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ARTICLE

IMPACT OF DISTURBANCE ON FOREST STRUCTURE AND TREE SPECIES COMPOSITION IN A TROPICAL DRY FOREST OF SOUTH ECUADOR

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Abstract. Tropical dry forests (TDFs) are often degraded and fragmented through human impact, which is also the case in Southern Ecuador, where land-use pressure is high. In this context we studied tree species composition and forest structure in a protected and adjacent disturbed TDF at altitudes between 560-1080 m asl. Fabaceae and Malvaceae were identified as the most important tree families in both forest types. The disturbed forest displayed lower tree species richness than the protected forest, and the gap in species richness between the two forest types increased with increasing altitude. Ten species of the protected forest were not recorded in the disturbed forest, two of them endemic. The disturbed site was further characterized by a lower number of stems but with larger diameters, in comparison with the protected forest. The majority of the most abundant tree species in the disturbed forest had rather low wood densities, but also the combination of high wood density with browsing tolerance and high resprouting capacity was encountered, and seems to be advantageous for getting established in such sites. Although certain tree species were well represented in the disturbed forest, some endemic species with relatively low abundances (e.g. *Simira ecuadorensis*, *Prockia crucis*) should receive more conservation attention.

Keywords: Altitude, Importance Value Index, species richness, Tumbesian dry forest, wood density

INTRODUCTION

Tropical dry forests (TDFs) are unique and species-rich ecosystems. Nevertheless they are considered the most endangered ecosystem type in tropical regions and continue to be a hotspot for human colonization and conversion (Gillespie et al. 2000, Janzen et al. 1988, Miles et al. 2006, Stoner & Sanchez-Azofeifa 2009). TDFs occur in tropical regions with pronounced seasonality of rainfall and several months of drought (Money et al. 1995). Rainfall seasonality has a strong impact on the structure and functioning of these forests, and is the determining factor generating patterns of tree phenology and growth (Eamus 1999). Nearly all dry forests are exposed to multiple threats, since they have a high level of suitability for livestock and rain-fed crops thereby sustaining rural livelihoods (Griscom & Ashton 2011, Miles et al. 2006, Shackleton et al. 2007). This conflict results in degraded forests and fragmented forest landscapes. It has been reported, for example, that only 27% of the original cover of Mexican TDFs remains as intact forest (Trejo & Dirzo 2000). DRYFLOR (2016) estimated that, for the entire Neotropics, less than 10% of the original dry forest area remains, of which only a small part is formally protected. Accordingly it is important to assess the conservation value of degraded forests, which inevitably play an increasing role in the conservation of forest biodiversity (Chazdon et al. 2009).

Fifty-four percent (ca 570000 km^2) of worlds TDFs are located in South America (Miles et al. 2006). Ecuador has a current TDF extent of 6443 km^2, of which 3097 km^2 are located in South Ecuador (Portillo-Quintero & Sánchez-Azofeifa 2010, Tapia-Armijos et al. 2015). The relatively low extent and high fragmentation of TDFs in Ecuador make this forest type a high priority for conservation (Portillo-Quintero & Sánchez-Azofeifa 2010, Tapia-Armijos et al. 2015). The most common threats to TDFs in South Ecuador are overgrazing and browsing by cattle and goats, expanding agricultural frontiers and selective harvesting of wood from species such as *Hadroanthus chrysanthus*, *Loxopterigium huasango* and *Simira ecuadorensis* (Paladines 2003). The use of dry forests by the rural population, however, is an important component of land use diversification, and contributes to an increased stability of farm income (Ochoa et al. 2016). Ochoa et al. (2019) further emphasize that forest use for goat grazing presents a viable alternative to converting forest to cropland. Recent estimations show that from 1976 to 2008 51% of South Ecuadorian TDFs became degraded, and a further 30% were converted to pasture (Tapia-Armijos et al. 2015). Biodiversity patterns and the conservation status of Ecuadorian dry forests have been little studied, and there is a strong need for conservation efforts to be developed conjointly with local communities (Escribano-Avila et al. 2017).

Because of the prevailing climatic conditions, reproduction in dry forests is highly seasonal and succession is slower in terms of plant growth compared with wet forests (Murphy & Lugo 1986, Quesada et al. 2009). Yet dry forests have the potential to recover to a mature state more quickly. This resilience reflects the simpler structure of the mature forest (Murphy & Lugo 1986). Understanding vegetation dynamics in TDFs is critical for the development of forest conservation strategies, but this forest type has received less attention compared with, for example, wet tropical forests (Chaturvedi et al. 2012, Griscom & Ashton 2011, Sagar et al. 2008, Quesada et al. 2009).

The high conservation priority and current lack of knowledge on the impact of disturbance in this endangered ecosystem lead us to compare the status of a disturbed with an adjacent protected TDF in South Ecuador. The disturbed forest was influenced by continuous grazing by animals (cattle and goats), which is a common silvopastoral practice in the region. We were able to use the intact protected forest as a baseline for comparative purposes.

We addressed the following research questions:

(i) How does silvopastoral use alter forest structure and tree species composition compared with a protected TDF?

(ii) How does altitude influence forest structure and tree species composition in the two forest types?

We thereby hypothesized that (a) forest disturbance will significantly alter forest structure and tree species composition, with a negative effect on species diversity, and (b) altitudinal differences in structure and species composition will be less pronounced in the disturbed forest.

MATERIALS AND METHODS

Study sites and data collection

The present study was conducted in a protected dry forest and an adjacent disturbed forest located near Macará in South Ecuador close to the Peruvian border. This area belongs to the Tumbesian dry forest ecoregion and is characterized by a pronounced seasonality. It has a rainy season lasting from January to May, and a dry season from June to December. At 600 m asl annual mean temperature is 23.7°C and annual rainfall is approximately 540 mm, but year to year variability in rainfall can be high (Pucha Cofrep 2015, Spannl et al. 2016). Due to low amounts of annual rainfall and dry conditions during large parts of the year the majority of tree species are deciduous, although these co-exist with smaller numbers of evergreen species. The area is hilly covering altitudes from 600 to 1400 m asl.

The protected forest is within the private Laipuna Forest Reserve, which totals 1680 ha and is owned and administrated by the NGO Nature and Culture International (NCI). In 2010-2012 a tree inventory was conducted along an altitudinal gradient ranging from 560-1320 m asl, in which 31 rectangular plots each of 400 m^2 were established. However, for the present study only plots at altitudes below 1080 m asl were considered (resulting in 18 inventory plots), to match the available altitudes within the disturbed forest. The disturbed forest is located in a 7400 ha buffer zone around the forest reserve, and is mainly impacted upon by the grazing of cattle and goats. Ochoa et al. (2016) estimated current stocking rates of 0.22 cattle ha^{-1} and 0.33 goats ha^{-1} in the buffer zone around the Laipuna Reserve. According to the local villagers, this type of silvopastoral land use became common in the middle of the last century. The tree inventory in the disturbed forest was conducted in May 2015 using a systematic sampling approach. A grid of 300 x 200 m was laid over the area of the disturbed forest at altitudes of 600-1100 m asl, and 52 circular plots each with a size of 531 m^2 were established at the intersections of the grid. These inventory plots of the disturbed forest were located at distances of 0.1-1.96 km from the protected forest (mean ± SD: 1.09 km ± 0.49 km). In all inventory plots diameter at breast height (DBH) was measured using a diameter tape, and tree height was measured with a hypsometer (Vertex IV, Haglöf, Sweden) for all trees with diameter > 10 cm. All trees were identified to

Table 1. Plot characteristics, number of tree species, Shannon diversity and evenness at different altitudes in the protected and disturbed forest.

Forest type	Altitude range (m asl)		No. of plots	Total area sampled (ha)	No. of tree species	Shannon- index (H')	Evenness (%)
Protected	Low	560-720	6	0.24	11	80.45	80.45
	Mid	720-900	6	0.24	15	86.29	86.29
	High	900-1080	6	0.24	25	83.48	83.48
Disturbed	Low	560-720	13	0.69	16	74.28	74.28
	Mid	720-900	26	1.38	18	80.64	80.64
	High	900-1080	13	0.69	14	79.01	79.01

species. The study plots were grouped into three altitude levels: 'low' (560-720 m asl), 'mid' (720-900 m asl) and 'high' (900-1080 m asl) as indicated in Table 1.

Data analysis and statistics

We calculated Evenness (*E*) for every species to characterize the spread in the number of individuals, and the Shannon diversity index (*H*) to account for both abundance and evenness of species present. Rarefaction curves were used to plot the statistical expectation of sample-based species accumulation, which is useful under different sampling methods (Longino et al., 2002).

Importance Value Index (IVI) was calculated according to Curtis and McIntosh (1951) for each species:

IVI = relative abundance + relative dominance + relative frequency

Where:

Abundance = number of individuals ha^{-1}
Dominance = basal area (m^2 ha^{-1})
Frequency = percentage of plots in which a species occurred

A detrended correspondence analysis (DCA) on the species abundance data from the inventory plots was performed using Canoco 5.0 (Ter Braak & Šmilauer 2012). To check for changes in compositional dispersion between disturbed and protected forest plots, we used the 'betadisper' function in the R package 'vegan' followed by Tukey's HSD test.

For each species wood density values were taken from the Global Wood Density Database (Chave et al. 2009, Zanne et al. 2009) and averaged for all tree individuals in each inventory plot. Linear regressions were used to explore the relationship between wood density and altitude in the two forest types. Significant differences ($P < 0.05$) in stem density and basal area between forest types and altitude were identified using a Kruskal-Wallis test, which was followed by a Mann-Whitney two-sample test (U-test) for pairwise comparisons. Calculations were done with RStudio version 3.2.2 (R Development Core Team 2015).

RESULTS

In the Laipuna Reserve between 560 and 1320 m asl we recorded 30 tree species belonging to 20 families, whereas in the adjacent disturbed forest the number of species was reduced to 22 tree species belonging to 12 families. In the protected forest the number of tree species increased with increasing altitude, whereas in the disturbed forest the highest numbers were recorded at mid-altitude (Table 1). Highest Shannon indices were found at mid-altitude in both forest types. Evenness ranged from 74-86 % across all sites, with highest values at the mid-altitude and lowest values at the low altitude in both forest types. The difference in evenness between the protected and disturbed forest decreased with increasing altitude (Table 1). Tree species rarefaction curves indicated lower species richness in the disturbed forest compared with the protected forest. The difference in species richness between the protected and disturbed forests was largest at the highest altitude (Fig. 1). A DCA of tree species abundance data depicted closer distances among plots in the protected forest, whereas this pattern was absent in the disturbed forest (Fig. 2). Protected forest plots were significantly more homogeneous in their species composition (p=0.012; Turkey's HSD test) compared with the disturbed forest plots.

The most common tree families in the protected forest were Fabaceae, representing nearly 20% of individuals, followed by Malvaceae and Bignoniaceae. In the disturbed forest Fabaceae and Malvaceae also were the most common tree families, together representing 50% of all individuals censussed. Convolvulaceae was identified as the third most important tree family in the disturbed forest, but the family was only represented by one species (*Ipomoea*

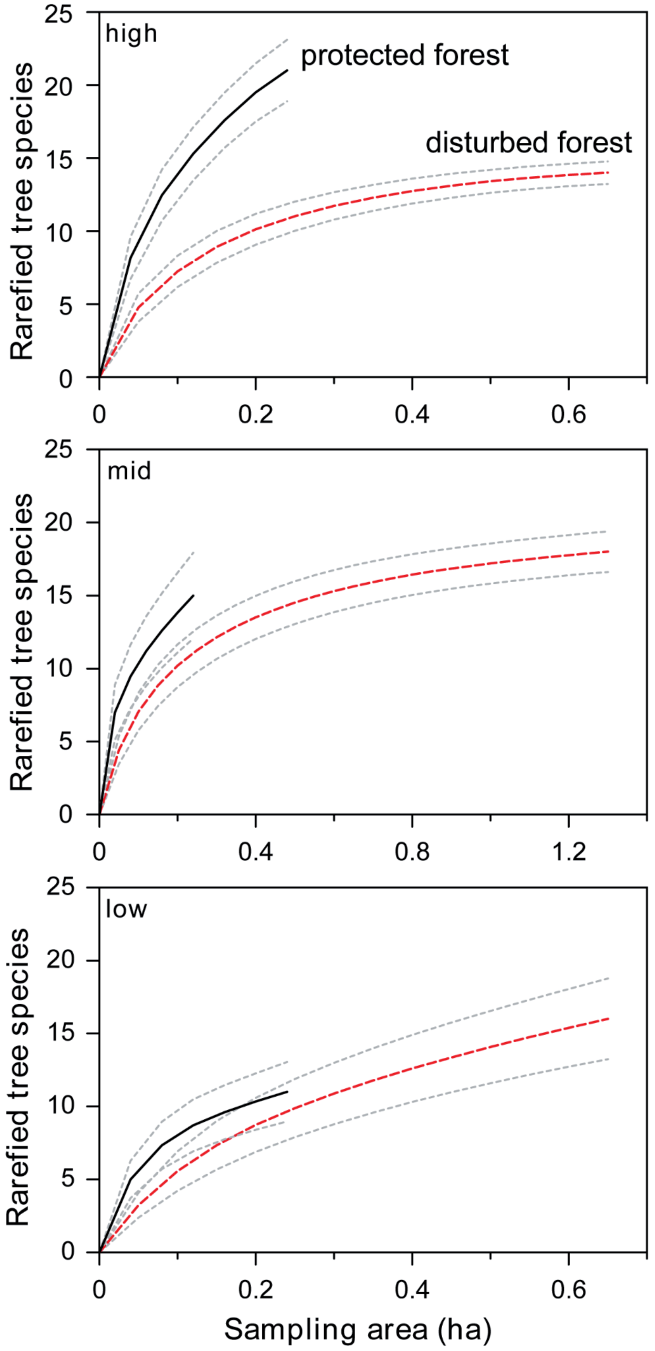

Figure 1. Plot-based tree species rarefaction curves for the protected and disturbed forest at three altitude levels. Dashed grey lines represent one standard error.

wolcottiana subsp. *calodendron*) that accounted for 22% of all trees (Table 2). Ten species found in the plots in the protected forest were absent from those in the disturbed forest. Two of these species are endemic to the Tumbesian dry forest ecoregion (*Prockia crucis, Simira ecuadorensis,* Table S1). Overall, we recorded eight evergreen tree species, whereas all other species were drought deciduous.

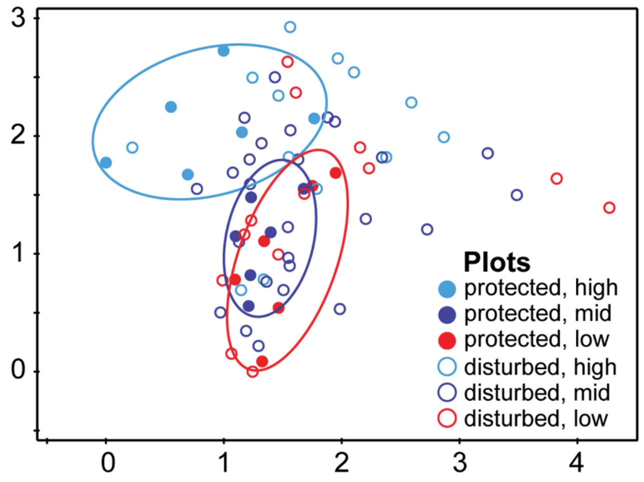

Figure 2. DCA ordination of tree species abundance in the protected and disturbed forest of the Laipuna dry forest reserve.

The most abundant evergreen species were *Capparis scabrida*, *Geoffrea spinosa* and *Caesalpinia glabrata*, which occurred across all altitudes. Evergreen trees had a share of 5-11% among all tree individuals, with no pronounced difference between the two forest types (Table 3).

At the low altitude plots in the protected forest the species with highest IVI was *Eriotheca ruizii*, followed by *Ceiba trichistandra* whereas, at the mid-altitude, this pattern was reversed, with *C. trichsistandra* ranked first, and *E. ruizii* ranked second (Fig. 3). At both altitudes *Bursera graveolens* and *I. wolcottiana* were ranked third and fourth, respectively. At the high altitude plots in the protected forest the species with highest IVI was *E. ruizii*, followed by *Erythrina velutina*, *Machaerium millei* and *I. wolcottiana*. Importance value indices changed through forest disturbance, with certain species increasing in IVI and others disappearing (Fig. 3). We note, however, that the larger area that was sampled in the disturbed forest could have potentially influenced the frequency of occurrence of species.

At the low and mid-altitude, respectively, *E. ruizii* and *C. trichistandra* remained as species with highest IVI, but most pronounced increases were observed for *E. velutina* at both altitudes. In addition, species appeared that were not, or only rarely, found in the protected forest, such as *Agonandra excelsa*, *Prosopis juliflora* and *Vachellia macracantha*. At the high altitude in the disturbed forest new species appeared with high IVI, namely *I. wolcottiana*, *C. trichistandra* and *Pisonia aculeata*, which were not among the top ranked species in the protected forest at this altitude (Fig. 3).

Stem density in the protected forest increased from 333 stems ha^{-1} at the low altitude to 500 stems ha^{-1} at high altitude. Overall stem density was significantly reduced in the

Table 2. Composition of tree assemblages in the protected and disturbed forest based on plant families.

Natural	Total individuals counted	%	Disturbed	Total individuals counted	%
Fabaceae	87	19.4	Fabaceae	124	26.3
Malvaceae	74	16.6	Malvaceae	114	24.2
Bignoniaceae	58	13.0	Convolvulaceae	104	22.0
Convolvulaceae	38	8.5	Burseraceae	45	9.5
Burseraceae	31	6.9	Nyctaginaceae	29	6.1
Combretaceae	24	5.4	Bixaceae	17	3.6
Asteraceae	22	4.9	Capparaceae	13	2.8
Capparaceae	20	4.5	Anacardiaceae	9	1.9
Polygonaceae	14	3.1	Combretaceae	8	1.7
Boraginaceae	12	2.7	Rhamnaceae	6	1.3
Moraceae	12	2.7	Opiliaceae	2	0.4
Hippocrateaceae	11	2.5	Boraginaceae	1	0.2
Nyctaginaceae	11	2.5	*Total*	*472*	*100*
Anacardiaceae	8	1.8			
Bixaceae	7	1.6			
Myrtaceae	6	1.3			
Flacourtiaceae	4	0.9			
Rhamnaceae	3	0.7			
Caricaceae	1	0.2			
Celastraceae	1	0.2			
Rubiaceae	1	0.2			
Sapindaceae	1	0.2			
Solanaceae	1	0.2			
Total	*447*	*100*			

disturbed forest, most prominently so at high altitude (Fig. 4). Small diameter trees (DBH 10-20 cm) increased in abundance with elevation in the protected forest, and generally composed the largest group of diameter classes. The disturbed forest showed a similar but less pronounced trend (Fig. 5). The number of stems generally decreased with increasing diameter class in the protected forest, although there was a slightly increase again towards large trees with diameters > 60 cm. This increase is due to the abundance of *C. trichistandra* and *E. ruizii* that can reach very large diameters. The reduction of stems through disturbance was most pronounced in the smallest diameter class, whereas larger diameter classes were less affected (Fig. 5). Basal area was significantly reduced through disturbance at the low and mid-altitude, whereas it remained almost equal to the protected forest at the high altitude. Unlike for stem density there was no influence of altitude on basal area in the protected forest (Fig. 4).

The largest individuals of the five common species of trees, *C. trichistandra*, *E. ruizii*, *B. graveolens*, *E. velutina* and *I. wolcottiana*, were encountered in the disturbed forest (Fig. 6). The largest differences in tree size between the protected and disturbed forest were observed for the two species of Malvaceae (*C. trichistandra*, *E. ruizii*). Mean wood density increased with increasing altitude in the protected forest, whereas no such trend was observed in the disturbed forest (Fig. 7).

Table 3. Percentage evergreen trees in the protected and disturbed forest.

Forest type / Altitude	low	mid	high
Natural	7.5	9.0	5.0
Disturbed	9.9	11.4	5.2

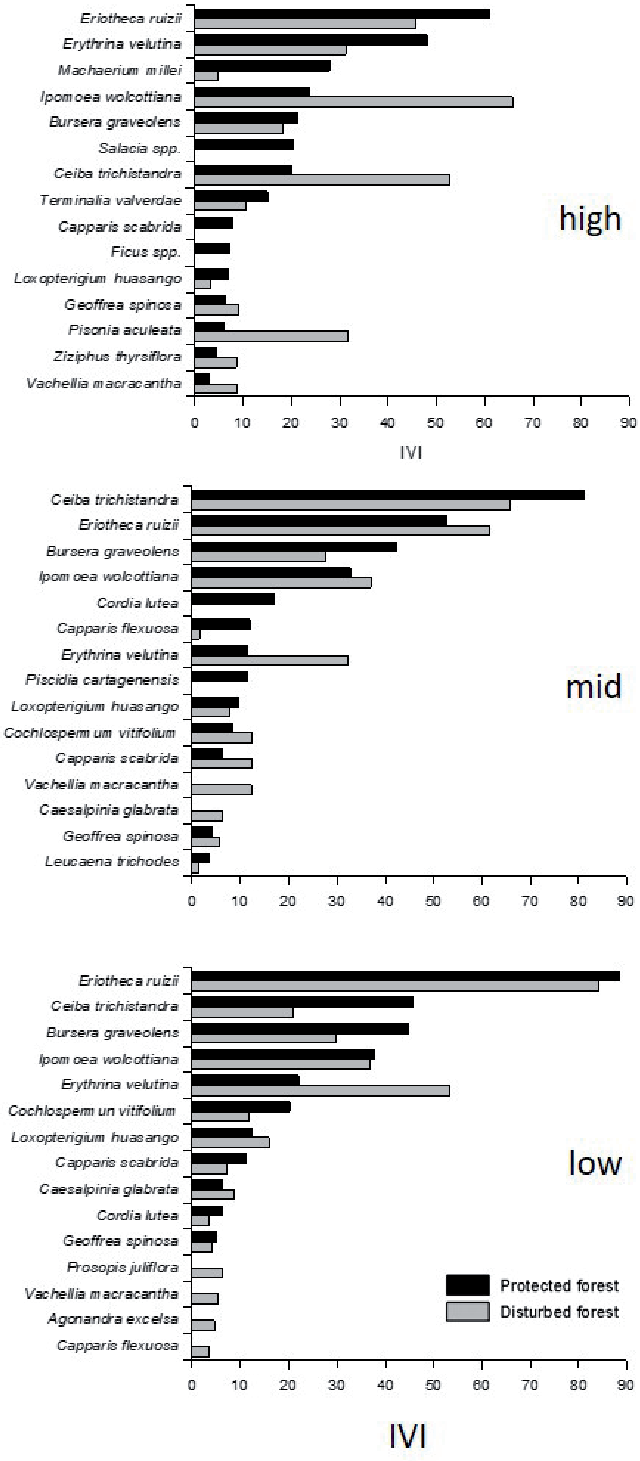

Figure 3. Importance Value Indices (IVI) of the 15 most important species at different altitudes in the protected and disturbed forest.

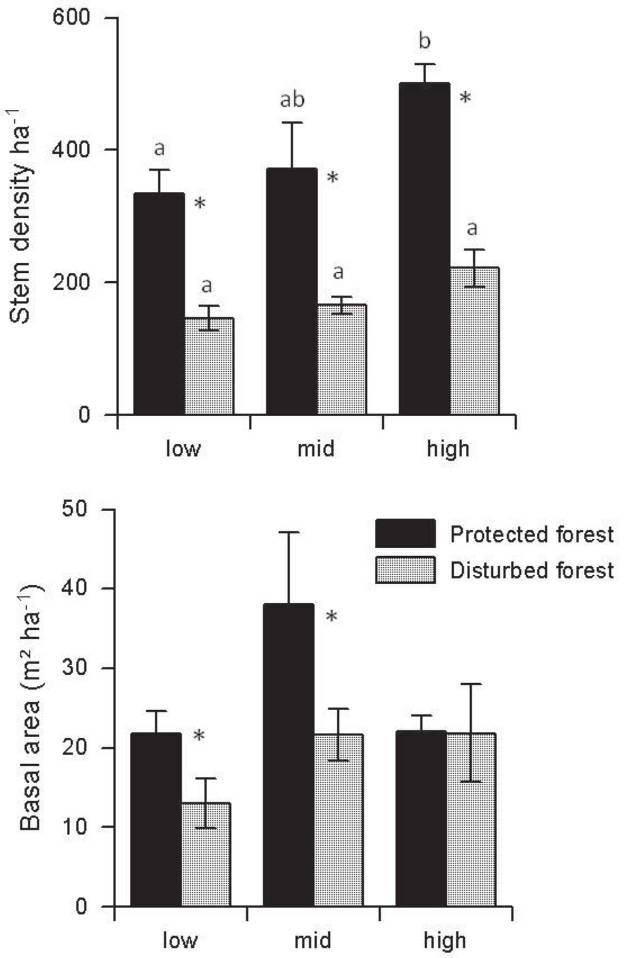

Figure 4. Stem density (left) and basal area (right) of trees with DBH >10 cm at different altitudes in the protected and disturbed forest. Different letters indicate significant differences between altitudes in one forest type, asterisks indicate significant differences between forest types at one altitude ($p<0.05$). In the right-hand figure we excluded one outlier from the mid altitude of the disturbed forest that had a projected basal area of 149 m^2 ha^{-1} due to two individuals of *C. trichistandra* with DBH > 200 cm.

DISCUSSION

Tree species richness in the protected and disturbed forest

The size and shape of the units sampled influence results on species richness and diversity, which are statistics that cannot be scaled to convert to a standard size of sampling plots (Kindt & Coe 2005). This circumstance may have also biased results in the present study, since the inventories in the two forest types had different sampling approaches resulting in a larger area and more replicates sampled in the disturbed forest. Nevertheless it became evident that

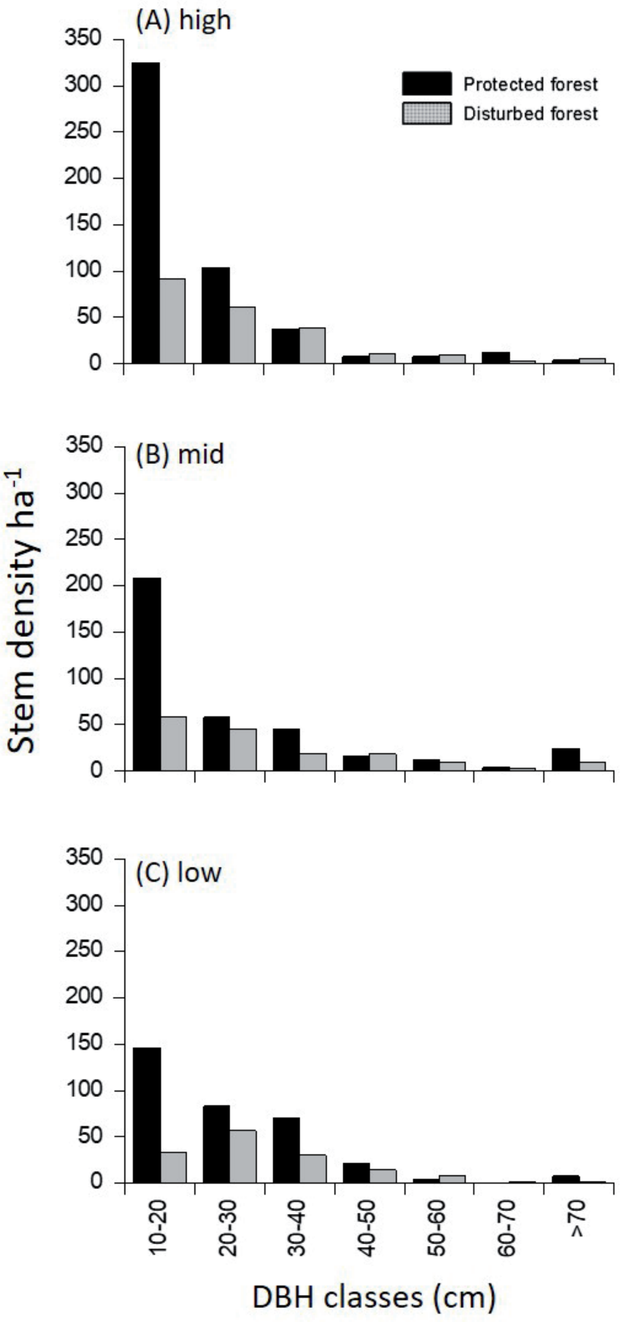

Figure 5. Stem diameter distribution (DBH >10 cm) at three altitude levels in the protected and disturbed forest.

forest disturbance reduced tree species richness even though species appeared in the disturbed forest which were not, or only rarely, recorded in the protected forest. These additions included species such as *P. juliflora* and *V. macracantha* which are light demanding species associated with reduced canopy cover. We assume that those species are browse-tolerant with high resprouting capacity; furthermore, their fruits and pods are preferred fodder for animals. Evergreen trees may have been left in the landscape as shade providers and are partly used as fodder in the dry season.

Fabaceae has been identified as the most important tree family in other studies of undisturbed neotropical dry forests (Álvarez-Yépiz et al. 2008, Gillespie et al. 2000, Linares-Palomino et al. 2010, Rendón-Carmona et al. 2009, Romero-Duque et al. 2007). Linares-Palomino (2006) listed 193 woody plant species in the montane dry forests of Northern Peru at altitudes between 700-1800 m asl. This region belongs to the same phytogeographic unit as the South Ecuadorian TDF, and 36 species were considered endemic to the area. Linares-Palomino and Ponce Alvarez (2005) counted six to 25 species in 1 ha plots in a dry forest of Northern Peru where some of the sites were under selective timber extraction. Espinosa & Cabrera (2011) identified 102 species on 5.45 ha in a nearby South Ecuadorian dry forest. They also found a high predominance of Malvaceae, with three species of this family accounting for 40% of total basal area. DRYFLOR (2016) identified twelve floristic groups across Neotropical TDFs, and point to high rates of endemism and floristic turnover, with the consequence that only few species are widespread and shared across areas. This has strong spatial implications for conservation measures, since a failure to protect particular locations would result in loss of unique species diversity.

The high abundance of the *E. ruizii* and *C. trichistandra* (Malvaceae) in the disturbed forest may be due to both their ecological adaptations and a consequence of earlier management decisions. They are typically canopy trees with large ecological tolerances covering an altitudinal range of 1500 m (Best & Kessler 1995). Both species are able to cope with dry and harsh conditions through their water storing capacity in the stems (*C. trichistandra*) and roots (*E. ruizii*) which allows them, to a certain extent, to decouple soil and plant water status (Butz et al. 2017). Both species also have some value as non-timber forest products (NTFP). It is likely that local farmers may conserve these two species when exploiting new land for pasture and agricultural fields. This trend towards selective protection of valuable trees has been reported from other regions. The African baobab (*Adansonia digitata*), for example, is an iconic species in many African woodlands which shows a high abundance around fields and human settlements (Duvall 2007, Lisao et al. 2018). The moist root tubers of *E. ruizii* may be used in very dry years by farmers to feed cattle (personal communication with farmer). *C. trichistandra* is a tree that is difficult to cut due to its shape and size, and the fibres surrounding its seeds are occasionally used to fabricate mattresses and pillows. *E. velutina* is not endemic to the region, and showed a marked increase in the disturbed forest at

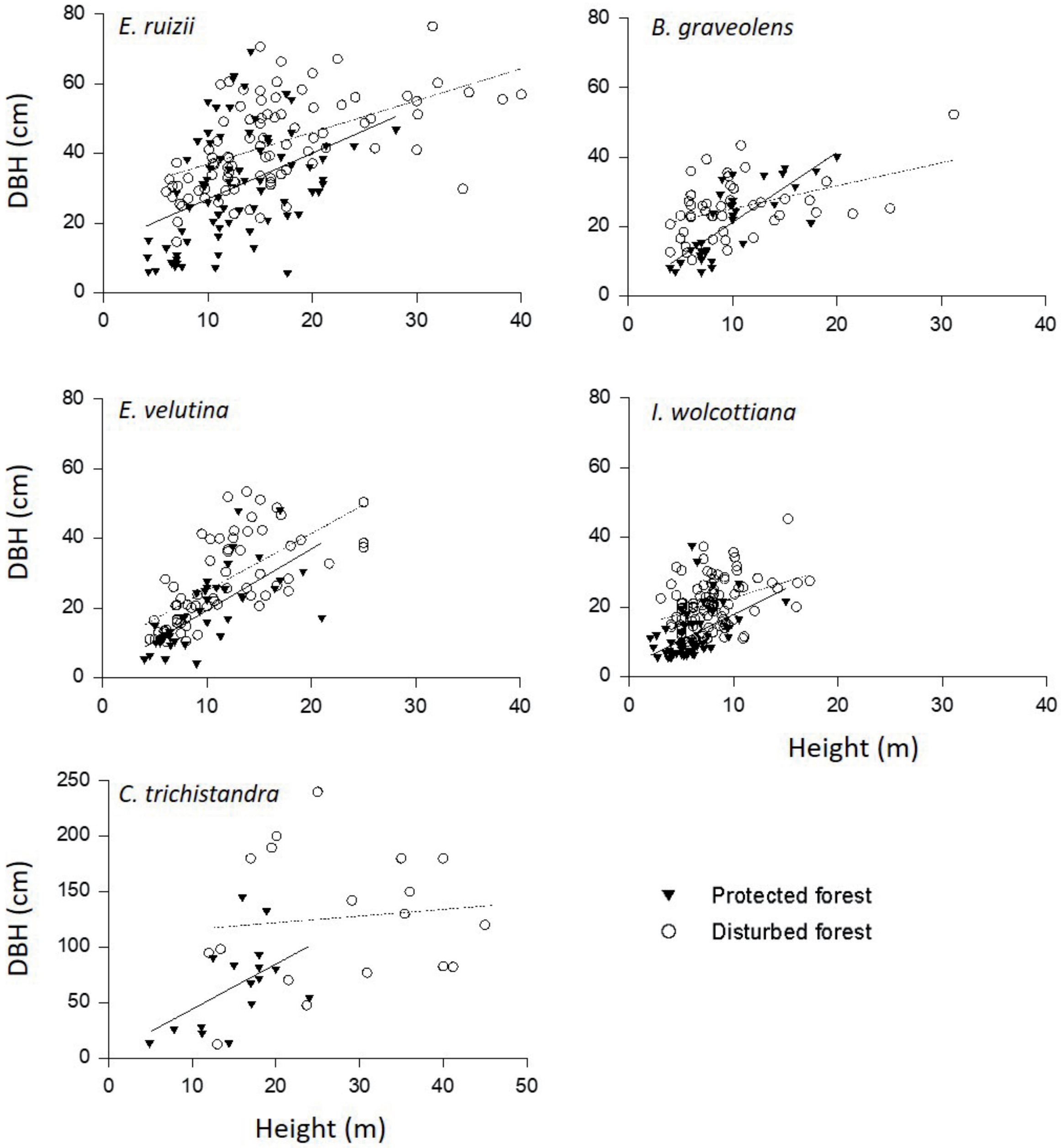

Figure 6. Diameter-height relationship of selected species in the protected and disturbed forest.

elevations below 900 m asl. It is a typical pioneer species with fast growth, drought resistance and thorny stems and, in Brazil, for example, is used for reforestation (Souza et al. 2016). *I. wolcottiana*, which was the species with highest IVI at high altitude in the disturbed forest, is a pioneer species endemic to the Tumbesian dry forest ecoregion. It seems to be more resistant to drought than other species due to its high sapwood water storage capacity (Pineda-García et al. 2013). *Ipomoea* species are known for their high alkaloid content that makes these plants unpalatable or even toxic.

Impact of forest disturbance on tree structure and regeneration

Trees in the disturbed forest grow under greater isolation, resulting in less competition for space and water, allowing trees to attain maximum stem growth. This was reflected in the occurrence of larger trees, especially of *C. trichistandra* and *E. ruizii*, which can reach very large DBH. *C. trichistandra* showed a more than two-fold increase in IVI at the high altitude of the disturbed forest compared with the protected forest. Álvarez-Yépiz et al. (2008) also encountered several

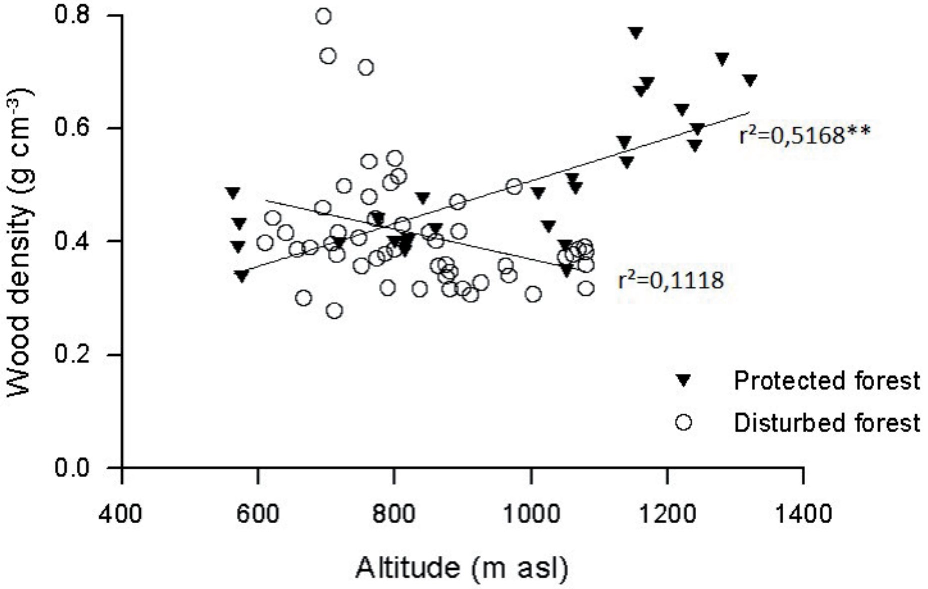

Figure 7. Mean wood density of trees in inventory plots, ** = $p < 0.01$. This figure also shows plots > 1080 m asl in the protected forest, for which no reference plots could be established in the disturbed forest.

old-growth individuals with thick trunks and high mean basal area in a secondary TDF in Northwestern Mexico.

Originally it was intended to assess regeneration in subplots of the main inventory plots, but signs of regeneration were apparent in only four out of the 52 plots in the disturbed forests. The occurrence of saplings (DBH < 5 cm, height ≥1.3 m) was observed only for *E. ruizii*, *E. velutina*, *I. wolcottiana*, *V. macracantha* and *P. juliflora,* which in the main are pioneer species. The micro-environment in disturbed sites is warmer and drier than in mature forests, favoring early successional species that are more drought-resistant and better able to cope with harsh environments (Lohbeck et al. 2013, Pineda-García et al. 2013). Survival of juvenile trees is affected by seasonal drought, as their immature root systems cannot reach deeper soil layers (Chaturvedi et al. 2012). Mortality of juvenile trees is further intensified through browsing and trampling, favoring species that are unpalatable to cattle and goats (Chaturvedi et al. 2012, Griscom & Ashton 2011). The impact of livestock on vegetation strongly depends on stocking rates. Vieira et al. (2006), for example, observed no effect of cattle on seedling survival in a dry forest of Central Brazil reflecting, in their view, the low stocking rate of 0.5 cattle ha^{-1}. In their study 57% of seedlings survived one year after being planted in forest fragments. Griscom et al. (2005) in contrast found a positive effect of cattle exclusion on the growth and survival of tree seedlings in a TDF in Panama, and cattle had clear browse preferences for certain species. McIntyre et al. (2003) counted similar numbers of species that decrease and increase with grazing in a subtropical grassland of Eastern Australia. Palatable seedlings are grazed upon preferentially, leading to a greater persistence of seedlings with chemical or mechanical protection, such as spines (Guevara et al. 1986). These defense mechanisms are also present in the dominant species, *C. trichistandra* and *E. velutina*, even in the juvenile stage.

A consequence of TDF degradation is simplification. Tree species remain that are stump sprouts, inedible to cattle, tolerant to desiccating conditions, have some human use or have been kept selectively (Griscom & Ashton 2011). This results in a change in the distribution of stem size-classes skewed towards a lower number of smaller stems, as observed in the present study. Generally, resprouting as a mechanism of regeneration offers resilience to disturbance in areas where regeneration of seedlings is affected by rainfall seasonality (McLaren & McDonald 2003, Vieira & Scariot 2006).

Our mean wood density values within the inventory plots were much lower than the mean of 0.645 g cm^3 reported for Central and South American forests in the meta-study of Chave et al. (2006). Most dominant species from our study area have relatively low wood densities (< 0.4 g cm^{-3}); whereas three species with high wood densities were found to increase in abundance in the disturbed forest (i.e. *P. julifora* 0.8 g cm^{-3}, *V. macracantha* 0.73 g cm^{-3}, *C. glabrata* 0.95 g cm^{-3}). We expected lower mean wood densities in the disturbed forest compared with the protected forest, since fast growing pioneer species are characterized by low wood density. In the event we observed this effect only at the high altitude sites. Species with higher wood density are better adapted to resist drought-induced embolism (Hacke et al. 2001), a trait that can be advantageous in secondary TDF environments. In this context two contrasting strategies optimize establishment in disturbed sites: (i) low wood density and fast growth, or (ii) high wood density (> 0.7 g cm^{-3}) together with browse-tolerance and high resprouting capacity.

CONCLUSIONS

Despite some imbalances in sampling design, this study provides evidence that disturbance of a Tumbesian dry forest reduced tree species richness and resulted in a shift of species composition, with certain species becoming more abundant in disturbed sites. Disturbance also changed forest structure towards a lower number of stems per hectare, but with larger diameters. Forest structure was also clearly influenced by altitude, with a larger number of small diameter trees present at higher altitudes. Certain endemic species showed good representation in disturbed forest, e.g. *C. trichistandra* and *E. ruizii*. However, other endemics with rather low abundance in the protected forest could not be detected at the disturbed sites, and should receive more attention through conservation efforts.

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SUPPLEMENTARY MATERIAL

Table S1. List of tree species encountered in the inventory plots of the protected and disturbed forest at altitudes of 560-1080 m asl. Shaded areas indicate the presence of a species in the respective forest type.

Species	Family	Protected forest	Disturbed forest	Endemic
Achatocarpus pubescens	Achatocarpaceae	🟩		
Agonandra excelsa	Opiliaceae		🟩	
Albizia multiflora	Fabaceae	🟩	🟩	x
Bauhinia aculeata	Fabaceae	🟩		
Bursera graveolens	Burseraceae	🟩	🟩	
Caesalpinia glabrata	Fabaceae	🟩	🟩	x
Casearia sp.	Flacourtiaceae	🟩		
Ceiba trischistandra	Malvaceae	🟩	🟩	x
Cochlospermum vitifolium	Bixaceae	🟩	🟩	
Colicodendron scabridum	Capparaceae	🟩	🟩	x
Cordia lutea	Boraginaceae	🟩	🟩	
Cynophalla flexuosa	Capparaceae	🟩	🟩	
Eriotheca ruizii	Malvaceae	🟩	🟩	x
Erythrina velutina	Fabaceae	🟩	🟩	
Ficus sp.	Moraceae	🟩		
Geoffroea spinosa	Fabaceae	🟩	🟩	
Handroanthus chrysanthus	Bignoniaceae	🟩		
Ipomoea wolcottiana	Convolvulaceae	🟩	🟩	x
Leucaena trichodes	Fabaceae	🟩	🟩	
Loxopterigium huasango	Anacardiaceae	🟩	🟩	x
Machaerium millei	Fabaceae	🟩	🟩	
Phyllanthus sp.	Euphorbiaceae	🟩		
Piscidia cartagenensis	Fabaceae	🟩		
Pisonia aculeata	Nyctaginaceae	🟩	🟩	
Prockia crucis	Flacourtiaceae	🟩		x
Prosopis juliflora	Fabaceae		🟩	
Salacia sp.	Hippocrateaceae	🟩		
Senna mollisima	Fabaceae	🟩	🟩	
Simira ecuadorensis	Rubiaceae	🟩		x
Terminalia valverdae	Combretaceae	🟩	🟩	x
Vachellia macracantha	Fabaceae	🟩	🟩	
Ziziphus thyrsiflora	Rhamnaceae	🟩	🟩	