Floristics and biogeography of vegetation in seasonally dry tropical regions

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SUMMARY

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

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

RESUMEN

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

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

RÉSUMÉ

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

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

INTRODUCTION

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

Major vegetation formations in seasonally dry regions of the tropics

In understanding the vegetation of lowland tropical regions, the distinction between savanna and forests is critical. We take the view that savannas are distinguished from other tropical forest formations by the presence of more or less continuous C4 grass cover and the prevalence of natural fire. This grass-layer and proneness to fire is found even in savannas with a dense tree canopy, such as the "cerradão", a sub-formation within the savannas ("cerrados") of Brazil (Oliveira-Filho and Ratter 2002). This contrasts with closed canopy forests, including wet forests and seasonally dry tropical forests (SDTF), where grasses are infrequent in the understory and where natural fire is rare. The distinction of savanna and forests by the key factors of C4 grass presence and prevalence to fire is followed by many workers at a global scale (Lehmann *et al*. 2011, McShea and Davies 2011, Ratnam *et al*. 2011, Scholes and Walker 1993, Suresh *et al*. 2011) and it is widely accepted in the Neotropics (Pennington *et al*. 2000, 2006).

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

It is perhaps unclear whether vegetation with the attributes of neotropical SDTF outlined above exists on other continents (Lock 2006). Monsoon vine thickets of northern Australia have attributes of SDTF – having a closed canopy and being largely deciduous (Bowman 2000). The dry scrub on the Horn of Africa and similar regions in Arabia and northwest India, which are rich in legumes and succulents, have been considered similar to cactus-rich drier formations of SDTF in the Neotropics, and both have been classified as a global “succulent biome” by Schrire *et al*. (2005). These formations have led to suggestions that there may be a “global metacommunity” of SDTF that has some plant lineages specific to it (Pennington *et al*., 2009). However, elsewhere, extensive areas of vegetation in seasonally dry regions of Asia and Africa that is named “forest” or “woodland” is C4 grass-rich and fire-prone – and hence in our view a form of savanna. Examples are dry deciduous forest" in India (Suresh *et al.* 2011), Miombo woodland in southern Africa (Campbell *et al.* 1995, Chidumayo 2013) and deciduous dipterocarp forest in continental Asia (Bunyavejchewin 1983, Bunyavejchewin *et al.* 2011).

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

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

METHODS

Data Sources

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

South America

Our plot data for South America primarily comes from RAINFOR plots curated in the ForestPlots.net database (Lopez-Gonzalez *et al*. 2011; www.forestplots.net; extraction date: Sept. 30th, 2013), which consists of a network of 1 ha tree plots that monitor the composition, structure, and biomass of forests across the Amazon. The RAINFOR plot network extends into drier areas at its eastern and southern borders, and we restricted analyses to plots in wet or moist forest (n = 60), SDTFs (n = 10), and savannas (n = 10) in the southern and eastern Amazon and neighbouring areas (found in Bolivia and Brazil). Additionally, we surveyed the published literature, obtaining tree plot data for SDTFs from the Brazilian states of Bahia, Goias, Distrito Federal, Mato Grosso, and Mato Grosso do Sul (n = 12; details in Table S1). Across all South American plots, 3.6% of individual stems were not identified to genus.

Africa

Our data for Africa come primarily from the AfriTRON network (Lewis *et al*. 2013), which is also curated in the ForestPlots.net database (Lopez-Gonzalez *et al*. 2011; www.forestplots.net; extraction date June 13th, 2013), which consists of 1 ha plot data from primarily wet or moist forests in the Congo basin and the West African Guinean region (n = 64). Several plots from the database are located in savanna at the northern edge of African wet forests (n = 5; see Fig. 1). Additionally we obtained data from five 1 ha plots in savanna in Sierra Leone (from Ottamba Killimi National Park; M.P. Bessike Balinga, unpubl. data). Two of the major habitat types in tropical Africa proper (between 23°S and 23°N) that have commonly been considered as a form of tropical dry forest are Miombo woodlands, which occur across Africa south of the Congo basin (Campbell *et al*. 1995, Chidumayo 2013), and thornveld or scrub forest in the Horn of Africa (Schrire *et al*. 2005). We were unable to obtain 1 ha plot data from the Horn of Africa, but do include data from a 10 ha plot in Miombo woodlands in the southeastern Democratic Republic of the Congo (J. Ilunga-Muledi and P. Meerts, unpubl. data), which we subdivided into 1 ha plots to allow for comparison with the other 1 ha plot data. Across all African plots, 2.8% of individual stems were not identified to genus.

Asia

There are extensive forested regions in tropical Asia in both India and Indochina. We obtained forest plot data for India from two primary sources: 1) a series of 1 ha plots from wet evergreen forest (n = 15) in the Western Ghats and dry evergreen forest (n = 16) from across southeastern India (Anbarashan and Parthasarathy 2008, 2013, Ayyappan and Parthasarathy 2001, Chittibabu and Parthasarathy 2000, Mani and Parthasarathy 2005, Muthuramkumar *et al*. 2006, Parthasarathy and Karthikeyan 1997a, 1997b, Parthasrathy and Sethi 1997, Srinivas and Parthasarathy 2000, Venkateswaran and Parthasarathy 2003) and 2) a series of 25 m x 25 m plots in wet evergreen (n = 155) and deciduous forest (n = 44) in the Western Ghats that sample individuals >10 cm in circumference at breast height (N. Page, unpubl. data). We combined neighbouring plots together where possible to approach the sample size, in terms of individuals, present in 1 ha plots (see Table S1).

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

Data Standardization and Analyses

We ran all datasets through the Taxonomic Name Resolution Service v3.2 (http://tnrs.iplantcollaborative.org; Boyle *et al*. 2013), which corrects misspellings and standardizes synonyms based on several botanical databases, most importantly, in this instance, the Missouri Botanic Garden’s Tropicos database (http://www.tropicos.org). As few species are found on more than one continent, we did not find species-level analyses to be appropriate for comparing floristic similarity of vegetation formations within and amongst continents. In contrast, no family was restricted to a single vegetation formation or a single continent, and we therefore did not consider that analyses at this taxonomic level would be useful for comparisons either; most plots show high floristic similarity with little variation in values. Consequently, we conducted all analyses at the genus level, excluding individuals that were not identified to genus. The final matrix for analysis comprised 1078 genera, 269 plots, and 120,691 individual trees.

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

We also used the Sorensen distance matrix as the basis for ordination of plots using non-metric multidimensional scaling (NMDS) in the vegan package (Oksanen *et al*. 2013) of the R Statistical Environment. We began the analysis with two axes and added axes until the stress value dropped below 0.1, an arbitrary threshold that indicates a reasonably stable solution (Borcard *et al*. 2011). In all cases, we used 20 random starts and ensured convergence among runs. All of the above analyses were repeated using Jaccard and Simpson distances among plots to assess the robustness of results to different distance indices.

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

RESULTS

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

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

Our ordination analyses also suggest the pre-eminence of geography in determining floristic relationships (Fig. 3A), while also demonstrating the clear importance of vegetation formation (Fig. 3B). We used an NMDS ordination with four axes, as this was the lowest number of axes that had a stress value under 0.1 (stress = 0.088). The first two axes clearly segregate plots from different continents, irrespective of their vegetation type. If an NMDS ordination is conducted with only two axes (results not shown, stress = 0.185), an identical result is obtained, suggesting that geography is the first factor that determines the floristic similarity of plots. The third and fourth axes separated plots in moist forests from those in savannas and other dry formations (e.g. SDTFs, Miombo woodlands). That all continents show this moist versus dry segregation within the same ordination does suggest that there is some floristic signal for moist versus drier formations that is the same on each continent. Nevertheless, African savannas are clearly floristically distinct from South American savannas, while there is also limited support, especially from the clustering analysis, for segregation of the different dry forest/woodland categories on different continents.

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

DISCUSSION

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

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

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

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

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

Thus, it seems that we cannot use these floristic analyses to determine whether the various dry vegetation formations in Africa and Asia correspond better to Neotropical savanna or SDTF. Rather, to classify palaeotropical dry vegetation types as savanna vs. SDTF (*sensu* Neotropical definitions), one would have to rely on information besides woody plant floristic composition, such as the presence vs. absence of C4 grasses and succulents or the frequency of fires (e.g., Torellos-Raventos *et al.* 2013). For example, based upon their ecological characteristics of richness in C4 grasses and propensity to burn, we suggest that many formations termed “forest” or “woodland” in Africa and Asia, including all of those analysed here, are better considered as savannas. We acknowledge that there are many types of vegetation in Africa and Asia that we have not assessed, *e.g. Baikiaea* (Leguminosae) woodlands (Piearce 1984) and *Cryptosepalum* (Leguminosae) dry forests in Angola, Democratic Republic of Congo, and Zambia (White 1983) and the coastal woodlands of Mozambique and Tanzania (Burgess and Clarke 2000), which may not have a propensity to burn and may be analogous to SDTF (*sensu* Neotropical definitions). The frequency of fires as a determinant of vegetation type in the tropics is supported by the observation that anthropogenic fires in SDTFs lead to their substitution by savannas (Saha and Howe 2003, Wanthongchai and Goldammer 2011). Conversely, in the absence of fire, savanna vegetation may eventually grow into a closed canopy forest (*i.e.* an SDTF) that can then exclude C4 grasses and fire, particularly on more fertile soils (Durigan 2006, Lawes et al. 2011, Woinarski *et al.* 2004).

Tropical savannas are geologically young, dating from the late Miocene (Beerling and Osborne 2006, Cerling *et al.* 1997, Jacobs *et al.* 1999), and SDTF in the Neotropics, though older, postdates the origin of tropical moist forests (Becerra 2005, Pennington *et al.* 2006). The antiquity of tropical moist forests relative to drought-adapted formations implies that the continentally structured floristic patterns we have found are largely a result of isolated continental floras evolving independently to occupy a seasonally dry environmental niche, rather than the result of the same drought-adapted lineages dispersing across the globe to reach dry environments. This result implies that though intercontinental migration has undoubtedly been important in tropical plant biogeography (e.g., Pennington and Dick 2004), the effect of *in situ* diversification on continents may have been greater. This can be illustrated by considering that only 88 of 477 genera (~20%) in our South American plots are even found in Africa and Asia. The fact that many eudicot families that are dominant in tropical vegetation date only to the late Cretaceous (Magallon *et al.* 1999) implies that the origin of most of these genera – a lower taxonomic level – will be later and therefore post-dates Gondwanan vicariance. Hence, long-distance dispersal is likely to have been important in their biogeography. A corollary suggestion is that the genera restricted to the Neotropics in our dataset (c. 80%) are likely to have had a neotropical origin. However, we note that this is a very approximate estimate as some of the 20% of widespread genera may also have had a neotropical origin, and some of the 80% apparently restricted to the Neotropics may be found in Africa and Asia outside of the plots we examined.

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

Implications for conservation and management

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

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

As our results have demonstrated, we cannot use floristic analyses to relate neotropical SDTF and savannas with palaeotropical dry vegetation. Dry forests that are physiognomically similar to neotropical SDTF (*sensu* Pennington *et al.* 2000) may cover only a small part of Africa (Lock 2006). Some possible examples are the deciduous bushlands and thickets of the Horn of Africa, which may be considered ecologically equivalent to the caatinga dry forest in northeastern Brazil (Lock 2006). In Asian dry forests, fire-sensitive succulents are almost absent and, due to their propensity to burn, we suggest that many Asian "dry forests" should be classified as savannas.

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

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

The result presented here – different vegetation types clustering floristically by continent – means that pantropical biological generalisations should be drawn with care, even within the ecologically defined savanna and SDTF categories. For example, while tropical savannas can be globally defined by an abundance of C4 grasses and propensity to burn, because they contain different woody plant lineages on each continent, it may be hard to generalise studies of resilience or ecosystem rehabilitation from one continent to another. With regard to forest management, the lack of floristic identity between neotropical and paleotropical SDTF and savannas makes cross-continental comparison in some contexts almost meaningless. For example, a species-specific analysis and a demographic approach are preconditions for evaluating whether timber and non-timber forest products harvesting is sustainable or not (Sutherland 2001).

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

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FIGURE LEGENDS

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

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

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

Figure 1

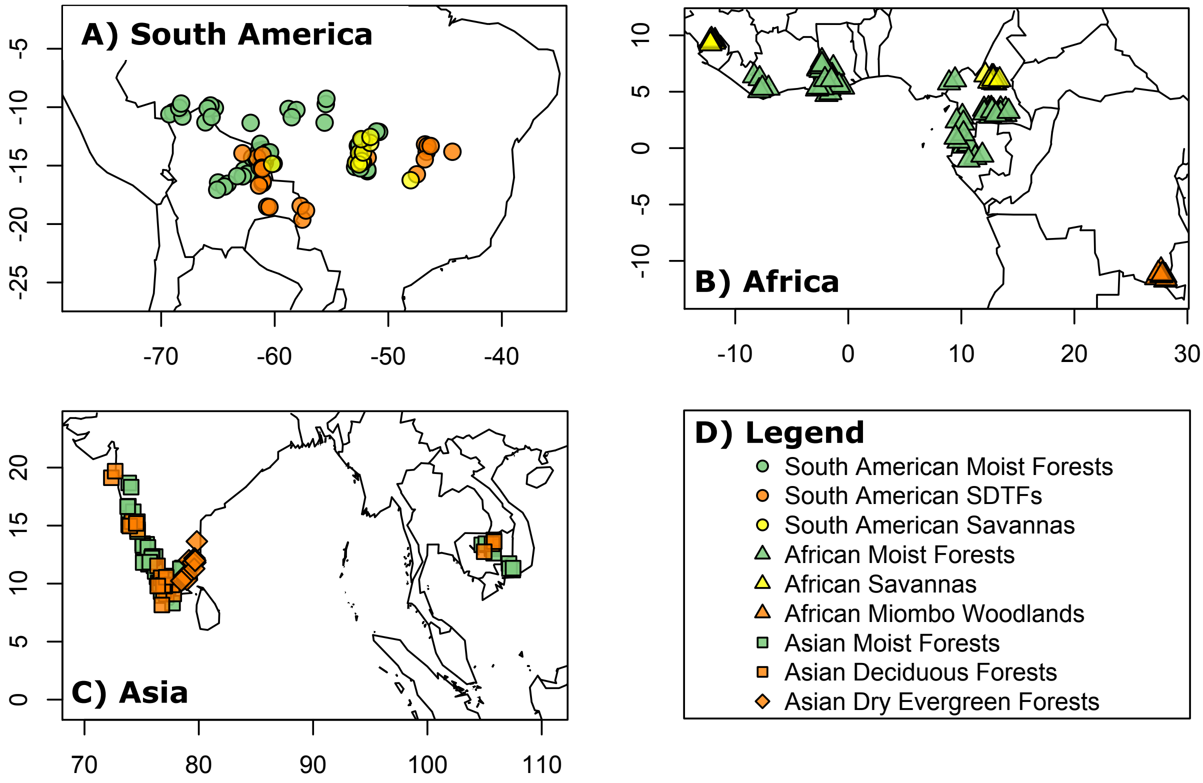
A) South America
-5
-10
-15
-20
-25
-70
-60
-50
-40
B) Africa
10
5
0
-5
-10
-10
0
10
20
30
C) Asia
20
15
10
5
0
70
80
90
100
110
D) Legend
● South American Moist Forests
● South American SDTFs
● South American Savannas
▲ African Moist Forests
▲ African Savannas
▲ African Miombo Woodlands
■ Asian Moist Forests
■ Asian Deciduous Forests
◆ Asian Dry Evergreen Forests

Figure 2

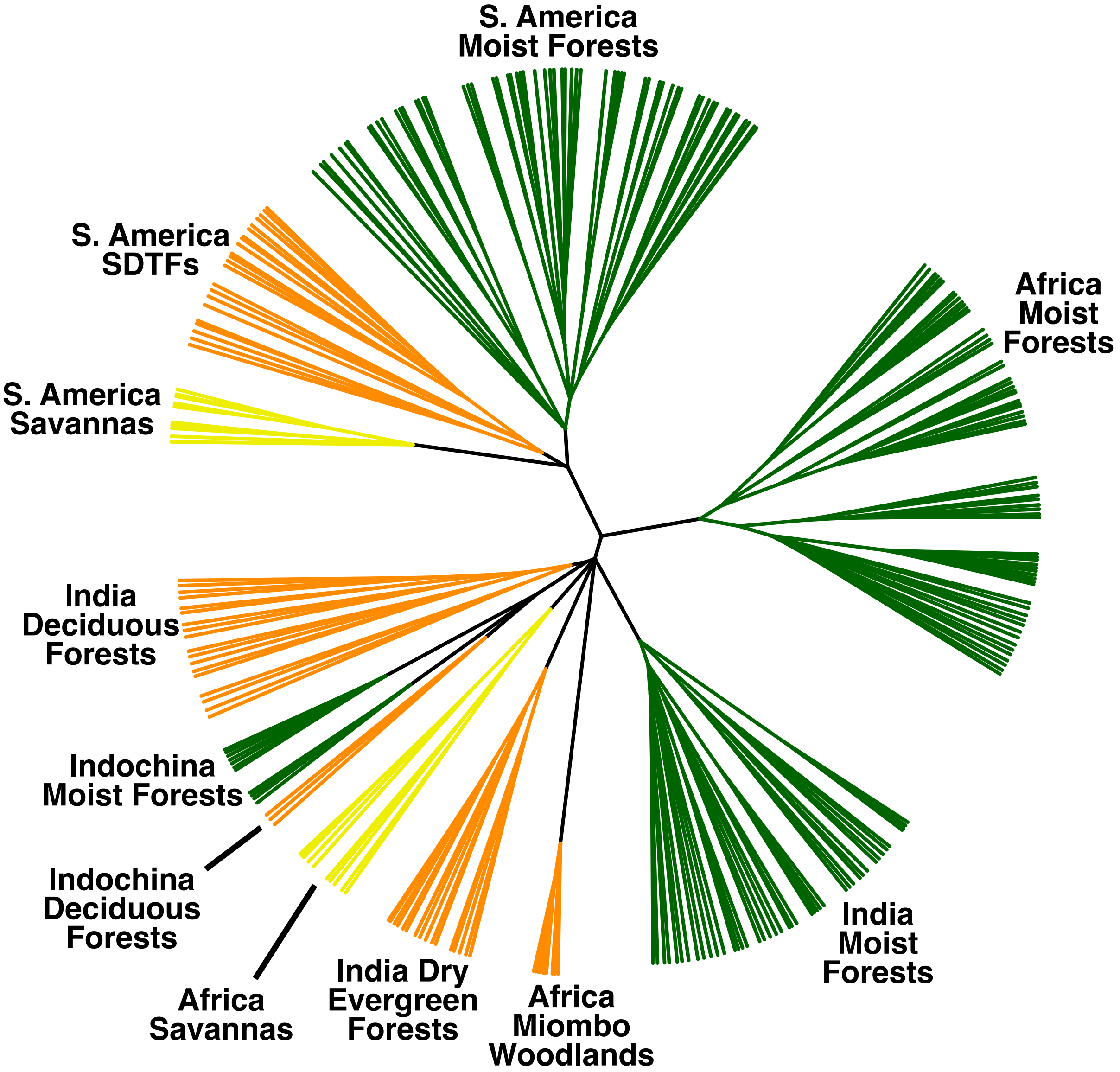
S. America Moist Forests
S. America SDTFs
S. America Savannas
Africa Moist Forests
India Deciduous Forests
Indochina Moist Forests
Indochina Deciduous Forests
Africa Savannas
India Dry Evergreen Forests
Africa Miombo Woodlands
India Moist Forests

Figure 3

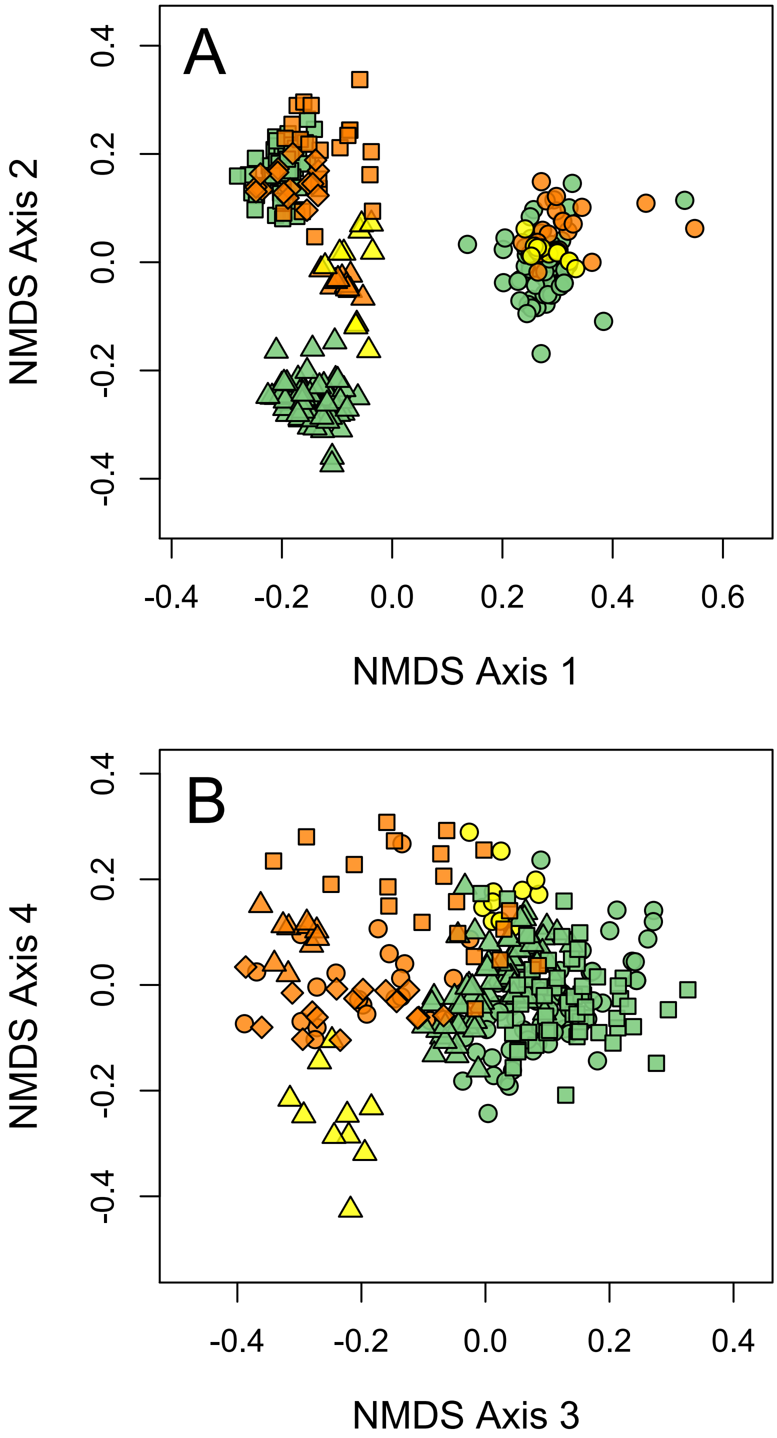
A
NMDS Axis 2
0.4
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
0.6
NMDS Axis 1
B
NMDS Axis 4
0.4
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
NMDS Axis 3

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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