in the NRC phylogeny. The ETS phylogeny supported recognition of B3 as a distinct clade, and B1b was not nested within the clade. Groups B1a and B1b were well-supported as clades in the 5-loci phylogeny, but the inclusion of *Dalling 54* reduced bootstrap support for B1a in the NRC phylogeny and for B1b in 5-loci phylogeny. In the ETS phylogeny and UPGMA dendrogram, *Dalling 54* and *Dalling 52* were distinguished by a long branch with strong bootstrap support (BS = 95%), indicating a unique genotype. In the ETS dataset, *Dalling 54* did not have any polymorphisms to indicate a potential hybrid origin. *Dalling 52* had a single nucleotide polymorphism at a position that is not variable across any Neotropical *Trema* lineages. Given the uncertain phylogenetic place of *Dalling 52* and *Dalling 54* these accessions are noted as "incertae sedis" in the phylogenetic trees. These specimens could potentially be a poorly sampled lineage within the complicated Central American *T. micrantha* B groups. In the plastome phylogeny, B1b did not form a distinct clade from B1a, and in the NRC phylogeny B1b was nested within *T. micrantha* B3, and not well-supported as a clade with B3. *T. micrantha* group B5 was recovered in the ETS analyses, where there was the greatest taxon sampling. Further

molecular sampling is required to understand its relationships within *T. micrantha*, but ETS data shows this lineage is potentially sister to group B3.

Phylogenetic conflict between nuclear and organellar phylogenies is well-documented in species-level phylogenies (Stull et al. 2020) and can occur due to incomplete lineage sorting (ILS), hybridization, chloroplast capture, and horizontal gene transfer (HGT). The incongruence observed between the NRC and plastome phylogenies for the placement of B1b may be a result of hybridization between *T. micrantha* B lineages, for which there are many likely instances (Table 3). For several accessions, polymorphisms were detected that are intermediates of the B1a and B1b genotypes and one accession had polymorphisms that shared both B1 and B3 genotypes (Table 3). B1a and B1b are sympatric in Mexico and northern Central America, and most B1a × B1b hybrids occur there (Figure 11). The ranges of B1a and B3 based on my samples do not overlap (Figure 11), but the presence of a hybrid between B1a and B3 suggests that the current ranges may be larger than I have estimated, or that they have contracted since the hybridization event. Based on the evidence obtained here, conflicting phylogenetic signal seems likely to be the result of hybridization between *T. micrantha* B clades. However, without further tests, incongruence due to ILS cannot be excluded as a possible explanation (Vargas et al. 2017).

There is also significant hybridization between group B1 and B2 where their distributions overlap in Mexico, Belize, and Nicaragua (Table 3, Figure 11). The ETS locus demonstrates these may be hybrids between B1b and B2, but the geographic distribution of the hybrids occurs where B1a and B2 overlap, thus the origin of the hybrids is difficult to distinguish. Frequent hybridization between *T. micrantha* B lineages is plausible. *Trema micrantha* likely experienced rapid diversification (note short branch lengths between B lineages), especially given the topographic and environmental heterogeneity across its distribution. When rapid diversification

happens in a brief period, it is expected that descendants are subject to interbreed before reproductive barriers develop (Vargas et al. 2017). Future estimates of divergence times within Neotropical *Trema* will provide more insight into diversification and admixture of these lineages.

Morphological recognition of major lineages

The morphological analyses demonstrate significant variability in *T. micrantha* group B as well as characters helpful in discriminating lineages. Several lineages in group B defined in the phylogenetic analyses are morphologically distinct in leaf shape. While not formally analyzed in the morphometric analyses presented here, trichome density and morphology are also important for characterizing *T. micrantha* lineages.

Group B2 is differentiated from B1a and B1b by longer and wider leaf apices, as shown in the ANOVA boxplots (Figure 9) and in PC2, which is a contrast between blade width (BW; with the positive value indicating contribution to the upper quadrants of PCA) and apex measurements (AL, AW; negative value indicating contribution to lower quadrants of PCA). Blade length is also most variable in group B2. Group B4 overlaps in morphological space with group B2 and was only significantly different from B2 in distance from the base of the blade to the widest point (BD). Distance from the base of the blade to the widest point can serve as a proxy measurement for overall leaf shape. For example, if the leaf is widest near the base of the blade, BD is smaller and vice versa. Group B4 has a mean BD value lower than B2, indicating B4 specimens may be more ovate in shape than B2. Group B3 shows the most morphological intermediacy of all the lineages, and was only significantly different from B1a in BD, where B3 (and all other B lineages) had a lower mean BD value than B1a. Groups B1a and B1b were significantly different in blade length (BL) and in BD, with B1a having a larger mean value for both characters. Accessions of B1b are more ovate in shape (smaller BD) with a cordate leaf

base, while B1a accessions are longer and more regularly shaped, or elliptic. Group B5 shows considerable morphological overlap with B1a but is mostly distinct from B1b. Further evaluations of potential species delimitation of Group B5 will require more morphological and molecular sampling.

Group B2 accessions are characterized by long, attenuate apices, leaf blades between 4 – 15cm long that are elliptic to lanceolate in shape, and asymmetric leaf bases. This morphological characterization is consistent with descriptions from local floras describing *T. micrantha* in the Caribbean and South America, but these descriptions do not discriminate between the clades identified in this study (Torres and Luca 2005; Philcox 1982; Legaard and Balslev 2014; Melo and Ussui-Fukugauti 1984; MacBride 1937; Berg 1992). Regarding trichome density and morphology, two different suites of characters have been found on the abaxial lamina. Group B2 leaves are scabrous, with sparse, short erect trichomes that are cystolithic at the base or leaves are soft, densely pubescent, with trichomes that are cystolithic at the base. Based on observations in this study, these suites of trichome morphologies are not geographically structured; both soft pubescent and scabrid specimens are found across the Caribbean and South America. Authors have also noted the morphological variation in South American *T. micrantha* with some describing the pubescent, South American *T. micrantha* as *Trema mollis* (Machado et al. 2019). Many accessions of B2 analyzed here share similarities to the *Celtis mollis* (= *T. micrantha*) type specimen (*Humbolt & Bonpland 359*). The lectotype of *Rhamnus micranthus* L., the basionym of *Trema micrantha* L. Blume, is an illustration (Brown 1756) from Jamaica making it difficult to make inferences about the similarities between *T. micrantha* lineages and the type specimen. Accessions representing group B2 look more similar to the illustration than any other *T. micrantha* B lineages. However, it is important to note that floras do not distinguish *T. micrantha*

B or *T. micrantha* A, which are very similar in leaf shape (Garwood et al. 2018) and overlap geographically. Additionally, herbarium specimens of *T. micrantha* A has been observed in Jamaica, while B2 has not.

Accessions representing group B4 are morphologically similar to group B2 based on personal observations and morphometric analyses. While the ANOVA rendered BD significantly different between B2 and B4, these clades significantly overlap in morphological space. Additionally, observations of trichome density and morphology reveal the same patterns for B4 as were found in B2. *Nee 47985*, *Serrano 7072c*, *Nee 44561*, and *Morrone 4128* all have sparse, scabrid pubescence, while *Nee 52336*, *Nee 54145,* and *Conrad 2636* are densely pubescent with soft trichomes.

Group B3 is very similar to B2 in leaf shape, with variability across specimens. Accessions observed here typically have long, acuminate to attenuate apices, are narrowly ovate to elliptic in shape with cordate to asymmetric leaf bases. While group B3 overlaps with B2 (and to a lesser extent B1a and B1b) in the morphometric analyses, it has unique trichome morphology. A majority of B3 accessions are white to gray on the abaxial surface due to being densely pubescent. Accessions typically have short, dense trichomes underlaying long erect trichomes. Observations presented here are consistent to floras published in the range of B3 (Costa Rica, Panama). Nevling's (1960) description of *T. micrantha* in Panama notes lanceolate to ovate-elliptic leaves with long attenuate apices and sparsely to densely villose trichomes on the abaxial surface, (1960) however Nevling does not differentiate *T. micrantha* and *T. domingensis* as the description includes entire and serrate leaf margins. In Costa Rica, Burger (1977) describes *T. micrantha* leaves as lanceolate to narrowly ovate, tapering to an acuminate apex, rounded at the unevenly truncate to cordate leaf base and the pubescence as lustrous and

densely to sparsely strigillose with pale grayish hairs. Burger's description (1977) of trichomes of Costa Rican *T. micrantha* is more similar to my observations of group B3 than the other B groups. Interestingly, Johnston (1949) notes a species, *T. canescens,* distinct from *T. micrantha,* growing in Panama. This species is described as having ovate-lanceolate, pale hairy leaves, with an obliquely cordate base (Johnston 1949). While this description generally fits the description of many specimens in group B3, the isotype of *Celtis canescens* Kunth (=*T. micrantha*) (*Humbolt s.n.*) looks more similar to accessions of group B1b or B5 and was collected in Mexico on the same volcano as *Eggler 133* (a representative of B5).

Accessions representing group B5, including *Cornejo-Tenorio 3705*, *Hinton 439*, *Hinton 7833*, *Miller 2947*, and *Miller 3097* are morphologically similar to the type specimen of *T. strigillosa* Lundell (*Schipp 439*) collected in Belize, with lanceolate to elliptic leaves, long acuminate apices, round bases, elevated veins, and appressed or strigillose hairs near the veins (Lundell 1939; Standley and Steyermark 1946). The three other specimens of group B5, *Eggler 133*, *Flores 1882*, and *Tenorio 16194* are more densely pubescent with short trichomes underlaying long, erect trichomes on the blade and veins of the abaxial leaf surface with a more cordate leaf base. *Eggler 133* and *Flores 1882* were collected atop volcanoes at high elevations, potentially explaining the more pubescent leaves.

Many accessions representing group B1b (e.g., *Abbott 19812*, *Contreras 5421*, *McDaniel 9166*, etc.) have the typical *T. floridana* Britton ex Small or *T. micrantha* var. *floridana* (Britton) Standl. & Steyerm. morphology. The leaves are ovate, finely serrate, with short acuminate apices, cordate leaf bases, and densely pubescent on the abaxial surface (Britton 1908; Adams 1972; Small 1903; Sauget & Liogier 1951; Nee 2015), sharing much resemblance with the *T. floridana* type specimen *Small & Nash 32*, from southern Florida. Other authors have described

T. micrantha in Florida as *T. mollis*, subsuming. *floridana* as a synonym (Sargent 1922; Sudworth 1927).

Generally, accessions of group B1a are morphologically distinct from B1b with more rounded to oblique leaf bases and longer leaf blades that are oblong-lanceolate in shape. Additionally, while B1b specimens are densely pubescent and often white on the abaxial surface, B1a specimens can be more scabrous with short, appressed trichomes or softly pubescent. Central American and Caribbean floras (Nee 2015; Stevens 2001) note morphology similar to group B1a found here, but these floras do not distinguish different *T. micrantha* lineages and thus could also include *T. micrantha* B2 and A. Many B1a specimens (*Cornejo-Tenorio 2526*, *Ibarra Manriquez 8*, *Kerber 394*, *Ventura 18114*, etc.) are morphologically similar to the *Celtis schiedeana* (Schltdl.) Blume (=*Trema schiedeana* (Schltdl.) Blume, a synonym of *Trema micrantha*) type with short appressed trichomes. The inclusion of *Dalling 54* reduced bootstrap support for the B1a clade, and *Dalling 54* + *Dalling 52* (both from the mountains of Panama) shared a long branch with strong support in the ETS phylogeny. Both these specimens have morphology similar to *T. schiedeana.*

Ecological recognition of major lineages

The AUC values exceeded 90% for each ecological niche model (ENM) except for group B2 (Table 6), which was 89.5%, indicating that the models estimate each lineage's ranges well and mostly excluded regions with false positives selected from background points (best AUC value 100%). The OER values were under 20% for groups B1a, B1b, B2, and B4 indicating that models predicted species presence and/or suitable habitat moderately well (best OER value 0%). The OER values for groups B3 and B5 were less than 5%, potentially demonstrating that restricted distributions may have performed effectively over wider distributions. Group B4 is

also restricted in its distribution, so a higher OER value may be due to exclusion of environmental variables that define its ecological niche. Some environmental variables were shared as important across lineages; however, all ENMs except for that of group B5 had unique variables contributing to habitat suitability. Bioclimatic variable 4 (temperature seasonality) was important for all ENMs except for group B3.

The ENM for group B2 was the lowest performing model (AUC=89.5%, OER=17.4%), likely due to the broad distribution and potentially generalist nature of this lineage. Group B2 is distributed throughout South America, Central America, and the Caribbean, typically in lowland habitats such as gallery forests, semideciduous seasonal forests, and tropical savannas (Machado et al. 2019). Only 7% of B2 specimens have elevations recorded at ≥ 1000 m and 84% of specimens have elevations ≤ 500 m. Mean diurnal air temperature range (bio2) is a measure of the mean difference of monthly maximum and minimum temperatures over a year (Karger et al. 2017). Supplemental figure 1 shows the distribution of B2 and the bio2 raster data. Group B2 is mostly found in areas with cooler colors, implying that group B2's modeled niche is partially defined by habitats with lower temperature fluctuations. Group B2's modeled niche is additionally defined by areas with soils of lower organic material and lower soil pH values, and areas with a less temperature change over the course of a year. These results are consistent with soil and climate characteristics of lowland tropical forests. Moist tropical forests have soils that are primarily Oxisols and Ultisols (Vitousek & Sanford 1986; Osman 2013), both of which are generally characterized as strongly leached acidic soils, low in organic matter.

Group B4 is a high-elevation lineage with a distinct distribution along the Cordillera Real within the Sub-Andean Zone in Bolivia and Argentina, contrasting with B2 which is a lowland lineage (Figure 10b). Mean monthly precipitation amount of the warmest quarter (bio18) had the

greatest contribution to habitat suitable in the ENM. Bio18 represents the mean precipitation during the warmest three months of year (Karger et al. 2017). Supplementary figure 2 demonstrates that B4 occurs in areas of relatively higher precipitation during the warmest months. Precipitation seasonality (bio15) was also an important variable in clade B4's ENM and this environmental variable is a measure of precipitation variability, with larger percentages presenting greater precipitation variability (Suppl. Fig. 3) (O'Donnell and Ignizio 2012). The inclusion of bio18, bio15, and bio4 (Table 7) demonstrates a relationship between B4's distribution and the humid subtropical climate and seasonality of the outer tropical Andes (Perry et al. 2017). The outer tropical Andes are well known for the distinct seasonality of precipitation, with a wet season from November to March and a dry season from April to October (Perry et al. 2017).

Mean monthly precipitation amount of the coldest quarter (bio19) was the highest contributing variable in group B3's ENM, implying that higher precipitation during dry season is important for habitat suitability. (Suppl. Fig. 4). Isothermality (bio3) and mean annual air temperature (bio1) also moderately (each <20%) contributed to the ENM. Isothermality is the measure of how much the day-to-night temperatures oscillate relative to the annual oscillations (O'Donnell and Ignizio 2012). Thus, B3 occurs in habitats with higher mean annual temperatures and lower temperature variability within an average month relative to the year.

Group B1a is distributed in humid, tropical-savanna and tropical-monsoon climates of Central America and is a moderate to high elevation lineage with 84% of occurrences with elevations ≥ 500 m and 56% of occurrences with elevations ≥ 1000 m (Table 1). Temperature seasonality (bio4), soil pH, and mean monthly precipitation amount of the coldest quarter (bio19) contributed most to the clade B1a ENM. Clade B1a occupies habitats with low annual

temperature variability (Suppl. Fig, 5), acidic to neutral soils, and dry seasons with lower precipitation.

Group B1b is a lowland species (only 2 accessions had elevations >1000 m) in Mexico, Guatemala, Belize, and southern Florida. Temperature seasonality (bio4) made the highest contribution to the model indicating clade B1b occurs in habitats with low annual temperature variability (Suppl. Fig. 5). Absolute depth to bedrock was also an important variable, with clade B1b occupying areas with generally lower depths to bedrock (Suppl. Fig. 6). While objective measures of model performance (AUC, OER) were good, visual inspection of the model shows moderately to highly suitable habitat across most of Central America and the Caribbean, potentially indicating that the environmental variables used here are not effective in discriminating suitable habitat for *T. micrantha* B1b or that sampling across the range of B1b was not adequate.

Group B5 is a montane lineage currently only documented in tropical deciduous, pine-oak forests along the Sierra Madre del Sur and Trans-Mexican Volcanic Belt. Precipitation seasonality (bio15) was the most important variable in the ENM, accounting for half of the habitat suitability, with soil pH and temperature seasonality (bio4) both contributing ~20%. Precipitation seasonality is high in B5's range (Suppl. Fig. 7), and this finding is consistent with the climate of the Sierra Madre del Sur (Marshall & Liebherr 2000; Morrone 2010; Santiago-Alvarado et al. 2016).

It is important to note that temperature seasonality (bio4) was an important variable in 5 of the 6 ENMs, and the most important variable for *T. micrantha* B1a and B1b. This bioclimatic variable is simply a measure of temperature change over the course of a year (Karger et al. 2017). Tropical environments are well-characterized by generally stable temperatures and bio4 is

not variable across *T. micrantha* group B's distribution (Suppl. Fig. 8). Models predicting bio4 as an important environmental factor for any *T. micrantha* clade provides little insight into specific ecological requirements of these lineages.

Conclusions

Taxonomists have long described the variability of *T. micrantha* and noted that satisfactory treatments of the group would necessitate a broad study of the genus. The 5-loci phylogeny of *Trema* has the greatest taxon sampling and supports recognition of 5 species within *T. micrantha* group B as well as recognition of clades A, C, and D as species based on the phylogenetic species concept (Wheeler and Meier 2000). While relationships within and between *T. micrantha* group B were conflicting between the NRC and plastome phylogenies, this is a phenomenon that is commonly recovered when comparing nuclear and organellar data, both of which are biologically different and demonstrate different evolutionary paths (Vargas et al. 2017). Even though group B1b was not monophyletic across all phylogenetic analyses, a combination of phylogenetic, morphometric, and biogeographic data provides support for its recognition.

Group B2 is distributed throughout lowland tropical forests and tropical savannas across the Neotropics, is phylogenetically distinct from all other *T. micrantha* lineages, and monophyletic in all phylogenetic analyses. Morphological data also supports recognition of *T. micrantha* B2, with long leaf blades, long acuminate apices, and oblique leaf bases being distinguishing characters. With the evidence presented here, group B2 satisfies the morphological (Mayr 1992), phylogenetic (Wheeler and Meier 2000), and ecological species concepts (Grant 1992).

Group B4 occupies a unique geographic range along the Cordillera Real in Bolivia and Argentina, with a niche defined by the humid subtropical climate and seasonal precipitation, strongly supporting the ecological species concept (Grant 1992) While group B4 did not show unique leaf shape features here, thus not fulfilling the morphological species concept, this lineage was monophyletic in all phylogenetic analyses, satisfying the phylogenetic species concept (Wheeler and Meier 2000).

Group B3 has a geographic distribution restricted to Costa Rica and Panama, where it commonly occurs in secondary forests. The ENM indicates that *T. micrantha* B3 occurs in habitats with relatively high precipitation. The ETS dataset demonstrates the possibility of two subclades within *T. micrantha* B3, one lowland and one montane group, however without more robust support, this hypothesis cannot yet be supported. Group B3 was well-supported and monophyletic in the 5-loci and plastome phylogenies, while in the NRC the inclusion of B1b accessions reduced bootstrap support. As discussed above, this incongruence is likely due to hybridization. Clade B3 could not be distinguished from B2 (and to some extent B1a and B1b) in the morphometric analyses, potentially due to a smaller sample size. However, this group has tomentose, white pubescence on the abaxial leaf surface and narrowly ovate to lanceolate leaves a combination of characters that discriminates the lineage from other *T. micrantha* lineages. The evidence presented here supports all three species concepts.

Group B1a can be supported as a species based on the phylogenetic species concept (Wheeler and Meier 2000) and morphological species concept (Mayr 1992). B1a and B1b are distinct clades in the 5-loci phylogeny. In the plastome phylogeny these lineages are not reciprocally monophyletic and in the NRC phylogeny B1a is monophyletic and well-supported (excluding *Dalling 54*). Additionally, the morphometric analyses demonstrate that B1a is

morphologically distinct from all other B lineages (except B5), with rounded to oblique leaf bases, oblong-lanceolate leaf shape, and scabrous to minutely pubescence on the abaxial surface. Group B1a is a moderate to high elevation species, making it distinct from *T. micrantha* B1b and B2. The ENM indicated that, within its range, B1a occupies niches similar to other lineages (most important variables in ENM were shared with other lineages), thus B1a does not completely satisfy the ecological species concept, but further tests (i.e. statistical niche overlap tests) would be necessary to adequately evaluate this.

While the phylogenetic position of group B1b was not consistent across datasets, the 5-loci phylogenies support the monophyly of B1b, thus meeting the criteria of the phylogenetic species concept (Wheeler and Meier 2000). This group is morphologically distinguishable, supporting the morphological species concept (Mayr 1992). Group B1b has distinct, ovate leaves with short acuminate apices, cordate leaf bases, and tomentose pubescence on the abaxial leaf surface. Group B1b is a lowland species found in southern Florida, Guatemala, Belize, and eastern Mexico, distinguishing it from B1a which is typically found at high elevations. However, the ENM did not discern a distinct niche for this lineage, thus there is not support for the ecological species concept.

Group B5 has a unique distribution along the Sierra Madre del Sur in western Mexico, where it occupies tropical deciduous, pine-oak forests. The ecological niche of *T. micrantha* B5 is unique to this lineage and distinguishable from other *T. micrantha* lineages, thus supporting the ecological species concept (Grant 1992). Clade B5 was only sampled for the ETS phylogeny, where it was well-supported and monophyletic. While more robust molecular data is required for this clade, the evidence presented here supports the phylogenetic species concept (Wheeler and

Meier 2000). With the current evidence here, there is not support for the morphological species concept (Mayr 1992), further morphological sampling is necessary.

This study is the first to evaluate the relationships of *T. micrantha* in detail and provides a more robust understanding of species circumscriptions within Neotropical *Trema*. This combination of biologically and taxonomically important evidence provides recognition of at least 6 species within *T. micrantha* group B and three additional species of *T. micrantha* noted as A, C, and D. Groups B1a, B1b, B2, B3, B4, and B5 satisfy the phylogenetic species concept *sensu* Mishler and Theriort in addition to the morphological species concept (B1a, B1b), or the ecological species concept (B3, B4, B5), or both (B2). Lastly, the work presented here highlights the utility of integrating a multi-faceted approach. With the inclusion of phylogenetic, morphometric, and biogeographic data, a more inclusive, robust, and biologically relevant species circumscription can be pursued through evaluation of several species' concepts.

EXHIBITS

Table 1. *Trema* accessions sampled for phylogenetic, morphometric, and ecological analyses. "X" represents accessions sampled, with "-" denoting no data. Clade abbreviation: **mic** = micrantha, **P** = *Parasponia*. Institution acronyms: **BM** =The Natural History Museum, **E** = Royal Botanic Garden Edinburgh. **DAO** = Agriculture and Agri-Food Canada, **FLAS** = Florida Museum of Natural History, **MO** = Missouri Botanical Garden, **NY** = New York Botanical Garden, **SIU** = SIU Herbarium, **UCWI** = University of the West Indies, Mona, **UPRRP** = University of Puerto Rico, **USF** = University of South Florida.
Country abbreviations: **BVI** = British Virgin Islands, **DR** = Dominican Republic, **USVI** = US Virgin Islands

Clade	Accession Name	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
africana	*St-Laurent 96-43*	DAO	Togo	-	-	-	x	x	x
aspera	*Michael 865*	BM	Australia	-	-	-	x	-	-
aspera	*Compton 511*	BM	New Caleldonia	-	-	-	x	-	-
aspera	*DamasLAE 64501*	E	PNG	-	-	-	x	-	-
aspera	*DamasLAE 74502*	E	PNG	-	-	-	-	x	x
cubensis	*Zanoni 34002*	NY	DR	-	-	-	x	x	x
cubensis	*Zanoni 40263*	NY	DR	-	-	-	x	-	-
domingensis	*Whitefoord 106231*	MO	Belize	-	-	-	x	-	-
domingensis	*Garwood 5-10*	SIU	Belize	-	-	-	x	x	x
domingensis	*Garwood 231*	SIU	Belize	-	-	-	x	-	-
domingensis	*Garwood 5-5*	SIU	Belize	-	-	-	x	-	-
domingensis	*Araujo 1112*	MO	Bolivia	-	-	-	x	-	-
domingensis	*Meneces 471*	MO	Bolivia	-	-	-	x	-	-
domingensis	*Cascante 1184*	MO	Costa Rica	-	-	-	x	x	x
domingensis	*Solano 258*	MO	Costa Rica	-	-	-	x	-	-
domingensis	*Dalling s.n.*	SIU	Costa Rica	-	-	-	x	-	-
domingensis	*Ekman 12293*	S	DR	-	-	-	x	-	-
domingensis	*Garwood 4545*	SIU	Ecuador	-	-	-	x	x	x
domingensis	*Garwood 4575*	SIU	Ecuador	-	-	-	x	-	x
domingensis	*Garwood 4514*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Garwood 4516*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Garwood 4541*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Garwood 4543*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Garwood 4544*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Garwood 4556*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Garwood 4557*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Villa 2144*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Villa 2052*	SIU	Ecuador	-	-	-	x	-	-
domingensis	*Lundell 16311*	MO	Guatemala	-	-	-	x	-	-
domingensis	*Salick 8089*	MO	Nicaragua	-	-	-	x	-	-
domingensis	*Hayden 4*	MO	Panama	-	-	-	x	-	-
domingensis	*Smith 1471*	MO	Peru	-	-	-	x	-	-
domingensis	*Timaná 3227*	MO	Peru	-	-	-	x	-	-
domingensis	*Irwin 54824*	MO	Suriname	-	-	-	x	-	-
lamarckiana	*Wunderlin 8253*	MO	Bahamas	-	-	-	x	x	x
lamarckiana	*Gentry 51023*	MO	Cuba	-	-	-	x	x	x
lamarckiana	*Dechamps 49688*	MO	Cuba	-	-	-	x	-	-
lamarckiana	*Wise X87*	NY	DR	-	-	-	x	-	-

Table 1. Continued.

Clade	*Accession Name*	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
lamarckiana	*Zanoni 13516*	NY	DR	-	-	-	x	-	-
lamarckiana	*Zanoni 15344*	NY	DR	-	-	-	x	-	-
lamarckiana	*Zanoni 16860*	NY	DR	-	-	-	x	-	-
lamarckiana	*Zanoni 31914*	NY	DR	-	-	-	x	-	-
lamarckiana	*Zanoni 31925*	NY	DR	-	-	-	x	-	-
lamarckiana	*Zanoni 31926*	NY	DR	-	-	-	x	-	-
lamarckiana	*Zanoni 31903*	NY	DR	-	-	-	-	x	x
lamarckiana	*Thompson 4105*	FLAS	Haiti	-	-	-	x	-	-
lamarckiana	*Proctor 36513*	MO	Jamaica	-	-	-	x	-	-
lamarckiana	*Taylor 10514*	MO	Puerto Rico	-	-	-	x	x	x
lamarckiana	*Axelrod 8130*	MO	Puerto Rico	-	-	-	x	-	-
lamarckiana	*Avery 905*	FLAS	US	-	-	-	x	-	-
lamarckiana	*Koop 5*	SIU	US	-	-	-	x	x	x
levigata	*Forrest 12604*	BM	China	-	-	-	-	x	x
levigata	*Gaoligong 8560*	E	China	-	-	-	x	-	-
mic A	*Whitefoord 1875*	BM	Belize	-	-	-	x	-	-
mic A	*Garwood 5-8*	SIU	Belize	-	-	-	-	x	-
mic A	*Terán 951*	MO	Bolivia	-	-	-	-	x	x
mic A	*Arias 27*	MO	Colombia	-	-	-	x	-	-
mic A	*FernándezCasas 10596*	MO	Cuba	-	-	-	x	-	-
mic A	*Basilio Augusto 1078*	NY	DR	-	-	-	x	-	-
mic A	*Zanoni 32716*	NY	DR	-	-	-	x	-	-
mic A	*Garwood 4548*	SIU	Ecuador	-	-	-	x	x	x
mic A	*Villa 2078*	SIU	Ecuador	-	-	-	x	x	x
mic A	*Villa 2133*	SIU	Ecuador	-	-	-	x	x	x
mic A	*Garwood 4554*	SIU	Ecuador	-	-	-	x	-	-
mic A	*Garwood 4559*	SIU	Ecuador	-	-	-	x	-	-
mic A	*Villa 2147*	SIU	Ecuador	-	-	-	x	-	-
mic A	*Villa 2153*	SIU	Ecuador	-	-	-	x	-	-
mic A	*Villa 2066*	SIU	Ecuador	-	-	-	x	-	-
mic A	*Villa 2131*	SIU	Ecuador	-	-	-	x	-	-
mic A	*Villa 2015*	SIU	Ecuador	-	-	-	-	x	x
mic A	*Garwood 4547*	SIU	Ecuador	-	-	-	-	x	-
mic A	*Galo 12*	BM	Honduras	-	-	-	x	-	-
mic A	*Adams 7513*	BM	Jamaica	-	-	-	x	-	-
mic A	*Proctor 23831*	NY	Jamaica	-	-	-	x	-	-
mic A	*Franck 3906*	USF	Jamaica	-	-	-	x	x	x
mic A	*Whitefoord 258*	BM	Panama	-	-	-	x	-	-
mic A	*Dalling 16*	SIU	Panama	-	-	-	x	-	-
mic A	*Dalling 18*	SIU	Panama	-	-	-	x	-	-
mic A	*Dalling 49*	SIU	Panama	-	-	-	x	-	-
mic A	*Dalling 55*	SIU	Panama	-	-	-	x	-	-
mic A	*Dalling 02*	SIU	Panama	-	-	-	-	x	x
mic A	*Rimachi 2449*	FLAS	Peru	-	-	-	x	-	-
mic A	*Suclli 2327*	MO	Peru	-	-	-	-	x	x
mic A	*Little 13046*	NY	Puerto Rico	-	-	-	x	-	-
mic A	*Worthington 18155*	MO	Trinidad & Tobago	-	-	-	-	x	x
mic B1a	*García 170*	MO	Costa Rica	x	x	x	x	x	x

Table 1. Continued.

Clade	*Accession Name*	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
mic B1a	*Monro 3604*	BM/SIU	El Salvador	-	x	x	x	-	x
mic B1a	*Galán 2668*	MO	El Salvador	-	x	x	-	-	-
mic B1a	*Martínez 114*	MO	El Salvador	-	x	x	-	-	-
mic B1a	*Monterrosa 1718*	MO	El Salvador	-	x	x	-	-	-
mic B1a	*Skutch 1337*	BM	Guatemala	-	x	x	-	-	-
mic B1a	*Garcia 96.5395*	MO	Guatemala	x	x	x	x	x	x
mic B1a	*Pérez 2087*	MO	Guatemala	-	x	x	-	-	-
mic B1a	*Wehncke 1-3*	SIU	Guatemala	-	x	x	x	x	x
mic B1a	*Williams 17399*	BM	Honduras	x	x	x	x	-	-
mic B1a	*Chorley 183*	BM	Honduras	-	x	x	-	-	-
mic B1a	*Galeano 100*	MO	Honduras	-	x	x	-	-	-
mic B1a	*Kerber 394*	BM	Mexico	-	x	x	-	-	-
mic B1a	*Ventura 17223*	MO	Mexico	x	x	x	x	x	x
mic B1a	*Croat 65937*	MO	Mexico	x	x	x	x	x	x
mic B1a	*Ibarra Manríquez 2480*	MO	Mexico	x	x	x	x	x	x
mic B1a	*Gómez Chagala 798*	MO	Mexico	x	x	x	x	-	-
mic B1a	*Ibarra Manríquez 1470*	MO	Mexico	x	x	x	x	-	-
mic B1a	*López Luna 0020*	MO	Mexico	x	x	x	x	-	-
mic B1a	*López Luna 0195*	MO	Mexico	x	x	x	x	-	-
mic B1a	*Ibarra Manríquez 3958*	MO	Mexico	x	x	x	x	-	-
mic B1a	*Nee 23721*	MO	Mexico	-	x	x	x	-	-
mic B1a	*Beaman 6060*	MO	Mexico	x	x	x	-	-	-
mic B1a	*Cornejo Tenorio 2526*	MO	Mexico	x	x	x	-	-	-
mic B1a	*Ibarra Manríquez 8*	MO	Mexico	x	x	x	-	-	-
mic B1a	*Nee 26002*	MO	Mexico	x	x	x	-	-	-
mic B1a	*Ventura 18114*	MO	Mexico	x	x	x	-	-	-
mic B1a	*Breedlove 24747*	MO	Mexico	-	x	x	-	-	-
mic B1a	*Breedlove 28625*	MO	Mexico	-	x	x	-	-	-
mic B1a	*Martínez 935*	MO	Mexico	-	x	x	-	-	-
mic B1a	*Hall 7682*	BM	Nicaragua	-	x	x	x	-	-
mic B1a	*Stevens 35309*	MO	Nicaragua	x	x	x	x	x	x
mic B1a	*Coronado 377*	MO	Nicaragua	-	x	x	-	-	-
mic B1a	*Coronado 862*	MO	Nicaragua	-	x	x	-	-	-
mic B1a	*Paguaga 168*	MO	Nicaragua	-	x	x	-	-	-
mic B1a	*Rueda 11383*	MO	Nicaragua	-	x	x	-	-	-
mic B1a	*Stevens 30108*	MO	Nicaragua	-	x	x	-	-	-
mic B1a	*Stevens 35513*	MO	Nicaragua	-	x	x	-	-	-
mic B1a	*Stevens 35942*	MO	Nicaragua	-	x	x	-	-	-
mic B1a	*Stevens 39513*	MO	Nicaragua	-	x	x	-	-	-
mic B1a	*Dalling 54*	SIU	Panama	x	x	x	x	x	x
mic B1a	*Dalling 52*	SIU	Panama	x	x	x	-	-	-
mic B1b	*Garwood B05*	SIU	Belize	x	x	x	x	-	-
mic B1b	*Garwood B06*	SIU	Belize	x	x	x	x	-	-
mic B1b	*Garwood B02*	SIU	Belize	x	x	x	-	-	-
mic B1b	*Tun Ortiz 990*	BM	Guatemala	-	x	x	x	-	-
mic B1b	*Contreras 5421*	BM	Guatemala	-	x	x	-	-	-
mic B1b	*Garcia 3828*	BM	Mexico	-	x	x	x	-	-
mic B1b	*Stafford 237*	BM	Mexico	-	x	x	x	-	-
mic B1b	*Reyes-Garcia 184*	BM	Mexico	-	x	x	x	-	-

Table 1. Continued.

Clade	*Accession Name*	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
mic B1b	*Mendez 395*	FLAS	Mexico	x	x	x	x	-	-
mic B1b	*Abbott 19812*	FLAS	Mexico	x	x	x	-	-	-
mic B1b	*Provance 3222*	MO	Mexico	x	x	x	x	-	-
mic B1b	*Aguilar 7231*	MO	Mexico	x	x	x	-	-	-
mic B1b	*Bacab 73*	MO	Mexico	x	x	x	-	-	-
mic B1b	*Téllez 3828*	MO	Mexico	x	x	x	-	-	-
mic B1b	*Álvarez 7485*	MO	Mexico	-	x	x	-	-	-
mic B1b	*Calónico 23574*	MO	Mexico	-	x	x	-	-	-
mic B1b	*Cortés 285*	MO	Mexico	-	x	x	-	-	-
mic B1b	*Germán 1106*	MO	Mexico	-	x	x	-	-	-
mic B1b	*Novelo 146*	MO	Mexico	-	x	x	-	-	-
mic B1b	*Abbott 25239*	FLAS	US	x	x	x	x	x	x
mic B1b	*Abbott 24973*	FLAS	US	x	x	x	x	-	-
mic B1b	*Little 15015*	FLAS	US	x	x	x	x	-	-
mic B1b	*McDaniel 9166*	FLAS	US	x	x	x	x	-	-
mic B1b	*Stern 2822*	FLAS	US	x	x	x	x	-	-
mic B1b	*Wunderlin 8857*	FLAS	US	x	x	x	x	-	-
mic B1b	*Koop 2*	SIU	US	x	x	x	x	x	x
mic B1b	*Garwood M2*	SIU	US	x	x	x	-	-	-
mic B1b	*Garwood M3*	SIU	US	x	x	x	-	-	-
mic B1b	*Koop 13*	SIU	US	x	x	x	-	-	-
mic B1b	*Garwood M1*	SIU	US	-	x	x	-	-	-
mic B2	*Renvoize 3269*	FLAS	Argentina	x	x	x	x	-	x
mic B2	*Deginani 1040*	MO	Argentina	x	x	x	x	-	-
mic B2	*Hunziker 11947*	MO	Argentina	-	x	x	-	-	-
mic B2	*Garwood 230*	SIU	Belize	-	x	x	x	-	-
mic B2	*Garwood 5-1*	SIU	Belize	-	x	x	x	-	-
mic B2	*Garwood 5-6*	SIU	Belize	-	x	x	x	-	-
mic B2	*Garwood 5-2*	SIU	Belize	-	x	x	-	-	-
mic B2	*Garwood 5-3*	SIU	Belize	-	x	x	-	-	-
mic B2	*Garwood B30*	SIU	Belize	-	x	x	-	-	-
mic B2	*Quevedo 2445*	FLAS	Bolivia	x	x	x	-	-	-
mic B2	*Lewis 40505*	MO	Bolivia	x	x	x	x	x	x
mic B2	*Lewis 40551*	MO	Bolivia	x	x	x	x	-	-
mic B2	*Boom 4048*	MO	Bolivia	-	x	x	-	-	-
mic B2	*Nee 57246*	MO	Bolivia	-	x	x	-	-	-
mic B2	*Prance 19244*	FLAS	Brazil	x	x	x	x	-	-
mic B2	*Thomas MT588*	FLAS	Brazil	x	x	x	x	-	-
mic B2	*GadelhaNeto 3484*	MO	Brazil	x	x	x	x	x	x
mic B2	*Teixeira 368*	MO	Brazil	x	x	x	x	x	-
mic B2	*Agra 5007*	MO	Brazil	x	x	x	x	-	-
mic B2	*Amaral 1141*	MO	Brazil	x	x	x	x	-	-
mic B2	*Amorim 1239*	MO	Brazil	x	x	x	x	-	-
mic B2	*Todzia 2231*	MO	Brazil	x	x	x	x	-	-
mic B2	*Agra 4800*	MO	Brazil	x	x	x	-	-	-
mic B2	*Luchiari 587*	MO	Brazil	x	x	x	-	-	-
mic B2	*Souza 4985*	MO	Brazil	x	x	x	-	-	-
mic B2	*Staviski 61*	MO	Brazil	x	x	x	-	-	-
mic B2	*Agra 4737*	MO	Brazil	-	x	x	-	-	-

Table 1. Continued.

Clade	*Accession Name*	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
mic B2	*Custodio Filho 931*	MO	Brazil	-	x	x	-	-	-
mic B2	*Mansano 517*	MO	Brazil	-	x	x	-	-	-
mic B2	*Nee 42396*	MO	Brazil	-	x	x	-	-	-
mic B2	*Silva 433*	MO	Brazil	-	x	x	-	-	-
mic B2	*Anderson 10136*	NY	Brazil	x	x	x	x	x	x
mic B2	*Anderson 36289*	NY	Brazil	x	x	x	x	-	-
mic B2	*Conceição 442*	NY	Brazil	x	x	x	x	-	-
mic B2	*dos Santos 3501*	NY	Brazil	x	x	x	x	-	-
mic B2	*Dusen s.n.*	NY	Brazil	x	x	x	x	-	-
mic B2	*Irwin 24178*	NY	Brazil	x	x	x	x	-	-
mic B2	*Irwin 34910*	NY	Brazil	x	x	x	x	-	-
mic B2	*Lasseign P21199*	NY	Brazil	x	x	x	x	-	-
mic B2	*Philcox 4028*	NY	Brazil	x	x	x	x	-	-
mic B2	*Thomas 11471*	NY	Brazil	x	x	x	x	-	-
mic B2	*Little 26124*	NY	BVI	x	x	x	x	x	x
mic B2	*Little 8231*	BM	Colombia	-	x	x	x	-	-
mic B2	*Gentry 18152*	FLAS	Colombia	x	x	x	-	-	-
mic B2	*Juncosa 981*	MO	Colombia	-	x	x	-	-	-
mic B2	*Zarucchi 4123*	MO	Colombia	-	x	x	-	-	-
mic B2	*Garwood 592*	BM	Costa Rica	-	x	x	x	x	x
mic B2	*Gomez 20761*	BM	Costa Rica	-	x	x	-	-	-
mic B2	*Jones 10116*	MO	Costa Rica	-	x	x	-	-	-
mic B2	*Liesner 2782*	MO	Costa Rica	-	x	x	-	-	-
mic B2	*Martínez 199*	MO	Costa Rica	-	x	x	-	-	-
mic B2	*Robles 1457*	MO	Costa Rica	-	x	x	-	-	-
mic B2	*Short 131*	MO	Costa Rica	-	x	x	-	-	-
mic B2	*Vargas 3380*	MO	Costa Rica	-	x	x	-	-	-
mic B2	*Whitefoord 4426*	BM	Dominica	x	x	x	x	-	-
mic B2	*Meija 7197*	MO	DR	-	x	x	-	-	-
mic B2	*BasilioAugusto 1637*	NY	DR	-	x	x	x	-	-
mic B2	*Ososki 151*	NY	DR	-	x	x	x	-	-
mic B2	*Valeur 706*	NY	DR	-	x	x	x	-	-
mic B2	*Zanoni 27258*	NY	DR	x	x	x	-	-	-
mic B2	*Gentry 72350*	MO	Ecuador	-	x	x	-	-	-
mic B2	*Gilmartin 67*	MO	Ecuador	-	x	x	-	-	-
mic B2	*Reyes 760*	MO	Ecuador	-	x	x	-	-	-
mic B2	*Rubio 2343*	MO	Ecuador	-	x	x	-	-	-
mic B2	*Cerón 15641*	MO	Ecuador	-	x	x	-	-	-
mic B2	*Cerón 3596*	MO	Ecuador	-	x	x	-	-	-
mic B2	*Villa 2061*	SIU	Ecuador	x	x	x	x	x	x
mic B2	*Villa 2142*	SIU	Ecuador	-	x	x	x	x	x
mic B2	*Villa 2145*	SIU	Ecuador	-	x	x	x	-	-
mic B2	*Villa 2033*	SIU	Ecuador	-	x	x	x	-	-
mic B2	*Villa 2064*	SIU	Ecuador	-	x	x	x	-	-
mic B2	*Villa 2102*	SIU	Ecuador	-	x	x	x	-	-
mic B2	*Villa 2143*	SIU	Ecuador	-		x	-	-	-
mic B2	*Villa 2148*	SIU	Ecuador	-	x	x	-	-	-
mic B2	*Villa 2149*	SIU	Ecuador	-	x	x	-	-	-
mic B2	*Villa 2028*	SIU	Ecuador	-	x	x	-	-	-

Table 1. Continued.

Clade	*Accession Name*	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
mic B2	*Villa 2034*	SIU	Ecuador	-	x	x	-	-	-
mic B2	*Croat 102471*	MO	French Guiana	x	x	x	x	-	-
mic B2	*McKey 01*	SIU	French Guiana	-	x	x	x	x	x
mic B2	*Popenoe 49*	FLAS	Guatemala	x	x	x	x	x	x
mic B2	*Jansen-Jacobs 658*	MO	Guyana	x	x	x	x	-	-
mic B2	*Boom 7324*	MO	Guyana	x	x	x	-	-	-
mic B2	*Henkel 2579*	MO	Guyana	-	x	x	-	-	-
mic B2	*McDowell 4352*	MO	Guyana	-	x	x	-	-	-
mic B2	*Proctor 32504*	BM	Honduras	x	x	x	-	-	-
mic B2	*Yuncker 8354*	BM	Honduras	-	x	x	-	-	-
mic B2	*Nee 25106*	BM	Mexico	x	x	x	-	-	-
mic B2	*Dressler 236*	MO	Mexico	x	x	x	-	-	-
mic B2	*Aguilar 11565*	MO	Mexico	-	x	x	-	-	-
mic B2	*Calzada 18950*	MO	Mexico	-	x	x	-	-	-
mic B2	*López 89-10-2*	MO	Mexico	-	x	x	-	-	-
mic B2	*Márquez 283*	MO	Mexico	-	x	x	-	-	-
mic B2	*Martínez 13791*	MO	Mexico	-	x	x	-	-	-
mic B2	*Martínez 7192*	MO	Mexico	-	x	x	-	-	-
mic B2	*Rzedowski 37422*	MO	Mexico	-	x	x	-	-	-
mic B2	*Soto 7133*	MO	Mexico	-	x	x	-	-	-
mic B2	*Buck 34377*	NY	Navassa Island	-	x	x	-	-	-
mic B2	*Hall 7794*	BM	Nicaragua	-	x	x	x	-	-
mic B2	*Stevens 30384*	MO	Nicaragua	-	x	x	x	x	x
mic B2	*Grijalva 2904*	MO	Nicaragua	-	x	x	-	-	-
mic B2	*Guadamuz 948*	MO	Nicaragua	-	x	x	-	-	-
mic B2	*Velázquez 65*	MO	Nicaragua	-	x	x	-	-	-
mic B2	*D'Arcy 12257*	BM	Panama	-	x	x	x	-	-
mic B2	*Garwood 1508*	BM	Panama	-	x	x	x	-	-
mic B2	*Dalling 09*	SIU	Panama	x	x	x	x	-	x
mic B2	*Dalling 08*	SIU	Panama	x	x	x	x	-	-
mic B2	*Dalling 72*	SIU	Panama	x	x	x	x	-	-
mic B2	*Dalling 83*	SIU	Panama	x	x	x	x	-	-
mic B2	*Dalling 05*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 48*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 60*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 66*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 67*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 68*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 69*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 70*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 71*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 76*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 77*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 80*	SIU	Panama	x	x	x	-	-	-
mic B2	*Dalling 38*	SIU	Panama	-	-	x	-	-	-
mic B2	*Dalling A1*	SIU	Panama	-	x	x	-	-	-
mic B2	*Dalling A2*	SIU	Panama	-	x	x	-	-	-
mic B2	*Benítez 579*	MO	Paraguay	x	x	x	x	-	x
mic B2	*Hahn 2307*	MO	Paraguay	x	x	x	x	-	-

Table 1. Continued.

Clade	*Accession Name*	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
mic B2	*Ortiz 1033*	MO	Paraguay	-	x	x	-	-	-
mic B2	*Stevens 31307*	MO	Paraguay	-	x	x	-	-	-
mic B2	*Stutz de Ortega 1887*	MO	Paraguay	-	x	x	-	-	-
mic B2	*Zardini 11061*	MO	Paraguay	-	x	x	-	-	-
mic B2	*Calatayud 4147*	MO	Peru	-	x	x	-	-	-
mic B2	*Campos de la Cruz 2643*	MO	Peru	-	x	x	-	-	-
mic B2	*Valenzuela 1905*	MO	Peru	-	x	x	-	-	-
mic B2	*Valenzuela 1927*	MO	Peru	-	x	x	-	-	-
mic B2	*Stimson 3009*	FLAS	Puerto Rico	x	x	x	-	-	-
mic B2	*Taylor 10129*	MO	Puerto Rico	x	x	x	x	-	-
mic B2	*Sustache s.n.*	SIU	Puerto Rico	x	x	x	x	x	x
mic B2	*Rifkin 1*	SIU	Puerto Rico	-	x	x	x	-	-
mic B2	*Rifkin 2*	SIU	Puerto Rico	-	x	x	x	-	-
mic B2	*Axelrod 14441*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Axelrod 7259*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Axelrod 8553*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Axelrod 9951*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Breckon 5922*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Cedeño-Maldonado 118*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Taylor 10097*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Trejo-Torres 1439*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Axelrod 12381*	UPRRP	Puerto Rico	-	x	x	-	-	-
mic B2	*Breckon 8040*	UPRRP	Puerto Rico	-	x	x	-	-	-
mic B2	*Miller 5950*	UPRRP	Puerto Rico	-	x	x	x	-	-
mic B2	*Croat 102457*	MO	Suriname	x	x	x	x	-	-
mic B2	*Bodle s.n.*	FLAS	US	x	x	x	x	-	-
mic B2	*Stuart s.n.*	FLAS	US	-	x	x	x	x	x
mic B2	*Pattison s.n.*	FLAS	US	-	x	x	x	-	-
mic B2	*Bradley s.n*	SIU	US	-	x	x	x	-	-
mic B2	*Mori 17017*	BM	USVI	x	x	x	x	-	-
mic B2	*Acevedo-Rodriguez 619*	NY	USVI	x	x	x	x	-	-
mic B2	*Díaz 493*	MO	Venezuela	x	x	x	-	-	-
mic B2	*Boom 6316*	MO	Venezuela	-	x	x	-	-	-
mic B2	*Gonto 01153*	MO	Venezuela	-	x	x	-	-	-
mic B2	*Gonto 595*	MO	Venezuela	-	x	x	-	-	-
mic B2	*Liesner 7352*	MO	Venezuela	-	x	x	-	-	-
mic B2	*Steyermark 107831*	MO	Venezuela	-	x	x	-	-	-
mic B2	*Zanoni 37078*	NY	DR	x	x	x	x	x	x
mic B3	*Khan 538*	BM	Costa Rica	-	x	x	x	x	x
mic B3	*Khan 447*	BM	Costa Rica	-	x	x	-	-	-
mic B3	*Alford 3021*	MO	Costa Rica	x	x	x	x	x	x
mic B3	*Fernández 1367*	MO	Costa Rica	x	x	x	-	-	-
mic B3	*Gómez 19706*	MO	Costa Rica	x	x	x	-	-	-
mic B3	*Rojas 90*	MO	Costa Rica	x	x	x	-	-	-
mic B3	*Vargas 353*	MO	Costa Rica	x	x	x	-	-	-
mic B3	*Wilbur 18248*	MO	Costa Rica	x	x	x	-	-	-
mic B3	*Kriebel 73*	MO	Costa Rica	-	x	-	-	-	-
mic B3	*Hamilton 960*	BM	Panama	-	x	-	-	-	-
mic B3	*Dalling 58*	SIU	Panama	x	x	x	x	x	x

Table 1. Continued.

Clade	*Accession Name*	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
mic B3	*Dalling 47*	SIU	Panama	x	x	x	-	-	-
mic B3	*Dalling 56*	SIU	Panama	x	x	x	-	-	-
mic B3	*Dalling 57*	SIU	Panama	x	x	x	-	-	-
mic B3	*Dalling 62*	SIU	Panama	x	x	x	-	-	-
mic B3	*Dalling 64*	SIU	Panama	x	x	x	-	-	-
mic B3	*Dalling 45*	SIU	Panama	-	x	x	x	x	-
mic B3	*Dalling 41*	SIU	Panama	x	x	x	-	-	-
mic B3	*Dalling 44*	SIU	Panama	x	x	x	-	-	-
mic B3	*Dalling 40*	SIU	Panama	-	x	-	-	-	-
mic B3	*Dalling 43*	SIU	Panama	-	x	-	-	-	-
mic B3	*Dalling 50*	SIU	Panama	-	x	-	-	-	-
mic B3	*Dalling 53*	SIU	Panama	-	x	-	-	-	-
mic B3	*Dalling 63*	SIU	Panama	-	x	-	-	-	-
mic B4	*Venturi 7580*	BM	Argentina	x	x	x	x	x	x
mic B4	*Conrad 2636*	MO	Argentina	-	x	x	x	-	-
mic B4	*Morrone 4128*	MO	Argentina	x	x	x	-	-	-
mic B4	*Nee 47985*	MO	Bolivia	x	x	x	x	x	x
mic B4	*Nee 53226*	MO	Bolivia	x	x	x	x	x	x
mic B4	*Nee 44561*	MO	Bolivia	x	x	x	-	-	-
mic B4	*Nee 54145*	MO	Bolivia	x	x	x	-	-	-
mic B4	*Serrano 7072c*	MO	Bolivia	x	x	x	-	-	-
mic B5	*Hinton 439*	BM	Mexico	-	-	x	-	-	-
mic B5	*Hinton 7833*	BM	Mexico	-	-	x	-	-	-
mic B5	*Cornejo 3705*	MO	Mexico	x	x	x	-	-	-
mic B5	*Flores 1882*	MO	Mexico	x	x	x	-	-	-
mic B5	*Miller 2947*	MO	Mexico	x	x	x	-	-	-
mic B5	*Miller 3097*	MO	Mexico	x	x	x	-	-	-
mic B5	*Eggler 133*	MO	Mexico	-	x	x	-	-	-
mic B5	*Tenorio 16194*	MO	Mexico	-	x	x	-	-	-
mic C	*Nee 51812*	BM	Bolivia	-	-	-	x	x	x
mic C	*Liogier 15415*	NY	DR	-	-	-	x	x	x
mic C	*Basilio Augusto 1522*	NY	DR	-	-	-	x	-	-
mic C	*Zanoni 25833*	NY	DR	-	-	-	x	-	-
mic C	*Zanoni 25862*	NY	DR	-	-	-	x	-	-
mic C	*Zanoni 26547*	NY	DR	-	-	-	x	-	-
mic C	*Palacios 2177*	MO	Ecuador	-	-	-	x	x	x
mic C	*Villa 2141*	SIU	Ecuador	-	-	-	x	x	x
mic C	*Villa 2128*	SIU	Ecuador	-	-	-	x	-	-
mic C	*Villa 2129*	SIU	Ecuador	-	-	-	x	-	-
mic C	*Villa 2134*	SIU	Ecuador	-	-	-	x	-	-
mic C	*Judd 4047*	FLAS	Haiti	-	-	-	x	x	x
mic C	*Adams 11328*	BM	Jamaica	-	-	-	x	-	-
mic C	*Ammann 427*	UCWI	Jamaica	-	-	-	x	-	-
mic C	*Adams 11328*	UCWI	Jamaica	-	-	-	x	-	-
mic C	*Perea 2530*	MO	Peru	-	-	-	-	x	-
mic C	*Vincent 15484*	UPRRP	Puerto Rico	-	-	-	x	x	x
mic D	*Huamantupa 7725*	MO	Peru	-	-	-	x	x	x
mic D	*Galiano 5749*	MO	Peru	-	-	-	x	-	-
mic D	*Galiano 4462*	MO	Peru	-	-	-	-	x	x

Table 1. Continued.

Clade	*Accession Name*	Institution	Country	Morph	ENM	ETS	5-gene	NRC	CPG
nitens	*St-Laurent 97-53*	DAO	Togo	-	-	-	x	x	x
nitida	*Xu 1995435*	MO	China	-	-	-	-	x	x
orientalis	*McKey 02*	SIU	Cameroon	-	-	-	-	x	x
orientalis	*Martin 5034*	BM	Indonesia	-	-	-	x	-	-
orientalis	*Armstrong 1067*	NY	Myanmar	-	-	x	-	x	x
orientalis	*Maxwell 10*	SIU	Thailand	-	-	-	x	x	x
orientalis	*St-Laurent 96-16*	DAO	Togo	-	-	x	x	-	-
orientalis	*St-Laurent 97-11*	DAO	Togo	-	-	-	x	x	x
P andersonii	*McKee 2849*	E	Fiji	-	-	-	x	-	-
P rigida	*Brass 13072*	BM	Indonesia	-	-	-	x	x	x
P rigida	*HentyLAE 72464*	E	PNG	-	-	-	x	-	-
P rigida	*HentyNGF 14332*	E	PNG	-	-	-	x	-	-
P rigida	*HentyNGF 49896*	E	PNG	-	-	-	x	-	-
politoria	*Grierson 2400*	E	Bhutan	-	-	-	x	x	x
politoria	*Grierson 4661*	E	Bhutan	-	-	-	-	-	-
politoria	*Kerr 2237*	BM	India	-	-	-	x	-	-
tomentosa	*Rahman 2554*	BM	Bangladesh	-	-	-	x	-	-
tomentosa	*Stainton 5381*	BM	India	-	-	-	x	-	-

Table 2. Primers used in this study for Sanger sequencing.

Locus/Primer	Primer Sequence	Reference
ITS		
ITS A	CGAGAAGTCCACTGAACCTTATC	Abbott (2009)
ITS B	TCTTYTCCTCCGCTTATTGATATGC	Abbott (2009)
ITS C	GCGTTCAAAGACTCGATGGTTC	Abbott (2009)
ITS D	GACTCTCGGCAACGGATATCTCGGC	Abbott (2009)
ETS		
ETS F	CGTTCGGTTTCCTGTGTTGG	Garwood et al. (2018)
ETS R	TACTGGCAGGATCAACCAGG	Garwood et al. (2018)
trnL-F		
C	CGA AAT CGG TAG ACG CTA CG	Taberlet et al. (1991)
D	GGG GAT AGA GGG ACT TGA AC	Taberlet et al. (1991)
E	GGT TCA AGT CCC TCT ATC CC	Taberlet et al. (1991)
F	ATT TGA ACT GGT GAC ACG AG	Taberlet et al. (1991)
trnH-psbA		
F	TGATCCACTTGGCTACATCCGCC	Xu et al. (2000)
R	GCTAACCTTGGTATGGAAGT	Xu et al. (2000)
rbcL		
rbcL Z1	ATGTCACCACAAACAGAAACTAAAGCAAGT	Clayton et al. (2007)

Table 2. Continued.

Locus/Primer	Primer Sequence	Reference
rbcL 3'	CTCGGAGCTCCTTTTAGTAAAAGATTGGGCCGA	Clayton et al. (2007)
rbcLaF	ATGTCACCACAAACAGAGACTAAAGC	Kress et al. (2012)
rbcLaR	GTAAAATCAAGTCCACCRCG	Kress et al. (2012)

Table 3. Hybrid accessions identified in the ETS dataset.

Accession	Hybrid Status	Country	Confidence
Aguilar 6397	B1 x B2	Mexico	high
Cabrera 89	B1 x B2	Mexico	high
Cabrera 255	B1 x B2	Mexico	high
Cowan 2008	B1 x B2	Mexico	high
Garwood B08	B1 x B2	Belize	high
Garwood B25	B1 x B2	Belize	high
Garwood B27	B1 x B2	Belize	high
Garwood B29	B1 x B2	Belize	high
LopezGomez 53	B1 x B2	Mexico	high
LopezGomez 64	B1 x B2	Mexico	high
MartinezCalderon 144	B1 x B2	Mexico	high
Nee 24870	B1 x B2	Nicaragua	high
Nee 46830	B1 x B2	Belize	high
Proctor 29471	B1 x B2	Belize	high
Ventura 15981	B1 x B2	Mexico	high
Ventura 17037	B1 x B2	Mexico	high
AlvaradoCardenas 227	B1a x B1b	Mexico	low
Argenal 156	B1a x B1b	Honduras	low
Breedlove 24636	B1a x B1b	Mexico	moderate
Calonico 22514	B1a x B1b	Mexico	high
Cortes 75	B1a x B1b	Mexico	high
D'Arcy 12069	B1a x B1b	Mexico	high
Dorantes 1241	B1a x B1b	Mexico	high
Garwood B01	B1a x B1b	Belize	high
Garwood B03	B1a x B1b	Belize	moderate
Garwood B04	B1a x B1b	Belize	moderate
Garwood B07	B1a x B1b	Belize	high
Garwood B09	B1a x B1b	Belize	high

Table 3. Continued.

Accession	Hybrid Status	Country	Confidence
Garwood B10	B1a x B1b	Belize	moderate
Garwood B11	B1a x B1b	Belize	high
Garwood B12	B1a x B1b	Belize	high
Garwood B13	B1a x B1b	Belize	moderate
Garwood B14	B1a x B1b	Belize	high
Garwood B15	B1a x B1b	Belize	high
Garwood B16	B1a x B1b	Belize	moderate
Garwood B18	B1a x B1b	Belize	moderate
Garwood B19	B1a x B1b	Belize	high
Garwood B21	B1a x B1b	Belize	high
Garwood B22a	B1a x B1b	Belize	high
Garwood B23	B1a x B1b	Belize	high
Garwood B24a	B1a x B1b	Belize	high
Garwood B26	B1a x B1b	Belize	high
Garwood B28	B1a x B1b	Belize	high
Garwood B40	B1a x B1b	Belize	moderate
Gereau 2232	B1a x B1b	Mexico	high
Harriman 14400	B1a x B1b	Mexico	low
Hernandez 436	B1a x B1b	Mexico	high
HernandezLopez 70a	B1a x B1b	Mexico	moderate
Hernandez Magana 5697	B1a x B1b	Mexico	high
Hughes 427	unknown	Guatemala	low
LopezGarcia 0013	B1a x B1b	Mexico	high
Mark 6425	B1a x B1b	Nicaragua	low
Martinez 611	B1a x B1b	Mexico	low
Martinez 801	B1a x B1b	Mexico	moderate
Monro 2062	B1a x B1b	El Salvador	low
Monro 3605	B1a x B1b	El Salvador	moderate
Nee 22975	B1a x B1b	Mexico	low
Perez-Farrera 2692	unknown	Mexico	low
Provance 3305	B1a x B1b	Mexico	high
ReyesGarcia 755	B1a x B1b	Mexico	low
ReyesGarcia 1537	B1a x B1b	Mexico	low
ReyesGarcia 6113	B1a x B1b	Mexico	low

Table 3. Continued.

Accession	Hybrid Status	Country	Confidence
Salinas 8180	B1a x B1b	Mexico	moderate
Snedaker D62	B1a x B1b	Guatemala	moderate
Stevens 39422	B1a x B1b	Nicaragua	moderate
Tenerio 11130	B1a x B1b	Mexico	high
Torres 1357	unknown	Mexico	low
Ventura 4607	B1a x B1b	Mexico	low
Dalling 42	B1a x B3	Panama	low
Romero 3120	B1b x B5	Mexico	low
Rudas 1672	unknown	Mexico	low
Chavarria 1464	B3 x B5	Costa Rica	low
Dalling 59	B2 x B3	Panama	low

Table 4. Results from the Principal Component Analysis of leaf shape characters.

Character	Variable	PC1 eigenvectors	PC2 eigenvectors
Petiole Length (mm)	PL	-0.03968	0.16473
Blade Length (mm)	BL	-0.91123	-0.01054
Blade Width (mm)	BW	-0.279857	0.54387
Distance from Base to Widest Point (mm)	BD	-0.20808	0.11135
Basal Indentation (mm)	BI	-0.01158	0.03392
Teeth Density (teeth/cm)	TD	0.03222	-0.01691
Apex Length (mm)	AL	-0.20021	-0.77268
Apex Width (mm)	AW	-0.07219	-0.25705

Table 5. Correlations values for the 19 bioclimatic variables. Only two decimals are shown, with values $r \geq 0.80$ are highlighted in red.

Layer	bio1	bio12	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio1	1.00	0.47	-0.59	0.43	-0.55	0.72	0.92	-0.58	0.83	0.85	0.83	0.94	0.53	0.14	-0.06	0.53	0.15	0.18	0.34
bio12	0.47	1.00	-0.75	0.52	-0.59	0.01	0.63	-0.68	0.25	0.49	0.17	0.58	0.92	0.71	-0.38	0.92	0.73	0.63	0.74
bio2	-0.59	-0.75	1.00	-0.53	0.73	0.01	-0.80	0.87	-0.33	-0.58	-0.23	-0.73	-0.72	-0.47	0.31	-0.72	-0.48	-0.41	-0.58
bio3	0.43	0.52	-0.53	1.00	-0.89	-0.17	0.68	-0.83	0.20	0.45	-0.08	0.68	0.59	0.20	0.21	0.59	0.21	0.26	0.39
bio4	-0.55	-0.59	0.73	-0.89	1.00	0.15	-0.81	0.97	-0.27	-0.54	0.01	-0.80	-0.69	-0.18	-0.18	-0.69	-0.19	-0.28	-0.41
bio5	0.72	0.01	0.01	-0.17	0.15	1.00	0.41	0.13	0.73	0.58	0.96	0.45	0.05	-0.11	-0.08	0.05	-0.11	-0.16	0.06
bio6	0.92	0.63	-0.80	0.68	-0.81	0.41	1.00	-0.85	0.66	0.84	0.56	0.99	0.70	0.23	-0.04	0.70	0.24	0.25	0.49
bio7	-0.58	-0.68	0.87	-0.83	0.97	0.13	-0.85	1.00	-0.30	-0.58	-0.06	-0.82	-0.73	-0.31	-0.01	-0.73	-0.33	-0.36	-0.50
bio8	0.83	0.25	-0.33	0.20	-0.27	0.73	0.66	-0.30	1.00	0.54	0.80	0.69	0.30	0.04	-0.05	0.30	0.05	0.18	0.11

Table 5. Continued.

Layer	bio1	bio12	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio9	0.85	0.49	-0.58	0.45	-0.54	0.58	0.84	-0.58	0.54	1.00	0.67	0.84	0.54	0.18	-0.04	0.54	0.19	0.08	0.45
bio10	0.83	0.17	-0.23	-0.08	0.01	0.96	0.56	-0.06	0.80	0.67	1.00	0.59	0.19	0.04	-0.19	0.19	0.04	0.00	0.16
bio11	0.94	0.58	-0.73	0.68	-0.80	0.45	0.99	-0.82	0.69	0.84	0.59	1.00	0.67	0.17	0.03	0.67	0.18	0.23	0.43
bio13	0.53	0.92	-0.72	0.59	-0.69	0.05	0.70	-0.73	0.30	0.54	0.19	0.67	1.00	0.45	-0.11	1.00	0.46	0.48	0.72
bio14	0.14	0.71	-0.47	0.20	-0.18	-0.11	0.23	-0.31	0.04	0.18	0.04	0.17	0.45	1.00	-0.64	0.45	1.00	0.66	0.48
bio15	-0.06	-0.38	0.31	0.21	-0.18	-0.08	-0.04	-0.01	-0.05	-0.04	-0.19	0.03	-0.11	-0.64	1.00	-0.11	-0.65	-0.38	-0.23
bio16	0.53	0.92	-0.72	0.59	-0.69	0.05	0.70	-0.73	0.30	0.54	0.19	0.67	1.00	0.45	-0.11	1.00	0.46	0.48	0.72
bio17	0.15	0.73	-0.48	0.21	-0.19	-0.11	0.24	-0.33	0.05	0.19	0.04	0.18	0.46	1.00	-0.65	0.46	1.00	0.67	0.49
bio18	0.18	0.63	-0.41	0.26	-0.28	-0.16	0.25	-0.36	0.18	0.08	0.00	0.23	0.48	0.66	-0.38	0.48	0.67	1.00	0.14
bio19	0.34	0.74	-0.58	0.39	-0.41	0.06	0.49	-0.50	0.11	0.45	0.16	0.43	0.72	0.48	-0.23	0.72	0.49	0.14	1.00

Table 6. Ecological Niche Modeling results.

Group	Sample size, post-rarification	Regularization Multipliers	Feature Classes	AUC	OER
B1a	36	0.5	Linear	0.936	0.139
B1b	21	5	Linear	0.911	0.15
B2	132	3	Hinge	0.895	0.174
B3	12	1.5	Hinge + Product + Linear + Quadratic	0.994	0.023
B4	8	1	Hinge	0.977	0.123
B5	6	4	Linear + Quadratic	0.982	0.037

Table 7. Variable contributions for ENMs of each clade.

Group	Variable full name (abbreviation)	% contribution
B1a	temperature seasonality (bio4)	21.7
	pH index measure in water solution (phihox)	17.3
	mean monthly precipitation amount of the coldest quarter (bio19)	13.3
	annual precipitation amount (bio12)	10.5
	isothermality (bio3)	10.3
	Total Variable Contribution:	**73.1**
B1b	temperature seasonality (bio4)	53
	absolute depth to bedrock (bdticm)	33.1
	mean diurnal air temperature range (bio2)	12.5
	Total Variable Contribution:	**98.6**
B2	mean diurnal air temperature range (bio2)	27.5

Table 7. Continued.

Group	Variable full name (abbreviation)	% contribution
	soil organic carbon content (orcdrc)	22.8
	temperature seasonality (bio4)	14.9
	pH index measure in water solution (phihox)	13.1
	Total Variable Contribution:	**78.3**
B3	mean monthly precipitation amount of the coldest quarter (bio19)	43.1
	isothermality (bio3)	15.6
	mean annual air temperature (bio1)	10.7
	Total Variable Contribution:	**69.4**
B4	mean monthly precipitation amount of the warmest quarter (bio18)	42.4
	precipitation seasonality (bio15)	23.4
	volumetric percentage of coarse fragments (crfvol)	20.5
	temperature seasonality (bio4)	10.7
	Total Variable Contribution:	**97**
B5	precipitation seasonality (bio15)	50.6
	pH index measure in water solution (phihox)	19.9
	temperature seasonality (bio4)	19.3
	Total Variable Contribution:	**89.8**

REFERENCES

Abbott, J.R. 2009. Phylogeny of Polygalaceae and a revision of *Badiera*. PhD dissertation. University of Florida, Gainesville, Florida.

Acevedo-Rodriguez, P. and Strong, M.T. 2012. *Catalogue of seed plants of the West Indies*. Smithsonian Institution, Washington, D.C.

Adams, C.D. 1972. *Flowering Plants of Jamaica*. University of the West Indies, Jamaica.

Alvarado-Serrano, D.F. and Knowles, L. L. 2014. Ecological niche models in phylogeographic studies: applications, advances and precautions. *Molecular Ecology Resources* **14**: 233-248.

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A. et al. 2021. SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology* **19**(5): 455-477. doi: https://doi.org/10.1089/cmb.2012.0021

Berg, C.C. 1992. *Trema* In: Gorts-Van Rijn, A.R.A. *Flora of the Guianas*, *Series A, Phanerogams, Fascile* **11**: 6-9. Koeltz Scientific Books, Koenigstein, FRG.

Bolger, A.M., Lohse, M., and Usadel, B. 2014. Trimmomatic: A flexible trimmer for Illumina Sequence Data. *Bioinformatics* **30**(15): 2114-2120. doi: 10.1093/bioinformatics/btu170

Britton, N.L. 1908. *North American tress being descriptions and illustrations of the tree growing independently of cultivation in North America, North of Mexico, and the West Indies.* Henry Holt and Company, New York.

Brown, J. 2014. SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution* **5**(7): 694-700. doi:10.1111/2041-210X.12200.

Brown, J.L., Bennet, J.R., and French, C.M. 2017. SDMToolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ* **5**:e4095. doi: 10.7717/peerj.4095.

Browne, P. (1756) *The Civil and Natural History of Jamaica in Three Parts.* P. Browne, London. http://dx.doi.org/10.5962/bhl.title.10826

Burger, W. 1977. Flora Costaricensis. *Fieldiana: Botany 40.* Field Museum of Natural History, Chicago, IL.

Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K., and Madden, T.L. 2009. BLAST+: architecture and applications. *BMC Bioinformatics* **10**. doi: https://doi.org/10.1186/1471-2105-10-421.

Cascales, J., Bracco, M., Garberoglio, M.J., Poggio, L., and Gottlieb, A.M. 2017. Integral phylogenomic approach over *Illex* L. species from southern South America. *Life* **7**: 1-18.

Chase, M.W., Christenhusz, M.J.M., Faye, M.F, et al. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181**: 1-20.

Clayton, J.W., Fernando, E.S., Soltis, P.S., and Soltis, D.E. 2007. Molecular phylogeny of the tree-of-heaven family (Simaroubaceae) based on chloroplast and nuclear markers. *International Journal of Plant Sciences* **168**(9): 1325-1339.

Doyle, J. and Doyle, J. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* **19**: 11-15.

Edgar, R. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**(5): 1792-1797. doi: 10.1093/nar/gkh340.

Elith, J. and Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**: 677-697.

ESRI, A.D. 2011. ArcMap release 10 documentation manual. Environmental Systems Research Institute, Redlands, California.

Garica-Orth, X. and Martinez-Ramos, M. 2011. Isolated trees and grass removal improve performance of transplanted *Trema micrantha* (L.) Blume (Ulmaceae) saplings in tropical pastures. *Restoration Ecology* **19**(1): 24-34.

Garwood, N.C., Jordan, K., Humphreys, A.M., Russel, S.J., and Neubig, K.M. 2018. *Trema domingensis* rises like a phoenix from the ashes of *Trema integerrima*: A reassessment of the entire-leaved species of neotropical *Trema* (Cannabaceae). *Journal of Botanical Research Institute of Texas* **12***(2)*: 555-577.

Grant, V. 1992. Comments on the ecological species concept. *Taxon* **41**(2): 310-312.

He, J., Yao, M., Lyu, R.D., Lin, L., Liu, H., Pei, L., Yan, S., Xie, L., and Cheng, J. 2019. Structural variation of the complete chloroplast genome and plastid phylogenomics of the genus *Asteropyrum* (Ranunculaceae). *Scientific Reports* **9** (15285).

Hengl, T, de Jesus, JM, MacMillan, RA, Batjes, NH, Heuvelink, GBM, et al. (2014) SoilGrids1km - Global Soil Information Based on Automated Mapping. PLoS ONE **9**(8): e105992.

Jin, J., Yu, W., Yang, J., Song, Y., dePamphilis, C.W., Yi, T., and Li, D. 2020. GetOrganelle: a fast and versatile toolkit for accurate de novo assembly of organelle genomes. *Genome Biology* **21**(241). https://doi.org/10.1186/s13059-020-02154-5

Johnston, I.M. 1949. The botany of San Jose Island (Gulf of Panama). *Sargentia.* The Arnold Arboretum of Harvard University. Jamaica Plain, Massachusetts.

Kabir, M., AL-Noman, A., Kumar, D. B., Hasan, M., Akhter, S., and Rahman, M. 2019. *Trema orientalis* (Linn.) leaves promote anticancer activity in Ehrlich ascites carcinoma (EAC) in Swiss albino mice. *Journal of Basic and Clinical Physiology and Pharmacology*. 10.1515/jbcpp-2019-0121

Kalyaanamoorthy, S., Minh, B. Q., Wong, T., von Haeseler, A., and Jermiin, L.S. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**: 587–589.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P., Kessler, M. 2017. Climatologies at high resolution for the Earth land surface areas. *Scientific Data*. **4**(170122). https://doi.org/10.1038/sdata.2017.122

Katoh, S. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772-780.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P., and Drummond, A. 2012. Geneious Basic: an integrated and extendable desktop software platform for organization and analysis of sequence data. *Bioinformatics* **28**: 1647-1649.

Kim, K., Lee, S., Lee, J., et al. 2015. Complete chloroplast and ribosomal sequences of 30 accessions elucidate evolution of *Oryza* AA genome species. *Scientific Reports* **5** (15655).

Kress, W.J., Lopez, I.C., and Erickson, D.L. 2012. Generating plant DNA barcodes for trees in long-term forest dynamic plots. In: Kress, W.J. and Erickson D.L. DNA barcodes: Methods and protocols. *Methods in Molecular Biology* **858**: 441-458.

Langmead, B. and Salzberg, S.L. 2012. Fast gapped-read alignment with Bowtie2. *Nature Methods* **9**: 357-359.

Legaard, S. and Balslev, H. 2014. *Trema.* In: Persson, C. and Stahl, B. *Flora of Ecuador* **91**: 66-71. University of Gothenburg, Sweden.

Li, X, Xu, J., He, Y., Shen, S., Zhu, J., and Shen, Z. 2016. The complete nuclear ribosomal DNA (nrDNA) cistron sequence of *Pyropia yezoensis* (Bangiales, Rhodophyta). *Journal of Applied Phycology* **28**: 663-669.

Lundell, C.L. 1939. New or otherwise noteworthy plants from Mexico and Central America. *Phytologia* **1**: *337-340.*

MacBride, J.F. 1937. *Flora of Peru* **8**(2), no. 2. Field Museum of Natural History, Chicago, IL.

Machado, A.F.P, Oliveira da Silva, M.F., de Oliveira, R.P., Giulietti, A.M, and Torres, D.S.C. 2019. Flora de Bahia: Cannabaceae. *Sitientibus series Biological Sciences*. DOI: 10.13102/scb3781

Marshall, C.J. and Liebherr J.K. 2000. Cladistic biogeography of the Mexican transition zone. *Journal of Biogeography* **27**: 203-216.

Mayr, E. 1992. A local flora and the biological species concept. *American Journal of Botany* **79**(2): 222-238.

Melo, M.M.R.F, Ussui-Fukugauti, S.Y. 1984. Flora Fanerogamica da Reserva do parque estadual das fontes do ipiranga, Ulmaceae (Sao Paulo, Brazil). *Hoehea* **11**: 68-69.

Morrone, J.J. 2010. Fundamental biogeographic patterns across the Mexican Transition Zone: an evolutionary approach. *Ecography* **33**: 355-361.

Nasir Uddin, S., Akond, M.A., Mubassara, S., and Nazma, Y. M. 2008. Antioxidant and antibacterial activities of *Trema cannabina*. *Middle-East Journal of Scientific Research* **3**(2): 105-108.

Nauheimer, L., Cui, L., Clarke, C., Crayn, D.N., Bourke, G., and Nargar, K. 2019. Genome skimming provides well resolved plastid and nuclear phylogenies, showing patterns of deep reticulate evolution in the tropical carnivorous plant genus *Nepenthes* (Caryophyllales). *Australian Systematic Botany* **32**: 243-254.

Nee, M. 2015. *Trema.* In: Davidse, G., Sousa Sanchez, M., Knapp S., and Chiang Cabrera, F. *Flora Mesoamericana* **2**(3): 176-177. Missouri Botanical Garden, St. Louis, Missouri.

Neubig, K., Whitten, W.M., Abbott, J., Elliot, S., Soltis, D., and Soltis, P. 2014. Variables affecting DNA preservation in archival plant specimens. In: Applequist, W. and Campbell, L. *DNA banking for the 21st century: Proceedings of the U.S. Workshop on DNA Banking*. Missouri Botanical Garden, St. Louis, Missouri.

Nevling, L.I. 1960. Flora of Panama. Part IV. Fascicle II. *Annals of the Missouri Botanical Garden* **47***(2)*. Missouri Botanical Garden, St. Louis, Missouri.

Nguyen, L.T., Schmidt, H.A, von Haeseler, A., and Quang Minh B.Q. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution* **32**: 268-274.

O'Donnell, M.S. and Ignizio, D.A. 2012. Bioclimatic predictors for supporting ecological applications in the coterminous United States. U.S. Geological Survey Data Series 691.

Osman, K. 2013. Forest types and their associated soils. In: *Forest Soils*. Springer International Publishing, Switzerland.

Oyebola, O.E., Morenikeji, O.A., and Ademola, I.O. 2017. In-vivo antimalarial activity of aqueous leaf and bark extracts of *T. orientalis* against *Plasmodium berghei* in mice. *Journal of Parasitic Diseases* **41***(2)*: 398-404.

Perry, L.B., Seimon, A. Andrade-Flores, M.F., et al. 2016. Characteristics of precipitating storms in glacierized tropical Andean Cordilleras of Peru and Bolivia. *Annals of the American Association of Geography* **107**(2): 309-322.

Peters, C. M., Rosenthal, J., and Urbina, T. 1987. Otomi Bark Paper in Mexico: Commercialization of a Pre-Hispanic Technology. *Economic Botany* **41**(3): 423-432.

Philcox, D. 1982. *Ulmaceae.* In: *Flora of Trinidad and Tobago* **2**(6). Ministry of Agriculture, Lands and Food Production, Trinidad and Tobago.

Phillips, S.J., Anderson, R.P., and Schapire, R.E. 2006. Maximum Entropy, modeling of species geographic distributions. *Ecological Modelling* **190**: 231-259.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rambaut, A. 2007. FigTree, a graphical viewer of phylogenetic trees.

Rasband, WS, (1997-2016). ImageJ 1.49v. U.S. National Institutes of Health, Bethesda, Maryland, U.S.A.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539-542.

Rosauer, D. F., Catullo, R. A., VanDerWal, J., Moussalli, A., and Moritz, C. 2015. Lineage range estimation method reveals fine-scale endemism linked to Pleistocene stability in Australian rainforest herpetofauna. *PLoS ONE* **10**(5): e0126274. doi:10.1371/journal.pone.0126274.

Santiago-Alvarado, M., Montano-Arias, G., and Espinosa, D. 2016. Areas de endemismo de la Sierra Madre del Sur. In: Luna-Vega, I., Espinosa, D., Contreras-Medina, R. *Biodiversidad de la Sierra del Sur.* Ciudad de Mexico, Universidad Nacional Autonoma de Mexico.

Sargent, C.S. 1922. *Manual of the trees of North America (exclusive of Mexico)*. Houghton Mifflin Company, The Riverside Press Cambridge, New York.

Sauget J.S. & Liogier E.E. 1951. Flora de Cuba Vol. II. *Contribuciones ocasionales del Museo De Historia Natural Del Colegio De La Salle* **10**: 41-42.

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

Small, J.K. 1903. *Flora of Southeastern United States: Being descriptions of the seed plants, ferns, and fern-allies growing naturally in North Carolina, South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, Louisiana, and the Indian Territory, and in Oklahoma, and Texas East of the One-Hundredth Meridian.* 1st edition. J.K. Small, New York.

St. Laurent, L., Baum, B.R., Akpagana, K., and Arnason, J.T. 2000. A numerical taxonomic study of *Trema* (Ulmaceae) from Togo, West Africa. *Systematic Botany* **25***(3)*: 399-413.

Standley, P.C. and Steyermark, J.A. 1946. Flora of Guatemala. *Fieldiana: Botany* **24**(4). Chicago Natural History Museum, Chicago, IL.

Stevens, W.D., Ulloa, C.U., Pool, A., and Montiel, O.M. 2001. *Flora De Nicaragua*. Missouri Botanical Garden Press, St. Louis, Missouri.

Stolarski, O.C., Gorenstein, M.R., Lubke,, M., Lubke L., Helena, P., O'Connor, P., and Bechara, F.C. 2018. *Trema micrantha* (L.) Blume. in plantations for ecological restoration: Early development in the Brazilian subtropical forest. *Ciencia Florestal, Santa Maria* **28**(3): 1217-1229.

Stull, G.W., Soltis, P.S., Soltis, D.E., Gitzendanner, M.A., and Smith S.A. 2020. Nuclear phylogenomic analyses of asterids conflict with plastome trees and support novel relationships among major lineages. *American Journal of Botany* **107**(5): 790-805.

Sudsworth, G.B. 1927. Checklist of the forest trees of the United States their names and range. Miscellaneous Circular **92**. US Dept. Of Agriculture.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Taberlet, P., Gielly, L., Pautou, G., and Bouvet J. 1991. Universal primers for amplication of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* **17**: 1105-1109. doi:10.1007/BF00037152

Tillich, M., Lehwark, P., Pellizzer, T., Ulbricht-Jones, E.S., Fischer, A., Bock, R., and Greiner, S. 2017. GeSeq - versatile and accurate annotation of organelle genomes. *Nucleic Acids Research* **45**(W1): W6-W11.

Torres, R.B. and Luca, A.Q. 2005. *Parte integrante de Flora Fanerogamica do Estado de Sao Paulo, Ulmaceae*. In: Wanderley, M.G.L., Shepard, G.J., Melhem, T.S., Martins, S.E.

Kirizawa, M., and Giulietti, A.M. *Flora de Fanerogamica do Estado de Sao Paulo*. Instituto de Botanica, Sao Paulo. 361-370.

Vargas, O., Ortiz, E., and Simpson, B. 2017. Conflicting phylogenomic signals reveal a patternof reticulate evolution in a recent high-Andean diversification (Asteraceae: Astereae: Diplostephium). *New Phytologist* **214**(4): 1736–1750.

Vazquez-Yanes, C. 1998. *Trema micrantha* (L.) Blume (Ulmaceae): A promising neotropical tree for site amelioration of deforested land. *Agroforestry Systems* **40**: 97-104.

Vitousek, P.M and Sanford, R.L. 1986. Nutrient cycling in moist tropical forests. *Annual Review of Ecology and Systematics* **17**: 137-167.

Wang, H.X., Liu, H., Moore, M.J., et al. 2019. Plastid phylogenomic insights into evolution of the Caprifoliaceae *s.l.* (Dipsacaes). *Molecular Phylogenetics and Evolution* **142** (106641). doi: 10.1016/j.ympev.2019.106641

Wheeler, Q.D. and Meier, R. 2000. *Species concepts and phylogenetic theory: A debate.* Columbia University Press, New York.

World Flora Online. 2022. *Trema* Lour. Published on the internet. http://www.worldfloraonline.org/taxon/wfo-4000038807.

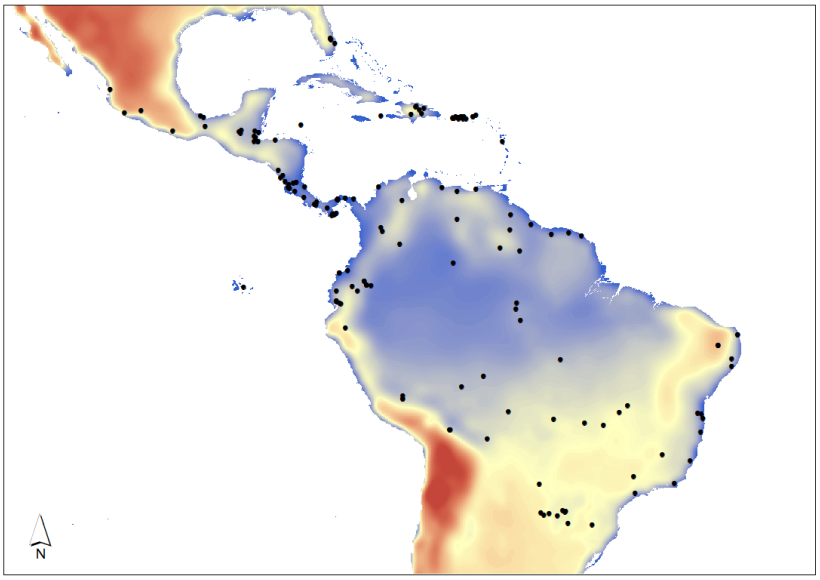
Xu, D.H., Abe, J., Sakai, M., Kanazawa, A., and Shimamoto, Y. 2000. Sequence variation of non-coding regions of chloroplast DNA of soybean and related wild species and its implications for the evolution of different chloroplast haplotypes. *Theoretrical and Applied Genetics* **101**: 724-732. doi:10.1007/s001220051537.

Yesson, C., Russel, S.J., Parrish, T., Dalling, J.W., and Garwood, N.C. 2004. Phylogenetic framework for *Trema* (Celtidaceae). *Plant Systematics and Evolution* **248**: 85-109.

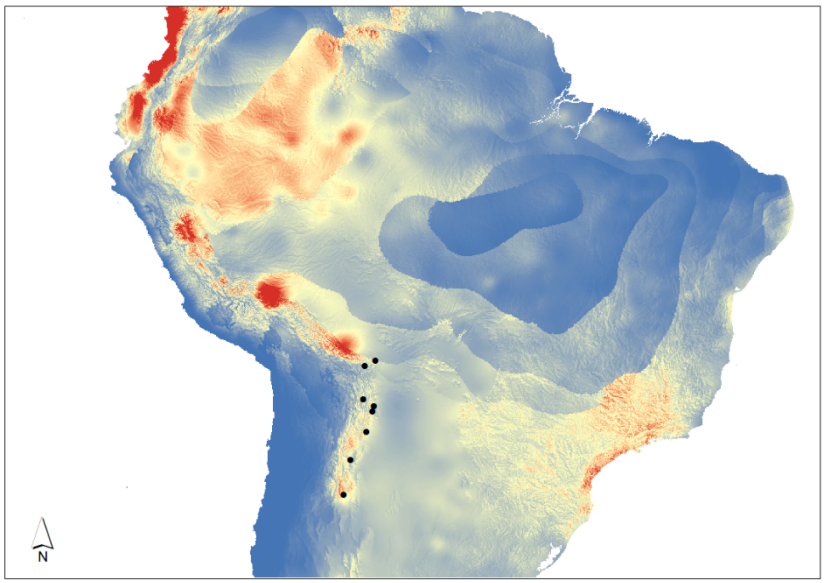
Zhang, H., Jin, J.J., Moore, M.J., Tingshuang, Y., and Dezhu, L. 2018. Plastome characteristics of Cannabaceae. *Plant Diversity* **40**: 127-137.

APPENDIX

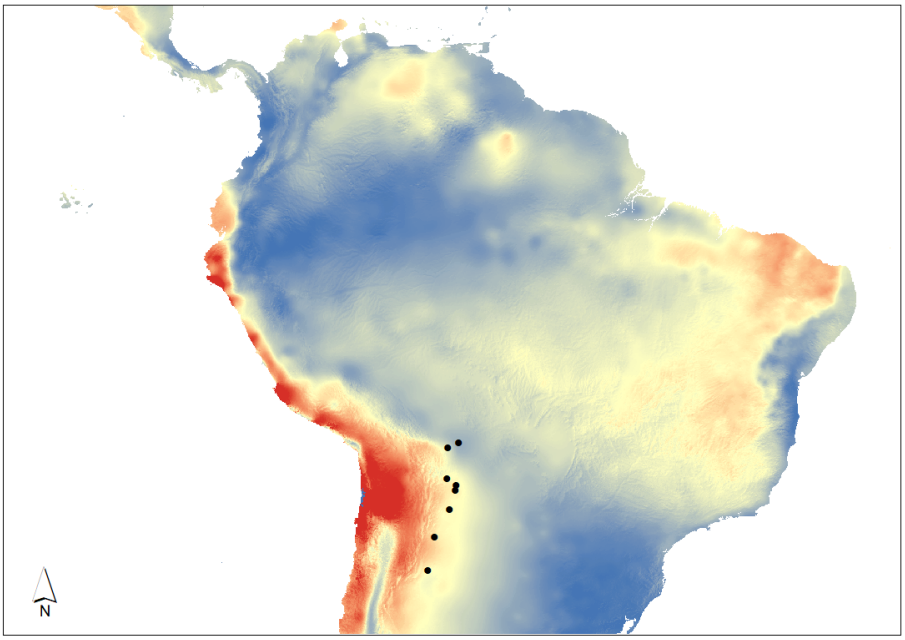
SUPPLEMENTARY FIGURES



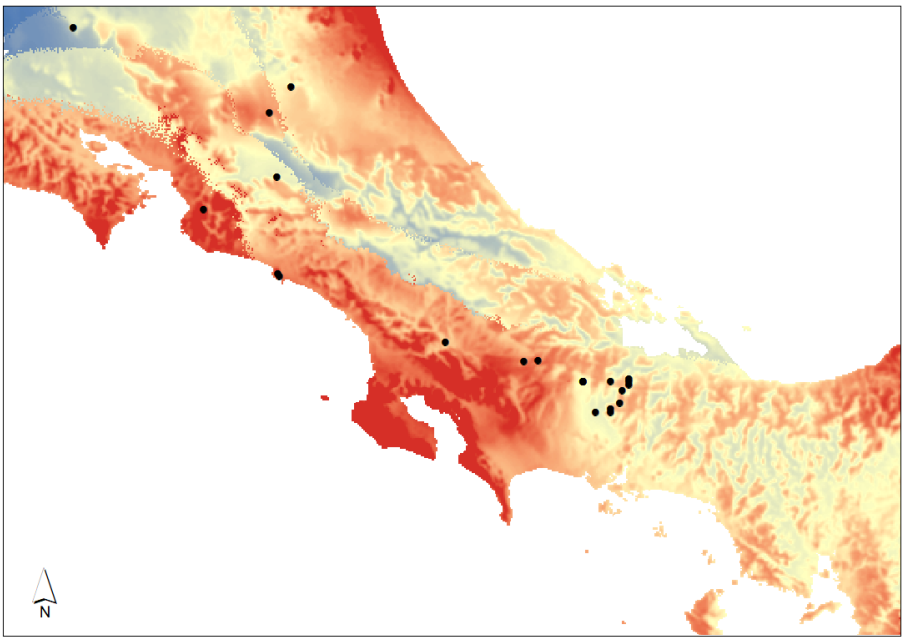
Supplementary Figure 1. Mean diurnal air temperature range (bio2) raster layer with group B2 distribution. Bio2 contributed 27.5% to B2 ENM. Cool colors represent lower values (smaller range in temperature), warm colors represent higher values.



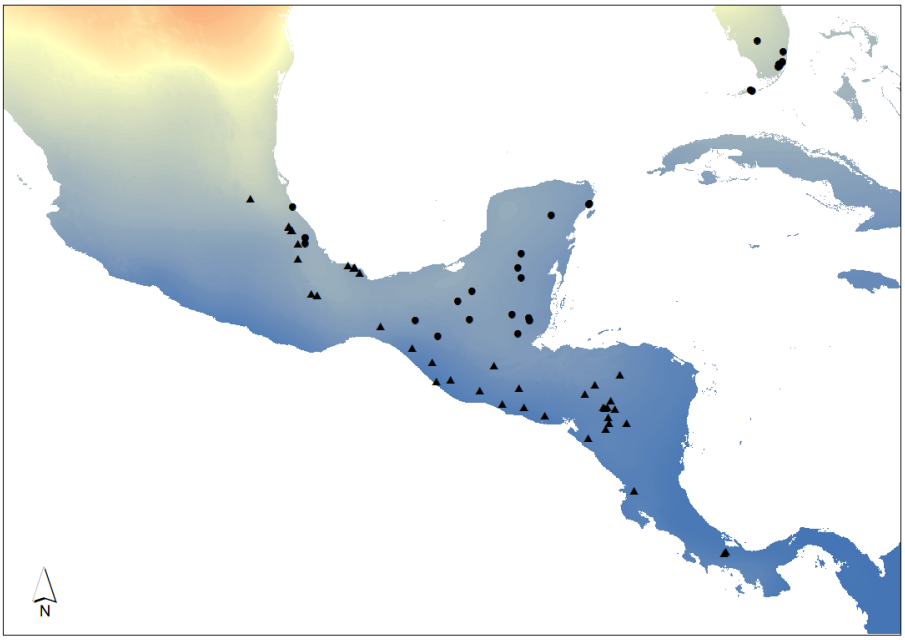
Supplementary Figure 2. Mean monthly precipitation amount of the warmest quarter (bio18) with group B4 distribution. Bio18 contributed 42.4% to B4 ENM. Cool colors represent lower values, warm colors represent higher values.



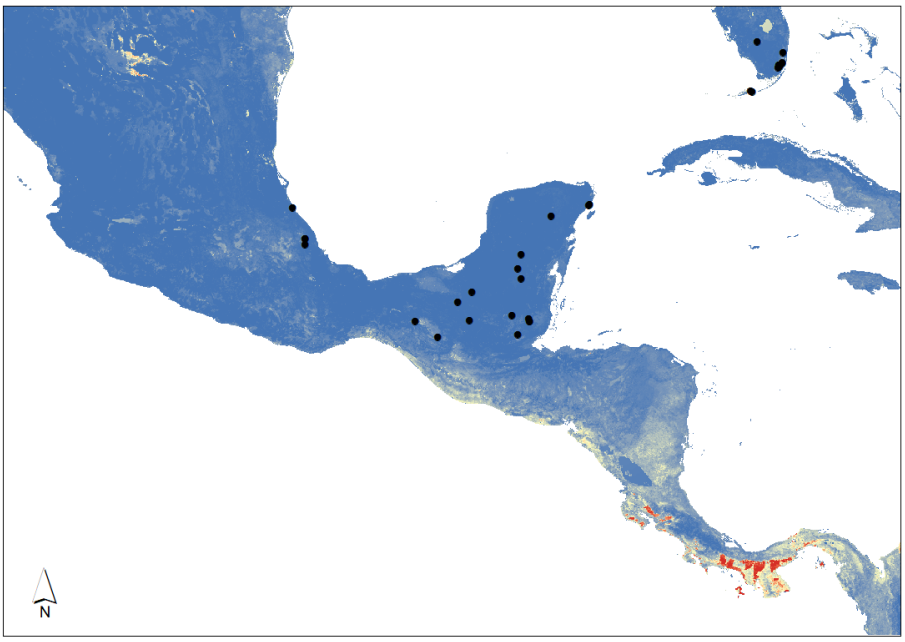
Supplementary Figure 3. Precipitation seasonality (bio15) with group B4 distribution. Bio15 contributed 23.4% to B4 ENM. Cool colors represent lower values (less precipitation seasonality), warm colors represent higher values.



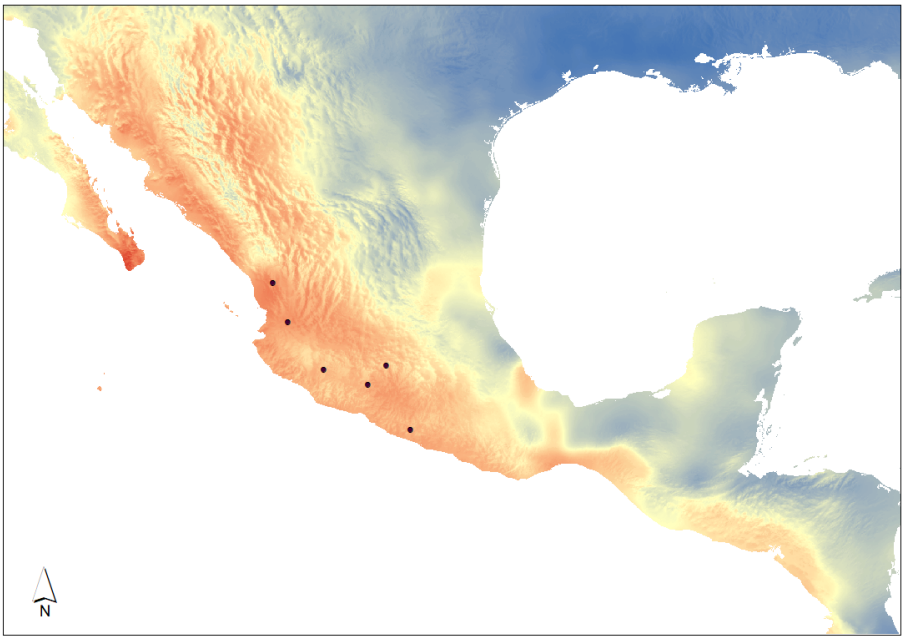
Supplementary Figure 4. Mean monthly precipitation amount of the coldest quarter (bio19) with the group B3 distribution. Bio19 contributed 43.1% to B3 ENM. Cool colors represent lower values (lower rainfall), warm colors represent higher values.



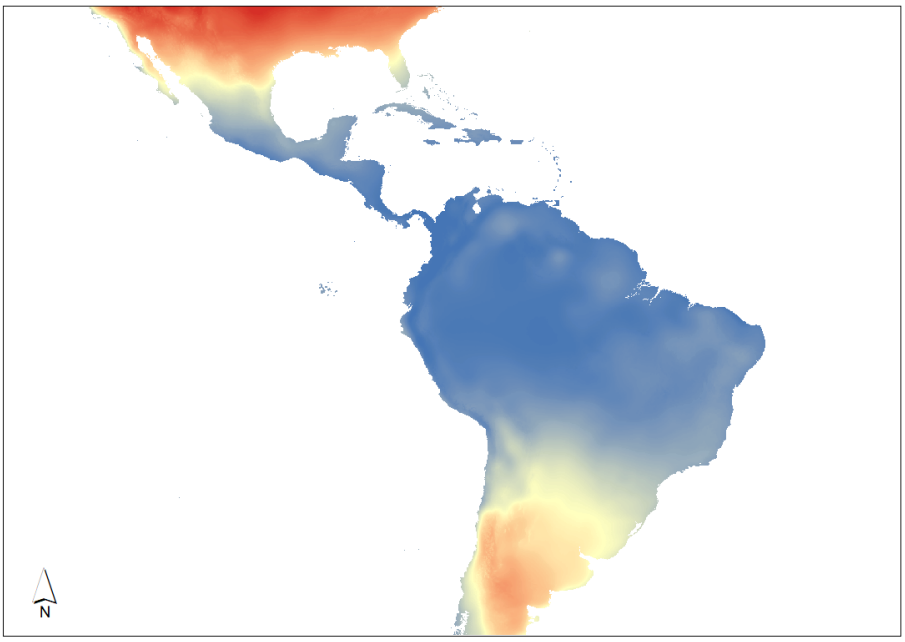
Supplementary Figure 5. Temperature seasonality (bio4) with B1a (black triangles) and B1b (black circles) distribution. Bio4 contributed 21.7% to B1a ENM and 53% to B1b ENM. Cool colors represent lower values of seasonality, warm colors represent higher values.



Supplementary Figure 6. Absolute depth to bedrock (bdticm) with B1b distribution. Bdticm contributed 33.1% to B1b ENM. Cool colors represent lower values (less distance to bedrock), warm colors represent higher values.



Supplementary Figure 7. Precipitation seasonality (bio15) with group B5 distribution. Bio15 contributed 50.6% to B5 ENM. Cool colors represent less precipitation seasonality, warm colors represent areas with more precipitation seasonality.



Supplementary Figure 8. Raster layer for temperature seasonality (Bio4). Cool colors represent lower values, warm colors represent higher values.

Supplementary Table 1. *Trema micrantha* B accessions used in this study, with elevation (in meters) included.

Clade	Accession Name	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
incertea sedis	*Dalling 54*	840	Panama	x	x	x	x	x	x
micrantha B1a	*García 170*	550	Costa Rica	x	x	x	x	x	x
micrantha B1a	*Garcia 96.5395*	1680	Guatemala	x	x	x	x	x	x
micrantha B1a	*Stevens 35309*	1095	Nicaragua	x	x	x	x	x	x
micrantha B1a	*Ventura 17223*	1000	Mexico	x	x	x	x	x	x
micrantha B1a	*Croat 65937*	1550	Mexico	x	x	x	x	x	x
micrantha B1a	*Ibarra Manríquez 2480*	250	Mexico	x	x	x	x	x	x
micrantha B1a	*Wehncke 1-3*	1900	Guatemala	-	x	x	x	x	x
micrantha B1a	*Monro 3604*	780	El Salvador	-	x	x	x	-	x
micrantha B1a	*Gómez Chagala 798*	480	Mexico	x	x	x	x	-	-
micrantha B1a	*Ibarra Manríquez 1470*	100	Mexico	x	x	x	x	-	-
micrantha B1a	*López Luna 0020*	1600	Mexico	x	x	x	x	-	-
micrantha B1a	*López Luna 0195*	1600	Mexico	x	x	x	x	-	-
micrantha B1a	*Williams 17399*	1700	Honduras	x	x	x	x	-	-
micrantha B1a	*Ibarra Manríquez 3958*	1100	Mexico	x	x	x	x	-	-
micrantha B1a	*Hall 7682*	1000	Nicaragua	-	x	x	x	-	-
micrantha B1a	*Nee 23721*	100	Mexico	-	x	x	x	-	-
micrantha B1a	*Beaman 6060*	100	Mexico	x	x	x	-	-	-
micrantha B1a	*Cornejo Tenorio 2526*	550	Mexico	x	x	x	-	-	-
micrantha B1a	*Dalling 52*	960	Panama	x	x	x	-	-	-
micrantha B1a	*Ibarra Manríquez 8*	900	Mexico	x	x	x	-	-	-
micrantha B1a	*Nee 26002*	1250	Mexico	x	x	x	-	-	-
micrantha B1a	*Ventura 18114*	800	Mexico	x	x	x	-	-	-
micrantha B1a	*Breedlove 24747*	1450	Mexico	-	x	x	-	-	-
micrantha B1a	*Breedlove 28625*	700	Mexico	-	x	x	-	-	-
micrantha B1a	*Chorley 183*	480	Honduras	-	x	x	-	-	-
micrantha B1a	*Coronado 377*	800	Nicaragua	-	x	x	-	-	-
micrantha B1a	*Coronado 862*	1143	Nicaragua	-	x	x	-	-	-
micrantha B1a	*Galán 2668*	1164	El Salvador	-	x	x	-	-	-
micrantha B1a	*Galeano 100*	1057	Honduras	-	x	x	-	-	-
micrantha B1a	*Kerber 394*	1000	Mexico	-	x	x	-	-	-

Supplementary Table 1. Continued.

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha B1a	*Martínez 114*	600	El Salvador	-	x	x	-	-	-
micrantha B1a	*Martínez 935*	1568	Mexico	-	x	x	-	-	-
micrantha B1a	*Monterrosa 1718*	1279	El Salvador	-	x	x	-	-	-
micrantha B1a	*Paguaga 168*	1488	Nicaragua	-	x	x	-	-	-
micrantha B1a	*Pérez 2087*	896	Guatemala	-	x	x	-	-	-
micrantha B1a	*Rueda 11383*	1275	Nicaragua	-	x	x	-	-	-
micrantha B1a	*Skutch 1337*	1160	Guatemala	-	x	x	-	-	-
micrantha B1a	*Stevens 30108*	935	Nicaragua	-	x	x	-	-	-
micrantha B1a	*Stevens 35513*	1200	Nicaragua	-	x	x	-	-	-
micrantha B1a	*Stevens 35942*	1630	Nicaragua	-	x	x	-	-	-
micrantha B1a	*Stevens 39513*	1450	Nicaragua	-	x	x	-	-	-
micrantha B1b	*Abbott 25239*	3	United States	x	x	x	x	x	x
micrantha B1b	*Koop 2*	2	United States	x	x	x	x	x	x
micrantha B1b	*Abbott 24973*	5	United States	x	x	x	x	-	-
micrantha B1b	*Garwood B05*	660	Belize	x	x	x	x	-	-
micrantha B1b	*Garwood B06*	660	Belize	x	x	x	x	-	-
micrantha B1b	*Little 15015*	1	United States	x	x	x	x	-	-
micrantha B1b	*McDaniel 9166*	1	United States	x	x	x	x	-	-
micrantha B1b	*Mendez 395*	25	Mexico	x	x	x	x	-	-
micrantha B1b	*Provance 3222*	1100	Mexico	x	x	x	x	-	-
micrantha B1b	*Stern 2822*	1	United States	x	x	x	x	-	-
micrantha B1b	*Wunderlin 8857*	4	United States	x	x	x	x	-	-
micrantha B1b	*Garcia 3828*	8	Mexico	-	x	x	x	-	-
micrantha B1b	*Stafford 237*	750	Mexico	-	x	x	x	-	-
micrantha B1b	*Tun Ortiz 990*	525	Guatemala	-	x	x	x	-	-
micrantha B1b	*Reyes-Garcia 184*	1550	Mexico	-	x	x	x	-	-
micrantha B1b	*Abbott 19812*	680	Mexico	x	x	x	-	-	-
micrantha B1b	*Aguilar 7231*	360	Mexico	x	x	x	-	-	-
micrantha B1b	*Bacab 73*	260	Mexico	x	x	x	-	-	-
micrantha B1b	*Garwood M2*	4	United States	x	x	x	-	-	-
micrantha B1b	*Garwood M3*	4	United States	x	x	x	-	-	-
micrantha B1b	*Garwood B02*	500	Belize	x	x	x	-	-	-

Supplementary Table 1. Continued.

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha B1b	*Koop 13*	1.2	United States	x	x	x	-	-	-
micrantha B1b	*Téllez 3828*	-	Mexico	x	x	x	-	-	-
micrantha B1b	*Álvarez 7485*	136	Mexico	-	x	x	-	-	-
micrantha B1b	*Calónico 23574*	158	Mexico	-	x	x	-	-	-
micrantha B1b	*Contreras 5421*	180	Guatemala	-	x	x	-	-	-
micrantha B1b	*Cortés 285*	20	Mexico	-	x	x	-	-	-
micrantha B1b	*Garwood M1*	4	United States	-	x	x	-	-	-
micrantha B1b	*Germán 1106*	-	Mexico	-	x	x	-	-	-
micrantha B1b	*Novelo 146*	53	Mexico	-	x	x	-	-	-
micrantha B2	*Anderson 10136*	740	Brazil	x	x	x	x	x	x
micrantha B2	*GadelhaNeto 3484*	50	Brazil	x	x	x	x	x	x
micrantha B2	*Lewis 40505*	1825	Bolivia	x	x	x	x	x	x
micrantha B2	*Little 26124*	152	British Virgin Islands	x	x	x	x	x	x
micrantha B2	*Popenoe 49*	15	Guatemala	x	x	x	x	x	x
micrantha B2	*Sustache s.n.*	20	Puerto Rico	x	x	x	x	x	x
micrantha B2	*Villa 2061*	175	Ecuador	x	x	x	x	x	x
micrantha B2	*Zanoni 37078*	100	Dominican Republic	x	x	x	x	x	x
micrantha B2	*Garwood 592*	50	Costa Rica	-	x	x	x	x	x
micrantha B2	*McKey 01*	8	French Guiana	-	x	x	x	x	x
micrantha B2	*Stevens 30384*	55	Nicaragua	-	x	x	x	x	x
micrantha B2	*Stuart s.n.*	6	United States	-	x	x	x	x	x
micrantha B2	*Villa 2142*	250	Ecuador	-	x	x	x	x	x
micrantha B2	*Teixeira 368*	320	Brazil	x	x	x	x	x	-
micrantha B2	*Benítez 579*	200	Paraguay	x	x	x	x	-	x
micrantha B2	*Dalling 09*	40	Panama	x	x	x	x	-	x
micrantha B2	*Renvoize 3269*	300	Argentina	x	x	x	x	-	x
micrantha B2	*Acevedo-Rodriguez 619*	360	US Virgin Islands	x	x	x	x	-	-
micrantha B2	*Agra 5007*	905	Brazil	x	x	x	x	-	-
micrantha B2	*Amaral 1141*	420	Brazil	x	x	x	x	-	-
micrantha B2	*Amorim 1239*	550	Brazil	x	x	x	x	-	-
micrantha B2	*Anderson 36289*	1000	Brazil	x	x	x	x	-	-
micrantha B2	*Bodle s.n.*	4	United States	x	x	x	x	-	-

Supplementary Table 1. Continued.

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha B2	*Conceição 442*	47	Brazil	x	x	x	x	-	-
micrantha B2	*Dalling 08*	40	Panama	x	x	x	x	-	-
micrantha B2	*Dalling 72*	75	Panama	x	x	x	x	-	-
micrantha B2	*Dalling 83*	285	Panama	x	x	x	x	-	-
micrantha B2	*Deginani 1040*	600	Argentina	x	x	x	x	-	-
micrantha B2	*dos Santos 3501*	50	Brazil	x	x	x	x	-	-
micrantha B2	*Dusen s.n.*	750	Brazil	x	x	x	x	-	-
micrantha B2	*Hahn 2307*	230	Paraguay	x	x	x	x	-	-
micrantha B2	*Irwin 24178*	1000	Brazil	x	x	x	x	-	-
micrantha B2	*Irwin 34910*	750	Brazil	x	x	x	x	-	-
micrantha B2	*Jansen-Jacobs 658*	200	Guyana	x	x	x	x	-	-
micrantha B2	*Lasseign P21199*	80	Brazil	x	x	x	x	-	-
micrantha B2	*Lewis 40551*	1500	Bolivia	x	x	x	x	-	-
micrantha B2	*Mori 17017*	90	US Virgin Islands	x	x	x	x	-	-
micrantha B2	*Philcox 4028*	560	Brazil	x	x	x	x	-	-
micrantha B2	*Prance 19244*	720	Brazil	x	x	x	x	-	-
micrantha B2	*Taylor 10129*	350	Puerto Rico	x	x	x	x	-	-
micrantha B2	*Thomas 11471*	575	Brazil	x	x	x	x	-	-
micrantha B2	*Thomas MT588*	80	Brazil	x	x	x	x	-	-
micrantha B2	*Todzia 2231*	55	Brazil	x	x	x	x	-	-
micrantha B2	*Whitefoord 4426*	200	Dominica	x	x	x	x	-	-
micrantha B2	*Croat 102457*	40	Suriname	x	x	x	x	-	-
micrantha B2	*Croat 102471*	39	French Guiana	x	x	x	x	-	-
micrantha B2	*Axelrod 14441*	10	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Axelrod 7259*	275	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Axelrod 8553*	850	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Axelrod 9951*	650	Puerto Rico	-	x	x	x	-	-
micrantha B2	*BasilioAugusto 1637*	-	Dominican Republic	-	x	x	x	-	-
micrantha B2	*Bradley s.n*	8	United States	-	x	x	x	-	-
micrantha B2	*Breckon 5922*	350	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Cedeño-Maldonado 118*	300	Puerto Rico	-	x	x	x	-	-
micrantha B2	*D'Arcy 12257*	170	Panama	-	x	x	x	-	-

Supplementary Table 1. Continued

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha B2	*Garwood 1508*	30	Panama	-	x	x	x	-	-
micrantha B2	*Garwood 230*	50	Belize	-	x	x	x	-	-
micrantha B2	*Garwood 5-1*	20	Belize	-	x	x	x	-	-
micrantha B2	*Garwood 5-6*	350	Belize	-	x	x	x	-	-
micrantha B2	*Hall 7794*	70	Nicaragua	-	x	x	x	-	-
micrantha B2	*Little 8231*	240	Colombia	-	x	x	x	-	-
micrantha B2	*Miller 5950*	20	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Ososki 151*	704	Dominican Republic	-	x	x	x	-	-
micrantha B2	*Pattison s.n.*	9	United States	-	x	x	x	-	-
micrantha B2	*Rifkin 1*	11	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Rifkin 2*	310	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Taylor 10097*	50	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Trejo-Torres 1439*	350	Puerto Rico	-	x	x	x	-	-
micrantha B2	*Valeur 706*	250	Dominican Republic	-	x	x	x	-	-
micrantha B2	*Villa 2145*	250	Ecuador	-	x	x	x	-	-
micrantha B2	*Villa 2033*	100	Ecuador	-	x	x	x	-	-
micrantha B2	*Villa 2064*	60	Ecuador	-	x	x	x	-	-
micrantha B2	*Villa 2102*	200	Ecuador	-	x	x	x	-	-
micrantha B2	*Agra 4800*	905	Brazil	x	x	x	-	-	-
micrantha B2	*Boom 7324*	500	Guyana	x	x	x	-	-	-
micrantha B2	*Dalling 05*	40	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 48*	325	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 60*	35	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 66*	145	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 67*	3	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 68*	1	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 69*	95	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 70*	110	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 71*	170	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 76*	90	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 77*	190	Panama	x	x	x	-	-	-
micrantha B2	*Dalling 80*	40	Panama	x	x	x	-	-	-

Supplementary Table 1. Continued

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha B2	*Díaz 493*	50	Venezuela	x	x	x	-	-	-
micrantha B2	*Dressler 236*	345	Mexico	x	x	x	-	-	-
micrantha B2	*Gentry 18152*	330	Colombia	x	x	x	-	-	-
micrantha B2	*Luchiari 587*	-	Brazil	x	x	x	-	-	-
micrantha B2	*Nee 25106*	326	Mexico	x	x	x	-	-	-
micrantha B2	*Proctor 32504*	8	Honduras	x	x	x	-	-	-
micrantha B2	*Quevedo 2445*	155	Bolivia	x	x	x	-	-	-
micrantha B2	*Souza 4985*	920	Brazil	x	x	x	-	-	-
micrantha B2	*Staviski 61*	-	Brazil	x	x	x	-	-	-
micrantha B2	*Stimson 3009*	300	Puerto Rico	x	x	x	-	-	-
micrantha B2	*Zanoni 27258*	935	Dominican Republic	x	x	x	-	-	-
micrantha B2	*Agra 4737*	905	Brazil	-	x	x	-	-	-
micrantha B2	*Aguilar 11565*	125	Mexico	-	x	x	-	-	-
micrantha B2	*Axelrod 12381*	275	Puerto Rico	-	x	x	-	-	-
micrantha B2	*Boom 4048*	200	Bolivia	-	x	x	-	-	-
micrantha B2	*Boom 6316*	90	Venezuela	-	x	x	-	-	-
micrantha B2	*Breckon 8040*	35	Puerto Rico	-	x	x	-	-	-
micrantha B2	*Buck 34377*	75	Navassa Island	-	x	x	-	-	-
micrantha B2	*Calatayud 4147*	925	Peru	-	x	x	-	-	-
micrantha B2	*Calzada 18950*	15	Mexico	-	x	x	-	-	-
micrantha B2	*Campos de la Cruz 2643*	700	Peru	-	x	x	-	-	-
micrantha B2	*Custodio Filho 931*	-	Brazil	-	x	x	-	-	-
micrantha B2	*Dalling 38*	-	Panama	-	-	x	-	-	-
micrantha B2	*Dalling A1*	-	Panama	-	x	x	-	-	-
micrantha B2	*Dalling A2*	-	Panama	-	x	x	-	-	-
micrantha B2	*Garwood 5-2*	20	Belize	-	x	x	-	-	-
micrantha B2	*Garwood 5-3*	25	Belize	-	x	x	-	-	-
micrantha B2	*Garwood B30*	530	Belize	-	x	x	-	-	-
micrantha B2	*Gentry 72350*	175	Ecuador	-	x	x	-	-	-
micrantha B2	*Gilmartin 67*	-	Ecuador	-	x	x	-	-	-
micrantha B2	*Gomez 20761*	360	Costa Rica	-	x	x	-	-	-
micrantha B2	*Gonto 01153*	650	Venezuela	-	x	x	-	-	-

Supplementary Table 1. Continued

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha B2	*Gonto 595*	55	Venezuela	-	x	x	-	-	-
micrantha B2	*Grijalva 2904*	600	Nicaragua	-	x	x	-	-	-
micrantha B2	*Guadamuz 948*	60	Nicaragua	-	x	x	-	-	-
micrantha B2	*Henkel 2579*	-	Guyana	-	x	x	-	-	-
micrantha B2	*Hunziker 11947*	-	Argentina	-	x	x	-	-	-
micrantha B2	*Jones 10116*	660	Costa Rica	-	x	x	-	-	-
micrantha B2	*Juncosa 981*	700	Colombia	-	x	x	-	-	-
micrantha B2	*Liesner 2782*	50	Costa Rica	-	x	x	-	-	-
micrantha B2	*Liesner 7352*	120	Venezuela	-	x	x	-	-	-
micrantha B2	*López 89-10-2*	370	Mexico	-	x	x	-	-	-
micrantha B2	*Mansano 517*	376	Brazil	-	x	x	-	-	-
micrantha B2	*Márquez 283*	-	Mexico	-	x	x	-	-	-
micrantha B2	*Martínez 13791*	220	Mexico	-	x	x	-	-	-
micrantha B2	*Martínez 199*	40	Costa Rica	-	x	x	-	-	-
micrantha B2	*Martínez 7192*	160	Mexico	-	x	x	-	-	-
micrantha B2	*McDowell 4352*	107	Guyana	-	x	x	-	-	-
micrantha B2	*Meija 7197*	1200	Dominican Republic	-	x	x	-	-	-
micrantha B2	*Nee 42396*	-	Brazil	-	x	x	-	-	-
micrantha B2	*Nee 57246*	360	Bolivia	-	x	x	-	-	-
micrantha B2	*Ortiz 1033*	-	Paraguay	-	x	x	-	-	-
micrantha B2	*Reyes 760*	200	Ecuador	-	x	x	-	-	-
micrantha B2	*Robles 1457*	80	Costa Rica	-	x	x	-	-	-
micrantha B2	*Rubio 2343*	400	Ecuador	-	x	x	-	-	-
micrantha B2	*Rzedowski 37422*	915	Mexico	-	x	x	-	-	-
micrantha B2	*Short 131*	650	Costa Rica	-	x	x	-	-	-
micrantha B2	*Silva 433*	1200	Brazil	-	x	x	-	-	-
micrantha B2	*Soto 7133*	280	Mexico	-	x	x	-	-	-
micrantha B2	*Stevens 31307*	185	Paraguay	-	x	x	-	-	-
micrantha B2	*Steyermark 107831*	40	Venezuela	-	x	x	-	-	-
micrantha B2	*Stutz de Ortega 1887*	-	Paraguay	-	x	x	-	-	-
micrantha B2	*Valenzuela 1905*	1525	Peru	-	x	x	-	-	-
micrantha B2	*Valenzuela 1927*	1525	Peru	-	x	x	-	-	-

Supplementary Table 1. Continued

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha B2	*Vargas 3380*	1100	Costa Rica	-	x	x	-	-	-
micrantha B2	*Velázquez 65*	150	Nicaragua	-	x	x	-	-	-
micrantha B2	*Villa 2143*	250	Ecuador	-		x	-	-	-
micrantha B2	*Villa 2148*	250	Ecuador	-	x	x	-	-	-
micrantha B2	*Villa 2149*	250	Ecuador	-	x	x	-	-	-
micrantha B2	*Villa 2028*	100	Ecuador	-	x	x	-	-	-
micrantha B2	*Villa 2034*	100	Ecuador	-	x	x	-	-	-
micrantha B2	*Yuncker 8354*	-	Honduras	-	x	x	-	-	-
micrantha B2	*Zardini 11061*	700	Paraguay	-	x	x	-	-	-
micrantha B2	*Zarucchi 4123*	230	Colombia	-	x	x	-	-	-
micrantha B2	*Cerón 15641*	1190	Ecuador	-	x	x	-	-	-
micrantha B2	*Cerón 3596*	450	Ecuador	-	x	x	-	-	-
micrantha B3	*Dalling 58*	395	Panama	x	x	x	x	x	x
micrantha B3	*Alford 3021*	1048	Costa Rica	x	x	x	x	x	x
micrantha B3	*Khan 538*	60	Costa Rica	-	x	x	x	x	x
micrantha B3	*Dalling 47*	325	Panama	x	x	x	-	-	-
micrantha B3	*Dalling 56*	675	Panama	x	x	x	-	-	-
micrantha B3	*Dalling 57*	545	Panama	x	x	x	-	-	-
micrantha B3	*Dalling 62*	1015	Panama	x	x	x	-	-	-
micrantha B3	*Dalling 64*	945	Panama	x	x	x	-	-	-
micrantha B3	*Fernández 1367*	900	Costa Rica	x	x	x	-	-	-
micrantha B3	*Gómez 19706*	-	Costa Rica	x	x	x	-	-	-
micrantha B3	*Rojas 90*	500	Costa Rica	x	x	x	-	-	-
micrantha B3	*Vargas 353*	100	Costa Rica	x	x	x	-	-	-
micrantha B3	*Wilbur 18248*	900	Costa Rica	x	x	x	-	-	-
micrantha B3	*Khan 447*	20	Costa Rica	-	x	x	-	-	-
micrantha B3	*Dalling 45*	1575	Panama	-	x	x	x	x	-
micrantha B3	*Dalling 41*	1465	Panama	x	x	x	-	-	-
micrantha B3	*Dalling 44*	1555	Panama	x	x	x	-	-	-
micrantha B4	*Nee 47985*	1600	Bolivia	x	x	x	x	x	x
micrantha B4	*Nee 53226*	540	Bolivia	x	x	x	x	x	x
micrantha B4	*Venturi 7580*	800	Argentina	x	x	x	x	x	x
micrantha B4	*Conrad 2636*	1125	Argentina	-	x	x	x	-	-
micrantha B4	*Morrone 4128*	-	Argentina	x	x	x	-	-	-
micrantha B4	*Nee 44561*	500	Bolivia	x	x	x	-	-	-
micrantha B4	*Nee 54145*	630	Bolivia	x	x	x	-	-	-
micrantha B4	*Serrano 7072c*	1630	Bolivia	x	x	x	-	-	-

Supplementary Table 1. Continued

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha B5	*Cornejo 3705*	1910	Mexico	x	x	x	-	-	-
micrantha B5	*Flores 1882*	1700	Mexico	x	x	x	-	-	-
micrantha B5	*Miller 2947*	800	Mexico	x	x	x	-	-	-
micrantha B5	*Miller 3097*	1500	Mexico	x	x	x	-	-	-
micrantha B5	*Eggler 133*	955	Mexico	-	x	x	-	-	-
micrantha B5	*Hinton 439*	1300	Mexico	-	-	x	-	-	-
micrantha B5	*Hinton 7833*	1800	Mexico	-	-	x	-	-	-
micrantha B5	*Tenorio 16194*	1300	Mexico	-	x	x	-	-	-
micrantha B3	*Dalling 40*	1380	Panama	-	x	-	-	-	-
micrantha B3	*Dalling 43*	1575	Panama	-	x	-	-	-	-
micrantha B3	*Dalling 50*	735	Panama	-	x	-	-	-	-
micrantha B3	*Dalling 53*	1035	Panama	-	x	-	-	-	-
micrantha B3	*Dalling 63*	1120	Panama	-	x	-	-	-	-
micrantha B3	*Hamilton 960*	2200	Panama	-	x	-	-	-	-
micrantha B3	*Kriebel 73*	1256	Costa Rica	-	x	-	-	-	-
micrantha A	*Franck 3906*	729	Jamaica	-	-	-	x	x	x
micrantha A	*Garwood 4548*	250	Ecuador	-	-	-	x	x	x
micrantha A	*Villa 2078*	485	Ecuador	-	-	-	x	x	x
micrantha A	*Villa 2133*	650	Ecuador	-	-	-	x	x	x
micrantha A	*Adams 7513*	305	Jamaica	-	-	-	x	-	-
micrantha A	*Arias 27*	930	Colombia	-	-	-	x	-	-
micrantha A	*Basilio Augusto 1078*	400	Dominican Republic	-	-	-	x	-	-
micrantha A	*Dalling 16*	80	Panama	-	-	-	x	-	-
micrantha A	*Dalling 18*	40	Panama	-	-	-	x	-	-
micrantha A	*Dalling 49*	325	Panama	-	-	-	x	-	-
micrantha A	*Dalling 55*	700	Panama	-	-	-	x	-	-
micrantha A	*FernándezCasas 10596*	260	Cuba	-	-	-	x	-	-
micrantha A	*Galo 12*	80	Honduras	-	-	-	x	-	-
micrantha A	*Garwood 4554*	250	Ecuador	-	-	-	x	-	-
micrantha A	*Garwood 4559*	250	Ecuador	-	-	-	x	-	-
micrantha A	*Little 13046*	244	Puerto Rico	-	-	-	x	-	-
micrantha A	*Proctor 23831*	610	Jamaica	-	-	-	x	-	-
micrantha A	*Rimachi 2449*	170	Peru	-	-	-	x	-	-
micrantha A	*Villa 2147*	250	Ecuador	-	-	-	x	-	-
micrantha A	*Villa 2153*	1000	Ecuador	-	-	-	x	-	-
micrantha A	*Villa 2066*	340	Ecuador	-	-	-	x	-	-
micrantha A	*Villa 2131*	675	Ecuador	-	-	-	x	-	-
micrantha A	*Whitefoord 258*	15	Panama	-	-	-	x	-	-
micrantha A	*Whitefoord 1875*	130	Belize	-	-	-	x	-	-

Supplementary Table 1. Continued

Clade	*Accession Name*	Elevation (m)	Country	Morph	ENM	ETS	5-gene	NRC	Plastome
micrantha A	*Zanoni 32716*	700	Dominican Republic	-	-	-	x	-	-
micrantha A	*Suclli 2327*	1500	Peru	-	-	-	-	x	x
micrantha A	*Terán 951*	630	Bolivia	-	-	-	-	x	x
micrantha A	*Villa 2015*	1100	Ecuador	-	-	-	-	x	x
micrantha A	*Worthington 18155*	457	Trinidad & Tobago	-	-	-	-	x	x
micrantha A	*Dalling 02*	50	Panama	-	-	-	-	x	x
micrantha A	*Garwood 5-8*	350	Belize	-	-	-	-	x	-
micrantha A	*Garwood 4547*	250	Ecuador	-	-	-	-	x	-
micrantha C	*Judd 4047*	1545	Haiti	-	-	-	x	x	x
micrantha C	*Liogier 15415*	1700	Dominican Republic	-	-	-	x	x	x
micrantha C	*Nee 51812*	1950	Bolivia	-	-	-	x	x	x
micrantha C	*Palacios 2177*	1300	Ecuador	-	-	-	x	x	x
micrantha C	*Villa 2141*	1714	Ecuador	-	-	-	x	x	x
micrantha C	*Vincent 15484*	1170	Puerto Rico	-	-	-	x	x	x
micrantha C	*Adams 11328*	975	Jamaica	-	-	-	x	-	-
micrantha C	*Ammann 427*	1400	Jamaica	-	-	-	x	-	-
micrantha C	*Basilio Augusto 1522*	-	Dominican Republic	-	-	-	x	-	-
micrantha C	*Villa 2128*	720	Ecuador	-	-	-	x	-	-
micrantha C	*Villa 2129*	675	Ecuador	-	-	-	x	-	-
micrantha C	*Villa 2134*	1242	Ecuador	-	-	-	x	-	-
micrantha C	*Zanoni 25833*	1700	Dominican Republic	-	-	-	x	-	-
micrantha C	*Zanoni 25862*	1700	Dominican Republic	-	-	-	x	-	-
micrantha C	*Zanoni 26547*	1575	Dominican Republic	-	-	-	x	-	-
micrantha C	*Adams 11328*	976	Jamaica	-	-	-	x	-	-
micrantha C	*Perea 2530*	1679	Peru	-	-	-	-	x	-
micrantha D	*Huamantupa 7725*	2710	Peru	-	-	-	x	x	x
micrantha D	*Galiano 5749*	2500	Peru	-	-	-	x	-	-
micrantha D	*Galiano 4462*	1980	Peru	-	-	-	-	x	x

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- SIUC Masters Fellowship (2020)
- S-STEM Symposium Travel Awardee (2019)
- Students United in Preserving, Exploring, and Research Biodiversity (SUPERB) Scholarship (2019)
- James E. Ozment Natural History Award (2019)
- SIU Sustainability Environmental Ambassador Award (2018, 2019)
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Phylogenetic, morphometric, and biogeographic investigations of *Trema micrantha* (Cannabaceae)

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