Phytogeography and conservation of neotropical dry forest with emphasis on Colombia

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Declaration

I hereby declare that the work contained in this thesis is my own, unless otherwise acknowledged and cited. This thesis has not in whole or in part been previously presented for any degree.

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15th December, 2016

Abstract

Dry forest is one of the most threatened tropical forests in the world. Human impact has caused its massive transformation but conservation of dry forest has often been neglected across Latin America. In Colombia, less than 10% of the original extension of dry forest remains. This thesis studies the phytogeography of neotropical dry forest and its relevance for conservation using data from 1602 tree species inventories made in dry forests across Latin America and the Caribbean synthesised by The Latin American Seasonally Dry Tropical Forest Floristic Network (DRYFLOR). Clustering and ordination analyses were used to explore the floristic relationships of dry forest across the entire Neotropics, revealing distinctive regional clusters defined by their tree species composition. Colombian dry forests are shown to be part of two wider clusters, one including neighbouring forests in Venezuela and southern Central America, and the second including the inter-Andean dry forests. The high turnover of floristic diversity and endemism within and amongst the main floristic groups demonstrates that to conserve the full species diversity in dry forests across Latin America and the Caribbean will require protecting it simultaneously across multiple regions.

A regionally focused study of floristic relationships in the Central American and northern South American dry tropical forest group, using quantitative approaches to conservation prioritization, including a new Conservation Priority Index (CPI), suggests that conservation priority should be placed on the South American Caribbean Coast in the cross-border area of Colombia and Venezuela. This emphasises the need for a biogeographical approach to conservation that cannot be restricted by political borders. Within Colombia, new quantitative floristic data were used to investigate controls of floristic composition in dry forests. Multivariate analyses showed that space related variables explain a larger fraction of the variance of the floristic composition than climatic or edaphic variables. The importance of spatial variables implies that biogeography is a key element in understanding the structure of communities, and that the Andean cordilleras might be acting as geographical barriers isolating these seasonally dry formations.

The value of floristic inventory data for assessing the conservation status of tree species using IUCN criteria was assessed in a case of study of the Andean Piedmont dry forest. By combining inventory data from the DRYFLOR database and herbarium records, the number of species for which we have sufficient information to make conservation assessments increases by 16% and the accuracy of predictive species distribution improves for 84% of the species. Together, these results reveal the importance of ecological inventory data as a complementary data source in conservation assessment for dry forest trees in the Neotropics.

Finally, the conclusions chapter places these results in the context of conservation planning for Colombian dry forests, including some suggestions for research, policies and actions. These actions include restoration programmes focusing on sustainable harvesting of native dry forest tree species, for example for firewood and other forest resources such as fruits, fibres and medicines. A land use mosaic, including forest fallows and strict conservation areas, may help to guarantee the long-term maintenance dry forest species in Colombia.

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Sábato says you don't choose the topic, the topic chooses you. Knowledge is not the result of applying scientific rules. Rather, it is an act of inspiration, the origin of which is refused, but responsibility for which is demanded. Listening and writing are twin actions that drive creation.

Creation hides utopia, the aspiration to a new and different world that can be all the more real the simpler it is.

Alfredo Molano Bravo

Introduction

Seasonally dry tropical forest is a formation dominated by trees and usually with a closed canopy, which occurs on fertile soils in frost-free regions where the rainfall is less than c. 1800 mm per year, with a period of 3–6 months receiving less than 100 mm per month (Murphy & Lugo, 1986; Gentry, 1995; Sanchez-Azofeifa et al., 2005). During the dry season, the vegetation is mostly deciduous. In Latin America, dry forest occurs as fragments of varying size from northwest Mexico and the Caribbean islands to northern Argentina and southwest Brazil (Pennington et al., 2006). International conservation interest in this neglected formation is increasing as it represents the world's most threatened tropical forest type due to its frequently fertile soils being suitable for agriculture (Miles et al., 2006). In comparison to rain forest such as Amazonia, which remains ~80% intact (Soares-Filho et al., 2006; ter Steege et al., 2015) dry forest is in a critical state, and in Colombia, only 8% of the original extension remains (García et al., 2014). Fewer areas of dry forest are protected than other forest types (Miles et al., 2006). For example, only 1.2% of the total Caatinga region of dry forest in Brazil is fully protected compared to 9.9% of the Brazilian Amazon (Ministério do Meio Ambiente Brasil., 2016). Although varying in structure and species composition, dry forests comprise a recognized biome (Pennington et al., 2000; 2009;). Neotropical dry forests have been attracting increasing scientific curiosity due to the belief that their disjunct distribution and high occurrence of endemic species has been influenced by historical climatic fluctuations (Prado & Gibbs, 1993). As such, their study can provide insights into historical climate and vegetation change, and biodiversity evolution and maintenance.

The recent development of a unified scientific interpretation of neotropical dry forest (Linares-Palomino et al., 2011; Portillo-Quintero et al., 2015; Sánchez-Azofeifa et. al.,

2009) has established the foundation to allow continental scale biogeographic analyses of this biome to be undertaken. Such analyses can frame national and regional conservation prioritisation in an international context. As an example, few areas of dry forest in inter-Andean valleys in Ecuador and Peru have any protection (Linares-Palomino, 2006), reflecting lack of attention at a national level of their uniqueness, which is illustrated by their high numbers of endemic species. Because their geographic area and overall species diversity is smaller than neighbouring biomes such as rain forests, their conservation has often been ignored.

The biogeographic analyses presented in this thesis are the first based upon robust floristic data from across the full geographical extent of neotropical dry forest. A preliminary attempt at such analyses of dry forest throughout the Neotropics (Linares-Palomino et al., 2011) highlighted the need for more complete floristic information from several regions, including Colombia, which is the focus of this thesis. To address this lack of floristic information, the Latin American Seasonally Dry Tropical Forest Floristic Network (DRYFLOR) was formed in 2012. It has placed floristic data for neotropical dry forest that is scattered in often inaccessible scientific literature into a single, open-access database. One strength of the DRYFLOR data is that local floristic experts have evaluated the quality of the surveys included and resolved taxonomic ambiguities (i.e., synonyms - different names used for the same species in different surveys) to enable data from all dry forest countries to be compatible. These data are derived from quantitative inventory plots, transects and more general floristic lists for specific areas. I became the lead DRYFLOR network partner for Colombia before starting my PhD, during which I liaised with 24 Colombian researchers who contributed floristic lists, as well as carrying out new surveys. I was responsible for cleaning and entering these data into the DRYFLOR database.

This first chapter of this thesis analyses dry forest tree diversity patterns and their implications for conservation at continental scale using all 1602 tree species inventories in the DRYFLOR database. This broad-scale study helps to contextualise Colombian dry forest at a continental scale, providing a framework for regional and national biogeographic analyses and their implications for conservation in Colombia presented in subsequent chapters.

The second chapter aims to describe diversity patterns of the Central American and northern South American dry tropical forest group that was identified in the continental scale analysis. It frames regional conservation priorities using quantitative approaches to the assessment of the relative conservation value of different areas.

The third chapter uses new quantitative inventory data to investigate patterns of species composition and dominance in Colombian dry forest. The dataset has abundance data for species that is lacking in the DRYFLOR dataset and also includes new surveys that I made in the field. It analyses the influence of climatic, edaphic and anthropogenic variables in the assemblage of the different dry forest tree communities across Colombia and discusses the implications of the results for conservation.

The fourth chapter evaluates the value of the DRYFLOR inventory data as a complement to herbarium specimen records for assessing the conservation status of dry forest tree species.

The final conclusions chapter attempts to synthesise the results of all the chapters in the context of the conservation of dry forest in Colombia at a critical moment in the country's history when the cessation of sixty years of conflict may offer unprecedented opportunities for the preservation and sustainable use of biodiversity.

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Chapter 1 Floristic distinctiveness in neotropical seasonally dry forest and its implications for conservation

This chapter has been published in Science magazine as DRYFLOR, 2016⊕ see Appendix 1

1.1 Summary

The phytogeographic relationships of neotropical seasonally dry tropical forest (dry forest) tree communities were examined across their entire range in Latin America and the Caribbean using data from the DRYFLOR Network. Using detailed species inventories for tree plant species from 1602 areas of dry forest, I explored the implications of species richness patterns, floristic turnover and endemism for the conservation of neotropical dry forest. Analyses were performed using a 'neotropical dry forest *sensu stricto*' definition, excluding semi-deciduous sites from southern South America. Ordination and classification methods were used to analyse 835 areas that include 4660 species from 983 genera and 147 families. Twelve floristic groups were identified, within which more than 65% of the species (3115) are confined (exclusive) to a single group. High dissimilarity values (Simpson index mean 0.90) amongst the sites and within each region (mean 0.79) demonstrate high beta diversity, reflecting that few species are widespread and shared across many areas of neotropical dry forest. The six Andean regions showed high levels of endemism (38% exclusive species) and clearly distinct floras. Despite this, less than 3% of the Andean dry forest areas in our database lie within protected areas, which, combined with their fragmented nature, suggests that should be considered as a conservation priority. In general, these findings suggest that to conserve the full diversity of dry forest, which is highly threatened across Latin America and the Caribbean, will require protecting it simultaneously within multiple regions.

⊕ DRYFLOR (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. Science 23 Sep 2016: Vol. 353, Issue 6306, pp. 1383-1387, DOI: 10.1126/science.aaf5080

1.2 Introduction

Seasonally dry tropical forest (dry forest) in the Neotropics is a biome with a wide and fragmented distribution, found from Mexico to Argentina (Figure 1). The definition of dry forest using physiognomy and/or floristic composition can be highly dissimilar within and between countries (Murphy & Lugo, 1986; Mooney et al., 1995; Olson et al., 2001; Sanchez-Azofeifa et al., 2005; Miles et al., 2006; Pennington et al., 2006). The Phytoecological Glossary of the Americas, compiled by Huber and Riina, (1997) reports 79 terms and concepts for dry forest *sensu lato* used in South America (excluding Brazil): 52 related to “dry” forest, 11 to “xerophytic” forest, 11 for ”cactus dominated” vegetation, and five for “very dry” forest. The wide variety of names for dry forests reflects different criteria used for naming them (e.g., physiognomy or location) as well as their broad ecological and geographical range. For example, “deciduous seasonal forest” in Colombia grows from 0-1000 m.a.s.l. (Espinal & Montenegro, 1963), whereas “Andean montane dry forest” in Peru is found between 2500-3200 m.a.s.l. (ORNERN, 1976). This wide range of names and varying definitions complicates communication amongst researchers and policy makers.

Despite this plethora of local names, a consensus has started to emerge that in a broad sense, neotropical dry forest is a formation dominated by trees and usually with a closed canopy, which occurs on fertile soils in frost-free regions where the rainfall is less than c. 1800 mm per year, with a period of 3–6 months receiving less than 100 mm per month (Murphy & Lugo, 1986; Gentry, 1995; Sanchez-Azofeifa et al., 2005). During the dry season, the vegetation is mostly deciduous. Leguminosae is the most species-rich family, and additional woody families are abundant and characterize this vegetation including Capparaceae, Zygophyllaceae, Malvaceae subfamily Bombacoideae, and Cactaceae (Pennington et al., 2009). Unlike in savanna, fire cannot be frequent in dry forest in its natural state because the flora shows little or no adaptations to it (Pennington et al., 2009).

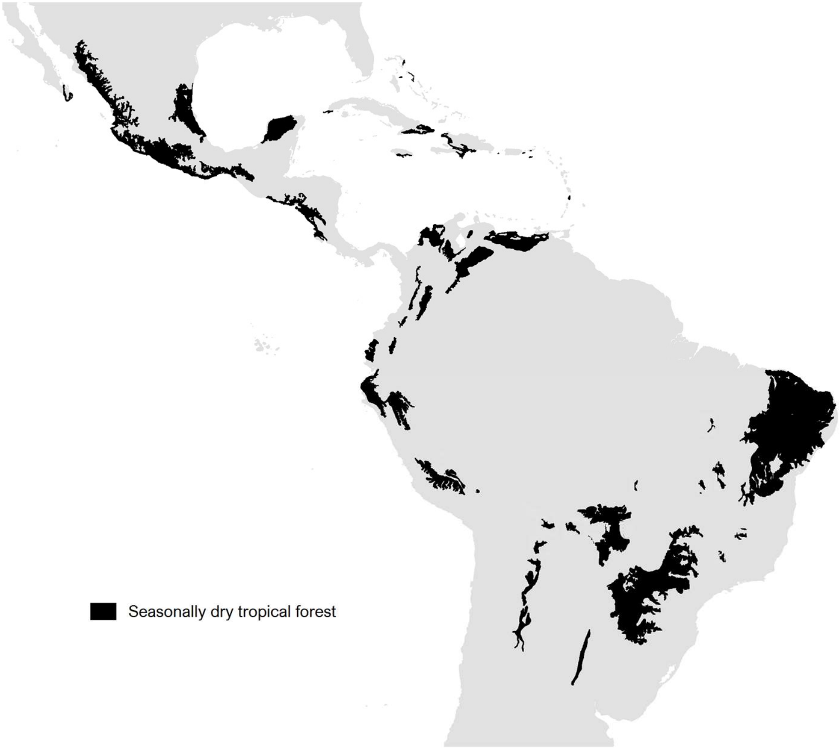

Figure 1. Schematic distribution of dry forest in the Neotropics, based on Pennington et al. (2000), Linares-Palomino et al. (2011), Olson et al. (2001) and the location of DRYFLOR inventory sites (see Figure 3).

Interest in the biogeography of neotropical dry forest has increased since Prado and Gibbs (1993) and Pennington et al. (2000) proposed a hypothesis that during glacial times of cooler and drier climate, dry forests were much more extensive than at present, perhaps forming contiguous forests across wide areas of tropical South America. According to this hypothesis, the supposed dry forest extensions during the Last Glacial Maximum went through subsequent fragmentation during the Last Glacial–Holocene transition (marked by increased temperature and precipitation levels), which resulted in the current isolated areas of dry forest, which were suggested as present-day refugia (Prado & Gibbs, 1993). This hypothesis of widespread glacial dry forests became known as the “Pleistocenic Arc” of seasonally dry vegetation and was based upon the distributions of a number of widespread dry forest species (Prado & Gibbs, 1993; Gentry, 1995; Pennington et al., 2000). However, dry forest has subsequently been shown to have high species turnover (beta diversity) among areas (Trejo & Dirzo, 2000; Linares-Palomino et al., 2011). Phylogenetic studies suggest that this 1high beta diversity may reflect that dry forest is an old biome, dating from the Miocene, with limited dispersal amongst its separate areas, resulting in in-situ diversification and therefore high species endemism in its separate areas (Becerra, 2005; Pennington et al., 2009; Särkinen et al., 2012). The concept of dispersal limitation as a mechanism to explain differences in plant community composition in dry forests has been taken further by some authors (e.g., Linares-Palomino & Kessler, 2009). It may be particularly relevant in island-like habitats, which is the case of the neotropical dry forest.

Dry forest is perhaps the most threatened tropical forest in the world (Janzen, 1988; Miles et al. 2006) with human impact having driven massive ecosystem transformation. Areas that support dry forest have been favoured for human settlements because of their drier climates and fertile soils, resulting in higher population densities and an increasing demand for energy and land, enhancing the their degradation (Blackie et al., 2014).

Agricultural activities are the main causes of dry forest habitat alteration, due to its relatively fertile soils. Pastures and large extensions of monocrops (e.g., sugar cane, rice, soy, and African oil palm) now dominate many dry forest landscapes. Other threats, such as mining, extraction of fuel wood, charcoal burning, and alien species, are playing an important role in the transformation of dry forest at regional and local scales. In a climatic change scenario dry forest areas are highly vulnerable to desertification, which results in the most severe form of soil degradation (Maass et al., 2005; Sieck et al.,2011). However, global warming might increase temperature and droughts in humid tropical areas, and in this context dry forest species will be key future resources for climatic change adaptation and mitigation programmes.

Dry forest is in a critical state and requires urgent and concrete action to preserve its biodiversity and the goods and services it provides. Protected areas are the main tool of biodiversity conservation, but dry forest is poorly represented in protected areas in the Neotropics (Miles et al., 2006; Sanchez-Azofeifa & Portillo-Quintero, 2011). Recently, most efforts have been at local scale, concentrated towards creating new protected areas that ensure the conservation of small relics of dry forest. However, it is also necessary to call the attention of policy makers and governments to consider conservation action with a broader national, regional and continental perspective.

Using the DRYFLOR database, in this chapter, I analysed the floristic composition, beta diversity patterns and distinctiveness of dry forest areas across the Neotropics, and explore the phytogeographic relationships amongst them.

The research questions are:

1. What are the main groups of neotropical dry forest based upon floristic composition?
2. How do patterns of species diversity and endemism vary amongst these groups?
3. How does species composition turnover amongst dry forest communities? This question tests the hypothesis that high diversity turnover as found at

regional level for dry forests (e. g. Mexico, Trejo & Dirzo, 2000) will be a general pattern at continental scale.

4. What are the implications for framing regional and national conservation prioritisation for neotropical dry forest in an international context?

1.3 Methods

1.3.1 DRYFLOR floristic data

Large biodiversity datasets (e.g. Encyclopedia of Life [http://eol.org], Global Biodiversity Facility [http://www.gbif.org], Salvias [http://www.salvias.net/pages/index.html], and RAINFOR: Amazon Forest Inventory Network [http://www.rainfor.org]) have been developed in the last decades, using different data-types such as museum specimens and forest inventory plots. There are 183 databases for vegetation data worldwide (Dengler et al., 2012). These initiatives make evident that networking of scientists and collections-based institutions promotes synthesis of dispersed biodiversity information.

The DRYFLOR Network is an initiative coordinated from the Royal Botanic Garden Edinburgh, which involves scientific and conservation partnerships from across Latin America including Argentina, Paraguay, Brazil, Peru, Ecuador, Venezuela, Colombia, Antilles and Mexico (http://elmer.rbge.org.uk/dryflor/). DRYFLOR has developed the first comprehensive dataset of the woody flora of dry forest across the Neotropics. The main goal of the network is to improve the floristic knowledge of dry forests, building a foundation for future research to contribute to their conservation.

The DRYFLOR database contains 192.264 occurrence records from 1602 sites across Latin America and the Caribbean covering 6958 species of woody plants from

1169 genera and 159 families. DryFlor includes sites of neotropical dry forest *sensu lato* (Beard, 1955, Gentry, 1982, Murphy & Lugo, 1995, Prado & Gibbs, 1993), covering tall semi-deciduous forests on moister sites to thorn woodland and cactus scrub in more arid areas.

Inventories in the DRYFLOR database include all woody plants reaching 3 m in height, excluding lianas or climbers, following NeoTropTree (Tree Flora of the Neotropical Region) guidelines (Oliveira-Filho, 2014; Ary Oliveira-Filho is the Brazilian DRYFLOR partner). The data comprise mostly floristic surveys or ecological inventories. Every floristic list is restricted to a site that is defined as a circular area of 10 km diameter covering a specific vegetation type. DRYFLOR data compilation began with a review of bibliography (journal articles, books, technical reports, student theses), followed by contacting local researchers who could provide unpublished floristic lists. Within the DRYFLOR network, I was lead partner for Colombia, and coordinating data compilation for 125 sites.

The treatment of the data follows DRYFLOR protocols where the judgment of the quality of the species identifications in a given survey is crucial. Taxonomic concepts for families followed the classification of the Angiosperm Phylogeny Group III system (APG III). To correct misspellings, the species list was tested in the Taxonomic Name Resolution Service v3.2 (http://tnrs.iplantcollaborative.org; Boyle et al. 2013). Synonyms and nomenclature were checked by gathering a thesaurus of more than 11700 names using the most updated taxonomic resources such as Catalogue of Seed Plants of the West Indies (Acevedo & Strong, 2012) and Flora do Brasil (Rio de Janeiro Botanical Garden, http://floradobrasil.jbrj.gov.br/). In cases where these sources were in conflict, taxonomic specialists were contacted whenever possible.

The database does not use infraspecific taxonomic ranks. I coordinated data treatment across the entire DRYFLOR dataset.

1.3.2 Data analysis

Quantitative analyses were performed to identify the main regions of neotropical dry forest and to describe the relationships in terms of floristic affinities amongst them. All the analyses were run in the R Statistical Environment v. 3.2.1 (R Core Development Team 2015) using the packages vegan (Oksanen et al., 2016), recluster (Dapporto, et al., 2013), and pvclust (Suzuki & Shimodaira, 2015).

Pairwise distances were calculated to assess differences in floristic composition amongst sites and subsequently amongst the main groups. The Simpson dissimilarity index was used to build the distance matrix to explore the dataset through ordination and classification methods. The Simpson distance is less affected by variation in species richness than other metrics such as Sørensen or Jaccard distance (Lennon, 2001; Koleff et al. 2003, Kreft & Jetz, 2010), and this is an important factor in our dataset, with numbers of species per site varying from 4 to 305. The Simpson dissimilarity index (β sim) calculates the compositional distance between pairs of sites β 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. Choosing the minimum value of the exclusive species between the sites reduces the influence that local species richness gradient has on dissimilarity (Lennon, 2001).

Non-metric multidimensional scaling (NMDS) ordinations were applied using the function metaMDS of the vegan library (Oksanen et al. 2016). This method is considered the most robust unconstrained ordination approach (Minchin, 1987). It attempts to represent compositional variation in a few dimensions (Legendre & Legendre, 1998), which helps to identify groups of sites and transitional areas. NMDS was performed using 1000 random starts with increasing numbers of dimensions until the stress value was below 0.2. Stress values calculated as the sum of the squared differences between fitted and original distances were used to assess the performance of the ordination. Values ranged from 0 to 1, with smaller values indicating better fits (Legendre & Legendre, 1998).

Classification hypotheses of the sites were estimated using hierarchical clustering techniques, which are commonly applied for biogeographical purposes (Kreft & Jetz, 2010; Holt et al., 2013; Dapporto et al., 2013; Gonzalez-Orozco et al., 2014). The unweighted pair-group method was used, applying arithmetic averages (UPGMA) as an algorithm to link the clusters, after comparing its performance to Ward's minimum variance method. Performance was assessed with the cophenetic correlation between the original dissimilarity matrix and the Simpson dissimilarity index. The Ward method showed a low correlation (r= 0.37) and UPGMA gave the best performance (r=0.65) (Appendix 2)

The Simpson dissimilarity index 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 will be strongly 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 tree will be clustered together. To avoid this bias, the recluster package (Dapporto et al., 2013), which performs a random re-order of the sites (recluster.cons function), was used for the clustering analysis.

In order to establish relationships amongst the major groups identified by clustering analyses (12 groups; see below), a pooled species list was built for each and then clustering analyses were conducted on a species x 'major group' matrix. A pvclust approach was used to estimate support for relationships amongst these groups. This method provides the Approximately Unbiased (AU) support values per cluster which is computed by multiscale bootstrap resampling of the species. Clusters with high AU values (e.g. >0.95) are considered strongly supported by the data (Suzuki & Shimodaira, 2015).

In order to assess the floristic similarity within and among the major groups to compare them with published floristic similarity values from other biomes (e.g., Bridgewater et al., 2004; Linares-Palomino et al., 2011), I calculated Simpson and also Sørensen dissimilarity values. These calculations included singletons.

I also evaluated the diversity gradients in terms of distance from the equator in the 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.

Overlaying the distribution of the dry forest sites and the dataset of protected areas across the Neotropics, I conducted an approximate assessment of the conservation status of dry forest to evaluate the proportion of the sites that are under protection. I considered conservation units from the World Database on Protected Areas (WDPA) reported by 2015 (IUCN & UNEP-WCMC, www.protectedplante.net).

1.3.3 Dataset exploration

Preliminary analyses were necessary to standardize and explore the nature and structure of the dataset. The first step was building a binary matrix of species versus sites, based on the whole DRYFLOR database, excluding all the taxa that were not identified to species as well as singleton species (1836 species that occur at just one site). Secondly, 105 sites with few species presences were removed. Knowing that some areas of the dry forest in the Andes have complete floristic inventories with few 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 (Lennon, 2001; Kreft & Jetz, 2010). The matrix for these preliminary analyses contained 5443 tree species and 1524 dry forest sites.

A clustering analysis was run, permuting the order of the sites 10000 times, which was summarized using a 50 % majority rule consensus tree. In an exploratory analysis a high number of clusters and a flexible threshold are suggested as a means to reach a consistent representation for the original matrix and data generated by randomization (Dapporto et. al, 2013). A consensus tree based upon such repeated analyses re-ordering sites ensures more general biogeographic meaning (Dapporto, 2013) in comparison to other approaches (i.e. pvclust) where a single hierarchical cluster is applied.

The preliminary consensus tree showed the sites assembling in 11 groups: 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 (Figure 2).

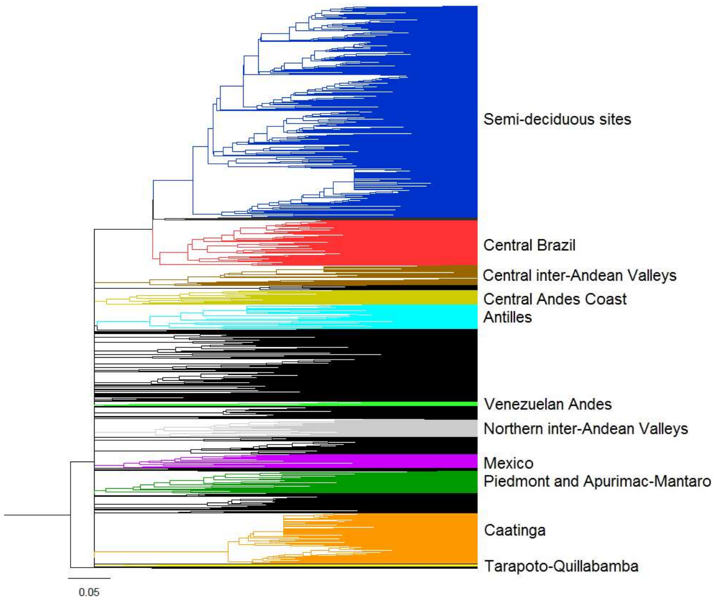

Figure 2. Hierarchical clustering of 1467 DRYFLOR sites based upon 10000 random site order-addition excluding singleton species and using Simpson dissimilarity and UPGMA as the linkage method. Sites from Central America and northern South America indicated in black.

The separation of the Central Andes (inter-Andean Ecuador and most of the Peruvian inter-Andean sites) and Antilles as groups is well documented and supported by high levels of species endemism in those areas (Pennington et al., 2000, 2006, 2009; Linares-Palomino et al., 2011). The Piedmont group is also well known, defined as one of the dry forest ‘nuclei’ (Prado & Gibbs, 1993; Pennington et al., 2000, 2006, 2009; Linares-Palomino et al., 2011), which follows the flanks of the Andes from Santa Cruz de la Sierra in Bolivia to Tucuman and the Sierras of the North West of Argentina.

The Venezuelan Andes group is not related to the rest of the Andean dry formations. These sites occur exclusively in the Merida region, from 1800 to 2400 metres altitude (Aranguren, 2009) and their dry season is relatively short – three months maximum. Due to their proximity to areas of cloud forest, their species lists include 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*). These sites were considered initially in the broad definition of dry forest because they are traditionally called “seasonally dry premontane” and “seasonally dry montane” forests and the purpose was to test their floristic affinities at a broad scale.

A massive group contains sites from Bolivia and Brazil. Within this group a cluster is evident, which includes the seasonally dry semi-deciduous formations from the Atlantic Forest and Cerrado Domain (riverine forest), and the sites known as the Misiones nucleus. Semi-deciduous formations are tall forests in areas with a seasonal rainfall regime, where between 30 and 60% of the leaf mass is lost during the dry season (Ary T. Oliveira-Filho, 2009).

The semi-deciduous sites include humid elements that are common in the Atlantic forest, and can also be found within Cerrado Domain, entering through river courses as part of gallery forest. Such gallery forest elements also enter the Misiones sites because this nucleus includes the Paraguay-Parana river systems. In the Misiones, typical species from southern South American dry forests (e.g. *Anadenanthera colubrina, Amburana cearensis*) are common but not dominant elements in the community (Prado & Gibbs, 1993). In general, the proximity of dry forest areas to different major biomes - e.g., savanna in the Cerrado region or rain forest (Pennington et al., 2009) - promotes the incursion of different floristic elements into transitional areas.

The influence of transitional semi-deciduous sites in the database is evident in terms of species composition. In semi-deciduous sites, the genera with most records are *Eugenia, Miconia, Myrcia*, and *Ocotea*, which are not typical or dominant elements from drier forest formations. In contrast, excluding those sites, genera from more characteristic dry forest families such as Leguminosae and Bignoniaceae (e.g., *Senna, Bauhinia, Machaerium and Handroanthus*) become the taxa with higher frequency. Based on the multiple moist forest elements present in the transitional areas, the semi-deciduous sites and the Venezuelan Andes group were excluded in the subsequent floristic analyses, resulting in a dataset containing sites from 'neotropical dry forest *sensu stricto*', plus the Misiones region that has a less severe dry season (as measured by precipitation of the driest quarter [Hijmans et al., 2005]), but which is a widely recognized dry forest nucleus (Prado & Gibbs, 1993, Pennington et al., 2000).

Additionally, a few sites that belong to poorly represented regions in the database were removed after they were identified as outliers according to the NMDS scores (e.g. Estoraques and Tuparro tablelands in Colombia; Laguna in Baja California, Mexico).

1.4 Results and discussion

1.4.1 The main groups of neotropical dry forest and their relationships

After data exploration, the final dataset focusing on the drier formations, including Misiones sites, and after removing sites with less than eight species presences, contained 835 sites, 147 families, 983 genera and 4660 species of which 1504 (32 %) are singletons, found at just one site. Silhouette values were used to determine the optimal number of groups (using recluster.regions function from Dapporto et al., 2013). This is a measure of how much an object belongs to its cluster compared to how close it is to objects in its nearest neighbouring clusters (Rousseeuw, 1987).

According to the silhouette values curve, I chose the partition of data into 12 clusters. NMDS was also performed and the ordination plots allowed inference of the floristic distances among and within biogeographical regions. The ordination plot shows the 12 main groups (Appendix 3). The clustering analyses identified 12 main dry forest 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 (Figure 3).

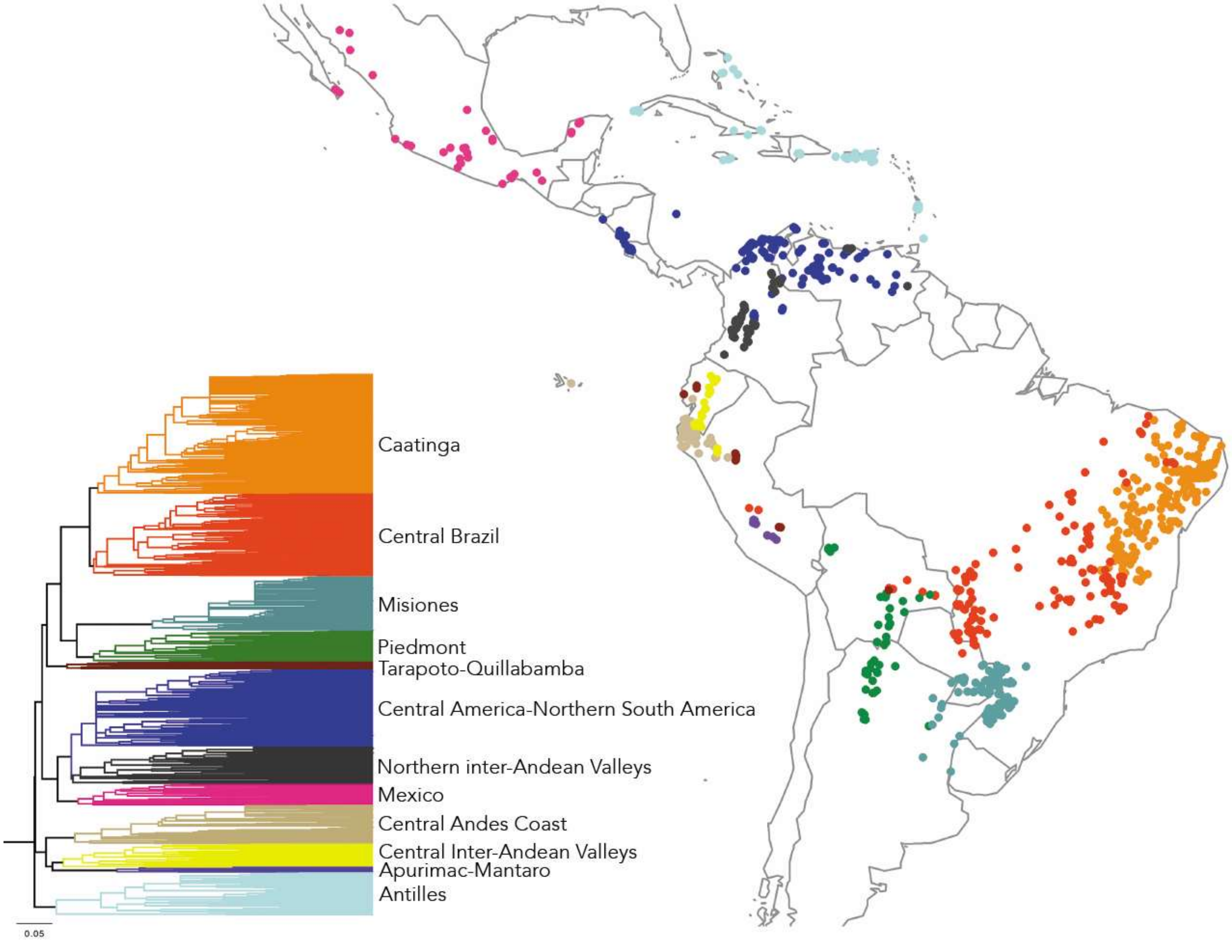

Figure 3. Geographical representation of the hierarchical clustering of 835 dry forest sites using the Simpson dissimilarity index and excluding singleton species.

A similar topology to the 835 site classification (Figure 3) was obtained in the consensus tree clustering the 12 groups with the *Approximately Unbiased* (AU) support values per cluster (using the pvclust package) (Figure 4).

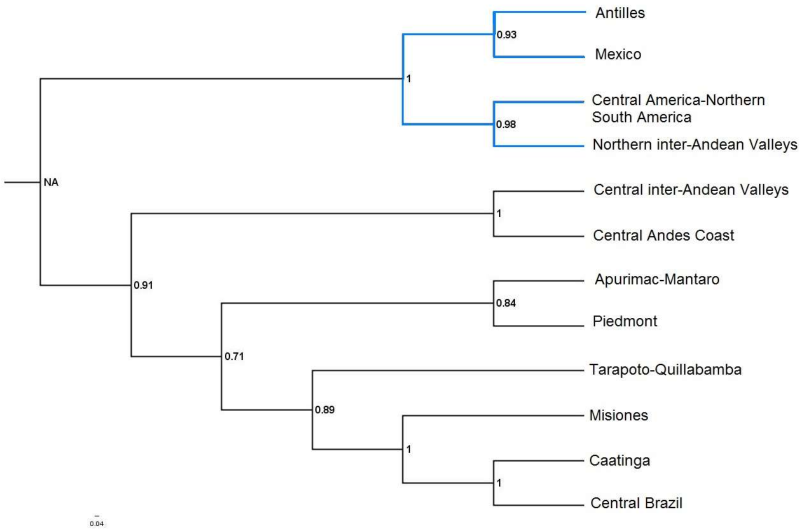

Figure 4. Hierarchical classification of the 12 dry forest floristic groups with approximately unbiased bootstrap values (AU) (nboot=10000). The northern cluster is indicated with blue lines.

A northern cluster of areas (Mexico, Antilles, Central America-northern South America) is resolved with 100% support (AU value); this northern group is also clear in the ordination (Figure 5).

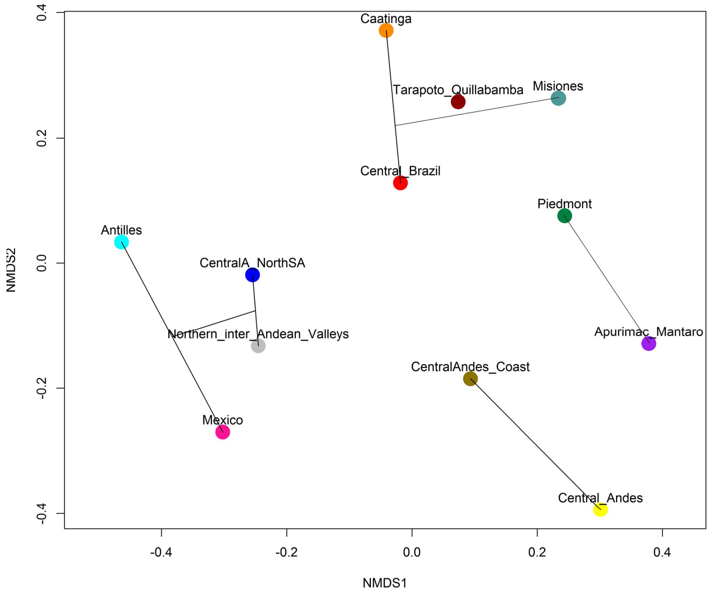

Figure 5. NMDS ordination of the 12 dry forest floristic groups in two dimensions, stress values= 0.116, tr =100. Relationships inferred from a classification using the UPGMA method (Figure 4) are indicated by lines.

There are few studies that have examined the relationships of the floras of these areas at a continental scale, and the strong support for this group confirms a north-south division in neotropical dry forest that was suggested by Linares-Palomino et al (2011). The individual distinctiveness of Mexican dry forest has been widely recognised (Rzedowski, 1978; Gentry, 1995) and the Caribbean is considered a distinctive neotropical phytogeographic region (Gentry, 1982) not only because of its notable level of endemism (Acevedo & Strong, 2012; Maunder et al., 2008) but also for the particularities of the Antillean dry forest in terms of structure and edaphic preferences (Gentry, 1995).

With the exception of the northern South American areas in Colombia and Venezuela, all other South American areas form a single cluster (Figure 4). This division of the dry forest of Colombia and Venezuela from all areas further south 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 (1982).

The northern Andean valleys of the Rio Magdalena and Cauca are part of the northern South American group, and within the wider South American group, five additional groups of Andean dry forests are resolved (Figure 3). Therefore, there are six separate Andean dry forest groups, which reflects the great floristic heterogeneity of dry Andean valleys, which was first highlighted by Sarmiento (1975).

The Central inter-Andean Valleys (mostly Ecuadorean) and Central Andes Coast groups have strong affinities, and sites from the Marañón valley in Peru group in both clusters. A close floristic relationship of southern Ecuadorian and northern Peruvian inter-Andean valleys was reported by Lewis et al. (2006) and Linares-Palomino

(2006). The relationship of the Marañón valley sites with the adjacent coast may reflect the ease of migration across the Andean cordillera in the Huancabamba depression, where the Andean cordillera reaches only c. 2100m (Bridgewater et al., 2003).

The floristic affinities of the Tarapoto Valley in Amazonian Peru have been considered uncertain (Bridgewater et al. 2003), which is reflected here in its isolated position in the ordination (Figure 5). Tarapoto falls in a group with Quillabamba and two additional sites from the Pacific Ecuadorian coast. The grouping of these sites on opposite sides of the Andes may be related to the effect of humid floristic elements from the adjacent moist forests of the Amazon (Tarapoto and Quillabamba) and the Chocó region in Ecuador. The position of Puerto Ocopa sites in the Central Brazil cluster may also reflect the influence of humid floristic elements, but the low number of sites is not sufficient to reach a clear conclusion about the floristic affinities of the area.

Southern Andean areas have been previously shown to be floristically distinct (Kessler & Helme**,** 1999, López & Beck**,** 2002) but their relationships in prior studies were uncertain, especially with regard to Bolivian and central/southern Peruvian sites (Linares et al., 2011). Here, the Peruvian inter-Andean valleys of the Mantaro and Apurimac are a distinct group, and the Bolivian Andean areas group with sites from the Andean Piedmont of Argentina.

The eastern and southern South American areas fell into two clusters, the first one formed by the Central Brazil, Caatinga, Misiones and Tarapoto-Quillabamba, and the second by the Piedmont and the Andean groups of Central Andes and Apurimac-

Mantaro (Figure 4). The Misiones group shares a significant number of species with the Central Brazil group (409 spp. Table 1, Appendix 4), Caatinga (264 spp.) and Piedmont (232 spp.). The Misiones group, with its intermediate geographic position amongst other dry forest groups, and influenced by surrounding more humid forests, shows the complexity of the community assemblage of semi-deciduous formations.

1.4.2 Diversity patterns and endemism

Confirming previous studies showing the dominance of Leguminosae in dry forest (Gentry, 1995; Lavin & Matos, 2008; Pennington et al., 2009), this family had by far the highest richness in terms of number of genera (152) and species (944), and was also the most recorded family, with 14192 presences, suggestive of its dominance in terms of frequency across our dataset. Myrtaceae, Euphorbiaceae and Malvaceae were the next most diverse families with more than 200 species, and Myrtaceae is the second most frequent family with 2970 occurrences of 223 species. Cactaceae is also a very important element in dry forests, with 41 genera, 137 species and more than 1300 records. The most commonly reported genera were *Cordia* (Boraginaceae), *Senna* (Leguminosae), *Eugenia* (Myrtaceae), *Aspidosperma* (Apocynaceae), and *Bauhinia* (Leguminosae) with more than 900 records each. The genera with the highest species-richness were *Eugenia* (Myrtaceae; 96 spp.), *Croton* (Euphorbiaceae; 70 spp.), *Bursera* and *Ficus* (Burseraceae and Moraceae; 59 spp.).

Taxonomic composition in all the 12 dry forest floristic groups is variable except for the consistent dominance of legumes (Appendix 5). This supports the idea of the floristic heterogeneity of neotropical dry forest (Pennington et al., 2006). Aside from legumes, other dominant families vary amongst the dry forest groups. For example, the second most species-rich family in Central Brazil, Caatinga and Misiones is

Myrtaceae; in Mexico, Central inter-Andean valleys and Apurimac-Mantaro it is Euphorbiaceae, and Central Andes Coast it is Cactaceae. In terms of generic diversity, 78% of the most species-rich genera are not common to more than three groups. In fact, 50% of the most species-rich genera are exclusive to a single dry forest group. However, it is also important to note that six genera: *Cordia* (Boraginaceae), *Ficus* (Moraceae), *Zanthoxylum* (Rutaceae), *Senna* (Fabaceae), *Croton* (Euphorbiaceae) and *Eugenia* (Myrtaceae), show high species richness in at least nine of the main floristic groups.

The number of species in the floristic lists from the 835 sites ranged from 8 to 305, partly reflecting the heterogeneity of methodologies used to obtain the data (e.g., from plots and transects of varying sizes or vegetation surveys), which precludes any definitive discussion of alpha diversity at individual sites. However, because our surveys provide a reasonable geographical coverage of the dry forest areas across the Neotropics, this variation likely also reflects the high heterogeneity in regional species richness patterns.

The Central Brazil, Caatinga and Mexican groups contain the most species (1344, 1112 and 1072 respectively, Table 1), whilst some inter-Andean valleys contain the least (Central inter-Andean valleys and Apurimac - Mantaro with 165 and 78 species respectively). Overall, regional species richness may reflect an integrated time-area effect (Fine & Ree, 2006). The small number of species in inter-Andean dry forests is perhaps unsurprising given their small and fragmented area; the dry forest of the Marañón, Apurimac and Mantaro inter-Andean valleys in Peru are estimated to occupy just c. 3100 km^2 in total (INRENA, 1995) compared to c. 850,000 km^2 estimated for the Caatinga (Paganucci de Queiroz, 2006), which has 1112 species in the dataset. Whilst species restricted to one of the 12 main dry forest groups ("exclusive" species in Table 1) may not be strictly endemic to these groups (because they may be found elsewhere, for example in non-dry forest vegetation or in unsampled dry forest in the geographic region of other groups), they do serve as a proxy for endemism. Mexican and Antillean dry forests have the highest percentage of exclusive species (73 and 65% respectively). The lowest percentages of exclusive species are found in Misiones, reflecting the large numbers of species shared with neighbouring areas (see below). Despite their close geographical proximity, Andean sites have c. 30-40% exclusive species, reflecting high beta diversity at relatively small spatial scales.

Table 1. 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

1.4.3 Diversity turnover

Pairwise dissimilarity values between individual sites computed across the whole dataset (835 sites) show a mean value of 0.90 for Simpson dissimilarity (median = 0.94) and 0.94 for Sørensen dissimilarity (median = 0.97). These values are slightly higher than reported by Linares-Palomino et al., (2011; Sørensen = 0.86) who included relatively few floristic lists from Central America and northern South America areas.

Pairwise dissimilarity values among the 12 main groups (computed using the pooled species lists) are high, ranging 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 (Appendix 6). They suggest high levels of diversity turnover not only at a continental scale, but also at a regional scale. Geographical patterns in beta diversity in Figure 6 show the dry forest groups connected to each other by lines proportional to the number of shared species. Most of the lines represent less than 100 species shared between dry forest groups. The stronger affinities are found in only two areas: one in the south, where the dry forest from Central Brazil (red circle; Figure 6) show high levels of similarity mainly with Caatinga, sharing more than 695 species, but also with Piedmont and Misiones; and the second in Central America and northern South America (blue circle; Figure 6) involving the Mexican dry forest and the northern inter-Andean Valleys.

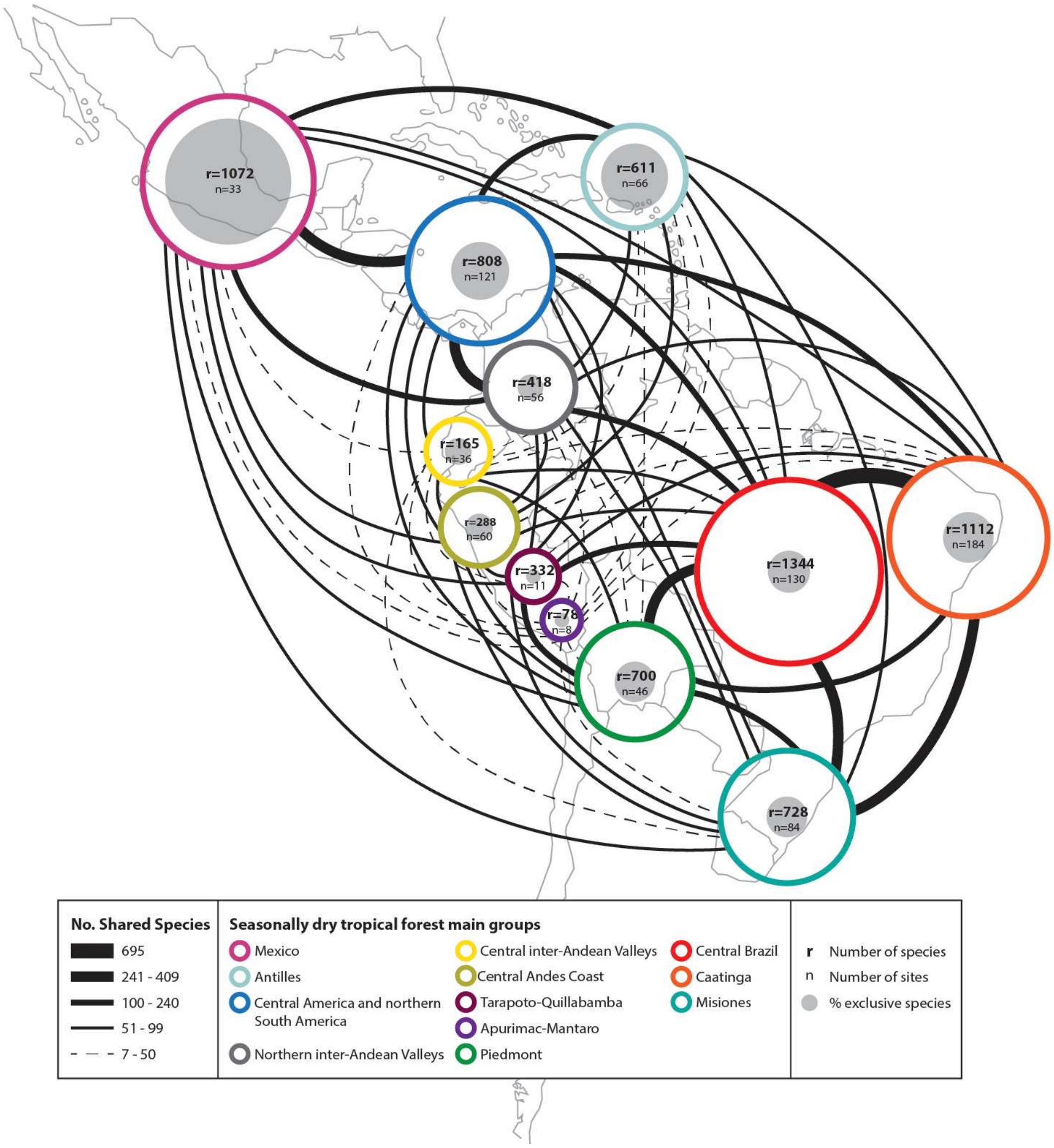

Figure 6 Geographical patterns of species turnover among dry forest regions. Size of the circles is proportional to the number of the species per group, coloured circles represent the total number of species and grey circles the number of exclusive species (r= number of species, n=number of sites). The species turnover among the areas is described by having the line width based on the number of species shared (values from Table 1, Appendix 4).

The high beta diversity reflects that few species are widespread and shared across many areas of neotropical dry forest. No species is found in all 12 dry forest regions, there are only three species shared amongst 11 groups and nine species amongst ten groups (Table 2, Appendix 4). Some of the most recorded species (i.e., those recorded across most sites) are widespread ecological generalists such as *Maclura* *tinctoria, Guazuma ulmifolia* and *Celtis iguanaea,* which are common in other biomes as well as dry forest. Some of these species tend to grow in disturbed areas, so their presence in many sites could be a consequence of the level of degradation and fragmentation of dry forest. In other cases, highly recorded species are dry forest specialists, such as *Anadenanthera colubrina,* which occurs in more than 60% of the sites in the Caatinga, Central Brazil and Piedmont, and *Cynophalla flexuosa* that is commonly recorded in Antilles, Caatinga and Central Andes Pacific coast (~40% of the sites).

Although frequently recorded dry forest specialist species may be abundant and dominant, there is little evidence for any oligarchy of species that dominates in neotropical dry forest as a whole, as suggested by Linares-Palomino et al. (2011) and Pennington et al. (2006), probably reflecting limited dispersal between isolated areas. These patterns contrast strongly with other tropical biomes, such as rain forest (Pitman et al., 2001; ter Steege et al., 2013) and savanna (Bridgewater et al., 2004), which are often dominated by a suite of oligarchic species over large geographic areas.

Frequently recorded species are seldom shared between any of the floristic groups. Eighty-five percent of the most recorded species, identified as top 20 frequency (Appendix 5), are recorded in a single main floristic group, with a few exceptions where the same species was recorded across several groups (e.g. *Anadenanthera colubrina* and *Guazuma ulmifolia* in five groups each). Widespread species that are common in various and disjunct dry forest areas, such as *Anadenthera colubrina* or *Geoffroea spinosa*, which were emphasised in early discussions of neotropical dry forest biogeography, are the exception.

In other cases, there is a particular set of species characteristic of 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. Another example to illustrate this trend is the set of species in common between Mexico and Antilles dry forest, which share two species of *Sideroxylon* - a common genus of Sapotaceae from dry areas (*S. salicifolium* and *S. foetidissimum)*, *Exostema caribaeum* (Rubiaceae), *Krugiodendron ferreum* (Ramnaceae) and *Bauhinia divaricata* (Leguminosae).

Beta diversity is also high within all major regions of dry forests with median Sørensen values ranging from 0.74 within the Caatinga to 0.90 within the Tarapoto-Quillabamba group (the median value is slightly lower at 0.70 within the semi-deciduous Misiones group). This result of high local beta diversity has only been previously shown only for Mexican dry forest (Trejo & Dirzo, 2002). Excluding the Tarapoto-Quillabamba group, Mexico has the highest beta diversity (Sørensen = 0.88, Simpson = 0.79) and also high species richness, both of which have been stated in previous studies (Trejo & Dirzo, 2002; Balvanera & Lott, 2002; Rzedowski & De Rzedowski, 2013).

There is a clear geographical differentiation in the frequency patterns of the dissimilarity values within groups. The southern groups showed a bell-shaped distribution (Figure 1, Appendix 7). In contrast, the northern group, including Antilles, Mexico and Central America and northern South America, showed a high frequency of 100 % of dissimilarity amongst sites (Figure 2, Appendix 7). A third distribution is shown by the Andean groups (Figure 3, Appendix 7), which have a mixture of patterns with high levels of heterogeneity.

The Caatinga has high regional species richness, similar to that in Mexico and also has high species richness at individual sites. However, its beta diversity value is the lowest, which may reflect that the Caatinga region is the biggest continuous area of dry forest in the Neotropics, and lacks barriers formed by mountains, so community composition is less affected by dispersal limitation. It is interesting that there may be a peak in regional dry forest species richness around 20 degrees' latitude (Figure 7), which may support a "reverse latitudinal gradient" stated by Gentry (1995).

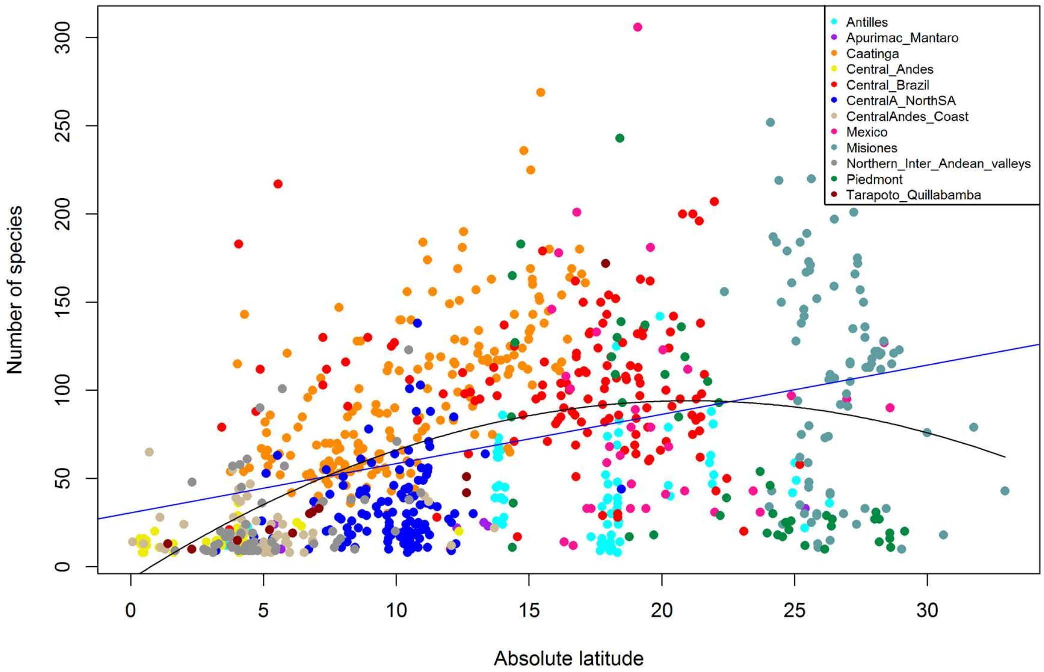

Figure 7. Fitted lines plot for polynomial (black line, R^2= 0.2196) and linear (blue line, R^2= 0.159) regression of absolute latitude versus total number of species of 835 dry forest sites.

1.4.4 Conservation implications

This study demonstrates high beta diversity for all neotropical dry forest, with each major floristic group having a particular set of species, underlined by high pairwise floristic dissimilarity (mean values for the whole dataset of 0.90 for the Simpson dissimilarity index and 0.79 for the Sørensen index). This high floristic turnover makes clear a need to conserve dry forests in each of the major groups, meaning that many protected areas will be needed.

However, overlaying the distribution of DRYFLOR sites on to a data set of protected areas shows that the existing level of protection of dry forest across the Neotropics is inadequate. It is shocking that 86% of dry forest sites in the DRYFLOR dataset, which were selected as well preserved areas, are situated outside protected areas. Andean dry forests are particularly poorly protected. For instance, Apurimac-Mantaro and Tarapoto-Quillabamba sites are not protected under any conservation category. Only 5% of the Northern inter-Andean Valleys dry forest sites - one of the most transformed land areas in Colombia (Forero-Medina & Joppa, 2010; Vargas, 2012) - are protected, representing just 1.4% (3846 ha) of the total remaining extension of dry forest in this region (García et al., 2014). Only 14% of the Central inter-Andean Valleys, 13% of the Central Andes Pacific Coast, and 12% of Piedmont sites occur within a protected area. Major dry forest regions such as Mexico and the Caatinga are also under-represented with less than 15% of the sites under protection. In fact, only 1.2% of the total Caatinga region of in Brazil is fully protected (Ministério do Meio Ambiente Brasil., 2016). Both Mexico and the Caatinga are home to more than a thousand woody species, and the high beta diversity within them means that to protect this diversity fully will require multiple, geographically dispersed protected areas.

The six dry forest Andean groups showed high levels of endemism (38% of species are exclusive to them in the DRYFLOR dataset) and high floristic dissimilarity. Andean dry forests groups are highly neglected in terms of conservation, and setting up regional or national reserves in these areas should be a priority in an international context.

Furthermore, there is an opportunity to refine and extend existing protected area networks in the Central America and northern South America and the Antilles floristic groups where representation in protected areas is slightly higher at 23% and 18% respectively. Given the precarious state of the remnants and the high level of fragmentation of natural vegetation in these areas, connectivity of dry forest patches might be a key issue in the long-term viability of reserves.

1.5 Conclusions

Based upon floristic composition, this study identified 12 major floristic groups of neotropical dry forest. The analyses suggest great floristic turnover across neotropical dry forest both within and between the major floristic groups. There are some commonalities of floristic composition, such as the dominance of legumes, but these are all at higher taxonomic level rather than at species level. At species level, the data suggest high levels of endemism to each group and little evidence for many widespread species shared amongst groups. These conclusions are underlined by the mean pairwise floristic dissimilarity values for the whole dataset of 0.90 for the Simpson dissimilarity index and 0.79 for the Sørensen index.

Sampling effort evaluated using species accumulation curves (Appendix 1-Supplementary material, Fig. S3), showed a robust floristic dataset for the southern areas (Piedmont, Misiones, Central Brazil, Caatinga), in contrast to other areas, in which more survey work is required especially the Andean valleys in Peru and Ecuador (e.g., Tarapoto-Quillambamba, Apurimac-Mantaro, Central inter-Andean).

In summary, these findings provide a scientific framework within which, for the first time, national decision makers can contextualise the significance of their dry forests at a regional and continental scale. They clearly suggest that to conserve the full dry forest diversity across Latin America and the Caribbean will require protecting it simultaneously within multiple regions.

1.6 Appendices

Appendix 1

RESEARCH ARTICLE S
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).

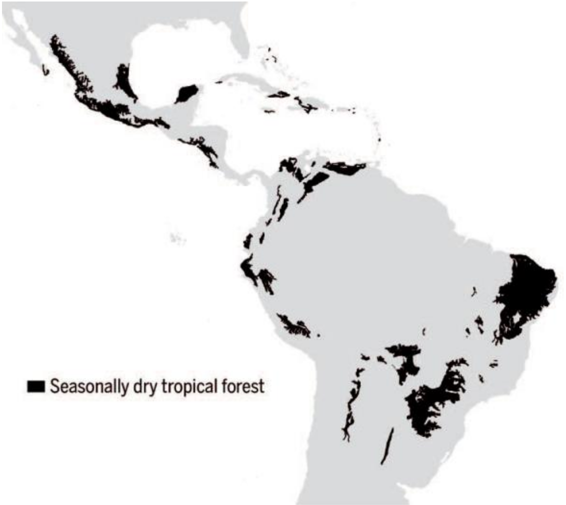

Fig. 1. Schematic dry forest distribution in the Neotropics. [Based on Pennington *et al.* (*13*), Linares-Palomino *et al.* (*2*), Olson *et al.* (*45*), and the location of DRYFLOR inventory sites (see Fig. 2)]

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

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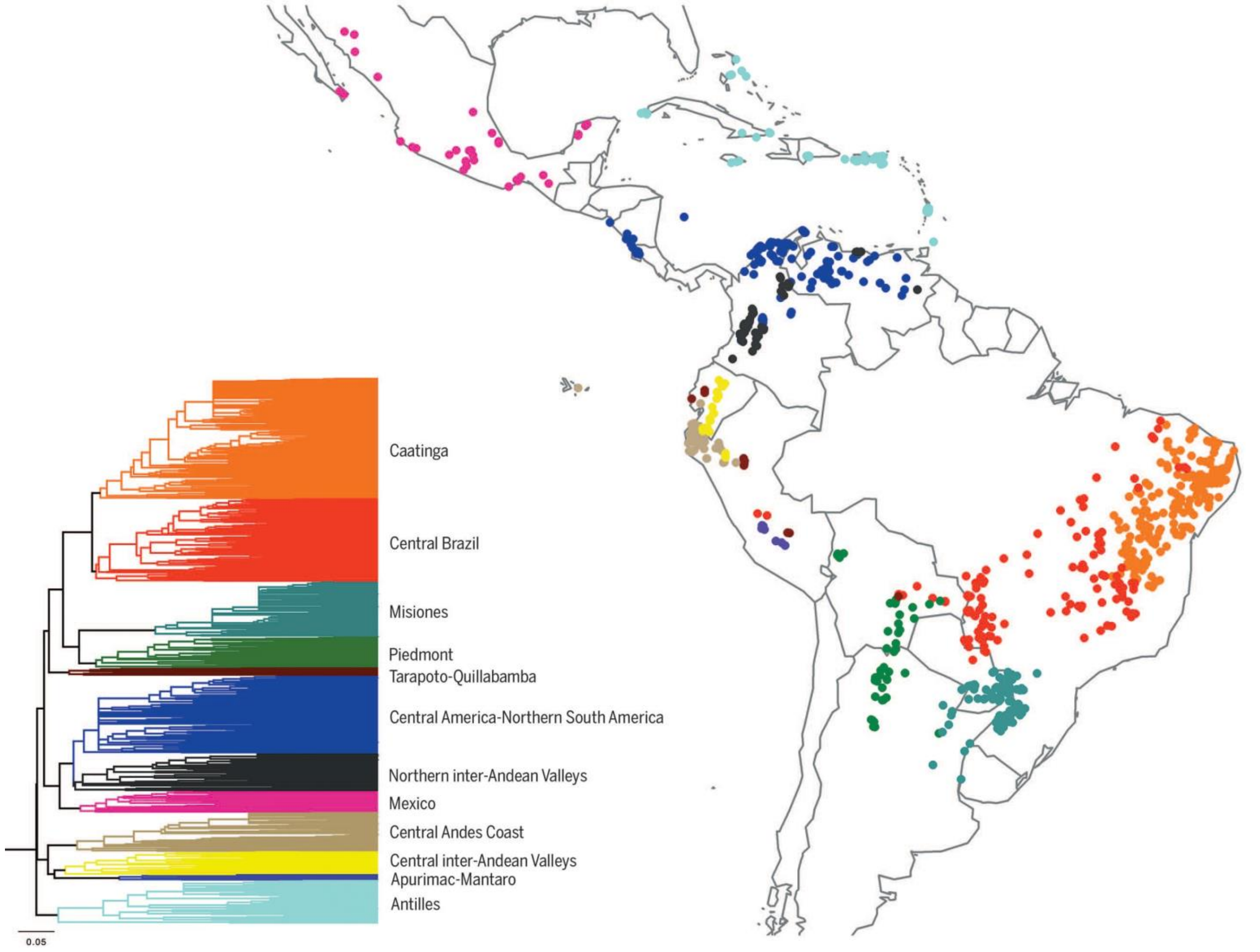

Fig. 2. Neotropical dry forest floristic groups based on woody plants. Geographical representation of UPGMA clustering of 835 dry forest sites using the Simpson dissimilarity index as a measure of distance.

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

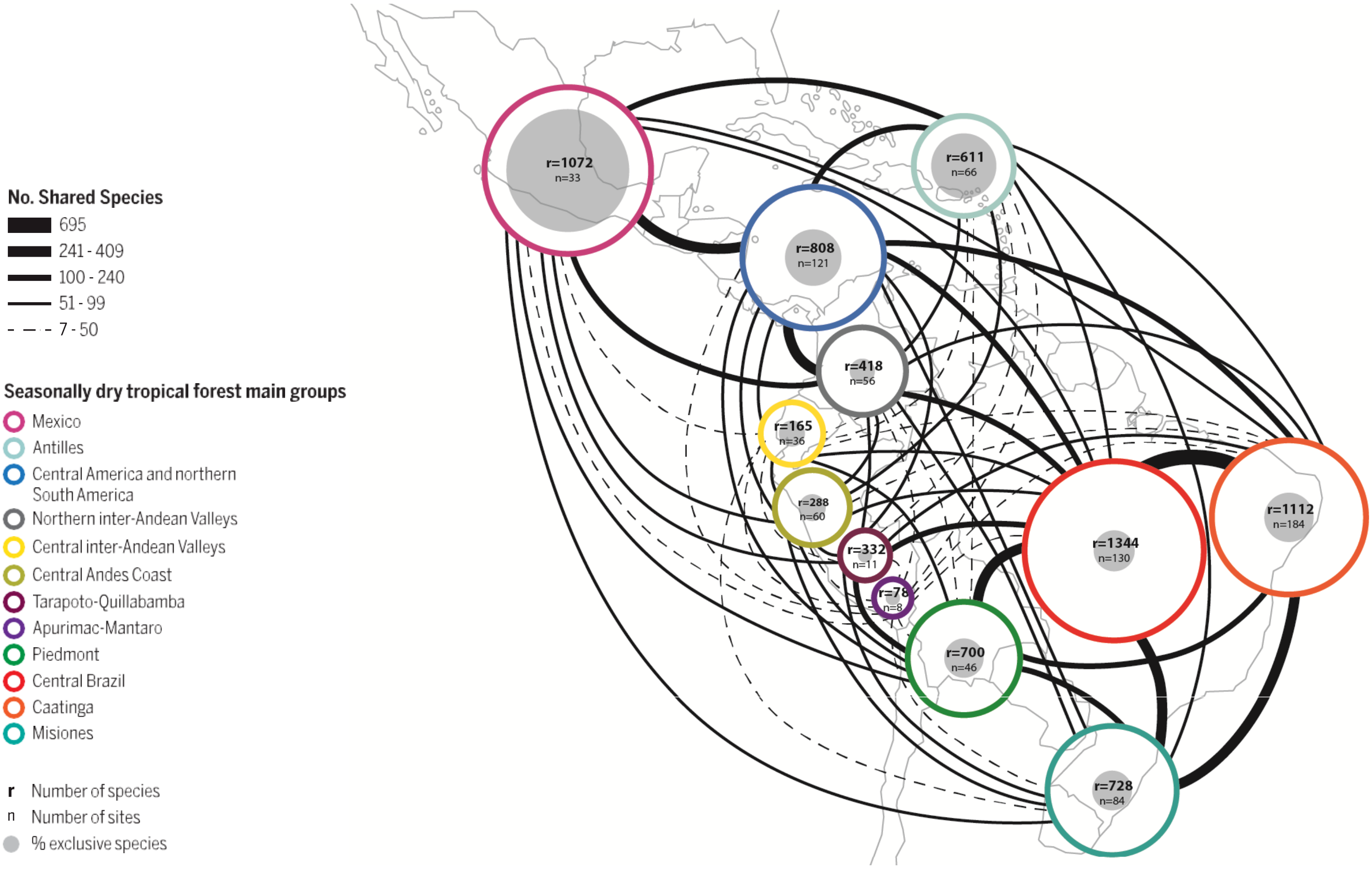

Fig. 3. Geographical patterns of species turnover among 12 dry forest floristic groups. (Fig. 2). Size of the circles is proportional to the number of species per group; size of colored circles is proportional to the total number of species and of gray circles to the number of exclusive species. The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

REFERENCES AND NOTES

1. R. T. Pennington, M. Lavin, A. Oliveira-Filho, *Annu. Rev. Ecol. Evol. Syst.* 40, 437–457 (2009).
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 *et al.*, *J. Biogeogr.* 33, 491–505 (2006).
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, *Annu. Rev. Ecol. Syst.* 17, 67–88 (1986).
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.*, *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. 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.
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, *Int. J. Climatol.* 25, 1965–1978 (2005).
13. R. T. Pennington, D. E. Prado, C. A. Pendry, *J. Biogeogr.* 27, 261–273 (2000).
14. D. E. Prado, P. E. Gibbs, *Ann. Mo. Bot. Gard.* 80, 902–927 (1993).
15. D. E. Prado, *Candollea* 48, 145–172 (1993).
16. H. Kreft, W. Jetz, *J. Biogeogr.* 37, 2029–2053 (2010).
17. M. Maunder *et al.*, *Bot. Rev.* 74, 197–207 (2008).
18. P. Acevedo-Rodríguez, M. T. Strong, *Smithsonian Contrib. Bot.* 98, 1–1192 (2012).
19. A. H. Gentry, *Ann. Mo. Bot. Gard.* 69, 557–593 (1982).
20. 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.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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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

DRYFLOR, Karina Banda-R, Alfonso Delgado-Salinas, Kyle G. Dexter, Reynaldo Linares-Palomino, Ary Oliveira-Filho, Darién Prado, Martin Pullan, Catalina Quintana, Ricarda Riina, Gina M. Rodríguez M., Julia Weintritt, 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 Graveson, 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)

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Editor's Summary

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Supplementary Materials for

Plant diversity patterns in neotropical dry forests and their conservation implications

DRYFLOR.

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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/treeatlan/). 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 (β sim) calculates the compositional distance between pairs of sites $\beta \text{ sim} = 1 - J / [J + \min(A, B)]$, 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 × 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 (UICN &UNEP-WCMC, www.protected planet.net).

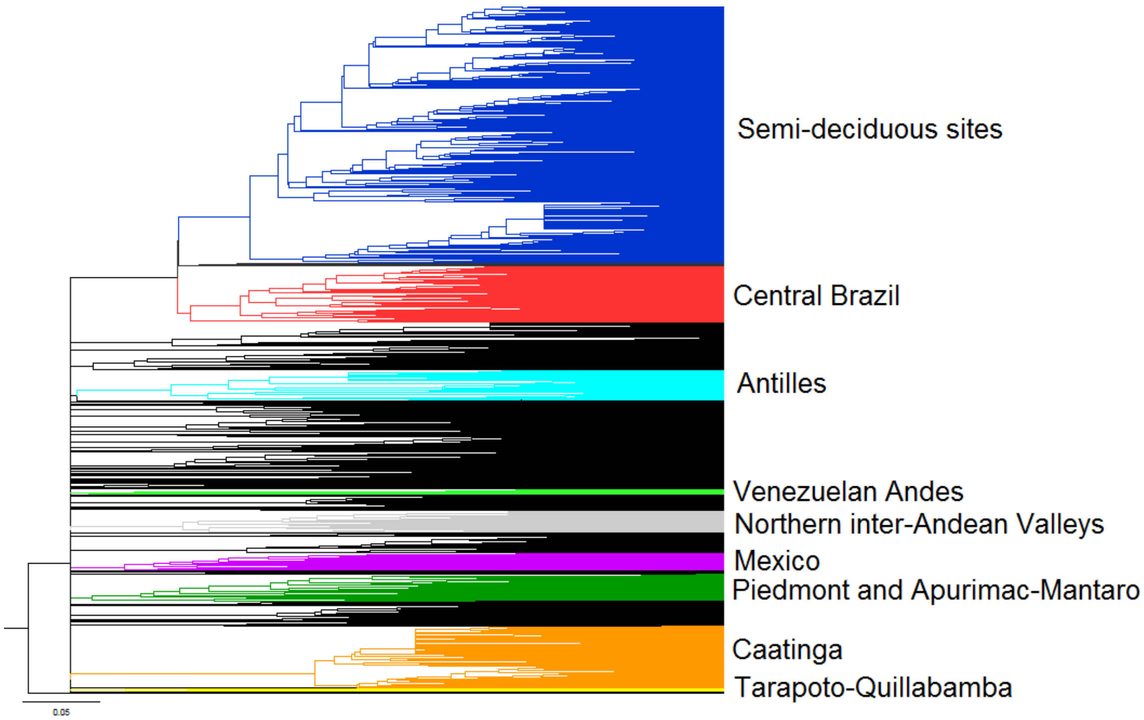


Fig. S1.

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.

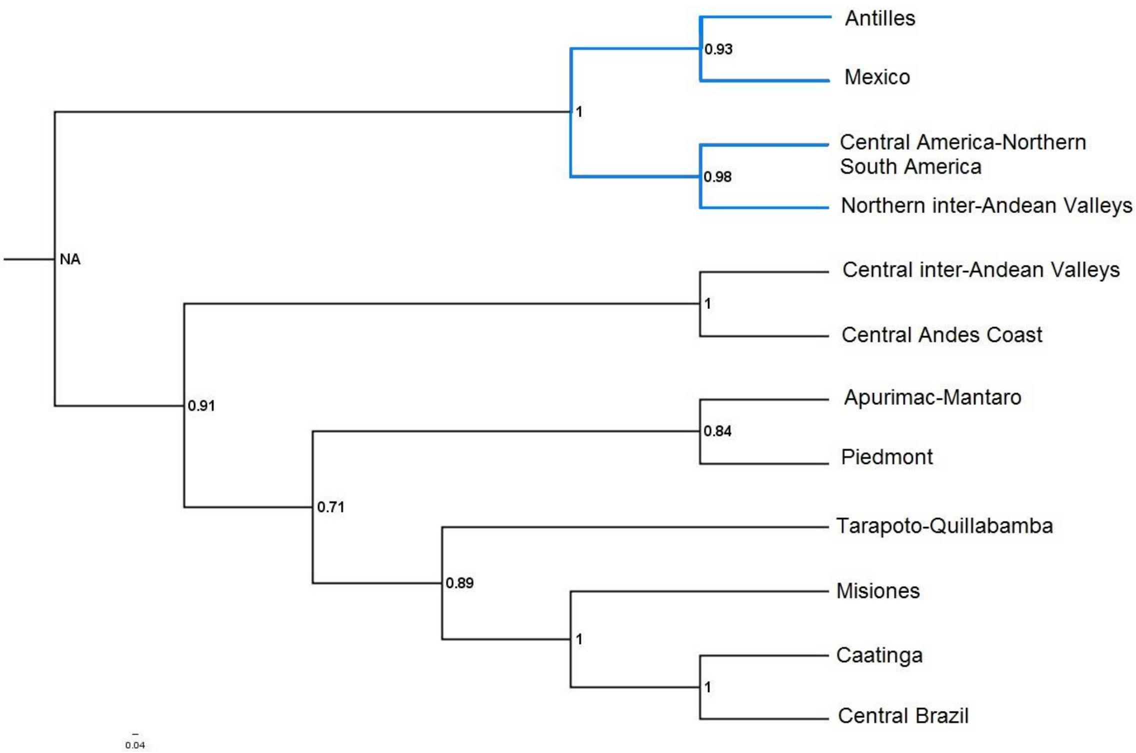


Fig. S2

Hierarchical classification of the12 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.

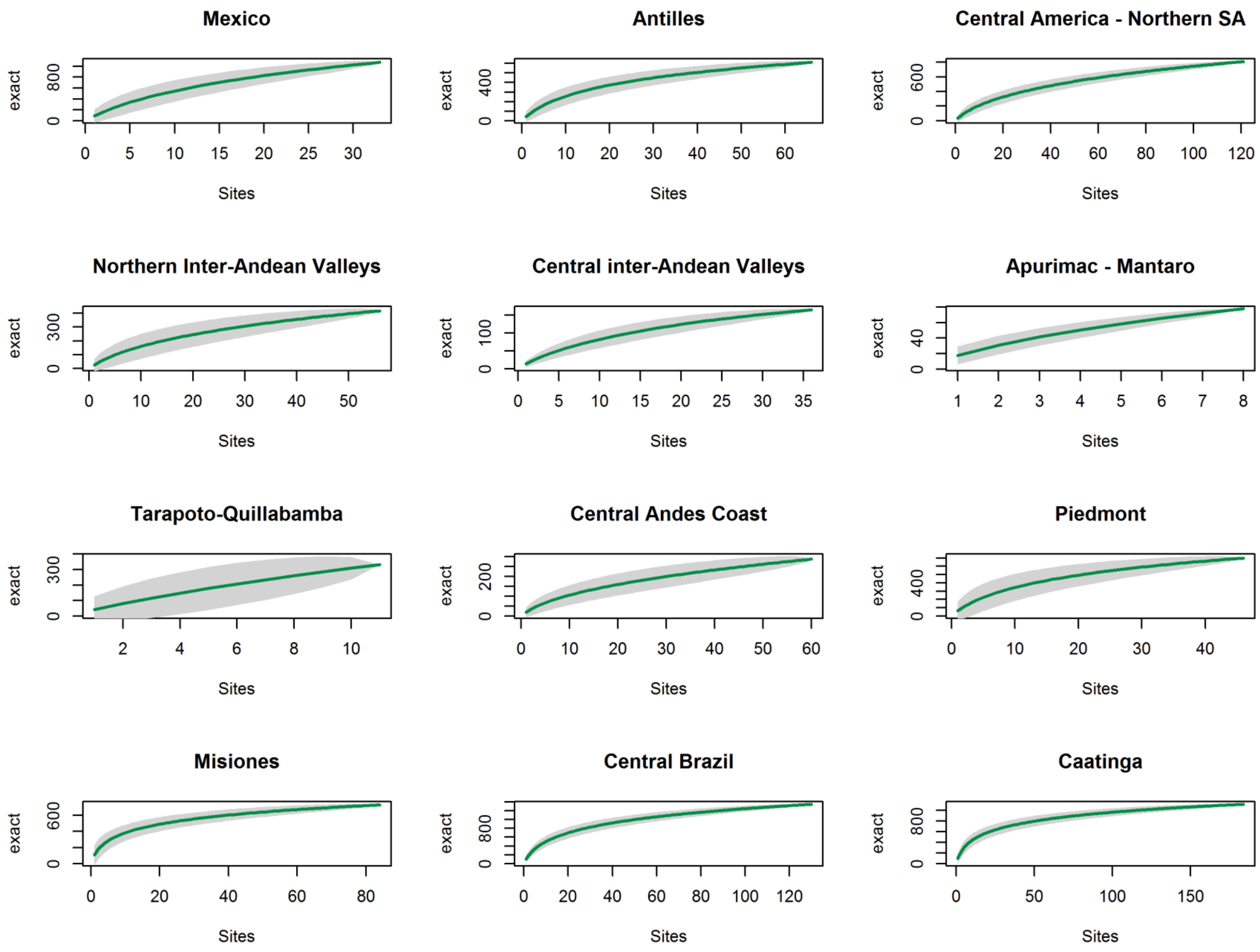


Fig. S3

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

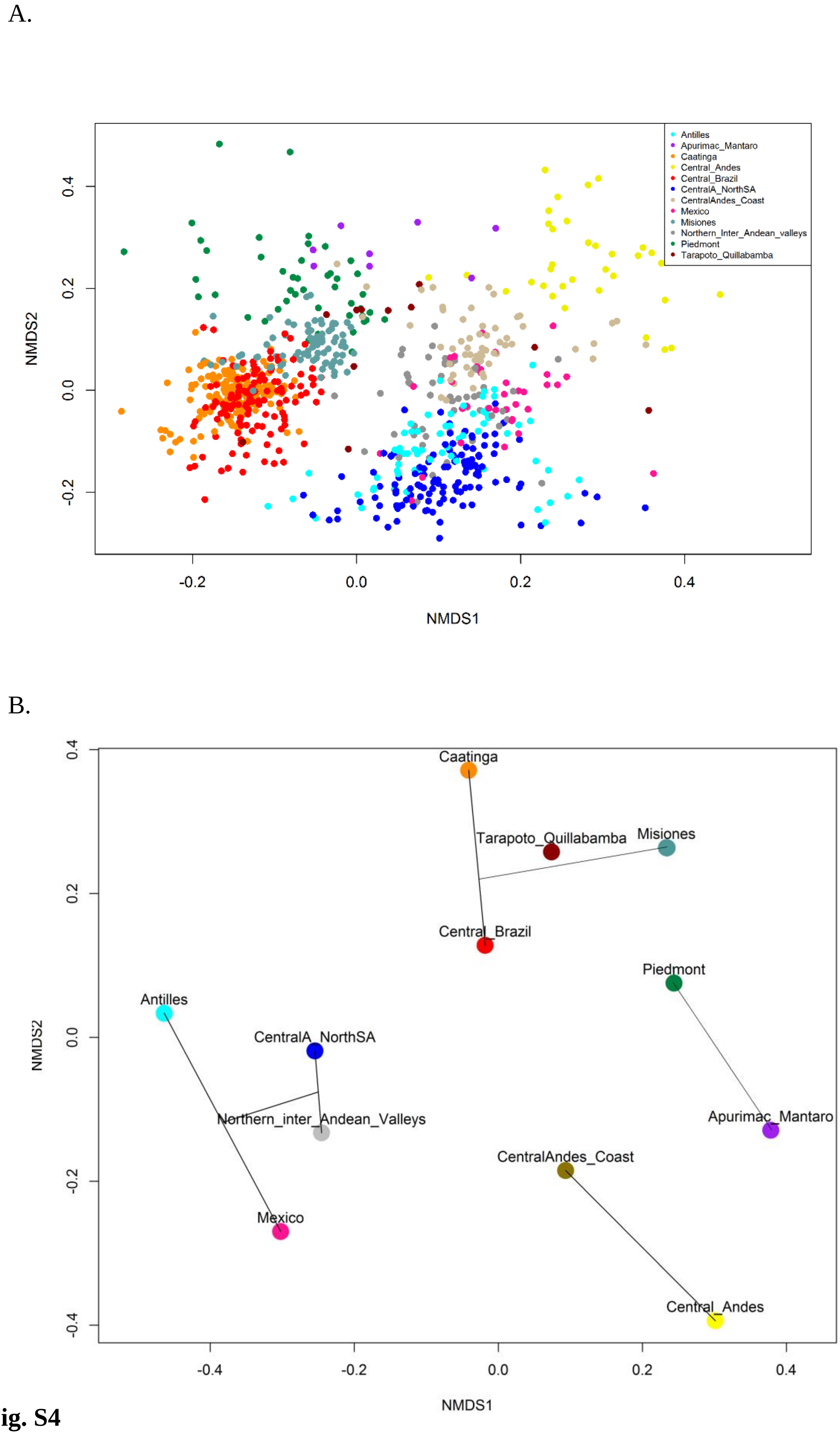


Fig. S4

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.

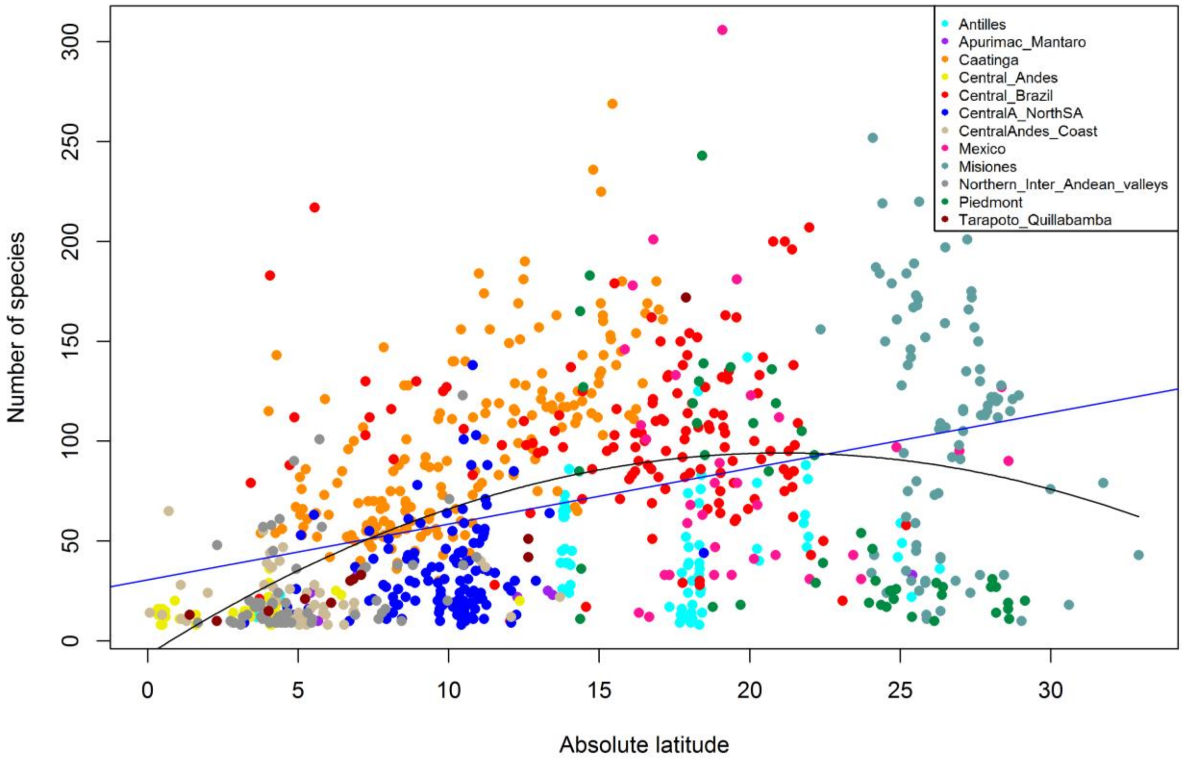


Fig. S5

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.

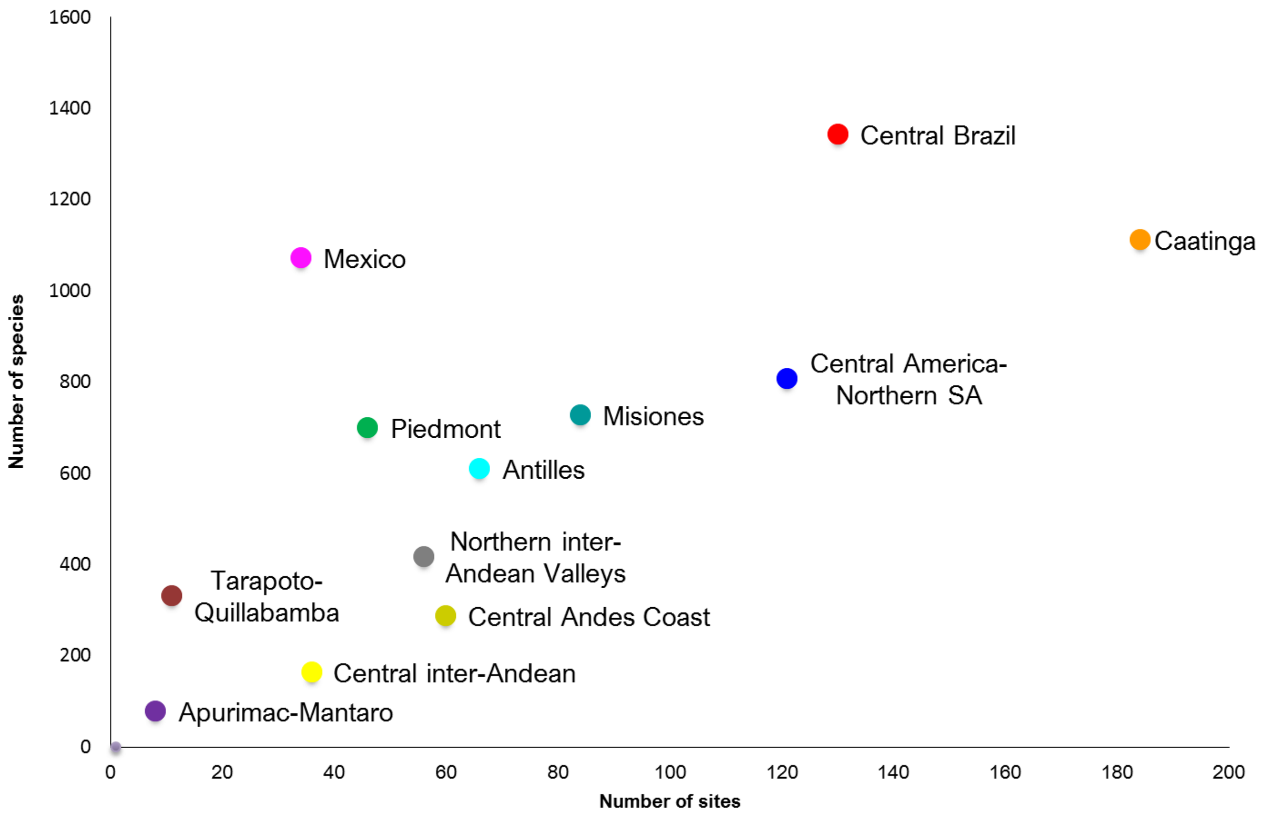


Fig. S6
Scatter plot of number of sites versus the total number of species per dry forest floristic group.

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
Cynophalla flexuosa	x	x	x	x		x	x	x	x	x	x	x
Sapindus saponaria		x	x	x	x	x	x	x	x	x	x	x
Trema micrantha	x	x	x	x		x	x	x	x	x	x	x
Celtis iguanaea	x		x	x		x	x	x	x	x	x	x
Cordia alliodora	x		x	x	x	x	x	x		x	x	x
Guazuma ulmifolia	x		x	x		x	x	x	x	x	x	x
Maclura tinctoria	x		x	x		x	x	x	x	x	x	x
Randia armata	x		x	x	x	x	x	x	x	x	x	
Tecoma stans	x	x	x		x	x	x	x	x	x	x	
Urera caracasana		x	x	x		x	x	x	x	x	x	x
Ximenia americana	x		x	x		x	x	x	x	x	x	x
Zanthoxylum fagara	x		x	x	x	x	x	x	x	x	x	
Cedrela odorata	x		x	x		x	x	x	x	x		x
Prockia crucis	x		x	x		x	x	x	x		x	x
Senegalia polyphylla			x	x		x	x	x	x	x	x	x
Trichilia hirta	x		x	x		x	x	x	x	x	x	
Vachellia macracantha	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)	*Bursera simaruba (54)*
	Rubiaceae (46)	Coccoloba (15)	*Bourreria succulenta (41)*
	Myrtaceae (33)	Ficus (13)	*Guapira fragrans (39)*
	Boraginaceae (27)	Cordia (11)	*Citharexylum spinosum (34)*
	Euphorbiaceae (21)	Guettarda (11)	*Eugenia monticola (33)*
	Arecaceae (18)	Erythroxylum (9)	*Randia aculeata (33)*
	Lauraceae (17)	Zanthoxylum (9)	*Cynophalla hastata (32)*
	Malvaceae (16)	Casearia (8)	*Amyris elemifera (31)*
	Moraceae (16)	Croton (8)	*Krugiodendron ferreum (29)*
	Sapotaceae (16)	Miconia (8)	*Gymnanthes lucida (27)*
	Bignoniaceae (15)	Tabebuia (8)	*Picramnia pentandra (26)*
	Polygonaceae (15)	Maytenus (7)	*Schaefferia frutescens (26)*
	Rhamnaceae (15)	Bourreria (6)	*Tabebuia heterophylla (25)*
	Rutaceae (15)	Caesalpinia (6)	*Cynophalla flexuosa (24)*
	Salicaceae (14)	Comocladia (6)	*Erythroxylum rotundifolium (24)*
	Apocynaceae (13)	Diospyros (6)	*Guettarda scabra (24)*
	Sapindaceae (13)	Guapira (6)	*Quadrella indica (24)*
	Melastomataceae (12)	Plumeria (6)	*Canella winterana (22)*
	Cactaceae (11)	Calyptranthes (5)	*Ficus citrifolia (22)*
	Celastraceae (11)	Clusia (5)	*Nectandra coriacea (22)*
	Malpighiaceae (11)	Coccothrinax (5)	*Sideroxylon foetidissimum (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)	*Dodonaea viscosa (6)*
	Euphorbiaceae (11)	Croton (3)	*Vachellia aroma (6)*
	Malvaceae (6)	Ipomoea (3)	*Aloysia scorodonioides (5)*
	Asteraceae (5)	Lantana (3)	*Anadenanthera colubrina (5)*
	Bignoniaceae (5)	Tecoma (3)	*Ipomoea pauciflora (5)*
	Solanaceae (4)	Baccharis (2)	*Aralia soratensis (4)*
	Cannabaceae (3)	Celtis (2)	*Eriotheca discolor (4)*
	Convolvulaceae (3)	Clusia (2)	*Lantana camara (4)*
	Urticaceae (3)	Eriotheca (2)	*Nicotiana glutinosa (4)*
	Verbenaceae (3)	Jatropha (2)	*Vasconcellea quercifolia (4)*
	Clusiaceae (2)	Manihot (2)	*Aeschynomene tumbezensis (3)*

	Sapindaceae (2)	Nicotiana (2)	*Furcraea andina (3)*
		Prosopis (2)	*Jatropha augusti (3)*
		Solanum (2)	*Leucaena trichodes (3)*
		Vachellia (2)	*Schinus molle (3)*
			Tecoma fulva (3)
			Trema micrantha (3)

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Caatinga (184)	Leguminosae (279)	Eugenia (33)	*Aspidosperma pyrifolium (149)*
	Myrtaceae (88)	Erythroxylum (24)	*Myracrodruon urundeuva (149)*
	Euphorbiaceae (46)	Senna (23)	*Cereus jamacaru (137)*
	Rubiaceae (44)	Ficus (21)	*Anadenanthera colubrina (136)*
	Malvaceae (38)	Myrcia (20)	*Handroanthus impetiginosus (135)*
	Rutaceae (35)	Mimosa (19)	*Jatropha mollissima (135)*
	Cactaceae (34)	Bauhinia (17)	*Cynophalla hastata (131)*
	Asteraceae (29)	Casearia (16)	*Schinopsis brasiliensis (131)*
	Erythroxylaceae (24)	Machaerium (16)	*Commiphora leptophloeos (129)*
	Moraceae (24)	Psidium (16)	*Mimosa tenuiflora (126)*
	Bignoniaceae (23)	Pilosocereus (15)	*Annona leptopetala (124)*
	Sapotaceae (23)	Senegalia (15)	*Senna spectabilis (124)*
	Apocynaceae (22)	Aspidosperma (13)	*Guapira laxa (123)*
	Salicaceae (21)	Cordia (13)	*Ziziphus joazeiro (117)*
	Annonaceae (19)	Ocotea (13)	*Bauhinia cheilantha (113)*
	Malpighiaceae (18)	Byrsonima (12)	*Maytenus rigida (112)*
	Lauraceae (17)	Pouteria (12)	*Spondias tuberosa (109)*
	Vochysiaceae (17)	Zanthoxylum (12)	*Senna macranthera (103)*
	Arecaceae (16)	Chamaecrista (11)	*Cordia trichotoma (102)*
	Sapindaceae (16)	Maytenus (11)	*Croton blanchetianus (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)	*Vachellia macracantha (28)*
	Euphorbiaceae (17)	Ficus (6)	*Lantana rugulosa (17)*
	Asteraceae (14)	Cestrum (4)	*Opuntia soederstromiana (16)*
	Malvaceae (13)	Lantana (4)	*Dodonaea viscosa (15)*
	Solanaceae (12)	Opuntia (4)	*Baccharis latifolia (14)*
	Cactaceae (9)	Acalypha (3)	*Tara spinosa (14)*
	Moraceae (8)	Baccharis (3)	*Lycianthes lycioides (13)*
	Boraginaceae (7)	Byttneria (3)	*Tecoma stans (12)*
	Sapindaceae (5)	Ceiba (3)	*Schinus molle (10)*
	Verbenaceae (5)	Cordia (3)	*Cyathostegia mathewsii (9)*
	Anacardiaceae (4)	Duranta (3)	*Lantana camara (8)*
	Bignoniaceae (4)	Myrcianthes (3)	*Abutilon ibarrense (7)*
	Lauraceae (4)	Solanum (3)	*Mimosa albida (7)*
	Myrtaceae (4)	Tecoma (3)	*Mimosa quitensis (7)*
	Capparaceae (3)	Tournefortia (3)	*Schinus areira (7)*

	Meliaceae (3)		*Tournefortia fuliginosa (7)*
	Berberidaceae (2)		*Varronia macrocephala (7)*
	Malpighiaceae (2)		*Zanthoxylum fagara (7)*
	Piperaceae (2)		*Acalypha padifolia (6)*
	Rubiaceae (2)		*Berberis pichinchensis (6)*
	Rutaceae (2)		*Croton abutiloides (6)*
	Urticaceae (2)		Croton menthodorus (6)

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Central America-northern South America (121)	Leguminosae (171)	Casearia (18)	*Guazuma ulmifolia (87)*
	Rubiaceae (50)	Cordia (16)	*Astronium graveolens (77)*
	Euphorbiaceae (38)	Lonchocarpus (16)	*Spondias mombin (71)*
	Salicaceae (29)	Coccoloba (14)	*Bursera simaruba (68)*
	Malvaceae (26)	Croton (13)	*Hura crepitans (47)*
	Annonaceae (24)	Ficus (12)	*Cochlospermum vitifolium (46)*
	Boraginaceae (23)	Machaerium (11)	*Platymiscium pinnatum (46)*
	Moraceae (22)	Annona (10)	*Cecropia peltata (41)*
	Polygonaceae (22)	Inga (10)	*Quadrella odoratissima (40)*
	Capparaceae (21)	Erythroxylum (9)	*Ceiba pentandra (39)*
	Arecaceae (18)	Eugenia (8)	*Sterculia apetala (38)*
	Bignoniaceae (17)	Randia (8)	*Samanea saman (36)*
	Myrtaceae (17)	Trichilia (8)	*Maclura tinctoria (35)*
	Rutaceae (17)	Zanthoxylum (8)	*Albizia niopoides (34)*
	Apocynaceae (16)	Guapira (7)	*Pseudobombax septenatum (34)*
	Sapindaceae (16)	Bauhinia (6)	*Enterolobium cyclocarpum (32)*
	Meliaceae (15)	Bunchosia (6)	*Libidibia coriaria (32)*
	Nyctaginaceae (14)	Cynophalla (6)	*Prosopis juliflora (32)*
	Cactaceae (13)	Erythrina (6)	*Handroanthus billbergii (31)*
	Primulaceae (13)	Handroanthus (6)	*Pithecellobium dulce (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)	*Bursera graveolens (39)*
	Cactaceae (24)	Cordia (8)	*Colicodendron scabridum (36)*
	Malvaceae (18)	Opuntia (7)	*Cordia lutea (34)*
	Euphorbiaceae (15)	Croton (6)	*Loxopterygium huasango (32)*
	Moraceae (13)	Senna (6)	*Vachellia macracantha (32)*
	Rubiaceae (11)	Mimosa (5)	*Eriotheca ruizii (29)*
	Boraginaceae (9)	Psidium (5)	*Libidibia glabrata (29)*
	Bignoniaceae (8)	Trichilia (5)	*Pithecellobium excelsum (28)*
	Capparaceae (8)	Vachellia (5)	*Ceiba trischistandra (25)*
	Meliaceae (8)	Armatocereus (4)	*Cynophalla flexuosa (25)*
	Solanaceae (8)	Browningia (4)	*Cochlospermum vitifolium (24)*
	Myrtaceae (6)	Ceiba (4)	*Geoffroea spinosa (22)*
	Polygonaceae (6)	Inga (4)	*Guazuma ulmifolia (22)*

	Sapindaceae (5)	Annona (3)	*Prosopis pallida (20)*
	Anacardiaceae (4)	Celtis (3)	*Coccoloba ruiziana (18)*
	Apocynaceae (4)	Coccoloba (3)	*Leucaena trichodes (17)*
	Asteraceae (4)	Cynophalla (3)	*Albizia multiflora (15)*
	Cannabaceae (4)	Eriotheca (3)	*Piscidia carthagenensis (15)*
	Nyctaginaceae (4)	Erythrina (3)	*Beautempsia avicenniifolia (14)*
	Verbenaceae (4)	Simira (3)	*Bougainvillea spectabilis (14)*
		Tecoma (3)	*Erythrina smithiana (14)*
		Zanthoxylum (3)	

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Central Brazil (130)	Leguminosae (298)	Eugenia (33)	*Guazuma ulmifolia (112)*
	Myrtaceae (78)	Erythroxylum (21)	*Anadenanthera colubrina (109)*
	Rubiaceae (66)	Ficus (21)	*Handroanthus impetiginosus (109)*
	Malvaceae (50)	Bauhinia (20)	*Myracrodruon urundeuva (102)*
	Euphorbiaceae (49)	Aspidosperma (18)	*Astronium fraxinifolium (101)*
	Rutaceae (35)	Senna (18)	*Maclura tinctoria (92)*
	Annonaceae (33)	Cordia (16)	*Tabebuia roseoalba (90)*
	Lauraceae (31)	Inga (15)	*Dilodendron bipinnatum (88)*
	Moraceae (30)	Myrcia (15)	*Enterolobium contortisiliquum (87)*
	Salicaceae (28)	Trichilia (15)	*Sterculia striata (87)*
	Solanaceae (28)	Byrsonima (14)	*Acrocomia aculeata (82)*
	Apocynaceae (27)	Casearia (14)	*Aspidosperma subincanum (81)*
	Sapindaceae (26)	Machaerium (14)	*Senegalia polyphylla (81)*
	Arecaceae (24)	Mimosa (14)	*Aspidosperma cuspa (77)*
	Meliaceae (24)	Ocotea (14)	*Albizia niopoides (75)*
	Malpighiaceae (23)	Psidium (14)	*Terminalia argentea (74)*
	Cactaceae (22)	Annona (13)	*Cecropia pachystachya (71)*
	Bignoniaceae (21)	Miconia (13)	*Cordia glabrata (71)*
	Erythroxylaceae (21)	Senegalia (13)	*Talisia esculenta (70)*
	Chrysobalanaceae (20)	Solanum (13)	*Cordia trichotoma (69)*
	Combretaceae (20)		

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Mexico (33)	Leguminosae (297)	Bursera (54)	*Vachellia farnesiana (21)*
	Euphorbiaceae (69)	Lonchocarpus (32)	*Plumeria rubra (20)*
	Burseraceae (56)	Croton (25)	*Pithecellobium dulce (19)*
	Malvaceae (49)	Ficus (21)	*Senna atomaria (19)*
	Rubiaceae (40)	Mimosa (19)	*Tecoma stans (18)*
	Apocynaceae (32)	Caesalpinia (16)	*Vachellia campechiana (18)*
	Boraginaceae (31)	Quercus (16)	*Vachellia pennatula (18)*
	Moraceae (27)	Pithecellobium (15)	*Bauhinia divaricata (17)*
	Rutaceae (24)	Senna (15)	*Haematoxylum brasiletto (16)*
	Malpighiaceae (22)	Diospyros (13)	*Lysiloma divaricatum (16)*
	Salicaceae (19)	Calliandra (12)	*Spondias purpurea (16)*

	Sapotaceae (18)	Vachellia (12)	*Bursera fagaroides (15)*
	Asteraceae (16)	Bauhinia (11)	*Ceiba aesculifolia (15)*
	Celastraceae (16)	Eugenia (11)	*Comocladia engleriana (15)*
	Fagaceae (16)	Randia (11)	*Ficus cotinifolia (15)*
	Myrtaceae (16)	Sideroxylon (11)	*Guazuma ulmifolia (15)*
	Sapindaceae (16)	Diphysa (10)	*Caesalpinia pulcherrima (15)*
	Anacardiaceae (15)		*Apoplanesia paniculata (14)*
	Capparaceae (14)		*Amphipterygium adstringens (14)*
	Polygonaceae (14)		*Bursera grandifolia (14)*
			Lysiloma acapulcense (14)

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Misiones (84)	Leguminosae (110)	Eugenia (28)	*Cordia americana (75)*
	Myrtaceae (72)	Solanum (18)	*Chrysophyllum gonocarpum (67)*
	Solanaceae (40)	Ocotea (17)	*Ruprechtia laxiflora (65)*
	Rubiaceae (35)	Miconia (11)	*Chrysophyllum marginatum (64)*
	Lauraceae (33)	Ficus (10)	*Allophylus edulis (63)*
	Euphorbiaceae (27)	Myrcia (10)	*Eugenia uniflora (63)*
	Asteraceae (22)	Nectandra (10)	*Holocalyx balansae (63)*
	Bignoniaceae (18)	Cestrum (9)	*Syagrus romanzoffiana (63)*
	Melastomataceae (16)	Erythroxylum (9)	*Luehea divaricata (62)*
	Moraceae (16)	Annona (8)	*Cedrela fissilis (61)*
	Rutaceae (16)	Handroanthus (8)	*Peltophorum dubium (61)*
	Salicaceae (16)	Inga (8)	*Cupania vernalis (60)*
	Meliaceae (15)	Myrsine (8)	*Diatenopteryx sorbifolia (60)*
	Sapindaceae (15)	Piper (8)	*Pilocarpus pennatifolius (60)*
	Anacardiaceae (14)	Trichilia (8)	*Cabralea canjerana (59)*
	Malvaceae (13)	Casearia (7)	*Parapiptadenia rigida (59)*
	Annonaceae (12)	Ilex (7)	*Sorocea bonplandii (59)*
	Arecaceae (12)	Maytenus (7)	*Casearia sylvestris (58)*
	Apocynaceae (10)	Senegalia (7)	*Trichilia catigua (57)*
	Celastraceae (10)	Senna (7)	*Cordia trichotoma (56)*
		Zanthoxylum (7)	*Sebastiania brasiliensis* (56)

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Northern inter-Andean Valleys (56)	Leguminosae (77)	Ficus (10)	*Guazuma ulmifolia (39)*
	Rubiaceae (25)	Zanthoxylum (9)	*Ochroma pyramidale (26)*
	Euphorbiaceae (22)	Piper (8)	*Senna spectabilis (25)*
	Moraceae (18)	Croton (7)	*Pithecellobium dulce (24)*
	Lauraceae (14)	Erythroxylum (7)	*Zanthoxylum fagara (24)*
	Myrtaceae (14)	Eugenia (7)	*Anacardium excelsum (22)*
	Malvaceae (13)	Inga (7)	*Erythrina poeppigiana (22)*
	Arecaceae (12)	Miconia (7)	*Pseudosamanea guachapele (22)*
	Rutaceae (10)	Coccoloba (6)	*Ficus insipida (18)*
	Salicaceae (10)	Machaerium (6)	*Cupania americana (17)*
	Urticaceae (10)	Senna (6)	*Psidium guineense (17)*

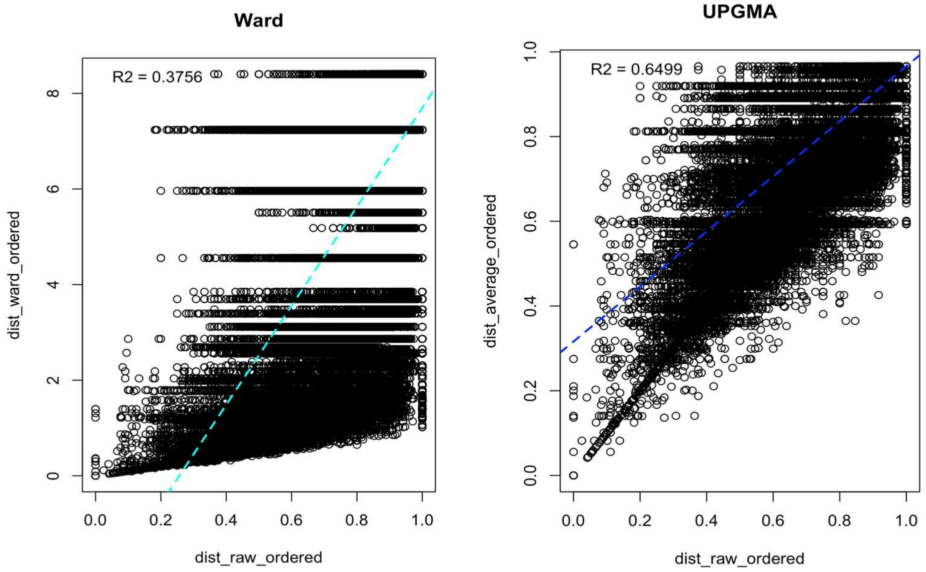
	Bignoniaceae (9)	Casearia (5)	*Croton gossypiifolius (16)*
	Melastomataceae (9)	Clusia (5)	*Zanthoxylum rhoifolium (16)*
	Meliaceae (9)	Cordia (5)	*Brosimum alicastrum (15)*
	Annonaceae (8)	Acalypha (4)	*Sapindus saponaria (15)*
	Boraginaceae (8)	Bactris (4)	*Achatocarpus nigricans (14)*
	Piperaceae (8)	Bauhinia (4)	*Attalea butyracea (14)*
	Polygonaceae (8)	Brownea (4)	*Ocotea veraguensis (14)*
	Anacardiaceae (7)	Calliandra (4)	*Astronium graveolens (13)*
	Capparaceae (7)	Cecropia (4)	*Cecropia peltata (13)*
	Clusiaceae (7)	Lonchocarpus (4)	*Ceiba pentandra (13)*
	Erythroxylaceae (7)	Nectandra (4)	*Euphorbia cotinifolia (13)*
	Primulaceae (7)	Ocotea (4)	*Machaerium capote (13)*
	Sapindaceae (7)	Solanum (4)	*Muntingia calabura (13)*
		Trichilia (4)	
		Vachellia (4)	

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Piedmont (46)	Leguminosae (157)	Inga (20)	*Anadenanthera colubrina (39)*
	Euphorbiaceae (33)	Senegalia (11)	*Achatocarpus praecox (29)*
	Asteraceae (32)	Senna (11)	*Myracrodruon urundeuva (27)*
	Cactaceae (32)	Eugenia (10)	*Pisonia zapallo (23)*
	Myrtaceae (28)	Prosopis (10)	*Vachellia aroma (23)*
	Bignoniaceae (22)	Machaerium (9)	*Parapiptadenia excelsa (22)*
	Anacardiaceae (21)	Solanum (9)	*Enterolobium contortisiliquum (21)*
	Malvaceae (21)	Aspidosperma (8)	*Tipuana tipu (21)*
	Solanaceae (20)	Celtis (8)	*Allophylus edulis (20)*
	Rubiaceae (18)	Maytenus (8)	*Libidibia paraguariensis (20)*
	Apocynaceae (16)	Schinus (8)	*Ruprechtia apetala (20)*
	Sapindaceae (16)	Cereus (7)	*Celtis iguanaea (19)*
	Rutaceae (14)	Croton (7)	*Senegalia praecox (19)*
	Capparaceae (13)	Ficus (7)	*Handroanthus impetiginosus (18)*
	Moraceae (13)	Coccoloba (6)	*Pterogyne nitens (18)*
	Nyctaginaceae (13)	Cordia (6)	*Tecoma stans (18)*
	Polygonaceae (13)	Erythroxylum (6)	*Vachellia caven (18)*
	Salicaceae (13)	Luehea (6)	*Amburana cearensis (17)*
	Celastraceae (11)	Zanthoxylum (6)	*Cynophalla retusa (17)*
	Meliaceae (10)	Baccharis (5)	*Phyllostylon rhamnoides (17)*
		Bauhinia (5)	*Ruprechtia laxiflora (17)*
		Bougainvillea (5)	*Senna spectabilis (17)*
		Erythrina (5)	*Trichilia claussenii (17)*
		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)	*Trichilia elegans (7)*
	Moraceae (18)	Inga (7)	*Brosimum alicastrum (6)*
	Rubiaceae (15)	Neea (7)	*Triplaris cumingiana (6)*
	Euphorbiaceae (13)	Trichilia (7)	*Erythroxylum ulei (5)*
	Meliaceae (12)	Coccoloba (6)	*Inga umbellifera (5)*
	Malvaceae (11)	Allophylus (5)	*Morisonia oblongifolia (5)*
	Lauraceae (10)	Eugenia (5)	*Zanthoxylum rhoifolium (5)*
	Sapindaceae (10)	Ocotea (5)	*Ceiba insignis (4)*
	Nyctaginaceae (9)	Capparidastrum (4)	*Celtis iguanaea (4)*
	Polygonaceae (9)	Casearia (4)	*Coccoloba padiformis (4)*
	Sapotaceae (9)	Chrysophyllum (4)	*Handroanthus serratifolius (4)*
	Apocynaceae (8)	Cordia (4)	*Anadenanthera colubrina (3)*
	Arecaceae (8)	Erythroxylum (4)	*Aspidosperma rigidum (3)*
	Capparaceae (8)	Ficus (4)	*Brosimum guianense (3)*
	Annonaceae (7)	Machaerium (4)	*Cedrela fissilis (3)*
	Bignoniaceae (7)	Nectandra (4)	*Ceiba boliviana (3)*
	Myrtaceae (7)	Piper (4)	*Chrysophyllum venezuelanense (3)*
	Urticaceae (7)	Terminalia (4)	*Clarisia biflora (3)*
	Boraginaceae (6)	Urera (4)	*Cordia alliodora (3)*
	Cactaceae (6)		*Coussapoa villosa (3)*
	Salicaceae (6)		*Croton abutiloides (3)*
			Drypetes amazonica (3)
			Manilkara bidentata (3)
			Neea hermaphrodita (3)
			Phytelephas aequatorialis (3)
			Platymiscium stipulare (3)
			Preslianthus 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)

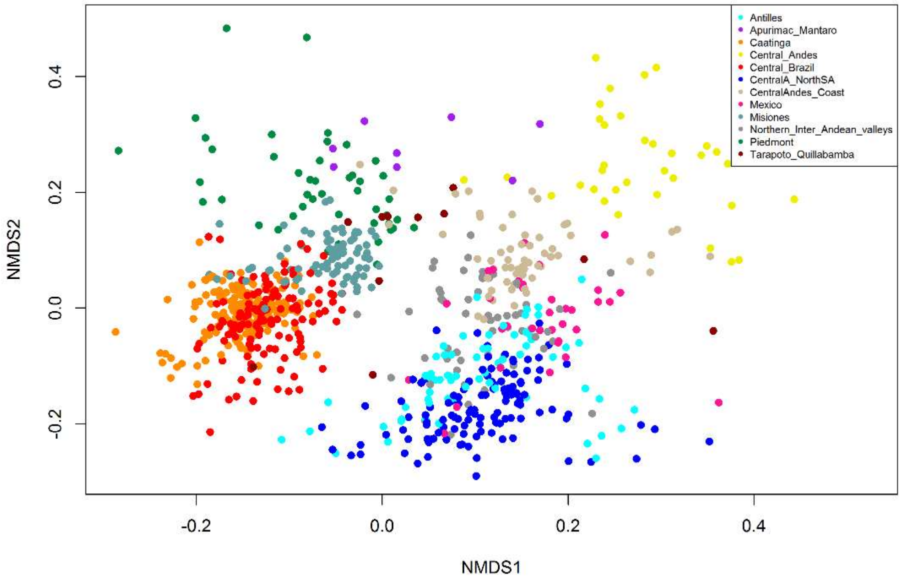
Appendix 2

Figure. Cophenetic correlation plots to evaluate the performance of clustering methods.



Appendix 3.

Figure. NMDS ordination plot of the 835 dry forest sites colouring by floristic group (1000 iterations, 2 dimensions, stress=0.124)



Appendix 4.

Table 1. Matrix of shared species among the 12 neotropical dry forest groups.

	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 2. Species recorded in more than nine dry forest 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
Cynophalla flexuosa	x	x	x	x		x	x	x	x	x	x	x
Sapindus saponaria		x	x	x	x	x	x	x	x	x	x	x
Trema micrantha	x	x	x	x		x	x	x	x	x	x	x
Celtis iguanaea	x		x	x		x	x	x	x	x	x	x
Cordia alliodora	x		x	x	x	x	x	x		x	x	x
Guazuma ulmifolia	x		x	x		x	x	x	x	x	x	x
Maclura tinctoria	x		x	x		x	x	x	x	x	x	x
Randia armata	x		x	x	x	x	x	x	x	x	x	
Tecoma stans	x	x	x		x	x	x	x	x	x	x	
Urera caracasana		x	x	x		x	x	x	x	x	x	x
Ximenia americana	x		x	x		x	x	x	x	x	x	x
Zanthoxylum fagara	x		x	x	x	x	x	x	x	x	x	
Cedrela odorata	x		x	x		x	x	x	x	x		x
Prockia crucis	x		x	x		x	x	x	x		x	x
Senegalia polyphylla			x	x		x	x	x	x	x	x	x
Trichilia hirta	x		x	x		x	x	x	x	x	x	
Vachellia macracantha	x	x	x		x	x		x	x	x	x	

Appendix 5.

Table. 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)	*Bursera simaruba (54)*
	Rubiaceae (46)	Coccoloba (15)	*Bourreria succulenta (41)*
	Myrtaceae (33)	Ficus (13)	*Guapira fragrans (39)*
	Boraginaceae (27)	Cordia (11)	*Citharexylum spinosum (34)*
	Euphorbiaceae (21)	Guettarda (11)	*Eugenia monticola (33)*
	Arecaceae (18)	Erythroxylum (9)	*Randia aculeata (33)*
	Lauraceae (17)	Zanthoxylum (9)	*Cynophalla hastata (32)*
	Malvaceae (16)	Casearia (8)	*Amyris elemifera (31)*
	Moraceae (16)	Croton (8)	*Krugiodendron ferreum (29)*
	Sapotaceae (16)	Miconia (8)	*Gymnanthes lucida (27)*
	Bignoniaceae (15)	Tabebuia (8)	*Picramnia pentandra (26)*
	Polygonaceae (15)	Maytenus (7)	*Schaefferia frutescens (26)*
	Rhamnaceae (15)	Bourreria (6)	*Tabebuia heterophylla (25)*
	Rutaceae (15)	Caesalpinia (6)	*Cynophalla flexuosa (24)*
	Salicaceae (14)	Comocladia (6)	*Erythroxylum rotundifolium (24)*
	Apocynaceae (13)	Diospyros (6)	*Guettarda scabra (24)*
	Sapindaceae (13)	Guapira (6)	*Quadrella indica (24)*
	Melastomataceae (12)	Plumeria (6)	*Canella winterana (22)*
	Cactaceae (11)	Calyptranthes (5)	*Ficus citrifolia (22)*
	Celastraceae (11)	Clusia (5)	*Nectandra coriacea (22)*
	Malpighiaceae (11)	Coccothrinax (5)	*Sideroxylon foetidissimum (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)	*Dodonaea viscosa (6)*
	Euphorbiaceae (11)	Croton (3)	*Vachellia aroma (6)*
	Malvaceae (6)	Ipomoea (3)	*Aloysia scorodonioides (5)*
	Asteraceae (5)	Lantana (3)	*Anadenanthera colubrina (5)*
	Bignoniaceae (5)	Tecoma (3)	*Ipomoea pauciflora (5)*
	Solanaceae (4)	Baccharis (2)	*Aralia soratensis (4)*
	Cannabaceae (3)	Celtis (2)	*Eriotheca discolor (4)*
	Convolvulaceae (3)	Clusia (2)	*Lantana camara (4)*
	Urticaceae (3)	Eriotheca (2)	*Nicotiana glutinosa (4)*
	Verbenaceae (3)	Jatropha (2)	*Vasconcellea quercifolia (4)*
	Clusiaceae (2)	Manihot (2)	*Aeschynomene tumbezensis (3)*
	Sapindaceae (2)	Nicotiana (2)	*Furcraea andina (3)*
		Prosopis (2)	*Jatropha augusti (3)*
		Solanum (2)	*Leucaena trichodes (3)*
		Vachellia (2)	*Schinus molle (3)*
			Tecoma fulva (3)
			Trema micrantha (3)

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Caatinga (184)	Leguminosae (279)	Eugenia (33)	*Aspidosperma pyrifolium (149)*
	Myrtaceae (88)	Erythroxylum (24)	*Myracrodruon urundeuva (149)*
	Euphorbiaceae (46)	Senna (23)	*Cereus jamacaru (137)*
	Rubiaceae (44)	Ficus (21)	*Anadenanthera colubrina (136)*

	Malvaceae (38)	Myrcia (20)	*Handroanthus impetiginosus (135)*
	Rutaceae (35)	Mimosa (19)	*Jatropha mollissima (135)*
	Cactaceae (34)	Bauhinia (17)	*Cynophalla hastata (131)*
	Asteraceae (29)	Casearia (16)	*Schinopsis brasiliensis (131)*
	Erythroxylaceae (24)	Machaerium (16)	*Commiphora leptophloeos (129)*
	Moraceae (24)	Psidium (16)	*Mimosa tenuiflora (126)*
	Bignoniaceae (23)	Pilosocereus (15)	*Annona leptopetala (124)*
	Sapotaceae (23)	Senegalia (15)	*Senna spectabilis (124)*
	Apocynaceae (22)	Aspidosperma (13)	*Guapira laxa (123)*
	Salicaceae (21)	Cordia (13)	*Ziziphus joazeiro (117)*
	Annonaceae (19)	Ocotea (13)	*Bauhinia cheilantha (113)*
	Malpighiaceae (18)	Byrsonima (12)	*Maytenus rigida (112)*
	Lauraceae (17)	Pouteria (12)	*Spondias tuberosa (109)*
	Vochysiaceae (17)	Zanthoxylum (12)	*Senna macranthera (103)*
	Arecaceae (16)	Chamaecrista (11)	*Cordia trichotoma (102)*
	Sapindaceae (16)	Maytenus (11)	*Croton blanchetianus (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)	*Vachellia macracantha (28)*
	Euphorbiaceae (17)	Ficus (6)	*Lantana rugulosa (17)*
	Asteraceae (14)	Cestrum (4)	*Opuntia soederstromiana (16)*
	Malvaceae (13)	Lantana (4)	*Dodonaea viscosa (15)*
	Solanaceae (12)	Opuntia (4)	*Baccharis latifolia (14)*
	Cactaceae (9)	Acalypha (3)	*Tara spinosa (14)*
	Moraceae (8)	Baccharis (3)	*Lycianthes lycioides (13)*
	Boraginaceae (7)	Byttneria (3)	*Tecoma stans (12)*
	Sapindaceae (5)	Ceiba (3)	*Schinus molle (10)*
	Verbenaceae (5)	Cordia (3)	*Cyathostegia mathewsii (9)*

	Anacardiaceae (4)	Duranta (3)	*Lantana camara (8)*
	Bignoniaceae (4)	Myrcianthes (3)	*Abutilon ibarrense (7)*
	Lauraceae (4)	Solanum (3)	*Mimosa albida (7)*
	Myrtaceae (4)	Tecoma (3)	*Mimosa quitensis (7)*
	Capparaceae (3)	Tournefortia (3)	*Schinus areira (7)*
	Meliaceae (3)		*Tournefortia fuliginosa (7)*
	Berberidaceae (2)		*Varronia macrocephala (7)*
	Malpighiaceae (2)		*Zanthoxylum fagara (7)*
	Piperaceae (2)		*Acalypha padifolia (6)*
	Rubiaceae (2)		*Berberis pichinchensis (6)*
	Rutaceae (2)		*Croton abutiloides (6)*
	Urticaceae (2)		Croton menthodorus (6)

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Central America-northern South America (121)	Leguminosae (171)	Casearia (18)	*Guazuma ulmifolia (87)*
	Rubiaceae (50)	Cordia (16)	*Astronium graveolens (77)*
	Euphorbiaceae (38)	Lonchocarpus (16)	*Spondias mombin (71)*
	Salicaceae (29)	Coccoloba (14)	*Bursera simaruba (68)*
	Malvaceae (26)	Croton (13)	*Hura crepitans (47)*
	Annonaceae (24)	Ficus (12)	*Cochlospermum vitifolium (46)*
	Boraginaceae (23)	Machaerium (11)	*Platymiscium pinnatum (46)*
	Moraceae (22)	Annona (10)	*Cecropia peltata (41)*
	Polygonaceae (22)	Inga (10)	*Quadrella odoratissima (40)*
	Capparaceae (21)	Erythroxylum (9)	*Ceiba pentandra (39)*
	Arecaceae (18)	Eugenia (8)	*Sterculia apetala (38)*
	Bignoniaceae (17)	Randia (8)	*Samanea saman (36)*
	Myrtaceae (17)	Trichilia (8)	*Maclura tinctoria (35)*
	Rutaceae (17)	Zanthoxylum (8)	*Albizia niopoides (34)*
	Apocynaceae (16)	Guapira (7)	*Pseudobombax septenatum (34)*

	Sapindaceae (16)	Bauhinia (6)	*Enterolobium cyclocarpum (32)*
	Meliaceae (15)	Bunchosia (6)	*Libidibia coriaria (32)*
	Nyctaginaceae (14)	Cynophalla (6)	*Prosopis juliflora (32)*
	Cactaceae (13)	Erythrina (6)	*Handroanthus billbergii (31)*
	Primulaceae (13)	Handroanthus (6)	*Pithecellobium dulce (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)	*Bursera graveolens (39)*
	Cactaceae (24)	Cordia (8)	*Colicodendron scabridum (36)*
	Malvaceae (18)	Opuntia (7)	*Cordia lutea (34)*
	Euphorbiaceae (15)	Croton (6)	*Loxopterygium huasango (32)*
	Moraceae (13)	Senna (6)	*Vachellia macracantha (32)*
	Rubiaceae (11)	Mimosa (5)	*Eriotheca ruizii (29)*
	Boraginaceae (9)	Psidium (5)	*Libidibia glabrata (29)*
	Bignoniaceae (8)	Trichilia (5)	*Pithecellobium excelsum (28)*
	Capparaceae (8)	Vachellia (5)	*Ceiba trischistandra (25)*
	Meliaceae (8)	Armatocereus (4)	*Cynophalla flexuosa (25)*
	Solanaceae (8)	Browningia (4)	*Cochlospermum vitifolium (24)*
	Myrtaceae (6)	Ceiba (4)	*Geoffroea spinosa (22)*
	Polygonaceae (6)	Inga (4)	*Guazuma ulmifolia (22)*
	Sapindaceae (5)	Annona (3)	*Prosopis pallida (20)*
	Anacardiaceae (4)	Celtis (3)	*Coccoloba ruiziana (18)*
	Apocynaceae (4)	Coccoloba (3)	*Leucaena trichodes (17)*
	Asteraceae (4)	Cynophalla (3)	*Albizia multiflora (15)*
	Cannabaceae (4)	Eriotheca (3)	*Piscidia carthagenensis (15)*
	Nyctaginaceae (4)	Erythrina (3)	*Beautempsia avicenniifolia (14)*

	Verbenaceae (4)	Simira (3)	*Bougainvillea spectabilis (14)*
		Tecoma (3)	*Erythrina smithiana (14)*
		Zanthoxylum (3)	

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Central Brazil (130)	Leguminosae (298)	Eugenia (33)	*Guazuma ulmifolia (112)*
	Myrtaceae (78)	Erythroxylum (21)	*Anadenanthera colubrina (109)*
	Rubiaceae (66)	Ficus (21)	*Handroanthus impetiginosus (109)*
	Malvaceae (50)	Bauhinia (20)	*Myracrodruon urundeuva (102)*
	Euphorbiaceae (49)	Aspidosperma (18)	*Astronium fraxinifolium (101)*
	Rutaceae (35)	Senna (18)	*Maclura tinctoria (92)*
	Annonaceae (33)	Cordia (16)	*Tabebuia roseoalba (90)*
	Lauraceae (31)	Inga (15)	*Dilodendron bipinnatum (88)*
	Moraceae (30)	Myrcia (15)	*Enterolobium contortisiliquum (87)*
	Salicaceae (28)	Trichilia (15)	*Sterculia striata (87)*
	Solanaceae (28)	Byrsonima (14)	*Acrocomia aculeata (82)*
	Apocynaceae (27)	Casearia (14)	*Aspidosperma subincanum (81)*
	Sapindaceae (26)	Machaerium (14)	*Senegalia polyphylla (81)*
	Arecaceae (24)	Mimosa (14)	*Aspidosperma cuspa (77)*
	Meliaceae (24)	Ocotea (14)	*Albizia niopoides (75)*
	Malpighiaceae (23)	Psidium (14)	*Terminalia argentea (74)*
	Cactaceae (22)	Annona (13)	*Cecropia pachystachya (71)*
	Bignoniaceae (21)	Miconia (13)	*Cordia glabrata (71)*
	Erythroxylaceae (21)	Senegalia (13)	*Talisia esculenta (70)*
	Chrysobalanaceae (20)	Solanum (13)	*Cordia trichotoma (69)*
	Combretaceae (20)		

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Mexico (33)	Leguminosae (297)	Bursera (54)	*Vachellia farnesiana (21)*

	Euphorbiaceae (69)	Lonchocarpus (32)	*Plumeria rubra (20)*
	Burseraceae (56)	Croton (25)	*Pithecellobium dulce (19)*
	Malvaceae (49)	Ficus (21)	*Senna atomaria (19)*
	Rubiaceae (40)	Mimosa (19)	*Tecoma stans (18)*
	Apocynaceae (32)	Caesalpinia (16)	*Vachellia campechiana (18)*
	Boraginaceae (31)	Quercus (16)	*Vachellia pennatula (18)*
	Moraceae (27)	Pithecellobium (15)	*Bauhinia divaricata (17)*
	Rutaceae (24)	Senna (15)	*Haematoxylum brasiletto (16)*
	Malpighiaceae (22)	Diospyros (13)	*Lysiloma divaricatum (16)*
	Salicaceae (19)	Calliandra (12)	*Spondias purpurea (16)*
	Sapotaceae (18)	Vachellia (12)	*Bursera fagaroides (15)*
	Asteraceae (16)	Bauhinia (11)	*Ceiba aesculifolia (15)*
	Celastraceae (16)	Eugenia (11)	*Comocladia engleriana (15)*
	Fagaceae (16)	Randia (11)	*Ficus cotinifolia (15)*
	Myrtaceae (16)	Sideroxylon (11)	*Guazuma ulmifolia (15)*
	Sapindaceae (16)	Diphysa (10)	*Caesalpinia pulcherrima (15)*
	Anacardiaceae (15)		*Apoplanesia paniculata (14)*
	Capparaceae (14)		*Amphipterygium adstringens (14)*
	Polygonaceae (14)		*Bursera grandifolia (14)*
			Lysiloma acapulcense (14)

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Misiones (84)	Leguminosae (110)	Eugenia (28)	*Cordia americana (75)*
	Myrtaceae (72)	Solanum (18)	*Chrysophyllum gonocarpum (67)*
	Solanaceae (40)	Ocotea (17)	*Ruprechtia laxiflora (65)*
	Rubiaceae (35)	Miconia (11)	*Chrysophyllum marginatum (64)*
	Lauraceae (33)	Ficus (10)	*Allophylus edulis (63)*
	Euphorbiaceae (27)	Myrcia (10)	*Eugenia uniflora (63)*
	Asteraceae (22)	Nectandra (10)	*Holocalyx balansae (63)*

	Bignoniaceae (18)	Cestrum (9)	*Syagrus romanzoffiana (63)*
	Melastomataceae (16)	Erythroxylum (9)	*Luehea divaricata (62)*
	Moraceae (16)	Annona (8)	*Cedrela fissilis (61)*
	Rutaceae (16)	Handroanthus (8)	*Peltophorum dubium (61)*
	Salicaceae (16)	Inga (8)	*Cupania vernalis (60)*
	Meliaceae (15)	Myrsine (8)	*Diatenopteryx sorbifolia (60)*
	Sapindaceae (15)	Piper (8)	*Pilocarpus pennatifolius (60)*
	Anacardiaceae (14)	Trichilia (8)	*Cabralea canjerana (59)*
	Malvaceae (13)	Casearia (7)	*Parapiptadenia rigida (59)*
	Annonaceae (12)	Ilex (7)	*Sorocea bonplandii (59)*
	Arecaceae (12)	Maytenus (7)	*Casearia sylvestris (58)*
	Apocynaceae (10)	Senegalia (7)	*Trichilia catigua (57)*
	Celastraceae (10)	Senna (7)	*Cordia trichotoma (56)*
		Zanthoxylum (7)	*Sebastiania brasiliensis* (56)

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Northern inter-Andean Valleys (56)	Leguminosae (77)	Ficus (10)	*Guazuma ulmifolia (39)*
	Rubiaceae (25)	Zanthoxylum (9)	*Ochroma pyramidale (26)*
	Euphorbiaceae (22)	Piper (8)	*Senna spectabilis (25)*
	Moraceae (18)	Croton (7)	*Pithecellobium dulce (24)*
	Lauraceae (14)	Erythroxylum (7)	*Zanthoxylum fagara (24)*
	Myrtaceae (14)	Eugenia (7)	*Anacardium excelsum (22)*
	Malvaceae (13)	Inga (7)	*Erythrina poeppigiana (22)*
	Arecaceae (12)	Miconia (7)	*Pseudosamanea guachapele (22)*
	Rutaceae (10)	Coccoloba (6)	*Ficus insipida (18)*
	Salicaceae (10)	Machaerium (6)	*Cupania americana (17)*
	Urticaceae (10)	Senna (6)	*Psidium guineense (17)*
	Bignoniaceae (9)	Casearia (5)	*Croton gossypiifolius (16)*
	Melastomataceae (9)	Clusia (5)	*Zanthoxylum rhoifolium (16)*

	Meliaceae (9)	Cordia (5)	*Brosimum alicastrum (15)*
	Annonaceae (8)	Acalypha (4)	*Sapindus saponaria (15)*
	Boraginaceae (8)	Bactris (4)	*Achatocarpus nigricans (14)*
	Piperaceae (8)	Bauhinia (4)	*Attalea butyracea (14)*
	Polygonaceae (8)	Brownea (4)	*Ocotea veraguensis (14)*
	Anacardiaceae (7)	Calliandra (4)	*Astronium graveolens (13)*
	Capparaceae (7)	Cecropia (4)	*Cecropia peltata (13)*
	Clusiaceae (7)	Lonchocarpus (4)	*Ceiba pentandra (13)*
	Erythroxylaceae (7)	Nectandra (4)	*Euphorbia cotinifolia (13)*
	Primulaceae (7)	Ocotea (4)	*Machaerium capote (13)*
	Sapindaceae (7)	Solanum (4)	*Muntingia calabura (13)*
		Trichilia (4)	
		Vachellia (4)	

Group (sites)	Family (species)	Genus (species)	*Species (number of sites in which recorded)*
Piedmont (46)	Leguminosae (157)	Inga (20)	*Anadenanthera colubrina (39)*
	Euphorbiaceae (33)	Senegalia (11)	*Achatocarpus praecox (29)*
	Asteraceae (32)	Senna (11)	*Myracrodruon urundeuva (27)*
	Cactaceae (32)	Eugenia (10)	*Pisonia zapallo (23)*
	Myrtaceae (28)	Prosopis (10)	*Vachellia aroma (23)*
	Bignoniaceae (22)	Machaerium (9)	*Parapiptadenia excelsa (22)*
	Anacardiaceae (21)	Solanum (9)	*Enterolobium contortisiliquum (21)*
	Malvaceae (21)	Aspidosperma (8)	*Tipuana tipu (21)*
	Solanaceae (20)	Celtis (8)	*Allophylus edulis (20)*
	Rubiaceae (18)	Maytenus (8)	*Libidibia paraguariensis (20)*
	Apocynaceae (16)	Schinus (8)	*Ruprechtia apetala (20)*
	Sapindaceae (16)	Cereus (7)	*Celtis iguanaea (19)*
	Rutaceae (14)	Croton (7)	*Senegalia praecox (19)*
	Capparaceae (13)	Ficus (7)	*Handroanthus impetiginosus (18)*

	Moraceae (13)	Coccoloba (6)	*Pterogyne nitens (18)*
	Nyctaginaceae (13)	Cordia (6)	*Tecoma stans (18)*
	Polygonaceae (13)	Erythroxylum (6)	*Vachellia caven (18)*
	Salicaceae (13)	Luehea (6)	*Amburana cearensis (17)*
	Celastraceae (11)	Zanthoxylum (6)	*Cynophalla retusa (17)*
	Meliaceae (10)	Baccharis (5)	*Phyllostylon rhamnoides (17)*
		Bauhinia (5)	*Ruprechtia laxiflora (17)*
		Bougainvillea (5)	*Senna spectabilis (17)*
		Erythrina (5)	*Trichilia claussenii (17)*
		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)	*Trichilia elegans (7)*
	Moraceae (18)	Inga (7)	*Brosimum alicastrum (6)*
	Rubiaceae (15)	Neea (7)	*Triplaris cumingiana (6)*
	Euphorbiaceae (13)	Trichilia (7)	*Erythroxylum ulei (5)*
	Meliaceae (12)	Coccoloba (6)	*Inga umbellifera (5)*
	Malvaceae (11)	Allophylus (5)	*Morisonia oblongifolia (5)*
	Lauraceae (10)	Eugenia (5)	*Zanthoxylum rhoifolium (5)*
	Sapindaceae (10)	Ocotea (5)	*Ceiba insignis (4)*
	Nyctaginaceae (9)	Capparidastrum (4)	*Celtis iguanaea (4)*
	Polygonaceae (9)	Casearia (4)	*Coccoloba padiformis (4)*
	Sapotaceae (9)	Chrysophyllum (4)	*Handroanthus serratifolius (4)*
	Apocynaceae (8)	Cordia (4)	*Anadenanthera colubrina (3)*

	Arecaceae (8)	Erythroxylum (4)	*Aspidosperma rigidum (3)*
	Capparaceae (8)	Ficus (4)	*Brosimum guianense (3)*
	Annonaceae (7)	Machaerium (4)	*Cedrela fissilis (3)*
	Bignoniaceae (7)	Nectandra (4)	*Ceiba boliviana (3)*
	Myrtaceae (7)	Piper (4)	*Chrysophyllum venezuelanense (3)*
	Urticaceae (7)	Terminalia (4)	*Clarisia biflora (3)*
	Boraginaceae (6)	Urera (4)	*Cordia alliodora (3)*
	Cactaceae (6)		*Coussapoa villosa (3)*
	Salicaceae (6)		*Croton abutiloides (3)*
			Drypetes amazonica (3)
			Manilkara bidentata (3)
			Neea hermaphrodita (3)
			Phytelephas aequatorialis (3)
			Platymiscium stipulare (3)
			Preslianthus 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)

Appendix 6.

Table. 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

Appendix 7.

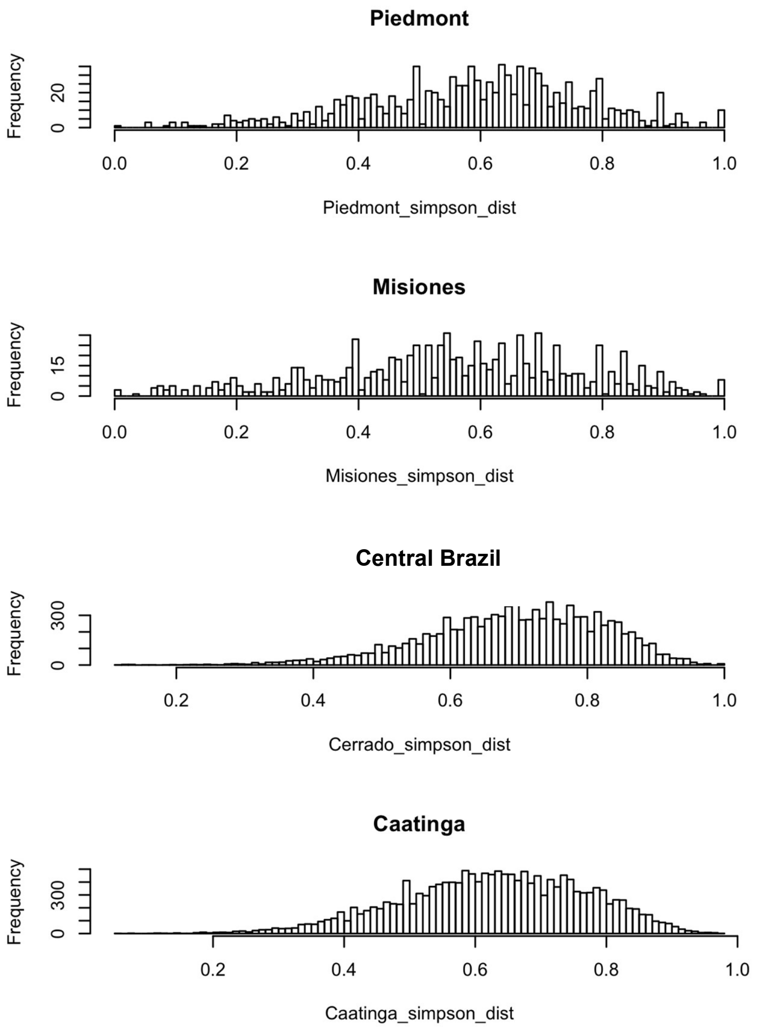


Figure 1. Histograms of dissimilarity values for the southern dry forest groups, using the Simpson dissimilarity index.

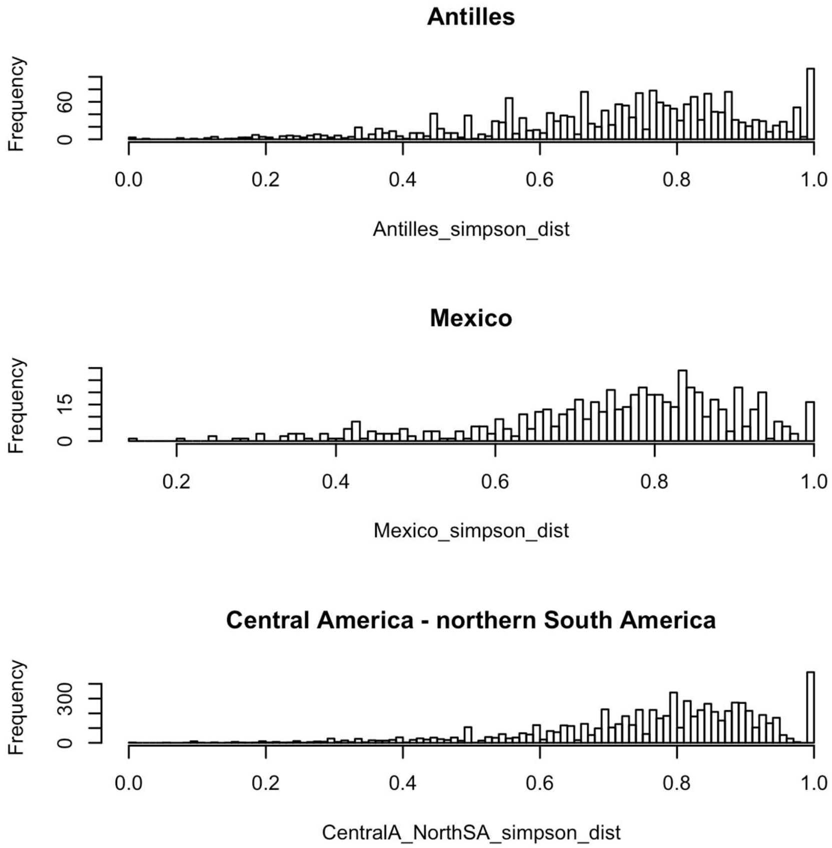


Figure 2. Histograms of dissimilarity values for the northern dry forest groups, using the Simpson dissimilarity index.

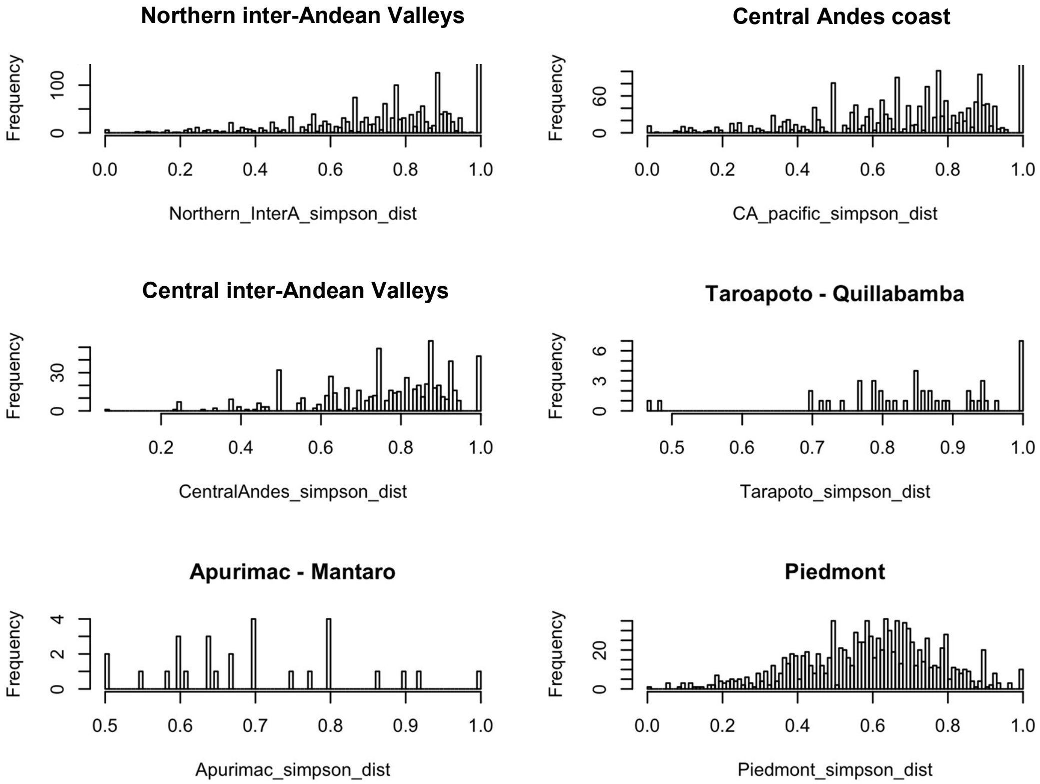


Figure 3. Histograms of dissimilarity values for the Andean dry forest groups, using the Simpson

Chapter 2 Tree diversity patterns and regional conservation priorities in Central American and northern South American dry forests

2.1 Summary

This chapter aims to describe floristic affinities and diversity patterns of Central American and northern South American seasonally dry tropical forests, and to frame their conservation prioritization in a regional context. Classification methods were used to analyze 113 areas in this region from the DRYFLOR database that include 1725 species of trees, finding ten floristic groups. I assessed two quantitative indices to assess the priority conservation value of these groups: i. Genetic Heat Index (GHI) as a measure of global rarity; and ii. a new Conservation Priority Index (CPI), which includes diversity metrics, endemism, and threats. Results of the two indices were significantly different, and due to the valuable information that both supplied, I suggest a modified CPI where the weight of the endemism parameter is doubled. According to this modified CPI, conservation should be focused on the South American Caribbean Coast, inter-Andean Valleys and in the Llanos dry forests. A biogeographical approach should be used as a framework for conservation planning, and furthermore, binational initiatives are urgently needed between Colombia and Venezuela. These should include a regional protected areas network across political borders, with the aim to promote the connectivity and preservation of dry forest remnants and their appropriate management.

2.2 Introduction

Tropical dry forest has been considered one the most threatened tropical forests worldwide for two decades (Gentry, 1995; Janzen, 1988; Miles et al., 2006). Although interest in dry forest from scientists and policy-makers has risen considerably, efforts in conservation have been insufficient. In some countries, the remaining dry forest covers only 8% of its original extent, and it is found in highly transformed anthropogenic landscapes, mainly as small fragments (García et al., 2014). The high fertility of its soil has led its transformation over millennia by intensive agriculture with associated urbanization. More recently, threats with irreversible effects such as mining have caused soil degradation, serious erosion and desertification processes that could be dramatically enhanced in scenarios of climatic change.

The Convention on Biological Diversity (Aichi Biodiversity Target 11) aims to expand the world’s protected area network to 17% of the land surface by 2020, and to achieve this, tropical dry forest requires conservation strategies at different scales - from the global to the local. These strategies might be included in international agreements and long-term national policies, followed by local on-the-ground actions that are consistent over time. In order to optimize efforts and limited financial resources, there is an urgent need for prioritization at a regional and national level to set conservation targets (Brooks et al. 2006; Kier et al. 2009; Marris 2007; Powney & Isaac 2015). The first step to achieving this is to identify wider areas of dry forest as the units to which the policies will be applied.

2.2.1 Delimitation of the regional area of dry forest in this study

Based on floristic similarity, using a large database of floristic inventories from across the Neotropics, the Latin American Seasonally Dry Tropical Forest Floristic Network (DRYFLOR, 2016; Chapter 1) identified 12 groups of dry forest which represent biologically meaningful units based on their floristic composition. This continental-scale analysis revealed that tree communities in dry forests show a substantial signal for geographical structure in floristic clustering, which is also found at a global scale (Dexter et al., 2015). One of the 12 groups, representing an independent floristic unit, is the Central American and northern South American dry forests, including the northern inter-Andean valleys, which will be the focus of this chapter.

2.2.2 Conservation prioritization

Systematic conservation planning (SCP) is the field in conservation biology that refers to a multidisciplinary, methodical and rigorous process to set and accomplish conservation targets (Kukkala & Moilanen, 2013; Margules & Pressey, 2000). SCP consists of a first step of prioritising sites and a second one in which the planning is participative, including collaborative implementation of the strategies designed, and deciding which actions might be applied locally. The complexity of the second step, facing the competing land uses, socio-economic and political realities that vary among countries and regions (Margules & Pressey, 2000; Levin et al., 2015), make SCP difficult to deploy effectively at large geographic scales (Pressey et al., 2007). With that in mind, this chapter is focused on the first step of SCP, setting priorities areas for conservation actions at a regional scale.

Conservation actions have the goal to ensure the maintenance of biodiversity and critical ecosystem processes (Mace, 2000). Prioritization of these actions should be made based on evidence (Brooks et al., 2006; Sutherland et al., 2004), trying to find a balance amongst rigour, feasibility and cost-effectiveness. Numerical analyses of specimen and inventory data can be used for assessing conservation priorities. For example, biodiversity auditing, recommended for well-characterized areas, combines distribution records with autecological information to suggest conservation management priorities (Dolman et al., 2012). However, this kind of approach requires a huge amount of detailed information that usually is not available for species of tropical ecosystems (Socolar et al., 2016b). In the absence of such information, conservation planning has analysed biodiversity patterns by identifying areas with high numbers of endemic species (e.g., global biodiversity hotspots [Myers et al., 2000]). Another quantitative approach, which is applicable at different scales, is to use geographic distributions of species to calculate the Genetic Heat Index (GHI) for conservation value (Hawthorne, 1996; Hawthorne & Marshall, 2015). GHI does not use genetic methods such as population genetics or molecular ecology. Rather, it is based on the concept that endemic and rare species are limited genetic resources that are more valuable than those represented by populations of other species with wider distribution ranges; in this context, GHI, based on a single criterion, scales conservation priorities associated with areas rich in globally rare species, which has the drawback of the inherent limitations of species occurrence records upon which it is based (i.e. incomplete distribution records, misidentification, inacurate georrefences). GHI has been used in dry forest to assess the conservation value of landscapes in Mexico and Honduras (Gordon et al., 2004), to set conservation priorities for rain forest in Cameroon (Tchouto et al., 2006), and recently to identify 'botanical high conservation value areas' in Trinidad and Tobago (Baksh-comeau et al., 2016).

Previous studies have demonstrated low geographical overlap between species-rich areas and concentration of endemic or rare species (i.e., Prendergast et al., 1993), for example in Britain using plant and animal distribution data, and globally for bird species (Orme et al. 2005) and terrestrial vertebrates (Lamoreux et al. 2006). Moreover, each approach – emphasising either species richness or species endemism – depends on spatial scale and are criticised for the use of a single criterion by which conservation assessment is made (Brooks et al., 2006; Kier et al., 2009; Mace, 2000). Here, I compare species-richness and global rarity species methods, and suggest an alternative

Conservation Priority Index (CPI) to identifying conservation priorities in the Central American and northern South American Dry Forest. The CPI aims to be synthetic by being based on metrics that capture species richness, beta diversity, endemism (GHI as a measure of global rarity), and threat (assessed by the absence of protected areas).

This chapter has two aims: (i) to describe floristic affinities and diversity patterns of the Central American and northern South American seasonally dry tropical forest; (ii) to frame regional conservation prioritization in this region in the context of two quantitative conservation indices, the GHI and CPI.

The research questions are: i. how many groups can we identify in terms of tree composition within the Central American and northern South American dry forests, including the northern inter-Andean valleys region? ii. what are the diversity patterns of the subgroups identified? Furthermore, due to the critical conservation status of the dry forest in this region, I analysed diversity patterns, geographical range and level of threats with the aim to frame regional conservation prioritization, raising two more research questions: iii. How well does the GHI, as a measure of endemism in a quantitative conservation index, perform for this region?; and iv. Is a multi-criteria conservation index valuable to capture biodiversity values of the dry forest?

2.3 Materials and methods

2.3.1 Floristic dataset

The tree inventory data analysed here have been gathered for the DRYFLOR initiative (Latin American and Caribbean seasonally dry forest floristic network-http://www.dryflor.info/). The data include plants that reach at least 3 m in height, excluding lianas or climbers, following the criteria of NeoTropTree (Tree Flora of the Neotropical Region; http://www.icb.ufmg.br/treeatlan/). In DRYFLOR, a site corresponds to a homogeneous vegetation type with an area of maximum 5 km radius.

The regional subset of Central America and northern South America includes 113 dry forest sites containing 1725 species. This subset avoided species-poor sites (<8 species) that are likely to represent incomplete floristic surveys and which add noise into the analyses (Kreft & Jetz, 2010; Lennon et al., 2001).

2.3.2 Data analyses

Clustering and biodiversity turnover

Multivariate analyses were run in the R Statistical Environment v. 3.2.3 using the packages recluster (Dapporto 2013) and pvclust (Suzuki & Shimodaira 2015) with the aim to identify floristic groups in the Central American and northern South American dry forest sites, and the floristic turnover among them.

Pairwise floristic distances were calculated using the Simpson dissimilarity index (β sim), which is less affected by variation in species richness (Kreft & Jetz, 2010). Singleton species (494 species) were excluded. $\beta \text{ sim} = 1 - J / [J + \min (A, B)]$, where A and B are the number of species unique to each site, and J is the number of species common to both sites. In order to treat the high percentage of tied values in the dissimilarity matrix (76.5%), I used the recluster.cons function, which performs a random re-order of the sites to obtain a hierarchical classification (50% consensus rule from 1000 trees). The final clustering analyses with the Approximately Unbiased (AU) support values per cluster were obtained via multiscale bootstrap by resampling the species order (pvclust function, 1000 bootstrapping). The unweighted pair-group method was used applying arithmetic averages (UPGMA) as an algorithm to link the clusters.

In addition, Simpson similarity values were calculated between pairs of sites within the floristic groups identified, in order to assess the floristic similarity within them. These calculations include singleton species in order to capture the whole diversity of the groups.

2.3.3 Quantitative conservation prioritisation

With the purpose to set and suggest a conservation value categorization for the Central American and Northern South American dry forest, I assessed an endemism-based metric (GHI) and compared it with a new Conservation Priority Index (CPI) that aims to capture endemism, species richness, beta diversity and threat.

Measuring endemism using the Genetic Heat Index

The Genetic Heat Index (GHI) is a metric of the concentration of restricted range species in a sample (Gordon et al., 2004; Hawthorne & Marshall, 2015), in this case confined to each dry forest floristic group identified by my cluster analyses. Essentially, species are rated into four “star” categories based on global geographic range calculated from distribution records (e.g., those found in GBIF): Green (widespread), Blue (continentally widespread), Golden (significant global rarity value) and Black (rare or local endemics). Each star category has an average geographical range and a specific weight based upon a study of global plant species distributions, calculated in degree squares (Hawthorne & Marshall, 2015). These values are based on the maximum geographical range of 72 degrees square as default baseline for the globally widespread species (green star). This averange, and also the weight of the star, are three times smaller than that of the next rarest category (Hawthorne & Marshall, 2015). For each category, the average geographical range is 72 (green star), 24 (72/3 blue star), 8 (24/3 golden star), and 2.67 (8/3= black star). Therefore the star weights and the ideal mean range by category are: 72/2.67 = 27 (**black**), 72/8= 9 (**golden**), 72/24= 3 (**blue**) and 72/72= 1 (0 for the GHI calculation **green**). Even though the weight of the stars might vary regionally and possibly be adjusted with extensive fieldwork, in order to be comparable globally, Hawthorne and Marshall (2015) suggested using the same standard set of weights for the star system. The calculation of the index is:

GHI = 100 X (No. black spp X 27 +No. golden spp X 9 + No. blue spp X 3+ No. green X 0)/ No total spp

The star categorization for 55% of the species (867) in the Central America and Northern South America dataset was obtained from existing calculations (Hawthorne's work at the University of Oxford, pers. comm.). The remaining species (718) were placed in a star category using herbarium-specimen based distribution and the inventory data from DRYFLOR. Herbarium occurrences were obtained mainly from the Global Biodiversity Information Facility (GBIF, www. gbif.org, [data dowloaded 15/06/2016]), using the R package rgbif (Chamberlain et al., 2016); in particular cases, where the species were absent or GBIF's taxonomy was outdated, records from Tropicos (www.tropicos.org) were also incorporated. Herbarium record data were cleaned by removing records that indicate problems with geographical issues (e.g., invalid coordinates, locality mismatch, geodetic datum invalid) and insufficient collection information (e.g., basis of record impossible to interpret or unlikely date). As means of testing my approach, 100 species with existing star categories (already evaluated by Hawthorne [pers. comm.] were evaluated using herbarium plus DRYFLOR data records, showing the same results, validating the compilation of GHI values generated using both approaches.

Conservation Priority Index (CPI)

Although endemism is particularly useful to indicate highly valuable areas in terms of biodiversity, conservation prioritization is a complex process which might include other factors to increase the effectiveness of conservation policies. Here, I suggest a new index that incorporates endemism and additional metrics of diversity and threat.

CPI corresponds to the sum of the four factors (**CPI= ghi+ Rsr+Rbeta+Psup)**

ghi: Relative Genetic Heat Index is obtained dividing the GHI per floristic group with the highest value observed in any dry forests group in the region. This variable is designed to capture information about species endemism.

Endemism, as a measure of biodiversity uniqueness, represents a means of assessing unique genetic resources (Brooks et al. 2006; Kier et al. 2009), and is considered as a surrogate for conservation value (Myers et al. 2000; Lamoreux et al., 2006). Taking into account plant species endemism might be a sensible decision in the attempt to capture the biological distinctiveness of dry forests.

Rsr: Relative species richness is obtained dividing the mean species number per site for each group (alpha diversity- α) by the highest value observed in any dry forest group in the region. This variable is designed to capture information about species richness.

For forest ecosystems, species richness or alpha diversity of trees is a simple and important metric of conservation value because high plant species diversity is considered crucial to maintaining ecosystem processes, function, and services (Isbell et al., 2011). Although richness patterns in plant species might vary for different life forms as Linares-Palomino (2008) reported for the dry forest in the Bolivian piedmont, the use of trees as an indicator is facilitated by the quality of tree inventory data in terms of taxonomic resolution and relatively homogeneous sampling methods. For example, fertile collections of lianas are rare if data do not come from monitoring plots, and data for herbs or epiphytes across the region are insufficient as these life forms are usually not recorded in the floristic inventories.

Rβ: Relative beta diversity. The number of floristic compositional units in a dry forest group dividing per the highest value in any of the groups. This variable is designed to capture the variation in species assemblage.

$$R\beta=\beta/\max\beta$$

$$\beta=\text{Total number species in the group } (\gamma) \text{ / Mean spp-richness in the group } (\alpha)$$

Regional-to-local diversity ratio (Tuomisto, 2010) quantifies how many times as rich in species diversity a floristic group is than its sites are on average. In this case, this diversity ratio represents the number of distinctive sets of species - or community assemblages - in a given floristic group.

Incorporating a beta diversity metric into the CPI calculation captures compositional heterogeneity. Several studies and approaches recognise the value of beta diversity in conservation planning (Bush, et al., 2016; Ferrier & Guisan, 2006; Socolar et al., 2016b; Ferrier et al., 2007; Ball et al., 2009). However, is important to note that higher values of beta diversity are not always significant in conservation. For instance, anthropogenic impacts drive species loss and invader establishment which might cause an increase in beta diversity (Socolar et al., 2016). However, in this study, floristic data gathered by DRYFLOR (which is the most robust dry forest dataset available) included mostly inventory data from well-conserved areas, avoiding highly disturbed sites or secondary forest.

Psup: Proportion of sites of each floristic group falling outside protected areas; 1 is not protected at all and 0 is fully protected. This variable is designed to capture information about threat. Representativeness of dry forest sites in protected areas was assessed by overlying them on to the coverage of protected areas. I used conservation units from the World Database on Protected Areas (WDPA) reported by 2015 (UICN &UNEP-WCMC, www.protected planet.net).

The majority of potential threats to dry forests are related to human activities (Miles et al., 2006). Protected areas are the main tools of biodiversity conservation (Sieck et al, 2011), and areas without any protection are extremely vulnerable to intensified land use, fragmentation, and probably destined to disappear. Despite acknowledging that protected areas are not always effective, often being understaffed, underfunded, and facing external threats (Saout et al., 2013; Watson et al., 2014), some studies reveal that protected areas actually can reduce natural-cover loss (Ament & Cumming, 2016; Geldmann et al., 2013). In this context, the assumption that protected areas are effective in reducing land cover changes within their borders seems reasonable and using the absence of protected areas is therefore a practical approach to measuring level of threat for dry forest.

In order to give equal weight to each factor in calculating the CPI, each metric was scaled with the minimum observed value being zero (0) and the maximum observed value being one (1). The maximum theoretically possible value of CPI is four (4), which means "Top conservation priority", and the minimum theoretically possible value is zero (0).

2.4 Results and discussion

2.4.1 Floristic affinities and diversity patterns

Classification of dry forest sites in the study region was carried out using a matrix of 113 sites x 1231 species (excluding singletons), obtaining a consensus tree which shows clear geographical structure across five main floristic groups: i. South American Caribbean Coast; ii. Central America and San Andres and Providencia; iii. Inter-Andean Valleys in Colombia; iv. dry forests within the Llanos; and v. Montane dry forest in Venezuela (Appendix 1). The Venezuelan montane forests were excluded from further analyses because they were identified as an outlier group, reflecting the strong representation of mesic montane floristic elements in them. For example, in this group the most frequently recorded species are *Calycolpus moritzianus* (Myrtaceae), *Clusia minor* (Clusiaceae), *Miconia theizans* (Melastomataceae*)* and *Viburnum tinoides* (Adoxaceae), all of which are characteristic of mesic forests.

In order to assess support for floristic groups, I ran bootstrapping analyses for the dataset, excluding the Venezuelan montane forest, using 106 sites in total. I then identified ten floristic groups supported by at least 0.9 AU: 1. Central America Pacific Coast; 2. Central America semi-deciduous; 3. Central America; 4. South American Caribbean Coast; 5. Caracas-Cerrejón; 6. Xerophytic South American Caribbean Coast; 7. Inter-Andean Valleys; 8. Inter-Andean middle Magdalena Valley; 9. Llanos semi-deciduous; and 10. Llanos flooded. (Figure 2).

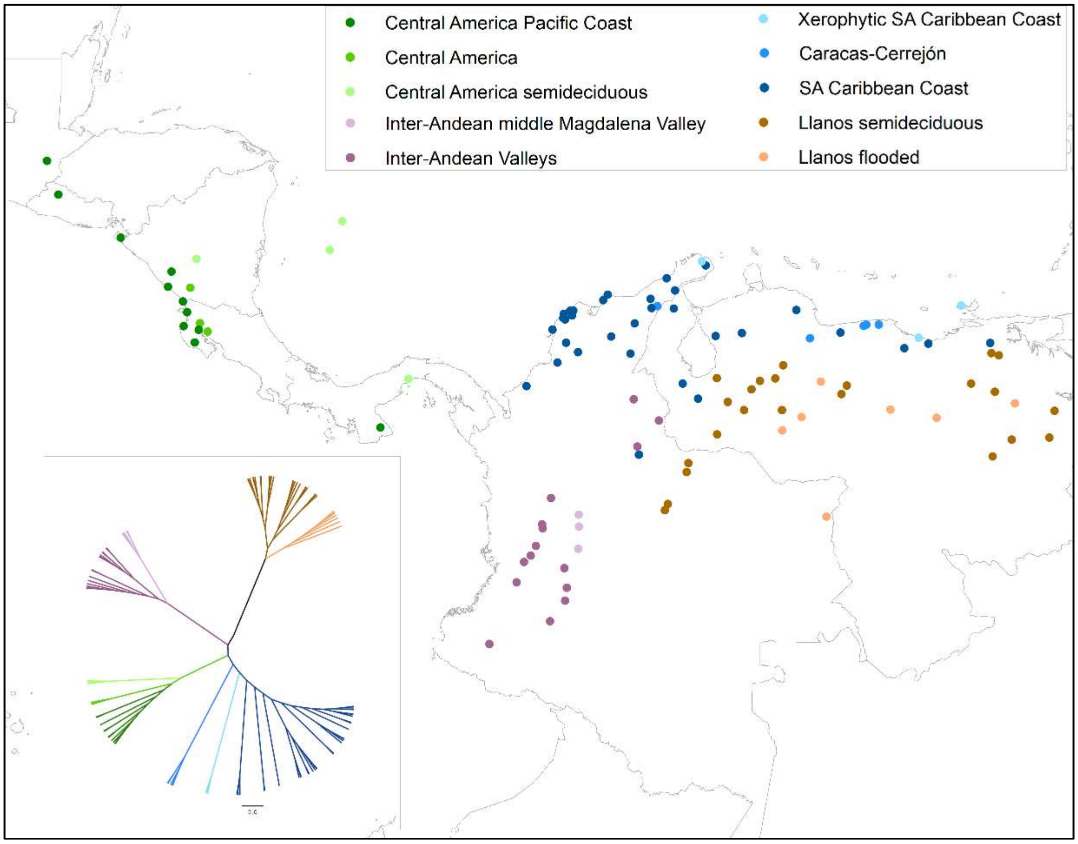


Figure 1. Geographic representation of the UPGMA classification of the 106 dry forest sites in the region, showing ten floristic groups supported by bootstrap values (pvclust, AU<0.9).

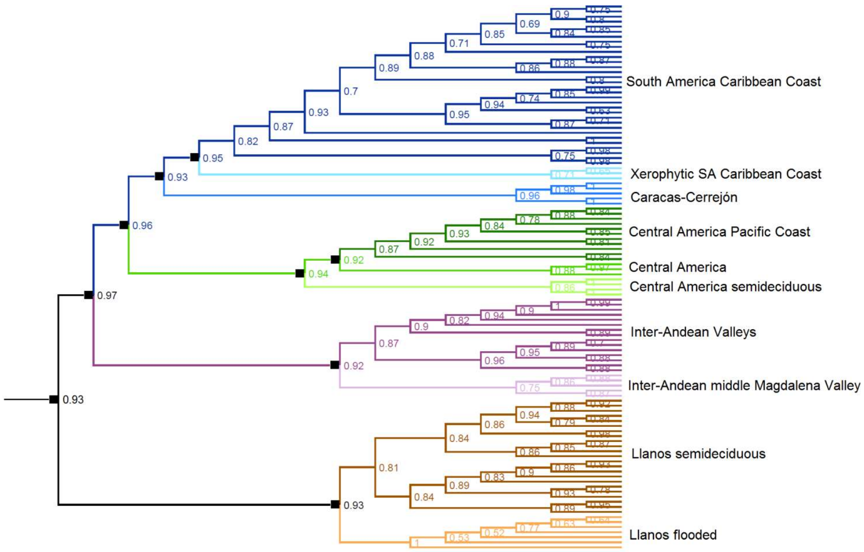


Figure 2. Hierarchical cluster of 106 dry forest sites in the region using UPGMA and Simpson dissimilarity index as the measure of distance. Ten floristic groups with AU >0.90 bootstrap are indicated by colours.

Leguminosae is the most species-rich family in the ten floristic groups, followed by Euphorbiaceae, Rubiaceae and Malvaceae (see Chapter 1 for discussion of dominant families in neotropical dry forests). Capparaceae is the second most species-rich family in the Xerophytic group; this family is a predominant component in the driest neotropical areas as reported by Gentry (1995). Meanwhile Myrtaceae is important in the Llanos semi-deciduous group, as it is in the semi-deciduous forest in southeastern Brazil (Lopes et al. 2012). Arecaceae, which is a dominant element in gallery forests (Correa-Gomez & Stevenson, 2010) and in the adjacent moist forest (Pitman et al., 2001; Gosling et at., 2009; ter Steege et al., 2013), is common in the Llanos flooded group.

Species-rich genera vary among groups. *Lonchocarpus* and *Ficus* are the most diverse genera in the Central American groups and *Casearia* and *Coccoloba* in the South American Caribbean Coast and Xerophytic groups. Surprisingly, being a genus characteristic of humid habitats, *Inga* is one of the most species-rich genera in five of the floristic groups: Central America semi-deciduous, Inter-Andean Valleys, Inter-Andean middle Magdalena Valley, Llanos semi-deciduous, and Llanos flooded. However, *Inga* species are highly recorded only in the Llanos groups where other evergreen floristic elements characteristic of wet forest are common (e.g., *Virola surinamensis, Callophylum brasiliense* [Aymard & González 2014]); elsewhere it is represented only by occasional records, and it is unlikely to be abundant. In support of this, according to quantitative inventory data, *Inga* species represent 6% of stems per plot in Llanos sites in Venezuela (Aymard & Farreras unpublished) in contrast to only 1% of stems in Inter-Andean Cauca Valley sites (Ruíz & González, 2014). This underlines the great value of quantitative inventory data to describe plant community patterns and to identify dominant species (see Chapter 3).

There are 12 species recorded in all ten regional groups: *Astronium graveolens, Bursera simaruba, Casearia sylvestris, Ceiba pentandra, Cynophalla flexuosa, Enterolobium cyclocarpum, Hamelia patens, Hymenaea courbaril, Maclura tinctoria, Pithecellobium lanceolatum, Sapindus saponaria,* and *Spondias mombin.* This appears to contrast with the continental-scale patterns in which no species are shared among all the main dry forest floristic groups across the Neotropics (DRYFLOR, 2016; Chapter 1), but the spatial scale here is smaller and most of these species are ecological generalists, like the most widespread species found at a neotropical scale.

Overall, the data reveal high levels of beta diversity across the region (Simpson index: mean = 0.79, median = 0.81; Sørensen index: mean = 0.84, median = 0.85), which is consistent with studies of dry forest floristic turnover at continental scale (DRYFLOR, 2016; Chapter 1), and also at regional scale (Trejo & Dirzo, 2002); Mexico). However, values of dissimilarity are lower within floristic groups, ranging from 0.68 (Simpson median) in the Llanos semi-deciduous and inter-Andean valleys to 0.33 (Simpson median) in the Llanos flooded (Table 1).

Strong floristic affinities were indicated by the lowest dissimilarity values between geographically neighbouring groups - e.g., Central America and Central America Pacific Coast (Simpson=0.09) and South America Caribbean Coast and Xerophytic groups (Simpson=0.08) (Table 1, Appendix 2).

The South American Caribbean Coast group shows strong floristic affinities with the Llanos semi-deciduous and inter-Andean Valleys, supported by the high number of species shared between them, 238 and 201 respectively (Table 2, Appendix 2,).

Table 1. Description of the dry forest floristic groups in the region.

Group	No. sites	No. families	No. genera	No. species	Mean No. species per site	Median Simpson	Mean Simpson
Central America	3	53	158	234	122.67	0.56	0.54
Inter-Andean middle Magdalena Valley	3	57	170	245	126.67	0.49	0.55
Xerophytic SA Caribbean Coast	3	32	91	126	57.67	0.60	0.55
Central America semi-deciduous	4	73	282	470	171.25	0.67	0.60
Caracas-Cerrejón	5	50	132	178	78.00	0.43	0.45
Llanos flooded	7	52	151	212	115.00	0.33	0.35
Central America Pacific Coast	11	66	232	397	137.27	0.53	0.54
Inter-Andean Valleys	15	65	238	414	95.87	0.68	0.63
Llanos semi-deciduous	23	78	306	657	122.17	0.68	0.67
SA Caribbean Coast	32	65	270	499	82.06	0.57	0.57

The Caribbean Coast - Llanos semi-deciduous relationship has been reported previously by Sarmiento (1975) and Rangel-Ch (2014), and the Caribbean Coast -inter-Andean Valleys relationship by Pizano et al., (2014). The Llanos semi-deciduous forest is found mainly in piedmont landscapes, which are moderate Andean slopes of up to 500 metres elevation (Rangel-Ch et al., 1995). These affinities could reflect a formerly continuous extension of dry vegetation before the Andean uplift or the connection of these areas through arid corridors during the Pleistocene (Hernández 1992).

2.4.2 Regional conservation prioritisation

The categorisation of species into star categories -the first step for the GHI calculation- is based on their biogeographical range. The most common floristic elements in the dry forests of the region are widespread dry-tolerant species (57% of the species are in the green star category, Figure 3.), which are often also components of wet forest communities (Gentry 1995). Examples are *Hura crepitans* (Euphorbiaceae), *Bixa orellana* (Bixaceae), *Ficus insipida* (Moraceae), *Hamelia patens* (Rubiaceae) and *Attalea butyracea* (Arecaceae) which occur in both dry and rain forests. The globally rarest species (black star) are the least represented in the region, making up only 5% of the total species (Appendix 3), with most of them concentrated in drier formations in the South American Caribbean Coast groups. For example, *Machaerium grandifolium, Libidibia granadillo, Caesalpinia mollis* (Fabaceae), *Cynophalla linearis* (Capparaceae) and *Croton heliaster* (Euphorbiaceae) are restricted to the South American Caribbean Coast and Xerophytic groups.

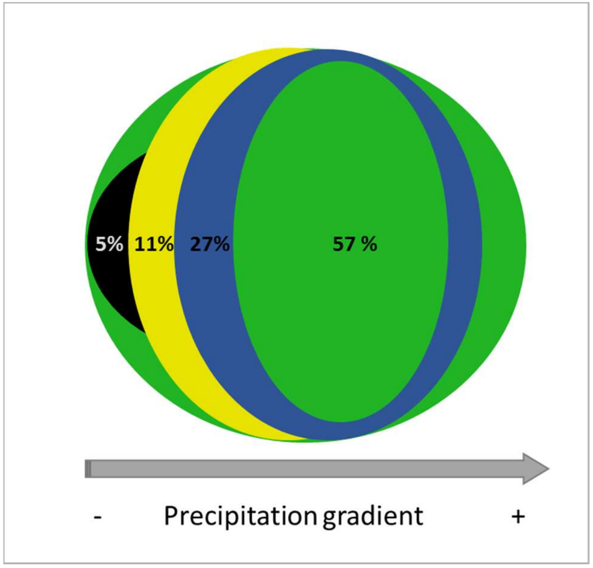


Figure 3 Proportion of the tree species in the region belonging to each star category across the precipitation gradient: Green (widespread) and Blue (continentally widespread) species occur across a wider precipitation range in comparison to the Golden (significant global rarity value) and Black (rare or local endemics) species, which are more restricted to lower precipitation values.

According to the GHI total values, the South American Caribbean Coast groups and the inter-Andean Valleys are the top four priorities (Table 2). Like the species distribution patterns, the GHI calculated for this study appears to be highly related to rainfall (Figures

3 and 4) with the highest GHI values found in areas where the annual precipitation values are lower and water deficit stronger.

In this context, GHI is highlighting drier formations because of their higher levels of species endemism, which might reflect the phylogenetic niche conservatism described for some lineages characteristic of these arid areas (e.g., robinioid legumes; Pennington et al., 2009). In terms of providing support or adaptation services to human communities, it is well-know that drier areas, can be central to achieving broader food security objectives as agriculture is occurring in surrounding areas with evident ecological links (Blackie et al., 2014). Furthermore, drylands are possibly the most vulnerable areas in climate change scenarios in the region, since intensified extreme climatic conditions such as prolonged drought may trigger desertification or increments in rainfall can enhance soil erosion because they are not protected by closed canopies.

Table 2. Genetic Heat Index. Values correspond to the total number of species by star category per floristic group.

Star (weight) Group	BLACK (27)	GOLDEN (9)	BLUE (3)	GREEN (0)	Total No. species	No. sites	GHI
Caracas-Cerrejón	14	14	27	123	178	5	329
SA Caribbean Coast	29	52	104	314	499	32	313
Xerophytic SA Caribbean Coast	6	11	26	83	126	3	269
Inter-Andean Valleys	17	36	83	277	413	15	250
Central America Pacific Coast	8	32	138	219	397	11	231
Inter-Andean middle Magdalena Valley	8	15	43	179	245	3	196
Llanos semideciduous	17	40	107	493	657	23	174
Central America semideciduous	12	27	79	350	468	4	172
Central America	4	12	57	161	234	3	165
Llanos flooded	2	10	27	173	212	7	106

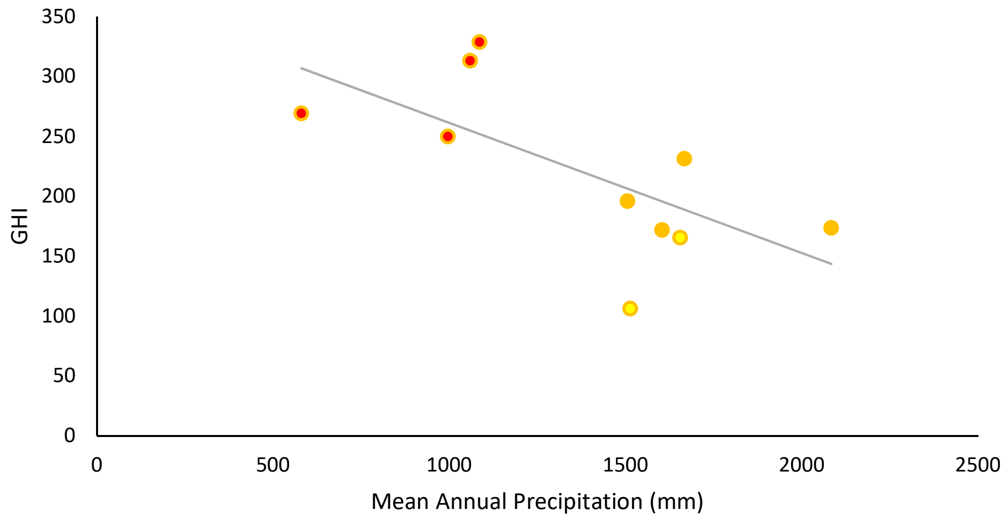


Figure 4. Scatter plot of the Mean Annual Precipitation values (Worldclim database- Hijmans et al., 2005) and GHI values per floristic group in the region. Linear regression R^2 = 0.449

The CPI results highlight the top priority conservation groups (more than 55% of the maxCPI value: CPI >2.2) as the South American Caribbean Coast, Llanos semi-deciduous, and inter-Andean Valleys. The Llanos flooded and the Xerophytic South American Caribbean Coast groups are lowest on the CPI scale (Table 3). This ranking is substantially different to the priorities identified by the GHI in which drier areas are highly ranked. CPI incorporates a set of metrics that emphasize different aspects of the value of dry forest biodiversity. However, I am aware that it could be missing relevant aspects for conservation assessments, for example, phylogenetic and functional diversity, which have been recently taken into account in conservation planning (Ashley et al., 2003). In addition, other relevant threats such as climatic change are not captured by the CPI metric of threat that assesses only the lack of protected areas in the dry forest groups in the region.

Table 3. Conservation Priority Index per floristic group (equal metrics weight). Ranking was selected at 35% maxCPI (1.4) for intermediate and 55% maxCPI (2.2) for top priority level.

Group	**No. sites**	**ghi**	**Rsr**	**Rβ**	**Psup**	**CPI**
SA Caribbean Coast	32	0.93	0.21	1.00	0.63	2.77
Llanos semi-deciduous	23	0.30	0.57	0.83	0.74	2.44
Inter-Andean Valleys	15	0.65	0.34	0.58	0.87	2.43
Inter-Andean middle Magdalena Valley	3	0.40	0.61	0.02	1.00	2.03
Central America Pacific Coast	11	0.56	0.70	0.25	0.45	1.97
Caracas-Cerrejón	5	1.00	0.18	0.10	0.60	1.88
Central America	3	0.27	0.57	0.02	1.00	1.85
Central America semi-deciduous	4	0.30	1.00	0.21	0.00	1.51
Llanos flooded	7	0.00	0.50	0.00	0.71	1.22
Xerophytic SA Caribbean Coast	3	0.73	0.00	0.08	0.33	1.15

My goal in developing the CPI was to keep the principle of complementarity in setting conservation priorities,which recognises the need for maximizing the inclusion of as many components of biodiversity as possible (Bush et al., 2016; Ferrier & Wintle, 2009) whilst simultaneously highlighting the value and urgency of sustainable land management. However, the results of the CPI do not select some of the drier areas as top priorities, which seems unsatisfactory because, as explained above, these areas house most endemic species in the region and may be highly vulnerable to climatic change. I therefore decided to recalculate the CPI, giving double weight to the endemism metric (relative GHI). With this modified CPI, I identified the conservation priority groups with at least 2.75 CPI (55% of the maxCPI, Table 4, maxCPI=5, minCPI=0) which include the South American Caribbean Coast, Caracas-Cerrejón, inter-Andean Valleys and Llanos semi-deciduous. In comparison to the previous CPI calculation, Caracas-Cerrejón and the Xerophytic group move further up the prioritisation scale.

Table 4. Modified CPI, calculated per floristic group with ghi double weighted. Ranking was selected at 35% maxCPI (1.75) for intermediate and 55% maxCPI (2.75) for top priority level.

Group	No. sites	ghiX2	Rsr	Rβ	Psup	CPI
SA Caribbean Coast	32	1.86	0.21	1.00	0.63	3.70
Inter-Andean Valleys	15	1.29	0.34	0.58	0.87	3.08
Caracas-Cerrejón	5	2.00	0.18	0.10	0.60	2.88
Llanos semi-deciduous	23	0.61	0.57	0.83	0.74	2.75
Central America Pacific Coast	11	1.12	0.70	0.25	0.45	2.53
Inter-Andean middle Magdalena Valley	3	0.81	0.61	0.02	1.00	2.44
Central America	3	0.53	0.57	0.02	1.00	2.12
Xerophytic SA Caribbean Coast	3	1.46	0.00	0.08	0.33	1.88
Central America semi-deciduous	4	0.59	1.00	0.21	0.00	1.80
Llanos flooded	7	0.00	0.50	0.00	0.71	1.22

The South American Caribbean Coast, the top priority group identified by the modified CPI, has the maximum number of globally rare species in the study region (29 black star species, Table 2). Caracas-Cerrejón, placed third in the CPI ranking and with the highest GHI value, also has a significant level of endemism. Both these regions extend across the borders of Colombia and Venezuela, but their valuable endemic species are not included in the national conservation agendas (e.g., IUCN red listing,) because of the political connotation that endemism usually implies (i.e., they are not endemic to Colombia or Venezuela). To ameliorate this, conservation strategies might be urgently switched to a more biogeographical approach.

Although efforts in the establishment of new reserves have been made recently in the Caribbean, forest fragmentation in this region is massive, and these protected areas are isolated and immersed in an agricultural matrix. Consequently, actions to promote connectivity amongst patches, whether they are protected or not, must be implemented in order to ensure population viability and ecological processes.

The Inter Andean Valleys is the second priority group. These valleys have a remarkable bioclimatic and geographical variability (Flórez, 2003). Inter-Andean dry forests are confined to the piedmont areas, where orientation of the mountains creates dry climatic conditions mainly as the result of rain-shadow effects (Galvis & Mesa S, 2014; Sarmiento, 1975). However, these rain shadows are less pronounced where the valleys are wide, and on these flat valley bottoms more humid vegetation may be found (Vargas et al., 2014). The Inter Andean valleys are one of the most transformed areas in Colombia. For example, the Cauca Valley has less than 6% of forest cover (CVC, 2007), and the remnants are small fragments (in most of the cases less than 9 ha [Arcila-Cardona et al., 2012]) in an extensive agricultural landscape. This floristic group represents the least protected dry forest in Colombia (García et al., 2014 and Appendix 4) and holds an interesting community assemblage with high levels of beta diversity and might be considered as a clear priority for conservation planning.

The Llanos semi-deciduous is also part of the top priority conservation groups for the modified CPI. As a whole, the Llanos is an extremely heterogeneous region of approximately 563.000 Km^2 (Aymard & González, 2014). It is characterized by a combination of physiognomies, from fire-prone savannas with a continuous herbaceous layer and an open tree layer to savanna woodlands with ~80% tree cover, which are found in the piedmont area (Sarmiento 1984). This continuous savanna landscape is interrupted by different vegetation types such as semi-deciduous forest and gallery forest, due mainly to small-scale environmental changes including edaphic conditions and topography (Mistry, 2000, Aymard & González, 2014; Rangel-Ch & Minorta-Cely, 2014). The semi-deciduous forest in the Llanos represents a particular closed-canopy formation in the region, with high values of alpha and beta diversity. It is also highly threatened by cattle-raising and agricultural activities, which have occurred since colonial times but have more recently expanded and intensified in the form of palm and rice monocrops. Oil extraction by multinationals, which has been the pillar of the regional economy, is an additional concern in the Llanos. But most worrying are new methods for hydrocarbon extraction such as fracking that carry a significant environmental cost.

After double weighting the endemism metric, the Xerophytic group was in the last place of the intermediate priority range of the CPI. This shrub formation, dominated by columnar cacti, is common in the driest areas of the South American Caribbean Coast, where different vegetation physiognomies, highly related ecologically, are integrated (Sarmiento, 1975). I suggest that special attention should be paid to these xerophytic areas. It is clear that keeping traditional land use management – which in La Guajira region in Colombia, for example, includes wood fuel production and goat ranching as well as industrial-scale coal mining, will result in irremediable soil degradation, habitat loss and extinction of endemic species.

The South American Caribbean Coast, Caracas-Cerrejón, Llanos semi-deciduous and Xerophytic groups require urgent conservation attention and co-operation between the Colombian and Venezuelan authorities to underpin and coordinate binational initiatives for the planning of a new protected area network, which should include active management at landscape level, working hand in hand with local communities.

2.5 Conclusions

In this study, I identified ten dry forest floristic groups in the Central American and northern South America region. These groups, statistically well-supported, show a strong geographical structure. Dissimilarity values within the floristic groups range from 0.68 to 0.33 (Simpson median) with mean of 0.55 on average. These values are lower on average than those reported at a continental-scale and presented in Chapter 1 (mean 0.73).

More than 50% of the tree species in the dry forests of the region are droght-tolerant, but widespread in various other habitats. In the next chapter, I will examine the dominance of these ecological versatile floristic elements, particularly in the Colombian dry forest, using quantitative inventory data.

Significant differences between the conservation priority indices GHI and CPI were found. GHI, based on the single criterion of endemism (measured as the concentration of globally rare species) highlights the importance of the drier areas, represented by Caracas-Cerrejón, South American Caribbean Coast, and Xerophytic groups. In contrast, CPI that includes diversity metrics, endemism, and threats - with the idea to include different biodiversity components in conservation planning- highlights the South American Caribbean Coast, Llanos semi-deciduous, and inter-Andean valleys. Due to the valuable information that both indices supplied, capturing different aspects of biodiversity plus vulnerability in future scenarios, I suggest a modified CPI in which the endemism parameter is double-weighted and added to the alpha diversity, beta diversity, and level of threat values. As a result, this modified CPI index set the South American Caribbean

Coast (including Caracas-Cerrejón), inter-Andean Valleys and Llanos semi-deciduous as the top conservation priorities and the Xerophytic group as an intermediate priority.

The value of a biotic community for conservation can also be assessed by measuring phylogenetic diversity (Ashley et al., 2003), which might capture functional diversity as well. Furthermore, other relevant threats such as climatic change are not captured by the CPI. In this context, I suggest that future conservation prioritisation exercises should incorporate a phylogenetic diversity metric and analyses of threats. Including evolutionary principles and climatic change vulnerability might be a way to increase the effectiveness of conservation over the long term (Mace & Purvis, 2008).

The high priority areas for conservation (e.g., South American Caribbean Coast, Caracas-Cerrejón, and Xerophytic groups) have numerous endemic species spread across national borders, which highlights the importance of a biogeographical approach to setting conservation priorities. The usual approaches, defined by political borders, are failing to protect these endemic species. Therefore, concrete actions coordinated as binational initiatives between Colombia and Venezuela are urgently needed. A regional protected areas network must be planned with the aim to promote the cross-border connectivity and preservation of the dry forest remnants, and the appropriate management of the land.

2.6 Appendices

Appendix 1.

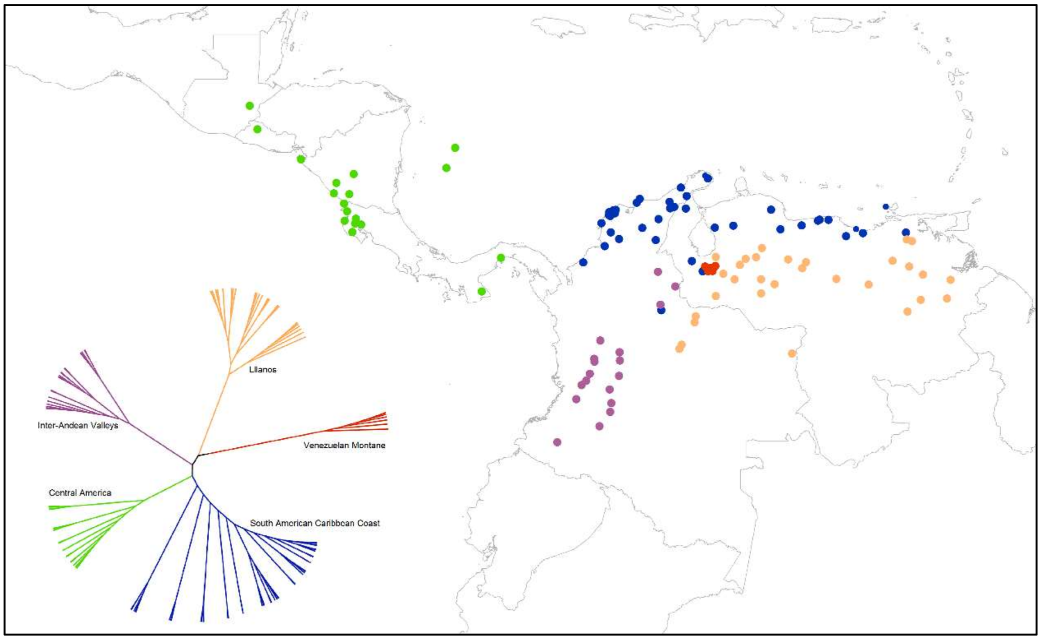


Figure. Geographic representation of the 50% consensus tree of 113 dry forest sites

Appendix 2.

Table 1. Distance matrix among the Central America and northern South America dry forest floristic groups using Simpson dissimilarity index.

	Caracas-Cerrejón	Caribbean Coast	Central America Pacific Coast	Central America semideciduos	Central America	Inter-Andean Magdalena medio	Inter-Andean Valleys	Llanos semideciduos	Llanos flooded	Xerophytic
Caracas-Cerrejón	0.00	0.27	0.62	0.60	0.69	0.70	0.47	0.33	0.74	0.56
Caribbean Coast		0.00	0.61	0.66	0.48	0.51	0.51	0.52	0.50	0.08
Central America Pacific Coast			0.00	0.67	0.09	0.72	0.71	0.72	0.75	0.53
Central America semideciduos				0.00	0.55	0.57	0.64	0.65	0.70	0.67
Central America					0.00	0.76	0.58	0.58	0.77	0.63
Inter-Andean Magdalena medio						0.00	0.39	0.50	0.74	0.68
Inter-Andean Valleys							0.00	0.55	0.64	0.50
Llanos semideciduos								0.00	0.22	0.39
Llanos flooded									0.00	0.71
Xerophytic										0.00

Table 2. Number of species shared between pair floristic groups. Grey scale indicates greatest values

	Caracas-Cerrejón	Caribbean Coast	Central America Pacific Coast	Central America semideciduos	Central America	Inter-Andean Magdalena medio	Inter-Andean Valleys	Llanos semideciduos	Llanos flooded	Xerophytic
Caracas-Cerrejón	178	130	67	72	56	54	94	119	47	56
Caribbean Coast		499	156	161	122	121	201	238	107	116
Central America Pacific Coast			397	130	214	69	114	110	54	59
Central America semideciduos				470	106	105	149	164	64	42
Central America					234	57	99	98	49	46
Inter-Andean Magdalena medio						245	150	123	56	40
Inter-Andean Valleys							414	185	77	63
Llanos semideciduos								657	165	77
Llanos flooded									212	37
Xerophytic										126

Appendix 3.

Table. Black star species list per floristic group in the study region.

Species	Caracas-Cerrejón	SA Caribbean Coast	Central America Pacific Coast	Central America semi-deciduous	Central America	Inter-Andean middle Magdalena Valley	Inter-Andean Valleys	Llanos semi-deciduous	Llanos flooded	Xerophytic SA Caribbean Coast
Total number of species	14	29	8	12	4	8	17	17	2	6
Bourreria cumanensis	X	X						X		X
Lecythis ollaria	X	X					X	X		
Libidibia punctata	X	X						X		X
Brasilettia mollis	X	X								X
Libidibia granadillo	X	X								X
Lonchocarpus dipteroneurus	X	X						X		
Albizia barinensis								X	X	
Aniba bracteata						X	X			
Brasilettia velutina			X		X					
Citharexylum subthyrsoideum	X	X								
Croton micans						X	X			
Croton scaber	X						X			
Cymbopetalum costaricense			X		X					
Cynophalla linearis		X								X
Eugenia casearioides	X	X								
Guettarda malacophylla							X	X		
Lonchocarpus macrocarpus		X						X		
Machaerium goudotii						X	X			
Pithecellobium roseum		X						X		
Pityrocarpa leucoxylon		X						X		
Poincianella eriostachys			X		X					

Species	Caracas-Cerrejón	SA Caribbean Coast	Central America Pacific Coast	Central America semi-deciduous	Central America	Inter-Andean middle Magdalena Valley	Inter-Andean Valleys	Llanos semi-deciduous	Llanos flooded	Xerophytic SA Caribbean Coast
Prockia flava	x	x								
Tabernaemontana odontadeniiflora			x		x					
Trichilia oligofoliolata						x	x			
Ampelocera albertiae							x			
Annona hayesii				x						
Apoplanesia cryptopetala		x								
Astrocaryum triandrum						x				
Bathysa pittieri	x									
Bulnesia carrapo						x				
Calanthea stenosepala										x
Calycolpus warscewiczianus				x						
Capparidastrum tenuisiliquum		x								
Cavanillesia chicamochae		x								
Cecropia mutisiana							x			
Chomelia protracta				x						
Clusia cochliformis							x			
Coccoloba manzinellensis				x						
Coccoloba portuguesana								x		
Cordia macuirensis		x								
Coussarea curvigemma				x						
Croton draco				x						
Croton heliaster		x								
Croton malambo		x								
Croton pedicellatus							x			
Cupania seemannii				x						

Species	Caracas-Cerrejón	SA Caribbean Coast	Central America Pacific Coast	Central America semi-deciduous	Central America	Inter-Andean middle Magdalena Valley	Inter-Andean Valleys	Llanos semi-deciduous	Llanos flooded	Xerophytic SA Caribbean Coast
Erythroxylum jaimei							X			
Erythroxylum undulatum	X									
Eugenia mcvaughii	X									
Eugenia pachystachya								X		
Ficus lapathifolia			X							
Guatteria jefensis				X						
Guettarda krugii		X								
Helietta plaeana		X								
Inga nubigena				X						
Karwinskia colombiana				X						
Ledenbergia seguierioides	X									
Libidibia ebano		X								
Licania subrotundata									X	
Lonchocarpus crucisrubierae								X		
Lonchocarpus penthaphyllus				X						
Machaerium grandifolium		X								
Machaerium striatum							X			
Montanoa grandiflora			X							
Muellera broadwayi		X								
Neea bracteosa								X		
Neea nigricans		X								
Neocalyptrocalyx muco								X		
Ormosia panamensis				X						
Pilosocereus tillianus		X								
Poincianella exostemma			X							

Species	Caracas-Cerrejón	SA Caribbean Coast	Central America Pacific Coast	Central America semi-deciduous	Central America	Inter-Andean middle Magdalena Valley	Inter-Andean Valleys	Llanos semi-deciduous	Llanos flooded	Xerophytic SA Caribbean Coast
Rauia subtruncata								x		
Rudgea trujilloi								x		
Simira cesariana		x								
Sloanea bolivarensis								x		
Stenocereus aragonii			x							
Sterculia caribaea		x								
Styphnolobium sporadicum							x			
Talisia stricta						x				
Trichilia carinata						x				
Vasconcellea sphaerocarpa							x			
Xylopia pittieri		x								
Zanthoxylum gentryi							x			
Ziziphus cyclocardia							x			

Appendix 4.

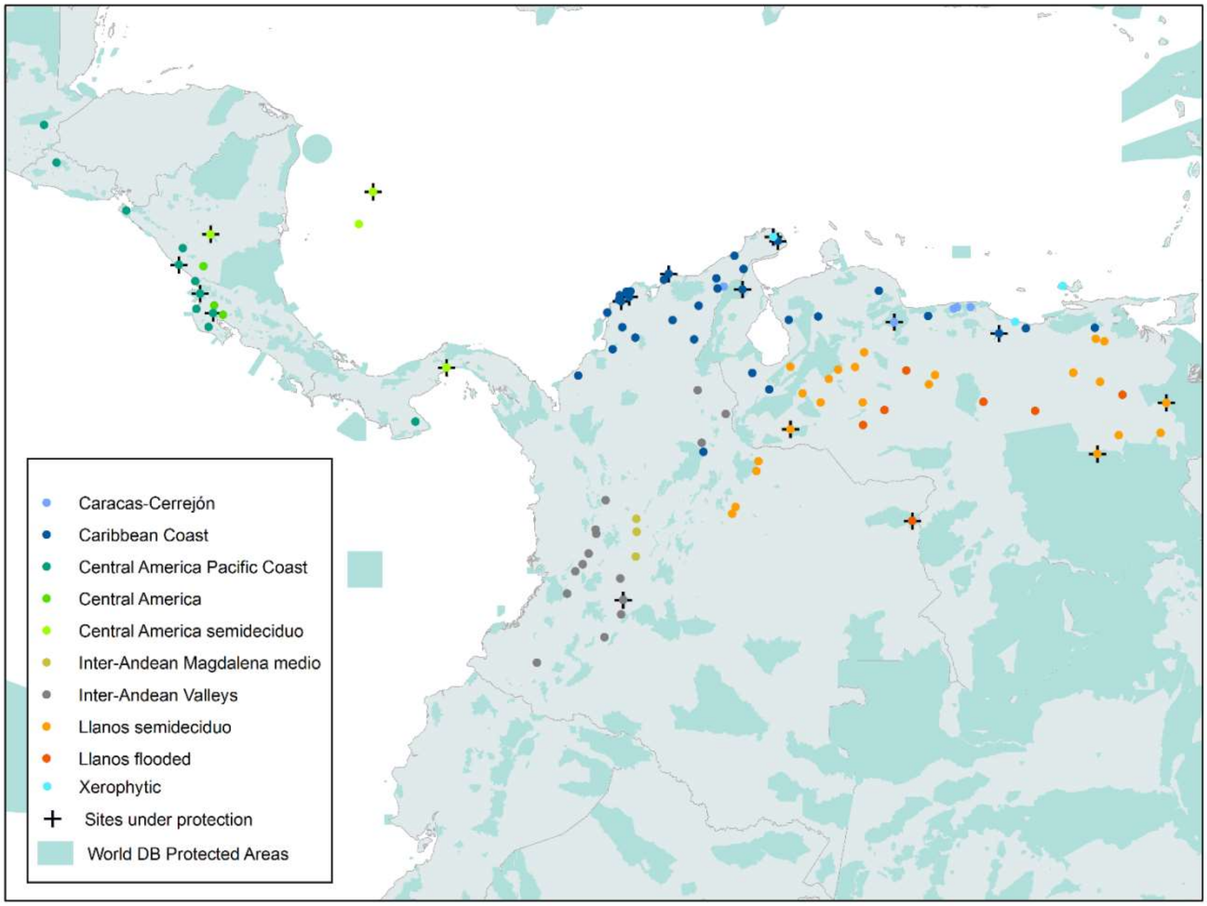


Figure. Representativeness of the dry forest floristic groups in protected areas (WDBP, 2015-UICN &UNEP-WCMC, www.protected planet.net)

Chapter 3 Understanding tree community patterns in Colombian dry forests

3.1 Summary

Dry forest is one of the most threatened ecosystems in Colombia. Investigating how its communities are structured and which environmental or spatial factors control their assembly might heplp to underpin more efficient conservation actions and to develop recovery plans for threatened species. Data from 39 inventories of trees from dry forest formations in Colombia that recorded abundance of each species were used to describe community patterns. The sample sites belong to three major dry forest floristic groups: Caribbean Coast, inter-Andean Valleys, and Llanos. Eighty-four percent of the 596 species recorded were not shared among these groups. Each dry forest group is characterized by a different set of dominant species, so there is no evidence of an oligarchy of species dominating these dry forest communities. The effects of environmental control of floristic composition were investigated using climatic, edaphic and anthropogenic variables. Mesotrophic soils were found in most areas with pH values between 5 and 7 and high contents of nutrients, except in the Llanos sites which have acid and nutrient-poor soils. Multivariate analyses showed that space-related variables explain the largest fraction of the variance of the floristic composition in all sites and within the major floristic groups (Caribbean and inter-Andean Valleys). These results contrast with several studies conducted in southern areas in the Neotropics where environment is reported as the most important factor correlating with floristic variation. Disturbance regime, specifically grazing by goats, also explains a small portion of the variance. The importance of space implies that biogeography is a key element for understanding the structure of these communities, and the Andean Cordilleras might be acting as geographical barriers isolating these seasonal dry formations. The variation found across

space indicated that distinctive conservation programs should be planned for each dry forest group, including alternative land uses such as sustainable forestry systems (using native species) and forest-pasture systems for cattle management on small scales, but excluding goats, which have a devastating effect on the vegetation. In scenarios of drying climates, dry forest specialist species that are currently rare might become more common, so I also recommend including such species, which may not be necessarily endemic to Colombia, in a priority conservation assessment list of species.

3.2 Introduction

The critical state of Colombian dry forest has finally attracted the attention of policy makers in the last five years with the realisation that less than 10% of its original extension remains (García et al., 2014). However, the relevance and efficiency of policy guidance and on the ground conservation actions have been limited due to the lack of robust baseline biodiversity data and studies that allow a better knowledge of ecological processes in dry forests. This chapter aims to understand the factors that structure tree communities in Colombian dry forest, which species compose these communities, and which species are more abundant. The answers to these questions provide important foundations to build conservation plans for the remnant areas of dry forest or to develop recovery plans for threatened or endangered species.

Floristically, dry forest formations in Colombia belong to the Central America and Northern South America dry forest floristic group defined in Chapter 1 (DRYFLOR, 2016), which is composed by eight sub-groups (Chapter 2). A large proportion of its species are drought-tolerant, but also widespread in various other habitats. Whilst the presence-absence floristic data used in Chapters 1 and 2 are useful for uncovering wide-scale biogeographic patterns, this chapter presents quantitative inventory data for Colombian dry forests, including species abundances, which allow more detailed studies of dominance and the structure of communities.

Dry forest is characterized by great variation in structure, from open scrublands to closed canopy forest (Pennington et al., 2009). There are also differences in the abiotic conditions of the sites where it occurs – a broad range of climate, altitude and soil type (Murphy & Lugo, 1995). Land use and management, which cause biodiversity loss, may also shape the component assemblages and overall distribution of dry forest. For example, ‘savannization’, which is primarily a structural reference to loss of trees from tropical forest areas for logging, often followed by fires (Ratnam et al., 2011), is a degradation process that frequently affects dry forests, changing their physiognomy, composition and ecological structure. Examining how community patterns are driven by environmental or spatial controls at regional scale may facilitate efficient planning of the management and conservation of dry forests in scenarios of increased disturbance and climate change.

Abiotic factors are variables (i. e. climatic, physical, and chemical) that might control the composition and structure of the biotic elements of the ecosystem. If the abiotic factors are spatially structured, their patterns will be reflected in the community assembly (Borcard et al., 2011). The method of multivariate variation partitioning (Borcard et al., 1992) allows inference of how much of the association among species is linked to their common and unique relationships with the environmental variables (Peres-Neto et al., 2006).

This chapter addresses two research questions: i. what are the patterns of tree species composition and dominance in dry forest formations in Colombia?; and ii. which spatial, climatic, edaphic or disturbance variables are controlling the assemblage of these communities, and how much of the variance in floristic composition can be explained by them?

I then addressed the following hypotheses i. dominant species in Colombian dry forests are specialist (ecologically restricted) to seasonally dry areas ii. variation in species composition among Colombian dry forest areas is related to climatic and edaphic conditions.

3.3 Methods

3.3.1 Floristic data

Quantitative inventory data were gathered for a total of 39 sites (Figure 1), 35 of which come from the published and unpublished studies from DRYFLOR Colombia (Latin American and Caribbean seasonally dry forest floristic network; http://www.dryflor.info/). These data were gathered using transects covering at least 0.1 ha and also from 1 ha permanent plots that are part of the Colombian Monitoring Network of dry forest. Seventy five percent of the surveys included stems > 2.5 cm diameter at breast height (DBH, i.e. 1.3 m) and 25% included stems >10 cm DBH.

Four new tree inventories (all >2.5 cm DBH) were conducted in two regions of Colombia where floristic information was poor or absent:

1. In the Northern-Andean region one transect-type survey and a 1 ha permanent plot were established in the Department of Norte de Santander in collaboration with the Universidad de Pamplona and the regional Herbarium Catatumbo-

Sarare, where 280 herbarium vouchers were processed and deposited. In total, 112 morpho-species were recorded, with 70% of them identified to species.

2. In the Piedmont area, two transect-type surveys were completed, one in the Department of Casanare and the second in Arauca. 120 vouchers were collected from 89 morpho-species with 75% identified to species. Identification of the material was carried out in collaboration with the Instituto de Ciencias Naturales (Universidad Nacional de Colombia, Bogotá) and the Colombian National Herbarium (COL), where samples were deposited.

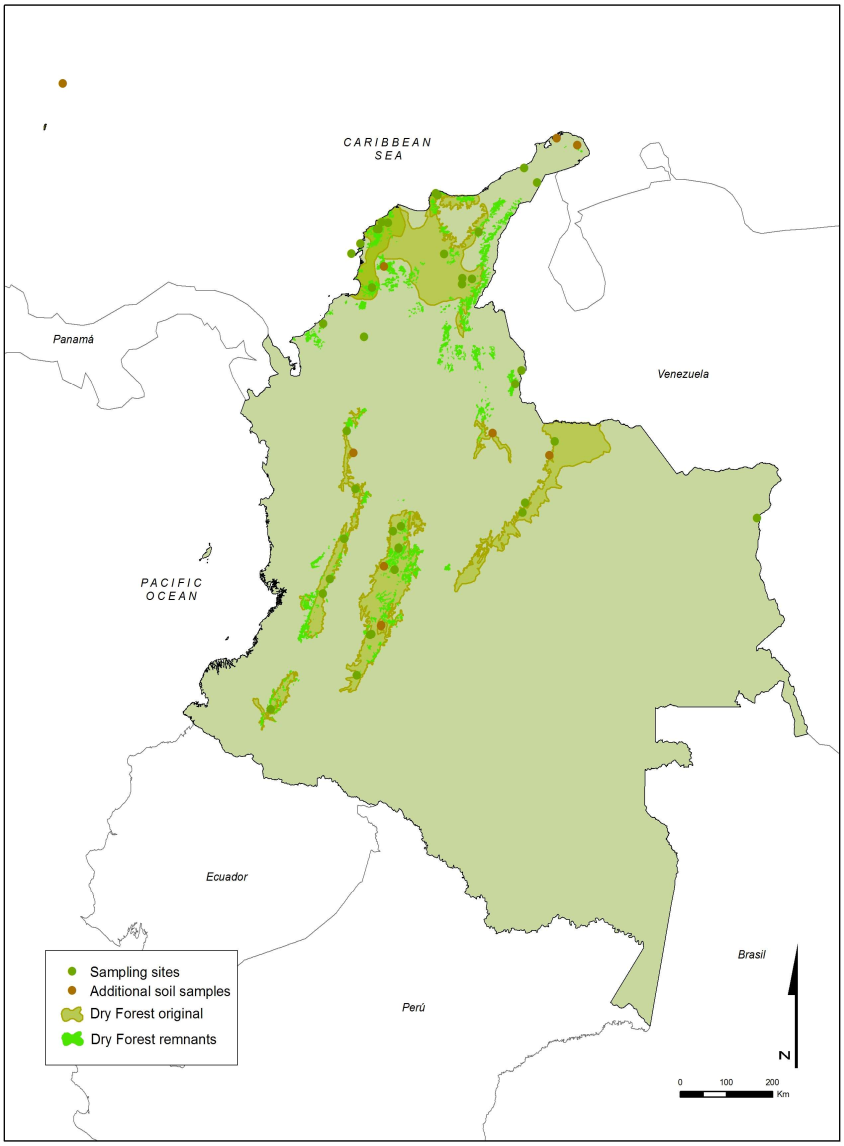


Figure 1. Sampling sites in the Colombian dry forest

Sampling sites are allocated throughout the whole distribution of dry forests in Colombia (Figure 1). They occur in relative well-conserved areas, avoiding highly disturbed zones. Some areas correspond to secondary forests because dry forest areas have a long history of land cover change, but these areas are at a late successional stage.

3.3.2 Environmental data

Soils

Soil samples were collected at 50 forest inventory sites, which included 39 for which tree species abundance data were available, plus an additional 11 chosen to ensure coverage of the broadest environmental gradient possible across Colombian dry forest (Figure 1). Sampling followed the protocol of Dexter & Baker (2013), in which four or five homogenous soil cores 30 cm long are extracted across the plot/transects (~30 cm depth after clearing the surface), then mixed and deposited in a paper bag (at least 500 g), leaving it to air dry. Samples were analysed in the Laboratory of Soils and Water of the Faculty of Agronomy at the Universidad Nacional de Colombia, Bogotá. In total, 13 parameters were measured: pH, exchangeable acidity, effective cation-exchange capacity (ECEC), Organic Carbon (OC), sodium (Na); content of the macronutrients nitrogen (N), calcium (Ca), potassium (K), magnesium (Mg) and phosphorus (P); and the proportion of clay, sand and silt particles as a measure of soil texture (Appendix 1).

Disturbance regime

Following the principles of Grounded Theory (Charmaz, 2006; Glaser & Strauss, 1967), in which through an inductive approach, qualitative data obtained from social research is analysed to develop a categorised model, a short-term history of land use was obtained by interviewing local inhabitants of dry forest sites during fieldwork. Interviews are considered an important tool that can provide detailed information about land use and local knowledge to understand the human-ecological relationship (Burguillos et al., 2008).

The open, informal interviews consisted of five questions about the forest site and surroundings: 1. How long have you been living here?; 2. As far as you know, has this area been always a forest?; 3. If not, what was it before and how long ago did the forest start to grow?; 4. Do people take timber from this forest?; and 5. Have people set fire to the forest and how often? Through the information gathered, five disturbance regimes that operated in the past were identified: cows, goats, crops, selective logging, and burning. Each of these disturbance regimes was classified using a linear time scale from 0.2 (most recent event) to 1 (none recorded) (Table 1). The whole disturbance dataset is in Appendix 2.

Table 1. Variables defined as a historical disturbance regime, fitted in a time-scale lineal model, for the Colombian dry forest sites.

	Time (years ago)				
Disturbance	<10	10 to 20	20 to30	>30	No recorded
Cows	0.2	0.4	0.6	0.8	1
Crops	0.2	0.4	0.6	0.8	1
Goats	0.2	0.4	0.6	0.8	1
Selective logging	0.2	0.4	0.6	0.8	1
Burning	<2	2 to 5	5 to10	>10	No recorded
	0.2	0.4	0.6	0.8	1

Climate

Climatic data for dry forest sites were obtained from the Worldclim database (Hijmans et al., 2005). The variables included 11 temperature and eight precipitation parameters (Table 2).

Table 2. Climatic variables taken from WorldClim (Hijmans et al. 2005)

Variable	**Description**
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

3.3.3 Statistical analyses

Exploratory analysis

Transformation of compositional community data was performed using the Hellinger distance, which is recommended for analysis of species abundance data (Rao, 1995; Legendre & Legengre, 1998; Legendre & Gallagher, 2001; Borcard et al., 2011). Transformations of the species data allow the use of ordination methods (e.g., PCA and RDA that are Euclidean distance-based) in data containing many zeros, a common situation when communities are highly dissimilar in species composition (Legendre & Gallagher, 2001),which is the case across Colombian dry forest. The Hellinger transformation offers a balance between linearity and resolution.

The floristic group, corresponding to those identified from the clustering analyses conducted in chapter 2, was also a variable taken into account. The Caribbean Coast, Inter-Andean Valleys, Llanos semi-deciduous and Llanos flooded are the Colombian dry forest floristic groups for which quantitative data were available. All Llanos sites were considered together because Llanos flooded was represented by just one site (Tuparro).

Spatial autocorrelation was quantified by calculating the Principal Coordinates of Neighbour Matrix (PCNM) among 38 sites samples (excluding Tuparro, the most distant site). Spatial autocorrelation describes the fact that proximal points in space are more correlated either positively (similar values) or negatively (dissimilar values) than randomly selected pairs (Borcard et al., 2011). Firstly, the function Rdist.earth (fields package in R, Nychka et al., 2016) was used to transform geographical coordinates into distance (Km). Secondly, using the R package vegan (Oksanen et al., 2016) the PCNM was calculated. This approach is recommended to detect spatial structure in ecological data where the distance between adjacent objects is preserved (Legendre et al., 2005). In a PCNM, spatial variables are used to determine the eigenvectors of the distance matrix focusing on neighbouring sites, where distances are decomposed into a new set of independent (orthogonal) spatial variables.

Multivariate analysis

Ecological processes occur at a variety of scales, showing complex, multiscale patterns. The multivariate approach provides a powerful tool for analysing community structure (Legendre & Gallagher, 2001). Here, the variation in community composition among the 38 sites based on raw or transformed data - the response floristic composition matrix - was evaluated with respect to several sets of explanatory variables.

Initially, I explored the relationship between the compositional data and the sets of variables by a simple Mantel test on distance matrices (Borcard et al., 2011; Mantel, 1967) for the species abundances (using the Bray-Curtis dissimilarity index) and for the principal components (PCA) of edaphic, climatic and disturbance variables, and also testing if differences in tree community composition among sites are due to spatial distance. The principal components correspond to a smaller number of factors, which are non-correlated after reducing dimensionality in the sets of variables. After running the Mantel test, Pearson (r) correlation values and the p-values for its significance were obtained.

Finally, I performed variation partitioning (Borcard et al., 1992) for the 38 sites samples and within the floristic groups. The aim of these analyses was to quantify the relative contribution of measured (edaphic, climatic and anthropogenic) and unmeasured, spatially-autocorrelated factors in explaining variation in the community composition. I used the function varpart in the R package Vegan (Oksanen et al., 2016) to get the unique and combined fractions of variation explained by several sources, using the adjusted R^2 in redundancy analysis ordination (RDA) (Borcard et al., 2011). RDA searches for a series of linear combinations of the explanatory variables that successively best explain the variation of the response matrix. The adjusted R^2 deals with the inflation of the amount of explained variance caused by random correlations.

3.4 Results

3.4.1 Floristic patterns

596 tree species from 316 genera and 75 families were found in 39 inventories. The first record of *Piranhea longepedunculata* (Picrodendraceae) in Colombia was made in the Northern-Andean region (La Garita permanent plot), a species previously known only from the Guiana Shield in Venezuela. Among the Caribbean Coast, Inter-Andean Valleys, and

Llanos groups - with 19, 16 and four surveys respectively - most of the species (496, 84% of the total) are restricted to one group and just 27 species (4.5%) are shared among all three.

The top 20 most dominant species were identified for each group (Table 3), of which only three species occur in more than one floristic group: *Astronium graveolens* (Anacardiaceae) and *Guazuma ulmifolia* (Malvaceae) dominate in the Caribbean and the Inter-Andean Valleys, and to a lesser extent *Spondias mombin* (Anacardiaceae) dominates in the Caribbean and Llanos groups.

Table 3. Dominant tree species (top 20 average relative abundance) per floristic group in the Colombian dry forest

Caribbean Coast		Inter-Andean Valleys		Llanos	
Species	Relative abund.	Species	Relative abund.	Species	Relative abund.
Astronium graveolens	7.2	*Guazuma ulmifolia*	5.3	*Genipa americana*	7.6
Guazuma ulmifolia	5.2	*Handroanthus chrysanthus*	5.1	*Tabebuia serratifolia*	6.3
Bursera simaruba	4.8	*Trichilia oligofoliolata*	4.7	*Bactris bidentula*	4.7
Hura crepitans	3.6	*Curatella americana*	3.7	*Triplaris weigeltiana*	3.5
Samanea saman	3.2	*Astronium graveolens*	3.3	*Cecropia engleriana*	3.2
Libidibia coriaria	2.9	*Casearia guianensis*	2.5	*Tapirira guianensis*	3.2
Pereskia guamacho	2.7	*Machaerium capote*	2.3	*Jacaranda obtusifolia*	3.2
Brosimum utile	2.2	*Mayna odorata*	2.2	*Cochlospermum vitifolium*	3.2
Capparidastrum frondosum	1.8	*Xylopia aromatica*	2.2	*Acrocomia aculeata*	2.7
Pithecellobium roseum	1.5	*Oxandra espintana*	1.9	*Eschweilera tenuifolia*	2.5
Quadrella odoratissima	1.5	*Eugenia procera*	1.8	*Annona edulis*	2.3
Spondias mombin	1.3	*Cupania americana*	1.7	*Tabernaemontana grandiflora*	2.2
Brosimum alicastrum	1.2	*Callicarpa acuminata*	1.5	*Protium guianense*	2.2
Bauhinia pauletia	1.2	*Myrcia splendens*	1.5	*Spondias mombin*	2.1
Attalea butyracea	1.2	*Clarisia biflora*	1.5	*Croton lechleri*	1.9
Tabernaemontana amygdalifolia	1.1	*Erythroxylum ulei*	1.5	*Gustavia augusta*	1.9
Coursetia ferruginea	1.1	*Cecropia peltata*	1.4	*Adenocalymma purpurascens*	1.7
Cochlospermum vitifolium	1.0	*Guarea guidonia*	1.3	*Derris utilis*	1.5
Triplaris weigeltiana	1.0	*Myriocarpa stipitata*	1.2	*Handroanthus chrysanthus*	1.5
Simira cordifolia	1.0	*Cupania latifolia*	1.2	*Himatanthus articulatus*	1.5

The most geographically restricted species, taking in account herbarium records,) are also the rarest for all the dry forest groups (Figure 2). For example, 6.3% of the stems recorded on the Caribbean coast are rare or local endemic species *Pithecellobium* *roseum, Muellera broadwayi* (Leguminosae), *Neea nigricans* (Nyctaginaceae), *Cynophalla linearis, Capparidastrum tenuisiliquum* (Capparaceae), and *Bourreria cumanensis* (Boraginaceae). In the Llanos group, only 1.5% of the stems correspond to the rarest two species recorded in the Tuparro National Park: *Licania subrotundata* (Chrysobalanaceae), which is a new record for Colombia (previously documented only for Venezuela), and the endemic *Pachira nukakika* (Malvaceae).

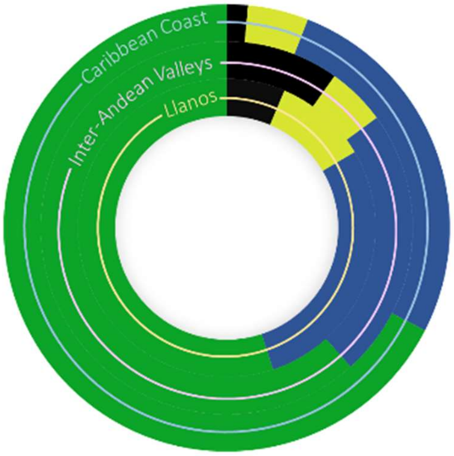


Figure 2. Proportion of the stems per floristic group belonging to each distribution range: Widespread (green), Continentally widespread (blue), Global rare (golden), Rare or local endemics (black).

3.4.2 Environmental patterns

Soils

Most of the soils fall into the mesotrophic category with pH values between 5 and 7 and high contents of magnesium and calcium of at least 2.0 me/100 gr and most of the sites with higher values. The Llanos sites differ, with acid (pH 4.4 on average) and dystrophic soils with low magnesium and calcium content (< 1.1 me/100 gr), except for Huron in the Piedmont (Appendix 1).

The drier environments have alkaline soils (pH 7.6-8.1). These include sites in La Guajira, the Tatacoa desert in the Magdalena Valley, the Chicamocha canyon in the Eastern

Cordillera, and calcareous sites from the Caribbean, including islands with a coral reef origin.

Soil texture for 90% of sites is sandy clay loam, with a balance of soil particle types with a low proportion of silt. The Llanos flooded site has a sandy loam and the drier areas (e.g., La Guajira, Tatacoa and Chicamocha) fall into the loamy sand category where the percentage of sand particles is high (<70%).

Disturbance

Selective logging and burning are the most generalized and intense disturbance regimes affecting the dry forest sites recently (average 0.55 and 0.77 respectively). Recent disturbance by cattle and crops is almost absent, which is consistent with the fact that most of the sites are late-stage forest successions. Hence intense grazing or crops, if they occurred, were probably more than 40 years ago. Goats are present in the drier areas in La Guajira.

Climate

Annual precipitation ranged from 380 mm in the driest areas in La Guajira to almost 3000 mm in the Piedmont sites. Removing these extreme values, 1,388 mm per year is the average rainfall (median = 1,355 mm). The mean annual temperature is 26°C. The highest temperature of the warmest month is in La Guajira (35°C) and the lowest in the inter-Andean Valleys (30°C).

3.4.3 Explaining the floristic variation of the dry forest tree communities

Correlations among variables showed a significant relationship between dissimilarity of species composition and geographic distance. The correlation between species composition and soils, climate or disturbance regime was not significant (r < 0.1 and p-values > 0.05, Figure 2).

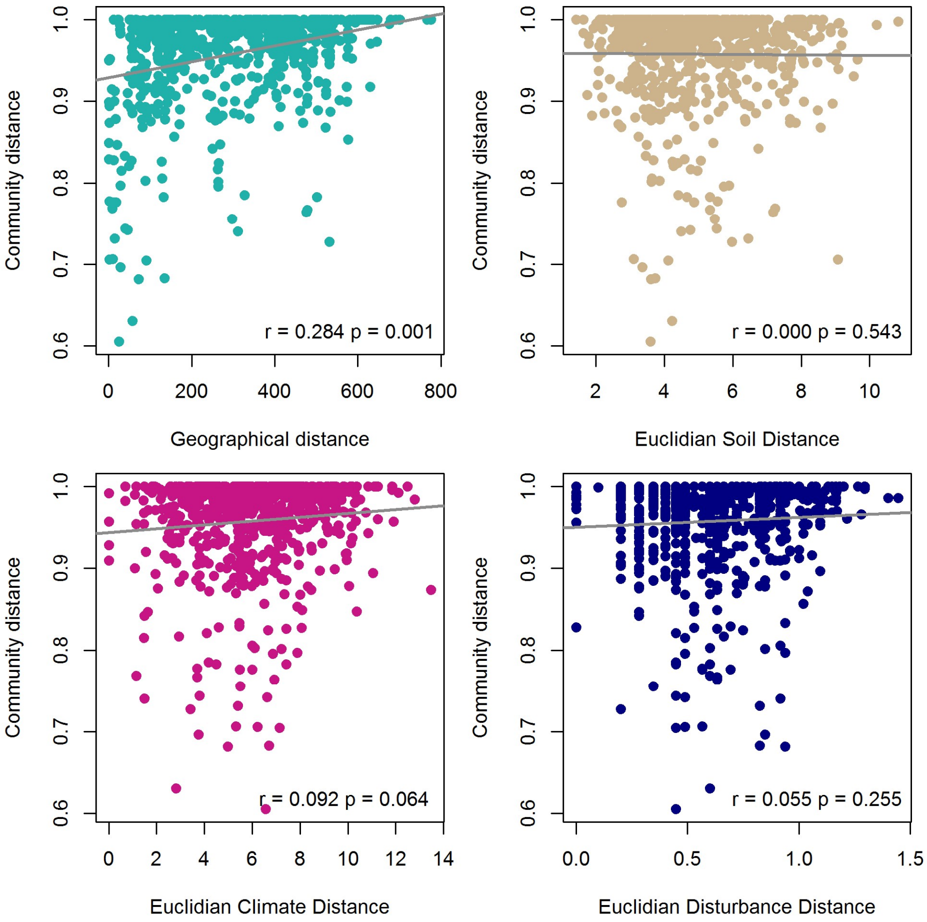
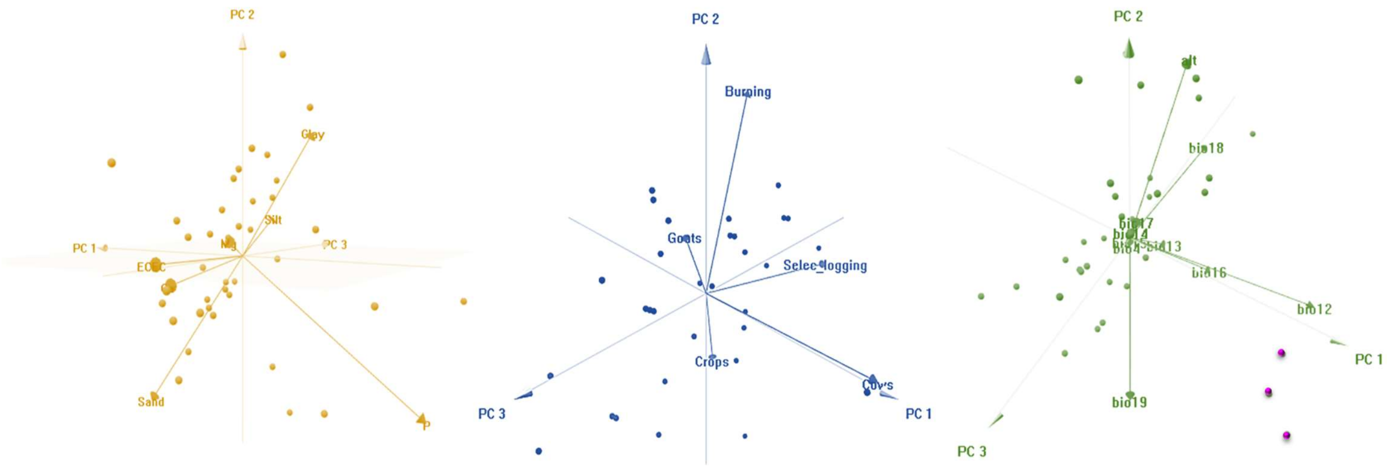


Figure 3. Correlation plots of the distance matrices of the external variables versus tree community composition of Colombian dry forest. Pearson correlation (r) and p-values (p) computed using simple Mantel tests are shown (999 permutations).

Principal components analyses (PCA) were plotted in three dimensions (Figure 4) allowing visualization of how variables are correlated. Most of the soil variables are correlated apart from potassium (P) content. For disturbance variables, goat livestock is non-correlated and falls apart from the principal components. For the climate variables, annual precipitation (bio12) and precipitation of coldest quarter (bio19) show a different pattern, separating the Llanos (purple dots, Figure 4) from the rest of the sites.



Soil variables

Disturbance variables

Climate variables

Figure 4. PCA plots

The major fraction of the variance in the community composition for the whole dataset (38 sites) was explained by the spatial arrangement of the sites (12%), the floristic grouping (2%), which is also a space-related variable, disturbance regime (1.3%) and the combinations of spatial arrangement-floristic group (1.5%), and spatial arrangement-floristic group-disturbance (0.09%). Edaphic and climatic characteristics explain very little of the variance (< 0.001). However, a great percentage of variation remained unexplained by the variables examined (Figure 5).

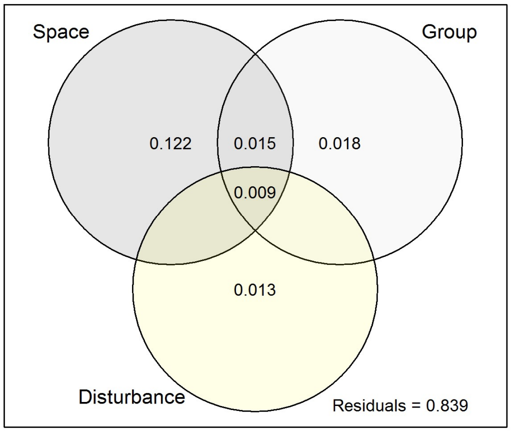


Figure 5. Venn diagram showing the fraction of the variance in dry forest species composition explained by the set of variables. Values < 0.001 are not shown.

Figure 6 illustrates the proportion of the variance explained in the main floristic groups: Caribbean (A) and inter-Andean (B) dry forest, excluding the Llanos group, which has a few sites (n=4 including the more distance site: Tuparro), less than the number of variables tested. These analyses within floristic groups allow control of the spatial correlation or biogeographic effect, assessing only the influence of the edaphic, climatic and disturbance variables on the community composition. In the Caribbean, 22% of the variance was explained by the variables evaluated, and climate and space together have the largest influence (6.8%). On the other hand, in the inter-Andean Valleys, only 4% of the variance of the dry forest community is explained with a relatively important contribution of the spatial arrangement (1%).

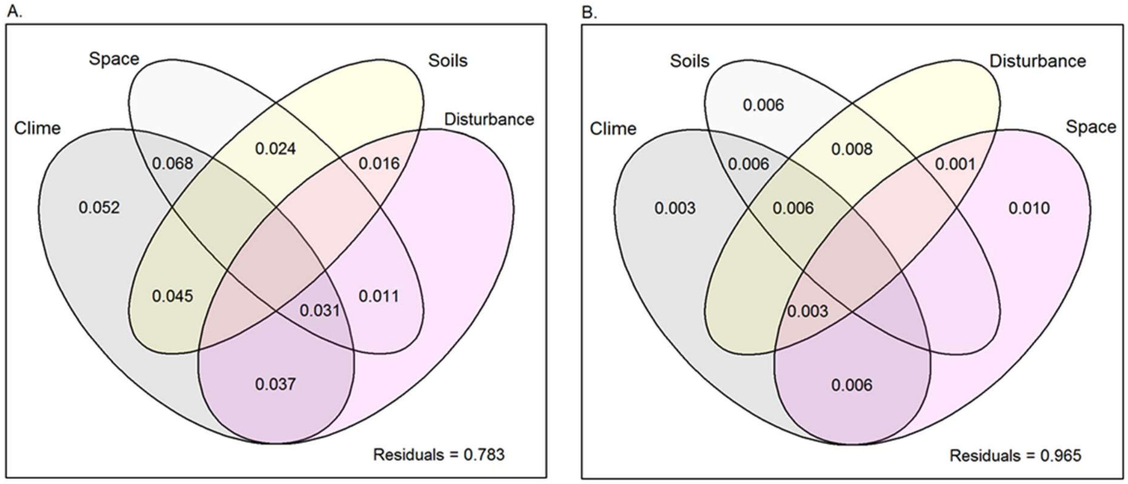


Figure 6. Venn diagram showing the fraction of the variance in species composition in A. Caribbean dry forest, (18 sites) and B. Inter-Andean dry forest ((17 sites), explained by the set of variables. Values < 0.001 are not shown.

3.5 Discussion

3.5.1 Tree community patterns

Across all sites, *Astronium graveolens* (Anacardiaceae), *Guazuma ulmifolia* (Malvaceae), *Bursera simaruba* (Burseraceae), *Handroanthus chrysanthus* (Bignoniaceae), *Trichilia* *oligofoliolata* (Meliaceae), *Hura crepitans* (Euphorbiaceae) *Curatella americana* (Dilleniaceae), *Casearia guianensis* (Salicaceae) and *Samanea saman* (Leguminosae) were identified as the most common species (>1.4% of total relative abundance, see Appendix 3). There is a great variety of distribution patterns and ecological range among these common species. For example, *T. oligofoliolata* is dry forest restricted, *C. americana* occurs in dry forest but is also characteristic of savannas, and *B. simaruba* and *G. ulmifolia* are found in both dry and wet formations. Geographically, *Trichilia oligofoliolata* is an endemic restricted to the Magdalena valley, *B. simaruba* is regionally widespread from Mexico to Venezuela, whereas *G. ulmifolia, H. chrysanthus* and *A. graveolens* are widespread across the Neotropics.

I rejected the hypothesis that dominant species in Colombian dry forests are specialist (ecologically restricted) to seasonally dry areas. Although the sample sites cover the best preserved areas of dry forest in Colombia, the fact that most of these abundant species are ecological generalist pioneers may reflect the disturbed nature of the vegetation. For the Colombian Caribbean, Castellanos-Castro and Newton (2015) reported that species turnover between successional stages may shift from ecological generalists to species more confined to dry forest in later stages. Furthermore, *G. ulmifolia* and *B. simaruba* are the species with the greatest number of uses reported in rural communities in the Colombian Caribbean region (Jiménez-Escobar & Estupiñán-González, 2011) and humans may be affecting their distribution patterns, both indirectly through degrading forest, making it a suitable habitat for these pioneer species, or directly by moving and planting them.

Some dry forest specialist species are also abundant, particularly in the Caribbean Coast group, (Table 3 and Appendix 3) including *Pereskia guamacho* (Cactaceae), *Libidibia* *coriaria, Bauhinia pauletia*, *Coursetia ferruginea* (Leguminosae) and *Quadrella odoratissima* (Capparaceae). Another set of dry forest specialist species are the least common, and of these the most geographically restricted species (black star in Figure 1) might be prioritized for conservation due to their constrained ecological preferences. They include *Bulnesia carrapo* (Zygophyllaceae)*, Capparidastrum tenuisiliquum, Cynophalla linearis* (Capparaceae)*, Bourreria cumanensis* (Boraginaceae), and *Muellera broadwayi* (Leguminosae). This pattern where endemic species are locally rare is also found in dry forest in the inter-Andean Valleys in Ecuador (Quintana, 2015).

Oligarchy in plant communities is defined as a group of common species that combine high frequency with high local abundance. This pattern of community structure has been reported for the savannas of central Brazil (Bridgewater et al., 2004) and for the Amazonian rain forest (Pitman et al., 2001; ter Steege et al., 2013), which are dominated by a few common species over large areas. In contrast, apart from *A. graveolens*, *G. ulmifolia* and *S. mombin,* which are abundant across more than one dry forest group, each Colombian dry forest group is characterized by a different set of dominant species (see Table 3), and 84% of all the species encountered were not shared among groups. This supports the suggestion from the continental scale dataset (Chapter 1) that there was no evidence of an oligarchy of species across more than one of the 12 major floristic dry forest groups.

3.5.2 Soils in Colombian dry forest

The general assumption of the relatively high fertility of neotropical dry forest soils (Fajardo et al., 2005; Oliveira-Filho & Ratter, 2002; Pennington et al., 2000) is confirmed for the Caribbean and inter-Andean dry forest sites in Colombia by the samples analysed here, which have pH values between 5 and 7 and high contents of nutrients. Mesotrophic soils with similar pH and nutrient status have been reported from the semi-deciduous “Cerradão” vegetation of the savannas in Central Brazil. According to studies conducted by Ratter (1973; 1978), there is a link between high soil nutrients and deciduousness of the dominant trees in the plant communities of Central Brazil, where soil fertility must be maintained by an efficient nutrient recycling process (Furley, 1996). Conversely, sites from the Andean Piedmont in the Llanos region had dystrophic and acid soils with pH lower than 4.9.

Soil fertility has also been inferred by a number of studies as a determinant in seasonal environments of the presence of grasslands (savannas) on poor, acid soils and forest on higher pH, richer soils (Goodland & Pollard, 1973; Lehmann et al., 2011; Lloyd et al., 2008; Stott, 1988). For example, in Peru, dry forests in inter-Andean sites have alkaline soils with pH values of 7.4 -8.0 and high levels of organic content, Ca, K and P, whereas savanna sites have acid soils with pH values from 5.1 to 5.4 and low nutrient levels (Pennington, unpublished). Similarly, in Central Brazil, savanna formations have poor and acid soils with pH lower than 5.5 in comparison to the more alkaline and nutrient-rich soils from dry semi-deciduous forest formations (Furley & Ratter, 1988; Ratter et al., 1978). Although the sampling in this study did not include savanna sites, dystrophic soils were found in the Andean Piedmont of the Llanos region and in the drier environments where trees are not dominant elements of the vegetation.

3.5.3 Drivers of tree community composition

Tree community composition in Colombian dry forest formations is most strongly related to their spatial arrangement (Figure 3). The floristic group to which each site belongs is also an important factor explaining the variation of these communities. This variable is also space-related since the groupings show strong geographical structure, separating sites of the Caribbean Coast, the Inter-Andean Valleys and those from the Andean Piedmont in the Llanos region.

The second hypothesis of this chapter, which states that variations in species composition among Colombian dry forest areas are related to climatic and edaphic conditions is also rejected. This result, emphasising space rather than environment, contrasts with several studies in which variation in species composition has been strongly related to precipitation gradients and evapotranspiration at wide geographic scales in the Neotropics (Gentry, 1995; Trejo & Dirzo, 2002). It also differs from studies made at more local scales, where different environmental variables - such as topography, altitude, climate, and soil variables related to water availability, soil nitrogen and slope - have been reported as drivers of species turnover (Lott et al., 1987; Oliveira-Filho et al.,1998; Espinosa et al., 2011).

At a broad geographic scale, in a study conducted in the dry diagonal in South America, covering the Central Brazil and Caatinga dry forest groups (Chapter 1), Neves et al. (2015) showed that temperature-related variables were the most significant factors controlling variation in species composition. For the Colombian dry forest, all temperature variables (Table 2) are similar across the sites analysed (+/- 1.56°C mean SD) whereas differences in temperature across the dry diagonal are larger due to the wide latitudinal gradient, with mild temperatures in the coldest month and a low annual temperature range in the northern compared with the southern areas.

At more local scales, edaphic control of floristic composition has been shown in several studies conducted across biome boundaries such as that between savannas and dry forests (Furley & Ratter, 1988; Oliveira-Filho & Ratter, 2002). According to the data analysed here, tree community composition within dry forest formations in Colombia is not driven by soil types (Figure 2, Figure 3), which was also shown in dry forests in Costa Rica (Powers et al., 2009). This may reflect the minor differences in pH and nutrient status of soils within the Colombian dry forest formations, which are less than those found between the acid, nutrient poor soils of savannas and the more fertile, high pH soils of dry forests in central Brazil.

Edaphic variables do not explain the variation in floristic composition within the different dry forest communities in Colombia but soil properties may affect the physiognomy of the vegetation. Along a gradient from sandy soils with low nutrient availability to clayey, nutrient-rich soils, there is a change from open, low cactus scrub in the drier or even semi-desert areas to much taller semi-deciduous forest. This gradient was also reported by Powers et al. (2009) for dry forest in Costa Rica.

Disturbance regime explained only a small fraction of the variation in community composition as was observed at landscape scales in the Colombian Caribbean (Castellanos-Castro & Newton 2015), in the inter-Andean Valleys in Ecuador (Quintana, 2015) and also in secondary dry forests of Mexico (Gordon et al., 2004; Williams-Linera & Lorea, 2009) and the Bahamas (Larkin et al., 2012). The goat grazing regime was the most important explanatory variable selected in the RDA; this disturbance regime affects the drier areas of Colombian dry forests. It is well known that goats are responsible for dramatic changes in vegetation cover, species composition, and soil compaction (Manzano & Návar, 2000), being able to graze even marginal lands (Eisler et al., 2014). In the driest areas of Colombia, (i.e., Chicamocha Canyon) goats are responsible for massive transformation of plant communities, loss of woody elements, and promoting the abundance of unpalatable species (Valencia-Duarte et al., 2012).

A large fraction of the variance in the community composition is not explained by the variables analysed. It is common in species composition studies to have a high percentage of residual variation (from 33 to 83%; Legendre et al., 2009; Oliveira-Filho et al., 2013; Castellanos-Castro & Newton, 2015; Neves et al., 2015) meaning that the complexity of processes driving community composition is not entirely captured. There are several factors that were not included in this study that are potentially important drivers in the community assembly of Colombian dry forest. These could be topography, successional stage of the vegetation, and ecological processes such as biotic interactions and dispersal mode.

Overall, the significance of space-related variables in controlling the variation of dry forest tree communities indicates the importance of biogeography in the understanding of the floristic composition of these formations. Differences in tree species composition might be related to the Andean cordilleras in Colombia acting as massive geographical barriers isolating these seasonal dry formations. The biggest extension of dry forest in Colombia occurs on the Caribbean coast whereas the other two main groups are Andean, one occurring along the inter-Andean Valleys of the Magdalena, Cauca and Patía rivers (Chapter 2), and the second one along the Piedmont of the Eastern Cordillera in the Llanos region.

The environmental conditions - for both climatic and edaphic variables - under which dry forests grow across the country are similar. In the inter-Andean Valleys, rain shadows maintain low precipitation, similar in magnitude to that on the Caribbean coast, where precipitation regime is determined by the intertropical convergence zone (ITCZ) (Seo et al., 2014). In both of these regions there is low seasonal rainfall, which causes low nutrient leaching, helping to maintain fertile soils where dry forests occur. This overall similarity in abiotic factors of climate and soil across Colombian dry forests may explain why it is less important as a control of floristic composition.

3.6 Conclusions and implications for conservation

Quantitative inventory data for Colombian dry forests confirm that the majority of the most abundant species there are drought-tolerant, ecological generalists, widespread in various other habitats. In contrast, dry forest specialist species are more geographical restricted and are also locally rare.

There is no evidence of an oligarchy of species dominating across large areas of dry forest in Colombia. The majority of the species recorded in all sites were not shared among major floristic groups. Apart from three widespread species (*Guazuma ulmifolia*, *Astronium graveolens* and *Spondias mombin*), each dry forest group is characterized by a different set of dominant species.

Currently, nationally endemic species of Colombian dry forest are prioritized for conservation assessments. However, I recommend including in this priority list species that are dry forest specialist and locally rare, but which may not be endemic to Colombia, such as: *Capparidastrum tenuisiliquum, Cynophalla linearis* (Capparaceae), *Bourreria cumanensis* (Boraginaceae), and *Muellera broadwayi* (Leguminosae). Extreme climatic events may lead to changes in composition and abundance of plant species in seasonally dry formations. Protecting rare species, which might be the common species of the future, may well be critically relevant in times of climatic change.

Among the dry forest formations, tree species composition is spatially structured, so conservation actions should consider the biogeographic structure uncovered here. It is likely that spatially autocorrelated but unmeasured environmental variables such as dispersal limitation, or historical biogeographic fragmentation are causing neighbouring dry forest sites to be similar, and distant sites to be different, in tree composition. In this context, particular conservation programs should be planned and implemented for each dry forest group, including alternative land use for surrounding areas of dry forests across the country. For example, sustainable forestry systems for long term timber production using native species and small scale forest-pasture systems for cattle management may be feasible options. Avoiding goats as livestock is desirable because they cause massive vegetation degradation, promoting desertification processes in drylands.

3.7 Appendices

Appendix 1.

Table. Soil data for 39 dry forest sites in Colombia, which belong to three floristic groups Caribbean Coast, Inter-Andean Valleys and Llanos and 11 additional samples across the environmental gradient.: pH, proportion of Organic Carbon (OC) and nitrogen (N); meq per 100 gr of exchangeable acidity (Acidity), effective cation-exchange capacity (ECEC), sodium (Na), calcium (Ca), potassium (K), magnesium (Mg) and phosphorus (P); and soil texture: proportion of clay, silt and sand

No.	Site-Department	pH	OC	N	Ca	K	Mg	Na	Acidity	ECEC	P	Clay	Silt	Sand
1	LaLoma-Cesar	5.1	0.57	0.05	0.73	0.08	0.16	0.03	0.52	1.51	55.40	6	15	79
2	Maicao-La Guajira	5.4	0.64	0.09	6.67	0.70	6.19	0.36	0.21	14.10	3.75	46	23	31
3	Tayrona-Magdalena	5.4	1.20	0.20	2.86	0.34	2.65	0.34	0.94	7.13	3.05	30	34	35
4	Canalete-Córdoba	5.7	1.33	0.20	4.35	0.73	7.81	0.43	0.00	13.30	1.37	72	27	1
5	Rkalashe-Magdalena	5.9	1.46	0.16	5.80	0.16	1.25	0.19	0.00	7.41	3.35	12	18	69
6	ElCeibal-Bolívar	6.0	1.80	0.19	2.49	1.14	10.50	0.50	0.00	14.70	21.00	64	33	3
7	Palomar-Atlántico	6.0	1.33	0.14	9.81	0.38	2.61	0.14	0.00	12.90	4.47	20	23	57
8	Becerril1-Cersar	6.2	0.65	0.29	18.70	1.06	3.07	0.17	0.00	23.00	95.20	62	23	15
9	Luriza-Atlántico	6.4	1.19	0.15	9.02	0.37	2.85	0.08	0.00	12.30	13.50	10	10	79
10	Manaure-La Guajira	6.5	0.39	0.05	6.78	0.75	1.70	0.19	0.00	9.42	4.67	28	22	49
11	ElCopey-Cesar	6.6	2.27	0.26	14.90	0.89	3.46	0.09	0.00	19.40	88.70	26	27	47
12	Besotes-Cesar	6.7	3.19	0.29	8.24	0.42	1.20	0.03	0.00	9.89	10.80	16	16	67
13	SanJorge-Córdoba	6.8	2.90	0.24	2.61	0.37	9.20	0.21	0.00	12.40	9.69	36	19	45
14	Rosales-Atlántico	7.0	2.21	0.25	20.80	0.48	3.27	0.10	0.00	24.60	35.90	18	15	67
15	IslaRosario-Bolívar	7.1	4.13	0.44	1.93	0.39	3.72	3.91	0.00	9.95	13.50	20	16	63
16	Tierrabomba'Bolívar	7.3	2.25	0.26	12.10	0.98	2.25	0.23	0.00	15.50	12.00	56	22	21
17	Becerril2-Cesar	7.4	2.92	0.34	5.63	0.40	1.35	0.11	0.00	7.49	116.00	58	38	3
18	Coloso-Sucre	7.4	1.76	0.20	1.02	1.04	2.93	0.12	0.00	5.10	7.62	34	32	34
19	Pozo-Huila	4.5	1.32	0.10	1.47	0.12	0.87	0.06	1.63	4.15	0.70	18	36	46
20	ElRaizon-Norte de Santander	4.7	4.38	0.31	2.62	0.25	0.67	0.06	1.37	4.97	8.65	16	13	71
21	Patia-Nariño	5.1	2.62	0.14	26.10	0.33	5.00	0.17	0.32	32.00	43.80	30	30	40
22	Demo-Huila	5.2	1.99	0.16	4.18	0.25	1.80	0.08	0.21	6.53	7.67	16	20	64
23	Muro-Huila	5.5	2.14	0.30	13.40	0.44	5.23	0.08	0.00	19.20	53.00	46	38	16

No.	Site-Department	pH	OC	N	Ca	K	Mg	Na	Acidity	ECEC	P	Clay	Silt	Sand
24	Zorra-Tolima	5.7	2.65	0.25	8.78	0.06	5.99	0.14	0.00	15.00	1.38	18	36	46
25	Chispidial-Huila	5.8	1.02	0.08	6.62	0.20	2.75	0.10	0.00	9.67	27.20	20	42	38
26	Tulua-Valle del Cauca	6.0	5.32	0.45	30.20	0.85	6.00	0.51	0.00	37.60	40.10	36	28	36
27	Tasajero-Norte de Santander	6.1	2.65	0.32	8.97	0.78	5.47	0.06	0.00	15.30	5.00	40	29	31
28	Pereira-Risaralda	6.2	3.86	0.49	14.30	0.47	6.20	0.08	0.00	21.00	0.70	32	22	46
29	Tamesis-Antioquia	6.2	0.71	0.08	4.08	0.18	1.14	0.10	0.00	5.50	42.50	6	12	82
30	Limones1-Tolima	6.5	3.01	0.31	13.30	0.77	3.31	0.07	0.00	17.40	25.00	20	22	58
31	Quimbo-Huila	6.7	1.68	0.15	10.90	0.29	3.73	0.13	0.00	15.00	1.76	18	46	36
32	Limones2-Tolima	6.8	3.22	0.31	16.20	0.55	4.44	0.08	0.00	21.30	7.57	26	30	44
33	Mendez-Tolima	6.8	1.54	0.18	19.40	0.31	4.22	0.11	0.00	24.00	14.20	18	24	58
34	Vinculo-Valler del Cauca	6.9	3.77	0.65	22.40	0.84	14.80	0.13	0.00	38.20	0.70	42	26	32
35	Neme-Tolima	7.5	2.36	0.26	28.60	0.38	1.46	0.13	0.00	30.60	34.50	22	32	46
36	Malvinas-Arauca	4.1	2.27	0.20	1.10	0.06	0.23	0.01	0.27	1.66	1.32	8	28	64
38	Tuparro-Vichada	4.4	2.77	0.22	0.49	0.27	0.14	0.09	1.33	2.32	8.60	14	18	68
39	LaVirgen-Casanare	4.4	1.27	0.10	0.63	0.14	1.08	0.12	6.90	8.87	0.70	44	30	26
42	Huron-Casanare	4.9	0.86	0.09	2.39	0.13	0.35	0.05	1.36	4.28	3.77	20	14	66
37	ElOso-Arauca	4.4	0.68	0.06	0.34	0.18	0.38	0.18	3.11	4.19	1.36	26	46	28
40	UribeUribe-Santander	4.3	1.37	0.15	2.00	0.08	0.26	0.08	4.16	6.58	0.98	26	24	50
41	LaGarita-Norte de Santander	4.8	3.63	0.31	6.33	0.72	2.29	0.04	0.17	9.55	4.74	36	38	26
43	Eucalipto-Cesar	4.9	0.53	0.03	0.19	0.14	0.08	0.01	0.37	0.79	2.22	2	15	83
44	Peak-San Andrés y Providencia	6.0	1.91	0.28	13.30	0.59	5.85	0.51	0.00	20.20	10.60	20	24	56
45	HdaAltamira-Tolima	6.7	3.88	0.35	16.70	0.21	3.26	0.23	0.00	20.40	26.60	18	32	50
46	Chicamocha-Santander	7.2	5.42	0.59	1.16	1.44	2.12	0.07	0.00	4.80	116.00	16	15	69
47	Tatacoa2_Huila	7.4	1.79	0.22	13.60	0.48	1.71	0.04	0.00	15.80	94.20	8	14	78
48	AltaGuajira-LaGuajira	7.5	0.27	0.02	5.55	0.88	5.63	8.46	0.00	20.50	49.20	22	6	71
49	PtaGallinas-LaGuajira	8.1	0.51	0.05	15.80	0.74	1.24	0.38	0.00	18.20	45.90	16	8	75
50	Tatacoa_Huila	8.8	0.08	0.03	27.10	0.49	3.79	9.67	0.00	41.10	116.00	40	26	34

Appendix 2.

Table. Disturbance data which include five variables defined through interviews to local inhabitants around dry forest sites

	Sites	cows	crops	burning	selec_logging	goats
1	LaLoma-Cesar	0.20	1.00	0.40	0.60	1.00
2	Maicao-La Guajira	0.80	1.00	0.80	0.60	0.20
3	Tayrona-Magdalena	1.00	1.00	0.80	1.00	1.00
4	Canalete-Córdoba	0.60	1.00	0.60	0.80	1.00
5	Rkalashe-Magdalena	0.60	0.60	1.00	0.80	1.00
6	ElCeibal-Bolívar	1.00	1.00	0.40	0.40	1.00
7	Palomar-Atlántico	0.40	0.30	1.00	0.40	1.00
8	Becerril1-Cersar	1.00	0.60	1.00	0.40	1.00
9	Luriza-Atlántico	0.40	1.00	1.00	0.40	1.00
10	Manaure-La Guajira	0.80	1.00	0.20	0.80	0.20
11	ElCopey-Cesar	0.20	1.00	0.80	0.60	1.00
12	Besotes-Cesar	0.80	1.00	0.80	0.80	1.00
13	SanJorge-Córdoba	0.80	1.00	0.80	0.60	1.00
14	Rosales-Atlántico	0.80	1.00	0.40	0.40	1.00
15	IslaRosario-Bolívar	1.00	1.00	0.40	0.80	1.00
16	Tierrabomba'Bolívar	0.40	0.40	1.00	0.40	1.00
17	Becerril2-Cesar	0.80	1.00	0.40	0.20	1.00
18	Coloso-Sucre	1.00	1.00	1.00	0.60	1.00
19	Pozo-Huila	0.80	1.00	0.60	0.60	1.00
20	ElRaizon-Norte de Santander	1.00	1.00	0.80	0.20	1.00
21	Patia-Nariño	0.60	0.80	0.60	0.20	1.00
22	Demo-Huila	8.00	1.00	0.60	0.60	1.00
23	Muro-Huila	0.80	0.20	0.60	0.80	1.00
24	Zorra-Tolima	0.80	1.00	1.00	0.80	1.00
25	Chispidial-Huila	0.80	1.00	0.20	0.60	1.00
26	Tulua-Valle del Cauca	0.80	0.80	1.00	0.60	1.00
27	Tasajero-Norte de Santander	1.00	1.00	0.80	0.40	1.00
28	Pereira-Risaralda	0.80	1.00	0.80	0.60	1.00
29	Tamesis-Antioquia	0.80	1.00	0.80	0.80	1.00
30	Limones1-Tolima	0.80	1.00	0.80	0.40	1.00
31	Quimbo-Huila	0.60	1.00	0.80	0.40	1.00
32	Limones2-Tolima	0.80	1.00	0.80	0.40	1.00
33	Mendez-Tolima	1.00	1.00	1.00	0.80	1.00
34	Vinculo-Valler del Cauca	1.00	1.00	1.00	0.60	1.00
35	Neme-Tolima	1.00	1.00	1.00	0.60	1.00
36	Malvinas-Arauca	0.80	1.00	1.00	0.60	1.00
38	ElOso-Arauca	1.00	1.00	1.00	0.20	1.00
39	Tuparro-Vichada	1.00	1.00	0.80	1.00	1.00
42	LaVirgen-Casanare	1.00	1.00	1.00	0.20	1.00

	Sites	cows	crops	burning	selec_logging	goats
37	UribeUribe-Santander	NA	NA	NA	NA	NA
40	LaGarita-Norte de Santander	1.00	1.00	1.00	0.20	1.00
41	Huron-Casanare	0.80	1.00	1.00	0.60	1.00
43	Eucalipto-Cesar	0.00	0.00	0.00	0.00	0.00
44	Peak-San Andrés y Providencia	1.00	1.00	1.00	0.80	1.00
45	HdaAltamira-Tolima	NA	NA	NA	NA	NA
46	Chicamocha-Santander	0.80	0.60	0.80	0.60	0.20
47	Tatacoa2_Huila	0.80	1.00	0.40	0.60	0.20
48	AltaGuajira-LaGuajira	NA	NA	NA	NA	NA
49	PtaGallinas-LaGuajira	NA	NA	NA	NA	NA
50	Tatacoa_Huila	1.00	1.00	1.00	0.80	0.20

Appendix 3.

Table. The top 20 species with the highest average relative abundance in all the Colombian dry forest sites.

Family	Species	Relative abundance
Anacardiaceae	*Astronium graveolens*	4.9
Malvaceae	*Guazuma ulmifolia*	4.9
Burseraceae	*Bursera simaruba*	2.8
Bignoniaceae	*Handroanthus chrysanthus*	2.6
Meliaceae	*Trichilia oligofoliolata*	2.1
Euphorbiaceae	*Hura crepitans*	1.8
Dilleniaceae	*Curatella americana*	1.6
Salicaceae	*Casearia guianensis*	1.5
Leguminosae	*Samanea saman*	1.5
Leguminosae	*Libidibia coriaria*	1.3
Cactaceae	*Pereskia guamacho*	1.2
Moracae	*Brosimum utile*	1.2
Leguminosae	*Machaerium capote*	1.1
Annonaceae	*Xylopia aromatica*	1.1
Polygonaceae	*Triplaris weigeltiana*	1.0
Achariaceae	*Mayna odorata*	1.0
Rubiaceae	*Genipa americana*	0.9
Anacardiaceae	*Tapirira guianensis*	0.9
Moraceae	*Brosimum alicastrum*	0.9
Annonaceae	*Oxandra espintana*	0.8

Chapter 4 Tree inventory data as a valuable tool for IUCN red list assessments: The Piedmont dry forest as a case study

4.1 Summary

This chapter evaluates the value of a floristic database for more than 1600 tree species inventories across Latin America and the Caribbean assembled by the DRYFLOR network for assessing species conservation status of species in highly threatened dry forests. It presents a case study of a regional IUCN assessment for 193 tree species from the Andean Piedmont dry forest. Data on the distribution and conservation status of species provide the foundation for making informed conservation decisions and the International Union for Conservation of Nature (IUCN) Red List is a commonly used conservation tool that underpins priority setting processes from single species to entire ecosystems. The conservation assessment used herbarium records (GBIF) and inventory data (DRYFLOR) to estimate extents of occurrence (EOO) and area of extension (AOE). These two parameters were calculated using a mapping tool developed directly by DRYFLOR and also by GeoCAT (interface from Royal Botanic Gardens, Kew). EOO and AOO values calculated from DRYFLOR and GBIF are dissimilar. I found that combining inventory and herbarium records increases the number of species for which information is sufficient to make conservation assessments by 15%, and improves the accuracy of the distribution data for 84% of tree species. Therefore, these data sources may provide complementary information. The IUCN is increasingly integrating spatial databases of species to expand the cover of conservation assessments, including the use of species distribution modelling (SDM). The additional use of empirical data from ecological inventories is a valuable alternative approach assessing impacts of climate change, which does not run the risk of over-prediction of species distributions, as is sometimes the case with SDMs. Here, the

importance of ecological inventory data as a complementary data source in conservation assessment for dry forest trees in the Andean Piedmont is demonstrated, suggesting its potential use across all the Neotropics.

4.2 Introduction

Dry forest supports the livelihoods of many people, but centuries of destruction by colonial agriculture, extensive cattle ranching, monocrops and large-scale mining mean that its conservation status is now critical. It is considered the most threatened tropical forest in the Neotropics (Miles et al., 2006). At continental and regional scale, dry forest shows high floristic turnover, but it is underrepresented in the Latin American protected areas system (Chapter 1, DRYFLOR, 2016 and Chapter 2). Also, because of the dramatic reduction of their original extension - in some countries only 10% is left (García et al., 2014) - valuable ecosystem services that dry forest supplies are disappearing (Blackie et al., 2014). It is likely that many dry forest tree species are highly threatened due to habitat loss, but this has not been assessed quantitatively. Therefore, research and policy tools are urgently needed to address the critical state of dry forest at continental and national scales in the Neotropics. In this context, information on the distribution and conservation status of species provide the foundation for making informed conservation decisions.

The International Union for Conservation of Nature (IUCN) Red list is a commonly used conservation tool which underpins priority setting processes for single species and, when using multi-species data, entire ecosystems. IUCN Red List assessment includes two key elements: 1) a set of expert-reviewed data on species distribution, abundance, population trends, and threats; and 2) qualified application of IUCN agreed Categories and Criteria based on interpretation of these data (IUCN, 2013). IUCN Red List assessments rely principally on herbarium specimen data from natural history collections due to the absence of accurate population data or detailed distribution maps for the majority of plant species, especially in the tropics (Brummitt et al., 2015). However, additional sources of information such as field survey data have recently been included in the four-stage process of The Global Tree Assessment (GTA, https://www.bgci.org/plant-conservation/GlobalTreeSearch) to generate species distribution maps (A. Newton et al., 2015). GTA is an ambitious initiative which has the aim to conduct a complete assessment of the conservation status of the world’s tree species by 2020, to ensure that conservation efforts are directed at species at the highest risk of extinction.

Red listing of all national endemic species is the basis for national conservation policy (IUCN, 2013; Schatz, 2009), which is a good starting point as these are global species conservation assessments by definition. However, species may have a small range that spans borders between two or more countries, and national efforts are not fully appropriate for these. In the case of neotropical dry forests, high levels of endemism are found in the Central Andean dry forests groups, with 30 to 40% exclusive species restricted to very small areas of dry forest that span the Ecuadorian and Peruvian borders (Linares-Palomino et al., 2011; Chapter 1, Dryflor, 2016). These species are would not be represented in initiatives prioritizing national endemics. For this reason, the development of regional assessments based on a biogeographical approach has been recommended (Chapter 2, Gentili et al., 2011).

Inventory data for almost 7000 dry forest tree species across Latin America and the Caribbean have been gathered by the DRYFLOR network (Latin American and Caribbean seasonally dry forest floristic network- http://www.dryflor.info/), which has developed a detailed floristic database from more than 1600 neotropical dry forest sites. DRYFLOR comprises a group of researchers and conservationists from throughout Latin America, who are dry forest floristic experts. DRYFLOR inventory data and the expertise of the network partners might both be important elements to help to assess the conservation status of dry forest tree species.

The aim of this study is to estimate the value of the DRYFLOR data for assessing the conservation status of dry forest trees, specifically, calculating the parameters needed for IUCN assessments. Using a biogeographical approach, the Andean Piedmont group, which is one of the 12 floristic groups in the Neotropics identified in chapter 1 (DRYFLOR, 2016), was selected as a case study. Approximately 86% of the dry forest tree species of the Andes are not evaluated into IUCN categories, so new conservation assessments developed for this region make a concrete contribution to priority-setting for species preservation in the Andes.

The research questions in this chapter are: i. Are the inventory data complementary or redundant to the herbaria records for the tree species distribution of the Piedmont dry forest? And ii. Are conclusions from the Piedmont dry forests applicable to other dry forest areas?

4.3 Methods

4.3.1 Study area and species distribution records

The utility of inventory data was evaluated by calculating the parameters for a preliminary regional IUCN assessment for 193 species of trees from the Piedmont dry forest group which covers the eastern flanks of the northern Argentinean and southern Bolivian Andes.

The Piedmont group was one of the six Andean groups that represent biologically meaningful units based on their floristic composition (dots in colours Figure 1. and Chapter 1, DRYFLOR, 2016).

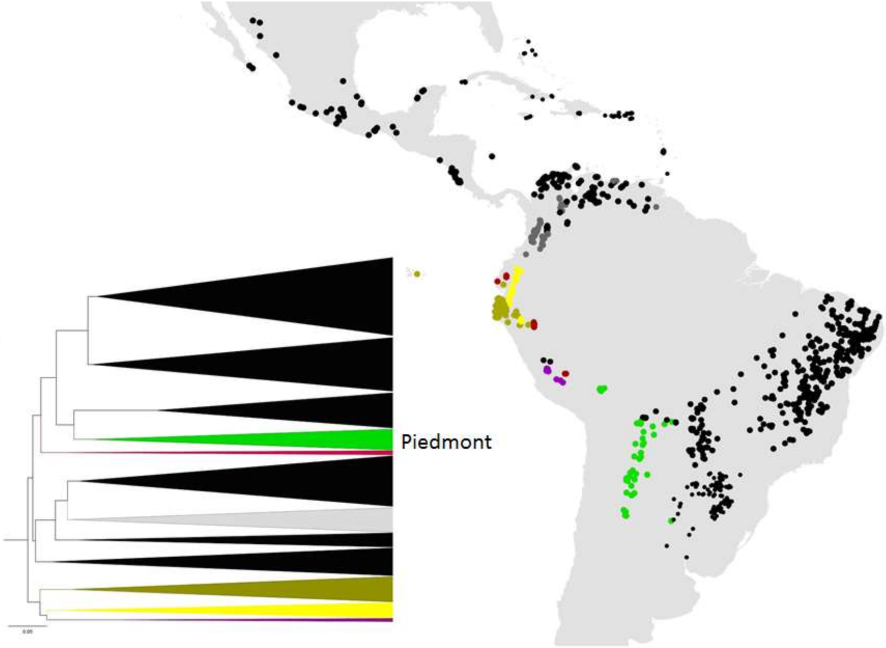


Figure 1. DRYFLOR inventory sites. Andean dry forest groups in colours. Piedmont group is highlighted in green.

The evaluation estimated extents of occurrence (EOO) and area of extension (AOO) (see details below) in three ways: first considering DRYFLOR inventory data; secondly using only herbarium records; and finally using combined inventory and herbarium records.

Tree inventory data for the Andean Piedmont analysed here have been gathered for the DRYFLOR initiative (see dry forest sites in Figure 1), and in total include 2848 records from 700 species. The species exclusive to the Piedmont in the DRYFLOR dataset were chosen as an initial basis for the case study. Of these, scrutiny of herbarium records on GBIF showed 109 species to be endemic to the Piedmont. A total of 193 species of trees was analysed here, including 84 that are not Piedmont endemics. This has the additional benefit of assessing the value of the DRYFLOR data in areas beyond the Piedmont, especially in Paraguay and southern Brazil.

Species records from herbarium specimens were obtained using the rgbif package (Chamberlain et al., 2016), to connect to the Global Biodiversity Information Facility website (GBIF, www. gbif.org, [data dowloaded 15/10/2015]). 13 species out of 193 were not found in GBIF because of lack of records or because GBIF's taxonomy was outdated. Herbarium records were cleaned by removing duplicates and those had geographical issues (e.g. invalid coordinates, locality mismatch, geodetic datum invalid) or insufficient collection information. Fifteen percent of all the GBIF records had some issues in terms of the quality of the data, such as records without georreferences, incomplete georreferences, and incorrect georeferences that wereidentified as implausible records by their location.

4.3.2 Risk of extinction parameters

IUCN assessments include five criteria (A-E) to evaluate if a species belongs to a threatened category (Critically Endangered, Endangered or Vulnerable). Criteria A, C, D and E refer to population measurements related to size and trends such as decline of populations or concerns about viability. Criteria B and D are related to the species' geographical range (IUCN, 2016). Criterion B is measured exclusively in terms of the two parameters analysed here, Extent of occurrence (EOO) and the Area of occupancy (AOO).

EOO is the area covered by the smallest polygon that can be drawn including all distribution records. AOO is the area obtained by the sum of the occupied grid squares within the EOO (Figure 2). These two parameters related to extinction risk for Criterion B (geographical range), were calculated using a mapping tool developed directly by DRYFLOR and GeoCAT (conservation assessment interface from the Royal Botanic Gardens, Kew). EOO needs a-minimum of three occurrences to draw a polygon.

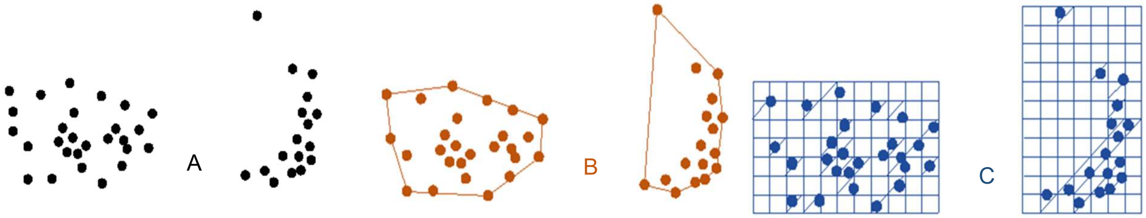


Figure 2. Distinction between EOO (B) and AOO (C) from known spatial distribution records (A) (taken from IUCN, 2001, Categories & Criteria - Version 3.1)

4.3.3 Statistical test

In order to measure the strengths of association between both sources of occurrence records, a non-parametric correlation was conducted using Spearan's rho coephicient. The Wilcoxon signed-rank test was used to examine differences between inventory and herbaria data in calculating EOO and AOO. This test is an example of a non-parametric or distribution free test, which is based on paired difference scores, also taking into account the magnitude of the observed differences (Bauer, 1972). The null hypothesis states that the parameters of risk of extinction (EOO and AOO) calculated from DRYFLOR and herbaria data have identical distributions, at 0.05 significance level, without assuming the data have a normal distribution.

Assessing whether inventory data are complementary or redundant with respect to herbarium records, I compared the AOO values, which are directly proportional to the number of records obtained, with herbarium data and inventory data alone and in combination.

4.4 Results

EOO and AOO were measured for the Piedmont tree species meeting the three records requirement: 170 using GBIF data and 138 using DRYFLOR data. These calculations show a positive correlation (Figure 3), and a dissimilar pattern in frequency distribution (Figure 4) , being the values based on herbaria specimens (GBIF) larger than those calculated based on DRYFOR data (Table 1).

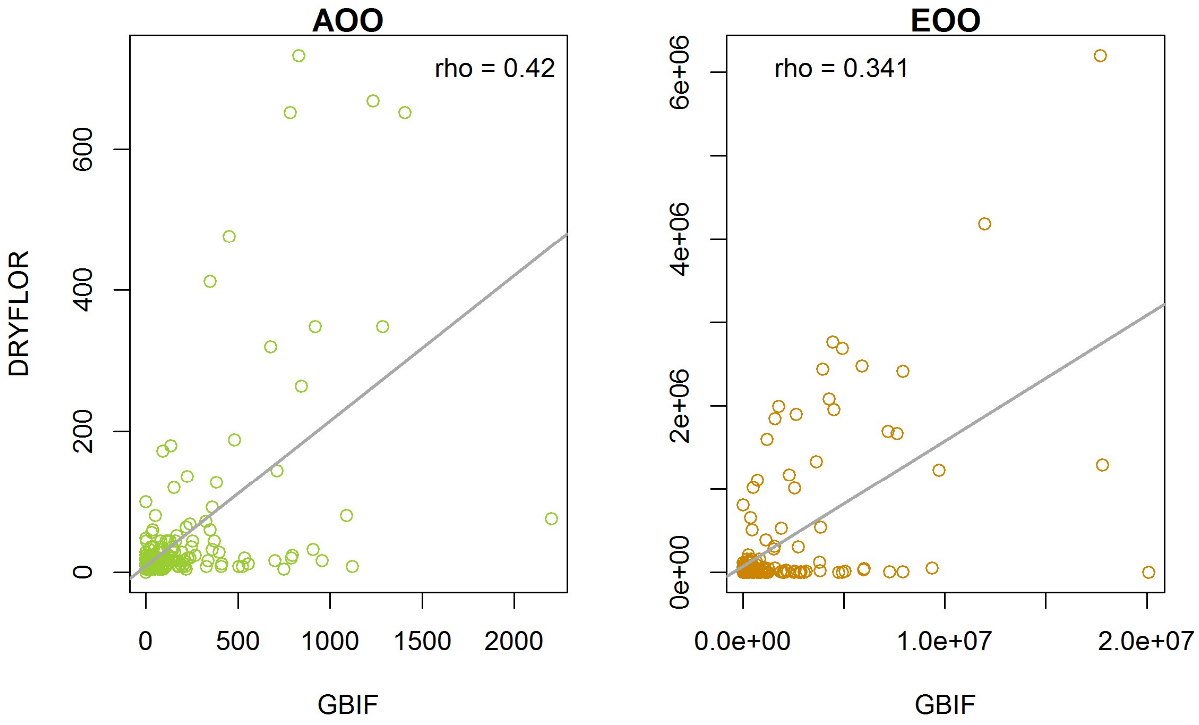


Figure 3. Correlations 1:1 GBIF vs DRYFLOR for the calculation of AOO and EOO, the association was measured by Spearman's rho coephicient (rho).

Table 1. Quantitative summary of the EOO and AOO calculated from DRYFLOR and GBIF records.

		Mean	*Median*	*SD*
EOO	DRYFLOR	293,566.6	10,227.2	780,460.3
	GBIF	1,587,758.7	363,696.8	3,086,402.2
AOO	DRYFLOR	48.6	16.0	113.6
	GBIF	191.7	80.0	305.9

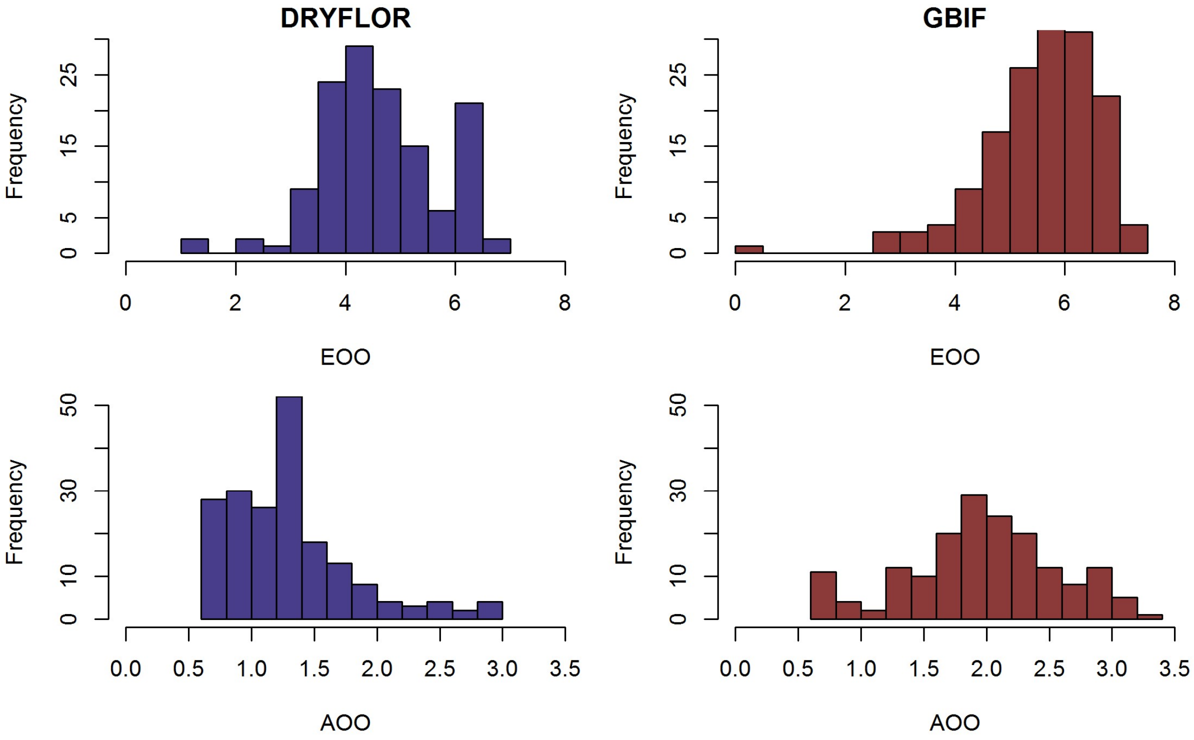


Figure 4. Histograms of the EOO and AOO parameters (log10 transformed), calculated from DRYFLOR and GBIF records.

The Wilcoxon sign-rank test (α= 0.5 AOO: V = 1547.5, p-value < 2.2e-16; EOO: V = 1083, p-value < 2.2e-16), rejected the null hypothesis showing that EOO and AOO values calculated independently from DRYFLOR and GBIF are dissimilar. The relationship between herbarium voucher records and combined data is shown in Figure 3A, indicating that combined data captured more distribution records. Figure 3B shows that using only herbarium specimen data there are some species for which there are insufficient records to calculate EOO.

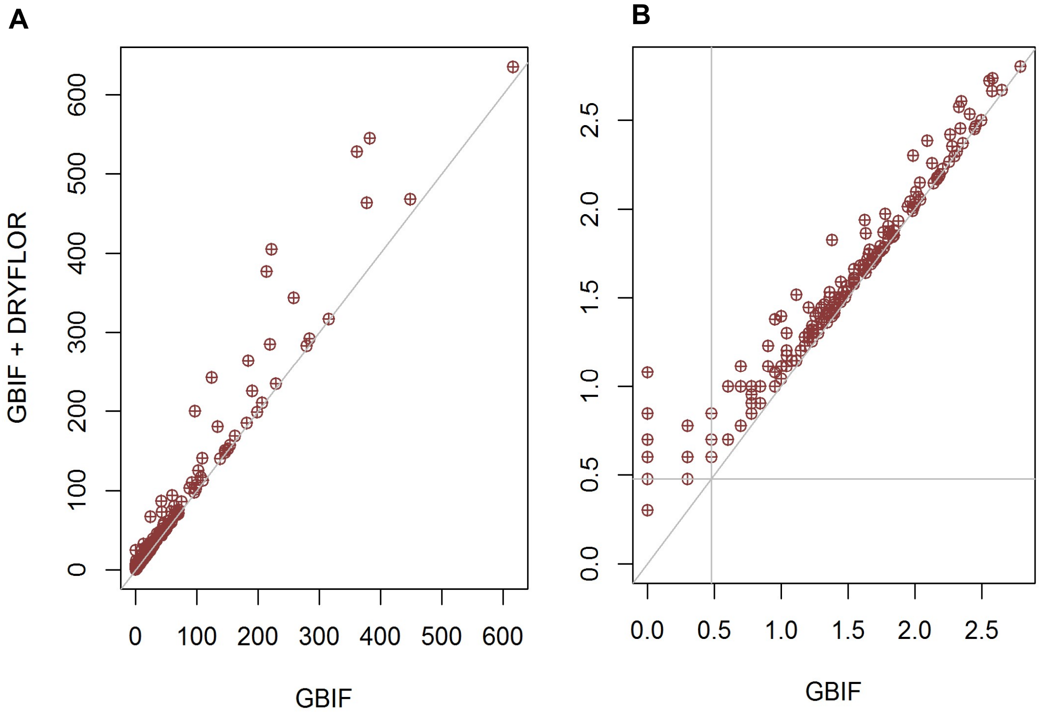


Figure 3. Scatter plot herbarium voucher records (GBIF) and combined data. A. Raw record data B. Log10 transformed records; the vertical and horizontal line is the cut-off for being able to calculate EOO (3 log10 transformed)

Comparing the AOO values based on herbarium data and inventory data alone and in combination, I found that only 16% of the species had lower AOO values using the combined data than the sum of AOO from herbarium and inventory data, which indicates redundancy. So, for 84% of the tree species in the Piedmont dry forest, inventory data complement herbarium records (see Figure 4 for examples of complementary, nonoverlapping records). Figure 4 also shows the overlapping EOO calculated with herbarium data and the amplified EOO calculated by combining data. These results indicate that both sources of records are providing complementary information about species distributions, improving the accuracy of the subsequent calculation of the extincion risk parameters AOO and EOO for individual species.

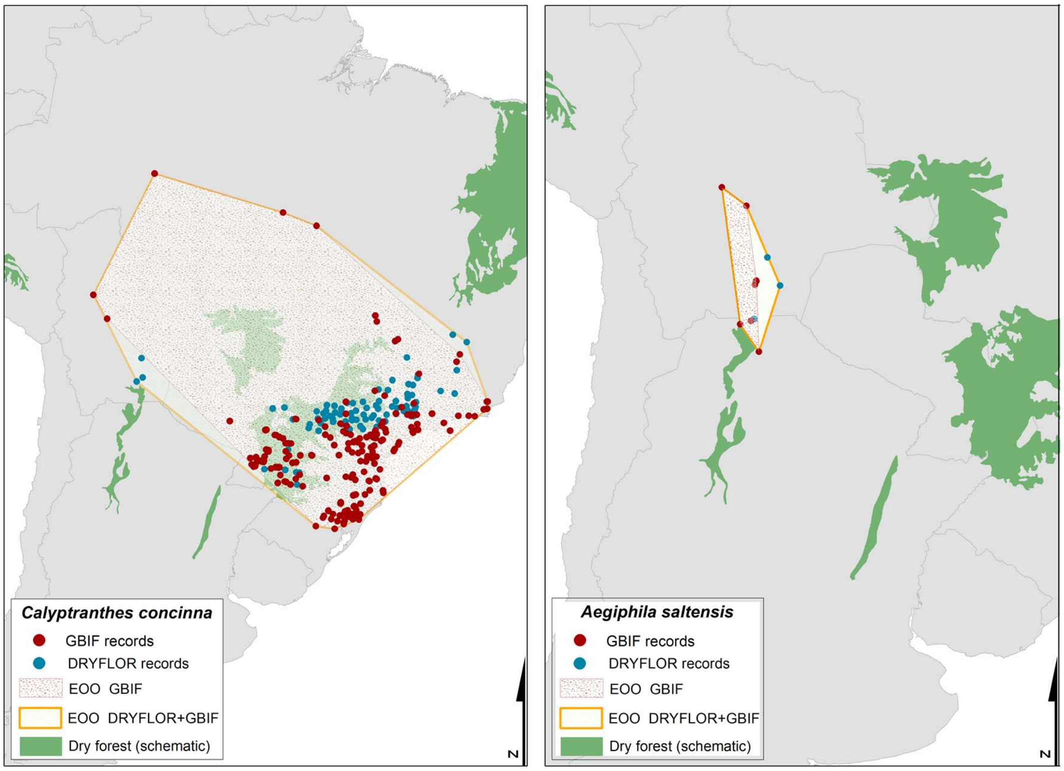


Figure 4. Distribution records and extend of occurrence (EOO) calculated for Calyptranthes concinna (Myrtaceae) and Aegiphilia saltensis (Lamiaceae).

DRYFLOR data complement the distribution records of 23 species for which herbarium records available in GBIF were insufficient to calculate EOO (Appendix 1; see examples in Figure 5). However, even combining both data sources, there are still nine species with less than three records *Lithrea ternifolia, Achatocarpus microcarpus, Barnadesia macrocephala, Bernardia hassleriana, Cereus huilunchu, Juglans soratensis, Koeberlinia* *holacantha, Plectrocarpa tetracantha, and Zygia bangii*. Those species were preliminarily assessed as Data Deficient (DD).

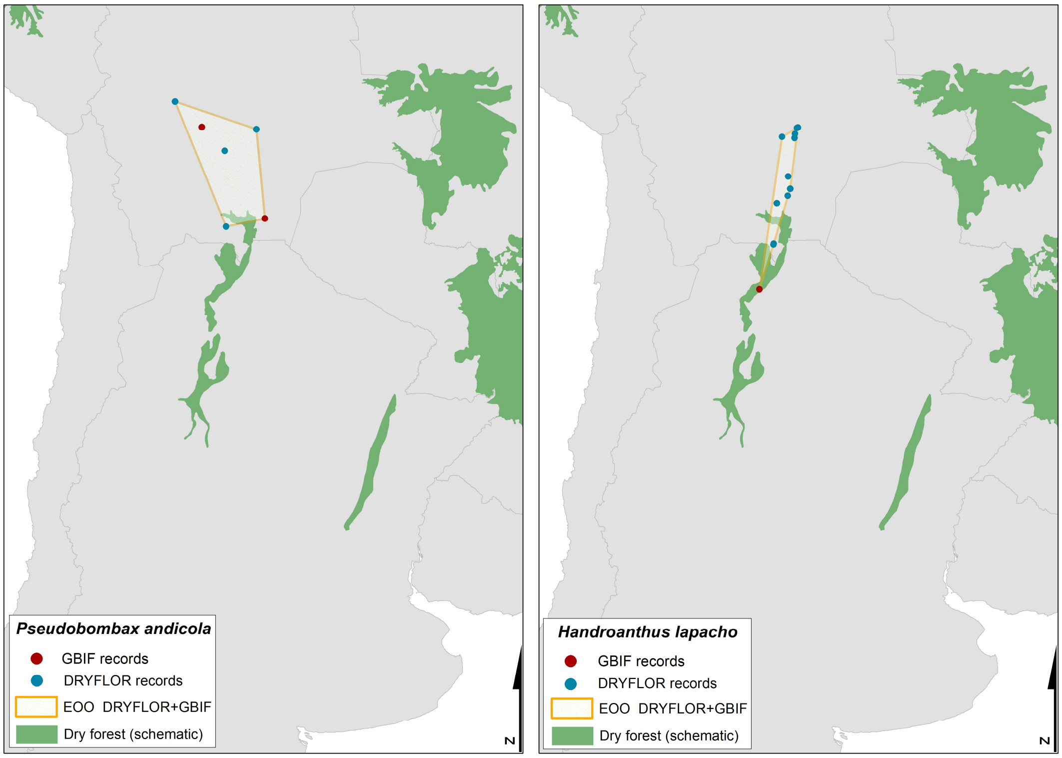


Figure 5. Distribution records and extend of occurrence (EOO) calculated for Pseudobombax andicola (Malvaceae) and Handroanthus lapacho (Bignoniaceae)

4.5 Discussion

4.5.1 Inventory data for conservation assessments of dry forest species

Red list conservation assessments measure extinction risk by examining several species-specific aspects, including population size, distribution and decline. However, the rate of new assessments of extinction risk is slow (Brummitt et al., 2015), due in part to the lack of detailed information for individual plant species. This highlights the importance of identifying sources of reliable species distribution data to increase the number of species for which assessment can be made. This study shows that combining inventory and herbarium records improves the accuracy of the species distribution data and increases the number of dry forest tree species for which we have sufficient information to make conservation assessments.

These results using DRYFLOR data might be general for other areas of dry forest in the Neotropics. For example, examining the distribution records for *Bursera simaruba*, a widespread species that occurs from Mexico to Venezuela and the Caribbean, Franklin et al. (2016) showed that 123 records from DRYFLOR fill gaps in northern South America and the Lesser Antilles in comparison to other sources of information including GBIF (see Figure 6). Therefore, the use of data from ecological inventories, like DRYFLOR, can be a useful data source to strengthen the quality of dry forest tree conservation assessments.

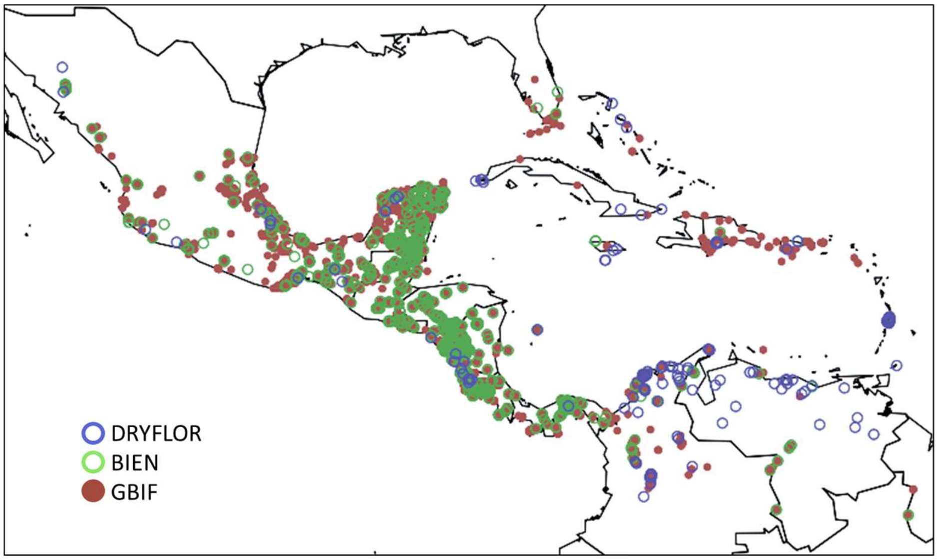


Figure 6. Occurrence records for Bursera simaruba (Burseraceae) from DRYFLOR (Latin American and Caribbean seasonally dry forest floristic network), BIEN (Botanical Information and Ecology Network in America), and GBIF (Global Biodiversity Facility). Taken from Franklin et al., 2016.

4.5.2 Data quality of occurrence records for conservation assessments

Efforts to create large biodiversity databases have been made in the three last decades (Franklin et al., 2016). The Encyclopedia of Life (http://eol.org), Global Biodiversity Facility (http://www.gbif.org), and Salvias (http://www.salvias.net/pages/index.html), are initiatives of this type based upon herbarium and museum specimens. In contrast, RAINFOR: Amazon Forest Inventory Network (http://www.rainfor.org) and DRYFLOR use forest inventory plot data. In the era of 'big data', species occurrence records are limited by the gaps in taxonomic coverage and in coverage of full geographical ranges (Soberón & Peterson, 2004). In order to tackle these limitations, Meyer et al. (2016) suggested developing procedures for data cleaning or ultimately for incorporating data limitations into the analyses.

In contrast to herbarium specimen collections, records that come from inventory data have the advantage of capturing occurrences of rare species due systematic and extensive sampling methods in the field (Baker et al., 2017). In addition, inventory sites give opportunities for monitoring over time, which is limited with herbarium data (Johnson et al., 2011). However, the use of inventory data for making conservation assessments is only feasible if these can be considered an accurate source of species distribution records.

The DRYFLOR database is a single relational database, centralised and hosted at the Royal Botanic Garden Edinburgh, and all the network partners across the Neotropics can enter data directly into it. This offers enormous advantages, especially in terms of ensuring consistency of data entry by different users because the system automatically manages taxonomic synonymy based upon the most updated resources (see Chapter 1, e.g., Catalogue of Seed Plants of the West Indies and Flora do Brasil) and the opinion of taxonomic specialists. A drawback compared to data from herbarium specimens is that in most cases the inventory records are not backed by an archived herbarium voucher and therefore they cannot be re-verified. Therefore, judgement of the original quality of species identifications in a survey is essential, and this is evaluated by regional network partners who are responsible for assessing data quality. If they have concerns about a survey, for example if several species recorded are unlikely to occur in the specific area or habitat of the survey, the inventory is rejected. Whilst DRYFLOR sites may reflect species lists from surveys covering different areas, all provide valuable species distribution data, though larger plots may capture rare species more effectively. Thus, DRYFLOR is a reliable source of information for tree inventory data of dry forests across the Neotropics.

The IUCN is increasingly integrating not only spatial databases of species to expand the coverage of conservation assessments, but also using species distribution modelling (SDM). Static SDMs are based on the relationship between species and climatic conditions (Franklin, 2010). For IUCN assessments, SDMs are used to estimate extents of occurrence and to explore potential impacts of climate change on species distribution (Cassini, 2011; Syfert et al., 2014). However, using SDMs to produce distribution maps for dry forest trees might run the risk of over-prediction of their distributions because dry forests show high species turnover at continental and regional scale and geographically separate areas of dry forest have similar environmental conditions but different species compositions (e.g. Colombian dry forest, Chapter 3). Spatial modelling for dry forest species probably would not capture accurate distribution patterns for these species, which in some cases (e.g., Colombia; Chapter 3) are not controlled by climate.

Regarding the temporal bias mentioned above, herbarium data have limitations for re-assessing conservation species status due to the static information that specimen records supply (Brummitt et al., 2015). Inventory data, especially from permanents plots, represent an alternative data source to assess species population trends over time.

4.6 Conclusions

The use of inventory data improves the accuracy of distribution estimates for the majority of tree species (86%) in the Andean Piedmont region, and also the subsequent calculation of the extinction risk parameters AOO and EOO. This demonstrates that for making conservation assessments, herbarium and inventory records are best used in combination. In addition, combining herbarium and DRYFLOR inventory data increases the number of dry forest tree species for which we have sufficient information (three or more records) to make conservation assessments by 15%. A further advantage of ecological inventory data is that permanent inventory plots allow the status of species to be re-assessed through time.

These conclusions were demonstrated for species of trees in the Piedmont dry forests, but I expect them to be general for other areas of dry forest in the Neotropics, as demonstrated for the Central America and Northern of South America by Franklin et al. (2016), and also for the species with larger geographical range that are not endemic to the Piedmont region.

4.7 Appendix

Species list from the Piedmont dry forest by which combined data (DRYFLOR AND GBIF) allowed the preliminary conservation assessment

	DRYFLOR			GBIF			Combined records
Species	Records	EOO (Km^2)	AOO (Km^2)	Records	EOO (Km^2)	AOO (Km^2)	
Cereus cochabambensis	3	23177.7	12.0	--	--	--	3
Koeberlinia holacantha	2	0.0	8.0	1	0	2	3
Mimosa woodii	1	0.0	4.0	2	0	8	3
Plectrocarpa tetracantha	1	0.0	4.0	2	0	8	3
Trichocereus tacaquirensis	3	1608.8	12.0	--	--	--	3
Kaunia gynoxymorpha	3	5101.0	12.0	--	--	--	3
Pedersenia cardenasii	3	19.8	12.0	1	0	2	4
Cantua bicolor	3	4023.8	12.0	1	0	2	4
Barnadesia macrocephala	2	0.0	8.0	2	0	4	4
Amomyrtella guili	4	5156.0	16.0	--	--	--	4
Bauhinia tuichiensis	4	213.7	16.0	--	--	--	4
Schinus venturii	4	9287.5	16.0	--	--	--	4
Myrocarpus emarginatus	4	43482.0	16.0	--	--	--	4
Hyaloseris camataquiensis	4	23177.7	16.0	1	0	2	5
Myrcia barituensis	5	5726.3	20.0	--	--	--	5
Azara salicifolia	5	12874.3	20.0	--	--	--	5
Viposia integerrima	5	128044.5	20.0	--	--	--	5
Pseudobombax andicola	4	61874.2	16.0	2	0	8	6
Kaunia catamaquiensis	6	61874.2	24.0	--	--	--	6
Leucochloron bolivianum	6	45060.5	24.0	1	0	2	7
Ocotea porphyria	7	22612.8	28.0	--	--	--	7
Handroanthus lapacho	11	15466.2	44.0	1	0	2	12
Gymnanthes edwalliana	25	808470.8	100.0	--	--	--	25

Chapter 5 Conclusions

5.1 Phytogeographic patterns of the neotropical dry forest

Based upon floristic composition, 12 major floristic groups of neotropical dry forest were identified. The analyses suggest great floristic turnover across neotropical dry forest, both within and between the major floristic groups. There are some commonalities of floristic composition among dry forest groups, such as the dominance of legumes, but these are all at higher taxonomic level rather than at species level. At species level, the data suggest high levels of endemism to each dry forest group and little evidence for many widespread species shared amongst groups. Only in the Southern dry diagonal (Caatinga, central Brazil, Misiones and Piedmont) the number of species shared amongst their floristic groups is relative large. These shared species are found mainly in geographical proximal groups (i.e. central Brazil-Caatinga, central Brazil-Misiones, central Brazil-Piedmont). However, the significance of these shared species in dominance patterns must be tested in future studies using quantitative data, which was no possible with current DRYFLOR data.

Some sites from the extremes of the environmental range of dry forest were considered initially in the broad definition of dry forest because they are traditionally called “seasonally dry formations” and the purpose was to test their floristic affinities at a broad scale. This was the case for the semi-deciduous formations from the Atlantic Forest in Brazil and the Venezuelan Andean group. Both groups were identified in the exploratory analyses and excluded from further analyses (see supplementary material, Appendix 1, Chapter 1). Semi-deciduous formations were also recognised in the regional analysis. For example, most of the dry forest areas from the Caribbean Coast, the Inter-Andean Valleys and the dry forests of San Andrés and Providencia Islands have a large proportion of their tree species, though drought-tolerant, are widespread in various habitats including rain forest. This was also the case for forests in the Colombian Llanos region (both the semi-deciduous and flooded groups), which have significantly different floras from the rest of the Colombian dry forest formations, which is reflected in their environmental differences (high rainfall and nutrient-poor and acid soils). The inclusion of semi-deciduous sites probably affected the values of dissimilarity in species composition. In the semi-deciduous sites the incursion of different floristic elements might be common due to their proximity to different major biomes, for example savanna (Cerrado region) or rain forest in the Atlantic forest, and montane forest in the case of the Venezuelan Andean sites and the Llanos in the Colombian piedmont. This mixture of biotas might have less range-restricted species and consequently less strong floristic turnover.

A broader ecological approach may be needed to improve the understanding of the floristic affinities of semi-deciduous formations. Analyses including wet habitats across the Neotropics will be necessary to understand the biogeography of semideciduous vegetation.

The high diversity turnover revealed in this study provides a scientific framework within which, for the first time, national decision makers can contextualise the significance of their dry forests at a regional and continental scale. These conclusions are underlined by the mean pairwise floristic dissimilarity values for the whole dataset of 0.90 for the Simpson dissimilarity index and 0.79 for the Sørensen index. They suggest that to conserve the full dry forest diversity across Latin America and the Caribbean will require protecting it simultaneously within multiple regions.

At regional level, ten groups in the Central American and northern South America dry forests were identified based upon floristic composition. These statistically well-supported groups show strong geographical structure. Dissimilarity values within these groups are lower on average (from 0.68 to 0.33 Simpson median with mean of 0.55) than those reported at a continental-scale. More than 50% of the tree species in the dry forests of the region are drought-tolerant, but widespread in various other habitats.

Dominance patterns in the Colombian dry forest, were examined using quantitative inventory data, finding that the most abundant species for the Colombian dry forest are ecological generalists that are widespread in various other habitats. In contrast, dry forest specialist species are more geographically restricted and are also locally rare. Furthermore, there is no evidence of an oligarchy of species dominating across large areas of dry forest in Colombia because most of the species recorded in all sites within major groups were not shared among them. Except for three widespread and common species (*Guazuma ulmifolia*, *Astronium graveolens* and *Spondias mombin*), each dry forest group is characterized by a different set of dominant species.

The finding of high levels of beta diversity, reflecting few dry forest species that are shared across Latin America, supports the idea of dispersal limitation as a mechanism shaping the composition of these formations, which contrasts with implications of the “Pleistocenic arc” theory. This theory suggested that dry forests were much more extensive during glacial periods than they are at present - forming contiguous forests across wide areas of tropical South America- and implies that beta diversity should be low.

Further studies might focus on analysing species dominance patterns using abundance data and traits related to dispersal of the dry forest species in the neotropics. Species abundance data would allow a more nuanced view of beta diversity and dominance and better understanding of dispersal syndrome and distance decay of seed dispersal may help to understand the mechanistic basis of these patterns.

5.2 Conservation tools for the neotropical dry forest

Regional and local actions are urgently needed to conserve dry forest on the ground. To achieve this, it is crucial to develop tools to inform policy makers. Using the information available (e.g. a large inventory dataset, herbarium records), these tools can be developed efficiently in terms of time and cost, whilst being scientifically reliable. Here, I suggest a Conservation Priority Index (CPI) based on a multicriteria approach to capture various biodiversity aspects. CPI includes an endemisim parameter (double-weighted), alpha diversity, beta diversity, and level of threat represented by the absence of protected areas. This CPI, when applied to the Central American and Northern South American dry forest region, set the South American Caribbean Coast (including Caracas-Cerrejón), inter-Andean Valleys and Llanos semi-deciduous as the top conservation priorities and a Xerophytic group (mostly the La Guajira area) as an intermediate priority.

The high priority areas for conservation (e.g., South American Caribbean Coast, Caracas-Cerrejón, and Xerophytic groups) have numerous endemic species spread across the national border between Colombia and Venezuela. Therefore, concrete actions coordinated as binational initiatives between the two countries are urgently needed. The requirement of a biogeographical approach for more effective conservation initiatives across the Neotropics is one of the main conclusion of this thesis. The usual methods, defined by political borders, are failing to protect dry forest species with distributions that are restricted but cross national borders.

Regarding species conservation assessments, I demonstrated in Chapter 4 that the use of inventory data improves the accuracy of distribution estimates for the majority of tree species (86%) in the Andean Piedmont region, and also the subsequent calculation of the extinction risk parameters area of occupancy (AOO) and extend of ocurrence (EOO). This demonstrates that for making conservation assessments, herbarium and inventory records are best used in combination. In addition, combining herbarium and DRYFLOR inventory data increases the number of dry forest tree species for which we have sufficient information (three or more records) to make conservation assessments by 15%. A further advantage of ecological inventory data is that permanent inventory plots allow the status of species to be re-assessed through time. These conclusions were demonstrated for species of trees in the Piedmont dry forests, but I expect them to be general for other areas of dry forest in the Neotropics, as demonstrated for the Central America and Northern of South America by Franklin et al. (2016), and also for the species with larger geographical range that are not endemic to the Piedmont region.

5.3 Data limitations and further data analyses

The DRYFLOR network has made efforts using local experts to ensure that only high-quality surveys are included – i.e., those by well qualified authors with good ability to make taxonomic determinations. However, I am aware that large biodiversity datasets have a percentage of error that is inevitable. In the case of DRYFLOR, such errors will mostly be related to species identifications. Problems in plant taxonomy are common across Latin American countries because of the absence of taxonomic specialists and the difficulties of exchanging herbarium specimens amongst countries. In the case of an inventory-based dataset such as DRYFLOR a fundamental problem is that in most cases species records are not backed by herbarium vouchers so verifying identifications is highly problematic. However, the rate of species misidentification in dry forest will be smaller in comparison to the wetter tropical forest (e.g. Choco and Amazon forest) which hold a greater number of species. Furthermore, inventory data have the advantage of highly accurate spatial data; occurrence records from herbarium specimens (e.g., from GBIF) are more susceptible to errors associated with GPS accuracy or precision in georeferencing.

DRYFLOR data include inventories obtained using heterogeneous methodologies, for example plots and transects of varying sizes or general floristic surveys, meaning that sampling effort is dissimilar among sites and regions. In order to evaluate how well DRYFLOR has captured the woody plant diversity across the continent, expected species accumulation curves were calculated (see figure 1, also in Chapter 1). The curves for the southern areas (Piedmont, Misiones, Central Brazil, Caatinga) level off more than those for other areas and therefore show that the DRYFLOR dataset is particularly robust for these areas. In other areas, especially some of the Andean valleys (e.g., Tarapoto-Quillambamba, Apurimac-Mantaro, Central inter-Andean) the more steeply rising curves underline the conclusion that more survey work is required there.

Because of the limitations of the DRYFLOR dataset, performing sensitivity analyses is recommended to evaluate how changes in the database can alter results and conclusions. Running a predictive model based on well-known sample sites to analyse the origin of possible errors (i.e. geographical, taxonomic) might help to validate the robustness of the database understanding the origin and magnitude of its limitations. These models refer to how well the data work on alternate subset.

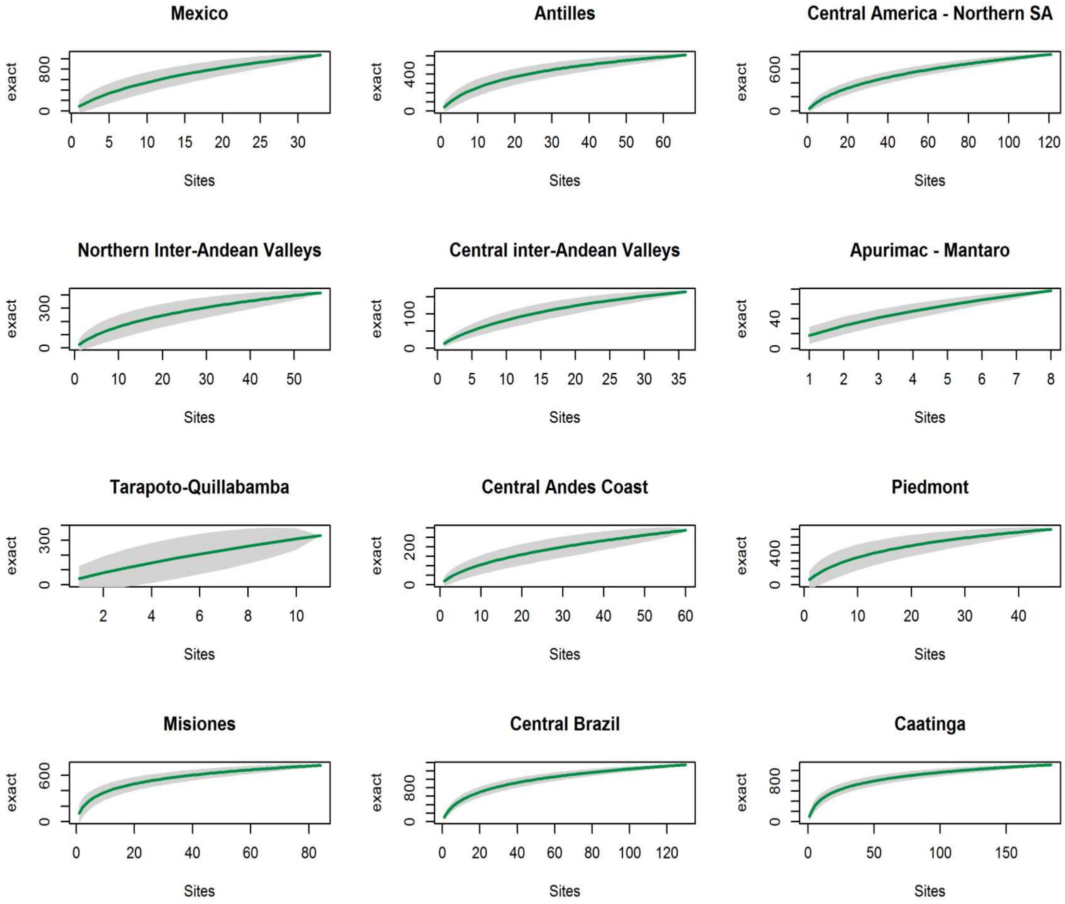


Figure 1. Species accumulation curves for each dry forest group calculated using a sample-based rarefaction method. Grey shadow shows confidence intervals from the standard deviation.

5.4 Tree diversity of Colombian dry forest and its conservation

Dry forests in Colombia are floristically dissimilar from those found in the southern dry areas of the American continent. They belong to the Central American and northern South American dry forest group, which is one of the 12 units defined in Chapter 1 based on floristic similarity, using the DRYFLOR database of floristic inventories from across the Neotropics (DRYFLOR, 2016). Within this Central American and northern South American group, Colombian dry forest is separated into eight sub-groups (Chapter 2): 1. South American Caribbean Coast; 2. Caracas-Cerrejón; 3. Xerophytic South American Caribbean Coast; 4. inter-Andean Valleys; 5. inter-Andean middle Magdalena Valley; 6. Llanos semi-deciduous; 7. Llanos flooded, and 8. San Andres and Providencia that are part of the Central America semi-deciduous group (Figure 1). .

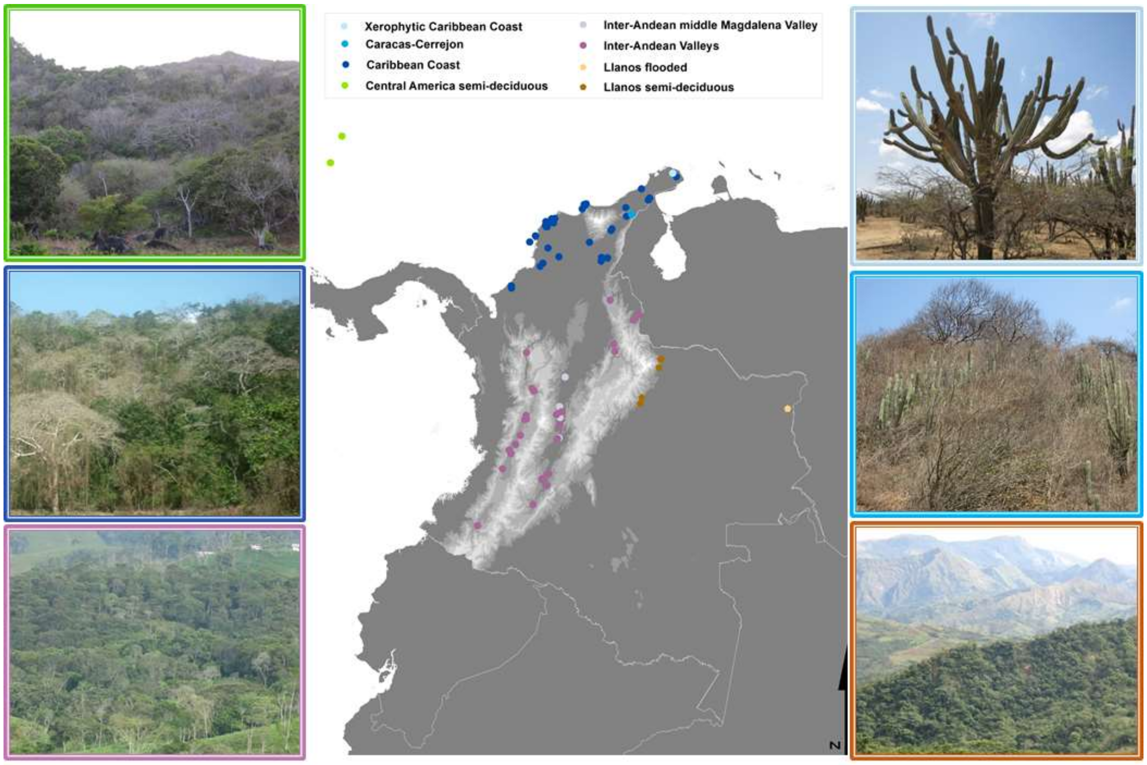


Figure 1. Colombian dry forest floristic groups

Most of the dry forest areas from the Caribbean Coast, the Inter-Andean Valleys and the dry forests of San Andrés and Providencia Islands (part of the Central American dry forest floristic group; Chapter 2) might be considered as semi-deciduous vegetation types because a large proportion of their tree species, though drought-tolerant, are widespread in various habitats including rain forest. These widespread species with high ecological plasticity are abundant in semi-deciduous areas in contrast to the most range-restricted species, which are locally rare and confined to the driest areas (Chapter 2 and 3). Semi-deciduous formations are found throughout the Neotropics, and in the wider DRYFLOR dataset are represented in Brazil (e.g., the Misiones region), Bolivia (some areas in the Chiquitano), Peru (e.g., Puerto Ocopa, Tarapoto) and Mexico (known locally as “bosque semi-caducifolio”). These semi-deciduous forests in Colombia may be analogous to the “cerradão” vegetation of Central Brazil, which are also semi-deciduous and with similar mesotrophic soils (Ratter et al., 1978).

This study also found that forests in the Llanos region (both the semi-deciduous and flooded groups), have significantly different floras (Chapter 2 and 3) from the rest of the Colombian dry forest formations. This may reflect their environmental differences. For example, Llanos sites have high rainfall (some sites have >2000 mm per year) and nutrient-poor and acid soils.

The driest areas of the Colombian Caribbean (belonging to the Caracas-Cerrejón and Xerophytic sub-groups), could be considered as equivalent to the “succulent biome” described in the dry southern areas of South America (i.e. much of the Caatinga: Oliveira-Filho et al., 2013; Schrire et al., 2005), which is a formation restricted to the more drought-prone end of the tropical seasonality gradient where annual precipitation is less than 1200 mm and cacti are abundant.

The composition and structure of the dry forests in Colombia may have been particularly affected by the complex and interesting biogeographical history of northern South America, which has been driven by the uplift of the tropical Andes and the formation of the Panama isthmus (Gentry, 1982; Richardson et. al., 2001; Stone, 2013; Bacon et al., 2015). The development of dry climates currently found in inter-Andean Valleys originated when the mountains became high enough to cause a rain shadow effect. The Northern Andean uplift in Colombia seems to be more recent (~11 mya years for the eastern cordillera and 8-11 mya for the northwest [Graham, 2011; Richardson et al., 2015]) than the orogeny of the Central Andes in Peru (ca. 20 mya [Gregory-Wodzicki, 2000; Särkinen et al., 2012]). The Colombian Inter-Andean Valleys are long and extensive areas with a mixture of environments influenced by montane and humid floristic elements (i.e. Cauca Valley, Vargas, 2012 and middle Magdalena Valley, Chapter 2). Having existed for a relatively shorter period of time than the long-isolated dry forests of the valleys in the central Andes (DRYFLOR, 2016; Särkinen et al., 2012), the Colombian Inter-Andean Valleys have accumulated fewer endemic dry forest specialist species (only 4% tree species are endemic to inter-Andean Valleys in Colombia, Chapter 3).

On the Caribbean Coast, regression and transgression episodes of the Caribbean Sea (Flórez, 2003) serin the recent Holocene (Toscano et al., 2011) have influenced the development of dry forests. The last marine regression was approximately 1 mya (Flórez, 2003), meaning coastal dry forest formations are geologically young, allowing even less time for endemic species to evolve in low-lying areas (2.5% trees species are endemic, Chapter 3).

As a caveat to drawing general conclusions about the floristic nature and origin of Colombian dry forests, it should be noted that all the patterns described in this thesis are based on tree species, and there is evidence that diversity patterns in tropical dry forests differ among life forms (Quintana, 2015 in Ecuador; Linares-Palomino & Kessler, 2009 in Bolivia). Future research should therefore concentrate on the investigation of ecological patterns of herbs, lianas and epiphytes in Colombia and across neotropical dry forests.

Future research could also focus on the phylogenetics and population genetics of species occupying the different kinds of dry forest formations in Colombia. Evolutionarily old, geographically structured phylogenies and genetically differentiated populations might be expected to be uncovered in the drier formations, especially those isolated by mountain barriers (Schrire et al., 2005; Pennington et al., 2009; Särkinen et al., 2012). In contrast, one might expect semi-deciduous formations on the Caribbean coast to have been assembled more recently, with widespread species showing patterns of recent population expansion, as described for some rain forest tree species in southern Amazonia (Honorio et al., 2015).

5.5 Why is Colombian dry forest important?

Tropical dry forest holds significant plant diversity - ca. 7000 tree species in the Neotropics and ca. 2700 in Colombia, based only on inventory data (Chapter 1, DRYFLOR, 2016). However, it is unfortunately considered one the most threatened tropical forests worldwide (Janzen, 1988; Gentry, 1995; Miles et al., 2006). It has been transformed across the Neotropics by centuries of colonial agriculture, extensive cattle ranching, cultivation of monocrops and large-scale mining. Intensification of land use has driven an increasing change in the composition of ecological assemblages in Colombian vegetation (Echeverría-Londoño et al., 2016). In Chapter 3, I found that anthropogenic-related variables are an important factor controlling the community composition of dry forest in Colombia. If land-use can be managed to allow dry forests to be preserved and to regenerate, this could have a substantial global impact. Species loss in forests around the world could significantly reduce forest productivity and therefore compromise the global forest carbon sink (Liang et al., 2016). Analysis of the biomass dynamics of Amazon rain forest shows a long-term declining trend of carbon accumulation (Brienen et al., 2015). In scenarios of changing climate and atmospheric composition, carbon sequestration in the dry forest might play a key role because its species are adapted to survive extreme climatic conditions. For example, recent studies highlight the potential role of secondary dry forests in mitigating climate change through carbon sequestration (Chazdon et al. 2016; Poorter et al. 2016). There are also studies that show the value of some dry forest legume trees as a carbon sink. Planting of species such as *Caesalpinia platyloba* (Mexican dry forest) and *Samanea saman* (one of the dominant species in Colombian dry forests, Appendix 2, Chapter 3) has been suggested to achieve optimal CO_2 absorption (Diaz-Gustavo et al. 2015, Suwanmontri et al., 2013). Regenerating dry forests could be critical to carbon sequestration, though more studies are required on their growth rates and carbon storage.

Apart from carbon sequestration, dry forest also plays an important role preserving soil water (Portillo-Quintero et al., 2015) and delaying erosion and desertification, which are intimately related to poverty due to the rapid soil degradation after deforestation (Maass et al., 2005; Newton, 2008). The prioritisation of dry forest ecosystem services delivery over forest-based economics may result in social and environmental benefits, including improving the livelihoods of forest-dependent people (Headley, 2016).

5.6 Future prospects and conservation recommendations for Colombian dry forests

The post-conflict scenario starting in 2017 is unprecedented in recent Colombian history and represents a huge challenge for the academic community and society in general. There is the opportunity, for the first time, to execute expeditions in dry forest areas that have been unexplored due to security issues (e.g., Montes de Maria in the department of Bolivar, and in the department of Sucre, which has the lowest number of plant collections in Colombia [Bernal et al., 2015]).

The Land Restitution Programme aims to return land to individuals and communities displaced by the armed conflict in Colombia. This programme has been running slowly since 2011, but is now central in the implementation of the recent peace agreement. Forty seven percent of the municipalities where land restitution has been claimed (URT, https://www.restituciondetierras.gov.co/ [31/10/2016]) are concentrated in dry forests. There is therefore a great opportunity to build a programme in dry forest regions where social justice and environmental sustainability work hand in hand.

Here, I present a proposal for future prospects for Colombian dry forests that include some suggestions for research, conservation tools, policies and actions.

5.6.1 Research

A research route is proposed and illustrated in the diagram below (Figure 2), which focuses on two actions: Inventories and Experiments; and three research lines: i) Origin and evolution, ii) Function and iii) Ecosystem services.

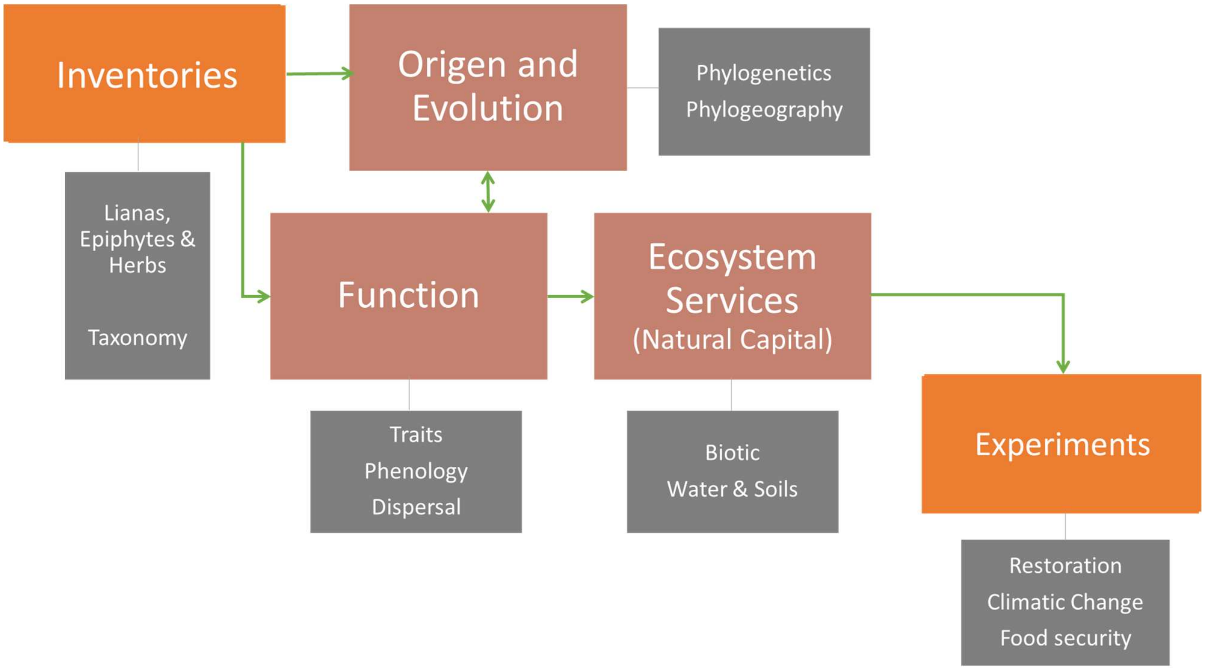


Figure 2. Research route for Colombian dry forest

Inventories and taxonomy comprise the baseline to improve the understanding of plant community patterns of dry forests. In particular, if floristic data are gathered from permanent inventory plots they should cover all growth forms, and there is also an opportunity to investigate phenology, population trends and carbon sequestration. There are direct connections among the research lines, firstly concerning function and evolution, which might provide the foundation to understand ecological assembly processes affecting the evolution of species' traits. Secondly, functional traits such as plant height, leaf dry matter content, leaf nitrogen and phosphorus concentration and flowering onset can help to quantify ecosystem function (Maes et al. 2013), something that has been neglected in Colombian dry forest (Calvo-Rodriguez et al., 2016).

Studies of phylogeny and population genetics of clades and species occupying the different kinds of dry forest formations in Colombia might be relevant for plant groups such as Cactaceae (e.g, *Pereskia*) and legumes (e.g., *Senna*, *Anadenanthera*), *Anacardium excelsum* (Anacardiaceae) and *Bursera simaruba* (Burseraceae). Such studies could elucidate the history of Colombian dry forests, for example the nature of connections between the Caribbean coast and inter-Andean valleys, and the age of separation of the inter-Andean forests by the various cordilleras.

Experiments to develop propagation protocols for native species are needed for effective restoration programmes. Specific projects to build biological corridors for the establishment of a regional protected areas network might promote ‘living edges’ in rural landscapes at local scales (see some details below), and also should consider the connectivity of remnants forests at larger scales (e.g. the jaguar corridor initiative, which seeks to connect forest remnants across large areas of modified landscapes across countries [https://www.panthera.org]).

Understanding which factors or traits allows the success of dominant tree species in seasonally dry areas might shed light on their response to climatic change. It might be particularly important to focus on legumes, which are the most species-rich and often dominant plant group in dry forests (Chapter 1 and Chapter 2). Experiments simulating different environmental conditions (i.e., light, soils moisture and soils nutrients) to compare germination, growth and physiology have been carried out in dry forest in Costa Rica (Powers et al., 2016), and might be a model for Colombia.

Permaculture projects are a possible solution to food security and desertification, and could be most relevant in La Guajira and other very dry areas, where hunger and child malnutrition were responsible for more than 50 deaths in 2016 in indigenous communities (https://www.minsalud.gov.co). Permaculture refers to agricultural systems intended to be sustainable and self-sufficient (Veteto & Lockyer, 2013).

5.6.2 Tools: conservation assessments

The critical state of dry forests requires conservation tools to drive and implement effective policies. Plant species conservation assessments are an important basic tool for planning biodiversity conservation. However, progress in making assessments is slow due to the huge numbers of plant species in the tropics, including many yet to be described scientifically. Identifying species at risk of extinction that require conservation intervention needs both substantial up-scaling and prioritisation of efforts to collect and enhance the quality of available occurrence information (Meyer et al., 2016). In terms of baseline information about distributions, here I demonstrated that tree inventory data are a complementary source of information, increasing the ability to assess tree species under the IUCN criteria (Chapter 4). My study also highlights range-restricted species spread across national borders, especially between Colombia and Venezuela (Chapter 2). Such species are neglected by projects that are currently operating in Colombia, which are focused on the conservation of national endemics (Castellanos-Castro, pers. comm. 2016). This highlights the importance of a biogeographical approach to setting conservation priorities. In this case, concrete actions coordinated as binational initiatives between Colombia and Venezuela are urgently needed.

Currently, 56 plant species have been selected for the “Red list of the Colombian plants project” by the Instituto Alexander von Humboldt based on endemism at national level and level of threat. Following a biogeographical approach to define endemism, I suggest incorporation into the priority list species that are range-restricted but found across the Colombia and Venezuela border region. Such species would include *Pereskia guamacho* (Cactaceae), *Belensita nemorosa* (Capparaceae), and *Handroanthus billbergii* (Bignoniaceae). I also suggest inclusion of species that are dry forest specialists and locally rare, which may not be endemic to Colombia (Chapter 3), such as *Cynophalla linearis, Capparidastrum tenuisiliquum* (Capparaceae), *Bourreria cumanensis* (Boraginaceae), and *Muellera broadwayi* (Leguminosae).

The rate of new assessments of extinction risk for individual plant species approximates the rate at which new plant species are described (Brummit et al., 2015). In Colombia, the biodiversity of many remote places remains poorly known and it is estimated that there are ~9000 new vascular plant species to be discovered (Bernal pers. comm., 2013). Therefore, Colombia urgently needs to increase exploration to expand the number of both collections and medium and long term ecological studies. This biotic exploration in turn requires underpinning by extensive taxonomic work in all plant groups to improve the quality of data. This latter problem is illustrated by my own dry forest inventories where ~25% of the morpho-species are not taxonomically identified.

Initiatives that promote scientific networking, such as DRYFLOR, can help to improve fundamental baseline inventory and taxonomic data. They can enhance collaboration of regional researchers with specialists around the world in many fields (taxonomy, genetics, ecology and horticulture), facilitating an increase in knowledge and conservation of Colombian dry forest.

5.6.3 Planning – Conservation Policies

Despite dry forest having been identified as a strategic ecosystem in Colombia (http://www.minambiente.gov.co/), national polices are not meeting the urgent need to preserve it. For example, cattle pasture is the main cause of deforestation in dry forest areas across the country, especially on the Caribbean Coast. According to the national agency of geography (IGAC, 2012), more than 50% of the land in Colombia used for cattle pasture is not optimal for this activity, which highlights the need to reconcile land use more effectively within a national framework.

Policies to ensure the conservation of biodiversity have to involve alternatives to the current development model, which has driven the conversion of dry forest to extremely intense land use. Such is the case of mining, which is considered the engine of the Colombian economy (PDN 2014-2018), but which is also responsible for dry forest destruction. Apart from the irremediable damage to biodiversity, water sources and terrain than mining causes, mining compensation programs, which aim to mitigate the environmental cost, also fail. For example, soil samples taken in Eucalyptus (*E. grandis*) plantations during my fieldwork in the department of Cesar, which are part of the compensation program in the mining complex of “La Jagua”, show devastating effects on soil quality, creating a dystrophic soil with low N, Mg and Ca content (< 0.08 me/100 gr) in comparison to the samples taken in adjacent areas of dry forest remnants (Chapter 3). Large scale mining of coal has been developed in this area by multinational companies since the adoption of economically liberal policies in the 1990s and the collapse of cotton crops, ignoring the potential of non-extractive activities in the highly fertile soils of this region. Environmental compensation programmes for mining require revaluation, and an alternative could be restoration programs involving local communities.

5.6.4 Conservation Actions

Successful conservation of Colombian dry forests will need to preserve the remaining small forests, and to improve livelihoods of local communities. Studies in Mexico show the importance of a forested landscape with diverse land-uses (i.e., small forest patches, secondary and fallow forests) in conserving dry forest biodiversity (Gordon et al., 2004). There are also benefits for communities being close to forest rather than intensified land use systems (Ickowitz et al., 2016). Solutions in Colombia might therefore create a diverse mosaic of land uses and link dry forest landscapes to diets via sustainable agroforestry, as well as using strict conservation areas.

Tree species composition is spatially structured among dry forest formations in Colombia (Chapter 3), so conservation actions should consider the biogeographic structure revealed in this study. Particular conservation programmes should be planned and implemented for each dry forest group. As an example, in the final sections below I suggest some conservation actions for the Caribbean Coast and the inter-Andean dry forest groups, which were identified as top conservation priorities in Chapter 2.

Caribbean Coast

New reserves have been established recently in the Caribbean, but forest fragmentation in this region is massive, and these protected areas are isolated and immersed in an agricultural matrix. Consequently, promotion of connectivity among patches, whether they are protected or not, must be implemented in order to ensure population viability and long-term maintenance of ecological processes.

Restoration programmes that aim to connect dry forest remnants should be focused on sustainable forestry systems. These programmes could focus on sustainable cutting of timber for firewood and the harvesting of other forest resources (i.e., fruits, fibres and medicines), using native dry forest species.

Several useful trees of the Caribbean dry forests (Jiménez-Escobar & Estupiñán-González, 2011; Rodríguez, 2012), have high ecological plasticity and wide environmental range (Chapters 1-3), which may make them able to survive changing climates. These species are also abundant (Chapter 3) and might be considered as part of alternative systems to the traditional land use of grazing. For example, *Bursera simaruba* (Burseraceae) is a fast-growing species, a good competitor in open areas, and is a possible basis for honey production (Castellanos-Potenciano et al., 2012), and therefore has potential in forest restoration programs focusing on sustainable use of dry forest. Other useful species that could be emphasised in restoration programmes are *Brosimum allicastrum* (Moraceae), which has been used for c. 2000 years (Graham, 2011) for its nutritious fruits and *Spondias mombim* (Anacardiaceae), which has potential for its medicinal properties form bark and flowers (analgesic and antibacterial), as well as edible fruits that are a good source of vitamins (Orwa et al.2009).

Inter-Andean Valleys

The inter-Andean valleys are one the most transformed areas in Colombia. For example, the Cauca Valley has less than 6% of forest cover (CVC, 2007). Industrial sugarcane plantations dominate the landscape and the dry forests remnants are small fragments (in most cases less than 9 Ha [Arcila-Cardona et al., 2012]). Sustainable forestry and silvopastoral projects with smallholders are needed in the inter-Andean

Valleys to maximize biodiversity conservation, instead of on relying on strictly protected areas.

Forestry systems for long term, sustainable timber harvesting can be implemented using native and common species (Chapter 3) such as *Cordia alliodora* (Boraginaceae) and *Cedrela odorata* (Meliaceae), both of which have established protocols for seed storage and germination in the region (Villanueva, pers. comm. 2016). There are also species of legumes with good timber that might be considered for restoration programs, such as *Pseudosamanea guachapele* and *Chloroleucon bogotense* that are key elements in the intermediate successional stage of the inter-Andean Valley dry forests (Vargas & Ramírez, 2014).

Silvopasture is a rotational grazing system that combines grasses, herbs, bushes and trees for nutritious forage. Using species of legumes (i.e., *Gliricidia sepium* and *Chloroleucon bogotense*) that fix atmospheric nitrogen, adding to soil fertility and reducing the need for artificial fertiliser for grasses, might be an option for efficient cattle raising for small farmers, increasing profit and reducing land demand, which nowadays is enormous (1.4 ha of grass is required per cow [Palmer, 2016]). Silvopastoral systems should exclude goats, which have a devastating effect on soils and vegetation.

References

Acevedo, P., & Strong, M. T. (2012). Catalogue of seed plants of the West Indies. *Smithsonian Contributions to Botany*, *98*, 1–1192.

Ament, J. M., & Cumming, G. S. (2016). Scale dependency in effectiveness, isolation, and social-ecological spillover of protected areas. *Conservation Biology*, *30*(4), 846–855. http://doi.org/10.1111/cobi.12673

Aranguren, A. (2009). *Caracterizacización de comunidades leñosas estacionalmente secas premontanas y montanas del estado de Mérida*. Universidad de los Andes, Venezuela.

Arcila-Cardona, A., Valderrama-Ardilla, C., & Chacón-Ulloa, P. (2012). Estado de la fragmentación del bosque seco de la cuenca alta del río Cauca, Colombia. *Biota Colombiana*, *13*, 86–101.

Ashley, M. V., Willson, M. F., Pergams, O. R. W., O'Dowd, D. J., Gende, S. M., & Brown, J. S. (2003). Evolutionarily enlightened management. *Biological Conservation*, *111*(2), 115–123. http://doi.org/10.1016/S0006-3207(02)00279-3

Aymard, G. A., & González, V. (2014). Los bosques de los llanos de Venezuela: Aspectos de su estructura, composición florística y estado actual de conservación. In J. O. Rangel-Ch (Ed.), *Colombia Diversidad Biótica XIV* (pp. 483–532). Bogotá D.C., Colombia: Universidad Nacional de Colombia.

Bacon, C. D., Silvestro, D., Jaramillo, C., Smith, B. T., Chakrabarty, P., & Antonelli, A. (2015). Biological evidence supports an early and complex emergence of the Isthmus of Panama. *Proceedings of the National Academy of Sciences*, *112*(19), 6110–6115. http://doi.org/10.1073/pnas.1423853112

Baker, T. R., Pennington, R. T., Dexter, K. G., Fine, P. V. A., Fortune-Hopkins, H., Honorio, E. N., … Vasquez, R. (2017). Maximising Synergy among Tropical Plant Systematists, Ecologists, and Evolutionary Biologists. *Trends in Ecology & Evolution*, *xx*, 1–10. http://doi.org/10.1016/j.tree.2017.01.007

Baksh-comeau, Y. S., Maharaj, S. S., Adams, C. D., & Hawthorne, W. D. (2016). An annotated checklist of the vascular plants of Trinidad and Tobago with analysis of vegetation types and botanical "hotspots." *Phytotaxa*, *250*(1), 1–431.

Balvanera, P., & Lott, E. (2002). Patterns of β-diversity in a Mexican tropical dry forest. *Journal of Vegetation Science*, *13*, 145–158. http://doi.org/10.1111/j.1654-1103.2002.tb02034.x

Bauer, D. F. (1972). Constructing confidence sets using rank statistics. *Journal of the American Statistical Association*, *67*(339), 687–690. http://doi.org/10.2307/2284469

Becerra, J. X. (2005). Timing the origin and expansion of the Mexican tropical dry forest. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(31), 10919–23. http://doi.org/10.1073/pnas.0409127102

Blackie, R., Baldauf, C., Gautier, D., Gumbo, D., Kassa, H., Parthasarathy, N., … Sunderland, T. (2014). *Tropical dry forests: The state of global knowledge and recommendations for future research*. Bogor, Indonesia.

Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical Ecology with R*. (R. Gentleman, G. G. Parmigiani, & K. Hornik, Eds.). New York: Springer.

Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological a variation. *Ecology*, *73*(3), 1045–1055. http://doi.org/10.2307/1940179

Bridgewater, S., Pennington, R. T., Reynel, C. A., Daza, A., & Pennington, T. D. (2003). A preliminary floristic and phytogeographic analysis of the woody flora of seasonally dry forests in northern Peru. *Candollea*, *58*(1), 129–148.

Bridgewater, S., Ratter, J. A., & Felipe Ribeiro, J. (2004). Biogeographic patterns, β-diversity and dominance in the cerrado biome of Brazil. *Biodiversity and Conservation*, *13*(12), 2295–2318. http://doi.org/10.1023/B:BIOC.0000047903.37608.4c

Brooks, A. T. M., Mittermeier, R. A., Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., … Hoffmann, M. (2006). Global biodiversity conservation priorities. *Science*, *313*(5783), 58–61. http://doi.org/10.1126/science.1064397

Brummitt, N. A., Bachman, S. P., Griffiths-Lee, J., Lutz, M., Moat, J. F., Farjon, A., … Lughadha, E. M. N. (2015). Green plants in the red: A baseline global assessment for the IUCN Sampled Red List Index for plants. *PLoS ONE*, *10*(8), 1–23. http://doi.org/10.1371/journal.pone.0135152

Brummitt, N., Bachman, S. P., Aletrari, E., Chadburn, H., Griffiths-Lee, J., Lutz, M., … Nic Lughadha, E. M. (2015). The sampled red list index for plants, phase II: ground-truthing specimen-based conservation assessments. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *370*(1662), 20140015. http://doi.org/10.1098/rstb.2014.0015

Burguillos, L., Parra, L., & Wagner, E. (2008). Human, ecologican, and biophysical dimensions of tropical dry forests. In J. M. Nassar, J. P. Rodriguez, G. A. Sánchez-Azofeifa, T. Garvin, & M. Quesada (Eds.), *Manual of methods. Human, Ecologican, and Biophysical Dimensions of Tropical Dry Forests* (p. 134). Caracas, Venezuela.: TROPI-DRY.

Bush, A., Harwood, T., Hoskins, A. J., Mokany, K., & Ferrier, S. (2016). Current uses of beta-diversity in biodiversity conservation: A response to Socolar et al. *Trends in Ecology and Evolution*, *31*(5), 337–338. http://doi.org/10.1016/j.tree.2016.02.020

Cassini, M. H. (2011). Ranking threats using species distribution models in the IUCN Red List assessment process. *Biodiversity and Conservation*, *20*(14), 3689–3692. http://doi.org/10.1007/s10531-011-0126-9

Castellanos-Castro, C., & Newton, A. C. (2015). Environmental heterogeneity influences successional trajectories in Colombian seasonally dry tropical forests. *Biotropica*, *47*(6), 660–671. http://doi.org/10.1111/btp.12245

Castellanos-Potenciano, B., Ramírez-Arriaga, E., & Zaldivar-Cruz, J. (2012). Análisis del contenido polínico de mieles (Apidae) en el estado de Tabasco , México. *Acta Zoológica Mexicana*, *28*(1), 13–36.

Chamberlain, S., Ram, K., Barve, V., & Mcglinn, D. (2016). Package ' rgbif ' Interface to the Global Biodiversity Information Facility "API." Retrieved from https://cran.r-project.org/web/packages/rgbif/rgbif.pdf

Charmaz, K. (2006). *Constructing Grounded Theory: A Practical Guide through Qualitative Analysis*. London: Sage.

CVC. (2007). *Plan de acción trienal 2007-2009, Corporación Autónoma Regional del Valle del Cauca.* Santiago de Cali.

Dapporto, L., Ramazzotti, M., Fattorini, S., Talavera, G., Vila, R., & Dennis, R. L. H. (2013). Recluster: an unbiased clustering procedure for beta-diversity turnover. *Ecography*, *36*(10), 1070–1075. http://doi.org/10.1111/j.1600-0587.2013.00444.x

Dexter, K. G., & Baker, T. R. (2013). Soil sampling protocol. Edinburgh and Leeds, UK.: Adapted from RAINFOR.

Dexter, K. G., Smart, B., Baldauf, C., Baker, T. R., Balinga, M. P. B., Brienen, R. J. W., & Fauset, S. (2015). Floristics and biogeography of vegetation in seasonally dry tropical regions. *International Forestry Review*, *17*(S2), 10–32.

Dolman, P. M., Panter, C. J., & Mossman, H. L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology*, *49*(5), 986–997. http://doi.org/10.1111/j.1365-2664.2012.02174.x

DRYFLOR. (2016). Plant diversity patterns of neotropical dry forest and their conservation implicatons. *Science*, *353*(6306), 1383–1387.

Eisler, M. C., Lee, M. R. F., Tarlton, J. F., Martin, G. B., Beddington, J., Dungait, J. A. J., … Winter, M. (2014). Agriculture: Steps to sustainable livestock. *Nature*, *507*(7490), 32–34. http://doi.org/10.1038/507032a

Espinal, L. S., & Montenegro, E. (1963). *Formaciones vegetales de Colombia. Memoria explicativa sobre el mapa ecológico.* Bogotá D.C., Colombia: Instituto Geográfico “Agustín Codazzi”. Departamento Agrológico.

Espinosa, C. I., Cabrera, O., Luzuriaga, A., & Escudero, A. (2011). What factors affect diversity and species composition of endangered tumbesian dry forests in southern Ecuador? *Biotropica*, *43*(1), 15–22. http://doi.org/10.1111/j.1744-7429.2010.00665.x

Fajardo, L., Gonzalez, V., Nassar, J. M., Lacabana, P., Portillo, Q., Carlos, a., … Rodriques, J.-P. (2005). Tropical dry forests of Venezuela: characterisation and current conservation status. *Biotropica*, *37*(4), 531–546.

Ferrier, S., & Guisan, A. (2006). Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, *43*(3), 393–404. http://doi.org/10.1111/j.1365-2664.2006.01149.x

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, *13*(3), 252–264. http://doi.org/10.1111/j.1472-4642.2007.00341.x

Ferrier, S., & Wintle, B. (2009). Quantitative approaches to spatial conservation prioritization: Matching the solution to the need. In A. Moilanen, K. A. Wilson, & H. P. Possingham (Eds.), *Spatial conservation prioritization: Quantitative methods and computational tools* (p. 328). Oxford: Oxford, Biology.

Fine, P. V., & Ree, R. H. (2006). Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *The American Naturalist*, *168*(6), 796–804. http://doi.org/10.1086/508635

Flórez, A. (2003). *Colombia: evolución de sus relieves y modelados* (Primera). Bogotá D.C., Colombia: Universidad Nacional de Colombia.

Forero-Medina, G., & Joppa, L. (2010). Representation of global and national conservation priorities by Colombia's protected area network. *PLoS ONE*, *5*(10), e13210. http://doi.org/10.1371/journal.pone.0013210

Franklin, J. (2010). Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, *16*(3), 321–330. http://doi.org/10.1111/j.1472-4642.2010.00641.x

Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Big data for forecasting the impacts of global change on plant communities. *Global Ecology and Biogeography*. http://doi.org/10.1111/geb.12501

Furley, P. A. (1996). The influence of slope on the nature and distribution of soils and plant communities in the central Brazilian cerrado. In M. G. Anderson & S. M. Brooks (Eds.), *Advances in Hillslope Processes* (pp. 327–346). John Wiley & Sons Ltd.

Furley, P. A., & Ratter, J. A. (1988). Soil resources and plant communities the central Brazilian cerrado and their development. *Journal of Biogeography*, *15*(1), 97–108.

Galvis, G., & Mesa S, L. M. (2014). Consideraciones históricas sobre la distribución actual del bosque seco en Colombia. In C. Pizano & H. García (Eds.), *El Bosque seco Tropical en Colombia* (pp. 24–32). Bogotá D.C., Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH).

García, H., Corzo, G., Isaacs, P., & Etter, A. (2014). Distribución y estado actual de los remanentes del bioma de bosque seco tropical en Colombia: Insumos para su gestión. In C. Pizano & H. García (Eds.), *El Bosque Seco Tropical en Colombia* (First, pp. 228–251). Bogotá D.C., Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH).

Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M., & Burgess, N. D. (2013). Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biological Conservation*, *161*, 230–238. http://doi.org/10.1016/j.biocon.2013.02.018

Gentili, R., Rossi, G., Abeli, T., Bedini, G., & Foggi, B. (2011). Assessing extinction risk across borders: Integration of a biogeographical approach into regional IUCN assessment? *Journal for Nature Conservation*, *19*(2), 69–71. http://doi.org/10.1016/j.jnc.2010.06.001

Gentry, A. H. (1982). Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden*, *69*, 557–593.

Gentry, A. H. (1995). Diversity and floristic composition of neotropical dry forests. In S. Bullock, H. Mooney, & E. Medina (Eds.), *Seasonally Dry Tropical Forests*. (pp. 146–194). Cambridge, UK: Cambridge University Press.

Gina M. Rodríguez, Karina Banda-R, S. P. R. B. y A. C. E. G. (2012). Lista comentada de las plantas vasculares de bosques secos prioritarios para la conservación en los departamentos de Atlántic y Bolívar (Caribe colombiano). *Biota Colombiana*, *13*(2), 7–39.

Glaser, B. G., & Strauss, A. L. (1967). *The Discovery of Grounded Theory: Strategies for Qualitative Research*. New York: Aldine de Gruyter.

Goodland, R., & Pollard, R. (1973). The Brazilian cerrado vegetation : A fertility gradient. *Journal of Ecology*, *61*(1), 219–224.

Gordon, J. E., Hawthorne, W. D., Reyes-García, A., Sandoval, G., & Barrance, A. J. (2004). Assessing landscapes: A case study of tree and shrub diversity in the seasonally dry tropical forests of Oaxaca, Mexico and southern Honduras. *Biological Conservation*, *117*(4), 429–442. http://doi.org/10.1016/j.biocon.2003.08.011

Graham, A. (2011). *A Natural History of the New World: the Ecology and Evolution of Plants in the Americas*. Chicago and London: The University of Chicago Press.

Gregory-Wodzicki, K. M. (2000). Uplift history of the Central and Northern Andes: A review. *Geological Society of America Bulletin*, *112*(7), 1091–1105. http://doi.org/10.1130/0016-7606(2000)112<1091:uhotca>2.0.co;2

Hawthorne, W. D. (1996). Holes in sums of parts in Ghanaian forest: regeneration scale and sustainable use. *Proceedings of the Royal Society of Edinburgh*, *104 (B)*, 75–176.

Hawthorne, W. D., & Marshall, C. A. M. (2015). *A Manual for a Rapid Botanic Survey (RBS) and Measurement of Vegetation Bioquality* (July 2015). Oxford: Dept. plant Scienc, University of Oxford, U.K.

Headley, M. (2016). Keynote address: Forest management, climate change, and biodiversity: Advancing an understanding of Caribbean forest dynamics and creating long-term regional networks. *Caribbean Naturalist*, *1*(Special Issue), 18’24.

Hernández, G., & Acevedo, A. (2009). Implementación de la metodología CORINE LAND CORVER con imágenes IKONOS. *Revista Ingenierías Universidad de Medellín*, *8*(15), 39–52.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. http://doi.org/10.1002/joc.1276

Honorio Coronado, E. N., Dexter, K. G., Pennington, R. T., Chave, J., Lewis, S. L., Alexiades, M. N., … Phillips, O. L. (2015). Phylogenetic diversity of Amazonian tree communities. *Diversity and Distributions*, n/a-n/a. http://doi.org/10.1111/ddi.12357

Huber, O., & Riina, R. (Eds.). (1997). *Glosario fitoecológico de las Américas* (Vol: 1). Caracas, Venezuela.: Fundación Instituto Botánico de Venezuela.

Ickowitz, A., Rowland, D., Powell, B., Salim, M. A., & Sunderland, T. (2016). Forests, trees, and micronutrient-rich food consumption in Indonesia. *PLoS ONE*, *11*(5), 1–15. http://doi.org/10.1371/journal.pone.0154139

INRENA. (1995). *Mapa ecológico del Perú: guía explicativa.* Lima, Peru: Ministerio de Agricultura, Instituto Nacional de Recursos Naturales (INRENA).

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., … Loreau, M. (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, *477*(7363), 199–202. http://doi.org/10.1038/nature10282

IUCN. (2001). *IUCN Red List Categories and Criteria: version 3.1. IUCN species survival commission*. (I. species survival Commission., Ed.). Gland, Switzerland and Cambridge, UK: IUCN.

IUCN. (2013). *The IUCN Red List of Threatened Species™: Strategic Plan 2013 - 2020. Version 1.0. Red List Committee*.

IUCN. (2016). *Guidelines for Using the IUCN Red List Categories and Criteria* (Vol. Version 12). Standards and Petitions Subcommittee.

IUCN, & UNEP-WCMC. (2014). The World Database on Protected Areas (WDPA) [On-line]. Retrieved January 1, 2014, from www.protectedplanet.net

Janzen, D. H. (1988). Tropical dry forests: The most endangered major tropical ecosystem. In E. O. Wilson. (Ed.), *Biodiversity* (pp. 130–137). Washington, DC: National Academy Press.

Jiménez-Escobar, N. D., & Estupiñán-González, A. C. (2011). Useful trees of the Caribbean region of Colombia. *Bioremediation, Biodiversity and Bioavailability*, *5*(Special Issue 1), 65–79.

Johnson, K. G., Brooks, S. J., Fenberg, P. B., James, K. E., Glover, A. G., Lister, A. M., … Stewart, J. R. (2011). Climate change and biosphere response: unlocking the collections vault. *BioScience*, *61*(2), 147–153. http://doi.org/10.1525/bio.2011.61.2.10

Kessler, M., & Helme, N. (1999). Floristic diversity and phytogeography of the central Tuichi valley, an isolated dry forest locality in the Bolivian Andes. *Candollea*, *54*, 341–366.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., … Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(23), 9322–7. http://doi.org/10.1073/pnas.0810306106

Kreft, H., & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, *37*(11), 2029–2053. http://doi.org/10.1111/j.1365-2699.2010.02375.x

Kukkala, A. S., & Moilanen, A. (2013). Core concepts of spatial prioritisation in systematic conservation planning. *Biological Reviews*, *88*(2), 443–464. http://doi.org/10.1111/brv.12008

Lamoreux, J. F., Morrison, J. C., Ricketts, T. H., Olson, D. M., Dinerstein, E., McKnight, M. W., & Shugart, H. H. (2006). Global tests of biodiversity concordance and the importance of endemism. *Nature*, *440*(7081), 212–214. http://doi.org/10.1038/nature04291

Larkin, C. C., Kwit, C., Wunderle, J. M., Helmer, E. H., Stevens, M. H. H., Roberts, M. T. K., & Ewert, D. N. (2012). Disturbance type and plant successional communities in Bahamian dry forests. *Biotropica*, *44*(1), 10–18. http://doi.org/10.1111/j.1744-7429.2011.00771.x

Lavin, M., & Matos, A. B. (2008). The impact of ecology and biogeography on legume diversity, endemism, and phylogeny in the Caribbean region: A new direction in historical biogeography. *The Botanical Review*, *74*(1), 178–196. http://doi.org/10.1007/s12229-008-9006-8

Legendre, P., Borcard, D., & Peres-Neto, P. R. (2005). Analyzing beta diversity: partitioning the spastial variation of community composition data. *Ecological Monographs*, *75*(4), 435–450. http://doi.org/10.1890/05-0549

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. http://doi.org/10.1007/s004420100716

Legendre, P., & Legengre, L. (1998). *Numerical Ecology* (2nd ed.). Amsterdam: Elsevier.

Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I. F., & He, F. (2009). Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology*, *90*(3), 663–674. http://doi.org/10.1890/07-1880.1

Lehmann, C. E. R., Archibald, S. A., Hoffmann, W. A., & Bond, W. J. (2011). Deciphering the distribution of the savanna biome. *The New Phytologist*, *191*(1), 197–209. http://doi.org/10.1111/j.1469-8137.2011.03689.x

Lennon, J. J., Koleff, P., Greenwood, J. J. D., & Gaston, K. J. (2001). The geographical structure of British bird distributions: Diversity, spatial turnover and scale. *Journal of Animal Ecology*, *70*(6), 966–979. http://doi.org/10.1046/j.0021-8790.2001.00563.x

Levin, N., Mazor, T., Brokovich, E., Jablon, P.-E., & Kark, S. (2015). Sensitivity analysis of conservation targets in systematic conservation planning. *Ecological Applications*, *25*(7), 1997–2010. http://doi.org/10.1890/14-1464.1

Lewis, G. P., Klitgaard, B. B., & Schrire, B. D. (2006). Seasonally dry forests of southern Ecuador in a continental context: Insights from legumes. In R. T. Pennington, G. P. Lewis, & J. A. Ratter (Eds.), *Neotropical Savannas and Seasonally Dry Forests. Plant Diversity, Biogeography and Conservation.* (pp. 281–314). Boca Raton, FL, USA.: CRC Press, Boca Raton.

Linares-Palomino, R. (2006). Phytogeography and floristics of seasonally dry tropical forests in Peru. In R. T. Pennington, G. P. Lewis, & J. A. Ratter (Eds.), *Neotropical Savannas and Seasonally Dry Forests. Plant Diversity, Biogeography and Conservation.* (pp. 257–280). Boca Raton, FL, USA.: CRC Press, Boca Raton.

Linares-Palomino, R., & Kessler, M. (2009). The role of dispersal ability, climate and spatial separation in shaping biogeographical patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. *Journal of Biogeography*, *36*(2), 280–290. http://doi.org/10.1111/j.1365-2699.2008.02028.x

Linares-Palomino, R., Oliveira-Filho, A. T., & Pennington, R. T. (2011). Neotropical seasonally dry forests: diversity, endemism, and biogeography of woody plants. In R. Dirzo, H. S. Young, H. A. Mooney, & G. Ceballos (Eds.), *Seasonally Dry Tropical Forest: Ecology and Conservation*. Washington, DC: Island Press/Center for Resource Economics. http://doi.org/10.5822/978-1-61091-021-7

Lloyd, J., Bird, M. I., Vellen, L., Miranda, A. C., Veenendaal, E. M., Djagbletey, G., … Farquhar, G. D. (2008). Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate. *Tree Physiology*, *28*(3), 451–468.

http://doi.org/10.1093/treephys/28.3.451

López, R. P., & Beck, S. G. (2002). Phytogeographical affinities and life form composition of the Bolivian Prepuna. *Candollea*, *57*, 77–96.

Lott, E., Bullock, S. H., & Solis-Magallanes, A. J. (1987). Floristic diversity and structure of upland and arroyo forests of coastal Jalisco. *Biotropica*, *19*(3), 228–235.

Maass, J. M., Balvanera, P., Castillo, A., Daily, G. C., Mooney, H. A., Ehrlich, P., … Ayala, R. (2005). Ecosystem services of tropical dry forests : Insights from long- term ecological and social research on the Pacific Coast of Mexico.

Mace, G. M. (2000). It's time to work together and stop duplicating conservation efforts …. *Nature*, (correspondence), 393–394. http://doi.org/10.1038/35013247

Mace, G. M., & Purvis, A. (2008). Evolutionary biology and practical conservation: Bridging a widening gap. *Molecular Ecology*, *17*(1), 9–19. http://doi.org/10.1111/j.1365-294X.2007.03455.x

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, *27*, 209–220.

Manzano, M. G., & Návar, J. (2000). Processes of desertification by goats overgrazing in the Tamaulipan thornscrub (matorral) in north-eastern Mexico. *Journal of Arid Environments*, *44*, 1–17. http://doi.org/10.1006/jare.1999.0577

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, *405*(6783), 243–253. http://doi.org/10.1038/35012251

Marris, E. (2007). Conservation priorities: what to let go. *Nature*, *450*(November), 152–155. http://doi.org/10.1038/450152a

Maunder, M., Leiva, A., Santiago-Valentín, E., Stevenson, D. W., Acevedo-Rodríguez, P., Meerow, A. W., … Francisco-Ortega, J. (2008). Plant conservation in the Caribbean island biodiversity hotspot. *The Botanical Review*, *74*(1), 197–207. http://doi.org/10.1007/s12229-008-9007-7

Meyer, C., Weigelt, P., & Kreft, H. (2016). Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecology Letters*, *19*(8), 992–1006. http://doi.org/10.7287/peerj.preprints.1326v2

Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., … Gordon, J. E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, *33*(3), 491–505. http://doi.org/10.1111/j.1365-2699.2005.01424.x

Ministério do Meio Ambiente Brasil. (2016). Unidades de Conservação por Bioma Publication: CNUC/MMA. www.mma.gov.br/images/arquivo/80112/CNUC_PorBiomaFev16.pdf.

Mistry, J. (2000). *World Savannas, Ecology and Human Use*. Edinburgh: Pearson Education Limited.

Murphy, P. G., & Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, *17*, 67–88.

Murphy, P., & Lugo, A. E. (1995). Dry forests of Central America and the Caribbean. In S. Bullock, H. Mooney, & E. Medina (Eds.), *Seasonally Dry Tropical Forests.* (pp. 9–34). Cambridge, UK: Cambridge University Press.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–8. http://doi.org/10.1038/35002501

Neves, D. M., Dexter, K. G., Pennington, R. T., Bueno, M. L., & Oliveira Filho, A. T. (2015). Environmental and historical controls of floristic composition across the South American dry diagonal. *Journal of Biogeography*, *42*, 1566–1576. http://doi.org/10.1111/jbi.12529

Newton, A. C. (2008). Restoration of dryland forests in Latin America: The ReForLan project. *Ecological Restoration*, *26*(1), 10–14.

Newton, A., Oldfield, S., Rivers, M., Mark, J., Schatz, G., Garavito, N. T., … Miles, L. (2015). Towards a global tree assessment. *Oryx*, *49*(3), 1–6. http://doi.org/10.1017/S0030605315000137

Nychka, D., Furrer, R., Paige, J., & Sain, S. (2016). “fields”: Tools for spatial data. R package version 8.4-1, 202.

Oksanen, A. J., Blanchet, F. G., Kindt, R., Minchin, P. R., Hara, R. B. O., Simpson, G. L., … Wagner, H. (2016). Package “ vegan .” Retrieved from https://cran.r-project.org/web/packages/vegan/vegan.pdf

Oliveira-Filho, A. T. (2009). Classificação das fitofisionomias da América do Soul cisandina tropical e tropical: Proposta de um novo sistema-prático e flexível- ou uma injeção a mais caos? *Rodriguésia*, *60*(2), 237–258.

Oliveira-Filho, A. T., Cardoso, D., Schrire, B. D., Lewis, G. P., Pennington, R. T., Brummer, T. J., … Lavin, M. (2013). Stability structures tropical woody plant diversity more than seasonality: Insights into the ecology of high legume-succulent-plant biodiversity. *South African Journal of Botany*. http://doi.org/10.1016/j.sajb.2013.06.010

Oliveira-Filho, A. T., Curi, N., Vilela, E. A., & Carvalho, D. A. (1998). Effects of canopy gaps, topography, and soils on the distribution of woody species in a central Brazilian deciduous dry forest. *Biotropica*, *30*(3), 362–375.

Oliveira-Filho, A. T., & Ratter, J. A. (2002). Vegetation physiognomies and woody flora of the cerrado biome. In A. T. de Oliveira-Filho & J. A. Ratter (Eds.), *The Cerrados of Brazil. Ecology and Natural History of a Neotropical Savanna* (pp. 91–120). New York: Columbia University Press.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., … Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *BioScience*, *51*(11), 933. http://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. a, … Owens, I. P. F. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, *436*(7053), 1016–9. http://doi.org/10.1038/nature03850

ORNERN. (1976). *Mapa ecológico del Perú. Guía explicativa. Mapa 1:1.000.000*.

Paganucci de Queiroz, L. (2006). The Brazilian Caatinga: Phytogeographical patterns inferred from distribution data of Leguminosae. In T. D. Pennington, G. P. Lewis, & J. A. Ratter (Eds.), *Neotropical Savannas and Seasonally Dry Forests. Plant Diversity, Biogeography and Conservation.* (pp. 121–157). Boca Raton, FL, USA.: CRC Press.

Palmer, N. (2016). What’s your beef? Why it might be time give livestock a break. Retrieved November 30, 2016, from http://blog.ciat.cgiar.org/whats-your-beef-why-it-might-be-time-give-livestock-a-break/

Pennington, R. T., Lavin, M., & Oliveira-Filho, A. (2009). Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 437–457.

http://doi.org/10.1146/annurev.ecolsys.110308.120327

Pennington, R. T., Lewis, G. P., & Ratter, J. A. (2006). An overview of the plant diversity, biogeography and conservation of neotropical savannas and seasonally dry forest. In R. T. Pennington, G. P. Lewis, & J. A. Ratter (Eds.), *Neotropical Savannas and Seasonally Dry Forests. Plant Diversity, Biogeography and Conservation.* (pp. 1–30). Boca Raton, FL, USA.: CRC Press, Boca Raton.

Pennington, R. T., Prado, D. E., & Pendry, C. A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, 261–273.

Peres-Neto, P., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices : Estimation and comparison of fractions. *Ecology*, *87*(10), 2614–2625. http://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Pitman, N. C. A., Terborgh, J. W., Silman, M. R., Núñez, P. V., Neill, D. a., Cerón, C. E., … Aulestia, M. (2001). Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology*, *82*(8), 2101–2117. http://doi.org/10.1890/0012-9658(2001)082[2101:DADOTS]2.0.CO;2

Portillo-Quintero, C., Sanchez-Azofeifa, A., Calvo-Alvarado, J., Quesada, M., & do Espirito Santo, M. M. (2015). The role of tropical dry forests for biodiversity, carbon and water conservation in the neotropics: lessons learned and opportunities for its sustainable management. *Regional Environmental Change*, *15*(6), 1039–1049. http://doi.org/10.1007/s10113-014-0689-6

Powers, J. S., Becknell, J. M., Irving, J., & Pèrez-Aviles, D. (2009). Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. *Forest Ecology and Management*, *258*(6), 959–970. http://doi.org/10.1016/j.foreco.2008.10.036

Powney, G. D., & Isaac, N. J. B. (2015). Beyond maps: a review of the applications of biological records. *Biological Journal of the Linnean Society*, *115*(April 2015), 532–542. http://doi.org/10.1111/bij.12517

Prado, D. E., & Gibbs, P. E. (1993). Patterns of species distributions in the dry seasonal forest of South America. *Annals of the Missouri Botanical Garden*, *80*(4), 902–927.

Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C., & Gibbons, D. W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, *365*(6444), 335–337. http://doi.org/Doi 10.1038/365335a0

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology and Evolution*, *22*(11), 583–592. http://doi.org/10.1016/j.tree.2007.10.001

Quintana, C. (2015). *Diversity and ecological ranges of plant species from dry inter-Andean valleys*. Ph.D. Thesis. Aarhus University.

Rangel-ch, J. O., & Minorta-Cely, V. (2014). Los tipos de vegetación de la Orinoquia colombiana. In J. O. Rangel-Ch (Ed.), *Colombia Diversidad Biótica XIV* (pp. 533–612). Bogotá D.C., Colombia: Universidad Nacional de Colombia.

Rao, C. R. (1995). A review of canonical coordinates and an alternative to correspondence analysis using Hellinger distance. *Questiio*, *19*(1–3), 23–63.

Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. a., Archibald, S., Lehmann, C. E. R., … Sankaran, M. (2011). When is a “forest” a savanna, and why does it matter? *Global Ecology and Biogeography*, *20*(5), 653–660. http://doi.org/10.1111/j.1466-8238.2010.00634.x

Ratter, J. A., Askew, G. P., Montgomery, R. F., & Gifford, D. R. (1978). Observations on forest of some mesotrophic soils in central Brazil. *Revista Brasileria de Botánica*, (1), 47–58.

Ratter, J. A., Richards, P. W., Argent, G., & Gifford, D. R. (1973). Observations on the vegetations of northeastern Mato Grosso 1. The woody vegetation types of the Xavantina-Cachimbo expedition area. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, (266), 449–492.

Richardson, J. E., Whitlock, B. A., Meerow, A. W., & Madriñán, S. (2015). The age of chocolate: a diversification history of Theobroma and Malvaceae. *Frontiers in Ecology and Evolution*, *3*(November), 1–14. http://doi.org/10.3389/fevo.2015.00120

Richardson, J., Pennington, R. T., Pennington, T. D., & Hollingsworth, P. M. (2001). Rapid Diversification of a species-rich genus of neotropical rain forest trees. *Science*, *293*(5538), 2242–2245. http://doi.org/10.1126/science.1061421

Rio de Janeiro Botanical Garden. (n.d.). List of Species of the Brazilian Flora. Retrieved from http://floradobrasil.jbrj.gov.br/%3E

Ruíz, D., & González, R. (2014). Composición florística y estructura de una parcela permanente en bosques secos tropicales del municipio de Pereira, Risaralda. 1943 registros, aportados por: Gonzáles, R. (Contacto del recurso), Ruiz, D. (Creador del recurso), Quintana, A. (Proveedor de m. *Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Universidad Tecnológica de Pereira*, *Versión 7.*

Rzedowski, J. (1978). *Vegetación de Mexico*. Mexico: Editorial Limusa.

Rzedowski, J., & De Rzedowski, G. C. (2013). Datos para la apreciación de la flora fanerogámica del bosque tropical caducifolio de méxico. *Acta Botanica Mexicana*, (102), 1–23.

Sanchez-Azofeifa, G. A., Nassar, J. M., Stoner, K. E., Castillo, A., Arturo, G. S., Zent, L., … Garvin, T. (2005). Research priorities for neotropical dry forests. *Biotropica*, *37*(4), 477–485.

Saout, S. Le, Hoffmann, M., Shi, Y., & Hughes, A. (2013). Protected Areas and Effective Biodiversity Conservation. *Science*, *342*, 803–805. http://doi.org/10.1126/science.1239268

Särkinen, T., Pennington, R. T., Lavin, M., Simon, M. F., & Hughes, C. E. (2012). Evolutionary islands in the Andes: persistence and isolation explain high endemism in Andean dry tropical forests. *Journal of Biogeography*, *39*(5), 884–900. http://doi.org/10.1111/j.1365-2699.2011.02644.x

Sarmiento, G. (1975). The dry plant formations of South America and their floristic connections. *Journal of Biogeography*, *2*(4), 233–251.

Schatz, G. E. (2009). Plants on the IUCN Red List: setting priorities to inform conservation. *Trends in Plant Science*, *14*(11), 638–642. http://doi.org/10.1016/j.tplants.2009.08.012

Schrire, B. D., Lavin, M., & Lewis, G. P. (2005). Global distribution patterns of the Leguminosae: insights from recent phylogenies. In I. Friis & H. Balslev (Eds.), *Plant Diversity and Complexity Patterns: Local, Regional and Global Dimensions* (pp. 375–422). Biologiske Skrifter.

Seo, J., Kang, S. M., & Frierson, D. M. W. (2014). Sensitivity of intertropical convergence zone movement to the latitudinal position of thermal forcing. *Journal of Climate*, *27*(8), 3035–3042. http://doi.org/10.1175/JCLI-D-13-00691.1

Sieck, M., Ibisch, P. L., Moloney, K. A., & Jeltsch, F. (2011). Current models broadly neglect specific needs of biodiversity conservation in protected areas under climate change. *BMC Ecology*, *11*(1), 12. http://doi.org/10.1186/1472-6785-11-12

Soberón, J., & Peterson, T. (2004). Biodiversity informatics: managing and applying primary biodiversity data. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *359*(1444), 689–698. http://doi.org/10.1098/rstb.2003.1439

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016a). How should beta-diversity inform biodiversity conservation? *Trends in Ecology and Evolution*, *31*(1), 67–80. http://doi.org/10.1016/j.tree.2015.11.005

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016b). Sparse data necessitate explicit treatment of beta-diversity: A reply to Bush et al. *Trends in Ecology and Evolution*, *31*(5), 338–339. http://doi.org/10.1016/j.tree.2016.02.019

Stone, R. (2013). Battle for the Americas. *Science*, *341*(6143), 230–233. http://doi.org/10.1126/science.341.6143.230

Stott, P. (1988). The forest as phoenix : Towards a biogeography of fire in mainland South East Asia. *The Geographical Journal*, *154*(3), 337–350.

Sutherland, W. J., Pullin, A. S., Dolman, P. M., & Knight, T. M. (2004). The need for evidence-based conservation. *Trends in Ecology and Evolution*, *19*(6), 305–308. http://doi.org/10.1016/j.tree.2004.03.018

Suzuki, R., & Shimodaira, H. (2015). Package " pvclust " Hierarchical Clustering with P-Values via Multiscale Bootstrap Resampling, *1.3-2*.

Syfert, M. M., Joppa, L., Smith, M. J., Coomes, D. A., Bachman, S. P., & Brummitt, N. a. (2014). Using species distribution models to inform IUCN Red List assessments. *Biological Conservation*, *177*, 174–184. http://doi.org/10.1016/j.biocon.2014.06.012

Tchouto, M. G. P., Yemefack, M., De Boer, W. F., De Wilde, J. J. F. E., Van Der Maesen, L. J. G., & Cleef, A. M. (2006). *Biodiversity hotspots and conservation priorities in the Campo-Ma'an rain forests, Cameroon*. *Biodiversity and Conservation* (Vol. 15). http://doi.org/10.1007/s10531-005-0768-6

ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., … Silman, M. R. (2013). Hyperdominance in the Amazonian tree flora. *Science*, *342*, 1243092. http://doi.org/10.1126/science.1243092

Toscano, M. A., Peltier, W. R., & Drummond, R. (2011). ICE-5G and ICE-6G models of postglacial relative sea-level history applied to the Holocene coral reef record of northeastern St Croix, U.S.V.I.: Investigating the influence of rotational feedback on GIA processes at tropical latitudes. *Quaternary Science Reviews*, *30*(21–22), 3032–3042. http://doi.org/10.1016/j.quascirev.2011.07.018

Trejo, I., & Dirzo, R. (2000). Deforestation of seasonally dry tropical forest : a national and local analysis in Mexico. *Biological Conservation*, *94*, 133–142.

Trejo, I., & Dirzo, R. (2002). Floristic diversity of Mexican seasonally dry tropical forests. *Biodiversity and Conservation*, *11*(11), 2063–2084. http://doi.org/10.1023/A:1020876316013

Tuomisto, H. (2010). A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, *33*(1), 2–22. http://doi.org/10.1111/j.1600-0587.2009.05880.x

Valencia-Duarte, J., Trujillo, L. N., & Vargas, O. (2012). Dinámica de la vegetación en un enclave semiárido del río Chicamocha, Colombia. *Biota Colombiana*, *13*(2), 40–65.

Vargas, W. (2012). Los bosques secos del Valle del Cauca, Colombia: una aproximación a su flora actual. *Biota Colombiana*, *312*(2), 102–164.

Vargas, W., Castaño, A., & Idárraga, Á. (2014). Las plantas de los bosques secos de Colombia, Valle geográfico del rio Cauca. In C. Pizano & H. García (Eds.), *El Bosque seco Tropical en Colombia* (pp. 76–77). Bogotá D.C., Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH).

Vargas, W., & Ramírez, W. (2014). Lineamientos generales para la restauración del bosque seco tropical en Colombia. In C. Pizano & H. García (Eds.), *El Bosque seco Tropical en Colombia* (Primera ed, pp. 253–286). Bogotá D.C., Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH).

Veteto, J., & Lockyer, J. (2013). *Environmental Anthropology Engaging Ecotopia*. New York: Berghahn Books.

Watson, J. E. M., Dudley, N., Segan, D. B., & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, *515*(7525), 67–73. http://doi.org/10.1038/nature13947\rhttp://www.nature.com/nature/journal/v515/n7525/abs/nature13947.html#supplementary-information

Williams-Linera, G., & Lorea, F. (2009). Tree species diversity driven by environmental and anthropogenic factors in tropical dry forest fragments of central Veracruz, Mexico. *Biodiversity and Conservation*, *18*(12), 3269–3293. http://doi.org/10.1007/s10531-009-9641-3