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Disentangling the environmental heterogeneity, floristic distinctiveness and current threats of tropical dry forests in Colombia

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Supplementary material for this article is available online

Abstract

Tropical dry forests (TDFs) have been defined as a single biome occurring mostly in the lowlands where there is a marked period of drought during the year. In the Neotropics, dry forests occur across contrasting biogeographical regions that contain high beta diversity and endemism, but also strong anthropogenic pressures that threaten their biodiversity and ecological integrity. In Colombia, TDFs occur across six regions with contrasting soils, climate, and anthropogenic pressures, therefore being ideal for studying how these variables relate to dry forest species composition, successional stage and conservation status. Here, we explore the variation in climate and soil conditions, floristic composition, forest fragment size and shape, successional stage and anthropogenic pressures in 571 dry forest fragments across Colombia. We found that TDFs should not be classified solely on rainfall seasonality, as high variation in precipitation and temperature were correlated with soil characteristics. In fact, based on environmental factors and floristic composition, the dry forests of Colombia are clustered in three distinctive groups, with high species turnover across and within regions, as reported for other TDF regions of the Neotropics. Widely distributed TDF species were found to be generalists favored by forest disturbance and the early successional stages of dry forests. On the other hand, TDF fragments were not only small in size, but highly irregular in shape in all regions, and comprising mostly early and intermediate successional stages, with very little mature forest left at the national level. At all sites, we detected at least seven anthropogenic disturbances with agriculture, cattle ranching and human infrastructure being the most pressing disturbances throughout the country. Thus, although environmental factors and floristic composition of dry forests vary across regions at the national level, dry forests are equally threatened by deforestation, degradation and anthropogenic pressures all over the country, making TDFs a top priority for conservation in Colombia.

1. Introduction

Tropical dry forests (TDFs) occur in America, Asia and Africa, where mean annual temperature is greater than 17 °C, annual rainfall ranges from 250–2000 mm and potential evapotranspiration is higher than precipitation (Holdridge 1967, Murphy and Lugo 1986, Kalacska *et al* 2004, Dirzo *et al* 2011). However, climatic limits of dry ecosystems are still unclear, as the dry biome occurs across different rainfall regimes (e.g. dry savannas can have up to 2500 mm rainfall·year^{-1}, Lehmann *et al* 2011) and vary dramatically in soil conditions (Rundel and Boonpragob 1995, Sampaio 1995) and elevation. Therefore, TDFs are generally defined by their seasonality, with 3–6 dry months (precipitation < 100 mm·month^{-1}, Portillo-Quintero and Sanchez-Azofeifa 2010), which determines the deciduous phenology of many woody plants, and the biological cycles of these forests as a whole (Pennington *et al* 2009, Dirzo *et al* 2011). In terms of floristic composition, TDFs strongly differ between South America, Africa and Asia (Dexter *et al* 2015), and have a high plant species turnover across the Neotropics, where species of different floristic groups are commonly restricted to a single region (DRYFLOR *et al* 2016).

Although TDFs are used to represent 42% of all the worlds' tropical forests (Brown and Lugo 1982), only 1000 000 km^2 are left worldwide (Miles *et al* 2006, Portillo-Quintero and Sanchez-Azofeifa 2010, Powers *et al* 2011), with more than 50% left in South America (Miles *et al* 2006). These forests have been recognized as highly endangered ecosystems (Murphy and Lugo 1986, Janzen 1988). However, research in the tropics has been concentrated on more humid forests (Powers *et al* 2011, Sánchez-Azofeifa and Portillo-Quintero 2011). This imbalance in knowledge has also been reflected in a general absence of studies that assess the different environmental conditions under which dry forests occur, and their degree of degradation and fragmentation across Latin America (Sánchez-Azofeifa *et al* 2005, Portillo-Quintero and Sánchez-Azofeifa 2010, Sánchez-Azofeifa and Portillo-Quintero 2011). For instance, recent studies showed high floristic turnover among different regions in the Neotropics (DRYFLOR *et al* 2016), but little is known on how differences in species composition may be related to climate and soil factors.

Accurate measurements of TDF extent and successional status are key tools for the conservation and landscape planning for these forests (Hesketh and Sánchez-Azofeifa 2014), and are necessary for addressing their ecological importance and as providers of ecosystem services (Calvo-Rodríguez *et al* 2016). The only analysis of TDF cover at the global scale revealed that deforestation was six times higher in Latin America (12%) compared to Asia and Africa (2%) between 1980 and 2000 (Miles *et al* 2006). Similarly, Olson *et al* (2001) and Portillo-Quintero and Sánchez-Azofeifa (2010) showed that 66% of dry forest in Latin America has been lost due to deforestation, and only 4.5% is subject to protection. At the regional level, similar efforts to map the distribution and loss of TDFs have been published for Mexico (Trejo and Dirzo 2000, Sánchez-Azofeifa *et al* 2009), Puerto Rico (Martinuzzi *et al* 2013), Venezuela (Fajardo *et al* 2005) and the Antilles (Helmer *et al* 2008). However, few studies have evaluated the successional status and anthropogenic pressures of dry forests in the field (e.g. Larkin *et al* 2012), which is key information for addressing their real conservation status. Furthermore, few studies have explored how in addition to fragmentation and successional status of dry forests, environmental conditions and species composition vary across different regions, which is crucial for implementing more effective conservation and management plans for TDFs.

In Colombia, TDFs originally covered 8'882 854 ha, but around 90% of its cover was replaced by pastures, agricultural fields, and urbanization by the end of the 20th century (Etter *et al* 2008, García *et al* 2014). In fact, only 8% (720 000 ha) of TDF original cover is left in land mosaics in which successional forest covers at least 30% of the territory (384 416 ha) (García *et al* 2014). This means that less than 4% of the original TDFs remain as mature forests. Moreover, only 5% of what is left is preserved in protected areas (García *et al* 2014). Given this critical situation and the lack of information on the conservation status of this ecosystem in Colombia (Fernández-Méndez *et al* 2014, Pizano *et al* 2014), the purpose of this study was to evaluate the variation of environmental conditions, floristic composition and conservation status of TDFs at the national level by doing extensive field surveys. Specifically, we intended to answer the following three questions: (1) How do environmental conditions and floristic composition of TDFs vary across six geographic regions? (2) What are the land-cover status and successional stages of TDFs across these regions? (3) Which are the main anthropogenic pressures impacting dry forests? This information will not only contribute to our understanding of the abiotic, biotic and anthropogenic factors that shape dry forests in Colombia, but can support better founded conservation and management strategies for this highly endangered ecosystem.

2. Methods

2.1. Study area

In Colombia, TDFs occur across altitudinal and climatic gradients and in transitions from humid forests to savannas (Pizano *et al* 2014). Therefore, we used the broad definition of TDFs being lowland to mid-elevation (up to 1200 m.a.s.l.) forests that experience at least three months of drought (<300 mm total rainfall, ∼100 mm·month^{-1}) (Mooney *et al* 1995). We used

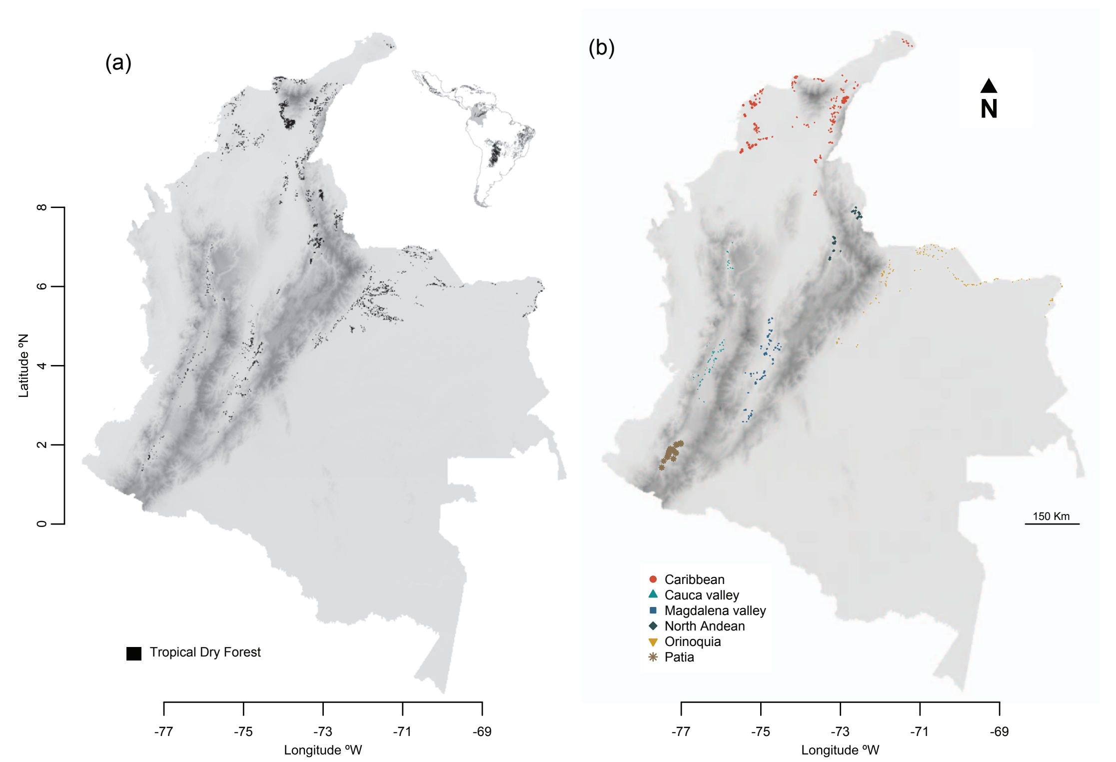

Figure 1. Current extent and distribution (*a*), and field sample sites across six regions of TDFs in Colombia (*b*), as defined by Pizano *et al* (2014a).

the 1:100 000 scaled national map of TDFs (Corzo and Delgado 2012) to randomly select 571 existing forest fragments (sites) within TDF landscapes in six geographic regions of Colombia suggested by Pizano *et al* (2014a) (figure 1, appendix table A1 available at stacks.iop.org/ERL/13/045007/mmedia). We excluded areas that appeared as dry forests in the national map, but were confirmed as not being TDFs by local experts. The number of sample sites was proportional to the extent of TDFs for each region, and it was validated by a field team of botanists, ecologists and spatial analysts.

2.2. Environmental variables

Climatic variables for TDF regions were estimated using the national climatic model developed by the Instituto de Hidrología, Meteorología y Estudios Ambientales and Instituto Humboldt (IAvH) of Colombia, based on 2046 weather stations around the country (monthly data in a resolution of 90 m). Selected climatic variables included mean annual temperature (MAT °C), total annual precipitation (TAP mm), total precipitation in the driest period (rainfall ≤ 300 mm in three continuous months ($\sim$100 mm·month^{-1}); TPdriest mm), number of dry seasons for which precipitation is < 300 mm (drySeason: 1 or 2 periods·year^{-1}) and number of dry months for which precipitation is < 100 mm (dryMonths: 1–12 months·year^{-1}) (appendix table A1). Soil variables included pH (in H_2O), soil organic carbon content (OCarbon g·kg^{-1}), sand content (% particles > 50–2000 μm), silt content (% particles 2–50 μm) and clay content (% particles < 2 μm), bulk density (BulkDens kg·m^{-3}), cation exchange capacity (CEC cmol$_c$·kg^{-1}), and absolute depth to bedrock (Bedrock cm). Soil variables where obtained from the global soil information system (SoilGrids 1–km, Hengl *et al* 2014) (appendix table A1).

2.3. Field sampling data

Field sampling was done between August 2013 and October 2014. Field teams collected the following information at each site: geographic coordinates (Lat./Long. decimal), altitude (m), presence of vascular plant species, successional stage of forest fragments, and the anthropogenic pressures present inside the forest fragment as well as in the surrounding matrix. For plant species data collection, field teams ran a linear transect inside each forest fragment sampled, in which plant species were sampled, photographed and identified by local botanists who also collected reference specimens. All plants of height ≥ 1.3 m were sampled including palms, shrubs, lianas and cacti. For plants with dubious identity, 1–3 specimens were collected for taxonomic identification (appendix table A2). All specimens were processed in a local herbarium (appendix table A2) and homologated based on duplicates in the Federico Medem Herbarium in Bogotá using the APG III classification system (Haston *et al* 2009).

2.4. Quantifying land-cover metrics

Forest fragment size and shape were quantified based on dry forest patches interpreted from a Landsat 8

Mosaic 2014 of TDF distribution published by the IAvH (15 × 15 m resolution) and developed following global models and protocols for image processing using remote sensing techniques (Xu and Becker 2012). Remote sensing resolution was improved using Google EarthPro© images from 2014–2015 (Yu and Gong 2012). Each fragment was mapped by visual interpretation, keeping a fixed digitalization height of 1500 m. This fixed scale assured fragment size and shape was correctly compared between and within regions. All 571 sample sites were re-interpreted using this method for land-cover metric evaluation during the field-sampling period. 77 sites were excluded from the analyses due to cloudiness in the images.

2.5. Successional stages and anthropogenic pressures

Botanists classified TDF successional stages in the field in four categories: no-forest (in some areas forest fragments had a different size or shape to those in the map due to difference in scale), early, intermediate, and late, based on the physiognomy and structural data including visually estimated canopy height and stem density, and the presence of pioneer and late successional species (Kalacska *et al* 2004, García-Millán *et al* 2014). Early successional forests were characterized by low stem density, open vegetation, dominance of pioneer species, and a canopy height of 10 m. Intermediate forests were defined as more dense vegetation in which intermediate-successional species were common, there was a second layer of young trees, a dense understory, and mature trees up to 15 m in height. Finally, late forests were distinguished by a multi-layer and heterogeneous canopy of more than 15 m in height with emergent trees, the presence of late-successional species, and a more open understory (Kalacska *et al* 2004, García-Millán *et al* 2014). At each sample site, anthropogenic pressures were recorded and categorized according to their impact level from the lowest to the highest as follows: ecotourism (1), hunting (2), non-timber forest product extraction (3), selective logging (4), cattle herding inside the forest (5), intensive logging (6), agriculture (7), cattle ranching (8), human infrastructure (9), hydrocarbons (10), fire (11), clear-cut mining (12) and erosion (13). Cattle herding inside the forest was classified as a different pressure to cattle ranching because herding means cattle browse in the understory of TDFs (particularly during the dry season), while forests are clear-cut for the establishment of cattle ranches. Categories 1–5 and fire were recorded based on interviews with local people, while all other pressures were visually assessed.

2.6. Data analyses

We ran a principal component analysis (PCA) to analyze environmental heterogeneity of TDFs across Colombia, reduce climate-soil dimensionality, and identify the principal axes of variation across regions. We also used the unweighted pair-group Simpson dissimilarity index (D_{Simpson}) to evaluate plant species turnover across TDF field sites, as other authors have suggested this is an effective measure of geographical regionalization (Kreft and Jetz 2010) and floristic clustering of TDFs at different geographic scales (Dexter *et al* 2015, DRYFLOR *et al* 2016). D_{Simpson} ranges between 0 and 1, where values close to the unit indicate maximum floristic dissimilarity. We then used the D_{Simpson} distance matrix as the basis for ordination of TDFs in regions using non-metric multidimensional scaling (NMDS, Borcard *et al* 2011). To test if TDF regions had significantly different mean D_{Simpson}, we used the analysis of similarity test (ANOSIM, Clarke 1993). Finally, we computed a redundancy analysis (RDA, with *Hellinger* transformation) to address how differences in species composition may be related to soil and environmental conditions, for which R^2 and adjusted R^2 were calculated to identify the percentage of the explained variance (Borcard *et al* 2011). The significance of the canonical axes in RDA was tested by a one-way analysis of variance (ANOVA) following Legendre *et al* (2011).

Total fragment size (area in hectares) was estimated based on land-cover data for each TDF region, as a key metric for estimating patch occupancy and conservation status in the landscape (McGarial and Marks 1995, Hill and Curran 2003). We also used land-cover data to calculate the shape index as the perimeter/area ratio. This index is defined as the fragment narrowing shape by which a theoretical zero value indicates an infinitely large perimeter around an infinitesimally small area (Berry 2007, Moser *et al* 2002). Hence, a lower value in the index indicates a more irregularly shaped form of forest fragments resulting from land-cover transformations. A one-way ANOVA and a post-hoc Tukey test were performed to compare forest fragment size (area) and shape index (perimeter/area ratio) across the six regions. Both metrics were $\log_{10}$-transformed to fit the assumption of normality.

Forest successional status relative frequency (%) was estimated as the sum of sites (s) in which we reported each successional category (C) divided by the total number of sites measured for each region (R) multiplied by 100: $F = 100 \times \sum_{i=1}^{s} C_i / \sum_{i=1}^{s} R_i$, a descriptive summary of the successional status of TDF fragments in each region. We also estimated the relative frequency (%) of each anthropogenic pressure inside forest fragments and in the surrounding matrix across regions (anthropogenic pressures: 1–13; section 2.3). To evaluate the impact of pressures and differences across the six regions, we performed a non-parametric one-way ANOVA (Kruskal–Wallis; Sokal and Rohlf 1995, McDonald 2014), and a multiple pair comparisons test (posthoc.kruskal.nemenyi.test; Dunn 1964, Pohlert 2016), using the mean ranks of pressures per region as the level of impact. In both analyses, values higher than 6.5 indicate a high level of anthropogenic pressures for a TDF region.

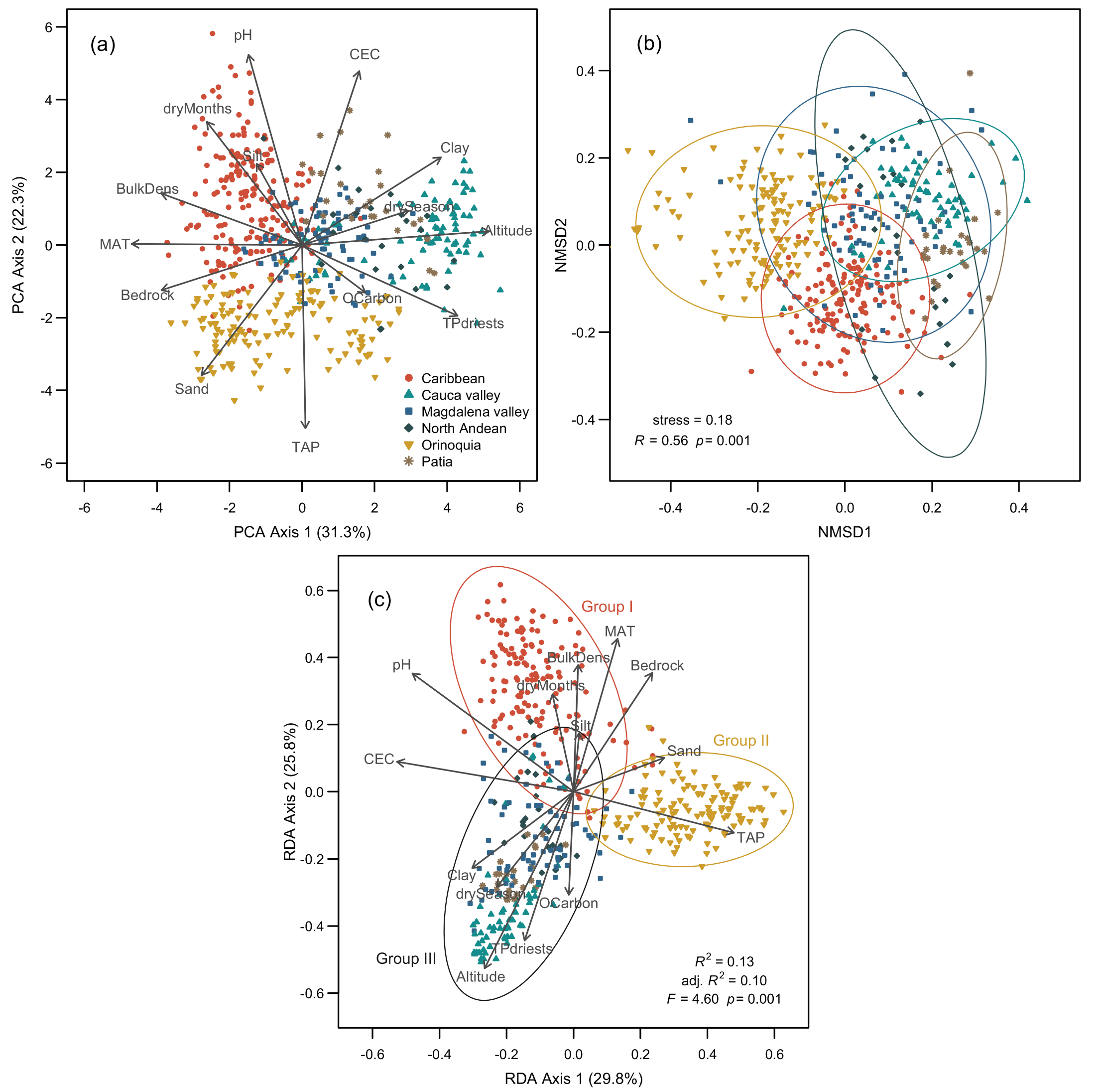

Figure 2. Variation in TDF environmental and soil conditions (*a*), plant species composition (*b*), and their correlation (*c*) across six TDF regions in Colombia. (*a*) Ordination space of environmental conditions (PCA, soil-climate variables, $N = 558$); (*b*) ordination space of TDF floristic composition (NMDS, $N = 464$) using the Simpson dissimilarity index as distance between pair-sites; and (*c*) RDA fitted for the floristic composition and climate-soil conditions (RDA, $N = 456$). Ellipses represent 95% confidence intervals for all analyses.

All statistical analyses were performed using the statistical program R (R Development Core Team 2005, version 3.2.2). We used the package 'vegan' (Oksanen *et al* 2007) for estimating the Simpson dissimilarity index, the NMDS and RDA, and 'PMCMR' package for calculating the Posthoc Kruskal-Nemenyi test (Pohlert 2016). For information on how many forest sampling sites were used for each analysis, please see appendix table A3.

3. Results

TDFs in Colombia occur in areas with high environmental and soil variation (figure 2(*a*)), with a mean annual temperature of 26.5 ± 1.6 °C, mean annual precipitation of 1575.1 ± 596.9 mm, and one to two annual dry seasons with a total precipitation of 115.3 ± 65.4 mm (~3 months continuous < 100 mm·month^{-1}) (appendix table A1). Soils varied from low fertility (pH < 5.5, CEC $= 11.3 \pm 4.1$ cmol$_c$·kg^{-1}), high sand content ($>40\%$) and low organic carbon content (< 13 g·kg^{-1}), to fertile due to high cation exchange capacity (>20 cmol$_c$·kg^{-1}), and higher content of finer textures (clay content $> 30\%$) and organic matter (>20 g·kg^{-1}) (appendix table A1).

Dry forest vegetation clustered in six different groups ($p = 0.001$), with a clear overlap between inter-Andean valley regions (figure 2(*b*)). Sites across the six TDF regions showed high floristic dissimilarity (mean $D_{\text{Sipmson}} = 0.89$, median $D_{\text{Sipmson}} = 0.92$), as 73.3% of plant species were found only in one region, 13.8% of species were shared between two regions, and 1.3%–4.3% species were found in 3–5 regions (appendix table A2). In fact, only three species were found in all six regions (*Guazuma ulmifolia*, *Ceiba pentandra* and *Ochroma pyramidale*, Malvaceae), and the

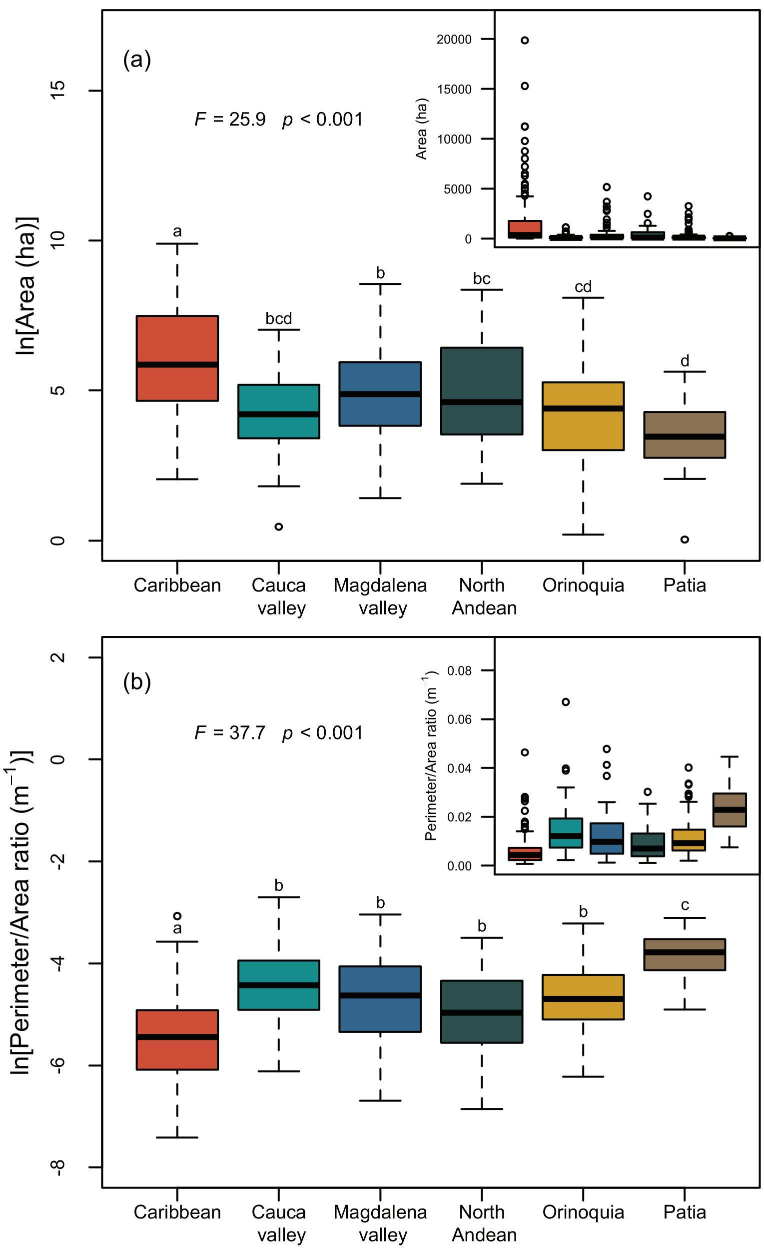

Figure 3. Fragment size in hectares (*a*) and shape index (perimeter/area) (*b*) for six regions of TDFs in Colombia. Different letters indicate statistically significant differences between groups ($p < 0.05$). The upper-right boxes show the forest fragment size and shape index without log transformation.

most frequently detected species varied in each region (appendix table A2). Correspondingly, we found a high floristic dissimilarity within regions, which ranged from 0.67 in Patia to 0.88 in the North Andean region in the median of D_{Sipmson}.

TDFs clustered in three main floristic groups associated to climate-soil conditions ($p = 0.001$, figure 2(*c*)): (1) the Caribbean, with high soil fertility (mean pH > 6.3, CEC > 20 cmol$_c$·kg^{-1}), the longest dry season (5.0 ± 1.7 months per dry period, TPdriest ~1–155 mm) and high aridity due to high temperatures (MAT = 27.3 ± 0.9 °C) (figure 2(*c*), appendix table A1); (2) the Orinoquia, with total annual precipitation above 2367 mm, but dry season (3.9 ± 0.8 months) precipitation of only 40–231 mm, and soils with the highest sand content (40.4 ± 7.4%) and the lowest fertility (pH < 5.3, CEC 11.3 ± 4.1 cmol$_c$·kg^{-1}) (figure 2, appendix table A1), and 3) the inter-Andean valleys with high soil fertility (CEC > 19.6 cmol$_c$·kg^{-1}, clay content > 36.5%) and the highest total precipitation during the driest period (45–298 mm), with two annual dry seasons (figure 2, appendix table A1), and valleys with different altitudes (Cauca Valley = 375–1211 m, Magdalena Valley = 227–906 m, North Andean = 188–1154 m and Patia = 555–953 m; figures 2(*a*)–(*c*) and appendix table A1). Environmental and soil factors explained 13% (R^2) and 10% (adjusted R^2) of the variation in species composition (figure 2(*c*)), with a large proportion of unexplained variance.

A total of 332 342 ha of TDFs were mapped and validated in the field (494 forest fragments). Forest fragment size had a median of 115.2 ha and a

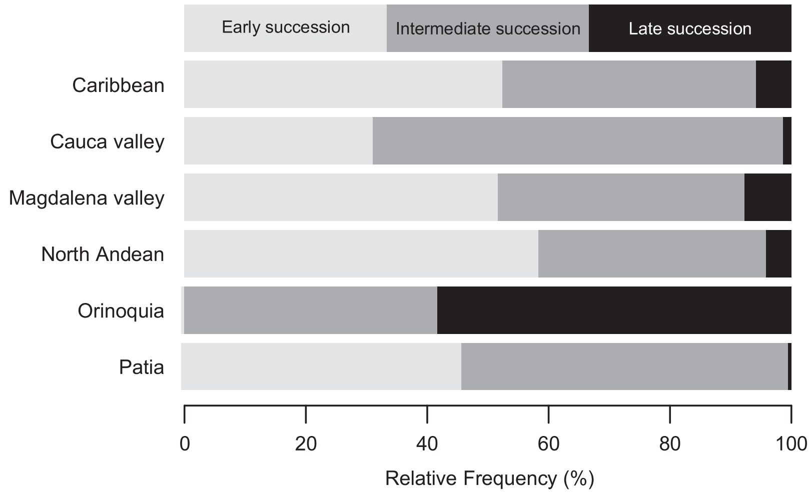

Figure 4. Relative frequency of three successional stages of dry forest fragments registered at each field sample site across six regions in Colombia.

perimeter/area ratio index of 0.008 at the national level (figure 3 (*a*)). The largest forest fragments where found in the Caribbean, where fragment size showed high variation (mean $A = 1530.4 \pm 2840.4$ ha), followed by the Cauca and Magdalena Valleys, North Andean and Orinoquia (figure 3(*a*)). The smallest forest fragments were found in the Patia Valley, where average fragment size was 56.9 ± 63.9 ha (figure 3(*a*)). In general, all forest fragments across the six regions had high narrowing values as a result of large perimeters around low area per patch (median shape index 0.004–0.025, figure 3(*b*)). In the Caribbean, although fragments were the biggest, they also had the highest narrowing, indicating high levels of transformation (median shape index 0.004, figures 3(*a*) and (*b*)). In contrast, the Patia region had the lowest fragment narrowing (median shape index 0.023, figures 3(*a*) and (*b*)) as a result of low forest patch size and regularly shaped fragment shapes. In terms of successional stages, except for the Orinoquia region, the relative frequency of late successional forests (mature forests) was lower than 7% for all regions (figure 4). An extreme case was the Patia region, where no mature forests could be found (figure 4). Correspondingly, dry forests in all regions were at either early (~31%–50%) or intermediate succession (~21%–63%), but in Orinoquia, where no early successional forests were found, and TDFs were either intermediate or mature (figure 4).

Anthropogenic pressure mean rank was higher than 6.5 inside the forest (7.2) and in the surrounding matrix (8.2) across all regions, except inside the forests in the Caribbean and Orinoquia regions (figure 5). In order of importance, the most frequent pressures for all regions inside the forests were: selective logging (reported presence 175, total represented percentage = 30.6%), herding (160, 28.0%), human infrastructure (150, 26.3%) and hunting (110, 19.3%). In contrast, the most frequently reported pressures in the surrounding matrix were: cattle-ranching (327, 57.3%), human infrastructure (314, 54.9%), agriculture (148, 25.9%) and fire (92, 16.1%). The Magdalena Valley, North Andean and Patia regions were the most threatened by high-impact levels inside the forest (Mean rank > 8.1, figure 5(*a*)), while high impact levels were present in the surrounding matrix of all regions (Mean rank > 8.2, figure 5(*b*)), with the highest in the Patia region.

4. Discussion

4.1. Floristic distinctiveness correlates with environmental heterogeneity of TDFs in Colombia

TDFs are commonly defined as a single biome characterized by a strong seasonality in precipitation (Pennington *et al* 2009, Portillo-Quintero and Sanchez-Azofeifa 2010). However, these forests vary significantly in rainfall seasonality (Murphy and Lugo 1986, Gentry 1995, Murphy and Lugo 1995, Pennington *et al* 2009), soil nutrients, soil texture (Peña-Claros *et al* 2012), soil water storage (Neves *et al* 2015), frost (Pennington *et al* 2006) and altitude (Gentry 1995). Correspondingly, TDF plants have been modeled as metacommunities historically adapted to dry conditions (Pennington *et al* 2009) with high species turnover and endemism as a result of historical fragmentation, dispersal limitation (Linares-Palomino *et al* 2011, Neves *et al* 2015) and environmental controls (Neves *et al* 2015, Williams *et al* 2017).

We found that TDFs in Colombia cannot be defined solely on rainfall parameters such as Total annual precipitation (as defined in methods) Mean annual temperature (as defined in methods) TAP or MAT/TAP ratio (Murphy and Lugo 1986, Gentry 1995, Pennington *et al* 2009). Taken together, all environmental variables measured across six TDF regions (appendix table A1) grouped dry forests in three clusters: the Caribbean, the Orinoquia, and the inter-Andean valleys (figure 2(*a*)). The Caribbean

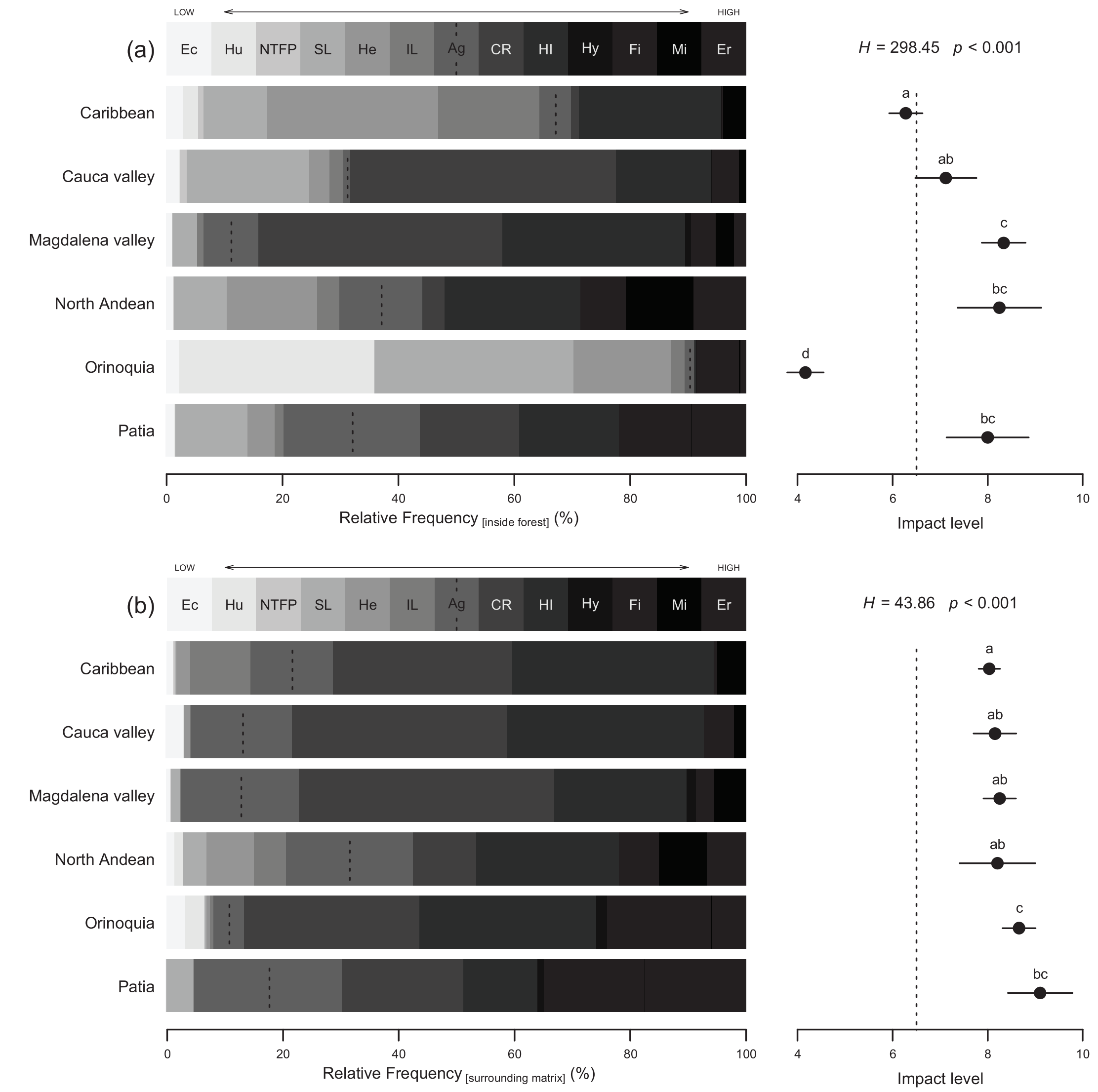

Figure 5. Frequency of anthropogenic pressures and their impact inside dry forest fragments (*a*) and in the surrounding matrix (*b*) in six regions of Colombia ($N = 457$). The arrows indicate the level of impact for each pressure from low (ecotourism (Ec), hunting (Hu), extraction of non-timber forest products (NTFP), selective logging (SL), herding inside the forest (He)) to high (intensive logging (IL), agriculture (Ag), cattle ranching (CR), human infrastructure (HI), hydrocarbons (Hy), fire (Fi), clear-cut mining (Mi), and erosion (Er)). Values higher than 6.5 (dashed line) in the plots indicate the presence of a high number of pressures in a given region based on the mean ranks (Kruskal–Wallis test, H). Different letters indicate statistically significant differences between groups ($p < 0.05$).

experiences the longest and harshest dry season with high MAT and low precipitation, similar to TDFs in Venezuela (Fajardo *et al* 2005) and Central America (Murphy and Lugo 1986, Gentry 1995), but contain mostly fertile soils, as a result of low nutrient leaching (Fajardo *et al* 2005). In contrast, the Orinoquia had a high TAP and low soil fertility as the result of high nutrient leaching (Malagón-Castro 2003) and high sand content, resulting in low soil water storage during the dry season (Medina and Silva 1990, Dezzeo *et al* 2008), an important determinant of dry forests across the Neotropics (Dezzeo *et al* 2008, Peña-Claros *et al* 2012, Neves *et al* 2015). Finally, the inter-Andean valleys had the highest soil fertility and a high variation in rainfall during the dry season (appendix table A1), with two annual dry seasons determined by Colombia's mountainous geography (Fernández-Méndez *et al* 2014). In addition to these marked differences in climate and soils, these three regions differed in altitude (appendix table A1).

Matching the variation in environmental conditions, we found that 73.3% of TDF plant species were only found in one region, and that the floristic composition of dry forests in Colombia is clustered in the same three groups: the Caribbean and the inter-Andean valleys (Patia, Cauca and Magdalena Valleys and North Andean), as suggested by (DRYFLOR *et al* 2016), and the Orinoquia ($p < 0.001$), a region where TDFs have been poorly studied, but has been suggested as a separate floristic entity by Espinal and Montenegro (1977) and Pizano *et al* (2014a) (figures 2(*b*)–(*c*)). In fact, environmental and soil factors explained 13% of the variation in plant species composition (figure 2(*c*)). Similar to other dry forests in the Neotropics, we found high species turnover for both across and within regions (Linares-Palomino *et al* 2011, Neves *et al* 2015, DRYFLOR *et al* 2016, Williams *et al* 2017), as well as high levels of endemism across TDF regions. Floristic composition in the Caribbean appears to be correlated with soils with a high pH and high bulk density, high mean annual temperature, and the longest dry season (figure 2(*c*)). Meanwhile, the presence of plants in the inter-Andean valleys was correlated with soils with high clay and organic carbon content, two dry seasons, and the highest altitudes (figure 2(*c*)). For example, *Trichilia carinata* and *Trichilia oligofoliolata* are restricted to the Magdalena Valley, although locally abundant (González-M *et al* 2016) (appendix table A2). Finally, dry forests of the Orinoquia, with the most unique flora, are characterized by sandy soils and the highest precipitation (figure 2(*c*)). This supports the hypothesis that TDFs in northern South America were isolated from other dry areas due to geography barriers such as rainy formations (Amazonia and Chocó), and the Andes (Gentry 1982, Pennington *et al* 2009). A caveat of our study is that we only sampled plant species of ≥ 1.3 m in height, therefore excluding species important for dry forests such as epiphytes and herbs (Linares-Palomino *et al* 2009, Pizano *et al* 2014a). On the other hand, although the correlation between environmental and soil conditions and floristic distinctiveness was clear, we failed to explained a large fraction (87%) of the variation in dry forest species composition (figure 2(*c*)). However, as reported before, given the many factors that determine plant species composition, this is a usual result of studies on floristic composition over similar spatial scales with species presence-absence data (Guisan *et al* 1999, Neves *et al* 2015).

We also found that the most widespread dry forest species were generalists that are favored by forest disturbance and early successional stages (appendix table A2), as reported by previous studies (Uribe *et al* 2001, López-Camacho *et al* 2012, Castellanos-Castro and Newton 2015, Williams *et al* 2017) for other TDFs (Newbold *et al* 2014), indicating the incipient successional status of dry forests at the regional level (Derroire *et al* 2016). Furthermore, we found an introduced invasive species (*V. farnesiana*) among the most common species of TDFs throughout the country, suggesting that TDFs are also highly susceptible to invasion (Pizano *et al* 2014a). This shows the importance of taking into account human land-cover disturbances as determinants of floristic composition and species turnover of TDFs (Larkin *et al* 2012).

4.2. Successional status and current threats of TDFs in Colombia

Previous studies using remotely sensed data have shown that TDFs are highly fragmented in the Neotropics (Fajardo *et al* 2005, Miles *et al* 2006, Rodríguez *et al* 2008, Portillo-Quintero and Sanchez-Azofeifa 2010). However, field-collected information on forest fragment shape and size, successional stage, species composition and forest conservation status, is rare. Anthropogenic pressures in TDFs vary from hunting, selective logging and local clearing with fire (for agriculture and cattle ranching) to complete deforestation and soil desertification (Janzen 1988, 1988a, García *et al* 2014), but are still fairly unexplored in the Neotropics. In particular, methods such as satellite image analysis are unable to detect subtle changes in the forest due to hunting, non-timber forest harvesting, selective logging, invasion of exotic species and understory thinning due to cattle herding (Peres *et al* 2006).

In an extensive and unique field survey at the national level, we found that TDFs in Colombia are highly fragmented, narrowly shaped, and comprise mostly early and intermediate successional stages, with very little mature forest (figures 3 and 4). At the national level, dry forest comprises very small and highly irregularly shaped forest fragments, with larger remnants only found in the Caribbean and the Magdalena Valley (figure 3). Furthermore, of the 332 342 ha of TDFs mapped across six regions, between 31%–50% of the fragments contained early, ~21%–63% intermediate, and less than 7% mature forest (except for Orinoquia) (figure 4).

On the other hand, high-impact disturbances such as human infrastructure and hunting were common inside dry forest fragments in all regions but Orinoquia, where lower-impact disturbances (cattle herding, hunting, non-timber forest product extraction, and ecotourism) were more important (figure 5(*a*)). Similarly, pressures in the surrounding matrix included higher-impact disturbances such as cattle ranching, human infrastructure, agriculture and fire in all regions (figure 5(*b*)). Orinoquia, an extensive area (285 440 km^2), had the least pressures inside the forest (figure 5(*a*)), and was the only region where mature TDFs still exist (figure 4). However, this is the new agricultural frontier as declared by the Colombian government, and therefore presented high-impact anthropogenic pressures in the surrounding matrix. Thus, in contrast to a tendency towards conservation, deforestation and degradation of TDFs, at the national level will probably tend to increase as a result of high-impact pressures detected in all regions. In particular, previous studies have shown that both high- and low-impact pressures may further degrade TDFs. For example, in the dry forests of Sonebhadra (India), an increase in human population led to increased illegal tree felling, extraction of non-timber resources and cattle herding, which led to significant declines in 52% of the population of all 65 forest plant species (Sagar and Singh 2004). Furthermore, degradation of TDFs may substantially increase carbon emissions, negatively impacting payment schemes such as the 'Reduced Emissions from Forest Deforestation and Degradation' (REDD), one of the most advocated conservation strategies for TDFs (Portillo-Quintero *et al* 2015). However, more extensive field work and satellite and remote sensing methods (Peres *et al* 2006, García-Millán *et al* 2014, Li *et al* 2017), as well as studies on the response of species to disturbance (Newbold *et al* 2014), need to be done to better estimate the extent and impact of anthropogenic pressures on TDFs.

5. Conclusions

Although considered a biome, TDFs have been shown to differ both environmentally and floristically at the regional scale (Murphy and Lugo 1986, Gentry 1995, Murphy and Lugo 1995, Pennington *et al* 2006, Pennington *et al* 2009, Peña-Claros *et al* 2012, Neves *et al* 2015). In this extensive field survey in Colombia, we found that both environmental and floristic characteristics of TDFs varied significantly across regions, and grouped dry forests in three separate entities: the Caribbean, the inter-Andean valleys, and the Orinoquia region. In fact, we found a high species turnover across and within regions (Linares-Palomino *et al* 2011, Neves *et al* 2015, DRYFLOR *et al* 2016), and high levels of regional endemism. At the same time, the most common dry forest tree species were generalists that are favored by forest disturbance and are common in early successional stages. Thus, disturbance is a key determinant of plant community composition in the dry forests of Colombia.

In addition to differences in environmental conditions and plant species across dry forest regions, our broad field study allowed us to verify that TDFs are highly fragmented, consisting of irregularly shaped forest fragments, and of mostly early and intermediate successional forests across the national level (Portillo-Quintero and Sanchez-Azofeifa 2010). Furthermore, anthropogenic pressures inside forest fragments and in the surrounding matrix were equally high across all regions of dry forest, with high-impact disturbance such as human infrastructure, fire, cattle ranching and agricultural plantations dominating TDFs across the country. Thus, the protection of TDF should be a priority in Colombia, where environmental, biotic, successional, and human dimensions need to be considered for assuring more effective management and conservation strategies of these unique forests.

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