

1 Floristics and biogeography of vegetation in seasonally dry tropical 2 regions

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76 SUMMARY

77 To provide an inter-continental overview of the floristics and biogeography of drought-
78 adapted tropical vegetation formations, we compiled a dataset of inventory plots in South
79 America, Africa, and Asia from savannas (subject to fire), seasonally dry tropical forests (not
80 generally subject to fire), and moist forests (no fire). We analysed floristic similarity across
81 vegetation formations within and between continents. Our dataset strongly suggests that
82 different formations tend to be strongly clustered floristically by continent, but that among
83 continents, superficially similar vegetation formations (e.g. savannas) are floristically highly
84 dissimilar. Neotropical moist forest, savanna and seasonally dry tropical forest are distinct,
85 but elsewhere there is no clear floristic division of savanna and seasonally dry tropical forest,
86 though moist and dry formations are separate. We suggest that because of their propensity to
87 burn, many formations termed “dry forest” in Africa and Asia are best considered as
88 savannas. The floristic differentiation of similar vegetation formations from different
89 continents suggests that cross-continental generalisations of the ecology, biology and
90 conservation of savannas and seasonally dry tropical forests may be difficult.

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94 KEYWORDS: savanna, seasonally dry tropical forest, moist forest, metacommunities,
95 resilience

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101 RESUMEN

102 Para proveer una visión inter-continental de la florística y biogeografía de formaciones
103 vegetales tropicales adaptadas a la sequía, hemos recopilado un base de datos de parcelas
104 forestales de América del Sur, África y Asia de sabanas (sujeto al fuego), los bosques
105 tropicales estacionalmente secos (no generalmente sujeta al fuego), y los bosques húmedos
106 (sin fuego). Analizamos similitud florística a través de formaciones de vegetación dentro y
107 entre continentes. Nuestros resultados sugiere que las diferentes formaciones tienden a estar
108 fuertemente agrupadas florísticamente por continente, pero que entre los continentes,
109 formaciones vegetales superficialmente similares (por ejemplo, sabanas) son florística muy
110 disímiles. En América del Sur, bosque húmedo, sabana y bosque tropical estacionalmente
111 seco son distintos, pero en otros lugares no existe una clara división florística entre sabana y
112 bosque tropical estacionalmente seco, aunque formaciones húmedas y secas están separados.
113 Le sugerimos que debido a su propensión a quemar, muchas formaciones denominadas
114 "bosque seco" en África y Asia están mejor considerados como sabanas. La diferenciación
115 florística de las formaciones vegetales similares de diferentes continentes sugiere que
116 generalizaciones a través continentes de la ecología, la biología y la conservación de las
117 sabanas y bosques tropicales estacionalmente secos pueden ser difíciles.

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120 PALABRAS CLAVES: sabana, bosque tropical estacionalmente seco, bosque húmedo,
121 metacomunidades, resiliencia

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124 RÉSUMÉ

125 Pour donner un vue inter-continental des floristique et biogéographie des formations
126 végétales tropicales adaptées à la sécheresse, nous avons compilé un base de données de
127 parcelles d'inventaire en Amérique du Sud, Afrique et Asie du savanes (exposées au feu), les
128 forêts tropicales saisonnière sèches (généralement pas soumis au feu), et les forêts humides
129 (pas du feu). Nous avons analysé le similitude floristique dans les formations végétales dans
130 et entre des continents. Notre résultats suggère fortement que différentes formations ont
131 tendance à être fortement groupées floristiquement par continent, mais entre des continents,
132 les formations végétales superficiellement similaires (par exemple les savanes) sont
133 floristiquement très dissemblables. Dans Amérique de Sud, les forêts humides, les savanes, et
134 les forêts tropicales saisonnière sèches sont distincts, mais ailleurs il n'y a pas une division
135 floristique claire entre la savane et la forêt tropicale saisonnière sèche, bien que formations
136 humides et sèches sont séparées. Nous suggérons qu'en raison de leur propension à brûler,
137 des nombreuses formations appelées "forêt sèche" en Afrique et en Asie sont mieux
138 considérés comme savanes. La différenciation floristique des formations végétales similaires
139 de différents continents suggère que les généralisations transcontinentaux de l'écologie, de la
140 biologie et la conservation des savanes et des forêts tropicales saisonnière sèches peut être
141 difficile.

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144 MOTS-CLÉS: savane, forêt tropicale saisonnière sèche, forêt humide, métacommunautés,
145 resilience

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147 INTRODUCTION

148 This paper examines the relationships amongst different formations of vegetation in
149 seasonally dry regions throughout the tropics, especially in their floristic composition, and
150 also in terms of their ecology. Our approach is to undertake a novel pantropical analysis of
151 the floristic composition of dry forest, savanna and moist forest formations, and to place the
152 results in the context of their structure and key ecological attributes, such as propensity to
153 burn. We stress that it is not our intention to re-visit labyrinthine debates of the definition of
154 vegetation formations (e.g. Gentry 1995, Leimgruber *et al.* 2011, McShea and Davies 2011,
155 Torellos-Raventos *et al.* 2013, Veenendaal *et al.* 2014) or to attempt to make precise
156 definitions of “seasonally tropical dry forest” or “tropical savannas” on different continents.
157 Our analyses address fundamental biogeographic questions, such as whether there is
158 coherence in floristic composition in vegetation formations that are structurally and
159 ecologically similar across continents. However, in the context of the papers in this volume,
160 another goal is to help to understand the generality of case studies in ecology and
161 conservation from a particular seasonally dry tropical region. For example, can the lessons of
162 a study of resilience to fire in “tropical dry forest” in Indochina be applied to “tropical dry
163 forest” in South America?

164

165 **Major vegetation formations in seasonally dry regions of the tropics**

166 In understanding the vegetation of lowland tropical regions, the distinction between savanna
167 and forests is critical. We take the view that savannas are distinguished from other tropical
168 forest formations by the presence of more or less continuous C4 grass cover and the
169 prevalence of natural fire. This grass-layer and proneness to fire is found even in savannas
170 with a dense tree canopy, such as the “cerradão”, a sub-formation within the savannas
171 (“cerrados”) of Brazil (Oliveira-Filho and Ratter 2002). This contrasts with closed canopy

172 forests, including wet forests and seasonally dry tropical forests (SDTF), where grasses are
173 infrequent in the understory and where natural fire is rare. The distinction of savanna and
174 forests by the key factors of C4 grass presence and prevalence to fire is followed by many
175 workers at a global scale (Lehmann *et al.* 2011, McShea and Davies 2011, Ratnam *et al.*
176 2011, Scholes and Walker 1993, Suresh *et al.* 2011) and it is widely accepted in the
177 Neotropics (Pennington *et al.* 2000, 2006).

178 When climate is sufficiently dry in the tropics, moist forest gives way to savannas and
179 SDTF (Lehmann *et al.* 2011, Murphy and Lugo 1986, Pennington *et al.* 2006, Staver *et al.*
180 2011). In the Neotropics, SDTF experiences ≤ 1600 mm rainfall a year, has a dry period of at
181 least 5-6 months where precipitation is ≤ 100 mm/month and is mostly deciduous (Murphy
182 and Lugo 1986, Pennington *et al.* 2006). It grows on relatively fertile, often calcareous soils,
183 and where soils are poor and acid it is replaced by savanna, which differs in its evergreen
184 trees (Pennington *et al.*, 2006). Neotropical savannas, and those on other continents, can be
185 found under wetter conditions than SDTF (up to 2500 mm rainfall/yr; Lehmann *et al.* 2011,
186 Staver *et al.* 2011).

187 It is perhaps unclear whether vegetation with the attributes of neotropical SDTF
188 outlined above exists on other continents (Lock 2006). Monsoon vine thickets of northern
189 Australia have attributes of SDTF – having a closed canopy and being largely deciduous
190 (Bowman 2000). The dry scrub on the Horn of Africa and similar regions in Arabia and
191 northwest India, which are rich in legumes and succulents, have been considered similar to
192 cactus-rich drier formations of SDTF in the Neotropics, and both have been classified as a
193 global “succulent biome” by Schrire *et al.* (2005). These formations have led to suggestions
194 that there may be a “global metacommunity” of SDTF that has some plant lineages specific
195 to it (Pennington *et al.*, 2009). However, elsewhere, extensive areas of vegetation in
196 seasonally dry regions of Asia and Africa that is named “forest” or “woodland” is C4 grass-

197 rich and fire-prone – and hence in our view a form of savanna. Examples are dry deciduous
198 forest” in India (Suresh *et al.* 2011), Miombo woodland in southern Africa (Campbell *et al.*
199 1995, Chidumayo 2013) and deciduous dipterocarp forest in continental Asia
200 (Bunyavejchewin 1983, Bunyavejchewin *et al.* 2011).

201 In this paper we analyse forest inventory plot data from across the tropics using clustering
202 and ordination methods to explore the relationships in floristic composition of diverse
203 vegetation formations from South America, Africa, India, and Indochina that could be
204 broadly classified as tropical savannas or SDTF. We include moist or wet forest plots from
205 each continent to provide broader biogeographic context. The analyses are used to address the
206 following related questions:

- 207 1. Is there floristic commonality of savannas and dry forests amongst continents? This
208 examines, for example, the suggestion that there may be a global metacommunity of
209 SDTF (Pennington *et al.* 2009).
- 210 2. Alternatively, do different formations (savannas, moist forests, SDTF) cluster
211 floristically by continent? If they do cluster geographically, this would refute the
212 global metacommunity hypothesis and suggest independent evolutionary assembly of
213 the vegetation formations on each continent.
- 214 3. Do formations in Africa and Asia that are termed “dry forests” or “woodland” show
215 floristic relationships to Neotropical SDTF or savannas? A closer relationship with
216 Neotropical savannas might be expected if they are grass-rich and fire prone.

217

218 METHODS

219 **Data Sources**

220 To compare the floristic composition of different woody tropical vegetation formations
221 within and amongst continents, we assembled tree inventory data from South America,

222 Africa, and Asia - three continents with major portions of their area in the tropics (Fig. 1). We
223 aimed to obtain data from formations in dry as well as moist areas. Woody formations in
224 drier areas have been subject to many designations, including SDTF, deciduous forests,
225 woodlands, and savannas, while forests from moist areas have been more consistently
226 referred to as wet, moist, or rain forest. We classified plots into major vegetation formations
227 based on available metadata (i.e. from the associated journal article for published plots or
228 from the data provider for unpublished plots). We did not include data from islands as they
229 may confound analyses because of divergent floristic composition resulting from isolation.
230 We therefore did not include tropical Malesia (e.g. Borneo, New Guinea, etc.), which, while
231 comprising an extensive part of the Asian tropics, are also of lesser interest in this study as
232 they have little dry vegetation. The inventory data primarily consisted of 1 ha plots that
233 measured the diameter of and identified all trees >10 cm diameter at breast height (DBH),
234 except where noted in below or in Table S1. We only included plots where >90% of stems
235 were identified to genus.

236

237 **South America**

238 Our plot data for South America primarily comes from RAINFOR plots curated in the
239 ForestPlots.net database (Lopez-Gonzalez *et al.* 2011; www.forestplots.net; extraction date:
240 Sept. 30th, 2013), which consists of a network of 1 ha tree plots that monitor the composition,
241 structure, and biomass of forests across the Amazon. The RAINFOR plot network extends
242 into drier areas at its eastern and southern borders, and we restricted analyses to plots in wet
243 or moist forest (n = 60), SDTFs (n = 10), and savannas (n = 10) in the southern and eastern
244 Amazon and neighbouring areas (found in Bolivia and Brazil). Additionally, we surveyed the
245 published literature, obtaining tree plot data for SDTFs from the Brazilian states of Bahia,

246 Goias, Distrito Federal, Mato Grosso, and Mato Grosso do Sul (n = 12; details in Table S1).

247 Across all South American plots, 3.6% of individual stems were not identified to genus.

248

249 **Africa**

250 Our data for Africa come primarily from the AfriTRON network (Lewis *et al.* 2013), which

251 is also curated in the ForestPlots.net database (Lopez-Gonzalez *et al.* 2011;

252 www.forestplots.net; extraction date June 13th, 2013), which consists of 1 ha plot data from

253 primarily wet or moist forests in the Congo basin and the West African Guinean region (n =

254 64). Several plots from the database are located in savanna at the northern edge of African

255 wet forests (n = 5; see Fig. 1). Additionally we obtained data from five 1 ha plots in savanna

256 in Sierra Leone (from Ottamba Killimi National Park; M.P. Bessike Balinga, unpubl. data).

257 Two of the major habitat types in tropical Africa proper (between 23°S and 23°N) that have

258 commonly been considered as a form of tropical dry forest are Miombo woodlands, which

259 occur across Africa south of the Congo basin (Campbell *et al.* 1995, Chidumayo 2013), and

260 thornveld or scrub forest in the Horn of Africa (Schrire *et al.* 2005). We were unable to

261 obtain 1 ha plot data from the Horn of Africa, but do include data from a 10 ha plot in

262 Miombo woodlands in the southeastern Democratic Republic of the Congo (J. Ilunga-Muledi

263 and P. Meerts, unpubl. data), which we subdivided into 1 ha plots to allow for comparison

264 with the other 1 ha plot data. Across all African plots, 2.8% of individual stems were not

265 identified to genus.

266

267 **Asia**

268 There are extensive forested regions in tropical Asia in both India and Indochina. We

269 obtained forest plot data for India from two primary sources: 1) a series of 1 ha plots from

270 wet evergreen forest (n = 15) in the Western Ghats and dry evergreen forest (n = 16) from

271 across southeastern India (Anbarashan and Parthasarathy 2008, 2013, Ayyappan and
272 Parthasarathy 2001, Chittibabu and Parthasarathy 2000, Mani and Parthasarathy 2005,
273 Muthuramkumar *et al.* 2006, Parthasarathy and Karthikeyan 1997a, 1997b, Parthasarathy and
274 Sethi 1997, Srinivas and Parthasarathy 2000, Venkateswaran and Parthasarathy 2003) and 2)
275 a series of 25 m x 25 m plots in wet evergreen (n = 155) and deciduous forest (n = 44) in the
276 Western Ghats that sample individuals >10 cm in circumference at breast height (N. Page,
277 unpubl. data). We combined neighbouring plots together where possible to approach the
278 sample size, in terms of individuals, present in 1 ha plots (see Table S1).

279 We obtained data from Indochina from two sources. From Cambodia, we sourced data
280 from a series of 0.1 ha plots from the central plains region (Theilade *et al.* 2011, I. Theilade,
281 unpubl. data). We combined neighbouring plots within the same habitat type to create a total
282 of 10 ‘plots’ with sufficient sample size. The majority of the plots were in wet evergreen
283 forest (n = 7), such as riverine, swamp, or tall dipterocarp forest, while three plots were in
284 deciduous or semi-deciduous forest such as dry dipterocarp forest and sralao forest, a habitat
285 dominated by trees of the genus *Lagerstroemia* (Lythraceae). From Vietnam, we obtained
286 data for four 1 ha plots in evergreen forest from Cat Tien National Park from the literature
287 (Blanc *et al.* 2000). Across all Asian plots, 0.3% of individual stems were not identified to
288 genus.

289

290 **Data Standardization and Analyses**

291 We ran all datasets through the Taxonomic Name Resolution Service v3.2
292 (<http://tnrs.iplantcollaborative.org>; Boyle *et al.* 2013), which corrects misspellings and
293 standardizes synonyms based on several botanical databases, most importantly, in this
294 instance, the Missouri Botanic Garden’s Tropicos database (<http://www.tropicos.org>). As few
295 species are found on more than one continent, we did not find species-level analyses to be

296 appropriate for comparing floristic similarity of vegetation formations within and amongst
297 continents. In contrast, no family was restricted to a single vegetation formation or a single
298 continent, and we therefore did not consider that analyses at this taxonomic level would be
299 useful for comparisons either; most plots show high floristic similarity with little variation in
300 values. Consequently, we conducted all analyses at the genus level, excluding individuals that
301 were not identified to genus. The final matrix for analysis comprised 1078 genera, 269 plots,
302 and 120,691 individual trees.

303 We used the Sorensen distance (Sorensen 1948) to determine how divergent
304 individual pairs of plots were in their genus composition. The Sorensen distance for each pair
305 of plots was calculated as $(A+B-2*J)/(A+B)$ where A is the number of genera in plot A, B is
306 the number of genera in plot B, and J is the number of genera shared between plots A and B.
307 We used the Sorensen distance matrix as the basis for a hierarchical clustering analysis of
308 plots. We implemented the clustering using the recluster package (Dapporto *et al.* 2013) in
309 the R Statistical Environment v. 3.0.1 (R Core Development Team 2013). This approach is
310 advantageous because it adds plots randomly to the clustering analysis, repeats this process as
311 many times as the user decides (in our case 100 times, which was well above the threshold at
312 which a stable solution was reached), and generates a consensus tree from all random
313 addition replicates, thus avoiding biases in plot entry order to which other clustering
314 approaches are susceptible (Dapporto *et al.* 2013). We additionally conducted a bootstrap
315 analysis, resampling the same number of genera in the original plots with replacement 1000
316 times, to assess support for the clusters obtained. Finally, we used multiple agglomeration
317 methods to link clusters, including single linkage, complete linkage, average linkage, and
318 Ward's minimum variance method (Borcard *et al.* 2011).

319 We also used the Sorensen distance matrix as the basis for ordination of plots using
320 non-metric multidimensional scaling (NMDS) in the vegan package (Oksanen *et al.* 2013) of

321 the R Statistical Environment. We began the analysis with two axes and added axes until the
322 stress value dropped below 0.1, an arbitrary threshold that indicates a reasonably stable
323 solution (Borcard *et al.* 2011). In all cases, we used 20 random starts and ensured
324 convergence among runs. All of the above analyses were repeated using Jaccard and Simpson
325 distances among plots to assess the robustness of results to different distance indices.

326 In order to compare directly the influence of continent versus vegetation formation on
327 floristic similarity, we conducted a series of analyses of variance of distance matrices,
328 equivalent to permutational MANOVA (Anderson 2001), using functions in the vegan
329 package (Oksanen *et al.* 2013). We used continental region and vegetation formation as
330 explanatory variables, both individually and together. The moist vegetation formation was
331 found in all continental regions, while dry vegetation formations varied: savanna and SDTF
332 in South America, savanna and miombo woodland in Africa, deciduous and dry evergreen
333 forest in India, and deciduous forest in Indochina. Given uncertainty about whether dry
334 vegetation formations on different continents actually represent the same units, we compared
335 analyses with plots assigned to their original vegetation formation versus various possible
336 combinations of dry formations. The simplest scheme consisted of assigning all plots from
337 dry formations to a single category to contrast with moist forest. This categorisation allowed
338 us to assess statistically a potential interaction between continent and vegetation type. We
339 also considered schemes where different dry formations in Africa and Asia were lumped with
340 Neotropical savanna or SDTF. Additionally, we conducted an analysis where each vegetation
341 formation in each continental region was given a distinct vegetation category (*e.g.* the
342 savannas of South America and Africa were assigned to different categories). Lastly, given
343 observed floristic differentiation between India and Indochina, we conducted analyses both
344 where these were distinguished in continental region assignments and where they were
345 lumped together as ‘Asia’.

346

347 RESULTS

348 Plots from different continents consistently show high Sorensen distances, with a minimum
349 value of 0.71, indicating that the two most similar plots from different continents share 29%
350 of their genera, and a modal value of 1.00, indicating that most plots from different continents
351 do not share any genera at all. In contrast, plots within continents show a broad range of
352 Sorensen distances from 0.10 to 1.00.

353 All of the plots from a given vegetation formation on a given continent cluster
354 together, and we refer to these primary clusters as ecogeographic units (Fig. 2). The
355 relationships of ecogeographic units show some support for the role of geography in
356 determining floristic similarity, while vegetation formations from different continents never
357 cluster together. For example, all of the plots from South America form a well-supported
358 cluster (>70% bootstrap support), and the three major vegetation formations are clearly
359 distinct from each other. African wet forests are sister to the rest of the ecogeographic units
360 from Asia and Africa. The relationships of the remaining ecogeographic units from Africa
361 and Asia are unclear (Fig. 2). Moist and deciduous forests from Indochina cluster together,
362 rather than with the corresponding vegetation formation from India, showing that geography
363 is important even within Asia. These results were robust to the agglomeration method used to
364 link clusters.

365 Our ordination analyses also suggest the pre-eminence of geography in determining
366 floristic relationships (Fig. 3A), while also demonstrating the clear importance of vegetation
367 formation (Fig. 3B). We used an NMDS ordination with four axes, as this was the lowest
368 number of axes that had a stress value under 0.1 (stress = 0.088). The first two axes clearly
369 segregate plots from different continents, irrespective of their vegetation type. If an NMDS
370 ordination is conducted with only two axes (results not shown, stress = 0.185), an identical

371 result is obtained, suggesting that geography is the first factor that determines the floristic
372 similarity of plots. The third and fourth axes separated plots in moist forests from those in
373 savannas and other dry formations (e.g. SDTFs, Miombo woodlands). That all continents
374 show this moist versus dry segregation within the same ordination does suggest that there is
375 some floristic signal for moist versus drier formations that is the same on each continent.
376 Nevertheless, African savannas are clearly floristically distinct from South American
377 savannas, while there is also limited support, especially from the clustering analysis, for
378 segregation of the different dry forest/woodland categories on different continents.

379 Analyses of variance of the Sorensen distances among plots also showed a
380 predominant influence of geography. Continent alone explained 27.3% of the variation in
381 distance values, while the original vegetation formation delimitations explained 19.6%. When
382 continent and vegetation formation were combined in a multivariate analysis, continent
383 explained 27.3% and vegetation formation 18.3%. Any other possible scheme of combining
384 savanna and dry forest formations resulted in less variation explained by vegetation
385 formation. If we lumped all dry formations into one category to allow for an assessment of
386 interaction between continent and vegetation formation, we found that continent explained
387 27.2%, habitat 5.7%, and their interaction 8.6%. The best model, in terms of percentage of
388 variation explained (49.3%), was that which distinguished all vegetation formations on
389 different continents as belonging to different categories. When India and Indochina were
390 lumped together as one continental region, nearly identical results were obtained, although
391 the amount of variation explained by continent was reduced by an average of 2%. All results
392 were qualitatively similar when Jaccard or Simpson distances were used instead of Sorensen
393 distances for analyses.

394

395 DISCUSSION

396 **The floristics and biogeography of vegetation in seasonally dry regions of the tropics**

397 Moist forests in the Neotropics, Africa, and Asia are typically considered the same biome,
398 despite differences in floristic composition (Pennington *et al.* 2009). However, inter-
399 continental floristic and ecological comparisons of SDTF are exceedingly rare, and so the
400 idea of a global “dry forest” biome is still controversial and poorly tested. A previous
401 intercontinental analysis of the biogeography of the Leguminosae (Schrire *et al.* 2005)
402 suggested the existence of a “succulent” biome, which encompasses regions corresponding to
403 SDTF in both the Neotropics and the Paleotropics, whereas a floristic comparison of African
404 and Neotropical SDTF showed that the vegetation of the two continents, despite their
405 similarity in physiognomy, is made up of different assemblages of families and genera (Lock
406 2006).

407 The fundamental floristic units found in our hierarchical clustering analysis consist of
408 individual vegetation formations within continents (Fig. 2). Similar vegetation formations
409 from different continents (e.g. savanna) clearly do not cluster together, thus falsifying the
410 hypothesis that there are global metacommunities for different vegetation formations.
411 Meanwhile, there is a substantial signal for geography in the clustering results. For example,
412 the three vegetation formations from South America, while clearly distinct from each other,
413 form a strongly supported cluster, and all plots from Indochina cluster together rather than
414 with plots of the corresponding vegetation formation from India (Fig. 2). The ordination
415 analyses also support the pre-eminence of geography in determining the floristic similarity of
416 vegetation formations (Fig. 3A). Finally, our analyses of variance of Sorensen distance values
417 further highlight the importance of geography and clearly demonstrated that vegetation
418 formations on different continents are more divergent in floristic composition than any
419 vegetation formations within continents.

420 Our clustering results also suggest that South America is more isolated from Africa
421 and Asia than either of the latter two continents are from each other (Fig. 2). This conclusion
422 is supported by our NMDS analysis, the first axis of which clearly separated South American
423 plots from African and Asian plots (Fig. 3A). Indeed, of the 477 genera found in South
424 American plots, 67 are found in African plots and 64 are found in Asian plots, while African
425 and Asian plots share 96 genera overall (with 389 and 396 total genera respectively).

426 Our ordination analyses show a common floristic signal across continents for
427 segregation of wet versus dry vegetation formations (evident in Fig. 3B), but the analyses do
428 not allow us to classify the different dry formations across continents with respect to each
429 other. Only in the Neotropics are savanna and SDTF clearly distinguished in our floristic
430 analyses (Fig. 2), which corroborates their *a priori* distinction here and in the literature (e.g.,
431 Pennington *et al.* 2006). However, it is evident that plots classified *a priori* as savanna in
432 South America and Africa do not show great floristic similarity (Fig. 3B), while the various
433 dry forest formations from different continents all fall out as separate clusters in our
434 clustering analyses (Fig. 2). Furthermore, the analyses of variance demonstrate that the best
435 categorisation scheme incorporates different categories for superficially similar vegetation
436 formations on different continents (e.g. savanna from South America should comprise a
437 separate category from savanna in Africa). In other words, the analyses suggest that there
438 should not be any common vegetation units across continents, at least not based on floristics.

439 Thus, it seems that we cannot use these floristic analyses to determine whether the
440 various dry vegetation formations in Africa and Asia correspond better to Neotropical
441 savanna or SDTF. Rather, to classify palaeotropical dry vegetation types as savanna vs.
442 SDTF (*sensu* Neotropical definitions), one would have to rely on information besides woody
443 plant floristic composition, such as the presence vs. absence of C4 grasses and succulents or
444 the frequency of fires (e.g., Torellos-Raventos *et al.* 2013). For example, based upon their

445 ecological characteristics of richness in C4 grasses and propensity to burn, we suggest that
446 many formations termed “forest” or “woodland” in Africa and Asia, including all of those
447 analysed here, are better considered as savannas. We acknowledge that there are many types
448 of vegetation in Africa and Asia that we have not assessed, *e.g.* *Baikiaea* (Leguminosae)
449 woodlands (Pearce 1984) and *Cryptosepalum* (Leguminosae) dry forests in Angola,
450 Democratic Republic of Congo, and Zambia (White 1983) and the coastal woodlands of
451 Mozambique and Tanzania (Burgess and Clarke 2000), which may not have a propensity to
452 burn and may be analogous to SDTF (*sensu* Neotropical definitions). The frequency of fires
453 as a determinant of vegetation type in the tropics is supported by the observation that
454 anthropogenic fires in SDTFs lead to their substitution by savannas (Saha and Howe 2003,
455 Wanthongchai and Goldammer 2011). Conversely, in the absence of fire, savanna vegetation
456 may eventually grow into a closed canopy forest (*i.e.* an SDTF) that can then exclude C4
457 grasses and fire, particularly on more fertile soils (Durigan 2006, Lawes et al. 2011,
458 Woinarski *et al.* 2004).

459 Tropical savannas are geologically young, dating from the late Miocene (Beerling and
460 Osborne 2006, Cerling *et al.* 1997, Jacobs *et al.* 1999), and SDTF in the Neotropics, though
461 older, postdates the origin of tropical moist forests (Becerra 2005, Pennington *et al.* 2006).
462 The antiquity of tropical moist forests relative to drought-adapted formations implies that the
463 continentally structured floristic patterns we have found are largely a result of isolated
464 continental floras evolving independently to occupy a seasonally dry environmental niche,
465 rather than the result of the same drought-adapted lineages dispersing across the globe to
466 reach dry environments. This result implies that though intercontinental migration has
467 undoubtedly been important in tropical plant biogeography (*e.g.*, Pennington and Dick 2004),
468 the effect of *in situ* diversification on continents may have been greater. This can be
469 illustrated by considering that only 88 of 477 genera (~20%) in our South American plots are

470 even found in Africa and Asia. The fact that many eudicot families that are dominant in
471 tropical vegetation date only to the late Cretaceous (Magallon *et al.* 1999) implies that the
472 origin of most of these genera – a lower taxonomic level – will be later and therefore post-
473 dates Gondwanan vicariance. Hence, long-distance dispersal is likely to have been important
474 in their biogeography. A corollary suggestion is that the genera restricted to the Neotropics in
475 our dataset (c. 80%) are likely to have had a neotropical origin. However, we note that this is
476 a very approximate estimate as some of the 20% of widespread genera may also have had a
477 neotropical origin, and some of the 80% apparently restricted to the Neotropics may be found
478 in Africa and Asia outside of the plots we examined.

479 Recent work on the evolution of plant lineages found in the savannas of South
480 America and Africa corroborate the view of *in situ* continental evolution (Maurin *et al.* 2014,
481 Simon *et al.* 2009, Simon and Pennington 2012). Plants occupying these savannas have sister
482 groups in the other vegetation types of each continent such as moist forests and SDTF.
483 Woody lineages occupying the savannas in Africa and South America are not the result of a
484 dispersal of fire adapted species from another part of the global savanna biome, but are
485 instead a result of multiple local lineages evolving fire adaptations and expanding into the
486 savanna niche. It seems that the evolutionary barrier preventing the entry of lineages into
487 savannas is relatively weak, and that plants from other types of vegetation have evolved the
488 fire adaptations (such as root-sprouting and corky bark) needed to survive fire-prone
489 savannas relatively easily (Pennington and Hughes 2014, Simon and Pennington 2012). Our
490 results showing clustering of different vegetation types, including savanna, by continent,
491 support this idea of local lineages evolving *in situ* to fill niches in other environments.

492

493 **Implications for conservation and management**

494 Dry forests have been defined in many different ways. In the context of this journal volume,
495 it is worth considering that CIFOR has adopted the FAO's concept of "dry forests" (FAO,
496 2001), which encompasses both formations that we would classify as SDTF and as savanna.

497 In ecological terms, SDTF and savannas have features in common that are related to
498 rainfall seasonality. Rainfall is a dominant ecological force affecting temporal patterns of
499 biological activity such as growth and reproduction, which are synchronised with water
500 availability (McLaren and McDonald 2005, Murphy and Lugo 1986, Silva *et al.* 2011). Litter
501 production is also influenced by seasonality and occurs during the dry season, when litterfall
502 is at its maximum (Murphy and Lugo 1986), with cascading effects on the timing of essential
503 nutrient fluxes, microbial dynamics, and vegetation growth in savannas and dry forests
504 (Lawrence 2005). However, despite these similarities, SDTF and savannas are ecologically
505 distinct in the Neotropics (Pennington *et al.* 2000; see above), especially in the prevalence of
506 natural fires, which are much more frequent in savannas. Therefore, in terms of fire
507 resistance, dry forests and savannas require different management strategies. For example,
508 fire is an essential tool to maintain savanna structure and biodiversity, since in its absence the
509 woody plant cover increases (Durigan 2006, Lawes *et al.* 2011, Woinarski *et al.* 2004). In
510 contrast, a neotropical SDTF is adversely affected by fire, because its woody plants,
511 especially the succulent element from the Cactaceae family, lack the necessary adaptations to
512 fire.

513 As our results have demonstrated, we cannot use floristic analyses to relate
514 neotropical SDTF and savannas with palaeotropical dry vegetation. Dry forests that are
515 physiognomically similar to neotropical SDTF (*sensu* Pennington *et al.* 2000) may cover only
516 a small part of Africa (Lock 2006). Some possible examples are the deciduous bushlands and
517 thickets of the Horn of Africa, which may be considered ecologically equivalent to the
518 caatinga dry forest in northeastern Brazil (Lock 2006). In Asian dry forests, fire-sensitive

519 succulents are almost absent and, due to their propensity to burn, we suggest that many Asian
520 “dry forests” should be classified as savannas.

521 Although fire is considered a natural feature of “dry forests” in Africa and Asia, its
522 frequency is now probably much higher than it has been historically (McShea and Davies
523 2011, Timberlake *et al.* 2010), with possible negative consequences such as invasion by alien
524 species (Hiremath and Sundaram 2005). When burning frequency is inappropriate, dry forests
525 in the tropics often degrade to more open formations or convert to other land-use systems
526 (Wanthongchai and Goldammer 2011). In this context, and regardless of the classification
527 adopted, management systems need to be carefully designed to incorporate the peculiarities
528 of each landscape and their different levels of resistance to fire. Consequently, more research
529 is needed, particularly to address the spatial and temporal effects of burning, so as to design
530 appropriate fire management systems (Wanthongchai and Goldammer 2011).

531 A second, longer term management and conservation issue is the spectre of climate
532 change, and how this may change the distributions of moist forests, savannas and SDTFs. In
533 this context, the key differences in soil preference of SDTF and savannas needs consideration
534 in models such as dynamic global vegetation models (DGVMs). For example, if climates
535 warm and become more seasonal in moist forest areas, SDTF species will not spread into
536 these areas unless fertile soils are present. Whilst consideration of soil variables has been
537 included in some discussions of palaeovegetation changes (e.g., Pennington *et al.* 2000; Slik
538 *et al.* 2011), it has yet to be used in hind-casting of quantitative species-distribution models
539 (e.g., Werneck *et al.* 2012) or in DGVMs.

540 The result presented here – different vegetation types clustering floristically by
541 continent – means that pantropical biological generalisations should be drawn with care, even
542 within the ecologically defined savanna and SDTF categories. For example, while tropical
543 savannas can be globally defined by an abundance of C4 grasses and propensity to burn,

544 because they contain different woody plant lineages on each continent, it may be hard to
545 generalise studies of resilience or ecosystem rehabilitation from one continent to another.
546 With regard to forest management, the lack of floristic identity between neotropical and
547 paleotropical SDTF and savannas makes cross-continental comparison in some contexts
548 almost meaningless. For example, a species-specific analysis and a demographic approach
549 are preconditions for evaluating whether timber and non-timber forest products harvesting is
550 sustainable or not (Sutherland 2001).

551 Our findings that global SDTF or savanna biomes may not exist from the floristic
552 standpoint are not in disagreement with the proposition of a global conservation plan or
553 strategy for seasonally dry tropical regions. Both SDTF and savannas have experienced
554 extensive deforestation (Aide *et al.* 2013), so the adoption of a broad concept is strategic to
555 call attention to tropical dry biomes, which have been neglected historically in both research
556 and conservation efforts. Many of the global threats to SDTF and savannas are similar (e.g.,
557 mineral exploration, expansion of agricultural frontiers) and successful experiences to protect
558 the remaining vegetation, as well as contributions to sustainable livelihoods in dry areas,
559 certainly need to be shared. Because SDTF and savannas often occur as mosaics together and
560 with other vegetation types, conservation strategies should consider their inter-connections
561 and links with other types of vegetation and land-use systems at the landscape level.
562 However, we emphasise that any conservation strategy for SDTF and savannas should take
563 into account the distinctiveness of their flora in each tropical region.

564

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585

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864 FIGURE LEGENDS

865 **Figure 1:** Distribution of the 269 forest inventory plots used in this study from A) South
866 America, B) Africa, and C) Asia, along with D) vegetation type. All plots are from within the
867 tropics *sensu stricto* (between 23°S and 23°N).

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869 **Figure 2:** Hierarchical clustering of all plots using pairwise Sorensen distances between plots
870 and the average linkage method for grouping clusters. The different geographic/vegetation
871 type clusters are labeled and colored by the their *a priori* vegetation type designation (green =
872 wet forest; yellow = savanna; orange = dry forest/woodland).

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874 **Figure 3:** Results of the Non-metric Multidimensional Scaling (NMDS) analysis with four
875 axes (stress = 0.088; see text for details). **A)** The first two axes segregate plots by continent;
876 **B)** the third and fourth axes segregate the plots into dry versus wet vegetation types within
877 continents. Symbols are coloured by continent and vegetation type following the legend in
878 Figure 1D.

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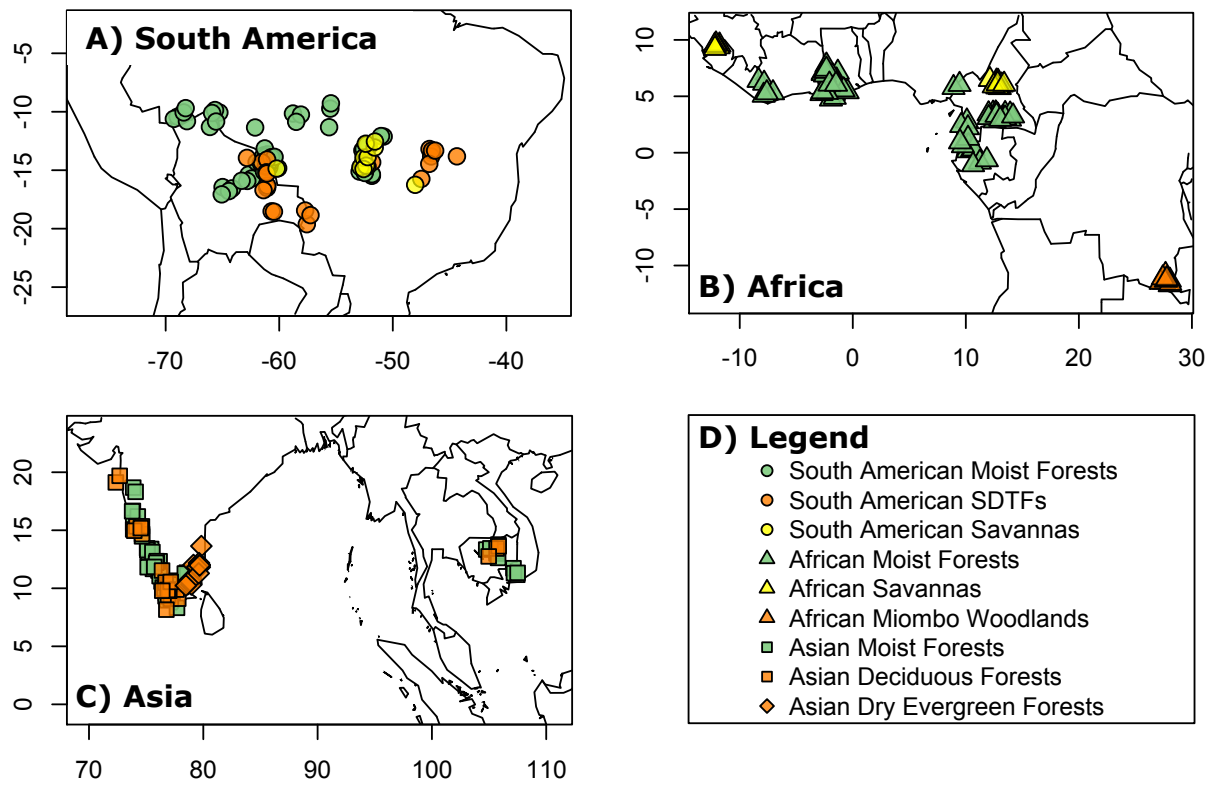
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889 **Figure 1**



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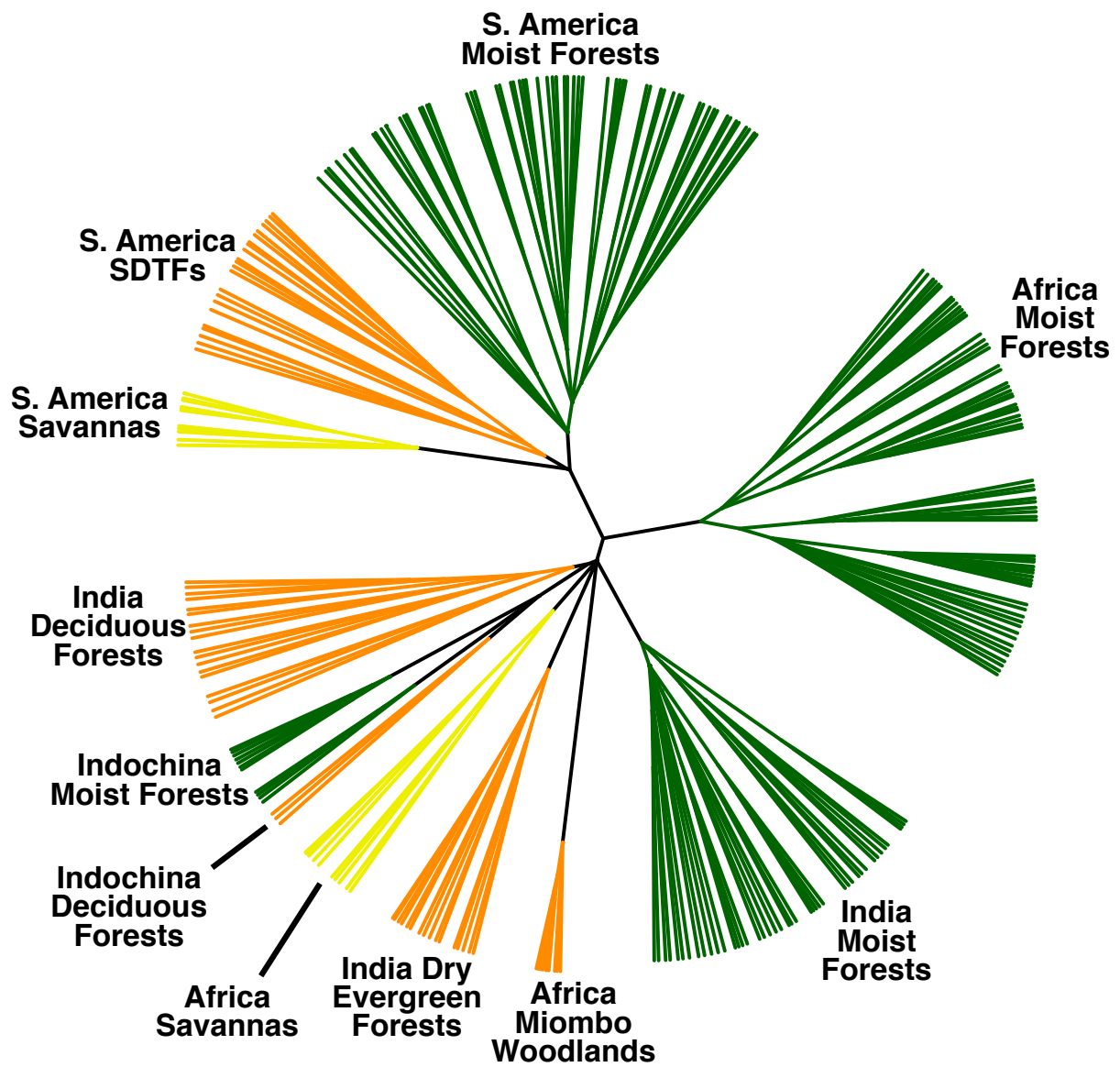
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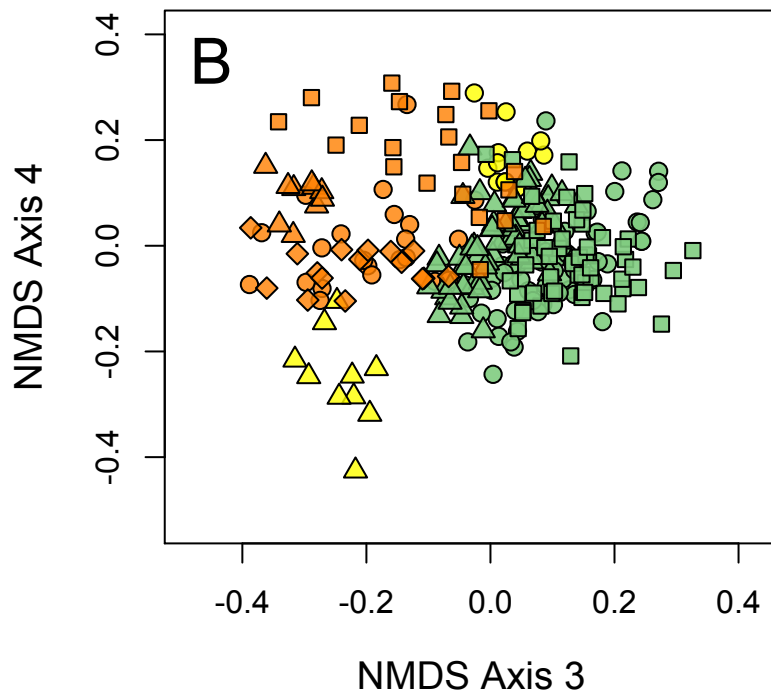
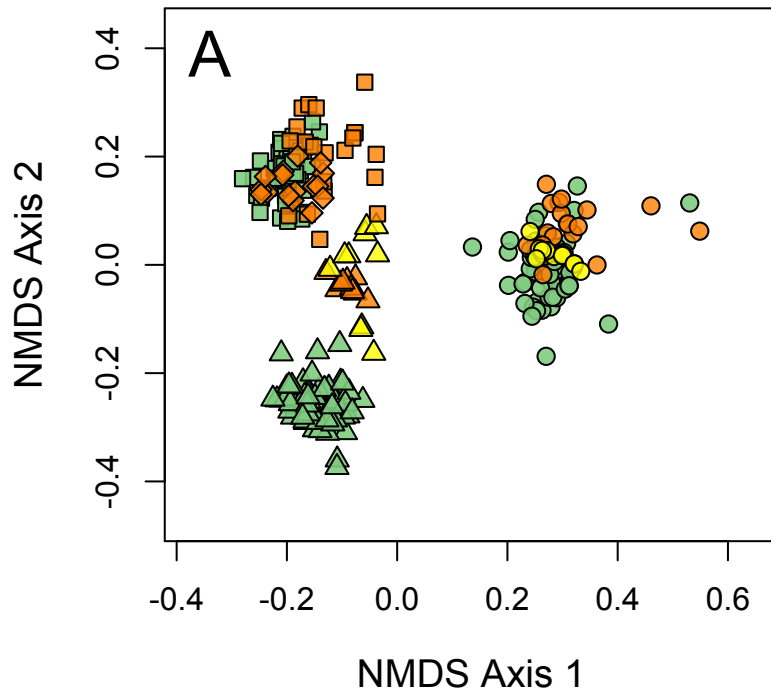
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919 **Table S1.** Metadata and relevant publications for all plots used in analyses.

Continent	Country	Vegetation Type	Plot Code	Latitude	Longitude	Total Area (ha)	Number of Plots	Min. Size (cm DBH)	Number of Individuals	Citation
Africa	DR Congo	Miombo Woodlands	mikembo1	-11.48	27.67	1	1	10	402	S1
Africa	DR Congo	Miombo Woodlands	mikembo2	-11.48	27.67	1	1	10	441	S1
Africa	DR Congo	Miombo Woodlands	mikembo3	-11.48	27.67	1	1	10	439	S1
Africa	DR Congo	Miombo Woodlands	mikembo4	-11.48	27.67	1	1	10	509	S1
Africa	DR Congo	Miombo Woodlands	mikembo5	-11.48	27.67	1	1	10	376	S1
Africa	DR Congo	Miombo Woodlands	mikembo6	-11.48	27.67	1	1	10	381	S1
Africa	DR Congo	Miombo Woodlands	mikembo7	-11.48	27.67	1	1	10	496	S1
Africa	DR Congo	Miombo Woodlands	mikembo8	-11.48	27.67	1	1	10	404	S1
Africa	DR Congo	Miombo Woodlands	mikembo9	-11.48	27.67	1	1	10	623	S1
Africa	DR Congo	Miombo Woodlands	mikembo10	-11.48	27.67	1	1	10	468	S1
Africa	Cameroon	Savanna	MDJ.02	6.16	12.82	1	1	10	135	S2
Africa	Cameroon	Savanna	MDJ.04	6.00	12.87	1	1	10	212	S2
Africa	Cameroon	Savanna	MDJ.06	6.00	12.89	1	1	10	309	S2
Africa	Cameroon	Savanna	MDJ.08	6.21	12.75	1	1	10	240	S2

Africa	Cameroon	Savanna	MDJ.09	6.01	12.89	0.4	1	10	43	S2
Africa	Sierra Leone	Savanna	OKNP01	9.67	12.14	1	1	10	270	S3
Africa	Sierra Leone	Savanna	OKNP02	9.70	12.15	1	1	10	225	S3
Africa	Sierra Leone	Savanna	OKNP03	9.61	12.48	1	1	10	382	S3
Africa	Sierra Leone	Savanna	OKNP04	9.76	12.49	1	1	10	227	S3
Africa	Sierra Leone	Savanna	OKNP05	9.83	12.38	1	1	10	285	S3
Africa	Ghana	Wet Forest	ASU.01	7.14	-2.45	1	1	10	347	S2, S4
Africa	Ghana	Wet Forest	ASU.02	7.13	-2.47	1	1	10	364	S5
Africa	Ghana	Wet Forest	ASU.88	7.16	-2.45	1	1	10	149	S6
Africa	Ghana	Wet Forest	ASU.99	7.13	-2.47	1	1	10	115	S5
Africa	Ghana	Wet Forest	BBR.14	6.71	-1.29	1	1	10	490	S7
Africa	Ghana	Wet Forest	BBR.16	6.70	-1.29	1	1	10	566	S7
Africa	Ghana	Wet Forest	BBR.17	6.69	-1.28	1	1	10	455	S7
Africa	Cameroon	Wet Forest	BIS.01	3.30	12.48	1	1	10	330	S8
Africa	Cameroon	Wet Forest	BIS.02	3.29	12.48	1	1	10	491	S8
Africa	Cameroon	Wet Forest	BIS.03	3.22	12.49	1	1	10	331	S8
Africa	Cameroon	Wet Forest	BIS.04	3.21	12.50	1	1	10	434	S8
Africa	Cameroon	Wet Forest	BIS.05	3.31	12.49	1	1	10	325	S8

Africa	Cameroon	Wet Forest	BIS.06	3.31	12.49	1	1	10	436	S8
Africa	Ghana	Wet Forest	BOR.05	5.35	-1.83	1	1	10	337	S7
Africa	Ghana	Wet Forest	BOR.06	5.35	-1.84	1	1	10	430	S7
Africa	Cameroon	Wet Forest	CAM.01	2.36	9.93	1	1	10	403	S8
Africa	Cameroon	Wet Forest	CAM.02	2.31	9.92	1	1	10	419	S8
Africa	Cameroon	Wet Forest	CAM.03	2.42	9.90	1	1	10	404	S8
Africa	Ghana	Wet Forest	CAP.09	4.85	-2.04	1	1	10	516	S8
Africa	Ghana	Wet Forest	CAP.10	4.80	-2.05	1	1	10	508	S8
Africa	Liberia	Wet Forest	CVL.01	6.19	-8.18	1	1	10	503	S8
Africa	Liberia	Wet Forest	CVL.11	6.19	-8.18	1	1	10	458	S8
Africa	Cameroon	Wet Forest	DJK.01	3.33	12.72	1	1	10	314	S8
Africa	Cameroon	Wet Forest	DJK.02	3.33	12.72	1	1	10	407	S8
Africa	Cameroon	Wet Forest	DJK.03	3.36	12.72	1	1	10	343	S8
Africa	Cameroon	Wet Forest	DJK.04	3.36	12.73	1	1	10	477	S8
Africa	Cameroon	Wet Forest	DJK.05	3.32	12.76	1	1	10	371	S8
Africa	Cameroon	Wet Forest	DJK.06	3.33	12.76	1	1	10	432	S8
Africa	Cameroon	Wet Forest	DJL.01	3.12	13.58	1	1	10	351	S8
Africa	Cameroon	Wet Forest	DJL.02	3.12	13.59	1	1	10	435	S8

Africa	Cameroon	Wet Forest	DJL.03	3.04	13.62	1	1	10	429	S8
Africa	Cameroon	Wet Forest	DJL.04	3.05	13.62	1	1	10	613	S8
Africa	Cameroon	Wet Forest	DJL.05	3.03	13.58	1	1	10	320	S8
Africa	Cameroon	Wet Forest	DJL.06	3.03	13.61	1	1	10	496	S8
Africa	Ghana	Wet Forest	DRA.04	5.16	-2.38	1	1	10	422	S7
Africa	Ghana	Wet Forest	DRA.05	5.21	-2.44	1	1	10	409	S7
Africa	Cameroon	Wet Forest	EJA.04	5.75	8.99	1	1	10	556	S8
Africa	Cameroon	Wet Forest	EJA.05	5.75	8.99	1	1	10	559	S8
Africa	Ghana	Wet Forest	ESU.18	5.86	-0.80	1	1	10	450	S7
Africa	Ghana	Wet Forest	ESU.20	5.83	-0.78	1	1	10	541	S6
Africa	Ghana	Wet Forest	FUR.07	5.56	-2.39	1	1	10	576	S7
Africa	Ghana	Wet Forest	FUR.08	5.58	-2.39	1	1	10	563	S7
Africa	Liberia	Wet Forest	GBO.01	5.39	-7.62	1	1	10	364	S8
Africa	Liberia	Wet Forest	GBO.11	5.39	-7.59	1	1	10	424	S8
Africa	Liberia	Wet Forest	GBO.20	5.41	-7.59	1	1	10	339	S8
Africa	Gabon	Wet Forest	LM	-0.19	11.58	1.2	15	10	488	S8
Africa	Gabon	Wet Forest	MDC.01	0.62	10.41	1	1	10	531	S8
Africa	Gabon	Wet Forest	MDC.02	0.62	10.41	1	1	10	547	S8

Africa	Gabon	Wet Forest	MDC.03	0.62	10.42	1	1	10	518	S8
Africa	Gabon	Wet Forest	MDC.04	0.47	10.28	1	1	10	506	S8
Africa	Gabon	Wet Forest	MDC.05	0.46	10.29	1	1	10	521	S8
Africa	Cameroon	Wet Forest	MDJ.01	6.17	12.83	1	1	10	558	S4
Africa	Cameroon	Wet Forest	MDJ.03	5.98	12.87	1	1	10	418	S4
Africa	Cameroon	Wet Forest	MDJ.07	6.01	12.89	1	1	10	449	S4
Africa	Cameroon	Wet Forest	MDJ.10	6.00	12.89	0.4	1	10	183	S4
Africa	Equat. Guinea	Wet Forest	MMI.01	1.39	9.92	1	1	10	416	S8
Africa	Equat. Guinea	Wet Forest	MMI.02	1.37	9.97	1	1	10	634	S8
Africa	Ghana	Wet Forest	TBE.05	7.01	-2.05	1	1	10	493	S7
Africa	Ghana	Wet Forest	TBE.08	7.02	-2.07	1	1	10	356	S6
Africa	Ghana	Wet Forest	TBE.09	7.02	-2.06	1	1	10	490	S6
Africa	Ghana	Wet Forest	TON.01	6.07	-2.12	1	1	10	458	S7
Africa	Ghana	Wet Forest	TON.08	6.04	-2.10	1	1	10	484	S7
Africa	Gabon	Wet Forest	WKA.09	-1.14	11.07	1	1	10	546	S8
Africa	Gabon	Wet Forest	WKA.10	-1.14	11.07	1	1	10	602	S8
Asia	India	Deciduous Forest	Akovil	9.52	77.45	0.125	2	3.18	188	S9
Asia	India	Deciduous Forest	Bathery	11.70	76.36	0.125	2	3.18	193	S9

Asia	India	Deciduous Forest	Bela	14.95	74.15	0.125	2	3.18	93	S9
Asia	India	Deciduous Forest	Bondla	15.43	74.10	0.125	2	3.18	166	S9
Asia	India	Deciduous Forest	Dand	15.16	74.63	0.375	6	3.18	284	S9
Asia	India	Deciduous Forest	Mbolly	10.37	76.88	0.125	2	3.18	206	S9
Asia	India	Deciduous Forest	Mulla	9.53	77.25	0.125	2	3.18	200	S9
Asia	India	Deciduous Forest	Mund	8.68	77.35	0.125	2	3.18	148	S9
Asia	India	Deciduous Forest	Nadke	14.99	74.21	0.125	2	3.18	182	S9
Asia	India	Deciduous Forest	Phan	18.65	73.00	0.375	6	3.18	740	S9
Asia	India	Deciduous Forest	Sthoppu	9.56	77.57	0.125	2	3.18	114	S9
Asia	India	Deciduous Forest	Tansa	19.60	73.24	0.125	2	3.18	100	S9
Asia	India	Deciduous Forest	Thek	9.59	77.17	0.125	2	3.18	327	S9
Asia	India	Deciduous Forest	Tkad	10.13	76.70	0.125	2	3.18	231	S9
Asia	India	Deciduous Forest	Top	10.49	76.84	0.125	2	3.18	63	S9
Asia	India	Deciduous Forest	Tyanai	8.53	77.50	0.125	2	3.18	111	S9
Asia	India	Deciduous Forest	Uthanni	10.13	76.72	0.125	2	3.18	158	S9
Asia	India	Deciduous Forest	Vasant	15.40	74.26	0.125	2	3.18	281	S9
Asia	Cambodia	Deciduous Forest (Dry Dipterocarp)	Cambodia1	12.92	105.61	0.5	10	10	302	S10

Asia	Cambodia	Deciduous Forest (Sralao)	Cambodia5	13.45	105.61	0.5	10	10	253	S10
Asia	Cambodia	Deciduous Forest (Sralao)	Cambodia6	13.44	105.53	0.6	12	10	203	S10
Asia	India	Dry Evergreen Forest	TDEF.AK	11.69	79.67	1	1	10	748	S11
Asia	India	Dry Evergreen Forest	TDEF.AR	10.45	79.08	1	1	10	511	S12
Asia	India	Dry Evergreen Forest	TDEF.CK	11.51	79.71	1	1	10	347	S13
Asia	India	Dry Evergreen Forest	TDEF.KK	11.72	79.67	1	1	10	654	S14
Asia	India	Dry Evergreen Forest	TDEF.KR	10.46	79.05	1	1	5	855	S12
Asia	India	Dry Evergreen Forest	TDEF.MM	10.48	79.11	1	1	10	358	S12
Asia	India	Dry Evergreen Forest	TDEF.OR	13.60	79.92	1	2	10	934	S11
Asia	India	Dry Evergreen Forest	TDEF.PP	12.55	79.87	1	1	10	870	S15
Asia	India	Dry Evergreen Forest	TDEF.PT	11.53	79.70	1	1	10	687	S16
Asia	India	Dry Evergreen Forest	TDEF.RP	10.00	78.81	1	1	10	522	S12
Asia	India	Dry Evergreen Forest	TDEF.SK	11.50	79.70	1	1	10	696	S16
Asia	India	Dry Evergreen Forest	TDEF.SP	9.98	78.81	1	1	10	470	S12
Asia	India	Dry Evergreen Forest	TDEF.SPD	11.67	79.70	1	1	10	292	S13
Asia	India	Dry Evergreen Forest	TDEF.SR	11.73	79.64	1	1	10	359	S13

Asia	India	Dry Evergreen Forest	TDEF.TM	11.72	79.68	1	1	10	390	S14
Asia	India	Dry Evergreen Forest	TDEF.VP	11.94	79.39	1	1	10	803	S13
Asia	India	Wet Forest	Ach	9.11	77.19	0.25	4	3.18	132	S9
Asia	India	Wet Forest	AG.1	13.52	75.08	1	1	10	600	S17
Asia	India	Wet Forest	AG.2	13.52	75.08	1	1	10	311	S17
Asia	India	Wet Forest	AG.3	13.52	75.08	1	1	10	580	S17
Asia	India	Wet Forest	Agu	13.51	75.08	0.375	6	3.18	214	S9
Asia	India	Wet Forest	Amb	15.94	74.00	0.375	6	3.18	242	S9
Asia	India	Wet Forest	Ans	15.01	74.38	0.5	8	3.18	410	S9
Asia	India	Wet Forest	Bhi	19.06	73.54	0.1875	3	3.18	87	S9
Asia	India	Wet Forest	Bra	12.08	75.80	1.25	20	3.18	714	S9
Asia	India	Wet Forest	COURT.1	9.25	77.25	1	1	10	546	S18
Asia	India	Wet Forest	Kat	14.27	74.75	0.6875	11	3.18	537	S9
Asia	India	Wet Forest	KMTR	8.59	77.35	0.6875	11	3.18	514	S9
Asia	India	Wet Forest	KO.KS	11.33	78.38	2	1	10	813	S19
Asia	India	Wet Forest	KO.MS	11.33	78.38	2	1	10	1190	S19
Asia	India	Wet Forest	KO.PS	11.33	78.38	2	1	10	1138	S19
Asia	India	Wet Forest	KO.VS	11.33	78.38	2	1	10	1309	S19

Asia	India	Wet Forest	Koy	17.44	73.71	0.1875	3	3.18	161	S9
Asia	India	Wet Forest	KS	10.47	76.83	0.375	6	3.18	252	S9
Asia	India	Wet Forest	Kud	13.24	75.16	0.5	8	3.18	356	S9
Asia	India	Wet Forest	Mak	12.09	75.76	0.1875	3	3.18	101	S9
Asia	India	Wet Forest	Nel	10.53	76.68	0.125	2	3.18	66	S9
Asia	India	Wet Forest	Nil	11.44	76.39	0.1875	3	3.18	106	S9
Asia	India	Wet Forest	Par	10.42	76.71	0.1875	3	3.18	93	S9
Asia	India	Wet Forest	Per	9.49	77.19	0.5625	9	3.18	381	S9
Asia	India	Wet Forest	Push	12.59	75.68	0.25	4	3.18	151	S9
Asia	India	Wet Forest	Rad	16.37	73.87	0.125	2	3.18	78	S9
Asia	India	Wet Forest	Radha	16.33	73.90	0.1875	3	3.18	223	S9
Asia	India	Wet Forest	Sch	8.88	77.14	0.4375	7	3.18	234	S9
Asia	India	Wet Forest	SilVal	11.12	76.44	0.625	10	3.18	399	S9
Asia	India	Wet Forest	Sub	12.63	75.65	0.1875	3	3.18	111	S9
Asia	India	Wet Forest	Tal	12.36	75.48	0.125	2	3.18	77	S9
Asia	India	Wet Forest	Tatte	10.12	76.77	0.1875	3	3.18	79	S9
Asia	India	Wet Forest	VA.AK	10.40	77.45	1	25	10	611	S20
Asia	India	Wet Forest	VA.IP	10.40	77.45	0.8	20	10	395	S20

Asia	India	Wet Forest	VA.LM	10.40	77.45	0.8	20	10	484	S20
Asia	India	Wet Forest	Valp	10.34	76.91	0.375	6	3.18	211	S9
Asia	India	Wet Forest	Vara	10.42	76.87	0.1875	3	3.18	120	S9
Asia	India	Wet Forest	Vazh	10.30	76.67	0.375	6	3.18	127	S9
Asia	India	Wet Forest	VG.ha1	10.42	76.87	1	1	10	285	S21
Asia	India	Wet Forest	VG.ha10	10.42	76.87	1	1	10	360	S21
Asia	India	Wet Forest	VG.ha20	10.42	76.87	1	1	10	381	S21
Asia	India	Wet Forest	VG.ha30	10.42	76.87	1	1	10	387	S21
Asia	Vietnam	Wet Forest	VietnamA	11.43	107.33	1	1	10	384	S22
Asia	Vietnam	Wet Forest	VietnamB	11.43	107.33	1	1	10	416	S22
Asia	Vietnam	Wet Forest	VietnamC	11.43	107.33	1	1	10	425	S22
Asia	Vietnam	Wet Forest	VietnamE	11.43	107.33	1	1	10	522	S22
Asia	India	Wet Forest	Vish	16.94	73.79	0.125	2	3.18	78	S9
Asia	India	Wet Forest	Wyn	11.84	75.81	0.125	2	3.18	66	S9
Asia	Cambodia	Wet Forest (Riverine)	Cambodia2	13.35	105.62	0.9	18	10	475	S10
Asia	Cambodia	Wet Forest (Riverine)	Cambodia3	13.25	105.58	0.5	10	10	285	S10
Asia	Cambodia	Wet Forest (Riverine)	Cambodia4	13.43	105.55	0.45	9	10	294	S10
Asia	Cambodia	Wet Forest (Swamp)	Cambodia7	13.34	105.60	0.95	19	10	486	S23

Asia	Cambodia	Wet Forest (Tall Dipterocarp)	Cambodia8	13.34	105.61	0.4	8	10	188	S10
Asia	Cambodia	Wet Forest (Tall Dipterocarp)	Cambodia9	13.25	105.58	0.55	11	10	280	S10
Asia	Cambodia	Wet Forest (Tall Dipterocarp)	Cambodia10	13.43	105.59	1.1	22	10	510	S10
South America	Brazil	Savanna	IBGE	-15.92	-47.88	3	4	10	305	S24, S25
South America	Bolivia	Savanna	LFB.03	-14.58	-60.83	1	1	10	204	S2
South America	Brazil	Savanna	NXV.01	-14.71	-52.35	1	1	10	385	S2
South America	Brazil	Savanna	NXV.02	-14.70	-52.35	1	1	10	571	S2
South America	Brazil	Savanna	NXV.03	-14.71	-52.35	0.5	1	5	1045	S2
South America	Brazil	Savanna	NXV.05	-14.71	-52.35	0.5	1	5	1179	S2
South America	Brazil	Savanna	NXV.09	-14.69	-52.35	0.5	1	5	916	S2
South America	Brazil	Savanna	SMT.01	-12.82	-51.77	1	1	10	381	S2
South America	Brazil	Savanna	SMT.02	-12.82	-51.77	1	1	10	444	S2
South America	Brazil	Savanna	SMT.03	-12.82	-51.77	1	1	10	209	S2
South America	Bolivia	SDTF	ACU.01	-15.25	-61.25	1	1	10	336	S2, S4
South America	Bolivia	SDTF	ACU.02	-15.25	-61.24	1	1	10	406	S24, S25

South America	Bolivia	SDTF	CRP.01	-14.54	-61.50	1	1	10	456	S24, S25
South America	Bolivia	SDTF	CRP.02	-14.54	-61.50	1	1	10	497	S24, S25
South America	Bolivia	SDTF	OTT.01	-16.39	-61.21	1	1	10	410	S2, S4
South America	Bolivia	SDTF	OTT.02	-16.39	-61.21	1	1	10	169	S2, S4
South America	Bolivia	SDTF	OTT.03	-16.42	-61.19	1	1	10	250	S2
South America	Bolivia	SDTF	SRQ.01	-14.40	-62.30	1	1	10	291	S24, S25
South America	Brazil	SDTF	TA_BA	-13.50	-44.24	1	25	5	881	S26
South America	Brazil	SDTF	TA_DF	-15.50	-47.30	1	25	5	1189	S26
South America	Brazil	SDTF	TA_GO	-13.15	-46.66	1	25	5	734	S26
South America	Brazil	SDTF	TA_GO_A	-14.06	-46.49	1	25	5	756	S27
South America	Brazil	SDTF	TA_GO_C	-13.66	-46.75	2.4	60	5	609	S28
South America	Brazil	SDTF	TA_GO_D	-13.83	-46.70	1	25	5	536	S29
South America	Brazil	SDTF	TA_GO_E	-13.52	-46.50	1	25	5	842	S30
South America	Brazil	SDTF	TA_GO_F	-13.69	-46.74	1	25	5	920	S31
South America	Brazil	SDTF	TA_MS_A	-19.03	-57.68	0.3	80	5	320	S32
South America	Brazil	SDTF	TA_MS_B	-19.03	-57.68	0.4	78	5	410	S32
South America	Brazil	SDTF	TA_MS_D	-19.21	-57.79	0.1	20	5	80	S33
South America	Brazil	SDTF	TA_MT	-14.35	-52.35	1	25	5	813	S26

South America	Bolivia	SDTF	TUC.01	-18.52	-60.81	1	1	10	828	S2, S4
South America	Bolivia	SDTF	TUC.03	-18.52	-60.81	1	1	10	152	S2, S4
South America	Brazil	Wet Forest	ALF.01	-9.60	-55.94	1	1	10	506	S2, S4
South America	Brazil	Wet Forest	ALF.02	-9.58	-55.92	1	1	10	537	S2, S4
South America	Bolivia	Wet Forest	BBC.01	-14.30	-60.53	1	1	10	515	S24, S25
South America	Bolivia	Wet Forest	BBC.02	-14.30	-60.53	1	1	10	537	S24, S25
South America	Bolivia	Wet Forest	BEE.01	-16.53	-64.58	1	1	10	571	S24, S25
South America	Bolivia	Wet Forest	BEE.05	-16.53	-64.58	1	1	10	544	S24, S25
South America	Bolivia	Wet Forest	CHO.01	-14.39	-61.15	1	1	10	623	S24, S25
South America	Bolivia	Wet Forest	CHO.02	-14.34	-61.16	1	1	10	519	S24, S25
South America	Brazil	Wet Forest	DOI.01	-10.57	-68.31	1	1	10	466	S2, S4
South America	Brazil	Wet Forest	DOI.02	-10.55	-68.31	1	1	10	244	S2, S4
South America	Brazil	Wet Forest	FEC.01	-10.07	-67.62	1	1	10	411	S2, S4
South America	Brazil	Wet Forest	FLO.01	-12.81	-51.85	1	1	10	608	S2, S4
South America	Bolivia	Wet Forest	FOB.01	-13.57	-61.02	1	1	10	224	S24, S25
South America	Bolivia	Wet Forest	HCC.11	-13.91	-60.82	1	1	10	534	S24, S25
South America	Bolivia	Wet Forest	HCC.12	-13.91	-60.82	1	1	10	690	S24, S25
South America	Bolivia	Wet Forest	HCC.21	-14.53	-60.74	1	1	10	556	S24, S25

South America	Bolivia	Wet Forest	HCC.22	-14.53	-60.73	1	1	10	609	S24, S25
South America	Bolivia	Wet Forest	HCC.23	-14.56	-60.75	1	1	10	638	S24, S25
South America	Bolivia	Wet Forest	HCC.24	-14.57	-60.75	1	1	10	488	S24, S25
South America	Brazil	Wet Forest	JFR.01	-10.48	-58.47	0.93	1	10	383	S24, S25
South America	Brazil	Wet Forest	JFR.02	-10.53	-58.50	0.525	1	10	168	S24, S25
South America	Brazil	Wet Forest	JFR.09	-10.47	-58.51	0.975	1	10	382	S24, S25
South America	Bolivia	Wet Forest	KEN.01	-16.02	-62.73	1	1	10	438	S24, S25
South America	Bolivia	Wet Forest	LCA.13	-15.68	-62.78	1	1	10	420	S24, S25
South America	Bolivia	Wet Forest	LCA.16	-15.68	-62.78	1	1	10	441	S24, S25
South America	Bolivia	Wet Forest	LCA.29	-15.68	-62.77	1	1	10	397	S24, S25
South America	Bolivia	Wet Forest	LCA.30	-15.68	-62.77	1	1	10	425	S24, S25
South America	Bolivia	Wet Forest	LFB.01	-14.58	-60.83	1	1	10	559	S2, S4
South America	Bolivia	Wet Forest	LFB.02	-14.58	-60.83	1	1	10	525	S2, S4
South America	Bolivia	Wet Forest	LGB.01	-14.80	-60.39	1	1	10	598	S24, S25
South America	Bolivia	Wet Forest	LSL.01	-14.40	-61.14	1	1	10	494	S24, S25
South America	Bolivia	Wet Forest	LSL.02	-14.40	-61.14	1	1	10	612	S24, S25
South America	Bolivia	Wet Forest	MBT.01	-10.07	-65.89	1	1	10	448	S24, S25
South America	Bolivia	Wet Forest	MBT.05	-10.03	-65.63	1	1	10	490	S24, S25

South America	Bolivia	Wet Forest	MBT.08	-9.94	-65.75	1	1	10	437	S24, S25
South America	Bolivia	Wet Forest	MVE.01	-15.01	-61.13	1	1	10	567	S24, S25
South America	Bolivia	Wet Forest	NCR.01	-14.64	-61.16	1	1	10	475	S24, S25
South America	Bolivia	Wet Forest	NCR.02	-14.71	-61.15	1	1	10	532	S24, S25
South America	Bolivia	Wet Forest	NEN.01	-13.63	-60.89	1	1	10	561	S24, S25
South America	Bolivia	Wet Forest	NEN.02	-13.63	-60.89	1	1	10	500	S24, S25
South America	Bolivia	Wet Forest	NLT.01	-13.65	-60.82	1	1	10	456	S24, S25
South America	Bolivia	Wet Forest	NLT.02	-13.65	-60.83	1	1	10	304	S24, S25
South America	Brazil	Wet Forest	NXV.06	-14.72	-52.36	0.47	1	5	480	S24, S25
South America	Brazil	Wet Forest	NXV.07	-14.72	-52.36	0.47	1	5	395	S24, S25
South America	Brazil	Wet Forest	NXV.08	-14.72	-52.36	0.47	1	5	571	S24, S25
South America	Brazil	Wet Forest	PEA.01	-12.15	-50.83	1	1	5	1600	S24, S25
South America	Brazil	Wet Forest	PEA.02	-12.32	-50.74	1	1	5	1311	S24, S25
South America	Brazil	Wet Forest	POR.01	-10.82	-68.78	1	1	10	527	S2, S4
South America	Brazil	Wet Forest	POR.02	-10.80	-68.77	1	1	10	501	S2, S4
South America	Brazil	Wet Forest	RBR.01	-11.00	-61.95	1	1	10	565	S24, S25
South America	Bolivia	Wet Forest	RET.06	-10.97	-65.72	1	1	10	523	S24, S25
South America	Bolivia	Wet Forest	RET.08	-10.97	-65.72	1	1	10	523	S24, S25

South America	Bolivia	Wet Forest	SCT.01	-17.09	-64.77	1	1	10	391	S24, S25
South America	Bolivia	Wet Forest	SCT.06	-17.09	-64.77	1	1	10	335	S24, S25
South America	Brazil	Wet Forest	SIP.01	-11.41	-55.32	1	1	10	349	S24, S25
South America	Brazil	Wet Forest	TAN.02	-13.09	-52.38	1	1	10	489	S24, S25
South America	Brazil	Wet Forest	TAN.03	-12.82	-52.36	1	1	10	577	S24, S25
South America	Brazil	Wet Forest	TAN.04	-12.92	-52.37	1	1	10	567	S2, S4
South America	Brazil	Wet Forest	VCR.01	-14.83	-52.16	1	1	10	523	S2, S4
South America	Brazil	Wet Forest	VCR.02	-14.83	-52.17	1	1	10	532	S2, S4

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