TECHNISCHE UNIVERSITÄT MÜNCHEN

TUM School of Life Sciences

Lehrstuhl für Waldbau

Impacts of anthropogenic disturbances and climate change on biodiversity and stand dynamics on Ecuadorian dry forest sites

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Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Forstwissenschaft (Dr. rer. silv.)

genehmigten Dissertation.

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Die Dissertation wurde am 07.07.2021 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 22.09.2021 angenommen.

Dedico este trabajo a mi esposa, quien me apoyó durante todo este proceso y ha sido el principal soporte familiar, gracias amor por tu tiempo y sacrificio. A mi hijo Mateo por haberme distanciado físicamente y perdido parte de su desarrollo personal. A mis hijos Gabriela, Alejandra y Matias para quienes representó dejar una forma de vida y sobrellevar las dificultades de crecer y formar parte de un mundo ajeno.

A mis padres Sonia y Eduardo por haber inculcado en sus hijos el deseo de formarse personal y profesionalmente, por los valores que sembraron en sus hijos y por su apoyo brindado en todo momento. A mis hermanos Eduardo, Robert y Sonia María; a mi cuñada Ma. Del Cisne y a mis sobrinos Martina, Edu y Luciana quienes durante todo momento han aportado mucho más que alegría y soporte espiritual.

Acknowledgments

Many people have been involved at different points in this research making it possible to conclude this dissertation in a satisfactory way.

Much respect and gratitude to my supervisor Prof. Dr. Michael Weber for his enormous support and valuable advice throughout the whole process. To my main advisor Dr. Patrick Hildebrandt, for his incalculable support at every stage of the research, because his experience and knowledge facilitated my work, to his family who have been one of the most important emotional supports for my family and myself during our time in Germany. To my co–supervisor Dr. Carlos Iván Espinosa, who with his knowledge of the ecosystem was a great support to help improve the scientific component of the research.

I wish to thank Prof. Dr. Thomas Knoke for his contribution to the publications and especially for being part of the assessing committee. To Prof. Dr. Peter Annighöfer, head of the assessing committee, many thanks. Special gratitude to Violeta Aramayo Schenk for her selfless support administratively and personally. To Lara von Dehn for her enormous contribution to language editing.

To Naturaleza y Cultura Internacional, Parque Nacional Cerros de Amotape and the communities Malvas, El Cardo, Piedras Blancas for allowing me to conduct this research in the reserves La Ceiba, Cazaderos, Cerros de Amotape National Park, Limones, Piedras Blancas and El Cardo. In addition, I would like to thank Elizabeth Gusmán, Diego González, Jorge Armijos, Geovanny Cango, Angel Gusmán, Johana Gusmán, Israel Medina, Yodán Zapata and Flavio Olaya for their support in data collection.

My thanks for the financial support to Secretaria de Educación Superior, Ciencia, Tecnología e Innovación (SENESCYT), Technical University of Munich (TUM), Universidad Técnica Particular de Loja (UTPL), German Research Foundation (DFG) project PAK 824/B3 and to Erzbischöfliches Ordinariat München.

Table of Contents

List of figures

List of tables

Abstract

Tropical and subtropical dry forests make up the world’s largest terrestrial ecosystem occupying 42% of the tropical forest area; 54.2% of this total is found in South America. Most parts of this ecosystem are heavily threatened by a combination of human disturbances and climate change whose threats also arise in the dry forest of southern Ecuador and northern Perú (called the Tumbesian region). In this region, the natural forests have been used to establish several productive activities, such as growing crops, rearing livestock and using the forest resources, due to their ease of access and climatic conditions, which has led to this ecosystem becoming highly threatened.

To understand the effects of these threats, which have not yet been appropriately assessed, we pose the objectives: a) examine the current situation of the dry forest in the central zone of the Tumbesian region in terms of structure and diversity of the adult forest as well as of natural regeneration; b) to identify drivers (human pressure, abiotic and soil variables) affecting the diversity and structure of adult forest and natural regeneration in the dry forest of the study area; c) to assess the effects of seasonality and grazing on the dynamics of natural regeneration in the dry forest.

The factors assessed to determine the impact on diversity and structure of the forest were: species richness, diversity, tree abundance for both mature forest and natural regeneration, species similarity and density in mature forest, mortality and recruitment in natural regeneration. Data for mature forest were obtained from 72 plots (60 × 60 m, total area 25.92 ha), which were randomly placed to cover a wide range of stand characteristics with different stand densities and elevations (from 200 to 1100 m a.s.l.). Data on natural regeneration was obtained from 288 fenced and unfenced plots (2 × 2 m, total area 1152 m^2) nested in the former ones with five surveys spanning a 2-years period. Generalized linear mixed models or linear mixed models were used to determine whether the analysed respond variables were affected by anthropogenic activities, climate and/or soil characteristics. The best models were chosen using the delta Akaike information criterion (ΔAIC $\leq$2).

The results show that human pressure index (HPI) was the most negative predictor for forest health of mature forest. Annual precipitation was the most important abiotic predictor for good health conditions in mature forest as well as for natural regeneration. Livestock grazing did not significantly change the diversity and structure of mature forest although the best models for species richness, diversity and abundance included this predictor; however, cattle grazing was a negative predictor for the abundance of seedlings.

Soil characteristics were also an important predictor for natural regeneration: soils deeper than 10 cm and well drained revealed positive effects on species richness; likewise, moderately

drained soils had a significant positive effect on the diversity and sites with clay loam and loam soils had a significantly higher diversity. Fencing had a major effect on reducing mortality of natural regeneration but did not improve the abundance or species diversity.

Zusammenfassung

Tropische und subtropische Trockenwälder bilden das größte terrestrische Ökosystem der Welt und nehmen 42% der tropischen Waldfläche ein; 54,2% dieser Fläche befinden sich in Südamerika. Die meisten Teile dieses Ökosystems sind durch eine Kombination aus menschlichen Störungen und Klimawandel stark bedroht, was auch für den Trockenwald im südlichen Ecuador und nördlichen Perú (die sogenannte Tumbesische Region) gilt. In dieser Region wurden die natürlichen Wälder aufgrund ihrer leichten Zugänglichkeit und der klimatischen Bedingungen zur Etablierung verschiedener produktiver Aktivitäten wie Ackerbau, Viehzucht und Nutzung der Waldressourcen genutzt, was zu einer starken Bedrohung dieses Ökosystems geführt hat.

Um die Auswirkungen dieser Bedrohungen, die bisher noch nicht angemessen bewertet wurden, zu verstehen, stellen wir die folgenden Ziele auf: a) die aktuelle Situation des Trockenwaldes in der zentralen Zone der Tumbesischen Region in Bezug auf Struktur und Diversität des erwachsenen Waldes sowie der natürlichen Verjüngung zu untersuchen; b) die Identifizierung von Einflussfaktoren (menschlicher Druck, abiotische und Bodenvariablen), die die Vielfalt und Struktur des erwachsenen Waldes und der natürlichen Regeneration im Trockenwald des Untersuchungsgebietes beeinflussen; c) die Bewertung der Auswirkungen von Saisonalität und Beweidung auf die Dynamik der natürlichen Regeneration im Trockenwald.

Die Faktoren, die bewertet wurden, um die Auswirkungen auf die Vielfalt und Struktur des Waldes zu bestimmen, waren: Artenreichtum, Diversität, Baumabundanz sowohl für den ausgewachsenen Wald als auch für die Naturverjüngung, Artenähnlichkeit und Dichte im ausgewachsenen Wald, Mortalität und Aufkommen in der Naturverjüngung. Die Daten für den ausgewachsenen Wald wurden aus 72 Parzellen (60 × 60 m, Gesamtfläche 25,92 ha) gewonnen, die nach dem Zufallsprinzip platziert wurden, um ein breites Spektrum an Bestandesmerkmalen mit unterschiedlichen Bestandesdichten und Höhenlagen (von 200 bis 1100 m ü. NN) abzudecken. Daten zur Naturverjüngung wurden von 288 eingezäunten und nicht eingezäunten Parzellen (2 × 2 m, Gesamtfläche 1152 m^2) gewonnen, die in den ersteren mit fünf Erhebungen über einen Zeitraum von zwei Jahren verschachtelt wurden. Allgemeine lineare gemischte Modelle oder lineare gemischte Modelle wurden verwendet, um zu bestimmen, ob die analysierten Antwortvariablen durch anthropogene Aktivitäten, Klima und/oder Bodeneigenschaften beeinflusst wurden. Die besten Modelle wurden anhand des Delta-Akaike-Informationskriteriums (ΔAIC $\leq$2) ausgewählt.

Die Ergebnisse zeigen, dass der Index des menschlichen Einflusses (HPI für das Akronym auf Englisch) die negativste erklärende Variable für die Waldgesundheit des reifen Waldes war. Der Jahresniederschlag war der wichtigste abiotische Prädiktor für einen guten Gesundheitszustand in

reifem Wald sowie für die natürliche Verjüngung. Die Beweidung mit Vieh veränderte die Vielfalt und Struktur des reifen Waldes nicht signifikant, obwohl die besten Modelle für den Artenreichtum, die Artenvielfalt und die Abundanz diesen Prädiktor enthielten; allerdings war die Beweidung mit Vieh ein negativer Prädiktor für die Abundanz von Setzlingen.

Bodeneigenschaften waren ebenfalls ein wichtiger Prädiktor für die Naturverjüngung: Böden, die tiefer als 10 cm und gut entwässert sind, zeigten positive Effekte auf den Artenreichtum; ebenso hatten mäßig entwässerte Böden einen signifikant positiven Effekt auf die Vielfalt und Standorte mit Lehm- und Tonböden hatten eine signifikant höhere Vielfalt. Die Umzäunung hatte einen großen Effekt auf die Verringerung der Mortalität der Naturverjüngung, verbesserte aber nicht die Abundanz oder die Artenvielfalt.

Resumen

Los bosques secos tropicales y subtropicales constituyen el mayor ecosistema terrestre del mundo y ocupan el 42% de los bosques tropical; el 54,2% de este total se encuentra en Sudamérica. La mayor parte de este ecosistema está fuertemente amenazado por una combinación de perturbaciones humanas y cambio climático, cuyas amenazas también se producen en el bosque seco del sur de Ecuador y el norte de Perú (conocido como Región Tumbesina). Debido a su facilidad de acceso y a las condiciones climáticas de esta región, los bosques naturales han sido utilizados para establecer diversas actividades productivas, como la agricultura, la cría de ganado y el aprovechamiento de los recursos del bosque, lo que ha llevado a este ecosistema a estar muy amenazado.

Para entender los efectos de estas amenazas, que aún no han sido debidamente evaluadas, nos planteamos los objetivos: a) examinar la situación actual del bosque seco en la zona central de la región tumbesina en términos de estructura y diversidad del bosque adulto, así como de la regeneración natural; b) identificar los factores (presión humana, variables abióticas y edáficas) que afectan a la diversidad y estructura del bosque adulto y de la regeneración natural en el bosque seco del área de estudio; c) evaluar los efectos de la estacionalidad y el pastoreo en la dinámica de la regeneración natural en el bosque seco.

Los factores evaluados para determinar el impacto sobre la diversidad y la estructura del bosque fueron: riqueza de especies, diversidad, abundancia de árboles tanto para el bosque maduro como para la regeneración natural, similitud de especies y densidad del bosque maduro, así como la mortalidad y el reclutamiento de la regeneración natural. Los datos del bosque maduro se obtuvieron a partir de 72 parcelas (60 × 60 m, con una superficie total de 25,92 ha) que se colocaron al azar para cubrir áreas con diferentes características en cuanto a densidades y elevaciones (de 200 a 1100 m s.n.m.). Los datos sobre la regeneración natural se obtuvieron en 288 parcelas valladas y no valladas (2 × 2 m, superficie total de 1152 m^2) anidadas en las primeras, con cinco muestreos realizados en un periodo de 2 años. Se utilizaron modelos lineales mixtos generalizados o modelos lineales mixtos para determinar si las variables de respuesta fueron afectadas por las actividades antropogénicas, el clima y/o las características del suelo. Los mejores modelos se eligieron utilizando el criterio de información delta Akaike (ΔAIC $\leq$2).

Los resultados muestran que el índice de presión humana (HPI) fue el predictor más negativo para la condición de los bosques maduros. La precipitación anual fue el predictor abiótico más importante influye en las buenas condiciones de salud del bosque maduro, así como de la regeneración natural. El pastoreo de ganado no cambió significativamente la diversidad y la estructura

del bosque maduro, aunque los mejores modelos para la riqueza, diversidad y abundancia de especies incluyeron este predictor; sin embargo, el pastoreo de ganado vacuno fue un predictor negativo para la abundancia de plántulas.

Las características del suelo también fueron un predictor importante para la regeneración natural: los suelos de más de 10 cm de profundidad y bien drenados revelaron efectos positivos en la riqueza de especies; asimismo, los suelos moderadamente drenados tuvieron un efecto positivo y significativo en la diversidad. Los sitios con suelos franco-arcillosos y francos tuvieron una diversidad significativamente mayor. El cercado tuvo un efecto importante en la reducción de la mortalidad de la regeneración natural, pero no mejoró la abundancia ni la diversidad de especies.

1. Introduction

1.1. Tropical Dry Forest

The global assessment of predominant habitat types identified 14 major terrestrial habitat types (Olson, *et al.*, 2000), among them, tropical and subtropical dry forest ecosystems, which collectively represent 42% of the tropical forest of the world, making it the largest ecosystem in the tropics (Miles, *et al.*, 2006).

According to Pennington *et al.* (2000), seasonally dry tropical forest occurs where the precipitation is less than 1,600 mm/year and dry periods vary between 5–6 months in the year (Gentry, 1995). This forest type has a closed canopy (Murphy & Lugo, 1986; Banda-R. *et al.*, 2016) and occurs on fertile soils (Ratter *et al.*, 1978; Pennington, Prado & Pendry, 2000).

Traditionally, the tropical dry forest has been considered less species rich than moist forests (Banda-R., *et al.*, 2016; Gentry, 1988). However, a recent comparison suggests that dry forests may contain as many or even more plant species as the Amazon rainforest (Pennington, Lehmann & Rowland, 2018).

Around two-thirds of the original neotropical dry forest on the globe has been converted to other types of land uses (Portillo-Quintero, *et al.*, 2010). In Latin America, only 10% of tropical dry forest remained intact compared to 80% of the Amazon rain forest (Pennington *et al.*, 2018). Those rates mean that more extensive efforts are still required to learn about the ecosystem: its diversity, functionality, the consequences of the most harmful activities and how to harmoniously handle them.

The remaining area of tropical dry forest is estimated at about 1,048,700 km^2 of which around 54.2% is located in South America, especially across Brazil, Bolivia, Paraguay, Argentina, Venezuela and Colombia (Miles, *et al.*, 2006). Other smaller and isolated areas are located in dry valleys of the Andes in Bolivia, Peru, Ecuador and Colombia as well as at the coasts of Ecuador and northern Peru (Pennington *et al.*, 2000). Despite their high ecological importance, dry forests are exposed to many threats (Maalouf, *et al.*, 2012; Miles, *et al.*, 2006; Olson, *et al.*, 2000; Semper-Pascual, *et al.*, 2018), such as deforestation, fragmentation, overgrazing, fire, conversion to agriculture and drought.

1.2. The Tumbesian Region

The Tumbesian region is a substantial area (approximately 103,000 km^2), predominantly of tropical dry forest, located at the coast of the southwestern part of Ecuador, which extends to the northwest of Peru (Hasnat, *et al.*, 2020). It belongs to the “Chocó / Darien Western Ecuador”, an area identified as one of the 25 global biodiversity hotspots with a high number of endemic species (85 birds, 60 mammals, 63 reptiles, 210 amphibians and 2,250 plants) (Myers, *et al.*, 2000).

The region extends from 0 to 3,000 m above sea level (a.s.l.). It encloses dry forest, wet forest and in the highest altitudes sometimes even paramos (Figure 1a) (Aguirre M., Kvist, & Sánchez T., 2006a). It is characterized by gentle slopes where rivers only rarely form deep valleys (Best, *et al.*, 1995). Several soil types form the region: desertic areas have poorly developed soils (northern Peru and the Santa Elena Peninsula in Ecuador); regions with seasonal climates have well-developed, nutrient-rich and cultivable soils (e.g., the Loja Andean foothills); extremely fertile soils are found along rivers; and deeply developed soils can be found in permanent humid areas (e.g., the Andean foothills south of El Oro Province) (Best, *et al.*, 1995).

Actually, 5% of the original cover of the region is still overgrown by forest (Dodson, *et al.*, 1991). But only 5% of that is protected by either the state or private owners, which represents around 2,500 km^2 of seasonally dry forest under protection in both countries (Figure 1b) (Linares-Palomino, *et al.*, 2010).

The dry part of the Tumbesian region has a surface of approximately 64,500 km^2 (Dinerstein, *et al.*, 1995). Due to its isolation, a high endemism in woody species has been determined (Hasnat, *et al.*, 2020): 21% of the species in this region were reported endemic (Linares-Palomino *et al.*, 2009) which equals about 1/5 of the species of the Ecuadorian dry forest (Dodson, *et al.*, 1991). According to Aguirre *et al.* (2006) Ecuador registers seven types of dry forest: spiny dry scrub, deciduous dry forest, semi–deciduous dry forest, low montane dry forest, southern inter–Andean dry forest, eastern inter–Andean dry forest and northern inter–Andean dry forest. The semi–deciduous dry forest (located between 200 and 1,100 m a.s.l.) is the most diverse formation, followed by the deciduous dry forest (located from sea level to 700 m a.s.l.).

This region is cyclically affected by El Niño events, which occur every 3–7 years. The intense warming of the waters of the Pacific Ocean causes heavy rains, which affects the climate of the region (Trenberth, 2019) and strongly influences forest structure and dynamics.

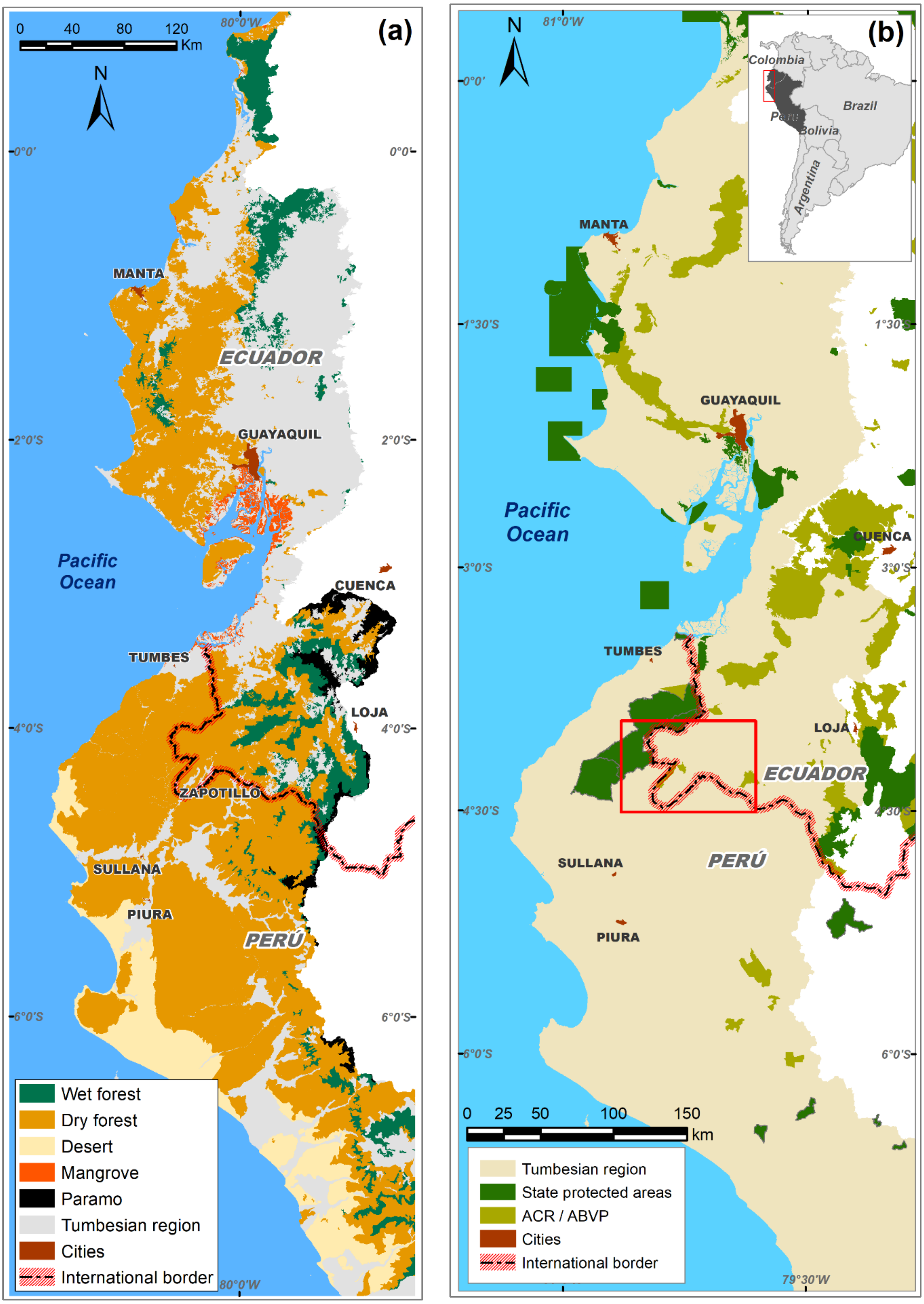


Figure 1. The Tumbesian region. **(a)** Map of remaining vegetation of the Tumbesian region. **(b)** Map of protected areas. ACR = Areas of regional conservancy from Peru; ABVP = Areas of protective forests and other vegetation from Ecuador. The red square in the middle of the map represents the study area.

1.3. Problem Statement

Seasonally dry forests have been declared the most threatened tropical forests globally (Miles, *et al.*, 2006). Dry forests of the Tumbesian region are also part of this reality. According to reports, these forests were colonized by hunters and gatherers of pre-Columbian civilizations (Hocquenghem, 1998), which means that this territory has been occupied for more than 5,000 years, which has undoubtedly induced a shift in the landscape composition to reach its current state (Banda-R., *et al.*, 2016).

Domestic animals were introduced into the area a long time ago. Goats for instance, arrived on the continent with the Spanish conquest and colonization (Rodero, *et al.*, 1992). They have successfully adapted to the site and the way they are bred. Nevertheless, their management nowadays is deficient or non-existent: goats stay in corrals at night, but they are released into the forest to look for food and water during the day. Cattle roam permanently free in the forest, but mainly in the higher parts. Horses and donkeys generally stay with the cattle (except when they are used as pack animals) but are less frequent (Leal-Pinedo, *et al.*, 2005).

In the 60s and 70s of the last century, a period of intensive logging of *Handroanthus chrysanthus* (Jacq.) S.O.Grose and *H. billbergii* (Bureau & K.Schum.) S.O.Grose lasted for almost two decades. In southwest Ecuador this was stopped in 1978 by the declaration of 'closed areas' in lands below 1,000 m a.s.l (Ministerio de Agricultura y Ganadería, *et al.*, 1978). However, timber extraction for domestic use (generally of selected species) continues until today because it is a permitted activity on state lands (Ministerio de Agricultura *et al.*, 1978), and illegal extraction has not been completely eliminated (Aguirre-Mendoza, *et al.*, 2005; Leal-Pinedo, *et al.*, 2005).

In the Ecuadorian part of the study area, the 'Zapotillo irrigation system', in operation since 2010, has stimulated the cultivation of new agricultural fields and an increase in the number of free-grazing goat and bovine herds in nearby forests (Hurtado, 2015). Furthermore, the Peruvian government promotes the creation of a dam in the central part of the Tumbesian region. If successful, this would provoke flooding of large areas in addition to the activities mentioned earlier.

Actions like those are responsible for the loss of species and the reduction of genetic variability, while leading to homogenizing the landscape and the ecosystem as they increase the abundance of certain species (Baskin, 1998; Mckinney, *et al.*, 1999). A clear instance of species loss due to anthropogenic activities was shown by Semper-Pascual *et al.* (2018), who revealed the influence of land conversion on the richness of animals in the Chaco of Argentina: the local extinction of birds and mammals was reported to be 56% in areas recently turned to pastures and 29% in areas converted to crop fields.

Additionally to the anthropogenic activities, the risk of degradation of dry forests due to the effects of climate change is increasing (Geist, *et al.*, 2004). Some authors argue that the combination of anthropogenic pressure, variability in climatic conditions and climate change turns tropical dry forests into particularly vulnerable regions (Miles, *et al.*, 2006; Sanchez-Azofeifa, *et al.*, 2013). Climate change has been identified as the most significant factor of uncertainty, as it might cause species extinction, changes in species spatial distribution and/or loss of biodiversity (Thomas, *et al.*, 2004).

Some changes have already been identified in the region, e.g., an increase of the mean temperature by 0.13°C per decade on the one hand and of precipitation by 8% on the other (Peters, *et al.*, 2013). Projections for southwestern Ecuador suggest an increase in temperature of 2°C to 5°C and an increase of 10% to 40% in rainfall by the end of the century (Marengo, *et al.*, 2010). This would severely affect the floristic composition of the region (Peters, *et al.*, 2013) and lead to changes in the distribution range of tree species (Feeley, *et al.*, 2011; Rehm, *et al.*, 2013).

1.4. Objectives and hypotheses

Considering the situation described above, this study strives to improve current knowledge about the dry forests in the central zone of the Tumbesian region and to identify if and how human activities and climate change impact forest conditions. To this end, it includes the following objectives:

a) To examine the current situation of dry forests in the central zone of the Tumbesian region in terms of its structure and diversity, focusing on the mature forest and natural regeneration.

b) To determine if anthropogenic pressure (especially livestock farming), abiotic factors and soil variables are already affecting the diversity and structure of the adult forest and the natural regeneration of the dry forests in the study area.

c) To determine whether seasonality or grazing has a greater influence on the dynamics of the natural regeneration of dry forests.

This research is based on the following hypotheses:

a) Livestock activities and other anthropogenic pressures have a strong influence on the structure and diversity of the mature forest and the natural regeneration of the dry forests of the Tumbesian region, resulting in different levels of density in the current forests.

b) Seasonality has a heavy influence on the mortality of natural regeneration. About 50% of dead seedlings could be caused by drought compared to those caused by grazing and other human activities.

1.5. Papers Contributions

This thesis includes two publications. The paper titles, short summaries and author contributions are presented below.

1.5.1. Publication 1

Jorge Cueva Ortiz, Carlos Iván Espinosa, Carlos Quiroz Dahik, Zhofre Aguirre Mendoza, Eduardo Cueva Ortiz, Elizabeth Gusmán, Michael Weber and Patrick Hildebrandt. (2019). *Influence of anthropogenic factors on the diversity and structure of a dry forest in the central part of the Tumbesian region (Ecuador-Perú).* Forests, 10(1), 1–22. https://doi.org/10.3390/f10010031.

The article identifies the conditions of adult dry forests in the central zone of the Tumbesian region in terms of structure and diversity and answers the question if those aspects are affected by anthropogenic and climatic factors and soil conditions. The results, derived by means of linear mixed models, revealed that anthropogenic factors (expressed by the human pressure index – HPI) was the most negative predictor and annual precipitation was the most important abiotic predictor of forest health conditions. Livestock grazing did not significantly change the diversity and structure of the mature forest. The mean annual temperature influenced only the basal area. The species composition was not affected by the HPI but was strongly determined by annual precipitation.

The authors contributed as follow: the research design was developed by J. Cueva, P. Hildebrandt and C. I. Espinosa; in the methodological aspects participated J. Cueva, P. Hildebrandt, C. I. Espinosa, Z. Aguirre and E. Cueva; the data collection was performed by J. Cueva and E. Gusmán; the manuscript was written by J. Cueva and reviewed by C. I. Espinosa, C. Quiroz, Z. Aguirre, E. Cueva, M. Weber and P. Hildebrandt.

1.5.2. Publication 2

Jorge Cueva Ortiz, Carlos Iván Espinosa, Zhofre Aguirre Mendoza, Elizabeth Gusmán, Michael Weber and Patrick Hildebrandt. (2020). *Natural Regeneration in the Tumbesian Dry Forest: Identification of the Drivers Affecting Abundance and Diversity*. Scientific Reports, 10(9786), 1–13. https://doi.org/10.1038/s41598-020-66743-x.

This article evaluates the effects of anthropogenic pressures and several abiotic variables on the natural regeneration of dry forests in the Tumbesian region. Natural regeneration was most positively affected by the rainy season precipitation, but soil conditions also played an important role. Short-term fences had a major effect on reducing mortality but did not improve the abundance or diversity, whereas cattle grazing significantly affected the abundance of seedlings.

In this document, J. Cueva, P. Hildebrandt and C. I. Espinosa designed the research; J. Cueva performed the fieldwork, the data analyses and wrote the document; J. Cueva and E. Gusmán undertook the data curation; J. Cueva, P. Hildebrandt and M. Weber discussed the results; P. Hildebrandt, M. Weber, C. I. Espinosa and Z. Aguirre reviewed the manuscript.

2. State of the Art

2.1. Forest characterization

To know the forest conditions is the first and most essential step before starting any kind of evaluation. In that order, measures that provide objective and quantitative appraisals are often used (Magurran, 1989) to determine the forests' diversity and structure. According to Magurran (1989), there are three reasons for the concern of ecologists about biological diversity: a) diversity is a central theme in ecology; b) diversity is often used as an indicator for well-functioning ecosystems; c) the existence of strong debates about measuring diversity.

2.2. Drivers affecting the dry forests

2.2.1. Climate change

In the 20th century, the combined mean of global land and sea temperature increased by 0.8 °C (IPCC, 2014). For the tropical Andes, a temperature increase of 0.13 °C per decade was reported for the period between 1950–2010 (Vuille *et al.*, 2015). However, the reasons for the high increase in this region still cause controversial discussions (Geist, *et al.*, 2004).

According to Feeley *et al.* (2011), the reactions of plants to climate change can be expressed in several ways: In the simplest cases, species with good adaptation ability can shift the boundaries of their distribution, and they will quickly adapt their behaviour to the new environmental conditions; in the worst cases, the response capacity is not suitable to adapt through migration, which will affect the abundance of the species (due to the death of individuals) leading to a probable extinction caused by the inability to perform their functions adequately.

It has been reported that tropical species are susceptible to climatic variation (Janzen, 1967). This sensitivity has been confirmed by Cuesta *et al.* (2019), who revealed that species closest to the equator have showcased narrower thermal niches than those with further extending ranges.

Parmesan & Yohe (2003), based on a global review of several documents, found that climate change affected the ranges of distribution and abundance of 84% of the species assessed throughout 20 years. Similar results could be observed in the Peruvian Andes, where 62% of the genera experienced an increase in their mean elevation by around 2.5 m year^{-1} between 2003 – 2008 (Feeley, *et al.*, 2011).

However, soon more drastic effects than species displacement might occur. According to projections of Miles *et al.* (2006), 37% of southern America's dry forests are at risk of severe climate change (computed as the average of the five general circulation models used) by the year 2055. These projections forecast a significant decrease in precipitation in many parts of tropical America, which may cause the current dry forests to turn into deserts while new areas would become climatically suitable for developing dry forests.

2.2.2. Forest resources use

Due to its long-standing exploitation, dry forests became probably the most threatened ecosystems in the world (Janzen, 1988). Cardoso da Silva & Fernandes Barbosa, (2017) stated that at least 63.3% of the Caatinga dry forest consist of anthropogenic forests. It has also been mentioned that it is unlikely that any remains of a forest might not have been used, at least as a source for firewood or charcoal production (Murphy, *et al.*, 1986).

Deforestation, habitat fragmentation, overgrazing, forest fires, land conversion and drought are some of the parameters identified as the primary drivers of ecosystem alterations (Best, *et al.*, 1995; Gentry, 1995; Janzen, 1988; Miles, *et al.*, 2006). The impacts of most of them tend to be more severe in the dry forest due to the high anthropogenic pressure to which this type of forest is subjected (Aguirre M. & Kvist, 2005; Espinosa, *et al.*, 2012; Murphy & Lugo, 1986), resulting in discontinuous and/or degraded forests.

2.2.3. Livestock grazing

Domestic animals have been listed as one of the main causes for the loss of biodiversity and density in the dry forest (Aguirre-Mendoza, *et al.*, 2005; Miles, *et al.*, 2006), mainly because the free-range cattle grazing is the most practiced way of raising livestock in this ecosystem (Piana, *et al.*, 2014).

In Costa Rica, the floristic composition of the dry forest was compared between two protected areas: one of them with intermittent cattle grazing and the other one with no sign of grazing. This research concluded that cattle grazing reduced the relative abundance and density of tree species and changed the species composition and structure of dry forests (Stern *et. al.*, 2002).

One research conducted in the upper parts of the Tumbesian region reported fewer species and lower cover of perennial plants in grazed areas than bush patches. No exclusive species were recorded in open areas (Espinosa *et al.*, 2014). In the Peruvian part of the study area, Cerros de Amotape National Park, on the other hand, the cattle grazing intensity was in negative correlation with the average canopy height and the percentage of vegetation cover (Piana, *et al.*, 2014). A crucial factor in this context is the grazing intensity. For instance, Schulz *et al.* (2018) found that in the Caatinga dry forest emergent trees were significantly less abundant in sites with high grazing intensity than those with low intensity, although tree density was not directly related to grazing intensity. Abou

Rajab *et al*. (2010) compared the natural regeneration under three different regimes of grazing: grazing allowed (no control), a limited number of cows and deer allowed (limited grazing) and no grazing. They found that abundance was directly related to the grazing level with the highest abundance in the no grazing area. More tall trees were found in the grazed areas, while more small trees were recorded in the limited grazing areas.

Likewise, Rodriguez (2006) reported a meaningful difference when comparing the effect of goats on species richness and abundance in fenced and unfenced plots: although the number of individuals was similar in fenced and unfenced plots, higher species richness was reported in fenced plots.

Due to the findings described above, dry forests exposed to extensive grazing were named "living dead forests" as livestock can completely suppress natural regeneration in these areas (Best, *et al.*, 1995; Janzen, 1986).

On the other hand, domestic animals, as long as they are correctly handled, have also been suggested as a way to reduce forest fires, as the grass-feeding reduces fuel and thus the fire risk in the next dry season; furthermore, animals help to disperse seeds throughout the forest (Janzen, 1988; Stoner, *et al.*, 2004).

In our study area, livestock breeding is a common and necessary activity for the local population. The income generated by keeping goats was identified as an essential mechanism to diversify the income of the local communities and reduce the financial risk of farmers (Ochoa M., *et al.* 2016).

2.2.4. Anthropogenic pressure

In the Americas, 66% of the original extension of the tropical dry forests has already been lost (Portillo-Quintero, *et al.*, 2010). Due to the geographic, climatic and productive conditions and the increasing population, the threats for the remaining dry forest are still growing (Lambin, *et al.*, 2003). The main reasons for the population increase are related to: (a) relatively flat landscapes; (b) usually fertile soils; (c) a marked seasonality, which allows producing short-cycle crops, (d) forests with small trees facilitating clearing and (e) the dry climate limits the spread of diseases transmitted by mosquitoes (Murphy & Lugo, 1986; Portillo-Quintero *et al.*, 2015).

Many authors (e.g., Best & Kessler, 1995; Gentry, 1995; Janzen, 1988; Miles *et al.*, 2006; Olson *et al.*, 2000) identified several human activities, including deforestation, fragmentation, overgrazing, fire and conversion to agriculture, as especially important for the loss of the ecosystem, because dry forests are susceptible to most of these activities which quickly alter the natural forests leading to desertification (Olson *et al.*, 2000).

As an effect of disturbing, in the Caatinga dry forest Leal *et. al.* (2014) found that at sites with low disturbance the mean dispersal distance of seed carried out by ants was four times higher compared to highly disturbed sites. Therefore, a likely negative implication on forest composition and structure of myrmecochorous plants in sites subject to high anthropogenic disturbance has been stated.

A recent study published by Rivas *et al.* (2020), determined that the Ecuadorian dry forests are under critical conditions: 83% of its area has very low connectivity; 70% was classified as highly fragile and 86% highly threatened. Despite this situation and the high endemism of the region, only 13% (1,069 km^2) is under protection by the Ecuadorian State.

Tapia-Armijos *et al.* (2015) revealed that between 1976 and 2008, deforestation of the natural cover in the study area amounted to 33% for seasonally dry forest and 18% for shrublands. In both cases the area turned into grasslands.

3. Study Area, Sampling Design and Datasets

3.1. Study area

3.1.1. Location and topography

The research was conducted in the dry forests of the Tumbesian region, within the deciduous and semi-deciduous formations (according to Aguirre M., Kvist, *et al.*, 2006a). The area is located between the coast of the Pacific Ocean and the Andes western cordillera, a lowlands area approximately 80 km wide, with a hot and arid climate.

The research area is located in southern Ecuador and northern Peru, in an altitudinal range from 200 m to 1,100 m a.s.l. Politically, the area belongs to the Tumbes department and the Loja province of Peru and Ecuador respectively (between 3°53’41.25’’ to 4°25’02.53’’ S and from 80°35’09.15’’ to 79°51’34.26’’ W) (Figure 2). Only two permanent rivers intersect this area: the Catamayo–Chira and the Puyango–Tumbes, both of which flow directly into the sea. In this area, the cordillera drops out of the two continuous mountain chains (called Eastern and Western Cordillera), departs from its north-south direction and splits up into many low mountains (peaks <4,000 m a.s.l.) running into different directions. This region is known as Huancabamba Depression (Best, *et al.*, 1995).

3.1.2. Climate and soils

The mean annual temperature ranges from 20–26 °C, although it can exceed 35 °C during the rainy season (Leal-Pinedo, *et al.*, 2005). According to Fick & Hijmans (2017) data, the annual precipitation recorded for our plots and their surroundings ranges from 440 to 1,270 mm. Nevertheless, as in the whole Tumbesian region, two seasons can be distinguished depending on the presence or absence of rainwater: a rainy season from January to April (nearly 85% of annual rainfall) and a dry season from May to December with two or three critically dry months (September–November).

The soils in the study area can be described as well-developed, slightly leached and rich in montmorillonite. The prevailing soil types are Vertisols, Luvisols, Mollisols and Planosols, which vary in their depth, drainage capacity, clay content and base saturation, but they are mostly rich in nutrients and cultivable (Best, *et al.*, 1995).

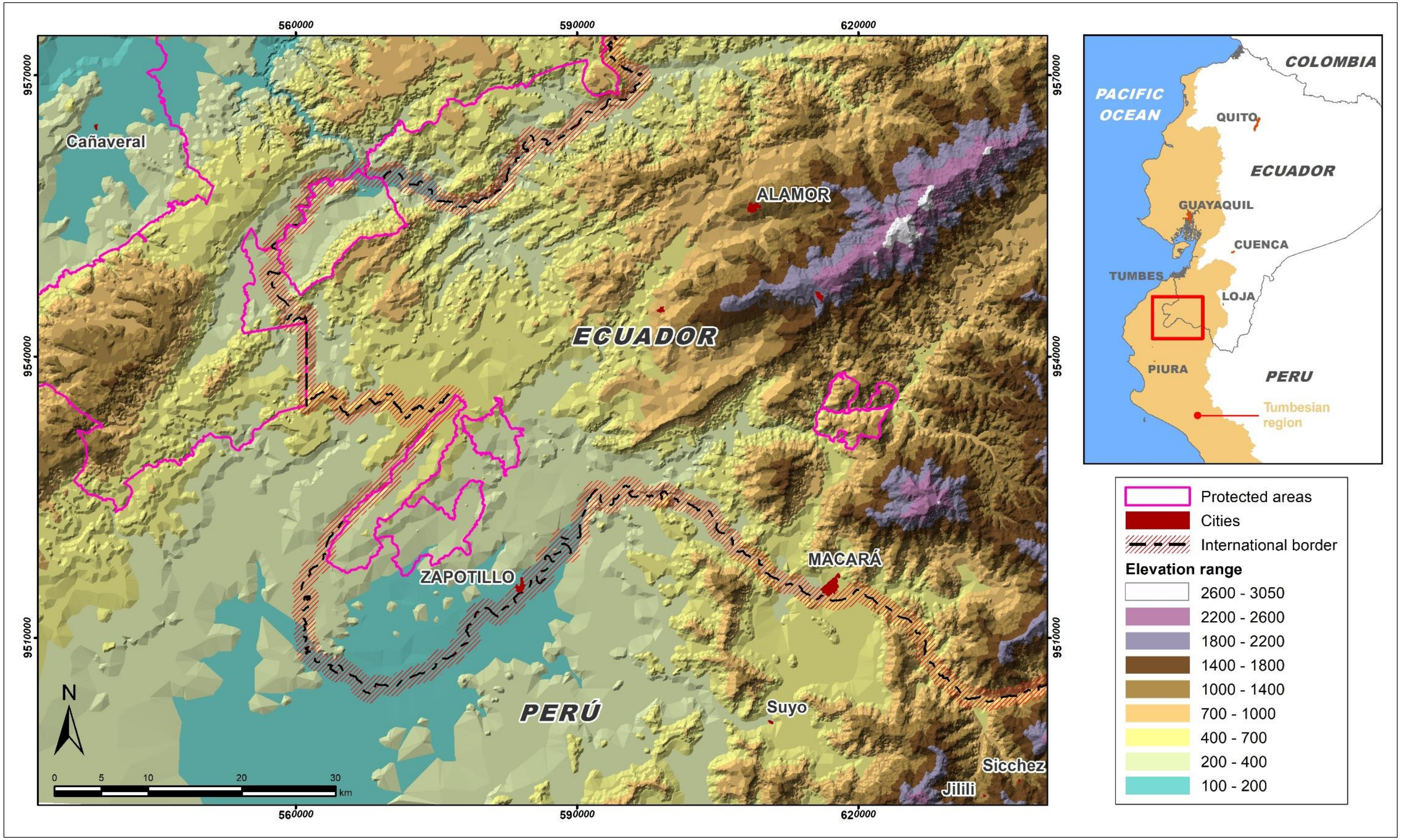


Figure 2. Map of elevation and protected areas of the research area.

Due to its volcanic and sedimentary origin, the soils in the region (Dodson, *et al.*, 1991) have a high agricultural potential. Since the seasonally dry forest occurs on fertile soils with a moderate to high pH level, good content of nutrients and low levels of aluminium, they are at high risk to be converted into agricultural land (Best, *et al.*, 1995; Linares-Palomino, *et al.*, 2011; Pennington, *et al.*, 2000).

3.1.3. Floristic composition

By compiling different studies and herbarium records, a total of 313 species in the dry forests of Ecuador and Peru were revealed, of which 184 belong to deciduous and semi–deciduous formations (Aguirre M., Linares-Palomino, & Kvist, 2006b; Linares-Palomino *et al.*, 2010).

According to (Espinosa *et al.*, 2011), the most abundant species in the Ecuadorian dry forests are *Simira ecuadorensis* (Rubiaceae), *Handroanthus chrysanthus* (Bignoniaceae) and *Eriotheca ruizii* (Malvaceae), which could be recorded in more than 40% of their inventory area. The research also recorded seven species listed as endangered: *Juglans neotropica* (Juglandaceae), *Siparuna eggersii* (Siparunaceae) both critically endangered and *Oreopanax rosei* (Araliaceae), *Verbesina pentantha* (Asteraceae), *Cavanillesia platanifolia* (Malvaceae), *Pradosia montana* (Sapotaceae) and *Erythrina smithiana* (Leguminosae).

Aguirre M. *et al*. (2009, 2006b) listed the following as characteristic species of the deciduous dry forest in the study area: *Ceiba trichistandra*, *Acacia macracantha*, *E. smithiana*, *Bouganvillea peruviana*, *Bursera graveolens*, *Loxopterygium huasango*, *Terminalia valverdeae*, *Handroanthus chrysanthus* and *Handroanthus billbergii*. For the semi–deciduous dry forest they reported: *Triplaris cumingiana*, *Bauhinia aculeata*, *Caesalpinia glabrata, Centrolobium ochroxylum*, *Machaerium millei*, *Cochlospermum vitifolium*, *Gallesia integrifolia*, *Delostoma integrifolium*, *Pisonia aculeata* and *Senna mollisima*.

Some endemic species to Ecuador and Peru have been recorded: *Mauria membranifolia*, *Ficus jacobii*, *Fulcaldea laurifolia*, *Armatocereus godingianus subsp. brevispinus*, *Coccoloba ruiziana*, *Mauria membranifolia*, *Handroanthus bilbergii*, *Tecoma weberbaueriana*, *Carica parviflora*, *Armatocereus cartwrightianus*, *Erythroxylum glaucum* and others (Aguirre-Mendoza, Linares-Palomino, *et al.*, 2006b). Nevertheless, several of them have been exposed to strong extraction processes in the past.

3.1.4. Threats

3.1.4.1. Deforestation and land use changes

Similar to the findings stated by Kalacska *et al*. (2005) and Sanchez-Azofeifa & Portillo-Quintero (2011) about other tropical dry ecosystems, agricultural land–use has been identified as the activity which does the most harm to the dry forest in the Tumbesian region. (Espinosa, *et al.*, 2012; Ochoa M., 2018).

In only three decades the natural cover in the study area changed dramatically: Tapia-Armijos *et al.* (2015) reported a deforestation rate of 33% for seasonally dry forest between 1978 and 2008. The land was mainly converted into pastures or corn, rice and onion crops.

In addition, the increasing clearing of new areas to make space for crop plantations in the region still continues (Tapia-Armijos, *et al.*, 2015). It is expected that changes in land–use due to the Zapotillo irrigation system will be growing, because until 2020 only 40% of total projected area had been really irrigated (Sistema de riego Zapotillo, 2020).

Furthermore, legal and illegal selective logging continues (Leal-Pinedo, *et al.*, 2005). There has been a substantial decrease thanks to the creation of private reserves promoted by the governmental conservation program Socio Bosque and more recently by the recognition of the 'Bosques de Paz' Transboundary Biosphere Reserve (Ministerio de Ambiente del Ecuador, 2015).

3.1.4.2. Grazing Livestock

Breeding of domestic animals and agriculture are the most important economic activities in the study area (Hurtado, 2015). Goats, donkeys, horses, cattle and pigs usually have poor or inexistent management: goats are the largest group. They stay in the forest to feed during the days and are in corrals only at night. Cattle, donkeys and horses stay permanently in the forest and move between the lower and higher parts of the area depending on grass availability; pigs only remain at the pens for at least two weeks before being slaughtered.

The research about the effects that animals have on the forest, especially on natural regeneration, is poor. The mechanisms to regulate the presence of these animals in the forest or their management has not yet been established (Aguirre-Mendoza, *et al.*, 2005; Hurtado, 2015). That is why traditional breeding in the forest is the most popular option in the region and the knowledge about its impacts is still underdeveloped.

3.1.4.3. Climate change

A recent study conducted in southern Ecuador by Eguiguren-Velepucha *et al*. (2016) evaluated the effects of climate change up to the year 2050 under two scenarios (Representative Concentration Pathway – RCP 2.6 and RCP 8.5). This research revealed an increase in the annual average temperature of 1.46°C in the RCP 2.6 scenario and 2.37°C in the RCP 8.5 scenario and an increase in annual rainfall in both scenarios, mainly affecting the deciduous formation in the study area. In the best case, these changes would only cause a displacement of the borders of both species and ecosystems (Feeley, *et al.*, 2011).

Under the RCP 2.6 scenario, 42% of the deciduous dry forest revealed moderate vulnerability and 58 % low vulnerability (the research cited used five categories of vulnerability: very low, low, moderate, high and very high); for the semi–deciduous dry forest, 74% and 24% were categorized as moderate and low vulnerability respectively. In the RCP 8.5 scenario, the vulnerability is of real concern because 73% of the deciduous and 85% of the semi–deciduous formation were identified to be highly vulnerable (Eguiguren-Velepucha, *et al.*, 2016).

3.2. Sampling design and data collection

Based on the information provided by Aguirre-Mendoza *et al*. (2006a), Lozano (2002) and Cueva & Chalán (2010), the study area was separated into strata in order to cover a broad range of the structural variation. In the inventory, two formations (deciduous and semi-deciduous) and three forest density levels (dense, semi-dense and sparse) in each formation were considered. This resulted in six strata (Figure 3), which were considered to equivalently represent most of the forest variability in the study area (Cueva O. *et al.*, 2019).

In every stratum, four inventory clusters comprising three plots of 60 m × 60 m, each with a nested subplot of 20 m × 20 m were established in an L-shape (Figure 4) and randomly distributed, as described in the methodology of the National Forestry Assessment of Ecuador (Cueva, *et al.*, 2012). Thus, 24 clusters (20 in Ecuador and four in Peru) containing 72 plots were inventoried, which altogether covered 25.92 ha (Cueva O. *et al*., 2019).

In the 60 × 60 m plots, all trees with a diameter at breast height (DBH) ≥10 cm were inventoried. Within the nested subplots, we also registered trees between 5 and 10 cm DBH and shrubs ≥5 cm DBH (Cueva O. *et al*., 2019). In all plots and subplots, all trees and shrubs were codified, and their species, DBH, total height and location in the plot were recorded. The species were identified in the field, and where necessary, botanical samples were collected for identification in the herbarium of the Universidad Técnica Particular de Loja (UTPL). The scientific names were reviewed and corrected according to The Plant List (2013).

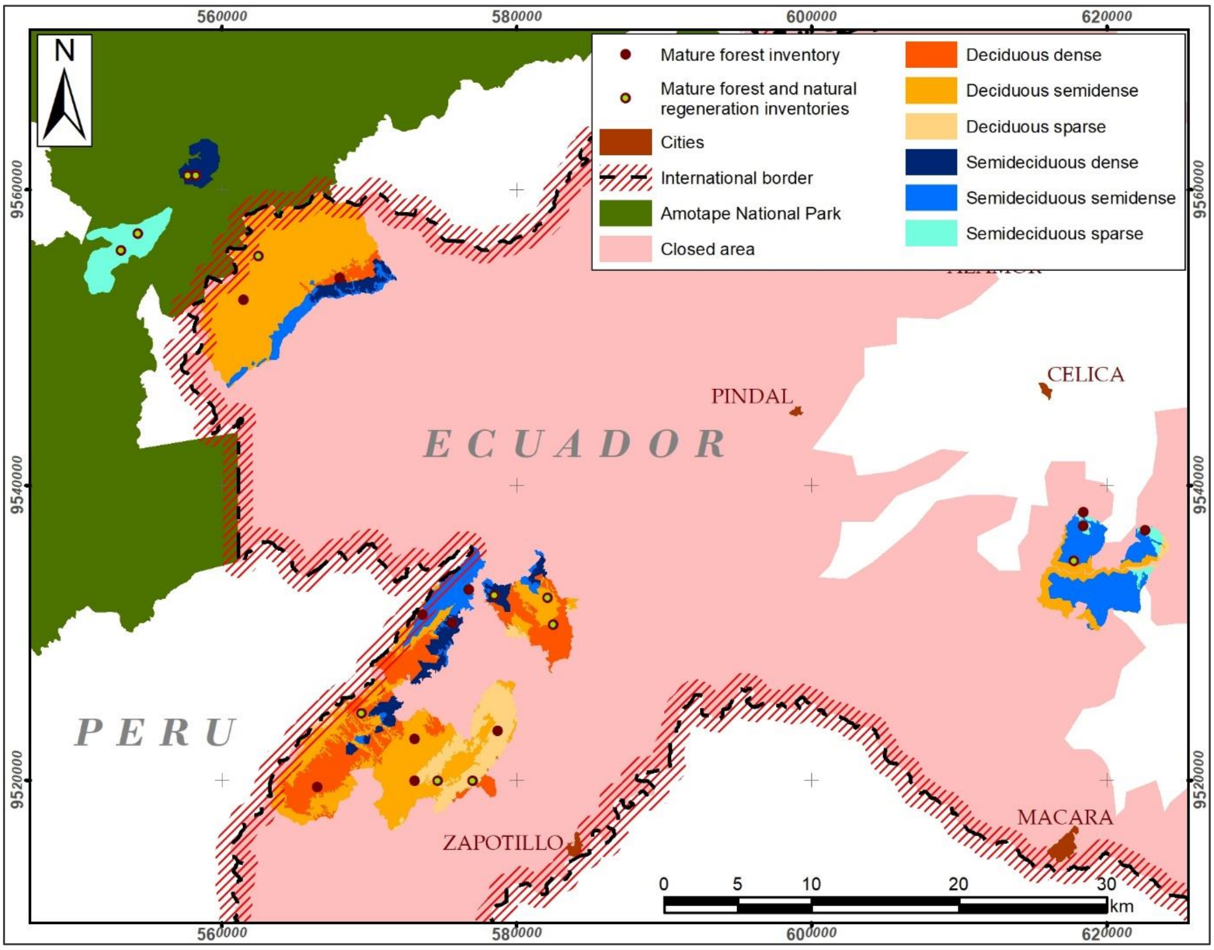


Figure 3. Stratification of the study area and locations of the plots.

Also nested in the 20 m × 20 m subplots, four 2 × 2 m sub–subplots (Figure 4) were installed to collect natural regeneration data. After the first regeneration inventory, 12 clusters were selected from a matrix of high, medium and low regeneration abundances and species diversity. In all 12 selected clusters, additional sub–subplots were installed afterward and fenced (four per large plot) (Figure 4), resulting in four unfenced and four fenced sub–subplots per large plot (288 sub–subplots in total: 144 fenced and 144 unfenced). Since the distance between the sub–subplots was only 16 m, and no variability was perceptible, they were grouped and treated as a single sample (Figure 4). Thus, 12 clusters (8 in Ecuador and 4 in Peru) containing 72 samples (36 per treatment) over a total area of 1,152 m^2 were used to assess natural regeneration (Cueva O. *et al*., 2020).

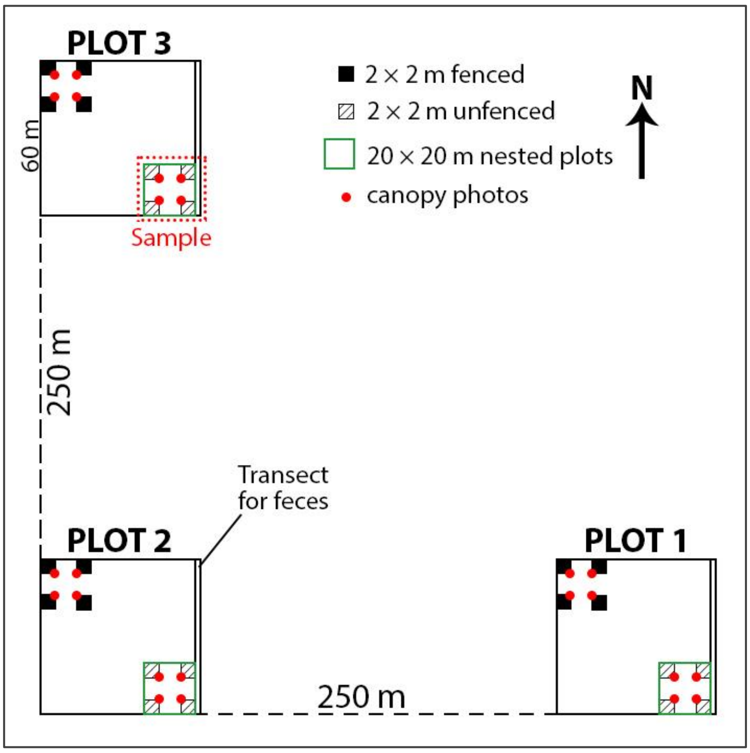


Figure 4. Diagram of the cluster design.

In the course of the study period of almost two years, five surveys (Dec. 2014, Jul. 2015, Jan. 2016, May 2016 and Nov. 2016) in the unfenced plots and four surveys in the fenced plots were simultaneously carried out (except Dec. 2014). In each survey, all seedlings of trees and shrubs that were >5 cm tall were identified and recorded. In addition, from the second survey onwards, all dead seedlings were recorded and all recruited seedlings were labelled. Thus, from the third survey onwards mortality and recruitment of saplings could be computed (Cueva O., *et al.*, 2020).

Furthermore, we collected and weighted the excrement of livestock within a 1 m × 60 m transect along the eastern edge of each plot (Figure 4). The excrements were dried and weighted to use the information as an indicator of grazing intensity (see Table 1).

3.3. External sources

WorldClim.org (Fick, *et al.*, 2017; Hijmans, *et al.*, 2005) was the primary source for obtaining abiotic variables. Temperature, precipitation and several related variants were used in the two publications as shown in table 1. The dataset had an approximate spatial resolution of 1 × 1 km.

Soil information was obtained from three sources: SoilGrids.org (Hengl *et al.*, 2014; Shangguan *et al.*, 2017) from which three topographical variables were used (soil classification, depth to bedrock and soil organic carbon stock); the Geopedological Map of Zapotillo and Celica of the Instituto Espacial Ecuatoriano (Instituto Espacial Ecuatoriano, 2018), from which the predictors organic material (OM), soil depth (SDepth), drainage (Drain), stoniness (Ston) and texture (Text) were used; and the Soil Classification Map of the Oficina Nacional de Evaluación de Recursos Naturales (ONERN), (2015) to identify the soil types for the Peruvian part. Unfortunately, this map does not include specific information about the soil characteristics, so they were assumed to be identical to those of the same soil type in the nearest localities on the Ecuadorian side.

The complete list of variables considered in this study and how they were used in each document is shown in table 1.

Table 1. Variables used by topics. Superscript numbers in the code correspond to how they were used by publication. The units in which the variables were expressed are in square brackets. Additional information about the variable is mentioned in parentheses. The letters in the source mean: a = generated in this research; b = Worlclim.org; c = Instituto Espacial Ecuatoriano (Cueva O., *et al.*, 2020, 2019).

Variable	Code	Pub. 1	Pub. 2	Source
Treatment				
Treatment: fenced and unfenced plots [open; exclude]	Treat^{2}		×	a
Biotic				
Dry feces of goats [gr]	Goats$^{1-2}$	×	×	a
Dry feces of cattle [gr]	Cattle$^{1-2}$	×	×	a
Dry feces of horses and donkeys [gr]	Equine$^{1-2}$	×	×	a
Human Pressure Index [index]	HPI$^{1-2}$	×	×	a
Canopy coverage [%]	Canp^{2}		×	a
Abiotic				
Annual mean temperature [ºC]	Temper^{1} - MTemp^{2}	×	×	b
Annual precipitation [mm]	Ann.Prec^{1}	×		b
Precipitation of wettest month [mm]	Mth.Prec^{1}	×		b
Precipitation seasonality (periods) [mm]	SPrec^{2}		×	b
Altitude of plot above sea level [m]	Altitude^{1} - Alt^{2}	×	×	a
Soil				
Soil organic content [Low; medium; high]	OM^{2}		×	c
Effective soil depth [0–10; 11–20; 21–50; 51–100; >100 cm]	Soil.depth^{1} - SDepth^{2}	×	×	c
Drainage [Good; moderate; poor]	Drainage^{1} - Drain^{2}	×	×	c
Stoniness [Without; very few; few; frequent; abundant]	Stoniness^{1} - Ston^{2}	×	×	c
Texture [Loam; sandy loam; clay loam; clay–sandy loam]	Texture^{1} - Text^{2}	×	×	c

4. Methods

4.1. Data Processing

The data processing before the statistical analyses has been described in detail in Cueva O., *et al.*, (2020, 2019). The following is a brief overview.

As a measure of the anthropogenic impact intensity due to activities such as wood extraction, fruit or plants gathering, human or livestock trampling and so on, the Hegyi's competition index (Hegyi, 1974) was adapted to compute the Human Pressure Index (HPI), which was defined as shown in equation 1.

$$\text{HPI} = \sum_{i=1}^{n} \frac{F_i}{B \times dist_i}. \qquad \text{(Eq. 1)}$$

F_i = number of families in the *ith* neighbouring village;

B = total basal area of trees and shrubs per plot projected to hectares (m^2/ha);

$dist_i$ = horizontal distance from the *ith* neighbouring village to the studied plot (m);

For the calculation, all neighbouring villages within a distance of 3 km around each plot were taken into account. To avoid a circular argument, the basal area was excluded from the HPI when assessing the number of individuals and the basal area (Cueva O. *et al.*, 2019).

Species richness was calculated as the total number of species of trees and shrubs in each plot. Diversity was calculated using the Simpson reciprocal index (Magurran, 2004). Abundance was obtained by counting the individuals per plot. However, to correct for the different plot sizes, the numbers of individuals were projected to the number of individuals per hectare before adding the numbers of shrubs. For natural regeneration, individuals were counting per sample, treatment and survey and it was projected to one hectare.

How individuals were distributed by diametric classes was obtained by using the records of the 24 clusters (72 plots). In addition, the distribution of 6 species was drawn up since, due to their use, they were considered as indicators of anthropogenic activities: *Ceiba trischistandra, Cavanillesia platanifolia, Bursera graveolens, Loxopterygium huasango, Handroanthus chrysanthus* and *Piscidia carthagenensis*.

Species similarity was obtained among plots within the same cluster, and it was determined by the Sørensen index (Magurran, 2004) using the "vegan" package (Oksanen, *et al.*, 2018) for R.

Mortality of the natural regeneration was computed as a percentage by relating the number of dead individuals from a survey to the total number of alive individuals from the previous survey. The recruitment rate was obtained by calculating the percentage of recruited individuals in a survey related to the total number of individuals in the same survey.

The images to calculate the canopy coverage were processed by Geigl (2018) using Gap Light Analyzer v2.0 software (Frazer, *et al.*, 1999). Canopy coverage was computed as a percentage, and the average of the four sub–subplots (fenced and unfenced plots were averaged separately) was used for each sample.

4.2. Analyses of factors affecting the conditions in mature forest and natural regeneration

Generalized linear mixed models (GLMMs) and linear mixed models (LMMs) (Bates *et al.* 2015; Bolker *et al.*, 2009; Cayuela, 2014; Seoane, 2014) were used to determine whether the mature forest and natural regeneration parameters are affected by biotic, abiotic, soil and treatment predictor variables. 12 predictor variables for mature forest and 14 for natural regeneration were used (Table 1).

Pearson's correlation coefficient was calculated for all combinations of variables. To avoid collinearity in model building, strongly correlated variables were not included in the same model. Furthermore, overfitting was avoided by limiting the number of variables in any model to five (Neo *et al.*, 2017).

86 candidate models were built to evaluate all mature forest parameters; 186 for diversity and abundance parameters of the natural regeneration and 13 candidate models were built for assessing the dynamic parameter of natural regeneration (See supplementary information (SI) Table 1, SI Table 2 and SI Table 3).

Formation and cluster were considered as random effects (plots were nested within clusters, and clusters were nested within formations). When natural regeneration was assessed, time was included as a random slope to account for the repeated measures.

The influence of predictor variables on species richness in both the mature forest and for natural regeneration was estimated using GLMMs with the Poisson error distribution and Laplace approximation (Bolker *et al.*, 2011, 2009; Cayuela, 2014; Di Rienzo *et al.* 2017; Neo *et al.*, 2017; Seoane, 2014). Species similarity, diversity (for the mature forest and natural regeneration), abundance in the mature forest and basal area were assessed via the restricted maximum likelihood approach (REML) (Bolker, *et al.*, 2009). Abundance of natural regeneration was assessed using the maximum likelihood approach with a negative binomial error distribution (Di Rienzo, *et al.*, 2017). The effects on mortality were assessed using the REML approach and Bayesian fitting to deal with singular fitting (Bolker, 2019b). Finally, the effect on recruitment was assessed using a GLMM with a Gaussian error distribution and link identity as 22% of the recruitment values were zeros (Bolker, 2019a).

Delta Akaike information criterion ($\Delta AIC < 2$) (Burnham, *et al.*, 2002) was used to select the best models selection. In all cases and for all selected models, the marginal and conditional variance (*R2m* and *R2c*, respectively) were computed to determine the proportion of the variance that was explained in each model (Nakagawa, *et al.*, 2013).

All analyses were performed in the R programming environment v3.4.0 and v3.5.3 (R Core Team, 2019).

Additional details about the procedures, R–packages used and more, can be found in Cueva O. *et al.* (2019) and Cueva O. *et al.* (2020).

5. Results

5.1. Forest characterization

We recorded a total of 117 species: 91 for mature trees and shrubs and 85 species for natural regeneration (Table 2). 83 species could be completely identified, 15 to genus level, 5 species only to family level and 14 could not be identified. In the inventory of mature forest 7,815 individuals were recorded as well as 7,791 different seedlings in all five surveys of natural regeneration. The identified species belong to 35 families: Leguminosae was the most diverse family with 25 species, Malvaceae had 9 species and 5 species belonged to Bignoniaceae and Apocynaceae.

Table 2. Families and species recorded in the mature forest and natural regeneration. Modified from Cueva O. *et al.*, (2019, 2020).

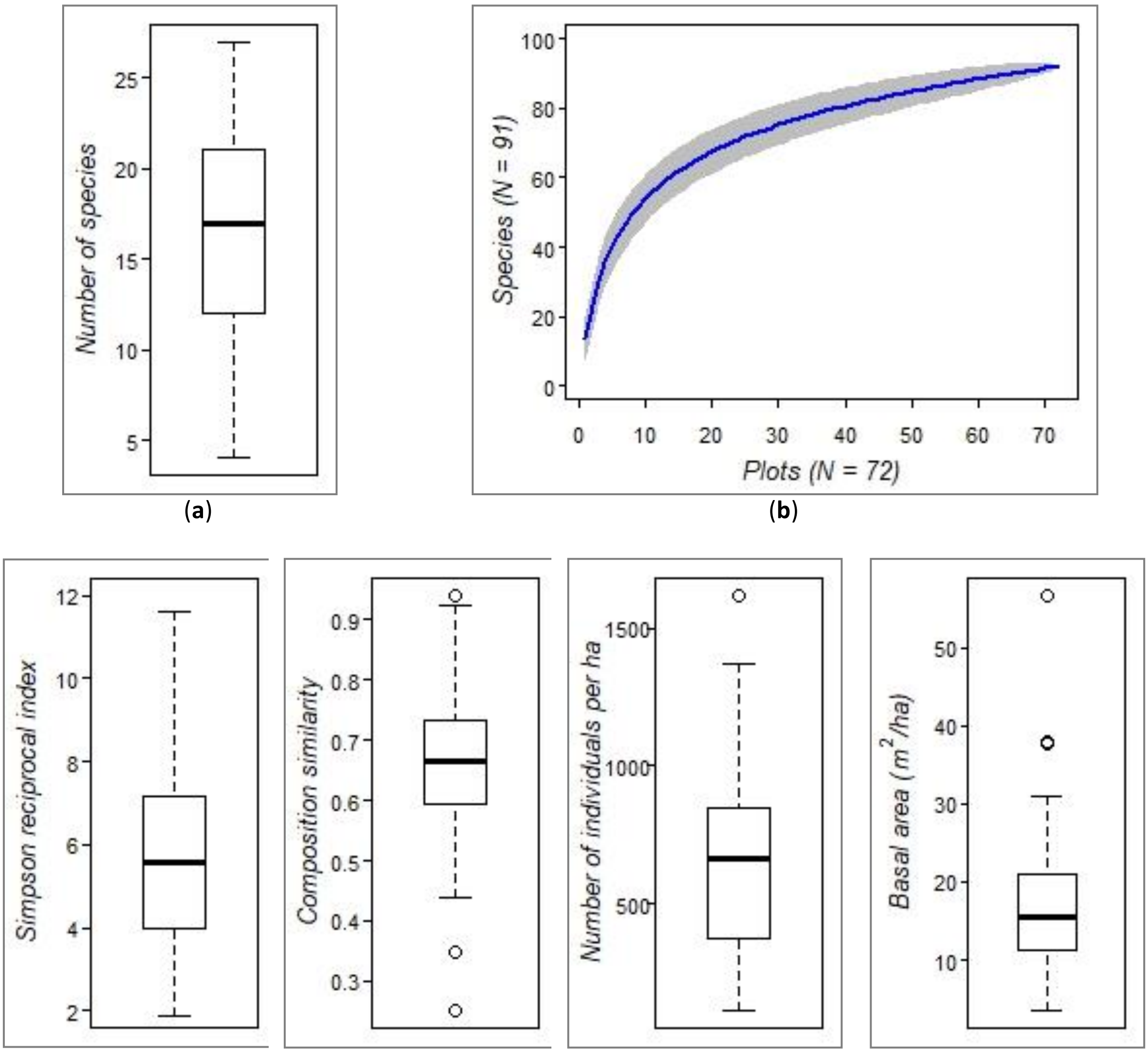
Family	Species	Trees + Shrubs	Nat Reg
Achatocarpaceae	*Achatocarpus pubescens* C. H. Wright	X	X
Anacardiaceae	*Loxopterygium huasango* Spruce ex Engl.	X	X
	Spondias purpurea L.	X	
Annonaceae	*Annona muricata* L.	X	
Apocynaceae	*Aspidosperma* sp.	X	X
	Aspidosperma sp. 2	X	X
	Prestonia mollis Kunth		X
	Rauvolfia tetraphylla L.		X
	Vallesia glabra (Cav.) Link		X
Asteraceae	*Fulcaldea laurifolia* (Bonpl.) Poir.	X	X
	Spp. 13		X
Bignoniaceae	*Anemopaegma* sp.	X	X
	Bignonia longiflora Cav.		X
	Handroanthus billbergii (Bureau & K.Schum.) S.O.Grose	X	X
	Handroanthus chrysanthus (Jacq.) S.O.Grose	X	X
	Tecoma stans (L.) Juss. ex Kunth	X	X
Bixaceae	*Cochlospermum vitifolium* (Willd.) Spreng.	X	X
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	X	X
	Cordia lutea Lam.	X	X
	Cordia macrantha Chodat	X	
	Cordia macrocephala (Desv.) Kunth		X
	Cordia sp.		X
Burseraceae	*Bursera graveolens* (Kunth) Triana & Planch.	X	X
Cactaceae	*Cereus diffusus* (Britton & Rose) Werderm.	X	
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg.	X	X
	Celtis loxensis C.C. Berg	X	X
Capparaceae	*Colicodendron scabridum* (Kunth) Seem	X	X
	Cynophalla flexuosa (L.) J.Presl	X	X
	Cynophalla sclerophylla (Iltis & Cornejo) Cornejo & Iltis		X
	Cynophalla sp.	X	

Family	Species	Trees + Shrubs	Nat Reg
Caricaceae	*Vasconcellea parviflora* A. DC.	X	X
Celastraceae	*Salacia* sp.	X	X
Combretaceae	*Terminalia valverdeae* A.H. Gentry	X	X
Convolvulaceae	*Ipomoea carnea* Jacq.		X
	Ipomoea pauciflora M. Martens & Galeotti	X	
	Ipomoea sp.	X	
	Ipomoea wolcottiana subsp. calodendron (O'Donell) McPherson		X
Erythroxylaceae	*Erythroxylum glaucum* O. E. Schulz	X	X
Euphorbiaceae	*Croton* sp.	X	X
	Hura crepitans L.		X
	Jatropha curcas L.	X	
	Spp. 5	X	
Leguminosae	*Acacia macracantha* Humb. & Bonpl. ex Willd.	X	X
	Albizia multiflora (Kunth) Barneby & J.W. Grimes	X	X
	Bauhinia aculeata L.	X	X
	Bauhinia sp.	X	X
	Caesalpinia glabrata Kunth	X	
	Caesalpinia spinosa (Molina) Kuntze	X	X
	Calliandra taxifolia (Kunth.) Benth.		X
	Centrolobium ochroxylum Rose ex Rudd	X	X
	Chloroleucon mangense (Jack.) Britton & Rose	X	X
	Erythrina velutina Willd.	X	X
	Geoffroea spinosa Jacq.	X	X
	Leucaena trichodes (Jacq.) Benth.	X	X
	Machaerium millei Standl.	X	X
	Mimosa acantholoba (Willd.) Poir.	X	X
	Mimosa pigra L.	X	
	Mimosa sp.	X	
	Myroxylon balsamum (L.) Harms.	X	
	Piptadenia flava (Spreng. ex DC.) Benth.	X	X
	Piscidia carthagenensis Jacq.	X	X
	Pithecellobium excelsum (Kunth) Mart.	X	X
	Prosopis juliflora (Sw.) DC.	X	X
	Senna bicapsularis (L.) Roxb.	X	
	Senna incarnata (Pav. & Benth.) H.S. Irwin & Barneby	X	X
	Senna mollissima (Willd.) H.S. Irwin & Barneby	X	
	Senna spectabilis (DC.) H.S. Irwin & Barneby.	X	
Malvaceae	*Byttneria* sp.		X
	Cavanillesia platanifolia (Bonpl.) Kunth	X	
	Ceiba insignis (Kunth) P.E. Gibbs & Semir	X	X
	Ceiba trischistandra (A.Gray) Bakh.	X	
	Eriotheca roseorum (Cuatrec.) A.Robyns	X	
	Eriotheca ruizii (K. Schum.) A. Robyns	X	X
	Guazuma ulmifolia Lam.	X	X

Family	Species	Trees + Shrubs	Nat Reg
	Malvastrum sp.		X
	Waltheria ovata Cav.		X
Meliaceae	*Trichilia hirta* L.	X	
Moraceae	*Ficus jacobii* Vázq. Avila	X	
	Ficus obtusifolia Kunth.	X	
	Maclura tinctoria (L.) Steud.	X	X
Muntingiaceae	*Muntingia calabura* L.	X	
Myrtaceae	*Psidium guajava* L.	X	X
	Psidium sp.	X	
	Spp. 1	X	
Nyctaginaceae	*Bougainvillea peruviana* Bonpl.	X	X
	Pisonia aculeata L.	X	X
	Pisonia floribunda Hook. F.	X	
	Spp. 3	X	
Opiliaceae	*Agonandra excelsa* Griseb.	X	X
Phytolaccaceae	*Gallesia integrifolia* (Spreng.) Harms	X	X
Piperaceae	*Piper* sp.		X
Polygonaceae	*Coccoloba ruiziana* Lindau	X	X
	Triplaris cumingiana Fisch. & C.A.Mey.	X	X
Rhamnaceae	*Ziziphus thyrsiflora* Benth.	X	X
Rubiaceae	*Phialanthus* sp.	X	
	Randia armata (Sw.) DC.	X	X
	Simira ecuadorensis (Standl.) Steyerm.	X	X
	Spp. 12		X
Salicaceae	*Prockia crucis* P. Browne ex L.	X	X
Sapindaceae	*Sapindus saponaria* L.	X	X
Solanaceae	*Acnistus arborescens* (L.) Schltdl	X	X
	Solanum albidum Dunal		X
Verbenaceae	*Citharexylum poeppigii* Walp	X	X
Unknown	Spp. 2	X	X
	Spp. 4	X	
	Spp. 6	X	
	Spp. 7	X	
	Spp. 8	X	
	Spp. 9	X	X
	Spp. 10		X
	Spp. 11		X
	Spp. 14		X
	Spp. 15		X
	Spp. 16		X
	Spp. 17		X
	Spp. 18		X
	Spp. 19		X
35	**117**	**91**	**85**

5.1.1. Mature forest

The number of species found per plot ranged between 4 and 27 species (Figure 5a). In the species accumulation curve (Figure 5b), it can be seen that 67% of the species were registered in 15 plots and 90% in 45 plots. The Simpson reciprocal indices ranged from 1.88 to 11.59 (Figure 5c).



(**a**) (**b**)

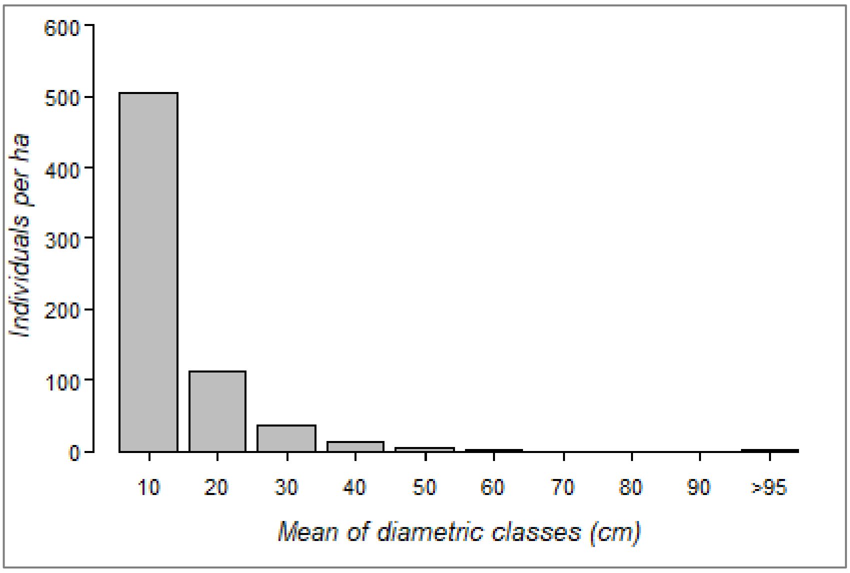
(c) **(d)** **(e)** **(f)**

Figure 5. Diversity and structural situation of the mature forest in the study area: (a, c–f) ranges of the different parameters in the plots; (b) species accumulation curve obtained via the Coleman method with confidence of 95% (grey buffer). Taken from Cueva O., *et al.* (2019).

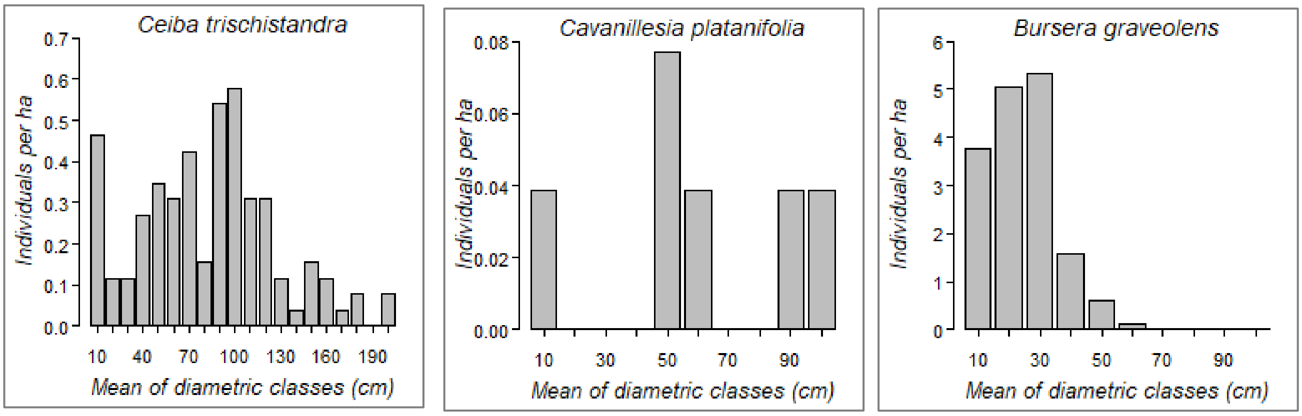
In most clusters, Sørensen indices showed a mean of 0.65 (see Figure 5d), which indicate high composition similarity among the plots in each cluster and can be explained by its close proximity. Overall, the structural parameters of the mature forest were found to be quite diverse. The number of individuals per hectare ranged from 108 individuals in plots located in sparse forests to 1620 individuals per hectare in forests with higher individuals' density (Figure 5e). The average DBH ranged from 15.2 to 33 cm, the basal area from 3.5 to 56.7 m^2 per hectare (Figure 5f).

The diameter frequency distribution of all individuals followed a negative exponential relationship, as expected in natural forests (Figure 6a). However, some characteristic species show a behaviour that distinctly deviates from this trend: e.g., *Ceiba trichistandra* and *Cavanillesia platanifolia* don't reach one individual/ha. In the best, the mid-ranges held the highest with 0.6 individuals/ha (85–105 cm DBH) and 0.08 (45–55 cm DBH) respectively, practically no individuals of these two species were found in the higher dbh–classes (Figures 6b, c).

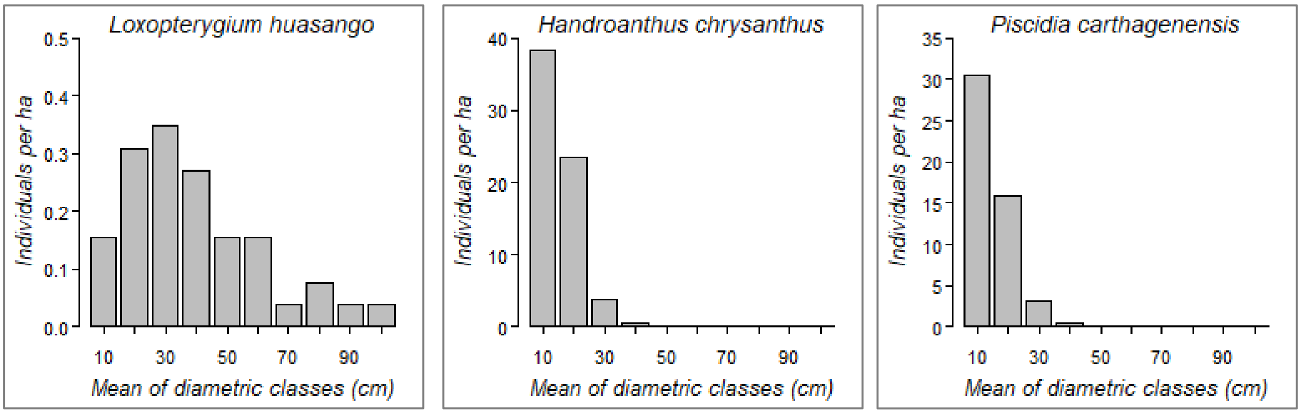
Bursera graveolens and *Loxopterygium huasango* Spruce ex Engl. showed most individuals in the range 25–35 cm DBH (Figure 6d–e). No individuals of *Handroanthus chrysanthus* and *Piscidia carthagenensis* with DBH >45 cm were found (Figure 6f, g), probably because the bigger trees were already harvested.



(a)



(b) (c) (d)

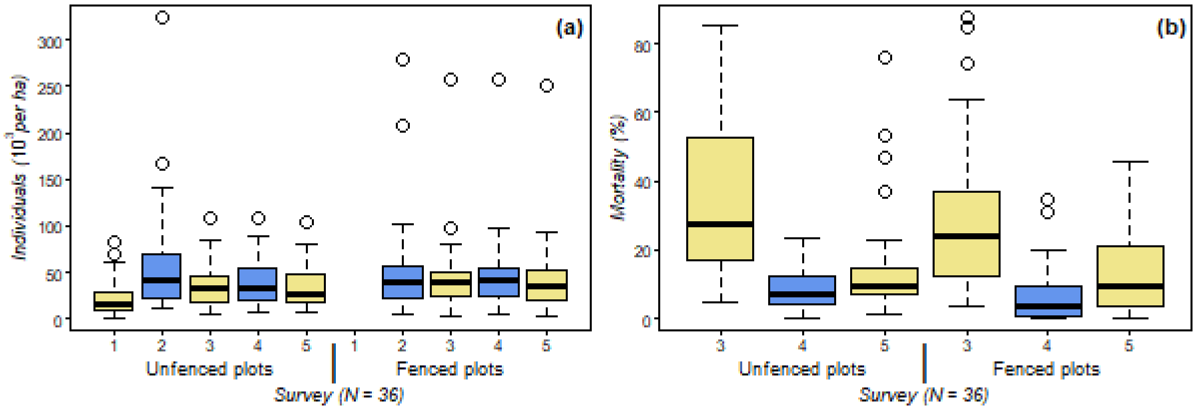


(e) (f) (g)

Figure 6. Diameter class distributions of individuals per ha: (a) all species; (b–g) distributions of selected species. Taken from Cueva O. *et al.* (2019). Considering that *C. trichistandra* regularly reach the largest diameters in the forest, the figure b was modified with respect to the other ones to conveniently cover its real distribution range.

5.1.2. Natural regeneration

In the evaluated area, the total number of individuals recorded in fenced and unfenced plots were: 6,280; 4,751; 5,069 and 4,572 individuals in surveys 2, 3, 4 and 5 respectively. The average number of seedlings per plot referred to the hectare, and survey number ranged from 21,900 to 57,200 individuals in unfenced plots and from 43,500 to 51,800 individuals per ha in fenced plots (Figure 7a). Evidently, the average abundance decreased slightly from the rainy season to the dry season. This seasonal effect was less pronounced in the fenced plots than in the unfenced plots due to a lower dry season mortality (Figure 7b), resulting in similar numbers of individuals occurring in the two seasons (median number of individuals per ha = 35,300–41,200 in fenced plots and 26,900–40,600 in unfenced plots).



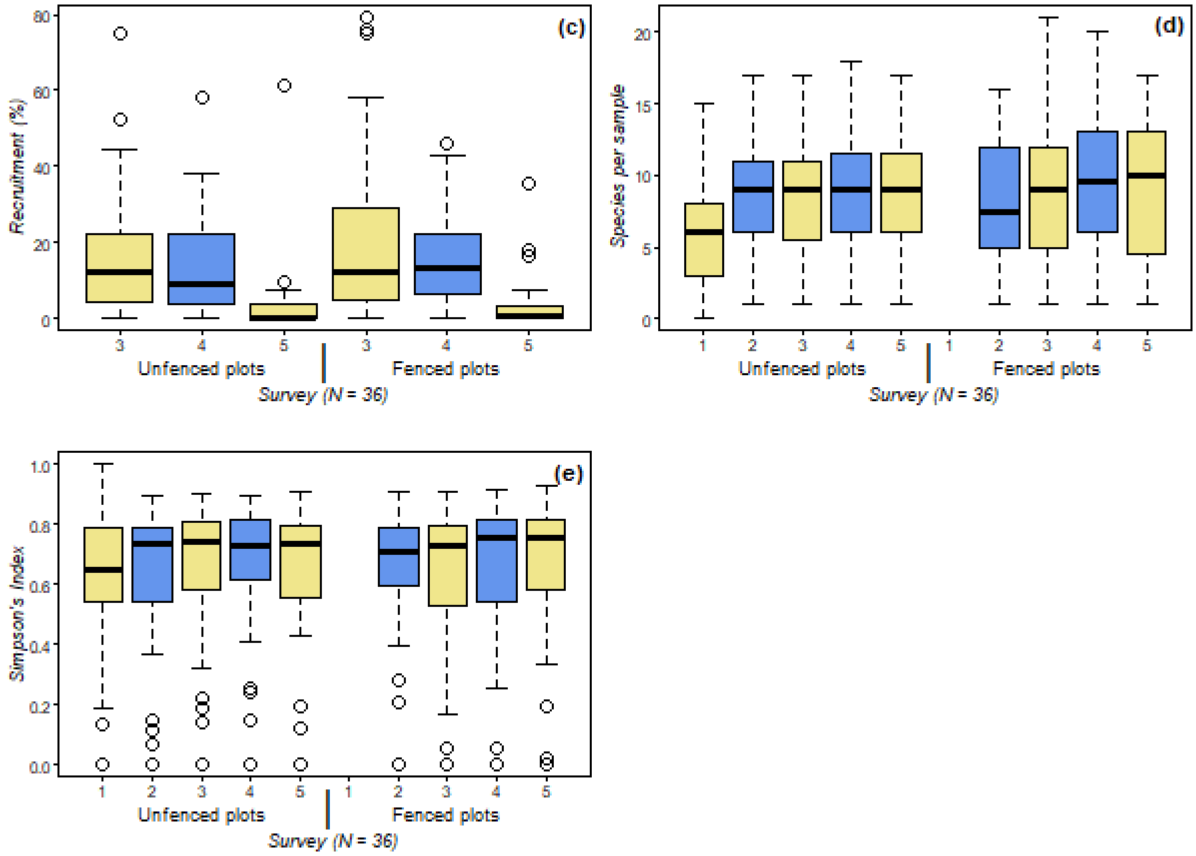


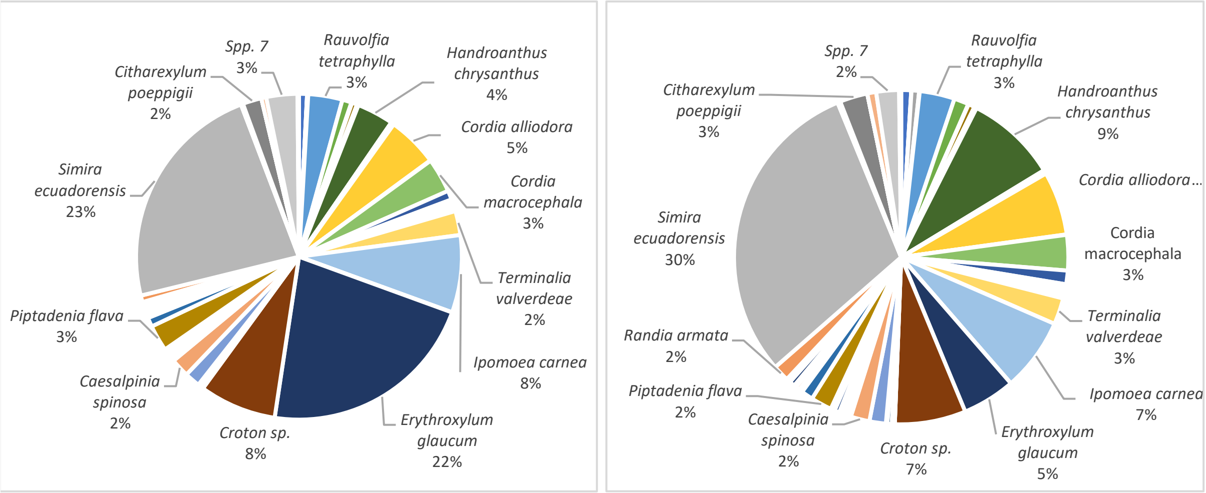
Figure 7. Natural regeneration parameters over time and treatment. (a) Abundance, (b) mortality, (c) recruitment, (d) species richness and (e) diversity of seedlings per survey in unfenced and fenced plots. Fenced plots were not assessed in survey 1 because they were selected based on the first evaluation of the unfenced plots. Numbers from 1 to 5 correspond to consecutive surveys (1 = 0 months; 2 = 7; 3 = 14; 4 = 17; 5 = 23). Yellow = dry season, blue = rainy season. Taken from Cueva O. et al. (2020).

In the first rainy season, *Simira ecuadorensis* and *Erythroxylum glaucum* had the highest abundances in the entire study area (12,560 and 11,900 individuals/ha, respectively. Figure 8a). *S. ecuadorensis* showed good resistance to the dry season, with 13,550 individuals/ha recorded in the final survey. In contrast, most *E. glaucum* individuals died during the dry season, with only 2,300 individuals/ha recorded alive in the final survey (Figure 8b).

The results show that the mortality of plants was highly influenced by seasonality, increasing from an average of 9.0% in the rainy season to 35.8% in the dry season. This pattern was observed across both treatments (Figure 7b). However, mortality was slightly lower in the fenced plots than in the unfenced plots. Substantial recruitment was recorded in the fenced plots in surveys 3 and 4 (21.4% and 16.6%, respectively), whereas recruitment was very low (3.1%) in the final survey. In the unfenced plots, recruitment decreased over time from 16.1% to 3.7%, even during the rainy season (Figure 7c).

The number of species remained almost the same across surveys 2 to 5 in the unfenced plots (mean = 8.8, 8.6, 9.1 and 8.7 species per plot, respectively) but showed a slight increase over time in the fenced plots (mean = 8.4, 8.8, 9.6 and 9.4 species per plot) (Figure 7d). A similar pattern was also observed for the Simpson's index, which had mean values ranging from 0.62 in survey 1 to 0.67 in survey 4 for the unfenced plots and 0.62 in survey 3 to 0.66 in survey 4 for the fenced plots (Figure 7e).

It should be emphasized that during the evaluation, zero seedlings were recorded for some of the characteristic species of the study area, including *Ceiba trischistandra*, *Cavanillesia platanifolia*, *Eriotheca roseorum* and *Myroxylon balsamum*. For other prominent species, such as *Centrolobium ochroxylum* and *Loxopterygium huasango*, only a few individuals (1 and 2 respectively) were recorded.



(a) (b)

Figure 8. Comparison of species' abundance between surveys 2 and 5. Only the most abundant species were tagged. (a) Abundances' distribution in survey 2; (b) Abundances' distribution in survey 5.

5.2. Drivers of the modification of the dry forest

5.2.1. Effects of pressure factors on mature forest

Table 3 shows the best models for each response variable of the mature forest together with all models with ΔAICs <2. The anthropogenic variables (HPI and livestock) and precipitation evidently had a strong influence on all analysed parameters of the mature forest. In all cases, the explained variance by fixed + random effects ranged from 27% to 63%.

Table 3. Best models explaining the influence of biotic and abiotic factors on the response variables of mature forest. df = degrees of freedom; AIC = Akaike's information criterion; ΔAIC = Delta Akaike's information criterion; *R2m* = marginal variance explained by fixed effects; *R2c* = conditional variance explained by random and fixed effects. In models with HPI.BA, the basal area of trees and shrubs was included in the human pressure index.

Model	df	AIC	ΔAIC	*R2m*	*R2c*
Species richness					
~1 + HPI.BA + Ann.Prec	4	412.44	0.00	0.26	0.63
~1 + HPI.BA	3	413.38	0.95	0.21	0.63
~1 + Goats + HPI.BA + Ann.Prec	5	414.33	1.89	0.26	0.63
~1 + Equine + HPI.BA + Ann.Prec	5	414.34	1.90	0.26	0.63
~1 + Cattle + HPI.BA + Ann.Prec	5	414.38	1.94	0.26	0.63
Diversity					
~1 + Goats + Cattle + Equine + HPI.BA + Ann.Prec	8	282.50	0.00	0.28	0.31
~1 + Goats + Ann.Prec + Drainage	7	282.66	0.17	0.31	0.37
~1 + Goats + Cattle + HPI.BA + Ann.Prec	7	282.67	0.17	0.27	0.32
~1 + Goats + Equine + HPI.BA + Ann.Prec	7	283.61	1.11	0.31	0.31
~1 + Goats + HPI.BA + Ann.Prec	6	283.81	1.31	0.30	0.31
~1 + Cattle + Equine + HPI.BA + Ann.Prec	7	284.48	1.99	0.27	0.31
Similarity of species composition					
~1 + HPI.BA + Ann.Prec	5	-69.54	0.00	0.17	0.29
~1 + HPI.BA	4	-68.74	0.80	0.10	0.27
~1 + Temper + Mth.Prec	5	-68.19	1.35	0.08	0.31
~1 + Ann.Prec	4	-67.88	1.66	0.11	0.30
Number of individuals					
~1 + Goats + Cattle + HPI + Stoniness	7	959.85	0.00	0.20	0.54
~1 + Goats + Equine + HPI + Stoniness	7	960.57	0.72	0.20	0.54
~1 + Cattle + Equine + HPI + Stoniness	7	961.42	1.58	0.19	0.54
Basal area					
~1 + Temper + Mth.Prec	5	-25.59	0.00	0.17	0.36
~1 + HPI + Ann.Prec	5	-25.16	0.43	0.23	0.33
~1 + Temper	4	-24.71	0.89	0.12	0.35
~1 + Equine + HPI + Ann.Prec	6	-23.60	1.99	0.26	0.35

Species richness

The species richness in mature forests is highly influenced by the HPI, the annual precipitation and the livestock. As inferred from table 3, these factors were respectively present in 5, 4 and 3 of the best models.

HPI negatively influenced the species richness of the mature forest in a significant way (Table 4, Figure 9a). In contrast, annual precipitation exerted a positive but non–significant influence (Table 4, Figure 9b).

Table 4. Influence of predictors included in the best models on structure and diversity of the mature forest. According to GLMM, n = 72.

Predictor	Estimate	Std. Error	p (<0.05)	
Species richness				
HPI.BA	-7.82	2.22	2.4×10^{-4}	***
Ann.Prec	0.77	0.44	0.09	†
Diversity				
Goats	1.78	1.83	0.33	
Cattle	-1.28	1.17	0.40	
Equine	0.55	1.03	0.49	
HPI.BA	-20.38	9.34	0.03	*
Ann.Prec	7.74	1.72	1.2×10^{-5}	***
Species similarity				
HPI.BA	-0.31	0.13	0.02	*
Ann.Prec	-0.64	0.30	0.03	*
Number of individuals				
Goats	-205.80	266.51	0.42	
Cattle	-143.93	162.62	0.37	
HPI	-2411.17	777.20	2.9×10^{-3}	**
Stoniness	-20.67	32.84	0.50	
Basal area				
Temper	-4.92	2.06	0.02	*
Mth.Prec	0.67	0.39	0.07	†

*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; † = $p < 0.1$

Diversity index

The diversity index was influenced by livestock, HPI and annual precipitation (Table 3). Six models with ΔAIC <2 were selected. Five of which included goats, three models included horses and donkeys and two models featured cattle. The negative effect of HPI (Table 4, Figure 9c) is linked to the distance between forests and villages. In forests separated from villages, a higher diversity was observed than in forests close to villages. Furthermore, the village population affected the diversity as well: forests near villages with fewer families were more diverse than those near crowded villages.

Annual precipitation exerted a significant positive influence on the diversity index (Table 4). Thus, wetter sites were more diverse than drier ones (Figure 9d).

Additional predictors in the best model did not significantly influence the diversity. Cattle revealed a negative influence on diversity (Table 4, Figure 9e), while goats and horses showed a positive influence (Table 4, Figures 9f and 9g respectively).

One extreme value of goat excrement (Figure 9f) strongly influenced species diversity in our model. After replacing this high value with the average and re-standardizing the variable, the effect of goat excrements became negative but remained non–significant (Estimate (E) = –0.4684, p-value (p)

= 0.73037). Nevertheless, no authoritative reason to remove the extremity was found because it was not an outlier; instead, the value reflects a common situation in areas near goat paddocks.

Soil predictors scarcely affected species richness and diversity of the mature forest in the study area. Soil drainage presented a positive impact (E = 0.09505, p = 0.8239443) in the second-best diversity model with a high goodness of fit (ΔAIC = 0.16825).

Similarity of species composition

Similarity of the species composition was mainly affected by HPI and annual precipitation (Table 3). These two predictors were included in the best model both wielding significant negative effects (Table 4). The species composition across the plots was more heterogenous when the HPI increased, which was strange considering the fact that heterogeneous forests are expected to become more homogeneous with an increase in anthropogenic interventions. Nevertheless, keeping in mind that the similarity index represents the species similarity among nearby plots (with a distance of 160m between each other), the increase in heterogeneity caused by HPI might be explained by a direct intervention that affects only one plot in the cluster.

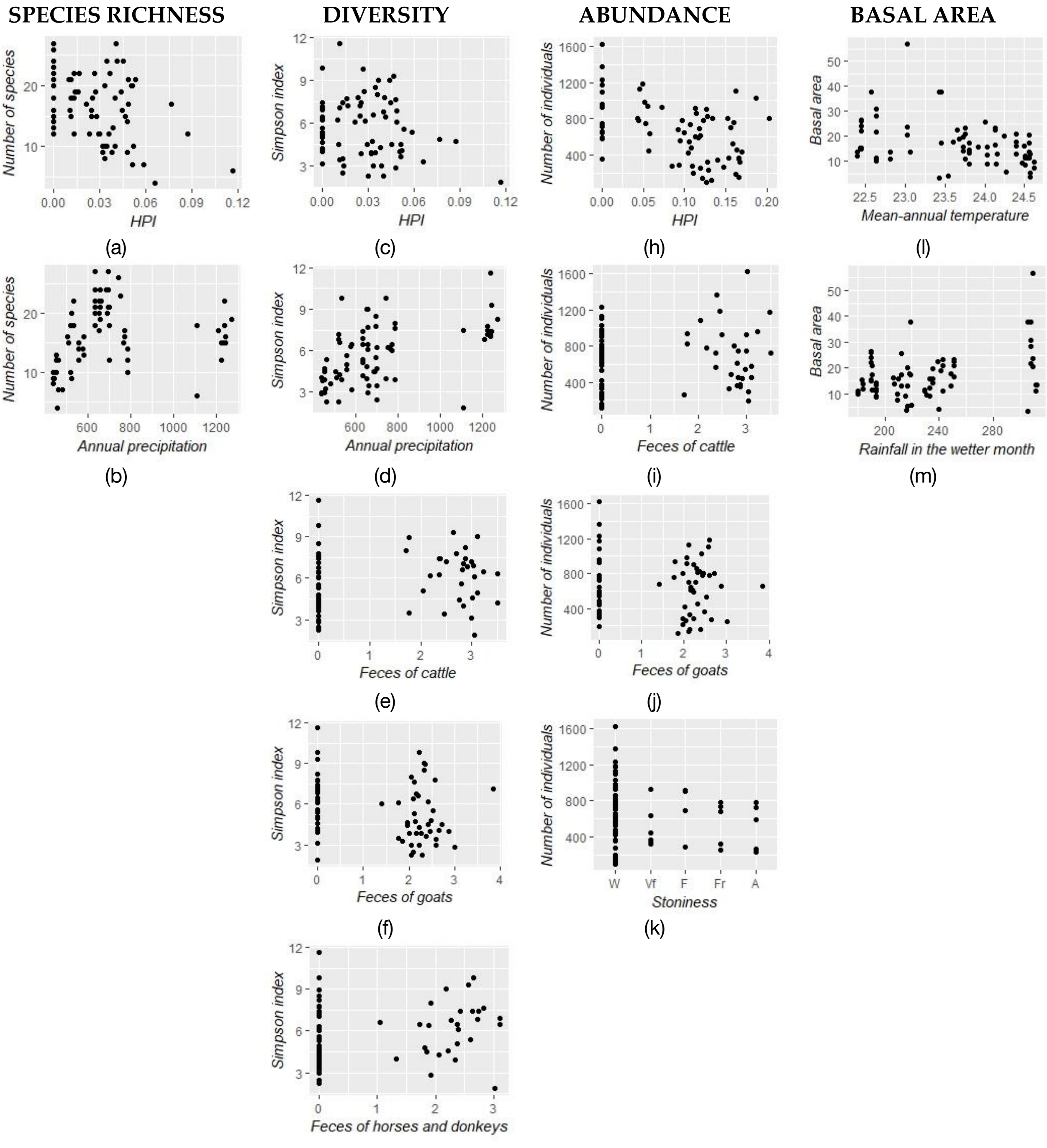
Number of individuals

Livestock, HPI and stoniness exerted a substantial effect on the number of individuals in mature forests. Goats, horses and cows were each included in two of these models, and HPI and stoniness in every one of the three best models (Table 3).

The best model included HPI, cattle, goats and stoniness, all of them with negative influence. However, only the effect of HPI was significant (Table 4). The number of individuals declined with increasing human pressure (Figure 9h). A specific negative influence of cattle and goats could not be confirmed by our data (Figure 9i, j), even the extreme value of goats did not significantly influence the results of this model. A similar effect was detected for stoniness (Table 4, Figure 9k).

Basal area

The mean annual temperature only affected the basal area of the mature forest with a significant negative influence (Table 4, Figure 9l). The best model also included precipitation in the wettest month with a positive non–significant effect (Table 4, Figure 9m).



(a) (c) (h) (l)

(b) (d) (i) (m)

(e) (j)

(f) (k)

(g)

Figure 9. Relationship between predictors that partially contribute to the best models on the mature forest. Under each parameter assessed, the predictors of the best model are presented.

Nevertheless, annual precipitation had a significant positive effect in the second-best model (E = 0.697, $p = 4.5 \times 10^{-4}$). However, it is well–established that water availability enhances the growth of trees and shrubs. Livestock presence exerted no direct effect on the basal area, while HPI influenced the basal area in the second-best model in a strongly negative way (E = –0.8826, $p = 3.0 \times 10^{-2}$).

5.2.2. Effects of pressure factors on the natural regeneration

The best models for each response variable of natural regeneration (ΔAICs <2) are listed in table 5. The explained variance by fixed + random effects ranged from 53% to 72%.

Number of individuals

As in mature forests, livestock had a strong influence on the number of individuals in terms of natural regeneration, mainly in interaction with treatment (fences). Only the best model included the presence of cows as an independent predictor (Table 5). Nevertheless, the rainy season precipitation seemed to be the most influential predictor since it is the only predictor which was part of all four best models (Table 5).

Table 5. Best models explaining the influence of biotic and abiotic factors on the response variables of natural regeneration. df = degrees of freedom; AIC = Akaike's information criterion; ΔAIC = Delta Akaike's information criterion; *R2m* = marginal variance explained by fixed effects; *R2c* = conditional variance explained by random and fixed effects.

Model	df	AIC	ΔAIC	*R2m*	*R2c*
Number of individuals					
~1 + Equine * Treat + SPrec + Cattle	8	3158.11	0.00	0.10	0.57
~1 + Goats * Cattle * Equine * Treat + SPrec	19	3159.10	0.99	0.13	0.60
~1 + Equine * Treat + Cattle * Treat + SPrec	9	3159.94	1.83	0.10	0.57
~1 + Equine * Treat + SPrec	7	3159.97	1.86	0.10	0.56
Richness					
~1 + SPrec + Treat + Soil.depth + Drain	12	1530.18	0.00	0.63	0.72
~1 + SPrec + Soil.depth + Drain	11	1530.45	0.28	0.62	0.72
~1 + Equine + SPrec + Treat + Soil.depth + Drain	13	1531.73	1.56	0.63	0.72
~1 + Cattle + SPrec + Treat + Text	10	1531.82	1.65	0.51	0.72
~1 + Equine + SPrec + Soil.depth + Drain	12	1532.01	1.83	0.63	0.72
Diversity					
~1 + Drain + Text	8	-233.70	0.00	0.40	0.53
Mortality					
~1 + SPrec + Treat + Time	8	587.18	0.00	0.36	0.56
Recruitment					
~1 + SPrec * Time + Treat	10	657.59	0.00	0.35	0.61
~1 + SPrec + Time	8	659.20	1.62	0.30	0.60

Table 6. Influence of predictors included in the best models of natural regeneration. The *p*-values of 0.05 for Cattle (0.047) as a predictor of abundance and DrainGood (0.049) as a predictor of species richness were achieved due to rounding.

Predictor	**Estimate**	**Std. Error**	***p* (<0.05)**
Number of individuals			
(Intercept)	3.17	0.25	$< 2 \times 10^{-16}$ ***
Equine	0.93	0.23	7.0×10^{-5} ***
Treatopen	-0.01	0.07	0.89
SPrec	0.39	0.08	0.00 ***
Cattle	-0.37	0.18	0.05 *
Equine:Treatopen	-0.99	0.27	0.00 ***
Species richness			
(Intercept)	-0.15	0.30	0.61
SPrec	0.15	0.05	3.6×10^{-3} **
Treatopen	-0.06	0.04	0.13
Soil.depth11 - 20 cm	1.32	0.28	2.2×10^{-6} ***
Soil.depth21 - 50 cm	1.93	0.27	1.2×10^{-12} ***
Soil.depth51 - 100 cm	1.45	0.26	1.7×10^{-8} ***
Soil.depth> 100 cm	2.06	0.29	6.1×10^{-13} ***
DrainModerated	0.45	0.16	0.01 **
DrainGood	0.28	0.14	0.05 *
Diversity			
(Intercept)	0.19	0.07	0.01 **
DrainModerated	0.16	0.08	0.04 *
DrainGood	-0.05	0.08	0.52
TextClay loam	0.17	0.08	0.04 *
TextLoam	0.22	0.06	2.0×10^{-4} ***
TextSandy loam	-0.12	0.10	0.27
Mortality			
(Intercept)	8.02	0.59	
SPrec	-1.61	0.15	$< 2.2 \times 10^{-16}$ ***
Treatopen	0.33	0.11	0.00 **
Time	-0.11	0.02	0.00 ***
Recruitment			
(Intercept)	-9.35	5.52	0.09 †
SPrec	7.67	2.80	0.01 **
Time	0.63	0.32	0.05 †
Treatopen	-0.10	0.14	0.44
SPrec:Time	-0.42	0.16	0.01 *

The number of individuals showed a significant positive effect of equine and rainy season precipitation (Table 6, Figure 10a, b); in contrast, cattle had a significant negative effect (Table 6; Figure 10c), indicating that the amount of natural regeneration decreases with the grazing of cows. Fencing did not affect the number of individuals when used as main predictor (Figure 10d). However, in interaction with equine it had a significant negative effect (Table 6; Figure 10e), demonstrating that the abundance of regenerating seedlings in unfenced sites, where horses were still present, was lower than in fenced sites where horses had previously been present but no longer are.

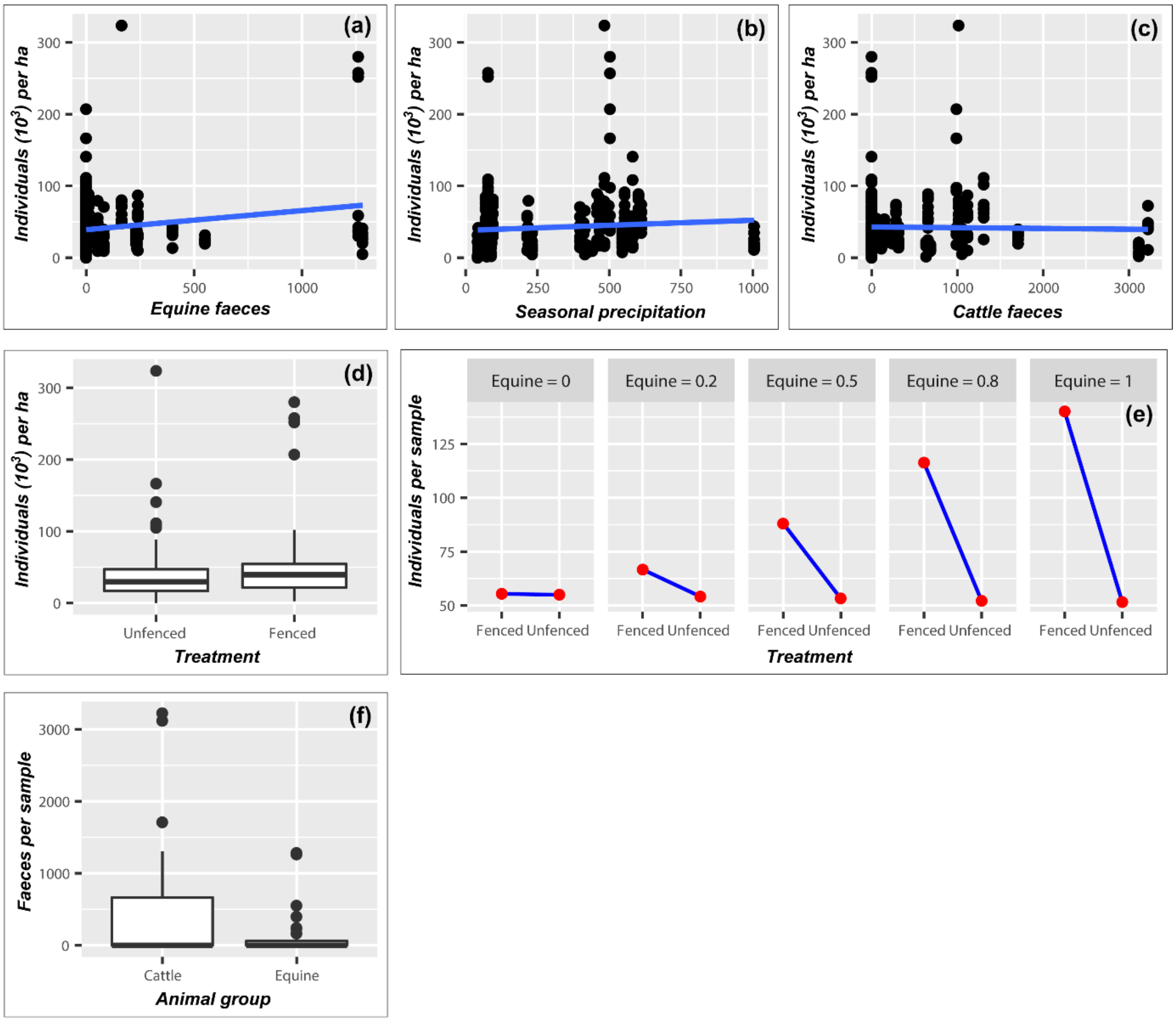


Figure 10. Relationship between predictors that partially contribute to the best models of natural regeneration.

Species richness

Species richness of natural regeneration is under the influence of precipitation, soil (depth and drainage), livestock variables and treatment. In contrast to the mature forest, no influence of HPI on natural regeneration species richness was detected in this research (Table 5).

Rainy season precipitation positively influenced species richness (Table 6), indicating that species richness is higher in the rainy season. Likewise, soil predictors played a preponderant role in natural regeneration: species richness was significantly higher on sites with deeper soils than on sites with shallow soils (<10 cm) and also higher on sites with moderately and well-drained soils than on sites with compacted or non–permeable soils (Table 6).

Diversity index

The single best model for the diversity index included the soil predictors drainage and texture (Table 5). Moderately drained soils had a significant positive effect on the diversity of natural regeneration compared with poorly drained soils, while sites with clay loam and loam soils had a significantly higher diversity than those with clay–sandy loam soils (Table 6).

Mortality

Regarding the dynamics of natural regeneration, only one model was identified to adequately explain mortality, which included rainy season precipitation, treatment and elapsed time (Time) as fixed effects (Table 5). Both rainy season precipitation and time had a significant negative effect on mortality (Table 6), indicating that mortality was lower in the rainy season than in the dry season and decreased with elapsed time in the monitored period. In addition, the mortality of natural regeneration was significantly higher in unfenced plots than in fenced plots.

Recruitment

Recruitment was best explained by rainy season precipitation and time (Table 5). The first one had a significant positive effect on recruitment (Table 6). However, the interaction of the two predictors had a significant negative effect illustrating that the effect of the rainy season precipitation decreased as time elapsed or that the effect of time decreased as rainfall increased. Fences did not affect the rate of recruitment (Table 5).

6. Discussion

6.1. Structure and Diversity of the Dry Forest – Present status.

To understand the potential effects of anthropogenic activities, climate and soil on the dry forest, this research examined the present status of the forest in terms of structure and diversity of the mature forest and natural regeneration levels.

The 91 species identified in the mature forest confirm the status of the region as a diversity hotspot. Our results suit those reported by other studies performed in the study region: Andrade M. & Jaramillo M. (2012) and Cueva O. *et al.* (2012) reported 111 species, Aguirre-Mendoza *et al.* (2013) recorded 58 species and Espinosa *et al.* (2011) recorded 102 species, including trees and shrubs with DBH $\geq$5 cm. Nevertheless, our numbers correspond to only 63% of the number of species reported in Aguirre-Mendoza *et al*., (2006b) for the dry forest in the Loja Province. Based on a compilation of several field studies and herbarium reviews, they derived 184 woody species in the deciduous and semi-deciduous formations.

However, for natural regeneration the total number of species (85) was considerably higher than the 21 species reported by Aguirre-Mendoza *et al.* (2013) for the Ecuadorian part of the same study area. They also exceed the 53 species reported by Lieberman & Li (1992) in a small 120-ha tropical dry forest patch in Ghana.

An alarming result of our inventory was that several of characteristic species of the study area (Aguirre-Mendoza, *et al.*, 2009), such as *Ceiba trischistandra*, *Cavanillesia platanifolia*, *Eriotheca roseorum* and *Myroxylon balsamum*, were recorded in the mature forest but are absent in the natural regeneration inventory. Explanations could be: i) the characteristic species suffered strong perturbations (e.g., due to climatic events or a high presence of selective seedling predators as reported by Albán, Matorel, Trías, & Vera (2002)); ii) a poor seed bank in the region (Espinosa, *et al.*, 2012). Aguirre-Mendoza *et al.* (2013) had already pointed out this finding, it was attributed to the existence of only a few species having abundant regeneration on the one hand and strong perturbations on the other.

The highest concentration of characteristic species has been reported in southwestern Ecuador (Manchego, *et al.*, 2017). Taking into account the entire southern region of Ecuador, 7,048 species of vascular plants (of the 18,198 reported in Ecuador) were recorded (Aguirre-Mendoza, *et al.*, 2015) for every ecosystem, resulting in the fact that the region is recognized as the most diverse in the country (Aguirre-Mendoza, *et al.*, 2015; Lozano C., 2002). Furthermore, this region has been internationally acknowledged as one of the most important diversity hotspots in Ecuador and the planet (Barthlott *et al.*, 2007; Myers *et al.*, 2000).

Diversities of the mature forest similar to that reported in this research (Simpson reciprocal index from 1.88 to 11.59) were reported by Aguirre-Mendoza *et al.* (2013; 2006a) and Muñoz e*t al.* (2014) in the Ecuadorian part of our study area and also for the Peruvian area in a study carried out by Linares-Palomino & Ponce A. (2005) at the Cerros de Amotape Cordillera, who reported Simpson values between 2.04 and 10.48. Similar to the situation of the natural regeneration in the present study, Rodriguez (2006) found a small difference in species richness between treatments, with a slightly higher number of species and diversity index in fenced plots. However, in contrast to our findings, the same study reported a decrease of the number of species over time in fenced plots, which could be related to the fact that the recruitment of new individuals was not accounted for Rodriguez's research. Therefore, species that were recorded in the initial survey with only a small number of individuals may not have been recorded in the following due to the death of those few individuals. On the contrary and in accordance with our results, Cabin *et al*. (2000) found that plots in a preserved area that had been fenced for 40 years had a larger number of species than unfenced plots, as well as a larger number of native species in comparison to exotic ones.

Regarding structural aspects, the anomalous distribution of diametric classes in the mature forest of some species, such as *C. trichistandra* (species palatable to animals) and *C. platanifolia* (Figures 6b and 6c respectively), is directly associated with the browsing and trampling of seedlings. As previously demonstrated, the abundance of individuals in the first stages decreases with animals grazing and increases in fenced areas. This occurrence could also be the case with the lower diameter classes of *B. graveolens*, while the few individuals in the diameter classes >45 cm (Figure 6d) can be explained by the fact that the larger trees are harvested for their wood which is used as flavouring and as repellent (Sanchez, *et al.*, 2006).

The low number of individuals of *H. chrysanthus*, *P. carthagenensis* and *L. huasango* found in the upper diameter classes of mature forests indicates that these valuable species have been excessively and selectively felled (Aguirre-Mendoza, *et al.*, 2005). This probably happened until 1978, i.e., before the region was declared a closed area (Ministerio de Agricultura y Ganadería, *et al.*, 1978). Thus, this can be clearly considered as a consequence of past utilization.

The number of individuals widely differed throughout the forest in both the mature forest and the natural regeneration as well as the basal area in the mature forest (Figure 5e, 8a). In several cases, the less abundant plots were found at the lowest and driest areas; however, this finding cannot be generalized. For instance, one plot with only a few individuals (located at 255 m a.s.l.; annual precipitation 457 mm) held 108 ind./ha with a basal area of 3.8 m^2/ha, whereas another plot with similar characteristics (247 m a.s.l., annual precipitation 467 mm) held 911 ind./ha with a basal area of 15.9 m^2/ha. Similar situations were relatively common and found with regards to species composition, indicating that factors other than abiotic factors also induce these spatial differences. For this reason, pressure predictors and soil characteristics were included in this study.

Seasonality had a strong influence on the number of individuals of natural regeneration. As expected, the abundance increased during the rainy season and decreased during the dry season over the course of the study (Figure 7a). This difference was particularly evident in the unfenced plots. In contrast, Rodriguez (2006) found a decrease in the number of individuals (with a non-significant difference) over one year of evaluation in both unfenced and fenced plots, even during the rainy season. Similar to our results, an evaluation of the effects of ungulates (cattle and goats) in Hawaii, Cabin *et al*. (2000) detected a much higher abundance of seedlings in a year that was catalogued as being rainy (1997) compared with an exceptionally arid year (1998). In the drier year, they observed a marked decrease in the number of seedlings across both treatments and no new individuals even of the most abundant species [*Diospyros sandwicensis* (A.DC.) Fosberg] were found throughout the year.

The almost constant number of individuals recorded in the fenced plots (Figure 7a) over time and seasonality shows that the effect of browsing is greater than the effect of seasonality. Livestock has a lot of food available during the rainy season, which does not occur during the dry season because much of the vegetation dries out or has already been consumed. The animals need to be quite meticulous in looking for their food and need to be able to eat even low palatable species (Fleming *et al.*, 2016). Thus, the fences play a relevant role during the dry season when food availability is lower.

As the present work, previous studies have also found that the mortality of regeneration is highly seasonal (Cabin, *et al.*, 2000; Lieberman, *et al.*, 1992; Rodriguez, 2006). For example, in the unfenced plots Rodriguez (2006) reported maximum mortalities of 20% in the rainy season and 67% in the dry season (across four and two months, respectively) and Lieberman & Li (1992) reported maximum mortalities of 12% in the rainy season and 33% in the dry season (across two months in both cases) of a tropical dry forest in Ghana. Similarly, in the present study, we obtained maximum mortality values of 23% for the rainy season and 85% for the dry season (across four and six months, respectively). Comparing the fenced plots in the same way, the maximum values reported by Rodriguez (2006) were 23% for the rainy season and 36% for the dry season (across two months in both cases) compared to 35% in the rainy season and 87.5% in the dry season (across four and six months, respectively) in the present study. However, this has to be interpreted carefully as the number of individuals was very low in some samples, and thus the proportion of dead seedlings was very high when only two of three seedlings died.

Like mortality, recruitment in the tropical dry forest is highly seasonal (Cabin, *et al.*, 2000; Lieberman, *et al.*, 1992; Vieira, *et al.*, 2006), with higher mortality in the dry season and higher recruitment in the rainy season. Nevertheless, a continuous decrease in recruitment in the unfenced plots was found, even during the rainy season (Figure 7c). However, recruitment in the fenced plots was closer to Cabin and Vieira's prediction – for example, there was similar recruitment between the first dry period (survey 3) and the subsequent wet period (survey 4), followed by a sharp decrease in the second dry period (survey 5) (Figure 7c).

Unfortunately, a part of the monitoring period fell in a phase with unusual climatic conditions, which could explain the high recruitment during survey 3, performed in the dry season. During the previous rainy season, the precipitation was restricted to only two or three relevant events in January, almost no rainfall in February and a short rainy period from March to May, followed by some light showers quite late in June, which contrasts with the continuous rains usually occurring from December to March. Therefore, it is probably the case that several seedlings that established during the wet period (after our assessment) were recorded in the dry period in survey 3.

It is well-known that seed banks in tropical dry forests contain low numbers of seeds and species (Ceccon *et al.* 2006; Espinosa *et al.*, 2012). Ceccon *et al*. (2006) and Ray & Brown (1994) argued that the main cause for the low number of species with high seed germination rates and seed mortality rates are environmental stress, predation and dispersal restrictions. According to Espinosa *et al*. (2012), the same factors have caused low seed availability in our study area, which resulted in shoot propagation being considered more important than seed propagation in the area (Aguirre-Mendoza, Betancourt Figueras, & Geada López, 2013; Espinosa, *et al.*, 2012).

6.2. Drivers affecting the diversity and structure of the mature forest

As pointed out before, anthropogenic activity is the most negative driver of forest loss. Former studies performed in southwestern Ecuador's dry deciduous forests identified an approximate deforestation rate of 29 and 57 km^2/year in the periods 1976 – 1989 and 1989 – 2008, respectively (Tapia-Armijos, *et al.*, 2015), while for the period between 2008 – 2014 was stated an average loss by deforestation of 71 km^2/year (± 43.9 SD) for the 17 characteristic species (Manchego, *et al.*, 2017). That shows that despite the measures imposed by national and local governments years ago, the forests loss continues increasing. On the other hand, forest loss resulting from climate change projections reached 21 km^2/year (± 26.4 SD) without accounting for potential spatial distribution gain (i.e., potential new favourable areas) indicating a relative annual average in area reduction of 1.4% and 0.6% due to deforestation and climate, respectively. In terms of spatial coverage and effect severity, deforestation may pose a higher threat to species distribution than climate change. Nevertheless, climate change may affect a greater number of forest areas, which are not subject to conversion (Manchego, *et al.*, 2017).

Precipitation during the dry season has been suggested as the most critical predictor for determining vegetation patterns (Malhi, *et al.*, 2008) as water is main factor driving the physiological processes of tropical trees (van Der Sleen, *et al.*, 2015). Three different precipitation characteristics have been identified as the most significant positive predictor in the study area. For 17 characteristic species of dry forest, precipitation during the year's driest quarter was the main determinant for the spatial distribution (Manchego, *et al.*, 2017). In terms of species richness, diversity and forest heterogeneity, our study identified the mean annual precipitation as the most influential predictor (Tables 3 – 4; Figure 9b, d). Precipitation in the rainy season had the strongest positive influence on the abundance of seedlings, the number of species, recruitment and mortality when its effect on natural regeneration was assessed (Tables 5 – 6).

Precipitation was mentioned as a poor predictor of species richness in the dry forest of Central America (Gentry, 1995; Gillespie *et al.,* 2000) and had a negative correlation with plant diversity in the study area (Espinosa, *et al.*, 2011). Nevertheless, both Gentry (1988) and Clinebell *et al.* (1995) were able to correlate these two factors when a dry–wet gradient existed in the forest. Our study area comprised an altitudinal gradient from 200 to 1,100 m a.s.l. with a semi-deciduous dry forest in the lower areas followed by a low montane dry forest in the higher areas. The latter formation has a mixture of tropical dry and pre–montane floristic elements, which means a transitional formation between the dry and wet forest (Aguirre-Mendoza, Kvist, *et al*., 2006a; Lozano C., 2002).

Several authors have identified deforestation and human presence as the greatest threats to dry forest ecosystems in both Ecuador (Manchego, *et al.*, 2017; Portillo-Quintero, *et al.*, 2010; Tapia-Armijos, *et al.*, 2015) and the world (Gentry, 1995; Janzen, 1988; Olson, *et al.*, 2000). Our results support those findings in the study area.

The human pressure index was a powerful predictor in this research, reducing species richness and the abundance of trees and shrubs (Figure 9a, h). Similar results were reported for species richness in a region located approximately 100 km east of our study area (Espinosa, *et al.*, 2011). The reduction in the number of species and of the abundance was also registered for a dry forest in Central America (Gillespie, *et al.*, 2000); in addition, significant differences in species richness, basal area and abundance among samples with different disturbance levels were reported in India by Sagar *et al.* (2003).

The HPI includes several activities that contribute to the negative effects of this factor: agricultural activities must be considered as a hazardous activity in the study area. For instance, throughout the rainy season, corn cultivation is the most frequent activity in the whole area, particularly in the higher parts to take advantage of the humidity. This leads to changes in the land use, mainly in the natural forests. Usually, the land is completely cleared until the soil is exposed, while the use of chemical agents frequently causes the pollution of soils and water. Even though wood logging is less practiced as a form of selective extraction, it is still allowed if the wood is used on–site. The extraction of firewood, fruits or curative plants affect the forest mainly because of the trampling of seedlings during the first stage. The effects of livestock can't be excluded when evaluating the general pressure, therefore, it is also considered in the HPI.

Cattle exerted a negative influence on the abundance of individuals (Figure 9i) as well as the diversity of the mature forest (Figure 9e). It has been identified that this group of animals reduces the number of individuals, especially during the seedling stage (Cueva O., *et al.*, 2020), but probably as well during the seed germination stage. This effect is provoked by soil compaction caused by the trampling as well as by browsing of seedlings. This observation is consistent with Stern *et al.* (2002) who stated that cattle grazing affected the diversity and structure of the forests in two protected areas in Costa Rica (Parque Nacional Palo Verde and Reserva Biológica Lomas Barbudal). The same effect was reported by Gillespie *et al.* (2000) for Costa Rica and Nicaragua. According to their research, cattle reduce the capacity of seeds to germinate, and intensive grazing can promote forests with spiny and unpalatable species.

The presence of goats was expected having a strong influence on parameters such as species richness and the number of individuals. Even though we could detect a negative influence (Figure 9j) the effect was non–significant, probably because the number of animals was still within the amount the forest can tolerate.

Considering these results, it is essential to note that our evaluation of the influence of animals was based on faecal samples, which decompose when exposed to environmental conditions such as the sun, wind and water. Therefore, the effects of animals should be interpreted with caution.

Surprisingly, we found that human pressure heterogenized the mature forest rather than homogenized it. At least in our analysis, human-induced homogeneity was not identifiable in nearby plots (Table 6). Considering that the driest areas support the fewest species, the extraction of one individual could promote the loss of that species in the plot. This might explain the differences in the numbers of species among nearby samples in our study and the consequent heterogenization. This finding clearly differs from other studies that identified homogenization as the main effect of anthropogenic perturbation of a forest (Espinosa, *et al.*, 2012; Mckinney, *et al.*, 1999).

The mean annual temperature only affected the basal area (Figure 9l) in a significantly negative way, probably because higher temperatures provoke higher evapotranspiration of plants. Hence, the growth of individuals would be affected, even the DBHs of some species could temporary decrease (Cueva O., E. 2019), especially during the water deficit phases. Contrary to Espinosa *et al.* (2011), no relation between this predictor and species richness was detected. However, as the mean annual temperature is strongly correlated with both annual rainfall and altitude (SI Table 5), we cannot rule out its effect on any of the assessed factors.

We conclude that measures to avoid deforestation in the southernmost coastal region should be promoted. Concurrently, conservation should be encouraged in the southwestern border with Peru (Cuesta, *et al.*, 2017), where the highest concentration of species has been predicted to occur (Manchego, *et al.*, 2017). Currently, there is no representation included in the national protected areas system of Ecuador. Further research is recommended, which should incorporate information about deforestation and modelling scenarios for northern Peru where the causes for deforestation are similar (Linares-Palomino, 2004; Wunder, 2000) and social processes such as demographics, economics and politics play an important role in this (Ochoa M., 2018).

6.3. Drivers of natural regeneration

As in the mature forest, precipitation was the most important predictor for natural regeneration. For this case, seasonal precipitation was used. It positively affected abundance, species richness, mortality and recruitment (Table 5). However, the HPI was not relevant for natural regeneration. One potential reason might be that fencing restricted the human activities as well as the presence of animals within the plots. Furthermore, HPI was strongly correlated with 10 of the 13 predictors we used (all except seasonal precipitation, treatment and stoniness; see SI Table 4), which may have limited the inclusion of this predictor in the models, causing the restriction of including correlated predictors in a single model.

In our study, plant diversity of natural regeneration increased in the rainy season. Similar effects were stated by Cabin *et al*. (2000), Espinosa *et al.* (2012), Lieberman & Li (1992) and Vieira & Scariot (2006). These effects can be linked to the higher water availability, the accelerated decomposition of organic matter (Espinosa, *et al.*, 2012) and the higher concentration and uptake of nutrients accumulating in the soil during the dry season when the vegetation is absorbing less (Roy, *et al.*, 1995).

Cattle exerted a negative influence on the abundance of individuals of natural regeneration (Figure 10c). In addition to browsing the vegetation, cattle are trampling the soil, causing compaction, reducing the volume and presence of pores, and therefore the availability of water and air (Maass, 1995).

In contrast to cattle, horses exerted a positive influence on the number of individuals (Figure 10a). A possible explanation for this might be the input of micronutrients to the soil. These micronutrients facilitate plant growth, as reported by García-Moreno *et al.* (2014) for *Quercus ilex* L. in a Mediterranean open forest. They found significantly higher N and Mg concentrations in the leaves of trees growing in intensively grazed areas, as well as an increase of inorganic N in the soil.

A second explanation might be the currently number of horses and donkeys in the area (Figure 10f). Because of similar physical traits between cattle and horses and food preferences, one would expect their impact on the forest to be similar as well, implying that the number of animals is a critical factor for the level of impact. The use of these animals has drastically changed over the last decades: horses and donkeys as means of transport have been replaced by motorcycles, while the number of cattle has been maintained or even increased to produce meat and milk or to put up the animals for sale.

Fencing had a significant positive effect only on the mortality of natural regeneration and in interaction with Equine on abundance, although treatment was included in the best models for all response variables, except diversity (Table 5). Our outcomes are consistent with the findings of Rodriguez (2006). Fences reduce the impact of animals eating and trampling seedlings and of people damaging individual plants when they walk through the forests or carry out extractive activities. In contrast to Rodriguez (2006) and Cabin *et al.*

Figure 11. Young individual of *Bursera graveolens* observed in a private area with approximately eight years of exclusion.

(2000), who found significant differences between unfenced and fenced plots for both species richness and abundance, in the present study, species richness and recruitment exhibited non–significant differences between fenced and unfenced samples (Table 5). However, on adjacent private land, which has been fenced for approximately eight years, well-established young individuals between 2–3 m height were found (Figure 11). During the research, zero individuals of that condition were recorded, and only a few individuals have been reported in the study area (Aguirre-Mendoza, Betancourt Figueras, & Geada López, 2013). Therefore, we believe that our observation time of two years was not enough to reveal direct fencing effects.

Lieberman & Li (1992) identified canopy closure as an essential predictor of forest density. However, that influence was not found in this research. Taking into account that canopy closure is highly correlated with several of the predictors considered in this study (see SI Table 4), its influence cannot be discarded entirely, especially as we found that the number of species and the abundance of individuals tended to increase with canopy closure (Figure 12). A closed canopy favours seed germination and seedling growth as it partially prevents seeds from becoming desiccated through high temperatures in the dry season. Furthermore, it also keep fresh fruits and seeds from being washed away during heavy rainfall (Griz, *et al.*, 2001).

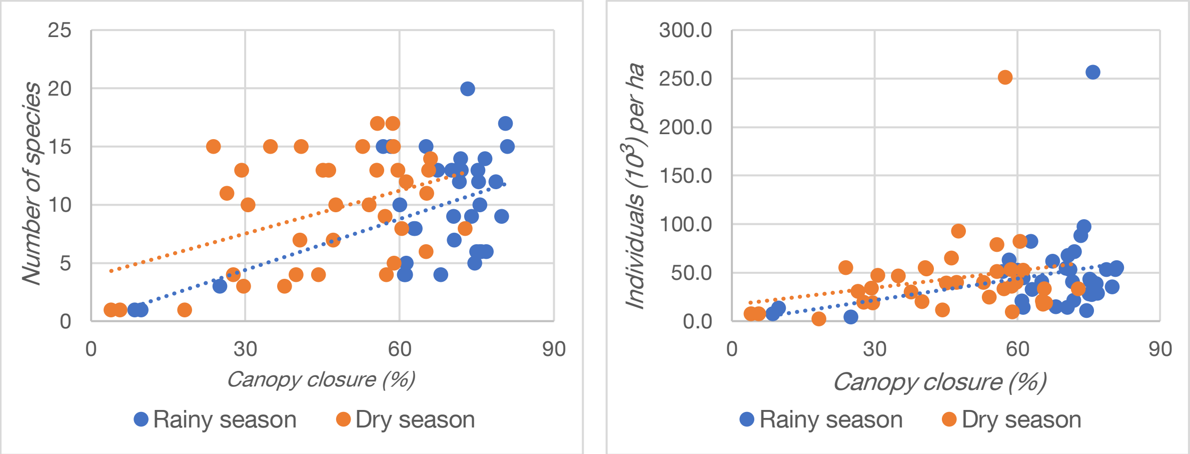


Figure 12. Relation of canopy closure on two parameters of natural regeneration. (a) Relation between canopy closure and species richness; (b) Relation between canopy closure and the number of individuals.

Elapsed time was an important predictor of mortality and recruitment (Table 5). Similarly, Rodriguez (2006) showed that mortality exhibited a constant decrease over time disrupted only by the rainy season. This effect was expected as the number of individuals decreases throughout the dry season whereas the surviving individuals will adapt to those conditions, resulting in decreasing mortality.

Soil characteristics played a much bigger role for natural regeneration than for the mature forest: in the latter, only stoniness had a negative influence on the number of individuals (see Figure

9k). However, unfavourable soil conditions for seed germination increased the mortality rate of seedlings, thereby reducing the number of individuals that reach maturity. In our models, soil depth and drainage turned out to be important predictors for species richness: well–drained soils that were deeper than 10 cm had a larger number of species (Table 5). Albán *et al.* (2002) reported that seeds of *Prosopis pallida*, sown superficially (5 cm depth), were damaged or eaten by ants and lizards, while surface seeds were accessible to birds and rodents. Furthermore, nutrients are transported by leaching rainwater towards deeper soils (Roy, *et al.*, 1995), leading to a better nutritional status of deeper seeds compared to those at the surface. Since this leaching depends on the soil drainage capacity, the lower species richness and diversity that occurs on poorly drained soils can also be explained by fewer nutrients moving into the soil.

The most important deficiency in this research is probably the lack of information regarding the number of animals across the area as well as adequate data on the soil characteristics in the Peruvian part of the study area. Thus, further research is recommended to close these gaps.

7. Conclusions

Our models confirm that anthropogenic pressure has already largely modified the diversity and structure of the dry forest. Estimates in this research indicate that in regions such as southwestern Ecuador, measures to avoid deforestation should be prioritized over climate change adaptation measures. The creation of protected areas would contribute to stopping deforestation and increasing the surface of this ecosystem under conservation, which currently only covers 2.3% of the total protected area in the entire country (Portillo-Quintero, *et al.*, 2010).

If the protection of individual species is prioritized, attention should be put on *Albizia multiflora*, *Ceiba trichistandra*, *Cavanillesia platanifolia* and *Cochlospermum vitifolium* as they are heavily threatened by deforestation, climate change and by negative effects of domestic animals grazing in the forest. These factors have probably already induced the lack (or reduced existence) of seedlings of the above-mentioned species in the natural regeneration, which may lead to a future homogenization of the ecosystem. Moreover, because these species can be used for timber production and agroforestry systems (Aguirre-Mendoza, 2012; Sanchez, *et al.*, 2006), we recommend focussing on sustainable management practices and gene pool conservation of these species.

Cattle management should be considered in particular, since this group of animals puts a high risk on species richness, diversity and abundance in the two main forest's strata: the mature forest and natural regeneration. At the same time, goat management should not be neglected due to its effects on abundance on both strata meaning a heavy change in the forest density.

We emphasize that our results and conclusions about animal effects should be taken with caution as our results are based on faeces, which only allow an approximate number of the animals present in the forest. Thus, further research is urgently recommended.

Among the abiotic factors, precipitation was the most important positive predictor of species richness, diversity and abundance despite the briefness of the rainy period. Unfortunately, the rainy season is also the period posing the greatest pressure due to the high availability of food for animals, fruits, or medicinal plants mostly in production during the rainy season. Therefore, to help to halt the loss of abundance and species richness due to aspects not related to drought, the introduction of suitable management strategies is recommended, such as: restricting cattle in largely affected areas and areas of high biological importance, establishment and control of maximum numbers of animals allowed in the forest per family or promotion of semi-stabled animal breeding, which should be supported by measures for species conservation, e.g., potential gen-ecological zone identification or gene pool variability tests in combination with enrichment planting efforts, the establishment of seed orchards and in vitro propagation.

Using fences to exclude all types of activities with a negative impact on natural regeneration seems only effective when they are established over a minimum period of six years, taking into account the experience of neighbours to the study area, which obviously should be assessed. Therefore, fences could be helpful if they are maintained on a medium- to long-term basis.

Soil conditions have a much more significant effect on natural regeneration than on the mature forest in the study area. Texture, drainage and soil depth are all important predictors with the capacity to generate changes concerning species richness and diversity of natural regeneration. Thus, areas with suitable conditions should be identified, fenced and used as seedling production sites.

Our results indicate that the mortality of natural regeneration is affected by both seasonality and the activities of animals and humans. The use of temporary fences, as suggested earlier in this paper, could be an efficient alternative to decrease mortality provoked by the two agents mentioned above: first, there would be the obvious effect of preventing animals from eating and trampling the seedlings; second, the vegetation would become denser and although the herbs will die, the rest of them will remain on site providing shade for seedlings and thus, decreasing the mortality caused by seasonality.

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9. List of Publications

- Quiroz Dahik, C., Crespo, P., Stimm, B., Mosandl, R., **Cueva, J**., Hildebrandt, P., Weber, M. (2021). Impacts of pine plantations on carbon stocks of páramo sites in Southern Ecuador. Carbon Balance Manag. 16:5. https://doi.org/10.1186/s13021-021-00168-5

- **Cueva-O., J**., Espinosa, C. I., Aguirre-Mendoza, Z., Gusmán-Montalván, E., Weber, M., & Hildebrandt, P. (2020). Natural Regeneration in the Tumbesian Dry Forest: Identification of the Drivers Affecting Abundance and Diversity. Scientific *Reports*, *10*(9786), 1–13. https://doi.org/10.1038/s41598-020-66743-x

- **Cueva O., J**., Espinosa, C. I., Quiroz D., C., Aguirre-Mendoza, Z., Cueva O., E., Gusmán, E., … Hildebrandt, P. (2019). Influence of anthropogenic factors on the diversity and structure of a dry forest in the central part of the Tumbesian region (Ecuador-Perú). Forests, 10(1), 1–22. https://doi.org/10.3390/f10010031

- Manchego, C. E., Hildebrandt, P., **Cueva O., J.,** Espinosa, C. I., Stimm, B., & Günter, S. (2017). Climate change versus deforestation: Implications for tree species distribution in the dry forests of southern Ecuador. *PLoS ONE*, *12*(12), 1–19. https://doi.org/10.1371/journal.pone.0190092

- **Cueva O., J.**, & Chalán, L. A. (2010). *Cobertura vegetal y uso actual del suelo de la provincia de Loja. Informe técnico* (1st ed.). Retrieved from Gráficas Amazonas website: http://www.naturalezaycultura.org/docs/Informe Cobertura Vegetal.pdf

10. Appendix

10.1. Appendix A. Supplementary information.

SI Table 1. Candidate models used to assess the mature forest's parameters.

ID	Model
1	~1
2	~1 + Goats
3	~1 + Goats + Cattle
4	~1 + Goats + Equine
5	~1 + Goats + HPI
6	~1 + Goats + Temper
7	~1 + Goats + Altitude
8	~1 + Goats + Ann.Prec
9	~1 + Goats + Mth.Prec
10	~1 + Goats + Soil.depth
11	~1 + Goats + Drainage
12	~1 + Goats + Stoniness
13	~1 + Goats + Texture
14	~1 + Goats + Cattle + Equine
15	~1 + Goats + Cattle + HPI
16	~1 + Goats + Cattle + Ann.Prec
17	~1 + Goats + Cattle + Mth.Prec
18	~1 + Goats + Cattle + Stoniness
19	~1 + Goats + Equine + HPI
20	~1 + Goats + Equine + Ann.Prec
21	~1 + Goats + Equine + Mth.Prec
22	~1 + Goats + Equine + Soil.depth
23	~1 + Goats + Equine + Stoniness
24	~1 + Goats + Equine + Texture
25	~1 + Goats + HPI + Ann.Prec
26	~1 + Goats + HPI + Stoniness
27	~1 + Goats + Temper + Mth.Prec
28	~1 + Goats + Ann.Prec + Drainage
29	~1 + Goats + Mth.Prec + Soil.depth
30	~1 + Goats + Mth.Prec + Drainage
31	~1 + Goats + Soil.depth + Drainage
32	~1 + Goats + Drainage + Texture
33	~1 + Goats + Cattle + Equine + HPI
34	~1 + Goats + Cattle + Equine + Ann.Prec
35	~1 + Goats + Cattle + Equine + Mth.Prec
36	~1 + Goats + Cattle + Equine + Stoniness
37	~1 + Goats + Cattle + HPI + Ann.Prec
38	~1 + Goats + Cattle + HPI + Stoniness
39	~1 + Goats + Equine + HPI + Ann.Prec
40	~1 + Goats + Equine + HPI + Stoniness
41	~1 + Goats + Equine + Mth.Prec + Soil.depth
42	~1 + Goats + Mth.Prec + Soil.depth + Drainage
43	~1 + Goats + Cattle + Equine + HPI + Ann.Prec
44	~1 + Goats + Cattle + Equine + HPI + Stoniness
45	~1 + Cattle
46	~1 + Cattle + Equine
47	~1 + Cattle + HPI
48	~1 + Cattle + Ann.Prec
49	~1 + Cattle + Mth.Prec
50	~1 + Cattle + Stoniness
51	~1 + Cattle + Equine + HPI
52	~1 + Cattle + Equine + Ann.Prec
53	~1 + Cattle + Equine + Mth.Prec
54	~1 + Cattle + Equine + Stoniness
55	~1 + Cattle + HPI + Ann.Prec
56	~1 + Cattle + HPI + Stoniness
57	~1 + Cattle + Equine + HPI + Ann.Prec
58	~1 + Cattle + Equine + HPI + Stoniness
59	~1 + Equine
60	~1 + Equine + HPI
61	~1 + Equine + Ann.Prec
62	~1 + Equine + Mth.Prec
63	~1 + Equine + Soil.depth
64	~1 + Equine + Stoniness
65	~1 + Equine + Texture
66	~1 + Equine + HPI + Ann.Prec
67	~1 + Equine + HPI + Stoniness
68	~1 + Equine + Mth.Prec + Soil.depth
69	~1 + HPI
70	~1 + HPI + Ann.Prec
71	~1 + HPI + Stoniness
72	~1 + Temper
73	~1 + Temper + Mth.Prec
74	~1 + Altitude
75	~1 + Ann.Prec
76	~1 + Ann.Prec + Drainage
77	~1 + Mth.Prec
78	~1 + Mth.Prec + Soil.depth
79	~1 + Mth.Prec + Drainage
80	~1 + Mth.Prec + Soil.depth + Drainage
81	~1 + Soil.depth
82	~1 + Soil.depth + Drainage
83	~1 + Drainage
84	~1 + Drainage + Texture
85	~1 + Stoniness
86	~1 + Texture

SI Table 2. Candidate models used to assess the natural regeneration's abundance and diversity parameters.

ID	Model
1	~1
2	~1 + Goats
3	~1 + Goats + Cattle
4	~1 + Goats + Equine
5	~1 + Goats + SPrec
6	~1 + Goats + Treat
7	~1 + Goats + Drain
8	~1 + Goats + Text
9	~1 + Goats + Cattle + Equine
10	~1 + Goats + Cattle + Canp
11	~1 + Goats + Cattle + SPrec
12	~1 + Goats + Cattle + Treat
13	~1 + Goats + Cattle + Text
14	~1 + Goats + Equine + SPrec
15	~1 + Goats + Equine + Treat
16	~1 + Goats + Equine + Drain
17	~1 + Goats + Equine + Text
18	~1 + Goats + SPrec + Treat
19	~1 + Goats + SPrec + Drain
20	~1 + Goats + SPrec + Text
21	~1 + Goats + Treat + Drain
22	~1 + Goats + Treat + Text
23	~1 + Goats + Drain + Text
24	~1 + Goats + Cattle + Equine + SPrec
25	~1 + Goats + Cattle + Equine + Treat
26	~1 + Goats + Cattle + Equine + Text
27	~1 + Goats + Cattle + Canp + SPrec
28	~1 + Goats + Cattle + Canp + Treat
29	~1 + Goats + Cattle + SPrec + Treat
30	~1 + Goats + Cattle + SPrec + Text
31	~1 + Goats + Cattle + Treat + Text
32	~1 + Goats + Equine + SPrec + Treat
33	~1 + Goats + Equine + SPrec + Drain
34	~1 + Goats + Equine + SPrec + Text
35	~1 + Goats + Equine + Treat + Drain
36	~1 + Goats + Equine + Treat + Text
37	~1 + Goats + Equine + Drain + Text
38	~1 + Goats + SPrec + Treat + Drain
39	~1 + Goats + SPrec + Treat + Text
40	~1 + Goats + SPrec + Drain + Text
41	~1 + Goats + Treat + Drain + Text
42	~1 + Goats + Cattle + Equine + SPrec + Treat
43	~1 + Goats + Cattle + Equine + SPrec + Text
44	~1 + Goats + Cattle + Equine + Treat + Text
45	~1 + Goats + Cattle + Canp + SPrec + Treat
46	~1 + Goats + Cattle + SPrec + Treat + Text
47	~ 1 + Goats + Equine + SPrec + Treat + Drain
48	~1 + Goats + Equine + SPrec + Treat + Text
49	~1 + Goats + Equine + SPrec + Drain + Text
50	~1 + Goats + Equine + Treat + Drain + Text
51	~1 + Goats + SPrec + Treat + Drain + Text
52	~1 + Cattle
53	~1 + Cattle + Equine
54	~1 + Cattle + Canp
55	~1 + Cattle + SPrec
56	~1 + Cattle + Treat
57	~1 + Cattle + SDepth
58	~1 + Cattle + Ston
59	~1 + Cattle + Text
60	~1 + Cattle + Equine + SPrec
61	~1 + Cattle + Equine + Treat
62	~1 + Cattle + Equine + SDepth
63	~1 + Cattle + Equine + Ston
64	~1 + Cattle + Equine + Text
65	~1 + Cattle + Canp + SPrec
66	~1 + Cattle + Canp + Treat
67	~1 + Cattle + SPrec + Treat
68	~1 + Cattle + SPrec + SDepth
69	~1 + Cattle + SPrec + Ston
70	~1 + Cattle + SPrec + Text
71	~1 + Cattle + Treat + SDepth
72	~1 + Cattle + Treat + Ston
73	~1 + Cattle + Treat + Text
74	~1 + Cattle + Equine + SPrec + Treat
75	~1 + Cattle + Equine + SPrec + SDepth
76	~1 + Cattle + Equine + SPrec + Ston
77	~1 + Cattle + Equine + SPrec + Text
78	~1 + Cattle + Equine + Treat + SDepth
79	~1 + Cattle + Equine + Treat + Ston
80	~1 + Cattle + Equine + Treat + Text
81	~1 + Cattle + Canp + SPrec + Treat
82	~1 + Cattle + SPrec + Treat + SDepth
83	~1 + Cattle + SPrec + Treat + Ston
84	~1 + Cattle + SPrec + Treat + Text
85	~1 + Cattle + Equine + SPrec + Treat + SDepth
86	~1 + Cattle + Equine + SPrec + Treat + Ston
87	~1 + Cattle + Equine + SPrec + Treat + Text
88	~1 + Equine
89	~1 + Equine + SPrec
90	~1 + Equine + Alt
91	~1 + Equine + Treat
92	~1 + Equine + SDepth
93	~1 + Equine + Drain
94	~1 + Equine + Ston
95	~1 + Equine + Text
96	~1 + Equine + SPrec + Alt
97	~1 + Equine + SPrec + Treat
98	~1 + Equine + SPrec + SDepth
99	~1 + Equine + SPrec + Drain
100	~1 + Equine + SPrec + Ston
101	~1 + Equine + SPrec + Text
102	~1 + Equine + Alt + Treat
103	~1 + Equine + Treat + SDepth
104	~1 + Equine + Treat + Drain
105	~1 + Equine + Treat + Ston
106	~1 + Equine + Treat + Text
107	~1 + Equine + SDepth + Drain
108	~1 + Equine + Drain + Text
109	~1 + Equine + SPrec + Alt + Treat
110	~1 + Equine + SPrec + Treat + SDepth
111	~1 + Equine + SPrec + Treat + Drain
112	~1 + Equine + SPrec + Treat + Ston
113	~1 + Equine + SPrec + Treat + Text
114	~1 + Equine + SPrec + SDepth + Drain
115	~1 + Equine + SPrec + Drain + Text
116	~1 + Equine + Treat + SDepth + Drain
117	~1 + Equine + Treat + Drain + Text
118	~1 + Equine + SPrec + Treat + SDepth + Drain
119	~1 + Equine + SPrec + Treat + Drain + Text
120	~1 + HPI.BA
121	~1 + HPI.BA + SPrec
122	~1 + HPI.BA + Treat
123	~1 + HPI.BA + Ston
124	~1 + HPI.BA + SPrec + Treat
125	~1 + HPI.BA + SPrec + Ston
126	~1 + HPI.BA + Treat + Ston
127	~1 + HPI.BA + SPrec + Treat + Ston
128	~1 + Canp
129	~1 + Canp + SPrec
130	~1 + Canp + Treat
131	~1 + Canp + SPrec + Treat
132	~1 + SPrec
133	~1 + SPrec + Alt
134	~1 + SPrec + Treat
135	~1 + SPrec + OM
136	~1 + SPrec + SDepth
137	~1 + SPrec + Drain
138	~1 + SPrec + Ston
139	~1 + SPrec + Text
140	~1 + SPrec + Alt + Treat
141	~1 + SPrec + Treat + OM
142	~1 + SPrec + Treat + SDepth
143	~1 + SPrec + Treat + Drain
144	~1 + SPrec + Treat + Ston
145	~1 + SPrec + Treat + Text
146	~1 + SPrec + SDepth + Drain
147	~1 + SPrec + Drain + Text
148	~1 + SPrec + Treat + SDepth + Drain
149	~1 + SPrec + Treat + Drain + Text
150	~1 + MTemp
151	~1 + MTemp + Treat
152	~1 + Alt
153	~1 + Alt + Treat
154	~1 + Treat
155	~1 + Treat + OM
156	~1 + Treat + SDepth
157	~1 + Treat + Drain
158	~1 + Treat + Ston
159	~1 + Treat + Text
160	~1 + Treat + SDepth + Drain
161	~1 + Treat + Drain + Text
162	~1 + OM
163	~1 + SDepth
164	~1 + SDepth + Drain
165	~1 + Drain
166	~1 + Drain + Text
167	~1 + Ston
168	~1 + Text
169	~1 + Goats * Cattle + SPrec + Treat
170	~1 + Goats * Equine + SPrec + Treat
171	~1 + Cattle * Equine + SPrec + Treat
172	~1 + Goats * Cattle * Equine + SPrec + Treat
173	~1 + Goats * SPrec + Treat
174	~1 + Cattle * SPrec + Treat
175	~1 + Equine * SPrec + Treat
176	~1 + HPI.BA * SPrec + Treat
177	~1 + SPrec * Treat + OM
178	~1 + SPrec * OM + Treat
179	~1 + SPrec * SDepth + Treat
180	~1 + SPrec * Treat + SDepth
181	~1 + Goats * Treat + SPrec
182	~1 + Cattle * Treat + SPrec
183	~1 + Equine * Treat + SPrec
184	~1 + Equine * Treat + SPrec + Cattle
185	~1 + Equine * Treat + Cattle * Treat + SPrec
186	~1 + Goats * Cattle * Equine * Treat + SPrec

SI Table 3. Candidate models used to assess the dynamic's parameters of natural regeneration.

ID	Model
1	~1
2	~1 + SPrec
3	~1 + SPrec + Treat
4	~1 + SPrec + Time
5	~1 + SPrec + Treat + Time
6	~1 + SPrec * Treat
7	~1 + SPrec * Treat + Time
8	~1 + SPrec * Time + Treat
9	~1 + SPrec + Treat * Time
10	~1 + Treat
11	~1 + Treat + Time
12	~1 + Treat * Time
13	~1 + Time

SI Table 4. *P–values* that shows the correlation among variables used to computed effects on natural regeneration. Values shaded on light grey means correlated variables.

	Goats	**Cattle**	**Equine**	**HPI**	**Canp**	**SPrec**	**MTemp**	**Alt**	**Treat**	**OM**	**SDepth**	**Drain**	**Ston**	**Text**
Goats	0													
Cattle	5.4×10^{-2}	0												
Equine	0.192	0.86	0											
HPI.BA	2.3×10^{-4}	4.9×10^{-3}	3.3×10^{-2}	0										
Canp	9.3×10^{-4}	5.9×10^{-2}	3.6×10^{-4}	1.2×10^{-27}	0									
SPrec	0.106	0.522	0.630	4.5×10^{-2}	0.780	0								
MTemp	3.4×10^{-12}	1.8×10^{-11}	7.9×10^{-8}	1.7×10^{-23}	1.6×10^{-14}	3.2×10^{-28}	0							
Alt	8.4×10^{-4}	1.1×10^{-2}	6.1×10^{-2}	2.0×10^{-7}	3.5×10^{-20}	6.7×10^{-2}	1.7×10^{-44}	0						
Treat	1.000	1.000	1.000	1.000	6.3×10^{-2}	0.696	0.699	1.000	0					
OM	2.0×10^{-3}	0.000	6.0×10^{-3}	0.000	1.0×10^{-3}	0.757	0.000	0.000	1.000	0				
SDepth	0.000	0.101	0.283	0.000	0.000	6.6×10^{-2}	0.000	0.000	1.000	0.000	0			
Drain	6.8×10^{-2}	1.0×10^{-2}	4.9×1^{-2}	0.000	0.000	0.259	0.000	1.5×10^{-2}	1.000	0.000	0.134	0		
Ston	0.000	0.738	0.875	0.169	1.3×10^{-2}	5.1×10^{-2}	0.000	0.000	1.000	0.000	7.0×10^{-3}	1.0×10^{-3}	0	
Text	0.938	4.5×10^{-2}	9.3×10^{-2}	0.000	0.000	0.110	0.000	2.2×10^{-2}	1.000	0.000	0.000	5.3×10^{-3}	2.6×10^{-2}	0

SI Table 5. *P-values* obtained in the Pearson´s correlation test of predictor variables of mature forest. Correlated variables are shaded.

	Goats	Cattle	Equine	HPI	Temper	Altitude	Ann.Prec	Mth.Prec	Soil.depth	Drainage	Stoniness	Texture
Goats	0											
Cattle	0.266	0										
Equine	0.367	0.338	0									
HPI	0.464	0.044	0.794	0								
Temper	0.120	5.2×10^{-7}	0.004	2.1×10^{-4}	0							
Altitude	0.107	7.2×10^{-5}	0.021	0.023	1.0×10^{-28}	0						
Ann.Prec	0.111	0.160	0.108	0.816	1.3×10^{-4}	3.1×10^{-11}	0					
Mth.Prec	0.701	0.381	0.635	0.010	0.355	6.4×10^{-5}	1.7×10^{-14}	0				
Soil.depth	0.578	0.012	0.181	0.000	0.000	0.000	0.034	0.136	0			
Drainage	0.412	0.000	0.011	0.023	1.0×10^{-3}	0.020	0.551	0.397	0.191	0		
Stoniness	0.912	0.536	0.831	0.949	0.000	0.000	0.000	0.000	0.000	1.0×10^{-3}	0	
Texture	0.795	0.005	0.159	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.013	0

10.2. Appendix B. Publications

Publication 1.

Title:	Influence of anthropogenic factors on the diversity and structure of a dry forest in the central part of the Tumbesian region (Ecuador-Perú)
Authors:	Cueva O., J., Espinosa, C. I., Quiroz D., C., Aguirre-Mendoza, Z., Cueva O., E., Gusmán, E., Weber, M., Hildebrandt, P.
Journal:	Forests
Published:	January 5, 2019

forests

Article

Influence of Anthropogenic Factors on the Diversity and Structure of a Dry Forest in the Central Part of the Tumbesian Region (Ecuador–Perú)

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Received: 1 November 2018; Accepted: 2 January 2019; Published: 5 January 2019

Abstract: The dry forest of southern Ecuador and northern Perú (called the Tumbesian region) is known for its high diversity, endemism, and healthy conservation state. Nevertheless, the forest is exposed to many threats linked with human activities. To understand the effects of these threats, which have not been appropriately assessed, we pose two questions: (a) What are the diversity and structural situations of the forest? (b) Are anthropogenic activities affecting the composition and structure of the forest? The assessed factors were species richness, diversity, species similarity, abundance, and density. Forest information was obtained from 72 plots (total area 25.92 ha) randomly placed to cover a wide range of stand densities (from 200 to 1100 m a.s.l.). After constructing linear mixed models and selecting the most influential one, we determined the individual influences of 12 predictors. The human pressure index (HPI) was the most negative predictor of forest health, and annual precipitation was the most important abiotic predictor of good health conditions. Livestock grazing did not significantly change the diversity and structure of mature forest. The mean annual temperature and stoniness influenced only the basal area and number of individuals, respectively. The species composition in our study area was not affected by the HPI, but was strongly predicted by annual precipitation.

Keywords: Ecuador; Perú; dry forest; Tumbesian region; species richness; diversity; similarity; goats; human pressure

1. Introduction

In a global assessment of predominant habitat types, Olson [1] identified 14 major terrestrial habitat types. Among these, tropical and subtropical dry forest ecosystems collectively represent 42% of all tropical forests [2].

The remains of tropical dry forests presently cover 1,048,700 km^2. Most of these remains (54.2%) are found in South America, mainly in northeastern Brazil, in the southeast of Bolivia and Paraguay, and north of Argentina. These regions are the largest continuous dry forests registered on the globe [2]. Other important but smaller areas are found in the Yucatan peninsula (Mexico), in the northern parts of

Venezuela and Colombia, and in Asia (Thailand, Vietnam, Laos, and Cambodia). Tropical dry forests with smaller coverage have also been reported in the north of Panama, the west of Mexico, Australia, Africa, and along the Pacific coast of South America, between Ecuador and Perú [3–5]. Isolated areas exist in the inter-Andean valleys of Ecuador, Perú, Colombia, and Bolivia.

Tropical dry forests are well-known as important ecosystems, yet they are exposed to many threats [1–3,6–9], including deforestation, fragmentation, overgrazing, fire, conversion to agriculture, and drought. These factors are mainly responsible for loss of species (or reduced genetic variability); however, they can also increase the abundance of other species, thereby homogenizing the landscape and the ecosystem [10–12]. A clear instance of these effects was shown by Semper et al. [8], who revealed the influence of land conversion on the richness of animals in Chaco, Argentina: the local extinction of birds and mammals here was estimated as 56% in areas recently turned to pastures, and 29% in areas converted to crop fields.

The future of dry forests has roused great concerns. This is because dry forests are highly accessible owing to their convenient topographic and climatic conditions, making them easy targets for homogenization, which reduces the genetic variability both within species and among populations [12].

The Tumbesian region is a substantial area (approximately 135,000 km^2) of dry forest located on the coast of the southwestern part of Ecuador, which extends to the northwest of Perú [5]. The Tumbesian region belongs to the "Chocó/Darien Western Ecuador", an area identified as one of the 25 global biodiversity hotspots with a large number of endemic species (85 birds, 60 mammals, 63 reptiles, 210 amphibians, and 2250 plants) [13]. For this reason, Olson [1] recommended including this area in the regional strategy plans for the "Tumbesian–Andean Valleys Dry Forests" in the Terrestrial Ecoregion.

Although dry forests have been characterized in several studies, their functionality remains poorly understood [14]. This applies to equatorial forests in general, but mainly in the Ecuadorian–Peruvian dry forest [15]. In particular, there exists a lack of knowledge regarding the effects of human activities such as cattle raising or selective timber extraction on the diversity and structure of the Ecuadorian dry forest.

In the Ecuadorian dry forests, seven distinct formations has been identified [5,16]—spiny dry scrub, deciduous dry forest, semi-deciduous dry forest, low montane dry forest, southern inter-Andean dry forest, eastern inter-Andean dry forest, and northern inter-Andean dry forest—of which semi-deciduous dry forest (located between 200 and 1100 m a.s.l.) is the most diverse formation, followed by deciduous dry forest (located from sea level to 700 m a.s.l.). For this reason, our study was carried out in these two formations.

Currently, local livestock farmers and conservationists from the study region are in the midst of an intense discussion. The first group is arguing that livestock grazing supports conservation, because animal sales generate income for families and hence prevent forest clearance for other purposes [17]; furthermore, grazing reduces the fuel load and risk of forest fires, as reported in Central America's dry forest [3,18]. In contrast, some conservationists argue that extensive grazing impedes the natural regeneration of forests, affecting their structure and diversity [19]. Owing to the lack of suitable information, no political recommendations for livestock handling are available.

Our study strives to improve the current knowledge on dry forests and to identify whether human activities significantly impact forest conditions. To this end, we pose the following research questions: (a) What are the structural and diversity situations of the dry forest in the central zone of the Tumbesian region? (b) Are anthropogenic activities affecting the diversity and structure of the tropical dry forest in this region?

2. Materials and Methods

2.1. Study Area

The research was conducted in the dry forest of the cantons Macará and Zapotillo of the Loja province in southern Ecuador, and the department and province of Tumbes in the northwest of Perú. This area constitutes the central part of the Tumbesian region (Figure 1). The altitudinal range of the deciduous and semi-deciduous dry forest formations varies between 200 and 1100 m a.s.l. [5,7]. The annual mean temperature in the area ranges between 20 °C and 26 °C, and the annual rainfall ranges from 300 mm in the lower lands to 700 mm in the highlands [19].

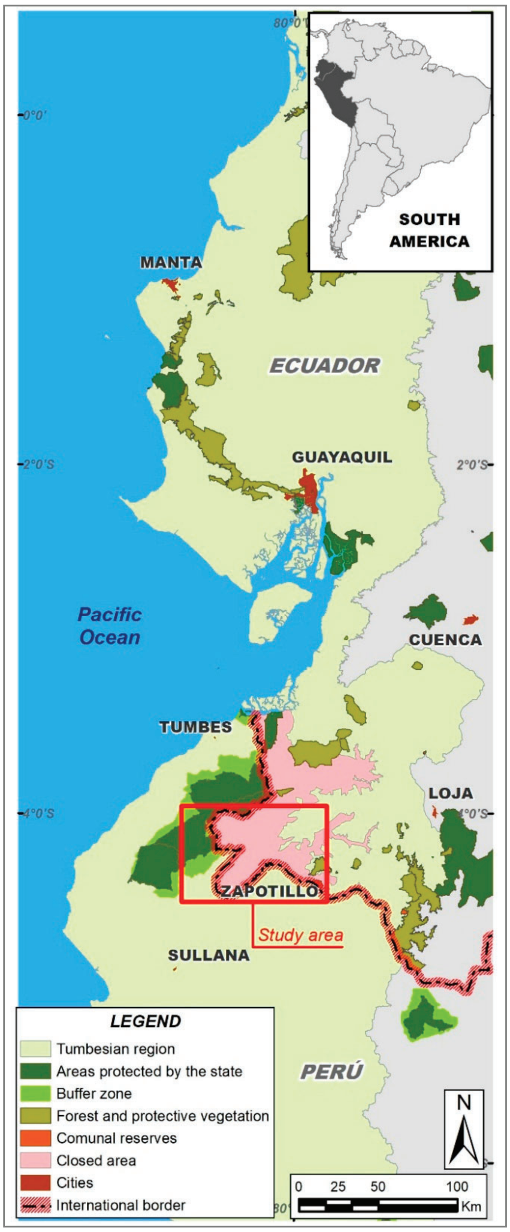


Figure 1. Study area in the Tumbesian region. Modified from "*La Región Tumbesina–una riqueza compartida*" [20].

Some species characteristic to the study area have been reported: *Ceiba trichistandra* (A.Gray) Bakh., *Cavanillesia platanifolia* (Bonpl.) Kunth, *Eriotheca ruizi* (K. Schum.) A. Robyns, *Handroanthus chrysanthus* (Jacq.) S.O.Grose, *Terminalia valverdae* A.H. Gentry, *Bursera graveolens* (Kunth) Triana & Planch., and *Piscidia carthagenensis* Jacq., among others [14,21]. Likewise, some species endemic to Ecuador and Perú have been recorded: *Ficus jacobii* Vázq. Avila, *Coccoloba ruiziana* Lindau, *Mauria membranifolia* Barfod & Holm-Niels., *Armatocereus brevispinus* Madsen, and others [21]. Nevertheless, several of them have been exposed to strong extraction processes.

During the 60s and 70s, many *H. chrysanthus* and *Handroanthus billbergii* (Bureau & K.Schum.) S.O.Grose were extracted for supplying the parquet industry. Accordingly, the coastal forests of southwestern Ecuador up to 1000 m a.s.l. were declared "closed areas" in May 1978 [22]. Although logging continues to operate today, the declaration has substantially decreased this activity. During the last few decades, the natural cover in the study area has dramatically changed: deforestation rates of 33% for seasonally dry forest and 18% for shrublands were reported between 1978 and 2008. In both cases, the area has been mainly converted into pastures [23]. Another relevant problem in the region is the increasing clearing of new areas for crop plantations [23]. The Zapotillo irrigation system, which came into operation approximately 8 years ago, has stimulated the cultivation of new agricultural fields and increased the number of free-grazing goat and bovine herds in nearby forests [24]. Finally, in recent years, the province has experienced extreme climatic conditions (drought or water saturation due to the El Niño phenomenon) that will probably have future impacts [25] on diversity and species composition, the recurrence of which would enhance their effects.

2.2. Data Collection

2.2.1. Forest Inventory

Following the information provided by Aguirre et al. [5], Lozano [16], and Cueva et al. [26], we separated the study area into strata [27]. In our inventory we considered two formations (deciduous and semi-deciduous) and three density levels (dense, semi-dense, and sparse) in each type. This resulted in six different strata, which were considered to equivalently cover most of the forest variability.

In every stratum, four inventory clusters comprising three plots of 60 m × 60 m (each with a nested subplot of 20 m × 20 m) were arranged in an L-shape (Figure 2) and randomly distributed, as described in the methodology of the National Forestry Assessment of Ecuador [28]. However, for more detailed information, we reduced the diameter at breast height (DBH) of the tree inventory from 20 cm to ≥10 cm. Within the nested subplots, we also registered trees between 5 and 10 cm DBH and shrubs with ≥5 cm DBH. In addition, we collected and weighed livestock excrement within a 1 m × 60 m transect along the eastern edge of each plot as an indicator of grazing intensity. Thus, we inventoried 24 clusters (20 in Ecuador and four in Perú) containing 72 plots, which altogether covered 25.92 ha.

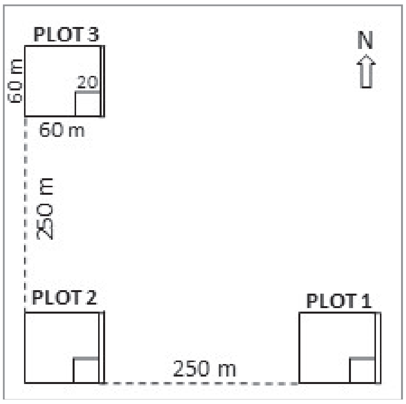


Figure 2. Cluster design. Shrubs were inventoried in the subplot in the southeast corner of each plot, and animal excrement was collected from the transect at the eastern edge.

In each plot, all trees and shrubs were labeled and their species, DBH, and total height were recorded. The species were identified in the field, and where necessary, botanical samples were collected for subsequent identification in the herbarium of the Universidad Técnica Particular de Loja (UTPL). The scientific names were reviewed and corrected based on Reference [29].

2.2.2. Biotic and Abiotic Factors

The number of grazing animals in the forest was estimated on the basis of the excrement amounts. Goats and cattle feces were separated, as these animals were the most common livestock in the study area. The excrement of horses and donkeys (Equine) was also collected, but was summed for each plot. Cattle, horses and donkeys are common throughout the area, but it is difficult to find goats in the highest zones.

As a proxy of the intensity of anthropogenic impact on the forest (due to activities such as woody extraction, grazing, and trampling), we computed the human pressure index (HPI). Adapted from Hegyi's competition index [30], the HPI is defined as:

$$\mathrm{HPI} = \sum_{i=1}^{n} \frac{F_i}{B \times dist_i}. \tag{1}$$

where:

F_i = number of families in the *ith* neighboring village;
B = total basal area of trees and shrubs per plot, projected to hectares (m^2/ha);
$dist_i$ = horizontal distance from the *ith* neighboring village to the studied plot (m).

To calculate the HPI, we considered all neighboring villages around each plot within a distance of 3 km, and collected information regarding the number of families in each village. The horizontal distances between the neighboring villages and the respective plots were calculated on a QGIS Desktop 2.8.7 [31]. The basal areas of trees and shrubs in our inventory data were used to consider the competitiveness among the vegetation at each site. The anthropogenic pressure ranged between 0 (no pressure) and 0.01367. To avoid a circular argument, the basal area was excluded from the HPI when assessing the structural aspects (i.e., number of individuals and basal area). In this case, the pressure ranged between 0 and 0.04117.

Herein, climatic data reporting gridded climate data to 30-arc second resolution (approximately 1 km^2) were used [32]. At each plot, we recorded the total annual precipitation (Ann.Prec), precipitation in the wettest month (Mth.Prec), and the mean annual temperature (Temper). In the study area, the ranges of Ann.Prec, Mth.Prec, and Temper were 442–1271 mm, 180–312 mm, and 22.39 °C–24.63 °C, respectively.

Ecuadorian part soil information was obtained from the Geopedological Map of Zapotillo and Celica of the Instituto Espacial Ecuatoriano [33]. The soil parameters were soil depth (five categories: 0–10, 11–20, 21–50, 51–100, and >100 cm), drainage (three categories: poor, moderate, and good), stoniness (five categories: without, very few, few, frequent, and abundant), and texture (four categories: loam, sandy loam, clay loam, and clay–sandy loam). The Peruvian part soil type was identified from the Soil Classification Map of the Oficina Nacional de Evaluación de Recursos Naturales (ONERN) [34]. As specific soil characteristics were unavailable, they were assumed to be identical to those in the nearest area with the same soil type on the Ecuadorian side.

Values of each predictor can be found as Supplementary Material (Table S1).

2.3. Data Analysis

2.3.1. Data Processing

Species richness was calculated as the total number of species of trees and shrubs in each plot. Diversity was calculated using the Simpson reciprocal index, which is considered to be one of most effective and robust diversity measures [35]. Furthermore, the species accumulation curve was obtained by calling the function specaccum() in the R programming environment [36] using the Coleman method [35] in the "vegan" package [37].

To correct for the different plot sizes, the numbers of individuals were projected onto numbers of individuals per hectare before adding the numbers of trees and shrubs. Individuals' distribution by diametric classes were obtained for the forest and for some species, because they could be indicators of anthropogenic activities. Basal area of a tree was computed using the equation $0.7854 \times \text{DBH}^2$ [38]; the total basal area was obtained by summing the basal areas of all individual trees and shrubs inside the plot and projected to ha. Multi-stemmed individuals whose branches had minimum DBH were treated as the same individual to compute most parameters, whereas to compute the basal area per plot, each stem with minimum DBH was treated as a separate individual.

The species similarity among plots of the same cluster was determined by computing the Sørensen index [35] in the "vegan" package [37]. The Sørensen index tells us how similar two samples are, in terms of presence/absence of species [35].

2.3.2. Effects on Diversity, Structure, and Species Similarity

To determine whether the diversity, structure, and species similarity are affected by anthropogenic activities, climate, and/or soil characteristics in the study area, we applied generalized linear mixed models (GLMMs) or linear mixed models (LMMs) [39–42]. We used species richness and the Simpson reciprocal index as diversity indicators. When identifying the effect of anthropogenic activities on similarity, we used the Sørensen index as the dependent variable. In addition, the number of individuals and basal area per ha were the response variables when analyzing impacts on the forest structure.

In all cases, we considered 12 predictor variables: four biotic indicators (Goats, Cattle, Equine, HPI), four abiotic factors (Temper, Altitude, Ann.Prec, Mth.Prec), and four soil variables (Soil.depth, Drainage, Stoniness, Texture). Pearson's correlation coefficient was calculated for all combinations of variables (Table 1). To avoid collinearity in model building, strongly correlated variables were not included in the same model. Furthermore, overfitting was avoided by limiting the number of variables in any model to five [43] (Table A1). Formation and cluster were considered as random effects, taking into account that plots are nested within clusters, whereas clusters are nested within formations. Interactions between variables were not considered because we wished to identify variables' influence per se, the purpose was to facilitate the implementation of mitigation measures in the field, if necessary.

The influence of each predictor on species richness was estimated in GLMMs with the Poisson error distribution and Laplace approximation. Laplace approximation was used to achieve true likelihood, which cannot be obtained through penalized quasi-likelihood (PQL) approach [40,44]. The influence of the predictor variables on species similarity, the Simpson index, number of individuals per hectare, and basal area was assessed via the restricted maximum likelihood approach (REML), which was chosen because we were dealing with continuous response variables and normal distribution [40].

The best models were chosen using the delta Akaike information criterion ($\Delta\text{AIC} \leq 2$) [45], and the residuals distribution of each best model are presented as Supplementary Material (Figures S1–S5). We also computed the marginal and conditional variances (*R2m* and *R2c*, respectively) [46] using the MuMIn package [47] in R, which provides the proportion of the variance explained by the models. The models were tested for overdispersion.

To improve the model fittings, the abiotic variables and altitude were log-transformed and the HPI was transformed using the square root function. For comparison, the excrement amount of each type of livestock was standardized to 1.

All GLMMs and LMMs analyses were performed using the lme4 v 1.1-14 package [39] in the R v 3.4.0 programming environment [36].

Table 1. *p*-Values obtained in the Pearson's correlation test of predictor variables. Correlated variables are shaded.

	Goats	**Cattle**	**Equine**	**HPI**	**Temper**	**Altitude**	**Ann.Prec**	**Mth.Prec**	**Soil.depth**	**Drainage**	**Stoniness**	**Texture**
Goats	0											
Cattle	0.266	0										
Equine	0.367	0.338	0									
HPI	0.464	0.044	0.794	0								
Temper	0.120	5.2×10^{-7}	0.004	2.1×10^{-4}	0							
Altitude	0.107	7.2×10^{-5}	0.021	0.023	1.0×10^{-28}	0						
Ann.Prec	0.111	0.160	0.108	0.816	1.3×10^{-4}	3.1×10^{-11}	0					
Mth.Prec	0.701	0.381	0.635	0.010	0.355	6.4×10^{-5}	1.7×10^{-14}	0				
Soil.depth	0.578	0.012	0.181	0.000	0.000	0.000	0.034	0.136	0			
Drainage	0.412	0.000	0.011	0.023	1.0E-03	0.020	0.551	0.397	0.191	0		
Stoniness	0.912	0.536	0.831	0.949	0.000	0.000	0.000	0.000	0.000	1.0×10^{-3}	0	
Texture	0.795	0.005	0.159	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.013	0

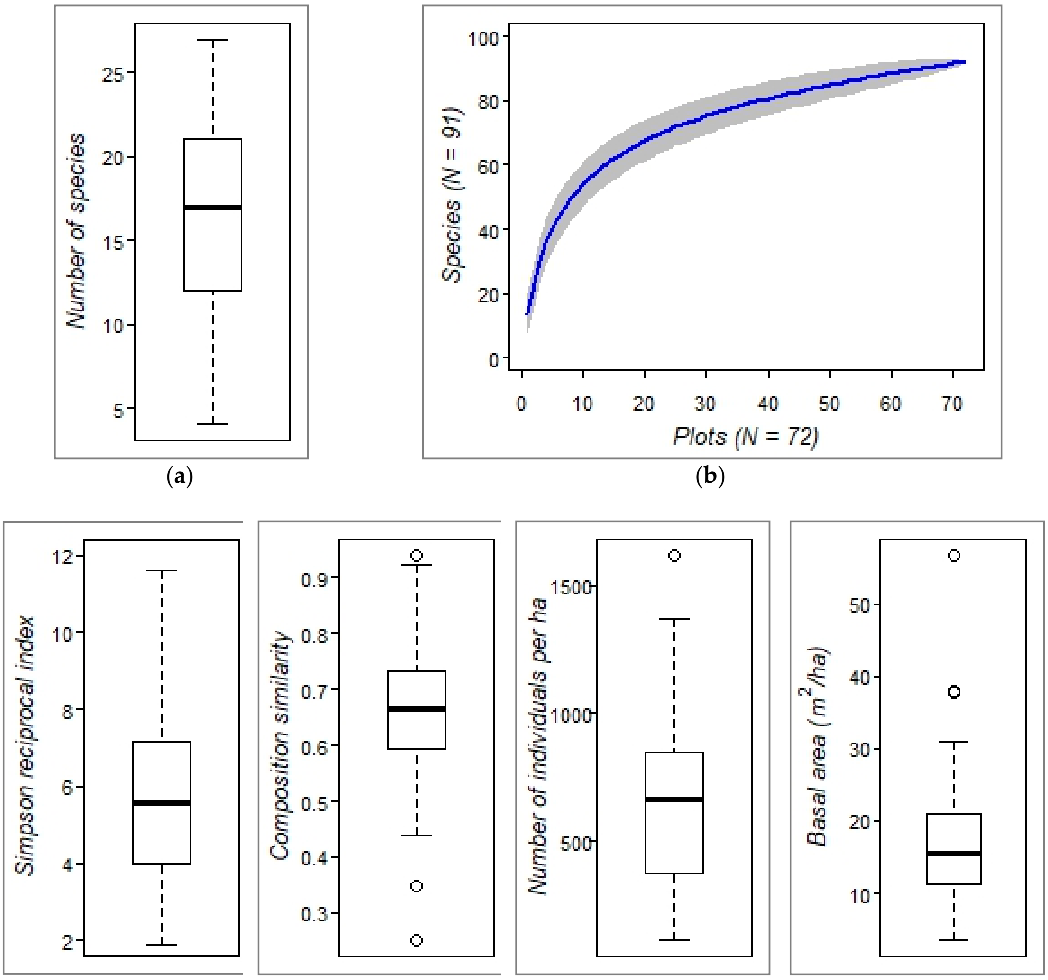
Several ways to assess the predictors' influence on one response variable are available, for instance, the stepwise procedure has been frequently used, however, it has been bypassed due to a lack of confidence in the model selection [45,48]. Without intending to criticize the procedure, we preferred to use a widely reliable process [40,41].

3. Results

3.1. Tree and Shrub Species Diversity, Composition Similarity, and Forest Structure

We recorded 7815 individuals from 91 species belonging to 34 families (Table A2). From these species, 71 were identified up to species level, 11 up to genus level, and 3 up to family level only. Six species (totaling 49 individuals) were unidentifiable and were classified as unknown. Leguminosae was the most diverse family with 24 species, followed by Malvaceae with six species. The species with the highest number of individuals were *Handroanthus chrysanthus* (1662) and *Piscidia carthagenensis* (1042).

The examined plots contained 4–27 species (Figure 3a). In the species accumulation curve (Figure 3b), 67% of the species were registered in 15 plots, and 90% were found in 45 plots. Similar results were presented in Aguirre [49]. The Simpson reciprocal indices ranged from 1.88 to 11.59 (Figure 3c). These results confirm large species diversity in the forests, reflecting the different species compositions and density landscapes in the study area.



(**a**) (**b**)

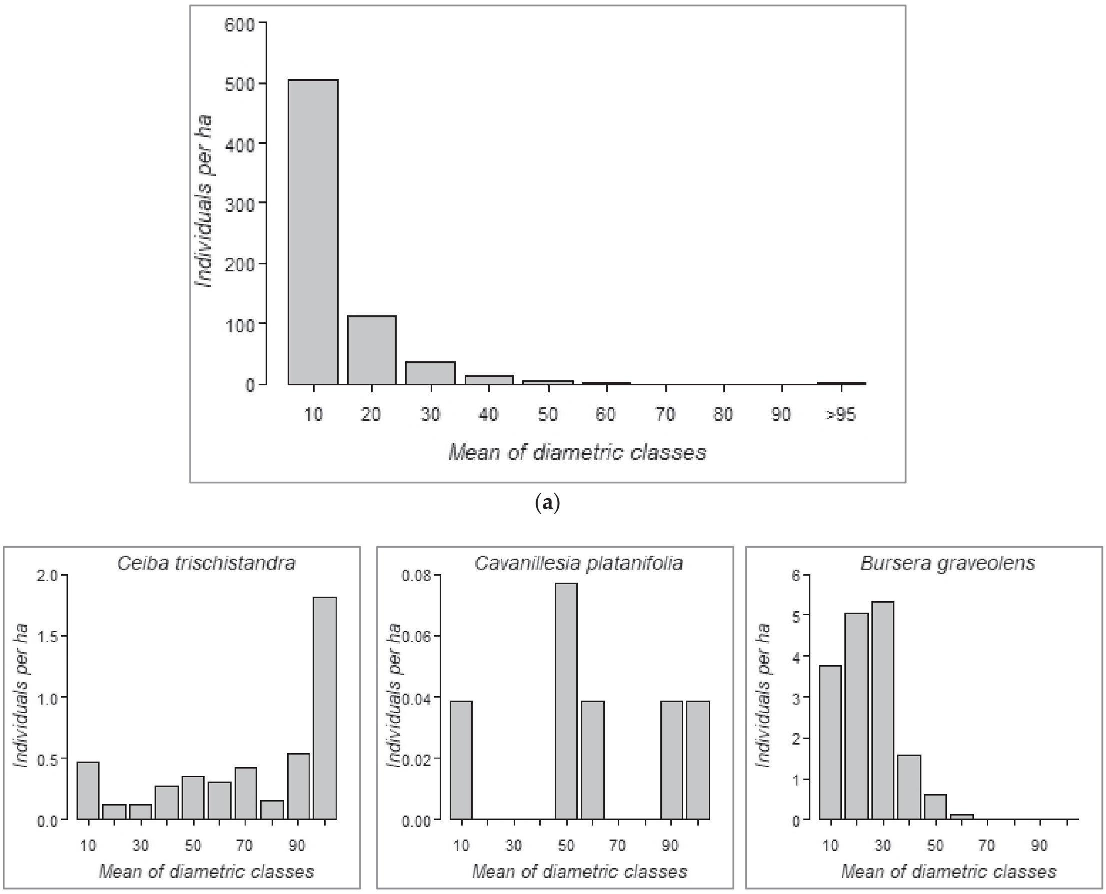
(**c**) (**d**) (**e**) (**f**)

Figure 3. Current diversity and structure situations of the forests in the study area: (**a**, **c**–**f**) ranges of species parameters in the plots; (**b**) species accumulation curve obtained via the Coleman method with confidence of 95% (grey buffer).

The Sørensen indices of the clusters (>0.6 in most clusters; see Figure 3d) evidence high similarity among the plots in each cluster. This result can be explained by the close proximity of the plots. In the single exception with low similarity among its plots, one plot was separated by a brook and located on steep land, and was hence difficult to access.

Overall, the structural parameters of the forest were found to be quite diverse. The average DBH ranged from 15.2 to 33 cm. The number of individuals per hectare ranged between 108 individuals in plots located in sparse forests (the lowest and driest parts of the ecosystem) to 1620 individuals per hectare in forest regions with higher vegetal cover (Figure 3e). The basal area ranged from 3.5 to 56.7 m^2 per hectare (Figure 3f).

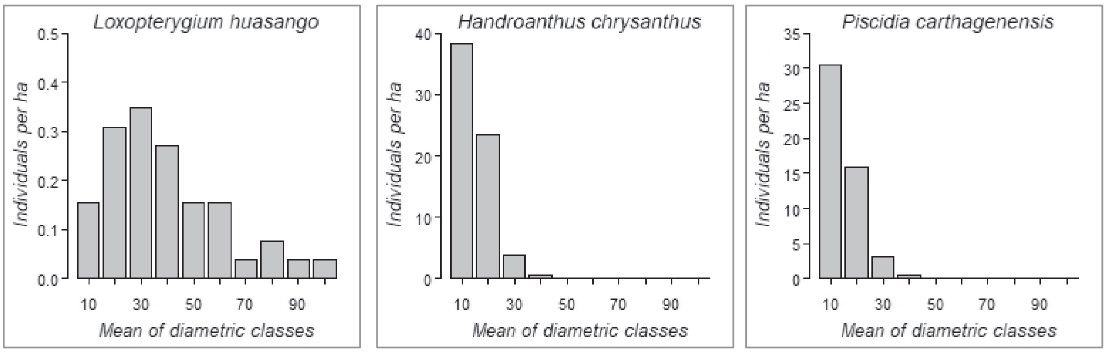
The diameter frequency distribution of all individuals followed a negative exponential relationship, as expected in natural forests (Figure 4a). However, some species distinctly deviated from this trend; for instance, the DBH exceeded 80 cm in many *Ceiba trichistandra* individuals (Figure 4b), was typically in the mid-range (15–55 cm) for *Cavanillesia platanifolia*, *Bursera graveolens*, and *Loxopterygium huasango* Spruce ex Engl. (Figure 4c–e), and never exceeded 45 cm in *H. chrysanthus* and *P. carthagenensis* (Figure 4f,g).



(**a**)

(**b**) (**c**) (**d**)

Figure 4. *Cont.*



(**e**) (**f**) (**g**)

Figure 4. Diameter class distributions of individuals per ha: (**a**) all species; (**b**–**g**) distributions of selected species.

To briefly compare the formations: we recorded 4012 individuals from 65 species, with a diversity index that varied from 2.86 to 9.81 for deciduous forest, and 4833 individuals from 82 species and Simpson reciprocal indices from 1.88 to 11.59 in semi-deciduous forest. 25 families were recorded in the deciduous formation and 34 in the semi-deciduous formation. The basal area ranged from 3.70 to 37.71 m^2/ha in deciduous and from 345 to 56.72 m^2/ha in semi-deciduous forest.

3.2. Anthropogenic Influences on Species Diversity, Similarity, and Forest Structure

Table 2 shows the best models for each response variable together with all models with ΔAICs below 2. The anthropogenic variables and annual precipitation strongly influenced all analyzed parameters.

Table 2. Best models of the five response variables. df = degrees of freedom; AIC = Akaike's information criterion; ΔAIC = Delta Akaike's information criterion; *R2m* = marginal variance explained by fixed effects; *R2c* = conditional variance explained by random and fixed effects. In models with HPI.BA, the basal area of trees and shrubs was included in the human pressure index.

Model	df	AIC	ΔAIC	*R2m*	*R2c*
Richness					
~1 + HPI.BA + Ann.Prec	4	412.44	0	0.26	0.63
~1 + HPI.BA	3	413.38	0.95	0.21	0.63
~1 + Goats + HPI.BA + Ann.Prec	5	414.33	1.89	0.26	0.63
~1 + Equine + HPI.BA + Ann.Prec	5	414.34	1.90	0.26	0.63
~1 + Cattle + HPI.BA + Ann.Prec	5	414.38	1.94	0.26	0.63
~1	2	424.54	12.10	0	0.56
Diversity					
~1 + Goats + Cattle + Equine + HPI.BA + Ann.Prec	8	282.50	0	0.28	0.31
~1 + Goats + Ann.Prec + Drainage	7	282.66	0.17	0.31	0.37
~1 + Goats + Cattle + HPI.BA + Ann.Prec	7	282.67	0.17	0.27	0.32
~1 + Goats + Equine + HPI.BA + Ann.Prec	7	283.61	1.11	0.31	0.31
~1 + Goats + HPI.BA + Ann.Prec	6	283.81	1.31	0.30	0.31
~1 + Cattle + Equine + HPI.BA + Ann.Prec	7	284.48	1.99	0.27	0.31
~1	3	311.06	28.56	0	0.20
Species similarity					
~1 + HPI.BA + Ann.Prec	5	−69.54	0	0.17	0.29
~1 + HPI.BA	4	−68.74	0.80	0.10	0.27
~1 + Temper + Mth.Prec	5	−68.19	1.35	0.08	0.31
~1 + Ann.Prec	4	−67.88	1.66	0.11	0.30
~1	3	−66.30	3.24	0	0.28

Table 2. *Cont.*

Model	df	AIC	ΔAIC	*R2m*	*R2c*
Number of individuals					
~1 + Goats + Cattle + HPI + Stoniness	7	959.85	0	0.20	0.54
~1 + Goats + Equine + HPI + Stoniness	7	960.57	0.72	0.20	0.54
~1 + Cattle + Equine + HPI + Stoniness	7	961.42	1.58	0.19	0.54
~1	3	1010.08	84.38	0	0.56
Basal area					
~1 + Temper + Mth.Prec	5	−25.59	0	0.17	0.36
~1 + HPI + Ann.Prec	5	−25.16	0.43	0.23	0.33
~1 + Temper	4	−24.71	0.89	0.12	0.35
~1 + Equine + HPI + Ann.Prec	6	−23.60	1.99	0.26	0.35
~1	3	−17.64	7.95	0	0.33

In the goodness of fit tests for species richness, 21%–26% of the variances were explained by fixed predictors (*R2m* in Table 2), and up to 63% of the variances were explained by both random and fixed predictors (*R2c* in Table 2). In the models of the Simpson index, 27%–31% of the variances were explained by fixed predictors and 30%–36% of the variances were attributed to fixed and random predictors. In the structural parameters, fixed and fixed + random predictors explained 19%–20% and 54% of the variances in terms of number of individuals respectively; in terms of basal area, fixed and fixed + random predictors explained approximately 26% and 35% of the variances, respectively. Overall, these results confirm a high contribution of fixed and random factors to the variations in the richness and number of individuals, but a lesser contribution to the variations in the Simpson index, species similarity and basal area.

Species richness is highly influenced by the HPI, annual precipitation, and presence of animals (Table 2). In the five models with ΔAIC below 2, the HPI was presented in all models and annual precipitation was included in four models. Both factors were predictors of the best model: the HPI exerted a significant negative influence (Table 3, Figure 5a). The annual precipitation exerted a positive but insignificant influence on species richness (Table 3), which seemed to culminate in the highest species number at an intermediate level of precipitation (Figure 5b).

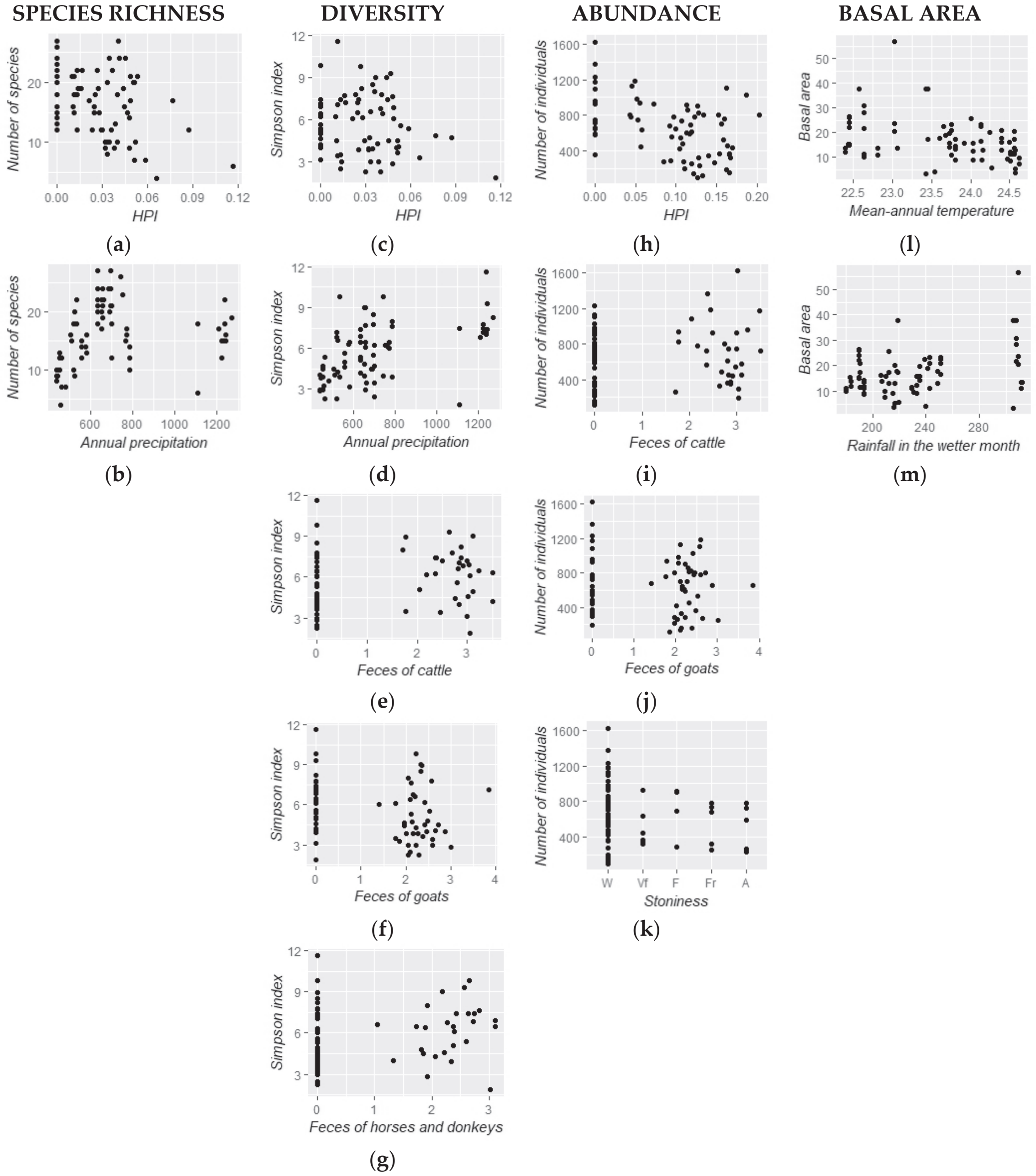
Table 3. Influence of predictors included in the best models on richness, diversity, species similarity, number of individuals, and basal area according to GLMM, *n* = 72.

Predictor	Estimates	Std. Error	*p* (<0.05)	
Richness				
HPI.BA	−7.82	2.22	2.4×10^{-4}	***
Ann.Prec	0.77	0.44	0.09	†
Diversity				
Goats	1.78	1.83	0.33	
Cattle	−1.28	1.17	0.40	
Equine	0.55	1.03	0.49	
HPI.BA	−20.38	9.34	0.03	*
Ann.Prec	7.74	1.72	1.2×10^{-5}	***
Species similarity				
HPI.BA	−0.31	0.13	0.02	*
Ann.Prec	−0.64	0.30	0.03	*
Number of individuals				
Goats	−205.80	266.51	0.42	
Cattle	−143.93	162.62	0.38	
HPI	−2411.17	777.20	2.9×10^{-3}	**
Stoniness	−20.67	32.84	0.50	

Table 3. *Cont.*

Predictor	Estimates	Std. Error	p (<0.05)	
Basal area				
Temper	−4.92	2.06	0.02	*
Mth.Prec	0.67	0.39	0.07	†

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; † $p < 0.1$.



(**a**) (**c**) (**h**) (**l**)

(**b**) (**d**) (**i**) (**m**)

(**e**) (**j**)

(**f**) (**k**)

(**g**)

Figure 5. Relationships among the predictors that partially contribute to the best models of each assessed variable. In (**a**,**c**,**h**) HPI is log-transformed. In (**k**), the horizontal axis represents the stoniness categories: W = Without; Vf = Very few; F = Few; Fr = Frequent; A = Abundant. In (**e**–**g**,**i**–**j**) the feces are expressed in grams log-transformed.

Animals exerted an apparent influence on the diversity index. Among the six models with ΔAIC lower than 2, five models included Goats, HPI, and annual precipitation; three models included horses and donkeys; two models featured cattle; and one model included soil drainage. HPI exerted a significant negative influence on the diversity index (Table 3), wherein more diversity was observed in forests that were separated from villages than in forests near villages, and more diversity was observed in forests near villages with fewer families than in forests near crowded villages (Figure 5c). Annual precipitation exerted a significant positive influence on species diversity (Table 3), suggesting that wetter places are more diverse than drier ones (Figure 5d).

Additional predictors on the best model did not significantly influence the diversity. Cattle exerted a negative influence (Table 3, Figure 5e), and goats and horses showed a positive influence (Table 3, Figure 5f,g respectively).

One extreme value of goat excrement (Figure 5f) strongly influenced species diversity. After replacing this high value by the average value and re-standardizing the variable, the effect of goat excrement was negative but insignificant (Estimate (E) = -0.4684, *p*-value (*p*) = 0.73037). Nevertheless, we found no authoritative reason to remove the extremity because it was not an outlier; rather, the value reflects a common situation in areas near goat paddocks.

Factors such as soil predictors, temperature, rainfall in the wettest months, and altitude scarcely affected the richness and diversity in this part of the forest. Soil drainage presented a positive impact (E = 0.09505, $p = 0.8239443$) in the second-best diversity model with a high goodness of fit (ΔAIC = 0.16825).

Four models substantially influenced the similarity of the species composition (Table 2). The best model included the HPI and annual precipitation. In this model, both predictors exerted significant negative effects (Table 3), thus, the species composition among the plots was more heterogenous when the HPI increased. The similarity index, which represents the species similarity among plots in the same cluster, must be high among nearby plots; therefore, the greater heterogeneity might be explained by local intervention, which affects only in one plot in the cluster.

The annual rainfall exerted a negative influence on species similarity; thus, the species composition became more heterogenous under wetter conditions.

HPI and stoniness were predictors of all three models, in terms of number of individuals with ΔAIC below 2. Goats, horses, and cows were each presented in two of these models.

Table 2 also indicates the influences of HPI, stoniness, and animals on the number of tree and shrub individuals. The best model included HPI, cattle, goats, and stoniness, all of which exerted a negative influence. However, only the HPI exerted a significant effect (Table 3). The number of individuals decreased with increasing human pressure (Figure 5h). However, a specific negative influence of cattle and goats cannot be confirmed by our data (Figure 5i,j). The extreme value of goats did not affect the results of this model. The influence of stoniness on the number of individuals was also negative but not significant (Table 3, Figure 5k).

The only variable influenced by temperature was the basal area. The best model (among four models with ΔAICs below 2) included the mean annual temperature and the rainfall amount of the wettest month. The mean annual temperature exerted a significant negative influence (Table 3), implying that the basal area decreases with increasing temperature (Figure 5l).

Precipitation in the wettest month exerted an insignificantly positive effect on the basal area (Table 3) in the best model (Figure 5m); nevertheless, a significantly positive effect on the same parameter was shown by the annual rainfall in the second-best model (E = 0.697, $p = 0.0004477$). Water availability enhances the growth of trees and shrubs. Animal presence exerted no direct effect on the stand density, although horses featured in the fourth model of the basal area. HPI exerted a significantly negative effect on the basal area in the second-best model (E = -0.8826, $p = 0.0296971$). Concordant with the number of individuals, the basal area was reduced because of wood logging.

4. Discussion

4.1. Floristic Aspects

With 91 species, our richness results are similar to those of other research performed in the study region: Andrade & Jaramillo [50] and Cueva et al. [51] reported 111 species, Aguirre [49] recorded 58 species, and Espinosa et al. [52] recorded 102 species, including trees and shrubs with DBH $\geq$5 cm. However, in a compilation of different studies and herbarium reviews, Aguirre et al. [21] reported 184 woody species in the deciduous and semi-deciduous formations of the dry forest in the Loja Province, which is double the number of species recorded herein.

Diversities similar to that reported in this research (Simpson reciprocal index from 1.88 to 11.59) were reported by Aguirre [5,49] and Muñoz et al. [53] in the Ecuadorian part of our study area; likewise, similar diversity values were reported in samples located on the Cerros de Amotape Cordillera in the Peruvian area, which was also included in our research, Linares-Palomino [54] reported Simpson values between 2.04 and 10.48.

Regarding structural aspects, species such as *C. trichistandra* (species palatable to animals), and *C. platanifolia*, (characteristic species of dry forest [5,16]), exhibited a non-habitual distribution of diametric classes. The low numbers of individuals in the lower classes might be associated with the browsing of seedlings [19]. *B. graveolens* is also palatable to animals, but the wood of old individuals is in addition used as a flavoring and repellent [55]. In contrast, we found few *H. chrysanthus*, *P. carthagenensis*, and *L. huasango* individuals in the upper classes, suggesting that these valuable species could have been selectively felled until 1978 [19], i.e., before the region was declared closed area, therefore, the latter result may be a consequence of past utilization.

The numbers of individuals and basal area widely differed throughout the forest (Figure 3d,e). In several cases, the less abundant samples occupied the lowest and driest areas; however, this finding cannot be generalized. For instance, one plot with few individuals (located at 255 m a.s.l where the annual precipitation is 457 mm) spanned 108 ind./ha with a basal area of 3.8 m^2/ha, whereas another plot with similar characteristics (247 m a.s.l., annual precipitation 467 mm) spanned 911 ind./ha with a basal area of 15.9 m^2/ha. Similar situations were relatively common, and were also found in species composition, indicating that factors other than abiotic factors promote these spatial differences. For this reason, pressure predictors and soil characteristics were included in this study.

4.2. Diversity, Similarity, and Structure

In our study, HPI most powerfully predicted the richness and abundance of trees and shrubs in the forest, because it negatively influenced four of the five analyzed parameters (Figure 5a,c,h). The basal area of trees and shrubs was less sensitive to the HPI. Espinosa [52] reported the same effect of anthropogenic disturbance on species richness in a dry forest in the Tumbesian region (approximately 100 km east of our study area). Gillespie [56] also found a significant correlation between these factors in dry forests from Central America, and Sagar [57] reported significant differences in species richness, basal area, and abundance among samples with different disturbance levels in India. Thus, our results confirm the findings of other authors [1,3,7], who identified human presence as the primary cause of dry forest degradation.

Agricultural activities could be most dangerous to this area of dry forest. Corn cultivation is common throughout the area during the rainy season, but more so in higher parts to take advantage of the humidity. This activity means a complete change of land use since it eases sowing, cleaning and harvesting tasks. Wood logging is less practiced nowadays; it is allowed for local use, in which case it is a selective extraction. These could be some causes for the high influence of HPI.

Herein, cattle exerted a negative influence on three of our assessed parameters (but exerted no effect on basal area) (Figure 5e,i). In addition to browsing on the vegetation, cattle can trample the soil, preventing the growth of new seedlings. These observations are consistent with Stern et al.'s [58] report that in two protected areas in Costa Rica (Parque Nacional Palo Verde and Reserva Biológica

Lomas Barbudal), both the diversity and structure of the forests have been significantly influenced by cattle grazing. The same conclusion was reported by Gillespie [56] in Central America, wherein he asserted that cattle reduce the capacity of seeds to germinate and that intensive grazing can generate spiny and unpalatable forests. However, as the livestock density in our study has only been estimated from feces, the respective results have to be interpreted with caution.

In contrast to cattle, goats and horses exerted a positive influence on species richness and diversity (Figure 5f,g). This can be explained by the lower food selectivity of these animals and their input of micronutrients to the soil. These micronutrients favor plant growth, as reported by García-Moreno et al. [59] for *Quercus ilex* L. in a Mediterranean open forest. They found significantly higher N and Mg concentrations in the leaves of trees growing in intensively grazed areas, together with elevated inorganic N in the soil. Nevertheless, the negative influence of goats on the number of individuals is explained by the loss of individuals that are eaten or trampled, particularly when seedlings are small [19], which is common in dry forests; this is because seedlings are especially vulnerable to such losses.

Our results revealed a clear but differentiated effect of livestock, indicating a need for more suitable information regarding livestock activities. Detailed counting of animals may improve the results; however, such counting requires much higher efforts on the part of researchers and farmers. Hence, our method and other similar methods should be used and improved upon in future work.

We found that human pressure heterogenized rather than homogenized the forest; at least, human-induced homogeneity was not identifiable in nearby plots. Considering that the driest areas support the fewest species, the extraction of one individual could promote the loss of that species in the plot. This might explain the differences in the numbers of species among nearby samples in our study, and the consequent heterogenization. These results differ from McKinney et al. [11] who stated that homogenization of a forest is the main effect of anthropic perturbation.

We also found that high annual rainfall increased the heterogeneity among the plots. This reflects the higher species richness observed in the wetter areas than the drier areas of our studied ecosystem. Likewise, in all models with a partial contribution of annual precipitation, the predictor positively affected species richness and diversity (Figure 5b,d).

According to Gentry [7] and Gillespie [56], precipitation is a poor predictor of plant diversity in the dry forest of Central America. Furthermore, Espinosa [52] predicted a negative correlation between precipitation and plant diversity. Nevertheless, both Gentry [60] and Clinebell et al. [61] were able to correlate these two factors when a dry–wet gradient existed in the forest. Considering the altitudinal gradient of our study area (200–1100 m a.s.l.) and that the semi-deciduous dry forest lies directly below the low montane dry forest [5,16], we confirmed a transitional formation between the dry and wet forest in our study area. This transition occurs from 1000 m a.s.l in Lozano [16] and from 900 m a.s.l in Aguirre [5].

The negative influence of stoniness on the number of individuals (see Figure 5k) is probably most relevant in the seed germination stage. When seeds meet unfavorable conditions for germinating, their mortality rate should increase, thereby reducing the number of individuals that reach maturity. Unfortunately, we found no previous study that investigated this predictor; hence, a comparison of our results is not possible.

The mean annual temperature only weakly affected the analyzed factors. The exception was the basal area of trees and shrubs, which was significantly negatively influenced by mean temperature (Figure 5l). This trend can be explained by the increased evapotranspiration of plants at high temperatures, which reduces their growth. Contrary to Espinosa [52], we found no relation between this predictor and species richness; however, as the mean annual temperature is strongly correlated with both annual rainfall and altitude (Table 1), we cannot neglect its effect on any of the assessed factors.

The influence of anthropogenic predictors was rarely reported in our reviewed literature. With the exception of Espinosa [52], the methodologies of these studies differed from ours.

For instance, Gillespie et al. [56] assessed the influence of human activities by correlating them with forest parameters; Stern, et al. [58] compared the situations in areas with and without grazing; and García-Moreno et al.'s [59] study focused on one species.

5. Conclusions

The composition and structure of the forest in the study area is primarily influenced by abiotic and human pressure factors. The soil characteristics exert weak effects at most.

Similar to other dry forests around the globe, our models confirmed that anthropogenic pressure has already largely modified the diversity and structure of the dry forest in the central part of the Tumbesian region. In fact, this factor affected all studied parameters. Cattle exert the most damaging effects on species richness, diversity, and abundance. Protective measures, such as prohibiting or restricting cattle in largely affected areas and areas of high biological importance, and reducing cattle ownership per family, should be considered.

Goats do not affect the species richness or diversity in the mature forests of our study area, but they reduce the abundance of individuals. Horses and donkeys did not affect any of the analyzed aspects. However, to identify the long-term effects, assessing the influence on the natural regeneration of the forest is necessary.

We emphasize that our results and conclusions about animal effects should be taken with caution, since we consider that feces, while it provides an approximation of animal number, is subject to high inaccuracy, due to decomposition provoked, for instance, by climatic factors.

Among the abiotic factors, annual precipitation was the most important positive predictor of species richness and diversity in the central zone of the Tumbesian region, despite the briefness of the rainy period.

Human pressure has not affected forest heterogeneity among nearby plots in our study area, where environmental conditions are constant and the human pressure is almost identical in different plots. The annual rainfall is the most important predictor of species heterogeneity in this part of the forest.

The diversity and structural parameters were consistent with similar research on this dry forest. However, complementary studies are necessary to clarify the influencers of characteristic species and to clarify whether unusual behaviors result from human or animal interventions, or arise from environmental conditions.

The most important deficiency in this research is probably the lack of information regarding the number of animals throughout the area, and soil characteristics in the Peruvian part of the study area. When these details are known, a better approximation of the true situation can likely be achieved.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1. Figures S1–S5. Residuals distribution of the best model of each of the assessed variables. Figure S1. Residuals distribution of the best model of richness. Figure S2. Residuals distribution of the best model of diversity. Figure S3. Residuals distribution of the best model of abundance. Figure S4. Residuals distribution of the best model of basal area. Figure S5. Residuals distribution of the best model of species similarity. Table S1. Dataset of assessed variables and, biotic and abiotic predictors of the central part of the Tumbesian region. Values are given for each sample.

Author Contributions: Conceptualization: J.C.O., P.H. and C.I.E.; Methodology: J.C.O., P.H., C.I.E., Z.A.M. and E.C.O.; Formal Analysis: J.C.O.; Investigation: J.C.O.; Data Curation: J.C.O. and E.G.; Writing—Original Draft Preparation: J.C.O.; Writing—Review & Editing: J.C.O., C.I.E., C.Q.D., Z.A.M., E.C.O., M.W. and P.H. Visualization: J.C.O. and P.H.; Supervision: M.W.; Funding Acquisition: J.C.O., P.H., C.I.E. and M.W.

Funding: This research was funded by the DFG project PAK 824/B3, project PROY_CCN_0030 under Universidad Técnica Particular de Loja, and project PIC-13-ETAPA-005 under Secretaria de Eduación Superior, Ciencia, Técnología e Innovación (SENESCYT). J.C.O. and C.Q.D. were funded via scholarships of SENESCYT. J.C.O. received support from Erzbischöfliches Ordinariat München. In addition, this work was supported by the German Research Foundation (DFG) and the Technical University of Munich (TUM) in the framework of the Open Access Publishing Program.

Acknowledgments: We wish to thank Thomas Knoke for his contribution to data analysis, also to Proofreading Service of TUM Graduate School and Elizabeth Gosling for their contribution with the language revision. We are also grateful to Naturaleza y Cultura Internacional, Parque Nacional Cerros de Amotape, and the communities

Malvas, El Cardo, and Piedras Blancas for allowing us to conduct this research on the reserves of La Ceiba, Cazaderos, Cerros de Amotape National Park, Limones, Piedras Blancas and El Cardo. Furthermore, we would to thank Diego González, Jorge Armijos, Geovanny Cango, Angel Gusmán, Johana Gusmán, Israel Medina, Yodán Zapata, Flavio Olaya, and the different communities for their support in data collection.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Candidate Models (Constructed from Predictor Variables Only).

ID	Model	ID	Model
1	~1	44	~1 + Goats + Cattle + Equine + HPI + Stoniness
2	~1 + Goats	45	~1 + Cattle
3	~1 + Goats + Cattle	46	~1 + Cattle + Equine
4	~1 + Goats + Equine	47	~1 + Cattle + HPI
5	~1 + Goats + HPI	48	~1 + Cattle + Ann.Prec
6	~1 + Goats + Temper	49	~1 + Cattle + Mth.Prec
7	~1 + Goats + Altitude	50	~1 + Cattle + Stoniness
8	~1 + Goats + Ann.Prec	51	~1 + Cattle + Equine + HPI
9	~1 + Goats + Mth.Prec	52	~1 + Cattle + Equine + Ann.Prec
10	~1 + Goats + Soil.depth	53	~1 + Cattle + Equine + Mth.Prec
11	~1 + Goats + Drainage	54	~1 + Cattle + Equine + Stoniness
12	~1 + Goats + Stoniness	55	~1 + Cattle + HPI + Ann.Prec
13	~1 + Goats + Texture	56	~1 + Cattle + HPI + Stoniness
14	~1 + Goats + Cattle + Equine	57	~1 + Cattle + Equine + HPI + Ann.Prec
15	~1 + Goats + Cattle + HPI	58	~1 + Cattle + Equine + HPI + Stoniness
16	~1 + Goats + Cattle + Ann.Prec	59	~1 + Equine
17	~1 + Goats + Cattle + Mth.Prec	60	~1 + Equine + HPI
18	~1 + Goats + Cattle + Stoniness	61	~1 + Equine + Ann.Prec
19	~1 + Goats + Equine + HPI	62	~1 + Equine + Mth.Prec
20	~1 + Goats + Equine + Ann.Prec	63	~1 + Equine + Soil.depth
21	~1 + Goats + Equine + Mth.Prec	64	~1 + Equine + Stoniness
22	~1 + Goats + Equine + Soil.depth	65	~1 + Equine + Texture
23	~1 + Goats + Equine + Stoniness	66	~1 + Equine + HPI + Ann.Prec
24	~1 + Goats + Equine + Texture	67	~1 + Equine + HPI + Stoniness
25	~1 + Goats + HPI + Ann.Prec	68	~1 + Equine + Mth.Prec + Soil.depth
26	~1 + Goats + HPI + Stoniness	69	~1 + HPI
27	~1 + Goats + Temper + Mth.Prec	70	~1 + HPI + Ann.Prec
28	~1 + Goats + Ann.Prec + Drainage	71	~1 + HPI + Stoniness
29	~1 + Goats + Mth.Prec + Soil.depth	72	~1 + Temper
30	~1 + Goats + Mth.Prec + Drainage	73	~1 + Temper + Mth.Prec
31	~1 + Goats + Soil.depth + Drainage	74	~1 + Altitude
32	~1 + Goats + Drainage + Texture	75	~1 + Ann.Prec
33	~1 + Goats + Cattle + Equine + HPI	76	~1 + Ann.Prec + Drainage
34	~1 + Goats + Cattle + Equine + Ann.Prec	77	~1 + Mth.Prec
35	~1 + Goats + Cattle + Equine + Mth.Prec	78	~1 + Mth.Prec + Soil.depth
36	~1 + Goats + Cattle + Equine + Stoniness	79	~1 + Mth.Prec + Drainage
37	~1 + Goats + Cattle + HPI + Ann.Prec	80	~1 + Mth.Prec + Soil.depth + Drainage
38	~1 + Goats + Cattle + HPI + Stoniness	81	~1 + Soil.depth
39	~1 + Goats + Equine + HPI + Ann.Prec	82	~1 + Soil.depth + Drainage
40	~1 + Goats + Equine + HPI + Stoniness	83	~1 + Drainage
41	~1 + Goats + Equine + Mth.Prec + Soil.depth	84	~1 + Drainage + Texture
42	~1 + Goats + Mth.Prec + Soil.depth + Drainage	85	~1 + Stoniness
43	~1 + Goats + Cattle + Equine + HPI + Ann.Prec	86	~1 + Texture

Table A2. List of Species in the Study Area.

Family	Species
Achatocarpaceae	*Achatocarpus pubescens* C. H. Wright
Anacardiaceae	*Loxopterygium huasango* Spruce ex Engl. *Spondias purpurea* L.
Annonaceae	*Annona muricata* L.
Apocynaceae	*Aspidosperma* sp. *Aspidosperma* sp. 2
Asteraceae	*Fulcaldea laurifolia* (Bonpl.) Poir.
Bignoniaceae	*Anemopaegma* sp. *Handroanthus billbergii* (Bureau & K.Schum.) S.O.Grose *Handroanthus chrysanthus* (Jacq.) S.O.Grose *Tecoma stans* (L.) Juss. ex Kunth
Bixaceae	*Cochlospermum vitifolium* (Willd.) Spreng.
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken *Cordia lutea* Lam. *Cordia macrantha* Chodat
Burseraceae	*Bursera graveolens* (Kunth) Triana & Planch.
Cactaceae	*Cereus diffusus* (Britton & Rose) Werderm.
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg. *Celtis loxensis* C.C. Berg
Capparaceae	*Colicodendron scabridum* (Kunth) Seem *Cynophalla flexuosa* (L.) J.Presl *Cynophalla* sp.
Caricaceae	*Vasconcellea parviflora* A. DC.
Celastraceae	*Salacia* sp.
Combretaceae	*Terminalia valverdeae* A.H. Gentry
Convolvulaceae	*Ipomoea pauciflora* M. Martens & Galeotti *Ipomoea* sp.
Erythroxylaceae	*Erythroxylum glaucum* O. E. Schulz
Euphorbiaceae	*Croton* sp. *Jatropha curcas* L. Spp. 5
Leguminosae	*Acacia macracantha* Humb. & Bonpl. ex Willd. *Albizia multiflora* (Kunth) Barneby & J.W. Grimes *Bauhinia aculeata* L. *Bauhinia* sp. *Caesalpinia glabrata* Kunth *Caesalpinia spinosa* (Molina) Kuntze *Centrolobium ochroxylum* Rose ex Rudd *Chloroleucon mangense* (Jack.) Britton & Rose *Erythrina velutina* Willd. *Geoffroea spinosa* Jacq. *Leucaena trichodes* (Jacq.) Benth. *Machaerium millei* Standl. *Mimosa acantholoba* (Willd.) Poir. *Mimosa pigra* L. *Mimosa* sp. *Myroxylon balsamum* (L.) Harms. *Piptadenia flava* (Spreng. ex DC.) Benth. *Piscidia carthagenensis* Jacq. *Pithecellobium excelsum* (Kunth) Mart. *Prosopis juliflora* (Sw.) DC. *Senna bicapsularis* (L.) Roxb. *Senna incarnata* (Pav. & Benth.) H.S. Irwin & Barneby *Senna mollissima* (Willd.) H.S. Irwin & Barneby *Senna spectabilis* (DC.) H.S. Irwin & Barneby.

Table A2. *Cont.*

Family	Species
Malvaceae	*Cavanillesia platanifolia* (Bonpl.) Kunth *Ceiba insignis* (Kunth) P.E. Gibbs & Semir *Ceiba trischistandra* (A.Gray) Bakh. *Eriotheca roseorum* (Cuatrec.) A.Robyns *Eriotheca ruizii* (K. Schum.) A. Robyns *Guazuma ulmifolia* Lam.
Meliaceae	*Trichilia hirta* L.
Moraceae	*Ficus jacobii* Vázq. Avila *Ficus obtusifolia* Kunth. *Maclura tinctoria* (L) Steud.
Muntingiaceae	*Muntingia calabura* L.
Myrtaceae	*Psidium guajava* L. *Psidium* sp. Spp. 1
Nyctaginaceae	*Bougainvillea peruviana* Bonpl. *Pisonia aculeata* L. *Pisonia floribunda* Hook. F. Spp. 3
Opiliaceae	*Agonandra excelsa* Griseb.
Phytolaccaceae	*Gallesia integrifolia* (Spreng.) Harms
Polygonaceae	*Coccoloba ruiziana* Lindau *Triplaris cumingiana* Fisch. & C.A.Mey.
Rhamnaceae	*Ziziphus thyrsiflora* Benth.
Rubiaceae	*Phialanthus* sp. *Randia armata* (Sw.) DC. *Simira ecuadorensis* (Standl.) Steyerm.
Salicaceae	*Prockia crucis* P. Browne ex L.
Sapindaceae	*Sapindus saponaria* L.
Solanaceae	*Acnistus arborescens* (L.) Schltdl
Unknown	Spp. 2 Spp. 4 Spp. 6 Spp. 7 Spp. 8 Spp. 9
Verbenaceae	*Citharexylum poeppigii* Walp
33	91

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Publication 2.

Title:	Natural Regeneration in the Tumbesian Dry Forest: Identification of the Drivers Affecting Abundance and Diversity
Authors:	Cueva O., J., Espinosa, C. I., Aguirre-Mendoza, Z., Gusmán-Montalván, E., Weber, M., & Hildebrandt, P.
Journal:	Scientific *Reports*
Published:	Juny 17, 2020

www.nature.com/scientificreports

SCIENTIFIC
REPORTS
natureresearch

Natural Regeneration in the Tumbesian Dry Forest: Identification of the Drivers Affecting Abundance and Diversity

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Tropical and subtropical dry forests make up the world's largest terrestrial ecosystem. However, these forests have been used to establish several productive activities, such as growing crops, rearing livestock, and using the forest resources, due to their ease of access and climatic conditions, which has led to this ecosystem becoming highly threatened. Therefore, this research assessed the effects of anthropogenic pressures and a number of abiotic variables on natural regeneration in dry forests in the Tumbesian region by addressing three research questions: (a) What is the status of natural regeneration in terms of abundance and diversity? (b) Does livestock grazing and the anthropogenic pressure affect the abundance and diversity of natural regeneration? (c) Does seasonality or grazing have the greatest influence on the regeneration dynamics? Data were obtained from 72 samples (36 fenced and 36 unfenced) during five surveys spanning a 2-year period, and the seedling abundance, mortality, recruitment, species richness and diversity were evaluated using linear mixed models. Natural regeneration was most positively affected by rainy season precipitation, but soil conditions also played an important role. Short-term fences had a major effect on reducing mortality but did not improve the abundance or diversity, whereas cattle grazing significantly affected the abundance of seedlings.

Scientists have been depicting the threats that tropical dry forests are exposed to for many years[1–6] and have identified some parts of this ecosystem as places of tremendous diversity and endemism[7–9]. These insights have supported the establishment of new protected areas in several regions of the world–for instance, the Brazilian Minister of the Environment identified 52 priority areas for conservation in the Caatinga in 2002, 27 of which were catalogued as an extreme priority[10]; Koleff *et al.*[11] stated in 2012 that 42% of the Mexican tropical dry forests should be protected; several private and state-owned areas were added to the list of protected areas in Ecuador, including the 'Bosques de Paz' Biosphere Reserve, in 2017[12]; and one of the most representative areas of Peru was placed under protection by the Amazonas Department in 2018[13]. However, although the number of protected areas has increased and a large amount of research has been undertaken on the biophysical aspects of tropical dry forests of Latin America, Caribbean and Africa[14,15], little is known about the ecology and regeneration of tropical dry forests[16] or the effects of domestic animals and other threats on the natural regeneration of these forests, which are still diminishing in size[14].

The tropical dry forest that extends along the Pacific coast from the southwest of Ecuador to the northwest of Peru covers approximately 64,500 km^2 [17] and faces similar issues[18]. This region, which is named the 'Tumbesian region', is known for its high level of endemism among woody species[7,19] and for being one of the better preserved areas in the region[20,21]. Some effort has been made to understand the ecosystem functionality and the effects of animals on the forest in this region, examples of which include the studies of Jara-Guerrero *et al.*[22], Espinosa *et al.*[18,23,24], Piana & Marsden[25] and Cueva *et al.*[26], who evaluated the influence of environmental conditions, anthropogenic disturbances or soil characteristics on seed dispersal or composition of mature dry forest. However, little attention has been paid to the natural regeneration, which has rarely been studied in the region (neither that

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generated by sprouts nor by seeds), despite this being a key component of the sustainability of the forest[27]. Studies that have been conducted include an assessment of the effect of goats in one village of Ecuador by Rodriguez in 2006[28], a very short report on a protected area in Peru by Abou *et al*. in 2010[29], and a structural and compositional characterisation of regeneration in three dry forest types in Ecuador by Aguirre *et al*. in 2013[30].

As with most tropical dry forests, natural regeneration in the Tumbesian region is affected by seasonality, which is characterised by a long period of drought for 7 months of the year[31], as well as by human activities, particularly the grazing of domestic animals[20]. However, the extent to which natural regeneration is affected by these biotic and abiotic factors remains poorly understood. Therefore, in this study, we attempted to fill these knowledge gaps by addressing the following research questions: (a) What is the status of natural regeneration in the dry forest in terms of abundance and diversity, taking into account seasonality and grazing? (b) Do livestock grazing and other anthropogenic pressures affect the abundance and diversity of natural regeneration in the dry forest? (c) Does seasonality or grazing have the greatest influence on the dynamics of natural regeneration in the dry forest?

Results

Status of natural regeneration. Measurements were made across a total of 1,152 m^2 of dry forest during five surveys (four in fenced plots), that were carried out over a nearly 2-year period. The total number of seedlings recorded in fenced plus unfenced plots in the evaluated area were: 6,280; 4,751; 5,069 and 4,572 individuals in surveys 2, 3, 4 and 5 respectively. The average number of seedlings per plot projected to one hectare and computed for each survey varied from 21,900 to 57,200 individuals in unfenced plots and from 43,500 to 51,800 individuals per ha in fenced plots (Fig. 1a). The average abundance decreased slightly from the rainy season to the dry seasons, but remained relatively constant when measurements from the same season and treatment were compared. This seasonal effect was less pronounced in the fenced plots than the unfenced plots due to the lower dry season mortality (Fig. 1b) resulting in similar numbers of individuals occurring in the two seasons (median number of individuals per ha = 35,300–41,200 in fenced plots and 26,900–40,600 in unfenced plots).

In the first rainy season, *Simira ecuadorensis* (Standl.) Steyerm and *Erythroxylum glaucum* O. E. Schulz had the highest abundances in the study area (1,447 and 1,371 individuals, respectively). *Simira ecuadorensis* showed good resistance to the dry season, with 1,561 individuals being recorded in the final survey. By contrast, most *E. glaucum* individuals died during the dry season, with only 265 individuals being recorded alive in the final survey.

During the monitoring period, the mortality of plants was influenced by seasonality, increasing from an average of 9.0% in the rainy season to 35.8% in the dry season, with the same pattern being observed across both treatments (Fig. 1b). However, mortality was slightly lower in the fenced plots than in the unfenced plots. Substantial recruitment was recorded in the fenced plots in surveys 3 and 4 (21.4% and 16.6%, respectively), whereas recruitment was very low in the final survey (3.1%). By contrast, recruitment decreased over time from 16.1% to 3.7% in the unfenced plots, even during the rainy season (Fig. 1c).

A total of 85 species from 31 families were recorded in the study area (see Supplementary Table S1), which included 37 tree species, 36 shrub species and 12 species that could not be identified. The number of species remained almost the same across surveys 2 to 5 in the unfenced plots (mean = 8.8, 8.6, 9.1 and 8.7 species per plot, respectively) but showed a slight increase over time in the fenced plots (mean = 8.4, 8.8, 9.6 and 9.4 species per plot) (Fig. 1d). A similar pattern was also observed for Simpson's index, which had mean values ranging from 0.62 in survey 1 to 0.67 in survey 4 for the unfenced plots and 0.62 in survey 3 to 0.66 in survey 4 for the fenced plots (Fig. 1e). Surprisingly, during the evaluation period no seedlings were recorded for some of the characteristic species[32] of the study area, including *Ceiba trischistandra* (A.Gray) Bakh., *Cavanillesia platanifolia* (Bonpl.) Kunth, *Eriotheca roseorum* (Cuatrec.) A.Robyns and *Myroxylon balsamum* (L.) Harms. Furthermore, only a few individuals of other species were recorded, such as *Centrolobium ochroxylum* Rose ex Rudd (one individual) and *Loxopterygium huasango* Spruce ex Engl. (two individuals).

Effects of biotic and abiotic factors on natural regeneration. Model selection revealed that the amount of variance in abundance that could be explained by the best models ranged from 10% to 13% for the fixed effects and from 56% to 60% for the fixed + random effects. Abundance appears to be more influenced by pressure predictors (Table 1). By contrast, the amount of variance in species richness that could be explained by the best models ranged from 51% to 63% for the fixed effects and equated to 72% for the fixed + random effects. The diversity was explained only by the soil predictors; just one model was selected, which explained 40% of the variance using the fixed effects and 53% of the variance using both fixed + random effects.

Four models were identified as best explaining the abundance of natural regeneration (Table 1). All of these models included rainy season precipitation (SPrec) and three included the interaction between the presence of horses and donkeys (Equine) and treatment (Treat). Only the best model included the presence of cows and bulls (Cattle) as an independent predictor, while the second and third best model include this predictor as a term of interaction. The four-way interaction between the presence of goats (Goats), Cattle, Equine and Treat was included in the second-best model, and the interaction between Cattle and Treat was included in the third-best model.

Both Equine and SPrec had significant positive effects on the abundance of natural regeneration, with the latter having the most evident positive effect (Table 2; Fig. 2a,b). By contrast, Cattle had a significant negative effect on abundance (Table 2; Fig. 2c), indicating that natural regeneration is affected by the grazing of cows and bulls. While fences (Treatopen) did not affect the number of individuals when it was used as main predictor (Fig. 2d), the interaction Treat and Equine had a significant negative effect (Table 2; Fig. 2e), demonstrating that the abundance of regenerating seedlings was lower in unfenced sites where horses were present than in fenced sites where horses had previously been present.

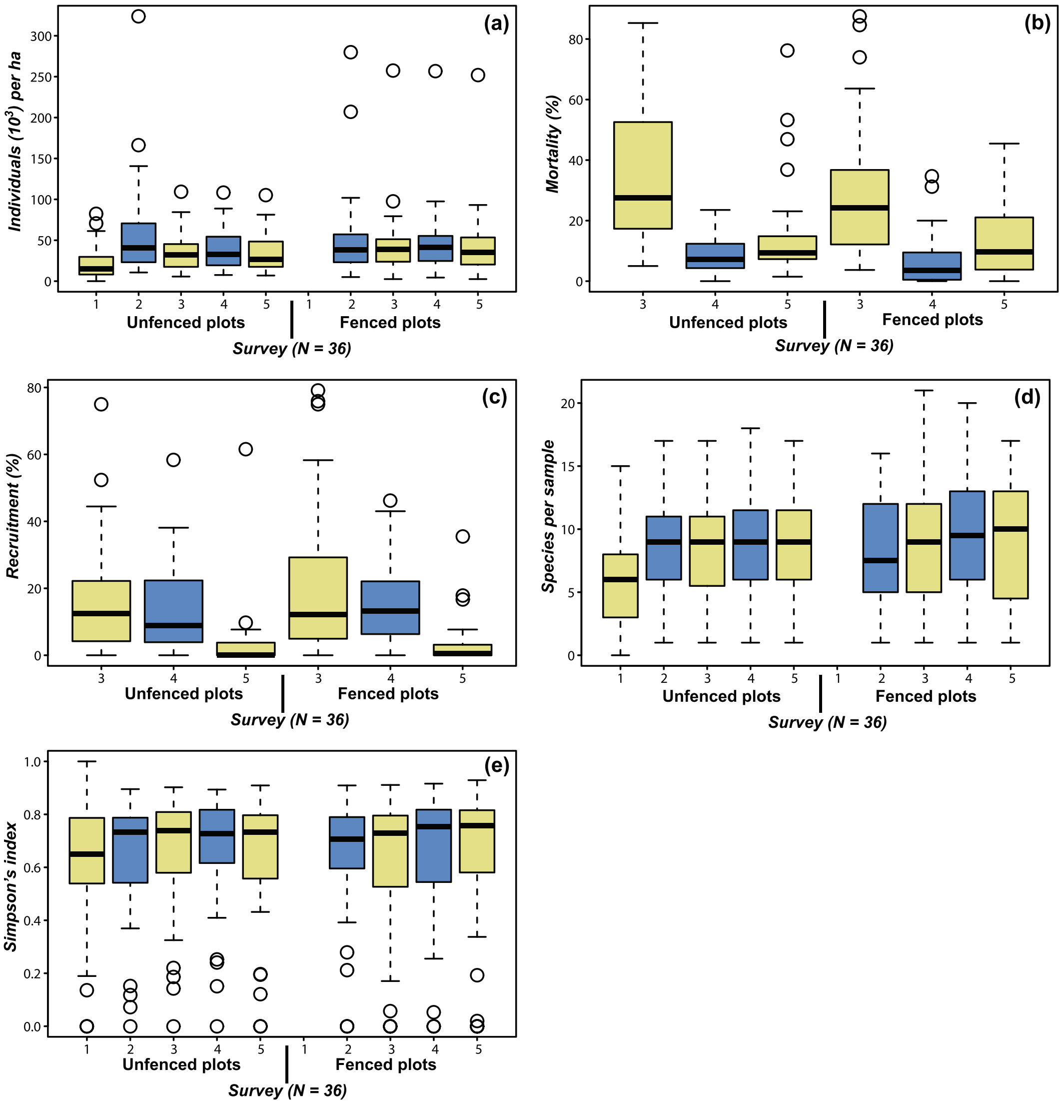

Figure 1. Changes in the natural regeneration parameters through time and under different treatments. **(a)** Abundance, **(b)** mortality, **(c)** recruitment, **(d)** species richness and **(e)** diversity of seedlings on each survey date in unfenced and fenced plots. Fenced plots were not assessed in survey 1 because they were selected based on the first evaluation of the unfenced plots. Numbers from 1 to 5 correspond to consecutive surveys, which spanned a 2-year period. Yellow = dry season, blue = rainy season.

Species richness was best explained by five models, all of which included SPrec, four of which included soil depth (SDepth) and drainage (Drain), and three of which included Treat (Table 1). All of these predictors were included in the best model.

SPrec had a significant positive influence on species richness (Table 2), indicating that species richness was higher in the rainy season. Species richness was also significantly higher in sites with deeper soils than in sites with shallow soils (<10 cm) and in sites with moderately and well-drained soils than in sites with compacted or non-permeable soils (Table 2). As seen for abundance, fences did not affect the species richness in our study area.

Only one model was selected for diversity, which included soil drainage and texture (Text) as predictors (Table 1). Moderately drained soils had a significant positive effect on the diversity compared with poorly drained soils, and sites with clay loam and loam soils had a significantly higher diversity than those with clay–sandy loam soils (Table 2).

Regarding the dynamics of natural regeneration, 36% and 56% of the variance in mortality was explained by the fixed and fixed + random effects, respectively, that were included in the best model, while 30–35% and 60–61% of the variance in recruitment was explained by the fixed and fixed + random effects, respectively (Table 3).

Only one model was identified as best explaining mortality, which included SPrec, Treat and elapsed time (Time) as fixed effects (Table 3). Both SPrec and Time had significant negative effect on mortality (Table 4), indicating that mortality was lower in the rainy season than in the dry season and also decreased with elapsed

Model	df	AIC	ΔAIC	*R2m*	*R2c*
Abundance					
~1 + Equine * Treat + SPrec + Cattle	8	3158.11	0.00	0.10	0.57
~1 + Goats * Cattle * Equine * Treat + SPrec	19	3159.10	0.99	0.13	0.60
~1 + Equine * Treat + Cattle * Treat + SPrec	9	3159.94	1.83	0.10	0.57
~1 + Equine * Treat + SPrec	7	3159.97	1.86	0.10	0.56
Species richness					
~1 + SPrec + Treat + SDepth + Drain	12	1530.18	0.00	0.63	0.72
~1 + SPrec + SDepth + Drain	11	1530.45	0.28	0.62	0.72
~1 + Equine + SPrec + Treat + SDepth + Drain	13	1531.73	1.56	0.63	0.72
~1 + Cattle + SPrec + Treat + Text	10	1531.82	1.65	0.51	0.72
~1 + Equine + SPrec + SDepth + Drain	12	1532.01	1.83	0.63	0.72
Diversity					
~1 + Drain + Text	8	−233.70	0.00	0.40	0.53

Table 1. Best models explaining the influence of biotic and abiotic factors on the response variables abundance, species richness and diversity. Linear mixed models were computed using a negative binomial error distribution for abundance, the Poisson distribution with the Laplace approximation for species richness and the restricted maximum likelihood (REML) approach for diversity. Models were selected and ordered according to the delta Akaike information criterion ($\Delta AIC < 2$). *R2m* and *R2c* represent the amount of variance that was explained by the fixed effects and fixed + random effects, respectively.

time through the monitoring period. In addition, the mortality of natural regeneration was significantly higher in unfenced plots than in the fenced plots.

The two best models explaining recruitment both included SPrec and Time as predictors (Table 3). While both of these predictors had a positive influence on recruitment, only SPrec was significant (Table 4), indicating that the recruitment of new individuals increases during the rainy season. There was also a significant negative interaction between these predictors on the recruitment of new seedlings, demonstrating that the effect of the rainy season precipitation decreased as time elapsed or the effect of time decreased as rainfall increased. Fences did not affect the rate of recruitment.

Discussion

State of natural regeneration.

Seasonality had a large influence on the number of individuals throughout the study period, with the abundance increasing during the rainy season and decreasing during the dry season, as would be expected (Fig. 1a). This difference was particularly evident in the unfenced plots. By contrast, Rodriguez[28] found that the number of individuals decreased over time in both unfenced and fenced plots in a smaller part of the same study area, even during the rainy season. Our finding that there was an almost constant number of individuals in the fenced plots showed that a fencing effect mainly occurred during the dry season, when food availability was lower and animals needed to be meticulous in searching for food. Similarly, in an evaluation of the effects of ungulates (cattle and goats) in Hawaii, Cabin *et al.*[33] found that there was a much higher abundance of seedlings in a year that was catalogued as being rainy (1997) compared with a year that was exceptionally dry (1998), when there was a marked decrease in the number of seedlings across both treatments and no additional individuals of the most abundant species [*Diospyros sandwicensis* (A.DC.) Fosberg] throughout the year.

Previous studies have also found that mortality is highly seasonal[28,33,34]. For example, Rodriguez[28] reported maximum mortalities of 20% in the rainy season and 67% in the dry season (across 4 and 2 months, respectively), and Lieberman & Li[34] reported maximum mortalities of 12% in the rainy season and 33% in the dry season (across 2 months in both cases). Similarly, in the present study, we obtained maximum mortality values of 23% for the rainy season and 85% for the dry season (across 4 and 6 months, respectively). If we make the same comparison for the fenced plots, the maximum values were 23% for the rainy season and 36% for the dry season (across 2 months for each) in the study of Rodriguez[28] and 35% in the rainy season and 87.5% in the dry season (across 4 and 6 months, respectively) in the present study. These findings indicate that mortality during the dry season was much higher in the present study than has previously been reported, which may have resulted from the low

Predictor	Estimate	Std. Error	p (<0.05)
Abundance			
(Intercept)	3.17	0.25	$<2.0 \times 10^{-16}$***
Equine	0.93	0.23	7.0×10^{-5}***
Treatopen	−0.01	0.07	0.89
SPrec	0.39	0.08	5.7×10^{-7}***
Cattle	−0.37	0.18	0.05*
Equine:Treatopen	−0.99	0.27	3.1×10^{-4}***
Species richness			
(Intercept)	−0.15	0.30	0.61
SPrec	0.15	0.05	3.6×10^{-3}**
Treatopen	−0.06	0.04	0.13
SDepth11–20 cm	1.32	0.28	2.2×10^{-6}***
SDepth21–50 cm	1.93	0.27	1.2×10^{-12}***
SDepth51–100 cm	1.45	0.26	1.7×10^{-8}***
SDepth >100 cm	2.06	0.29	6.1×10^{-13}***
DrainModerated	0.45	0.16	0.01**
DrainGood	0.28	0.14	0.05*
Diversity			
(Intercept)	0.19	0.07	0.01**
DrainModerated	0.16	0.08	0.04*
DrainGood	−0.05	0.08	0.52
TextClay loam	0.17	0.08	0.04*
TextLoam	0.22	0.06	2.0×10^{-4}***
TextSandy loam	−0.12	0.10	0.27

Table 2. Effects of structure and diversity predictors on the response variables abundance, species richness and diversity in the best models. The p-values of 0.05 for Cattle as a predictor of abundance and DrainGood as a predictor of species richness were due to rounding. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

number of individuals in some samples resulting in most or all of the seedlings (e.g. two from a total of three seedlings) dying before the next evaluation.

Lieberman & Li[34], Cabin *et al.*[33] and Vieira & Scariot[35] stated that both mortality and recruitment are highly seasonal in tropical dry forests, with higher mortality in the dry season and higher recruitment in the rainy season. By contrast, we found that there was a continuous decrease in recruitment in the unfenced plots, even during the rainy season (Fig. 1c). However, recruitment in the fenced plots was closer to their prediction – for example, there was similar recruitment between the first dry period and the next wet period, followed by a sharp decrease in the second dry period (Fig. 1c). The unclear seasonal influence in our study area could be explained by the unusual climatic situation during the previous rainy season (survey 2), when precipitation was restricted to only two or three relevant events in January, almost no rainfall in February and a short rainy period from March to May, followed by some light showers even in June, which contrasts with the continuous rains that usually occur from December to March. Therefore, it is likely that several seedlings that established during the wet period (after our assessment) were recorded in the dry period in survey 3.

It has previously been noted that seed banks in tropical dry forests contain low numbers of seeds and species[18,36]. Ceccon *et al.*[36] and Ray & Brown[37] argued that the low number of species with high seed germination rates and high mortality rates was mainly caused by environmental stress, predation and dispersal restrictions and, according to Espinosa *et al.*[18], our study area is also affected by these conditions. Therefore, since the low availability of seeds negatively affects the species richness and abundance, shoot propagation is considered more important than seed propagation in the study area[18,30].

The total number of species we recorded was considerably higher than the 21 species reported by Aguirre *et al.*[30] for the Ecuadorian part of the same study area and the 53 species reported by Lieberman & Li[34] in a small 120-ha tropical dry forest patch located in Ghana. As in the present study, Rodriguez[28] detected a small difference in species richness between treatments, with a slightly higher number of species and diversity index in fenced plots. However, unlike our results, Rodriguez[28] also found that the number of species decreased over time in fenced plots, which could be related to the fact that recruitment was not accounted for. Similarly, Cabin *et al.*[33] found that plots in a preserved area that had been fenced for 40 years had a larger number of species than unfenced plots, as well as a larger number of native than exotic species.

Species that were characteristic of the study area[32], such as *Ceiba trischistandra*, *Cavanillesia platanifolia*, *Eriotheca roseorum* and *Myroxylon balsamum*, were previously recorded in a mature forest inventory[26] and, according to Aguirre & Kvist[20], populations of the first two of these species have been maintained or may even have recovered. However, we did not record seedlings of these species in our study, and seedlings of *Centrolobium ochroxylum* and *Loxopterygium huasango* were scarce. This situation was also pointed out by Aguirre *et al.*[30], who

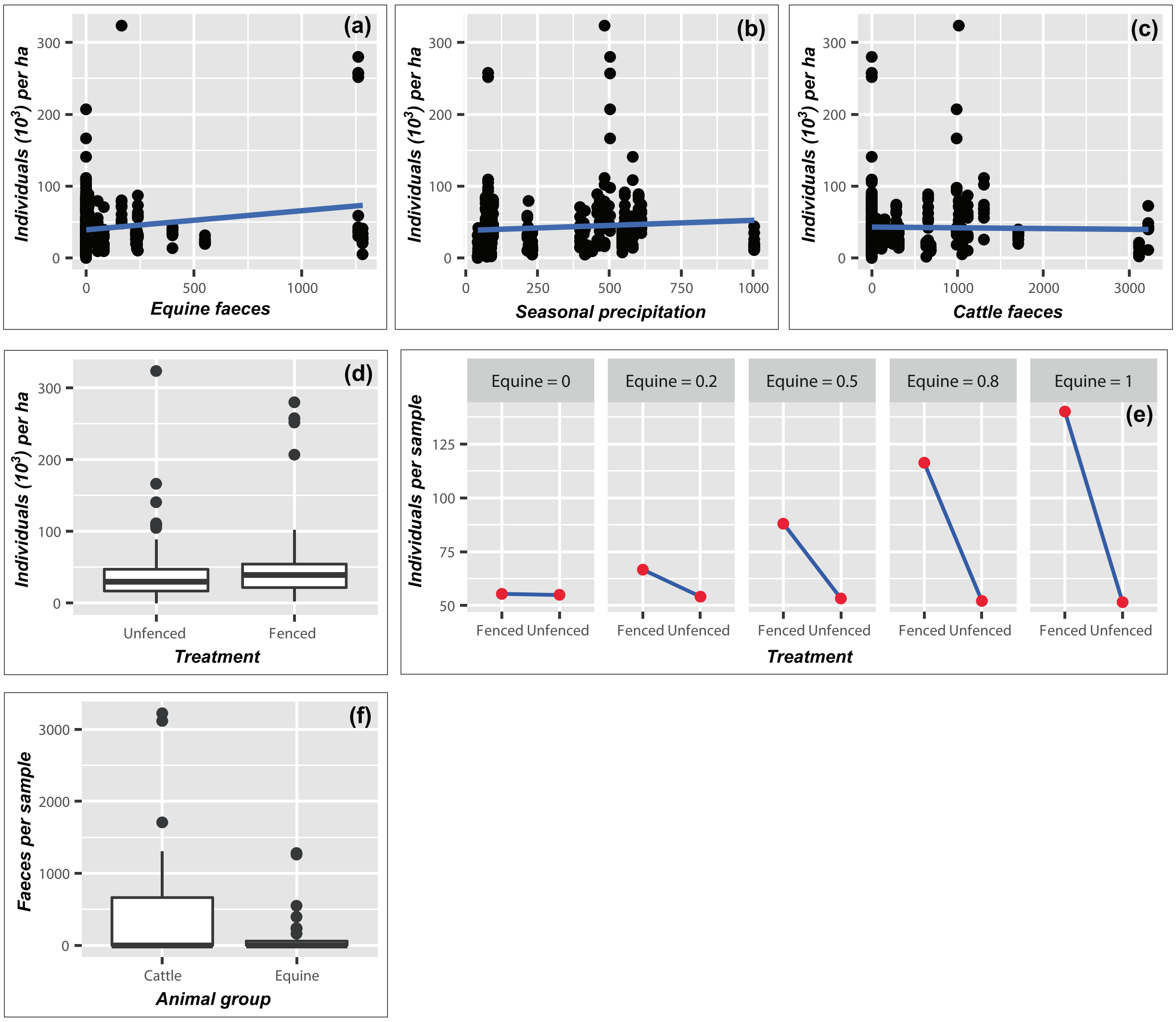

Figure 2. Relationship between the abundance of regenerating seedlings and the predictors. **(a)** equines, **(b)** seasonal precipitation, **(c)** cattle, **(d)** treatment and **(e)** the treatment–equine interaction. **(f)** A comparison of the amounts of cattle and equine faeces in the study area, presented as dry weights.

Model	df	AIC	ΔAIC	*R2m*	*R2c*
Mortality					
~1 + SPrec + Treat + Time	8	587.18	0.00	0.36	0.56
Recruitment					
~1 + SPrec * Time + Treat	10	657.59	0.00	0.35	0.61
~1 + SPrec + Time	8	659.20	1.62	0.30	0.60

Table 3. Best models explaining the dynamics of natural regeneration. Linear mixed models were computed using the restricted maximum likelihood (REML) approach with a Bayesian fit for mortality and a Gaussian error distribution for recruitment. Models were selected and ordered according to the delta Akaike information criterion ($\Delta AIC < 2$). *R2m* and *R2c* represent the amount of variance that was explained by the fixed effects and fixed + random effects, respectively.

attributed it to a few species having abundant regeneration in dry forests and strong perturbations. However, it may also be caused by the low diversity in the seed bank in this region[18] or the presence of selective seed or seedling predators.

Predictor	Estimates	Std. Error	p (<0.05)
Mortality			
(Intercept)	8.02	0.59	
SPrec	−1.61	0.15	$<2.2 \times 10^{-16}$***
Treatopen	0.33	0.11	3.7×10^{-3}**
Time	−0.11	0.02	3.0×10^{-5}***
Recruitment			
(Intercept)	−9.35	5.52	$0.09^{\dagger}$
SPrec	7.67	2.80	0.01**
Time	0.63	0.32	$0.05^{\dagger}$
Treatopen	−0.10	0.14	0.44
SPrec:Time	−0.42	0.16	0.01*

Table 4. Effects of predictors of mortality and recruitment that were included in the best models. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; $^{\dagger}p < 0.1$.

Predictors affecting the natural regeneration. One factor that has been shown to determine the establishment, survival and development of natural regeneration in dry forest is the availability of water[18,38]. Similarly, in the present study, seasonal precipitation (the rainy season) had the highest positive influence on all of the parameters analysed except diversity, with the abundance of seedlings, the number of species and recruitment increasing significantly and mortality decreasing significantly during the rainy season (Tables 2 and 4). Similar results were also presented by Espinosa *et al.*[18], Lieberman & Li[34], Cabin *et al.*[33] and Vieira & Scariot[35]. These effects can be attributed to the higher water availability, the accelerated decomposition of organic matter[18], and the higher concentration and uptake of nutrients that accumulate in the soil through the dry season when the uptake by vegetation is lower[39].

It is well known that unusual events such as El Niño bring major changes in the atmosphere, with temperatures that can exceed the normal average by 2 °C, while the rainfall over Peru and Ecuador can greatly increase the vegetation cover of dry lands[40]. Therefore, a longer assessment could allow the effects of these events on natural regeneration to be analysed.

Although treatment was included in the best models for all of the parameters except diversity, fencing only had a significant positive effect on mortality and by interaction with Equine on abundance. By contrast, Rodriguez[28] and Cabin *et al.*[33] found a meaningful difference between unfenced and fenced samples for aspects such as species richness and abundance. In the present study, species richness and recruitment exhibited only small differences between fenced and unfenced plots (Tables 2 and 4). Furthermore, although well-established young individuals between 2–3 m of height were found on private land with longer exclusion times (approximately 6 years), these were not recorded in any of our plots and only a few have been reported in the study area[30]. Therefore, we believe that our observation time of 2 years may not have been sufficient to reveal direct fencing effects.

Fences were found to be associated with decreased mortality (Table 3), which is consistent with the findings of Rodriguez[28]. This is because fences reduce the impact of animals that eat and trample seedlings[20] and of people that damage individual plants when they walk through the forests or carry out extractive activities.

Animals affected only the abundance of seedlings, with cattle having significant negative effects and horses and donkeys having significant positive effects (Table 2). This difference may have been caused by the current numbers of these animals in the area. It has previously been shown that cattle exert a negative effect on the structure of mature forests, particularly in terms of the abundance of individuals[41–43], but there is little information about the effects of horses or donkeys on mature and young plants. Since these groups of animals have similar physical traits and food preferences, we believe that they are highly likely to have a similar impact on the forest, suggesting that the number of animals is a critical factor for the level of impact, i.e. a high number of horses or cows would lead to a high impact. Horses and donkeys were once an essential means of transport, but this function has decreased since the introduction of motorcycles. By contrast, cattle are used for meat, milk or sale, leading to a considerable increase in number (Fig. 2f). The reduced number of horses could have favoured regeneration through the contribution of manure, the scarification or distribution of seeds, reduced trampling and the low number of seedlings being eaten. When considering these results, it is important to note that our evaluation of the influence of animals was based on faecal samples, which decompose following exposure to environmental conditions such as sun, wind and water. Therefore, the effects of animals should be interpreted with caution.

Wild animals could also affect natural regeneration as well as leaf litter covering the seedlings. However, they were not considered in this study, because of the difficulty to obtain suitable data and the limited budget.

Soil depth and drainage were important predictors of species richness, with soils that were >10 cm deep and better drained hosting larger numbers of species (Table 2). Alban *et al.*[44] previously reported that *Prosopis pallida* seeds that were sown superficially (5 cm depth) were damaged or eaten by ants and lizards, and surface seeds will also be accessible to selective birds and rodents. Furthermore, nutrients are transported by leaching rainwater towards deeper soils[39], leading to a better nutritive status of deeper seeds compared to those at the surface. Since this leaching will depend on the soil drainage capacity, the lower species richness and diversity that occurs in poorly drained soils can also be explained by lower nutrient movement into the soil.

Soil texture was a significant predictor of diversity, with clay loam and loam soils having higher levels of diversity than clay–sandy loam soils (Table 2). This can be explained by the high nutrient and water storage capacity, good aeration, and good root penetration of loam soils compared with sandy soils, all of which favour germination and plant development[45].

Elapsed time was an important predictor of mortality and recruitment (Table 3). Similarly, Rodriguez[28] showed that mortality exhibited a constant decrease over time that was disrupted only by the rainy season. This effect was expected because the number of individuals decreases throughout the dry season and the surviving individuals will have adapted to those conditions, thus decreasing mortality.

In contrast to our findings in the mature forest[26], there was no evidence that the human pressure index (HPI) affected natural regeneration. One likely reason for this is that fencing restricted the activities of humans as well as animals within the plots. We also found that there was a high correlation between HPI and 10 of the other 13 predictors we used [all except SPrec, Treat and stoniness (Ston); see Supplementary Table S2], which may have limited the inclusion of this predictor in the models.

Lieberman & Li[34] identified canopy closure as an important predictor of forest density. However, as for HPI, canopy closure was highly correlated with several of the predictors considered in our study and was considered in only 12 models (see Supplementary Table S3). However, we found that both the number of species and the abundance of individuals tended to increase with canopy closure. This would be expected if we consider that a closed canopy favours seed germination and seedling growth because it helps to prevent the seeds of species that are dispersed by wind and gravity, which are usually produced in the dry season[46,47], from becoming desiccated by high temperatures. Furthermore, a closed canopy also helps to prevent fresh fruits and seeds that are dispersed by animals, which mainly occur in the rainy season[47], from being washed away during heavy rainfall.

Conclusions

Seasonal precipitation is a highly influential predictor of natural regeneration in the dry forest. However, unfortunately, the rainy season is also the period with the greatest pressures due to the high availability of food for animals. Therefore, suitable management strategies should be introduced to help halt the loss of abundance and richness due to aspects not related to drought. These programmes could be coordinated by local government and supported by farmers' organisations and communities and could include compensation for farmers for losses during the temporary closure of certain areas for 5 years or more.

Since an almost constant species richness was recorded during the 2 years of assessment, we assume that this parameter is not affected by anthropogenic activities or abiotic factors in our study area in the medium term. Furthermore, a substantial number of seedlings was recorded during the rainy period. However, more accurate information on the mortality, recruitment and abundance of individuals during the distinct phases of regeneration is essential for determining whether the forest structure will be affected in the near future.

While the use of fences to exclude all types of activity is important in the study area, this will not affect the diversity and structure of the future forest if they are only established for a short period of time. Therefore, fences must be maintained on a medium- to long-term basis.

Cattle currently deserve special attention, as they are affecting the abundance of seedlings. Control measures have already been introduced at some sites in the study area, such as regulating the number of cows per family that are allowed in the forest. However, this research shows that this rule is not working either because it is not being complied with or because the proposed limit is still too high. Since our approach of estimating the intensity of animal impact from faeces has several weaknesses, more precise animal inventories are recommended in the future, as well as determination of the carrying capacity of the forest.

Soil conditions have a much larger effect on natural regeneration than on the mature forest in the study area. Texture, drainage and soil depth are all important predictors that can generate changes in the species richness and diversity of natural regeneration. Thus, areas with suitable conditions should be identified, fenced and used as seedling production sites.

Finally, our results indicate that mortality is vulnerable to both seasonality and the actions of animals and humans, whereas recruitment is mostly affected by the former.

Methods

Study area.

This research was conducted in the central part of the Tumbesian region, in southwestern Ecuador and north-western Peru (Fig. 3a). This area ranges from 200 to 1,100 m above sea level (a.s.l.)[48,49] and has a mean annual temperature of 20–26 °C, although this can exceed 35 °C during the rainy season[50]. The annual precipitation ranges from 300 to 700 mm[20], but nearly 85% of this is registered in the 4 months from January to April and there are two or three critically dry months (September–November). Consequently, two seasons can be clearly identified according to the presence or absence of rainwater. The region is affected by El Niño events, which occur every 3–7 years and bring intense rains that cause a change in the climate[40].

Colonisation of the area dates back to the pre-Columbian civilisations[51], which means that there has been quite a long period of intervention in the dry forest ecosystem, with increasingly harmful management practices being undertaken. This induced a shift in the landscape until it reached its current state. A period of intensive logging of *Handroanthus chrysanthus* (Jacq.) S.O.Grose and *H. billbergii* (Bureau & K.Schum.) S.O.Grose that had occurred for almost two decades was stopped in 1978 through the declaration of 'closed areas' in lands below 1,000 m a.s.l in southwest Ecuador[52]. However, timber extraction for domestic use (generally of selected species) continues today because it is a permitted activity on state lands[52], and illegal extraction has not been completely eliminated in either country[20,50]. Furthermore, livestock management is deficient or inexistent, with goats, cattle, horses and donkeys being released to graze freely in the forest.

Data collection.

Natural regeneration. Based on the dry forest types described by Lozano[53] and Aguirre *et al.*[49], we considered two formations (deciduous and semi-deciduous) and following Cueva & Chalán[54] three

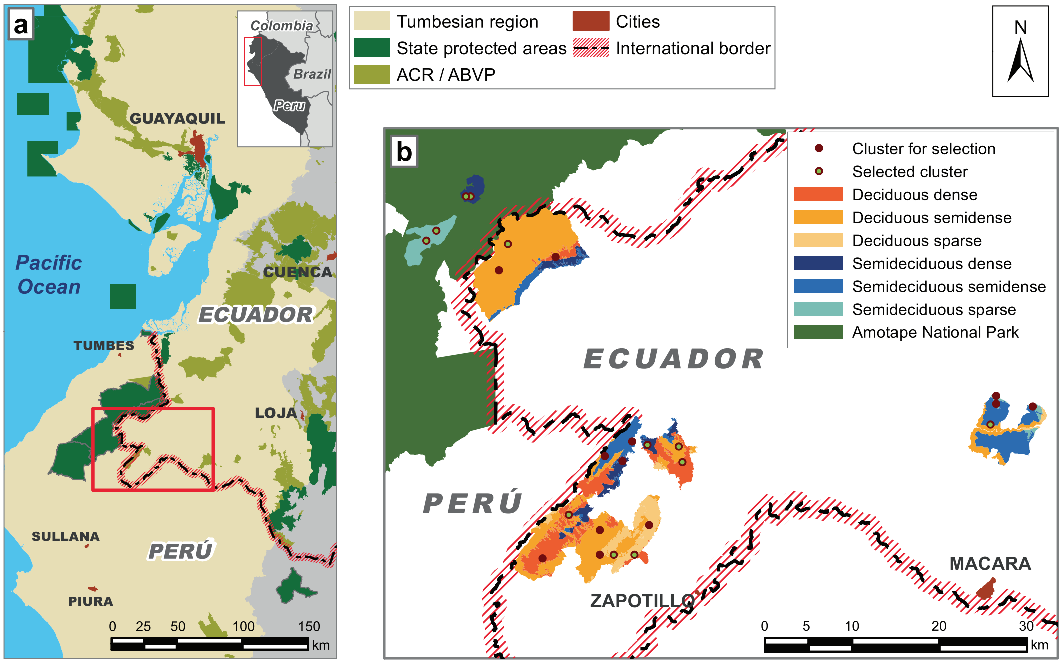

Figure 3. Geographic location of the study area. The maps were built using QGIS Desktop v. 2.8.7[76] (http://qgis.osgeo.org) (**a**) Locations of the study area and protected areas within the Tumbesian region. 'ACR/ABVP', areas of regional conservancy of Perú and area of protective forests and other vegetation of Ecuador. Modified from *"La Región Tumbesina–una riqueza compartida*[77]*"* (**b**) Distribution of clusters in the study area.

density levels (dense, semi-dense and sparse). This resulted in six different types of forest, which were considered to adequately cover most of the forest variability.

Four clusters were installed in each type of forest to give 24 clusters in total (Fig. 3b). Each of these clusters comprised three 60 × 60 m plots, within of which there were four 2 × 2 m sub-plots. After the first regeneration inventory, 12 clusters were selected from a matrix of high, medium and low regeneration abundances and species diversities. Additional sub-plots were then installed and fenced in each of these 12 clusters (four per large plot) (Fig. 4) to give four unfenced and four fenced sub-plots per plot (or 288 sub-plots in total: 144 fenced and 144 unfenced). Since the distance between the sub-plots was only 16 m and no variability was perceptible, they were grouped and treated as a single sample (Fig. 4). Thus, 12 clusters (8 in Ecuador and 4 in Peru) containing 72 samples (36 per treatment) were assessed over a total area of 1,152 m^2.

Over the almost 2-year study period, five surveys of the unfenced plots were carried out in Dec. 2014, Jul. 2015, Jan. 2016, May 2016 and Nov. 2016, and four surveys of the fenced plots were carried out at the same times with the exception of Dec. 2014. During each survey, all of the seedlings of trees and shrubs that were >5 cm tall were identified and recorded. In addition, from survey 2 onwards, any dead seedlings were recorded and all live seedlings were labelled. Thus, mortality and recruitment were computed from survey 3 onwards.

Biotic and abiotic factors. To estimate the number of grazing animals, in the first survey the faeces of goats, cows, horses and donkeys were collected along a 1 m × 60 m transect placed along the eastern border of the larger plots (Fig. 4) and separated according to the animal group. The dry weights of these samples were then obtained, combining the values for horses and donkeys.

To estimate the intensity of general anthropogenic pressure caused by activities such as firewood or timber extraction, trampling, grazing, etc., Hegyi's competition index was adapted[55], using the expression defined in Cueva *et al.*[26] to compute the HPI.

To characterise the light conditions in the plots, photographs of the canopy (Canp) were captured with a Canon EOS 300D DIGITAL camera using an 8-mm fisheye lens. One photograph was taken at the internal corners of each 2 × 2 m sub-plot (Fig. 4) in both the rainy and dry seasons. The camera was always placed 1.30 m above the ground facing north.

We included the available abiotic variables that are considered to have high influence on the structure and species composition of the tropical dry forest ecosystem[1,2].

Climatic information gridded to a resolution of 30 arc-seconds (approximately 1 km^2) was obtained from Fick & Hijmans[31]. The seasonal precipitation (SPrec) was obtained by summing separately the rainfall from January to April to obtain the amount of precipitation in the rainy season and the rainfall from May to December to obtain the amount of rainfall in the dry season. The mean annual temperature (MTemp) was obtained as an average. The altitude (Alt) was measured in the field for each plot.

For the Ecuadorian part of the study area, soil data were obtained from the Geopedological Map of Zapotillo and Celica of the Instituto Espacial Ecuatoriano[56]. The soil parameters used were organic material (OM), soil

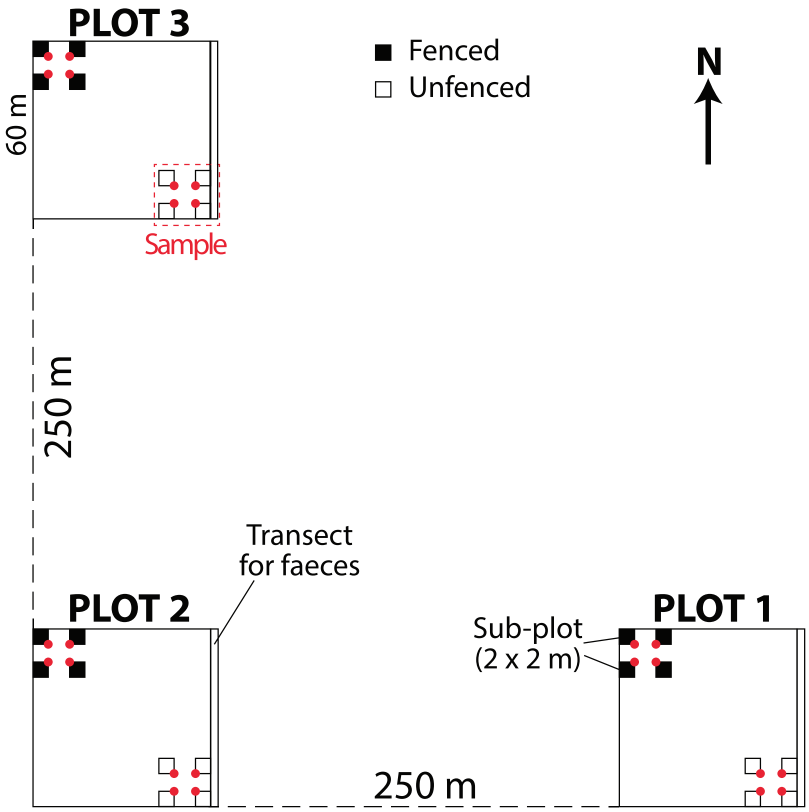

Figure 4. Diagram of the cluster design. Red dots indicate the places where photographs of the canopy were captured. Transects along the eastern edges (1 × 60 m) were used to collect faeces.

depth (SDepth), drainage (Drain), stoniness (Ston) and texture (Text). For the Peruvian part of the study area, the Soil Classification Map of the Oficina Nacional de Evaluación de Recursos Naturales (ONERN)[57] was used to identify the soil type. Unfortunately, this work does not include specific information about the soil characteristics, so they were assumed to be identical to those of the same soil type in the nearest localities on the Ecuadorian side.

Time was considered as the number of elapsed months since the first survey. Treatment (Treat) comprised two groups: open for unfenced plots and exclusion for fenced plots.

The ranges or levels of all predictors can be found in Supplementary Table S4, the full database used to evaluate structure and diversity is provided in the Supplementary Table S5 and the dataset to evaluate dynamics in the Supplementary Table S6.

Data analysis. *Data processing.* Abundance (Ind) and species richness (Spp) were calculated by counting the number of live individuals and species, respectively, of tree and shrub seedlings in each sample, treatment and survey period. Mortality (Mort) was computed by considering the percentage of dead individuals in relation to the number of individuals in the previous survey. The recruitment rate (Recr) was obtained by calculating the percentage of new individuals in a survey in relation to the total number of individuals in the same survey. Diversity was computed by calculating Simpson's index (Simp), as this is considered an effective and robust diversity measure[58].

The canopy images were processed by Geigl[59] using Gap Light Analyzer v2.0 software[60] (available on https://www.caryinstitute.org/science/our-scientists/dr-charles-d-canham/gap-light-analyzer-gla). Canopy coverage was computed as a percentage, and the average among the four sub-plots (unfenced and fenced plots were averaged separately) was used for each sample.

Statistical analysis. Generalized linear mixed models (GLMMs)[61–63] were applied to identify the effects of various predictors on the parameters evaluated. The response variables were the abundance of regeneration as a structure indicator; mortality and recruitment as indicators of the dynamics; and species richness and Simpson's index as indicators of the diversity of natural regeneration.

A total of 14 predictors were used: five biotic indicators (Goats, Cattle, Equine, HPI and Canp); eight abiotic variables related to climate, geography and soil (SPrec, MTemp, Alt, OM, SDepth, Drain, Ston and Text); and treatment (Treat). To improve the model fitting the predictor variables were transformed as shown in the Supplementary Table S4.

Correlations among all of the predictor variables were tested (Supplementary Table S2) and models were then built by considering that strongly correlated predictors could not be included in the same model to avoid collinearity. In addition, a maximum of five predictors were included in each model to avoid overfitting[64], resulting in 168 candidate models. A further 18 models were also built that included interactions between variables representing anthropogenic pressure and those that Cueva *et al.*[26] identified as having a relevant influence on the structure and diversity of the mature forest. Thus, a total of 186 candidate models were tested (see Supplementary Table S3). The asterisk (*) between interaction terms represents both the higher-order interaction term as well as the lower-order main effects.

The predictors SPrec, Treat and Time and their interactions were chosen to predict mortality and recruitment. In this instance, we only evaluated the effect of these three predictors because our goal was to assess if animals are more influential than seasonality, which would allow us to say if management policies are required to improve conditions in the dynamic of natural regeneration. Thirteen models were built for this purpose (see Supplementary Table S7). In all cases, formation and cluster were considered as random effects (plots were nested within clusters, and clusters were nested within formations), and Time was considered as a random slope to account for the repeated measures.

The effects of the predictors on abundance were assessed using the maximum likelihood approach with a negative binomial error distribution to deal with overdispersion[65]. The effects of the predictors on species richness were assessed using a GLMM with a Poisson error distribution and the Laplace approximation to get a true likelihood[62,66]. The effects of the predictors on diversity were assessed using the REML approach[62]. All of these analyses were performed using the lme4 package[61] v1.1–21. The effects on mortality were assessed using the REML approach and Bayesian fitting to deal with singular fitting[67] using the blme package[68] v1.0–4. Finally, the effects of the predictors on recruitment were assessed using a GLMM with a Gaussian error distribution and link identity because 22% of the recruitment values were zeros. The glmmTMB package[69] was used, as this is able to deal with zero-inflated model[70].

Model selection was carried out using the delta Akaike information criterion ($\Delta AIC < 2$)[71]. For all models, we computed the marginal and conditional variance (*R2m* and *R2c*, respectively)[72] to determine the proportion of the variance that was explained by each model. *R2m* and *R2c* were calculated using the MuMIn package[73] v1.42.1 when the lme4 and blme packages were used and the sjstats package[74] v0.17.4 when the glmmTMB package was used.

All analyses were performed in the R programming environment v3.5.3[75].

Data availability

The datasets are available as supplementary information. R scripts available upon request. Please email to jorge.cueva@tum.de for R scripts derived from freely available R packages: see material and methods for more details.

Received: 2 September 2019; Accepted: 26 May 2020;

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Acknowledgements

We wish to thank to those who funded this research: to German Research Foundation (DFG) project PAK 824/B3; to Universidad Técnica Particular de Loja (UTPL), who leads the projects PROY_CCN_0030 funded for UTPL and PIC-13-ETAPA-005 funded for Secretaria de Eduación Superior, Ciencia, Tecnología e Innovación (SENESCYT). J.C.O. received the support of SENESCYT and Erzbischöfliches Ordinariat München, many thanks. This work was supported by DFG and the Technical University of Munich (TUM) in the framework of the Open Access Publishing Program. Also, we want to thank to Proofreading Service of TUM Graduate School. To Naturaleza y Cultura Internacional, Parque Nacional Cerros de Amotape, and the communities Malvas, El Cardo, and Piedras Blancas for allowing us to conduct this research on their reserves. Furthermore, to Diego González, Jorge Armijos, Geovanny Cango, Angel Gusmán, Johana Gusmán, Israel Medina, Yodán Zapata and Flavio Olaya for their support in the fieldwork.

Author contributions

J.C.O., P.H. and C.I.E. designed the study. J.C.O. performed the fieldwork, data analyses and wrote the document. J.C.O. and E.G.-M. undertook the data curation. J.C.O., P.H. and M.W. discussed the results. P.H., M.W., C.I.E. and Z.A.M. reviewed the paper.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41598-020-66743-x.

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