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.

Neotropical 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 compiled by the Latin American and Caribbean Seasonally Dry Tropical Forest Floristic Network [DRYFLOR, www.dryflor.info; (*11*)].

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 (*11*). 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 (*11*).

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 nonmetric multidimensional scaling (NMDS) ordination (fig. S4A for all sites and fig. S4B pooling all species in each floristic group) recognizes a higher-level northern

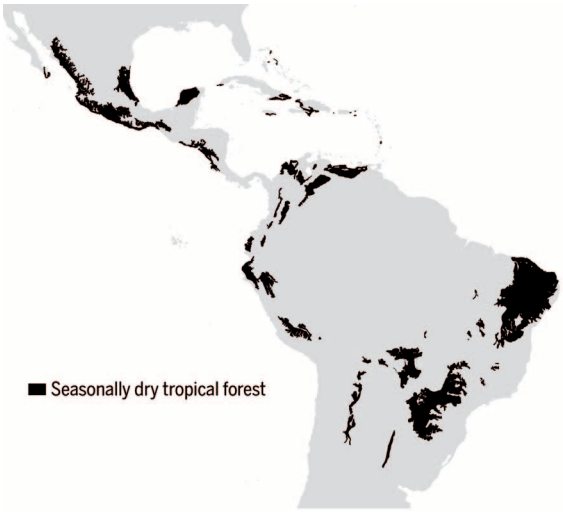

Fig. 1. Schematic dry forest distribution in the Neotropics. [Based on Pennington *et al.* (*13*), Linares-Palomino *et al.* (*2*), Olson *et al.* (*45*), and the location of DRYFLOR inventory sites (see Fig. 2)]

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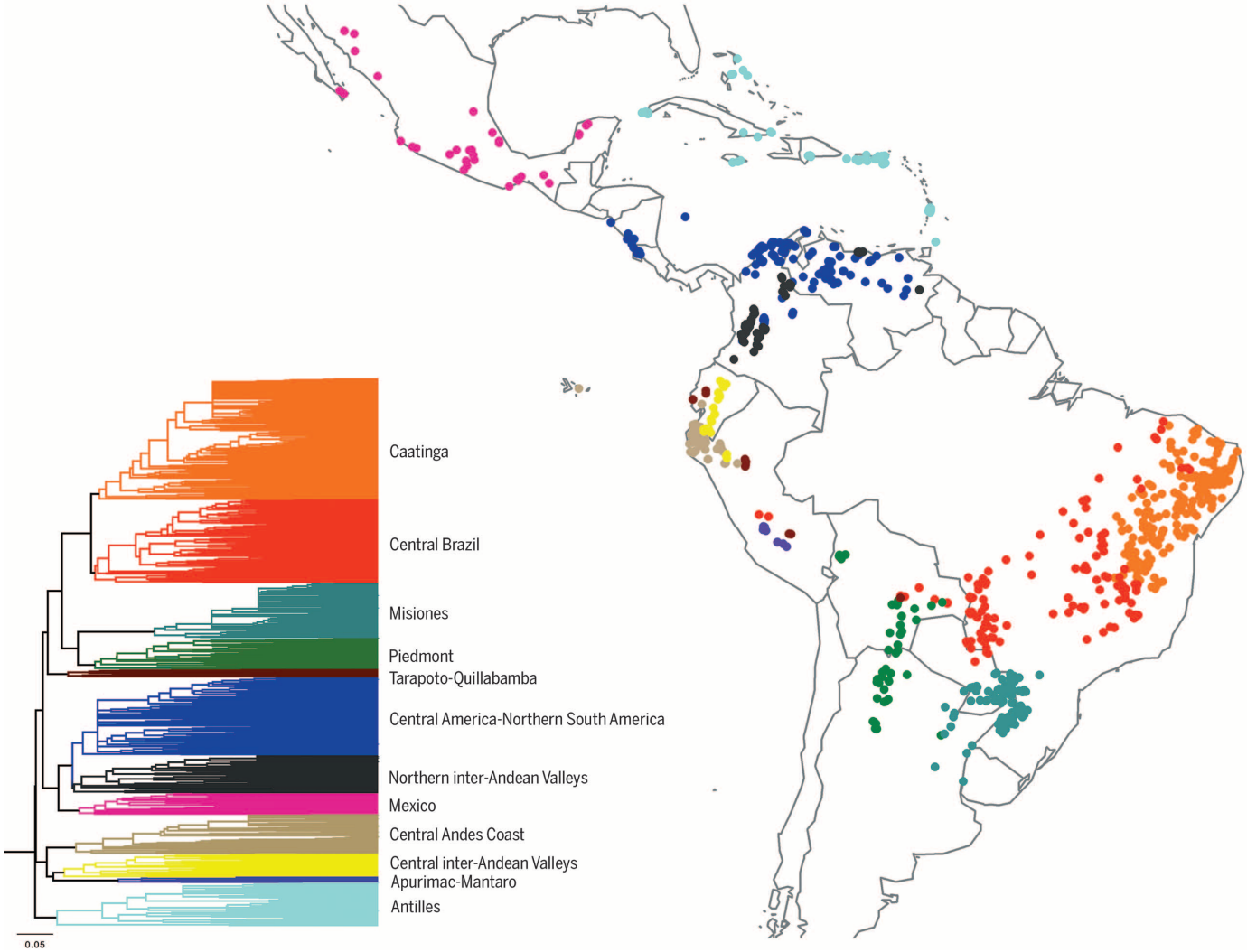

Fig. 2. Neotropical dry forest floristic groups based on woody plants. Geographical representation of UPGMA clustering of 835 dry forest sites using the Simpson dissimilarity index as a measure of distance.

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^2 in total (*24*) compared with ~850,000 km^2 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^2 (*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 *Maclura 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, Apurimac-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

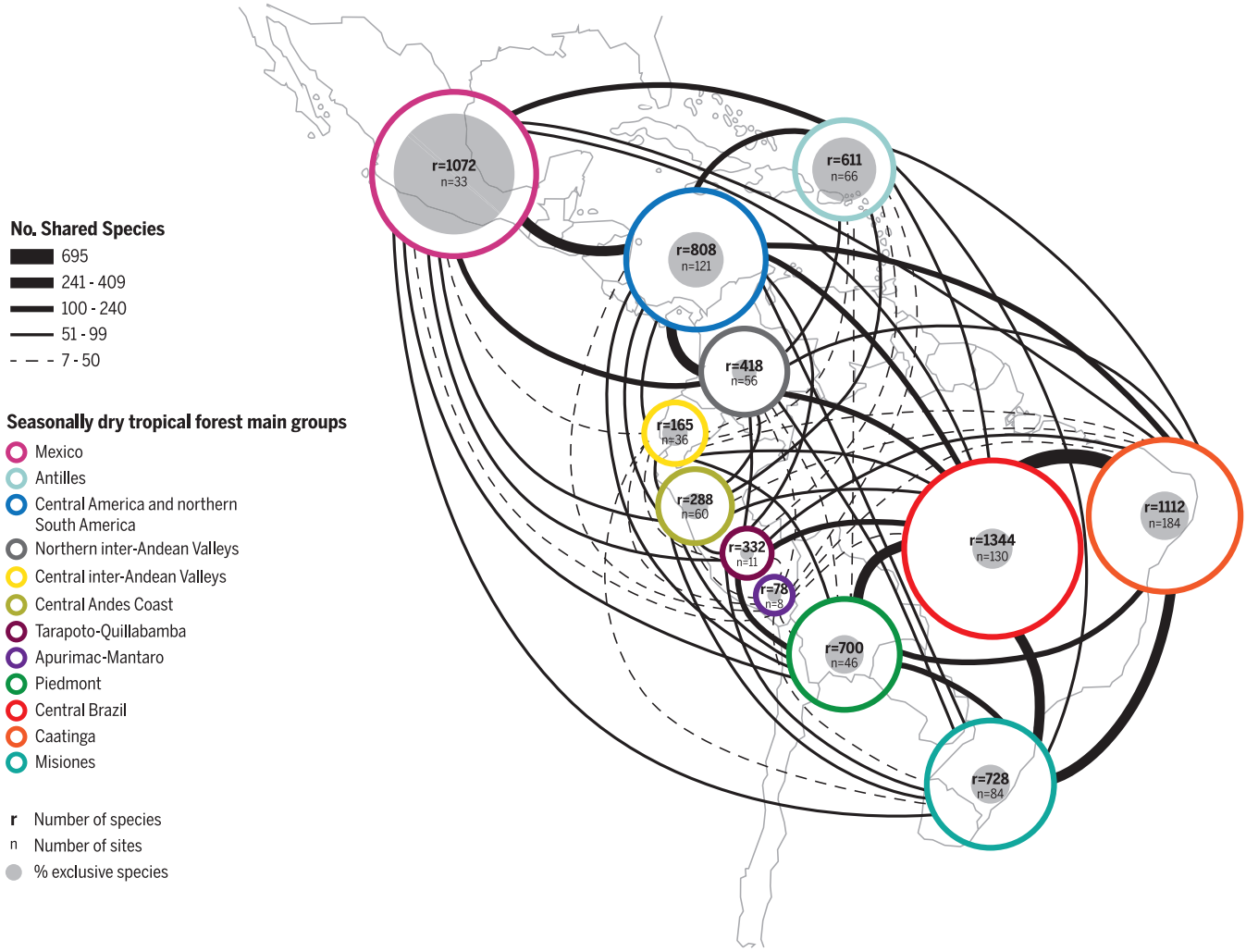

Fig. 3. Geographical patterns of species turnover among 12 dry forest floristic groups. (Fig. 2). Size of the circles is proportional to the number of species per group; size of colored circles is proportional to the total number of species and of gray circles to the number of exclusive species. The 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.

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SUPPLEMENTARY MATERIALS

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INFECTIOUS DISEASE

Replication of human noroviruses in stem cell–derived human enteroids

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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 noncultivatable pathogens, and allows the assessment of methods to prevent and treat HuNoV infections.

Human 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

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