What Factors Affect Diversity and Species Composition of Endangered Tumbesian Dry Forests in Southern Ecuador?

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ABSTRACT

This paper reports a study on species richness and composition of Tumbesian dry forest communities. We tested two alternative hypotheses about species assemblage processes in tropical dry forests: (1) species assemblage is determined by the filtering effect of environmental conditions and (2) species assemblage is determined by facilitative processes along the gradient of water availability, and thus, species richness and evenness increase as water becomes limited. In addition, we also explored the effect of climate and soil conditions on species composition in tropical dry forests. Species composition was sampled in 109 plots in terms of cover and tree diameter at breast height. Climatic, edaphic, topographic and anthropogenic degradation variables were obtained for each plot. We used generalized linear models and canonical correspondence analyses to evaluate the effect of environmental variables on species composition, richness and evenness. Water availability negatively affected richness and significantly determined the species assemblage. Species richness increased from ridges to valleys and evenness increased at higher altitudes. Soil characteristics showed no effect on richness and evenness but soil moisture, nitrogen concentration and soil temperature explained significant fractions of species composition. Although timber extraction and livestock in our study area were of low intensity, it negatively affected richness but had only a minor effect on species composition. Our results suggest that species composition in these endangered tropical dry forests may be at least partially explained by the stress-gradient hypothesis, with higher species richness at drier conditions probably induced by facilitation processes.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: anthropogenic degradation; community diversity; environmental constraints; precipitation; soil physical–chemical features; temperature; tropical dry forest; vegetation.

SINCE THE SEMINAL WORK OF JANZEN (1988), tropical dry forests have been recognized as one of the most threatened habitats in the world. Nevertheless, Neotropical dry forests are disappearing at an incredibly high rate and now occur in a tiny fraction of their historic range (Fajardo *et al*. 2005). Vanishing dry forests are reduced to small isolated remnants from Mexico to Argentina (Maass 1995) due to timber extraction, fuel wood extraction and grazing by cattle (Fajardo *et al*. 2005, Leal-Pinedo & Linares-Palomino 2005). Only some remnants of these dry forests— < 38 percent—are currently included in some category of protection (Miles *et al*. 2006). Despite evidence of extreme threats and forest losses quickly accumulating (Janzen 1988), Neotropical dry forests receive far less attention than other types of more humid tropical forests (Miles *et al*. 2006). Tropical dry forests have smaller stature and lower basal area than tropical rain forests (Murphy & Lugo 1986), they are diverse both locally and regionally (Givnish 1999) and although less known, they are almost as diverse as tropical rain forests. Ecological processes are strongly seasonal, and net primary productivity is lower than in rain forests because growth only takes place during the wet season (Pennington *et al*. 2000).

This conservation scenario worsens in southern Ecuador. From Gentry (1977), Ecuadorian dry forests are included among the most threatened ecosystems in this megadiverse country. More recently, Sierra (1999) explicitly pointed out that dry forest of the Loja province at the southern tip of the country should be the first national conservation priority. These Ecuadorian dry forests are part of the poorly explored Tumbesian region (Dinerstein *et al*. 1995) which is recognized as one of the most endangered hotspots in the world and probably one of the least known (Janzen 1988). The Tumbesian region covers a narrow fringe of land between the Pacific Ocean and Los Andes range and comprises the southwest tip of Ecuador and the northwestern edge of Peru. The Tumbesian region embraces altitudes from sea level to 2000 m and occasionally to 3000 m and it is extended over 87,000 km^2 (Best & Kessler 1995, Dinerstein *et al*. 1995). The most important ecosystem is the seasonal dry forest which is characterized by the so-called ceiba (*Ceiba trichistandra*) and their *Bombacaceae* relatives (Aguirre *et al*. 2006). These forests are extremely species-rich and shelter an extraordinary assembly of narrow endemisms of very different taxonomic groups (Best & Kessler 1995). Unfortunately, they are

currently not protected in Ecuador and only a tiny portion of them is protected in Peru in Cerros de Amotape National Park.

Knowledge of diversity patterns and environmental filtering factors is essential for proper management and conservation purposes of Neotropical dry forests (Sánchez-Azofeifa et al. 2005), especially in the case of declining tropical dry forests (Balvanera & Aguirre 2006). Even more, increasing our knowledge about how these dry forests vary in species composition and other community attributes and their responses to environmental changes, both natural and anthropogenic, is a priority (Aguirre et al. 2006). To unveil these relationships, we should consider that water availability is probably the main driver of species coexistence in these forests (Balvanera & Aguirre 2006). It is well known that variation in climate—rainfall, temperature and range of temperatures—together with some local factors such as slope, geologic substratum and soil features can control evapotranspiration and, consequently, reduce water availability in the field. This may create a local water availability gradient that would likely affect species composition and species richness by either of two ways: (1) water availability acting as a critical factor that filters those species able to survive or (2) plant–plant interactions through competition and facilitation. Under lower water conditions it is expected that positive interactions will prevail (stress gradient hypothesis; Bertness & Callaway 1994). This kind of interaction should favor plant recruitment out of the species optimum in more stressful low water conditions. Relative importance of climate and local factors as drivers of community assemblages is a central issue in ecology and biogeography (Hubbell 2001, Ricklefs 2004). While the high local species richness of tropical dry forests is well documented (Valencia et al. 2004, Sánchez-Azofeifa et al. 2005), factors that control local species composition at spatial scales important for conservation management are poorly known. Accordingly we sampled dry forests in southern Ecuador and tested how regional (climate) and local (soil features, topography and anthropogenic degradation) factors may be related to composition, and diversity attributes of Tumbesian dry forests. We tested two alternative hypotheses explaining species richness in these forests: (1) these community traits are determined by environmental filtering so we would expect more benign sites to be richer in species and (2) species assemblage was determined by plant–plant interactions along the gradient of water availability, and, thus, species richness and evenness would increase toward the more stressful water conditions where facilitation should dominate, whereas in more wet sites, species are excluded by competitive exclusion. Moreover, we described the different floristic forest communities and investigated the connections of this diversity with measurable variables such as temperature, precipitation and altitude thresholds. In this sense, our working hypothesis is that forest species composition should hierarchically reflect first, the effect of climate and second, other local effects, such as soil characteristics. To examine the small but predicted anthropogenic effect on composition, we also included this source of variation in our models.

This study will contribute to understanding of the biodiversity of this unknown and threatened megadiverse region, the role that environmental heterogeneity plays in shaping tree assemblages of dry Tumbesian forests and generation of base information for conservation management.

METHODS

STUDY AREA.—Tumbesian dry forests cover a territory about 87,000 km^2 that spans from the southwest tip of Ecuador to the northwestern extreme of Peru (Dinerstein et al. 1995). Our study area comprised nearly 1864 km^2 in the province of Loja (Zapotillo, Macara and Celica districts; 120–2640 m asl) in one of the largest and best conserved remnants of the Tumbesian dry forests (Aguirre & Kvist 2005). In all this vast territory, land management has been of low intensity during the last decades. We surveyed relatively well-conserved stands that did not suffer deforestation, and with very little anthropogenic perturbation. Average annual temperature in the region is ca 24°C (range: 10–33°C). Mean annual precipitation is ca 500 mm/yr.

These dry forests are the habitat of several endangered species including Juglans neotropica (Juglandaceae), Siparuna eggersii (Monimiaceae), both of which are critically endangered (see Joergensen & León-Yánez 1999, Valencia et al. 2000)

FIELDWORK.—We located 109 rectangular plots (10 × 50 m) on 48 forest stands in a stratified sampling design based on the available preliminary landscape maps in the zone (O. Cabrera, G. Guamán, W. Quizhpe, Z. Aguirre, R. Alvarado, unpubl. data) and with the aim of including the whole range of environmental conditions (Fig. S1). Two or three plots per forest stand were sampled. Plot size was chosen to ensure representation of diversity richness and composition of a typical dry forest in the region (Balvanera & Aguirre 2006). Total surveyed area was 5.45 ha. This sampling may not be efficient enough to explore processes occurring at smaller spatial scales like those related to fine soil heterogeneity which may critically affect recruitment processes; however, it is adequate for classification purposes, for testing some biogeographical hypotheses and mainly to generate basic information for conservation management. Altitude and slope of each plot were recorded with an altimeter and with a clinometer in a wooden rule of 3 m located in the center of the plot. Topographic location of each plot was measured on a semi-quantitative scale. This topographic gradient was presumed to reflect a water availability gradient (ridge > hillside > valley). Within each rectangular plot, we identified the species and measured the diameter at breast height (dbh) of all individual trees and shrubs with diameter ≥ 5 cm. Soil was characterized by means of five soil cores of 5-cm diam and 5-cm deep, taken in the center, and at each of the four plot corners. We measured soil temperature at 30-cm deep. Percentage of soil moisture was calculated by subtracting the dry weight to the water saturated weight of each sample. After taking this moisture value, the five subsamples were thoroughly merged before analyses to minimize soil heterogeneity at the plot scale. We measured percentage of total nitrogen content (Kjeldahl method), bulk density (g/cm^3) and pH. Although our study area was well conserved, we visually estimated anthropogenic degradation related to firewood and timber extraction and livestock. The anthropogenic degradation variable

summarized presence and amount of stumps—which are good surrogates of selective logging intensity—and evidence of cattle grazing activities in a semi-quantitative scale index: high, medium and low degradation.

Our regional scale predictors were related to climate. These variables were estimated with the Worldclim data base (Hijmans *et al.* 2005). Worldclim interpolated the climate variables to our 109 plots on the basis of the eight existing meteorological stations nearby the study area. This online tool estimates climate parameters derived from monthly values of temperature and rainfall of the latest 50 yr. Selected climatic variables represented annual trends (annual temperature and annual precipitation) seasonality (annual temperature range and annual precipitation range) and extreme environmental factors (temperature of the coldest and the warmest months, and precipitation in the wettest and driest months). We detected high correlations and variation inflation factors (VIF) between many of these variables, so hereafter we only considered in our analyses four climatic variables that showed low level of correlation: annual precipitation, precipitation in the driest month, annual temperature range and maximum temperature in the warmest month.

Although some uncertainty has been reported especially of rainfall values in mountainous areas after using this interpolation tool (Hijmans *et al.* 2005), the values interpolated for our plots are reliable because the eight meteorological stations are regularly distributed throughout the study area and tropical dry forests are usually located in the foothills of the Andes.

STATISTICAL ANALYSES.—Total species richness and evenness (Pielou 1966) were modeled by means of generalized linear models (GLMs, McCullagh & Nelder 1989). GLMs allow handling larger distribution types in addition to Gaussian distribution for the response variable than standard linear regressions. We applied a quasi-likelihood estimation of the regression coefficients because it allows estimating regression coefficients in datasets without fully knowing the error distribution of the response variable (Guisan *et al.* 2002). We built a saturated model with all 13 predictor variables (annual precipitation, precipitation in the driest month, annual range of temperature, maximum temperature in the warmest month, anthropogenic degradation, altitude, slope, topographic location, soil temperature, soil moisture, pH, total nitrogen content and bulk density). The significant terms of the model were identified using a forward stepwise approach (Guisan & Zimmermann 2000) and to avoid multiple comparison problems typical of forward stepwise analyses, we fixed the threshold for significance in $P < 0.01$. GLMs were built with S-PLUS statistical software (MathSoft 1999).

We built two main matrices (species per plot), one for density values (number of individuals of each species per plot) and the other for total plant basal area of each species (109 plots in rows and 102 species in columns). Detrended correspondence analysis showed that axes lengths were $> 3\,SD$ units in both main matrices and so canonical constrained analyses (CCA) were performed (ter Braak 1986, Legendre & Anderson 1999). Our null hypothesis (H_0) was that the environmental variables did not exert any effect significantly different from random on species composition in terms of density and basal area of each species. Plant data were square root transformed and down weighing of rare species was performed. Five constraining matrices were built: (1) the climate matrix included four variables: maximum temperature in the warmest month, annual temperature range, precipitation in the driest month and annual average precipitation; (2) the topography matrix was built with one continuous variable with values 1 for valley, 2 for hillside and 3 for ridge with represent decay in water availability; (3) the matrix with the intensity of degradation consisted in one vector coded as a continuous variable which values 1 for low degree of degradation, 2 for medium and 3 for high degradation; (4) the soil matrix included five variables: soil temperature, soil moisture, total nitrogen content, pH and bulk density; and (5) a complete environmental data matrix including all the above-mentioned predictors, except for the 'annual temperature range' variable which was eliminated from the complete dataset due to the high VIF values. Thus, the complete matrix contained 12 variables. Total variation explained by each constraining matrix was calculated as the sum of all canonical extracted axes (Borcard *et al.* 1992). Monte Carlo permutation tests were performed to determine the accuracy of the relationships (1000 randomizations) between each pair of datasets (Legendre & Anderson 1999, ter Braak & Smilauer 2002). To reduce the number of explaining variables and to select the best predictors, we used a forward selection procedure; the selected variables were used to construct a reduced model. Partial CCAs were run for each of the constrained models to identify the effect of each environmental matrix independently of the rest (Borcard *et al.* 1992). Partial CCAs with climate, soil and topography matrices were performed two by two and the intersection of the three matrices was calculated following the procedure used by Vincent *et al.* (2006). All these analyses were performed with CANOCO for Windows version 4.5 (ter Braak & Smilauer 2002).

To build a classification of species assemblages, the species densities dataset was subject to an agglomerative cluster analysis with complete linkage as the clustering algorithm. Data were fourth root transformed and the similarity matrix was built with the Bray Curtis distance among samples (Clarke & Gorley 2006). This cluster analysis was tested by means of a similarity profile permutation test (SIMPROF procedure) and a similarity percentage analysis (SIMPER procedure) was performed to identify the species responsible for the floristic differences between groups in each node of the dendrogram, so maintaining the hierarchical structure of the classification (Anderson *et al.* 2008). To identify the environmental variables that underlied this classification, we labeled each sample with the environmental variable thresholds obtained after a BIOENV analysis followed by a LINKTREE procedure. These analyses were undertaken with the PRIMER v6. statistical program (Clarke & Gorley 2006).

RESULTS

Our results showed that the Tumbesian tropical dry forests had on average 625 individuals/ha ($\pm\,294\,SD$). Our $500\,\mathrm{m}^2$ plots had on average 9.1 species ($\pm\,3.6\,SD$). Mean dbh was 33.4 cm. We recorded 102 species (69 trees and 29 shrubs) in the 109 plots

surveyed (Table S1). Average values and ranges of each predictor in our study area are given in Table 1. Three Bombacaceae species accounted for 40.3 percent of the area at breast height (*C. trichistandra*, *Cavanillesia platanifolia* and *Eriotheca ruizii*). The most abundant species were *Simira ecuadorensis* (Rubiaceae), *Tabebuia chrysantha* (Bignoniaceae) and *E. ruizii*, which appeared in > 40 percent of the plots. On the other hand, most species (54%) appeared in < 5 percent of the plots. We also recorded seven enlisted endangered species: *J. neotropica*, *S. eggersii* both critically endangered, and *Oreopanax rosei* (Araliaceae), *Verbesina pentantha* (Asteraceae), *C. platanifolia* (Bombacaceae), *Pradosia montana* (Sapotaceae), *Erythrina smithiana* (Fabaceae).

Species richness was negatively affected by annual temperature range, annual precipitation, anthropogenic degradation and topographic location (species richness increased from ridges to valley bottoms), whereas evenness showed a positive relationship with altitude only (Table 2). Species composition in terms of both density and basal area showed similar patterns when they were constrained with any of the explaining matrices (Table S2). Climate, topography and soil datasets explained fractions of total variation (12–16%), whereas anthropogenic degradation only explained a low but significant fraction of species composition (< 4%). Climate was the constraining matrix that explained the highest percentage of species composition variability after excluding the overlap with the rest of datasets, followed by soil physicochemical variables (Fig. 1). Climate, soil and topography matrices showed slight overlap in the variation explained, and anthropogenic degradation became nonsignificant after adjusting for the variability explained by the rest of environmental matrices. In the forward stepwise procedure for the densities and basal areas, nine and eight environmental variables were selected, respectively (Table 3). Variables related to water availability explained the largest fraction of variability in species composition, *i.e.*, altitude, precipitation in the

driest month, annual precipitation, soil moisture and temperature in the warmest month.

Agglomerative cluster analyses and the corresponding permutation tests (SIMPROF procedure) classified our samples into seven groups in terms of taxonomic affiliation (Fig. 2). At each node, the discriminating species between both groups were identified which gives an idea of the hierarchy underlying the classification (SIMPER procedure; Table S3). Thus, *Triplaris cumingiana* (Polygonaceae) and *S. ecuadorensis* (Rubiaceae) were the species that discriminated between the two main groups of Tumbesian dry forests. In the two subsequent nodes the diagnostic species were *Myrcia fallax* (Myrtaceae) and *Styrax* sp. (Styraceaeae) in the first and *S. ecuadorensis* and *Coccoloba ruiziana* (Polygonaceae) in the second node. Our seven floristic groups were also linked to conspicuous differences in altitude, annual precipitation and rainfall in the driest month (Fig. 2). Both Group 1 and 2 were > 650 m, but Group 2 occurred where the precipitation of the driest month was higher. In the range 300–800 m we found samples from Groups 6 and 7 which differed in the annual average precipitation and precipitation in the driest month. Group 7 occurred in drier conditions than Group 6. Group 4 included samples occurring at altitudes of 600–800 m and related to high precipitation values. In altitudes of 200–590 m and in the absence of precipitation in the driest months, two different groups were identified, Group 5 with higher mean annual precipitation values and Group 3 in drier conditions.

DISCUSSION

Our results support only one of our hypotheses: Tumbesian dry forests have higher richness in sites with greater water stress, consistent with the interpretation that facilitation processes are important to structuring of plant communities. As expected, our results showed that species richness and evenness were mainly affected by two factors underlying water availability: (1) climate, as shown by the significant effect of some climatic predictors such as annual rainfall, precipitation of the driest month and annual range of temperature in both community traits; and (2) altitude, in the case of evenness. Predictors related to water availability in areas with a marked seasonality in precipitation have already been associated with some components of diversity (Trejo 1998, White & Hood 2004). As a norm it has been suggested that availability of water increases productivity and consequently diversity (Dickson & Foster 2008); however, our results are aligned with those of Gentry (1995), who suggested that this relationship does not occur in the dry tropics. In fact, our results showed that drier conditions increased richness which suggests that our plant–plant interaction hypothesis seems more plausible. Thus, the negative relationship between water availability and richness could be explained, at least partially, by the well-known stress-gradient hypothesis, a conceptual model predicting that the relative frequency of facilitation and competition will vary inversely across gradients of physical stress or ecosystem productivity (Bertness & Callaway 1994). In consequence, the number of species packed in more stressful conditions was higher than expected by chance, whereas in more competitive conditions some species may competitively be excluded. In our

TABLE 1. *Range, mean values (± SD) of all the predictor and response variables measured in our study area.*

	Mean ± *SD*	Range
Species richness	9.10 ± 3.7	1–19
Evenness	3.94 ± 1.1	0–6.6
Slope (%)	17.3 ± 12.9	0–45
Altitude (m)	605 ± 284	200–1580
pH	5.75 ± 0.4	4.78–7
Organic matter (%)	4.51 ± 2	0.03–13
Soil temperature (°C)	25.8 ± 3.4	19–34
Organic carbon (%)	2.65 ± 1.2	0.04–7.55
Total nitrogen (%)	0.19 ± 0.1	0.01–0.6
Soil bulk density (g/cm^3)	1.18 ± 0.1	1.02–1.42
Soil moisture (%)	9.59 ± 7.8	1.05–28.7
Temperature in warmest month (°C)	31.0 ± 1.4	27–32.9
Annual temperature range (°C)	14.9 ± 0.7	13.8–16.6
Precipitation in the driest month (°C)	1.17 ± 1.5	0–4
Annual precipitation (°C)	747 ± 253	270–1284

TABLE 2. *The significantly selected variables after a forward stepwise procedure of the generalized linear models with 108 samples (one outlier was eliminated). Two response variables: species richness and evenness. Coef., regression coefficient; Resid. Dev., residual deviance; Cumul. D^2, cumulative D^2 (i.e., % variance explained). The p threshold to select significant terms was p < 0.01 to avoid multiple comparison problems.*

Variable	Coef.	SE	t-value	P	df	Resid. Dev.	F	P	Cumul. D^2
Species richness									
Null					108	1462			
Intercept	90.5	15.0	6.03	2.25E–08					
Annual temperature range	− 4.24	0.92	− 4.63	1.02E–05	107	1016	62.7	< 0.0001	0.305
Anthropogenic degradation	− 1.48	0.42	− 3.5	6.83E–04	106	919	13.6	0.0004	0.371
Annual average precipitation	− 0.01	0.003	− 3.82	2.19E–04	105	829	12.7	0.0006	0.433
Topographic location	− 1.58	0.49	− 3.19	1.83E–03	104	762	9.39	0.0028	0.479
Evenness									
Null					108	125			
Intercept	3.69	0.41	9.04	6.66E–15					
Altitude	0.001	0.0004	3.06	2.76E–03	107	110	14.3	0.0003	0.116

study area, the stress may be induced by water deficiency and nurse plant may improve their facilitative effect mainly by means of shade conditions on seedlings. Shadows caused by neighbors improve water availability by decreasing the vapor pressure difference between the leaf of the beneficiary and ambient air. This occurs without a substantial resource cost to the benefactor (Brooker *et al.* 2008) and leads to higher diversity than in more competitive scenarios.

Surprisingly, species richness patterns in these tropical dry forest areas were not affected by soil characteristics. This result should be taken with caution because it is well known that soil hetero-

geneity and ground surface variability are critical for the demography of some species, but at finer spatial scales (Hook *et al.* 1991). At the medium-size scale we are working on, however, soil fine heterogeneity seems not to affect species richness, although species composition was affected.

Some studies have shown the effect of topographic location to be commonly associated with diversity and also mediated by water availability (*e.g.*, Oliveira-Filho *et al.* 1998). Species richness and evenness increased from ridges to valleys, first because probably at ridges environmental conditions are harsher (*e.g.*, strong winds, shallower soils) and these extreme environmental conditions may restrict the amount of species able to survive in these rough conditions, and second because rock outcrops at ridges may significantly reduce the available space for trees (Escudero 1996).

On the other hand, total richness varied inversely along a human disturbance gradient. This is relevant because the intensity
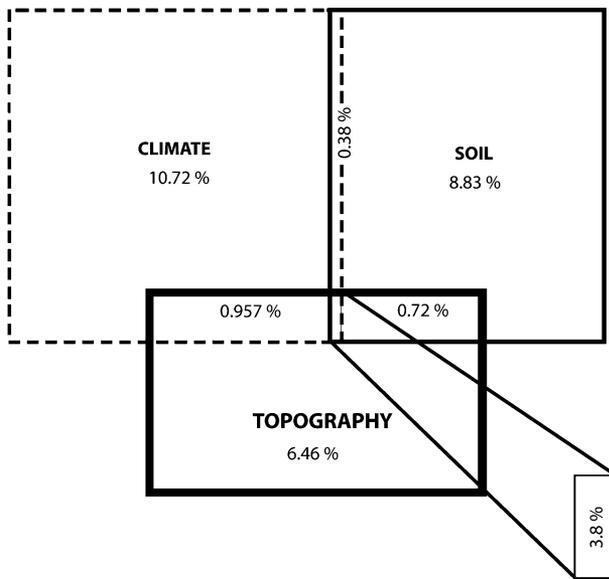

FIGURE 1. Variation in plant density explained by each of the constraining data matrices: topography, soil and climate and the overlap of the variation explained among matrices after undertaking the partial canonical constrained analyses (CCA) (see Methods). The effect of anthropogenic degradation became nonsignificant after adjusting the rest matrices as covariables in the partial CCA so it was not represented in this figure.

TABLE 3. *Environmental variables selected in the forward stepwise selection in the canonical constrained analysis on tree species densities and plant basal area (see Methods; p-value after Monte Carlo permutation test and Bonferroni adjustment). λ, variation explained.*

| Variable	Tree densities			Plant basal area		
	λ	F	P	λ	F	P
Altitude	0.49	8.18	0.001	0.47	6.83	0.001
Precipitation of driest month	0.26	4.53	0.001	0.26	3.79	0.001
Annual precipitation	0.23	4.09	0.001	0.25	3.71	0.001
Soil moisture	0.19	3.42	0.001	0.17	2.68	0.001
Nitrogen	0.13	2.42	0.001	0.16	2.58	0.001
Temperature of warmest month	0.15	2.92	0.001	0.15	2.28	0.001
Anthropogenic degradation	0.13	2.42	0.001			
Slope	0.12	2.32	0.001	0.12	1.94	0.001
Soil temperature	0.12	2.35	0.001	0.14	2.21	0.001
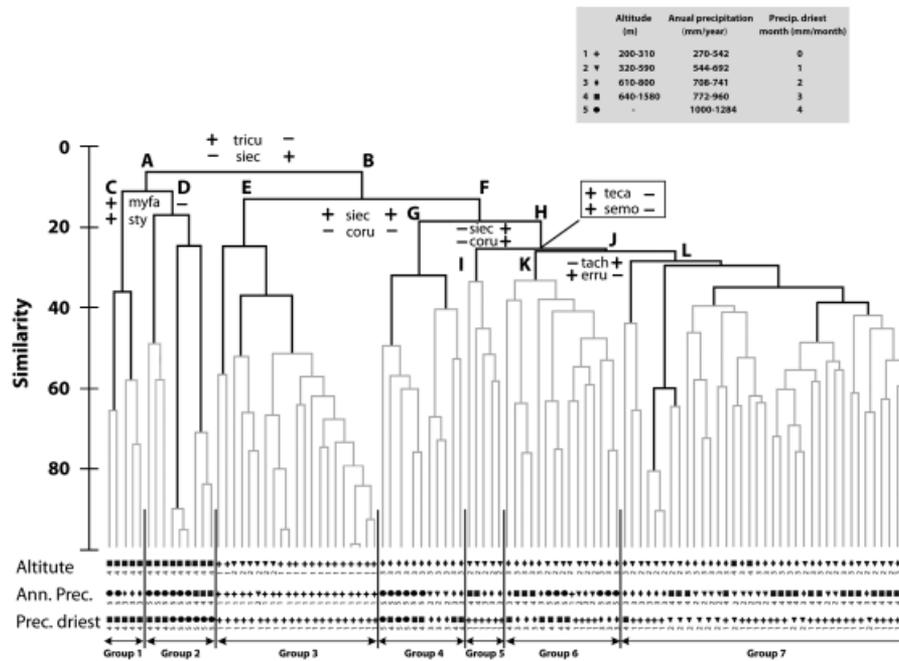
FIGURE 2.   Dendrogram of the agglomerative cluster of 103 samples (six outliers were excluded). Solid lines represent significant differences among groups by means of the permutation procedure SIMPROF. Data were fourth root transformed and the resemblance matrix was built by means of Bray Curtis distances. Species that contributed to the discrimination between groups are indicated in each node (SIMPER procedure). − and + symbols indicate in which groups the species were more abundant. *Y*-axis represents similarity percentage among groups. Capital letters indicate each node (for more details on SIMPER, see Table S3). Ann. Prec., Annual precipitation; Prec. Driest, precipitation in the driest month; tricu, *Triplaris cumingiana*; siec, *Simira ecuadorensis*; myfa, *Myrcia fallax*; sty, *Styrax* sp.; coru, *Coccoloba ruiziana*; teca, *Tecoma castanifolia*; semo, *Senna mollisima*; tach, *Tabebuia chrysantha*; erru, *Eriotheca ruizii*. The seven groups of samples obtained after the SIMPROF procedure, labeled with the environmental variables ranges identified in the LINKTREE analysis: altitude, annual precipitation and precipitation in the driest month.

of disturbance in the sampled stands is low and there is a dramatic increase of this pressure especially in more accessible areas. Timber extraction and cattle grazing affected forest richness but not composition (see below). This suggests that extraction is not selective, so the number of species is maintained at least in this low-pressure state.

Species composition of the Tumbesian dry forests was mainly determined by climate, topography and soil. It is worth noting that densities and basal area datasets showed similar results. The climate dataset explained the highest fraction of nonoverlapping information. Relevance of water was also highlighted because the selected climatic variables were also surrogates of this factor: temperature of the warmest month and rainfall of the driest month. Water availability has been recognized as one of the most important factors in determining species composition in tropical dry forests (Gentry 1995, White & Hood 2004). Soil predictors also played an important role in determining species composition in the line of other studies (Chytry *et al.* 2008). Soil variables related to water availability such as soil moisture and soil temperature were selected together with soil nitrogen concentration. Although soil features did not affect richness, they significantly controlled species composition, through surrogates of ecosystem productivity like nitrogen content. This implies that composition shifted in richer soils.

Altitude was also a significant predictor of species composition of these dry forests (Aguirre *et al.* 2006). This result was probably

related to the fact that at higher altitudes the transition region between mountain and genuine dry forest communities appears. Several Andean species that have their lower distribution limits in our study area appeared at higher altitudes (*e.g.*, *J. neotropica*, *T. cumingiana*, *V. pentantha*, *Clusia* sp.) implying an increase in diversity attributes typical of ecotones.

Our floristic classification in seven groups was in agreement with other floristic approaches carried out in this vast territory (Aguirre & Kvist 2005, Aguirre *et al.* 2006). For instance, the group dominated by *Myrcia falax* and *Styrax* sp., and the group dominated by *S. ecuadorensis* and *T. chrysantha*, which appeared at the higher and medium altitudes of the tropical dry forest was almost coincident with a well-defined vegetation type by Aguirre and Kvist (2005). All these floristic groups were strongly segregated by altitude and water availability (Fig. 2).

In conclusion, the species assemblage in tropical dry forests seems to be controlled mainly by altitude (proximity to the Mountain Forest ecotone) and water availability. Reduction in water availability in the tropical dry forest generated communities with more species, probably in response to the stress, facilitation processes became dominant. Our results fill, at least partially, the gap in the knowledge of dry forests ecology in South America (Sánchez-Azofeifa *et al.* 2005) and provide basic information for conservation management of poorly studied Tumbesian forests (Dinerstein *et al.* 1995, Aguirre *et al.* 2006).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Individuals density for plot and groups in terms of taxonomic affiliation.*

TABLE S2. *CCA models with the main matrix being the densities dataset and the basal area dataset.*

TABLE S3. *Breakdown of average dissimilarity between the groups segregated in the cluster analysis into contributions from each species by means of a Similarity Percentage procedure.*

FIGURE S1. Study area and plots location (black triangle) in the Loja province, Southern Ecuador.

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