

## Taxon-specific or universal? Using target capture to study the evolutionary history of rapid radiations

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1            *Abstract* - Target capture has emerged as an important tool for phylogenetics and  
2 population genetics in non-model taxa. Whereas developing taxon-specific capture probes  
3 requires sustained efforts, available universal kits may have a lower power to reconstruct  
4 relationships at shallow phylogenetic scales and within rapidly radiating clades. We present  
5 here a newly-developed target capture set for Bromeliaceae, a large and ecologically-diverse  
6 plant family with highly variable diversification rates. The set targets 1,776 coding regions,  
7 including genes putatively involved in key innovations, with the aim to empower testing of a  
8 wide range of evolutionary hypotheses. We compare the relative power of this taxon-specific  
9 set, Bromeliad1776, to the universal Angiosperms353 kit. The taxon-specific set results in  
10 higher enrichment success across the entire family, however, the overall performance of both  
11 kits to reconstruct phylogenetic trees is relatively comparable, highlighting the vast potential  
12 of universal kits for resolving evolutionary relationships. For more detailed phylogenetic or  
13 population genetic analyses, e.g. the exploration of gene tree concordance, nucleotide di-  
14 versity or population structure, the taxon-specific capture set presents clear benefits. We  
15 discuss the potential lessons that this comparative study provides for future phylogenetic  
16 and population genetic investigations, in particular for the study of evolutionary radiations.

17

18 **Keywords**— target capture, plant radiation, Bromeliaceae, *Tillandsia*, population structure, phy-  
19 logenomics

## 20 **1 Introduction**

21            Targeted sequencing approaches have emerged as a promising tool for studying evolutionary  
22 relationships in non-model taxa, enabling researchers to retrieve large data sets while requiring few  
23 genomic resources (Bossert & Danforth, 2018; Escudero, Nieto-Feliner, Pokorny, Spalink, & Viruel,  
24 2020; McDonnell et al., 2021; Soto-Gomez et al., 2019). Using custom baits, the method largely  
25 retrieves the same loci across a wide taxonomic scale, obtains comparable and mergeable data sets,  
26 and may be combined with genome-skimming (E. M. Lemmon & Lemmon, 2013; Weitemier et al.,

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27 2014). Pre-existing knowledge of the targeted loci further provides opportunities to address specific  
28 questions on both deep and shallow timescales (Hale, Gardner, Viruel, Pokorny, & Johnson, 2020;  
29 A. R. Lemmon, Emme, & Lemmon, 2012). Finally, the method does not necessarily require a refer-  
30 ence genome, is highly cost-effective, and with the ability to sequence herbarium samples, reduces  
31 the need for extensive sampling campaigns (Blaimer, Lloyd, Guillory, & Brady 2016; Hale et al.  
32 2020; Weitemier et al., 2014). Target capture has been successfully applied to resolve phylogenies  
33 in diverse groups, from arthropods such as bees (*Xylocopa*, Blaimer et al., 2016; Apidae, Bossert  
34 et al., 2019) and Araneae (Hexathelidae, Hedin, Derkarabetian, Ramírez, Vink, & Bond, 2018) to  
35 mammals (Cetacea, McGowen et al., 2020), and in numerous plant groups (*Heuchera*, Folk, Mandel,  
36 & Freudenstein, 2015; Gesneriaceae, Ogutcen et al., 2021; Zingiberales, Sass, Iles, Barrett, Smith,  
37 & Specht, 2016 to name a few). The method’s utility for studies at micro-evolutionary scales has  
38 been to date marginally explored, but several studies have pointed to the ability to analyze genomic  
39 diversity and estimate population genomic parameters (Choquet et al., 2019; Christmas, Biffin,  
40 Breed, & Lowe, 2017; de La Harpe et al., 2019; Derrien & Ramos-Onsins, 2020; Sanderson, DiFazio,  
41 Cronk, Ma, & Olson, 2020). Nonetheless, the development of probes for target enrichment may  
42 pose several challenges: first, the need to identify regions conserved enough to ensure recovery,  
43 yet polymorphic enough to provide ample information (Soto-Gomez et al., 2019; Villaverde et al.,  
44 2018). Second, probe design requires detecting regions without pervasive copy number polymor-  
45 phism (Kadlec, Bellstedt, Maitre, & Pirie, 2017; A. R. Lemmon et al., 2012), a particular challenge  
46 for angiosperms and other groups, where duplication events are ubiquitous (Van de Peer, Mizrachi,  
47 & Marchal, 2017).

48 In contrast, universal kits offer an attractive alternative that require reduced efforts to estab-  
49 lish, and provide comparable data sets across wider ranges of taxa (Johnson et al., 2019; Kadlec et  
50 al., 2017). Such kits were designed to retrieve single-copy markers, for example, in the broad scope  
51 of amphibians (Hime et al., 2021), anthozoans (Quattrini et al., 2018), vertebrates (A. R. Lemmon  
52 et al., 2012) or angiosperms (Johnson et al., 2019). In the latter example, the Angiosperms353 kit  
53 is designed to target 353 single-copy genes across angiosperms. So far the kit has been employed  
54 successfully in resolving phylogenies, including but not limited to *Nepenthes* (Murphy et al., 2020),

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55 *Schefflera* (Shee, Frodin, Cámara-Leret, & Pokorny, 2020) and the rapid radiations of *Burmeistera*  
56 (Bagley, Uribe-Convers, Carlsen, & Muchhala, 2020) and *Veronica* (Thomas et al., 2021), estab-  
57 lishing the kit as an eminent tool in macroevolutionary research. Its utility at microevolutionary  
58 levels is yet to be fully realized, although several works have established its suitability to deliver  
59 informative signals at a lower taxonomic level (Beck et al., 2021) and in acquiring population ge-  
60 nomics parameters (Slimp, Williams, Hale, & Johnson, 2021). The use of highly-conserved markers  
61 in a universal kit may, however, limit resolution power. Generally, taxon-specific baits are expected  
62 to deliver a higher information content and hence more accurate results (Kadlec et al., 2017), as  
63 enrichment success is known to drop with the level of divergence between sequences used for probe  
64 design and the targeted taxa (Liu et al., 2019). However, one study comparing the power of the  
65 universal Angiosperms353 kit and a taxon-specific kit to resolve phylogenomic relationship in Cyper-  
66 aceae reported surprisingly similar performance (Larridon et al., 2020) and similar findings were  
67 reported in Malinae (Ufimov et al., 2021) and in Ochnaceae (Shah et al., 2021). It remains to be  
68 established whether these findings apply to other taxa and other evolutionary scales, including at  
69 population level, where ample genomic variability is required to resolve intra-specific relationships  
70 and investigate patterns of genetic differentiation.

71       Until recently, the technology available to investigate evolutionary questions in rapidly evol-  
72 ving groups featuring high net diversification rates has presented major obstacles, in particular for  
73 non-model groups. Decreasing costs of sequencing coupled with an ever-growing plethora of bioin-  
74 formatic tools for data processing and downstream analysis has led to an increase in the use of  
75 methods like whole-genome sequencing, RNA sequencing and restriction site associated DNA se-  
76 quencing (RAD-Seq) in lieu of traditional methods employing few conserved markers (de La Harpe  
77 et al., 2017; McKain, Johnson, Uribe-Convers, Eaton, & Yang, 2018; Weitemier et al., 2014; Zimmer  
78 & Wen, 2013). Whole-genome sequencing however remains costly, posing barriers for research tar-  
79 geting large numbers of samples, organisms with large genomes and non-model organisms, for which  
80 the availability of high-quality genomic resources is often limited (Hollingsworth, Li, van der Bank,  
81 & Twyford, 2016; Supple & Shapiro, 2018). While RAD-seq is an affordable alternative and widely  
82 used in population genetics, the resulting data sets may fall short when screened for homologous

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83 sequences across distantly related lineages (but see e.g., Heckenhauer, Samuel, Ashton, Abu Salim,  
84 & Paun, 2018). Additionally, RAD-seq is less feasible when using degraded DNA from herbarium  
85 samples, and the use of short and inconsistently-represented loci across phylogenetic sampling may  
86 result in low information content and difficulties in assessing paralogy (E. M. Lemmon & Lemmon,  
87 2013; McKain et al., 2018; Jones & Good, 2016).

88 Rapid evolutionary radiations are key stages in the evolutionary history across the Tree of  
89 Life and highly recurrent, hence an essential part of biodiversity research (Gavrilets & Losos, 2009;  
90 Givnish et al., 2014; Hughes, Nyffeler, & Linder, 2015; Soltis, Folk, & Soltis, 2019; Soltis & Soltis,  
91 2004). Fast evolving groups provide potent opportunities to investigate important questions in  
92 evolutionary biology, such as the interplay between ecological and evolutionary processes in shaping  
93 biodiversity. A few notable study systems are the cichlid fish (McGee et al., 2020; Salzburger, 2018),  
94 *Heliconius* butterflies (Dasmahapatra et al., 2012; Moest et al., 2020), *Anolis* lizards (McGlothlin  
95 et al., 2018; Stroud & Losos, 2020), Darwin’s finches (Lamichhaney et al., 2015; Zink & Vázquez-  
96 Miranda, 2019), white-eyes birds (Moyle, Filardi, Smith, & Diamond, 2009) and New World lupins  
97 (Nevado, Atchison, Hughes, & Filatov, 2016). Nevertheless, much remains unknown about the  
98 genomic basis underlying species diversification outside these intensively studied systems.

99 Research of rapidly diversifying lineages presents several challenges. First, a brief diversi-  
100 fication period typically leads to imperfect reproductive barriers and incomplete lineage sorting,  
101 reflected in significant gene tree discordance and ambiguous relationships (Degnan & Rosenberg,  
102 2009; Lamichhaney et al., 2015; Pease, Haak, Hahn, & Moyle, 2016; Straub et al., 2014). In addition,  
103 understanding ‘speciation through time’ poses a methodological challenge, and requires connecting  
104 two conceptual worlds: macroevolutionary investigations, concerned with spatial and ecological pat-  
105 terns over deeper timescales, and microevolutionary approaches, providing insight into the processes  
106 acting during population divergence and speciation (Bragg, Potter, Bi, & Moritz, 2016; de La Harpe  
107 et al., 2017). Resolving phylogenomic relationships and disentangling the contribution of different  
108 genomic processes through time typically requires large-scale genomic datasets and thorough taxon  
109 sampling efforts (E. M. Lemmon & Lemmon, 2013; Linder, 2008; Straub et al., 2012).

110 Here, we present Bromeliad1776, a new bait set for targeted sequencing, designed to address

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111 a wide range of evolutionary hypotheses in Bromeliaceae: from producing robust phylogenies to  
112 studying the interplay of genomic processes during speciation and the genetic basis of trait shifts,  
113 such as photosynthetic and pollination syndrome. This highly diverse Neotropical radiation provides  
114 an excellent research system for studying the drivers and constraints of rapid adaptive radiation  
115 (Benzing, 2000; Givnish et al., 2011; Loiseau et al., 2021; Mota et al., 2020; Palma-Silva & Fay, 2020;  
116 Wöhrmann, Michalak, Zizka, & Weising, 2020). Bromeliaceae as a whole is considered an adaptive  
117 radiation (Benzing, 2000; Givnish et al., 2011) and contains several rapidly radiating lineages, most  
118 notably within Bromelioideae (Aguirre-Santoro, Salinas, & Michelangeli, 2020) and Tillandsioideae  
119 (Loiseau et al., 2021). It is a species-rich and charismatic monocot family, consisting of over 3,000  
120 species, including crops in the genus *Ananas* and other economically important species (Luther,  
121 2008). Members of the family are characterized by a distinctive leaf rosette that often impounds  
122 rainwater in central tanks (phytotelmata). A diversity of arthropods and other animal species  
123 and microbes reside in bromeliad tanks, in some cases even leading to protocarnivory and other  
124 forms of nutrient acquisition (Givnish, Burkhardt, Happel, & Weintraub, 1984; C. Leroy, Carrias,  
125 Céréghino, & Corbara, 2016). Bromeliads present a diversity of repeatedly evolving adaptive traits,  
126 which allowed them to occupy versatile habitats and ecological niches (Benzing, 2000). CAM  
127 photosynthesis, water-absorbing trichomes, formation of tank habit, extensive rates of epiphytism  
128 and a diversity of pollination syndromes are some of the adaptations correlated with high rates  
129 of diversification within the family (Benzing, 2000; Crayn, Winter, & Smith, 2004; Givnish et al.,  
130 2014; Kessler, Abrahamczyk, & Krömer, 2020; Quezada & Gianoli, 2011).

131 To assess the utility of the Bromeliad1776 kit, we performed a comparison between our taxon-  
132 specific kit and the universal Angiosperms353 kit using several methods across different evolutionary  
133 time-scales. We present Bromeliad1776 in the light of methodological considerations on bait design,  
134 data handling, analyses and other practical considerations.

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## 135 2 Materials and Methods

### 136 2.1 Custom bait design

137 Whole-genome sequences and gene models from *Ananas comosus* v.3 (Ming et al., 2015)  
138 were used to design a bait set aiming to target i) single-copy protein coding genes distributed  
139 across the whole genome, ii) genes previously described as associated with key innovation traits in  
140 Bromeliaceae (see below), iii) markers previously used for phylogenomic inference in Bromeliaceae  
141 and iv) genes orthologous to those in the Angiosperms353 bait set. The 1776 selected genes are  
142 detailed in Supporting information Table S1.

143 Genes in subset *i* were selected based on genetic diversity parameters calculated using whole-  
144 genome sequence and RNAseq data previously published by de La Harpe et al., (2020; data publicly  
145 available online at SRA Bioproject PRJNA649109) with the PopGenome R package v.2.1.6 (Pfeifer,  
146 Wittelsbürger, Ramos-Onsins, & Lercher, 2014). Genomic regions were retained in this category  
147 if they shared at least 70% identity between *A. comosus* and *T. sphaerocephala*, and if they had  
148 nucleotide diversity ( $\pi$ ) values not exceeding the 90% quantile of the ( $\pi$ ) distribution across genes  
149 for four *Tillandsia* species (*Tillandsia australis*, *Tillandsia fasciculata*, *Tillandsia floribunda* and  
150 *T. sphaerocephala*; data and analysis performed by de La Harpe et al. (2020). We further excluded  
151 genes with a total exonic size smaller than 1,100 bp, or individual exons smaller than 120 bp.  
152 Next, copy-number variation was calculated based on clustering of *A. comosus* and *Tillandsia*  
153 transcriptome assemblies to generate three copy number categories - "single copy", "low copy" (i.e.,  
154 less than five copies) and "high copy" (i.e., five or more copies). We included only single-copy genes  
155 in the design for bait subset *i*. Finally, we excluded genes that were located in genomic regions  
156 outside those assigned to linkage groups in the *A. comosus* reference (Ming et al., 2015). A total of  
157 1,243 genes were identified for this part.

158 The bait subset of genes associated with key innovative traits in Bromeliaceae (subset *ii*  
159 above) included (1) genes putatively under positive selection along branches relevant to C3/CAM  
160 shifts (de La Harpe et al., 2020), (2) genes that exhibit differential gene expression between CAM



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161 and C3 *Tillandsia* species (de La Harpe et al., 2020) and (3) genes putatively associated with pho-  
162 tosynthetic and developmental functions, or with flavonoid and anthocyanin biosynthesis, according  
163 to the literature (e.g. Ming et al., 2015; Palma-Silva, Ferro, Bacci, & Turchetto-Zolet, 2016; Wai et  
164 al., 2017; Goolsby, Moore, Hancock, Vos, & Edwards, 2018). *Ananas comosus* genes with the high-  
165 est match scores (calculated as lowest E-score in BLASTP, Madden (2013) against the sequences  
166 of genes from the literature were added to the bait set (see Supporting information Table S2 for  
167 details). A total of 1,612 genes underpinning innovative traits were included in the bait design,  
168 regardless of criteria used for subset *i* for size, similarity and duplication rate.

169 Markers previously used for phylogenomic inference in Bromeliaceae (subset *iii*) were ob-  
170 tained from the literature, spanning 13 genes (e.g. Barfuss et al., 2016; Machado et al., 2020;  
171 Schulte, Barfuss, & Zizka, 2009, see TS2 for full list). Genes orthologous to those in the An-  
172 giosperms353 bait set (Johnson et al., 2019) were identified using the orthologous gene models from  
173 *A. comosus* based on gene annotations (Ming et al., 2015) or using BLASTP (Madden, 2013),  
174 totalling 281 genes.

175 Finally, we used a draft genome of *T. fasciculata* (Jaqueline Hess, personal communication)  
176 to exclude from all candidates genes that exhibited multiple BLASTN hits, if they have not been  
177 previously described as duplicated within the genus (de La Harpe et al., 2020). Specifically, we  
178 excluded genes that matched another genomic sequence of at least 100bp with high similarity  
179 score ( $> 80\%$ ) and low E-value ( $< 10^{-5}$ ). In an additional round of filtering performed by the  
180 manufacturer of the final bait set, Arbor Biosciences (Ann Arbor, MI, USA), multi-copy genes with  
181 sequences that are more than 95% identical were collapsed into a single sequence and baits with more  
182 than 70% GC content or containing at least 25% repeated sequences were excluded. In addition,  
183 targets including exons smaller than 80 bp were completed with regions flanking the exons according  
184 to the *A. comosus* reference genome. The final kit included 1776 genes: 801 genes in subset *i*, 681  
185 genes associated with key innovative traits, 13 genes representing phylogenetic markers and 281  
186 genes orthologous to the Angiosperms353 set. Probes were designed with 57,445 80-mer baits tiling  
187 across targets in 2x coverage, targeting approximately 2.3Mbp. The kit is subsequently referred  
188 to as the Bromeliad1776 bait set. Further specifications can be found in Supporting information



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189 Tables S1 and S2 and in the github repository: [https://github.com/giyany/Bromeliad1776/tree/](https://github.com/giyany/Bromeliad1776/tree/main/MS_2021_scripts)  
190 [main/MS\\_2021\\_scripts](https://github.com/giyany/Bromeliad1776/tree/main/MS_2021_scripts).

## 191 **2.2 Plant material collection**

192 We sampled a total of 70/72 Bromeliaceae samples (for Angiosperms353 and for Bromeliad1776,  
193 accordingly; Supporting information Table S3), including 56 accessions from the Tillandsioideae sub-  
194 family and 16 representing the other subfamilies, except Navioideae. The divergence time between  
195 Tillandsioideae and subfamily Bromelioideae to which *A. comosus* belongs is estimated at 15Mya  
196 (according to Givnish et al. 2014). Within Tillandsioideae, we sampled 38/40 individuals from  
197 five species of the *Tillandsia* subgenus *Tillandsia* ('clade K' in Barfuss et al. (2016); Sampling in  
198 Mexican populations illustrated in Supporting information Figure S1).

## 199 **2.3 Library preparation & enrichment**

200 DNA extractions were performed using a modified CTAB protocol (Doyle & Doyle, 1987),  
201 purified using Nucleospin® gDNA cleanup kit from Macherey-Nagel (Hudlow et al., 2011) follow-  
202 ing the supplier's instructions with a two-fold elution step and finally quantified with Qubit® 3.0  
203 Fluorometer (Life Technologies, Ledeberg, Belgium).

204 For each sample, 200ng DNA was sheared using Bioruptor® Pico sonication device (Diagen-  
205 ode, Seraing, Belgium) aiming for an average insert size of 350bp, dried in a speed vacuum Eppen-  
206 dorf concentrator 5301 (Eppendorf, Germany) and eluted in 30 L ddH<sub>2</sub>O. Genomic libraries were  
207 prepared using the NEBNext® Ultra TM II DNA Library Prep Kit for Illumina® (New England  
208 Biolabs, Ipswich, MA, United States) using reagents at half volumes following Hale et al. (2020)  
209 and using 11 PCR cycles, increased up to 13 cycled for libraries with low genomic output. Sam-  
210 ples were double-indexed with NEBNext® Multiplex Oligos for Illumina® (New England Biolabs,  
211 Ipswich, MA, USA). Fragment sizes were inspected with Agilent Bioanalyzer (Agilent Technologies,  
212 Santa Clara, CA, USA) and concentrations were measured with Qubit® 3.0 Fluorometer. Subpools  
213 of 11-14 equimolar genomic libraries were prepared using phylogenetic proximity and DNA concen-

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214 trations of the genomic libraries, which ranged from 2.62 to 118.0 ng/ L, following Soto-Gomez et  
215 al. (2019).

216 We used the Angiosperms353 and the Bromeliad1776 bait sets from Arbor Biosciences (Ann  
217 Arbor, MI, USA) to enrich each subpool of genomic libraries independently with a single hybridiza-  
218 tion reaction of myBaits<sup>®</sup> target capture kits from Arbor Biosciences (Ann Arbor, MI, USA),  
219 following Hale et al. (2020). Average fragment size and DNA yield were estimated for each subpool  
220 using Agilent Bioanalyzer and Qubit<sup>®</sup> 3.0 Fluorometer. Subpools were then pooled in equimo-  
221 lar conditions and sequenced at Vienna BioCenter Core Facilities (Vienna, Austria) on Illumina<sup>®</sup>  
222 NextSeq<sup>™</sup> 550 (2x150bp, Illumina, San Diego, CA). Sequencing was conducted independently for  
223 either bait kit.

## 224 **2.4 Data processing**

225 The raw sequence data in BAM format was demultiplexed using deML v.1.1.3 (Renaud,  
226 Stenzel, Maricic, Wiebe, & Kelso, 2015) and samtools view v.1.7 (Li et al., 2009), converted to  
227 fastq using bamtools v.2.4.0 (Barnett, Garrison, Quinlan, Strömberg, & Marth, 2011) and quality  
228 checked using FastQC v.0.11.7 (Andrews, 2010). Reads were then trimmed for adapter content and  
229 quality using TrimGalore v.0.6.5 (Krueger, 2019), a wrapper tool around FastQC and Cutadapt,  
230 using settings `-fastqc -retain unpaired`. Sequence quality and adapter removal was confirmed with  
231 FastQC reports.

232 Quality and adapter-trimmed reads were aligned to *A. comosus* reference genome v.3 (Ming  
233 et al., 2015) using bowtie2 (Langmead & Salzberg, 2012) with the `-very-sensitive-local` option to  
234 increase sensitivity and accuracy. Samtools (Li et al., 2009) was then used to remove low quality  
235 mapping and sort alignments by position, and PCR duplicates were marked using MarkDupli-  
236 cates from PicardTools v.2.25 (*Picard Toolkit*, 2019). Summary statistics of the mapping step  
237 were generated using samtools stats. Variants were called using freebayes v1.3.2-dirty (Garrison  
238 & Marth, 2012) and sites marked as MNP/complex were decomposed and normalized using the  
239 script ‘vcfallelicprimitives’ from vcflib (Garrison, 2012). Next, AN/AC field was calculated using  
240 bcftools v.1.7 (Li, 2011) and variant calls were filtered using vcflib (Garrison & Marth, 2012) and

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241 bcftools. Given that freebayes does not perform automatic variant filtering steps, we identified  
242 sets of parameters that generate reliable final SNP sets, based on two independent criteria: the  
243 highest transition/transversion ratios as reported by SnpSift (SnpEff suite, Cingolani et al., 2012)  
244 and the lowest  $\pi_N/\pi_S$  (see section 2.7 below). After a detailed evaluation, we used the following  
245 criteria to generate two high quality SNP sets, one for each bait-set: we considered genotype calls  
246 with per-sample coverage below  $10\times$  as missing (NA) and excluded variants (i) marked as indels  
247 or neighboring indels within a distance of 3 bp, (ii) with depth of coverage at the SNP level lower  
248 than  $500\times$ , (iii) with less than ten reads supporting the alternate allele at the SNP level, or (iv)  
249 with more than 40% missing data. All genes in the Bromeliad1776 that passed the filtering criteria  
250 were included in the SNP set, regardless of their function. Summary statistics of the final SNP sets  
251 were generated using the script `vcf2genocountsmatrix.py`, namely the total number of SNPs, the  
252 proportion of on-target SNPs and the proportion of SNPs in some specific genomic contexts, with  
253 *A. comosus* genome v.3 as a reference. The full data processing script `align_and_trim.sh` and the  
254 `vcf2genocountsmatrix.py` script are both available at <https://github.com/giyany/Bromeliad1776>.

## 255 **2.5 Bait specificity and efficiency**

256 To explore bait specificity, we calculated the percentage of high quality trimmed reads on-  
257 target using samtools stats and bedtools intersect v2.25.0 (Quinlan & Hall, 2010) using the script `cal-`  
258 `culat_bait_target_specifity.sh` (available from <https://github.com/giyany/Bromeliad1776>). Tar-  
259 gets for Bromeliad1776 were defined as the bait sequences plus their 500 bp flanking regions. Targets  
260 for Angiosperms353 were defined using orthogroups to *A. comosus*: gene annotations from the bait  
261 set were used to assign genes to orthogroups using OrthoFinder (Emms & Kelly, 2019). When  
262 several orthogroups were found for a single Angiosperms353 gene, we included all, resulting in 559  
263 *A. comosus* genes assigned to orthogroups. Within the orthogroups, targets were again defined as  
264 exonic regions plus their 500 bp flanking regions.

265 To provide insights into determinants of bait capture success, we calculated bait efficiency for  
266 all baits of Bromeliad1776. For each bait, efficiency was calculated as the number of high-quality  
267 reads uniquely mapping to each bait target region, averaged over samples. We then tested for the

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268 correlation of capture efficiency to several bait characteristics (copy number, GC content, number  
269 and size of exons in targeted gene, size of baits and phylogenetic distance to *A. comosus*) with a  
270 generalized linear model or Kruskal-Wallis test in R v.4.0.3 (R Core Team, 2020) using a negative  
271 binomial family.

## 272 **2.6 Phylogenomic analyses**

273 We inferred phylogenomic relationships for all samples using two methods: a concatenation  
274 method, and a coalescent-based species tree estimation. The latter method was included as con-  
275 catenation methods do not account for gene tree incongruence, which may result in high support for  
276 an incorrect topology (Kubatko & Degnan, 2007), especially in the presence of notable incomplete  
277 lineage sorting. In addition, gene tree incongruence analysis provides insight into molecular genome  
278 evolution, including the extent of incomplete lineage sorting and other genomic processes such as  
279 hybridization and introgression (Galtier & Daubin, 2008; Wendel & Doyle, 1998).

280 We used the the variant and non-variant genotypes to create a phylip matrix with vcf2phylip  
281 v.2.0 (Ortiz, 2019) and constructed a maximum-likelihood species tree for each bait set with  
282 RAxML-NG v.0.9.0 (Kozlov, Darriba, Flouri, Morel, & Stamatakis, 2019), using 250 bootstrap  
283 replicates and a GTR model with an automatic MRE-based bootstrap convergence test. Next, we  
284 constructed a species tree using ASTRAL-III v.5.7.7 (hereafter: ASTRAL, Zhang, Rabiee, Sayyari,  
285 & Mirarab, 2018). For both the Angiosperms353 and the Bromeliad1776 sets, we separated the  
286 matrix into independent genomic windows, defining each window as a gene according to the known  
287 exons and a 500bp flanking region. For Angiosperms353, we extracted the 559 genes (assigned to  
288 orthogroups as explained above) as genomic windows using bedtools intersect. For Bromeliad1776,  
289 genomic windows were extracted using the *A. comosus* gene sequences included in bait design. All  
290 loci and all accessions were included in species tree inference regardless of the percentage of missing  
291 data, since taxon completeness of individual gene trees is important for statistical consistency of  
292 this approach, and we expected only low levels of fragmentary sequences (Mirarab, 2019; Nute,  
293 Chou, Molloy, & Warnow, 2018). After excluding genes with zero coverage, 269 genes and 1,600  
294 genes were included in species tree inference for Angiosperms353 and Bromeliad1776, respectively.

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295 For each gene, a maximum-likelihood gene tree was inferred using ParGenes (Morel, Kozlov,  
296 & Stamatakis, 2019) with RAxML-NG (Kozlov et al., 2019), using a GTR model with an automatic  
297 MRE-based bootstrap convergence test. Loci with insufficient signal may reduce the accuracy of  
298 species tree estimation (Mirarab, 2019), hence, in all gene trees, nodes with a bootstrap support  
299 smaller than ten were collapsed using Newick utilities (Junier & Zdobnov, 2010). A species tree was  
300 then generated in ASTRAL with quartet support and posterior probability for each tree topology.  
301 The number of conflicting gene trees was calculated using phyparts and visualized using the script  
302 phypartspiecharts.py (available from <https://github.com/mossmatters/MJPythonNotebooks>).

## 303 **2.7 Population structure and nucleotide diversity estimates**

304 To explore the genetic structure within the *Tillandsia* species complex, we focused on five  
305 species from 15 localities (Supporting information Table S3 and Supporting information Figure  
306 S1). We first used plink v.1.9 (Chang et al., 2015) to filter out SNPs in linkage disequilibrium.  
307 Population structure was further explored through individual ancestry analysis, with identity-by-  
308 descent matrix calculated by plink and inference of population structure using ADMIXTURE v.1.3.  
309 with K values ranging from one to ten, and 30 replicates for each K, using a block optimization  
310 method (Alexander & Lange, 2011). A summary of the ADMIXTURE results was obtained and  
311 presented using pong (Behr, Liu, Liu-Fang, Nakka, & Ramachandran, 2016). The set of LD-pruned  
312 biallelic SNPs was further filtered to allow a maximum of 10% missing data and used to perform  
313 a principal components analysis (PCA) with SNPRelate v.1.20.1 (Zheng et al., 2012). Finally, for  
314 each *Tillandsia* species, we used the strategy of T. Leroy et al. (2021) to compute synonymous  
315 ( $\pi_S$ ) and non-synonymous ( $\pi_N$ ) nucleotide diversities and Tajima's D, from fasta sequences using  
316 seq\_stat\_coding (T. Leroy et al., 2021).

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### 3 Results

#### 3.1 Higher mapping rates and capture efficiency for taxon-specific set

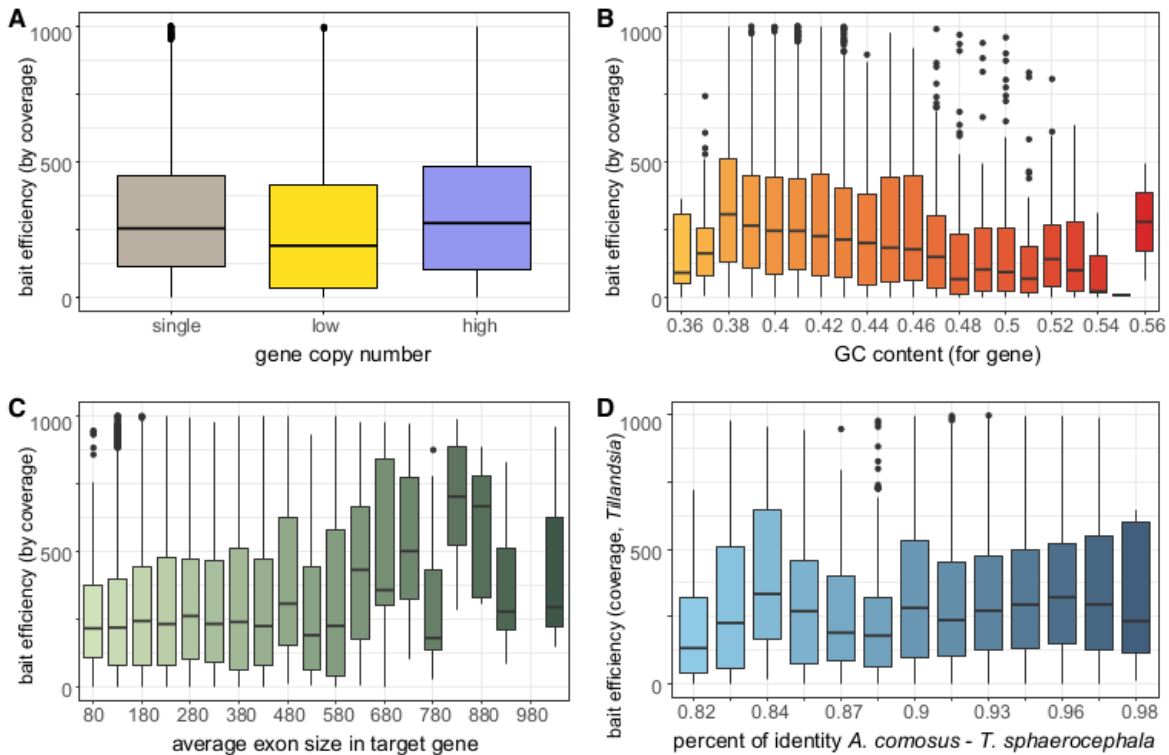
On average, 4,401,958 (803,464-12,693,516) paired-end reads per accession were generated per Angiosperms353 library and 2,962,023 (1,282,762-6,298,880) per Bromeliad1776 library. Overall, the mapping rates to the *A. comosus* reference genome were higher for libraries enriched with Bromeliad1776, with an average mapping rate of 82.3% (61.8%-95.9%) and 42.8% (22.1%-77.9%), for Bromeliad1776 and Angiosperms353, respectively (Supporting information Figure S2, Supporting information Table S4). Higher mapping rates were recorded for subfamilies Bromelioideae and Puyoideae, as compared to Tillandsioideae, for both the Angiosperms353 and Bromeliad1776 sets (see Supporting information Figures S3 and S4, respectively). This may reflect the effect of reference bias, and in the case of Bromeliad1776, it may be further amplified by our kit design based on *A. comosus* (subfamily Bromelioideae). Bait specificity was high for Bromeliad1776 with on average 90.4% reads on-target (76.5%-94.2%), while for Angiosperms353 bait specificity was 14.0% (4.6%-30.1%; see Supporting information Figure S2). Mapping rates and bait specificity were positively correlated for both bait sets (GLM,  $P < 0.01$ ).

#### 3.2 Bait efficiency depends on the genomic context

We investigated factors that may influence bait efficiency, starting with the contribution of gene copy number variation. We assumed three categories regarding the number of paralogs per orthogroup: single copy, low-copy (i.e., less than five copies) and high-copy (i.e., five or more copies). The number of gene copies had a significant effect on bait efficiency and post-hoc Dunn's test supported significant differences in efficiency for comparisons between low-copy and high-copy, and between single-copy and low-copy ( $P = 2.8^{-44}$ ). Low-copy genes exhibit the lowest enrichment success, suggesting that the bait efficiency is not simply correlated to the number of gene copies (Figure 1). We also recovered a significant effect of the intragenic GC content and GC content of the baits on bait efficiency (GLM,  $P = 1.5^{-68}$ ). Finally, we investigated the possible link between

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342 efficiency and gene structure. Average exon sizes ( $P < 2.0 \times 10^{-16}$ ) and total number of exons per gene  
343 ( $P = 1.1 \times 10^{-89}$ ) were also positively correlated with enrichment success. The size of the smallest exon for  
344 all targeted genes was however not correlated with bait efficiency. Sequence similarity, measured as  
345 percent of identity between *Tillandsia* sequences and those of *A. comosus*, was positively correlated  
346 with capture success ( $P = 4.8 \times 10^{-13}$ ; Figure 1).



347

348 **Figure 1** Effects of (A) putative gene copy number, (B) gene GC content, (C) average exon size,  
349 and (D) percent of identity on bait efficiency in Bromeliad1776 bait set, measured as the number of  
350 high-quality reads uniquely mapping to bait target region across samples. Continuous variable was  
351 binned and y-values higher than 1,000 excluded for visualization in B-D.

### 352 3.3 Both kits provided a large number of SNPs

353 After variant calling and filtering, we identified 47,390 and 209,186 high-quality SNPs for  
354 the Angiosperms353 and the Bromeliad1776 bait sets, respectively. On average, missing data  
355 represented 23.7% of genotype calls per individual in Angiosperms353, but only 6.3% for the



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356 Bromeliad1776 kit. The differences in amount of missing data are likely associated with the  
357 higher mean depth per site across the Bromeliad1776 kit (6,602), as compared to Angiosperms353  
358 (3,437). Focusing on the subgenus *Tillandsia*, we identified 15,622 SNPs for Angiosperms353  
359 (including a total of 18.9% missing data) compared to 65,473 polymorphic sites (2.9% missing  
360 data) for Bromeliad1776. In both full data sets and the subset including only *Tillandsia* sam-  
361 ples, Bromeliad1776 recovered more variants in intronic regions compared with Angiosperms353.  
362 Angiosperms353 recovered a large proportion of off-target SNPs, whereas in Bromeliad1776 approx-  
363 imately 15% of the SNPs were recovered from flanking regions (Table 1). We discuss ascertainment  
364 bias that may rise due to the non-random selection of markers in the supporting information.

### 365 **3.4 Similar phylogenomic resolution in concatenation method, Bromeliad1776** 366 **outperforms Angiosperms353 for species tree reconstruction**

367 The Angiosperms353 and Bromeliad1776-based maximum-likelihood phylogenetic trees re-  
368 covered the same backbone phylogeny of Bromeliaceae, clustering subfamily Tillandsioideae and  
369 the subgenus *Tillandsia* with high bootstrap values (Supporting information Figure S5). Neither  
370 set obtained high support for inter-population structure for *Tillandsia gymnobotrya*, but highly-  
371 supported nodes separated *T. fasciculata* accessions from Mexico and from other locations, and  
372 the populations of *T. punctulata* for the Bromeliad1776 data set were similarly separated. The  
373 tree topologies were identical, with the notable exception of the placements of *Tillandsia biflora* and  
374 *Racinaea ropalocarpa* and the genus *Deuterocohnia* (Supporting information Figure S5, purple ar-  
375 row). Overall, internal nodes are strongly supported for both sets, except for *Hechtia carlsoniae* as  
376 sister to Tillandsioideae, which is poorly supported for both sets. While several internal nodes are  
377 slightly less supported for the Angiosperms353 set, overall these results demonstrate the efficacy of  
378 both kits in phylogenomic reconstruction using concatenation approaches, indicating that as few as  
379 47k SNPs within variable regions provide reliable information to resolve phylogenetic relationships  
380 within the recent evolutionary radiation of *Tillandsia*.

381 Species trees as inferred with ASTRAL for both data sets likewise provided an overall strong  
382 local posterior support (Figure 2, see also Supporting information). Several nodes however exhibit

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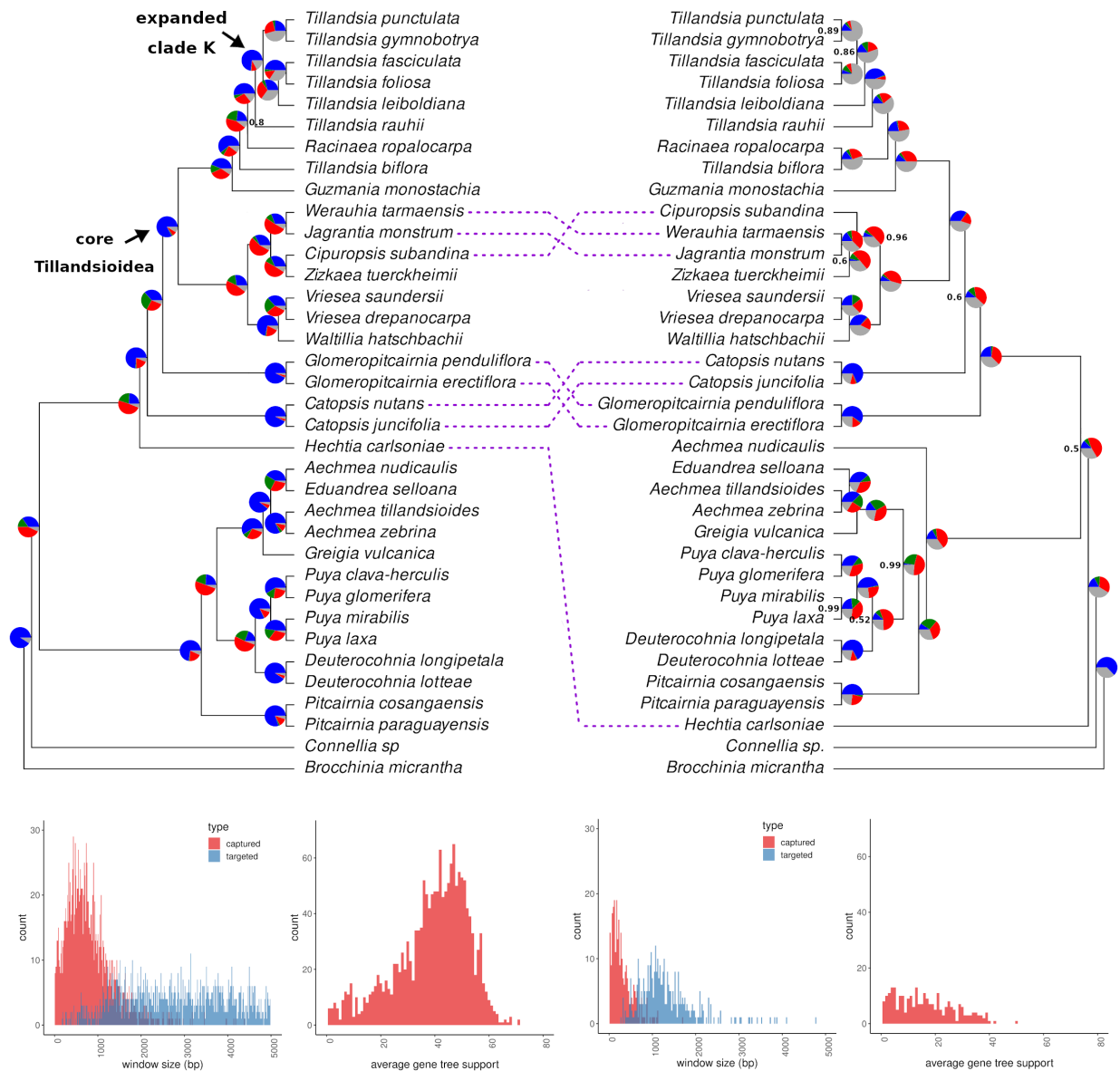
383 lower local posterior support values for the Angiosperms353 tree than for the Bromeliad1776 tree.  
384 The topology for the Bromeliad1776 ASTRAL tree was similar to the ML tree, but differed again by  
385 placing *Deuterocohnia* as sister taxa to *Puyoideae* only. In the Angiosperms353 tree, the topology  
386 differed from both ML trees and the ASTRAL Bromeliad1776 tree in several nodes. *H. carlsoniae*  
387 was placed as a sister taxa to all other subfamilies in the Angiosperm353 phylogeny. Notably,  
388 the placement of *Catopsis* and *Glomeropitcrania* differed, as well as the placement of *Cipurosis*  
389 *subandinai*, *T. biflora* and *R. ropalocarpa*. Several internal nodes were poorly supported, such  
390 as the node separating the tribe Catopsidae and core Tillandsioideae, and the nodes separating  
391 Tillandsioideae from all other subfamilies. The differences in topology between the Angiosperms353  
392 ASTRAL tree to all other trees (ML trees and Bromeliad1776 ASTRAL tree) together with the  
393 low posterior support suggest lower resolution power and a poor fit of this data set for resolving a  
394 species tree.

395 The length and average size of the input gene trees different among sets, with average window  
396 length of 304.6 bp and 819.9 bp and average gene tree support of 16.9 and 38.9 for Angiosperms353  
397 and Bromeliad1776 bait-sets, respectively (Figure 2). An examination of gene tree concordance  
398 constructed with Bromeliad1776 data set allowed us to identify variable levels of gene tree conflict  
399 among nodes (Figure 2). Gene tree discordance was especially high for the split between Tilland-  
400 sioideae and other subfamilies, as well as for the split between Puyoideae and taxa assigned to  
401 Bromelioideae. Furthermore, gene tree discordance and the proportion of un-informative gene trees  
402 was especially high for splits among clades within the K.1 and K.2 clades of subgenus *Tillandsia*. A  
403 similar analysis with Angiosperms353 yielded evidence for gene tree discordance, but a considerable  
404 number of gene trees were reported to be non-informative (grey part of the pie charts), especially  
405 within subgenus *Tillandsia* (Figure 2).

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**Bromeliad1776**

**Angiosperms353**



406

407 **Figure 2** Coalescent-based species trees generated ASTRAL-III for samples enriched with Bromeliad1776  
 408 (left) and Angiosperms353 (right, flipped for mirroring), on 269 and 1600 genes for each set, re-  
 409 spectively. Node values represent local posterior probabilities (pp) for the main topology and are  
 410 equal to 1 unless noted otherwise. Pie charts at the nodes show levels of gene tree discordance: the  
 411 percentages of concordant gene trees (blue), the top alternative bipartition (green), other conflicting  
 412 topologies (red) and uninformative gene trees (gray). At bottom, length and average bootstrap sup-  
 413 port for gene trees from either data set, according to the design of the bait set used for enrichment:

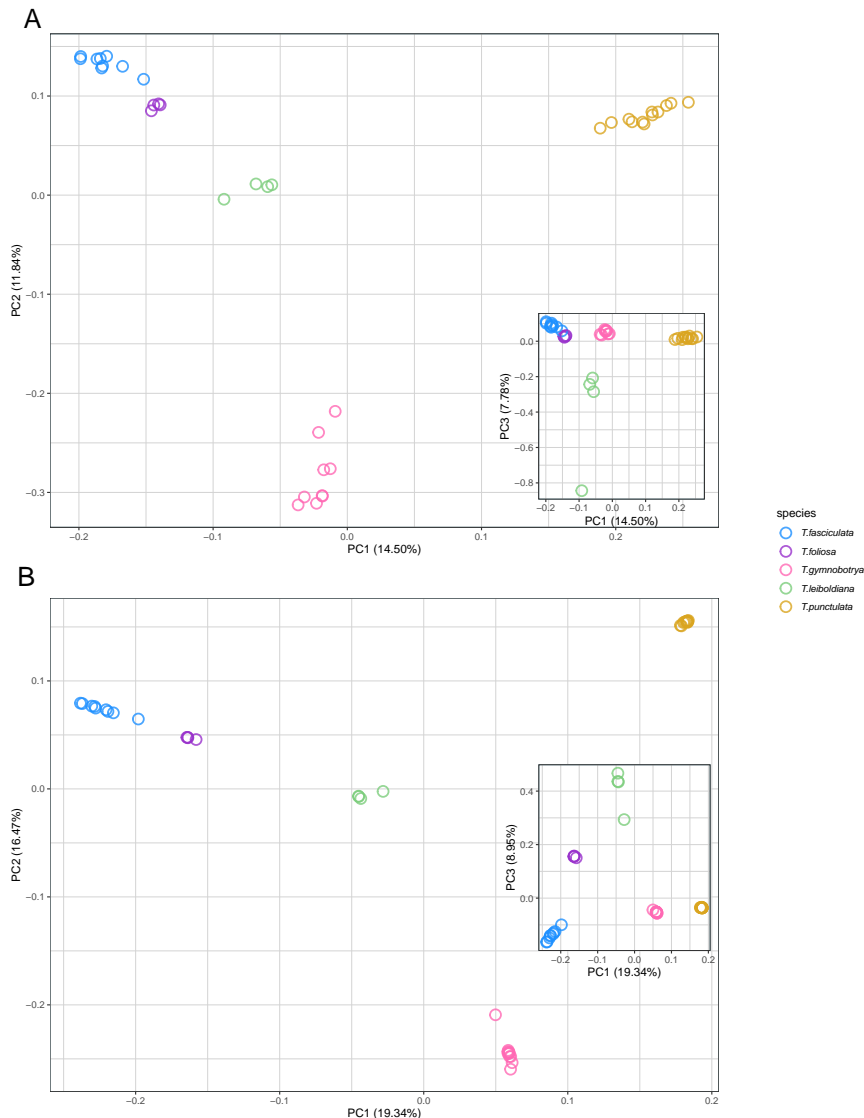
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414 *Angiosperms353 (right) and Bromeliad1776 (left). Each gene was considered a single genomic*  
415 *window.*

### 416 **3.5 Strong interspecific structure, but little evidence for within-species popula-** 417 **tion structure**

418 After LD-pruning and retaining maximum 10% missing data, 1,025 and 32,941 biallelic SNPs  
419 were included for the *Tillandsia* PCA analysis of the Angiosperms353 and Bromeliad1776 data  
420 sets, respectively. Overall, both data sets provided evidence for interspecific structure, but not for  
421 population structure, with Bromeliad1776 resulting in border-line higher resolution (slightly better  
422 separating *T. foliosa* from *T. fasciculata*). The percentage of explained variance was higher in  
423 the Bromeliad1776 set (19.3% and 16.5% for PC1 and PC2) as compared to the Angiosperms353  
424 data set (14.5% and 11.8%, see Figure 3, Supporting information Figure S6). Based on these two  
425 PCAs, we found no evidence for spatial genetic structure within each species, since accessions did  
426 not cluster by geographic origin on the two PCs presented, or any other PCs we investigated (See  
427 Supporting information Figure S6).

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428

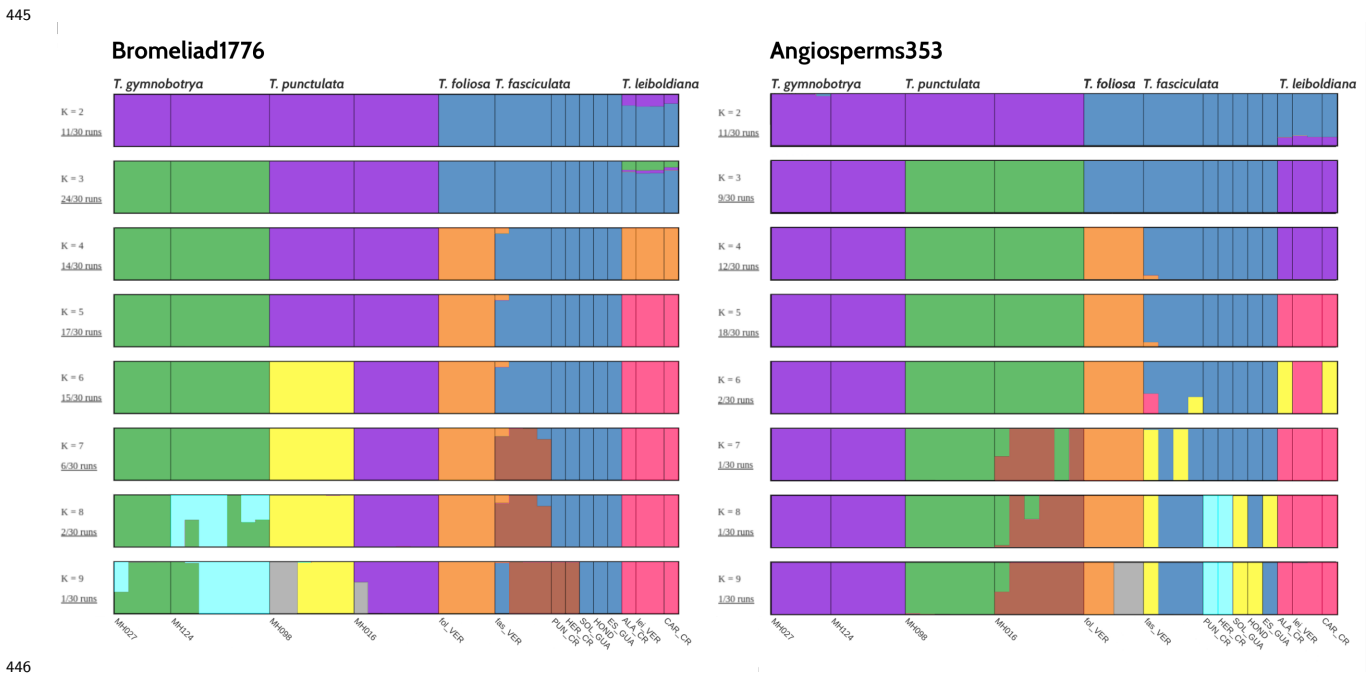
429 **Figure 3** *Principal Component Analysis (PCA) plot for samples of Tillandsia subgenus Tilland-*  
430 *sia enriched with two bait sets: A. Angiosperms353 (1,025 variants); B. Bromeliad1776 (32,941*  
431 *variants). Colors indicate different species according to legend.*

432

433 In addition to PCA, we performed ADMIXTURE analyses based on 9,804 and 42,613 variants  
434 for the Angiosperms353 and Bromeliad1776 sets, respectively (Figure 4). We used a cross-validation  
435 strategy to identify the best K and found clear support for K=5 for the Bromeliad1776 set (Sup-

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436 porting information Figure S7). In contrast, the CV pattern for the Angiosperms353 set varied  
 437 widely, providing limited information about the best K. Lowest CV values were however observed  
 438 for K=9 with locally low values for K=5 and K=3 (Supporting information Figure S7). We further  
 439 investigated the ADMIXTURE bar plots at different values of K. For K=5, very similar patterns  
 440 can be observed for both sets, with the recovered clusters reflecting the expected species bound-  
 441 aries. The main difference between the two data sets was the ability of the Bromeliad1776 set to  
 442 reach a more consistent solution (“consensus”) among 30 runs, especially at large K, as compared  
 443 to the runs based on the Angiosperms353 bait set. The Bromeliad1776 was also able to distinguish  
 444 between different sampling localities of *T. punctulata* and of *T. fasciculata* at K=7-8 (Figure 4).

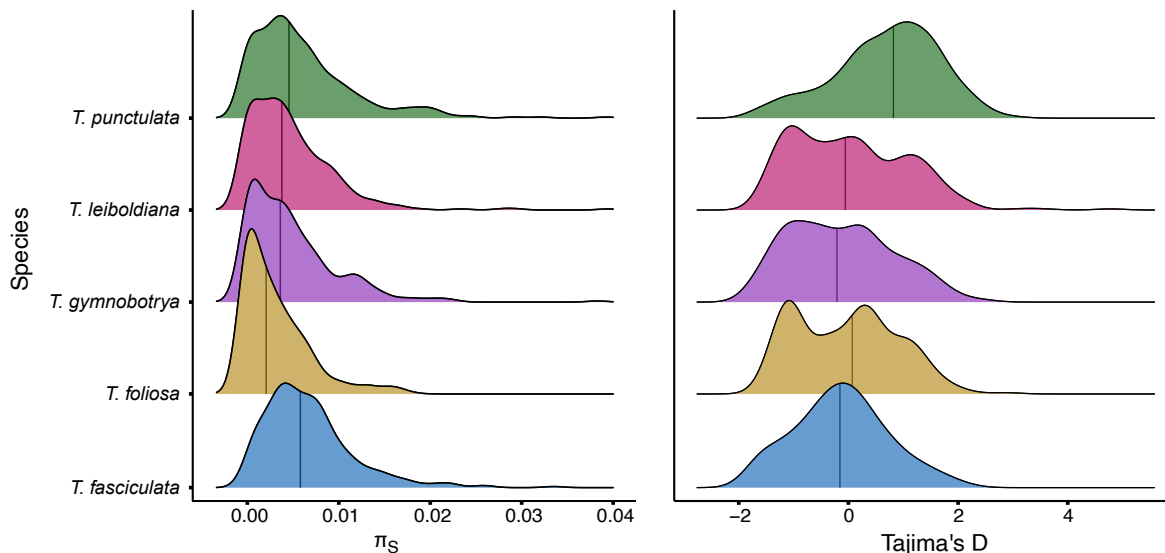


447 **Figure 4** Population structure of 5 *Tillandsia* subgenus *Tillandsia* species from 14 sampling  
 448 locations inferred with the ADMIXTURE software. Samples were enriched with either of two bait  
 449 sets: Angiosperms353 (9,804 variants after LD-pruning) and Bromeliad1776 (42,613 variants after  
 450 LD-pruning), showing values of K=2 to K=9. Colors represent genetically differentiated groups  
 451 while each accession is represented by a vertical bar.

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### 3.6 Distinct diversities hint at different demographic processes

Nucleotide diversity estimates were calculated for the Bromeliad1776 data-set only, due to difficulties obtaining a reliable SNP set with Angiosperms353 (see section 2.4). Averaged levels of nucleotide diversity at synonymous sites  $\pi_S$  greatly varied among species, from  $4.1 \times 10^{-3}$  to  $8.1 \times 10^{-3}$  for *T. foliosa* and *T. fasciculata*, respectively (Supporting information Table S5; Figure 5). Given the recent divergence of these different species and their roughly similar life history traits, they are expected to share relatively similar mutation rates, hence the observed differences in  $\pi_S$  are expected to translate into differences of long-term  $N_e$ . Looking at the distribution of  $\pi_S$  across genes, we found broader or narrower distributions depending on the species, which explains the observed differences in averaged  $\pi_S$ , as typically represented by the median of the distribution (vertical bars, Figure 5). Most species exhibit distributions of Tajima's D (Fig 5) that are centered around zero, with the notable exception of *T. punctulata*. The distribution of this species is shifted toward positive Tajima's D values, therefore indicating a recent population contraction, suggesting that this species experienced a unique demographic trajectory as compared to the other species.



466

467 **Figure 5** Distribution of Tajima's D and synonymous ( $\pi_S$ ) nucleotide diversity within each species  
468 for the Bromeliad1776 kit.



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## 469 4 Discussion

### 470 4.1 A taxon-specific bait set performs marginally better for phylogenomics

471 In this study, we compared the information content and performance of a taxon-specific bait  
472 set and a universal bait set for addressing questions on evolutionary processes at different scales  
473 in a highly diverse Neotropical plant group, including recently radiated clades. We found that the  
474 taxon-specific kit provided a greater number of segregating sites, yet contrary to our expectations,  
475 the abundance of information content did directly translate to a greater resolution power.

476 The universal and taxon-specific sets performed comparably when investigating macroevo-  
477 lutionary patterns: the inferred species trees are remarkably consistent between the two bait sets  
478 (Supporting information Figure S5, Figure 2). Notably, both sets were sufficiently informative to  
479 reconstruct the relationships among the fastest radiating clades. These results resonate with pre-  
480 vious comparative works (e.g. in *Burmeistera*, Bagley et al., 2020; in *Buddleja*, Chau, Rahfeldt,  
481 & Olmstead, 2018; and in *Cyperus*, Larridon et al., 2020), where taxon-specific markers provided  
482 higher gene assembly success, but a comparable number of segregating sites for phylogenetic infer-  
483 ence, indicating that universal bait sets are nearly as effective as taxon-specific bait sets, even in  
484 fast evolving taxa. The main advantage of the bromeliad taxon-specific set is its ability to provide  
485 additional resolution for deeper examination of gene tree incongruence (Figure 2), currently a fun-  
486 damental tool in phylogenomic research (Edwards, 2009; Morales-Briones et al., 2020; Pease et al.,  
487 2016).

488 The taxon-specific bait set performed marginally better to address hypotheses at more recent  
489 evolutionary scales and provided arguably clearer evidence for inference of species genomic structure  
490 using clustering methods. In fact, genetic markers obtained from both data sets provided sufficient  
491 information to infer species but no geographic structure, suggesting that *Tillandsia* could be char-  
492 acterized by high gene dispersal among populations. Considering that the Angiosperms353 kit has  
493 shown potential to provide within-species signal, as recently demonstrated by Beck et al. (2021) on  
494 *Solidago ulmifolia*, and to estimate demographic parameters from herbarium specimen (Slimp et al.,

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495 2021), we would expect the taxon-specific set to accurately reveal a geographical genetic structure.  
496 However, the present study is generally based on small sample sizes per species (n=4-8), mostly  
497 sampled within a limited geographic range, limiting our ability to draw robust conclusions on the  
498 levels of intra-specific population structure.

499 The Bromeliad1776 kit provided a substantially larger number of segregating sites (more  
500 than 200k vs. 47k in Angiosperms353; Table 1, Supporting information Figure S2) due to higher  
501 enrichment success, following the expectation for higher sequence variation in custom-made loci  
502 (Figure 1, see also Bragg et al., 2016; de La Harpe et al., 2019; Kadlec et al., 2017). We accordingly  
503 found that rates of molecular divergence are distinctly correlated with enrichment success in our  
504 sampling (Figure 1), following the expectation that a universal kit will provide fewer segregating  
505 sites.

506 However, the difference in resolution power between the kits cannot be ascribed solely to the  
507 different numbers of SNPs, but rather to the length and variability of the obtained regions. The  
508 topology obtained with the Angiosperm353 data set under the multi-species coalescent model was  
509 substantially different from all other inferred trees and the input gene trees provided a low power  
510 to detect patterns of gene tree discordance (Figure 2). We additionally observed that the highly  
511 conserved regions targeted by Angiosperms353 are shorter in comparison to Bromeliad1776 targets  
512 and thus result in shorter input windows for species tree inference (Figure 2). Hence, the patterns of  
513 gene tree discordance in the Angiosperms353 data set likely indicate incorrect gene tree estimation  
514 or other model misspecifications, rather than a biological signal. Specifically, coalescence-based  
515 methods are sensitive to gene tree estimation error (Zhang et al., 2018) and perform better with  
516 gene trees estimated from unlinked loci long enough and variable enough to render sufficient signal  
517 per gene tree - this is especially true for data sets with many taxa. The high rates of uninformative  
518 genes trees, found in almost half of the intergenic nodes in the Angiosperms353 data set, is expected  
519 with increased levels of gene tree error which in turn reduce the accuracy of ASTRAL (Mirarab, 2019;  
520 Sayyari & Mirarab, 2016). In contrast, the Bromeliad1776 ASTRAL tree (Figure 2, left) resolved  
521 phylogenetic relationships among taxa with high posterior probability and a topology similar to the  
522 ML tree. Gene tree discordance analysis revealed high incongruence around certain nodes, possibly

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523 reflecting rapid speciation events.

524 Since inference of phylogenetic relationships under the multi-species coalescent and explo-  
525 ration of gene tree discordance are both pivotal to phylogenomic research (Degnan & Rosenberg,  
526 2009; Edwards et al., 2016; Pease et al., 2016), a taxon-specific kit provides a clear advantage  
527 especially in recent rapid radiations, where gene tree conflict and incomplete lineage sorting are  
528 expected to be prevalent (Dornburg, Su, & Townsend, 2019; Kubatko & Degnan, 2007; Roch &  
529 Warnow, 2015). In that regard, inference of the species tree with the Bromeliad1776 is a tool to  
530 drive further hypotheses concerning evolutionary and demographic processes in the evolution of  
531 *Tillandsia*. Moreover, the features of the loci targeted provide an important opportunity to study  
532 selection (see section 4.3).

## 533 **4.2 Insights on Bromeliaceae phylogeny and demographic processes in *Tilland-*** 534 ***sia***

535 Both bait sets resolved the phylogeny of Bromeliaceae, including the fastest evolving lineages  
536 of the subfamily Tillandsioideae. The results generally agreed with previous findings of the rela-  
537 tionships among taxa (Givnish et al., 2011, 2014). Several findings that contrast with the expected  
538 known phylogeny may point at a complexity of genomic processes in the evolutionary history of  
539 Bromeliaceae subfamilies. Both the ML tree and species tree did not support a monophyly of the  
540 subfamily Pitcairnioideae, which was represented by four samples and two genera in our phylogeny:  
541 *Deuterochonia* and *Pitcarnia*. Rather, the genus *Deuterochonia* was sister to subfamily Puyoideae  
542 or sister to both Puyoideae and Bromelioideae subfamilies, inconsistent with the results of Barfuss  
543 et al. (2016) and Granados Mendoza et al. (2017). Interestingly, in a visualization of gene tree  
544 discordance we found high levels of incongruence and a high percentage of trees supporting an al-  
545 ternative topology in the node splitting the genera, indicating that several genomic processes such  
546 as hybridization and incomplete lineage sorting may have accompanied divergence in this group,  
547 contributing to the phylogenetic conflict and extending the challenges in resolving these evolution-  
548 ary relationships. Within the core Tillandsioideae, the tribes Tillandsieae and Vrieseae were found  
549 to be monophyletic, in accordance with previous work on the subfamily (Barfuss et al., 2016). Fi-

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550 nally, within our focal group *Tillandsia* subgenus *Tillandsia*, clade K as suggested by Barfuss et  
551 al. (2016) and clades K.1 and K.2 as proposed by Granados Mendoza et al. (2017) were all well  
552 supported, further in agreement with their interpretation of Mexico and Central America as a center  
553 of diversity for subgenus *Tillandsia*. Within *Tillandsia*, incongruence was prominent at the recent  
554 splits within clade K.1. and clade K.2 as expected in a recent rapid radiation, a result of high levels  
555 of incomplete lineage sorting, hybridization and introgression (Berner & Salzburger, 2015).

556 When applied to methods in population genetics, we obtained some evidence for a difference  
557 in demographic processes and in the level of genetic variation among species. This was especially  
558 true for the taxon-specific bait set: for example, the bait set differentiated between populations of  
559 *T. punctulata* and *T. fasciculata*, but not *T. gymnotrya* in a maximum likelihood tree and ances-  
560 try analysis (Supporting information Figure S5, Figure 4), indicating differences in inter-population  
561 genetic structure among species. The evidence for different demographic processes in these species  
562 extended to estimates of Tajima's D, where lower values may indicate a recent bottleneck. In addi-  
563 tion, we found a unique distribution of nucleotide diversity for *T. foliosa*, possibly reflecting a low  
564 effective population size for this endemic species in contrast with the closely related, but widespread  
565 *T. fasciculata*. In all cases, our limited sampling given the large size of the family constrains our  
566 ability to draw conclusions of a 'true' phylogeny and to account for population structure. Our find-  
567 ing however suggests that nuclear markers obtained with a target capture technique can highlight  
568 genomic processes and be further applied to address questions in population genomics with a wider  
569 sampling scheme.

### 570 **4.3 Future prospects and implications for research in Bromeliaceae and rapid** 571 **radiations**

572 Beyond the scope of this study, the availability of a bait set kit for Bromeliaceae provides a  
573 prime genetic resource for investigating several topical research questions on the origin and main-  
574 tenance of Bromeliaceae diversity. Manyfold studies of bromeliad phylogenomics set forth the chal-  
575 lenges of resolving species-level phylogenies with a small number of markers, particularly in young  
576 and speciose groups (Goetze, Zanella, Palma-Silva, Büttow, & Bered, 2017; Granados Mendoza

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577 et al., 2017; Loiseau et al., 2021; Versieux et al., 2012 ). This particularly curated bait set allows  
578 highly efficient sequencing across taxa: within our study, we found high mapping success with 82.3%  
579 average read mapping. As expected, we documented a difference in enrichment success among taxa,  
580 explained by divergence time to the reference used for bait design (see Supporting information Fig-  
581 ure S4), suggesting possible deviations from the assumptions of non-randomly distributed missing  
582 data that may mislead phylogenetic inference (A. R. Lemmon, Brown, Stanger-Hall, & Lemmon,  
583 2009; Streicher, Schulte, & Wiens, 2016; Xi, Liu, & Davis, 2016). However, given the large en-  
584 richment success, downstream analysis with deliberate methodology can account for possible biases  
585 and provide robust inference with strict data filtering (Molloy & Warnow, 2018; Streicher et al.,  
586 2016). Hence, target enrichment with Bromeliad1776 can produce large data sets with consistent  
587 representation between taxa, allowing repeatability between studies and retaining the possibility  
588 for global synthesis by including sequence baits orthologous to the universal Angiosperms353 bait  
589 set. Moreover, with specific knowledge of the loci targeted in this set, the ability to obtain the same  
590 sequences across taxa and experiments and to differentiate genic regions with the use of *A. comosus*  
591 models, this bait set offers a broad utility for research in population genomics.

592 Another important feature in the Bromeliad1776 set is the inclusion of genes putatively as-  
593 sociated with key innovative traits in Bromeliaceae with a focus on C3/CAM shifts. Little is known  
594 about the molecular basis of the CAM pathway, an adaptation to arid environments which evolved  
595 independently and repeatedly in over 36 plant families (Heyduk, Moreno-Villena, Gilman, Christin,  
596 & Edwards, 2019; Chen, Xin, Wai, Liu, & Ming, 2020; Silvera et al., 2010). CAM phenotypes are  
597 considered key adaptations in Bromeliaceae, associated with expansion into novel ecological niches.  
598 In *Tillandsia*, C3/CAM shifts were found to be particularly associated with increased rates of di-  
599 versification (Crayn et al., 2004; de La Harpe et al., 2020; Givnish et al., 2014). The Bromeliad1776  
600 bait set offers opportunities to address specific questions on the relationship between rapid diversi-  
601 fication and photosynthetic syndromes in this clade, including testing for gene sequence evolution.  
602 Additionally, the inclusion of multi-copy genes, combined with newly developed pipelines for study-  
603 ing gene duplication and ploidy (Morales-Briones et al., 2020; Viruel et al., 2019), are beneficial  
604 for studying the role of gene duplication and loss in driving diversification. With the increasing

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605 ubiquity of target baits as a genomic tool we expect to see additional pipelines and applications  
606 emerging, further expanding the utility of target capture for both macro-and microevolutionary  
607 research.

## 608 **5 Conclusions**

609 Even as whole genome sequencing becomes increasingly economically feasible, target capture  
610 is expected to remain popular due to its extensive applications in research. We found that evaluating  
611 the differences in resolution power between universal and taxon-specific bait sets is far from a  
612 trivial task, and we attempted to lay out a methodological roadmap for researchers wishing to  
613 reconstruct the complex evolutionary history of rapidly diversifying lineages. While a taxon-specific  
614 set offers exciting opportunities beyond phylogenomic and into research of molecular evolution, its  
615 development is highly time-consuming, requires community-based knowledge and may cost months  
616 of work when compared with out-of-the-box universal kits. Our results suggest that universal kits  
617 can continue to be employed when aiming to reconstruct phylogenies, in particular as this may  
618 offer the possibility to use previously published data to generate larger data sets. However, for  
619 those wishing to deeply investigate evolutionary questions in certain lineages, a taxon-specific kit  
620 offers certain benefits during data processing stages, where knowledge of the design scheme and  
621 gene models is extremely useful, and the possible return of costs is especially high for taxa emerging  
622 as model groups. We furthermore encourage groups designing taxon-specific kits to include also  
623 universal probes, furthering the mission to complete the tree of life.

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## 1059 **7 Data Accessibility**

1060 Targeted sequencing reads generated for this project are available at NCBI-SRA under Bio-  
1061 Project PRJNA759878; for accession numbers, see supporting information Table S4. The probe  
1062 set and the relevant supporting information are available in Dryad (doi:10.5061/dryad.mpg4f4r11).  
1063 The bioinformatics scripts are available at [https://github.com/giyany/Bromeliad1776/tree/main/](https://github.com/giyany/Bromeliad1776/tree/main/MS_2021_scripts)  
1064 MS\_2021\_scripts.

## 1065 **8 Author Contribution**

1066 CL, MP and GY conceived the study. CL provided funding. TK coordinated sample collec-  
1067 tion, MdLH, VGJ and GY collected data. Species identified by MHJB and WT. Bait kit designed  
1068 by GY, with guidance from JH and MP. Molecular work was performed by CGC, JV, NR, MHJB  
1069 and GY. The data was analyzed by GY and TL with feedback from JV and OP. The manuscript  
1070 was written by GY with significant input from all co-authors.

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## 1071 **9 Tables**

1072 **Table 1** Number and characteristics of the variants obtained for Angiosperms353 and Bromeliad1776.

1073



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	indv Nr.	SNP Nr.	site mean depth	SNPs			SNPs	SNPs	SNPs	SNPs	SNPs
				in exonic regions	in intronic regions	in intergenic regions	on-target SNPs	flanking SNPs	off-target SNPs		
<b><u>intragenic vcf</u></b>											
Angiosperms353	70	47,390	3447	40,628 (85.7%)	4,376 (9.2%)	2,386 (5.1%)	8,424 (17.8%)	3,488 (7.4%)	35,478 (74.8%)		
Bromeliad1776	72	209,186	6601.7	170,893 (81.7%)	35,790 (17.1%)	2,503 (1.2%)	162,924 (77.9%)	37,661 (18.0%)	8,601 (4.11%)		
<b><u>pop-level vcf</u></b>											
Angiosperms353	38	15,622	1,837.8	13,345 (85.5%)	1,442 (9.2%)	835 (5.3%)	3,032 (19.4%)	1,129 (7.22%)	11,461 (73.4%)		
Bromeliad1776	40	65,473	3914.9	54,636 (83.5%)	9,967 (15.2%)	870 (1.3%)	51,405 (78.5%)	10,588 (16.2%)	3,480 (5.3%)		

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## 1074 10 Supporting information

### 1075 10.1 Tables

1076 **Table S1** Genes included in the Bromeliad1776 bait design, with identifiers as annotated in  
1077 *Ananas comosus* genome v.3 (Ming et al., 2015). The table includes details about exon composition,  
1078 copy number and putatively associated pathways.

1079 **Table S2** Categories of pathways and traits used to choose genes of interest for the Bromeliad1776  
1080 bait set, including literature source and number of genes in each category.

1081 **Table S3** List of accessions used in this study. For samples of *Tillandsia* subgenus *Tillandsia*  
1082 locality codes are also indicated.

1083 **Table S4** Number of reads, numbers and percentage of read mapping to target in all samples for  
1084 both bait sets.

1085 **Table S5** Averaged levels of nucleotide diversity at synonymous ( $\pi_S$ ) and non-synonymous ( $\pi_N$ )  
1086 for 5 *Tillandsia* subgenus *Tillandsia* species.

### 1087 10.2 Figures

1088 **Figure S1** Map of sampling locations for *Tillandsia* subgenus *Tillandsia* accessions within Mex-  
1089 ico.

1090 **Figure S2** Mapping rates (A) and percentage of reads matching bait sequences (B) for Bromeliad  
1091 samples enriched with one of two bait sets: Angiosperms353 and Bromeliad1776. Reads were  
1092 mapped against *A. comosus* reference for both bait sets. Targets were defined as bait locations and  
1093 flanking 500 base-pairs. Bromeliad1776 targets were defined as the regions used for bait design and  
1094 Angiosperms353 targets were defined as *A. comosus* orthologous regions matching the genes used  
1095 for bait design.

1096 **Figure S3** A simplified phylogenetic tree, with branches colored according to read mapping per-  
1097 centage for samples enriched with Angiosperms353.

1098 **Figure S4** A simplified phylogenetic tree, with branches colored according to read mapping per-  
1099 centage for samples enriched with Bromeliad1776.

1100 **Figure S5** Maximum-likelihood (ML) phylogenetic tree inferred with RAxML-NG, based on vari-  
1101 ants called for data sets enriched with Bromeliad1776 bait set (left) and Angiosperms353 bait set  
1102 (right, flipped for mirroring). Branch lengths were calculated by number of substitutions per site.  
1103 Internal nodes are marked and colored according to bootstrap support. Nodes which differed among  
1104 trees are colored purple and have been marked by an arrow.

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1105 **Figure S6** Principal Component Analysis (PCA) plot for samples of *Tillandsia* subgenus *Tilland-*  
1106 *sia* enriched with two bait sets: A. Angiosperms353 (1,025 variants after LD-pruning) B. Bromeliad1776  
1107 (32,941 variants after LD-pruning). Colors indicate different species (following the scheme in Sup-  
1108 porting Figure S6) and shapes represent different geographic origins (populations).

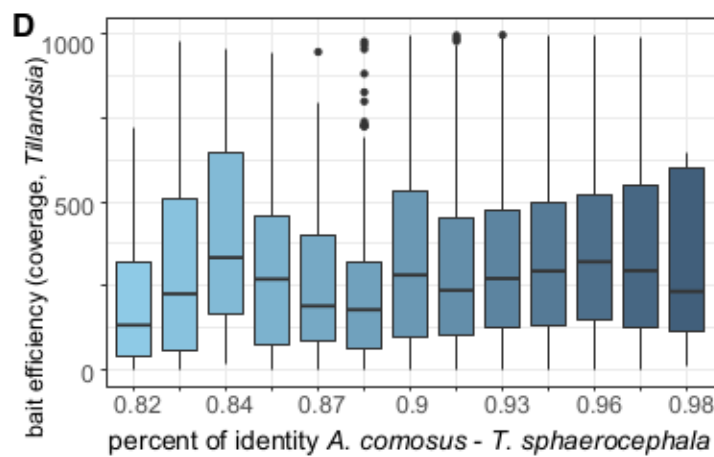
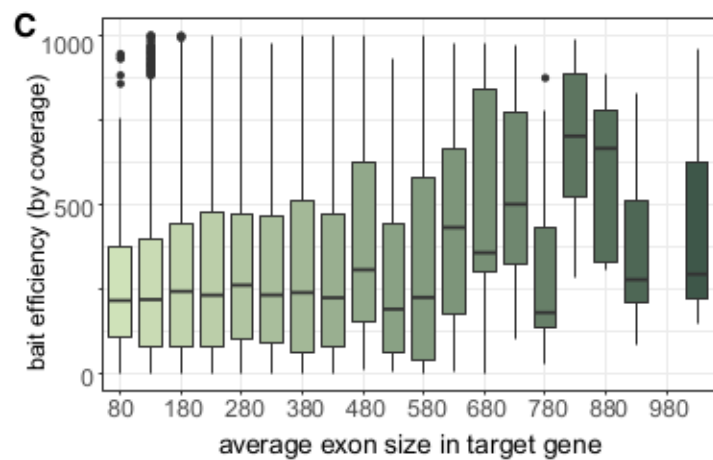
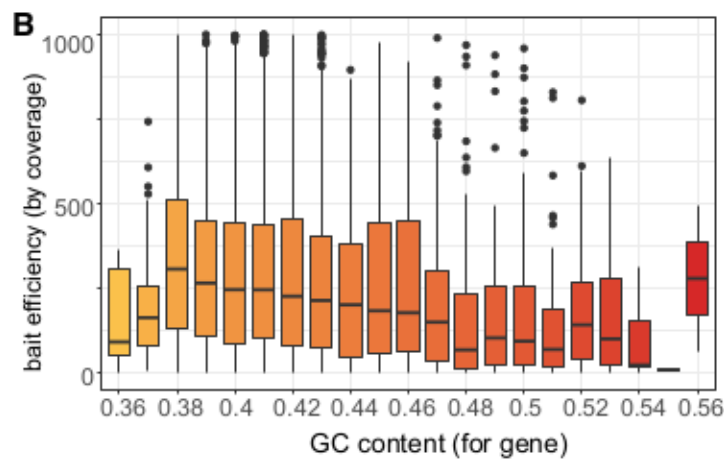
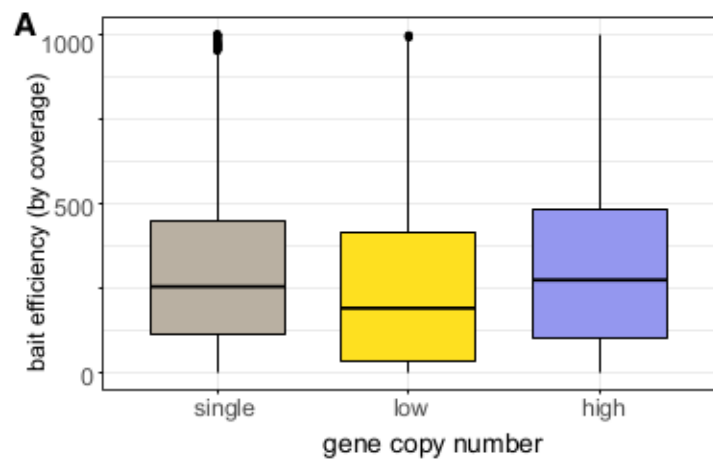
1109 **Figure S7** Admixture cross-validation errors (top) detected for values of K between 2 and 9 for  
1110 A. Angiosperms353 data set and B. Bromeliad1776 data set.

1111 **Figure S8** Coalescent-based species trees generated ASTRAL-III for samples enriched with An-  
1112 giosperms353 using 269 genes. Node values represent local posterior probabilities (pp) for the main  
1113 topology.

1114 **Figure S9** Coalescent-based species trees generated ASTRAL-III for samples enriched with Bromeliad1776  
1115 using 1600 genes. Node values represent local posterior probabilities (pp) for the main topology.

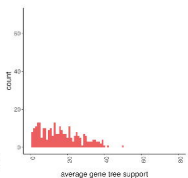
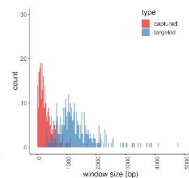
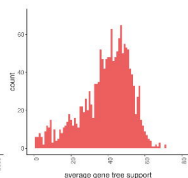
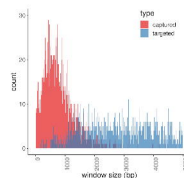
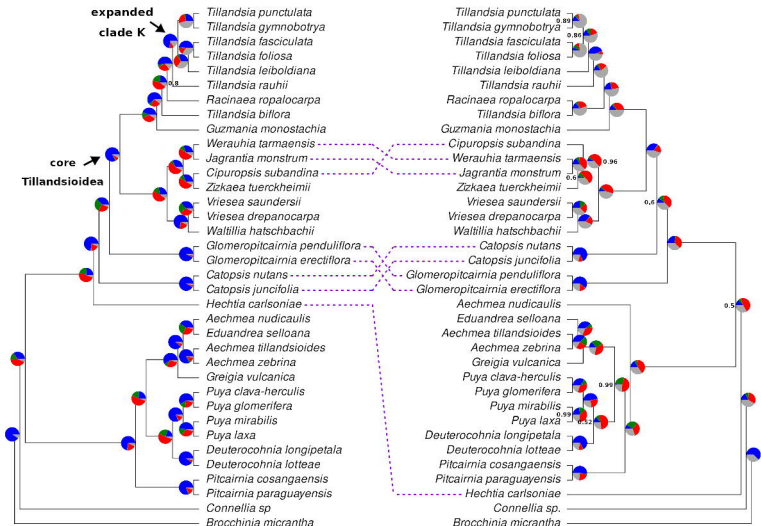
1116 **10.3 Files**

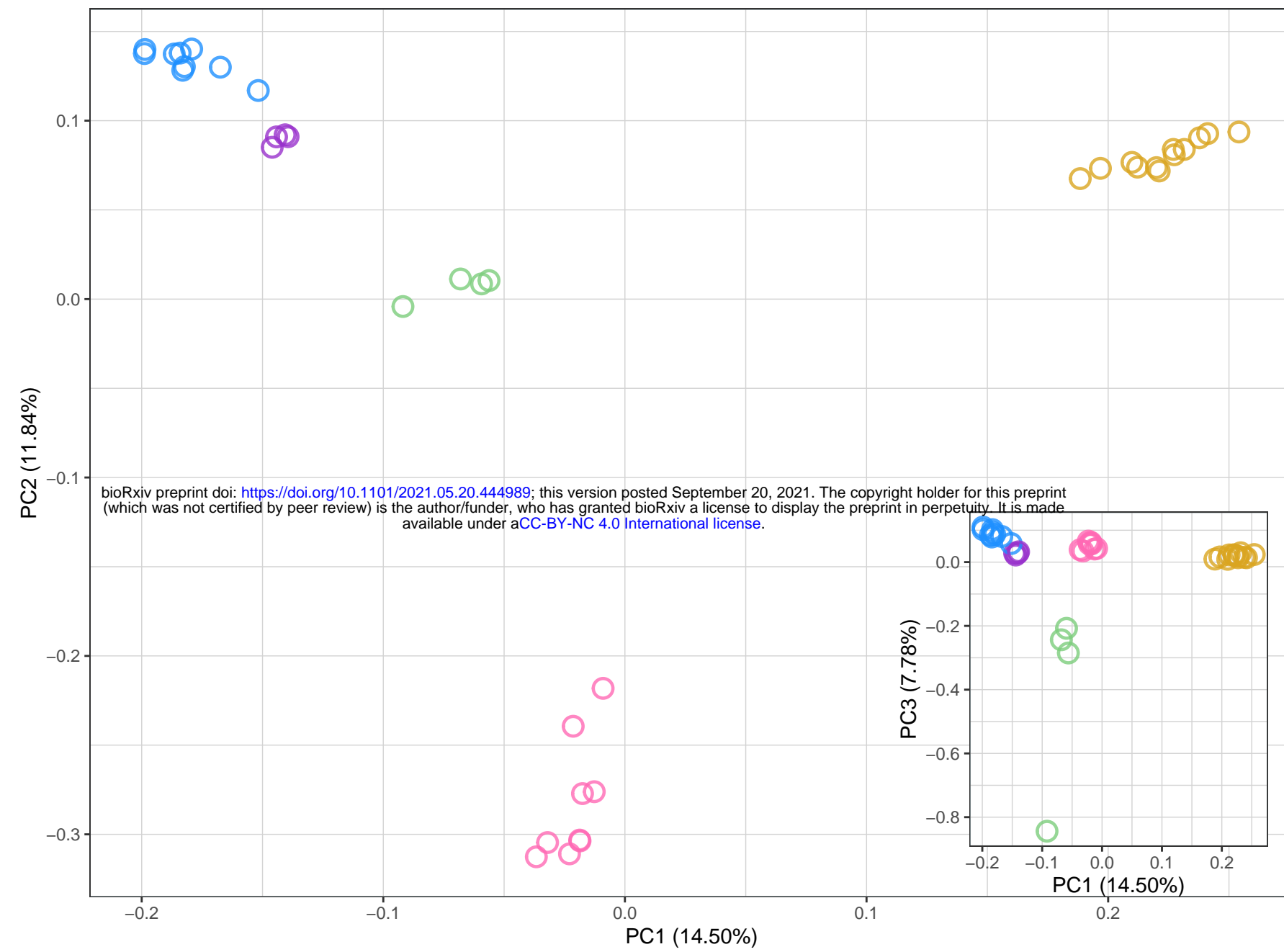
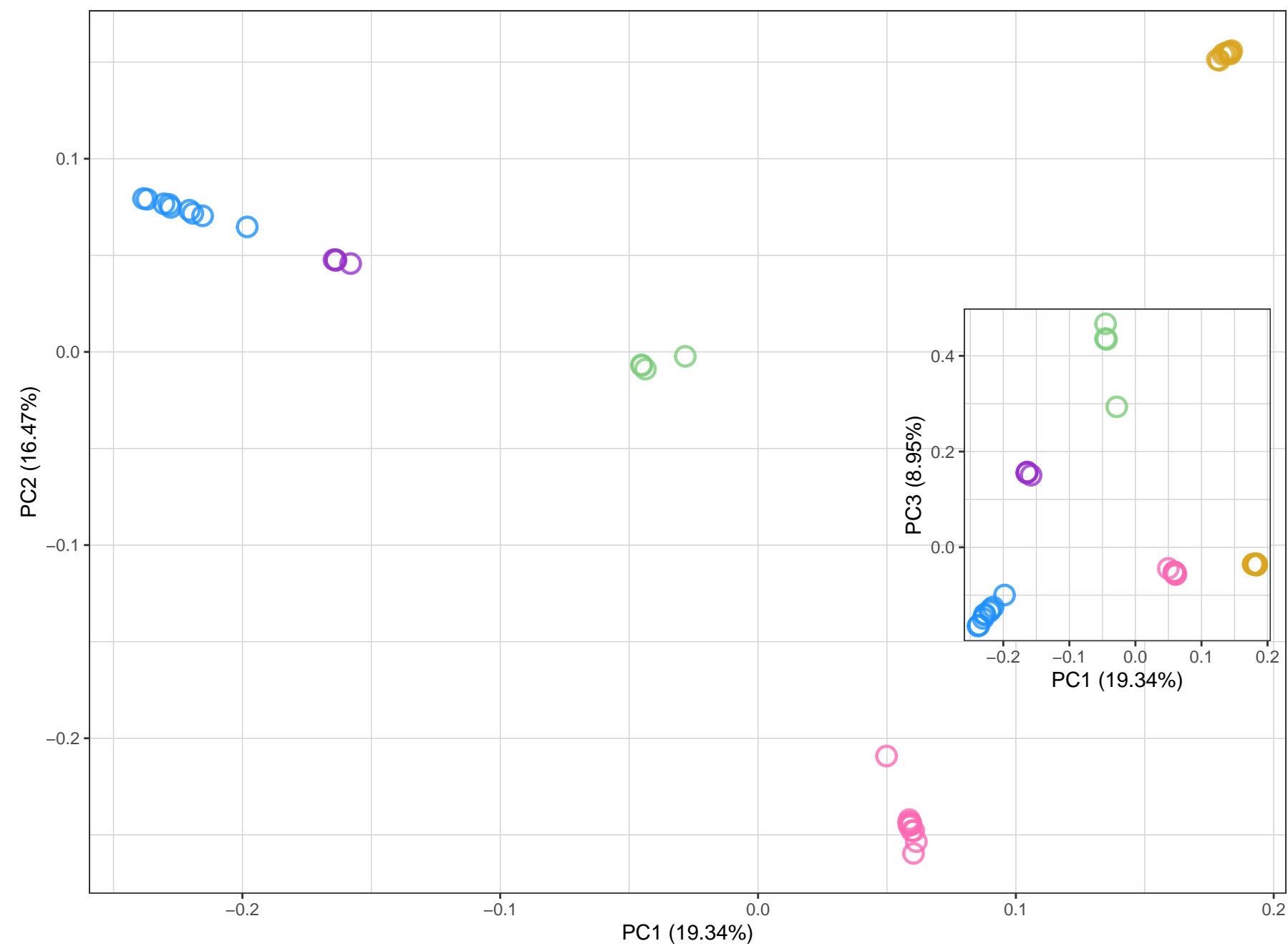
1117 **File S1** Estimation of ascertainment bias in target capture data using comparison with whole-  
1118 genome data



# Bromeliad1776

# Angiosperms353



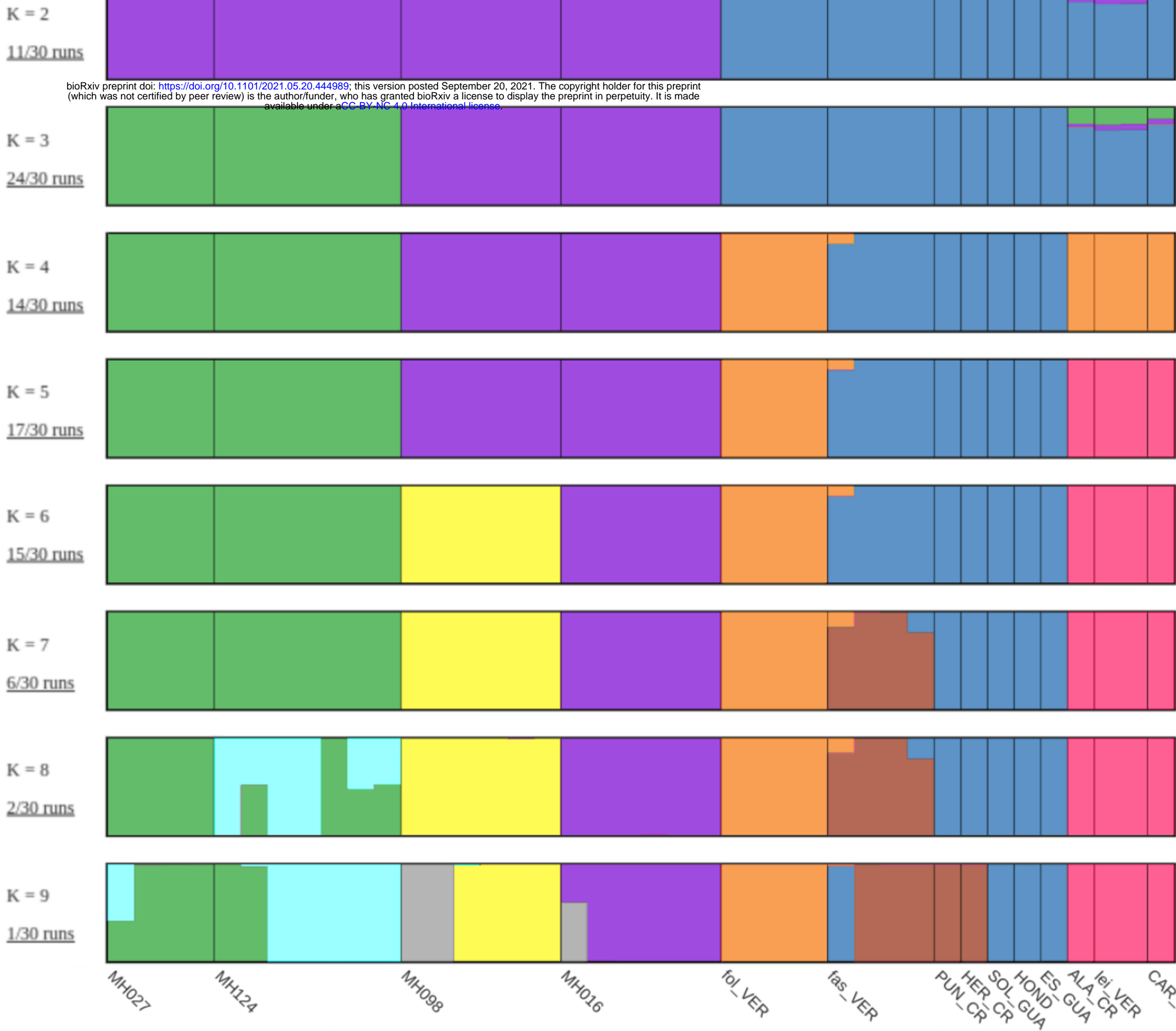
**A****B**

species

- *T.fasciculata*
- *T.foliosa*
- *T.gymnotrya*
- *T.leiboldiana*
- *T.punctulata*

# Bromeliad1776

*T. gymnobotrya*      *T. punctulata*      *T. foliosa* *T. fasciculata*      *T. leiboldiana*



# Angiosperms353

*T. gymnobotrya*      *T. punctulata*      *T. foliosa* *T. fasciculata*      *T. leiboldiana*

