

Would you live in a wood  
skyscraper? p. 1354

Yeast genetic interactions  
revealed p. 1381

Remote sensing for induced  
seismic hazard p. 1416

# Science

\$15  
23 SEPTEMBER 20  
[sciencemag.org](http://sciencemag.org)



## DRY FOREST

Diversity in the American  
tropics p. 1383

## RESEARCH ARTICLES

## FOREST ECOLOGY

# Plant diversity patterns in neotropical dry forests and their conservation implications

DRYFLOR\*†

Seasonally dry tropical forests are distributed across Latin America and the Caribbean and are highly threatened, with less than 10% of their original extent remaining in many countries. Using 835 inventories covering 4660 species of woody plants, we show marked floristic turnover among inventories and regions, which may be higher than in other neotropical biomes, such as savanna. Such high floristic turnover indicates that numerous conservation areas across many countries will be needed to protect the full diversity of tropical dry forests. Our results provide a scientific framework within which national decision-makers can contextualize the floristic significance of their dry forest at a regional and continental scale.

**N**eotropical seasonally dry forest (dry forest) is a biome with a wide and fragmented distribution, found from Mexico to Argentina and throughout the Caribbean (1, 2) (Fig. 1). It is one of the most threatened tropical forests in the world (3), with less than 10% of its original extent remaining in many countries (4).

Following other authors (5, 6), we define dry forest as having a closed canopy, distinguishing it from more open, grass-rich savanna. It occurs on fertile soils where the rainfall is less than ~1800 mm per year, with a period of 3 to 6 months receiving less than 100 mm per month (5–7), during which the vegetation is mostly deciduous. Seasonally dry areas, especially in Peru and Mexico, were home to pre-Columbian civilizations, so human interaction with dry forest has a long history (8). The climates and fertile soils of dry forest regions have led to higher human population densities and an increasing demand for energy and land, enhancing degradation (9). More recently, destruction of dry forest has been accelerated by intensive cultivation of crops, such as sugar cane, rice and soy, or by conversion to pasture for cattle.

Dry forest is in a critical state because so little of it is intact, and of the remnant areas, little is protected (3). For example, only 1.2% of the total Caatinga region of dry forest in Brazil is fully protected compared with 9.9% of the Brazilian Amazon (10). Conservation actions are urgently needed to protect dry forest's unique biodiversity—many plant

species and even genera are restricted to it and reflect an evolutionary history confined to this biome (1).

We evaluate the floristic relationships of the disjunct areas of neotropical dry forest and highlight those that contain the highest diversity and endemism of woody plant species. We also explore woody plant species turnover across geographic space among dry forests. Our results provide a framework to allow the conservation significance of each separate major region of dry forest to be assessed at a continental scale. Our analyses are based on a subset of a data set of 1602 inventories made in dry forest and related semi-deciduous forests from Mexico and the Caribbean to Argentina and Paraguay that covers 6958 woody species, which has been com-



**Fig. 1. Schematic dry forest distribution in the Neotropics.**

[Based on Pennington *et al.* (13), Linares-Palomino *et al.* (2), Olson *et al.* (45), and the location of DRYFLOR inventory sites (see Fig. 2)]

piled by the Latin American and Caribbean Seasonally Dry Tropical Forest Floristic Network [DRYFLOR, [www.dryflor.info](http://www.dryflor.info); (II)].

We present analyses that focus principally on DRYFLOR sites in deciduous dry forest vegetation growing under the precipitation regime outlined above (5–7), as measured using climate data from Hijmans *et al.* (12). We excluded most Brazilian sites in the DRYFLOR database with vegetation classified as “semi-deciduous” because these have a less severe dry season and a massive contribution of both the Amazonian and Atlantic rain forest floras (II). The only semi-deciduous sites retained from southeast Brazil were from the Misiones region, which has been included in numerous studies of dry forest biogeography [e.g., (13, 14)] (fig. S1), and we therefore wished to understand its relationships. We also excluded sites from the chaco woodland of central South America because it is considered a distinct biome with temperate affinities characterized by frequent winter frost (13, 15). Sites occurring in the central Brazilian region are small patches of deciduous forest that are scattered on areas of fertile soil within savanna vegetation known as “cerrado.” We performed clustering and ordination analyses on inventories made at 835 DRYFLOR sites that covered 147 families, 983 genera, and 4660 species (II).

## Floristic relationships, diversity, endemism, and turnover

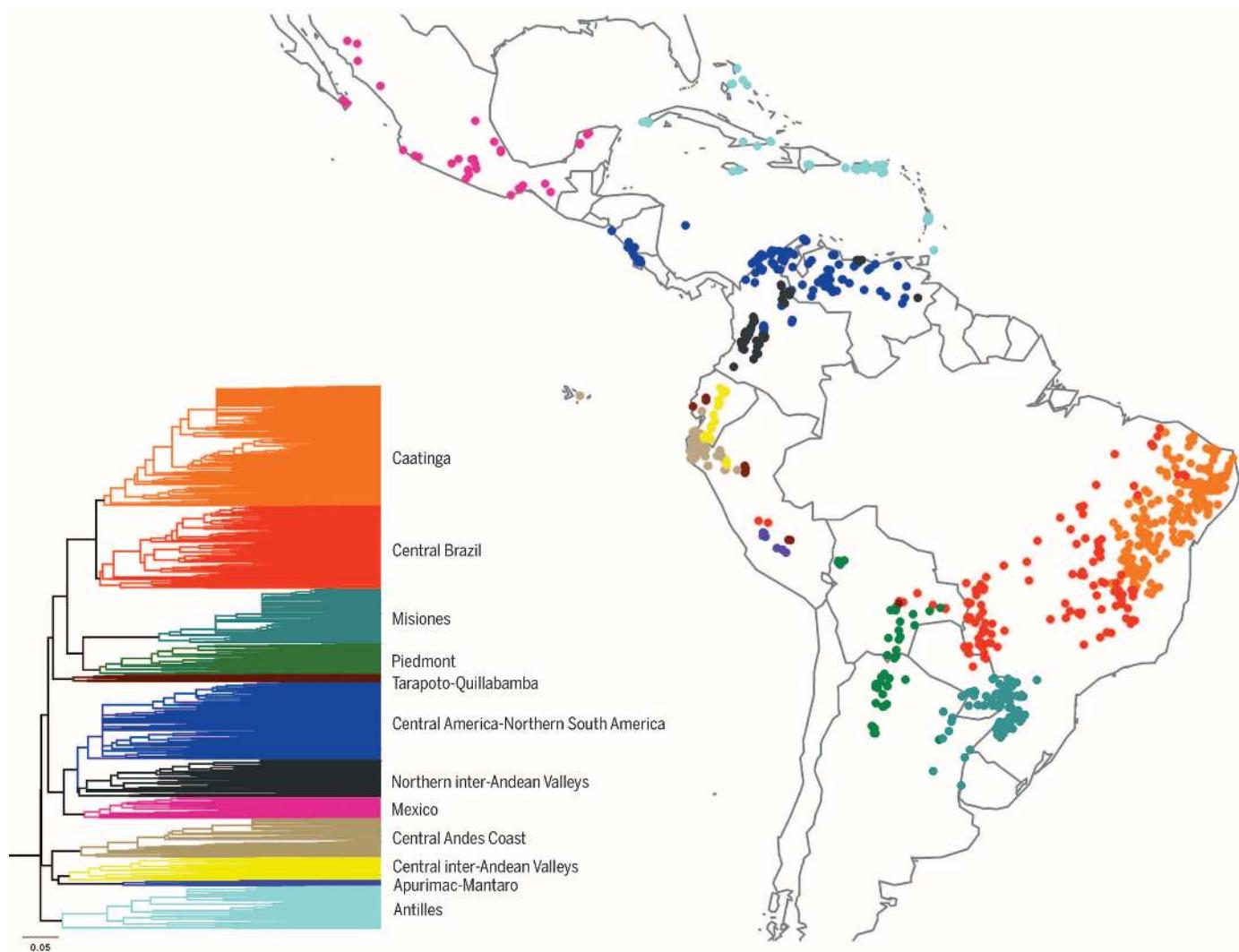
Our clustering analyses, based on the unweighted pair-group method with arithmetic mean (UPGMA) and using the Simpson dissimilarity index as a distance measure (16), identified 12 floristic groups: (i) Mexico, (ii) Antilles, (iii) Central America-northern South America, (iv) northern inter-Andean valleys, (v) central inter-Andean valleys, (vi) central Andes coast, (vii) Tarapoto-Quillabamba, (viii) Apurimac-Mantaro, (ix) Piedmont, (x) Misiones, (xi) central Brazil, and (xii) Caatinga (Fig. 2 and table S1).

The relationships among the floristic groups were similar in both the analysis of 835 sites (Fig. 2) and another that pooled all species lists from all sites in each of the 12 floristic groups in order to explore the support for relationships among them (fig. S2). The placement of the geographically small Peruvian inter-Andean groups of Apurimac-Mantaro and Tarapoto-Quillabamba is uncertain as previously reported by Linares-Palomino *et al.* (2), and differs in the two cluster analyses (Fig. 2 and fig. S2), which is reflected in low AU (approximately unbiased probability support) values (0.71) (fig. S2). More detailed floristic inventory is required in these poorly surveyed forests, which is also suggested by species accumulation curves that have not leveled in these geographic areas (fig. S3).

The analysis pooling all species lists in each floristic group (fig. S2) and a non-metric multidimensional scaling (NMDS) ordination (fig. S4A for all sites and fig. S4B pooling all species in each floristic group) recognizes a higher-level northern

Latin American and Caribbean Seasonally Dry Tropical Forest Floristic Network, Royal Botanic Garden Edinburgh, 20a Inverleith Row, Edinburgh, EH3 5LR, UK.

\*All authors with their affiliations appear at the end of this paper. †Corresponding author. Email: [t.pennington@rbge.ac.uk](mailto:t.pennington@rbge.ac.uk)



**Fig. 2. Neotropical dry forest floristic groups based on woody plants.** Geographical representation of UPGMA clustering of 835 dry forest sites using the Simpson dissimilarity index as a measure of distance.

cluster (Mexico, Antilles, Central America–northern South America, and northern inter-Andean valleys). The distinctiveness of Mexican dry forests has been widely recognized (6), and the well-supported Antillean floristic group reflects that the Caribbean is also a distinctive neotropical phytogeographic region with high endemism (17, 18). The support for a higher-level northern cluster confirms a north-south division in neotropical dry forest that was suggested by Linares-Palomino *et al.* (2) based on a data set that was more sparse in the northern Neotropics (57 sites compared with 276 here). The separation of a northern cluster of neotropical dry forests, which includes all areas in Colombia and Venezuela, from all other dry forest areas further south in South America may reflect the effectiveness of the rain forests of Amazonia and the Chocó as a barrier for migration of dry forest species, as suggested by Gentry (19).

A higher-level southern cluster comprises eastern and southern South American areas that divide into two subclusters, the first formed by Piedmont

and Misiones and the second by central Brazil and the Caatinga (Fig. 2). In the analysis of pooled species lists, the Misiones group clusters with the central Brazil and Caatinga floristic groups with strong support (1.0 AU) (fig. S2), which is due to the large number of species shared among them as a whole (Misiones shares 409 spp. with central Brazil and 264 spp. with Caatinga) (Fig. 3 and table S2).

There are six Andean dry forest floristic groups (northern inter-Andean valleys, central inter-Andean valleys, central Andes coast, Apurimac-Mantaro, Piedmont, and Tarapoto-Quillabamba), which are scattered across our UPGMA clusterings (Fig. 2 and fig. S2) and ordinations (fig. S4); this scattering reflects the great floristic heterogeneity of dry Andean regions first highlighted by Sarmiento (20). For example, the northern inter-Andean valleys of the Rio Magdalena and Cauca are placed within the higher-level northern South American cluster, whereas the Piedmont, Tarapoto-Quillabamba, and Apurimac-Mantaro floristic groups are placed in the higher-level southern cluster in our pooled analysis (fig. S2).

The central Brazil, Caatinga, and Mexico floristic groups contain the most species (1344, 1112, and 1072 species, respectively) (table S1), and the central inter-Andean valleys and Apurimac-Mantaro inter-Andean valleys contain the least (165 and 78 species, respectively). Overall regional species richness may reflect an integrated time-area effect (21). The age of the dry forest biome is not known throughout the Neotropics, but the fossil record and dated phylogenies suggest a Miocene origin in Mexico (22) and the Andes (23). Our data suggest that larger areas of dry forest, such as in the Caatinga and Mexico, have accumulated more species. The small number of species in inter-Andean dry forests reflects their tiny area; the dry forests of the Marañón, Apurimac, and Mantaro inter-Andean valleys in Peru are estimated to occupy 4411 km<sup>2</sup> in total (24) compared with ~850,000 km<sup>2</sup> estimated for the Caatinga (25). What is notable is the lack of an equatorial peak in regional species diversity (fig. S5). The northerly Mexican dry forests, which reach the Tropic of Cancer, have high species

numbers similar to the more equatorial Caatinga (1072 compared with 1112), despite being covered by far fewer surveys (33 compared with 184) (fig. S6) and in one-third of the land area [280,000 km<sup>2</sup>] (26). It is intriguing that there may be a peak in regional dry forest species richness around 20 degrees latitude (fig. S5), which may reflect a “reverse latitudinal gradient” of regional species richness in neotropical dry forest, which was suggested by Gentry (6). Our inventories used heterogeneous methodologies (e.g., plots and transects of varying sizes or general floristic surveys), which precludes any definitive discussion of alpha diversity at individual sites, but the high regional diversity of Mexican forests, which are distant from the equator, is remarkable. The high species richness of Mexican dry forests merits further investigation and may reflect their Miocene age combined with rates of species diversification that are potentially higher than in other dry forest regions.

Species restricted to one of the 12 floristic groups (“exclusive” species in table S1) may not be strictly endemic to them, because they may be found elsewhere in areas not covered by our surveys. However, we believe that they do serve as a proxy for species endemism, which is supported by independent evidence from floristic checklists. For example, Linares-Palomino (27) reported 43% endemism of woody plants for the Marañón valley, Peru, which forms a major part of our central Andean group and has 41% exclusive species. Mexican and Antillean dry forests have the highest percentages of exclusive species (73% and 65%, respectively). The lowest percentage of exclusive species is found in central Brazil dry forests, which reflects the larger numbers of species shared with neighboring floristic groups. Despite their close geographical proximity, Andean floristic groups each have about 30 to 40% of exclusive species, reflecting high floristic turnover at relatively small spatial scales, which may be caused by dispersal limitation among the geographic groups and in situ speciation within them (1, 28).

Pairwise dissimilarity values for the whole data set have a mean of 0.90 for Simpson dissimilarity (median of 0.94) and 0.94 for Sørensen dissimilarity (median of 0.97). The dissimilarity values among the 12 floristic groups (using the entire combined lists for each) (table S3, A and B) ranged from 0.38 to 0.94 (mean, 0.79; median, 0.82) for Simpson dissimilarity and 0.43 to 0.98 (mean, 0.87; median, 0.90) for Sørensen dissimilarity. High floristic turnover in dry forest has been shown in Mexico (29), but our data set allows a thorough assessment at a continental scale. In general, few species are shared among the floristic groups (Fig. 3), and this underlines the high levels of species turnover. It is also notable that dissimilarity values are high within all the deciduous dry forest floristic groups as well, with median Sørensen values ranging from 0.74 within the Caatinga to 0.90 within the Tarapoto-Quillabamba group (table S4) (the median value is slightly lower at 0.70 within the semi-deciduous Misiones group). These dissimilarity values are higher than those reported for the cerrado biome.

Bridgewater *et al.* (30) showed Sørensen dissimilarities with a lower mean value of 0.58 among cerrado floristic provinces separated by ~1000 km, based on floristic lists similar to those in the DRYFLOR data set. The probable higher species turnover in dry forests at continental, regional, and local scales is a result with considerable implications for conservation.

The strongest floristic affinities are found among (i) central Brazil, Caatinga, Piedmont, and Misiones and (ii) Central America and northern South America, Mexico and the northern inter-Andean valleys (Fig. 3). The relationship of the Caatinga and central Brazil dry forests, which share almost 700 species, has been highlighted previously (2, 14, 31), but what is striking elsewhere is the low levels of floristic similarity, even among geographically proximal floristic groups (e.g., northern and central inter-Andean valleys).

The high floristic turnover reflects that few species are widespread and shared across many areas of neotropical dry forest. No species is reported for all 12 floristic groups; there are only three species shared among 11 groups and nine species among 10 groups (table S5). Some of the species recorded across most sites are widespread ecological generalists like *Machura tinctoria* (Moraceae), *Guazuma ulmifolia* (Malvaceae), and *Celtis iguanaea* (Cannabaceae), which are common in other biomes, such as rain forest. These species tend to grow in disturbed areas, so their presence in many dry forest sites could be a consequence of their high level of degradation and fragmentation. In other cases, highly recorded species are dry forest specialists, such as *Anadenanthera colubrina* (Leguminosae)—which occurs in eight of the floristic groups and in more than 74% of the sites in the Caatinga, central Brazil, and Piedmont—and *Cynophalla flexuosa* (Capparaceae), which occurs in 11 groups and is commonly recorded (~40% of the sites) in the Antilles, Caatinga, and central Andes coast.

However, most frequently recorded species, defined as those registered in many sites, are seldom shared among any of our 12 floristic groups. For example, 85% of the top 20 most frequently recorded species in each floristic group (table S6) are restricted to a single group, with a few exceptions where the same species was frequent across several groups (e.g., *Anadenanthera colubrina* and *Guazuma ulmifolia*, in five groups each). In other cases, there is a particular set of species characteristic for pairs of geographically proximal floristic groups such as the central inter-Andean valleys and central Andes coast, where the dry forest specialist species, *Loxopterygium huasango* (Anacardiaceae), *Ceiba trichistandra* (Malvaceae), *Coccoloba ruiziana* (Polygonaceae), and *Pithecellobium excelsum* (Leguminosae), are recorded in >15% of the sites.

Our presence-absence database cannot assess abundance in terms of numbers of stems or basal area. However, the extensive field experience of the DRYFLOR network team suggests that when frequently recorded species are dry forest specialists, they tend to be locally abundant and

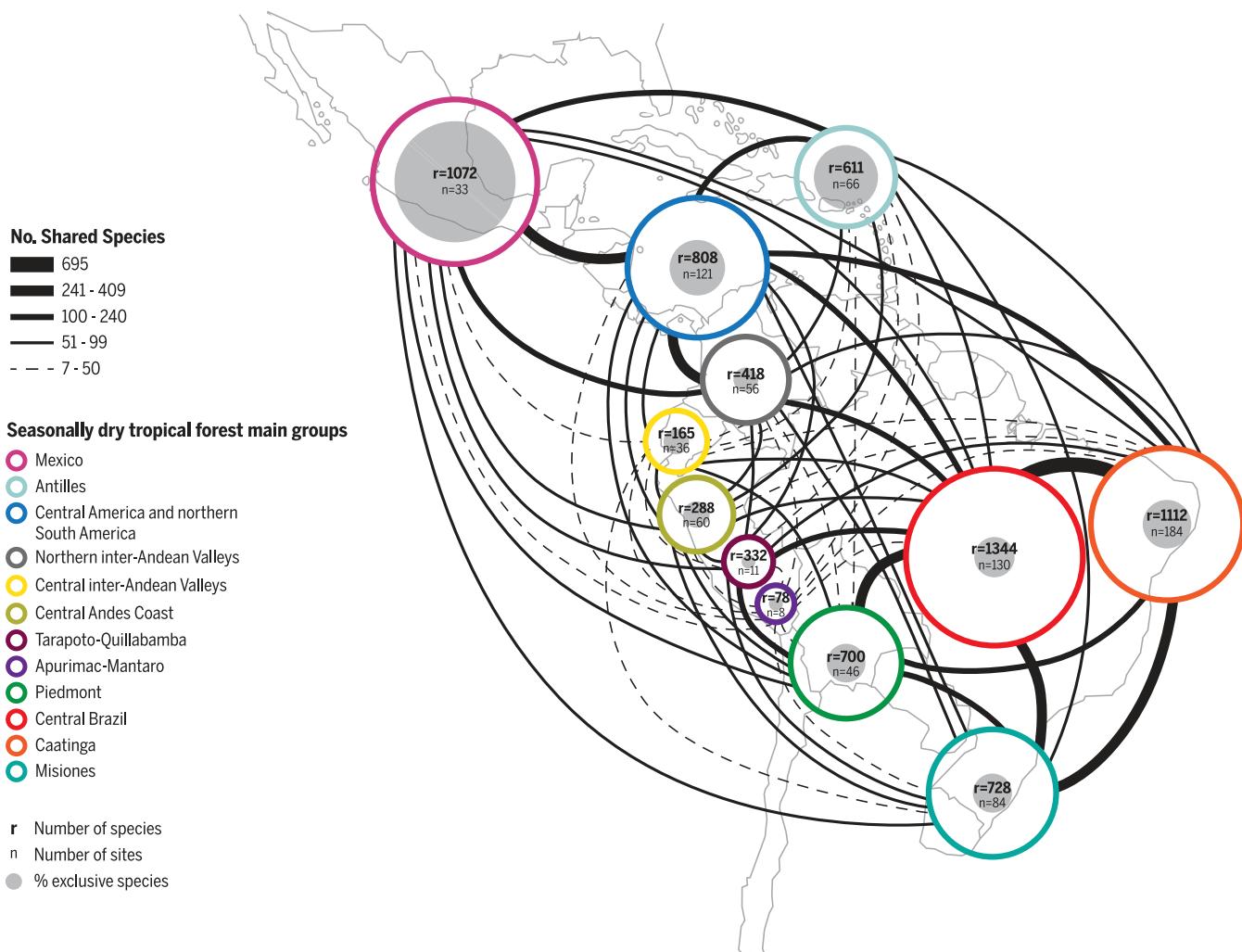
often dominant. Our observations are reinforced by quantitative inventory data that indicate that the most dominant species in dry forest plots represent 8.5 to 62.1% of stems per plot, with a median relative abundance of 17.9% (32). In contrast to dry forest specialist species, widespread and frequently recorded ecological generalist species are often not locally abundant.

Although frequently recorded dry forest specialist species in our data set may be locally abundant and dominant, they generally have geographically restricted total distributions. Widespread species that are common in more than one dry forest floristic group (Fig. 2), such as *Anadenanthera colubrina*, which was emphasized in early discussions of neotropical dry forest biogeography [e.g., (13, 14)], are the exception. In summary, there is little evidence for any oligarchy of species that dominates across neotropical dry forest as a whole. These patterns contrast strongly with the rain forests of Amazonia (33, 34) and the savannas of central Brazil (30), which are often dominated by a suite of oligarchic species over large geographic areas. The lack of an oligarchy of widespread, dominant dry forest species reflects the limited opportunities for dispersal and successful establishment among dry forest areas (1, 28).

## Conservation

Our data show that variation in floristic composition at a continental scale defines 12 dry forest floristic groups across the Neotropics. The floristic differentiation of these main dry forest groups is marked; 23 to 73% of the species found in each are exclusive to it. These figures are likely to indicate high levels of species endemism, which is illustrative of the high floristic turnover (beta diversity) that our data reveal. This high endemism and floristic turnover across the dry forest floristic groups indicate that failure to protect the forest in every one would result in major losses of unique species diversity.

The example of the Andean dry forest is illustrative in this context of the need for multiple protected areas. Andean dry forests fall into six floristic groups in our analysis (Fig. 2). Of these, two geographically small but highly distinct groups in Peru, Apurímac-Mantaro and Tarapoto-Quillabamba, have no formal protection at all. Only 1.4% (3846 ha) of the total remaining dry forest in the northern inter-Andean valleys—one of the most transformed land areas in Colombia (35)—are protected (4), well short of Aichi biodiversity target 11 that calls for conservation of 17% of terrestrial areas of importance for biodiversity (36). In other Andean areas, accurate maps of all remaining areas of dry forest are unavailable, but given that DRYFLOR sites were chosen because they represent well-preserved areas of dry forest, we can ask the question of how well protected these survey sites are. For example, only 14% of the central inter-Andean valleys, 18% of the central Andes coast, and 32% of Piedmont DRYFLOR sites occur within a protected area. If we are to conserve the full floristic diversity of Andean dry forest from north to south, future conservation planning must prioritize



**Fig. 3. Geographical patterns of species turnover among 12 dry forest floristic groups.** (Fig. 2). Size of the circles is proportional to the number of species per group; size of colored circles is proportional to the total number of species and of gray circles to the number of exclusive species. The species turnover among areas is described by line widths proportional to the number of species shared (values from table S2).

areas in Peru and elsewhere in the Andes that are globally unique but entirely unprotected. These Andean forests, like virtually all neotropical dry forests, have high local human populations and are exploited for agriculture and fuelwood. Conservation solutions therefore require a social dimension, including opportunities and incentives for human communities and private landowners (9).

Median pairwise floristic dissimilarity values within the floristic groups of 0.73 for Simpson dissimilarity and 0.85 for Sørensen dissimilarity show that floristic turnover is also high at regional scales, a result only previously shown for Mexico (29). Major dry forest regions, such as the Caatinga and Mexico, are each home to more than a thousand woody species, and the high floristic turnover within them means that to protect this diversity fully will require multiple, geographically dispersed protected areas. Conservation of some of these areas could be promoted by classifying their endemic species using International Union for the Conservation of Nature (IUCN) Red List criteria, for which the distribution data in the DRYFLOR database can provide a valuable basis.

Overall, only 14% of sites in the DRYFLOR database, which were chosen to cover the maximum remaining area of neotropical dry forest, fall within protected areas. Placed in the context of our data set, which shows high diversity, high endemism, and high floristic turnover, it is clear that current levels of protection for neotropical dry forest are woefully inadequate. It is our hope that our data set for Latin American and Caribbean dry forests and the results shown here can become a basis for future conservation decisions that take into account continental-level floristic patterns and thereby conserve the maximum diversity of these threatened but forgotten forests.

#### REFERENCES AND NOTES

- R. T. Pennington, M. Lavin, A. Oliveira-Filho, *Annu. Rev. Ecol. Evol. Syst.* **40**, 437–457 (2009).
- R. Linares-Palomino, A. T. Oliveira-Filho, R. T. Pennington, in *Seasonally Dry Tropical Forest: Ecology and Conservation*, R. Dirzo, H. S. Young, H. A. Mooney, G. Ceballos, Eds. (Island Press, 2011), pp. 3–21.
- L. Miles et al., *J. Biogeogr.* **33**, 491–505 (2006).
- H. García, G. Corzo, P. Isaacs, A. Etter, in *El Bosque seco Tropical en Colombia*, C. Pizano and H. García, Eds. (Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá D.C., Colombia, 2014), pp. 228–251.
- G. Murphy, A. E. Lugo, *Annu. Rev. Ecol. Syst.* **17**, 67–88 (1986).
- A. H. Gentry, in *Seasonally Dry Tropical Forests*, S. Bullock, H. Mooney, E. Medina, Eds. (Cambridge Univ. Press, Cambridge, 1995), pp. 146–194.
- G. A. Sanchez-Azofeifa et al., *Biotropica* **37**, 477–485 (2005).
- A. M. Hocquenghem, *Para Vencer la Muerte: Piura y Tumbes. Raíces en el Bosque Seco y en la Selva Alta-Horizontes en el Pacífico y en la Amazonia* [CNRS-IFEA (l'Institut Français d'Etudes Andines)], Lima, Peru, 1998.
- R. Blackie et al., “Tropical dry forests: The state of global knowledge and recommendations for future research” (2014 CIFOR Discussion paper 2; Center for International Forestry Research, Jawa Barat, Indonesia, 2014); <http://dx.doi.org/10.1728/cifor/004408>.
- Ministério do Meio Ambiente [Ministry of the Environment], Unidades de Conservação por Bioma (CNUC/MMA, Brasília-DF, Brasil, 2016); [www.mma.gov.br/images/arquivo/80112/CNUC\\_PorBiomaFev16.pdf](http://www.mma.gov.br/images/arquivo/80112/CNUC_PorBiomaFev16.pdf).
- Materials and methods are available as supplementary materials on Science Online.
- R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, *Int. J. Climatol.* **25**, 1965–1978 (2005).
- R. T. Pennington, D. E. Prado, C. A. Pendry, *J. Biogeogr.* **27**, 261–273 (2000).
- D. E. Prado, P. E. Gibbs, *Ann. Mo. Bot. Gard.* **80**, 902–927 (1993).
- D. E. Prado, *Candollea* **48**, 145–172 (1993).
- H. Kraft, W. Jetz, *J. Biogeogr.* **37**, 2029–2053 (2010).
- M. Maunder et al., *Bot. Rev.* **74**, 197–207 (2008).
- P. Acevedo-Rodríguez, M. T. Strong, *Smithsonian Contrib. Bot.* **98**, 1–112 (2012).
- A. H. Gentry, *Ann. Mo. Bot. Gard.* **69**, 557–593 (1982).
- G. Sarmiento, *J. Biogeogr.* **2**, 233–251 (1975).

21. P. V. A. Fine, R. H. Ree, *Am. Nat.* **168**, 796–804 (2006).  
 22. J. X. Becerra, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 10919–10923 (2005).  
 23. R. J. Burnham, N. L. Carranco, *Am. J. Bot.* **91**, 1767–1773 (2004).  
 24. Ministry of the Environment, Peru, *Mapa Nacional de Cobertura Vegetal: Memoria Descriptiva* (Ministerio del Ambiente, Lima, Perú, 2015).  
 25. L. P. de Queiroz, in *Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation*, R. T. Pennington, G. P. Lewis, J. A. Ratter, Eds. (CRC Press, Boca Raton, FL 2006) pp. 121–157.  
 26. J. Rzedowski, G. C. de Rzedowski, *Acta Bot. Mex.* **102**, 1–23 (2013).  
 27. R. Linares-Palomino, in *Neotropical Savannas and Seasonally Dry Forest: Plant Diversity, Biogeography and Conservation*, R. T. Pennington, G. P. Lewis, J. A. Ratter, Eds. (CRC Press, Boca Raton, 2006) pp. 227–280.  
 28. C. E. Hughes, R. T. Pennington, A. Antonelli, *Bot. J. Linn. Soc.* **171**, 1–18 (2013).  
 29. I. Trejo, R. Dirzo, *Biodivers. Conserv.* **11**, 2063–2084 (2002).  
 30. S. Bridgewater, J. A. Ratter, J. F. Ribeiro, *Biodivers. Conserv.* **13**, 2295–2317 (2004).  
 31. D. M. Neves, K. G. Dexter, R. T. Pennington, M. L. Bueno, A. T. Oliveira-Filho, *J. Biogeogr.* **42**, 1566–1576 (2015).  
 32. K. G. Dexter et al., *Int. For. Rev.* **17**, 10–32 (2015).  
 33. N. C. A. Pitman et al., *Ecology* **82**, 2101–2117 (2001).  
 34. H. ter Steege et al., *Science* **342**, 1243092 (2013).  
 35. G. Forero-Medina, L. Joppa, *PLOS ONE* **5**, e13210 (2010).  
 36. Convention on Biological Diversity, Quick guide to the Aichi Biodiversity Targets: Protected areas increased and improved, TARGET 11—Technical Rationale extended (COP/10/INF/12/Rev, Convention on Biological Diversity, 2011); <https://www.cbd.int/doc/strategic-plan/targets/T11-quick-guide-en.pdf>.

#### ACKNOWLEDGMENTS

This paper is the result of the Latin American and Caribbean Seasonally Dry Tropical Forest Floristic Network (DRYFLOR), which has been supported at the Royal Botanic Garden Edinburgh by a Leverhulme Trust International Network Grant (IN-074). This work was also supported by the U.K. Natural Environment Research Council grant NE/I028122/1; Colciencias Ph.D. scholarship 529; Synthesys Programme GBTAf-2824; the NSF (NSF 1118340 and 1118369); the Instituto Humboldt (IAvH)—Red colombiana de investigación y monitoreo en bosque seco; the Inter-American Institute for Global Change Research (IAI); Tropi-Dry, CRN2-021, funded by NSF GEO 0452325; Universidad Nacional de Rosario (UNR); and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). The data reported in this paper are available at [www.dryflor.info](http://www.dryflor.info). R.T.P. conceived the study. M.P., A.O.-F., K.B.-R., R.T.P., and J.W. designed the DRYFLOR database system. K.B.-R. and K.G.D. carried out most analyses. K.B.-R., R.T.P., and K.G.D. wrote the manuscript with substantial input from A.D.-S., R.L.-P., A.O.-F., D.P., C.Q., and R.R. All the authors contributed data, discussed further analyses, and commented on various versions of the manuscript. K.B.-R. thanks G. Galeano who introduced her to dry forest research. We thank J. L. Marcelo, I. Huamantupa, C. Reynel, S. Palacios, and A. Daza for help with fieldwork and data entry in Peru.

#### DRYFLOR authors

- Karina Banda-R,<sup>19</sup> Alfonso Delgado-Salinas,<sup>2</sup> Kyle G. Dexter,<sup>1,3</sup> Reynaldo Linares-Palomino,<sup>4,10</sup> Ary Oliveira-Filho,<sup>5</sup> Darién Prado,<sup>6</sup> Martín Pullan,<sup>1</sup> Catalina Quintana,<sup>7</sup> Ricardo Riina,<sup>8</sup> Gina M. Rodríguez M.,<sup>9</sup> Julia Weinritt,<sup>1</sup> Pedro Acevedo-Rodríguez,<sup>11</sup> Juan Adarve,<sup>12</sup> Esteban Álvarez,<sup>13</sup> Anairamíz Aranguren B.,<sup>14</sup> Julián Camilo Arteaga,<sup>15</sup> Gerardo Aymar,<sup>16</sup> Alejandro Castaño,<sup>17</sup> Natalia Ceballos-Mago,<sup>18</sup> Álvaro Cogollo,<sup>13</sup> Hermes Cuadros,<sup>19</sup> Freddy Delgado,<sup>20</sup> Wilson Devia,<sup>21</sup> Hilda Dueñas,<sup>15</sup> Laurie Fajardo,<sup>22</sup> Ángel Fernández,<sup>23</sup> Miller Ángel Fernández,<sup>24</sup> Janet Franklin,<sup>25</sup> Ethan H.Freid,<sup>26</sup> Luciano A. Galetti,<sup>6</sup> Reina Gonto,<sup>23</sup> Roy González-M.,<sup>27,44</sup> Roger Graveson,<sup>29</sup> Eileen H. Helmer,<sup>29</sup> Álvaro Idárraga,<sup>30</sup> René López,<sup>31</sup> Humfredo Marcano-Vega,<sup>29</sup> Olga G. Martínez,<sup>32</sup> Hernán M. Maturo,<sup>6</sup> Morag McDonald,<sup>33</sup> Kurt McLaren,<sup>34</sup> Omar Melo,<sup>35</sup> Francisco Mijares,<sup>36</sup> Virginia Mogni,<sup>6</sup> Diego Molina,<sup>30</sup> Natalia del Pilar Moreno,<sup>37</sup> Jafet M. Nasar,<sup>22</sup> Danilo M. Neves,<sup>1,45</sup> Luis J. Oakley,<sup>6</sup> Michael Oatham,<sup>38</sup> Alma Rosa Olvera-Luna,<sup>7</sup> Flávia F. Pezzini,<sup>1</sup> Orlando Joel Reyes Domínguez,<sup>39</sup> María Elvira Ríos,<sup>40</sup> Orlando Rivera,<sup>37</sup> Nelly Rodríguez,<sup>41</sup> Alicia Rojas,<sup>42</sup> Tiina Särkinen,<sup>1</sup> Roberto Sánchez,<sup>40</sup> Melvin Smith,<sup>28</sup> Carlos Vargas,<sup>43,44</sup> Boris Villanueva,<sup>35</sup> R. Toby Pennington<sup>1</sup>

<sup>1</sup>Royal Botanic Garden Edinburgh, 20a Inverleith Row, EH3 5LR, Edinburgh, UK. <sup>2</sup>Departamento de Botánica, Universidad Nacional Autónoma de México, México D.F., México. <sup>3</sup>School of GeoSciences, University of Edinburgh, Edinburgh, UK. <sup>4</sup>Universidad

Nacional Agraria La Molina, Avenida La Molina, Lima, Perú. <sup>5</sup>Universidade Federal de Minas Gerais (UFMG), Instituto de Ciências Biológicas (ICB), Departamento de Botânica, Avenida Antônio Carlos, 6627-Pampulha, Belo Horizonte, Minas Gerais, Brazil. <sup>6</sup>Cátedra de Botánica, IICAR-CONICET, Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, C.C. N° 14, S2125ZAA Zavalla, Argentina. <sup>7</sup>Pontificia Universidad Católica del Ecuador, Facultad de Ciencias Exactas, Escuela de Biología, Avenida 12 de Octubre 1076 y Roca, Quito, Ecuador. <sup>8</sup>Real Jardín Botánico, RJB-CSIC, Plaza de Murillo 2, 28014 Madrid, Spain. <sup>9</sup>Fundación Ecosistemas Secos de Colombia, Calle 5 A N° 70 C-31, Bogotá, Colombia. <sup>10</sup>Smithsonian Conservation Biology Institute, Los Libertadores 215, San Isidro, Lima, Perú. <sup>11</sup>Smithsonian National Museum of Natural History, West Loading Dock, 10th and Constitution Avenue, NW, Washington, DC 20560-0166, USA. <sup>12</sup>Parque Regional “El Vínculo”—INCIVA, El Vínculo—Kilometro 3 al sur de Buga sobre la Carretera Panamericana, Valle del Cauca, Colombia. <sup>13</sup>Jardín Botánico de Medellín José Joaquín Antonio Uribe,” Calle 73 No. 51D-14, Medellín, Colombia. <sup>14</sup>Instituto de Ciencias Ambientales y Ecológicas, Facultad de Ciencias, Núcleo Pedro Rincón, La Hechicería, 3er Piso, Universidad de los Andes (ULA), Mérida, Venezuela. <sup>15</sup>Herbario SURCO, Universidad Surcolombiana, Neiva, Colombia. <sup>16</sup>Programa de Ciencias del Agro y el Mar Herbario Universitario (PORT), UNELLEZ-Guámar, Mesa de Caucavas, Estado Portuguesa 3350, Venezuela. <sup>17</sup>Jardín Botánico “Juan María Céspedes” INCIVA, Mateguada, Tuluá, Valle del Cauca, Colombia. <sup>18</sup>Proyecto Mono de Margarita y Fundación Vuelta Larga, Isla de Margarita, Estado Nueva Esparta, Venezuela. <sup>19</sup>Universidad del Atlántico, Kilómetro 7 Vía Puerto, Barranquilla, Atlántico, Colombia. <sup>20</sup>Centro de Investigaciones y Servicios Ambientales (ECOVIDA), Delegación Territorial del Ministerio de Ciencia, Tecnología, y Medio Ambiente, Pinar del Río, Cuba. <sup>21</sup>Unidad Central del Valle del Cauca (UCEVA), Carrera 25 B No. 44-28, Tuluá, Valle del Cauca, Colombia. <sup>22</sup>Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 20632, Caracas 1020-A, Venezuela. <sup>23</sup>Centro de Biofísica y Bioquímica (Herbarium), Instituto Venezolano de Investigaciones Científicas, Apartado 20632, Caracas 1020-A, Venezuela. <sup>24</sup>Consultant Botanist, Yopal, Casanare, Colombia. <sup>25</sup>School of Geographical Sciences and Urban Planning, Arizona State University, Post Office Box 875302, Tempe, AZ 85287-5302, USA. <sup>26</sup>Bahamas National Trust, Leon Levy Native Plant Preserve, Eleuthera,

Bahamas. <sup>27</sup>Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Avenida Paseo Bolívar 16-20, Bogotá, D.C., Colombia. <sup>28</sup>Consultant Botanist, Cas in Bas Road, Gros Islet, St. Lucia. <sup>29</sup>Forest Service, Southern Research Station, International Institute of Tropical Forestry, Jardín Botánico Sur, 1201 Calle Ceiba, San Juan, PR00926, Puerto Rico. <sup>30</sup>Grupo de Estudios Botánicos, Universidad de Antioquia, AA 1226 Medellín, Colombia. <sup>31</sup>Universidad Distrital Francisco José de Caldas, Carrera 5 Este No. 15-82, Bogotá, Colombia. <sup>32</sup>Facultad de Ciencias Naturales, Universidad Nacional de Salta, Avenida Bolivia 5150, 4400 Salta, Argentina. <sup>33</sup>School of Environment, Natural Resources, and Geography, Thoday Building, Room G21, Bangor University, Bangor LL57 2DG, UK. <sup>34</sup>Department of Life Sciences, University of West Indies, Mona, Jamaica. <sup>35</sup>Universidad del Tolima, Barrio Santa Helena Parte Alta, Código Postal 730006299, Ibagué, Tolima, Colombia. <sup>36</sup>Fundación Orinoquia Biodiversa, Calle 15 No. 12-15, Tame, Arauca, Colombia. <sup>37</sup>Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Sede Bogotá, Código Postal 111321, Avenida Carrera 30 No. 45-03, Edificio 425, Bogotá, Colombia. <sup>38</sup>Department of Life Sciences, The University of The West Indies St. Augustine, Natural Sciences Building, Old Wing, Room 222, St. Augustine, Trinidad and Tobago. <sup>39</sup>Centro Oriental de Ecosistemas y Biodiversidad BIOECO, Cuba. <sup>40</sup>Universidad de Pamplona, Ciudad Universitaria, Pamplona, Norte de Santander, Colombia. <sup>41</sup>Departamento de Biología, Universidad Nacional de Colombia, Sede Bogotá, Código Postal 111321, Avenida Carrera 30 No. 45-03, Edificio 476, Bogotá, Colombia. <sup>42</sup>Jardín Botánico Eloy Valenzuela, Avenida Bucarica, Floridablanca, Santander, Colombia. <sup>43</sup>Jardín Botánico de Bogotá “José Celestino Mutis”, Avenida Calle 63 No. 68-95, Bogotá, Colombia. <sup>44</sup>Facultad de Ciencias Naturales y Matemática, Universidad del Rosario, Carrera 26 No. 63B-48, Bogotá, Colombia. <sup>45</sup>Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

#### SUPPLEMENTARY MATERIALS

[www.sciencemag.org/content/353/6306/1383/suppl/DC1](http://www.sciencemag.org/content/353/6306/1383/suppl/DC1)  
 Materials and Methods  
 Figs. S1 to S6  
 Tables S1 to S6  
 References (37–45)

26 February 2016; accepted 11 August 2016  
 10.1126/science.aaf5080

#### INFECTIOUS DISEASE

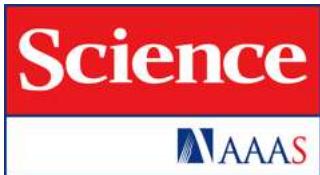
## Replication of human noroviruses in stem cell-derived human enteroids

**Khalil Ettayebi,<sup>1\*</sup> Sue E. Crawford,<sup>1\*</sup> Kosuke Murakami,<sup>1\*</sup> James R. Broughman,<sup>1</sup> Umesh Karandikar,<sup>1</sup> Victoria R. Tenge,<sup>1</sup> Frederick H. Neill,<sup>1</sup> Sarah E. Blutt,<sup>1</sup> Xi-Lei Zeng,<sup>1</sup> Lin Qu,<sup>1</sup> Baijun Kou,<sup>1</sup> Antone R. Opekun,<sup>2,3,4</sup> Douglas Burrin,<sup>3,4</sup> David Y. Graham,<sup>1,2,5</sup> Sasirekha Ramani,<sup>1</sup> Robert L. Atmar,<sup>1,2</sup> Mary K. Estes<sup>1,2†</sup>**

The major barrier to research and development of effective interventions for human noroviruses (HuNoVs) has been the lack of a robust and reproducible *in vitro* cultivation system. HuNoVs are the leading cause of gastroenteritis worldwide. We report the successful cultivation of multiple HuNoV strains in enterocytes in stem cell-derived, nontransformed human intestinal enteroid monolayer cultures. Bile, a critical factor of the intestinal milieu, is required for strain-dependent HuNoV replication. Lack of appropriate histoblood group antigen expression in intestinal cells restricts virus replication, and infectivity is abrogated by inactivation (e.g., irradiation, heating) and serum neutralization. This culture system recapitulates the human intestinal epithelium, permits human host-pathogen studies of previously noncultivable pathogens, and allows the assessment of methods to prevent and treat HuNoV infections.

**H**uman noroviruses (HuNoVs) are the most common cause of epidemic and sporadic cases of acute gastroenteritis worldwide, and are the leading cause of food-borne gastroenteritis (*1–3*). Since the introduction

of rotavirus vaccines, HuNoVs have become the predominant gastrointestinal pathogen within pediatric populations in developed countries (*4*). HuNoVs are highly contagious, with rapid person-to-person transmission directly through the fecal-oral route



## Plant diversity patterns in neotropical dry forests and their conservation implications

DRYFLOR, Karina Banda-R, Alfonso Delgado-Salinas, Kyle G. Dexter, Reynaldo Linares-Palomino, Ary Oliveira-Filho, Darién Prado, Martín Pullan, Catalina Quintana, Ricarda Riina, Gina M. Rodríguez M., Julia Weinritt, Pedro Acevedo-Rodríguez, Juan Adarve, Esteban Álvarez, Anairamiz Aranguren B., Julián Camilo Arteaga, Gerardo Aymard, Alejandro Castaño, Natalia Ceballos-Mago, Álvaro Cogollo, Hermes Cuadros, Freddy Delgado, Wilson Devia, Hilda Dueñas, Laurie Fajardo, Ángel Fernández, Miller Ángel Fernández, Janet Franklin, Ethan H. Freid, Luciano A. Galetti, Reina Gonto, Roy González-M., Roger Graverson, Eileen H. Helmer, Álvaro Idárraga, René López, Humfredo Marcano-Vega, Olga G. Martínez, Hernán M. Maturo, Morag McDonald, Kurt McLaren, Omar Melo, Francisco Mijares, Virginia Mogni, Diego Molina, Natalia del Pilar Moreno, Jafet M. Nassar, Danilo M. Neves, Luis J. Oakley, Michael Oatham, Alma Rosa Olvera-Luna, Flávia F. Pezzini, Orlando Joel Reyes Dominguez, María Elvira Ríos, Orlando Rivera, Nelly Rodríguez, Alicia Rojas, Tiina Särkinen, Roberto Sánchez, Melvin Smith, Carlos Vargas, Boris Villanueva and R. Toby Pennington (September 22, 2016)  
*Science* **353** (6306), 1383-1387. [doi: 10.1126/science.aaf5080]

### Editor's Summary

---

This copy is for your personal, non-commercial use only.

---

#### Article Tools

Visit the online version of this article to access the personalization and article tools:  
<http://science.sciencemag.org/content/353/6306/1383>

#### Permissions

Obtain information about reproducing this article:  
<http://www.sciencemag.org/about/permissions.dtl>

## Supplementary Materials for Plant diversity patterns in neotropical dry forests and their conservation implications

DRYFLOR

\*Corresponding author. Email: [t.pennington@rbge.ac.uk](mailto:t.pennington@rbge.ac.uk)

Published 23 September 2016, *Science* **353**, 1383 (2016)  
DOI: 10.1126/science.aaf5080

### This PDF file includes

Materials and Methods  
Figs. S1 to S6  
Tables S1 to S6  
References

## **Materials and Methods**

### Floristic data

We use data assembled by the Latin American and Caribbean seasonally dry forest floristic network (DRYFLOR; <http://www.dryflor.info/>). DRYFLOR has developed the first comprehensive dataset of the woody flora of neotropical dry forest *sensu lato* (15, 20, 38) across its full range, which covers tall semi-deciduous forests on moister sites to thorn woodland and cactus scrub on drier ones. The data are for woody plants at least 3 m in height and excluding lianas or climbers, following the criteria of NeoTropTree (Tree Flora of the Neotropical Region; <http://www.icb.ufmg.br/treetlan/>). Floristic lists come mainly from floristic surveys or ecological inventories, most of which are published in journal articles, books, technical reports and theses, as well as our own extensive field work. Every list covers a site of uniform vegetation type. The maximum size of a site is a circular area with a diameter of 10 km, but most are smaller. In some cases researchers and institutions provided unpublished floristic data to DRYFLOR. The DRYFLOR database contains 6958 species (the database includes only taxa identified to species and does not use infraspecific taxa) from 1169 genera and 159 families, obtained from 192,264 occurrence records from 1602 sites across Latin America and the Caribbean.

Taxonomic concepts of families are based upon the Angiosperm Phylogeny Group III system (39). To identify misspellings, the species list was tested in the Taxonomic Name Resolution Service v3.2 (<http://tnrs.iplantcollaborative.org>). Accepted species names and synonyms followed the most recently updated taxonomic resources for the Neotropics such as Catalogue of Seed Plants of the West Indies (19), Flora del Conosur (<http://www2.darwin.edu.ar/Proyectos/FloraArgentina/FA.asp>) and Flora do Brasil (<http://floradobrasil.jbrj.gov.br/>). In cases where these sources were in conflict, we contacted taxonomic specialists whenever possible.

### Dataset exploration

Preliminary analyses were necessary to standardize and explore the nature and structure of the dataset. We first built a binary matrix of species versus sites based on the DRYFLOR database, excluding chaco sites and singleton species (1836 species that occur at just one site). We removed sites with less than eight species presences (n=105). Knowing that some areas of dry forest in the Andes have complete floristic inventories with few woody species, eight species was the threshold chosen making a balance between keeping the greatest number of sites and avoiding the intrinsic noise that species-poor sites or incomplete sampling usually add (17). The matrix for these preliminary analyses contained 4999 tree species and 1467 dry forest sites.

A clustering analysis was run altering the order of the sites 10000 times, which was summarized using a 50% majority rule consensus tree, using Simpson dissimilarity as a distance measure and the unweighted pair-group method with arithmetic mean (UPGMA) as the linkage method (see “Data analysis” below). The consensus tree showed eleven groups, the relationships amongst which were not well resolved. The eleven groups are: i. Semi-deciduous vegetation types (including the Misiones region); ii. Central Brazil; iii. Central inter-Andean Valleys; iv. Central Andes Coast; v. Antilles; vi. Venezuelan Andes

(montane); vii. Northern inter-Andean Valleys; viii. Mexico; ix. Piedmont and Apurimac-Mantaro; x. Caatinga; and xi. Tarapoto-Quillabamba. Sites from Central America and northern South America form a series of groups, the relationships of which were unresolved (Fig. S1).

The cluster of 715 semi-deciduous sites is largely comprised of formations from the Atlantic Forest, central Brazil (mostly gallery forest) and the Misiones region. Semi-deciduous formations are tall forests in areas where between 30 and 60% of the leaf mass is lost during the dry season (40) but where the seasonal rainfall regime is less severe. The semi-deciduous sites include species more characteristic of humid environments such as the Atlantic and Amazon rain forests, which enter the savanna (“Cerrado”) region of central Brazil in gallery forest along rivers. The proximity of dry forest areas to different major biomes, for example savanna in the Cerrado region or rain forest and montane forest elsewhere (1), promotes the incursion of different floristic elements into transitional semi-deciduous areas. In the semi-deciduous sites, the genera with most records are *Eugenia*, *Myrcia*, *Miconia*, and *Ocotea*, which are not typical or dominant elements from drier forest formations. Based on the multiple moist forest elements present in the transitional areas, we decided to exclude most of the semi-deciduous sites. Similarly, we excluded the group of sites from the Venezuelan Andes because their species lists included elements from montane forest (i.e. *Viburnum tinoides*, *Miconia theizans*, *Clusia rosea* and *C. minor*) and other humid environments (i.e. *Myrsine coriacea* and *Vismia baccifera*). In contrast, we retained a set of semi-deciduous sites (n=84) from the Misiones region, which is a traditional recognized dry forest nucleus (1, 5) that extends from eastern Paraguay to north eastern Argentina, because we aimed to understand its relationships.

Our final dataset, focusing on the drier, deciduous formations plus the Misiones nucleus, contained 835 sites, 147 families, 983 genera and 4660 species of which 1504 (32%) are singletons, found at just one site.

#### Data analysis

We performed ordination and classification analyses, both of which excluded singleton species, to identify the main regions of neotropical dry forest and to describe the floristic affinities amongst them. Analyses were run in the R Statistical Environment v. 3.2.1 using the packages vegan (41), recluster (42), and pvclust (43). Pairwise floristic distances were calculated using the Simpson dissimilarity index because our dataset varied in numbers of species per site (from 8 to 305 species), and this index is less affected by variation in species richness than other measures (17). The Simpson dissimilarity ( $\beta$  sim) calculates the compositional distance between pairs of sites  $\beta$  sim =  $1 - J / [J + \min(A, B)]$ , where A and B are the number of species unique to each site, and J is the number of species common to both sites (44).

Non-metric multidimensional scaling (NMDS) ordinations used the function metaMDS - of the vegan library (41). In addition, we carried out a sensitivity analysis using monoMDS in order to explore the effects of tied dissimilarity values, which were found to not be significant (results not shown). NMDS was performed using 100 and 1000

random starts to reach a stable solution in two and four dimensions with stress values lower than 0.13. Classification hypotheses of the sites employed UPGMA hierarchical clustering (17, 42). The Simpson dissimilarity amongst sites had a high percentage of tied values, which implies that many equivalent trees are likely in the classification, and indicates that the results can be affected by the order of the sites in the species by site matrix. When the pairwise distance values are equal, the pairs first linked in the species by site matrix are more likely to be clustered. To avoid this bias, we used the recluster package (42) (`recluster.cons` function), performing 10000 random re-orderings of the sites.

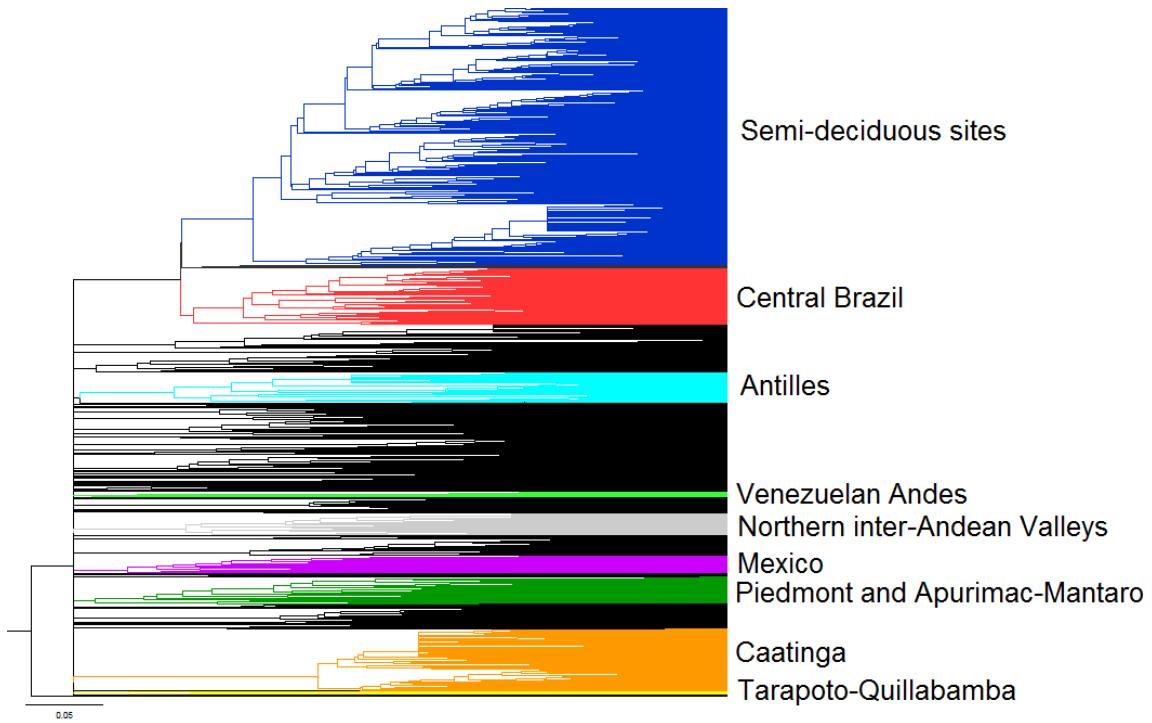
In order to investigate relationships amongst the floristic groups identified by the overall clustering analyses (12 floristic groups; see below), we pooled the species lists for each group into a single list and conducted clustering analyses on a species  $\times$  floristic group matrix. We used a `pvclust` approach, as here there are no tied values in the distance matrix. This method provides Approximately Unbiased (AU) support values per cluster, computed by multiscale bootstrap resampling; clusters with high AU values (e.g.,  $>0.95$ ) are strongly supported (43).

Using these pooled species lists for each floristic group we plotted the number of sites surveyed against the total number of species found in a given dry forest floristic group (Fig. S6). We also calculated Simpson and Sørensen dissimilarity values amongst the groups (Table S3) and amongst all sites within them (Table S4). We used Simpson because it is less affected by variation in species richness as explained above as well as Sørensen because it has been widely employed in prior studies of floristic turnover in tropical forests and allows for comparison with these studies. These calculations included singletons because we wished to capture fully the floristic dissimilarity between sites.

To assess how well the floristic diversity is captured in our dataset, we calculated expected species accumulation curves for each floristic group using a sample-based rarefaction method (45), from the “`specaccum`” function in the `vegan` library (41).

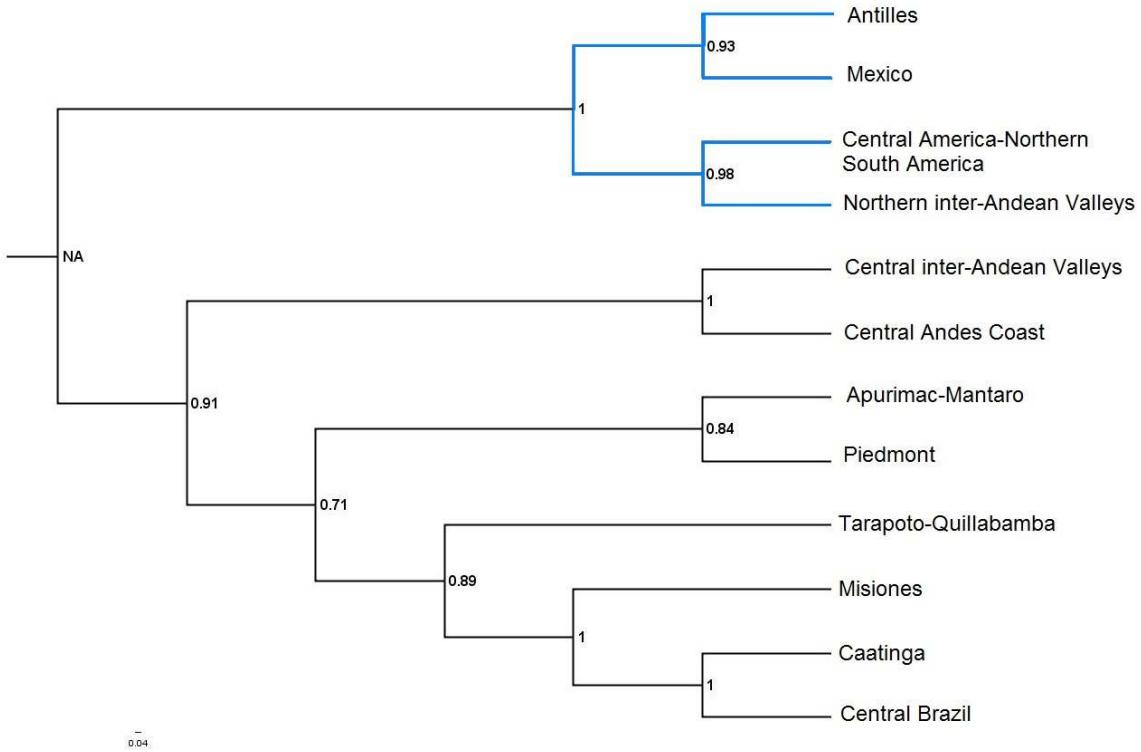
In order to evaluate diversity gradients in terms of distance from the equator in our final dataset a linear and a polynomial regression were fitted to a scatterplot of absolute latitude versus total number of species per dry forest site.

We conducted an assessment of the conservation status of dry forest by overlaying the distribution of our 835 sites on to the coverage of protected areas across the Neotropics. We used conservation units from the World Database on Protected Areas (WDPA) reported by 2015 (IUCN & UNEP-WCMC, [www.protectedplanet.net](http://www.protectedplanet.net)).



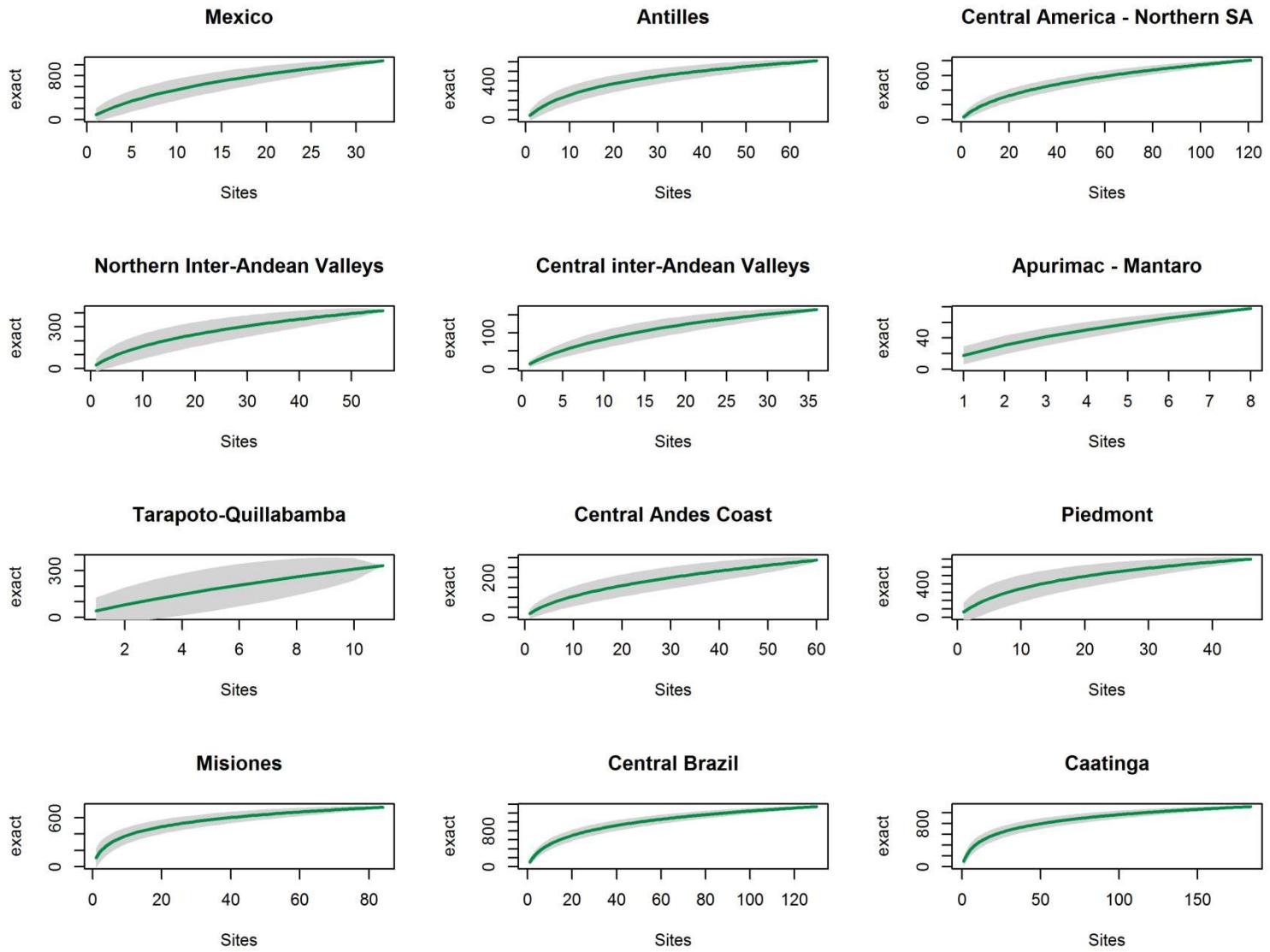
**Fig. S1.**

Fifty percent majority rule consensus tree based upon 10000 random site order-addition hierarchical clustering analyses of 1467 dry forest sites, excluding singleton species and using Simpson dissimilarity and UPGMA as the linkage method. Sites from central America and northern South America indicated in black.



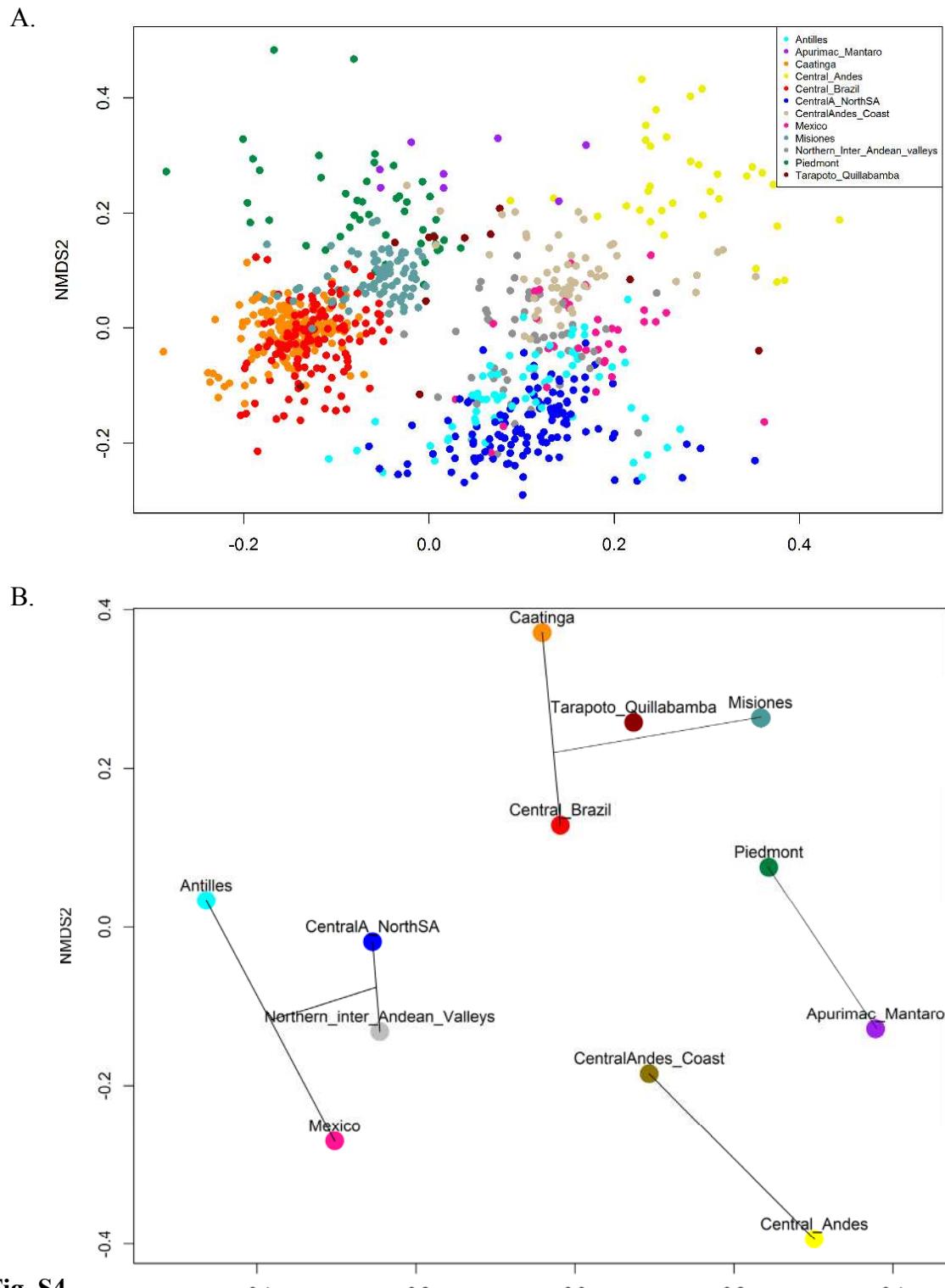
**Fig. S2**

Hierarchical classification of the 12 floristic dry forest groups using Simpson dissimilarity and UPGMA as the linkage method. The node values correspond to the approximately unbiased bootstrap (AU), obtained using 10000 iterations of multiscale bootstrap resampling. The higher-level northern cluster is indicated with blue lines.



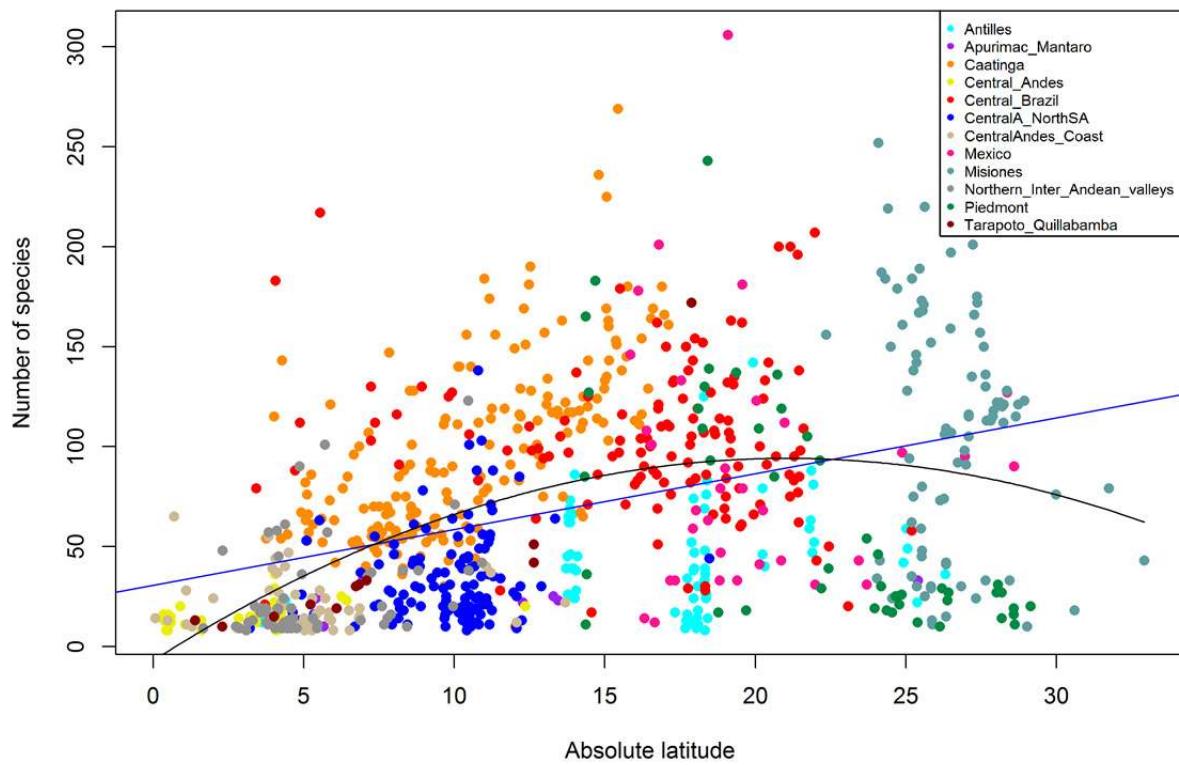
**Fig. S3**

Species accumulation curves for each dry forest group calculated using a sample-based rarefaction method. Grey shadow shows confidence intervals from the standard deviation.



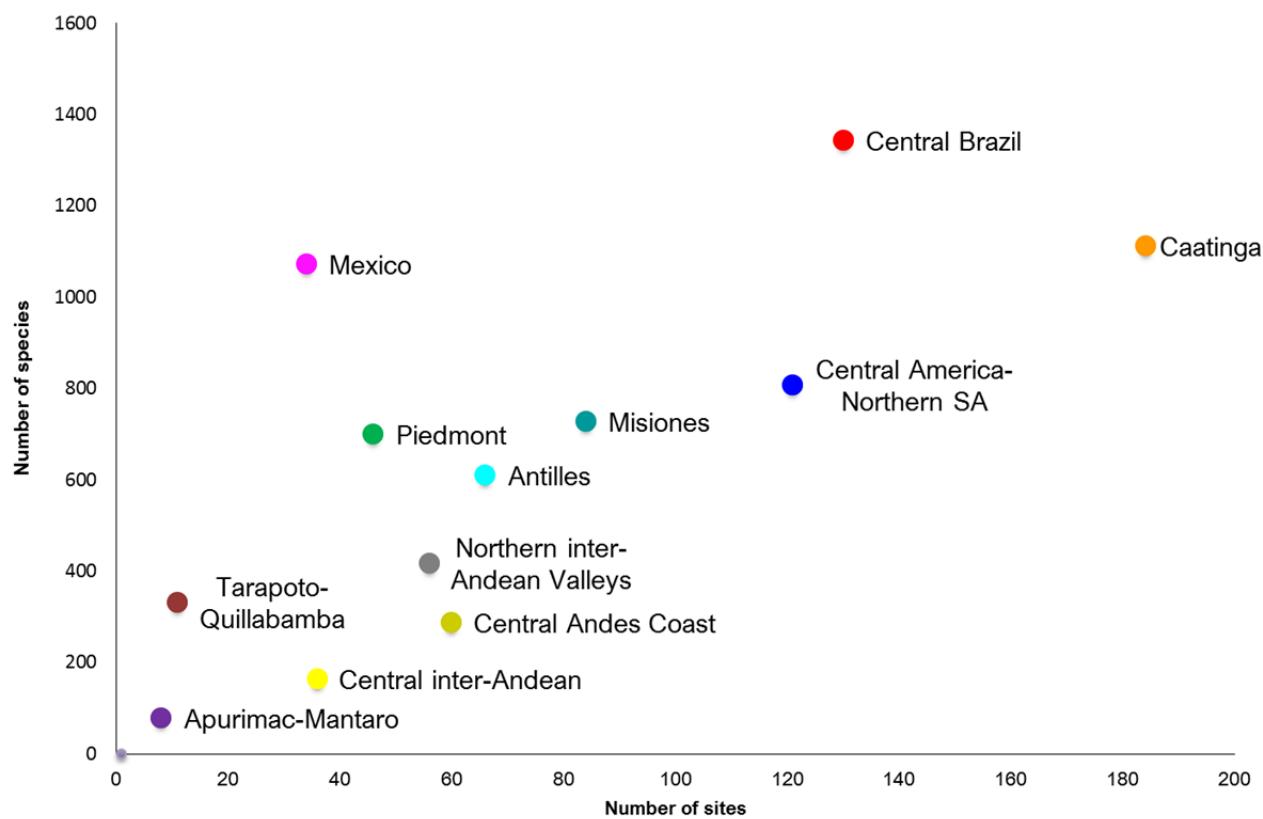
**Fig. S4**

NMDS ordination plots in two dimensions of dry forest floristic groups. A: 835 sites; stress values = 0.124, tr = 1000. B: 12 floristic groups; stress values = 0.116, tr = 100; relationships inferred from a classification using the UPGMA method (Fig. S2) are indicated by lines.



**Fig. S5**

Fitted lines plot for polynomial (black line,  $R^2= 0.2196$ ) and linear (blue line,  $R^2= 0.159$ ) regression of absolute latitude versus total number of species of 835 dry forest sites.



**Fig. S6**

Scatter plot of number of sites versus the total number of species per dry forest floristic group.

**Table S1.**

Description of dry forest floristic groups: numbers of sites, records, taxonomic diversity including singleton species and percentage of exclusive species

Group	Number of sites	Number of families	Number of genera	Number of species	Median of species per site	Mean of species per site	% exclusive species
Antilles	66	74	286	611	39	44.1	65
Apurimac-Mantaro	8	30	58	78	20	17.8	38
Central Andes Coast	60	54	178	288	16	19.7	35
Caatinga	184	80	369	1112	88	97.7	32
Central inter-Andean Valleys	36	40	111	165	13.5	13.8	41
Central America - Northern SA	121	81	377	808	27	33.1	40
Central Brazil	130	94	429	1344	99.5	103.3	23
Mexico	33	83	355	1072	78	98.1	73
Misiones	84	85	313	728	114	106.1	30
Northern inter-Andean Valleys	56	65	230	418	16.5	25.9	28
Piedmont	46	92	353	700	29.5	61.8	35
Tarapoto-Quillabamba	11	68	196	332	30	42.5	28

**Table S2.**

Shared species among dry forest floristic groups. Deeper grey shade indicates greater numbers of shared species, corresponding to line widths in Figure 3.

	Antilles	Apurimac-Mantaro	Central Andes Coast	Caatinga	Central inter-Andean	CentralA-NorthSA	Central Brazil	Mexico	Misiones	Northern Inter-Andean	Piedmont	Tarapoto-Quillabamba
Antilles	611	7	42	58	12	138	73	124	51	81	39	36
Apurimac-Mantaro		78	21	9	19	10	12	12	17	11	30	13
Central Andes Coast			288	48	64	79	70	63	51	64	71	50
Caatinga				1112	12	127	695	59	264	70	179	89
Central inter-Andean					165	21	21	20	22	23	32	17
CentralA-NorthSA						808	191	202	96	241	98	94
Central Brazil							1344	72	409	122	321	149
Mexico								1072	50	102	68	31
Misiones									728	75	232	90
Northern Inter-Andean										418	76	73
Piedmont											700	134
Tarapoto-Quillabamba												332

**Table S3.**

Dissimilarity values among dry forest floristic groups: A. Simpson; B. Sørensen. Deeper grey shade indicates greater values.

A.

	Antilles	Apurimac-Mantaro	Central Andes Coast	Caatinga	Central inter-Andean	CentralA-NorthSA	Central Brazil	Mexico	Misiones	Northern Inter-Andean	Piedmont	Tarapoto-Quillabamba
Antilles	0.00	0.91	0.85	0.91	0.93	0.77	0.88	0.80	0.92	0.81	0.94	0.89
Apurimac-Mantaro		0.00	0.73	0.88	0.76	0.87	0.85	0.85	0.78	0.86	0.62	0.83
Central Andes Coast			0.00	0.83	0.61	0.73	0.76	0.78	0.82	0.78	0.75	0.83
Caatinga				0.00	0.93	0.84	0.38	0.94	0.64	0.83	0.74	0.73
Central inter-Andean					0.00	0.87	0.87	0.88	0.87	0.86	0.81	0.90
CentralA-NorthSA						0.00	0.76	0.75	0.87	0.42	0.86	0.72
Central Brazil							0.00	0.93	0.44	0.71	0.54	0.55
Mexico								0.00	0.93	0.76	0.90	0.91
Misiones									0.00	0.82	0.67	0.73
Northern Inter-Andean										0.00	0.82	0.78
Piedmont											0.00	0.60
Tarapoto-Quillabamba												0.00

B.

	Antilles	Apurimac-Mantaro	Central Andes Coast	Caatinga	Central inter-Andean	CentralA-NorthSA	Central Brazil	Mexico	Misiones	Northern Inter-Andean	Piedmont	Tarapoto-Quillabamba
Antilles	0.00	0.98	0.91	0.93	0.97	0.81	0.93	0.85	0.92	0.84	0.94	0.92
Apurimac-Mantaro		0.00	0.89	0.98	0.84	0.98	0.98	0.98	0.96	0.96	0.92	0.94
Central Andes Coast			0.00	0.93	0.72	0.86	0.91	0.91	0.90	0.82	0.86	0.84
Caatinga				0.00	0.98	0.87	0.43	0.95	0.71	0.91	0.80	0.88
Central inter-Andean					0.00	0.96	0.97	0.97	0.95	0.92	0.93	0.93
CentralA-NorthSA						0.00	0.82	0.79	0.88	0.61	0.87	0.84
Central Brazil							0.00	0.94	0.61	0.86	0.69	0.82
Mexico								0.00	0.94	0.86	0.92	0.96
Misiones									0.00	0.87	0.68	0.83
Northern Inter-Andean										0.00	0.86	0.81
Piedmont											0.00	0.74
Tarapoto-Quillabamba												0.00

**Table S4.**

Floristic dissimilarity values within each dry forest floristic group as measured by Simpson and Sørensen dissimilarity index.

Group	Simpson index		Sorensen index	
	mean	median	mean	median
Antilles	0.72	0.75	0.82	0.85
Apurimac-Mantaro	0.70	0.68	0.76	0.76
Central Andes Coast	0.67	0.70	0.77	0.81
Caatinga	0.63	0.63	0.72	0.74
Central inter-Andean Valleys	0.77	0.80	0.81	0.85
Central America -Northern SA	0.77	0.80	0.85	0.87
Central Brazil	0.69	0.69	0.75	0.76
Mexico	0.77	0.79	0.86	0.88
Misiones	0.47	0.45	0.67	0.70
Northern inter-Andean Valleys	0.73	0.78	0.84	0.86
Piedmont	0.67	0.68	0.83	0.86
Tarapoto-Quillabamba	0.84	0.86	0.89	0.90

**Table S5.**

Tree species recorded in more than nine dry forest floristic groups.

Species \ Group	Antilles	Apurimac-Mantaro	Central Andes Coast	Caatinga	Central Inter-Andean	CentralA-NorthSA	Central Brazil	Mexico	Misiones	Northern Inter-Andean	Piedmont	Tarapoto-Quillabamba
<i>Cynophalla flexuosa</i>	x	x	x	x		x	x	x	x	x	x	x
<i>Sapindus saponaria</i>		x	x	x	x	x	x	x	x	x	x	x
<i>Trema micrantha</i>	x	x	x	x		x	x	x	x	x	x	x
<i>Celtis iguanaea</i>	x		x	x		x	x	x	x	x	x	x
<i>Cordia alliodora</i>	x		x	x	x	x	x	x		x	x	x
<i>Guazuma ulmifolia</i>	x		x	x		x	x	x	x	x	x	x
<i>Maclura tinctoria</i>	x		x	x		x	x	x	x	x	x	x
<i>Randia armata</i>	x		x	x	x	x	x	x	x	x	x	
<i>Tecoma stans</i>	x	x	x		x	x	x	x	x	x	x	
<i>Urera caracasana</i>		x	x	x		x	x	x	x	x	x	x
<i>Ximenia americana</i>	x		x	x		x	x	x	x	x	x	x
<i>Zanthoxylum fagara</i>	x		x	x	x	x	x	x	x	x	x	
<i>Cedrela odorata</i>	x		x	x		x	x	x	x	x		x
<i>Prockia crucis</i>	x		x	x		x	x	x	x		x	x
<i>Senegalia polyphylla</i>			x	x		x	x	x	x	x	x	x
<i>Trichilia hirta</i>	x		x	x		x	x	x	x	x	x	
<i>Vachellia macracantha</i>	x	x	x		x	x		x	x	x	x	

**Table S6.**

The 20 most species-rich families, the most species-rich genera and most recorded species, per dry forest floristic group.

Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Antilles (66)	Leguminosae (61)	Eugenia (16)	<i>Bursera simaruba</i> (54)
	Rubiaceae (46)	Coccoloba (15)	<i>Bourreria succulenta</i> (41)
	Myrtaceae (33)	Ficus (13)	<i>Guapira fragrans</i> (39)
	Boraginaceae (27)	Cordia (11)	<i>Citharexylum spinosum</i> (34)
	Euphorbiaceae (21)	Guettarda (11)	<i>Eugenia monticola</i> (33)
	Arecaceae (18)	Erythroxylum (9)	<i>Randia aculeata</i> (33)
	Lauraceae (17)	Zanthoxylum (9)	<i>Cynophalla hastata</i> (32)
	Malvaceae (16)	Casearia (8)	<i>Amyris elemifera</i> (31)
	Moraceae (16)	Croton (8)	<i>Krugiodendron ferreum</i> (29)
	Sapotaceae (16)	Miconia (8)	<i>Gymnanthes lucida</i> (27)
	Bignoniaceae (15)	Tabebuia (8)	<i>Picramnia pentandra</i> (26)
	Polygonaceae (15)	Maytenus (7)	<i>Schaefferia frutescens</i> (26)
	Rhamnaceae (15)	Bourreria (6)	<i>Tabebuia heterophylla</i> (25)
	Rutaceae (15)	Caesalpinia (6)	<i>Cynophalla flexuosa</i> (24)
	Salicaceae (14)	Comocladia (6)	<i>Erythroxylum rotundifolium</i> (24)
	Apocynaceae (13)	Diospyros (6)	<i>Guettarda scabra</i> (24)
	Sapindaceae (13)	Guapira (6)	<i>Quadrella indica</i> (24)
	Melastomataceae (12)	Plumeria (6)	<i>Canella winterana</i> (22)
	Cactaceae (11)	Calyptranthes (5)	<i>Ficus citrifolia</i> (22)
	Celastraceae (11)	Clusia (5)	<i>Nectandra coriacea</i> (22)
	Malpighiaceae (11)	Coccothrinax (5)	<i>Sideroxylon foetidissimum</i> (22)
	Meliaceae (11)	Myrcia (5)	
		Ocotea (5)	
		Reynosia (5)	
		Sideroxylon (5)	
		Thouinia (5)	
		Trichilia (5)	
		Ziziphus (5)	
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Apurimac-Mantaro (8)	Leguminosae (13)	Cnidoscolus (3)	<i>Dodonea viscosa</i> (6)
	Euphorbiaceae (11)	Croton (3)	<i>Vachellia aroma</i> (6)
	Malvaceae (6)	Ipomoea (3)	<i>Aloysia scorodonioides</i> (5)
	Asteraceae (5)	Lantana (3)	<i>Anadenanthera colubrina</i> (5)
	Bignoniaceae (5)	Tecoma (3)	<i>Ipomoea pauciflora</i> (5)
	Solanaceae (4)	Baccharis (2)	<i>Aralia soratensis</i> (4)
	Cannabaceae (3)	Celtis (2)	<i>Eriotheca discolor</i> (4)
	Convolvulaceae (3)	Clusia (2)	<i>Lantana camara</i> (4)

Urticaceae (3)	Eriotheca (2)	<i>Nicotiana glutinosa</i> (4)	
Verbenaceae (3)	Jatropha (2)	<i>Vasconcellea quercifolia</i> (4)	
Clusiaceae (2)	Manihot (2)	<i>Aeschynomene tumbezensis</i> (3)	
Sapindaceae (2)	Nicotiana (2)	<i>Furcraea andina</i> (3)	
	Prosopis (2)	<i>Jatropha augusti</i> (3)	
	Solanum (2)	<i>Leucaena trichodes</i> (3)	
	Vachellia (2)	<i>Schinus molle</i> (3)	
		<i>Tecoma fulva</i> (3)	
		<i>Trema micrantha</i> (3)	
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Caatinga (184)	Leguminosae (279)	Eugenia (33)	<i>Aspidosperma pyrifolium</i> (149)
	Myrtaceae (88)	Erythroxylum (24)	<i>Myracrodrodon urundeuva</i> (149)
	Euphorbiaceae (46)	Senna (23)	<i>Cereus jamacaru</i> (137)
	Rubiaceae (44)	Ficus (21)	<i>Anadenanthera colubrina</i> (136) <i>Handroanthus impetiginosus</i>
	Malvaceae (38)	Myrcia (20)	(135)
	Rutaceae (35)	Mimosa (19)	<i>Jatropha mollissima</i> (135)
	Cactaceae (34)	Bauhinia (17)	<i>Cynophalla hastata</i> (131)
	Asteraceae (29)	Casearia (16)	<i>Schinopsis brasiliensis</i> (131)
	Erythroxylaceae (24)	Machaerium (16)	<i>Commiphora leptophloeos</i> (129)
	Moraceae (24)	Psidium (16)	<i>Mimosa tenuiflora</i> (126)
	Bignoniaceae (23)	Pilosocereus (15)	<i>Annona leptopetala</i> (124)
	Sapotaceae (23)	Senegalia (15)	<i>Senna spectabilis</i> (124)
	Apocynaceae (22)	Aspidosperma (13)	<i>Guapira laxa</i> (123)
	Salicaceae (21)	Cordia (13)	<i>Ziziphus joazeiro</i> (117)
	Annonaceae (19)	Ocotea (13)	<i>Bauhinia cheilantha</i> (113)
	Malpighiaceae (18)	Byrsinima (12)	<i>Maytenus rigida</i> (112)
	Lauraceae (17)	Pouteria (12)	<i>Spondias tuberosa</i> (109)
	Vochysiaceae (17)	Zanthoxylum (12)	<i>Senna macranthera</i> (103)
	Arecaceae (16)	Chamaecrista (11)	<i>Cordia trichotoma</i> (102)
	Sapindaceae (16)	Maytenus (11)	<i>Croton blanchetianus</i> (101)
	Solanaceae (16)		
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Central inter-Andean Valleys (36)	Leguminosae (23)	Croton (9)	<i>Vachellia macracantha</i> (28)
	Euphorbiaceae (17)	Ficus (6)	<i>Lantana rugulosa</i> (17)
	Asteraceae (14)	Cestrum (4)	<i>Opuntia soederstromiana</i> (16)
	Malvaceae (13)	Lantana (4)	<i>Dodonaea viscosa</i> (15)
	Solanaceae (12)	Opuntia (4)	<i>Baccharis latifolia</i> (14)
	Cactaceae (9)	Acalypha (3)	<i>Tara spinosa</i> (14)
	Moraceae (8)	Baccharis (3)	<i>Lycianthes lycioides</i> (13)
	Boraginaceae (7)	Bytneria (3)	<i>Tecoma stans</i> (12)
	Sapindaceae (5)	Ceiba (3)	<i>Schinus molle</i> (10)

Verbenaceae (5)	Cordia (3)	<i>Cyathostegia mathewssii</i> (9)	
Anacardiaceae (4)	Duranta (3)	<i>Lantana camara</i> (8)	
Bignoniaceae (4)	Myrcianthes (3)	<i>Abutilon ibarrense</i> (7)	
Lauraceae (4)	Solanum (3)	<i>Mimosa albida</i> (7)	
Myrtaceae (4)	Tecoma (3)	<i>Mimosa quitensis</i> (7)	
Capparaceae (3)	Tournefortia (3)	<i>Schinus areira</i> (7)	
Meliaceae (3)		<i>Tournefortia fuliginosa</i> (7)	
Berberidaceae (2)		<i>Varronia macrocephala</i> (7)	
Malpighiaceae (2)		<i>Zanthoxylum fagara</i> (7)	
Piperaceae (2)		<i>Acalypha padifolia</i> (6)	
Rubiaceae (2)		<i>Berberis pichinchensis</i> (6)	
Rutaceae (2)		<i>Croton abutiloides</i> (6)	
Urticaceae (2)		<i>Croton menthodorus</i> (6)	
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Central America-northern South America (121)	Leguminosae (171)	Casearia (18)	<i>Guazuma ulmifolia</i> (87)
	Rubiaceae (50)	Cordia (16)	<i>Astronium graveolens</i> (77)
	Euphorbiaceae (38)	Lonchocarpus (16)	<i>Spondias mombin</i> (71)
	Salicaceae (29)	Coccoloba (14)	<i>Bursera simaruba</i> (68)
	Malvaceae (26)	Croton (13)	<i>Hura crepitans</i> (47)
	Annonaceae (24)	Ficus (12)	<i>Cochlospermum vitifolium</i> (46)
	Boraginaceae (23)	Machaerium (11)	<i>Platymiscium pinnatum</i> (46)
	Moraceae (22)	Annona (10)	<i>Cecropia peltata</i> (41)
	Polygonaceae (22)	Inga (10)	<i>Quadrella odoratissima</i> (40)
	Capparaceae (21)	Erythroxylum (9)	<i>Ceiba pentandra</i> (39)
	Arecaceae (18)	Eugenia (8)	<i>Sterculia apetala</i> (38)
	Bignoniaceae (17)	Randia (8)	<i>Samanea saman</i> (36)
	Myrtaceae (17)	Trichilia (8)	<i>Maclura tinctoria</i> (35)
	Rutaceae (17)	Zanthoxylum (8)	<i>Albizia niopoides</i> (34)
	Apocynaceae (16)	Guapira (7)	<i>Pseudobombax septenatum</i> (34)
	Sapindaceae (16)	Bauhinia (6)	<i>Enterolobium cyclocarpum</i> (32)
	Meliaceae (15)	Bunchosia (6)	<i>Libidibia coriaria</i> (32)
	Nyctaginaceae (14)	Cynophalla (6)	<i>Prosopis juliflora</i> (32)
	Cactaceae (13)	Erythrina (6)	<i>Handroanthus billbergii</i> (31)
	Primulaceae (13)	Handroanthus (6)	<i>Pithecellobium dulce</i> (31)
		Miconia (6)	
		Phyllanthus (6)	
		Senna (6)	
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Central Andes Coast (60)	Leguminosae (64)	Ficus (9)	<i>Bursera graveolens</i> (39)
	Cactaceae (24)	Cordia (8)	<i>Colicodendron scabridum</i> (36)
	Malvaceae (18)	Opuntia (7)	<i>Cordia lutea</i> (34)

Euphorbiaceae (15)	Croton (6)	<i>Loxopterygium huasango</i> (32)	
Moraceae (13)	Senna (6)	<i>Vachellia macracantha</i> (32)	
Rubiaceae (11)	Mimosa (5)	<i>Eriotheca ruizii</i> (29)	
Boraginaceae (9)	Psidium (5)	<i>Libidibia glabrata</i> (29)	
Bignoniaceae (8)	Trichilia (5)	<i>Pithecellobium excelsum</i> (28)	
Capparaceae (8)	Vachellia (5)	<i>Ceiba trischistandra</i> (25)	
Meliaceae (8)	Armatocereus (4)	<i>Cynophalla flexuosa</i> (25)	
Solanaceae (8)	Browningia (4)	<i>Cochlospermum vitifolium</i> (24)	
Myrtaceae (6)	Ceiba (4)	<i>Geoffroea spinosa</i> (22)	
Polygonaceae (6)	Inga (4)	<i>Guazuma ulmifolia</i> (22)	
Sapindaceae (5)	Annona (3)	<i>Prosopis pallida</i> (20)	
Anacardiaceae (4)	Celtis (3)	<i>Coccobola ruiziana</i> (18)	
Apocynaceae (4)	Coccobola (3)	<i>Leucaena trichodes</i> (17)	
Asteraceae (4)	Cynophalla (3)	<i>Albizia multiflora</i> (15)	
Cannabaceae (4)	Eriotheca (3)	<i>Piscidia carthagenensis</i> (15)	
Nyctaginaceae (4)	Erythrina (3)	<i>Beautempsia avicenniifolia</i> (14)	
Verbenaceae (4)	Simira (3)	<i>Bougainvillea spectabilis</i> (14)	
	Tecoma (3)	<i>Erythrina smithiana</i> (14)	
	Zanthoxylum (3)		
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Central Brazil (130)	Leguminosae (298)	Eugenia (33)	<i>Guazuma ulmifolia</i> (112)
	Myrtaceae (78)	Erythroxylum (21)	<i>Anadenanthera colubrina</i> (109) <i>Handroanthus impetiginosus</i> (109)
	Rubiaceae (66)	Ficus (21)	
	Malvaceae (50)	Bauhinia (20)	<i>Myracrodruon urundeuva</i> (102)
	Euphorbiaceae (49)	Aspidosperma (18)	<i>Astronium fraxinifolium</i> (101)
	Rutaceae (35)	Senna (18)	<i>Maclura tinctoria</i> (92)
	Annonaceae (33)	Cordia (16)	<i>Tabebuia roseoalba</i> (90)
	Lauraceae (31)	Inga (15)	<i>Diodendron bipinnatum</i> (88) <i>Enterolobium contortisiliquum</i> (87)
	Moraceae (30)	Myrcia (15)	
	Salicaceae (28)	Trichilia (15)	<i>Sterculia striata</i> (87)
	Solanaceae (28)	Byrsonia (14)	<i>Acromania aculeata</i> (82)
	Apocynaceae (27)	Casearia (14)	<i>Aspidosperma subincanum</i> (81)
	Sapindaceae (26)	Machaerium (14)	<i>Senegalia polyphylla</i> (81)
	Arecaceae (24)	Mimosa (14)	<i>Aspidosperma cuspa</i> (77)
	Meliaceae (24)	Ocotea (14)	<i>Albizia niopoides</i> (75)
	Malpighiaceae (23)	Psidium (14)	<i>Terminalia argentea</i> (74)
	Cactaceae (22)	Annona (13)	<i>Cecropia pachystachya</i> (71)
	Bignoniaceae (21)	Miconia (13)	<i>Cordia glabrata</i> (71)
	Erythroxylaceae (21)	Senegalia (13)	<i>Talisia esculenta</i> (70)
	Chrysobalanaceae (20)	Solanum (13)	<i>Cordia trichotoma</i> (69)
	Combretaceae (20)		

Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Mexico (33)	Leguminosae (297)	Bursera (54)	<i>Vachellia farnesiana</i> (21)
	Euphorbiaceae (69)	Lonchocarpus (32)	<i>Plumeria rubra</i> (20)
	Burseraceae (56)	Croton (25)	<i>Pithecellobium dulce</i> (19)
	Malvaceae (49)	Ficus (21)	<i>Senna atomaria</i> (19)
	Rubiaceae (40)	Mimosa (19)	<i>Tecoma stans</i> (18)
	Apocynaceae (32)	Caesalpinia (16)	<i>Vachellia campechiana</i> (18)
	Boraginaceae (31)	Quercus (16)	<i>Vachellia pennatula</i> (18)
	Moraceae (27)	Pithecellobium (15)	<i>Bauhinia divaricata</i> (17)
	Rutaceae (24)	Senna (15)	<i>Haematoxylum brasiletto</i> (16)
	Malpighiaceae (22)	Diospyros (13)	<i>Lysiloma divaricatum</i> (16)
	Salicaceae (19)	Calliandra (12)	<i>Spondias purpurea</i> (16)
	Sapotaceae (18)	Vachellia (12)	<i>Bursera fagaroides</i> (15)
	Asteraceae (16)	Bauhinia (11)	<i>Ceiba aesculifolia</i> (15)
	Celastraceae (16)	Eugenia (11)	<i>Comocladia engleriana</i> (15)
	Fagaceae (16)	Randia (11)	<i>Ficus cotinifolia</i> (15)
	Myrtaceae (16)	Sideroxylon (11)	<i>Guazuma ulmifolia</i> (15)
	Sapindaceae (16)	Diphysa (10)	<i>Caesalpinia pulcherrima</i> (15)
	Anacardiaceae (15)		<i>Apoplanesia paniculata</i> (14)
	Capparaceae (14)		<i>Amphipterygium adstringens</i> (14)
	Polygonaceae (14)		<i>Bursera grandifolia</i> (14)
			<i>Lysiloma acapulcense</i> (14)
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Misiones (84)	Leguminosae (110)	Eugenia (28)	<i>Cordia americana</i> (75)
	Myrtaceae (72)	Solanum (18)	<i>Chrysophyllum gonocarpum</i> (67)
	Solanaceae (40)	Ocotea (17)	<i>Ruprechtia laxiflora</i> (65)
	Rubiaceae (35)	Miconia (11)	<i>Chrysophyllum marginatum</i> (64)
	Lauraceae (33)	Ficus (10)	<i>Allophylus edulis</i> (63)
	Euphorbiaceae (27)	Myrcia (10)	<i>Eugenia uniflora</i> (63)
	Asteraceae (22)	Nectandra (10)	<i>Holocalyx balansae</i> (63)
	Bignoniaceae (18)	Cestrum (9)	<i>Syagrus romanzoffiana</i> (63)
	Melastomataceae (16)	Erythroxylum (9)	<i>Luehea divaricata</i> (62)
	Moraceae (16)	Annona (8)	<i>Cedrela fissilis</i> (61)
	Rutaceae (16)	Handroanthus (8)	<i>Peltophorum dubium</i> (61)
	Salicaceae (16)	Inga (8)	<i>Cupania vernalis</i> (60)
	Meliaceae (15)	Myrsine (8)	<i>Diatenopteryx sorbifolia</i> (60)
	Sapindaceae (15)	Piper (8)	<i>Pilocarpus pennatifolius</i> (60)
	Anacardiaceae (14)	Trichilia (8)	<i>Cabralea canjerana</i> (59)
	Malvaceae (13)	Casearia (7)	<i>Parapiptadenia rigida</i> (59)
	Annonaceae (12)	Ilex (7)	<i>Sorocea bonplandii</i> (59)
	Arecaceae (12)	Maytenus (7)	<i>Casearia sylvestris</i> (58)

	Apocynaceae (10)	Senegalia (7)	<i>Trichilia catigua</i> (57)
	Celastraceae (10)	Senna (7)	<i>Cordia trichotoma</i> (56)
		Zanthoxylum (7)	<i>Sebastiana brasiliensis</i> (56)
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Northern inter-Andean Valleys (56)	Leguminosae (77)	Ficus (10)	<i>Guazuma ulmifolia</i> (39)
	Rubiaceae (25)	Zanthoxylum (9)	<i>Ochroma pyramidalis</i> (26)
	Euphorbiaceae (22)	Piper (8)	<i>Senna spectabilis</i> (25)
	Moraceae (18)	Croton (7)	<i>Pithecellobium dulce</i> (24)
	Lauraceae (14)	Erythroxylum (7)	<i>Zanthoxylum fagara</i> (24)
	Myrtaceae (14)	Eugenia (7)	<i>Anacardium excelsum</i> (22)
	Malvaceae (13)	Inga (7)	<i>Erythrina poeppigiana</i> (22)
	Arecaceae (12)	Miconia (7)	<i>Pseudosamanea guachapele</i> (22)
	Rutaceae (10)	Coccoloba (6)	<i>Ficus insipida</i> (18)
	Salicaceae (10)	Machaerium (6)	<i>Cupania americana</i> (17)
	Urticaceae (10)	Senna (6)	<i>Psidium guineense</i> (17)
	Bignoniaceae (9)	Casearia (5)	<i>Croton gossypifolius</i> (16)
	Melastomataceae (9)	Clusia (5)	<i>Zanthoxylum rhoifolium</i> (16)
	Meliaceae (9)	Cordia (5)	<i>Brosimum alicastrum</i> (15)
	Annonaceae (8)	Acalypha (4)	<i>Sapindus saponaria</i> (15)
	Boraginaceae (8)	Bactris (4)	<i>Achatocarpus nigricans</i> (14)
	Piperaceae (8)	Bauhinia (4)	<i>Attalea butyracea</i> (14)
	Polygonaceae (8)	Brownea (4)	<i>Ocotea veraguensis</i> (14)
	Anacardiaceae (7)	Calliandra (4)	<i>Astronium graveolens</i> (13)
	Capparaceae (7)	Cecropia (4)	<i>Cecropia peltata</i> (13)
	Clusiaceae (7)	Lonchocarpus (4)	<i>Ceiba pentandra</i> (13)
	Erythroxylaceae (7)	Nectandra (4)	<i>Euphorbia cotinifolia</i> (13)
	Primulaceae (7)	Ocotea (4)	<i>Machaerium capote</i> (13)
	Sapindaceae (7)	Solanum (4)	<i>Muntingia calabura</i> (13)
		Trichilia (4)	
		Vachellia (4)	
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Piedmont (46)	Leguminosae (157)	Inga (20)	<i>Anadenanthera colubrina</i> (39)
	Euphorbiaceae (33)	Senegalia (11)	<i>Achatocarpus praecox</i> (29)
	Asteraceae (32)	Senna (11)	<i>Myracrodruon urundeuva</i> (27)
	Cactaceae (32)	Eugenia (10)	<i>Pisonia zapallo</i> (23)
	Myrtaceae (28)	Prosopis (10)	<i>Vachellia aroma</i> (23)
	Bignoniaceae (22)	Machaerium (9)	<i>Parapiptadenia excelsa</i> (22) <i>Enterolobium contortisiliquum</i> (21)
	Anacardiaceae (21)	Solanum (9)	
	Malvaceae (21)	Aspidosperma (8)	<i>Tipuana tipu</i> (21)
	Solanaceae (20)	Celtis (8)	<i>Alliophyllum edulis</i> (20)

Rubiaceae (18)	Maytenus (8)	<i>Libidibia paraguariensis</i> (20)	
Apocynaceae (16)	Schinus (8)	<i>Ruprechtia apetala</i> (20)	
Sapindaceae (16)	Cereus (7)	<i>Celtis iguanaea</i> (19)	
Rutaceae (14)	Croton (7)	<i>Senegalia praecox</i> (19)	
Capparaceae (13)	Ficus (7)	<i>Handroanthus impetiginosus</i> (18)	
Moraceae (13)	Coccoloba (6)	<i>Pterogyne nitens</i> (18)	
Nyctaginaceae (13)	Cordia (6)	<i>Tecoma stans</i> (18)	
Polygonaceae (13)	Erythroxylum (6)	<i>Vachellia caven</i> (18)	
Salicaceae (13)	Luehea (6)	<i>Amburana cearensis</i> (17)	
Celastraceae (11)	Zanthoxylum (6)	<i>Cynophalla retusa</i> (17)	
Meliaceae (10)	Baccharis (5)	<i>Phyllostylon rhamnoides</i> (17)	
	Bauhinia (5)	<i>Ruprechtia laxiflora</i> (17)	
Nyctaginaceae (13)	Bougainvillea (5)	<i>Senna spectabilis</i> (17)	
	Erythrina (5)	<i>Trichilia clausenii</i> (17)	
Vachellia (5)	Kaunia (5)		
	Myrsine (5)		
	Piptadenia (5)		
	Schinopsis (5)		
	Trichilia (5)		
Vachellia (5)			
Group (sites)	Family (species)	Genus (species)	Species (number of sites in which recorded)
Tarapoto-Quillabamba (11)	Leguminosae (46)	Aspidosperma (7)	<i>Trichilia elegans</i> (7)
	Moraceae (18)	Inga (7)	<i>Brosimum alicastrum</i> (6)
	Rubiaceae (15)	Neea (7)	<i>Triplaris cumingiana</i> (6)
	Euphorbiaceae (13)	Trichilia (7)	<i>Erythroxylum ulei</i> (5)
	Meliaceae (12)	Coccoloba (6)	<i>Inga umbellifera</i> (5)
	Malvaceae (11)	Allophylus (5)	<i>Morisonia oblongifolia</i> (5)
	Lauraceae (10)	Eugenia (5)	<i>Zanthoxylum rhoifolium</i> (5)
	Sapindaceae (10)	Ocotea (5)	<i>Ceiba insignis</i> (4)
	Nyctaginaceae (9)	Capparidastrum (4)	<i>Celtis iguanaea</i> (4)
	Polygonaceae (9)	Casearia (4)	<i>Coccoloba padiformis</i> (4)
	Sapotaceae (9)	Chrysophyllum (4)	<i>Handroanthus serratifolius</i> (4)
	Apocynaceae (8)	Cordia (4)	<i>Anadenanthera colubrina</i> (3)
	Arecaceae (8)	Erythroxylum (4)	<i>Aspidosperma rigidum</i> (3)
	Capparaceae (8)	Ficus (4)	<i>Brosimum guianense</i> (3)
	Annonaceae (7)	Machaerium (4)	<i>Cedrela fissilis</i> (3)
	Bignoniaceae (7)	Nectandra (4)	<i>Ceiba boliviiana</i> (3) <i>Chrysophyllum venezuelanense</i> (3)
	Myrtaceae (7)	Piper (4)	
	Urticaceae (7)	Terminalia (4)	<i>Clarisia biflora</i> (3)
	Boraginaceae (6)	Urera (4)	<i>Cordia alliodora</i> (3)
	Cactaceae (6)		<i>Coussapoa villosa</i> (3)

Salicaceae (6)

*Croton abutiloides* (3)  
*Drypetes amazonica* (3)  
*Manilkara bidentata* (3)  
*Neea hermaphrodita* (3)  
*Phytelephas aequatorialis* (3)  
*Platymiscium stipulare* (3)  
*Presbrianthus pittieri* (3)  
*Prunus rotunda* (3)  
*Pseudolmedia rigida* (3)  
*Rhamnidium elaeocarpum* (3)  
*Rollinia cuspidata* (3)  
*Solanum riparium* (3)  
*Sorocea sarcocarpa* (3)  
*Steriphoma peruvianum* (3)  
*Trichilia pleeana* (3)

---

## References and Notes

1. R. T. Pennington, M. Lavin, A. Oliveira-Filho, Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annu. Rev. Ecol. Evol. Syst.* **40**, 437–457 (2009). [doi:10.1146/annurev.ecolsys.110308.120327](https://doi.org/10.1146/annurev.ecolsys.110308.120327)
2. R. Linares-Palomino, A. T. Oliveira-Filho, R. T. Pennington, in *Seasonally Dry Tropical Forest: Ecology and Conservation*, R. Dirzo, H. S. Young, H. A. Mooney, G. Ceballos, Eds. (Island Press, 2011), pp. 3–21.
3. L. Miles, A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos, J. E. Gordon, A global overview of the conservation status of tropical dry forests. *J. Biogeogr.* **33**, 491–505 (2006). [doi:10.1111/j.1365-2699.2005.01424.x](https://doi.org/10.1111/j.1365-2699.2005.01424.x)
4. H. García, G. Corzo, P. Isaacs, A. Etter, in *El Bosque seco Tropical en Colombia*, C. Pizano and H. García, Eds. (Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá D.C., Colombia, 2014), pp. 228–251.
5. G. Murphy, A. E. Lugo, Ecology of tropical dry forest. *Annu. Rev. Ecol. Syst.* **17**, 67–88 (1986). [doi:10.1146/annurev.es.17.110186.000435](https://doi.org/10.1146/annurev.es.17.110186.000435)
6. A. H. Gentry, in *Seasonally Dry Tropical Forests*, S. Bullock, H. Mooney, E. Medina, Eds. (Cambridge Univ. Press, Cambridge, 1995), pp.146–194.
7. G. A. Sanchez-Azofeifa *et al.*, Research priorities for Neotropical Dry Forests. *Biotropica* **37**, 477–485 (2005).
8. A. M. Hocquenghem, *Para Vencer la Muerte: Piura y Tumbes. Raíces en el Bosque Seco y en la Selva Alta—Horizontes en el Pacífico y en la Amazonia* [CNRS-IFEA (l'Institut Français d'Études Andines), Lima, Peru, 1998].
9. R. Blackie *et al.*, “Tropical dry forests: The state of global knowledge and recommendations for future research” (2014 CIFOR Discussion paper 2; Center for International Forestry Research, Jawa Barat, Indonesia, 2014); <http://dx.doi.org/10.17528/cifor/004408>.
10. Unidades de Conservação por Bioma, Ministério do Meio Ambiente (CNUC/MMA), Brasília-DF, Brazil (2016); [www.mma.gov.br/images/arquivo/80112/CNUC\\_PorBiomaFev16.pdf](http://www.mma.gov.br/images/arquivo/80112/CNUC_PorBiomaFev16.pdf).
11. Materials and methods are available as supplementary materials on *Science Online*.
12. R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005). [doi:10.1002/joc.1276](https://doi.org/10.1002/joc.1276)
13. R. T. Pennington, D. E. Prado, C. A. Pendry, Neotropical seasonally dry forests and quaternary vegetation changes. *J. Biogeogr.* **27**, 261–273 (2000). [doi:10.1046/j.1365-2699.2000.00397.x](https://doi.org/10.1046/j.1365-2699.2000.00397.x)
14. D. E. Prado, P. E. Gibbs, Patterns of species distributions in the dry seasonal forests of South America. *Ann. Mo. Bot. Gard.* **80**, 902–927 (1993). [doi:10.2307/2399937](https://doi.org/10.2307/2399937)
15. D. E. Prado, What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco. V. *Candollea* **48**, 145–172 (1993).
16. H. Kreft, W. Jetz, A framework for delineating biogeographical regions based on species distributions. *J. Biogeogr.* **37**, 2029–2053 (2010). [doi:10.1111/j.1365-2699.2010.02375.x](https://doi.org/10.1111/j.1365-2699.2010.02375.x)

17. M. Maunder, A. Leiva, E. Santiago-Valentín, D. W. Stevenson, P. Acevedo-Rodríguez, A. W. Meerow, M. Mejía, C. Clubbe, J. Francisco-Ortega, Plant conservation in the Caribbean Island biodiversity hotspot. *Bot. Rev.* **74**, 197–207 (2008). [doi:10.1007/s12229-008-9007-7](https://doi.org/10.1007/s12229-008-9007-7)
18. P. Acevedo-Rodríguez, M. T. Strong, Catalogue of seed plants of the West Indies. *Smithsonian Contrib. Bot.* **98**, 1–1192 (2012). [doi:10.5479/si.0081024X.98.1](https://doi.org/10.5479/si.0081024X.98.1)
19. A. H. Gentry, Neotropical floristic diversity: Phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann. Mo. Bot. Gard.* **69**, 557–593 (1982). [doi:10.2307/2399084](https://doi.org/10.2307/2399084)
20. G. Sarmiento, The dry plant formations of South America and their floristic connections. *J. Biogeogr.* **2**, 233–251 (1975). [doi:10.2307/3037998](https://doi.org/10.2307/3037998)
21. P. V. A. Fine, R. H. Ree, Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *Am. Nat.* **168**, 796–804 (2006). [Medline](#) [doi:10.1086/508635](https://doi.org/10.1086/508635)
22. J. X. Becerra, Timing the origin and expansion of the Mexican tropical dry forest. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 10919–10923 (2005). [Medline](#) [doi:10.1073/pnas.0409127102](https://doi.org/10.1073/pnas.0409127102)
23. R. J. Burnham, N. L. Carranco, Miocene winged fruits of *Loxopterygium* (Anacardiaceae) from the Ecuadorian Andes. *Am. J. Bot.* **91**, 1767–1773 (2004). [Medline](#) [doi:10.3732/ajb.91.11.1767](https://doi.org/10.3732/ajb.91.11.1767)
24. Ministry of the Environment, Peru, *Mapa Nacional de Cobertura Vegetal: Memoria Descriptiva* (Ministerio del Ambiente, Lima, Perú, 2015).
25. L. P. de Queiroz, in *Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation*, R. T. Pennington, G. P. Lewis, J. A. Ratter, Eds. (CRC Press, Boca Raton, 2006) pp. 121–157.
26. J. Rzedowski, G. C. de Rzedowski, Datos para la apreciación de la flora fanerogámica del bosque tropical caducifolio de México. *Acta Bot. Mex.* **102**, 1–23 (2013).
27. R. Linares-Palomino, in *Neotropical Savannas and Seasonally Dry Forest: Plant Diversity, Biogeography and Conservation*, R. T. Pennington, G. P. Lewis, J. A. Ratter, Eds. (CRC Press, Boca Raton, 2006) pp. 227–280.
28. C. E. Hughes, R. T. Pennington, A. Antonelli, Neotropical plant evolution: Assembling the big picture. *Bot. J. Linn. Soc.* **171**, 1–18 (2013). [doi:10.1111/boj.12006](https://doi.org/10.1111/boj.12006)
29. I. Trejo, R. Dirzo, Floristic diversity of Mexican seasonally dry tropical forests. *Biodivers. Conserv.* **11**, 2063–2084 (2002). [doi:10.1023/A:1020876316013](https://doi.org/10.1023/A:1020876316013)
30. S. Bridgewater, J. A. Ratter, J. F. Ribeiro, Biogeographic patterns, diversity and dominance in the cerrado biome of Brazil. *Biodivers. Conserv.* **13**, 2295–2317 (2004). [doi:10.1023/B:BIOC.0000047903.37608.4c](https://doi.org/10.1023/B:BIOC.0000047903.37608.4c)
31. D. M. Neves, K. G. Dexter, R. T. Pennington, M. L. Bueno, A. T. Oliveira-Filho, Environmental and historical controls of floristic composition across the South American Dry Diagonal. *J. Biogeogr.* **42**, 1566–1576 (2015). [doi:10.1111/jbi.12529](https://doi.org/10.1111/jbi.12529)
32. K. G. Dexter *et al.*, Floristics and biogeography of vegetation in seasonally dry tropical regions. *Int. For. Rev.* **17**, 10–32 (2015).
33. N. C. A. Pitman, J. W. Terborgh, M. R. Silman, P. Núñez V, D. A. Neill, C. E. Cerón, W. A. Palacios, M. Aulestia, Dominance and distribution of tree species in upper Amazonian

terra firme forests. *Ecology* **82**, 2101–2117 (2001). doi:10.1890/0012-9658(2001)082[2101:DADOTS]2.0.CO;2

34. H. ter Steege, N. C. Pitman, D. Sabatier, C. Baraloto, R. P. Salomão, J. E. Guevara, O. L. Phillips, C. V. Castilho, W. E. Magnusson, J. F. Molino, A. Monteagudo, P. Núñez Vargas, J. C. Montero, T. R. Feldpausch, E. N. Coronado, T. J. Killeen, B. Mostacedo, R. Vasquez, R. L. Assis, J. Terborgh, F. Wittmann, A. Andrade, W. F. Laurance, S. G. Laurance, B. S. Marimon, B. H. Marimon Jr., I. C. Guimarães Vieira, I. L. Amaral, R. Brienen, H. Castellanos, D. Cárdenas López, J. F. Duivenvoorden, H. F. Mogollón, F. D. Matos, N. Dávila, R. García-Villacorta, P. R. Stevenson Diaz, F. Costa, T. Emilio, C. Levis, J. Schietti, P. Souza, A. Alonso, F. Dallmeier, A. J. Montoya, M. T. Fernandez Piedade, A. Araujo-Murakami, L. Arroyo, R. Gribel, P. V. Fine, C. A. Peres, M. Toledo, G. A. Aymard C, T. R. Baker, C. Cerón, J. Engel, T. W. Henkel, P. Maas, P. Petronelli, J. Stropp, C. E. Zartman, D. Daly, D. Neill, M. Silveira, M. R. Paredes, J. Chave, Dde. A. Lima Filho, P. M. Jørgensen, A. Fuentes, J. Schöngart, F. Cornejo Valverde, A. Di Fiore, E. M. Jimenez, M. C. Peñuela Mora, J. F. Phillips, G. Rivas, T. R. van Andel, P. von Hildebrand, B. Hoffman, E. L. Zent, Y. Malhi, A. Prieto, A. Rudas, A. R. Ruschell, N. Silva, V. Vos, S. Zent, A. A. Oliveira, A. C. Schutz, T. Gonzales, M. Trindade Nascimento, H. Ramirez-Angulo, R. Sierra, M. Tirado, M. N. Umaña Medina, G. van der Heijden, C. I. Vela, E. Vilanova Torre, C. Vriesendorp, O. Wang, K. R. Young, C. Baider, H. Balslev, C. Ferreira, I. Mesones, A. Torres-Lezama, L. E. Urrego Giraldo, R. Zagt, M. N. Alexiades, L. Hernandez, I. Huamantupa-Chuquimaco, W. Milliken, W. Palacios Cuenca, D. Paulette, E. Valderrama Sandoval, L. Valenzuela Gamarra, K. G. Dexter, K. Feeley, G. Lopez-Gonzalez, M. R. Silman, Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092 (2013). [Medline](#)
35. G. Forero-Medina, L. Joppa, Representation of global and national conservation priorities by Colombia's Protected Area Network. *PLOS ONE* **5**, e13210 (2010). [Medline](#) doi:10.1371/journal.pone.0013210
36. Convention on Biological Diversity, Quick guide to the Aichi Biodiversity Targets: Protected areas increased and improved, TARGET 11—Technical Rationale extended (COP/10/INF/12/Rev, Convention on Biological Diversity, 2011); <https://www.cbd.int/doc стратегический-план/tariffs/T11-quick-guide-en.pdf>.
37. P. Murphy, A. E. Lugo, in *Seasonally Dry Tropical Forests*, S. Bullock, H. Mooney, and E. Medina, Eds. (Cambridge Univ. Press, Cambridge, 2005) pp. 9–34.
38. The Angiosperm Phylogeny Group, An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* **161**, 105–121 (2009). doi:10.1111/j.1095-8339.2009.00996.x
39. A. T. Oliveira-Filho, Classificação das fitofisionomias da América do Sul cisandina tropical e subtropical: Proposta de um novo sistema -prático e flexível- ou uma injeção a mais caos? *Rodriguésia* **60**, 237–258 (2009).
40. A. J. Oksanen et al., Vegan: A community ecology package (The Comprehensive R Archive Network, 2016); <http://cran.r-project.org/web/packages/vegan/index.html>.
41. L. Dapporto, M. Ramazzotti, S. Fattorini, G. Talavera, R. Vila, R. L. H. Dennis, Recluster: Ordination methods for the analysis of beta-diversity indices (The Comprehensive R Archive Network, 2016); <http://cran.r-project.org/web/packages/recluster/index.html>.

42. R. Suzuki, H. Shimodaira, Pvclust: Hierarchical clustering with p-values via multiscale bootstrap resampling (The Comprehensive R Archive Network, 2016); <http://cran.r-project.org/web/packages/pvclust/index.html>.
43. J. J. Lennon, P. Koleff, J. J. D. Greenwood, K. J. Gaston, The geographical structure of British birds distributions: Diversity, spatial turnover and scale. *J. Anim. Ecol.* **70**, 966–979 (2001). [doi:10.1046/j.0021-8790.2001.00563.x](https://doi.org/10.1046/j.0021-8790.2001.00563.x)
44. R. K. Colwell, A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, J. T. Longino, Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J. Plant Ecol.* **5**, 3–21 (2012). [doi:10.1093/jpe/rtr044](https://doi.org/10.1093/jpe/rtr044)
45. D. M. Olson, E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettenberg, P. Hedao, K. R. Kassem, Terrestrial ecoregions of the world: A new map of life on earth. *Bioscience* **51**, 933–938 (2001). [doi:10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)