Systematics of the *Tillandsia fasciculata* Complex (Bromeliaceae)

By

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ABSTRACT

Both inter- and intraspecific approaches were employed in a series of studies to determine evolutionary patterns and processes within the *Tillandsia fasciculata* species complex, an epiphytic flowering plant in the pineapple family (Bromeliaceae). The *T. fasciculata* complex is a taxonomically challenging group due to a "mosaic" distribution of morphological characters that make it difficult to accurately diagnose its members across the Caribbean Basin – a biodiversity hotspot. The main goals of this study are to: 1) evaluate the circumscription and phylogenetic position of the *T. fasciculata* complex; 2) examine the genetic variation and structure of populations from Florida and the Bahamas, and 3) model the past, present, and future occurrence of *T. fasciculata* in geographic space.

For phylogenetic reconstruction both taxon and loci sampling of the *T. fasciculata* group were increased substantially over previously published studies. Concatenated data incorporating six ptDNA regions (*atp*B-*rbc*L, *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36 , *rps16*), rDNA (ETS) and a single low-copy nuclear gene (PRK) sequenced from 27 of the 33 taxa in the *T. fasciculata* complex clarified some taxonomic questions pertaining to the group, but others remain unresolved. Geography, more than morphology, plays an important role in delimiting several problematic taxa.

For population genetic studies, eight microsatellite loci (simple sequence repeats) were scored, and we identified at least three population clusters in the *T. fasciculata* group across its northern limit in Florida and the Bahamas (n=18 sites). The most genetically distinct population consists of the natural hybrid *T.* ×*floridana* and one of its purported parents, *T. bartramii*. Previously, relatedness of *T.* ×*floridana* and *T. bartrami* was based on speculation.

Species distribution models were generated using MaxEnt for eight bioclimatic layers based on MIROC-ESM from WorldClim, harmonized world soil data, and altitude data layers across past (last interglacial, last glacial maximum, mid-Holocene), current, and future (2050 and 2070). Jackknife results show that the most important single environmental data layer across taxa and across climatic conditions is soil data. Paleoclimatic data shed light on possible areas where some *T. fasciculata* varieties arose, and models for the future indicate areas will still be available for the persistence of these plants.

Chapter 1: Testing the Circumscription of the *Tillandsia fasciculata* complex (Bromeliaceae).

ABSTRACT

The *Tillandsia fasciculata* complex (Bromeliaceae) is a taxonomically challenging group that consists of eight subspecific varieties, 22 supravarietal taxa of uncertain rank, and three natural hybrids. This species complex occurs in and around the Caribbean Basin, a recognized biodiversity hotspot. Entities of this group have a perceived affinity to one another based on morphological characters such as castaneous leaf sheath, digitate inflorescence, generally glabrous floral bracts, and blue-violet corolla. The goal of this study is to reconstruct a more thoroughly sampled, well resolved phylogeny using a multigene approach to evaluate the circumscription and phylogenetic position of the *Tillandsia fasciculata* complex, and also to determine relationships within the complex. Six ptDNA regions (*atp*B-*rbc*L, *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36 , *rps16*), rDNA (ETS) and a single low-copy nuclear gene (PRK) were sequenced from 27 of the 33 taxa in the *T. fasciculata* complex. Results support the status of most of the taxa hypothesized to belong in this group. *Tillandsia beutelspacheri*, *T.* ×*polita*, and *T. rotundata* were hypothesized to be related to *T. fasciculata* but our phylogenetic results suggest otherwise. One of the most revealing results from our study is that *Tillandsia* plants that would historically be classified as "*T. fasciculata"* from northern South America form a clade separate from the *T. fasciculata* s.l. group. There is morphological, genetic, and biogeographic support for *T. fasciculata* var. *venosispica* (across Puerto Rico and the Lesser Antilles) and the small bracted *T. fasciculata* varieties from the Bahamas, Cuba, and Florida. *Tillandsia* ×*floridana*, a purported natural hybrid, shows incongruence between plastid and nuclear data. Biogeographic signal found in some of these clades may help delimit varieties. Our research

clarifies species boundaries within a group in the subgenus *Tillandsia*, and adds to the growing body of literature on plant Caribbean biogeography.

The *Tillandsia fasciculata* species complex is one of the most taxonomically challenging groups for both botanists and and bromeliad hobbyists. This species complex belongs to the subfamily Tillandsioideae (family, Bromeliaceae), which contains >1300 species and has some of the most widespread species of bromeliads in the Neotropics (Till 2000a). Tillandsioideae is characterized by entire leaf margins, ovaries superior or nearly so, and plumose-appendaged seeds (Till 2000a, Rauh 1979, Smith & Downs 1977). Molecular phylogenetic studies support the traditional morphological circumscription of this subfamily, finding it to be monophyletic (Gilmartin and Brown1989; Terry and Brown 1997; Horres et al. 2000; Barfuss et al. 2005; Givnish 2004, 2007) and positioned sister to all other bromeliad subfamilies except Brocchinioideae and Lindmanioideae (Givnish et al. 2011, Givnish et al. 2014). Tillandsioideae is hypothesized to have arisen roughly 15.4 million years ago (ma) in northern South America (Givnish et al. 2011) and has its greatest center of diversity in the northern Andes and Antilles (Till 2000a).

Six genera are traditionally recognized as belonging to Tillandsioideae (Smith and Down 1977): *Glomeropitcairnia*, *Catopsis*, and the core tillandsioids *Mezobromelia*, *Guzmania*, *Vriesea* and *Tillandsia*. In the mid 1990, based on floral and seed morphology, three core tillandsioid genera were recognized or resurrected, *Racinaea* (formerly *Tillandsia* subg. *Pseudocatopsis*; Spencer & Smith 1993), *Alcantarea* and *Werauhia* (formerly *Vriesea* subg. *Alcantarea*, and part of *Vriesea* subgenus *Vriesea* sect. *Xiphion*; Grant 1995a, 1995b). Molecular analyses (Barfuss et al. 2005, 2011) used plastid and nuclear loci to examine generic and infrageneric relationships of Tillandsioideae, with a focus on the core tillandsioids. In addition, Barfuss et al. 2011 proposed three new genera in the core tribe Tillandsieae: *Josemania*, *Lemeltonia*, and *Rothowia* (these species were formerly in the genus *Tillandsia* subgenus (non

monphyletic) *Phytarrhiza*). Givnish et al. (2011) found that within Tillandsioideae the core tillansioids have a stem age of ca. 14.2 ma, and crown age of 8.7 ma. Secondary centers of species richness are based on genera and subgenera (Till 2000a; Smith & Downs 1977). For example, *Alcantarea* (spp. 16) is endemic to eastern Brazil (Versieux et al.2012) and *Werauhia* (spp. 73) is located in Central America, whereas *Tillandsia* subgenus *Tillandsia* has its greatest center of diversity in Mexico (Till 2000a).

The genus *Tillandsia* (ca. 550 species, Till 2000b) varies tremendously in habit and inflorescence architecture. Plants are epiphytes, lithophytes or terrestrials, and range from the southeastern USA in the North to central Argentina and Chile in the South. The genus includes 6–7 subgenera according to differing systems of classification, and some of these have been divided further. For example, Gardner (1986) divided *Tillandsia* subgenus *Tillandsia* (ca. 200 species) into five groups, then based on floral structure and androecial characteristics divided one of these groups into eight subgroups. However, there have been few studies using molecular data published to evaluate the monophyly of these taxa and informal groups. Of the studies that have been conducted on species complexes within the genus *Tillandsia*, most have taken a morphometric approach. Donadio et al. (2015) used 85 morphological characters to examine the cladistic relationships of taxa in the subgenus *Diaphoranthema*, while Castello and Galetto (2013) used 35 morphological characters to study the five forms in the complex *T. capillaris*. Within the subgenus *Tillandsia*, Pinzón et al. (2011) took a morphometric approach to examine the *T. utriculata* complex. Chew et al. (2010) used nuclear ribosomal DNA markers to study 13 pseudobulbous *Tillandsia* species.

The *Tillandsia fasciculata* complex, which occurs in and around the entire Caribbean Basin, is an ideal lineage to address questions of Caribbean plant origins and assemblages, yet is

poorly understood. Plants of the *Tillandsia fasciculata* group are predominantly epiphytic, but also can be lithophytic, and are found in a variety of habitats from subtropical savannas and hardword hammocks to coastal rock plant communities and tropical mogotes. Generally, plants range from 50 to 75 cm in height, but can be taller than one meter or shorter than 25 cm. In 1788, Swartz described *T. fasciculata* based on a specimen collected in Jamaica (Smith & Downs 1977). Currently the taxonomic complex centered around *T. fasciculata* consists of eight varieties of the original species, 22 additional species, and three documented natural hybrids (Espejo & López-Ferrari 2005; Espejo et al. 2008; Luther 2001, 2008; Luther & Sieff 1994, 1997; Smith & Downs 1977; Figure 1, Table 1). Taxa classified in the *T. fasciculata* complex have presumed relationships to one another based on morphological characters such as castaneous leaf sheath, inflorescence architecture, floral bracts generally glabrous, and blue-violet corolla, but unambiguous synapomorphies for the complex are yet to be found. *Tillandsia fasciculata* var *fasciculata* is a diploid (base number n=25) (Brown & Gilmartin 1989), although Gauthe (1965) reported *T. fasciculata* 2*n*=64 and *T. fasciculata* var. *venosispica* 2*n*=56 (Cascante 2006). Species delimitation in the group is unclear, and even the issue of monophyly and circumscription (i.e., what taxa actually belong to this "complex"?) remains ambiguous.

Mez (1896) made significant contributions to our understanding of *Tillandsia fasciculata* systematics in his monograph. He designated eight infraspecific taxa, many of which are still recognized today (Table 1). Varieties were divided into two main categories based on length of spike and floral bract. The large-spiked group consisted of varieties that have spikes typically longer than 10 cm and floral bracts 33 mm long or longer. Mez further subdivided these taxa based on spike position (erect vs. nodding) and shape (flattened vs. not), and venation in the floral bract (prominent or obscure). The small-spiked group has spikes rarely longer than 10 cm

and floral bracts 25 mm long or less, with a peduncle that can be short or long. The flowers can be dense or loose, and the arrangement of spikes on the inflorescence can be feather or fan shaped.

Smith and Downs' (1977) monograph of the entire subfamily Tillandsioideae essentially upheld Mez's infraspecific classification of *Tillandsia fasciculata*. As with Mez, Smith and Downs relied heavily on floral characters such as size of spike and floral bract to circumscribe these taxa. Subsequent to Smith and Downs' (1977) monograph supravarietal taxa have been added to this species complex by various authors based on morphological structures (Table 1).

Although Barfuss et al.'s (2005) molecular systematic study of Tillandsioideae was ambitious and enlightenting, it focused on intergeneric relationships within the entire subfamily, and so only one accession of *Tillandsia fasciculata* was included to represent the entire complex in their study. They found that *T. fasciculata* is placed in the Tillandsioideae subgenus *Tillandsia*, and that it forms a clade with *T. remota*, *T. klausii*, *T. juncea*, *T. caput-medusae*, and *T. ionantha*. Historically, these five species have not been considered a part of the *T. fasciculata* complex sensu stricto. In a subsequent 2011 poster presentation (abstract only; study unpublished), Barfuss et al. included *T. beutelspacheri* and *T.* cf. *rhomboidea*, two of the 25 taxa that are hypothesized to be related to *T. fasciculata.* As with their previous study, Barfuss et al. (2011) confirmed that *T. fasciculata* belongs within the subgenus *Tillandsia*. They also found that *T. fasciculata* forms a clade with *T. beutelspacheri*, *T.* cf. *rhomboidea* and *T. exserta*. As a result of these previous morphological and molecular phylogenetic studies, questions of monophyly and cicumscription of the *T. fasciculata* complex remain unanswered since most of the "*T. fasciculata*" group were not included in that study.

The goal of this study is to reconstruct a more thoroughly sampled, well resolved phylogeny using a multigene approach to evaluate the circumscription and phylogenetic position of the *Tillandsia fasciculata* complex, and also to determine relationships within the complex. We also consider questions of biogeography. We address: 1) Do molecular data support the classification and relationships proposed using a morphology-based approach? 2) Within a phylogenetic framework, what taxa compromise the *T. fasciculata* complex? and 3) Within this complex, what are species relationships to one another? 4) What do our results indicate about evolutionary plant patterns in the Caribbean?

METHODS

Taxon sampling. Novel DNA sequence data from 27 out of 33 named taxa in the *Tillandsia fasciculata* complex were generated for this study. Vouchered plant material was collected in the Bahamas, Cuba, Dominican Republic, Guadeloupe, Jamaica, Mexico, St. Lucia, Trinidad, and USA (Florida, Puerto Rico, St. John, and St. Thomas). For taxa not found in the field, sequence data were generated using specimens from living research collections (Marie Selby Botanical Gardens and collaborators Drs. Germán Carnevali, Ivón Ramírez, and Adolfo Espejo), and nursery collections (Tropiflora (Sarasota, FL) and Bird Rock Tropical (Encinitas, CA)) (Figure 2, Supplementary Table 3).

Our strategy was two fold. First we wanted to evaluate monophyly of the "*T. fasciculata*" group. We started with ca. 200 sequences/molecular marker. If there were ambigous sequence(s), then that individual was excluded when concatenating a final dataset to obtain full coverage in the matrix. We further reduced this dataset to avoid over-representation of one taxon and/or from one collecting site. Care was taken to select taxa based on capturing the morphological

variability and distribution of individuals within and across islands. About 73 individuals were used for phylogenetic analyses unless stated otherwise (e.g., in BEAST analyses). Second, we wanted to take a phlyogeographic approach (see Network Analyses section). Because theses tests were run individually per marker and not concatenated, we returned to the ca. 200 individuals per locus (ca. 4–15 individuals/site).

Loci sampling. To test the monophyly of this group, the same plastid markers (*atp*B-*rbc*L spacer, *mat*K, and *rps*16 intron) employed by Barfuss et al. (2005) were used, along with others. Bromeliaceae phylogeny reconstructions are notorious for their lack of resolution. To address the low genetic variability among bromeliad taxa, more variable plastid regions such as *3'rps16-5'trnK* spacer (Shaw et al. 2005, 2007), low-copy nuclear genes (PRK: Schulte et al. 2009; rpb2, g3pdh: Sass & Specht 2010; PHYC: Jabaily & Sytsma 2010), and nr ITS and ETS (Chew et al. 2010; Sass & Specht 2010) were screened. Based on Polymerase Chain Reactions (PCR) amplification success, variability, and number of potentially informative characters, we selected *ndh*J-*trn*F, *psb*D-*trnt*T, *rpl14-rps8-infA-rpl*36, and PRK and ETS for use in this study. Our approach was to use *atp*B-*rbc*L spacer, *mat*K, and *rps*16 intron (hereafter referred to as MM "A", "B", and "C", respectively) so that we could test the placement of *T. fasciculata* within the subfamily Tillandsioideae. The more variable markers, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl14-rps8-infA-rpl*36, and ETS and PRK (hereafter referred to as MM "D", "E", "F", "G", "H", respectively, were used to test relationships among and within "*T. fasciculata*".

DNA extraction and PCR amplification. Several methods were used to obtain genomic plant DNA, depending on locality of collection. From 2010–2013, the Qiagen TissueLyser II was used to disrupt plant tissue and then the DNeasy Plant Mini kit (Qiagen, Valencia, CA) was used to extract total genomic DNA following provided instructions. From 2004–2007, either the BIO

101 FastDNA kit or Epicure Masterpure DNA Extraction protocol was used. Preparation of 25µL PCR reactions was dependent on molecular marker. Mixture and amplification parameters followed: Barfuss et al. (2005) for *atp*B-*rbc*L spacer, *mat*K, and *rps*16 intron; Shaw et al. (2007) for *ndh*J-*trn*F, *psb*D-*trnt*T, and *rpl*14-*rpl*36; Schulte et al. (2009) for PRK, and Chew et al. (2009) for ETS.

PCR products were run on a 1% agarose gel to visualize quality and purified using ExoSap-It (Affymetrix, Santa Clara, CA) at 37°C for 30 min and then 80°C for 20 min. Purified PCR products were cycle sequenced using BigDye (Applied Biosystems, Life Technologies, Grand Island, NY) following: 1 cycle at 95°C for 3 min, followed by 50 cycles (10 sec at 96°C, 4 min; 58°C), and then 7 min at 72°C. Agencourt CleanSeq magnetic beads (Beckman Coulter, Brea, CA) were used to purify the cycle sequencing products before samples were submitted to the University of Wisconsin-Madison Biotechnology Center for Sanger sequencing.

Phylogenetic Analyses

Sequences were edited and aligned using the software modules available in the Geneious 5.4 software package (http://www.geneious.com, Kearse et al., 2012), (MUSCLE (Edgar 2004)). Maximum Parismony (MP) analyses were run in PAUP*4.0 (Swofford 2002), Maximum Likelihood (ML) analyses were run using RAxML-HPC BlackBox (8.1.11) (Stamatakis 2014), and analyses based on Bayesian inference (BI) were run using MrBayes (Huelsenbeck et al. 2001; Ronquist & Huelsenbeck, 2003) 3.2.3 on XSEDE using the CIPRES Portal V. 3.3 (Miller et al. 2010).

To evaluate monophyly of *Tillandsia fasciculata,* a subset of hypothesized members of the group (73 novel sequences) were used to construct trees from *Tillandsia* DNA sequences available in Genbank or, if unpublished, provided by Barfuss. The datasets to evaluate

monophyly were: 1) MM A+B+C, 2) MM H, and 3) MM A+B+C+G+H. To examine relationships of the purported *T. fasciculata* group we looked at loci separately, concatenated with ILD, and then put them together: 1) MM A+B+C+D+E+F+G+H (plastid+nuclear), 2) MM A+B+C+D+E+F (plastid), 3) MM G+H (nuclear).

jMODELTEST v. 0.1.1 (Posada 2008) was used to select the best-fit model of nucleotide substitution for each individual molecular marker. BIONJ was selected to compute likelihoods, with Akaike Information Criterion (AIC) calculations. MP analyses were conducted for all single and combined gene regions under the following parameters: kept best trees only, 1000 random stepwise addition sequence replicate, held 10 trees at each step, tree bisection-reconnection (TBR) branch swapping using steepest descent. The following parameters were used for MP bootstrap analyses: 1000 replicates, kept best trees only, 100 random stepwise addition sequence replicates, held 10 trees at each step, TBR branch swapping using steepest descent. ML settings included: with a mixed/partitioned model when applicable, and estimated proportion of invariable sites (GTR (Rodriguez et al 1990) GAMMA + I). For BI, settings: substitution types (Nst=6), nucleotide substitution model (4x4), model for among-site variation (rates=invgamma), character sets, Parameters for MCMC: number of generations 20,000,000), number of runs 2, number of chains to run 4), Markov chain sampled (1000), fraction of the sampled values discarded as burnin-0.25. Sumt parameters: sumt burnin value: 10, fraction of samples to be discarded (burninfrac=0.25), sumt nruns=2, 1 tree in the sumt model, type of consensus tree: 50% majority rule. To analyze trace files from BI, the estimates and trace analysis tabs were used in Tracer v1.6 (Rambaut et al. 2014).

To test for congruence among plastid and nuclear data sets the incongruence length difference test (ILD, Farris et al. 1995) was used with the following heuristic search setting: kept

best trees only, 100 random stepwise addition sequence replicates, held 10 trees at each step, TBR branch swapping.

BUCKy (Ané et al. 2007, Larget et al. 2010) was also used to test concordance of multiple loci. mbsum was run from the MrBayes files. BUCKy was run twice with two different alpha scores, 1 and 100, otherwise default settings used. Topology of tree and concordance factors were then compared to test the effect of changing the *a priori* level of discordance among loci.

Network Analyses

To assess relationships of closely related taxa and evaluate if there are any associations with geography, Splits Tree4 (Huson & Bryant 2006) was performed on individual plastid datasets. This types of analyses is useful if there is hybridization, horizontal gene transfer, or recombination. For Split Tree4, settings included: distance uncorrected P, network selected NeighborNet which uses a neighbor joining algorithm.

There were two different sample size datasets run on each software program. The subset dataset was similar to that in the phylogenetic analyses (n=73), except *Catopsis nutans*, *Tillandsia usneoides,* and *Tillandsia* sp (accession#660) were not included. We used this smaller dataset first, to compare network results to phylogenetic tree results. The second dataset was more comprehensive (ranging from 114–242 individuals), similar to population level sampling where numerous individual plants were collected across a region or country to capture the morphological and possibly genetic variability.

Biogeographic Analyses:

BEAST v1.8 (Drummond et al. 2012) was used to place the *Tillandsia fasciculata* group within an evolutionary timescale. BEAST calibration points were based on Givnish et al. (2011)

with overlapping taxa, *Tillandsia usneoides* and *T. utriculata* (Givnish et al. 2011). One taxon set consisted of all *Tillandsia* tested and *Catopsis* excluded, monophyly was checked and estimated age of 14.2 ma given based on the split of the core tillandioids. The second taxon set was all *Tillandsia* tested except for those outside the subgenus *Tillandsia*: *T. heterophylla*, *T. multicaulis*, and *T. usneoides*, monophyly was checked and estimated age 6.5 ma. Substitution model was GTR+G, with a lognormal relaxed clock. Tree prior selected was the Yule Process. MCMC was set to length of chain 50,000,000 and 10,000. The BEUTI file was excuted and run twice on BEAST v1.8 via CIPRES. Trace files were then observed on Tracer. Then files were combined on LogCombiner, and run through Tree Annotator before being visualized in FigTree.

RESULTS

Testing the circumscription of the *Tillandsia fasciculata* complex

Plastid *atpB-rbcL, matK, + rps16* loci and a 137 taxa dataset:

To test the circumscription of the *Tillandsia fasciculata* complex and placement of focus taxa in the Tillandsioideae, we generated *atp*B-*rbc*L, *mat*K, and *rps16* sequence data for 73 taxa from the *T. fasciculata* comlex and combined these new sequences with those previously published in Barfuss et al.'s (2005) phylogenetic reconstruction. The final alignment includes 137 samples and is 8205 basepairs in length. Together these three plastid markers provide 111 (4.01%) parsimonious informative characters (Table 2). The MP, ML, BI analyses using MM A, B, and C strongly support (MP and ML >75% and PP 0.99) and reconfirm the monophyly of *Tillandsia* subgenus *Tillandsia* (Figure 3). However, relationships of the *T. fasciculata* group within this subgenus remain unresolved. We are surprised by the placement of *T. beutelspacheri* that was hypothesized at one time to be a part of or closely related to the *T. fasciculata* group.

Instead, it is sister to *T. rodrigueziana* and forms a polytomy with *T. guatelmalensis, T. utriculata,* and the remaining examined taxa in the subgenus. In contrast, taxa not previously hypothesized to be part of this complex (*T. capitata, T. palmasolana, T. tricolor, T. concolor, T. klausii*, and *T. caput-medusae*), are embedded within numerous taxa of the *T. fasciculata* group.

Several clades are weakly supported (bootstrap values and posterior probabilities for MP, ML and BI are respectively indicated in parenthesis) but some geographic signal is identified: *T.* aff. *fasciculata* plants from Colombia, Venezuela, and Trinidad (62/73/.99) form a clade. Most of the small bracted varieties from the Bahamas, Cuba, Florida and one collection from eastern Dominican Republic (59/63/.96 – accession DRBAY8) consistently group together; interestingly, one *T. fasciculata* var. *uncispica* plant from Cuba is not part of this clade.

Nuclear ribosomal ETS and 101 taxa dataset

Nuclear ribosomal ETS was similarly used to examine the circumscription of the *Tillandsia fasciculata* complex. The same 73 taxa dataset was added to data from Chew et al.'s (2009) phylogenetic study, resulting in an aligned matrix of 513 basepairs. This molecular marker has 88 (17.15%) parsimonious informative characters. In MP/ML/BI trees, few clades are well supported other than a *T. rothii, T. roland-gosselinii, T. concolor, T. palmsolana* group (87/93/1) and a *T. trelawniensis, T. compressa,* plus some *T. fasisculata* plants from the Dominican Republic (85/82/.91) (Supplementary Figure 1). The most notable change is that *T.* ×*floridana* is positioned in a strongly supported clade (84/95/1) with *T. juncea* and *T. balbisiana,* but not with other *T. fasciculata* varieties as in the plastid tree.

Plastid *atpB-rbcL*, *matK*, *rps16*, Nuclear ribosomal ETS + Nuclear PRK and an 81 taxa dataset

The five datasets (MM A+B+C+G+H) were concatenated to further assess circumscription of the *Tillandsia fasciculata* group. As with the abovementioned plastid phylogeny (MM A+B+C, 137 dataset), *Tillandsia rodrigueziana* and *T. beutelspacheri* are sister to each other (100/91/1) and fall outside the *T. fasciculata* group (Supplementary Figure 4). *Tillandsia rotundata* forms a clade with *T.* ×*polita*, *T. welzii*, and *T. tricolor*, again outside the *T. fasciculata* (63/75/.93) group. This result is surprising considering that *T. rotundata* was recognized as a variety of *T. fasciculata.* Similar to the ETS phylogenetic tree, a *T. rothii*, *T. roland-gosselinii*, *T. concolor*, *T. palmsolana* group is formed and outside the *T. fasciculata* group. Moreover, *T. marbascoensis* is included and there is strong statistical support for this clade (100/100/1). As with the ETS results, *T.* ×*floridana* did not form a clade with the *T. fasciculata* varieties from Bahamas, Cuba and FL. One of the most notable findings in our study is that the northern South America clade of plants is not a part of the *T. fasciculata* group. *Tillandsia* aff. *fasciculata* plants from Colombia, Venezuela, and Trinidad are strongly supported (99/100/1) that had previously only been hinted at (with weak or no statistical support) in the previous two tree analyses. Within the *T. fasciculata* group, clades are formed (e.g., small bracted *T. fasciculata* varieties from the Bahamas, Cuba, and Florida, and *T. fasciculata* var. *venosispica* from Puerto Rico and Lesser Antilles), but with weak statistical support (MP and ML <50%, PP<99%).

Testing relationship of the *Tillandsia fasciculata* focus group

*atp*B-*rbc*L

MP, ML, and BI results (n=76) (Supplementary, Figure 8) recover two weakly supported clades: *T. beutelspacheri* and *T. rodrigueziana*; (83/99/-) and *T.* aff. *fasciculata* plants from Colombia, Venezuela, and Trinidad (-/79/81).

*mat*K

One regional clade, the small bracted *Tillandsia fasciculata* varieties from Bahamas, Cuba, and Florida (63/100/.80) is found in MP, ML, and BI trees (n=76) (Supplementary Figure 9). However, several polytomy groups are formed including *T.* aff. *fasciculata* plants from Colombia, Venezuela, and Trinidad (86/100/.83) and *T. fasciculata* var. *venosispica* plants from Puerto Rico and the Virgin Islands plus one *T.* aff. *fasciculata* from the Dominican Republic.

rps16

Only two weakly supported clades are found in the MP, ML, and BI analyses (n=76): a *Tillandsia beutelspacheri* and *T. rodrigueziana* (55/100/.97) group and *T. acostae* (63/99/.86) clade (Supplementary Figure 10).

*ndh*F-*trn*F

In the *ndh*F-*trn*F 76 taxa dataset, the only recovered clades in the MP, ML, and BI trees are *Tillandsia usneoides* and #660 (74/98/1), and a mixture of taxa not even hypothesized to be related that included *T. beutelspacheri*, *T. rodrigueziana*. *T. concolor*, *T. flavobracteata*, and two *T.* aff. *fasciculata* plants, one from Costa Rica and another from Western Mexico (64/98/.94) (Supplementary Figure 12).

*psb*T-*trn*T

MP, ML, and BI analyses recovered several weakly supported clades not found in the previous locus datasets (n=76) (Supplementary Figure 13). *Tillandsia beutelspacheri* and *T. rodrigueziana* were sister to each other (-/88/.87). Also, a *T. jalsico-monticola* and *T. grossispicata* clade (61/61/-); *T. fasciculata* plants from Jamaica (63/50/.91); and a clade of *T. fasciculata* var. *venosispica* plants from Puerto Rico, Virgin Islands, and Guadeloupe(-/57/.83).

Splits Tree results (n=66), find three main clusters that are also suggested by phylogenetic analyses: small bracted *Tillandsia fasciculata* varieties from the Bahamas, Cuba, and Florida; *T. fasciculata* var. *venosispica* from Puerto Rico and the Virgin Island; and *T. fasciculata* plants from Jamaica (Figure 7).

With additional novel sequences added, Splits Tree4 results (n=114) reaffirm groups of: small bracted *Tillandsia fasciculata* varieties from the Bahamas, Cuba, and Florida + #561, #1111, #585, #1108, and #1180; *T. fasciculata* from Jamaica (except #818); and *T. fasciculata* var. *venosispica* from Puerto Rico and the Virgin Islands (Figure 8). Interestingly, neither St. Lucia nor Guadeloupe samples are a part of this cluster vs. phylogenetic analyses.

rpl14-rpl36

As with the other plastid locus MP, ML, and BI trees, the *rpl14-rpl36* 76 taxa dataset provides evidence for some weakly supported clades: the small bracted *Tillandsia fasciculata* varieties from the Bahamas, Cuba, and Florida + *T. botteri*, *T. inopinata* (1111), and *T. welzii*; and *T. kumae* (-/64/.70) including *T.* aff. *fasciculata* (Dominican Republic, BAY8) (Supplementary Figure 14).

Splits Tree results (n=73) finds groups comprised of: small bracted *Tillandsia fasciculata* varieties from the Bahamas, Cuba, and Florida, and *T. fasciculata* var. *venosispica* from Puerto Rico and the Virgin Islands group + *T. concolor*; and *T. beutelspacheri* and *T. rodrigueziana* (Figure 9).

Concatenated 6-plastid loci and a 76 taxa dataset

The combined datasets of *atpB-rbcL*, *matK*, *rps16*, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl14-rps8-infA-rpl*36 have 0.96% parsimonious informative characters. The ILD test shows that there is no significant difference when combining these two datasets (p=0.390000, sum of lengths for original partition 252). The loci used by Barfuss et. al (2005, MM A+B+C) vs. Shaw et. al (2007, MM D+E+F) was then compared to assess utility of the latter that have not been used on *Tillandsia* prior to this study. The percentage of parsimonious informative characters was low, 0.94%, for the molecular markers *atp*B-*rbc*L, partial *mat*K, and *rps16*. Of these, *mat*K was the most informative (1.36%) compared to *rps*16 (1.01%) and *atp*B-*rbc*L (0.50%) (Table 2). Molecular markers *ndh*F-*trn*F, *psb*D-*trn*T, and *rpl14-rpl36* were slightly more informative, 0.97%, with *psb*D-*trn*T (1.45%) higher than *rpl14-rpl36* (1.17%) and *ndh*F-*trn*F (0.32%) (Table 2).

For the 6-plastid loci tree, *Tillandsia beutelspacheri* and *T. rodrigueziana* are sister to each other and again outside the *T. fasciculata* group (Supplementary, Figure 5). The MM A+B+C (Supplementary Figure 7) and MM D+E+F (Supplementary Figure 11) trees also support this finding. *Tillandsia* aff. *fasciculata* plants from Colombia, Venezuela, and Trinidad form a weakly supported clade in the 6-plastid loci (64/79/.98) and MM A+B+C tree (63/97/95), but not the MM D+E+F tree. This pattern (6-loci and MM D+E+F, but not MM A+B+C) was also found in a mostly Jamaican plants clade (64/56/.94, 62/54/.94, respectively).

ETS + PRK with a 76 taxa dataset

The ETS and PRK dataset has more parsimonious informative characters than the plastid markers 9.86% vs. 0.96% (Table 2). ILD results suggest that the two datasets should not be combined (p=0.10000, sum of lengths for original partition, 381). However, topology does not seem to change whether the datasets were combined or when they were separate (Supplementary Figure 6).

With MP, ML, and BI analyses, several clades are resolved, and some with high support: *Tillandsia rothii, T. roland-gosselinii, T. concolor, T. palmasolana* (99/98/1); and *T.* aff. *fasciculata* plants from Colombia, Venezuela, and Trinidad clade (90/96/.99). One of the biggest surprises is that *T. beutelspacheri* and *T. rodrigueziana* are embedded with the *T. rotundata*/*T. tricolor* clade with weak statistical support (-/65/55), and are not separate as in the plastid analyses. Another notable change is that *T* ×*floridana* is not with other small bracted *T. fasciculata* varieties from the Bahamas, Cuba, and Florida compared to the plastid datasets.

Between these two markers tested, ETS (8.19%) was more parsimonious informative than PRK (6.1%). In the ETS MP, ML, and BI trees, the *Tillandsia rothii, T. roland-gosselinii, T. concolor, T. palmasolana, T. concolor, T.* ×*floridana* group was strongly supported (75/82/1) (Supplementary Figure 15). The other clades were weakly resolved and include: *T.* aff. *fasciculata* from Colombia, Venezuela, and Trinidad (62/67/.91), and *T. rotundata, T. welzii, T.* ×*polita,* and *T. tricolor* (65/68/.85). The PRK tree (Supplementary Figure 16) was similar in topology to the ETS tree. There was a weakly supported *T. rothii, T. roland-gosselinii, T. concolor, T. palmasolana, T. concolor,* and *T. ionantha* group (56/60/.56) (Supplementary Figure 16). There is strong support for *T.* aff. *fasciculata* plants from Venezuela, Colombia, and Trinidad (97/100/1).

Eight loci: *atpB-rbcL*, *matK*, *rps16*, *ndh*J-*trn*F, *psb*D-*trnt*T, *rpl14-rps8-infA-rpl*36, ETS and PRK

With a 76 taxa dataset

In MP, ML, and BI analyses we find that *Tillandsia beutelspacheri* and *T. rodrigueziana* are related to each other and this is strongly supported by confidence statistics (Figure 4). Results also suggest (74/88/.58) that they are sister to the *T. fasiculata* complex and other related taxa (Figure 4). Other strongly supported clades are: a *T. marabascoensis, T. palmasolana, T. concolor, T. rothii* and *T. roland-gosselnii* group (100/100/1), and a *Tillandsia* aff. *fasciculata* clade from plants in Colombia, Venezuela, and Trinidad (100/100/1) (Figure 5). Within the *T. fasciculata* group, there is support of taxa when multiple samples were included: *T. rhomboidea* (99/1001) and *T. jalsico-monticola* (90/94/1), *T. acostae* (85/90/1), and *T. kuzmae* (64/78/1). The *T. fasciculata* plants from Jamaica also form a clade (92/95/1).

With a 74 taxa dataset excluding two hybrids

Tests were conducted to examine the effect of removing the purported hybrids, *T. ×floridana* or *T. ×polita*, has on tree topology. There is little difference in overall topology when both purported hybrids (*Tillandsia ×floridana* and *T. ×polita*) are removed (Supplementary Figure 4). The *T. rotundata* group forms a grade when hybrids are excluded, whereas inclusion of hybrids results in a weakly supported clade (59/68/.58) (Figure 4). Separate tests were conducted to examine the effect of removing each individual hybrid, *T. ×floridana* or *T. ×polita*. Generally there is no difference in topology if one of the purported hybrids is excluded. The main change observed is placement of a mostly Jamaican taxa clade. When *T. ×floridana* is excluded, this mostly Jamaican taxa clade is embedded with and sister to the small bract varieties from the Bahamas, Cuba, and Florida (not shown). Whereas, when *T. ×polita* is excluded, the

mostly Jamaican taxa still form a clade but its placement is unresolved within the Caribbean clade (not shown).

Concordance Analysis

Although the ILD test found that the plastid and nuclear datasets should not be concatenated (p=0.010000, sum of lengths for original partition 661), there is no conflict in the position of strongly supported clades evident in topologies compared among trees of individual datasets.

There are no differences in topology between the two BUCKy analyses when the alpha, a priori, settings were changed, (alpha 1 (Supplementary Figure 17) and 100 (Figure 6)). Concordance factors, genomic support as a percentage of genes that have that clade, are also similar. Overall, the topology from the BUCKy trees is similar to the concatenated eight loci trees from MP, ML, and BI analyses (Figure 5) and the CF scores mirror trends in support levels seen in phylogenetic MP/ML/BI trees. For example, for the northern South American "T. aff. fasciculata" plants, MP/ML/BI values were 100/100/1, but and in the BUCKy trees, a CG of 0.658 with alpha as 100 (Figure 6) and a CF 0.657 with alpha as 1 (Supplementary Figure 17) The main difference is that the BUCKy tree finds *Tillandsia* ×*floridana* outside the small bract varieties from the Bahamas, Cuba, and Florida consistent with the nuclear dataset (Supplementary Figure 6) but not plastid (Supplementary Figure 5) or eight loci (Figure 5) dataset.

BEAST

Based on estimated times of the core tillandsioids and age of *Tillandsia usneoides* (Givnish et al. 2011), our results suggest that *Tillandsia fasciculata* s.l. arose about 1.75–4.75

ma, and that *T. fasciculata* s.s. arose about 1–3.2ma. (Figure 5). These findings are consistent with Givnish et al. (2011) with an estimated date of "older" crown age of *T. utriculata* as ca. 2.25-3.25 ma.

DISCUSSION

Monophyly and Circumscription of the *Tillandsia fasciculata* complex: excluded species

1) Does molecular data support the relationships proposed using a morphology-based approach?

Molecular data supports the inclusion of most of the taxa predicted to belong to the *Tillandsia fasciculata* complex sensu lato (related taxa include: *T. acostae, T. botteri. T. flavobrteata, T. grossipicata, T. hubertiana, T. inopinata, T. jalisco-monticola,* and *T. magnispica*; Table 1). *Tillandsia fasciculata* s.s taxa that were hypothesized to be in this group are supported from this study --*T. fasciculata* varieties and *T. compressa* (Table 1). Details regarding particular species and groups of species will be discussed in greater detail below. Some of the most interesting findings from our study are that *T. fasciculata* s.l. forms a clade only if: *T. trelawniensis* is included within it, and if *T. beutelspacheri, T. ×polita,* and *T. rotundata* are excluded. Additionally, taxa from northern South American (Colombia, Venezuela, and Trinidad) that would have historically been designated as "*T. fasciculata*" based on their morphology (e.g., digitate inflorescence) appear to be distantly related to the *T. fasciculata* clade.

Tillandsia trelawniensis

Morphological evidence based on similar spike characteristics indicated that the Jamaican endemic *Tillandsia trelawniensis* might be related to *T. polystachia* (Proctor 1982). The latter species was not included in our study because we lack material. However, we can state definitely that *T. trelawniensis* is part of the *T. fasciculata* s.s. clade, according to our results. Moreover, it is in a separate clade from other *T. fasciculata* plants collected in Jamaica, affirming its rank as a distinct species. Given their morphological similarity, we expect *T. polystachia* to be sister to *T. trelawniensis*, and so think it is likely that it is an element of the complex as well.

Tillandsia beutelspacheri and *T. rodrigueziana*

Three taxa (*Tillandsia beutelspacheri*, *T.* ×*polita*, and *T. rotundata*) hypothesized to be a part of the *T. fasciculata* species complex are not a part of this group according to our phylogenetic tree (Figure 4) and in all network results (Figure 9). *T. beutelscpacheri* (Smith 1974) was originally named *T. insignis* (Matuda 1971), although no morphological comparisons to existing species or hypothesized species relationship were given. Luther, however, later placed *T. beutelscpacheri* within the *T. fasciculata* complex. Our molecular phylogenetic reconstructions strongly support *T. beutelspacheri* as sister to *T. rodrigueziana*, with both taxa outside the *T. fasciculata* complex. Mez (1919) did not compare *T. rodrigueziana* to other *Tillandsia* plants in his species description, but it was considered to be morphologically similar to to *T. fasciculata* (Smith and Downs 1977).

The *Tillandsia rotundata* assemblage: *T. rotundata, T. welzii, T. ×polita*, and remarks on *T. tricolor*

Tillandsia rotundata has undergone nomenclatural changes mainly dealing with differing opinions on its rank. Smith (1945) described *T. fasciculata* var. *rotundata* based on plant material from Central America. He distinguished it as having "very short broad primary bracts and spikes" (Smith 1945). Later, Gardner (1984a, 1991) elevated *T. rotundata* to specific rank based on several morphological characters such as globose head with densely digitate spikes, cucullate, broad floral bracts, and its higher elevation habitat. Genetic evidence from this study finds that *T. rotundata* is outside the *T. fasciculata* s.l. group, thus supporting Gardner's hypothesis that *T. rotundata* is not a variety of *T. fasciculata*. Two different *T. rotundata* samples were included in this study. Even though both accessions are embedded in a clade with *T. welzii*, *T. ×polita*, and *T. tricolor*, the two *T. rotundata* samples are not sister to one another.

In Ehlers (1991) description of *Tillandsia welzii*, she compared the Guatemalan plant to both *T. fasciculata* var. *clavispica* and *T. rodrigueziana*. In contrast, phylogenetic trees from this study found that this plant is more closely related to the *T. rotundata*, *T. ×polita*, and *T. tricolor* clade (Figure 4–6, Supplementary Figure 6). In the plastid and MM C+D+E trees (Supplementary Figure 11), *T. welzii* is in the clade with small bracted *T. fasciculata* varieties from the Bahamas, Cuba, and Florida.

Based on morphometric analyses and pollen infertility, Gardner (1984b, 1991) classified *Tillandsia ×polita* as a natural hybrid between *T. rotundata* and T. *rodrigueziana*. The original species description by Smith (1941) compared *T. polita* as a reduced form *of T. fasciculata* but with exserted sepals. Treatment of *T. polita* as a species (Smith and Downs 1977, Luther 2008, Espejo et al. 2004), rather than a natural hybrid, is still being debated. Results from this study

found that overall tree topologies are not impacted when *T.* ×*polita* was included or excluded from analyses (vs. *T.* ×*floridana;* see below). However, the placement of *T.* ×*polita* in plastid (Supplementary Figure 5) vs. nuclear trees is incongruent, consistent with a result that might be expected from a recent hybrid. Nuclear (Supplementary Figure 6) and BUCKy trees based on all loci sampled (Figure 6 and Supplementary Figure 17) show an affinity between *T.* ×*polita* and many of the taxa in the *T. rotundata* group; whereas, in the plastid tree (Supplementary Figure 5), *T.* ×*polita* is embedded in a clade with samples of *T. rotundata* and *T. welzii*, and *T. acostae*, *T. magnispica*, *T. hubertiana*, and *T.* aff *fasciculata* from Guatemala, taxa typically not associated with *T.* ×*polita*. If this taxon is a natural hybrid, then our results detected a close relationship to one of its purported parents, *T. rotundata*, but no clear association with a second obvious parent, and certainly not a relationship with *T. rodrigueziana* as hypothesized by Gardner. It seems plausible to speculate that *T.* ×*polita* is a taxon of hybrid origin, that *T. rotundata* was one of its parents (maternal?), and that it has repeatedly backcrossed with that species and/or other taxa closely related to it.

There were no morphological comparisons in the original species description of *Tillandsia tricolor* (1831) to other species. Later *T. tricolor* was hypothesized to have a (morphological) affinity to *T. concolor* (280) and *T. lampropoda* outside of the *T. fasciculata* complex (Smith and Downs 1977, Luther 2008). Results from this study support the idea that *T. tricolor* is not a part of *T. fasciculata* s.l. Moreover, these results affirm Barfuss et al. (2011) findings in their phylogenetic study of the subfamily that *T. tricolor* is not a part of the *T. fasciculata* clade.

Revisiting classification of northern South American "*Tillandsia fasciculata*" plants

One of the more significant findings from this study is that *Tillandsia* plants from northern South America (Colombia, Venezuela, and Trinidad) that historically would have been designated as "*T. fasciculata*" are not part of the *T. fasciculata* s.l. clade. Typically any *Tillandsia* plants from this region that superficially resembles *T. fasciculata* have been lumped into this taxon. Molecular results from this study consistently find these plants positioned outside of *T. fasciculata* s.l. (Figures 4, 5, 6 and Supplementary Figures 6, 16, and 17) suggesting that northern South American '*T. fasciculata*' plants should be recognized as their own separate species. This study recommends a nomenclatural change back to its oldest name, *Tillandsia glaucophylla*. *Vriesia glaucophylla* is the oldest northern South American synonym associated with the name *T. fasciculata.* In 1848, Hooker described *Vriesia glaucophylla* from plant material from Colombia. Beer (1857) later recognized it as *Platystachys glaucophylla* and Baker (1887) designated it as *Tillandsia glaucophylla*. *Tillandsia compressa* var. *oligostachya* Baker ex André (1888) and *T. fasciculata* var. *bogotensis* André (1889) were also synonymized with *T. fasciculata*. Based on morphological similarity to *T. glaucophylla* and given the fact that the type descriptions are based on plants from Colombia, it is also recommended that these names be synonymized under *Tillandsia glaucophylla*.

The *Tillandsia roland-gosselinii* complex, including remarks on *T. concolor* and *T. palmasolana*

The *Tillandsia roland-gosselinii* group is hypothesized to consist of: *T. rothii, T. pacifica, T. marabasocensis*, and *T. macvaughii* (Luther 2008, Espejo and López-Ferrari 2005, Ehlers 1992). Within this group, additional taxa have been compared as well. Espejo and López-Ferrari (2005) compared *T. macvaughii* to *T. marabasocensis*, *T. maritima*, and *T. rothii*, while *T. maritima* has been compared to *T. fasciculata* (Matuda 1971). Relationships among taxa in the *T.*

roland-gosselinii complex and its relationship to *T. fasciculata* have been uncertain until this study. Phylogenetic trees from concatenated data finds strong support for a sister relationship between *T. roland-gosselinii* and *T. rothii* (Figure 5). Some even believe that *T. rothii* may be a hybrid between *T. roland-gosselinii* and *T. jalisco monticola*. (http://www.bromeliad.org.au/pictures/Tillandsia/rothii.htm). In trees with concatenated (Figure 5), plastid (Supplementary Figure 5), and nuclear data (Supplementary Figure 6), *T. rothii* and *T. roland-gosselinii* are embedded within the same clade, while *T. jalisco-monticola* is in a separate clade. Furthermore, in this investigator's field observations, *T. jalisco-monticola* is found in high elevation pine-oak habitats whereas *T. rothii* grows at lower elevations. There is also strong support for a clade that includes: *T. roland-gosselinii*, *T. rothii*, *T. concolor*, *T. palmasolana*, and *T. marabasocensis*, although there are minor topological discrepancies in the placement of *T. concolor*, *T. palmasolana*, and *T. marabasocensis* depending on individual marker used.

Traditional taxonomic treatments have not included either *Tillandsia concolor* or *T. palmasolana* within the *T. fasciculata* complex. However, several authors have hypothesized that *T. concolor* has an affinity to *T. fasciculata* based on morphological characters (Smith and Downs 1977, Luther 2008) while others suggested that *T. concolor* forms its own species complex with other taxa (Carnevali and Ramirez, per. comm). Phylogenetic results from this study consistently find that *T. concolor* is embedded in the *T. roland-gosselini* group (Figure 4). Matuda (1973) compared *Tillandsia palmasolana* to *T. tricolor*. As mentioned in the previous section, this study found that *T. tricolor* was more closely related to the *T. rotundata* group.

Circumscription of *Tillandsia fasciculata* s.l. (Table 1, Figure 4)

2) What taxa compromise the *T. fasciculata* complex?

3) Within this complex, what are species relationships to one another?

Tillandsia rhomboidea, with remarks on synonymy of *T. acostae*

Treatment and possible synonymy of *Tillandsia rhomboidea* and *T. acostae*, a pair of relatively small statured species, has been problematic. *Tillandsia rhomboidea* was described by André (1888) from a plant in Colombia. Smith and Downs (1977) recognized it in the subgenus *Allardtia*, but it was transferred to subgenus *Tillandsia*. Its stature is a smaller version of *T. fasciculata* and was believed to be a part of the *T. fasciculata* complex (Luther 1994). *Tillandsia acostae* was considered a synonym of *T. rhomboidea* by Luther (1994). *Tillandsia acostae* was described from a plant in Costa Rica by Mez & Tonduz (1916). Smith and Downs (1977) recognized that *T. acostae* loosely shared morphological characteristics with *T. fasciculata*. Molecular results from this study find that the two plant samples of *T. rhomboidea* and *T. acostae* each form separate clades (Figure 4, Supplementary Figure 4) that are not sister to each other, suggesting that they might very well be considered separate species. MP, ML, and BI analyses find that these taxa are positioned within the *T. fasciculata* s.l. group (Figure 4), while BUCKy analyses suggested they might be excluded from the *T. fasciculata* s.s. clade (Figure 6), but inconclusively in a polytomy with other tillandsias sampled in this study. Additionally, the Colombian samples of *T. rhomboidea* do not cluster with northern South America "*T.* aff. *fasciculata*" plants validating that *T. rhomboidea* is a species. In the BUCKy analyses *T. acostae* forms a clade with the *T. fasciculata* plant from Guatemala suggesting a Central American biogeographic affinity.

Tillandsia jalisco monticola and *T. magnispica* with remarks on MXCHAC6 and *T. lampropoda*

Several western Mexico tillandsias have been hypothesized to have an affinity to *Tillandsia fasciculata*. Morphologically, these plants tend to have 1 to few robust spike(s), and often inhabit higher elevation pine oak forests. Matuda (1975a) compared *T. jalisco-monticola* to *T. lampropoda* which itself was compared to *T. fasciculata* by Smith (1938). Matuda (1975a) described *Tillandsia jalisco-monticola* as having a simple, awl-shaped inflorescence, one of the largest (18-20 cm x 7.5 cm) in this species complex.

Tillandsia magnispica is another few branched, large inflorescence member of this group. According to Espejo et. al. (2009), the differences between *Tillandsia magnispica* and *T. jalisco-monticola* are: the former has thinner spikes, longer petals, and is endemic to Oaxaca while the latter is usually simple, with wider spikes and occurs in Colima, Jalisco, and Michoacan.

Results from this study find that the two samples of *Tillandsia jalisco-monticola*, one wild collected and one from a living research collection, formed a strongly supported clade. In the MP, ML, and BI analyses, even though *T. jalisco-monticola*, *T. magnispica*, *T. hubertiana* (See below description), and MX12CHAC6 (*Tillandsia* sp.) formed a clade, there is weak statistical support. MX12CHAC6 was collected at the same location as *T. magnispica*, but was not flowering and did not have a dried inflorescence to help with species classification. Results suggest it is either a new species or natural hybrid, as the plant co-occurs with another *Tillandsia* sp. Another, unlikely, scenario is that this sample is *T. magnispica* which makes *T. magnispica* paraphyletic.

Smith (1938) compared *Tillandsia lampropoda* to the larger varieties of *T. fasciculata*. *Tillandsia lampropoda* occurs throughout southern Mexico and Central America. He noted the

differences in leaf characters including how the scales are distributed in *T.fasciculata* (uniform across blade and sheath) vs. *T. lampropoda* (overlapping scales on blade, and separated, punctiform scales on sheath). Smith (1964) also described *T. lampropoda* var. *major* based on a plant from Guatemala and is known from the type locality only. Distinguishing morphological differences include: inflorescence digitate with ca. 3 spikes, and color of petal (white vs. yellow in *T. lampropoda*).

Miscellaneous western Mexico "*Tillandsia fasciculata*": *T. huberitana* and *T. grossipicata*

Tillandsia huberitana and *T. grossipicata* are two more species whose relationship to *T. fasciculata* was hypothesized but had yet been tested in a phylogenetic context. Matuda (1975b) described as the spikes of *T. hubertiana* longer and narrowly lanceolate compared to *T. fasciculata.* In the BUCKy analyses, even though *T. hubertiana* is embedded with the other Mexican species, it is more closely related to taxa from eastern Mexico (Figure 6, Supplementary Figure 17). But in MP, ML, and BI analyses, placement of *T. hubertiana* was with other western Mexico occurring taxa (Figure 4).

Tillandsia grossipicata is another western Mexico distributed species morphologically similar to *T. fasciculata*. *T. grossipicata* is delimited from *T. fasciculata* by its larger vegetative floral characters (Espejo et al. 2008), along with its range. While *T. grossipicata* is found in western Mexico, *T. fasciculata* s.s. occurs in eastern Mexico and the Caribbean. In the BUCKy analyses *T. grossipicata* is embedded within other western Mexican tillandsias (Figure 6, Supplementary Figure 17), although statistical support for a relationship between *T. grossipicata* and other western Mexican tillandsias was not found in MP, ML, and BI analyses (Figure 4).

Tillandsia flavobracteata, an endemic from eastern Mexico

Matuda (1975a) described *Tillandsia flavobracteata* from a plant collected in Veracruz and compared it to *T. achyrostachys* which was itself compared by Baker (1889) to *T. xiphostachys*. According to Matuda (1975), *T. flavobracteata* can be distinguished from *T. achrostachys* by its larger size and rigid, subulate-caudate leaves. Luther transferred it to subgenus *Tillandsia* and considered it within the *T. fasciculata* complex. Barfuss et al. (2011) study confirmed that *T. achyrostachys* belonged to the subgenus *Tillandsia* and is not closely related to *T. xiphostachys* which is itself a member of the Xiphioides clade. The results from this study indicate that the exact placement of *T. flavobracteata* within the *T. fasciculata* s.l. remains unclear, although in the BUCKy analyses *T. flavobracteata* formed a clade with the eastern Mexico tillandsias sampled (Figure 6, Supplementary Figure 17).

Circumscription of *Tillandsia fasciculata* s.s.

"*Tillandsia fasciculata*" from Eastern Mexico: *T. botterii and T. inopinata*

Tillandsia botterii and T. inopinata are two species occurring in eastern Mexico that have been compared to *T. fasciculata*. Baker's (1889) description of *T. botterii* is based on a Morren drawing from a plant sent by M. Devansaye. Baker (1889) considered *Tillandsia botterii* "scarcely more than a variety of *T. fasciculata*." It is known only from Veracruz, Mexico (Espejo et al. 2004). Another eastern Mexico "*T. fasciculata*" type plant is *T. inopinata*. Espejo et al. (2008) described *T. inopinata* as larger sized than *T. fasciculata* s.s., with more spikes (11-26.5 cm x 1.2 -2 cm) occurring in the Mexican biogeographic zones of Tamaulipas, Sierra Madre Oriental and Mexican Plateau (Morrone et. al. 2002). Molecular results from this study support

the placement of *T. botterii* in the *T. fasciculata* s.s. group; it tends to group with the smaller bracted *T. fasciculata* varieties from the Bahamas, Cuba, and Florida.

In the MP, ML, and BI trees of three plastid and both nuclear loci (Figure 5), "*Tillandsia inopinata"* appears scattered within the *T. fasciculata* group: one sample (#1111) consistently is sister to *T. botterrii* and in the *T. fasciculata* s.s. group while another sample #568 is in the *T. fasciculata* s.l. clade. In the BUCKy analyses (Figure 6, Supplementary Figure 17), both samples are in the *T. fasciculata* s.l. group, but still do not form a monophyletic clade. Even though both plants were collected near the type locality of *T. inopinata*, these findings suggest possible incomplete lineage sorting or hybridization.

Tillandsia kuzmae, a small *T. fasciculata* type plant from the Dominican Republic

Yet another small *Tillandsia fasciculata* looking plant is *T. kuzmae*. Ehlers (2000) described *T. kuzmae* as having spikes less than 10 cm with acuminate, nerved floral bracts. She also compared *Tillandsia kuzmae* to *T. fasciculata* var. *venosispica* (Ehlers 2000). This study supported Ehler's hypothesis that *T. kuzmae* is a unique entity that belongs to the *T. fasciculata* group. *Tillandsia kuzmae* forms a monophyletic clade, but it is sometimes embedded within or sometimes sister to *T. fasciculata* var. *venosispica* group from Puerto Rico and the Virgin Islands. In the MP, ML, and BI analyses of all loci sampled together (Figure 4), a *T. fasciculata* type plant also from the Dominican Republic (DRBAY8) was in the weakly supported *T. kuzmae* clade, but was not in the BUCKy analyses (Figure 6, Supplementary Figure 17).

Tillandsia compressa, a convoluted taxonomic treatment with comments on *T. buchii*

The taxonomy of *Tillandsia compressa* is convoluted. *Tillandsia compressa* was described by Shultes (1830) based on a plant from Jamaica. He compared this plant to *T.*

fasciculata. Since then, there have been numerous nomenclatural changes with some authors recognizing it as *T. fasciculata* var. *vensosispica* (Smith and Downs 1977) while others believing it to be a valid species. A varietal designation was ascribed to *T. compressa* var. *oligostachya* by Baker ex Andre (1888), but the name was synomized to *T. fasciculata* var. *fasciculata* by Smith and Downs (1977). The relatedness of *T. compressa* and the Haitian *T. buchii* (Urban 1917) is also contested. *Tillandsia buchii* was synonymized as *T. compressa* and later *T. fasciculata* var. *vensosispica*. Results from this study found that plants collected in Jamaica were part of the core *T. fasciculata* group. Even though several samples from Jamaica were included that would historically be classified as either *T. compressa*, *T. fasciculata*, or *T. fasciculata* var. *venosispica*, a monophyletic group was not formed.

Plants collected in the pine oak forest of the Dominican Republic morphologically resemble what would be considered *T. buchii*. Given the type location of *T. buchii* (Haiti), and the samples that were collected which had both a distinct morphology (thick branches) and habitat in high elevation pine oak forest, this study recommends that *T. buchii* be considered a synonym of *T. compressa* s.s. Based on field and herbarium observations, *T. compressa* s.s. is restricted to Hispaniola and Jamaica. Furthermore, *T. compressa* should not be confused with *T. fasciculata* var. *vensosispica* plants that are strongly associated with Puerto Rico, the Virgin Islands, and Lesser Antilles.

Tillandsia fasciculata var. venosispica s.s.

Tillandsia fasciculata var. *venosispica* was described by Mez in (1896). It belongs to the larger bracted varieties of *T. fasciculata*, but has nerved floral bracts. Molecular results from this study support *T. fasciculata* var. *venosispica* as a clade, although there is weak support and placement of *T. kuzmae* remains unresolved (Figure 5). Biogeographic signal suggests that this

clade is strictly from Puerto Rico and the Lesser Antilles, and that *T. fasciculata* var. *venosispica* type plants from Mexico, the Greater Antilles (excluding Puerto Rico), and northern South America should be reexamined.

Small floral bracted *T. fasciculata* varieties: *clavispica*, *densisipica*, *laxispica*, and *uncispica*

The smaller bracted *Tillandsia fasciculata* group, as divided by Mez (1896) consisted of: *T. fasciculata* var. *clavispica*, *T. fasciculata* var. *densispica*, *T. fasciculata* var. *laxispica*, and *T. fasciculata* var. *uncispica. Tillandsia fasciculata* var. *densispica* forma *alba*, was added by Foster (1953) and *T. fasciculata* var. *floridana* by Smith (1967, see section on FL hybrids below for more details). Confusion in morphological characters and distribution has been troublesome for taxonomists especially at the varietal rank: *T. fasciculata* var. *densispica*, *T. fasciculata* var. *laxispica*, and *T. fasciculata* var. *uncispica*.

Molecular results from this study show a clade of small bracted *Tillandsia fasciculata* in both phylogenetic analyses (Figure 4) and network analyses (Figures 7–9). Within this clade, the varieties are unresolved and formed a polytomy. Even though *T. fasciculata* var. *clavisipica* forms a polytomy with the other small bract varieties, there is morphological evidence (Sidoti, unpublished) and clear geographic boundaries (endemic to Cuba), that warrants its continued classification as a variety, and possibly even justification to species rank (Hechavarría, personal comm.). Two other *T. fasciculata* type specimens from Cuba are *T. fasciculata* var. *uncispica* and *T. fasciculata* var. *laxispica. Tillandsia fasciculata* var. *uncipica* is essentially a smaller version of *T. fasciculata*. Its distribution is mainly in Cuba, but some specimens have been recognized from plants from eastern Mexico and the Bahamas. In the MP, ML, and BI analyses (Figure 5), the two samples tested do not form a monophyletic group and one sample (#287) is

not even in the polytomy of other small bracted *T. fasciculata* varieties. In the BUCKy analyses both *T. uncispica* samples belong to the small bracted clade (Figure 6).

As currently classified, *Tillandsia fasciculata* var. *laxispica* is more widely distributed with specimens from the Bahamas, Cuba, and Mexico (Smith and Downs 1977). Differences between *T. fasciculata* var. *densispica* and *T. fasciculata* var. *laxispica* are mainly due to lax branching pattern. This study found that there is neither (phylogenetic) molecular nor morphological (Sidoti, unpublished) evidence to distinguish the two taxa. However, population genetic evidence supports recognition of this variety (Chapter 2).

Tillandsia fasciculata var. *densispica* and *Tillandsia fasciculata* var. *densispica* f. *alba* are described from plants in Florida. *Tillandsia fasciculata* var. *densispica* type looking plants are often classified with this varietal name if they have small branches and floral bracts. Molecular evidence from this study suggests this taxon is restricted to the Caribbean Islands and that taxa historically from outside the West Indies need to be reevaluated and reclassified. *Tillandsia fasciculata* var. *densispica* f. *alba* can co-occur with the purple flowered *Tillandsia fasciculata* var. *densispica*, but the white flowered form is more restricted in pockets in southern Florida than the more widespread purple form. This white petal color phenomenon has been observed in "*Tillandsia fasciculata* var. *densispica*" plants from Mexico (Ramriez 2004).

Florida hybrids:

In Florida there are two purported natural hybrids attributed to the complex: *Tillandsia* ×*floridana* L.B. Smith and *T.* ×*smalliana* (Luther 1985). The purported parents of *Tillandsia* ×*floridana* are the central to southern FL ranging *T. fasciculata* var. *densispica* and the northern to Central FL distributed *T. bartramii* (Luther 1985). Key morphological evidence suggests it is

intermediate in form being a medium sized plant with pink, lepidote floral bracts (Luther 1985). In the MP, ML, and BI analyses of this study, *T.*×*floridana* is positioned among the small bracted *T. fasciculata* varieties from the Bahamas, Cuba, and Florida based on plastid data (Supplementary Figure 5), but in the BUCKy analyses (Figure 6) and nuclear (Supplementary Figure 6) dataset it falls outside the *T. fasciculata s.l.* clade as would be expected for a hybrid taxon. The *psbT-trn*T Splits Tree analysis (Figure 8) affirms that *T.* ×*floridana* is clustered with one of its purported parents, *T. fasciculata* var. *densispica* from Florida and the Bahamas. *Tillandsia bartramii* clusters with the Florida, Bahamas, Cuba group with the Splits Tree analyses with *psbT-trn*T datasets.

Tillandsia fasciculata var. *densispica* and *T. balbisiana* are the purported parents of *T.* ×*smalliana* (Luther 1985). Distinguishing morphological characters are a mixture of the two parents: numerous, erect-arching leaves, and intermediate sized inflorescence (Luther 1985). *Tillandsia* ×*smalliana* clusters with the Florida and Bahaman *T. fasciculata* var. *densisipica* samples in the Splits Tree analyses for the *psbT-trn*T dataset (Figure 8). Unfortunately, the second parent, *T. balbsiana,* was not included in this study so confirmation of its hybrid origin still needs further investigation.

Biogeographic signal

4) What does it tell us about evolutionary patterns in the Caribbean?

The Caribbean islands are about 20 million years old (Graham 2003, 2010, 2011, Ricklefs & Bermingham 2007). Suitable habitats for colonization are dependent on the geologic history of islands, e.g., 40 ma for parts of Cuba and Hispaniola to 1 ma in Barbados (Graham

2010). Givnish et al. (2011) hypothesized that the core tillandsioids arose ca. 14.2 Ma in the Andes with modern lineages diverging ca. 8.7 Ma. *Tillandsia,* ca. 6 Ma, is a geologically young genus. Based on BEAST analysis from this study, *T. fasciculata* s.l. arose about 1.75–4.75 ma, and that *T. fasciculata* s.s. arose about 1–3.2 ma. Phylogenetic results from this study suggest that the *Tillandsia fasciculata* s.s. group originated in Mexico (mainland). This study corroborates many other plant studies that found Caribbean lineages originating from North America (e.g., *Lyonia*, *Poitea*, *Hebestigma*, *Pictetia*, and *Sabal* (Santiago & Olmstead 2004), *Pinus* subsection Australes (Jardon et al. 2011), *Rochefortia* (Ehretiaceae) (Irimia et al 2015)).

Northern South America: recognition of a distinct biogeographic "*Tillandsia fasciculata*" plant

A strong biogeographic signal is recovered in the South American "*Tillandsia fasciculata*" plants. These plants form a separate clade sister to other *Tillandsia* plants tested that historically are not associated with *T. fasciculata*. Trinidad is part of the South American continent shelf and given its recent separation (11-15,000 years) to northern South America these findings are consistent with biological studies (Hedges 2006, Hedges & Heinicke 2006, Camargo et al. 2009) that found connectedness between Trinidad and northern South America. The *T. fasciculata* var. *venosispica* plants from the Lesser Antilles (St. Lucia and Guadeloupe) are more closely related to *T. fasciculata* var. *venosispica* from Puerto Rico than "*T. fasciculata*" from northern South America, suggesting that the main direction of speciation of *T. fasciculata* is through the Greater Antilles into the Lesser Antilles.

Relationship of Jamaica taxa with Cuba and Hispaniola

Several studies have found a relationship of Jamaican flora to Cuba and Hispaniola (*Lasiocroton* in Jestrow et al. 2010, Santiago & Olmstead 2004). For the *Tillandsia fasciculata*

group, relationships are found between Jamaican samples and Hispaniola, but not Cuba. Jamaica is the type locality of *Tillandsia fasciculata* and several "*T. fasciculata"* plants are recognized to occur in this country: *T. fasciculata, T. fasciculata* var. *venosispica, T. fasciculata* var. *laxispica, T. compressa*, and *T. trelawniensis*. The Jamaican taxa tested did not form a monophyletic group. *Tillandsia trelawniensis* is more closely related to many of the Dominican Republic plant material, while most of the "*T. fasciculata"* samples form a strongly supported clade in both phylogenetic and network analyses. Cuba's *Tillandsia fasciculata* types are mostly restricted to the small bracted groups of the Bahamas and Florida, so there appears to be no relationship with Jamaica, at least with the small bracted varieties.

Relationship of Puerto Rican taxa with Hispaniola

Phylogenetic relationships have been found between Puerto Rican and Hispaniola plants (*Sabal, Lyonia, Poitea,* and *Goetzea* (Santiago & Olmstead 2004). This study also finds a similar pattern between Puerto Rico and Hispaniola. *Tillandsia kuzmae*, an endemic from Hispaniola is usually embedded but sometimes sister to *T. fasciculata* var. *venosispica,* Puerto Rico's most represented *Tillandsia fasciculata* plant (See section below for further details).

Greater Antillean-centered groups with representatives in the Virgin Islands or the Lesser Antilles

One of the most consistent taxonomic clades resolved in this study is *Tillandsia fasciculata* var. *venosispica* from Puerto Rico, Vieques, the US Virgin Islands (St. Thomas and St. John), and the Lesser Antilles (Guadeloupe and St. Lucia (in most analyses)). This suggests that the Puerto Rican *T. fasciculata* var. *venosispica* plants dispersed to the Virgin Islands and

then moved south through the Lesser Antilles. A similar dispersal pattern was observed in *Charianthus* (Melastomataceae) (Michelangeli et al 2008). Of note, *T. fasciculata* var. *vensosispica* is often found on limestone outcrops on many of these Lesser Antilles Islands vs. the islands closer to the mainland (Jamaica, Cuba, the Dominican Republic and Trinidad) where "*T. fasciculata*" like plants occur in different habitats. This suggests that these plants can more easily colonize various habitats, but prefer (or can outcompete other plants) in dry communities. Trejo-Torres and Ackerman (2002) found that humidity levels (i.e., dry type vegetation) played an important role in floristic links of limestone vegetation communities rather than geography (i.e., other islands).

CONCLUSIONS

This study increased both taxon and locus sampling of the *Tillandsia fasciculata* group. Concatenated data incorporating plastid regions, a low-copy nuclear gene, and nr ETS clarified some taxonomic questions pertaining to the hypothesized *T. fasciculata* group. Even though branch lengths were short, and statistical support low, some clades were resolved that support both the taxonomy and biogeography of the region (e.g., small bract varieties from the Bahamas, Cuba, and Florida). Geographic region plays an important role in delimiting several problematic taxa (e.g., *T. fasciculata* var. *venosispica* occurs in Puerto Rico and the Lesser Antilles, but not Mexico and Hispaniola as has been historically recognized). Loci sampling increased and included three new plastid markers. ETS, *psb*T-*trn*T, and *rpl14-rpl36* were helpful in resolving this group and should be added to future phylogenetic studies.

Within the "*Tillandsia fasciculata*" complex the lack of resolution among species is still prevalent despite sampling efforts. This could indicate a fast diversification episode in the

evolutionary history of this species, or of a recent colonization of the islands. Future directions should incorporate next generation sequencing such as rad seq that straddles phylogenetics and population genetics approaches.

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Table 1. Taxa and distribution of hypothesized *Tillandsia fasciculata* complex. BF=Bahamas, BH=Belize, BR=Brazil, CO=Colombia, CR=Curacao, CS=Costa Rica, CU=Cuba, DO=Dominica, DR=Dominican Republic, FG=French Guiana, GP=Guadeloupe, ES=El Salvador, GT=Guatemala, HA=Haiti, HO=Honduras, JM=Jamaica, MX=Mexico, NU=Nicaragua, PM=Panama, PR=Puerto Rico, SM=San Martin, ST=St. Lucia, NS=Suriname, TD=Trinidad and Tobago, US=United States, VC=St. Vincent & Grenadines VI=British Virgin Islands, VE=Venezuela.

Species	Distribution	This study
"*T. fasciculata* group"		
T. acostae	CS, GT, MX	related to
T. beutelspacheri Matuda	MX	outside *T. fasciculata* s.l.
T. botteri E. Morren ex Baker	MX	related to
T. copalaensis Ehlers	MX	no samples available
T. compressa Bertero ex Schultes f.	DR, HA, JM	sensu stricto
T. fasciculata var. *clavispica* Mez	CU, MX, US	sensu stricto
T. fasciculata var. *densispica* Mez	BF, CS, DR, GT, HA, MX, US	sensu stricto
T. fasciculata var. *densispica* forma *alba* Mez	US	sensu stricto
T. fasciculata Sw. var. *fasciculata*	BF, BH, BR, CO, CR, CS, DO, DR, ES, FG, GP, GT, HA, HO, JM, MX, NS, NU, PM, PR, SM, TD, VE	
T. fasciculata var. *laxispica* Mez	BF, CU, DR, HA, JM, MX	sensu stricto
T. fasciculata var. *pendulispica* Mez	Without locality or country, based on cultivated material	no samples available
T. fasciculata var. *uncispica* Mez	BF, CO, CS, CU, DR, GT, HA, PM, ST	sensu stricto
T. fasciculata var. *venosispica* Mez	CO, CS, CU, DR, ES, HA, JM, MX, PR, VC, VI	sensu stricto

T. flavobracteata Matuda	MX	related to
T.×*floridana* L.B. Smith	US	sensu stricto
T. grossipicata Espejo, Lopez-Ferrari & Till	MX	related to
T. hubertiana Matuda	MX	related to
T. inopinata Espejo, Lopez-Ferrari & Till	MX	related to
T. jalisco-monticola Matuda	MX	related to
T. kuzmae Ehlers	DR	sensu stricto
T. magnispica Espejo & Lopez-Ferrari	MX	related to
T. ×*polita* L.B. Smith	ES, GT, MX	outside *T. fasciculata* s.l.
T. rhomboidea André	CO	related to
T. rotundata (L.B. Smith) Gardner	GT, HO**,** MX	outside *T. fasciculata* s.l.
**T.* ×*smalliana* H. E. Luther	US	no samples available
T. zoquensis Ehlers	MX	no samples available

<u>"Related" taxa</u>

T. capitata Grisebach	CU, DR, MX	outside *T. fasciculata* s.l.
T. concolor L. B. Sm.	ES, MX	outside *T. fasciculata* s.l.
T. macvaughii Espejo & Lopez-Ferrari	MX	no samples available
T, maritima Matuda	MX	no samples available
T. marabascoensis Ehlers & Lautner	MX	outside *T. fasciculata* s.l.
T. rodrigueziana	ES, GT, HO, MX, NU	outside *T. fasciculata* s.l.
T. roland-gosselinii Mez	MX	outside *T. fasciculata* s.l.
T. rothii Rauh	MX	outside *T. fasciculata* s.l.
T. trelawniensis Proctor	JM	sensu stricto

T. tricolor var tricolor Schltdl. & Cham.	CS, GT, MX	outside *T. fasciculata* s.l.
T. verapazana Ehlers	GT	no samples available
T. welzii Ehlers	GT	outside *T. fasciculata* s.l.

Table 2a. Summary statistics table with character description, Consistency Index, Retention Index, Model

	Monophyly *atp*B-*rbc*L *matK* *rps16*	Monophyly ETS	Monophyly Subset *T.×floridana*	Monophyly Subset w/o *T.×floridana*
Total characters aligned	2767	513	4595	4595
Characters are constant	2499	285	4164	4164
Variable characters are parsimony-uniformative	157	140	279	277
Number of parsimony-informative characters	111	88	155	154
Ci	0.768	0.744	0.732	0.737
Ri	0.928	0.793	0.802	0.806
Length	384	367	638	630
model		GTR+G		

Table 2b. Summary statistics table with character description, Consistency Index, Retention Index, Model

	8-loci	Plastid	Barfuss	*atp*B-*rbc*L	*mat*K	*rps*16	Shaw	*ndh*F-*trn*F	*psb*D-*trn*T	*rpl*14-*rpl*36	Nuclear	ETS	PRK
Total characters aligned	8205	6380	2767	1000	879	888	3613	1245	1171	1197	1825	513	1312
Characters are constant	7690	6150	2678	979	843	856	3472	1206	1114	1152	1540	371	1169
Variable characters are parsimony-uniformative	349	169	63	16	24	23	106	35	40	31	180	100	80
Number of parsimony-informative characters	166	61	26	5	12	9	35	4	17	14	105	42	63
Ci	0.776	0.941	0.979	1	1	0.943	0.929	1	0.935	0.902	0.74	0.854	0.734
Ri	0.811	0.934	0.979	1	1	0.875	0.929	1	0.930	0.926	0.823	0.872	0.863
Length	696	254	97	22	40	35	155	40	62	51	407	174	207
model				TVM	TPM3uf +G	TPM1uf +G		TIM1	TVM+G	HKY+G		GTR+G	TrN+G

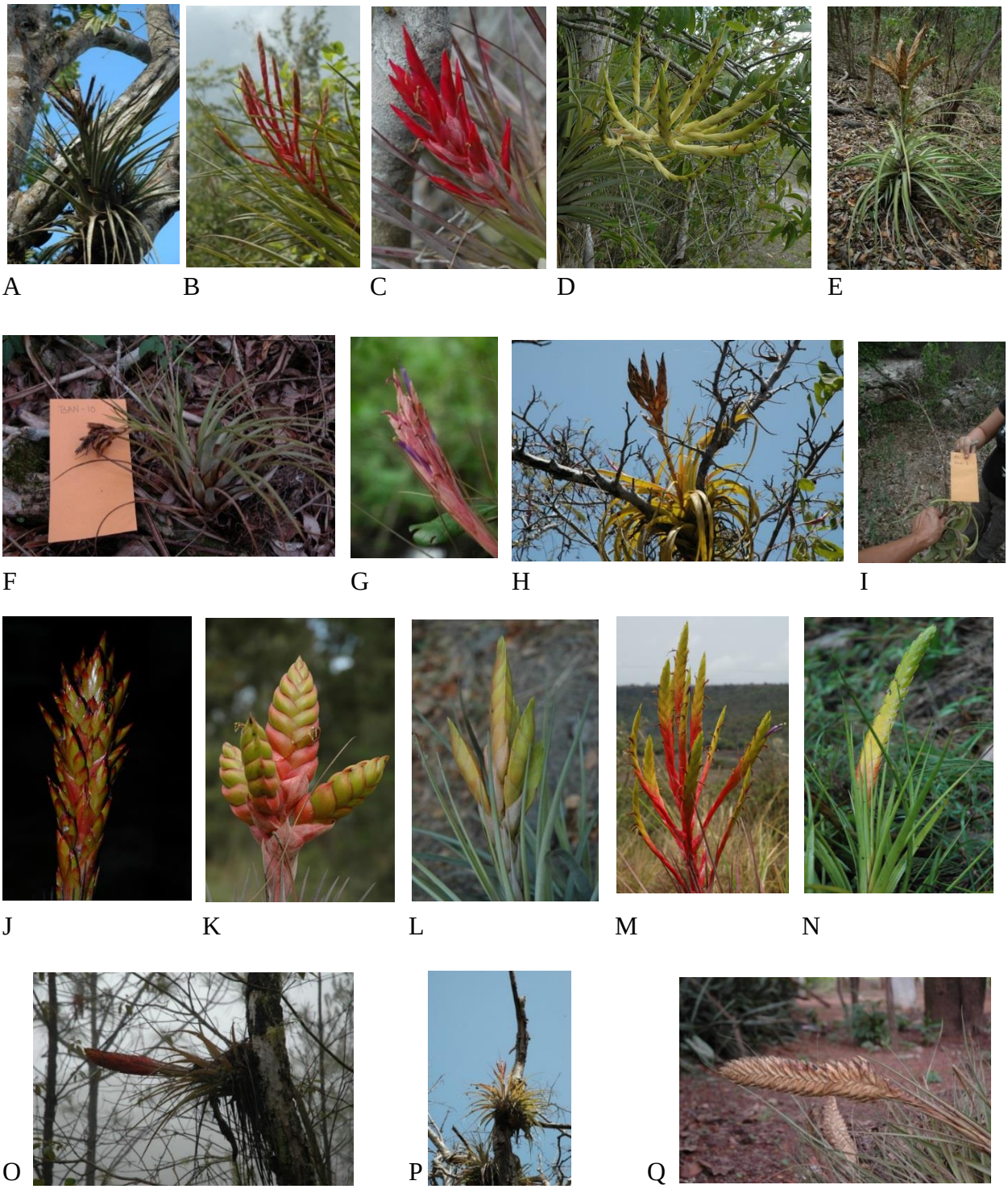


Figure 1. Morphological diversity of the *Tillandsia fasciculata* complex. A) *Tillandsia fasciculata* (Jamaica), B) *T. fasciculata* var. *clavispica* (Cuba), C) *T. fasciculata* var. aff. *laxispica* (Bahamas), D) *T. fasciculata* var. *densispica* f. *alba* (Florida), E) *T. fasciculata* var. *venosispica* (Puerto Rico), F) *T. fasciculata* var. *uncispica* (Cuba), G) *T.* ×*floridana* (Florida), H) *T. rothii* (Mexico), I) *T. maritma* (Mexico), J) *T xpolita* (Mexico), K) *T. compressa* (Dominican Republic), L) *T. grossipicata* (Mexico), M) *T. inopinata* (Mexico), N) *T. zoquensis* (Mexico), O) *T. jalisco-monticola* (Mexico), P) *T. huberitana* (Mexico), Q) *T. magnispica* (Mexico).

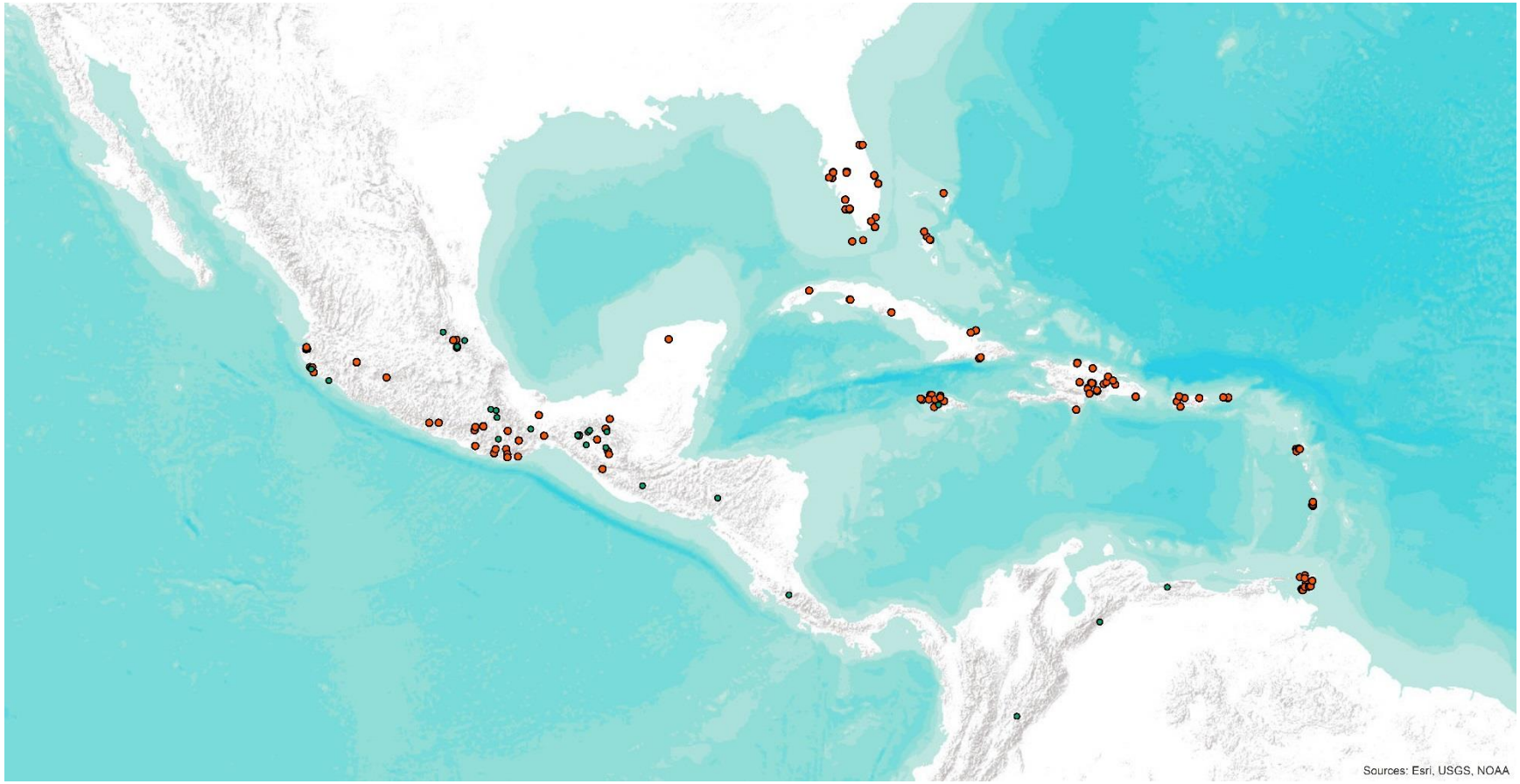


Figure 2. Taxon sampling of *Tillandsia fasciculata* complex. Refer to Supplementary Table 3 collection locality. Red dots by B. Sidoti. Green dots, other collectors.

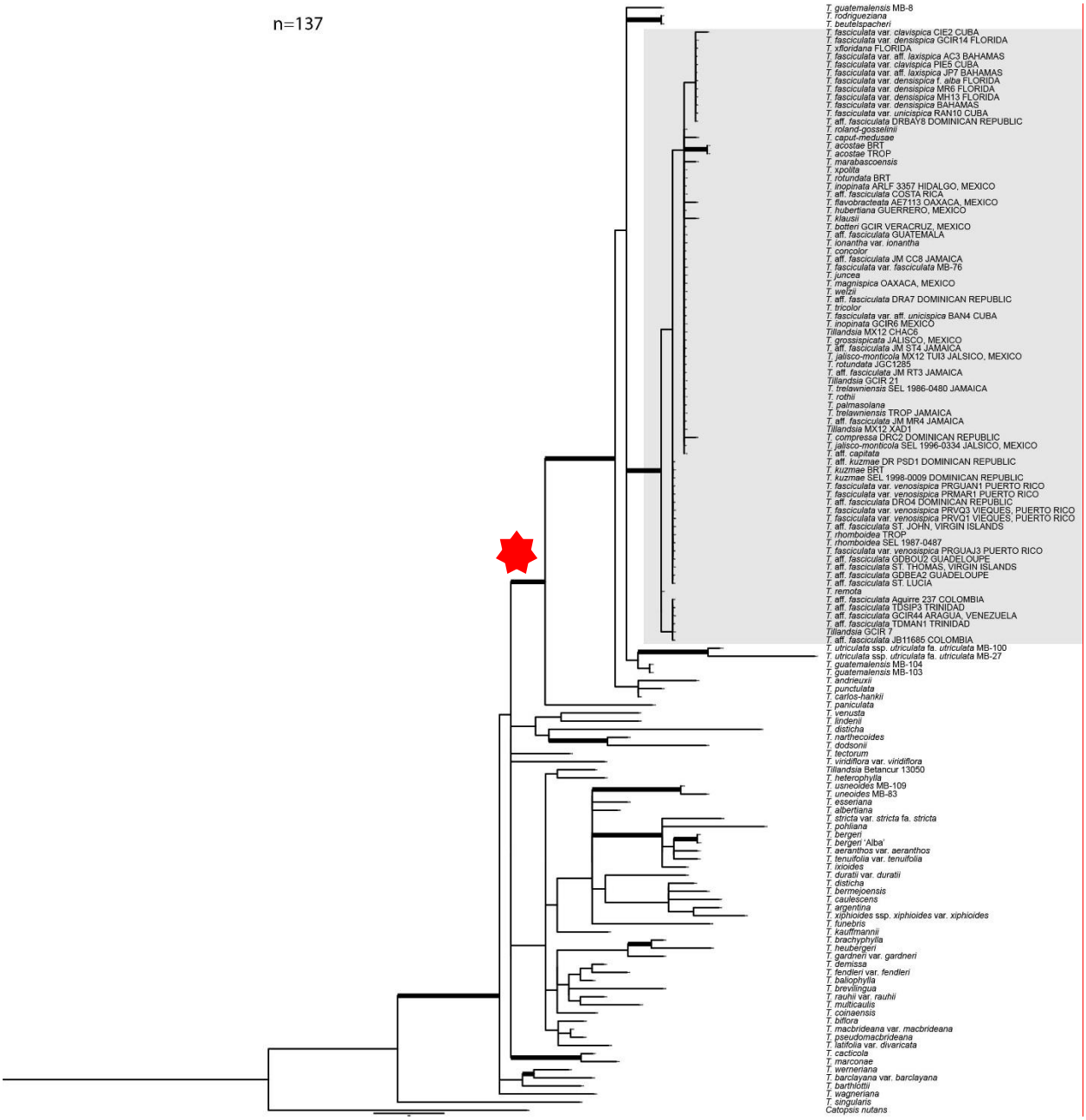


Figure 3. Maximum Likelihood tree of the *Tillandsia fasciculata* group (indicated in shaded grey box) based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, and *rps*16). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. N=137. Star indicates *Tillandsia* subgenus *Tillandsia* clade.

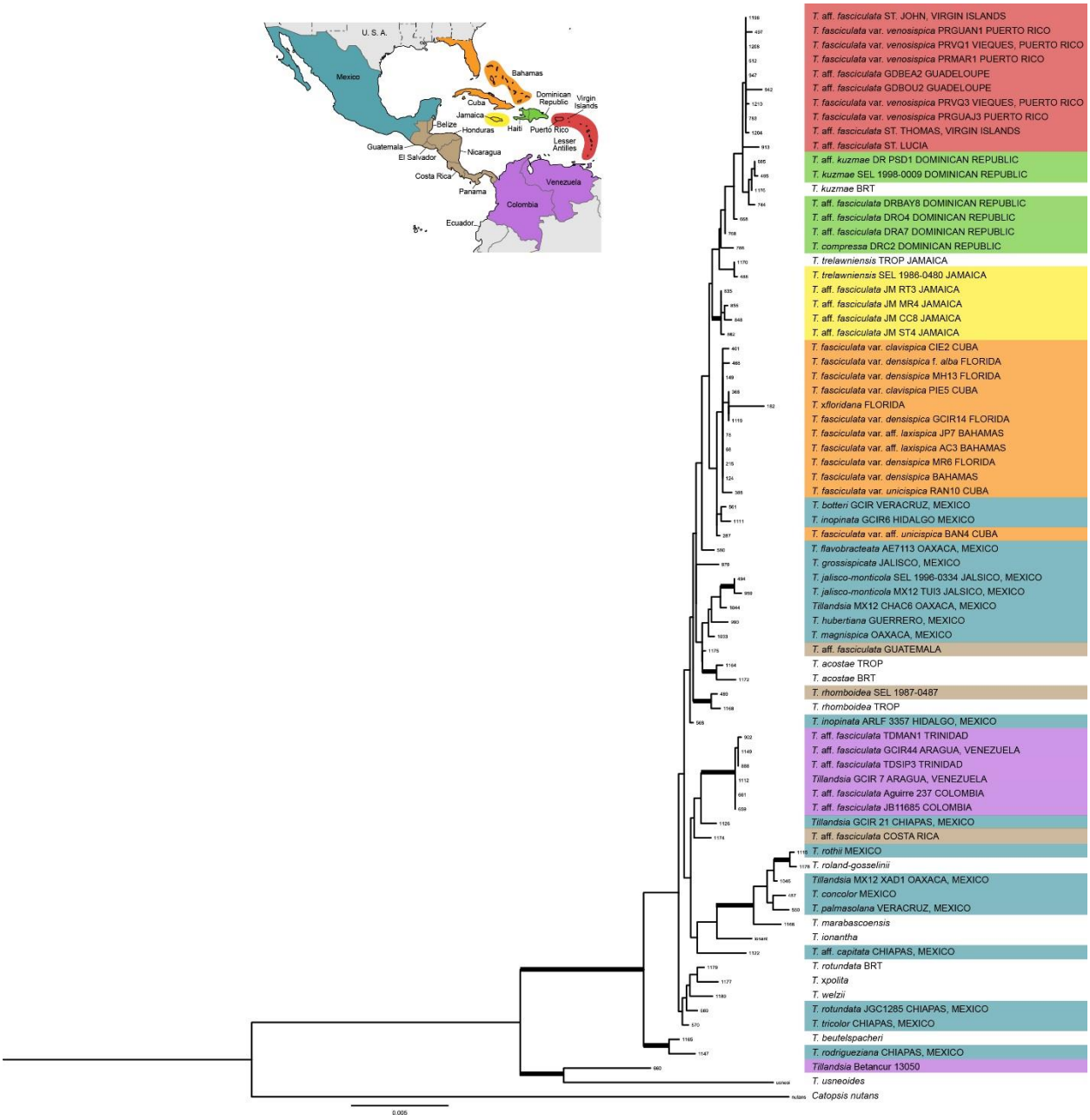


Figure 4. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36, *rps*16) and two nuclear loci (PRK and ETS). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. Concatenated (PLASTID + NUCLEAR) w/hybrid N=76. Non-colors, origin unknown.

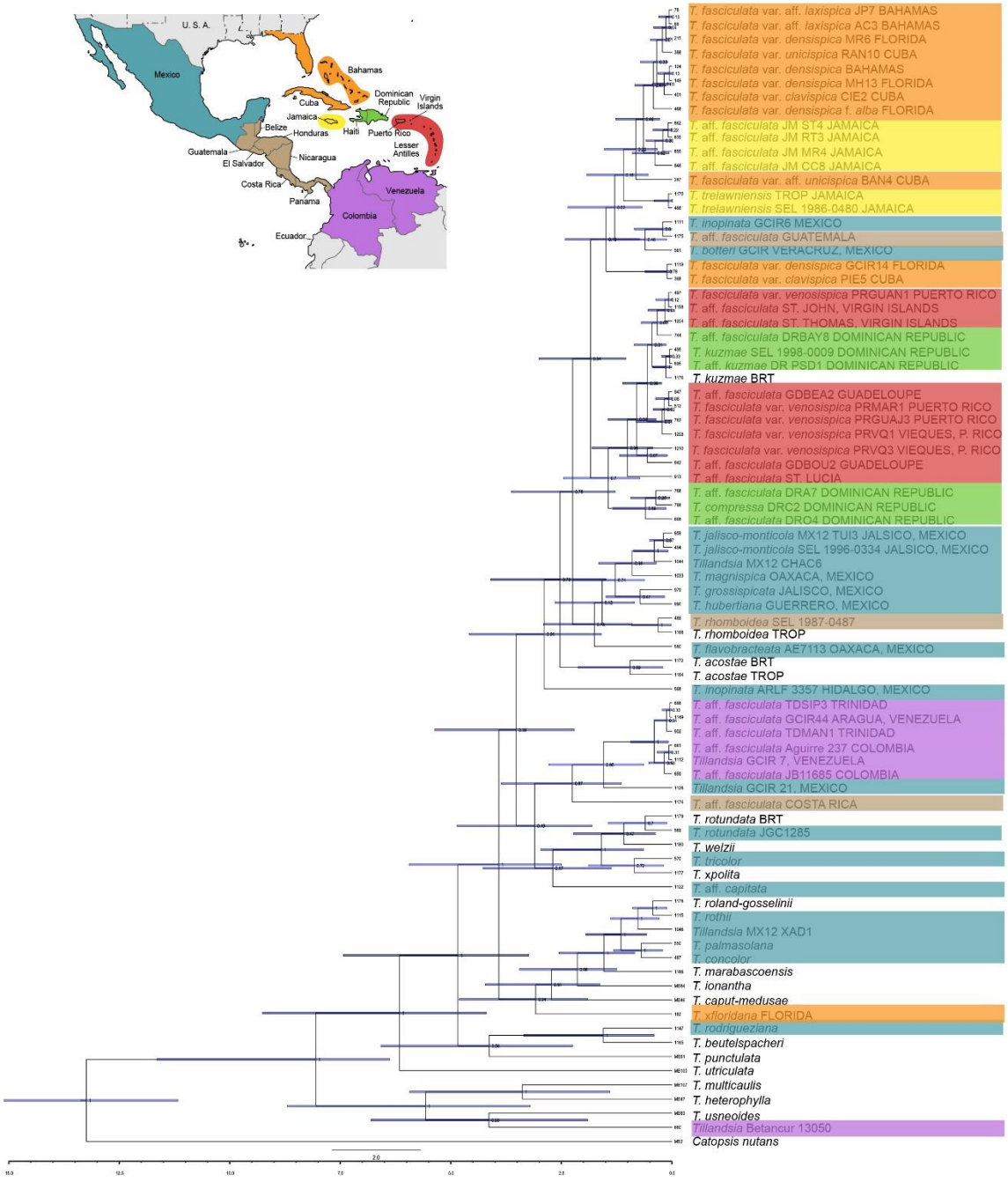


Figure 5. BEAST tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, *rps*16) and two nuclear loci (PRK and ETS). Blue horizontal bars = 95% highest probability density. Non-colors, origin unknown. n=76.

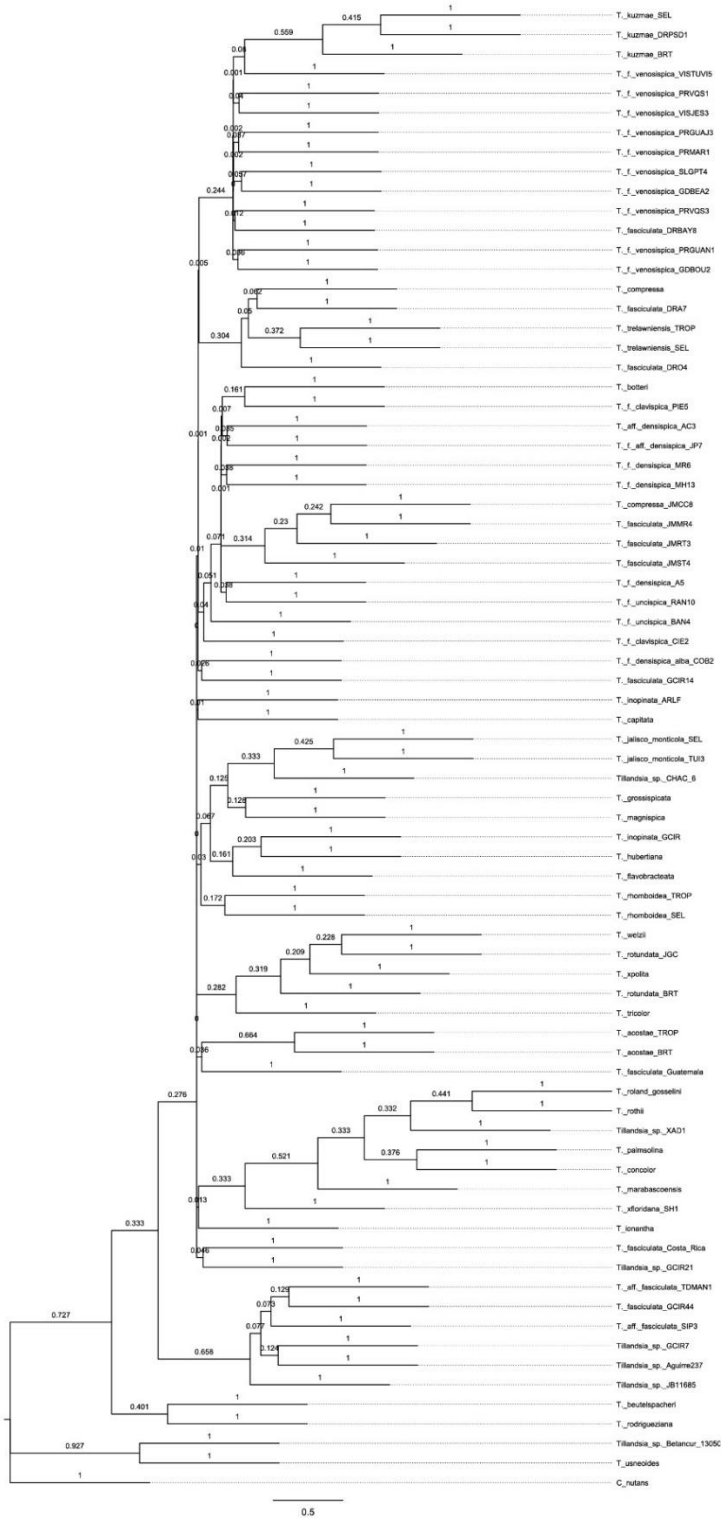


Figure 6. BUCKy tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36, *rps*16) and two nuclear loci (PRK and ETS). *a priori* level of discordance among loci set to 100. Concordance factor above nodes. n=76.

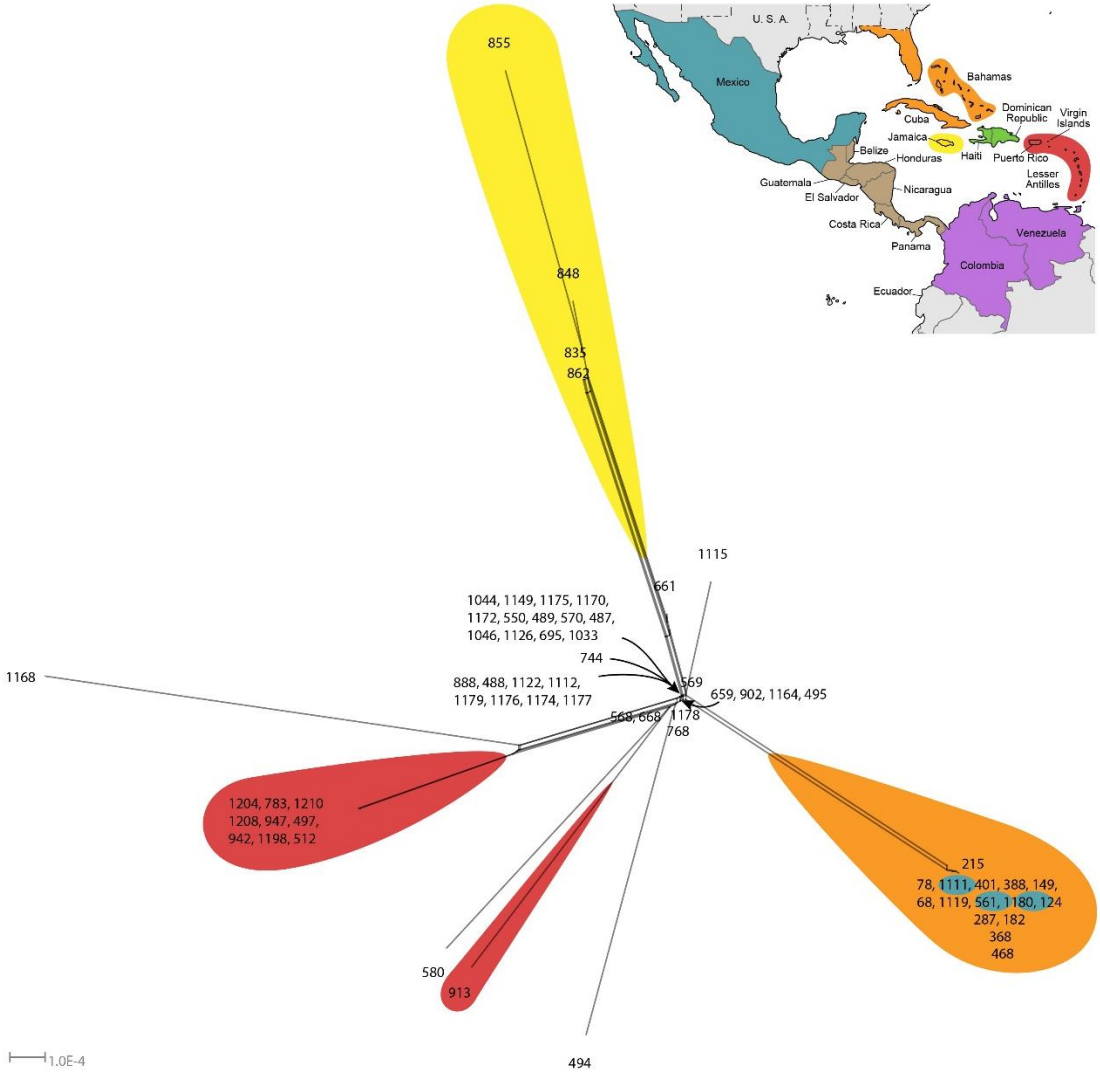


Figure 7. *psb*D-*trn*T neighbornet graph estimated from p-distances with SplitsTree of the *Tillandsia fasciculata* species complex. n=65. Refer to Supplementary Table 3 for collection number.

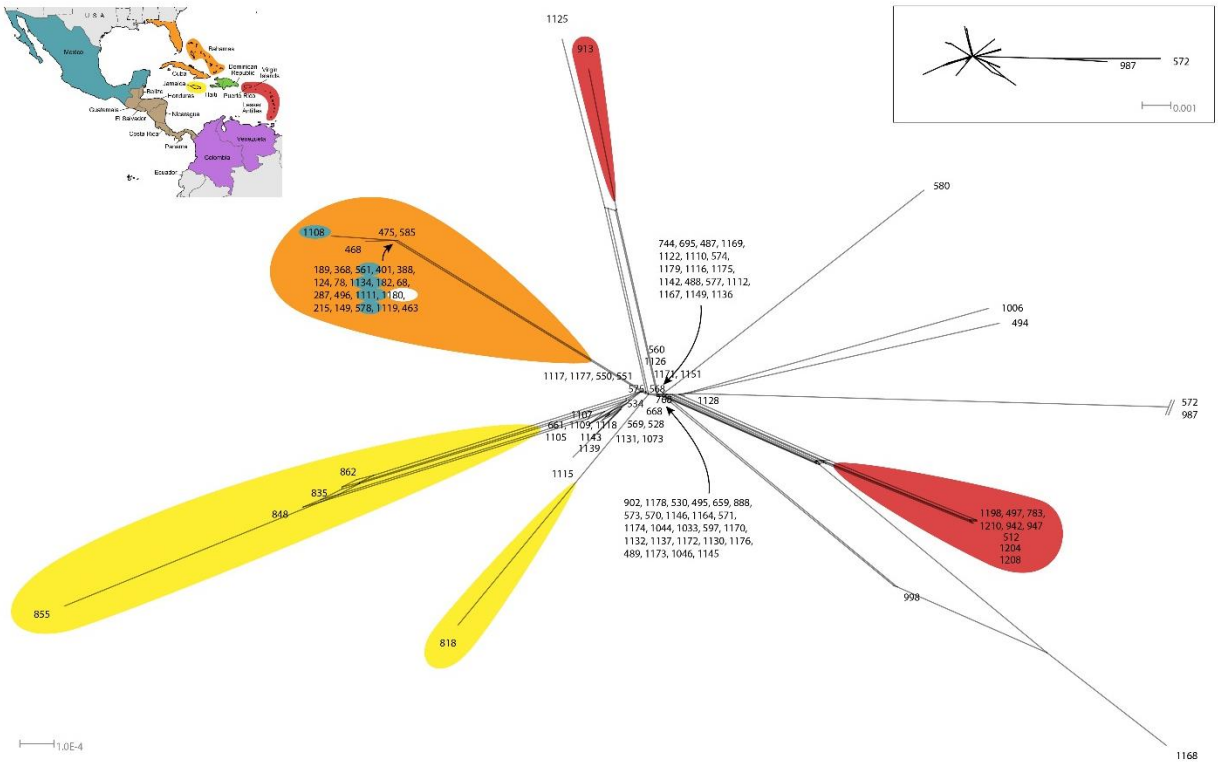


Figure 8. *psb*D-*trn*T neighbornet graph estimated from p-distances with SplitsTree of the *Tillandsia fasciculata* species complex. n=114. Refer to Supplementary Table 3 for collection number.

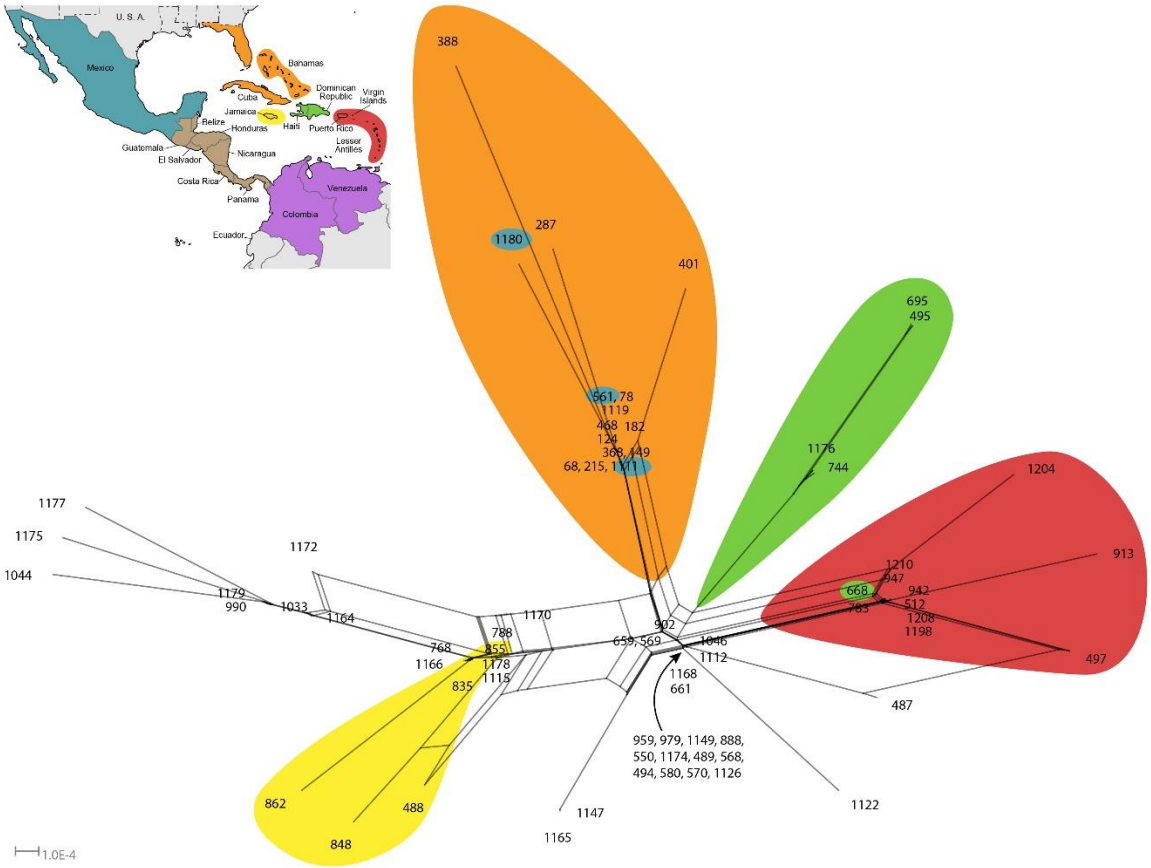
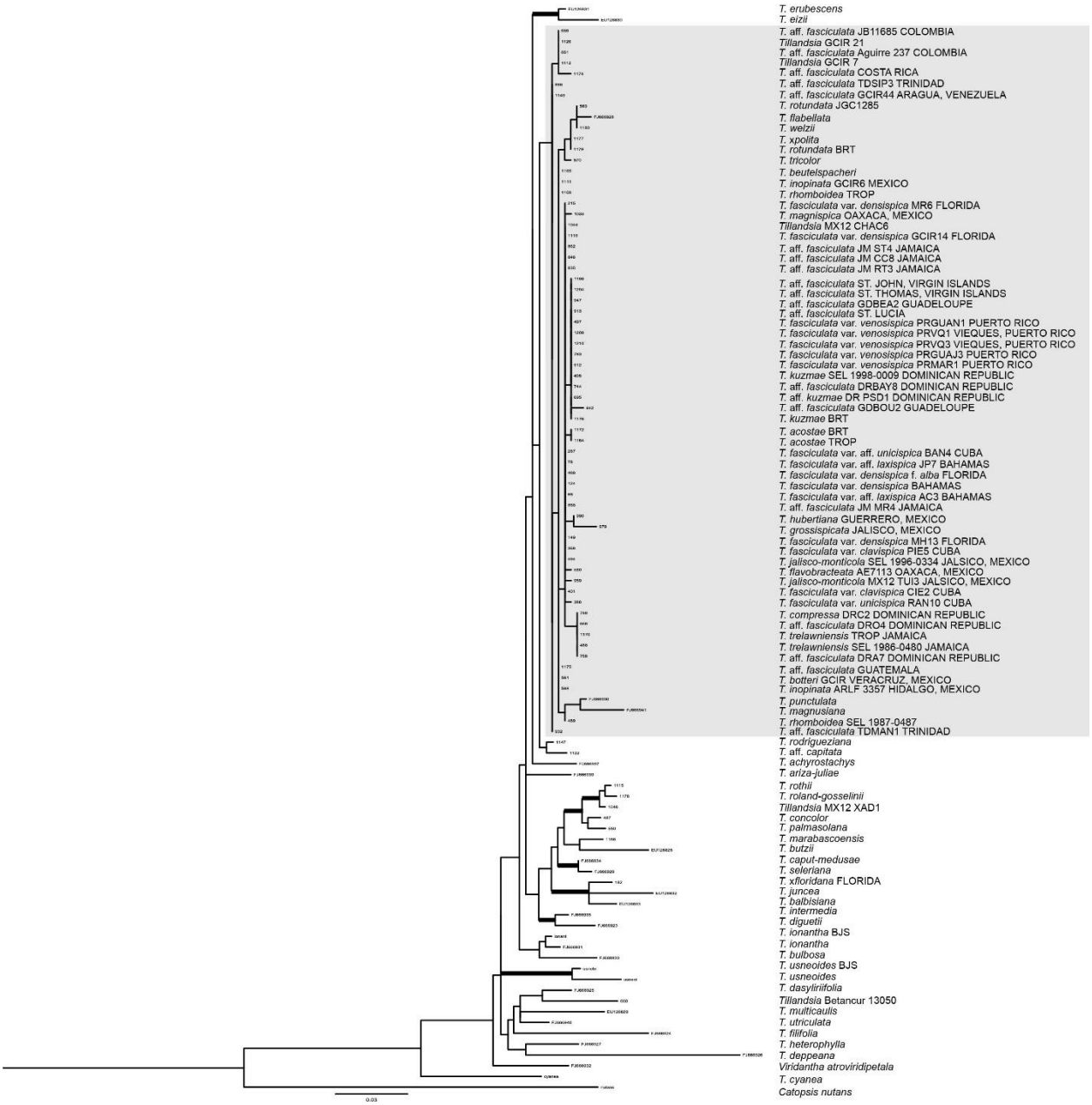
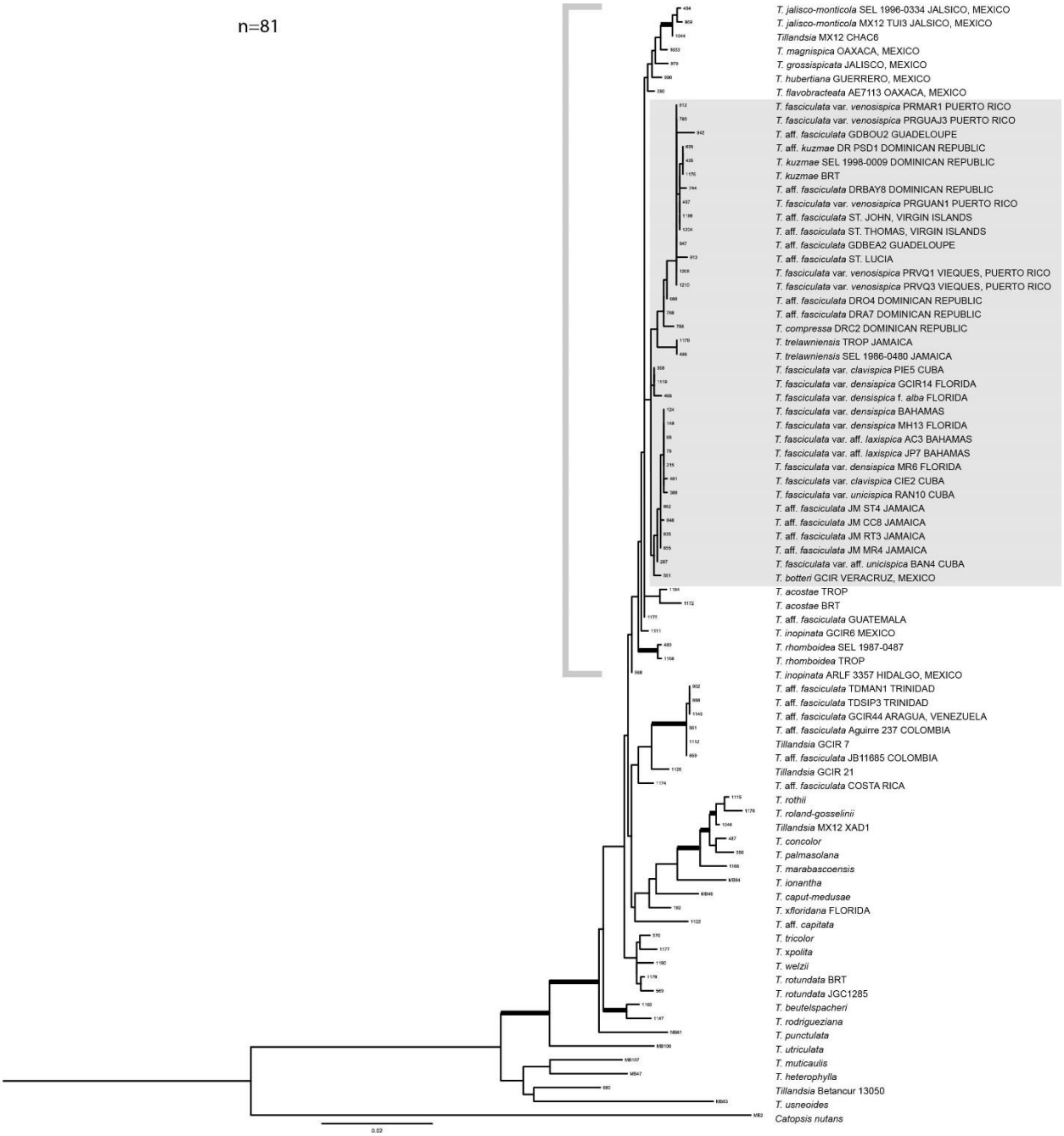


Figure 9. *rpl*14-*rpl*36 neighbornet graph estimated from p-distances with SplitsTree of the *Tillandsia fasciculata* species complex. n=72. Refer to Supplementary Table 3 for collection number.

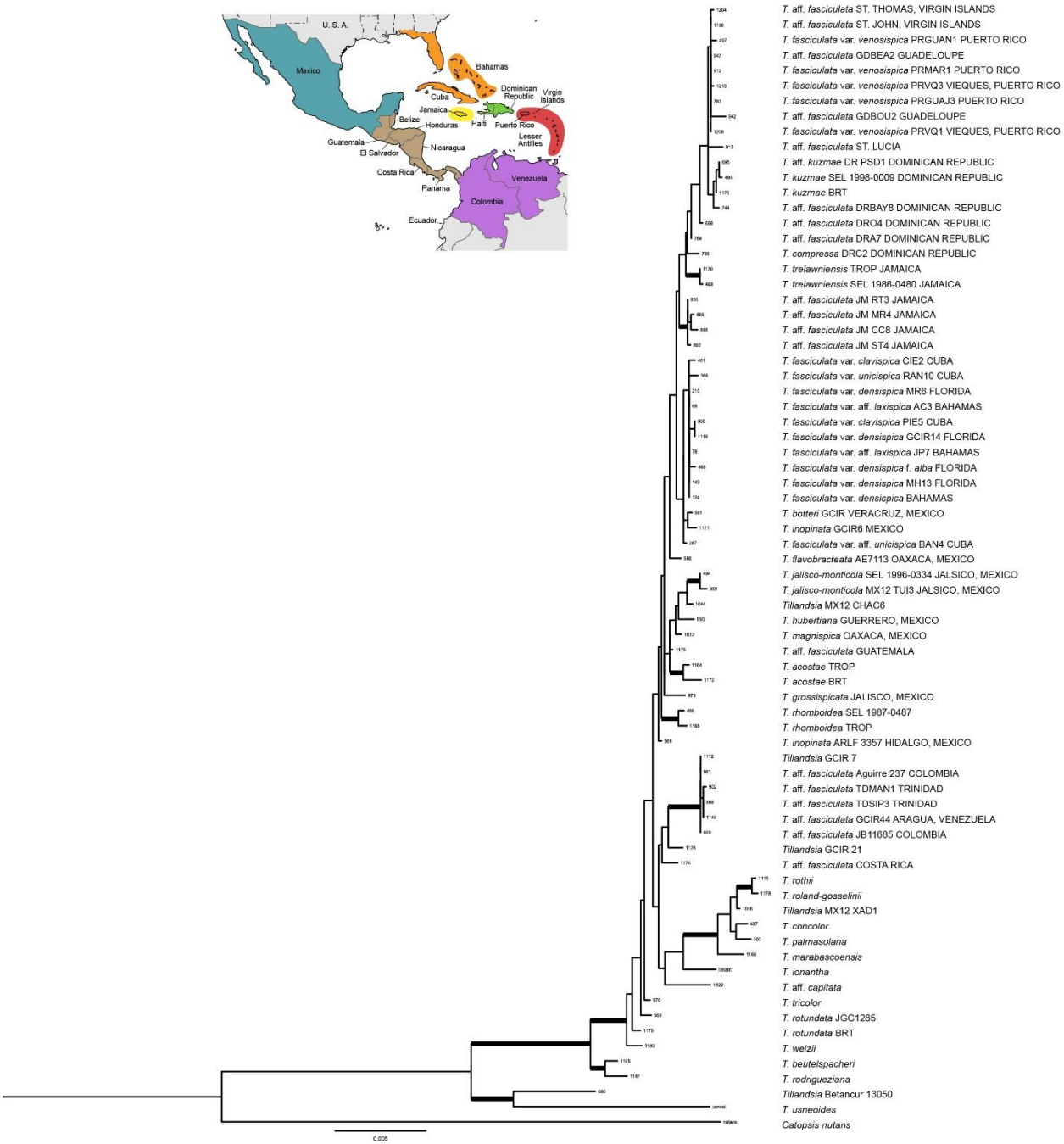


Supplementary Figure 1. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on nuclear locus ETS. Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. MONO ETS n=102

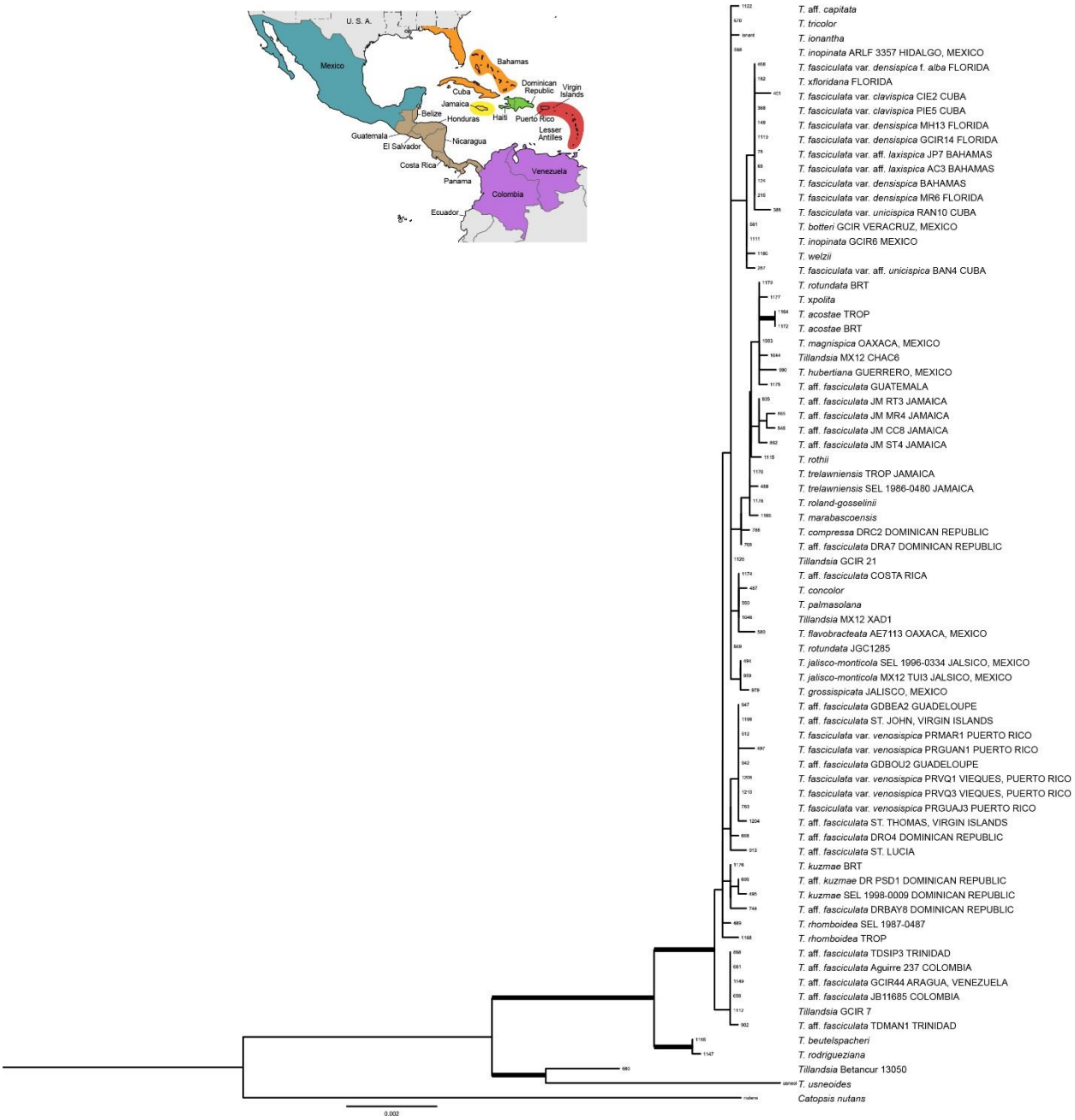


Supplementary Figure 2. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36, *rps*16) and two nuclear loci (PRK and ETS). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. n=81. MONO SUBSET

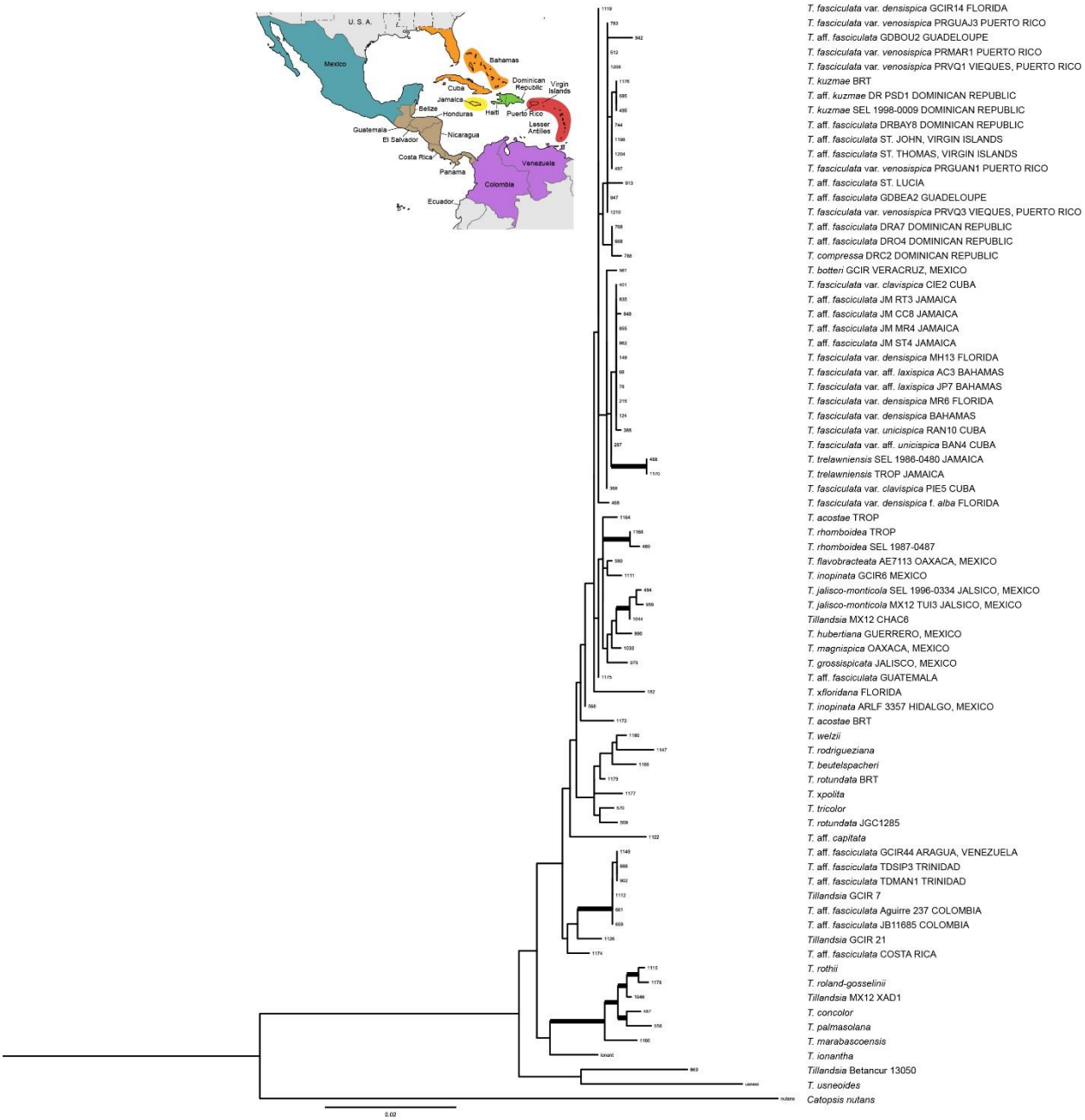
Supplementary Figure 3. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36, *rps*16) and two nuclear loci (PRK and ETS). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. n=80. MONO SUBSET2 (w/o *T.* ×*floridana*)



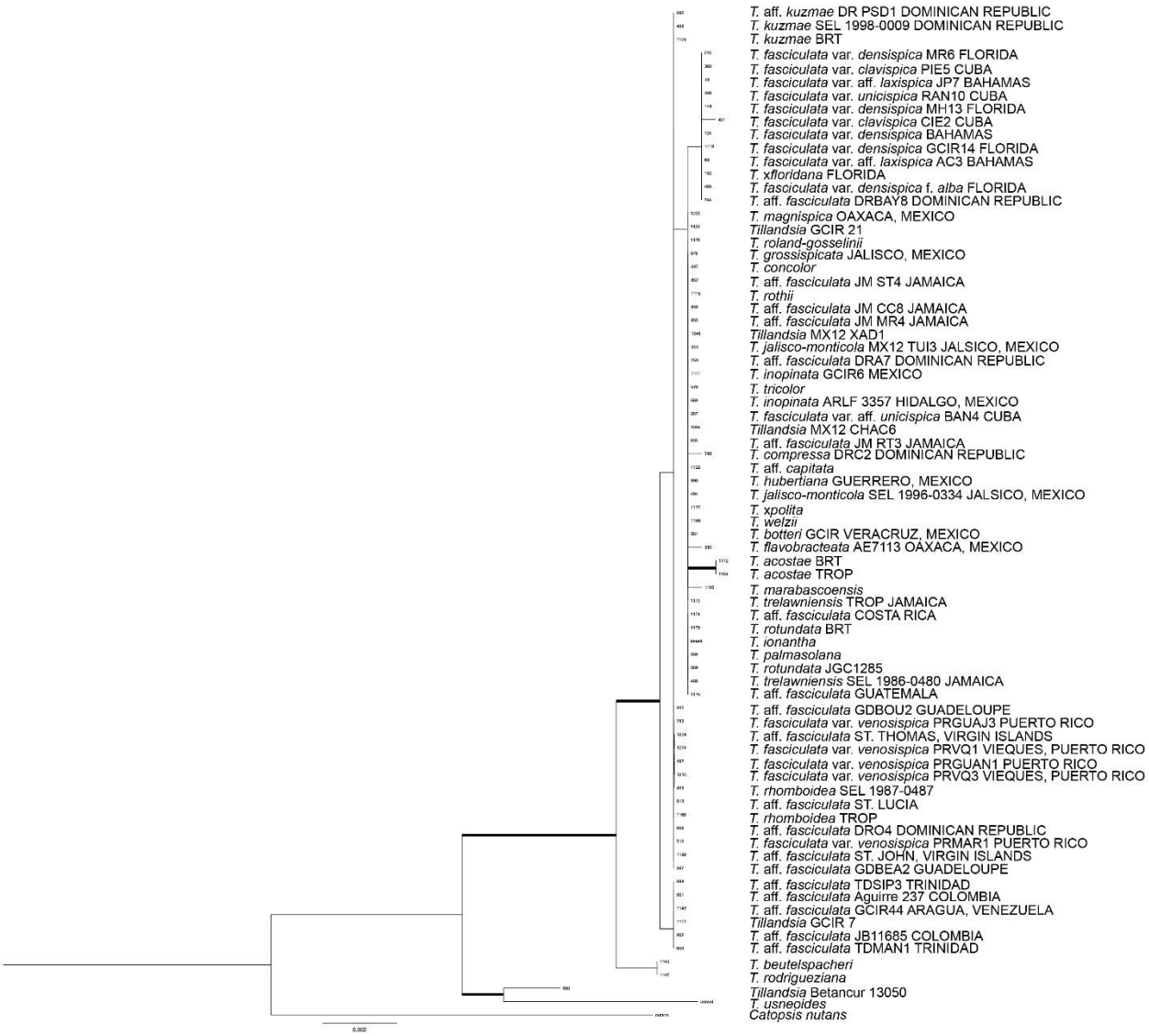
Supplementary Figure 4. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36, *rps*16) and two nuclear loci (PRK and ETS). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. Concatenated (PLASTID + NUCLEAR) excluding purported natural hybrids *T.* ×*floridana* and *T.* ×*polita* n=74



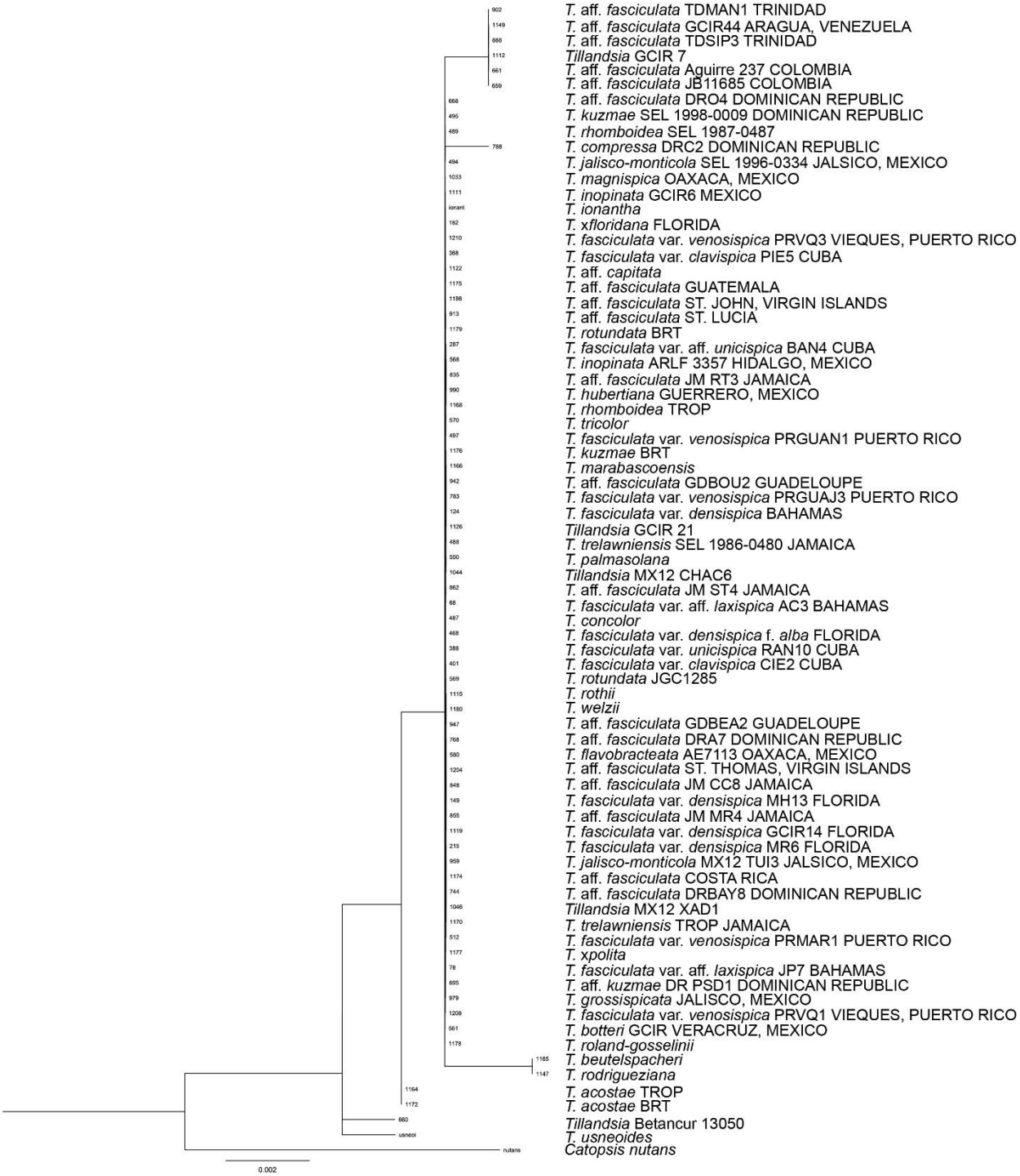
Supplementary Figure 5. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36, *rps*16). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. n=76 PLASTID (BARFUSS + SHAW)



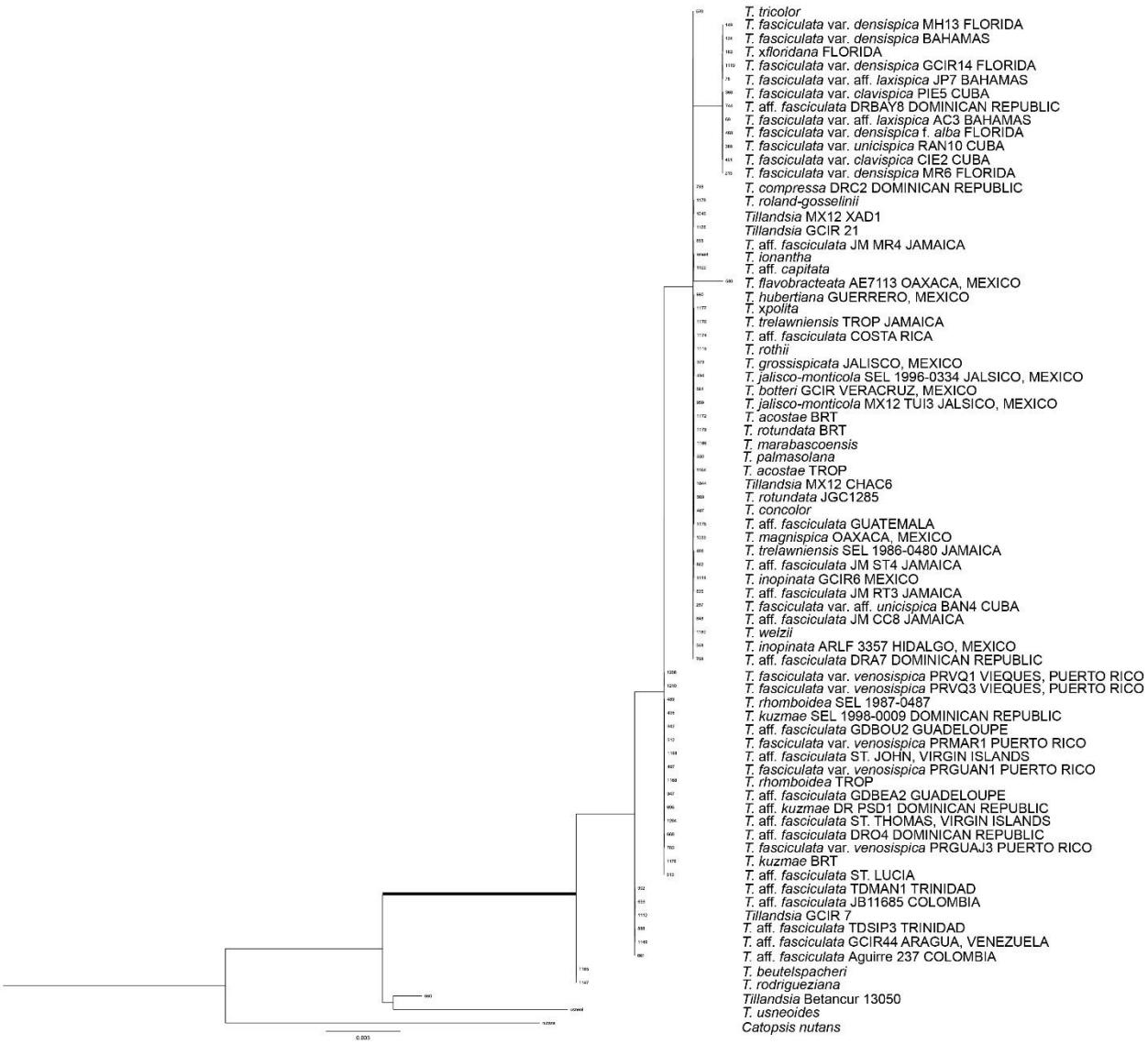
Supplementary Figure 6. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on combined nuclear loci (PRK and ETS). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. n=76 NUCLEAR (ETS + PRK)



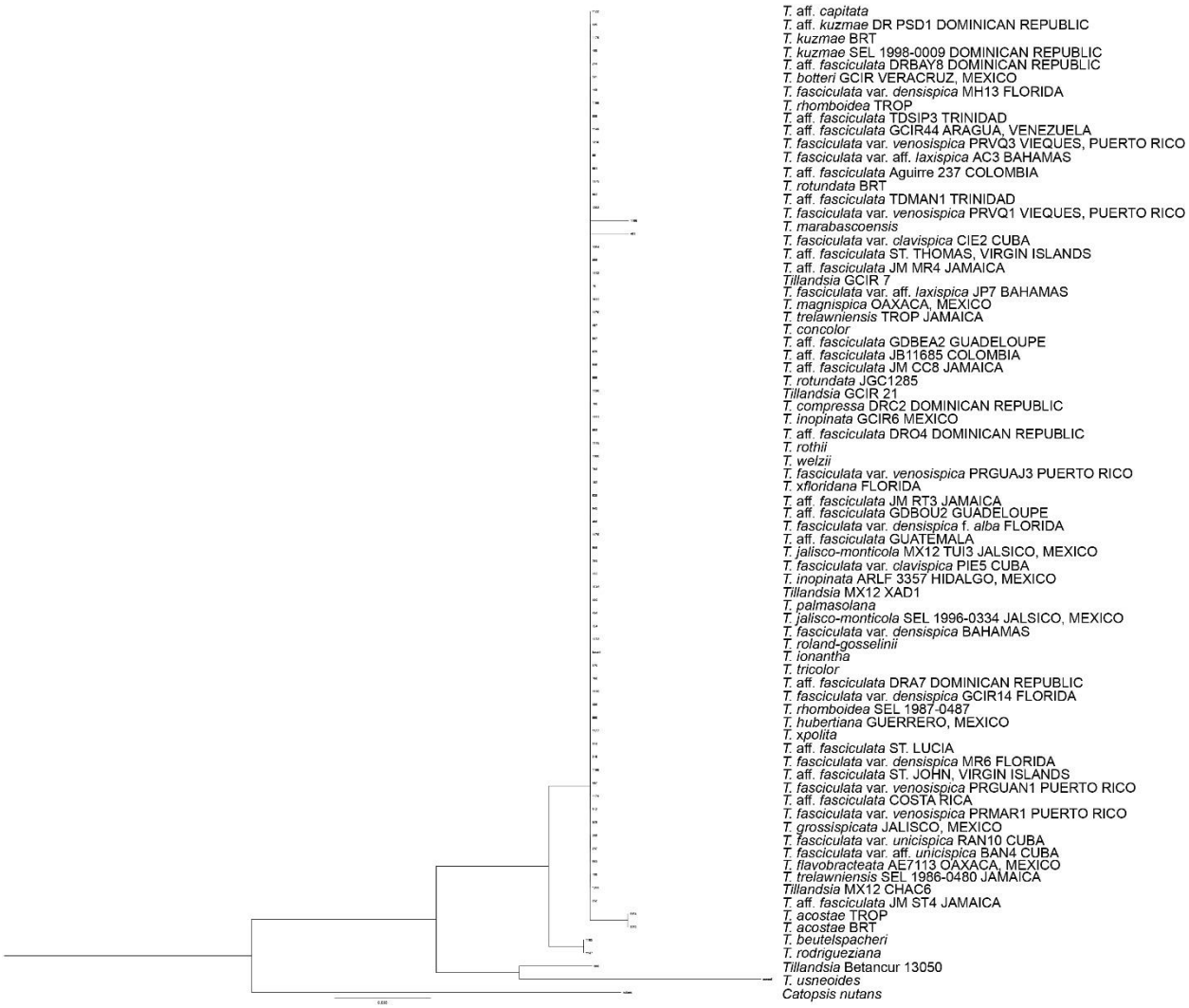
Supplementary Figure 7. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, and *rps*16). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99.



Supplementary Figure 8. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on *atp*B-*rbc*L. Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99.atpB-rbcL (n=76)

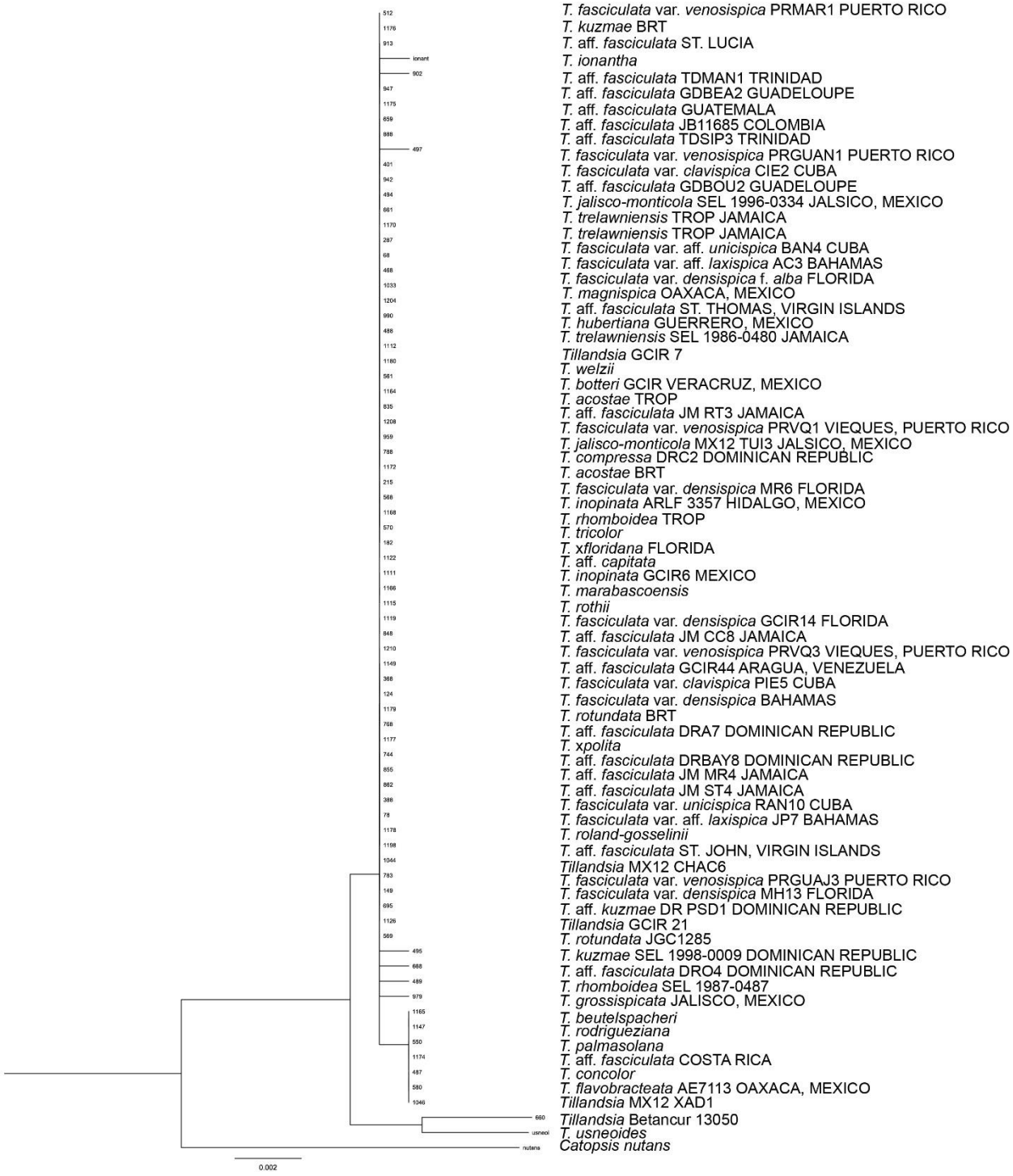


Supplementary Figure 9. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on partial *mat*K. Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. (n=76)

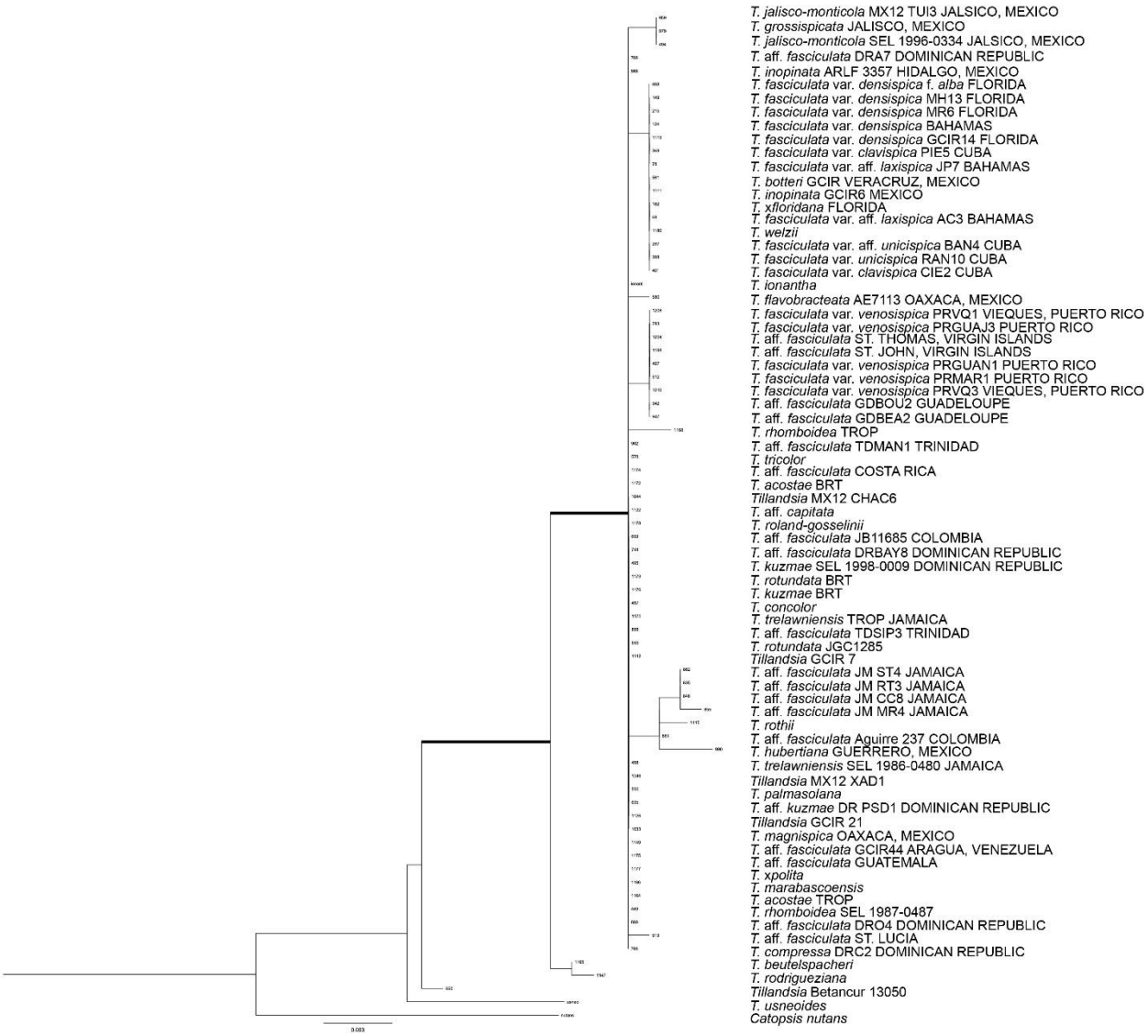


Supplementary Figure 10. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on *rps*16. (n=76)

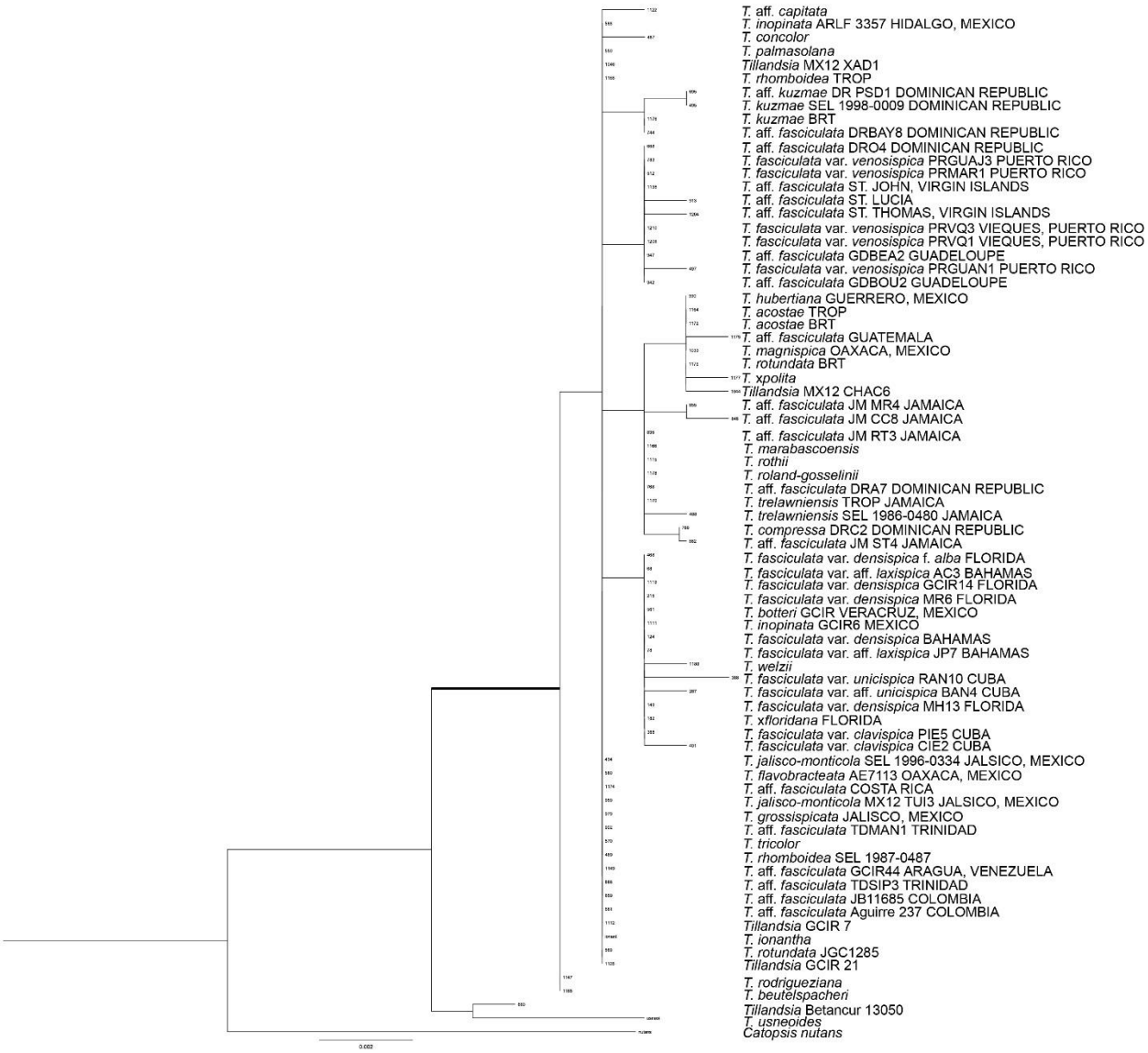
Supplementary Figure 11. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36). Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. (n=76)



Supplementary Figure 12. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on *ndh*J-*trn*F. Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. (n=76)



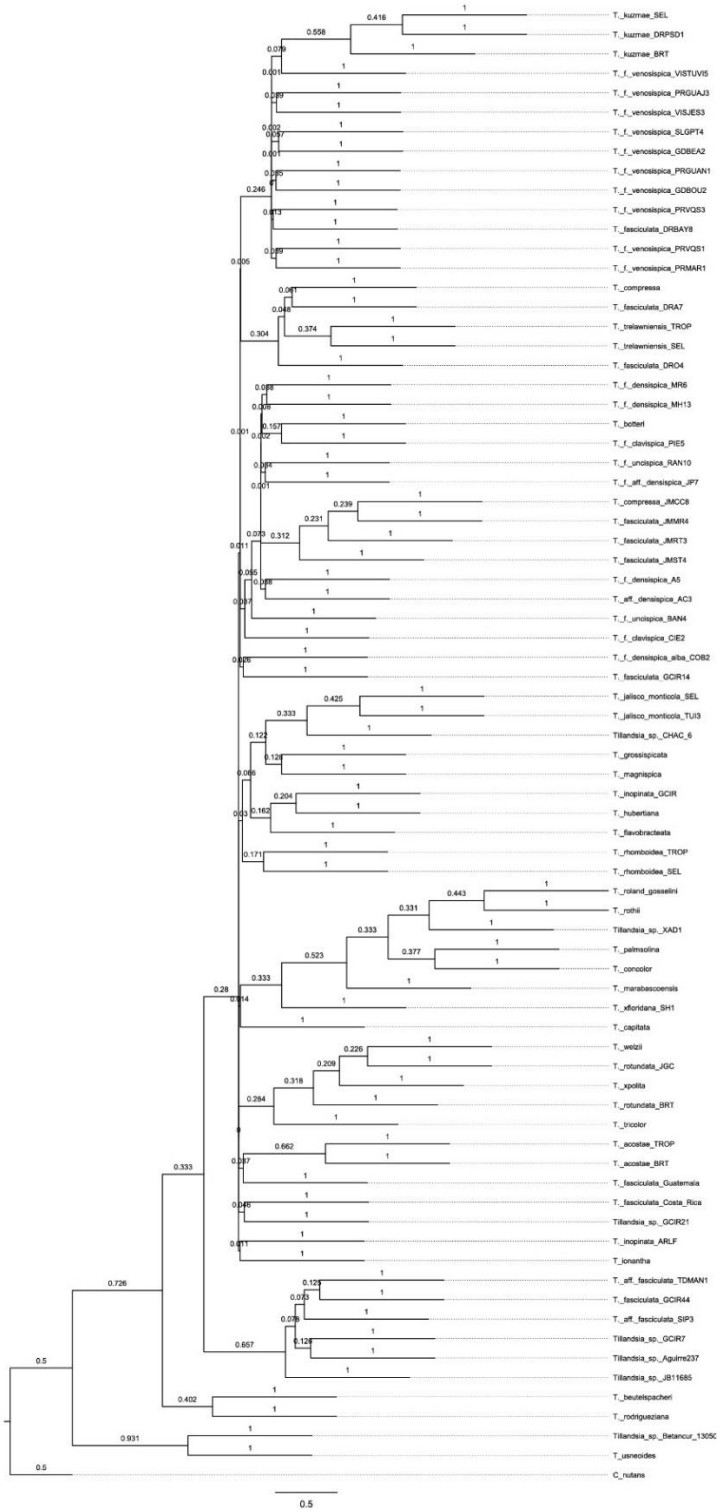
Supplementary Figure 13. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on *psb*D-*trn*T. Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. (n=76)



Supplementary Figure 14. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on *rpl*14-*rpl*36. Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. (n=76)

Supplementary Figure 15. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on ETS. Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. (n=76)

Supplementary Figure 16. Maximum Likelihood tree of the *Tillandsia fasciculata* group based on PRK. Thickened black bars indicate bootstrap values and posterior probabilities greater than 75% and 0.99. (n=76)



Supplementary Figure 17. BUCKy tree of the *Tillandsia fasciculata* group based on combined chloroplast loci (*atp*B-*rbc*L, partial *mat*K, *ndh*J-*trn*F, *psb*D-*trn*T, *rpl*14-*rpl*36, *rps*16) and two nuclear loci (PRK and ETS). *a priori* level of discordance among loci set to 1. Concordance factor above nodes. n=76.

Supplementary Table 3. Collecting sites for samples used in this study. Barfuss et al. (2005) sequences available on Genbank.

No.	Taxon	Source	Collection Date	Coll. Site	City	Country	Latitute (DD)	Longitude (DD)	Elevation	Habitat	Collector	Collectors
68	Tillandsia fasciculata var. laxispica	AC-3	16 April 2005	Atala Coppice		Bahamas	24.92333	-78.02350	10'	Coppice	Brian Sidoti	Jay Handelman
78	Tillandsia fasciculata var. aff. laxispica	JP-7	17 April 2005	on road to Red Bays, Jungle Pond		Bahamas	25.11053	-78.13393	9'	Coppice	Brian Sidoti	Jay Handelman
124	Tillandsia fasciculata var. densispica	A-5	20 April 2005			Bahamas	26.63413	-77.28440	4'	Coppice	Brian Sidoti	Jay Handelman
149	Tillandsia fasciculata var. densispica	MH13	14 June 2005	near site marker 11; Matheson Hammock	Miami	USA				Hardwood Hammock	Brian Sidoti	Jennifer Possley
182	Tillandsia fasciculata var. floridana	SH1	4 June 2005	Spring Hammock Preserve	Longwood	USA	24.71997	-81.30347		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
189	Tillandsia fasciculata var. floridana	T7	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	USA	28.51198	-80.97983		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
215	Tillandsia fasciculata var. densispica	MR6	8 June 2005	on west side along Main Park Drive, south of Power L, approx. 1.4 miles; Myakka River State Park	Sarasota	USA	27.24905	-82.29532		Hardwood Hammock	Brian Sidoti	Diana Donaghy
287	Tillandsia fasciculata var. uncispica	BAN4	27 September 2005	Reserva Ecologica "Alturas de Banao", Mogote Jarico	Banao	Cuba	23.86610	-79.58067	1453+/- 125 ft	Mogote	Brian Sidoti	Lucia Hechavarria Schwesinger and Maikel Canizares Morera
308	Tillandsia fasciculata var. uncispica	BAN25	27 September 2005	Reserva Ecologica "Alturas de Banao", Mogote Jarico	Banao	Cuba	21.86588	-79.57962	1453+/- 213 ft	Mogote	Brian Sidoti	Lucia Hechavarria Schwesinger and Maikel Canizares Morera

346	Tillandsia fasciculata var. clavispica	SIL13	29 September 2005	Silla de Gibara	Gibara	Cuba	21.02652	-76.08545	83+/-56 ft	Mogote	Brian Sidoti	Lucia Hechavarria Schwesinger, Maikel Canizares Morera, and Pedro Gonzalez Gutiérrez
368	Tillandsia fasciculata var. clavispica	PIE5	1 October 2005	La Gran Piedra	Gran Piedra	Cuba	20.01262	-75.64717	3330+/-20 ft	Bosque lluvioso	Brian Sidoti	Lucia Hechavarria Schwesinger, Maikel Canizares Morera, and Pedro Gonzalez Gutiérrez
373	Tillandsia fasciculata var. clavispica	PIE10	1 October 2005	La Gran Piedra	Gran Piedra	Cuba	20.01360	-75.65180	3182+/-39 ft	Bosque lluvioso	Brian Sidoti	Lucia Hechavarria Schwesinger, Maikel Canizares Morera, and Pedro Gonzalez Gutiérrez
388	Tillandsia fasciculata var. uncispica	RAN10	3 October 2005	Paredon de Bartolito=Paredon de la Jutice? De Alain, Rangel, Sierra del Rosario	San Cristobal	Cuba	22.74460	-83.19235	1799+/-184	Mogote	Brian Sidoti	Lucia Hechavarria Schwesinger and Maikel Canizares Morera
401	Tillandsia fasciculata var. clavispica	CIE2	4 October 2005	Laguna El Asiento, Cienaga de Zapata	Santo Tomas	Cuba	22.38467	-81.40347	25+/-16 ft	Swamp	Brian Sidoti	Lucia Hechavarria Schwesinger and Ramona Oviedo Prieto

402	Tillandsia fasciculata var. clavispica	CIE3	4 October 2005	Laguna El Asiento, Cienaga de Zapata	Santo Tomas	Cuba	22.38467	-81.40347	25+/-16 ft	Swamp	Brian Sidoti	Lucia Hechavarria Schwesinger and Ramona Oviedo Prieto
462	Tillandsia bartramii	MSBG	22 July 2006	2002-0032A							Brian Sidoti	
463	Tillandsia bartramii	MSBG	22 July 2006	1981-0769A							Brian Sidoti	
468	Tillandsia fasciculata var. densispica forma alba	COB2	10 April 2007	Camp Owaissa Bauer	Miami	USA	25.52232	-80.47177		edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
476	Tillandsia fasciculata var. densispica forma alba	COB10	10 April 2007	Camp Owaissa Bauer	Miami	USA	25.52439	-80.47011		edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
477	Tillandsia fasciculata var. densispica forma alba	COB11	10 April 2007	Camp Owaissa Bauer	Miami	USA	25.52459	-80.47010		edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
481	Tillandsia jalisco-monticola	MSBG	21 Mar 2010	1981-0786							Brian Sidoti	
483	Tillandsia fasciculata var. densispica	MSBG	21 Mar 2010	1981-2208							Brian Sidoti	
487	Tillandsia concolor	MSBG	21 Mar 2010	1985-1870							Brian Sidoti	
488	Tillandsia trelawniensis	MSBG	21 Mar 2010	1986-0480							Brian Sidoti	
489	Tillandsia rhomboidea	MSBG	21 Mar 2010	1987-0487							Brian Sidoti	
493	Tillandsia compressa	MSBG	21 Mar 2010	1994-0260							Brian Sidoti	
494	Tillandsia jalisco-monticola	MSBG	21 Mar 2010	1996-0334							Brian Sidoti	

495	Tillandsia kuzmae	MSBG	21 Mar 2010	1998-0009						Brian Sidoti	
496	Tillandsia xsmalliana	MSBG	21 Mar 2010	2000-0042						Brian Sidoti	
497	Tillandsia fasciculata var. venosispica	PR_GUAN1	23 May 2010	Bosque de Guanica, along Murcielago Trail	USA	17.96443	-66.86117	242ft+/-46		Brian Sidoti	Jay Handelman
498	Tillandsia fasciculata var. venosispica	PR_GUAN2	23 May 2010	Bosque de Guanica, along Murcielago Trail	USA	17.96443	-66.86117	242ft+/-46		Brian Sidoti	Jay Handelman
499	Tillandsia fasciculata var. venosispica	PR_GUAN3	23 May 2010	Bosque de Guanica, along Murcielago Trail	USA	17.96417	-66.86273	242ft+/-30		Brian Sidoti	Jay Handelman
512	Tillandsia fasciculata var. venosispica	PR_MAR1	24 May 2010	Near Bosque de Maricao, along Highway 105; approx. 5 miles west of park	USA	18.17795	-67.02513	2262ft+/-105		Brian Sidoti	Jay Handelman
524		EK1	8 June 2010	Eknakan on road	Mexico					Brian Sidoti	Rodrigo, Juan Pablo, Pan Li
528		EK5	8 June 2010	Eknakan on road	Mexico	20.75658	-89.36892	29 ft+/-105		Brian Sidoti	Rodrigo, Juan Pablo, Pan Li
530		PAL1	9 June 2010	Puente Shupa near bridge	Mexico	17.44770	91.96023	619ft+/-23		Brian Sidoti	German, Jose Luis, Jorge Carlos, Juan Pablo, Pan Li
534		ZO1			Mexico					Brian Sidoti	
535		ZO2			Mexico					Brian Sidoti	
537		PON_1			Mexico					Brian Sidoti	
550	Tillandsia palmsolina	MER5			Mexico					Brian Sidoti	
551		MER6			Mexico					Brian Sidoti	
560	Tillandsia botteri			Jalconolco	Mexico					Brian Sidoti	

561	Tillandsia botteri			Acazonica	Mexico					Brian Sidoti	
568	Tillandsia inopinata	ARLF3357			Mexico					Brian Sidoti	
569	Tillandsia rotundata	JGC1285			Mexico					Brian Sidoti	
570	Tillandsia tricolor	AE7203			Mexico					Brian Sidoti	
571	Tillandsia guenther-nolleri	AE6540			Mexico					Brian Sidoti	
572		JCR 2092			Mexico					Brian Sidoti	
573	Tillandsia sp. nov	JCR2108			Mexico					Brian Sidoti	
574	Tillandsia sp. nov	JCR2105			Mexico					Brian Sidoti	
575	Tillandsia sp. nov	AE7199			Mexico					Brian Sidoti	
576		AE7278			Mexico					Brian Sidoti	
577	Tillandsia concolor X T. circinnatioides	AE7373			Mexico					Brian Sidoti	
578	Tillandsia concolor	AE7372			Mexico					Brian Sidoti	
579	Tillandsia zoquensis	AE7227			Mexico					Brian Sidoti	
580	Tillandsia flavobracteata	AE7113			Mexico					Brian Sidoti	
581	Tillandsia polita var. elongata	AE7391			Mexico					Brian Sidoti	
582	Tillandsia aesii	ARLF3370			Mexico					Brian Sidoti	
583	Tillandsia sp	ARLF3326			Mexico					Brian Sidoti	
585		PVEN_2	17 June 2010		Mexico	20.41525	-98.68983	5919ft+/-46ft		Brian Sidoti	Adolfo, Ana

597		PVEN_14	17 June 2010		Mexico	20.45170	-98.67053	5107ft+/- 46ft	Brian Sidoti	Adolfo, Ana
659		JB 11685 Betancur			Colombia				Brian Sidoti	
660		13050			Colombia				Brian Sidoti	
661		Aguirre 237			Colombia				Brian Sidoti	
668		DR O4	25 June 2011	near Ovieado	Dominican Republic	17.83352	-71.45278		Brian Sidoti	Jennifer Possley
695		DR PSD1	28 June 2011	Pico San Diego Campo	Dominican Republic	19.55962	-70.71702	2568ft	Brian Sidoti	Theodoro, Jennifer
697		DR C2	29 June 2011	Near Constanza	Dominican Republic	18.94298	-70.75880	4959ft	Brian Sidoti	Theodoro, Jennifer
707		DR C12	29 June 2011	Near Constanza	Dominican Republic	18.95213	-70.77103	4713ft	Brian Sidoti	Theodoro, Jennifer
744		DR BAY8	1 July 2011	Baya hike	Dominican Republic	18.38057	-68.83148	64ft+/- 82ft	Brian Sidoti	Theodoro, Jennifer
768		DR A7	30 June 2011	Northwest of Azua, a few hundred meters south of La Guanabana	Dominican Republic	18.51215	-70.86055	822ft	Brian Sidoti	Theodoro, Jennifer
777		MX EK 3	8 June 2010	on delone regina (sp?)	Mexico	20.75913	-89.37127	73+/-161	Brian Sidoti	Rodrigo, Juan Pablo, Pan Li
778		WG 16							Brian Sidoti	
783		PR GUAJ3	25 May 2010	From Bosque de Guajataca, nearing Lago de Guajataca. Along Highway 149 N	USA	18.39087	-66.92472	598ft+/- 118	Brian Sidoti	Jay Handelman
788		DR C2		Near Constanza	Dominican Republic	18.94298	-70.75880	4959ft	Brian Sidoti	Theodoro, Jennifer
789	Tillandsia	John Taylor 17608							Brian Sidoti	
790	Tillandsia	Iltis 1561							Brian Sidoti	
791	Tillandsia fasciculata	Percy Gentle1301							Brian Sidoti	
792	Tillandsia fasciculata	Hugh O'Neill 8511			Mexico				Brian Sidoti	

798	Tillandisa jalisco-monticola	Santana 5938				Mexico					Brian Sidoti	
804	Tillandsia fasciculata	JM-SPGFLD 2a	18 January 2012	off of main road, A2, to Springfield. Negril overlook	Springfield	Jamaica	18.29715	-78.29543	136+/-43 ft	agriculture/forest	Brian Sidoti	Patrick Lewis & Bingi Burke
818	Tillandsia aff. trelawniensis	JM-MAL 5b	21 January 2012	near Malvern	Malvern	Jamaica	17.94395	-77.69812	2275 ft	pasture/dry forest	Brian Sidoti	Judeen Meikle
822	Tillandsia aff. compressa	JM-MAL 9	21 January 2012	near Malvern	Malvern	Jamaica	17.94413	-77.69753	2253 ft	pasture/dry forest	Brian Sidoti	Judeen Meikle
835	Tillandsia aff. compressa	JM-RT 3	19 January 2012	Road to Rat Trap	Rat Trap	Jamaica	18.26413	-77.92942	907+/-82 ft	Coffee Finca	Brian Sidoti	Patrick Lewis
848	Tillandsia aff. compressa	JM-CC 8	20 January 2012	Cockpit Country, NW of Troy	Troy	Jamaica	18.26760	-77.65507		dry forest	Brian Sidoti	Judeen Meikle & Nathan Hewitt
855	Tillandsia aff. fasciculata var. venosispica	JM-MR 4	24 January 2012	Mason River Preserve	Mason River	Jamaica	18.19570	-77.26273	2347+/-52 ft	dry forest	Brian Sidoti	Judeen Meikle, Jay Handelman, Christopher Daley, and Marcel Bruce
862	Tillandsia fasciculata	JM-ST 4	20 January 2012	along road to Stewart Town	Stewart Town	Jamaica	18.41458	-77.42387	965+/-184 ft	agriculture/dry forest	Brian Sidoti	Judeen Meikle
873	Tillandsia fasciculata	TD-CHG 4	14 February 2012	Along road towards Chaguaramas National Park, near Macqueripe	Chaguaramas	Trinidad	10.70748	-61.60903	82 ft		Brian Sidoti	Jennifer Possley with Tony (driver)
876	Tillandsia fasciculata	TD-CHG 7	14 February 2012	Along road towards Chaguaramas National Park, near Macqueripe	Chaguaramas	Trinidad	10.70695	-61.60897	77 ft		Brian Sidoti	Jennifer Possley with Tony (driver)
888	Tillandsia fasciculata	TD-SIP 3	15 February 2012	From Fyzabad heading east on road towards Siparia	Siparia	Trinidad	10.14747	-61.47720	57 ft		Brian Sidoti	Jennifer Possley with Ram (driver)

902	Tillandsia fasciculata	TD-MAN 1	16 February 2012	near Manzanilla	Manzanilla	Trinidad	10.54677	-61.06495	129 ft		Brian Sidoti	Jennifer Possley with Rishi (driver)
912	Tillandsia fasciculata	SL-GPT 3	20 Feb 2012	along trail of Gros Piton		St. Lucia	13.80438	-61.06545	889 ft	dry rain forest	Brian Sidoti	Jennifer Possley and Melvin Smith
913	Tillandsia fasciculata	SL-GPT 4	20 Feb 2012	along trail of Gros Piton		St. Lucia	13.80438	-61.06545	889 ft	dry rain forest	Brian Sidoti	Jennifer Possley and Melvin Smith
930	Tillandsia fasciculata	SL-SOU 4a	19 Feb 2012	along highway south of Sofriere, heading towards Choiseul.	south of Sofriere	St. Lucia	13.82930	-61.04850	1329 ft	agriculture/rain forest	Brian Sidoti	Jennifer Possley and Melvin Smith
938	Tillandsia fasciculata	GD-TV 2	23 Feb 2012	along D23, heading towards Mahaut on N2	near Mahaut	France	16.18380	-61.76970	738 ft	dry forest on W part of Basse Terre	Brian Sidoti	Jennifer Possley
941	Tillandsia fasciculata	GD-BOU 1	24 Feb 2012	south of Bouillante, off of highway N2, along side road D14 heading E towards National Park	south of Bouillante	France	16.10670	-61.75328	732 ft	dry forest on SW part of Basse Terre	Brian Sidoti	Jennifer Possley and Eric Francius
942	Tillandsia fasciculata	GD-BOU 2	24 Feb 2012	south of Bouillante, off of highway N2, along side road D14 heading E towards National Park	south of Bouillante	France	16.10670	-61.75328	732 ft	dry forest on SW part of Basse Terre	Brian Sidoti	Jennifer Possley and Eric Francius
947	Tillandsia fasciculata	GD-BEA 2	24 Feb 2012	along road, near Riv. De Beaugendre	south of Bouillante	France	16.09538	-61.75073	369 ft	dry forest on SW part of Basse Terre	Brian Sidoti	Jennifer Possley and Eric Francius
948	Tillandsia fasciculata	GD-BEA 3	24 Feb 2012	along road, near Riv. De Beaugendre	south of Bouillante	France	16.08488	-61.75997	252 ft	dry forest on SW part of Basse Terre	Brian Sidoti	Jennifer Possley and Eric Francius
957	Tillandsia jalisco-monticola	MX12 TUI 1	26 May 2012	La carretera Tuito-Vallarta y La Provincia, brecha a Zimapon a 7.3 km de la carretera	Tuito	Mexico	20.36032	-105.27645	3287 ft	Bosque Encino-Pino	Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro

959	Tillandsia jalisco-monticola	MX12 TUI 3	26 May 2012	La carretera Tuito-Vallarta, crucer a La Provincia-Zimapon, km 0.	Tuito	Mexico	20.35472	-105.31673	2447 ft	Bosque Encino-Pino	Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro
960	Tillandsia jalisco-monticola	MX12 TUI 4	27 May 2012	La carretera Tuito-Vallarta, km 9 al N de Tuito	Tuito	Mexico	20.38715	-105.31222	2227 ft	Bosque Encino-Pino	Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro
961	Tillandsia jalisco-monticola	MX12 TUI 5	27 May 2012	La carretera Tuito-Vallarta, km 9 al N de Tuito	Tuito	Mexico	20.38715	-105.31222	2227 ft	Bosque Encino-Pino	Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro
963	Tillandsia jalisco-monticola	MX12 TUI 7	27 May 2012	La carretera Tuito-Vallarta	Tuito	Mexico	20.43250	-105.30210		Bosque Encino-Pino	Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro
966	Tillandsia rothii	MX12 CHA 3	27 May 2012	Carretera Pto Vallarte ??? De Narridad (sp?)		Mexico	19.61238	-105.14802	76ft		Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro
975	Tillandsia sp.	MX12 PUR 1	27 May 2012	Camino a Purficacion: Carretera de Chomela a Villa purificacion		Mexico	19.60043	-105.04490	323ft		Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez,

											Ernesto de Castro
976	Tillandsia sp.	MX12 PUR 2	27 May 2012		Mexico	19.3832166666666 ??	-104.98087	29+/-???		Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro
977		MX12 ITZ 1			Mexico					Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro
979	T. grossispicata	MX12 MAZ 2	28 May 2012	Corretera de Tuxpan a Mazamitla (sp?)	Mexico	19.80357	-103.10048	4660ft		Brian Sidoti	Lucia Hechavarria Schwesinger, Antonio Vazquez, Ernesto de Castro
987		MX12 COM 1a	30 May 2012	Corretera de Nuevo Urechio a Miguel Silva (sp?)	Mexico	19.17928	-101.78462	4262ft		Brian Sidoti	Lucia Hechavarria Schwesinger and Miguel Muñiz Castro
990	T. hubertiana	MX12 VIA 2a	31 May 2012	Rincon de la Via cemino a la presa Corretera Chilpenzingo (sp?)	Mexico	17.28833	-99.48613	2436ft		Brian Sidoti	Lucia Hechavarria Schwesinger and Miguel Muñiz Castro

996	MX12 VIA 6	6 June 2012	Rincon de la Via cemino a la presa Corretera Chilpenzingo (sp?)	Mexico	17.28818	99.90000	2407ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
998	MX12 BON 1	6 June 2012	Some Bonitz Corretera transimice ????	Mexico	17.60692	-95.08248	140ft+/- 89ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1000	MX12 CAR 2	6 June 2012	Localidad Repo de T. Pinicole ??	Mexico	16.74345	-94.85090	899ft+/- 30ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1006	MX12 MAN 2	7 June 2012	Oaxaca El Manguito Santiago Varga RMO San Cristobal ??	Mexico	16.54247	-95.96273	4050ft+/- 15ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1008	MX12 MAN 4	7 June 2012	Oaxaca El Manguito Santiago Varga RMO San Cristobal ??	Mexico	16.53950	-95.96455	3920ft+/- 89ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1013	MX12 MIT 2	8 June 2012	Salide de le cemetera Milta-Oaxaca comino a la ruines de Yazul (sp?)	Mexico	16.94770	-96.45337	5422ft+/- 125ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali,

											and Juan Pablo Pinzon
1022		MX12 NUB 1	9 June 2012	Rancho Las Nules Corretera camino a San Jose del Pacifico dede Mia (sp?)	Mexico	16.18618	-96.51525	7815ft+/- 39ft		Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1024		MX12 GAL 2	9 June 2012	Pueblo de la Galera, Poclutla (sp???)	Mexico	15.96840	-96.47208	3816ft+/- 23ft		Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1033	T. magnispica	MX12 CHAC 2a	9 June 2012	Chacalapa Casa de Florinda ???	Mexico	15.83408	-96.46257	826ft+/- 26ft		Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1044		MX12 CHAC 6	11 June 2012	Chacalapa Casa de Florinda ???	Mexico	15.83408	-96.46257	826ft+/- 26ft		Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1046		MX12 XAD 1	11 June 2012	Desvio hacic Stz MS Xadanis Je la Corretera Poclutla (sp?)	Mexico	15.86245	-96.00233	548ft+/- 36ft		Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon

1054	MX12 GAB 1c	11 June 2012	San Gabriel de Mixtepec Oaxaca	Mexico	16.00572	-97.05342	2035+/- 23ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1055	MX12 GAB 1d	11 June 2012	San Gabriel de Mixtepec Oaxaca	Mexico	16.00572	-97.05342	2035+/- 23ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1056	MX12 GAB 2	11 June 2012	San Gabriel de Mixtepec Oaxaca	Mexico	16.00572	-97.05342	2035+/- 23ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1057	MX12 GAB 3	11 June 2012	Camino a le localided de A. oenigmatica (sp?)	Mexico	16.18125	-96.98502	5127+/- 194ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1058	MX12 AMA 1	11 June 2012	Carretera de Santiago Jameltepec y San Andre de Huaxpaltepec	Mexico	16.97065	-97.91073	2477ft+/- 39ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1067	MX12 AMA 11	11 June 2012	Salide herie Tlaxiaco desde San Pedro de los Malinas (sp?)	Mexico	17.13152	-97.51952	6439ft+/- 50ft	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali,

									and Juan Pablo Pinzon
1069		MX12 COR 2	11 June 2012		Mexico			Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1073		MX12 HUAX 1	11 June 2012		Mexico	16.31378	-97.88017	Brian Sidoti	Lucia Hechavarria Schwesinger, German Carnevali, and Juan Pablo Pinzon
1105		MX12 HUAX 29c	11 June 2012		Mexico	16.31378	-97.88017	Brian Sidoti	
1106	Tillandsia	MX12 GC IR 1	12 June 2012	6 km S de Enclliano Compostela Nueva	Mexico				
1107	Tillandsia	MX12 GC IR 2	12 June 2012	Cua. San Juan de los Moros	Mexico				
1108	Tillandsia	MX12 GC IR 3	12 June 2012	Oaxaca 19 km de Cucatlan.	Mexico				
1109	Tillandsia	MX12 GC IR 4	12 June 2012	Chichxulmiz (Puerto-Puebla?)	Mexico				
1110	Tillandsia	MX12 GC IR 5	12 June 2012	Hierve El Agua	Mexico				
1111	T. inopinata	MX12 GC IR 6	12 June 2012	ca. Pacula	Mexico				
1112	Tillandsia	MX12 GC IR 7	12 June 2012	El Castano Estado Aragua	Venezuela				
1113	Tillandsia	MX12 GC IR 8	12 June 2012	Kunana Perija	Venezuela				
1114	Tillandsia	MX12 GC IR 9	12 June 2012	Yosondua	Mexico				
1115	Tillandsia rothii	MX12 GC IR 10	12 June 2012		Mexico				

	Tillandsia aff.	MX12 GC	12 June	Rancho Rio Florida, ABA	
1116	fasciculata	IR 11	2012	SOLO	Mexico
		MX12 GC	12 June		
1117	Tillandsia	IR 12	2012	12 km N de Loxicha	Mexico
		MX12 GC	12 June		
1118	Tillandsia	IR 13	2012	GC Type locality 2 km S.	Mexico?
		MX12 GC	12 June		
1119	T. fasciculata	IR 14	2012		USA
	Tillandsia	MX12 GC	12 June		
1120	rothii	IR 15	2012	Chamela	Mexico
		MX12 GC	12 June		
1121	Tillandsia	IR 16	2012	MEX EEK1 Sidoti	Mexico
	Tillandsia aff.	MX12 GC	12 June	Canon del Gmjalba ca.	
1122	capitata	IR 17	2012	motozinthla	Mexico
		MX12 GC	12 June		
1123	Tillandsia	IR 18	2012	ca. Ocasingo	Mexico
	Tillandsia	MX12 GC	12 June		
1124	pringlei	IR 19	2012	Pacula	Mexico
		MX12 GC	12 June		
1125	Tillandsia	IR 20	2012	Yosondua	Mexico
		MX12 GC	12 June		
1126	Tillandsia	IR 21	2012	Oscingo, Tonina	Mexico
	Tillandsia	MX12 GC	12 June		
1127	inopinata	IR 22	2012	ex C. Hoqucanps?	Mexico
		MX12 GC	12 June		
1128	Tillandsia	IR 23	2012	El Mangioto ca. de El capagon?	Mexico
	Tillandsia	MX12 GC	12 June		
1129	botteri	IR 24	2012	Jalcomulco3	Mexico
	Tillandsia	MX12 GC	12 June		
1130	inopinata	IR 25	2012	Banac Meztitlan	Mexico
		MX12 GC	12 June		
1131	Tillandsia	IR 26	2012	Jamcocula sn. 1997	Mexico
	Tillandsia aff.	MX12 GC	12 June		
1132	fasciculata	IR 27	2012	G15	
		MX12 GC	12 June		
1133	Tillandsia	IR 28	2012	Uninajaz?	Mexico
	Tillandsia	MX12 GC	12 June		
1134	inopinata	IR 29	2012	Pacula	Mexico
		MX12 GC	12 June	Mirador La Coyota Canon del	
1135	Tillandsia	IR 30	2012	Sumidero	Mexico

		MX12 GC	12 June		
1136	Tillandsia	IR 31	2012	Santo Tomas Platanos	Mexico
	Tillandsia	MX12 GC	12 June		
1137	palmasolana	IR 32	2012		Mexico?
		MX12 GC	12 June		
1138	Tillandsia	IR 33	2012	10 km N Ocozocuatla	Mexico
		MX12 GC	12 June		
1139	Tillandsia	IR 34	2012	Puentea ca. Palenque.	Mexico
		MX12 GC	12 June		
1140	T. botterii	IR 35	2012	Jalcomilco2	Mexico?
	Tillandsia jalisco-	MX12 GC	12 June		
1141	monticola	IR 36	2012	IMR 1095	Mexico
		MX12 GC	12 June		
1142	Tillandsia	IR 37	2012	IMR-977	Mexico?
		MX12 GC	12 June		
1143	Tillandsia	IR 38	2012	Kivic	Mexico
		MX12 GC	12 June		
1144	Tillandsia	IR 39	2012	Cuzama	Mexico
		MX12 GC	12 June		
1145	Tillandsia	IR 40	2012	MXD13-1 Sidoti	Mexico?
		MX12 GC	12 June	San Miguel, Chimalapa,	
1146	Tillandsia	IR 41	2012	Carodulxo	Mexico
	Tillandsia	MX12 GC	12 June		
1147	rodrigueziana	IR 42	2012	Ocosingo-Altamisano	Mexico
	Tillandsia	MX12 GC	12 June	Arroyo la cariaga Tolimara	
1148	palmeri	IR 43	2012	Lana: Rio Claro?	Mexico
	Tillandsia aff.	MX12 GC	12 June		
1149	fasciculata	IR 44	2012	Barinitas	Venezuela
		MX12 GC	12 June		
1150	Tillandsia	IR 45	2012	CCI Tlacolula Cruz Verde	Mexico
		MX12 GC	12 June		
1151	Tillandsia	IR 46	2012	Lyotla	Mexico
		MX12 GC	12 June		
1152	T. botterii	IR 47	2012	Jalcomilco1	Mexico?
1164	T. acostae	Tropiflora			
1165	T. beutelspacheri	Tropiflora			
1166	T. marabascoensis	Tropiflora			

1167	T. x polita	Tropiflora										
1168	T. rhomboidea	Tropiflora										
1169	T. roland-gosselinii	Tropiflora										
1170	T. trelawniensis	Tropiflora										
1171	T. welzii	Tropiflora										
1172	T. acostae	Bird Rock Tropical		T293								
1173	T. copalaensis	Bird Rock Tropical		T374								
1174	T. fasciculata (Costa Rica)	Bird Rock Tropical		T073								
1175	T. fasciculata (Guatemala)	Bird Rock Tropical		T068								
1176	T. kuzmae	Bird Rock Tropical		T392								
1177	T. x polita	Bird Rock Tropical		T213								
1178	T. roland-gosselinii	Bird Rock Tropical		T162								
1179	T. rotundata	Bird Rock Tropical		T277								
1180	T. welzii	Bird Rock Tropical		T378								
1189	Tillandsia fasciculata aff. var. venosispica	VISJ-UR 4	18 December 2012		USA	18.32325	-64.76983		tropical dry rain forest?	Brian Sidoti	Jay Handelman and Gary Ray	
1194	Tillandsia aff. lineatispica	VISJ-UR 9	18 December 2012		USA	18.32438	-64.76950	542+/-39'	tropical dry rain forest?	Brian Sidoti	Jay Handelman and Gary Ray	
1195	Tillandsia lineatispica (hybrid?)	VISJ-UR 10	18 December 2012		USA	18.32438	-64.76950	542+/-39'	tropical dry rain forest?	Brian Sidoti	Jay Handelman and Gary Ray	
1198	Tillandsia fasciculata aff.	VISJ-ES 3	18 December 2012		USA	18.34212	-64.75985	ca. 652'	tropical dry rain forest?	Brian Sidoti	Jay Handelman	

	var. venosispica											and Gary Ray
1204	Tillandsia fasciculata aff. var. venosispica	VIST-UVI 5	20 December 2012		USA	18.34837	-64.97692	817'	tropical dry rain forest?	Brian Sidoti	Jay Handelman
1207	Tillandsia fasciculata aff. var. venosispica	MARPR?		Vieques	USA					Katie Frecker	
1208		PR-VQS1								Katie Frecker	

Chapter 2: Genetic variation and structure in the *Tillandsia fasciculata* (Bromeliaceae) complex of Florida and the Bahamas based on analysis of microsatellites

ABSTRACT

Florida is one of the most floristically diverse states in the USA. Increases in human population, agriculture, tourism, and invasive exotic species threaten the limited remaining natural vegetation. *Tillandsia fasciculata* (Bromeliaceae) is listed as a state endangered plant due to urbanization and the exotic weevil, *Metamasius callizona,* that consumes its meristematic tissue, resulting in death. Information on the genetic variation and structure of this group is lacking and taxonomic uncertainties persist since its original description in the 18th century. The aim of this study is to examine genetic variation and structure of *T. fasciculata* group in Florida and the Bahamas. Additionally, this study aims to address whether genetic structure among populations can help to delimit species boundaries. Furthermore, we also seek to evaluate purported parentage of the natural hybrid *T.* ×*floridana*. Leaf material of *T. fasciculata* var. *densispica* (n=160), *T. fasciculata* var. *densispica* f. *alba* (n=10), *T. bartramii* (n=12), and *T.* ×*floridana* (n=33) was collected across 18 populations (4–36 individuals/site) from Florida and the Bahamas. Results from eight microsatellite markers support high levels of heterozygosity. The average H_O and H_E over loci and populations is 0.684 (SE=0.023) and 0.561 (SE=0.016). F_{IS} are between -0.785 to 0.142, indicating low levels of inbreeding. STRUCTURE supports at least three population centers/clusters, 1) a *T. fasciculata* var. *densispica* f. *alba* group and purple flowered *T. fasciculata* var. *densispica* including individuals in Collier, St. Lucie, and Martin Counties, FL; 2) a southwestern Florida, southern Florida and Bahamas group; and 3) a *T.* ×*floridana* group that forms a genetic population with T. *bartramii*. Results for all AMOVA reveal greater variation within populations than among populations. When the Florida dataset is

reanalyzed with *T.* ×*floridana* and *T. bartramii* removed, F_{ST} values indicate a low degree of differentiation among populations. There are significant relationships between geographic and genetic distances for populations of the Florida and Bahamas "*Tillandsia fasciculata*" group. Treatment of Florida populations and Bahamas populations separately find significant isolation by distance.

Florida is the third most floristically diverse state in the US, with over 4,200 species of native or naturalized ferns and seed plants (Wunderlin et al. 2008). The state is unique in North America excluding Mexico for being home to several epiphytic flowering plants of Orchidaceae and Bromeliaceae that are characteristic of several southern Florida ecosystems. By 2060, the human population in Florida is projected to increase to 18 million and an estimated 7 million additional acres of land will be converted from rural and natural to urban uses (Zwick & Carr 2006). The impact on the biota will be great, especially considering that loss of habitat and habitat fragmentation can lead to inbreeding depression, genetic drift, and loss of evolutionary potential (Frankham et al. 2010). Future climate change scenarios, especially those that consider rising sea levels along the coasts, are also cause for alarm. Plants and animals unable to migrate or disperse to suitable habitats are likely to be impacted the most. Despite these threats to natural vegetation and ecosystems, there exist no population genetic studies of charismatic Bromeliaceae in Florida or within the larger Caribbean Basin floristic region.

Animal research plays a significant role in our understanding of diversification in the Caribbean, a recognized biodiversity hotspot. Based on phylogenetic data, *Anolis* lizards of the Greater Antilles are more closely related to one another on a given island than to *Anolis* from other islands. Moreover, research on *Eleutherodactylus* frogs, *Sphaerodactylus* geckos, and capromyid rodents suggest repeated and independent divergence of ancestral lineages (Ricklefs & Bermingham 2008). Recent radiations have been investigated using *Drosophila* as a study organism. Wilder and Hollocher (2003) found that the subgroup underwent two rounds of diversification, and that population bottlenecks linked to founder events played a minimal role.

In contrast, few studies have taken a plant population genetics approach (Francisco-Ortega et al. 2007, 2008) to address phylogeographic patterns across the Caribbean. Of those that

have, some studies compared genetic diversity among islands or between islands and the mainland. For example, lower genetic diversity was found in the population of *Pseudophoenix ekmanii* (Arecaceae) on Isla Beata than on Hispaniola (Namoff et al. 2011). Genetic variation within and among Cuba, Dominican Republic, and Puerto Rico was explored by Ackerman and Ward (1999). They found that populations of *Tolumnia variegata* (Orchidaceae) were very similar to one another within islands, and that among the islands gene flow was more restricted. Most research indicates plants originating from the mainland. Jardon-Barbolla (2011) found that the ancestral haplotypes of *Pinus* subsection Australes were from Central America. Conversely, results from Maskas and Cruzan's (2000) study on the systematics of *Piriqueta caroliniana* (Turneraceae) suggested that this species dispersed via long distance from the Bahamas to North America

Genetic variation and structure among bromeliad populations has been addressed in several studies, but all within mainland Central or South America (Zanella et al. 2012, Southcott & Ostevik 2011). Dominant markers have been used in several bromeliad population genetic studies: 1) AFLPs: *Billbergia* in Dal Vesco 2012; *Puya* in Sgorbati et al. 2004, and Schulte et al. 2010; *Fosterella* in Rex et al. 2007; and 2) RAPDs: *Puya* in Sgorbati et al. 2004, *Encholirium* in Mattos Cavallari et al. 2006. Co-dominant markers, such as microsatellites (SSRs) and allozymes (*Dyckia* in Hmeljevski et al. 2011) have also been used to study bromeliad population genetic diversity. Advantages to using SSRs are that they are highly polymorphic markers and PCR based with relatively low costs. SSRs have been used to study: *Puya* in Sgorbati et al. 2004, *Pitcairnia* in Sarthou et al. 2003 and Paggi et al. 2008, *Vriesea* and *Alcantarea* in Palma-Silva et al. 2007, *Vriesea* in Palma-Silva et al. 2009; *Pitcairnia* in Palma-Silva et al. 2011, *Guzmania* and *Tillandsia*, Boneh et al., 2003 and Cascante 2006, and *Alcantarea* in Barbara et al. 2007, 2008,

2009, *Orthophytum* in Aoki-Goncalves 2014, *Dyckia* in Krapp 2012 and Woehrmann 2013. There have been no studies published to date that consider population genetics within any of the three bromeliad genera indigenous to Florida. Among these genera, *Tillandsia* is the most diverse, with some 13 different species and two hybrids documented to occur on the Florida peninsula. Several of these species or their close relatives can also be found on islands of the Caribbean. This is especially true for taxa classified as part of the so-called '*Tillandsia fasciculata* complex'.

The *Tillandsia fasciculata* (Bromeliaceae) complex sensu lato (see Chapter 1) consists of 22 species, eight varieties, and three natural hybrids. These herbaceous plants are usually epiphytic and sometimes lithophytic. They occur throughout the Caribbean in a wide variety of habitats from subtropical savannas and hardwood hammocks to coastal rock plant communities and limestone outcrops. In Florida, *T. fasciculata* is a state endangered plant due not only to habitat loss, but also because the Mexican weevil, *Metamasius callizona (*Chevrolat*)*, consumes the meristematic tissue of adult plants, ultimately leading to the death of the plant.

We have conducted extensive fieldwork across Florida and the Caribbean over the past decade to locate and collect specimens and tissue from taxa in the species complex in order to evaluate genetic variation and structure among these plants. In particular we have focused our attention on populations from Florida and the nearby Bahamas using microsatellite loci. In addition to quantifying genetic variability within and among populations, this study also aims to address whether genetic structure among populations can help to delimit species boundaries of this group. We also seek to evaluate purported parentage of the natural hybrid *T.* ×*floridana* and to use population genetic data to explore conservation implications.

METHODS

Taxon sampling. All but two taxonomic members of the "*Tillandsia fasciculata*" complex known from Florida and the Bahamas were included in this study. We included this broad level of sampling, rather than restricting samples only to *T. fasciculata* or a subset of taxa, since phylogenetic results of the complex and its allies resulted in an unresolved clade indicating no clear phylogenetic delimitation among taxa (Chapter 1). Four taxa of the complex are documented to occur in Florida (Figure 1). *Tillandsia fasciculata* var. *densispica* is the most widespread, ranging from Central Florida to the Florida Keys. The other three Florida taxa have a more geographically restricted range. *Tillandsia fasciculata* var. *densispica* f. *alba*, has been recorded in southern Florida (Monroe and Miami-Dade counties), and *T.* ×*floridana* occurs in Central Florida (between the two ranges of its purported parents -- *T. fasciculata* var. *densispica* and *T. bartramii*). *Tillandsia* ×*smalliana*, another natural hybrid, occurs in southern Florida. Its purported parents are *T. fasciculata* var. *densispica* and *T. balbisiana*. Only one sample was obtained of this individual so it was excluded from this study. In the Bahamas, taxonomic delimitation of the group is unclear. Several individuals that would historically be classified as either *T. fasciculata* var. *laxispica* or *T. fasciculata* var. *densispica* were included in this study (Figure 1). Sampling of *Tillandsia fasciculata* var. *uncispica* on Crooked Island was not conducted. The only record of this taxon in the Bahamas is from an early 20th century herbarium specimen (Smith & Downs 1977). Two hundred and fifteen individuals were sampled and comprise: *T. fasciculata* var. *densispica* (n=160), *T. fasciculata* var. *densispica* f. *alba* (n=10), *T. bartramii* (n=12), and *T.* ×*floridana* (n=33). The number of individuals per site ranged from 4 to 36 (See Figure 2, Table 1, Supplementary Table 1). In the field, individuals were selected that represented the morphological diversity of the group with care being taken to not sample more

than five non-clonal individuals from a nearby location (ca. 40 ft; and never from the same tree). There were 12 sampling sites in Florida and six locations in the Bahamas.

DNA extraction. Total genomic DNA was extracted with one of two methods: either the BIO 101 FastDNA kit or Epicure Masterpure DNA Extraction protocol.

Microsatellite Primer sampling. Primers and PCR protocols were developed specifically for *Tillandsia fasciculata* and *Guzmania monostachia* by Boneh et al (2003). They designed five published (2003) (e6, p2p19, e19, e6b, CT5) and 10 unpublished (m11, CA21, 4-15, e18, CA 7, ale11, m7, CT4, e12, 4-20) primers (Table 2) with the intent of utilizing them in future ecological studies that compare secondary and mature Neotropical forests. Of these, eight loci were selected based on amplification and ease of genotyping. PCR amplifications followed Boneh et al. (2003) using the following mixture (25 µL): 13.8 µL water, 5 µL 5X Taq buffer, 0.5 µL $MgCl_2$, 0.5 µL dNTPs (10mM each), 1 µL bovine serum albumin (BSA), 1.0 µL F primer (10 mM), 1.0 µL R primer (10 mM), 0.2 µL Taq, and 1 µL, DNA template. Thermal cycling conditions followed Boneh et al. (2003). The PCR product was then diluted with water 1 µL PCR product: 99 µL water. Then that diluted product (5 µL) was added to a HiDi Formamide and Rox 500 size standard mixture. Samples were run at the UW-Madison Biotechnology Center.

Genotyping. Allele sizes were scored using Genemarker by SoftGenetics. Settings for Genemarker were: Raw data analysis (frame) 50-600, peak detection threshold 100, with 1% for global percentage and 25% for local region. To remove stutter peaks, the filter was set at the default for diploid fragment analyses, 95% left, and 40% right. The sample files were then run with the correct size template. Then, each sample file was checked for size calling and corrected if necessary. Panels were manually created for each locus, with ranges adjusted to account for

allele size. Sample files were rerun with this newly created panel and size standard. Genotyping of alleles was confirmed manually for each individual.

Statistical Analyses

For the frequency based analyses, we used GenAlEx v6.3 (Peakall & Smouse 2012) to assess allelic patterns across populations in Florida and the Bahamas. The percentage of polymorphic loci (P), the average number of alleles per locus (A), the observed heterozygosity (H_O), expected heterozygosity (H_E) across populations, and inbreeding coefficients (F_{IS}) were calculated per locus and per population in GenAlEx v6.3. This software was also used for χ^2 tests for Hardy-Weinberg Equilibrium. To compute an analysis of molecular variance (AMOVA) among populations and F_{ST} pairwise comparisons between populations we used GenAlEx v6.3. AMOVA analyses were run on the Bahamas and Florida dataset as two separate regions (N=215), Bahamas dataset only (n=61), Florida dataset only (n=154), Bahamas and Florida dataset as two separate regions without *T.* ×*floridana* and *T. bartramii* (n=170), and Florida dataset without *T.* ×*floridana* and *T. bartramii* (n=109).

To visualize genetic relationships among individuals, we employed Principal Component Analysis (PCA). We ran a pairwise genetic distance matrix among the 215 individuals and then performed a PCA in GenAlEx v6.3.

To assess potential population structure we used the software program STRUCTURE 2.3.4 which uses an approach based on Bayesian models (Pritchard et al. 2009). Settings implemented for STRUCTURE 2.3.4 were: admixture model with no prior knowledge of populations, length of burnin period was 500,000 and number of MCMC reps after burnin was 1,000,000. A project was built with predefined populations, K, set from 1 to 18 and run with 20

iterations. Otherwise default settings were used. Structure Harvester (Earl et al. 2012) was used to obtain the ΔK and infer best K (Evanno et al. 2005). Then CLUMPAK (Cluster Markov Packager Across K; Kopelman et al., in press) was implemented to help visualize structure results. A separate STRUCTURE analysis removed *T.* ×*floridana* and *T. bartramii* to test what effect these taxa had on genetic structure of the *T. fascisculata* group in the Bahamas and Florida (n=170).

To evaluate the relationship between genetic and geographic distances, we performed a Mantel test (1967). GenAlEx v6.3 was run with linearized F_{ST} (=F_{ST}/(1-F_{ST})) and geographic distance (log transformed locality data in degree decimal). Mantel tests were performed on the following datasets: *T. fasciculata* group in Florida and the Bahamas, Florida only, the Bahamas only, and Florida without *T.* ×*floridana* and *T. bartramii*.

RESULTS

Genetic Variation

Across the "*Tillandsia fasciculata*" plants sampled in Florida and the Bahamas (N=215), we find a total of 63 alleles at the eight loci sampled, ranging from 5 to 13 alleles per locus. The grand mean number of alleles over loci and populations is 3.632 (SE=0.135; Table 1). Private alleles are detected in five populations (Table 1). Three loci are monomorphic in three of the Bahamas populations (AC, M, A), while one locus is monomophic in one Florida population (MR). Percentage of polymorphic loci per population ranges from 75% to 100% (Table 1).

The average observed and expected heterozygosity over loci and populations is 0.684 (SE=0.023) and 0.561 (SE=0.016), respectively (Table 1). Chi-Square Tests for Hardy-Weinberg

Equilibrium finds that of the 144 locus/population combinations, 22 (P<0.05), 14 (P< (0.01) and 13 (P<0.001) shows deviation at corresponding levels of significance.

Values of F_{IS} are between -0.785 to 0.142 with a grand mean for all populations of -0.231 (SE=0.029) (Table 1). Of the 18 collecting sites, only four sites had positive mean F_{IS} scores, ranging from 0.008–0.142.

Population Genetic Structure and Differentiation

When individuals in the "*Tillandsia fasciculata*" group from Florida and the Bahamas are included in the PCA, only a few of the collection sites form distinct genetic groups (Figure 3). Populations from Central Florida consist of the purported natural hybrid *T.* ×*floridana* and *T. bartramii*. Percentage of variation explained by the first three axes are: 32.00%, 19.57% and 15.41% respectively. When a PCA is run without *T.* ×*floridana* and *T. bartramii* to test the taxon effect, the large cluster is not further divided (not shown).

Results from our eight loci STRUCTURE analysis find two genetic groups from the 18 collecting sites: 1) the natural hybrid *T.* ×*floridana* from central FL and one of its purported parents, *T. bartramii*, from northern Florida (Figure 4a); and 2) *T. fasciculata* var. *densispica* and *T. fasciculata* var. *densispica* f. *alba* from Florida, together with "*T. fasciculata*" from the Bahamas (ΔK=439.514932). The second and third highest ΔK suggest either three ((ΔK =141.284374 (Figure 4b)) or four groups (ΔK=7.050615). Recognition of three groups entails 1) *T.* ×*floridana* and *T. bartramii*; 2) *Tillandsia fasciculata* var. *densispica* f. *alba* and many individuals of *T. fasciculata* var. *densispica* from the southern counties of FL (except, Matheson Hammock); and 3) the remaining *T. fasciculata* var. *densispica* from the Bahamas and

southwestern and southern Florida (Figure 4b). In the case of four populations, these patterns become more pronounced.

To test the taxon effect of *Tillandsia* ×*floridana* and *T. bartramii*, we removed them from the dataset and conducted a separate STRUCTURE analyses. Results support the clustered groups seen in the previous analyses. With the highest ΔK score (ΔK=785.279879), the two populations are 1) *T. fasciculata* var. *densispica* f. *alba* and *T. fasciculata* var. *densispica* from Collier Co. in southwestern FL and the southeast counties of St. Lucie, and Martin, and 2) *T. fasciculata* var. *densispica* across the Bahamas and remaining counties (Figure 5). As K populations increase, *T. fasciculata* from the Bahamas and *T. fasciculata* var. *densispica* f. *alba* separately segregate from the rest of the groups, but there is no statistical support.

Results for all AMOVA reveal greater variation within populations than among populations (Tables 4–8). When all taxa are included, a significant portion is accounted for by variation within population (F_{ST}=0.172, P<0.001, Table 4).When only the Bahamas dataset is analyzed, within population difference again accounts for the largest percent variance in the Bahamas (94%, F_{ST}=0.056, P<0.001, Table 5). The same is true when only the Florida dataset is analyzed (87%, F_{ST}=0.128, P<0.001, Table 6). When *T.* ×*floridana* and *T. bartramii* are removed, again most of the variation is among populations (86%), while among populations accounts for 14% (5% among regions and 9% among populations within regions, Table 7) When the Florida dataset is reanalyzed and excludes *T.* ×*floridana* and *T. bartramii*, F_{ST} values indicate a lower degree of differentiation among populations than when these two taxa are included (F_{ST}=0.106, P<0.001, Table 7).

Isolation by Distance

There are significant relationships between geographic and genetic distance for the Florida and Bahamas "*Tillandsia fasciculata*" group (R_{XY}=0.395, R^2=0.1557, P<0.001, Figure 6). Separate Mantel tests were performed on the Bahamas dataset (R_{XY}=0.817, R^2=0.6678, P =0.016, Figure 7), Florida dataset (R_{XY}=0.215, R^2=0.0461, P=0.037, Figure 8) and Florida dataset without *T.* ×*floridana* and *T. bartramii* (R_{XY}=0.100, R^2=0.01, P =0.158, Figure 9). These results reveal significant isolation by distance for the separately treated Bahamas and Florida populations.

DISCUSSION

Genetic Variation

Polymorphic loci per population ranges from 75% to 100% (Table 1). Three loci were monomorphic in three of the Bahamas populations (Atala Coppice, Maidenhair, and Great Abaco), while one locus was monomorphic in one Florida population (Myakka River). This indicates that half of the islands may be experiencing lower levels of genetic variation due to isolation. The expected heterozygosity (H_E) results from our study falls within the range of Boneh et al. (2003). For CT5, e6b, and e19, Boneh et al. (2003), H_E was 0.732, 0.679, and 0.667, respectively. Our results for H_E are 0.612 (CT5), 0.660 (e6b), and 0.625 (e19).

In our study, the average observed heterozygosity (Ho) and H_E over loci and populations is 0.684 (SE=0.023) and 0.561 (SE=0.016), respectively. H_E scores between islands ranged from 0.371–0.579 in Bahamas populations vs. 0.447–0.715 in Florida populations. Cascante (2006) used many of the same loci developed by Boneh et al. (2003) to study Costa Rican *T. fasciculata*

populations in successional forests. The pooled Ho for his research was 0.683, almost identical to our study. His study found lower Ho in mature forest (0.330) than in early succession forest (0.776). In comparison to other bromeliad islands systems, Barbara et al (2008) studied genetic diversity and structure in four *Alcantarea* inselbergs. They found H_E ranging from 0.242 to 0.576. The H_E genetic diversity scores of the recent *Tillandsia fasciculata* in the Caribbean islands are similar to *Alcantarea* in the ancient Brazilian inselbergs.

Private alleles are detected in five populations, one in the Bahamas (Jungle Pond) and four in Florida (Jonathan Dickinson, Tosohatchee, Wingate Creek, and Highlands Hammock). All of the Florida sites are in the central park of the state, and T, WG, and HH have populations of *T.* ×*floridana* (Table 3). Except for locus CT5, the number of alleles found in our study (loci CA21, e6, e6b, p2p19) are nearly double that in Cascante (2006). This is probably due to the fact that they studied only *T. fasciculata* sensu stricto while we included other members of the *T. fasciculata* complex (*T.* ×*floridana*, *T. fasciculata* var. *densispica* , *T. fasciculata* var. *densispica* f. *alba*, and *T. fasciculata* var. aff. *laxispica* from the Bahamas).

F_{IS} scores range from -0.785 to 0.142 and are negative in 14 of the 18 populations tested (Table 1). Of the 18 collecting sites, only four sites had positive mean F_{IS} scores, ranging from 0.008–0.142. F_{IS} for *T. fasciculata* var. aff. *laxispica* population in the Bahamas was -0.075 vs. Florida populations with a F_{IS} of -0.302. This indicates that the Florida populations (mainland) have lower levels of inbreeding than the Bahamas (island). Within Florida, the *T. fasciculata* var. *densispica* f. *alba* has the lowest F_{IS} at -0.785. A white tubular flower with light green floral bracts suggests an insect pollinator. One possible explanation for the lowest F_{IS} is that insects are more common than hummingbird visitors. In Florida the bracts of *Guzmania monostachia* are pinkish-cream and less vibrant red in their more tropical counterparts where presumably there

are more hummingbirds. The pooled F_{IS} for each locus in Cascante (2006) was lower than our study. CA21: -0.505 vs -0.307; CT5: -0.487 vs -0.171; E6: -0.433 vs. -0.334; E6b:-0.493 vs. -0.170; and p2p19: -0.411 vs. -0.172). His more negative F_{IS} scores indicate that there is less inbreeding and more outbreeding on the mainland compared our mainland and island study system.

Population Genetic Structure and Differentiation

Molecular phylogenetic reconstructions based on DNA sequences from eight plastid and nuclear markers were not able to resolve relationships among *T. fasciculata* var. *densispica*, *T. fasciculata* var. *densispica* f. *alba*, and *T.* ×*floridana* (Chapter 1). Morphometric studies were equally uninformative and unable to significantly delimit *T. fasciculata* var. *densispica* plants from Florida and *T. fasciculata* var. aff. *densispica* and *T. fasciculata* var. aff. *laxispica* individuals from the Bahamas (Sidoti, unpublished). Our population-level approach provides greater resolution among these taxa into taxonomic or perhaps geographic clusters.

Results from our eight loci STRUCTURE analysis helps delimit T. ×*floridana* and *T. bartramii* from the rest of the *T. fasciculata* group tested. Prior to these results, relatedness of *Tillandsia* ×*floridana* and its purported parents *T. fasciculata* var. *densispica* and *T. bartramii* was only predicted from morphological characters and distribution. *Tillandsia fasciculata* var. *densispica* occurs in southern Florida and is relatively large (20–50” in tall) with a digitate inflorescence with glabrous, mostly red-green floral bracts on its branches (Luther 1985). *Tillandsia bartramii* is found in northern Florida, is smaller in comparison (16–18” tall) and has lepidote, pink floral bracts. *Tillandsia* ×*floridana* is distributed between these two taxa, in Central Florida. Its size is intermediate between the two (ca. 24” tall) and it has pink, lepidote floral bracts. Based on membership coefficient in STRUCTURE analyses, *T.* ×*floridana*

individuals clustered almost exclusively with *T. bartramii* (see Figure 3; predominantly in orange), rather than with its other purported parent, *T. fasciculata* var. *densispica* (predominant membership coefficient in blue, Figure 3).

Once these two taxa were removed, a separate STRUCTURE analysis was able to find better support for genetic groups that were hinted at previously. Based on the highest ΔK (ΔK=769.616818), again results suggest two genetic groups, but this time it is based on regions. Group 1 comprises: *T. fasciculata* var. *densispica* f. *alba* and *T. fasciculata* var. *densispica* from Collier Co. in southwestern FL and the southeast counties of St. Lucie, and Martin. Group 2 consists of: *T. fasciculata* var. *densispica* across the Bahamas and remaining counties (Figure 5). As K populations increases, *T. fasciculata* from the Bahamas segregates from the rest of the groups. This suggests they may be undergoing isolation. In a population genetic study on *Ipomoea microdatyla* (Convolvulaceae) in the same region, STRUCTURE results found two distinct clusters, Florida and Bahamas/Cuba (Geiger et al. 2012). Their findings are similar to ours, depending on inferred K. From a taxonomic standpoint, a separate Bahamas group helps to resolve the *T. fasciculata* var. *laxispica*/*T. fasciculata* var. *densispica* group (i.e., the former is found in the Bahamas). Another group that begins to separate from the other "*T. fasciculata*" as K increases is *T. fasciculata* var. *densispica* f. *alba* (see conservation implication below). PCA results were less informative than STRUCTURE analysis, but do support our first STRUCTURE analysis where *T.* ×*floridana* and *T. bartramii* form a separate group.

When we examine just variation among populations, a significant portion is accounted for by variation among regions (F_{RT}=0.067, P<0.001). Within regions, there is still significant variation among populations (F_{SR}=0.113, P<0.001). This is probably driven by variation within Florida because of the inclusion of *T.* ×*floridana* and *T. bartramii* ($SSWR_{Florida}$, 898.120 >

$SSWR_{Bahamas}$, 283.787). When the Bahamas and Florida datasets are treated separately, within population difference again accounts for the largest percent variance in the Bahamas (94%, F_{ST}=0.056, *P*<0.001, Table 5) and in Florida (87%, F_{ST}=0.128, *P*<0.001, Table 6).

Next we removed *Tillandsia ×floridana* and *T. bartramii* to test the effect they may have had on AMOVA results. As with the above treatment of Bahamas and Florida, this scenario shows a moderate degree of differentiation among populations (Fst=0.117, *P*<0.001, Table 7). Again, within regions there is still significant variation (F_{SR}=0.092, *P*<0.001). When *Tillandsia ×floridana* and *T. bartramii* are removed from the dataset, $SSWR_{Florida}$ decreases ($SSWR_{Florida}$, 605.229 > $SSWR_{Bahamas}$, 283.797). Even though there are significant differences among populations when only Florida *T. fasciculata* var. *densispica* plants (including the white flowered form) were analyzed (F_{ST}=0.106, *P*<0.001, Table 8), F_{ST} values indicate a low degree of differentiation among populations. This suggests low levels of population structuring in *T. fasciculata* var. *densispica* plants across Florida, a result supported by our STRUCTURE analysis.

The average F_{ST} over all populations for each locus was 0.180 (SE=0.007) which implies genetic differentiation (Frankham et al. 2010). A F_{ST} score of zero indicates complete panmixis, while a score of 1 implies population structuring. F_{ST} scores of other bromeliad studies were higher than our study. Our F_{ST} results are within the range of short-lived perennial, wind dispersed plants (Nybom et al 2004). Our F_{ST} results also fall within the range of other Tillandsioideae F_{ST} scores: *Tillandsia fasciculata*, 0.247 (Cascante 2006), *T. ionantha* 0.043 and *T. recurvata*, 0.906 and (Soltis et al. 1987), *T. achrostachys*, 0.391 (Gonzalez-Astorga et al. 2004), *Alcantarea geniculate*, 0.111. Barbara et al 2007, *A. glaziouana*, 0.217 Barbara et al 2009. And in *Bromelia*, a F_{ST}=0.224, Martini Zanella et al. 2001.

Isolation by distance

Three of our four Mantel tests on geographic and genetic distance matrices find low R^2 values indicating a weak positive relationship (exception the Bahamas populations). During the last interglacial (ca. 125 ka), much of the current range of the "*T. fasciculata*" group in Florida and the Bahamas would have been inundated. This relatively young group (1–3.2 ma for *T. fasciculata* s.s. group, Chapter 1) is likely influenced by these glacial cycles whose populations either may not have had enough time to become isolated or did not migrate to these regions until they became drier. Our STRUCTURE results weakly support clusters of plants based on separate regions. *Tillandsia fasciculata* var. *densispica* from Florida and *T. fasciculata* var. aff. *laxispica*, consistently form separate clusters when $K \geq 3$. Geiger et al (2012) found strong isolation by distance among the *Ipomea macrodatyla* populations across Florida and the Bahamas. Their geographic signal could be due to a more limited range of the plant. *Ipomea macrodatyla* occurs in the Everglades National Park and in Miami Dade Co. in the USA, the Bahamas, and Cuba (the latter not included in their IBD test), while the range of "*T. fasciculata*" in our study encompassed southern Florida up to the central part of the state and included Great Abaco in the Bahamas (both studies had samples from North Andros). Even though both studies focused on Florida and the Bahamas, their overall study sites had a narrower distribution range than ours.

Ploidy and Pollination

In interpreting our results, we were careful to consider the role that ploidy level and pollinator behavior might have on them. The proposed base chromosome number of Bromeliaceae is x=25 (Brown and Gilmartin 1989, Benzing 2000). Brown and Gilmartin (1989) found that two of the *Tillandsia fasciculata* var. *fasciculata* samples in their study had a base chromosome number of x=25. While most *Tillandsia* plants they sampled were diploid with base

chromosome number of x=25, a few exceptions were noted (e.g., *T. leiboldiana* x=19). Brown & Gilmartin chromosome count differed from Gauthe (1965) who reported *T fasciculata* 2*n*=64 and *T. fasciculata* var. *venosispica* 2*n*=56. They noted that the discrepancy may be due to no varietal designation given by Gauthe (1965) and in the highly polymorphic "*T. fasciculata*" group. Ploidy level is unknown in most members of the *T. fasciculata* group. While conducting our genotyping analyses we noticed that almost all samples exhibited either one (homozygous) or two (heterozygous) peaks. In only a very few instances did we observe what might be interpreted as three peaks, indicating a polyploid, but this pattern was not consistent among loci of the same individual, and the third peak was usually below the intensity threshold scored. As a result, we feel fairly confident in stating that all individuals sampled, including the supposed hybrids, are probably diploid.

Although we doubt the existence of polyploidy in the *Tillandsia fasciculata* complex, other researchers have hypothesized its prevalence in order to explain relatively high levels of heterozygosity observed in *T. fasciculata*. Castante (2006) supported this theory based on his breeding research of the taxon. He observed a long period of time that the exserted stigma and anther could touch, and through experiments found that this taxon is self-compatible. His SSR research also found that the offspring are identical to the maternal plant, thus claiming fixed heterozygosity, a condition associated with polyploidy. Castante (2006) hypothesized that these plants are pollinated primarily through selfing, and would thus exhibit low levels of heterozygosity. Because Castante found just the opposite, he proposed polyploidy to account for the unexpected result. We disagree, and instead note that we have observed hummingbirds visiting flowers of *T. fasciculata* in the field. Their floral morphology (e.g., red bracts, long

corolla) point to a bird-pollinated syndrome and not selfing as a primary mode of pollination and outcrossing.

Conservation implications

Tillandsia fasciculata var. *densispica* is listed as endangered in Florida, which is the northernmost range for the species complex. The taxa of the *T. fasciculata* group are otherwise distributed in Mexico, northern South America, and across the Caribbean. A detailed study on the genetic variation of this ecologically important plant group is critical to developing and implementing conservation measures for them. Levels of genetic variation within this and other populations were unknown until our study. F-statistics results indicating relatively high levels of heterozygosity and outcrossing are favorable for the long term viability of this variety in Florida. F_{IS} was low suggesting low levels of inbreeding. Furthermore, the genetic structure that does appear is a result of both taxonomy, *T.* ×*floridana* and *T. fasciculata* var. *densispica* f. *alba*, and region, *T. fasciculata* var. aff. *laxispica*. This suggests that if one or several populations become rare (e.g., in south Central Florida), those lost could be repatriated from another population (e.g. in southern Florida). This scenario could be especially important in maintaining extant populations of plants where the lethal weevil *Metamasius callizona* has yet to spread.

Because the weevil has decimated much of south Central Florida's *T. fasciculata* var. *densispica* (e.g., in HH, MR), all populations across the state should be managed to reflect the increasing rarity of this plant. Our population genetics data should be useful to park managers and local bromeliad societies that have an interest in *ex-situ* conservation efforts who want to know whether cultivated plants are representative of the full genetic variation and structure of their wild counterparts. If plants are repatriated, our results could aid in determining which

individual plants to return to the wild, and to where they should go (i.e., returning genetically similar, *ex situ* cultivated bromeliads to regions where their wild relatives once occurred *in situ*).

Finally, we wish to draw attention to an even less common taxon sampled in our study -- *T. fasciculata* var. *densispica* f. *alba*. Florida populations with a mean of 2.375 alleles (SE=0.263) at Camp Owaissa Bauer. Populations of *T. fasciculata* var. *densispica* f. *alba* are rare and are restricted to southern Florida. Depending on the interpretation of K value in STRUCTURE, morphometric results (Sidoti, unpublished) corroborate that this taxon may be distinct from its purple petal counterpart. Evidence from this study supports that they deserve to be elevated in taxonomic rank, which might help to draw further attention to their conservation status. We recommend that these populations be closely monitored and managed, since they likely represent something more than albino mutants.

CONCLUSION

We have demonstrated that microsatellites are useful in determining genetic variation and structure within and among populations of the *Tillandsia fasciculata* complex in Florida and the Bahamas. At least two populations of *T. fasciculata* var. *densispica* are identified: 1) *T. fasciculata* var. *densispica* f. *alba* and mostly *T. fasciculata* var. *densispica* individuals in Collier, FL and southeast counties, St. Lucie, and Martin and 2) a southwestern and southern Florida and Bahamas group. When factoring in morphometric results and geography, there is support to further subdivide these two groups to *T. fasciculata* var. *densispica* f. *alba* and *T. fasciculata* var. aff. *laxispica* from the Bahamas. The most genetically distinct population consists of the natural hybrid *T.* ×*floridana* and one of its purported parents, *T. bartramii*. Prior

to these results, relatedness of *T.* ×*floridana* and *T. bartrami* was only guessed at from morphological characters.

Further research should test and add more SSR loci that have been proven useful in other lineages of Tillandsioideae (e.g., used by Barabara et al. 2007, 2008, 2009, Palma-Silva et al. 2007, 2009) or take advantage of "next generation" methods such as Genotyping by Sequencing (GBS) or RAD-Seq. Furthermore, it would be advantageous in future studies of this group to include additional samples from across the Caribbean, so that phylogeographic patterns of biogeography can be considered across the region, and to help delimit this highly variable species complex.

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Table 1. Genetic diversity statistics for 18 populations of the *Tillandsia fasciculata* group: percent of polymorphic loci (P); mean number of alleles per locus (A);number of private alleles (A_{PV}); observed heterozygosity (H_O); expected heterozygosity (H_E); mean inbreeding coefficient per population (F_{IS}).

Population		*N*	*P*	*A*	A_{PV}	H_O	H_E	F_{IS}
Bahamas								
Atala Coppice	AC	6	75.00	2.750	0.000	0.438	0.460	0.058
Jungle Pond	JP	20	100.00	4.375	0.250	0.570	0.579	0.008
Rainbow Blue Hole	RBH	12	100.00	3.875	0.000	0.562	0.522	-0.090
Maidenhair	M	4	75.00	2.375	0.000	0.490	0.371	-0.306
Stafford Creek	SC	10	100.00	3.750	0.000	0.550	0.523	-0.080
Abaco	A	9	87.50	3.000	0.000	0.500	0.475	-0.039
Florida								
Key Largo Hammock	KLH	5	100.00	3.375	0.000	0.875	0.621	-0.421
Matheson Hammock	MH	12	100.00	3.375	0.000	0.586	0.460	-0.205
Corkscrew Swamp Sanctuary	CS	13	100.00	4.625	0.000	0.875	0.667	-0.331
Jonathan Dickinson	JD	12	100.00	4.875	0.125	0.615	0.715	0.142
Tosohatchee	T	11	100.00	2.875	0.125	0.920	0.549	-0.663
Myakka River	MR	8	87.50	2.375	0.000	0.556	0.447	-0.261
Collier-Seminole State Park 3	CLS	8	100.00	3.875	0.000	0.719	0.616	-0.172
Fakahatchee Strand	FS	14	100.00	4.375	0.000	0.826	0.655	-0.270
Savannas Preserve	SV	13	100.00	5.000	0.000	0.614	0.669	0.068
Wingate Creek	WG	12	100.00	3.250	0.250	0.863	0.582	-0.487
Highlands Hammock	HH	36	100.00	4.875	0.500	0.844	0.681	-0.242
Camp Owaissa Bauer	COB	10	100.00	2.375	0.000	0.913	0.506	-0.785
Mean			95.83	3.632	0.069	0.684	0.561	-0.231

Table 2. Microsatellite primers developed by Boneh et al. (2003). * denotes unpublished by Boneh.

Primer	Primer Forward	Primer Reverse	Product size	Microsatellite length
ale11*	TCTTTGGATGGCATAGACAA	GGGGCAGAAGGGTAAAGAAC	165	$CT_{(14)}$
CA21*	CCCTTCTCCTTCACTAGCA	AAAACATGGTAGAACACTCCA	157	$CAA_{(16)}$
CT5	AATGAGTTTCAGTTTTAGAAGC	CCAAGAAAAGAACGGATCA	189	$GA_{(25)}$
e6	AAACTATGGATTCCCCAACT	CGGTTCCTCCTTAGTCTTT	148	$CAA_{(14)}$
e6b	CGTACGAAGGTAAGCACAA	CCGTTGAAGAGGTTAGAGG	151	$CAA_{(12)}$
e18*	CAGTTAGACAGGCTCTTAGCATCA	TGCGCAAGTGAGACCAAATA	152	$CA_{(14)}$
m11*	GGCATAAATGTAAACTAACACAGAT	GCCAGAATGCGAAACTCC	225	$AG_{(39)}$AATAAAAAAAAA
p2p19	ATGCTGCCCACTGAAGATTT	TCCGTCCAAGGTTTATTTGC	204	$GAA_{(14)}$

Table 3. Genetic diversity statistics at eight microsatellite loci in the *Tillandsia fasciculata* group: number of alleles (A); observed heterozygosity (H_O); expected heterozygosity (H_E); among population genetic differentiation (F_{ST}).

Locus	*A*	H_O	H_E	F_{ST}
ale11	6	0.523	0.389	0.210
CA21	7	0.767	0.586	0.167
CT5	6	0.716	0.612	0.142
e6	7	0.772	0.493	0.179
e6b	13	0.657	0.660	0.181
e18	7	0.720	0.625	0.180
m11	5	0.508	0.432	0.205
p2p19	12	0.810	0.691	0.179
Mean	7.875	0.684	0.561	0.180

Table 4. Florida and Bahamas, all data (N=215). Analysis of molecular variance (AMOVA) based on eight microsatellite loci for 18 populations of the "*Tillandsia fasciculata*" group. F_{ST}=0.172, *P*<0.001.

Source of variation	d.f.	SS	MS	% of variation
Among regions	1	46.570	46.570	7
Among populations	16	156.644	9.790	10
Within populations	412	1025.263	2.489	83
Total	429	1228.477		100

Table 5. Bahamas only. Analysis of molecular variance (AMOVA) based on eight microsatellite loci for six populations of the "*Tillandsia fasciculata*" group in the Bahamas. n=61. F_{ST}=0.056, *P*<0.001.

Source of variation	d.f.	SS	MS	% of variation
Among populations	5	24.040	4.808	6
Within populations	116	259.747	2.239	94
Total	121	283.787		100

Table 6. Florida only. Analysis of molecular variance (AMOVA) based on eight microsatellite loci for twelve populations of the "*Tillandsia fasciculata*" group in Florida. n=154. F_{ST}=0.128, *P*<0.001.

Source of variation	d.f.	SS	MS	% of variation
Among populations	11	132.604	12.055	13
Within populations	296	765.516	2.586	87
Total	307	898.120		100

Table 7. Analysis of molecular variance (AMOVA) based on eight microsatellite loci for 14 populations of *Tillandsia fasciculata* var. *densispica* in Florida and *Tillandsia fasciculata* var. aff. *laxispica* in the Bahamas, as two regions. n=170. F_{ST}=0.142 , P<0.001.

Source of variation	d.f.	SS	MS	% of variation
Among regions	1	32.622	32.622	5
Among populations	15	107.696	7.180	9
Within populations	323	781.320	2.419	86
Total	339	921.638		100

Table 8. Analysis of molecular variance (AMOVA) based on eight microsatellite loci for eight populations of *Tillandsia fasciculata* var. *densispica* (including the white flowered form) in Florida n=109. F_{ST}=0.106 , *P*<0.001.

Source of variation	d.f.	SS	MS	% of variation
Among populations	10	83.657	8.366	11
Within populations	207	521.573	2.520	89
Total	217	605.229		100

Figure 1. Bahamas: A & B) *Tillandsia fasciculata* aff. *laxispica*. Florida: C) *T. fasciculata* var. *densispica* D) *T. fasciculata* var. *densispica* f. *alba*, E) *T.* ×*floridana*.

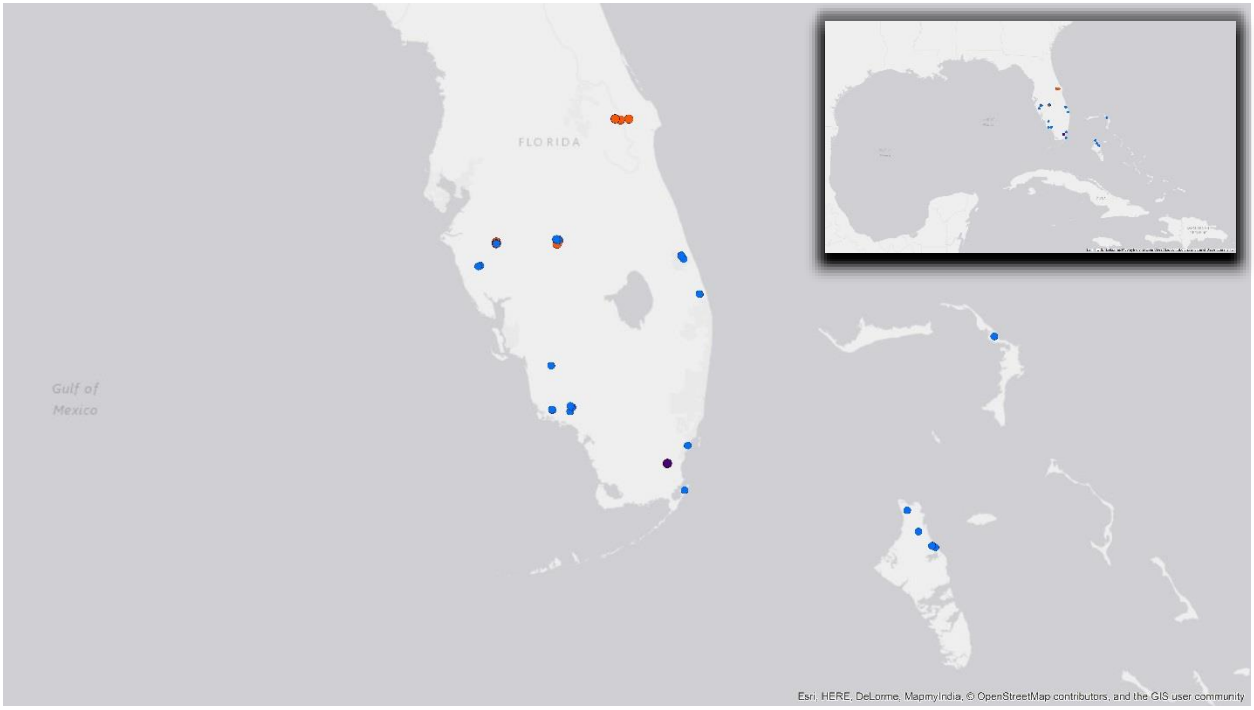


Figure 2. Collecting sites of *T. fasciculata* var. *densispica* and *T. fasciculata* aff. *laxispica* (in blue), *T. fasciculata* var. *densispica* f. *alba* (in purple), *T.* ×*floridana* (in orange), and *T. bartramii* (in orange). USA. Florida. William Beardall Tosohatchee State Reserve, Christmas, Orange Co. (N = 11); Dagny Johnson Key Largo Hammock Botanical State Park, Key Largo, Monroe Co. (N = 5); Jonathan Dickinson State Park, Hobe Sound, Martin Co. (N = 12); Matheson Hammock, Miami, Miami-Dade Co. (N = 12); Savannas Preserve State Park, Jensen Beach, Martin Co. (N = 12); Camp Owaissa Bauer, Miami, Miami-Dade Co. (N=10); Collier-Seminole State Park, Naples, Collier Co. (N = 8); Corkscrew Swamp Sanctuary, Naples, Collier Co. (N = 13); Fakahatchee Strand Preserve State Park, Copeland, Collier Co. (N = 14); Highlands Hammock State Park, Sebring, Highlands Co. (N =36); Myakka River State Park, Sarasota, Sarasota Co. (N = 8); Wingate Creek State Park, Manatee Co. (N=12). BAHAMAS. Andros: Atala Coppice (N = 6); Jungle Pond (n = 20); Rainbow Blue Hole (N = 12); Maidenhair (N = 4); Stafford Creek (N = 10); Abaco, near Abaco Heights (N = 9).

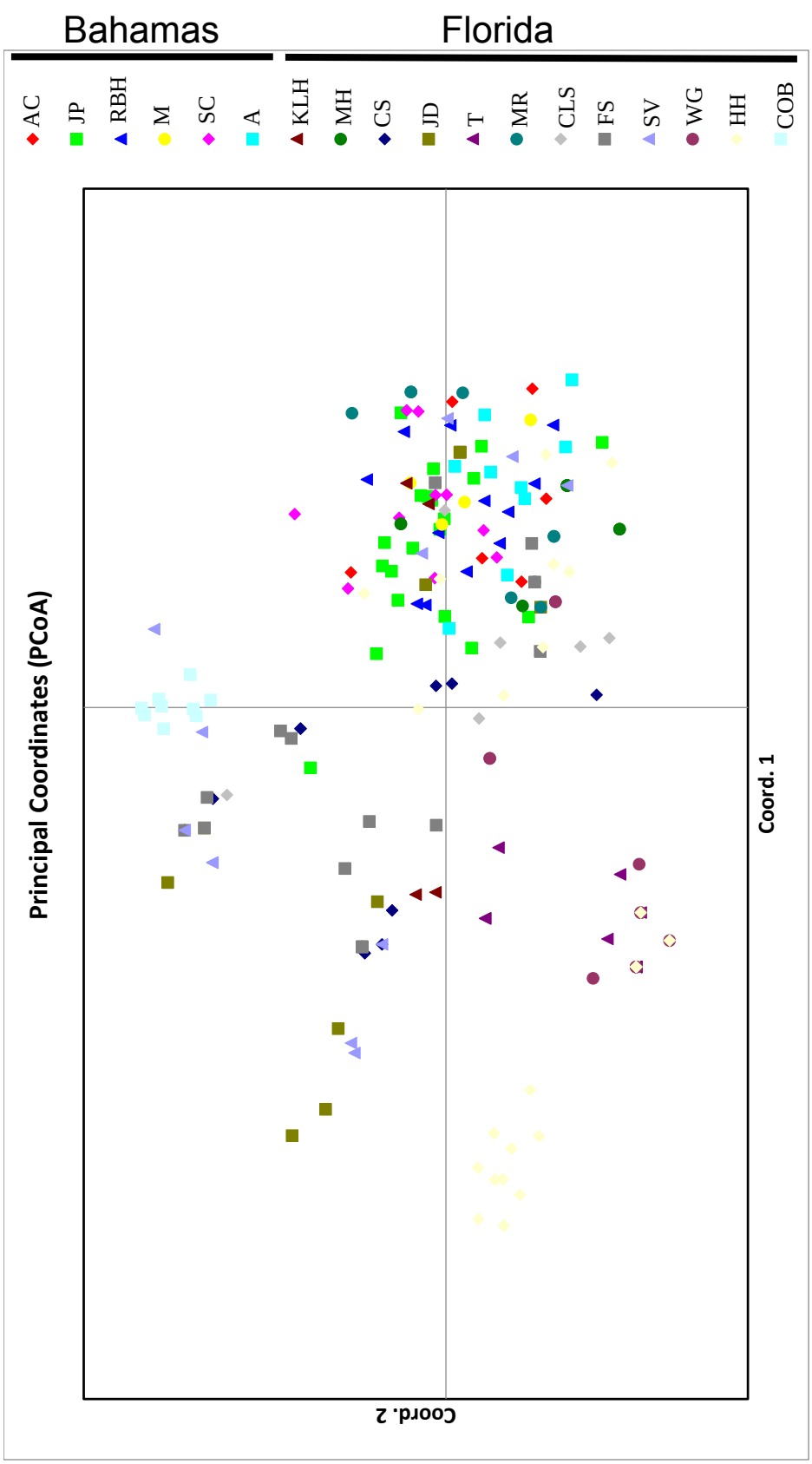
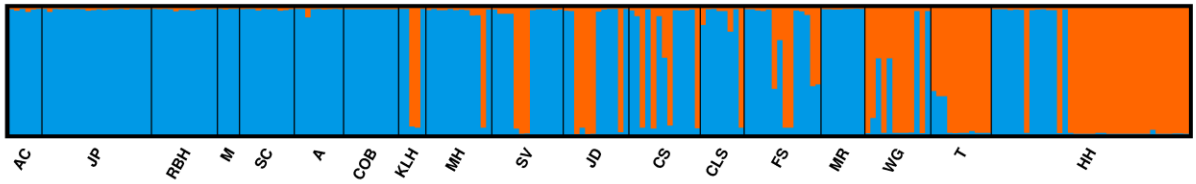


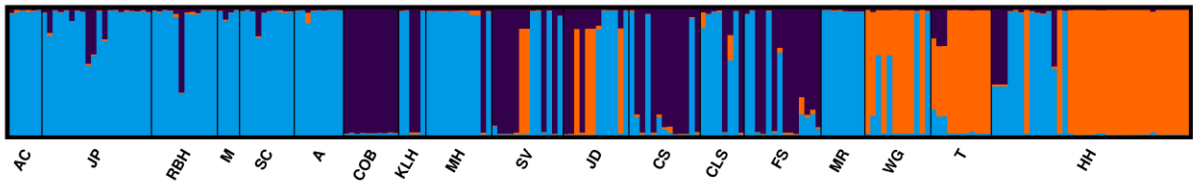
Figure 3. PCoA of *Tillandsia fasciculata* group in the Bahamas and Florida, based on SSR data. Percentage of variation explained by the first 3 axes are, 32.00%, 19.57% and 15.41% respectively. Lower, left quadrant are individuals of *T. bartramii* and *T. ×floridana*. N=215.

A)



K=2

B)



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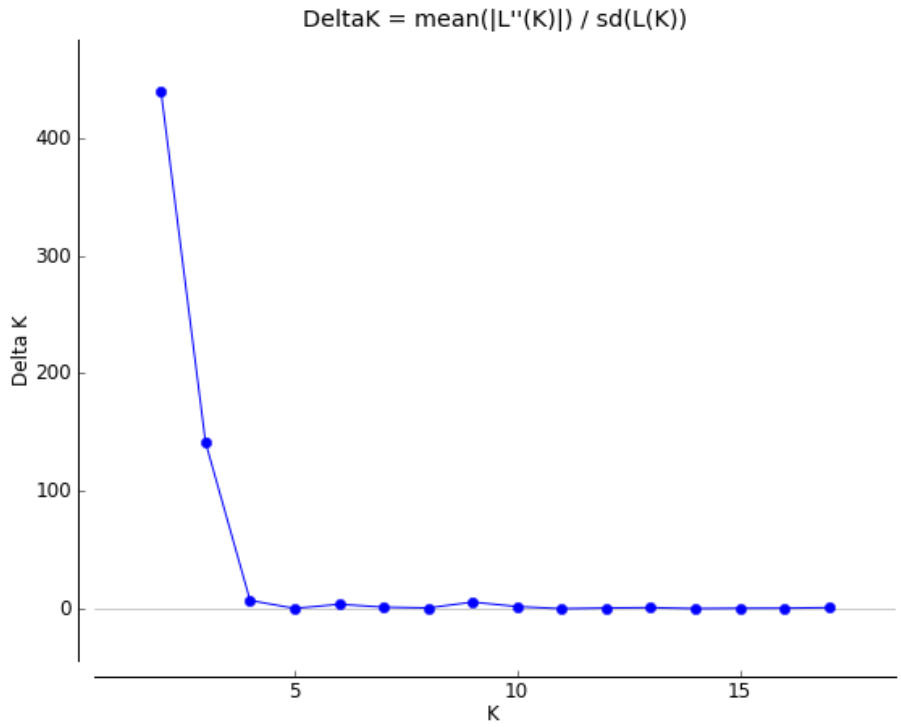
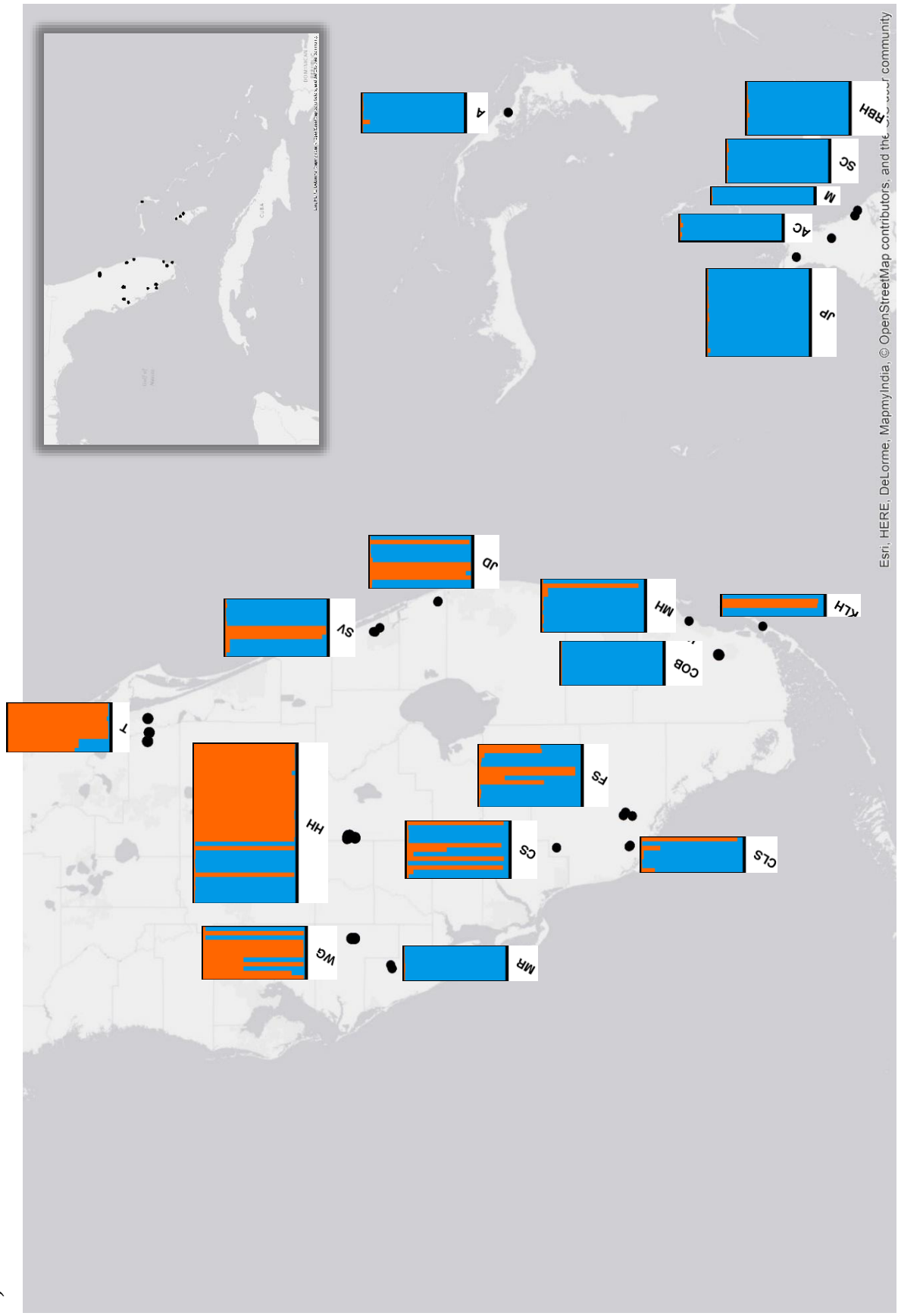


Figure 4. Microsatellite STRUCTURE analysis of Bahamas and Florida populations of *Tillandsia fasciculata* group. Each vertical line represents an individual from collecting site. Colors represent membership coefficient. Number of runs per K is 20. N=215. A) K=2, ΔK=439.514932. B) K=3, ΔK =141.284374. C) STRUCTURE analysis with map (following page).


A
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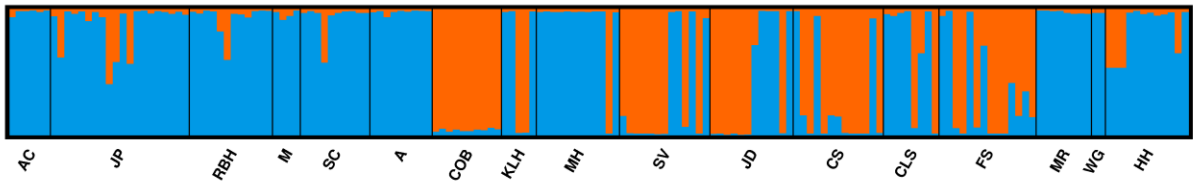
Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

C)

A)



K=2

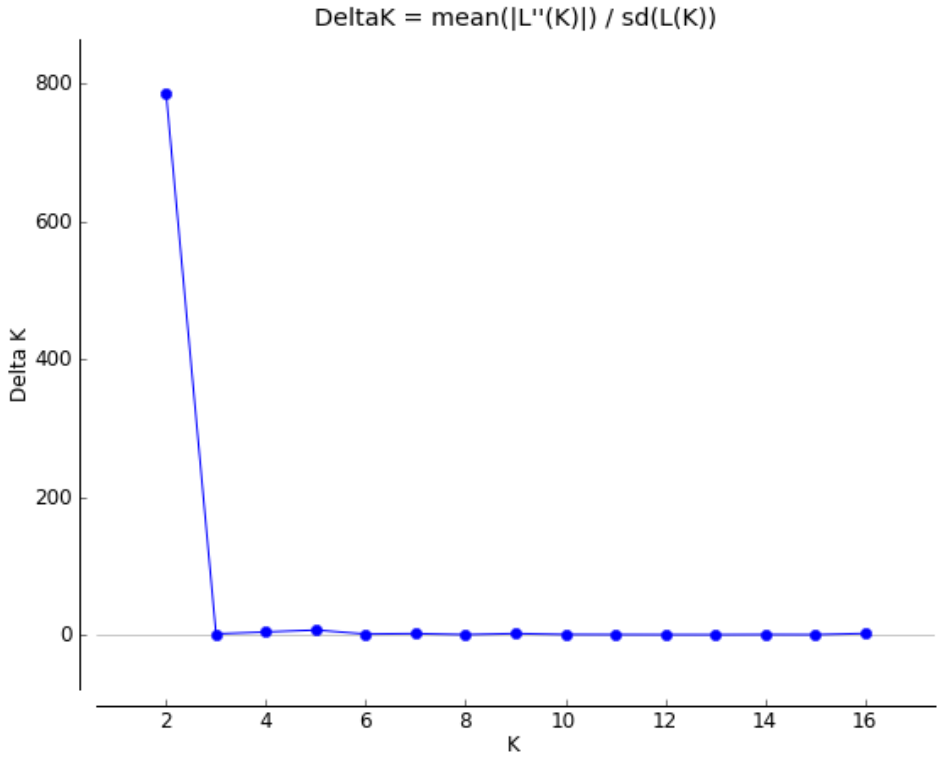
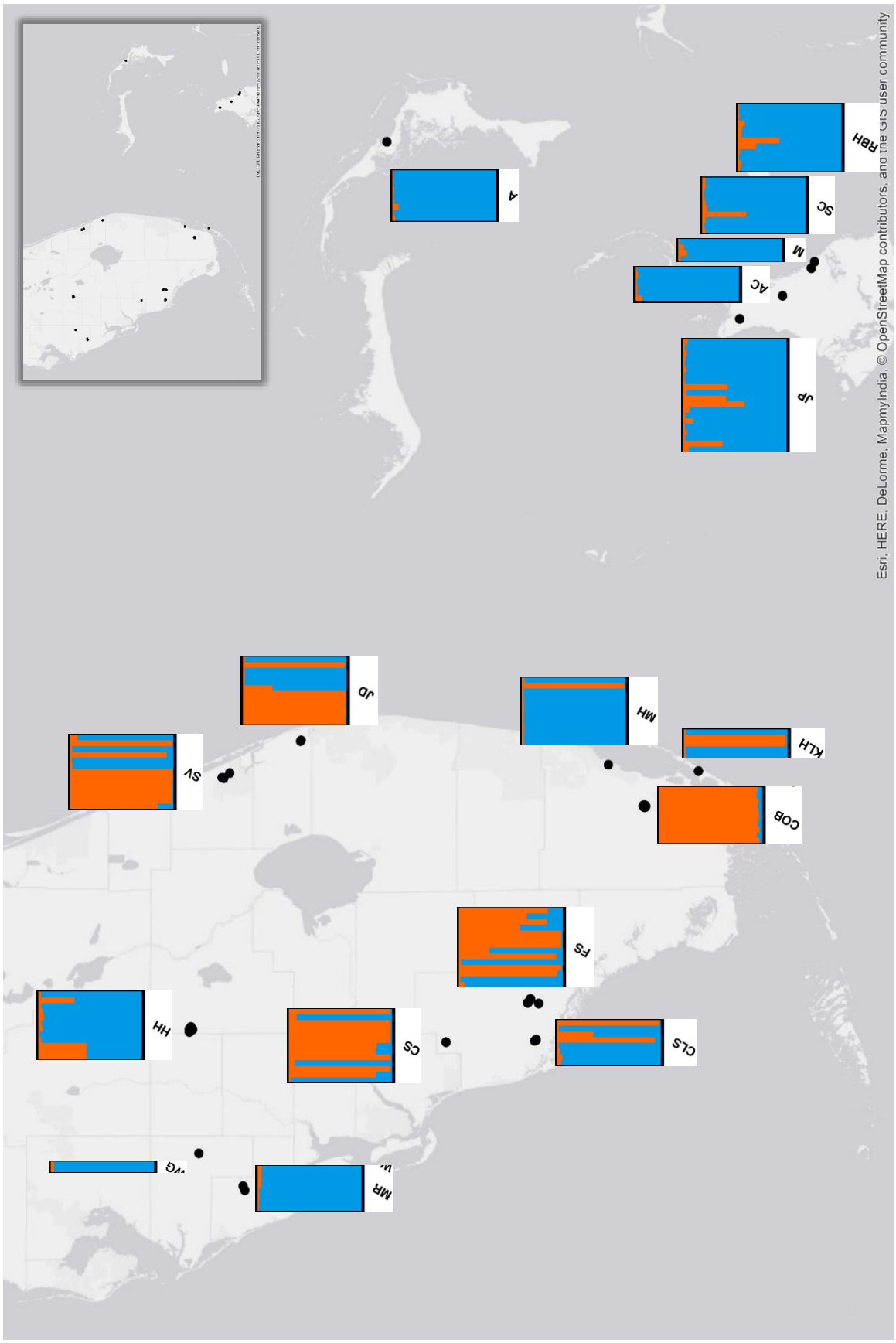


Figure 5. Microsatellite STRUCTURE analysis of Bahamas and Florida populations of *Tillandsia fasciculata* group without *T.* ×*floridana* and *T. bartramii*. Each vertical line represents an individual from collecting site. Colors represent membership coefficient. Number of runs per K is 20. n=170. A) K=2, ΔK=785.279879 B) STRUCTURE analysis with map (following page).

B)


A
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Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

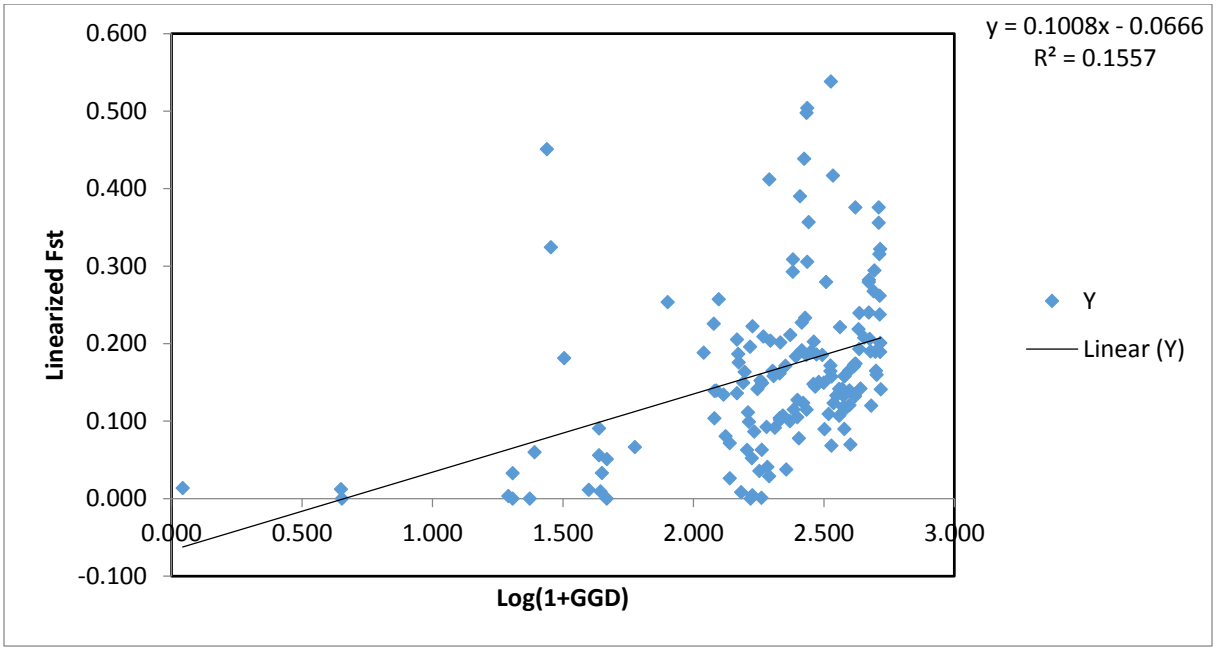

Figure 6. Association between geographic distance (log transformed degree decimal) and genetic distance (linearized $F_{ST}=F_{ST}/(1-F_{ST})$ among 18 populations of *Tillandsia fasciculata* group in the Bahamas and Florida (Mantel test of correlation, $P<0.001$).

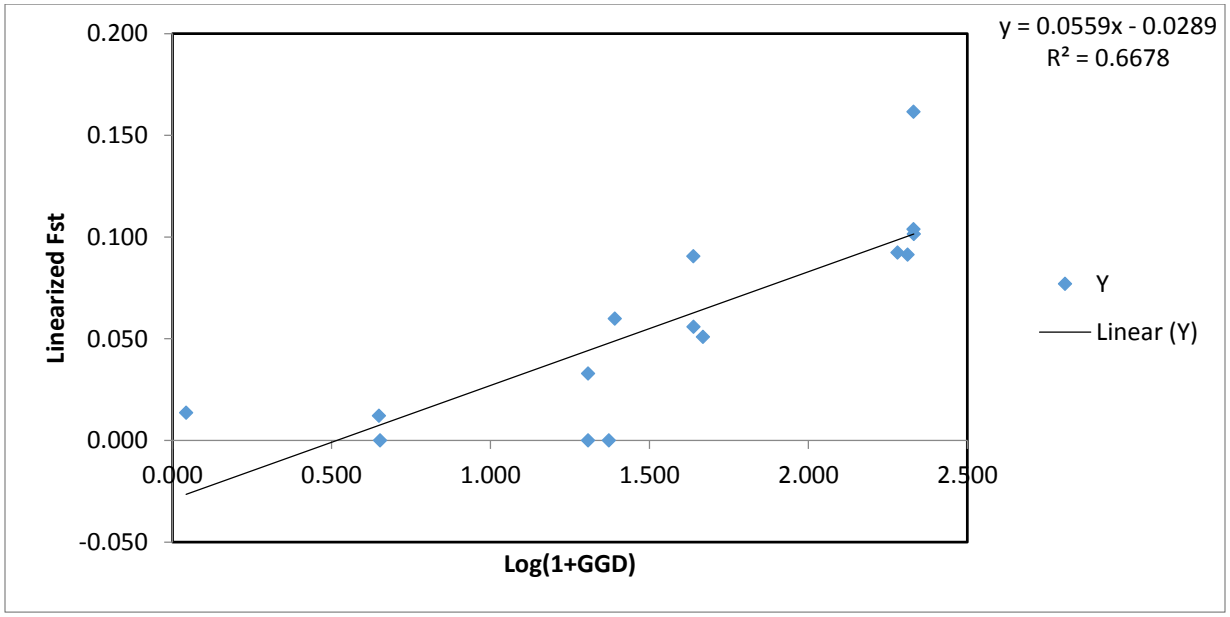

Figure 7. Association between geographic distance (log transformed degree decimal) and genetic distance (linearized $F_{ST}=F_{ST}/(1-F_{ST})$ among six populations of *Tillandsia fasciculata* group in the Bahamas (Mantel test of correlation, P=0.016).

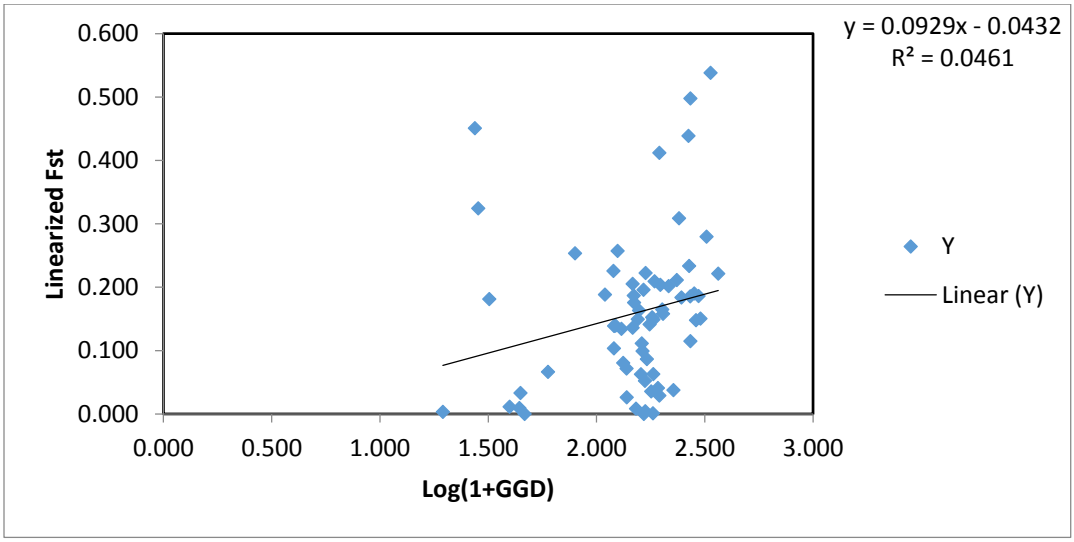

Figure 8. Association between geographic distance (log transformed degree decimal) and genetic distance (linearized $F_{ST}=F_{ST}/(1-F_{ST})$ among 12 populations of the *Tillandsia fasciculata* group in the Florida (Mantel test of correlation, P=0.037).

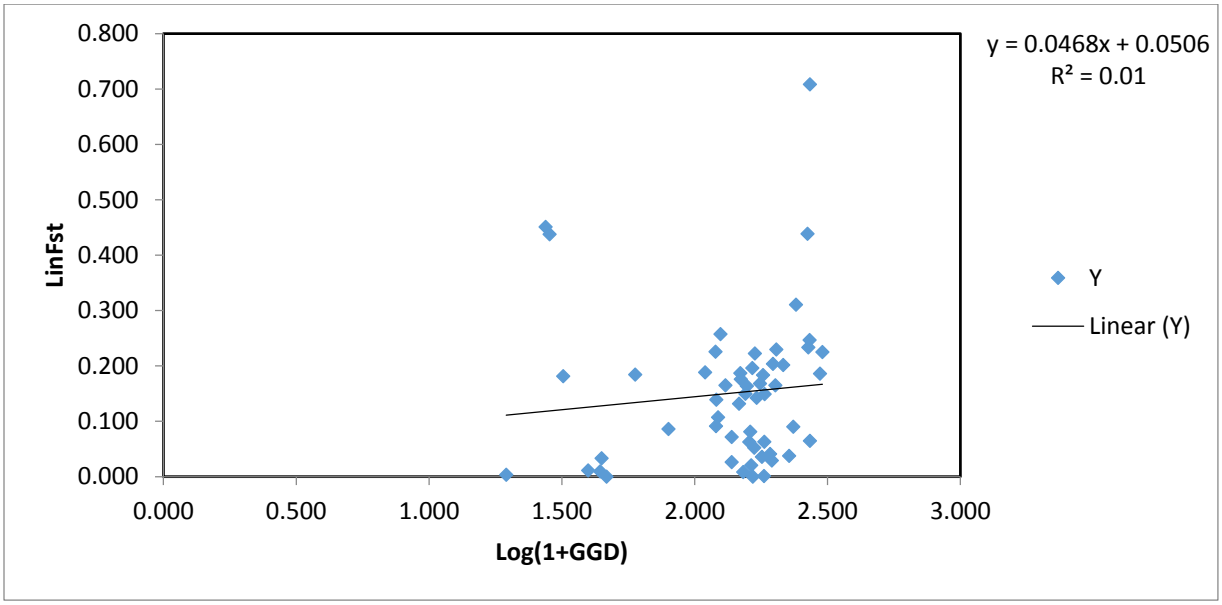

Figure 9. Association between geographic distance (log transformed degree decimal) and genetic distance (linearized $F_{ST}=F_{ST}/(1-F_{ST})$ among 11 populations of *Tillandsia fasciculata* group excluding *T.* ×*floridana* in the Florida (Mantel test of correlation, *P*=0.158).

Supplementary Table 1.

No.	Taxon	Collection Date	Coll. Site	City	County	State/Dept	Country	Latitude	Longitude	Elevation	Habitat	Collector	Collectors
66	Tillandsia fasciculata var. densispica	16 April 2005	Atala Coppice			Andros	Bahamas	24o55'40"N	78o01'41"W	10'	Coppice	Brian Sidoti	Jay Handelman
67	Tillandsia fasciculata var. densispica	16 April 2005	Atala Coppice			Andros	Bahamas	24o55'40"N	78o01'41"W	10'	Coppice	Brian Sidoti	Jay Handelman
68	Tillandsia fasciculata var. laxispica	16 April 2005	Atala Coppice			Andros	Bahamas	24o55'40"N	78o01'41"W	10'	Coppice	Brian Sidoti	Jay Handelman
69	Tillandsia fasciculata var. aff. laxispica	16 April 2005	Atala Coppice			Andros	Bahamas	24o55'40"N	78o01'41"W	10'	Coppice	Brian Sidoti	Jay Handelman
70	Tillandsia fasciculata var. densispica	16 April 2005	Atala Coppice			Andros	Bahamas	24o55'40"N	78o01'41"W	10'	Coppice	Brian Sidoti	Jay Handelman
71	Tillandsia fasciculata var. densispica	16 April 2005	Atala Coppice			Andros	Bahamas	24o55'40"N	78o01'41"W	10'	Coppice	Brian Sidoti	Jay Handelman
72	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
73	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
74	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
75	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
76	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
77	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
78	Tillandsia fasciculata var. aff. laxispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
79	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
80	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
81	Tillandsia fasciculata var. aff densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
82	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond			Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman

83	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
84	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
85	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
86	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
87	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
88	Tillandsia fasciculata var. aff. densispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
89	Tillandsia fasciculata var. aff. laxispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
90	Tillandsia fasciculata var. densispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
91	Tillandsia fasciculata var. laxispica	17 April 2005	on road to Red Bays, Jungle Pond	Andros	Bahamas	25o06.632N	78o08.036W	9'	Coppice	Brian Sidoti	Jay Handelman
92	Tillandsia fasciculata var. aff. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
93	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
94	Tillandsia fasciculata var. aff. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
95	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
96	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
97	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
98	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
100	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
101	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
102	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman

103	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
104	Tillandsia fasciculata var. densispica	18 April 2005	Rainbow Blue Hole	Andros	Bahamas	24o47.084N	77o51.601W	0'	Coppice	Brian Sidoti	Jay Handelman
105	Tillandsia fasciculata var. densispica	18 April 2005	Maidenhair	Andros	Bahamas	24o47.935N	77o53.429W	1'	Coppice	Brian Sidoti	Jay Handelman
106	Tillandsia fasciculata var. densispica	18 April 2005	Maidenhair	Andros	Bahamas	24o47.935N	77o53.429W	1'	Coppice	Brian Sidoti	Jay Handelman
108	Tillandsia fasciculata var. aff densispica	18 April 2005	Maidenhair	Andros	Bahamas	24o47.935N	77o53.429W	1'	Coppice	Brian Sidoti	Jay Handelman
109	Tillandsia fasciculata var. aff. densispica	18 April 2005	Maidenhair	Andros	Bahamas	24o47.935N	77o53.429W	1'	Coppice	Brian Sidoti	Jay Handelman
110	Tillandsia fasciculata var. aff. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
111	Tillandsia fasciculata var. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
112	Tillandsia fasciculata var. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
113	Tillandsia fasciculata var. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
114	Tillandsia fasciculata var. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
115	Tillandsia fasciculata var. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
116	Tillandsia fasciculata var. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
117	Tillandsia fasciculata var. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
118	Tillandsia fasciculata var. densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
119	Tillandsia fasciculata var. aff densispica	19 April 2005	Stafford Creek	Andros	Bahamas	24o47.898N	77o53.474W	3'	Coppice	Brian Sidoti	Jay Handelman
120	Tillandsia fasciculata var. densispica	20 April 2005		Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman
121	Tillandsia fasciculata var. densispica	20 April 2005		Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman
122	Tillandsia fasciculata var. densispica	20 April 2005		Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman

123	Tillandsia fasciculata var. densispica	20 April 2005				Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman
125	Tillandsia fasciculata var. densispica	20 April 2005				Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman
126	Tillandsia fasciculata var. densispica	20 April 2005				Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman
127	Tillandsia fasciculata var. densispica	20 April 2005				Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman
128	Tillandsia fasciculata var. aff. uncispica	20 April 2005				Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman
129	Tillandsia fasciculata var. densispica	20 April 2005				Abaco	Bahamas	26o38.048N	77o17.064W	4'	Coppice	Brian Sidoti	Jay Handelman
131	Tillandsia fasciculata var. densispica	27 May 2005	between posts 1-11; Dagny Johnson Key Largo Hammock Botanical State Park	Key Largo	Monroe County	FL	USA	25o17.343N	80o18.241W	0'	Hardwood Hammock	Brian Sidoti	Row Iliescu
132	Tillandsia fasciculata var. densispica	27 May 2005	between posts 1-11; Dagny Johnson Key Largo Hammock Botanical State Park	Key Largo	Monroe County	FL	USA	25o17.343N	80o18.241W	0'	Hardwood Hammock	Brian Sidoti	Row Iliescu
133	Tillandsia fasciculata var. densispica	27 May 2005	between posts 1-11; Dagny Johnson Key Largo Hammock Botanical State Park	Key Largo	Monroe County	FL	USA	25o17.343N	80o18.241W	0'	Hardwood Hammock	Brian Sidoti	Row Iliescu
135	Tillandsia fasciculata var. densispica	27 May 2005	between posts 1-11; Dagny Johnson Key Largo Hammock Botanical State Park	Key Largo	Monroe County	FL	USA	25o17.343N	80o18.241W	0'	Hardwood Hammock	Brian Sidoti	Row Iliescu
136	Tillandsia fasciculata var. densispica	27 May 2005	between post 29-30; Dagny Johnson Key Largo Hammock Botanical State Park	Key Largo	Monroe County	FL	USA	25o17.906N	80o17.772W	0'	Hardwood Hammock	Brian Sidoti	Row Iliescu
137	Tillandsia fasciculata var. densispica	1 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	ca. 25o40.805N	ca. 80o16.429W	ca. 20'	Hardwood Hammock	Brian Sidoti	
138	Tillandsia fasciculata var. densispica	1 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	ca. 25o40.805N	ca. 80o16.429W	ca. 20'	Hardwood Hammock	Brian Sidoti	
139	Tillandsia fasciculata var. densispica	1 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	ca. 25o40.805N	ca. 80o16.429W	ca. 20'	Hardwood Hammock	Brian Sidoti	

140	Tillandsia fasciculata var. densispica	1 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	ca. 25o40.805N	ca. 80o16.429W	ca. 20'	Hardwood Hammock	Brian Sidoti	
141	Tillandsia fasciculata var. densispica	1 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	ca. 25o40.805N	ca. 80o16.429W	ca. 20'	Hardwood Hammock	Brian Sidoti	
142	Tillandsia fasciculata var. densispica	1 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	ca. 25o40.805N	ca. 80o16.429W	ca. 20'	Hardwood Hammock	Brian Sidoti	
143	Tillandsia fasciculata var. densispica	1 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	ca. 25o40.805N	ca. 80o16.429W	ca. 20'	Hardwood Hammock	Brian Sidoti	
146	Tillandsia fasciculata var. densispica	1 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	ca. 25o40.805N	ca. 80o16.429W	ca. 20'	Hardwood Hammock	Brian Sidoti	
147	Tillandsia fasciculata var. densispica	14 June 2005	near site marker 11; Matheson Hammock	Miami	Miami-Dade County	FL	USA				Hardwood Hammock	Brian Sidoti	Jennifer Possley
149	Tillandsia fasciculata var. densispica	14 June 2005	near site marker 11; Matheson Hammock	Miami	Miami-Dade County	FL	USA				Hardwood Hammock	Brian Sidoti	Jennifer Possley
150	Tillandsia fasciculata var. densispica	14 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	25o40.805N	80o16.429W	20 ft	Hardwood Hammock	Brian Sidoti	Jennifer Possley
151	Tillandsia fasciculata var. densispica	14 June 2005	Matheson Hammock	Miami	Miami-Dade County	FL	USA	25o40.805N	80o16.429W	20 ft	Hardwood Hammock	Brian Sidoti	Jennifer Possley
152	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.777N	81o36.320W	24 ft	Bald Cypress	Brian Sidoti	Row Iliescu
153	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.777N	81o36.320W	24 ft	Bald Cypress	Brian Sidoti	Row Iliescu
156	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.794N	81o36.298W	33 ft	Bald Cypress	Brian Sidoti	Row Iliescu
157	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.794N	81o36.298W	33 ft	Bald Cypress	Brian Sidoti	Row Iliescu
158	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.794N	81o36.298W	33 ft	Bald Cypress	Brian Sidoti	Row Iliescu
159	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.794N	81o36.298W	33 ft	Bald Cypress	Brian Sidoti	Row Iliescu

160	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.794N	81o36.298W	33 ft	Bald Cypress	Brian Sidoti	Row Iliescu
161	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.777N	81o36.352W		Bald Cypress	Brian Sidoti	Row Iliescu
162	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.777N	81o36.352W		Bald Cypress	Brian Sidoti	Row Iliescu
163	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.777N	81o36.352W		Bald Cypress	Brian Sidoti	Row Iliescu
164	Tillandsia fasciculata var. densispica	2 June 2005	north of Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.777N	81o36.352W		Bald Cypress	Brian Sidoti	Row Iliescu
165	Tillandsia fasciculata var. densispica	2 June 2005	Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.519N	81o36.342W	75 ft	Bald Cypress	Brian Sidoti	Row Iliescu
166	Tillandsia fasciculata var. densispica	2 June 2005	Boardwalk; Corkscrew Swamp Sanctuary	Naples	Collier County	FL	USA	26o22.344N	81o36.705W		Bald Cypress	Brian Sidoti	Row Iliescu
168	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.059N	80o09.411W	37 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan
170	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.059N	80o09.411W	37 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan
171	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	ca. 27o00.059N	ca 80o09.411W	ca. 37 ft	Bald Cypress	Brian Sidoti	Jeremy Moynihan
172	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	ca. 27o00.059N	ca 80o09.411W	ca. 37 ft	Bald Cypress	Brian Sidoti	Jeremy Moynihan
173	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	ca. 27o00.059N	ca 80o09.411W	ca. 37 ft	Bald Cypress	Brian Sidoti	Jeremy Moynihan
174	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.208N	80o09.609W	32 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan
175	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.208N	80o09.609W	32 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan

177	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.208N	80o09.609W	32 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan
178	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.208N	80o09.609W	32 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan
179	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.208N	80o09.609W	32 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan
180	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.208N	80o09.609W	32 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan
181	Tillandsia fasciculata var. densispica	3 June 2005	Kitching Creek trail, Jonathan Dickinson State Park	Hobe Sound	Martin County	FL	USA	27o00.208N	80o09.609W	32 ft	Hardwood Hammock	Brian Sidoti	Jeremy Moynihan
183	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.197N	80o55.714W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
184	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.197N	80o55.714W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
185	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.193N	80o55.715W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
187	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.731N	80o58.808W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
188	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.743N	80o58.816W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
189	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.719N	80o58.790W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
190	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.716N	80o58.810W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
191	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.716N	80o58.817W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
192	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.716N	80o58.819W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
194	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.629N	80o50.795W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert
195	Tillandsia fasciculata var. floridana	4 June 2005	William Beardall Tosohatchee State Reserve	Christmas	Orange County	FL	USA	28o30.629N	80o50.795W		Hardwood Hammock	Brian Sidoti	Eliza Gilbert

197	Tillandsia fasciculata var. densispica	6 June 2005	south canal, 200 yd from curve, driving toward west; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o27.817N	81o32.598W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
199	Tillandsia fasciculata var. densispica	6 June 2005	south canal; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o27.817N	81o32.598W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
200	Tillandsia fasciculata var. densispica	6 June 2005	south canal; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o27.817N	81o32.598W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
201	Tillandsia fasciculata var. densispica	6 June 2005	loop road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.223N	81o32.943W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
202	Tillandsia fasciculata var. densispica	6 June 2005	loop road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.359N	81o32.641W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
203	Tillandsia fasciculata var. densispica	6 June 2005	loop road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.294N	81o32.929W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
204	Tillandsia fasciculata var. floridana	6 June 2005	loop road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.407N	81o33.023W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
205	Tillandsia fasciculata var. densispica	6 June 2005	ranger station; Highlands Hammock State Park	Sebring	Highlands County	FL	USA				Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
206	Tillandsia fasciculata var. densispica	6 June 2005	campground road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.292N	81o31.869W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
207	Tillandsia fasciculata var. densispica	6 June 2005	north dam road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.686N	81o32.416W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris

208	Tillandsia fasciculata var. densispica	6 June 2005	north dam road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.689N	81.32.805W	Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
209	Tillandsia fasciculata var. densispica	6 June 2005	north dam road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.697N	81o33.423W	Hardwood Hammock	Brian Sidoti	Andrea Bishop and Dorothy Harris
211	Tillandsia fasciculata var. densispica	8 June 2005	on west side along Main Park Drive, south of Power L, approx. 1.4 miles; Myakka River State Park	Sarasota	Sarasota County	FL	USA	27o14.934N	82o17.720W	Hardwood Hammock	Brian Sidoti	Diana Donaghy
212	Tillandsia fasciculata var. densispica	8 June 2005	on west side along Main Park Drive, south of Power L, approx. 1.4 miles; Myakka River State Park	Sarasota	Sarasota County	FL	USA	27o14.934N	82o17.720W	Hardwood Hammock	Brian Sidoti	Diana Donaghy
213	Tillandsia fasciculata var. densispica	8 June 2005	on west side along Main Park Drive, south of Power L, approx. 1.4 miles; Myakka River State Park	Sarasota	Sarasota County	FL	USA	27o14.938N	82o17.716W	Hardwood Hammock	Brian Sidoti	Diana Donaghy
214	Tillandsia fasciculata var. densispica	8 June 2005	on west side along Main Park Drive, south of Power L, approx. 1.4 miles; Myakka River State Park	Sarasota	Sarasota County	FL	USA	27o14.943N	82o17.719W	Hardwood Hammock	Brian Sidoti	Diana Donaghy
216	Tillandsia fasciculata var. densispica	8 June 2005	shop area, Myakka River State Park	Sarasota	Sarasota County	FL	USA	27o14.493N	82o18.956W	Hardwood Hammock	Brian Sidoti	Diana Donaghy
217	Tillandsia fasciculata var. densispica	8 June 2005	shop area, Myakka River State Park	Sarasota	Sarasota County	FL	USA	27o14.493N	82o18.956W	Hardwood Hammock	Brian Sidoti	Diana Donaghy
218	Tillandsia fasciculata var. densispica	8 June 2005	shop area, Myakka River State Park	Sarasota	Sarasota County	FL	USA	27o14.493N	82o18.956W	Hardwood Hammock	Brian Sidoti	Diana Donaghy
219	Tillandsia fasciculata var. densispica	8 June 2005	shop area, Myakka River State Park	Sarasota	Sarasota County	FL	USA	27o14.493N	82o18.956W	Hardwood Hammock	Brian Sidoti	Diana Donaghy
220	Tillandsia fasciculata var. densispica	8 June 2005	camp ground #1, Collier-Seminole State Park	Naples	Collier County	FL	USA	25o59.534N	81o35.654W	Hardwood Hammock	Brian Sidoti	Andrea Bishop and Christina Olson
222	Tillandsia fasciculata var. densispica	8 June 2005	camp ground #1, Collier-Seminole State Park	Naples	Collier County	FL	USA	25o59.467N	81.35.675W	Hardwood Hammock	Brian Sidoti	Andrea Bishop and

													Christina Olson
223	Tillandsia fasciculata var. densispica	8 June 2005	camp ground #2, Collier-Seminole State Park	Naples	Collier County	FL	USA	25o59.561N	81o35.723W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Christina Olson
224	Tillandsia fasciculata var. densispica	8 June 2005	camp ground #2, Collier-Seminole State Park	Naples	Collier County	FL	USA	25o59.561N	81o35.723W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Christina Olson
225	Tillandsia fasciculata var. densispica	8 June 2005	camp ground #2, Collier-Seminole State Park	Naples	Collier County	FL	USA	25o59.561N	81o35.723W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Christina Olson
226	Tillandsia fasciculata var. densispica	8 June 2005	ranger station, Collier-Seminole State Park	Naples	Collier County	FL	USA	25o59.495N	81o35.520W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Christina Olson
227	Tillandsia fasciculata var. densispica	8 June 2005	ranger station, Collier-Seminole State Park	Naples	Collier County	FL	USA	25o59.495N	81o35.520W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Christina Olson
229	Tillandsia fasciculata var. densispica	8 June 2005	Collier-Seminole State Park	Naples	Collier County	FL	USA	29o59.875N	81o35.954W		Hardwood Hammock	Brian Sidoti	Andrea Bishop and Christina Olson
235	Tillandsia fasciculata var. densispica	13 June 2005	Township 51, range 29, sect. 33; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	25o58.781N	81o25.131W	13 ft	Swamp	Brian Sidoti	Mike Owen
236	Tillandsia fasciculata var. densispica	13 June 2005	Township 51, range 29, sect. 33; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	25o58.781N	81o25.131W	13 ft	Swamp	Brian Sidoti	Mike Owen
237	Tillandsia fasciculata var. densispica	13 June 2005	Township 51, range 29, sect. 33; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	25o58.781N	81o25.131W	13 ft	Swamp	Brian Sidoti	Mike Owen

238	Tillandsia fasciculata var. densispica	13 June 2005	0.6 mi from gate #7; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	25o58.781N	81o25.208W	35 ft	Swamp	Brian Sidoti	Mike Owen
240	Tillandsia fasciculata var. densispica	13 June 2005	east main tram (gate 12) 0.9 mi, north side of tram; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o00.903N	81o23.884W		Swamp	Brian Sidoti	Mike Owen
241	Tillandsia fasciculata var. densispica	13 June 2005	east main tram (gate 12) 0.9 mi, north side of tram; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o00.903N	81o23.884W		Swamp	Brian Sidoti	Mike Owen
242	Tillandsia fasciculata var. densispica	13 June 2005	east main tram (gate 12) 0.9 mi, north side of tram; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o00.903N	81o23.884W		Swamp	Brian Sidoti	Mike Owen
243	Tillandsia fasciculata var. densispica	13 June 2005	east, main tram, near ditch, 1.1 mi; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o00.903N	81o23.884W		Swamp	Brian Sidoti	Mike Owen
244	Tillandsia fasciculata var. densispica	13 June 2005	Gate 15 tram; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o00.983N	81o23.820W	22 ft	Swamp	Brian Sidoti	Mike Owen
245	Tillandsia fasciculata var. densispica	13 June 2005	Gate 15 tram; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o01.573N	81o24.965W		Swamp	Brian Sidoti	Mike Owen
246	Tillandsia fasciculata var. densispica	13 June 2005	200-300 yrds from gate 15; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o01.707N	81o24.959W	42 ft	Swamp	Brian Sidoti	Mike Owen
247	Tillandsia fasciculata var. densispica	13 June 2005	east of gate 15 tram; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o01.707N	81o24.959W	42 ft	Swamp	Brian Sidoti	Mike Owen
248	Tillandsia fasciculata var. densispica	13 June 2005	east of gate 15 tram; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o01.633N	81o24.950W	19 ft	Swamp	Brian Sidoti	Mike Owen
249	Tillandsia fasciculata var. densispica	13 June 2005	near railroad tracks; Fakahatchee Strand Preserve State Park	Copeland	Collier County	FL	USA	26o01.633N	81o24.950W	19 ft	Swamp	Brian Sidoti	Mike Owen
251	Tillandsia fasciculata var. densispica	16 June 2005	Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA				Scrub	Brian Sidoti	Jeremy Moynihan

252	Tillandsia fasciculata var. densispica	16 June 2005	near railroad tracks; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA			Scrub	Brian Sidoti	Jeremy Moynihan
253	Tillandsia fasciculata var. densispica	16 June 2005	near railroad tracks; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA			Scrub	Brian Sidoti	Jeremy Moynihan
254	Tillandsia fasciculata var. densispica	16 June 2005	near railroad tracks; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA			Scrub	Brian Sidoti	Jeremy Moynihan
255	Tillandsia fasciculata var. densispica	16 June 2005	Halpatiokee part of North Fork on St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	27o18.33N	80o18.822W	Scrub	Brian Sidoti	Jeremy Moynihan
256	Tillandsia fasciculata var. densispica	16 June 2005	Halpatiokee part of North Fork on St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	27o18.33N	80o18.822W	Scrub	Brian Sidoti	Jeremy Moynihan
257	Tillandsia fasciculata var. densispica	16 June 2005	Halpatiokee part of North Fork on St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	27o18.33N	80o18.822W	Scrub	Brian Sidoti	Jeremy Moynihan
258	Tillandsia fasciculata var. densispica	16 June 2005	Halpatiokee part of North Fork on St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	27o18.33N	80o18.822W	Scrub	Brian Sidoti	Jeremy Moynihan
260	Tillandsia fasciculata var. densispica	12 August 2005	North Fork of St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	29o19.801N	80o20.031W	Scrub	Brian Sidoti	Jeremy Moynihan
261	Tillandsia fasciculata var. densispica	12 August 2005	North Fork of St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	29o19.801N	80o20.031W	Scrub	Brian Sidoti	Jeremy Moynihan
262	Tillandsia fasciculata var. densispica	12 August 2005	North Fork of St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	27o19.873N	80o20.295W	Scrub	Brian Sidoti	Jeremy Moynihan
263	Tillandsia fasciculata var. densispica	12 August 2005	North Fork of St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	27o20.329N	80o20.143W	Scrub	Brian Sidoti	Jeremy Moynihan
264	Tillandsia fasciculata var. densispica	12 August 2005	North Fork of St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	27o20.158N	80o20.088W	Scrub	Brian Sidoti	Jeremy Moynihan

265	Tillandsia fasciculata var. densispica	12 August 2005	North Fork of St. Lucie River; Savannas Preserve State Park	Jensen Beach	Martin County	FL	USA	27o20.030N	80o20.104W	Scrub	Brian Sidoti	Jeremy Moynihan Chris
416	Tillandsia fasciculata var. floridana	20 July 2006	north of Myakka River and east of Wingate Creek, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.228N	82o08.298W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen Chris
417	Tillandsia fasciculata var. floridana	20 July 2006	north of Myakka River and east of Wingate Creek, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.228N	82o08.298W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen Chris
418	Tillandsia fasciculata var. floridana	20 July 2006	north of Myakka River and east of Wingate Creek, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.228N	82o08.298W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen Chris
419	Tillandsia fasciculata var. floridana	20 July 2006	north of Myakka River and east of Wingate Creek, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.228N	82o08.298W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen Chris
420	Tillandsia fasciculata var. floridana	20 July 2006	north of Myakka River and east of Wingate Creek, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.228N	82o08.298W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen Chris
421	Tillandsia fasciculata var. floridana	20 July 2006	south of Myakka River, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.134N	82o08.311W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen Chris
422	Tillandsia fasciculata var. floridana	20 July 2006	south of Myakka River, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.134N	82o08.311W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen Chris
423	Tillandsia fasciculata var. floridana	20 July 2006	south of Myakka River, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.134N	82o08.311W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen Chris
424	Tillandsia fasciculata var. floridana	20 July 2006	south of Myakka River, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.134N	82o08.311W	bottom land forest	Brian Sidoti	Becker and Elizabeth Jensen

428	Tillandsia fasciculata var. densispica	20 July 2006	north of Myakka River and west of Wingate Creek, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.234N	82o08.302W	bottom land forest	Brian Sidoti	Chris Becker and Elizabeth Jensen
429	Tillandsia fasciculata var. floridana	20 July 2006	north of Myakka River and west of Wingate Creek, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.234N	82o08.302W	bottom land forest	Brian Sidoti	Chris Becker and Elizabeth Jensen
431	Tillandsia fasciculata var. densispica	20 July 2006	north of Myakka River and west of Wingate Creek, Wingate Creek State Park	Bradenton	Manatee County	FL	USA	27o26.234N	82o08.302W	bottom land forest	Brian Sidoti	Chris Becker and Elizabeth Jensen
432	Tillandsia bartramii	21 July 2006	cypress board walk; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o27.816N	81o31.887W	Bald Cypress	Brian Sidoti	Dorothy Harris and Elizabeth Jensen
436	Tillandsia fasciculata var. densispica	21 July 2006	near ranger station, Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o28.255N	81o31.950W	Hardwood Hammock	Brian Sidoti	Dorothy Harris and Elizabeth Jensen
438	Tillandsia bartramii	21 July 2006	cypress board walk; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o27.816N	81o31.887W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
439	Tillandsia bartramii	21 July 2006	cypress board walk; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o27.816N	81o31.887W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
440	Tillandsia bartramii	21 July 2006	cypress board walk; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o27.816N	81o31.887W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens

441	Tillandsia bartramii	21 July 2006	cypress board walk; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.130N	81o32.836W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
443	Tillandsia fasciculata var. floridana	21 July 2006	cypress board walk; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.130N	81o32.836W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
444	Tillandsia bartramii	21 July 2006	cypress board walk; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.130N	81o32.836W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
445	Tillandsia fasciculata var. floridana	21 July 2006	cypress board walk; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.130N	81o32.836W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
446	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.142N	81o32.749W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
447	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.142N	81o32.749W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
448	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.142N	81o32.749W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and

													Cathy Bergens
449	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.142N	81o32.749W		Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
450	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.142N	81o32.749W		Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
451	Tillandsia bartramii	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W		Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
452	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W		Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
453	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W		Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
454	Tillandsia bartramii	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W		Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens

456	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
457	Tillandsia fasciculata var. floridana	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
458	Tillandsia bartramii	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
459	Tillandsia bartramii	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
460	Tillandsia bartramii	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens
461	Tillandsia bartramii	21 July 2006	south property, end of Vaughn Road; Highlands Hammock State Park	Sebring	Highlands County	FL	USA	27o26.120N	81o32.822W	Bald Cypress	Brian Sidoti	Dorothy Harris, Elizabeth Jensen, and Cathy Bergens

468	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52232	-80.47177	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
469	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52197	-80.47208	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
470	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52224	-80.47184	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
471	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52286	-80.47194	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
472	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52331	-80.47181	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
473	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52216	-80.47259	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
474	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52210	-80.47289	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez

475	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52236	-80.47150	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
476	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52439	-80.47011	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez
478	Tillandsia fasciculata var. densispica forma alba	10 April 2007	Camp Owaissa Bauer	Miami	Miami-Dade County	FL	USA	25.52443	-80.46983	edge of hardwood hammock, near pine rockland	Brian Sidoti	Jennifer Possley and Cristina Rodriguez

Chapter 3: Past, present, and future species distribution modeling for four varieties of *Tillandsia fasciculata* (Bromeliaceae) throughout the Caribbean Basin

ABSTRACT

Species distribution models (SDM) offer biologists a spatial tool to better understand processes of evolution and biogeography. SDM may also aid in addressing questions such as which abiotic factors are most influential in determining suitable localities. Few studies have incorporated SDM in the Caribbean and no studies have applied SDM on bromeliads in this region. Our goals for incorporating species distribution models in our broader systematics work are to address the following questions: 1) Does the predicted geographic space corroborate the taxonomic and genetic groupings uncovered in earlier studies? 2) Can we determine which environmental factors contribute the most to *Tillandsia fasciculata* distribution in the past, present, and future? 3) Will paleoclimate data be valuable to explore areas in the Caribbean Basin that may have acted as past refugia for these taxa? and 4) What are implications of our results for applicable conservation measures today and tomorrow? We ran MaxEnt on eight bioclimatic layers based on MIROC-ESM from WorldClim across past (last interglacial, last glacial maximum, mid-Holocene), current, and future (2050 and 2070, each with 4.5 and 8.5 rcp) climatic conditions. Additional environmental data layers included in SDM were soil and altitude. Jackknife results find that the most important single environmental data layer across taxa and across different climatic conditions is harmonized world soil data. The ranking of bioclimatic data on suitable localities changes depending on the taxon studied. For *T. fasciculata* var. *densispica* the most important single variable is mean temperature of coldest quarter, reflecting its northernmost range which experiences frost. MaxEnt results support hypothesized past distributions, such as *T. fasciculata* var. *clavispica* in Mexico and northern Central America. Projected climatic

conditions in 2050 and 2070 suggest less suitable localities for all four taxa. While our SDM study was limited to soil, altitude, and bioclimatic data, we find SDM useful in aiding our understanding of past and future direction of the *T. fasciculata* group in the Caribbean.

Species distribution models (SDM) are a spatial tool that may help systematists, ecologists, and conservation biologists better understand processes of evolution and biogeography. SDM can be used to explain how past population ranges contribute to current patterns of divergence and diversity (Beatty & Provan 2011, Kozak et al, 2008, Knowles et al 2007), and how future distributions may be effected by climate change. SDM can also be used to assess how likely it will be that currently protected areas capture future distribution patterns, or prioritize areas for protection that currently are at risk of habit loss. SDM also aid in addressing questions such as "what role do environmental variables play in species distribution?" and "which abiotic factors are most influential in determining where a species grows?"

Only a limited number of published studies have incorporated SDM to help elucidate biogeographic patterns of organisms across the Caribbean – a biodiversity hotspot. Glor and Warren (2011) applied the SDM technique to examine the role of Merten's Line (low lying valley, xeric conditions) on the island of Hispaniola for two *Anolis* lizard species. Algar and Losos (2011) used a suite of both classic and modern approaches on their study of *Anolis* to address the paradox of why islands, which are predicted to be species poor compared to the mainland, host so many adaptive radiations.

There is scant literature on plant studies in the Caribbean that utilize SDM, and none that have considered vascular epiphytes or Bromeliaceae. In fact, the two papers most relevant to our study, because they also consider distribution patterns of epiphytes across the Caribbean, were published prior to the development of SDM techniques. Based on current species distributions of Orchidaceae (both terrestrial and epiphytic), Trejo and Ackerman (2001) showed that Caribbean island orchid floras grouped together based on similar geomorphologic or physiographic characters, e.g., low elevation, calcareous islands. In another study, Ackerman et al. (2007)

investigated the relationships of orchid species vs. island size (and/or vs. elevation) in the West Indies. They found that large montane islands are the best predictors for orchid species richness. Neither study employed SDM or considered past or future distribution scenarios.

There do exist a few published studies on bromeliads that have utilized predictive species modeling. Zizka et al. (2009) research on species richness of Chilean Bromeliaceae and placement over protected areas is the most applicable to our study. Additionally, Zizka et al. (2009) assessed species distribution and centers of diversity of Bromeliaceae in Chile. Barve et al. (2014) studied the widely-distributed "Spanish moss" (*Tillandsia usneoides*) and considered various environmental layers in their models. Likewise, Judith et al (2013) applied SDM to study bromeliads distribution across soilsealing areas in Merida, Venezuela. It is expected that more studies of these kinds will be forthcoming as bromeliad systematists begin to explore the value of SDM. In the meantime, bromeliad ecology and systematics continues to be examined by more traditional means.

Floristic inventories and ecological studies on epiphytic Bromeliaceae have shown that species abundance is greatest in moist mid-montane (1500–2500 m) ecosystems because of the large amount of lateral light and atmospheric moisture present in these habitats (Benzing 1980, Kromer 2006;). Kromer's (2005) research in Bolivia also supported bromeliad species richness peaks at mid-elevations. Beyond these basic conclusions stating a mid-elevation preference for bromeliads, few studies exist that predict their broader distributions in a way that may add to our understanding of which environmental factors influence epiphytic plant, and specifically Bromeliaceae, distributions across the landscape.

In contrast, there have been a handful of studies that consider Bromeliaceae diversification driven by biotic and abiotic factors in evolutionary time. For example, Givnish

(2010) suggested that recently uplifted, extensive montane regions play a role in bromeliad species diversification, in addition to biotic features of the plant such as evolution of the tank habit and absorptive foliar trichomes. Further research by Givnish et al. (2014) tied these traits and avian pollination to changes in net species diversification rates. Silverstro et al. (2014) also examined key innovations and net diversification in Bromeliaceae, but restricted their study to the effects of CAM photosynthesis and the water impounding tank habit in the subfamily Bromelioideae.

The research presented here, focused on four distinct varieties of *Tillandsia fasciculata*, is the first bromeliad study, and one of the few plant studies to date, that employs the contemporary methods of SDM across the Caribbean Basin. Our aims for incorporating species distribution models in our broader systematics work are to address the following questions: 1) Does the predicted geographic space corroborate the taxonomic and genetic groupings uncovered in earlier studies? 2) Can we determine which environmental factors contribute the most to *T. fasciculata* distribution in the past, present, and future? 3) Will paleoclimate data be valuable to explore areas in the Caribbean Basin that may have acted as past refugia for these taxa? and 4) What are implications of our results for applicable conservation measures today and tomorrow?

METHODS

Taxon Selection. Four varieties from the *Tillandsia fasciculata* complex were selected for this study, and each was analyzed independently. The distribution of the *T. fasciculata* group is Caribbean Basin, but *Tillandsia fasciculata* var. *densispica* (N=50), *Tillandsia fasciculata* var. *laxispica* (N=15), *T. fasciculata* var. *clavispica* (N=43), and *T. fasciculata* var. *venosispica*

(N=36) are generally restricted to Florida and the Bahamas, Cuba, and the Lesser Antilles, respectively (Supplemental Tables 1–4). They occur from sea level to ca. 1500 m, from coastal scrub and tropical hardwood hammock to pine-oak forests. The main criterion for selection of these taxa was clear taxonomic boundaries. *Tillandsia fasciculata* var. *densispica*, *T. fasciculata* var. *laxispica*, and *T. fasciculata* var. *clavispica* form a monophyletic clade (Chapter 1), but can be further delimited by morphometrics (*T. fasciculata* var. *clavispica*) or population genetics (*T. fasciculata* var. *densispica* and *T. fasciculata* var. *laxispica*, Chapter 2). *Tillandsia fasciculata* var. *venosispica* is genetically (Chapter 1) and morphologically distinct with clear biogeographic boundaries. Additional criteria for inclusion in this study was actual number of samples and representation. Taxa that had only a scarce number of collections were not considered (e.g., *T. kuzmae* or *T. trelawniensis*). Geographic breath of sampling across island or region of islands was also taken into account.

Data collection. Locality. For newly collected material, coordinates were recorded in the field with a GPS unit (Magellan eXplorist). When explicitly stated on the historical specimens, latitude and longitude coordinates were taken directly from herbarium labels. When latitude and longitude points were not provided on an herbarium sheet, coordinates were estimated from stated locations via georeferencing. A global gazetteer was used (http://www.fallingrain.com or http://www.latlong.net) when cities were given. In cases where more specific directions were provided, but still no coordinates given, points were georeferenced using Google maps. If latitude and longitude points were provided as Degrees Minutes Seconds or Degrees Minutes, they were converted to Decimal degrees (https://www.fcc.gov/encyclopedia/degrees-minutes-seconds-tofrom-decimal-degrees). . In total, data for 144 specimens were obtained from both, the new material and/or herbarium specimens, which came from the following 20 herbaria -- BM,

BH, F, FLAS, FTG, GH, HAC, HAJB, IJ, K, MAPR, NY, S, SEL, TEX, UPR, UPRRP, US, USF, and WIS. Data were then manually thinned to remove sites with duplicate latitude and longitude points, and any locality that was vaguely described. Although a greater number of records exist for these four taxa than what we used for this study, the final data locations used for each taxon were greatly reduced to avoid overfitting, a phenomenon that results in predicted distribution clustered near location points.

Data layers. Nineteen Bioclim layers were downloaded from the Worldclim database (Hijmans et al. 2005). Past, present, and future climatic conditions included: last interglacial period (ca. 120-140 kya), last glacial maximum (ca. 22 kya), mid Holocene (ca. 6 kya), current conditions (ca. 1950-2000), and climate forecasted for the year 2050 (2041–2060) and 2070 (2061–2080). For the future climate conditions we used two representative concentration pathways (rcp), 4.5 and 8.5. All climate data were downloaded with a spatial resolution of 30 arc-seconds (ca. 1 km), except for the last glacial maximum and mid-Holocene at 2.5 min—the highest resolution available. The Last glacial maximum and mid-Holocene climatic layers were changed to 30 arc-seconds using the resampled toolbox in ArcGIS. Altitude, soil data, and Florida protected regions were downloaded at 30 arc-seconds from WorldClim (Hijmans et al. 2005), Harmonized World Soil Data base v1.21 (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012), and Florida conservation lands (Florida Natural Areas Inventory 2015), respectively.

General Circulation Models (or global climate model, GCM). Of the listed GCMs on WorldClim, three models Community Climate System Model (CCSM4), Model for Interdisciplinary Research on Climate (MIROC-ESM), and Max Planck Institute (MPI-ESM-P), were available across periods of study interest. We used the climatic data calculated by the MIROC-ESM (Watanabe et al 2011). This model "couples the atmosphere, ocean and land

surface through the exchange of energy, momentum, water and important trace gases such as carbon dioxide" (Watanabe et al 2011).

ArcGIS v10.2. Once the data was downloaded, we followed Brown et al.'s protocol (2014) for SDM toolkit in MaxEnt. First, we opened one of the data files in ArcGIS. The region of study interest was selected including the recommended 50–100 km area outside region of distribution. WorldClim climate data were extracted by masking it, converted from raster to asci via the SDM toolbox, and then projected as WGS 1984. This process was repeated for all environmental data.

Next we tested autocorrelations of the 19 Bioclim data using the SDM toolbox. Data that was autocorrelated with a value above 80% was excluded. Autocorrelated variables were ranked by frequency to determine which ones to remove. For example, we removed precipitation of wettest quarter (BIO_{16}) because it is autocorrolated with annual mean temperature (BIO_1), isothermality (BIO_3), precipitation of driest quarter (BIO_{17}), and precipitation of coldest quarter (BIO_{19}). Bioclimatic layers such as temperature seasonality (BIO_4) and precipitation seasonality (BIO_{15}) were excluded because data are not original input climate data (Brown et al 2014). For this study, we used eight Bioclimatic data layers per climate condition (Table 1). A PCA and heterogeneity calculation were conducted to examine climate heterogeneity among the eight climatic conditions.

Species Distribution Modeling. MaxEnt (Phillips et al., 2004) has been found to be useful for presence only data, and successful at predicting the likelihood of species distribution (Baldwin, 2009; Elith and Graham, 2009, Ortega-Huerta & Townsend Peterson, 2008; Hernandez et al. 2008; Wisz et al. 2008). For each taxon, MaxEnt 3.3.3k was performed on paleoclimatic, current, and future climate conditions. Response curves were created and jackknife test conducted to

measure variable importance. Default settings were used except for: a 10% training threshold applied and 10,000 iterations.

RESULTS

Data layers

After removing 11 of the BioClim data layers due to autocorrelation, we conducted heterogeneity tests on the existing eight layers using the SDM toolkit box. Climate heterogeneity raster results find that the areas with highest areas of climate heterogeneity are the mountainous areas of Guatemala and Costa Rica, across the eight climatic conditions.

According to Jackknife of AUC, the harmonized world soil data layer is the most important single environmental layer for predicting suitable locality. Of the bioclimatic data tested, Jackknife results for *Tillandsia fasciculata* var. *densispica* indicate that the mean temperature of coldest quarter is the most important single variable for predicting suitable localities across the eight climatic conditions.

For *Tillandsia fasciculata* var. *laxispica*, the single variable scores for jackknife of regularized training gain and jackknife of test gain are much lower than the other three taxa. Based on jackknife of AUC, the most important single variables are harmonized world soil data, altitude, and precipitation of driest month.

Of the bioclimatic data tested, Jackknife results of AUC for *Tillandsia fasciculata* var. *clavispica* finds mean temperature of driest quarter to be the most important single variable

across the eight climate conditions. Temperature annual range is also important (in 7 of the 8 climatic conditions).

Jackknife results of AUC for *Tillandsia fasciculata* var. *venosispica* find three bioclimatic variables ranking higher than the harmonized world soil data. These results are opposite of the Jackknife results of AUC for *T. fasciculata* var. *densispica*, *T. fascisculata* var. *laxispica*, and *T. fasciculata* var. *clavispica* which ranks harmonized world soil data as first for the eight climatic conditions. The most important single bioclimatic data layer in determining suitability of *T. fasciculata* var. *venosispica* is maximum temperature of warmest month across the eight climatic conditions. Precipitation of driest month is the next most important single data layer.

SDM maps: past, present, future

We tested the Maxent model using four taxa for which we feel we have thorough sampling. *Tillandsia fasciculata* var. *densispica* current distribution is probably restricted to Florida, and the SDM reflect its limited range (Figure 1). Outside of Florida, suitable localities for *Tillandsia fasciculata* var. *densispica* are the Bahamas and Louisiana. Our study does not include sea level as a component to the SDM, and the projected suitable area for this taxon in southern Florida would have been inundated during the last interglacial (ca. 120–140 kya). Protected areas in Florida encompass the projected suitable localities for *Tillandsia fasciculata* var. *densispica* (Figure 2).

The past SDM for *Tillandsia fasciculata* var. *laxispica* suggest a wide range of suitable habitats across the Yucatán region, northern Cuba (last glacial maximum), and even northern

South America (mid-Holocene; Figure 3). Projected climate data in 2050 and 2070 show a narrower range. Across all climatic conditions, Antigua and Barbuda, Barbados, and the northern South American islands of Aruba and Curacao are suitable for *Tillandsia fasciculata* var. *laxispica* even though no records of this variety occur on these islands.

Tillandsia fasciculata var. *clavispica* is a Cuban endemic plant. The MaxEnt model predicts that suitable localities exist outside of Cuba for this taxon (Figure 4). The Yucatán Peninsula contains suitable localities especially during the last glacial maximum and mid-Holocene. In future projections 2050 and 2070 with rcp 4.5 and 8.5, suitable localities in Mexico and Central America diminish compared to paleoclimatic conditions.

For *Tillandsia fasciculata* var. *venosispica*, current distribution of this taxon is in Puerto Rico and the Lesser Antilles. In all eight climatic conditions tested, predicted suitable localities occur in eastern Hispaniola and Jamaica (Figure 5). Cuba and the Atlantic coast of Nicaragua also contain suitable localities in some of the models.

DISCUSSION

Repeated glacial cycles during the Pleistocene (ca. 1.8 kya–2.5 ma) greatly affected the landscape of Florida and the Bahamas. During the late Pleistocene (210–330 kya), the Wicomico shoreline was ca. 20–35 m above present level and reached the Lake Wales Ridge region (Myers & Ewel 1990). In contrast, during the last interglacial period (ca. 75–125 kya), the Pamlico terrace and shoreline were 2–8 m higher than they are today (Hine 2013). Southern Florida and much of the Bahamas were flooded at this time. The highest point on the Bahamas Bank is on Cat Island (63 m). During the last glacial maximum, ca 20 kya, northern North America was

covered with the Laurentide ice sheet causing the world's sea level to fall ca 125 m lower than today (Hine 2013).

Our results find that *Tillandsia fasciculata* group arose about 1.75–4.75 ma, and that the mostly Caribbean *T. fasciculata* s.s. arose about 1–3.2 ma (Chapter 1). Due to the fluctuating sea levels during these glacial cycles, the evolutionary processes and dispersal of *T. fasciculata* var. *densispica* and *T. fasciculata* var. *laxispica* would be most affected because they occur in regions of lower elevation compared to *T. fasciculata* var. *clavispica* in Cuba.

Case study: four Caribbean *Tillandsia fasciculata* varieties

The SDM for the four Caribbean taxa aids in our understanding of possible patterns of dispersal in past and future climate conditions. The actual distribution of *Tillandsia fasciculata* var. *densispica* (which these SDM are based on) is dependent on the recognized taxonomy and distribution of this taxon. Historically, *T. fasciculata* var. *densispica* is recognized to occur from Mexico and throughout the Greater Antilles. Our phylogenetic study (Chapter 1) and population genetic studies (Chapter 2) suggest *T. fasciculata* var. *densispica* range is much narrower than previously hypothesized. For our SDM, we restricted data points to Florida. Based on this, SDM suggest suitable localities outside Florida in nearby Bahamas and Cuba. Our SDM did not incorporate sea levels. Knowledge of past and future sea levels is critical to interpreting SDM. During the last interglacial, our SDM suggests southern Florida as a suitable locality even though it would be inundated. Likewise, future climatic conditions suggest southern Florida as suitable, but a projected rise in sea level would make these suitable localities inhospitable. Central Florida is the northern most range of the *T. fasciculata* group and the fact that the most important single variable to suitable localities for this taxon is mean temperature of coldest quarter is not surprising, i.e., frost is lethal to the plant.

Compared to SDM for the other tested taxa, *Tillandsia fasciculata* var. *laxispica* SDM exhibit a less narrow range of suitable habitats, especially under past climatic conditions. This may be due our sample size of only 15 individuals. Most of the herbarium collections in the Bahamas had to be georeferenced and ultimately were not included in this study due to possible errors with georeferencing (Chan et al. 2011). A balance is needed between obtaining enough locality data points that are ideally representative of their full climatic niches (Feeley 2011), and thinning data so as to not overfit it (Radosavljevic and Anderson 2013). While a sample size of five locations produces acceptable models, at least 30 locations are recommended (Baldwin 2009).

Suitable localities during the last glacial maximum, but especially during the mid-Holocene, suggest that *Tillandsia fasciculata* var. *clavispica* most likely originated in Mexico. These results are not surprising considering Mexico is one of the centers of diversity for the subgenus *Tillandsia* (Till 2000). Moreover, phylogenetic results (Chapter 1) support a Mexican origin. As climatic conditions change from current to projected, 2050 and 2070, SDM indicate that Mexico becomes less suitable. Although Hispaniola appears suitable, the biological reality is Haiti would not be a likely locality due to heavy deforestation. Puerto Rico also appears as a suitable location, but *T. fasciculata* var. *venosispica* is already established there. *Tillandsia fasciculata* var. *clavispica* would have to compete for the same resources and/or it would start to interbreed with *T. fasciculata* var. *venosispica*. Within Cuba, *T. fasciculata* var. *clavispica* is one of the most common tillandsias across the landscape. The central valley is deforested mainly due to agriculture, and our SDM reflect that (cooler colors).

Tillandsia fasciculata var. *venosispica* current distribution is restricted to Puerto Rico and the Lesser Antilles. Suitable localities for this taxon are found in Jamaica, eastern Hispaniola,

Trinidad and Tobago, and northern Venezuela for all eight climate models tested. Eastern Nicaragua is suitable for this taxon during the last glacial maximum and under current and projected climatic conditions remains so, albeit with a reduced range that borders Honduras. While these results suggest suitable habitat in Trinidad and Tobago and northern South America, the biologic reality is they will have to co-occur and compete with the already existing *T.* aff. *fasciculata.* Within Puerto Rico and the Lesser Antilles little change in suitable localities across different climatic conditions was observed, which may be a reflection of resolution (1 km) and size of islands.

Environmental variables and bromeliads

MaxEnt allows one to test the relative importance of environmental layers for predicting suitable localities. Across taxa and across different climatic conditions, our results find that harmonized world soil data is the most important single environmental data layer. Of the bioclimatic variables, annual temperature range (BIO_7) is the most important single variable for three of the four taxa. While there is overlap in the remaining bioclimatic data layers across the eight climatic conditions, the actual ranking varies. For example with *T. fasciculata* var. *densispica* the most important bioclimatic single variable is mean temperature of coldest quarter (BIO_{11}) which reflects its northernmost range which experiences frost. Mean temperature of coldest quarter was ranked as the third (7 of 8 climatic conditions) and second (last interglacial) most important single variable for *T. fasciculata* var. *clavispica.* Precipitation of driest month (BIO_{14}) is the most important bioclimatic single factor for *Tillandsia fasciculata* var. *laxispica* which suggests that the limiting factor is access to water. This bioclimatic variable ranks as the second most important single variable for *T. fasciculata* var. *venosispica*. For *T. fasciculata* var. *venosispica*, maximum temperature of warmest month (BIO_5) is the most important variable in

eight climatic conditions. For *T. fasciculata* var. *clavispica*, mean temperature of driest quarter (BIO_9) is the most important single bioclimatic variable in eight climatic conditions.

The main caveat to this study is that we only used the bioclimatic data available in WorldClim. Other data that should be incorporated in future research are humidity and land use, preferably at an even higher resolution. Creation of pseudo absence selection methods that incorporate bathymetric data is critical especially since low lying Florida and the Bahamas are effected by fluctuating sea levels.

Even though *Tillandsia fasciculata* is predominantly epiphytic, harmonized world soil data is the most important single environmental variable which may reflect phorophytes dependence on soil. Givnish et al (2014) found fertile, moist cordilleras to be one of the important factors to the net rates of species diversification in bromeliads. When focusing on just the Caribbean islands in our PCA and heterogeneity tests, Hispaniola is the most heterogeneous. These results confirm what is already known about that island. Hispaniola has five major mountain ranges and including Pico Duarte (3,098 m), the highest peak in the Antilles, and is comprised of four distinct ecoregions (moist forest, pine forest, dry forests, and grasslands). In Swenson & Umana (2014) phylofloristic study on the Lesser Antilles, they found that for non-endemic plants, environmental heterogeneity played a larger role in species assemblages on islands rather than spatial distance:

Future climatic conditions

Our SDM show there are suitable localities for *Tillandsia fasciculata* var. *densispica*, *T. fasciculata* var. *laxispica*, *T. fasciculata* var. *clavispica*, and *T. fasciculata* var. *venosispica*, and *T. fasciculata* var. *densispica* under future climatic conditions. While nearby islands offer possible solutions to where these taxa could disperse or be repatriated, the reality is these taxa

face much bigger threats such as habitat destruction and climate change (e.g., inundation from rising sea levels). Research suggests that projected sea level rise due to climate change is analogous to the 46 m rise experienced during the last interglacial (Clark & Huybers 2009), meaning much of the low lying suitable localities in Florida and the Bahamas are not suitable.

Another critical factor is that SDM does not include basic biological processes. Inclusion of *Tillandsia fasciculata* in several physiological bromeliad studies provide insight into how it may react to climate change. Germination and seedling establishment are critical phases to overcome, with water often being the limiting factor. Zotz and Thomas (1999) examined water movement in tank bromeliads. They found that *T. fasciculata* was less effective in maintaining moisture in their tanks than the soft leaved *Guzmania monostachia*. They also provided evidence that smaller individual plants dry out faster than larger plants. In a later study, Zotz et al (2010) found that water availability had a significant impact on growth rates of epiphytic bromeliads, but that elevated CO_2 had little effect. Within that study, they also found that *T. fasciculata* relative growth rates were most responsive to increase in nutrient solution, and that water supply did increase relative growth rates, but it was not statistically significant. On a community scale, most of the Caribbean islands already have well established varieties of *T. fasciculata* on them so introduction of new taxa would have to be able to compete for the same resources, namely space. Additionally, since these taxa are varieties possible interbreeding could occur.

Hurricanes

The number and intensity of cyclones (hurricanes in the Atlantic) are expected to increase due to climate change. Several studies track the projected frequency in the Caribbean Basin. Fraza and Elsner (2014) found that the central part of the Basin will experience more frequent hurricanes, but regions in the southern portion of the Basin will experience the highest intensity

hurricanes. Another study examining hurricane tracks supported a similar path. Gannon (2014) found that the region with the most return intervals, or location of hurricane strikes, was western Cuba.

Broad effects of hurricanes on forest ecosytems were proposed by Lugo (2000) and include such topics as sudden or delayed tree mortality, changes in successional direction, and biomass turnover. Long term studies have been conducted to test the effects hurricanes have on Caribbean ecosystems. Van Blem et al. (2006) examined forest structure in a Puerto Rican dry forest after Hurricane Georges. They examined stem mortality, and stem sprouting, and concluded that tropical dry forests are better able to withstand hurricanes because of their dense, short stature. Another long term study examined tree growth and mortality in the Blue Mountains of Jamaica after Hurricane Gilbert (Tanner et al. 2014). Their results found that topographic position, tree size, and species identity are important factors for crown damage by hurricanes. Knowledge about post hurricane effects on tree growth and mortality is fundamental to understand viability of epiphytic bromeliads since they are dependent on tree limbs for structural support. *Tillandsia fasciculata* s.l. does occur as a lithophyte, but the ground must be porous so as to not rot the plant.

The effects of hurricanes on epiphytes has been studied much less. Goode and Allen (2008) found 50% less observed vascular epiphytes in El Edén Ecological Reserve in Quintana Roo, Mexico than prior to Hurricane Wilma. They also found that epiphytic individuals in wetland areas sustained greater losses than mature forests, but that overall species composition remained the same. Oberbauer et al. (1996) studied the effects of Hurricane Andrew on the epiphytes in cypress domes in Everglades National Park. They found that overall epiphyte mortality was relatively low despite the large number of dead epiphytes, and suggested that

opening in the canopy may promote epiphyte establishment through increased light conditions. Oberbauer et al. (1996) did not include *T. fasciculata* in their overall analyses, but they found that this taxon sustained a 50% loss even though its roots are strongly attached to host plants.

The future does not look bleak for the widely distributed *Tillandsia fasciculata* group. In fact Zotz (2007) census work of vascular epiphytes suggests that more widely distributed taxa are more likely to increase in abundance in the future.

CONCLUSIONS

Even though our SDM study included only two environmental variables (harmonized world soil data and altitude) and was limited to bioclimatic data from WorldClim, we found these data layers informative. Paleoclimatic data were able to shed light on possible areas where some of the *Tillandsia fasciculata* varieties arose. Future climatic data also found suitable localities outside current distribution, although factors such as habitat destruction, rising sea levels, increase in number and intensity of hurricanes, and biologic interactions, need to be taken into consideration and play more of a critical role than these models can capture.

Future research should test other GCM, such as CCSM4 and MPI-ESM-P, to see how results compare to MIROC-ESM. Incorporation of other data layers land use, topography, and bathymetric data may prove useful. Finally, looking at these SDM in a phylogenetic sense may help better understand the evolutionary patterns of the *Tillandsia fasciculata* group.

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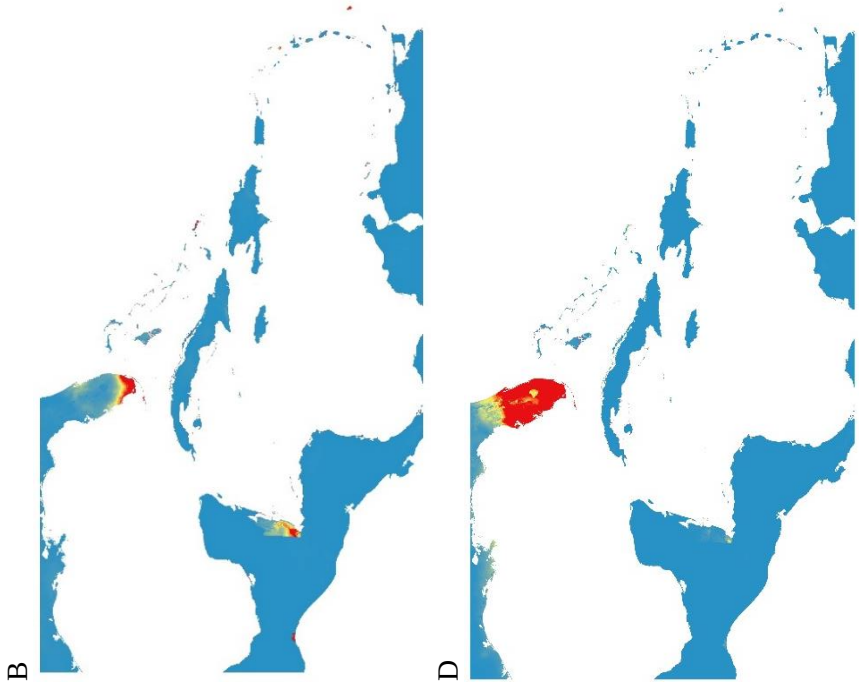
Table 1. Environmental data layers used in this study

Bioclimatic (BioClim) data from WorldClim (Hijmans et al. 2005):
BIO_1 = Annual Mean Temperature
BIO_5 = Max Temperature of Warmest Month
BIO_7 = Temperature Annual Range (BIO5-BIO6)
BIO_9 = Mean Temperature of Driest Quarter
BIO_{11} = Mean Temperature of Coldest Quarter
BIO_{12} = Annual Precipitation
BIO_{14} = Precipitation of Driest Month
BIO_{18} = Precipitation of Warmest Quarter
Other layers:
Altitude from WorldClim (Hijmans et al. 2005)
Harmonized World Soil Data Base v1.21 (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012)
Florida conservation lands (Florida Natural Areas Inventory 2015)

Figure 1. Species distribution models of *Tillandsia fasciculata* var. *densispica* (N=50) using MaxEnt. Based on A) last interglacial (ca. 120-140 kya), B) last glacial maximum (ca. 22 kya), C) mid-Holocene (ca. 6 kya), and D) current, and future projections E) 2050 with 4.5 rcp, F) 2050 with 8.5 rcp, G) 2070 with 4.5 rcp, and H) 2070 with 8.5 rcp climatic conditions. Spatial resolution for A, DH, 30" (ca. 1 km), and for B and C, originally 2.5' but resampled to 30" . Warmer colors indicate most suitable conditions.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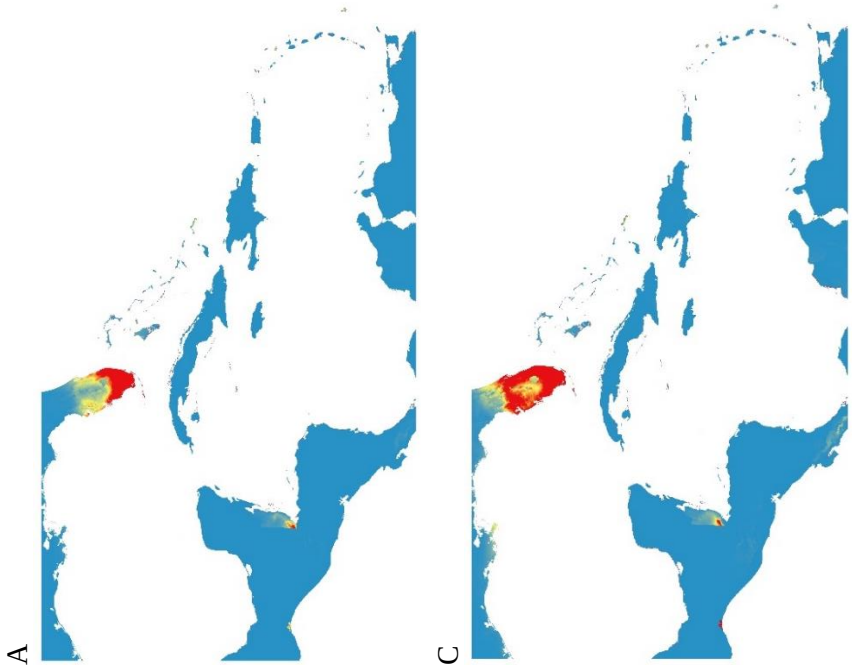
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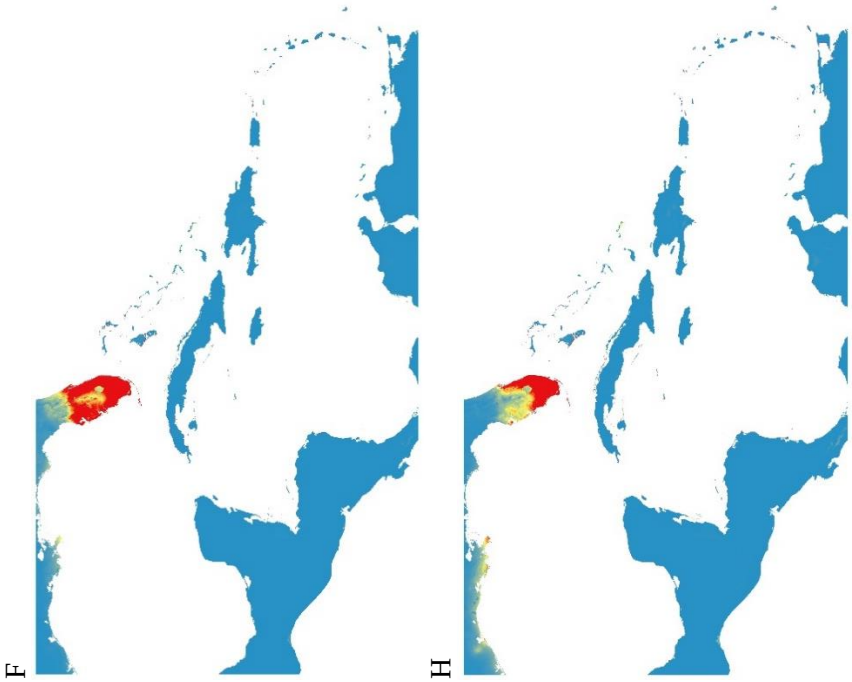
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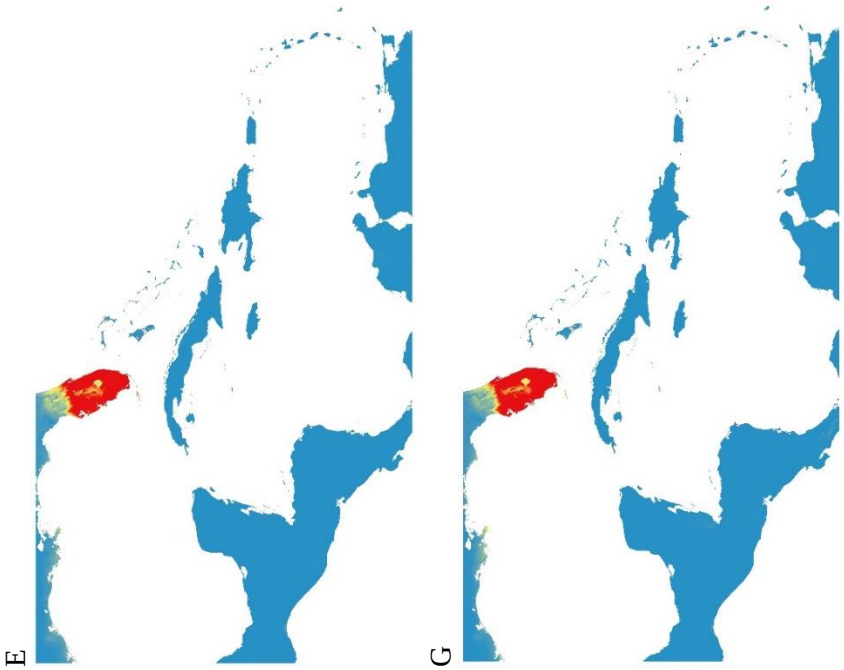
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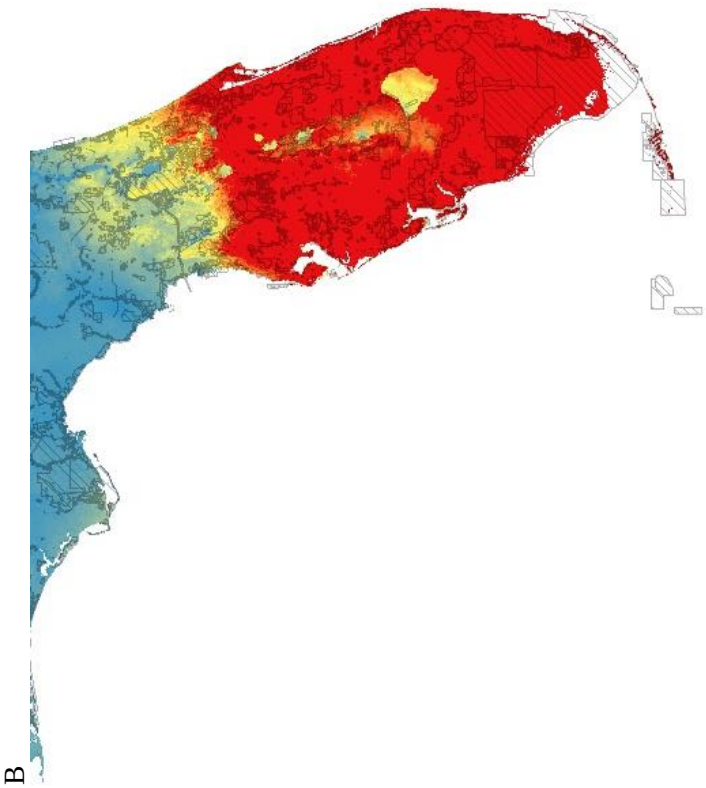
Figure 2. A) Locality points (red dots) and protected areas (green shading) of *Tillandsia fasciculata* var. *densispica* (N=50). Species distribution models of *Tillandsia fasciculata* var. *densispica* using MaxEnt. Based on B) current and future projections C) 2050 with 4.5 rcp, D) 2050 with 8.5 rcp, E) 2070 with 4.5 rcp, and F) 2070 with 8.5 rcp climatic conditions. Spatial resolution 30” (ca. 1 km). Warmer colors indicate most suitable conditions. Horizontal hash mark=protected areas



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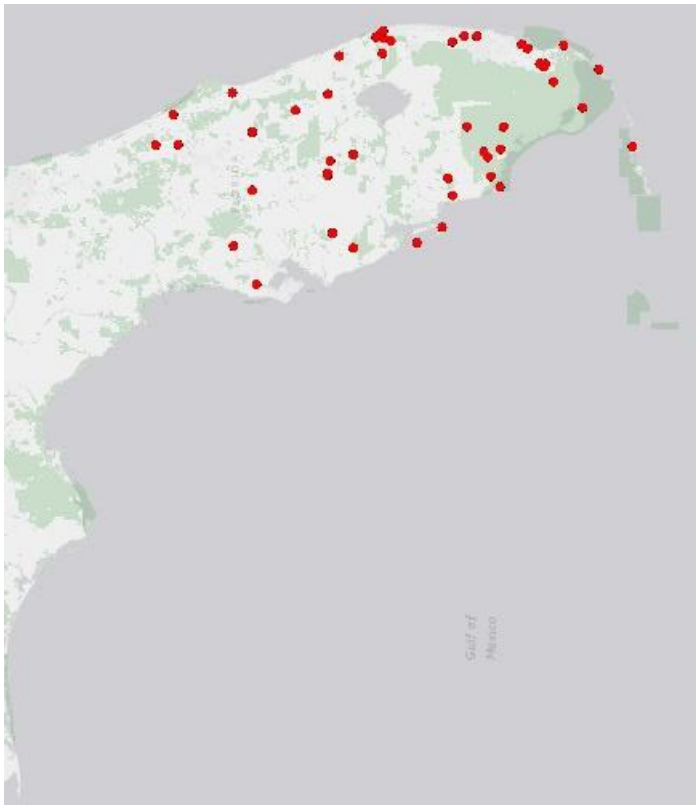

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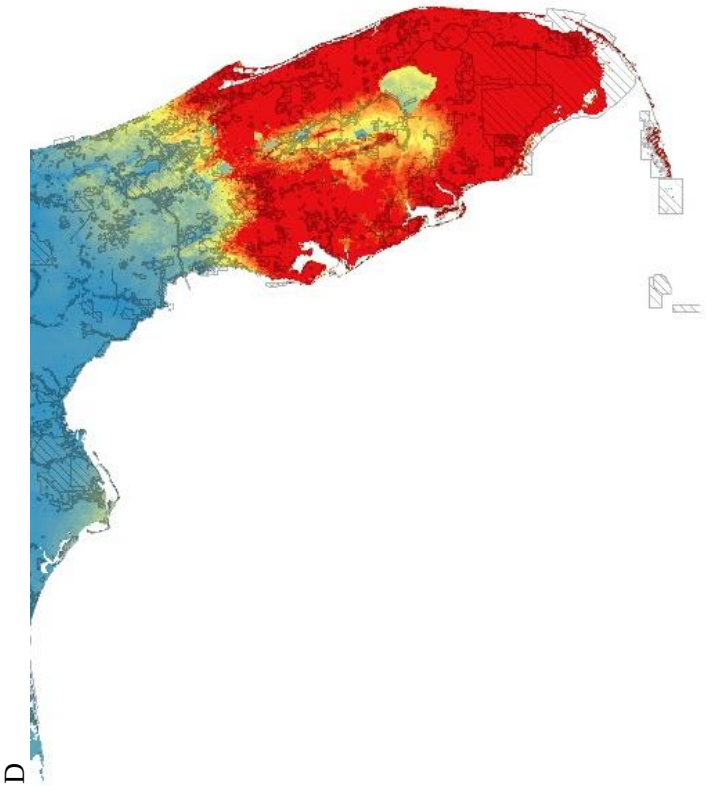

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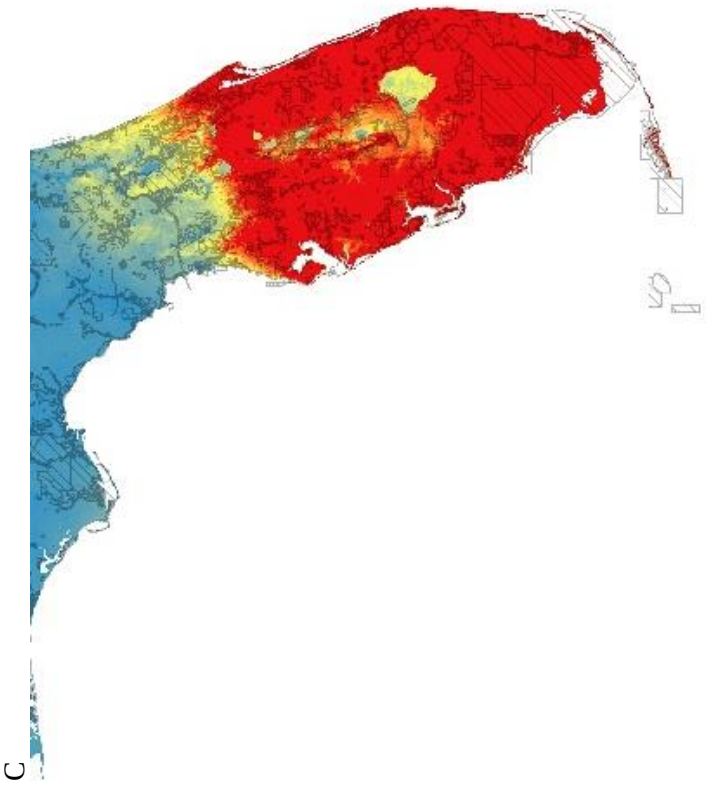

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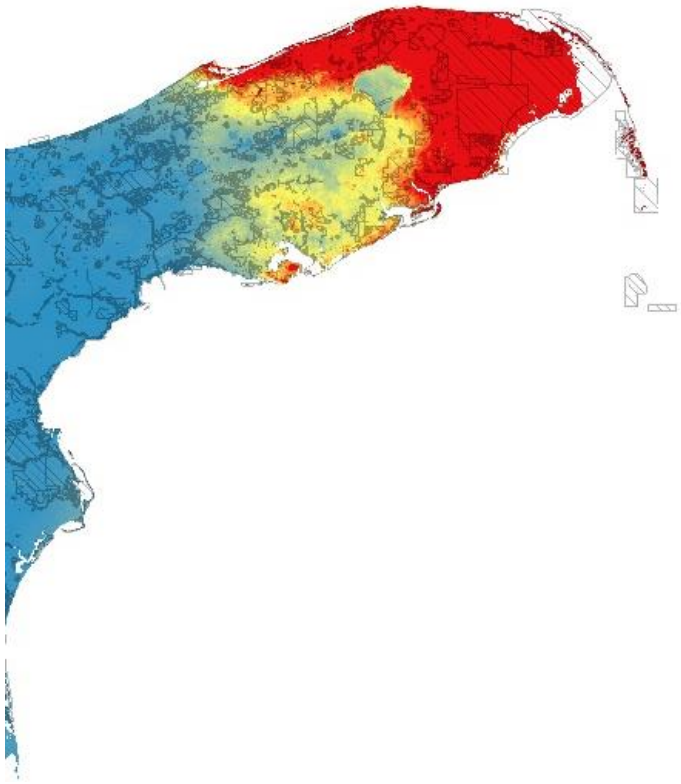

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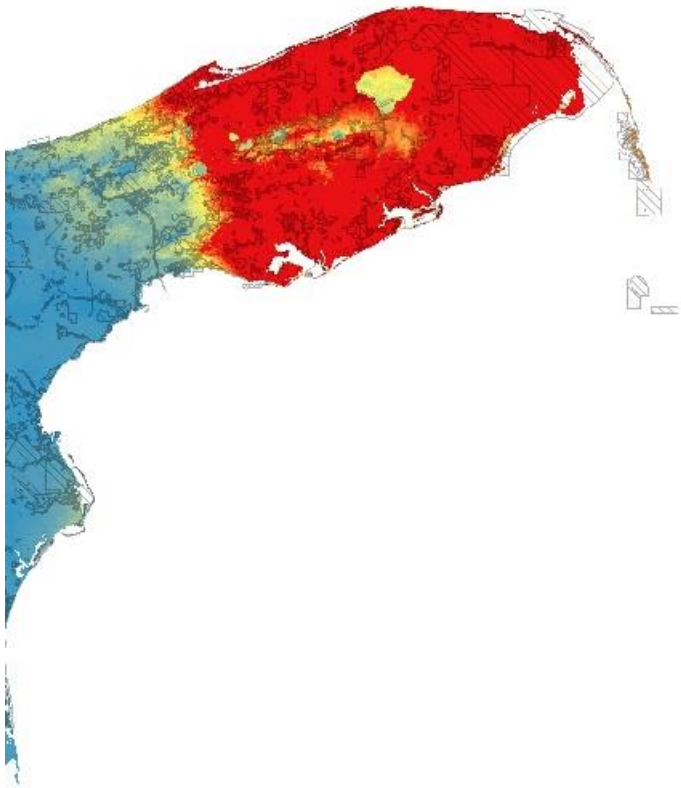

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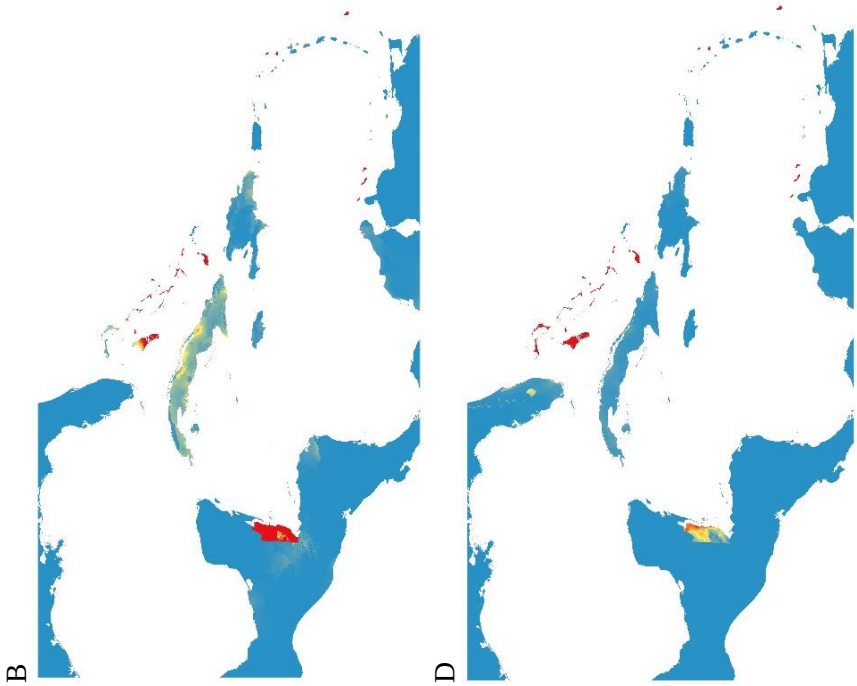
Figure 3. Species distribution models of *Tillandsia fasciculata* var. *laxispica* (N=15) using MaxEnt. Based on A) last interglacial (ca. 120-140 kya), B) last glacial maximum (ca. 22 kya), C) mid-Holocene (ca. 6 kya), and D) current, and future projections E) 2050 with 4.5 rcp, F) 2050 with 8.5 rcp, G) 2070 with 4.5 rcp, and H) 2070 with 8.5 rcp climatic conditions. Spatial resolution for A, DH, 30" (ca. 1 km), and for B and C, originally 2.5' but resampled to 30". Warmer colors indicate most suitable conditions.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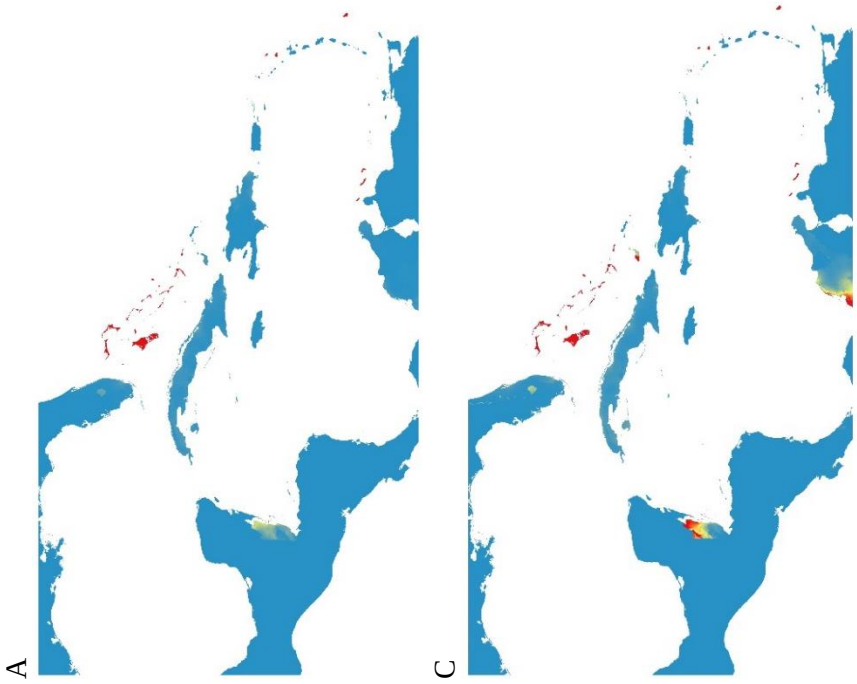
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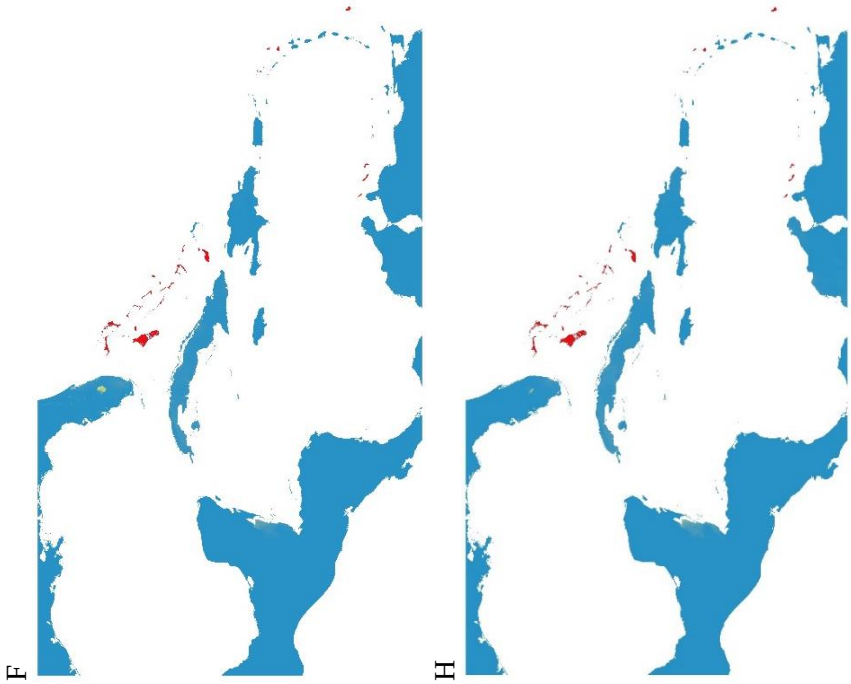
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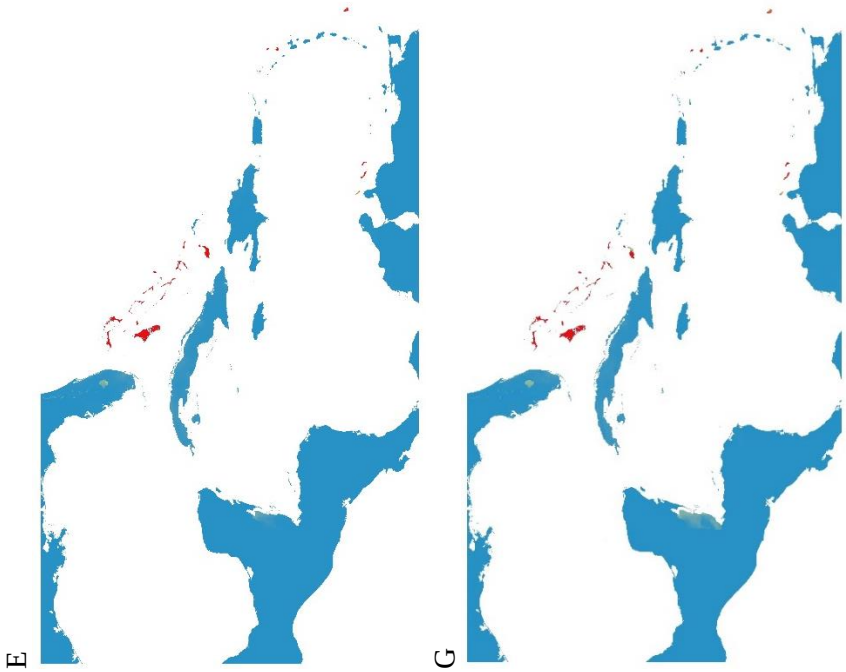
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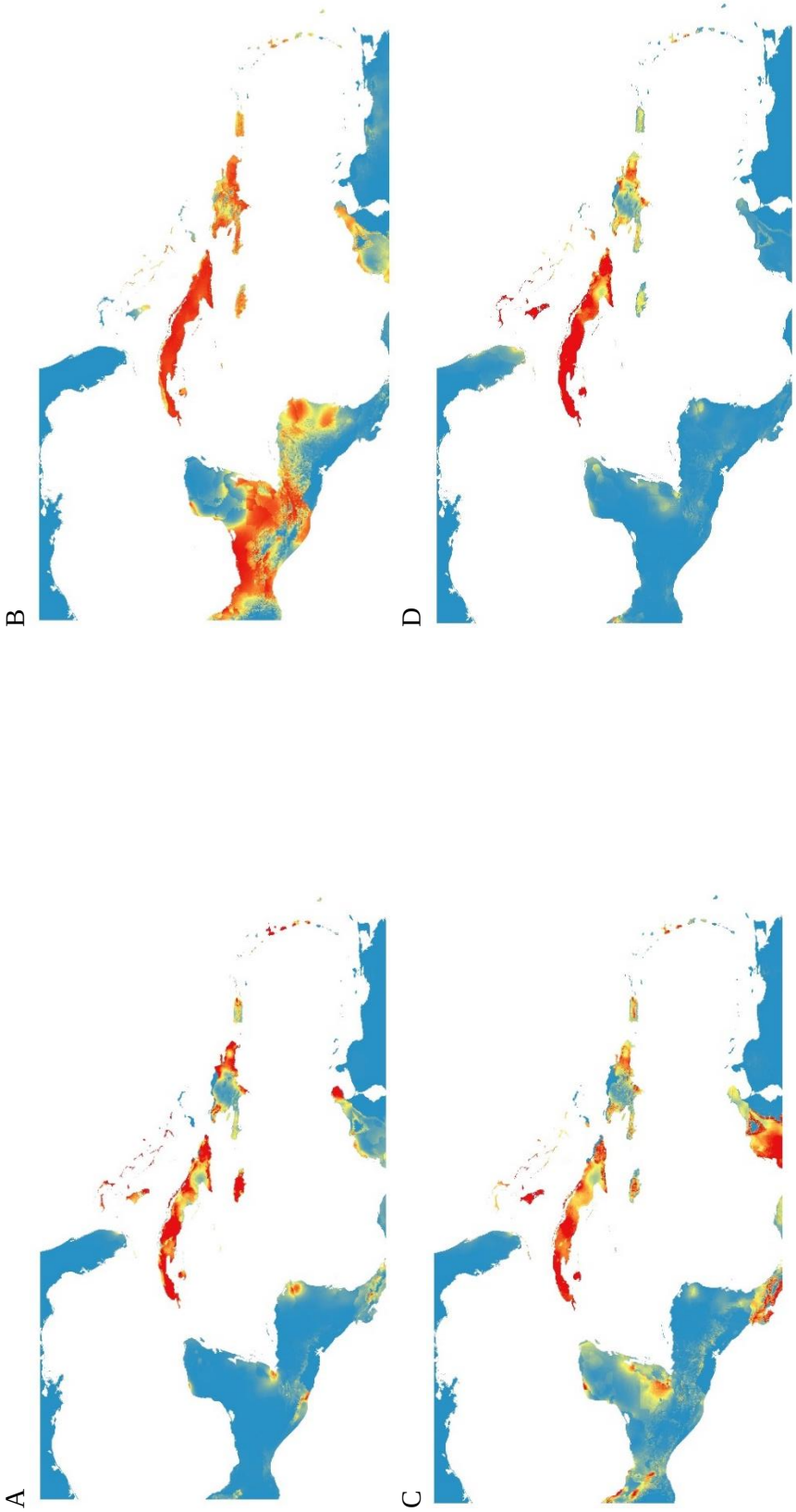
Figure 4. Species distribution models of *Tillandsia fasciculata* var. *clavispica* (N=43) using MaxEnt. Based on A) last interglacial (ca. 120-140 kya), B) last glacial maximum (ca. 22 kya), C) mid-Holocene (ca. 6 kya), and D) current, and future projections E) 2050 with 4.5 rcp, F) 2050 with 8.5 rcp, G) 2070 with 4.5 rcp, and H) 2070 with 8.5 rcp climatic conditions. Spatial resolution for A, DH, 30" (ca. 1 km), and for B and C, originally 2.5' but resampled to 30". Warmer colors indicate most suitable conditions


B
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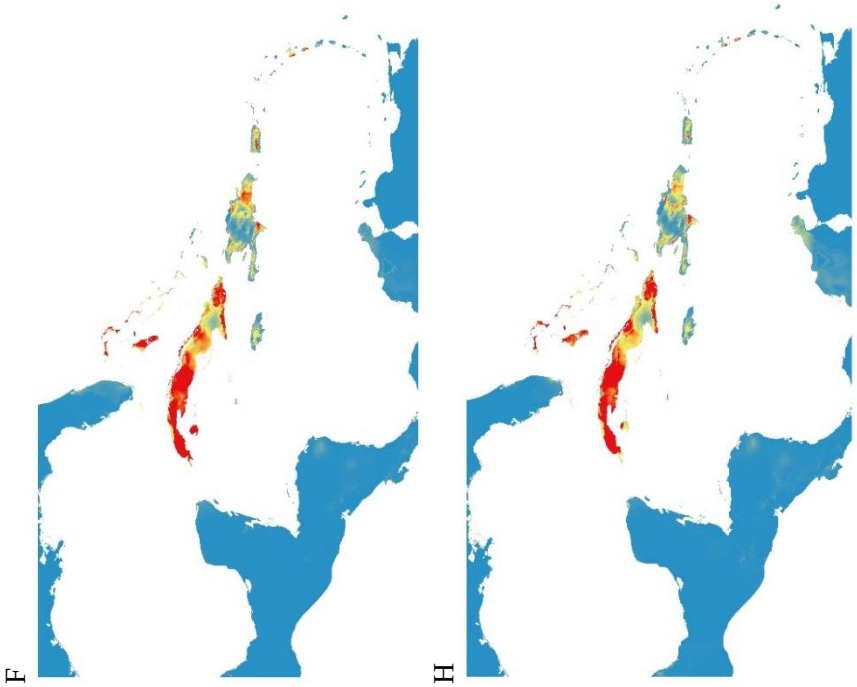
A
C


F
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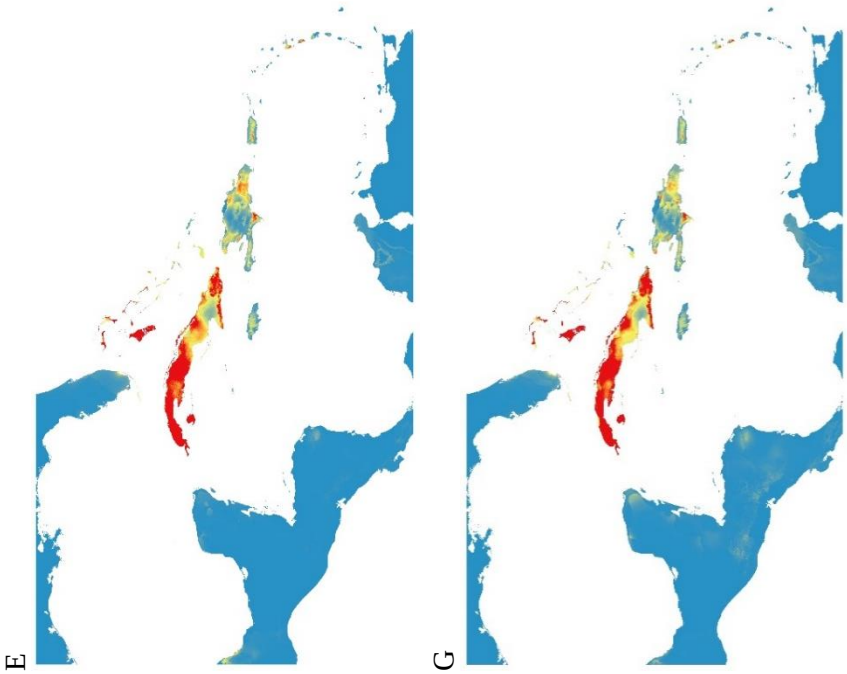
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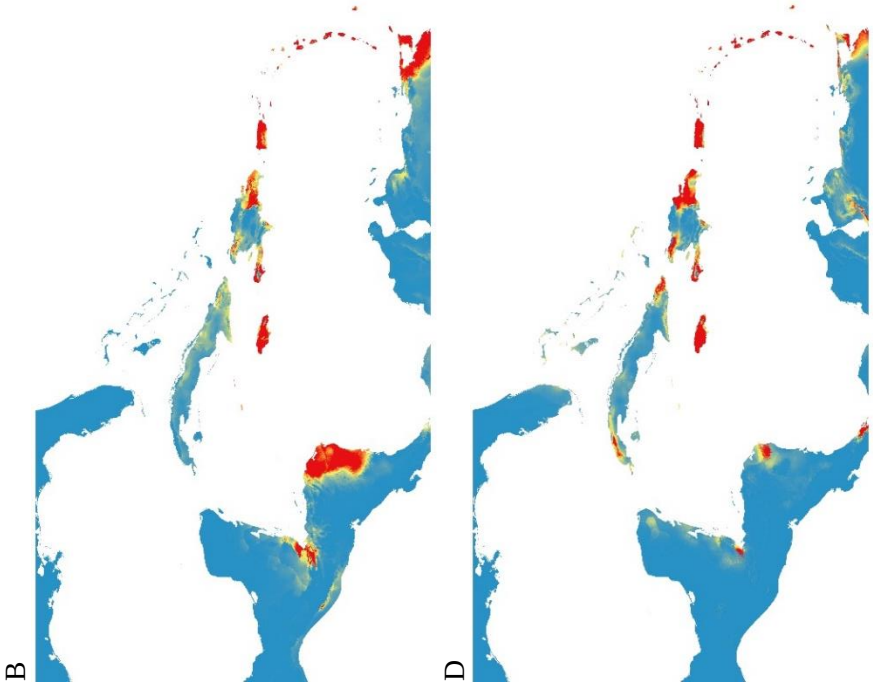
Figure 5. Species distribution models of *Tillandsia fasciculata* var. *venosispica* (N=36) using MaxEnt. Based on A) last interglacial (ca. 120-140 kya), B) last glacial maximum (ca. 22 kya), C) mid-Holocene (ca. 6 kya), and D) current, and future projections E) 2050 with 4.5 rcp, F) 2050 with 8.5 rcp, G) 2070 with 4.5 rcp, and H) 2070 with 8.5 rcp climatic conditions. Spatial resolution for A, DH, 30" (ca. 1 km), and for B and C, originally 2.5' but resampled to 30". Warmer colors indicate most suitable conditions.


B
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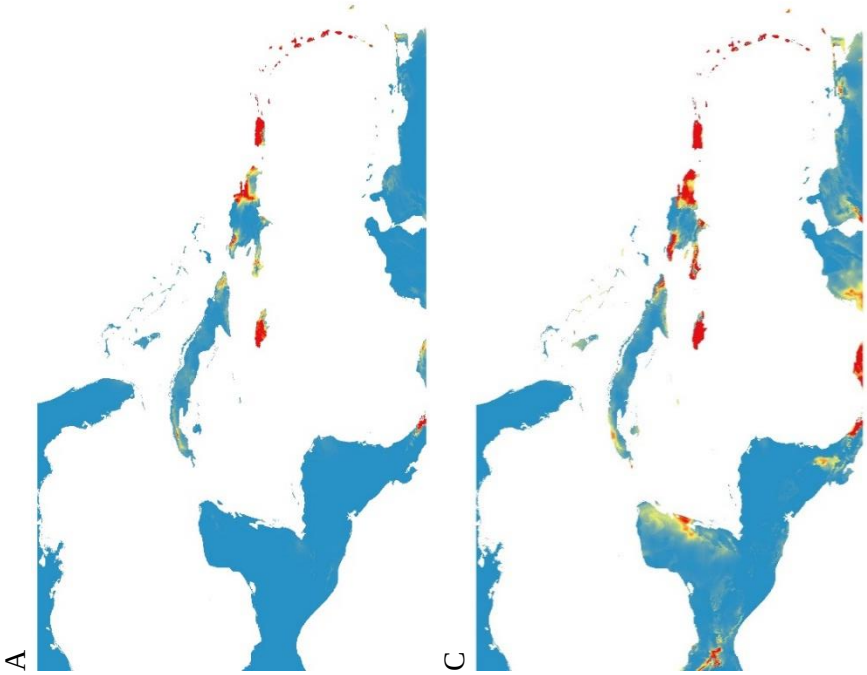
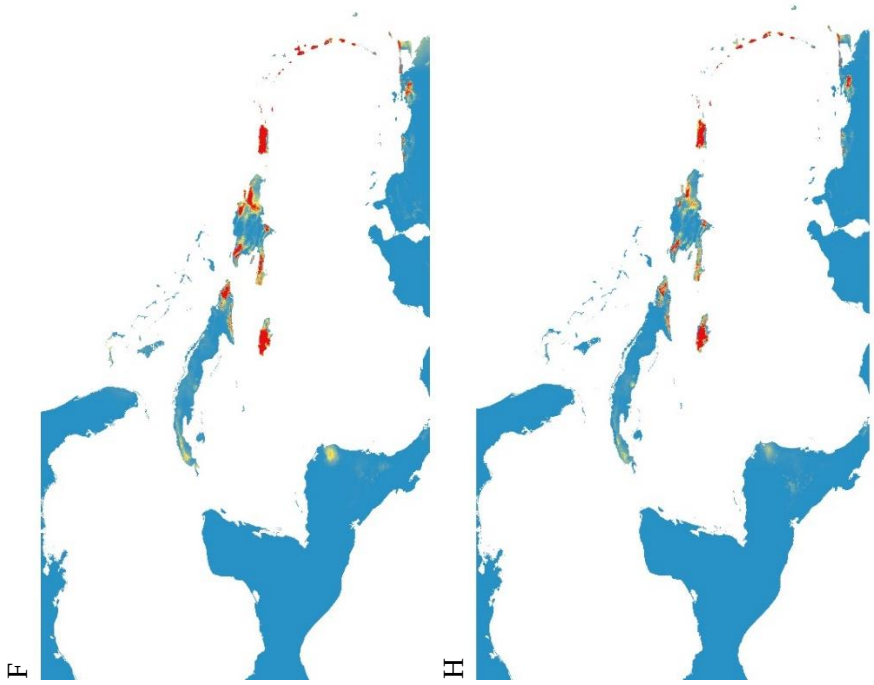
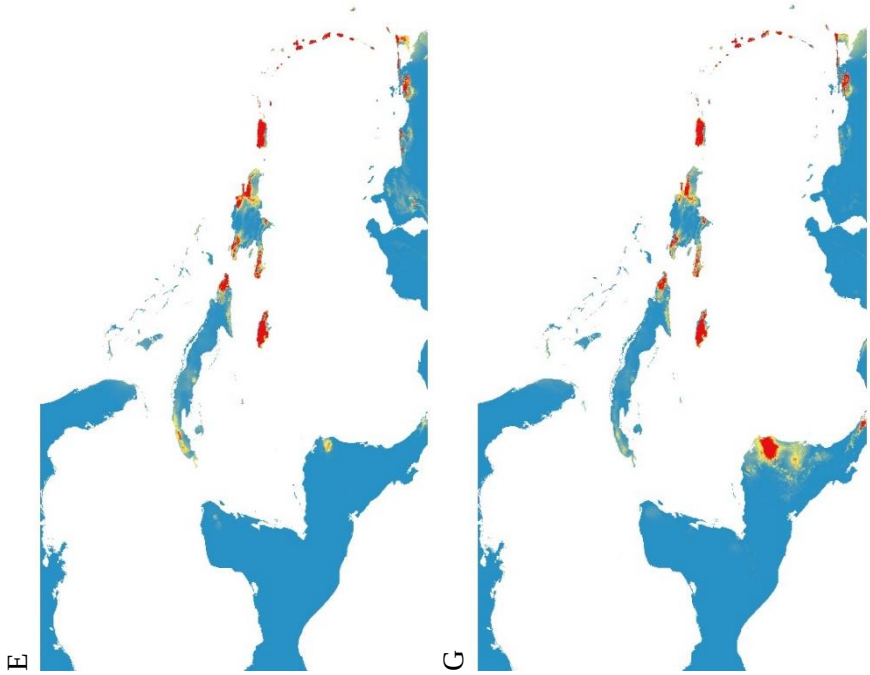

A
C


F
H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Supplementary Table 1. Specimens used for *Tillandsia fasciculata* var. *densispica.*

POLITICAL DIVISION 1	POLITICAL DIVISION 2	LOCALITY	Lat (Geo. Ref)	Long (Geo. Ref)	INITIALS	PRIMARY COLLECTOR	CO-COLLECTORS	Field Collector and number	Field Collection date	INSTITUTION	HERBARIUM SPECIMEN NO.
Florida	Palm Beach Co.	Pal-Mar *West Jupiter Wetlands). Ca. 2.2 miles west of SR 711, ca. 2.5 miles north of Indian Town Road (SR 706)	26.94685	-80.32275	Keith	Bradley	Steven Woodmansee	233	17-Jul-97	FTG	82555
Florida		No Name Key	24.69760	-81.32619	J.H.	Simpson		314	May 1891	F	231299
Florida	Highlands Co.	Bear Point, e side of Lake Placid (Lake Childs), sec. 29, T 37 S, R 30 E	27.23530	-81.34287	BTY			421	3-Apr-60	FLAS	75766
Florida	Highlands Co.	Desoto City North (High 39). Sec. 10, T35S, R29E (sebring quad). About 0.5-1.0 mile N. Red Beach Lake.	27.44611	-81.40497	Steven P.	Raymond		445	22-Apr-86	FLAS	193495
Florida	Osceola Co.	4 miles NE of the intersection of US 441 and Fla. Turnpike (Geo Ref. est 4 miles NE of intersection)	27.75064	-80.87646	B.C.	Bennett		549	31-Jan-82	FAU	20442
Florida	Lee Co.	Cayo-Costa Island	26.67075	-82.25018	Stephen	Young	Stanley Herwitz	583	10-Apr-91	USF	206443
Florida	Palm Beach Co.	Loxahatchee River Corridor. Ca. 0.4 milese south of Indian Town Road, ca. 1.15 miles west of Florida Turnpike	26.92992	-80.17020	Keith	Bradley	Steven Woodmansee	620	9-Oct-97	FTG	84001

Florida	Miami-Dade	Fuch's Hammock Park (Sykes Hammock). SW 304 St. & 194 Ave.	25.48411	-80.50616	Keith	Bradley		1350	28-Feb-98	FTG	104707; 108488
Florida	Osceola Co.	North side of US 441, 1 miles w of Holopaw, sec 11, T27S, R32 E. (Geo Ref. Google map estimate)	28.14750	-81.09261	D.B.	Ward	T. Myint	2006	8-Jun-60	FLAS	76872
Florida	Collier	Big Cypress near Deep Lake	26.05071	-81.34295	M.B.	Foster		2825	30-May	US	2120885
Florida		Merritt's Island, Indian River	28.31949	-80.68291	A.H.	Curtiss		2844	July	F	308520
Florida	Volusia Co.	Rt. 44, 7.5 miles W of Jct. with St. Rd. 415 W of Samsula (Geo Ref. Google Map estimate)	29.02436	-81.20224	Walter S.	Judd	with Angus Goulson and Robert Godfrey	3232	9-Apr-83	F	2090322
Florida	Collier Co.	TP Scrubsb (Coll28). Secs 2,3, & 10, T48S, R25E (Bonita Springs quad). (Geo Ref. Google Map estimate)	26.33981	-81.77870	Robin B.	Huck	Harvey A. Miller	3812	28-Mar-86	FLAS	164332
Florida	Lee	Sanivel Island, J.N. "Ding" Darling National Wildlife Refuge. Near abondoned homesite 0.9 mil W of Tarpon Bay Road on Sanibel-Captiva Road. T46S, R22, Sec. 27, NW of NE.	26.44037	-82.09803	Bruce	Hansen	Don Richardson	6146	10-Aug-79	USF	140251
Florida	Volusia Co.	Turnbull Hammock, Fla. 410, 14.7 mi e of Osteen, S29, T19S, R34E(Geo Ref. Turnbull Hammock Conservation Area)	28.86026	-80.89289	D.B.	Ward		6494	2-Jun-67	FLAS	98663

Florida	Okeechobee Co.	Along Fla. 68, 2.7 miles west of St. Lucie County line; 5.2 miles east of jct with US 441. T35S, R36E. Section 10, NE of NW (Geo Ref. Google Map estimate 5.2 mi east of US 441 and Hwy 68)	27.45042	-80.72507	Bruce	Hansen	Ruben Sauleda and Don Richardson	7279	29-May-80	USF	150779
Florida	Collier	Rooker Bay, National Estuarine Sanctuary. At large shell mound and just north, T50S, R25E, Sec. 36 & T51S, R51E, Sec. 1. (Geo Ref. Rookery Bay Natsional Estuarine Research Reserve)	25.91025	-81.70302	Bruce	Hansen	R.P Wunderlin, and George Robinson	8336	2-Jun-81	USF	166105
Florida	Broward Co.	Just S of Holmberg Road, 1.4 mi. W of jct. US441; ca. T48S, R41E, Sec. 2, NW of SE. (Geo Ref. Google Map estimate)	26.31048	-80.22850	Bruce	Hansen	George Robinson, and Ruben Sauleda	8379	2-Jul-81	USF	156657
Florida	Broward Co.	Along south side of FL 84, 0.5 miles west of I-95, Fort Lauderdale. T50S, R42E, Sec. 20., SW of NE (Geo Ref. Google Map estimate)	26.08586	-80.17691	Bruce	Hansen	Ruben Sauleda	10593	19-Oct-85	USF	188909
Florida	Pinellas Co.	Brooker Creek Preserve, ca. 3 miles north of Oldsmar; ca. 0.5 miles west of powerline; T 28S, R16E, Sec. 1. NW 1/4 (Geo Reference Brooker Creek Preserve and Environmental Education Center)	28.13285	-82.65560	Bruce	Hansen	R.P Wunderlin, and P. Douris	12164	12-May-93	USF	208677
Florida	Monroe Co.	Plantation Key	24.98614	-80.54607	W.C.	Muenscher	R.F. Thorne	18481	10-20 March 1947	BH	

Florida	Collier Co.	Monroe Station	25.86428	-81.09936	Alma L.	Moldenke	Harold N. Moldenke	29630	13-May-75	TEX	
Florida	Broward Co.	vicinity of Ft. Lauderdale Executive Airport (Geo Ref. Ft. Lauderdale Exec. Airport)	26.20056	-80.17144	D.S.	Correll		42502	2-Jul-74	FTG	22057
Florida	Collier Co.	Kissimee Billy, north of Alligator Alley	26.19564	-81.08646	D.S.	Correll	Nixon Smiley, and Percy Brown	47186	14-May-76	FTG	28589
Florida	Miami-Dade	Deering Estate, Cutler	25.62710	-80.31615	D.S.	Correll	John Popenoe	49810	21-May-78	FTG	33889
Florida	Polk Co.	On tree in cypress swamp, 5 mi nw of Haines City via Polk City Road (Geo Ref. estimate of 5 miles NW)	28.15863	-81.68979	H.S.	Conard			8-Apr-67	FLAS	98665
Florida	Seminole Co	Lake Monroe (Geo Ref. Lake Monroe Conservation Area)	28.82247	-81.20236	A.P.	Garber			March 1876	FLAS	69989
Florida	Monroe Co.	Flamingo, Everglades National Park (Geo Ref. Flamingo Visitor Center)	25.14123	-80.92376	F.C.	Craighead			Aug-60	FLAS	76929
Florida	Martin Co.	SW side of Loxahatchee River, sec. 16, T40 S, R 42 E (Geo Ref. Loxahatchee River Lake Worth Creek Aquatic Preserve)	26.95335	-80.11141	D.E.	Wilson			29-Dec-59	FLAS	75136
Florida	Collier Co.	Big Cypress (Geo Ref. Big Cypress National Preserve and Hwy 41)	25.89905	-81.32202	H	Luther			5-May-79	SEL	26487
Florida	Palm Beach Co.	Jupiter (Geo Ref. center of city of Jupiter)	26.93423	-80.09421	D.C.	Peattie			Jan-23	F	781070
Florida	Miami-Dade Co.	No Name Key	24.69760	-81.32619	J.H.	Simpson			May 1891	F	231299
Florida		Homestead Geo Ref. center of Homestead)	25.46872	-80.47756	Hugh	O'Neill			7-Oct-29	WIS	

Florida		St. Leo (Geo Ref. cener of St. Leo)	28.33723	-82.25842	Hugh	O'Neill				WIS	
Florida		Lake Monroe (Geo Ref. Lake Monroe Conservatio Area)	28.82247	-81.20219	A.P.	Garber			March 1876	GH	
Florida		Merritt's Island (Geo Ref. Merritt Island)	28.31811	-80.68198	William M	Canby			February 1889	GH	
Florida	Miami-Dade	North end Long Pine Key, Everglades National Park	25.39969	-80.65748	P.B.	Tomlinson			6/11/1965	FTG	222
Florida	West Palm Beach Co.	off Rt. 98 in the Loxahatchee slough west of West Palm Beach (Geo Ref. Loxahatchee Slough)	26.86736	-80.19814	Larry A.	Burmacki			1 Agusut 1977	FTG	36268
	Monroe County	Key Largo. between post 29-30; Dagny Johnson Key Largo Hammock Botanical State Park	25.29843	-80.29620	B.J	Sidoti	Row Iliescu	136		KLH7	
Florida	Miami-Dade County	Miami. Matheson Hammock	25.68008	-80.27382	B.J	Sidoti		137		MH1	
Florida	Collier County	Naples. north of Boardwalk; Corkscrew Swamp Sanctuary	26.37990	-81.60497	B.J	Sidoti	Row Iliescu	155		CS4	
Florida	Martin County	Hobe Sound. Kitching Creek trail, Jonathan Dickinson State Park	27.00098	-80.15685	B.J	Sidoti	Jeremy Moynihan	168		JD1	
Florida	Highlands County	Sebring. loop road; Highlands Hammock State Park	27.47157	-81.54882	B.J	Sidoti	Andrea Bishop and Dorothy Harris	203		HH7	
Florida	Sarasota County	Sarasota. on west side along Main Park Drive, south of Power L, approx. 1.4 miles; Myakka River State Park	27.24905	-82.29532	B.J	Sidoti	Diana Donaghy	214		MR5	
Florida	Collier County	Naples. camp ground #1, Collier-Seminole State Park	25.99112	-81.59458	B.J	Sidoti	Andrea Bishop and Christina Olson	222		CLS3	

Florida	Collier County	Copeland. east main tram (gate 12) 0.9 mi, north side of tram; Fakahatchee Strand Preserve State Park	26.01505	-81.39807	B.J	Sidoti	Mike Owen	240	FS6
Florida	Martin County	Jensen Beach. North Fork of St. Lucie River; Savannas Preserve State Park	27.33882	-80.33572	B.J	Sidoti	Jeremy Moynihan	263	SV13
Florida	Miami-Dade County	Miami. Camp Owaissa Bauer	25.52210	-80.47289	B.J	Sidoti	Jennifer Possley and Cristina Rodriguez	474	COB8
Florida	Manatee County	Bradenton. north of Myakka River and west of Wingate Creek, Wingate Creek State Park	27.43723	-82.13837	B.J	Sidoti	Chris Becker and Elizabeth Jensen	428	WG14
Florida	Highlands County	Sebring. near ranger station, Highlands Hammock State Park	27.47092	-81.53250	B.J	Sidoti	Dorothy Harris and Elizabeth Jensen	436	HH18

Supplementary Table 2. Specimens used for *Tillandsia fasciculata* var. *laxispica*

COUNTRY	POLITICAL DIVISION 1	LOCALITY	Lat (Ge. Ref)	Long (Geo. Ref)	INITIALS	PRIMARY COLLECTOR	CO-COLLECTORS	Field Collector and number	Field Collection date	INSTITUTION	HERBARIUM SPECIMEN NO.
Bahamas	New Providence	scrubland near W shore of Millars Sound (Geo Ref. Nassau)	25.06800	-77.30990	Birgitta	Svensson	Kare Bremer	699	26-Jan-75	S	
Bahamas	Inagua	Matthew Town to lower Savanah occasional in Flamingo Pond just n. of airport and Cockburn Town, w.	20.95000	-73.66670	Feo. V.	Nash	Norman Taylor	1451	4-Nov-04	NY	
Bahamas	San Salvador Island	side of island near Lisbon Creek, Mangrove	24.03330	-74.51670	R.R.	Smith		3953	Jun-75	FTG	47159
Bahamas	Andros	Cay about 1.5 miles west of airstrip (Geo Ref. estimated from South Andros	24.25000	-77.65000	J.K.	Small	J.J. Carter	8494	16-19 January 1910	NY	
Bahamas	South Andros	Airport)	24.15602	-77.61137	D.S.	Correll		43532	25-Sep-74	FTG	22066

Bahamas	Crooked Island	near pier, along road to Turtle Sound, west of Church Grove (Geo Ref. Church Grove)	22.75000	-74.21670	D.S.	Correll		44325	17-Feb-75	FTG	24453
Bahamas	West Grand Bahama	Freetown Community	26.56670	-78.45000	D.S.	Correll	John Popenoe	45382	23-May-75	FTG	25356
Bahamas	Cat Island	between Dolphin Head and Old Bight (Geo Ref. Old Bight)	24.25000	-75.35000	D.S.	Correll		46117	19-Nov-75	FTG	21943
Bahamas	Andros	Red Bays	25.12430	-78.16690	John I.	Northrop	Alice R. Northrup	439?	17 April 1890	F	130571
Bahamas	Andros	Atala Coppice	24.92333	-78.02350	B.J.	Sidoti	Jay Handelman	66	16 April 2005		
Bahamas	Andros	on road to Red Bays, Jungle Pond	25.11053	-78.13393	B.J.	Sidoti	Jay Handelman	72	17 April 2005		
Bahamas	Andros	Rainbow Blue Hole	24.78473	-77.86002	B.J.	Sidoti	Jay Handelman	92	18 April 2005		
Bahamas	Andros	Maidenhair	24.79892	-77.89048	B.J.	Sidoti	Jay Handelman	105	18 April 2005		
Bahamas	Andros	Stafford Creek	24.79830	-77.89123	B.J.	Sidoti	Jay Handelman	110	19 April 2005		
Bahamas	Abaco		26.63413	-77.28440	B.J.	Sidoti	Jay Handelman	120	20 April 2005		

Supplementary Table 3. Specimens used for *Tillandsia fasciculata* var. *clavispica*

COUNTRY	POLITICAL DIVISION 1	LOCALITY	Lat (Geo Ref.)	Long (Ge. Ref.)	INITIALS	PRIMARY COLLECTOR	CO-COLLECTORS	Field Collector and number	Field Collection date	INSTITUTION	HERBARIUM SPECIMEN NO.
Cuba	Pinar del Rio	in moutains near El Guama	23.11670	-82.21670	Wm.	Palmer	J.H. Riley	319	15-Mar-00	US	372567
Cuba	Isla de Pinos	Near Nueva Gerona	21.88170	-82.80700	A.H.	Curtiss		353	17-Feb-04	F	165262
Cuba	Habana	Vecindad de Santiago de las Vegas	22.97000	-82.38690		Baker	Nilson	633	5-Jul-04	HAC	
Cuba	Habana	Managua	22.97500	-82.28860		Baken?		1564	23-Sep-04	HAC	
Cuba	Oriente	Valley of Rio Matamoros South of Holguin	20.68083	-76.43333	J.A.	Shafer		1519	22-Apr-09	NY	
Cuba	Camaguey	Cayo Paloma	22.12861	-77.74972	J.A.	Shafer		2574	12-Oct-09	F	251089
Cuba	Pinar del Rio	near Mendoza (Paso Real)	22.16280	-84.09890	J.A.	Shafer		10611	29-Nov-11	GH	
Cuba	Pinar del Rio	Laguna del Bufeo to Laguna Alcatraz Grande	22.05153	-84.10972	J.A.	Shafer		11015	16-Dec-11	NY	
Cuba	Oriente	Guantanamo, Novalriches, in the coast forest	20.04110	-75.19170	E.L.	Ekman		2950	26-Sep-14	S	
Cuba	Oriente	Santiago de Cuba, Loma Bonete, on the top	20.02070	-75.82670	E.L.	Ekman		7688	23-Sep-16	S	

Cuba	Santa Clara	near Sagua la Grande; highest mogote, Pesquera	22.80670	-80.07560	Bro.?	Leon	A. Loustalot	9478	12-Aug-20	US	1047946
Cuba	Santa Clara	Belmonte, Soledad, Cienfuegos	22.12190	-80.36190	J.G.	Jack		7626	3-Feb-30	GH	
Cuba	Pinar del Rio	Vinales	22.61240	-83.71140	E.P.	Killip		13585	11-Dec-30	US	1480288
Cuba	Oriente	Lomas de Ensenada de Mora	19.88300	-77.31700	J.P.	Carabia	F.G. Walsingham	20	24-Mar-38	GH	
Cuba	Pinar del Rio	Puerto Cortez, Guanes (Geo. Ref. Guane)	22.20250	-84.08750	J.	Acuna		11134	1-Jul-40	HAC	
Cuba	Isla de Pinos	Finca Mamey, headwaters of Rio Las Casas (Geo. Ref. Gerona)	21.88170	-82.80700	E.P.	Killip		44678	5-Feb-55	US	2112809
Cuba	Las Villas	road from Santa Clara to Manicaragua, 4-8 km south of Santa Clara.	22.50954	-80.04047	R.E.	Schultes	A.S. Barclay, J.H. Beaman, J.A. Freeberg, T.B. Lee	828	25-Jul-55	FTG	13688
Cuba	Oriente	Monte Picote, a foothill at the southern end of Sierra de Nipe, near Palmarito del Cauto	20.31990	-75.91690	C.V.	Morton		9738	29-Jan-56	US	2351274
Cuba	Pinar del Rio	Gorge of the Taco Taco River, near Santa Cruz de los Pinos	22.68250	-83.12220	George R.	Proctor		16299	16-Mar-57	IJ	17374
Cuba	Oriente	Bez. Yateras. Srra. de Magueg. Kiefern-Laubmischwald 8 km se Gupeyal	20.49750	-75.05861	Kuban	Dtsch. A.	Humboldt Expedition	974	29-Jan-68	HAC	
Cuba	Granma	Montes al este de Alegria del Pio	19.90000	-77.55000	J.	Bisse	et al.	HAJB35380	23-Oct-77	HAC	34307
Cuba	Pinar del Rio	Los Palacios: Bano de Bermejales, pinares alreadedores de Campamento Galalon	22.58720	-83.24860	J.	Gutierrez	L. Gonzalez		18-Jan-80	HAJB	41623

Cuba	Pinar del Rio	Candelaria. Las Ter???, Loma Pelada de Cayajabos	22.60000	-83.38330	J.	Bisse	K.F. Gunther, F.K. Meyer, B. Mory, & L. Gonzalez		18-Mar-84	HAJB	51938
Cuba	Pinar del Rio	Minas de Matahambre. Sumidero. Mogote cerca del pueblo	22.58750	-83.94500	I.	Arias	R. Rankin		29-Aug-88	HAJB	66095/B
Cuba	Santi Spiritus	Sierra del Escambray; a largo de la carretera de Trinidad hacia topes de Coyantes (entre Pico mi Retiro y Hosteria Los Helechos)	21.91360	-80.02190	P.	Acevedo-Rodriguez	B. Buck, S. Hundorf, and L. Montes	5627	2-Jul-93	US	3262751
Cuba	Matanzas	10 km from Playa Larga, along road north toward Palpite	22.29040	-81.18210	P.	Acevedo-Rodriguez	M. Fernandez, K. de Queiroz, R. Oviedo, & L. Rodriguez	6259	8-Apr-94	US	3297661
Cuba	Oriente	South of lumber camp, crest of Sierra Nipe	20.46667	-75.81667	C.V.	Morton	Juliam Acuna	3052	16-17 October 1941	US	1782019-1782020
Cuba	Oriente	United States Naval Station, Guantanamo Bay	19.90101	-75.10615	N.L.	Britton		2091	17-30 March 1909	NY	

Cuba	Pinar del Rio	Vicinity of Sumidero	22.44125	-83.90195	J.A.	Shafer		13487	2-4 August 1912	NY	
Cuba	Santiago	Vicinity of Baracoa	20.34660	-74.49680	Charles L.	Pollard	Edward Palmer, and William Palmer	99	24-29 January 1902	F	125624
Cuba	Oriente	Guabairo, Soledad, Cienfuegos	22.15940	-80.31250	J.G.	Jack		6924	6 February 1928/9	GH	
Cuba		Rio Seco (~ Curuhey) (Geo. Ref. Curujey)	22.48330	-80.60000		Eggers		4730	Feb 1889	K	321815
Cuba	Habana	Cienaga de Lanier, Isla de Pinos	21.56600	-82.87900	Mision?	Rusa		87	May-June 1962	HAC	
Cuba	Pinar del Rio	parte oeste de Arlemisa? (Geo. Ref. as Artemisa)	22.81310	-82.76190	Carely?	Wilson?		1535	14-Sep-04	HAC	
Cuba	Habana	Balabano (Geo. Ref. as Batabano)	22.71640	-82.28810	Baker	Maclain?		2374	4-Oct-04	HAC	
USA	FL	Key West	24.55506	-81.77998	F.	Rugel		104	Feb 1866	NY	

Cuba	Sancti Spiritus	Banao. Reserva Ecologica "Alturas de Banao", Mogote Jarico	21.86588	-79.57962	B.J.	Sidoti	Lucia Hechavarria Schwesinger and Maikel Canizares Morera	309	27-Sep-05
Cuba	Holguin	Guardalavaca. Caletica	21.11720	-75.85877	B.J.	Sidoti	Lucia Hechavarria Schwesinger, Maikel Canizares Morera, and Pedro Gonzalez Gutiérrez	329	29-Sep-05
Cuba	Holguin	Silla de Gibara	21.02895	-76.08533	B.J.	Sidoti	Lucia Hechavarria Schwesinger, Maikel Canizares Morera, and Pedro Gonzalez Gutiérrez	334	29-Sep-05

Cuba	Santiago de Cuba	Reserva Ecologica Siboney-Jutici	19.96252	-75.71707	B.J.	Sidoti	Lucia Hechavarria Schwesinger, Maikel Canizares Morera, Pedro Gonzalez Gutiérrez, and Angel Eduardo Reyes Vázquez	354	30-Sep-05
Cuba	Santiago de Cuba	La Gran Piedra	20.01360	-75.65180	B.J.	Sidoti	Lucia Hechavarria Schwesinger, Maikel Canizares Morera, and Pedro Gonzalez Gutiérrez	369	1-Oct-05
Cuba	Pinar del Rio	San Cristobal. Paredon de Bartolito=Paredon de la Jutice? De Alain, Rangel, Sierra del Rosario	22.74460	-83.19235	B.J.	Sidoti	Lucia Hechavarria Schwesinger and Maikel Canizares Morera	379	3-Oct-05

Cuba	Matanzas	Santo Tomas. Laguna El Asiento, Cienaga de Zapata	22.38467	-81.40347	B.J.	Sidoti	Lucia Hechavarria Schwesinger and Ramona Oviedo Prieto	400	4-Oct-05	

Supplementary Table 4. Specimens used for *Tillandsia fasciculata* var. *venosispica*

COUNTRY	POLITICAL DIVISION 1	LOCALITY	Lat (Geo. Ref.)	Long (Geo. Ref.)	INITIALS	PRIMARY COLLECTOR	CO-COLLECTORS	Field Collector and number	Field Collection date	INSTITUTION	HERBARIUM SPECIMEN NO.
USA	Puerto Rico	Salinas. cerca de La Plena, carr. 712	18.05000	-66.20833	D.S.	Fernandez	D. Garcia, and J. Ackerman	12	18-Sep-88	UPRRP	11835
USA	Puerto Rico	Maricao: Bo. Maricao Afuera; SW of Hwy 120 km 17.1	18.15944	-66.99806	J.A.	Cedeno	O.J. Vazquez	823	7-Mar-96	MAPR	14802
Tortola		Long Bay East	18.39485	-64.68397	R.G.	D'Arcy		833		FLAS	94302
USA	Puerto Rico	Arecibo, Bo. Sabana Hoyos, Finca Las Abras.	18.33685	-66.60578	J.C.	Trejo-Torres	M. Curras	2229	10-Apr-03	UPR	25856
USA	St. John	Reef Bay, Fish Bay Gut.	18.32291	-64.76513	P.	Acevedo Rdgz.		2495	27-Jan-88	NY	
USA	Puerto Rico	Coamo, Las Piedras Chiquitas (trail from Rt 717, km 2.1). Along N spur of ridge	18.06885	-66.27045	F.	Axelrod	A. and B. Axelrod	2630	29-Jul-91	UPRRP	16490
USA	Puerto Rico	Municipio de Yauco, Barrio Susua Alta, Bosque Estatal de Susua. Approximadamente 200-300 m del cruce, en las margenes de Quebrada Peces, lado sur de la carretera que va a la oficina	18.07500	-66.92500	R.	Garcia		2950	26-Apr-90	MAPR	3132
USA	Puerto Rico	Bayamon: Bo. Hato Tejas; series of mogotes (haystack hills) W of Rt. 871, E mogote next to road through Cantera	18.40550	-66.18930	F.	Axelrod	L. Escobar	3108	15-Oct-91	UPRRP	17673

USA	Puerto Rico	Vieques, Monte Pirata Balneario Publico	18.09302	-65.55155	J.D.	Ackerman		3878	10-Sep-05	UPRRP	43217
USA	Isla Vieques	Sunbay, La Esperanza area; on east side of Playa Media Luna, 1.6 mi from Rt. 996	18.09715	-65.45805	Ruben P.	Sauleda	M. Ragan, R. and P. Adams	8496	5-Nov-83	FTG	54840
USA	Puerto Rico	Behind Holiday Inn on N side of Rt. 2, 2.8 mi W of Ponce; 0.5 mi W of junction with Rt. 591	17.97994	-66.67187	Ruben P.	Sauleda	M. Ragan, R. and P. Adams	8507	6-Nov-83	USF	176465
USA	Puerto Rico	Arecibo. Bo. Rio Arriba, area to N of temporary S end of new Rt 10, on top of mogote	18.33533	-66.67633	F.	Axelrod		9390	8-Nov-95	UPRRP	29955
St. Vincent		King's Hill	13.15640	-61.16720	R.A.	Howard		11132	1-7 April 1950	BM	883632
Grenadines	St. Vincent territory	Bequia	13.28330	-61.13330	R.A.	Howard		11234	26-31 March, 8-20 April 1950	BM	883629
USA	Puerto Rico	Arecibo: 0.5 km S of Biafara ca. 60 m	18.40222	-66.66472	P.	Acevedo Rdgz.	A. Siaca	11702	10-Jul-01	US	3429236
USA	Puerto Rico	Toa Baja: Bo. Sabana Seca, just W of dirt road N of Caribbean Primate Center and c. 0.5 km S from Rt 867.	18.43650	-66.20500	F.	Axelrod	N. Rios	13301	?	UPRRP	41890
Saba		level, area S. of Windwardside	17.63330	-63.23330	R.A.	Howard		18417	15-Jul-77	GH	
La Desirade		Ravine la Riviere (Geo. Ref. near La Riviere, & Grand Ravine)	16.32272	-61.05810	G.	Proctor		21261	11-Jun-60	IJ	62617

Dominica		St. Joseph Parish. Morne Raquette Road from coastal highway to Au Piton, 0-5 km east of town; 3.3 km E of Morne Raquette	15.45000	-61.45000	S.R.	Hill	D. Bradshaw	25562	18-Dec-93	NY	
USA	Puerto Rico	Airbonito: Bo. Honduras, Rt 726, km 1.6	18.15017	-66.25700	F.	Axelrod	E. Santiago, T. Carlo, J. Aukema		13 Feb ?	UPRRP	38719
USA	Puerto Rico	Bosque de Guanica, along Murcielago Trail	17.96372	-66.86287	B.J.	Sidoti	Jay Handelman	504	23 May 2010		
USA	Puerto Rico	Near Bosque de Maricao, along Highway 105; approx. 5 miles west of park	18.17795	-67.02513	B.J.	Sidoti	Jay Handelman	512	24 May 2010		
USA	Puerto Rico	From Bosque de Guajataca, nearing Lago de Guajataca. Along Highway 149 N	18.39087	-66.92472	B.J.	Sidoti	Jay Handelman	515	25 May 2010		
USA	Puerto Rico	Bosque de Rio Abajo. Behind fence of Cooperative and sign of Centro de Visitantes	18.32060	-66.68328	B.J.	Sidoti	Jay Handelman	518	25 May 2010		
USA	Puerto Rico	From Bosque de Carite. Near Lago Patillas. Route 184 heading south towards Patillas.	18.32155	-66.03592	B.J.	Sidoti	Jay Handelman	521	26 May 2010		
St. Lucia		along trail of Gros Piton	13.80443	-61.06498	B.J.	Sidoti	Jennifer Possley and Melvin Smith	916	20 Feb 2012		

St. Lucia	east of Fond Doux	along road, in riverbed	13.76595	-61.03447	B.J.	Sidoti	Jennifer Possley and Melvin Smith	922	20 Feb 2012
St. Lucia	north of Soufriere	along highway heading south towards Soufriere. Off highway near plantation.	13.87470	-61.04402	B.J.	Sidoti	Jennifer Possley and Melvin Smith	927	19 Feb 2012
St. Lucia	east of Anse La Raye	east of Anse La Raye, side road off of main highway heading east towards Forest Reserve	13.93533	-61.04042	B.J.	Sidoti	Jennifer Possley	934	21 Feb 2012
France	near Mahaut	along D23, heading towards Mahaut on N2	16.18380	-61.76970	B.J.	Sidoti	Jennifer Possley	937	23 Feb 2012
France	south of Bouillante	south of Bouillante, off of highway N2, along side road D14 heading E towards National Park	16.10670	-61.75328	B.J.	Sidoti	Jennifer Possley and Eric Francius	941	24 Feb 2012
France	south of Bouillante	along road, near Riv. De Beaugendre	16.08488	-61.75997	B.J.	Sidoti	Jennifer Possley and Eric Francius	948	24 Feb 2012
France	Domaine Duclos	parking lot of GUAD	16.20397	-61.66062	B.J.	Sidoti	Jennifer Possley and Eric Francius	949	24 Feb 2012
USA	St. John	on rock outcrop, near Upper Rendezuous area	18.32325	-64.76983	B.J.	Sidoti	Jay Handelman and Gary Ray	1189	18 Dec 2012
USA	St. John	on rock outcrop, near L'Esperance Trail, Virgin Islands National Park	18.34212	-64.75985	B.J.	Sidoti	Jay Handelman and Gary Ray	1196	18 Dec 2012

USA	St. Thomas	on rock outcrop along ?? Gut, near arts center? Of the University of Virgin Islands	18.34837	-64.97692	B.J.	Sidoti	Jay Handelman	1203	20 Dec 2012	