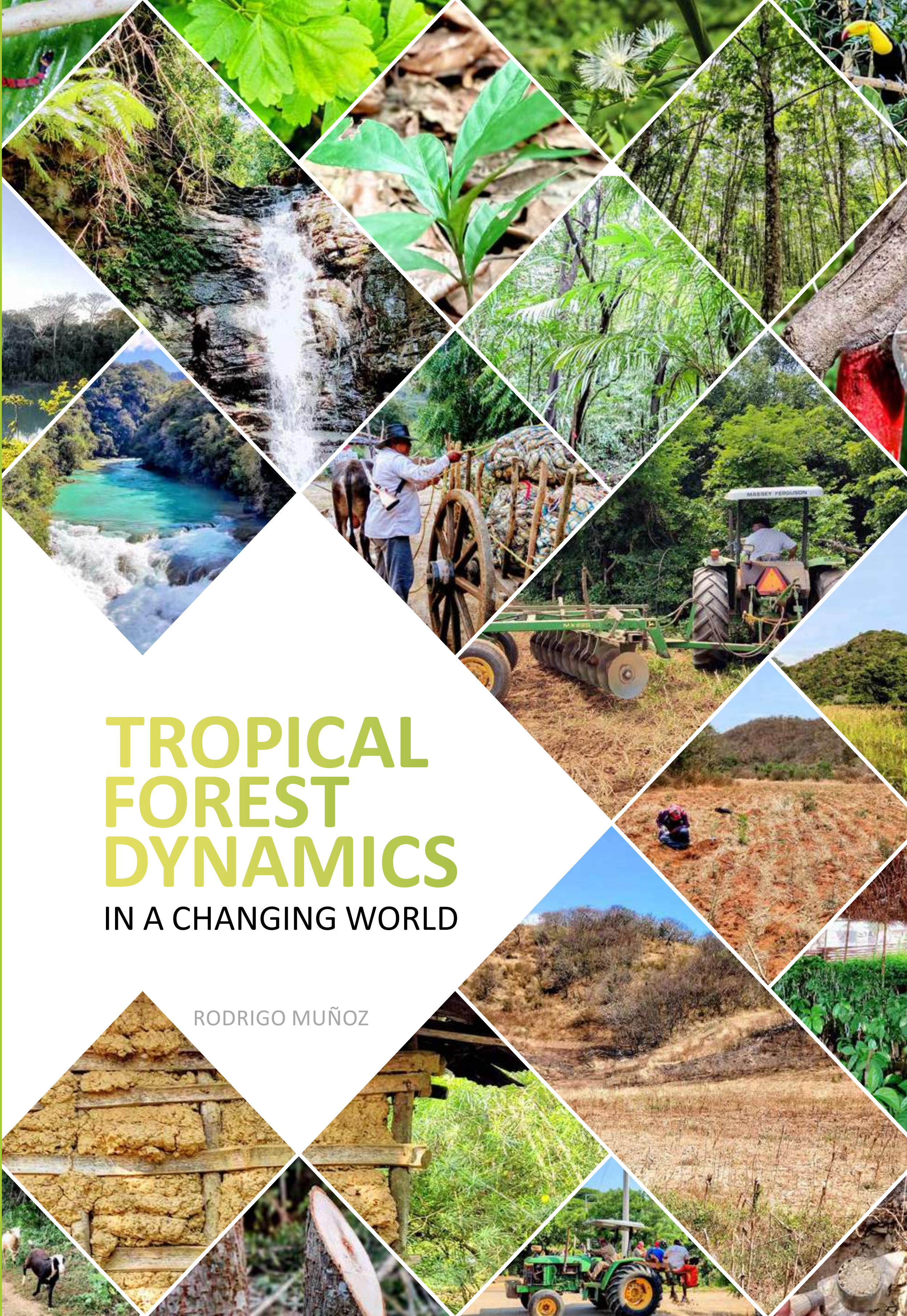

TROPICAL FOREST DYNAMICS

IN A CHANGING WORLD

RODRIGO MUÑOZ

Propositions

1. Forests behave like homeostatic living beings.
(this thesis)

2. As temperatures rise, a significant number of tropical dry forests will experience reduced productivity and will transition into different types of ecosystems.
(this thesis)

3. The value of empirical observation is underestimated in contemporary science.

4. Science, rather than a profession, is a philosophy.

5. The pursuit of sustainability still remains a luxury rather than a mandate.

6. Climate change will only worsen the already feeble control of the poorest over their own fate.

Propositions belonging to the thesis, entitled

Tropical forest dynamics in a changing world

Rodrigo Muñoz
Wageningen, 6 October 2023

TROPICAL FOREST DYNAMICS

IN A CHANGING WORLD

RODRIGO MUÑOZ

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TROPICAL FOREST DYNAMICS

IN A CHANGING WORLD

RODRIGO MUÑOZ

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Our biological duty is, above all else,
to respect life and to promote it

José Mujica

Former President of Uruguay
United Nations General Assembly
September 2013

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CHAPTER 1

General introduction

Rodrigo Muñoz

SUMMARY

The thesis “Tropical forest dynamics in a changing world” delves into the intricate dynamics of tropical forests, examining the interplay between autogenic regulation and allogenic factors, such as climatic conditions and substrates. Tropical forests, subject to diverse environmental changes including climatic variability, natural disturbances, and human interventions, remain essential ecosystems for biodiversity and ecosystem services. This study addresses the urgent need to comprehend how these factors shape forest stability, growth, and responses to change.

This general introduction chapter sets the stage by outlining the fundamental theoretical foundations of the thesis. Tropical forests, constantly exposed to environmental shifts, respond through autogenic regulation, a self-regulating mechanism that allows them to maintain relative stability over time. This internal process involves trees adjusting their physiological functions to new conditions, collectively resulting in forest dynamics. While extensively studied, the complex relationships between abiotic and biotic factors in these ecosystems still puzzle and challenge today’s ecologists.

The chapter highlights the crucial roles of climatic conditions, substrates, and disturbances as allogenic factors influencing forest dynamics. Climatic fluctuations and shifts, both cyclic and unprecedented due to climate change, impact resource availability, plant physiology, and vegetation type. Substrates, composed of bedrock and soils, shape spatial heterogeneity, species composition, and structural development across landscapes. Disturbances, whether abiotic or biotic, lead to changes in forest biomass, structure, and composition, setting the stage for recovery through autogenic regulation.

Drawing from extensive datasets of tropical dry and wet forests in Mexico, this research aims to illuminate how these theoretical underpinnings manifest in real-world contexts. By unraveling the complexities of autogenic regulation and allogenic factors, the study contributes to a more comprehensive understanding of tropical forest dynamics, aiding in informed conservation and management decisions for these vital ecosystems in an ever-changing global landscape.

Tropical forests are continuously exposed to changes in environmental conditions (Wright, 2005). Climatic variability and natural disturbances generate continuous changes in the abiotic environment of forests (Odum, 1969). Humans introduce additional pressure by clearing land, extracting goods from the forests, and by altering the climate. All these factors provoke changes in the state of tropical forests by removing biomass and by adding or removing resources from the environment. Trees in all forests respond by adjusting their physiological processes in accordance with the new conditions, which allows them to survive, grow and reproduce as efficiently as they can, given the conditions under which they live (Gleason, 1917; West et al., 2009). Collectively, these individual responses result in temporal fluctuations in the state of forests, known as forest dynamics (Frelich, 2016). The study of forest dynamics has been a fascinating topic for natural historians and ecologists for more than a century (Clements, 1916; Pickett et al., 2009). Yet, the complexity of forests and their environment is difficult to disentangle and understand. Much progress has been made in the study of tropical forest dynamics; yet many basic old questions remain, and new ones have emerged (Odum, 1969; Hartshorn, 1980; McDowell et al., 2020). Particularly, the novel pressures that humans exert on tropical forests demand urgent answers to fully understand their functioning, to better foresee their fate under current and future conditions, and to act accordingly to preserve these crucial ecosystems (Wright, 2005; Kopittke et al., 2019; Siyum, 2020).

In this thesis, I explore some of the most important factors inducing changes in tropical forests and analyze how these systems cope with them. I took advantage of two exceptionally long datasets: the secondary and old-growth tropical dry forest (TDF) dataset of Nizanda, and the secondary tropical wet forest (TWF) dataset of Marqués de Comillas, both from southern Mexico. Ultimately, I aim to advance scientific knowledge on tropical forest dynamics in forest stability and homeostasis, and the effects of climate and substrates. Understanding forest dynamics is needed more than ever in an era of exceptional natural and anthropic changes: a solid knowledge base is essential to manage and preserve tropical forests and the key ecosystem services they deliver in a changing world.

1 AUTOGENIC REGULATION: FOREST'S INTERNAL MECHANISM OF HOMEOSTASIS

1.1 Homeostasis in tropical forests

Forests are homeostatic systems. Homeostasis is the property of a system to remain relatively unchanged over time, even in the event of external changes (Billman, 2020). Think of the body temperature of humans, which remains close to 37 °C even if exposed to an external temperature of 10 °C or 50 °C. The human system adapts to remain within a certain range of operative conditions known as the dynamic regime or stability domain. In forests, this dynamic regime is determined by abiotic factors (such as solar energy, temperature, water balance, and soil nutrients) and biotic factors (such as plant species availability, their environmental requirements, and the way they complement and interact with each other) (Odum, 1969). The interplay between these abiotic and biotic factors underlies the development of a forest community and its dynamics, commonly fluctuating within the dynamic regime (Mayer and Rietkerk, 2004).

1.2 Mechanism of autogenic regulation

Plants capture and use resources (light, water, nutrients) for their growth, until one or more resources become limiting, and the vegetation attains its maximum biomass and enters in an overall stable state. This stable state is largely determined by the availability of resources and the physical conditions of the abiotic environment (Odum, 1969). Ultimately, however, the biotic component of a orest determines the realized amount of biomass a site holds, and the realized speed at which biomass accumulates. In other words, abiotic conditions determine the maximum amount of biomass and the maximum speed at which biomass is accrued, and biotic conditions determine the functioning of the realized community within abiotic boundaries.

Forests are inherently dynamic systems because they are composed of organisms that undergo a dynamic life cycle. Trees establish, grow, reproduce, and die, and all these processes induce changes in the state of the forest (Lewis et al., 2004a). When plants recruit and grow, the amount of forest biomass increases (Lewis et al., 2004b; van der Sande et al., 2017), increasing the demand for resources to sustain that biomass. The opposite occurs when plants die or decrease in size due to physical damage, releasing the captured resources to the environment (Lewis et al., 2004a). The resulting fluctuation in resource availability either promotes processes of biomass gain if resource availability is high and competition is mild, or biomass stagnation and/or loss if resource availability is low and competition is fierce (Odum, 1969). This process of autogenic regulation (*auto* = "self" and -*genic* = "produced or generated from") is an essential ecosystem property that generates stability in the state of a forest (Tansley, 1935). Autogenic regulation is also the essential mechanism behind ecosystem recovery, largely contributing to the resilience of tropical forests. Without autogenic regulation, forests would eventually disappear due to their inability to cope with change.

Autogenic regulation does not imply that forests do not undergo any change (Tansley, 1935), but rather that they will internally promote and suppress certain processes to achieve the maximum amount of biomass a forest can hold (given that the abiotic environment remains stable), yielding constrained variations over time (Odum, 1969; Lewis et al., 2004b). In the long term, stability is achieved by means of minor corrections in the biomass of a system, either through increased rates of survival, growth, and reproduction when the amount of biomass is suboptimal, or increased rates of mortality and plant physical damage (*e.g.*, due to insect outbreaks triggered by abundant plant biomass) when the amount of biomass exceeds the threshold value that can be sustained by the abiotic environment. Naturally, stability is not a programmed mechanism, but rather the consequence of the interplay between all individual plants and other living organisms that make up the forest (Gleason, 1917). Ultimately, autogenic regulation leads to a system that fluctuates within a defined dynamic regime, which is the range of values where biomass (or any other state variable) is relatively stable and fluctuates in the absence of external forcing (Mayer and Rietkerk, 2004).

1.3 Resilience and autogenic regulation

Resilience (*sensu* Hodgson et al. (2015), also known as engineering resilience) is a forest property that emerges from autogenic regulation. Resilience is the capacity of a forest to resist and recover after experiencing a disturbance (Holling, 1996; Ingrisch and Bahn, 2018). Resilience is determined by a forest's capacity to resist the impact of a disturbance and to recover from the potential perturbation produced. Recovery arises from the autogenic regulation mechanism of plants exploiting the available space and resources available after a forest is affected by an external/allogenic factor (Hodgson et al., 2015). Because recovery and autogenic regulation depend on the capacity of plants to exploit resources, they also depend on the functional profile (*i.e.*, set of functional attributes of a species assemblage) and niche of these plants (Peterson et al., 1998). Consequently, autogenic regulation and recovery may also differ between forests, especially if their functional profiles are contrasting enough. Autogenic regulation can be simply assessed by regressing the net rate of change of a forest state variable (ΔY) on the value of the state variable itself (Y). In principle, larger deviations from the stable state should produce larger rates of change: positive rates if the forest is below its stable state (high resource availability) and negative rates if the forest is above its stable state (high resource competition). Associating state variables and their rates of change is a very simple approach to assess autogenic regulation and recovery potential in forests. Yet, this approach has not been tested in the context of tropical forests. Steep slopes in the regression between state variable and their rates of change would suggest a strong autogenic regulation and fast recovery capacity.

2 ALLOGENIC FACTORS: FORESTS IN A CHANGING ENVIRONMENT

Allogenic factors (*allo* = "other" and *-genic* = "produced or generated from") can be defined as factors external and seemingly independent from the forest community[1] (Tansley, 1935; Pickett et al., 1989). Climate, forests' substrate, and natural and anthropogenic disturbances represent allogenic factors that may influence the structure, biodiversity, and ecosystem functioning (SBEF) of forests (*e.g.*, Arroyo–Rodríguez et al., 2017; Reed and Kaye, 2020; Sullivan et al., 2020; Callahan et al., 2022). Climatic conditions change continuously, leading to variations in resource availability and the conditions that affect plants' physiological processes (Choat et al., 2012; Sullivan et al., 2020). Substrates undergo slow changes, particularly in forests with a mild disturbance regime; nevertheless, they significantly shape the structure and diversity of forests (Durán et al., 2006; Fayolle et al., 2012; Peña-Claros et al., 2012). Disturbances occur in pulses, and intense disturbances only occur infrequently. When these allogenic factors change, plants may respond by adjusting their rates of survival, growth, or reproduction to the new conditions, producing changes in forest's state. Therefore, forests track the environment and remain in equilibrium with it, although this might not be an immediate response.

2.1 Climatic conditions

Climatic conditions fluctuate in very contrasting time scales, from days, to years to millennia. Daily and seasonal fluctuations are cyclic and predictable, and plants have developed strategies like circadian cycles and phenology to cope with these fast environmental changes

---

[1] However, the concept of allogenic factors is poorly defined in ecological literature.

(McClung, 2001; Cleland et al., 2007). Some plants are also adapted to interannual climatic variation in sites where year-to-year climatic conditions are little predictable, by storing nutrients and adapting their genetic and physiological processes in response to periodically unfavorable environmental conditions (Volaire, 2018; Zandalinas et al., 2018). However, plant and forest acclimation have limits. Climatic fluctuations beyond the adaptive capacity of forests result in changes in its SBEF. Therefore, major climatic shifts over ecological and geological time scales result in large ecosystem changes and very often in a shift in the vegetation type of a certain area.

Global climate change will inevitably modify SBEF parameters for most ecosystems. Although change can be said to be the only constant in nature, the speed at which climate is currently changing is unprecedented for human history (Berrang-Ford et al., 2011). For South America, temperature have increased at a rate of 0.14 °C per decade since 1910, which has risen to 0.22 °C since 1981 (NOAA, 2023). Yet, despite its urgency and importance, it remains difficult to foresee and assess the consequences of climate change for tropical forest SBEF (Wright, 2005), mostly because of the uncertainty in the effect of the drivers of forest dynamics (Mitchard, 2018). Regarding tropical forests, the dynamics of vegetation in the wet tropics has been far more studied than that of the dry tropics (Siyum, 2020), and the dynamics of secondary tropical forests (*i.e.*, forests recovering from complete or semi-complete vegetation removal) in response to climatic variation has only been barely examined (Wright, 2005; Martínez-Ramos et al., 2018; Souza et al., 2019; Becknell et al., 2021; Calvo-Rodriguez et al., 2021; Zutta et al., 2023). Worryingly, secondary forests younger than 60 years account for 35 % of the tropical forest area in the Americas (2.4 million km^2) (Chazdon et al., 2016), which implies that the effects of climate change are vaguely understood for an area larger than Mexico only in the Neotropical region. Unfortunately, knowledge on climate-vegetation responses from primary forests cannot be directly extrapolated to secondary forests (Zutta et al., 2023) because in the latter structure is less developed (Poorter et al., 2016), ecosystem functioning is simpler (Odum, 1969), and diversity is generally lower (Rozendaal et al., 2019; Poorter et al., 2021a). We can assume that temperature and vapor pressure deficit reduce forest productivity (Sullivan et al., 2020), and precipitation (Martínez-Ramos et al., 2018; Becknell et al., 2021) whereas solar irradiance increases forest productivity (Graham et al., 2003; Condit et al., 2004), given that secondary and old-growth forest are two states of the same ecosystem. However, these assumptions need to be validated and quantified with ground or satellite data.

2.2 Substrates

Substrates are composed of bedrock and soils, and they are the media where plants develop their root systems. They provide support and nutrients such as water and minerals to trees, and therefore they play a key role in forest development (Sollins, 1998). Substrates change at slower rates than climate, usually in time scales of millennia or millions of years (Wardle et al., 2004), although it is possible to see changes in some of their attributes over ecological times (*e.g.*, fertility or bulk density) (van der Sande et al., 2023b). However, for practical purposes, substrates are regarded as relatively stable elements of the abiotic environment in ecological literature. The role of substrates for vegetation is mostly seen at spatial scales, driving differences in species compositions and structure development across the landscape (Ribeiro et al., 2007; Peña-Claros et al., 2012; Díaz-Castellanos et al., 2022). Yet, they can influence forest dynamics by their interaction with climatic conditions (Vargas Gutiérrez et al., 2023). Substrates that can retain water for a longer time (due to finer soil texture or a more impermeable bedrock) can be beneficial for water-limited tropical dry forests by reducing water stress (Stahl et al., 2013; Allen et al., 2017), or detrimental for tropical wet forests by creating anoxic conditions that hamper root respiration (Gloor et al., 2015). They can also influence forest dynamics via their filtering effect on species composition (Durán et al., 2006; Terra et al., 2018), as species respond differentially to environmental changes (Powers et al., 2020). For instance, harsher substrate conditions may promote a conservative forest composition which can be more resilient to climatic extremes, hence impacting forest dynamics.

The effect that substrates play on the spatial heterogeneity of tropical forests has been well documented (*e.g.*, Durán et al., 2006; Peña-Claros et al., 2012; Terra et al., 2018; Díaz.Castellanos et al., 2022). Substrates largely determine spatial heterogeneity in species diversity (richness, composition and diversity) and structure development across landscapes and regions (ter Steege et al., 2006), and they are able to create sharp ecosystem differences even at small scales (Durán et al., 2006; Terra et al., 2018). However, there are still many deficiencies in our understanding of substrates effects on forest dynamics, probably because of the complexity of the substrate-dynamics relationship (see conceptual scheme in van der Sande et al., 2017 for example). These studies are required, apart from contributing to basic knowledge about ecosystem functioning, to assess potential differences in climate responses across landscapes of the same forest ecosystem, especially in the context of climate change (Vargas Gutiérrez et al., 2023). This information will provide insight on the spatial diversity of forest responses to a changing environment, especially at small spatial scales.

2.3 Disturbance

Disturbances are forest changes promoted by allogenic factors (Pickett et al., 1989). They encompass allogenic changes that result in the increase or decrease of biomass, individuals, or other forest state variables (Viljur et al., 2022). In the context of ecological succession, they are usually regarded as sudden changes in biotic or abiotic factors that result in biomass removal from the vegetation, with concomitant changes in abiotic and biotic conditions (Chazdon et al., 2016). Disturbances can be either caused by abiotic events (*e.g.*, droughts and floodings) or biotic events (*e.g.*, insect and pathogen outbreaks), and can exert a direct effect on forest state variables (*e.g.*, cutting or burning vegetation) or an indirect effect by modifying resources and conditions (*e.g.*, climatic anomalies), secondarily impacting the state of forests. Land use change is probably the most important source of disturbance for tropical forests (Wright, 2005), as agricultural expansion has promoted extensive forest clearing, biomass, and biodiversity losses (Chazdon, 2008; Asner et al., 2010). Many agricultural lands are abandoned shortly after when soil fertility decreases and crop or pasture productivity drops (Hölscher et al., 1996), enabling the development of secondary forest patches (Chazdon, 2008). Although natural forest regeneration restores previously lost tropical forest cover and function in several cases (Chazdon, 2014), the resulting new forests may also suffer SBEF modifications when compared to their pre-disturbance state (Sakschewski et al., 2016; Arroyo-Rodríguez et al., 2017; Wigneron et al., 2020).

The fact that secondary forests have a clearly distinct dynamics has been extensively recognized and studied (Clements, 1916; Gleason, 1917; Pickett et al., 2009). However, there are still important and worrying knowledge gaps in our understanding of successional dynamics, such as their responses to climatic changes, that are better known for old-growth forests than for secondary ones (Wright, 2005; Siyum, 2020). For instance, there is mixed evidence about the resilience of secondary forests, which can be less resilient to climatic disturbances due to their lower diversity (Peterson et al., 1998; Bezemer and van der Putten, 2007), or more resilient because their less-developed structure requires less resources (cf. Finegan et al., 2015) and their flora is better adapted to harsh environmental conditions (Pineda-Garcia et al., 2013; Poorter et al., 2021b). Fortunately, secondary tropical forests are being increasingly monitored (mainly in the Neotropics), and valuable data are being gathered to assess the impacts of climate change on these extensive and important ecosystems. This opens a great window of opportunity to study how the diversity of secondary tropical forests (which largely differ in fallow ages, climatic regimes, floristic composition, and land use histories) respond to a changing environment. Advancing this ecological knowledge is needed to improve our basic understanding of forest dynamics, to elucidate with better accuracy the consequences of climate change and, hopefully, to take better management decisions regarding tropical forests (Wright, 2005; Zuidema et al., 2013; McDowell et al., 2020; Strassburg et al., 2020; Hartmann et al., 2022).

3 THESIS OVERVIEW

3.1 Aims, questions and general hypothesis

The aim of this thesis is to advance ecological knowledge about the role of autogenic regulation and allogenic factors such as climatic conditions and substrates in the dynamics of old-growth and secondary tropical forests. This aim was addressed in three research chapters that evaluate the influence of the following factors in the dynamics of tropical forests:

1. Autogenic regulation (**Chapter 2**)
2. Variation in climatic conditions (**Chapter 3**)
3. Substrate heterogeneity across the landscape (**Chapter 4**)

My overall hypothesis was that allogenic factors determine resource availability and environmental conditions for plant growth, setting the boundaries for vegetation development. When allogenic factors change, they influence survival, growth, and reproduction rates in tropical forests, influencing their dynamics. The effect of allogenic factors on demographic processes is mediated by the floristic composition and functional diversity of the community. Disturbances affect forests by directly removing biomass (*e.g.*, logging or wildfires) or by indirectly affecting climatic conditions (*e.g.*, drought or storms) and substrates (*e.g.*, soils degradation). When a disturbance affects the forest, recruitment, growth, and mortality rates respond to the environmental changes, helping the forest return to equilibrium with its environment (**Figure 1.1**).

3.2 Thesis structure

The research questions of this thesis were addressed in five chapters designed to explore the role of autogenic and allogenic drivers of tropical forest dynamics.

Chapter 1 (General introduction) describes the rationale, questions, and structure of the thesis, sets the theoretical bases of forest dynamics to contextualize the study and its contribution to ecology, and places this thesis work within a broader picture to explain its relevance and timeliness.

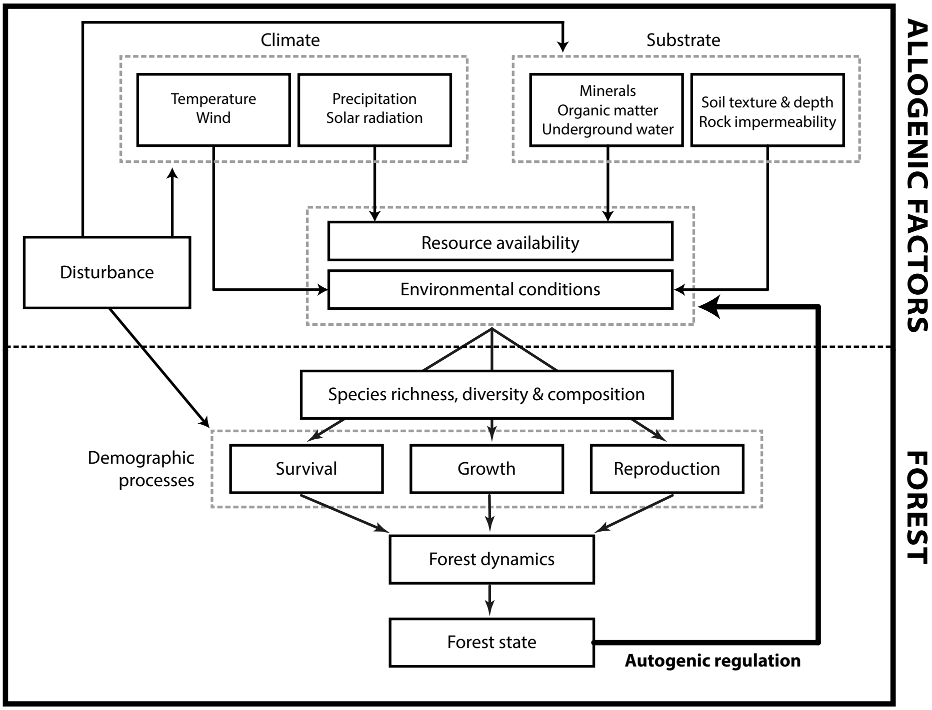


Figure 1.1

Conceptual diagram showing the hypothesized relationships between autogenic regulation and allogenic factors (climate, substrate, disturbance) driving forest dynamics. Climate and substrates influence resource availability and conditions for plant growth, which determine the abiotic boundaries for forest development. Autogenic regulation results from forest’s state on resource availability and environmental conditions for plant survival, growth, and reproduction. These demographic processes determine forest dynamics, and forest state in ultimate instance. Autogenic regulation results in a stabilizing effect on tropical forests’ state. Disturbances can either directly affect the forest by removing biomass (*e.g.*, logging) or indirectly by altering climatic conditions (*e.g.*, drought) on substrate properties (*e.g.*, land degradation after agricultural use).

Chapter 2 (Autogenic regulation in tropical dry forests) explores how autogenic regulation allows old-growth and secondary vegetation to recover from disturbance and remain stable over time in tropical dry forests. This chapter takes advantage of an exceptional dataset with 16 years of annual forest inventories to show how communities return to their old-growth dynamic regime after disturbance. It also shows how forests modulate recruitment, growth, and mortality to achieve the necessary rates of change that would allow them to return to their stable state, and shows how resource availability and competition are the driving forces behind autogenic regulation. To my knowledge, this is one of the few studies exploring in depth the concept of autogenic regulation for tropical forests and the first one to do so from a demographic perspective.

Chapter 3 (Climatic drivers of productivity in tropical secondary forests) examines how climatic conditions affect biomass productivity in wet and dry tropical secondary forests. For this study, I used up to 17 years of the dynamics of wet and dry tropical forests coupled with climatic records to assess the effect of precipitation, temperature, and photosynthetically active radiation (PAR), their seasonality and lagged effects on forest dynamics. This chapter shows that climatic sensitivity is ecosystem- and demographic process-specific. Here, we estimated the proportion of productivity explained by autogenic regulation and climatic conditions and quantified the impact of different climatic variables on forest dynamics. This is the first study to compare the influence of climatic conditions in secondary vegetation of wet and dry tropical forests.

Chapter 4 (Substrate effects in old-growth tropical dry forests dynamics) explores how forest structure, diversity, and their temporal dynamics differ across two substrates in a tropical dry forest landscape. To answer this question, I used a 12-year-long dataset of annual forest inventories to compare old-growth tropical dry forest fluctuations over time in limestone and siliciclastic phyllite substrates. This chapter compared the state and dynamics of seven forest attributes and analyzed differences in demographic rates between substrates. As a secondary aim, we also analyzed the effects of El Niño–Southern Oscillation (ENSO) phenomenon on TDF dynamics. This is one of the first studies to explore how substrates influence tropical forest dynamics, and probably the first one controlling for other environmental variables.

Chapter 5 (General discussion) goes back to the research questions underlying this thesis and confronts them with the results obtained in **Chapters 2-4**, with other studies, and with my general hypothesis (**Figure 1.1**).

4 STUDY SITES

For answering my research questions, I took advantage of two exceptional regions and datasets of tropical forest dynamics: the Nizanda Tropical Dry Forest Dataset and Marqués de Comillas Tropical Wet Forest Dataset (hereafter referred to simply as dry and wet forests), both located in southern Mexico (**Figure 1.2 A-B**).

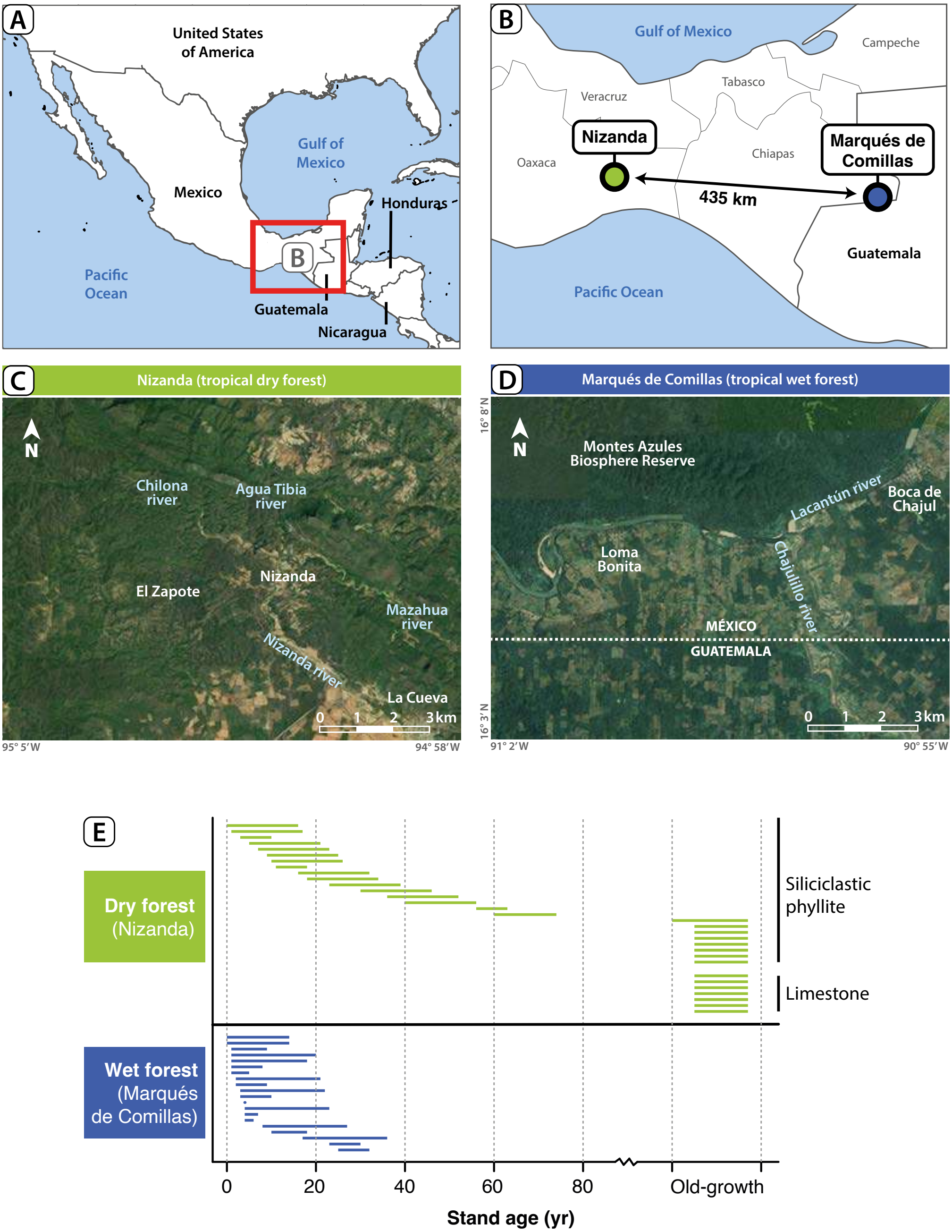
4.1 Tropical dry forest (Nizanda, Mexico)

The dry forest is located in the Mexican state of Oaxaca, in the Isthmus of Tehuantepec (16.66° N, 95.01° W; **Figure 1.2 A-C**, **Figure 1.3 left**) (Pérez-García et al., 2001). It has a mean annual precipitation of 900 mm yr^{1} and a mean annual temperature of 27.7 °C, with a dry season spreading over 6 months (rainfall < 50 mm month^{-1}). The region comprises several vegetation types, with tropical dry forest being the most widespread (Gallardo-Cruz et al., 2012) both on limestone- and siliciclastic phyllite-derived substrates (Pérez-Gutiérrez et al., 2009). The locality has been inhabited since pre-Columbian times, but significant agricultural activity started around the 1880's with the foundation of the Mena Nizanda settlement during the construction of the Trans-Isthmic Railway (Alonso Fernández, 2015). Because shifting agriculture has been the predominant cultivation method for most of the region's history, many secondary tropical dry forest patches are scattered across the landscape (**Figure 1.3 left top**) (Pérez-García et al., 2010). Nevertheless, landscape integrity remains relatively high, especially in areas relatively distant from human settlements (**Figure 1.2 C**) (Calzada et al., 2018).

A set of 17 secondary forest plots (400 m^{2}) was established in 2003-2005, and a set of comparable 14 old-growth forest plots (500 m^{2}) was established later in 2008 (Lebrija-Trejos et al., 2010; Muñoz et al., 2021a). To date, the Nizanda longitudinal chronosequence spans a successional range of 0-78 yr after land abandonment (oldest plot abandoned in 1945; **Figure 1.2 E**). In both plot sets, trees and shrubs were permanently tagged and identified to species, and plots were remeasured annually in September-October at the end of the rainy season. Survival, stem diameter and tree height were recorded for all trees in each forest inventory, and new in-growing plants meeting the inclusion criteria were added to the survey. To reduce sampling effort, vegetation was stratified in three classes: plants with a stem diameter at breast height (1.3 m, DBH) ≥ 5 cm (measured in 100 % plot area), plants with a DBH = 2.5–5 cm (measured in 50-75 % plot area), and plants with a DBH = 1–2.5 cm (measured in 25 % plot area). Most forest variables (*e.g.*, biomass) are expressed relative to 1 ha, considering the differing sampling area for each class.

4.2 Tropical wet forest (Marqués de Comillas, Mexico)

The wet forest is located in the Mexican state of Chiapas, in the Lacandon Rainforest region bordering with Guatemala (16.10° N, 91.00° W; **Figure 1.2 A-B, D**, **Figure 1.3 right**). It has a mean annual precipitation of 3000 mm yr^{1} and a mean annual temperature of 24.4 °C, with a short 3-month long dry season (rainfall < 100 mm month^{-1}). The area is located near the southern limit of the Montes Azules Biosphere Reserve. Since pre-Columbian times and up until the 1970's, the region was populated at low densities by the Lacandón people and


A
United States of America
Gulf of Mexico
Mexico
Honduras
B
Pacific Ocean
Guatemala
Nicaragua
B
Gulf of Mexico
Campeche
Tabasco
Veracruz
Nizanda
Chiapas
Marqués de Comillas
Oaxaca
435 km
Guatemala
Pacific Ocean
C
Nizanda (tropical dry forest)
16° 42′ N
16° 37′ N
N
Chilona river
Agua Tibia river
Nizanda
El Zapote
Mazahua river
Nizanda river
La Cueva
0 1 2 3 km
95° 5′ W
94° 58′ W
D
Marqués de Comillas (tropical wet forest)
16° 8′ N
16° 3′ N
N
Montes Azules Biosphere Reserve
Lacantún river
Boca de Chajul
Loma Bonita
Chajulillo river
MÉXICO
GUATEMALA
0 1 2 3 km
91° 2′ W
90° 55′ W
E
Dry forest (Nizanda)
Wet forest (Marqués de Comillas)
Siliciclastic phyllite
Limestone
0
20
40
60
80
Old-growth
Stand age (yr)

old-growth tropical wet forest was the dominant vegetation type. During the 1970's and 1980's, it experienced a sizeable immigration of Mexican and Guatemalan people (Berget et al., 2021). This sudden occupation led to a fast conversion of tropical forests into agricultural lands, especially to the south-west of the Lacantún river, outside of the Montes Azules Biosphere Reserve (Lohbeck et al., 2022). Nowadays, there is a sharp contrast between the landscape inside the Montes Azules reserve, which is very well preserved, and the occupied portion of the region, where only half of the old-growth forests remains mixed with patches of secondary forests and agricultural lands (**Figure 1.2 D**, **Figure 1.3 right top**) (Lohbeck et al., 2022).

A set of 14 secondary forest plots (500 m^2) was established in 2000-2005, and six more plots were added in 2012 (van Breugel et al., 2006). To date, the Marqués de Comillas longitudinal chronosequence spans a successional range of 0-36 yr after land abandonment (oldest plot abandoned in 1987; **Figure 1.2 E**). As with the dry forest dataset, trees were tagged and measured annually since plot establishment, either in September-October for the plots established in 2000-2005 or in February-March for those established in 2012. All stems with diameter at breast height ≥ 1 cm were included (*i.e.*, sampling was not stratified).

◀ **Figure 1.2**

Geographical description of the study sites and their permanent plots. **(A)** Nizanda (tropical dry forest) and Marqués de Comillas (tropical wet forest) are located in the southern part of Mexico, **(B)** in the states of Oaxaca and Chiapas, respectively, 435 km apart from each other. **(C)** The Nizanda region has been significantly inhabited by the Zapotec people since the 1880's; a low population density and the traditional practice of shifting agriculture have kept landscape integrity high to our days. **(D)** The Marqués de Comillas region was rapidly colonized during the 1970's and 1980's by Mexican and Guatemalan people, leading to high landscape fragmentation in a short period of time; the Montes Azules Biosphere Reserve north of the Lacantún River has allowed the tropical wet forest to remain relatively undisturbed in this area. **(E)** The longitudinal chronosequences at both sites use plots with different fallow ages to reconstruct the process of secondary succession; Nizanda has a longer history of agricultural practices, thus is has a chronosequence spanning a longer range of fallow ages (plus a set of old-growth forest plots).

Figure 1.3

Landscape and structure of the tropical forests studied in this thesis.

(Left) Tropical dry forest of Nizanda, Oaxaca state, Mexico. **(Left, top)** The landscape at the Nizanda region is a mosaic of mature and secondary tropical dry forest, xerophytic enclaves, riparian vegetation and agricutural lands, mostly devoted to seasonal crops. Landscape integrity remains relatively high, with agricultural lands occupying few and focalized areas around the floodplains of the region's rivers and streams. **(Left, bottom)** The structure of this tropical dry forest is characterized by a short-statured canopy (9-10 m height) that is thinner compared to wet forests. Species diversity is very high. Given the strong environmental constrains of this site (hot, dry, and highly seasonal), the diversity of drought-related functional traits is high. Legumes dominate

the canopy of these forests, probably because of treir heat and drought adaptations.

(Right) Tropical wet forest on Marqués de Comillas, Chiapas state, Mexico. **(Right, top)** The landscape of this region is comprised of mature and secondary tropical wet forest, riparian forest and agricultural lands for crops and cattle ranching. Landscape integrity is moderate, with high fragmentation but a sizable portion of tropical forest still standing. **(Right, bottom)** The structure of this tropical wet forest is remarkably massive and complex compared to its dry counterpart. Forest canopy is around 30 m tall and very thick, letting only small proportions of sunlight to pass through. Water is a very abundant resource, and light seems to be a strong filter for plants in these forests. Species diversity is also very high, with a wide diversity of traits related to light acquisition and growth.

CHAPTER 2

Autogenic regulation and resilience in tropical dry forest

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SUMMARY

Engineering resilience, a forest's ability to maintain its properties in the event of disturbance, comprises two components: resistance and recovery. In human-dominated landscapes, forest resilience depends mostly on recovery. Forest recovery largely depends on autogenic regulation, which entails a negative feedback loop between rates of change of forest state variables and state variables themselves. Hence community dynamics changes in response to deviations from forest equilibrium state. Based on the premise that autogenic regulation is a key aspect of the recovery process, here we tested the hypothesis that combined old-growth forest (OGF) and secondary forest (SF) dynamics should show autogenic regulation in state variables, and thus convergence towards OGF-based reference points, indicating forest resilience. We integrated dynamic data for OGF (11-year monitoring) and SF (16-year monitoring) to analyse three key state variables (basal area, tree density, species richness), their annual rates of change, and their underlying demographic processes (recruitment, growth, mortality). We examined autogenic regulation through generalized linear mixed-effects models (GLMMs) to quantify functional relationships between rates of change of state variables (and underlying demographic processes), and their respective state variables. State variables in OGF decreased moderately over time, against our prediction of OGF constancy. In turn, the three state variables analysed showed negative relationships with their respective rates of change, which allows the return of SF to OGF values after disturbance. In all cases, recruitment decreased with increasing values in state variables, while mortality increased. The observed negative relationships between state variables, their rates of change and their underlying demographic processes support our hypothesis of integrated OGF and SF dynamics showing autogenic regulation for state variables. Competition seems to be a major driver of autogenic regulation given its dependence on a resource availability that declines as forest structure develops.

Synthesis. Based on a straightforward and comprehensive approach to quantify the extent to which tropical forest dynamics is self-regulated, this study highlights the role of autogenic regulation in tropical dry forest as a basic component of its resilience. This approach is potentially valuable for a generalised assessment of engineering resilience of forests worldwide.

1 INTRODUCTION

Anthropogenic pressures acting on tropical forests are increasing worldwide (Hansen et al., 2013). Forest exploitation for timber and the expansion of land devoted to food production (Pendrill et al., 2019), currently operating mostly at industrial scales (Austin et al., 2017), represent serious threats to their existence. Hence, evaluating the ability of forests to persist and maintain their properties in the event of disturbance has become critical. This ability, known as resilience (Holling, 1973; Holling, 1996; Ingrisch and Bahn, 2018; Willis et al., 2018), is fundamental for the long-term maintenance of forest attributes, including standing biomass and biodiversity.

Engineering resilience, which concerns systems that only have a single basin of attraction (the set of system states that share a single equilibrium; Walker et al. (2004)), encompasses two major components: (1) resistance to disturbance, which is the capacity of a system to minimize state modifications in the face of a disturbance, and (2) recovery from disturbance, which is the capacity of a system to return to its pre-disturbance state (Holling, 1973; Holling, 1996; Peterson et al., 1998; Lloret et al., 2011; Ingrisch and Bahn, 2018). The interplay between these two components of resilience determines how successful a system will be in retaining its state properties over time (**Figure 2.1 A**) (Pimm, 1984; Peterson et al., 1998; Ives and Carpenter, 2007). However, in the context of human-driven land use change, forest resistance to disturbance loses importance: humans have developed tools and techniques that allow us to thoroughly remove vegetation no matter how resistant it is. For this reason, the resilience of human-disturbed forests fundamentally depends on its recovery component, making its understanding urgent.

Measuring the recovery component of engineering resilience in ecological systems is challenging because forest state is difficult to quantify directly. Quantification of recovery requires the use of several state variables that define the state of an ecological system at any given moment (Beisner et al., 2003; Walker et al., 2004; Müller et al., 2016; Ingrisch and

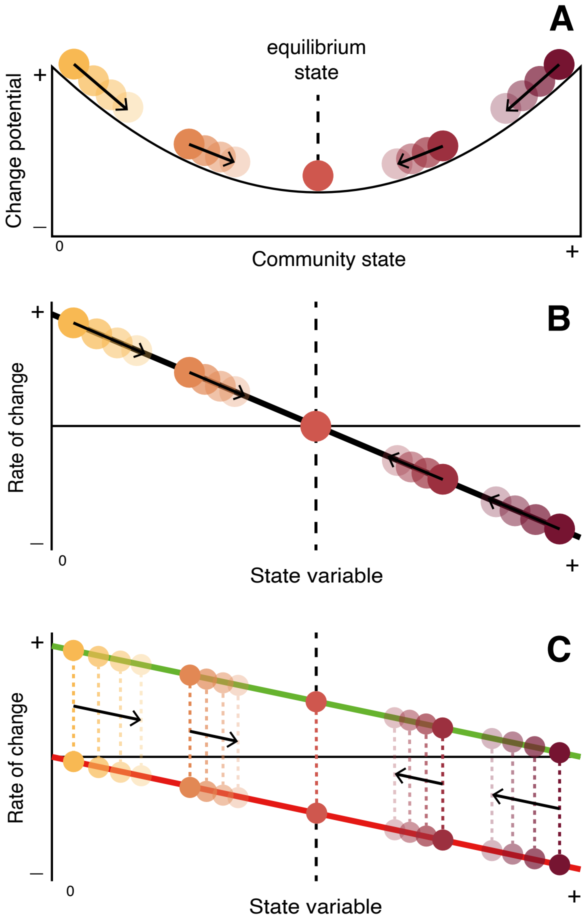


Figure 2.1

Conceptual overview of resilience in ecological systems. In all three panels, each circle/colour represents a different state of the same hypothetical community, while the arrows denote the dynamics of the community. **(A)** The concept of resilience, here represented with a ball-in-cup diagram, is a theoretical construct that is not amenable to direct evaluation in real ecosystems; neither the overall state of the community nor the potential of change is directly measurable. Thus, proxies for these theoretical variables are required. **(B)** We propose that resilience may be evaluated by substituting the overall state of the community by one or several state variables (*X*-axis), while the potential of change could be replaced by the rate of change in a state variable (*Y*-axis). We hypothesize that resilient systems show an overall negative relationship between state variables and their rates of change. **(C)** The rate of change of a given state variable results from the balance between antagonistic demographic processes. All changes in forest state variables are referred to as losses or gains, regardless of the underlying antagonistic processes. For example, mortality fluctuates from zero to large negative values, whereas recruitment fluctuates from high positive values to zero as the state variable values increase. Therefore, each community state has two different values, each corresponding to either gains (green line) or losses (red line). Below equilibrium, the net result should be positive, while above equilibrium it should be negative to allow for forest resilience. At equilibrium, positive and negative processes are offset, which results in no change of the state variable. In all panels, the dashed vertical line denotes the equilibrium state of the community.

Bahn, 2018). In forest ecosystems, commonly analysed state variables such as basal area, tree density and species richness (Nikinmaa et al., 2020), are the outcome of basic ecological processes occurring in the plant community (Chazdon, 2003; Norden et al., 2015). Basal area is an easily measurable variable that is closely related to biomass and thus to ecosystem productivity (Chave et al., 2014). Tree density is an essential demographic variable that can be used to estimate tree crowding and, thus, potential intra- and interspecific competition (Westoby, 1984). Species richness reflects the variety of ecological strategies of a certain forest community, as the requirements for resource and environmental conditions are different for individual species, which then influence the ecological performance of the plant community as a whole (Peterson et al., 1998).

Changes in forest state variables, and thus their recovery after disturbance, are driven by underlying demographic processes such as recruitment, growth, and mortality (*e.g.*, Lewis et al., 2004b; Rozendaal et al., 2016; van der Sande et al., 2017). These processes are antagonistic given their opposite effects on state variables; for instance, tree growth and recruitment increase forest basal area, whereas tree death reduces it (van der Sande et al., 2017). In relatively constant communities such as old-growth forests (OGF), the effects of antagonistic processes on state variables are balanced (Chambers et al., 2013). By contrast, in non-stable forest communities (Grimm and Wissel, 1997; Müller et al., 2016), such as secondary forests (SF) recovering from disturbance, such a balance is absent. In SFs, increases in state variables outweigh the losses, which results in a positive net change (*e.g.*, Poorter et al., 2016; Rozendaal et al., 2019). Similarly, under some circumstances forest state variables may exceed reference (equilibrium) values; for example, demographic inertia results when populations in successional communities grow beyond OGF values due to time lags in the action of regulating mechanisms (Koons et al., 2007). In these cases, antagonistic processes with negative effects outdo those with positive effects until balance is reached.

Depending on whether state variables are above, below, or at their reference value, changes resulting from the imbalance of the underlying antagonistic processes will result in gains, losses or no change (constancy) in state variables (Lewis et al., 2004a; Lewis et al., 2004b; Rozendaal and Chazdon, 2015; van der Sande et al., 2017). Such autogenic regulation should be apparent when the magnitude and direction of changes in community state variables are functions of the same state variables. Recovery, and thereby resilience, thus largely arises from autogenic regulation of the state variables in the community: autogenic regulation of forest state variables contributes to the recovery component of resilience through the continuous adjustment of forest dynamics in response to deviations from equilibrium. Derived from this reasoning, the premise of this study is that autogenic regulation is a key and distinctive aspect of the recovery process. This premise is fundamental to forest recovery through secondary succession but also for OGF, which also undergoes deviations from reference values.

Autogenic regulation of forest dynamics is fundamental for recovery in the context of engineering resilience, and together with the impact of external forces will result in the magnitude of changes in the state of the forest. Autogenic regulation implies a negative feedback loop between rates of change of forest state variables and the values of the state variables themselves, conforming to an overall negative relationship. Below-equilibrium values in a state variable lead to positive rates of change, equilibrium-state values lead to no change, and above-equilibrium values lead to negative rates of change in the state variable (**Figure 2.1 B**). These negative relationships between rates of change and state variables emerge because of the underlying negative relationships between recruitment, growth and mortality with state variables. It must be noted that the negative relationships between antagonistic processes and state variables hold regardless of the sign of these antagonistic processes (**Figure 2.1 C**).

A pervasive methodological limitation in the study of forest recovery is that the focus is generally restricted to either SF or OGF. This is regrettable: SF and OGF are alternative states of a forest continuum having a single basin of attraction; hence, the two of them are needed to examine the dynamics of the system over a broad range of forest states. Forests as a whole, regardless of successional status, are basically ruled by the same autogenic and allogenic forces. Therefore, the stability landscape of a forest (*sensu* Beisner et al., 2003) can be described by jointly monitoring the dynamics of SF and OGF within a same basin of attraction (**Figure 2.1 A**). However, quantifying the state of a forest and its potential for change is not straightforward in real life since these two concepts are theoretical constructs. To this end, state variables (as those discussed previously) can be used as proxies for the state of the forest, and the changes observed in them as proxies for the potential change of the forest.

In this study we integrated information gathered in both SF and OGF plots to examine community-level autogenic regulation in the basal area, tree density, and species richness of a Neotropical dry forest. To this end, we analysed the relationship between forest state variables, their rates of change, and their underlying demographic drivers based on multiannual dynamics of SF and OGF plots in a tropical dry forest in southern Mexico. We hypothesized that the integration of OGF and SF dynamic information should show autogenic regulation in forest state variables, and thus convergence towards OGF-based reference points, indicating forests in this study are resilient. Based on this hypothesis, we predicted that the state variables of OGF are constant over time due to the balanced effects of underlying antagonistic processes, while the forest state variables in SF change towards OGF equilibrium values due to an imbalance of their effects. To our knowledge, this is the first study to quantify autogenic regulation for tropical dry forests from a demographic perspective. It examines key community attributes separately to enable comparisons of the strength of autogenic regulation among them. Despite important efforts to assess tropical dry forest resilience (*e.g.*, Pulla et al., 2015; Poorter et al., 2016), this seems to be the first study to fully integrate dynamic information for the SF-OGF ecological continuum from a non-successional perspective; the integrated analysis of OGF and SF illustrates the displacement of a single ecological system within its stability landscape.

2 MATERIALS AND METHODS

2.1 Study site and vegetation sampling

The study was conducted in Nizanda (16.66° N, 95.01° W), a small village in southern Mexico located in a region where the natural vegetation cover is mostly seasonally dry tropical forest (**Figure 2.2**) (Pérez-García et al., 2010). Recent human colonization at this site occurred ca. 110 years ago and shifting agriculture has been practised since. Hence, SF representing a wide range of fallow ages are present, although well-preserved stands of OGF still dominate the landscape (Gallardo-Cruz et al., 2012). Together, OGF and SF span a broad range of values in basal area, tree density and species density (Lebrija-Trejos et al., 2008).

We used a total of 24 plots in both SF and OGF (**Figure 2.2 C**). Sixteen 400 m^2 SF plots and one OGF plot were set up as permanent plots in 2003 (Lebrija-Trejos et al., 2008), while seven additional 500 m^2 OGF plots were established in 2008. All plots are located on siliciclastic phyllite-derived soils. OGF plots were selected based on their structural heterogeneity, maximum tree size, OGF-specific species composition, and their conservation status (no evidence of logging or other obvious anthropogenic disturbances). The OGF forest in the region has not been exploited in its modern history and its structure, mostly because of the size of the largest trees, suggests that it could be several centuries old. SF plots range in time since abandonment from 0 to 74 years. All SF plots have re-grown after low intensity, non-mechanized shifting agriculture; land-use history was determined by interviewing landowners and fallow ages were verified by using tree ring counts (Brienen et al., 2009). Plots were fenced to avoid further human or cattle disturbance and monitored annually until 2019.

Stems with a diameter at breast height (DBH) ≥ 5 cm were tagged, identified to species, and measured annually. Stems from 1 to 2.5 cm DBH were monitored in 100 m^2 and

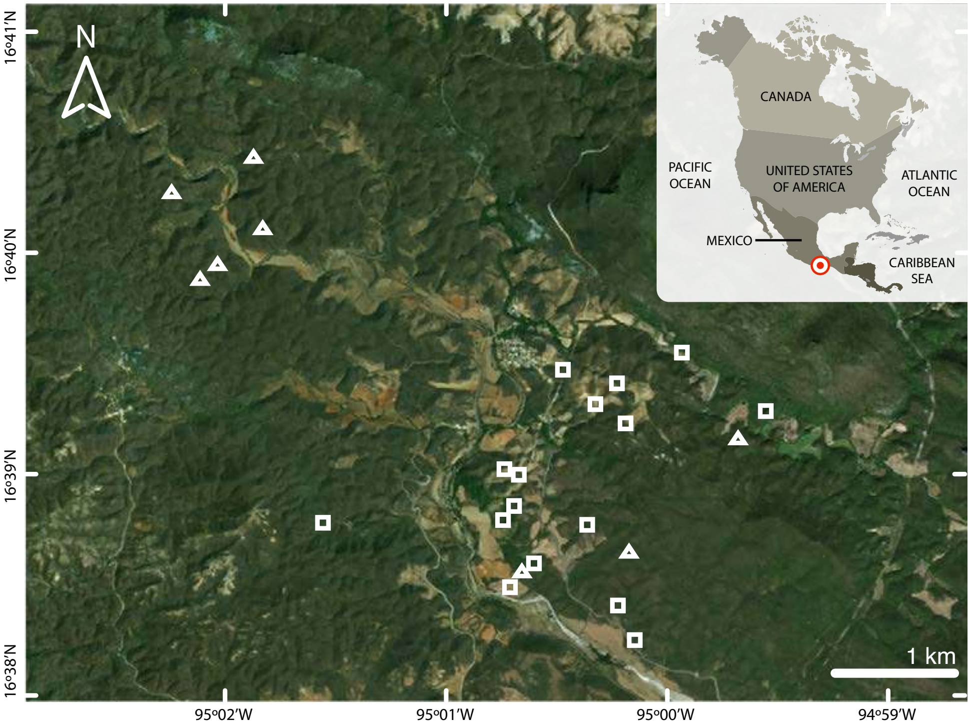


Figure 2.2

Location of study plots in the region of Nizanda. The study was conducted in southern Mexico **(inset)**. The region is a mosaic of well-preserved tropical dry forest, agriculture, pasture, and recovering forest with different times of abandonment. White triangles represent OGF permanent plots, and white squares represent SF permanent plots.

125 m^2 subplots in the SF and OGF plots, respectively. Similarly, stems from 2.5 to 5 cm DBH were monitored in 200 m^2 and 375 m^2 subplots in the SF and OGF plots, respectively (**Figure 2.S1** in Supp. mat.).

We calculated basal area (m^2 ha^{-1}), tree density (no. of stems ha^{-1}), and species richness (no. of species plot^{-1}) for each plot and census. Community-level basal area and tree density were estimated for each DBH category separately through the sums of individual values and expressed on a hectare basis. Species richness was standardized to 400 m^2 by randomly disregarding a 100 m^2 transect from the OGF plots (see legend of **Figure 2.S1** in Supp. mat.).

To assess taxonomic representativeness of our plots, we constructed individual-based rarefaction curves for a standardized area (400 m^2) for all SF and OGF plots for the last year of data (2019). Then, we computed the estimated total number of species per plot based on abundance data to provide an estimate of detected species. The observed species detection level for SF and OGF plots was satisfactory and representative of their forest community. For SF plots, an estimated 66 ± 16 % of species were detected, while for OGF plots the estimated detection was 69 ± 9 % (**Figure 2.S2** in Supp. mat.). These rarefaction analyses were conducted with the *R* package `vegan` (Oksanen et al., 2020; R Core Team, 2020).

2.2 Data analysis

We performed the analysis in three stages (**Figure 2.3**). First, we assessed OGF forest constancy by examining whether or not state variables of OGF plots showed directional changes. Next, we assessed autogenic regulation in forest state variables by examining whether state variables and their rates of change showed negative relations. Finally, we analysed the drivers of autogenic regulation by dissecting the rates of change of state variables into their underlying demographic processes (recruitment, growth, and mortality) to determine whether they were negatively related to the state variable.

To assess OGF constancy, we modelled the state variables as a function of time using generalized linear mixed-effects models (GLMMs), with a random intercept for plot to account for between-plot potential differences in soil properties and topography. A slope significantly different from zero would indicate a directional change over time in OGF dynamics.

To evaluate autogenic regulation of state variables in SF and OGF, we modelled the annual rate of change of a state variable as a function of the state variable using GLMMs, with a random intercept for the plots nested within forest type (SF or OGF), and a random intercept for year. The inclusion of a random intercept for each plot nested within forest type enabled us to assess both plot-to-plot differences in the relationship and account for consistently different effects of SF and OGF due to potential legacy effects in SF. We examined whether the slope was lower than zero (*i.e.*, negative relationship), which indicates state-variable resilience.

We analysed the drivers of forest autogenic regulation and recovery by identifying those demographic processes leading to changes in state variables (recruitment, growth, and mortality). We regressed the demographic processes on the state variable (*e.g.*, basal area loss due to mortality on basal area) using GLMMs, again including a random intercept for plots nested within forest successional stage (SF vs. OGF) and a random intercept for year. We forced the intercept for mortality to zero as no loss is possible when the value of the state variable is zero. We looked for negative relations between demographic processes and state variables. Negative relations imply that demographic processes respond to the state of the

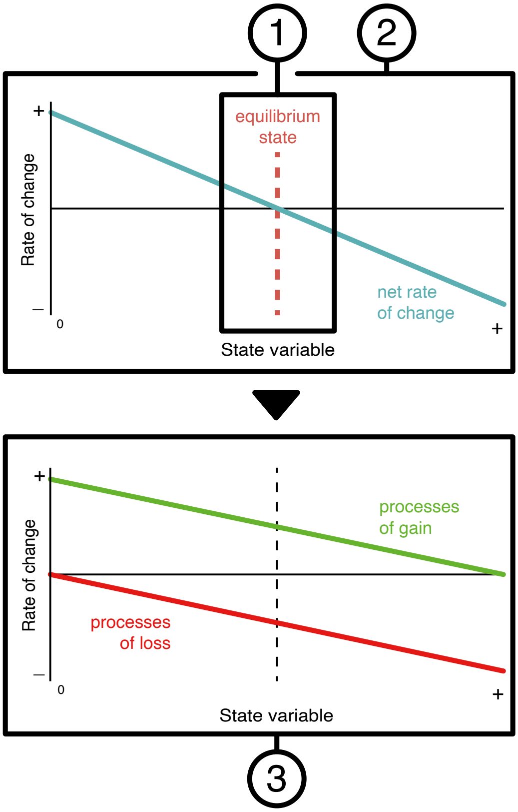


Figure 2.3

Data analysis strategy. **(1)** Assessment of OGF constancy and OGF reference values, including standard deviation. **(2)** Relationship between net rates of change and state variables. **(3)** Dissection of the rates of change into their underlying antagonistic processes and their relationship with state variables. Both panels depict a forest state variable in the horizontal axis and the net rate of change or the effect of an antagonistic process in the vertical axis (positive for recruitment and growth, and negative for mortality). In all cases, the three stages of the data analysis were repeated for each of the three state variables. The colour code matches the colours used to represent OGF dynamics (orange), net rates of change (blue), demographic gain processes (green), and demographic loss processes (red).

forest, and therefore drive the net rates of change that allow autogenic regulation in state variables. Covariance between net rates of change and between the same demographic processes across state variables was not considered in these models.

The random-effects structure in all models was selected a priori based on our hypotheses and experimental design (Harrison et al., 2018). We fitted the models using either the *lmer* (basal area and density) or *glmer* (species richness) function of the `lme4` package

(Bates et al., 2014) in *R* (R Core Team, 2020). Basal area and tree density were fitted using a Gaussian distribution, while a Poisson distribution was used for richness-related measures. In all cases, we estimated bootstrapped 95 % confidence intervals for model coefficients.

3 RESULTS

3.1 Old-growth forest dynamics

Basal area and tree density showed directional, negative changes over time in the OGF plots (**Figure 2.4**). Although the change over time for species richness was not significant, it showed a negative trend as its mean coefficient value was slightly negative. The three state variables markedly increased in the period 2011-2013 and sharply declined in the period 2015-2017.

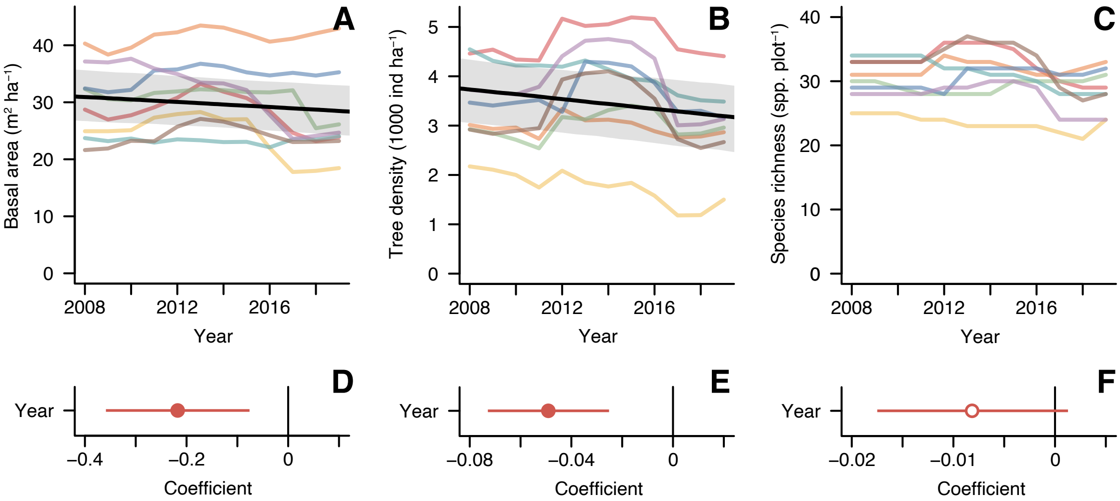
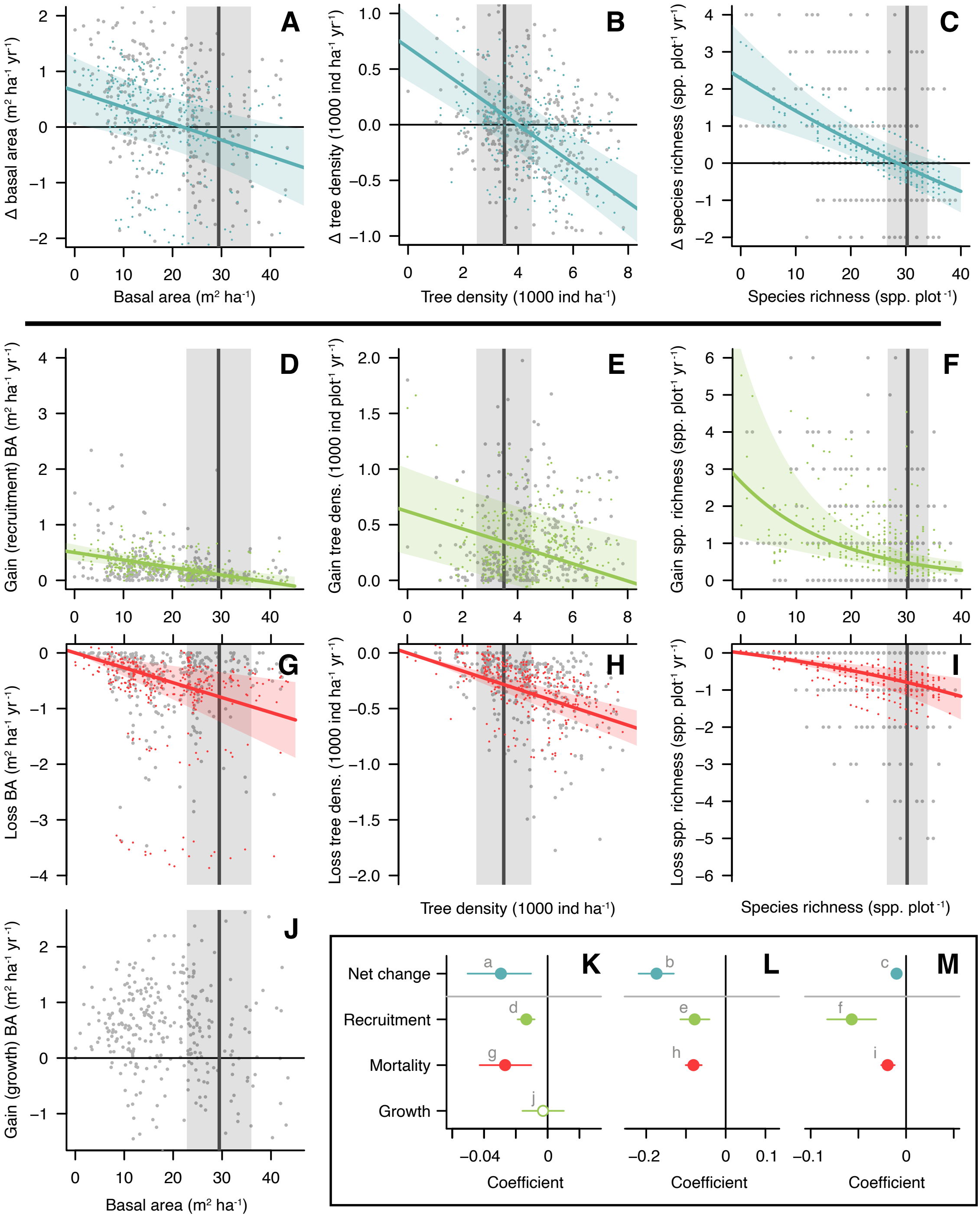


Figure 2.4

Dynamics of OGF state variables. **(A-C)** Basal area, tree density, and species richness dynamics in OGF plots from 2008 to 2018. Coloured lines represent a different OGF plot; solid, black lines depict the linear models with significant slopes; shaded areas around the significant models represent 95 % confidence intervals. **(D-F)** Bootstrapped 95 % confidence intervals for the slopes (coefficients) of basal area, tree density, and species richness as a function of census year. Slopes were estimated using linear mixed-effects models (LMMs).


A
Δ basal area (m² ha⁻¹ yr⁻¹)
2
1
0
−1
−2
0
10
20
30
40
Basal area (m² ha⁻¹)
B
Δ tree density (1000 ind ha⁻¹ yr⁻¹)
1.0
0.5
0.0
−0.5
−1.0
0
2
4
6
8
Tree density (1000 ind ha⁻¹)
C
Δ species richness (spp. plot⁻¹ yr⁻¹)
4
3
2
1
0
−1
−2
0
10
20
30
40
Species richness (spp. plot⁻¹)
D
Gain (recruitment) BA (m² ha⁻¹ yr⁻¹)
4
3
2
1
0
E
Gain tree dens. (1000 ind plot⁻¹ yr⁻¹)
2.0
1.5
1.0
0.5
0.0
F
Gain spp. richness (spp. plot⁻¹ yr⁻¹)
6
5
4
3
2
1
0
G
Loss BA (m² ha⁻¹ yr⁻¹)
0
−1
−2
−3
−4
H
Loss tree dens. (1000 ind ha⁻¹ yr⁻¹)
0.0
−0.5
−1.0
−1.5
−2.0
Tree density (1000 ind ha⁻¹)
I
Loss spp. richness (spp. plot⁻¹ yr⁻¹)
0
−1
−2
−3
−4
−5
−6
Species richness (spp. plot⁻¹)
J
Gain (growth) BA (m² ha⁻¹ yr⁻¹)
2
1
0
−1
Basal area (m² ha⁻¹)
K
L
M
Net change
Recruitment
Mortality
Growth
a
b
c
d
e
f
g
h
i
j
−0.04
0
−0.2
0
0.1
−0.1
0
Coefficient
Coefficient
Coefficient

◀ **Figure 2.5**

Relations between net rates of change, antagonistic demographic processes, and state variables in a tropical dry forest. **(A-C)** Response of the net rates of change to the value of the community state variable. **(D-J)** Response of the antagonistic demographic processes involved in the changes of the state variables to the value of the state variable. **(K-M)** Coefficients with 95 % confidence intervals for the slope of models shown in panels A-J. Solid lines and their colour-shaded areas represent the fitted models, excluding random effects, with 95 % confidence intervals; grey dots represent real plot-year observations; coloured dots indicate the model predictions including random effects; vertical grey lines and their shaded area show the OGF average value ± 1 standard deviation for each state variable. Lowercase letters in panels K-M indicate the correspondence with panels A-J. Overall, the relation between net rates of change and state variables was negative (A-C). Likewise, most demographic processes responded to changes in forest state variables (D-I), except for growth in basal area (J) and recruitment in tree density (E).

3.2 Rate of change in state variables

The rates of change showed a negative relationship with the state variables for all three state variables analysed, suggesting resilient behaviour (**Figure 2.5 A-C, K-M**). The fitted models intersected the *x*-axis (*i.e.*, predicted values reached zero) close to OGF average values for all three state variables, which implies that net rates of change approach zero as the forest approaches OGF values. Species richness was the state variable with the closest match between the OGF average and the point where the model intersected the *x*-axis. In contrast, the function for basal area crossed the *x*-axis at slightly lower values, while the function for tree density did so at slightly higher values than their respective OGF averages, but in all cases within their confidence intervals. These results were consistent with mean rates of change of state variables calculated for segments of the state variable range representing different stages of forest development (**Figure 2.S3** in Supp. mat.).

3.3 Relationship of demographic drivers with forest state

Demographic drivers of resilience showed different responses depending on the process and the state variable analysed (**Figure 2.5 D-M**, **Figure 2.S4** in Supp. mat.). For basal area, recruitment and mortality effects decreased and increased, respectively, with increasing values of the state variable, while growth did not show any response. For tree density and species richness, both recruitment and mortality responded clearly to changes in the state variable, decreasing and increasing with the state variable value, respectively. In other words, all the relationships except for growth were negative, since losses due to mortality result in negative changes by definition.

4 DISCUSSION

This study tested the hypothesis that dynamic information for tropical dry forest stands, in which no distinction is made between OGF and SF, should show autogenic regulation in forest state variables. Self-regulated forests should converge towards OGF-based reference points, implying forest resilience. Unexpectedly, OGF attributes were not overall constant, but decreased over time. However, as expected, we found negative relationships between state variables and their rate of change, suggesting that autogenic regulation drives the dynamics in forest attributes. We also found that demographic processes responded to changes in state variables but, interestingly, this was not the case for tree growth.

4.1 Old-growth forest dynamics

Against our expectations, state variables in the OGF (basal area, species richness, and density) showed mixed dynamic trends over time but all displayed decreasing trends over the sampling period, particularly towards its end. Equilibrium in natural systems occurs when the properties of a system show moderate variation over time (Pimm, 1984; Naselli-Flores et al., 2003; Jen, 2005; Ives and Carpenter, 2007). In our case, OGF dynamics showed a hump-shaped pattern that, overall, led to a significantly decreasing trend for basal area and tree density, and also a decreasing trend for species richness, although this was non-significant. Interestingly, this pattern was observed at most plots for the three state variables analysed. Such coordinated dynamics between plots is unlikely to be a stochastic event and thus suggests the existence of a regional-scale factor driving the observed OGF changes. Considering that tropical dry forests are systems strongly limited by water (Murphy and Lugo, 1986), climatic variability is likely to be largely responsible for these changes. The steep increases and decreases observed in the state variables coincided with La Niña and El Niño events, respectively. The 2011-2013 increase was coupled with La Niña event of 2010-2012, while the 2015-2017 decrease was coupled with the extreme El Niño event of 2015-2016 (Zhu et al., 2018; Wigneron et al., 2020). On the Pacific coastal region of Mexico, La Niña has been associated with above-average rainy years, while El Niño has been associated with droughts (Caso et al., 2007). Nonetheless, it is interesting that when the analysis focuses on the pre El Niño years, rates of change in the mature forest are zero for basal area and species richness, and slightly above zero for stem density (**Figure 2.S3** in Supp. mat.).

A directional dynamic in OGF does not necessarily imply that the system's state variables are not constant over time. A short-term directional behaviour could be part of a long-term cyclic pattern with a zero-mean rate of change. Antagonistic demographic processes could act with similar intensities over time, albeit not simultaneously. From our results for OGF, we infer that antagonistic demographic processes are not offsetting immediately, as gains did not offset losses during the study period (Lewis et al., 2004a; Lewis et al., 2004b; Chambers et al., 2013).

The directional dynamics observed for the OGF does not necessarily contradict our hypothesis. A possible interpretation for this result is that climate, an allogenic force, is occasionally capable of exerting a stronger influence than autogenic regulation in OGFs. OGFs are systems in relative equilibrium, where mean vegetation properties are largely driven by resource availability (Quesada et al., 2012; Seidl et al., 2012). As shown in the stability landscape depicted in **Figure 2.1 A**, the potential for change in vegetation is negligible close to OGF values (*i.e.*, the potential for change is lowest at or close to equilibrium). If true, this would imply that autogenic regulation (and, therefore, the potential for recovery) is also negligible at this point, allowing external forces to drive forest dynamics when the community approaches equilibrium. The topography at the bottom of the basin of attraction could determine how resistant the system is to allogenic forces once it achieves equilibrium. A flat and wide bottom could indicate a broad range of values defining the equilibrium of the system, wherein autogenic regulation may play a minor role in driving forest dynamics.

4.2. Rates of change in state variables

As the system moves farther away from equilibrium, autogenic regulation is likely to gain importance. Autogenic regulation should be highest when the state variables are either at zero or very large values, assuming that landscape and soil conditions remain undisturbed. The support for this reasoning is twofold. First, it is consistent with our observation of weakly self-regulated OGF attributes. Second, integrating SF and OGF dynamic information revealed the negative relationship between state variables and their net rates of change (**Figure 2.S4 A-C** in Supp. mat.). SF plots encompassed the lowest values for basal area and species richness, and the lowest and the highest values for tree density (*i.e.*, they are farther away from equilibrium than OGF; **Figure 2.S4** in Supp. mat.). Therefore, one may reasonably expect some SF (particularly very young stands) to undergo stronger autogenic regulation than OGF because the former lie farther away from the equilibrium state compared to the latter. Nevertheless, OGF can undergo strong autogenic regulation if considerably pushed away from equilibrium, as happened for some of our plots after the El Niño event that started in 2015. Similarly, autogenic regulation in SF plots whose attributes are already similar to OGF is expected to be weaker.

The hypothesis of negative relationships between state variables and their rates of change in the studied dry forest was supported by our results (**Figure 2.5 A-C**). Negative relationships imply that as the value of the state variable increases, the rates of change decrease, thereby resulting in a negative feedback loop. Under conditions of little vegetation development (low state variable values), as in early secondary succession, the rates of change will be positive until they reach their dynamic equilibrium state. Conversely, when the community exceeds the equilibrium state, forest state variables will decrease until they return to equilibrium. This result is consistent with previous findings on autogenic processes as relevant drivers of forest dynamics (van Breugel et al., 2006; Finegan et al., 2015; Lohbeck et al., 2015; Norden et al., 2015) and provides a mechanistic explanation for autogenic forest recovery.

Autogenic regulation is not equally strong for all state variables. Species richness showed the strongest autogenic regulation, as indicated by the relatively narrow confidence interval for the state variable-rate of change relationship (**Figure 2.5 C, Figure 2.S3 C** in Supp. mat.), and the fact that it was the most constant state variable in OGF plots over time (**Figure 2.4 C**). Basal area and stem density showed weaker autogenic regulation; these two variables exhibited a slightly directional OGF dynamics (**Figure 2.4 A-B**), the broadest confidence intervals for OGF reference values (**Figure 2.5 B-C**), and in the case of stem density, rates of change slightly above zero for plots close to OGF reference values (**Figure 2.S3 B**). This finding has important theoretical and practical implications. For the resilience theoretical framework, it points to the need of realising the multi-dimensional nature of stability landscapes and hence the different shapes of basins of attraction depending on the state variable/dimension being analysed (Walker et al., 2004; Nikinmaa et al., 2020); from a practical perspective, it shows why the perceived speed of the recovery process may vary depending on the variables used in the assessment (Poorter et al., 2016; Rozendaal et al., 2019).

4.3. Antagonistic demographic processes

Similar to our results for the net rates of change, most demographic processes showed clear relations with their state variables (**Figure 2.5 D-J**). This result largely agrees with our proposed mechanism of forest resilience through antagonistic demographic processes. Forest demographics responded to the state of the system, either with increased and/or decreased recruitment, growth or mortality, depending on the value of the state variables.

We suspect that the observed autogenic regulation, which ultimately leads to forest recovery, is driven mostly by competition. Forest structure development has a direct impact on the spatial arrangement of plants and their biotic interactions, yielding in turn changes in forest resource availability and environmental conditions (Lebrija-Trejos et al., 2011; van der Sande et al., 2017; Matsuo et al., 2021). As vegetation develops, competition for space, light, water, and nutrients increases (Uriarte et al., 2004). For any given tree, entering the community or increasing in size will be more difficult when the existing resources are shared with more and/or larger individuals (Rozendaal et al., 2020). In forests with higher tree density, species richness, and biomass, increased resource consumption is likely to result in (stronger) resource limitation. Resource limitation has direct impacts on recruitment by reducing the reproductive investment of mature trees (Allen et al., 2017b), and the probability of seedling establishment (Tripathi et al., 2018). Similarly, resource limitation affects the growth of established trees by reducing photosynthetic capacity and carbon fixation due to reduced water, light and/or nutrient availability (Quesada et al., 2012; van der Sande et al., 2017). Resource limitation increases tree mortality due to the reduction in photosynthetic uptake, which in turn could lead to a lower investment in defensive compounds against biotic agents (McDowell et al., 2008).

Unexpectedly, the analyses demonstrated that tree growth was not related to basal area. The lack of response in this variable is intriguing since some studies have suggested such a relationship (*e.g.*, Rozendaal and Chazdon, 2015; van der Sande et al., 2017; but see Toledo et al., 2011). Growth in basal area might be mostly driven by external factors in our study site, such as climate. Actually, rainfall and its seasonal distribution are likely the main factors influencing this process in tropical dry forests (Allen et al., 2017a). This is consistent with studies in other tropical forests, where not only growth but also mortality are largely driven by inter-annual changes in precipitation, particularly by severe droughts (Toledo et al., 2011; Aleixo et al., 2019; Saenz-Pedroza et al., 2020). Moreover, growth is affected by other environmental factors such as temperature or solar radiation, which change continuously (high intra- and inter-annual variability) but are unrelated to autogenic regulation (Lewis et al., 2004a).

4.4. Considerations for the assessment of autogenic recovery

The variability observed in the relationships between the three state variables and their rates of change/underlying demographic processes may arise from the existence of slightly different basins of attraction in each plot (Vandermeer et al., 2004). Even though our plots were carefully selected to be as similar as possible, as this is a requirement for establishing chronosequences (Johnson and Miyanishi, 2008; Mora et al., 2015), subtle inter-plot differences in soil attributes, topography, land-use history, or landscape context can shift the location of the bottom of the basin of attraction (representing the equilibrium state) as well as its shape (representing the relationship between forest state and potential of change; **Figure 2.1 A**). The inclusion of random effects in our mixed-effects models helped account for this fact, as in this way we were able to deal with differences in equilibrium states. Nonetheless, a key requirement of the approach in this study is that all plots should share a similar basin of attraction, as otherwise the interpretation of the overall trends shown by the models could be misleading. Highly heterogeneous environmental conditions could result in differences in the potential of vegetation development among stands (*e.g.*, Durán et al., 2006). Similarly, high landscape degradation and the associated seed-dispersal limitation could result in divergent species assemblages among stands, and thus also to different recovery pathways (Arroyo-Rodríguez et al., 2017). Therefore, it is essential to consider biotic and abiotic differences between sampling units when studying the recovery component of resilience, as they have an impact on the shape of the forest's basin of attraction.

The relatively uniform environmental conditions and the minimal impact of agriculture in our study region are ideal to test our hypothesis because this makes our forest unlikely to have multiple equilibrium states. The region has a low level of landscape fragmentation (Calzada et al., 2018; Gallardo-Cruz et al., 2018) and a high degree of naturalness (*sensu* Machado, 2004) compared to other tropical dry forests disrupted by agricultural practices. In SF plots, low-intensity (maximum of two harvesting cycles and no heavy machinery) (Lebrija-Trejos et al., 2008), traditional slash-and-burn agriculture was practiced prior to abandonment. In addition, soil properties are relatively similar across SF and OGF plots. The landscape context with a high connectivity of SF and OGF patches makes dispersal limitation unlikely at distances under 2.5 km (Gallardo-Cruz et al., 2010). These landscape conditions result from both a complex topography and the regional social context, characterised by a traditional indigenous community that has not yet fully embraced modern agricultural practices (Calzada et al., 2018).

Similar conditions may define many other areas in the tropics. However, landscapes with a very low degree of naturalness, a poor conservation state (*e.g.*, regions with flat topography, higher population density, higher income, lower cultural attachment, and/or more intense land-use), or with the presence of potentially hyper-dominant species may result in not one but several equilibrium forest states. Arrested forests, often reported in successional studies, represent systems having at least two alternative stables states: an OGF state and an arrested successional state. For instance, Mesquita et al. (2015) and Neto et al. (2019) reported strikingly different successional pathways in the central Amazon after abandonment of fields with clear-cut or pasture use, for both of which OGF was the original vegetation. Pastures were subjected to an intensive fire regime and soil compaction, changing soil properties and modifying seed and resprout banks at these sites. Land-use legacy in abandoned pastures led to hyper-dominance by plants of the *Vismia* genus, slowing down or arresting the recovery towards OGF reference values. Although arrested succession represents a system's new alternative stable state in which autogenic regulation may also operate, the relationships between state variables and demographic processes could be modified, having parameters leading to the arrested successional stable state rather than to the OGF state. As our approach is based on the engineering resilience framework, and therefore deals with systems with a single stable state in their stability landscape, it would not be possible to replicate our results in systems encompassing multiple stable equilibrium states.

A further consideration in assessing forest recovery is the selection of state variables to be analysed. In this study, we used basal area, tree density and species richness as state variables defining key forest attributes (Chazdon, 2003; Norden et al., 2015). Strictly, the conclusions from this study are valid regarding these state variables only, and the ecological processes they represent. Nonetheless, the negative feedback loops described by our recovery hypothesis are a necessary theoretical requirement for engineering resilience to be achieved, as otherwise recovery from disturbance would be dependent on contingency rather than being the result of autogenic regulation of forest dynamics. Therefore, we expect other forest attributes to resemble the patterns observed for the state variables analysed in this study.

4.5. Concluding remarks

Validation of our hypothesis in other biomes and landscape contexts (Arroyo-Rodríguez et al., 2017) is required before attempting to make broader generalizations. Nonetheless, our approach provides a simple and comprehensive way to quantify the extent to which forest dynamics is driven by autogenic factors. Certainly, a deeper and integrated study of autogenic and allogenic (in particular, climate variability) factors is needed to gain further insights into forest resilience mechanisms, and ultimately to predict the short- and mid-term dynamics of old-growth and secondary forests around the globe.

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AUTHORS' CONTRIBUTIONS

R.M. and J.A.M. developed the idea and led the writing of the manuscript; R.M. and J.A.M. performed field work; R.M. performed data analysis; D.M.A. and E.J.G. contributed to data analysis; F.B. and J.M.D. contributed to writing the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.s1rn8pk85 (Muñoz et al., 2021b).

CHAPTER 2

Supplementary material

Figure 2.S1 – Sampling design in OGF and SF permanent plots

Figure 2.S2 – Rarefied species richness per plot (for year 2019)

Figure 2.S3 – Alternative visualization of net rates of change (in discrete steps)

Figure 2.S4 – Alternative visualization of Figure 2.5 differentiating OGF and SF data points

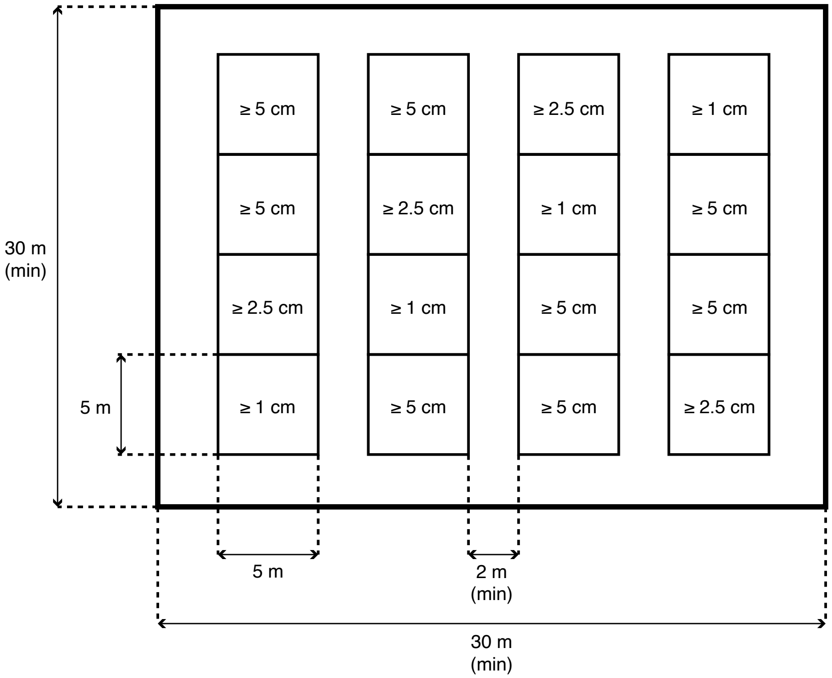


Figure 2.S1

Sampling design of the secondary forest (SF) and old-growth forest (OGF) plots. The figure depicts the configuration of a SF forest plot (and the 2003-established OGF forest plot). The sampling area of 400 m^2 was divided in four transects of 100 m^2 each. In turn, each transect was subdivided in four quadrats of 25 m^2 (5 × 5 m). Every quadrat was assigned to a specific DBH sampling criterion; either woody plants with a DBH ≥ 5 cm, DBH ≥ 2.5 cm, or DBH ≥ 1 cm, specified in the figure by the text within each quadrat. Such DBH criteria were randomly assigned to the quadrats of each transect, always keeping two 'DBH ≥ 5 cm' quadrats, one 'DBH ≥ 2.5 cm' quadrat, and one 'DBH ≥ 1 cm' quadrat per transect. Such configuration means that all plants with a DBH ≥ 5 cm are measured in the entire sampling area (as they are measured in all DBH-criteria quadrats; 400 m^2), plants with a DBH within 5 and 2.5 cm are measured in half of the sampling area (200 m^2), and plants with a DBH within 2.5 and 1 cm are measured in a quarter of the sampling area (100 m^2).

Transects were spaced by corridors of 2 m (although in few cases they were slightly larger). Such corridors were intended to minimize the impact of repeated walking on the dynamics of the vegetation (for instance, in seedling establishment). All the plots were fenced using barbed wire to stop further human disturbance by avoiding confusions on land use, as most of our SF plots were placed in areas that are being still used for productive purposes. The fencing consists of two lines of barbed wire roughly placed at 50 cm and 120 cm height from the ground. It stops people or cattle from getting into the plots but does not seem to affect the transit of wildlife; for instance, deer can jump over it and smaller fauna just walks below. The fenced area was usually of 30 × 30 m, which is the typical size of same-aged secondary vegetation patches in this region (low intensity slash-and-burn agriculture patches).

For the OGF plots established in 2008, the sampling area was increased to 500 m^2 by adding an additional transect. The sampling area proportions for the plants with DBH ≥ 5 cm and the plants within 2.5 and 1 cm remained the same (500 m^2 and 125 m^2, respectively). However, for the plants with DBH within 5 and 2.5 cm, the sampling effort was increased to three-quarters of the sampling area (325 m^2). Because space was not a limitation in OGF as in SF plots, the fenced area was extended to 50 × 50 m.

The standardisation of species richness between the 400 m^2 and the 500 m^2 plots was done by disregarding one whole 100 m^2 transect (*i.e.*, four contiguous quadrats) in OGF plots. The transect to be disregarded was randomly selected.

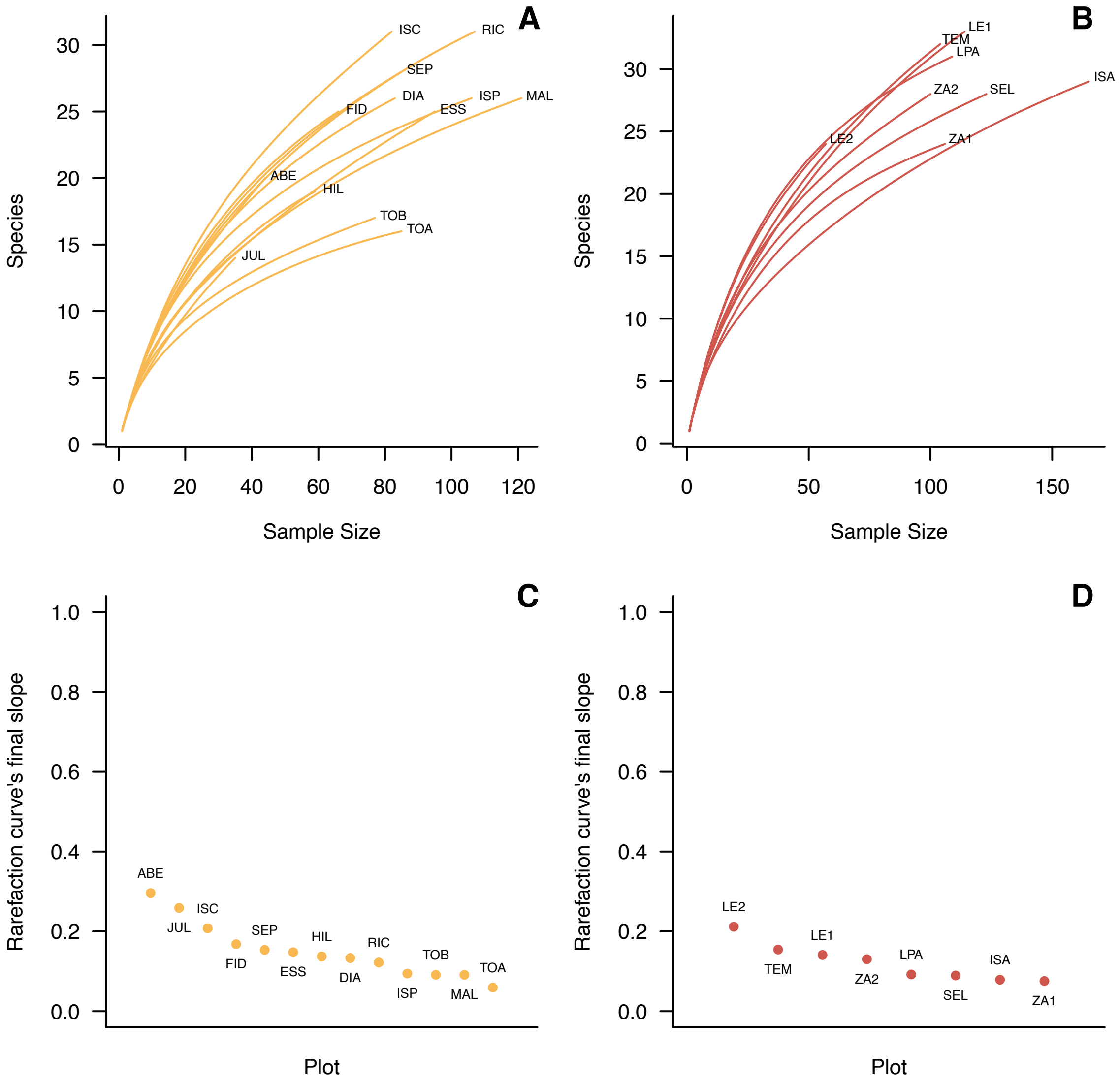


Figure 2.S2

Species rarefaction for SF and OGF plots with 2019 data. **(A)** Rarefaction curves for SF plots and **(B)** OGF plots, showing the number of individuals sampled in the *X* axis and the average number of identified species in the *Y* axis. Each line represents a different plot. **(C)** Final slope for the rarefaction curves of SF plots and **(D)** OGF plots. The value of the slopes is derived from the rarefaction curves in panels A and B. Each individual point represents the final slope for each plot. The slope of the rarefaction curves represents the average number of species that each new individual account for at the maximum number of individuals sampled in each plot. The lower the slope is, the more taxonomically-representative the data for each plot is.

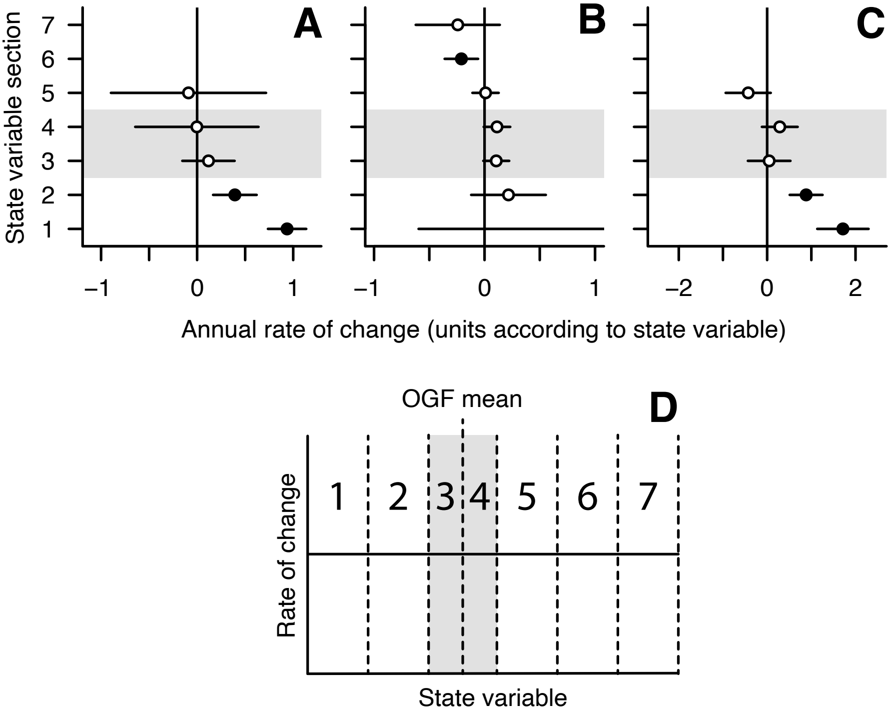
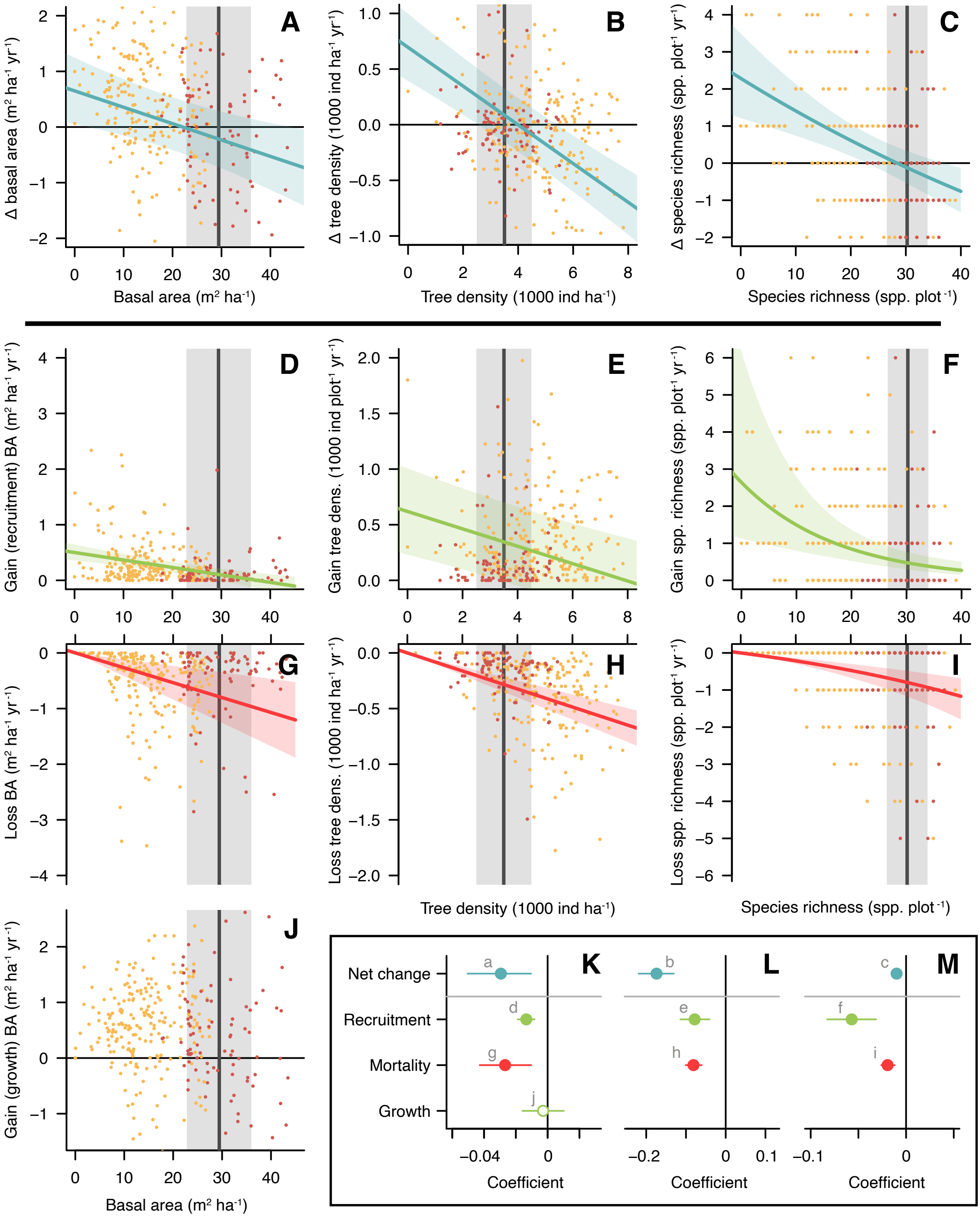


Figure 2.S3

Mean rates of change of state variables estimated for different sections of the state variable range separately. **(A)** Basal area, **(B)** tree density, and **(C)** species richness. Sections defined in **(D)** represent: 1, lower below-equilibrium; 2, upper below-equilibrium; 3, lower at-equilibrium; 4, upper at-equilibrium; 5, lower above-equilibrium; 6, upper above-equilibrium; 7, extreme upper above-equilibrium values. Circles and lines represent mean and 95 % confidence intervals; closed circles denote means significantly differing from zero. Gray bands in (A), (B) and (C) represents means within OGF confidence intervals, also shown in (D). Note that basal area (A) and species richness (C) had no data for sections 6 and 7, and that the mean value for section 1 in tree density (B) lies to the right of plot margin.


A
Δ basal area (m² ha⁻¹ yr⁻¹)
Basal area (m² ha⁻¹)
B
Δ tree density (1000 ind ha⁻¹ yr⁻¹)
Tree density (1000 ind ha⁻¹)
C
Δ species richness (spp. plot⁻¹ yr⁻¹)
Species richness (spp. plot⁻¹)
D
Gain (recruitment) BA (m² ha⁻¹ yr⁻¹)
E
Gain tree dens. (1000 ind plot⁻¹ yr⁻¹)
F
Gain spp. richness (spp. plot⁻¹ yr⁻¹)
G
Loss BA (m² ha⁻¹ yr⁻¹)
H
Loss tree dens. (1000 ind ha⁻¹ yr⁻¹)
Tree density (1000 ind ha⁻¹)
I
Loss spp. richness (spp. plot⁻¹ yr⁻¹)
Species richness (spp. plot⁻¹)
J
Gain (growth) BA (m² ha⁻¹ yr⁻¹)
Basal area (m² ha⁻¹)
K
L
M
Net change
Recruitment
Mortality
Growth
a
b
c
d
e
f
g
h
i
j
−0.04
0
−0.2
0
0.1
−0.1
0
Coefficient
Coefficient
Coefficient

◀ **Figure 2.S4**

Relations between net rates of change, antagonistic demographic processes, and state variables in a tropical dry forest, discerning SF and OGF datapoints. **(A-C)** Response of the net rates of change to the value of the community state variable. **(D-J)** Response of the antagonistic demographic processes involved in the changes of the state variables to the value of the state variable. **(K-M)** Coefficients with 95 % confidence intervals for the slope of models shown in panels A-J. Solid lines and their colour-shaded areas represent the fitted models, excluding random effects, with 95 % confidence intervals; red dots represent real OGF plot-year observations; yellow dots represent real SF plot-year observations; vertical grey lines and their shaded area show the OGF average value ± 1 standard deviation for each state variable. Lowercase letters in panels K-M indicate the correspondence with panels A-J.

CHAPTER 3

Climatic drivers of productivity in wet and dry tropical secondary forests

Rodrigo Muñoz | Lourens Poorter | Jorge A. Meave | Miguel Martínez-Ramos | Frans Bongers

In review

SUMMARY

Climate change affects the productivity and mitigation potential of forests worldwide, but it is unclear how climatic conditions impact the productivity of different tropical forest types due to the scarcity of long-term field observations. Here, we evaluate how annual changes in precipitation, temperature, and photosynthetically active radiation (PAR) drive changes in aboveground net primary productivity (ANPP) and its underlying components (recruitment, growth, mortality) in a wet and a dry tropical forest. We monitored 36 successional dry and wet Mexican tropical forest plots annually for an 18-yr period. Annual climatic data were matched with forest trajectories to assess the role of climatic conditions in forest dynamics. Climatic conditions showed a stronger effect on biomass dynamics in the secondary dry forest, whereas biomass dynamics was mainly driven by autogenic successional processes in the wet forest. ANPP was mainly driven by temperature, whereas precipitation and PAR had negligible effects. In the dry forest, climatic conditions in the previous year had significant legacy effects on forest productivity. Small temperature increases (+1 °C) reduced biomass growth in the wet (-1.94 Mg ha^{-1} yr $^{-1}$) and the dry forest (-3.65 Mg ha^{-1} yr $^{-1}$), and increased biomass mortality (+0.97 Mg ha^{-1} yr $^{-1}$) only in the dry forests. Our results strongly suggest that global warming will reduce the mitigation potential of secondary tropical forests, reducing long-term productivity and carbon stocks, especially for tropical dry forests.

1 INTRODUCTION

Climatic conditions determine to a large extent the aboveground net primary productivity (ANPP) and the global climate change mitigation potential of tropical forests (Sullivan et al., 2020). Key climatic variables for vegetation, such as precipitation, temperature and photosynthetically active radiation (PAR), vary across seasons and years, significantly affecting the metabolic and vital rates of plant (Yamori et al., 2014). Although these key climatic conditions largely determine tropical forests ANPP and global carbon cycling (Dusenge et al., 2019), most studies of forest-climate responses have mainly focused on rainfall without consideration of the effects of temperature and PAR (Suresh et al., 2010; Martínez-Ramos et al., 2018; Becknell et al., 2021).

The current study focuses on the effect of inter-annual climatic conditions of precipitation, temperature, and PAR on the dynamics of ANPP in secondary tropical forests. Secondary forests have a large potential to mitigate anthropogenic CO_2 emissions (Chazdon et al., 2016) as they account for more than half of the tropical forest area (FAO, 2020) and capture up to 11 times more carbon than old-growth forests (Poorter et al., 2016). Assessments of the effects of interannual climate variation on secondary tropical vegetation are very scarce, especially those analyzing various climatic conditions simultaneously. These analyses are much needed to further unravel how climate temporal dynamics affects tropical vegetation.

ANPP is driven by three underlying demographic processes: recruitment, growth, and mortality (Rozendaal et al., 2016; McDowell et al., 2020), with growth and mortality being the most important drivers of forest productivity (van der Sande et al., 2017). Previous research shows that the effects of climatic conditions depend on the demographic process analyzed (McDowell et al., 2020). There is evidence for tropical forests that high temperatures reduce tree growth (Clark et al., 2010; Sullivan et al., 2020) and increase mortality (Clark et al., 2010; Aleixo et al., 2019), whilst precipitation increases tree growth (Becknell et al., 2021) and reduces mortality (Suresh et al., 2010; Martínez-Ramos et al., 2018; Sullivan et al., 2020), and PAR increases tree growth (Graham et al., 2003; Schuur, 2003). Besides, not only the changes in climatic parameters affect ANPP, but also their timing of occurrence. Seasonality, for instance, is critical for biomass dynamics because some demographic processes occur with greater intensity during a specific period of the year (Clark et al., 2010; Saenz-Pedroza et al., 2020). Furthermore, legacy effects of climatic conditions in previous years may substantially impact ANPP in tropical forests (Suresh et al., 2010; Martínez-Ramos et al., 2018; Aleixo et al., 2019) as reduced carbon gain in the current year can result in fewer storage reserves for bud formation, leaf flushing, and stem diameter growth in the year after, or reduce tree vigor and long-term survival (Song et al., 2021).

This study aimed to evaluate the effect of annual and seasonal conditions in precipitation, temperature, and PAR on the ANPP of wet and dry tropical secondary forests. These forests experience contrasting climatic regimes and may potentially show different ANPP responses to interannual climatic variation. For both forest types, we took advantage of up to 18 years of annual inventories coming from permanent plots with 0-70 years of natural forest regeneration after agricultural abandonment.

Dry forests are subjected to strong water limitation (Allen et al., 2017), thus we hypothesized that increased water availability promotes gas exchange and leads to higher photosynthetic rates and productivity. Therefore, for dry forests, we predicted that ANPP would increase (via higher recruitment, growth, and survival) with higher precipitation and reduced temperature, as these conditions increase climatic water availability. By contrast, wet forests are typically light-limited (Matsuo et al., 2021), and thus we hypothesized that reduced cloudiness (which maximizes solar irradiance reaching the forest canopy) increases the photosynthetic uptake and productivity of these forests. Therefore, for wet forests, we predicted that ANPP would increase with higher PAR. Since seasonality and climatic legacy effects are likely relevant for the assessment of climate-vegetation responses, wet and dry seasons of the current and previous years (*i.e.*, climatic conditions on the preceding 24 months) were considered when conducting our analyses.

2 METHODS

2.1 Study site

The study was carried out in two Mexican tropical forest sites representing the extremes of the climatic gradient where tropical forests occur: the tropical dry forest of Nizanda (16.66° N, 95.01° E, mean annual precipitation [MAP] = 800 mm yr^{-1}, mean annual temperature [MAT]

= 27.7 °C) and the tropical wet forest of Marqués de Comillas (16.10° N, 91.00° E, MAP = 3,000 mm yr^{-1}, MAT = 24.4 °C). At both sites, agriculture and cattle ranching have resulted in the clearing of multiple vegetation patches (van Breugel et al., 2006; Lebrija-Trejos et al., 2010; Lohbeck et al., 2022). At the dry site, slash and burn agriculture has been practiced for nearly a century with livestock production increasing over the past years (Calzada et al., 2018). At the wet site, agriculture was introduced half a century ago and cattle ranching is currently the dominant land use (Zermeño-Hernández et al., 2016). At both sites, landscapes are heterogeneous and composed of patches of mature forest, secondary forests in different stages of recovery, agricultural fields, and pastures (Calzada et al., 2018; Berget et al., 2021).

2.2 Vegetation monitoring

Permanent plots in secondary forest patches were established at both sites. At the wet site 20 plots were established in abandoned cornfields ranging from 0 to 36 years of recovery. Plots were established in two stages, 14 plots in year 2000 and 6 plots in 2008. At the dry site, 16 plots were established in abandoned cornfields ranging from 0 to 74 years of recovery. Fourteen plots were established in 2003 and 2 plots in 2005 (**Figure 3.S1** in Supp. mat.). These longitudinal chronosequences are amongst the longest annually monitored secondary forest plots in the tropics. For this study, we used annual census data up to 2018.

Aboveground biomass (AGB) of individual trees was estimated by using the allometric equations developed specifically for tropical forests (Chave et al., 2014). Diameter at breast height (DBH) and wood density (WD) were used to calculate AGB at both sites, and tree height measurements were also used for estimating AGB at the dry site. WD data were obtained locally for 80 % of wet forest species (Lohbeck et al., 2014) and 50 % of dry forest species (Lohbeck et al., 2014; I.E. Romero-Pérez, *unpub. data*). For the remaining species, WD was retrieved from the Global Wood Density Database (Zanne et al., 2009) at the species level, preferably for values reported in Mexico or Central America. When no information at the species level was available, we used average genus- or family-level WD values. For those species lacking WD information, the basal-area-weighted WD mean for each forest was used. Tree AGB was aggregated per plot, and ANPP (Mg ha^{-1} yr^{1}) was calculated as the difference in AGB from one year to the next one for each census interval. Only individuals with a DBH ≥ 1 cm were considered for analysis.

Demographic components of ANPP were also estimated by calculating annual biomass gain due to recruitment (new trees reaching 1 cm DBH) and growth, and annual biomass loss due to mortality. We calculated these components per plot and year by analyzing the historical record of each individual stem (or tree for the dry site) and determining on an annual basis its fate (Muñoz et al., 2021a). Then, all stem or tree contributions to ANPP (*i.e.*, stem or tree AGB changes, either positive and negative) were summed per demographic process, plot, and year.

2.3 Meteorological information

We used long-term (2000 to present), high quality satellite information to estimate precipitation, temperature, and photosynthetically active radiation (PAR) for both sites. For precipitation, we used data from the Global Precipitation Measurement mission (GPM, product *GPM_3IMERGDF_06_precipitationCal*). For temperature and PAR, we used data from the Modern-Era Retrospective analysis for Research and Applications Version 2 (MERRA-2, products *M2SDNXSLV_5_12_4_T2MMEAN* and *M2TMNXLFO_5_12_4_PARDR*, respectively). All these data were retrieved from NASA EOSDIS in a monthly time resolution. We validated the satellite-retrieved data with climatic data measured in meteorological stations close to the study sites. For both variables at both sites, the minimum correlation coefficient was 0.79 (**Extended Methods 1** in Supp. mat.).

The effect of climatic conditions on ANPP and its demographic components may depend on seasonality (wet vs. dry season) and may also show delayed responses (also known as lagged or legacy effects). For this reason, the climatic variables were quantified for two seasons (wet and dry) and two lag years (current and previous), resulting in four periods per climatic predictor: current year wet season, current year dry season, previous year wet season, and previous year dry season. Because of the contrasting climatic regimes at the two study sites, the timing and duration of the wet and dry seasons were different. At the wet site, the wet season typically spans from May through January (9 months with an average precipitation ≥ 100 mm mo^{-1}), while at the dry site it spans from May through October (6 months with an average precipitation ≥ 50 mm mo^{-1}; a summary of interannual climate conditions per season can be found in **Figure 3.S2** in Supp. mat.).

2.4 Data analysis

Changes in ANPP and its demographic components were partitioned into four different sources or variation: (1) successional recovery of forest attributes, (2) identified climatic conditions (climatic predictors included in this study), (3) unidentified climatic conditions, and (4) random variation. To assess climatic effects, we first modelled successional recovery trends for ANPP and its three demographic components (analysis stage 1), then removed the successional trends and analyzed the residuals as a function of our climatic predictors (analysis stage 2).

For the successional detrending of productivity variables (stage 1), we modelled

ANPP variables as a function of abandonment age using linear, logarithmic, and inverse models, which were selected based on prior ecological knowledge of the successional patterns of productivity (van Breugel et al., 2006; Lebrija-Trejos et al., 2010; Poorter et al., 2016; Poorter et al., 2021a). To account for potential plot-specific conditions (*e.g.*, higher soil fertility leading to faster recovery), we used linear mixed-effects models (LMMs) and included permanent plots as a random effect. We compared models including random slopes with models including both random slopes and intercepts, as this allowed assessing the best suiting random-effect structure. We constructed seven models per site per response variable (ANPP, recruitment, growth, and mortality): six models including successional age as the fixed predictor variable (three mathematical functions × two random-effect structures) and a null model for reference (Table S1). We then selected for each response variable the best model based on the corrected Akaike Information Criterion for small samples (AICc). A threshold of two AICc units was set to distinguish between models with different performance; models with a difference in AICc ≤ 2 units were regarded as equally good.

For the climatic predictor analysis (stage 2), we extracted the residuals from the best performing models in stage 1 and then conducted a forward stepwise LMM. We modelled the residuals from stage 1 models as a function of 12 climatic predictors (precipitation, temperature, and PAR × four time periods). We started the model selection with a null model (response variable as a function of an intercept only) and added climatic predictors one by one until there was no improvement in model performance. To account for the effect of unidentified climatic conditions, we fitted a random intercept for each year included in the analysis. Therefore, the R^2_{marg} (marginal R^2) of these performed LMMs reflects variation explained solely by the climatic predictors included in each model, while the R^2_{cond} (conditional R^2) reflects the maximum year-attributable variability (including climatic predictors and other sources of annual variability). We constructed 95 % confidence intervals (by bootstrapping, 10,000 simulations) of the selected climatic predictors for the best models of stage 2. All climatic predictor coefficients were standardized ($\bar{x} = 0$, $s = 1$) so their effect size, as well as their confidence intervals, was comparable.

All statistical analyses were conducted in R (Team, 2021). LMMs were fitted with the `lme4` package (Bates et al., 2014). Marginal and conditional R^2 values were estimated with the `MuMIn` package (Bartoń, 2010).

3 RESULTS

3.1 Productivity patterns in tropical forest secondary succession

Aboveground net primary productivity (ANPP). Wet and dry forests showed different successional trajectories in ANPP (**Figure 3.1**). The wet forest showed consistently higher ANPP across all successional stages than the dry forest (**Figure 3.1 A-B**). In the wet forest, ANPP was relatively constant and positive during succession, implying that biomass recovery follows a linear trajectory over the observed successional period (0-35 yr after abandonment). In the dry forest ANPP strongly decreased during the first 10 years after which it became close to zero, implying that biomass recovers rapidly early in succession (0-15 yr after abonnement) and then slows down during mid and late successional stages (15-75 yr after abandonment).

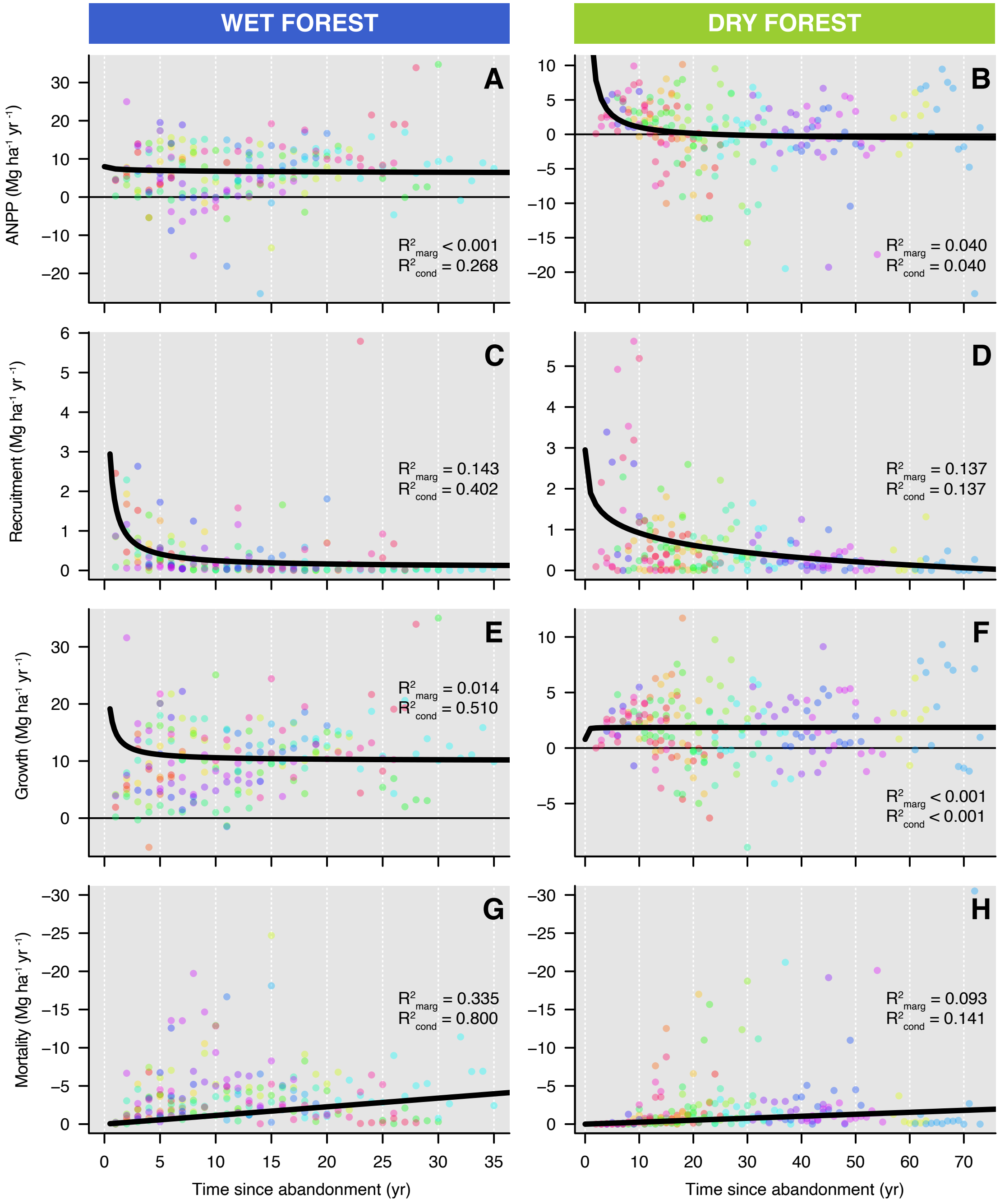
Recruitment. Both forest types showed qualitatively similar successional trajectories in the demographic components of ANPP. Recruitment was high during the first years of succession and declined exponentially over time. This decline was faster for the wet forest compared to the dry forest (**Figure 3.1 C-D**). For the dry forest, recruitment made significant contributions to ANPP gains even at mid-successional stages (15-30 years after abandonment).

Growth. Biomass growth was much higher for the wet forest than for the dry forest and showed slightly different successional patterns. In the wet forest, biomass growth decreased during the first years of succession and then remained constant. In the dry forest, growth has an initial increase after which it remained constant (**Figure 3.1 E-F**). Remarkably, at the dry forest, many year-plot combinations had negative biomass growth, especially during mid-successional stages (10-50 years).

Mortality. Biomass mortality increased linearly during succession in both forest types. Increase in mortality losses was faster in the wet forest than in the dry forest (**Figure 3.1 G-H**).

Figure 3.1 ▶

Successional trajectories in ANPP and its demographic components (Mg ha^{-1} yr^{-1}) during secondary succession for the wet (left panels) and dry (right panels) tropical forest sites. **(A, B)** ANPP, **(C, D)** recruitment, **(E, F)** growth, and **(G, H)** mortality. Bold black lines show the predicted trajectories of productivity variables after land abandonment based on the best LMMs for the successional detrending of productivity variables (*data analysis stage 1*, see *Methods*). Site average predictions are shown, excluding random effects (plots). Colors in data points represent plots at each site. For the wet site 20 plots were included in the analysis (2000-2018, n = 219), while for the dry site 16 plots were included (2003-2018, n = 227).


WET FOREST
DRY FOREST
A
B
C
D
E
F
G
H
ANPP (Mg ha⁻¹ yr⁻¹)
Recruitment (Mg ha⁻¹ yr⁻¹)
Growth (Mg ha⁻¹ yr⁻¹)
Mortality (Mg ha⁻¹ yr⁻¹)
R²marg < 0.001
R²cond = 0.268
R²marg = 0.040
R²cond = 0.040
R²marg = 0.143
R²cond = 0.402
R²marg = 0.137
R²cond = 0.137
R²marg = 0.014
R²cond = 0.510
R²marg < 0.001
R²cond < 0.001
R²marg = 0.335
R²cond = 0.800
R²marg = 0.093
R²cond = 0.141
30
20
10
0
−10
−20
5
−5
−15
6
4
3
2
1
−30
−25
−20
−15
−10
−5
0
5
10
15
20
25
30
35
40
50
60
70
Time since abandonment (yr)
Time since abandonment (yr)

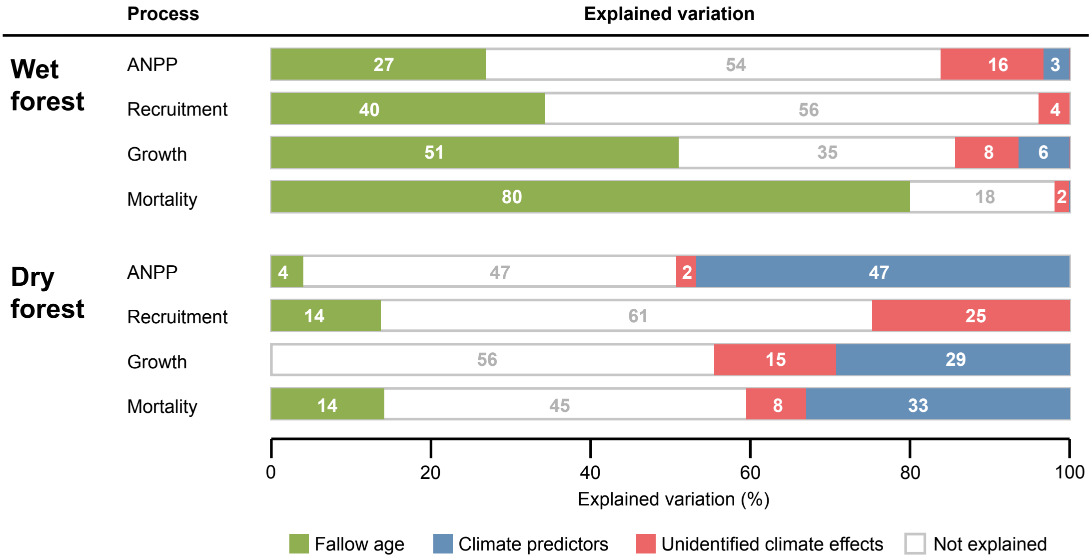


Figure 3.2

Interannual variation in aboveground net primary productivity (ANPP) and its underlying components explained by fallow age and climatic conditions for wet and dry secondary tropical forests. Stacked bars show the variation explained by fallow age (green), climatic predictors (blue), other unidentified climate effects (red), and not explained variation (white). Variation explained by fallow age was derived from the successional detrending of productivity variables (*data analysis stage 1*) and is represented by the R^2_{cond} of the productivity-successional models. Non-explained variation in *stage 1* was modelled as a function of up to 12 climatic predictors in the climatic predictor analysis (*data analysis stage 2*). From the climatic models of *stage 2*, R^2_{marg} indicated the variation explained by climatic predictors, $R^2_{cond} - R^2_{marg}$ indicated the variation explained by other unidentified climate variables (i.e., those variables affecting all stands in the same year), and $1 - R^2_{cond}$ indicated the variation not explained by any of the other three sources of variability (*i.e.*, not explained variation). Variation explained by the three categories of *stage 2* (climatic predictors, unidentified climate effects, and not explained variation) were made relative to non-explained variation of *stage 1* to produce this synthetic figure. See *Methods* for further details.

3.2 Succession and climate effects on biomass dynamics

Fallow age explained 27 % of ANPP variation in the wet forest, and only 4 % in the dry forest (**Figure 3.2**). In the wet forest, fallow age explained most of the variation in mortality (80 %), followed by growth (51 %) and recruitment (40 %). In the dry forest, fallow age explained much less variation in mortality and recruitment (14 %) and did not explain any variation in growth (0 %).

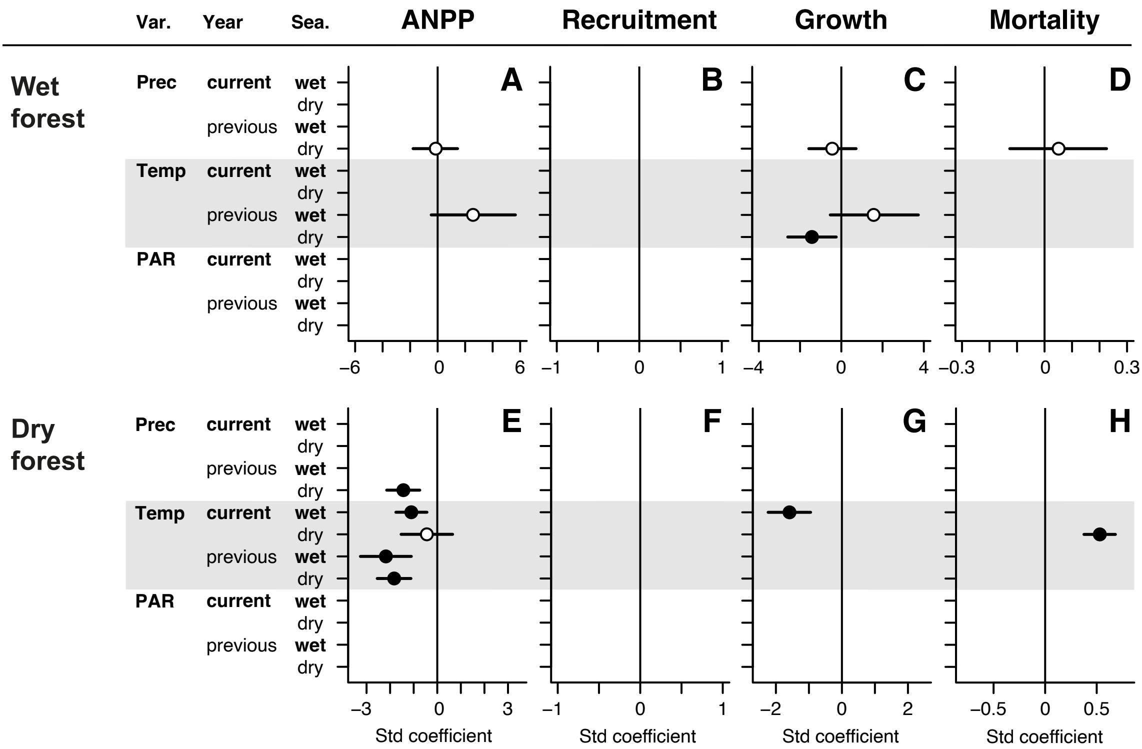


Figure 3.3

Effect of climatic conditions on **(A, E)** ANPP, **(B, F)** recruitment, **(C, G)** growth, and **(D, H)** mortality for wet **(top)** and dry **(bottom)** secondary tropical forests. Standardized coefficients for each climate predictor (circles), their 95 % confidence interval (black lines) and significance (solid circles significant, open circles non-significant) are indicated. Observed and predicted values for significant climatic predictors are shown in **Figure 3.S3** in *Supp. mat.*

3.3 Effects of climatic predictors on productivity

Climatic conditions explained a large share of inter-annual variation in ANPP and its demographic components in the dry forest (25-49 %, blue and red bars added). In contrast, the explained ANPP variation in the wet forest was substantially smaller (2-19 %; **Figure 3.2**). In the wet forest, our climatic predictors explained a negligible fraction of ANPP (0-6 %), whereas other unidentified climate factors (*i.e.*, other yearly variation affecting all stands in a similar manner) explained a larger share of variation (2-16 %; **Figure 3.2**). By contrast, in the dry forest climatic predictors explained most of the variation in ANPP (47 %), followed by mortality (33 %), growth (29 %) and recruitment (0 %), while unidentified climatic factors explained an additional 2-25 % (**Figure 3.2**).

In the wet forest, temperature in the previous dry season was the only climate predictor that had a significant effect on ANPP or their components, negatively affecting biomass growth (**Figure 3.3 C**). By contrast, in the dry forest temperature in the dry or wet seasons of the current or previous year had a significant negative effect on ANPP (**Figure 3.3 E**). Temperature in the wet season of current year had a negative effect on biomass growth (**Figure 3.3 G**), while temperature in the dry season of current year increased biomass mortality (**Figure 3.3 H**). Surprisingly, precipitation had only a significant negative effect on ANPP (**Figure 3.3 E**), whereas PAR did not affect biomass dynamics at all (**Figure 3.3**). Biomass recruitment was not affected by any climatic predictor at neither forest type (**Figure 3.3 B, F**). Climatic conditions in the previous year were as important as climatic conditions in the current year (4 vs. 3 significant cases), indicating important climate lag effects on these forest systems. Similarly, in the dry forest climate conditions during the dry season were as important as during the wet season (3 vs. 3 significant cases) indicating that harshness of conditions during the non-growing season matter for biomass growth and mortality.

4 DISCUSSION

We hypothesized that in dry forest ANPP would increase with precipitation and decrease with temperature. As predicted, temperature decreased ANPP by reducing growth and increasing mortality but, surprisingly, precipitation had a negative effect on ANPP. In wet forests, our results did not support the prediction of a positive effect of PAR on ANPP but, as in the dry forest, temperature reduced growth. In both forest types, climatic conditions in the previous year often affected ANPP or its underlying components, indicating that climatic temporal variation has legacy effects on ecosystem functioning.

4.1 Climatic conditions had a stronger effect on the dry forest

Climatic conditions (climatic predictors plus unidentified climatic factors) had a stronger effect on biomass dynamics in the dry forest (49 % explained variation) than in the wet forest (19 %). Such sensitivity of the dry forest cannot be explained by more variable climatic conditions at the site, as both sites share surprisingly similar coefficients of variation (CV) for precipitation, temperature, and irradiance (**Figure 3.S2** in Supp. mat.). Yet, in absolute terms, the dry site experienced harsher climatic conditions when compared to the wet site with lower precipitation (800 vs. 2680 mm yr^{-1}), hotter temperature (28.0 vs. 24.4 °C), and hence, more atmospheric and soil water stress. In addition, all wet forest plots are located relatively close to the perennial Lacantún river, possibly resulting in a shallow ground water table, and continuous plant access to ground water which reduces forest drought stress during dry atmospheric conditions (McDowell et al., 2019). Therefore, we infer that in the wet forest biomass dynamics during succession is mostly driven by autogenic processes than by climatic conditions (**Figure 3.1**) (Muñoz et al., 2021a). Other studies also show that harsher climatic conditions in dry forests result in lower aboveground biomass and ANPP in both secondary (Poorter et al., 2016) and old-growth forests (Schuur, 2003; Liu et al., 2014). The already harsh conditions at the dry forest might get exacerbated by small seasonal or annual changes in climatic conditions, thus resulting in a high sensitivity of dry forests to climatic variation (Allen et al., 2017).

4.2 Temperature reduces productivity and is its most important climatic driver

Precipitation. We hypothesized that dry forests would be water limited and therefore ANPP would increase with precipitation and decrease with temperature. Surprisingly, of the many potential precipitation effects analysed (2 forest types × 4 biomass response variables × 2 seasons × 2 years), only precipitation in the previous dry season significantly affected dry forest ANPP, exerting a negative effect (**Figure 3.3 E**). By contrast, other studies in secondary dry forests found that precipitation increased wood production in Costa Rica (Becknell et al., 2021) and understory plant growth and survival in Mexico (Martínez-Ramos et al., 2018).

Temperature. Temperature was the most important climatic driver of productivity, reducing growth in both forest types, and reducing ANPP and increasing mortality in the dry forest (**Figure 3.2**). Similarly, a pantropical study found maximum temperature to be the only climatic factor affecting ANPP, whereas precipitation and cloud cover (hence light availability) did not have an effect (Sullivan et al., 2020). High temperatures may reduce growth and survival through stomatal closure, increased respiration, and protein denaturation. Stomatal closure allows plants to avoid desiccation at the expense of reducing gas exchange, carbon gain, and growth (McDowell et al., 2008). At supra optimal temperatures, respiration can surpass photosynthetic rates, resulting in a negative net carbon gain (*i.e.*, net carbon loss) (Dusenge et al., 2019). Similarly, in a Costa Rican wet forest, high night-time temperatures increased stem respiration and reduced ANPP (Clark et al., 2010). In our dry forest, the mean annual temperature is already high (28 °C) and may reach values as high as 39 °C, although canopy temperatures get even higher due to solar exposure (Pau et al., 2018).

Dry season temperature increased biomass mortality in the dry forest, explaining as much as 33 % of the variation (**Figure 3.3 H**). Such temperature-driven mortality is most likely explained by increased stem respiration and carbon starvation. High temperatures lead to increased respiration (Dusenge et al., 2019; McDowell et al., 2020), which may deplete non-structural carbohydrate reserves during the dry season (McDowell et al., 2008; Aleixo et al., 2019) when the dry-deciduous forest is nearly leafless and unable to photosynthesize (Pérez-García et al., 2001; Luna-Nieves et al., 2022). Additionally, carbon starvation may result in reduced tree vigour and increased susceptibility to pests and pathogens, which may increase long-term mortality (McDowell et al., 2008; Hartmann et al., 2022).

Irradiance. We hypothesized that, in the wet forest, irradiance would increase ANPP because of light limitation due to cloud cover and high foliage density (Graham et al., 2003). However, we found no evidence of irradiance affecting ANPP on neither forest type, possibly because cloud cover at our sites does not reduce light availability below photosynthetic light saturation point (Schuur, 2003). Tropical forests in India, Puerto Rico and the USA have mean annual precipitations above 5000 mm yr^{-1} (Clark et al., 2001). At these very wet forests, climatic light limitation due to cloud cover can play a substantial role in reducing ANPP (Schuur, 2003).

4.3 Seasonality and legacy effects matter for temperature’s impact on ANPP

Climate conditions in the previous year often affected biomass dynamics in the current year, indicating that climate has important legacy effects on ecosystem functioning. In the wet forest, dry season temperature decreased growth in the following year (**Figure 3.3 C**) and in the dry forest, both dry and wet season temperature reduced ANPP in the following year. These legacy effects might be due to a combination of stomatal closure, increased stem respiration and carbon starvation, which could reduce carbohydrate reserves for bud break, leaf flushing, and cambial activity in the next year. Climate may have legacy effects beyond the one-year period that we considered. For instance, in the dry site, the 2015-2016 El Niño event produced extreme hot and dry conditions for more than 19 months (Liu et al., 2017). This extreme El Niño event also affected survival rates and plant density of understory woody plants of a similar dry secondary forest in western Mexico, affecting vegetation dynamics even beyond the duration of the El Niño event (Martínez-Ramos et al., 2018). Because tree growth occurs mostly during the wet season, and tree mortality occurs mostly during the dry season (Saenz-Pedroza et al., 2020), climatic conditions during each of these seasons have a different impact for different ANPP components.

4.4 Climate change implications: reduced mitigation potential of tropical forests

We found that temporal variation in heat, rather than variation in rainfall, affects productivity of secondary tropical forests, and that increasing heat leads to increased biomass mortality (*cf.,* Aleixo et al., 2019; Bauman et al., 2022b), reduced biomass growth (*cf.,* Bauman et al., 2022a) and, therefore, reduced ANPP (*cf.,* Sullivan et al., 2020), not only at the tree level, but also at the stand level. Our results complement the finding of Sullivan et al. (2020) that temperature reduces ANPP of tropical forests. However, while these authors used a spatial and static approach by comparing average conditions across sites, our study uses a temporal and dynamic approach by showing how changes in temperature across 18 years affect productivity. Our study presents therefore a direct test of the potential role of global warming for the carbon balance, functioning, and climate change mitigation potential of regrowing tropical forests. Brienen et al. (2015) found that over the past three decades (1985-2015) the mitigation potential of old-growth Amazonian forests has been declining because of increased CO_2 concentrations speeding up tree metabolism and reducing tree lifespan. Our study suggests that increasing temperatures may have a similar effect in secondary tropical forests. This is worrisome, as in our secondary forest sites temperatures have consistently increased over the course of the present study and will only continue to rise (**Figure 3.S2 D**). Conservative climate change projections predict by 2040 an average temperature increase of 1.5 °C compared to pre-industrial levels. This means that, within a few decades, there will be substantial reductions in tropical forest productivity (McDowell et al., 2020), especially for dry forests. Tropical dry forests species have evolved to withstand seasonal drought and harsh environmental conditions, especially for pioneer species (Lebrija-Trejos et al., 2010). However, our results suggest that biomass stocks and productivity in tropical dry forests will face strong negative consequences of global warming (*cf.,* Wright et al., 2009), with productivity reductions of up to 3.65 Mg ha^{-1} yr^{-1} per 1 °C increase in mean temperature (compared to 1.94 Mg ha^{-1} yr^{-1} per 1 °C at the wet forest; **Figure 3.S3** in Supp. mat.). The strong, negative impacts of temperature in dry forest ANPP are probably due to their proximity to their thermal limits and, possibly, long-term increases in temperature may result in a better drought-adapted flora with a lower productivity and biomass stocks (Allen et al., 2017). Hence, we conclude that tropical dry forests are more susceptible to undergo shifts in ecosystem properties due to global warming that wetter tropical forests (*cf.*, Bauman et al., 2022b).

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AUTHORS' CONTRIBUTIONS

R.M., F.B., and L.P. conceived the original idea of the study. R.M. performed data analyses. J.A.M., F.B. and M.M.-R. contributed data. All authors discussed, wrote, commented, revised, and approved the manuscript.

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DATA AVAILABILITY STATEMENT

The dataset will be made available in the Dryad repository upon acceptance of this manuscript.

CHAPTER 3

Supplementary material

Table 3.S1 – *Stage 1* model perfomance

Figure 3.S1 – Successional age span per site

Figure 3.S2 – Characterization of interannual climatic variability

Figure 3.S3 – Model predictions for significant climatic predictors

Extended methods – Validation of satellite-borne climatic data

Table 3.S1

Models used for successional detrending during *stage 1* of data analysis. A description of each model and their fixed- and random-effects formulas are provided. At the formulas, 'Int' indicates an intercept and '0' indicates no intercept. These models were fitted to data from the four response variables (ANPP, recruitment, growth, and mortality) and the two sites (wet and dry tropical secondary forests).

#	*Model description*	*Fixed effects*		*Random effects*
1	Null	Int	+	(Int I Plot)
2	Linear, random slope	Age	+	(0 + Age I Plot)
3	Linear, random slope and intercept	Age	+	(Int + Age I Plot)
4	Logarithmic, random slope	log (Age)	+	(0 + log (Age) I Plot)
5	Logarithmic, random slope and intercept	log (Age)	+	(Int + log (Age) I Plot)
6	Inverse, random slope	(1/Age)	+	(0 + (1/Age) I Plot)
7	Inverse, random slope and intercept	(1/Age)	+	(Int + (1/Age) I Plot)

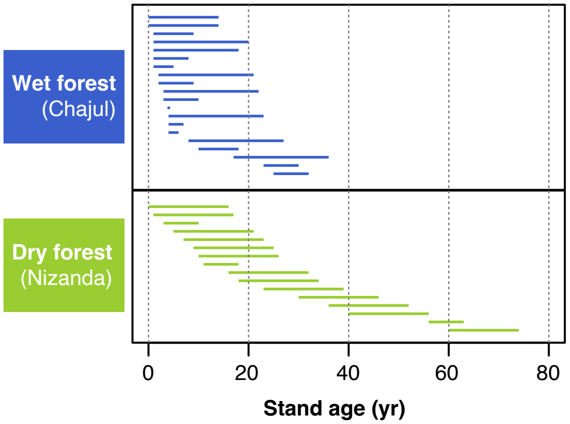


Figure 3.S1

Successional age span for the permanent plots used in this study, both at the wet (blue) and dry (green) forest sites. Each line represents a different plot, its starting position regarding the *x* axis (stand age) represents the initial age when the plot was established, and the length of the line represents for how long that plot has been monitored. Note that shorter lines show plots that were lost before 2018, mostly to fire.

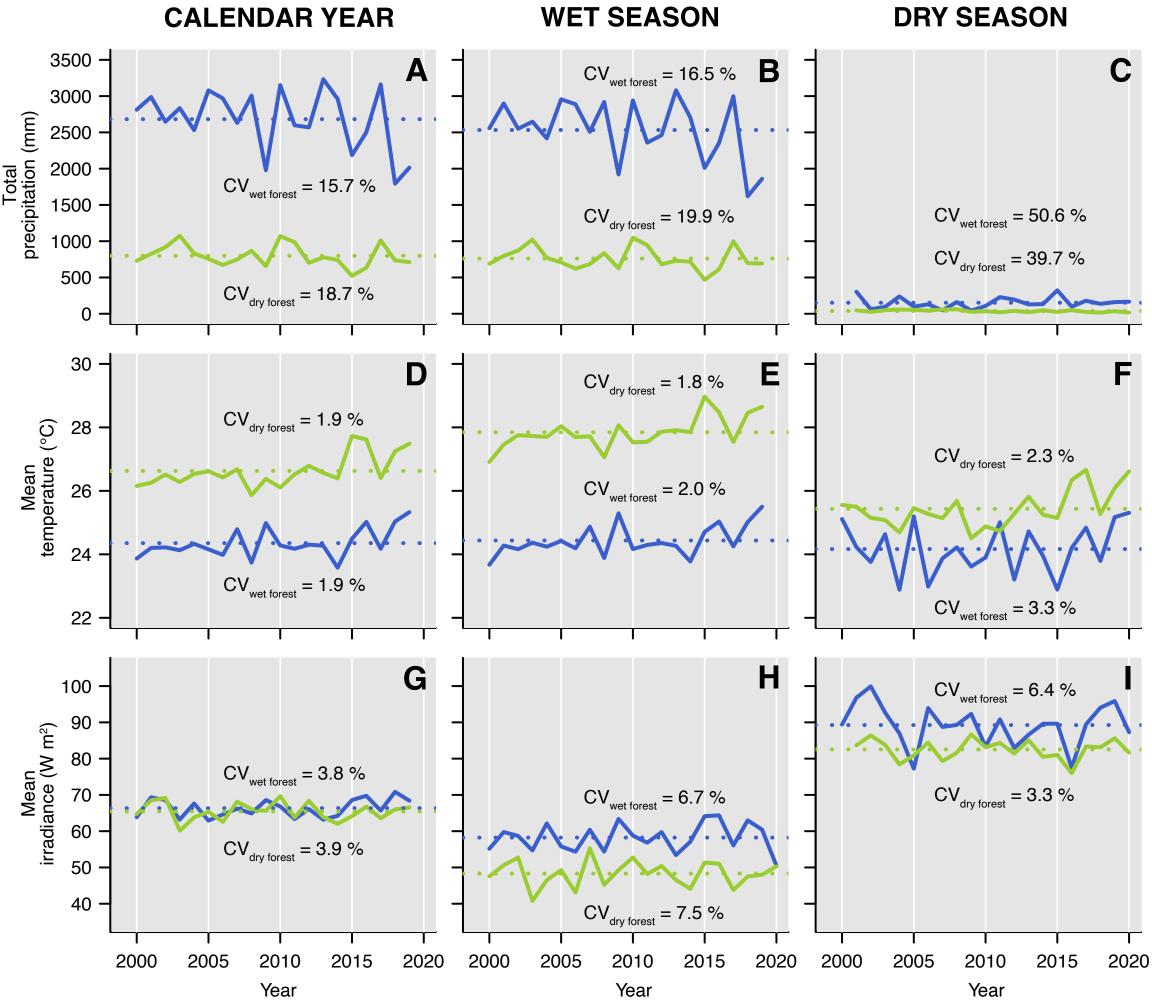
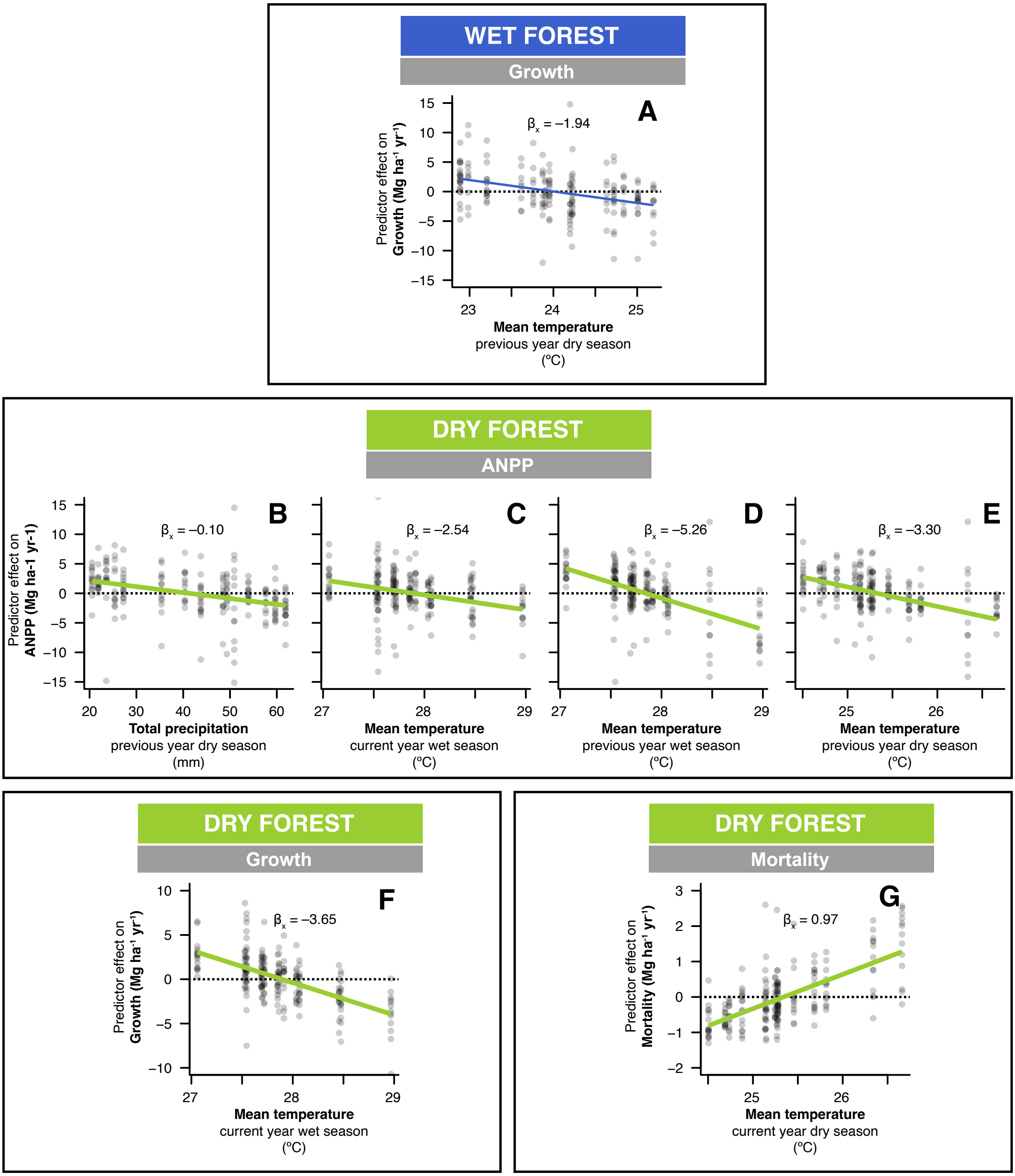


Figure 3.S2

Inter-annual dynamics of precipitation **(top)**, temperature **(middle)**, and irradiance **(bottom)** for calendar years **(left panels)**, the wet seasons **(center panels)** and dry seasons **(right panels)** for wet (blue line) and dry (green line) tropical forests. Calendar years span from January to December. Wet seasons span from May to January for the wet forest (3 mo), and from May to October for the dry forest (6 mo). Coefficients of variation (CV, %) across years are presented for each trend line. Total precipitation (mm), mean daily temperature (°C) and mean daily photosynthetically active radiation (W m^2) are presented for each period (calendar year, wet and dry seasons)


WET FOREST
Growth
A
βx = −1.94
Predictor effect on Growth (Mg ha-1 yr-1)
15
10
5
0
−5
−10
−15
23
24
25
Mean temperature
previous year dry season
(ºC)
DRY FOREST
ANPP
Predictor effect on ANPP (Mg ha-1 yr-1)
B
βx = −0.10
20
30
40
50
60
Total precipitation
previous year dry season
(mm)
C
βx = −2.54
27
28
29
Mean temperature
current year wet season
(ºC)
D
βx = −5.26
27
28
29
Mean temperature
previous year wet season
(ºC)
E
βx = −3.30
25
26
Mean temperature
previous year dry season
(ºC)
DRY FOREST
Growth
F
βx = −3.65
Predictor effect on Growth (Mg ha-1 yr-1)
10
5
0
−5
−10
27
28
29
Mean temperature
current year wet season
(ºC)
DRY FOREST
Mortality
G
βx = 0.97
Predictor effect on Mortality (Mg ha-1 yr-1)
3
2
1
0
−1
−2
25
26
Mean temperature
current year dry season
(ºC)

◀ **Figure 3.S3**

Model predictions for all significant climatic predictors. Observations are corrected for all other climatic variables included in their respective models. For the wet forest, **(A)** effect of precipitation in the previous year dry season on biomass growth. For the dry forest, effect of **(B)** precipitation on the previous year dry season, and temperature on the **(C)** current year wet season, **(D)** previous year wet season, and **(E)** previous year dry season on ANPP; **(F)** temperature on the current year wet season on biomass growth; and **(G)** temperature on the current year dry season on biomass mortality. The horizontal axis depicts the corresponding climatic predictor, while the vertical axis shows the effect in biomass change (in Mg ha^{-1} yr^{-1}). Slopes for the climatic predictors depicted in the horizontal axis (*X*) of each panel are presented (β_x) and depict the response in biomass change for one unit of the climatic predictor (in Mg ha^{-1} yr^{-1} *units-climatic-predictor*$^{-1}$). All observations are corrected for the other climatic predictors included in each model, so the effect of the target climatic predictor is isolated from the effect of all other climatic predictors (see **Figure 3.3** in the main text). The correction was made by generating a prediction excluding the target climatic predictor for each data point, and then subtracting that predicted value from the observed value. Therefore, each data point in these panels represents the variation explained by the target climatic predictor plus the unexplained variance of the model ($y_i = \alpha + \beta \cdot predictor_i + \varepsilon_i$)

EXTENDED METHODS: VALIDATION OF SATELLITE-BORNE CLIMATIC DATA

We conducted a validation of the satellite data available for the two tropical forest sites of this study by comparing it with data from weather stations located nearby our study sites. For the dry forest, 60 months of field data were available in non-continuous periods. For the wet forest, we took the period 2000-2015 from the Lacantún weather station, located 60 km away from the measuring plots (**Figure 3.EM1**). Out of the three climate variables analyzed in the study, only total precipitation and mean temperature were validated with ground data; photosynthetically active radiation could not be validated because the weather stations used did not measure such variable.

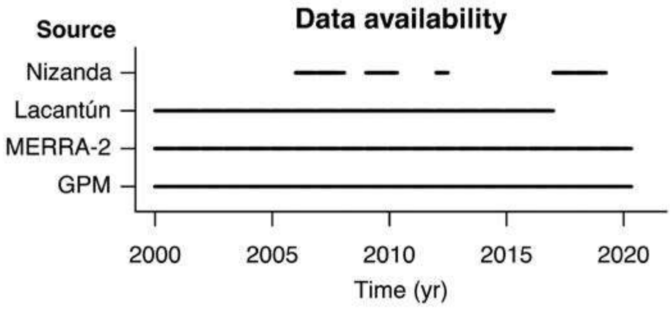


Figure 3.EM1

Temporal availability of ground and satellite data sources. Black lines indicate for what periods data is available at each source. Nizanda (dry forest) and Chajul (wet forest) labels represent the ground weather stations for each site (see Table EM1 below for more information). MERRA-2 data is available from 1980 to date, while GPM data availability spans from mid-2000 to date.

GPM (Global Precipitation Measurement) and MERRA-2 (Modern-Era Retrospective analysis for Research and Applications, version 2) data were retrieved through the Giovanni platform of NASA (giovanni.gsfc.nasa.gov). For precipitation, we used the final run of the daily accumulated precipitation (combined microwave-IR) estimate product (product code *GPM_3IMERGDF_06_precipitationCal*), which derives from the Integrated Multi-satellitE Retrievals for GPM (IMERG) algorithm. This product is available in a daily temporal resolution and a 0.1 × 0.1 ° spatial resolution. It provides an estimate of accumulated precipitation in mm per day. For temperature, we used the mean estimates of the 2-meter air temperature

Table 3.EM1

Location of the study sites, their weather stations, and retrieval coordinates of GPM (precipitation) and MERRA-2 (temperature) data. Mismatch between GPM and MERRA-2 coordinates is due to differences in spatial resolution and pixel size for each product.

Site	*Weather station*	*Coord. site (°)*	*Coord. w. station (°)*	*Coord. GPM (°)*	*Coord. MERRA-2 (°)*
Chajul (wet forest)	Lacantún (CFE)	16.099, -91.001	16.581, -90.702	16.550, -90.750	16.500, -90.625
Nizanda (dry forest)	Local	16.659, -95.011	16.659, -95.011	16.650, -95.050	16.500, -95.000

Table 3.EM2

Summary of correlations between satellite- and ground-based observations at daily, monthly, and yearly time resolutions. Number of observations (*n*), correlation coefficient estimate (*r*), and 95 % confidence interval for *r* (in brackets) are shown per site and climate variable. Significance level for *r* estimates is indicated with asterisks (see code for significance levels at the bottom of the table).

	Time resolution		
Site	*Daily*	*Monthly*	*Yearly*
Chajul (Lacantún weather station)	n = 6145 r = 0.227*** [0.203, 0.251]	n = 194 r = 0.869*** [0.830, 0.900]	n = 16 r = 0.821*** [0.549, 0.936]
	n = 5884 r = 0.731*** [0.719, 0.743]	n = 194 r = 0.790*** [0.730, 0.837]	n = 16 r = 0.167 [-0.359, 0.612]
Nizanda (local weather station)	n = 1629 r = 0.566*** [0.532, 0.598]	n = 60 r = 0.824*** [0.721, 0.892]	n = 4 r = 0.983* [0.402, 0.999]
	n = 1629 r = 0.862*** [0.849, 0.874]	n = 60 r = 0.855*** [0.767, 0.911]	n = 4 r = 0.731 [-0.774, 0.994]
	Significance: 0.05 * 0.01 ** 0.001 *** < 0.001		

product (product code *M2SDNXSLV v5.12.4*). The air temperature product is available on a daily temporal resolution and a 0.625 × 0.5 ° (longitude, latitude) spatial resolution. The geographical coordinates for the sites, reference weather stations, GPM and MERRA-2 data retrieval points are specified in **Table 3.EM1**.

To assess the accuracy of the satellite measurements, parametric correlations were performed between field and satellite observations, using as many observations as possible (*i.e.*, paired observations of ground and satellite data). Correlations were performed at daily, monthly, and yearly time resolutions.

As shown in **Table 3.EM2**, monthly observations had the highest correlation between satellite- and ground-based data in most cases. Association level between sources was good for all the variables and sites, with *r* values ranging between 0.79 and 0.87 and a significance level always below $P = 0.001$. Although association between sources was good, systematic biases were evident when plotting monthly satellite observations against ground observations (**Figure 3.EM2**).

Observations for all variables and sites showed a consistent bias, either positive or negative (*i.e.*, observations lie mostly above or below the 1:1 diagonal line in panels of **Figure 3.EM2**). For this reason, we computed the mean deviation for the satellite observations for each variable, site and month, and then introduced that 'correction factor' into all satellite-borne observations. We performed a parametric correlation using the corrected satellite observations, and then we compared it to the non-corrected version of the satellite data (**Figure 3.EM3**).

Correlation coefficients did not show any substantial difference between corrected and non-corrected observations (**Figure 3.EM3**). Therefore, considering the higher accuracy of bias-corrected satellite data, we used these observations in all analyses of climatic predictors of the study.

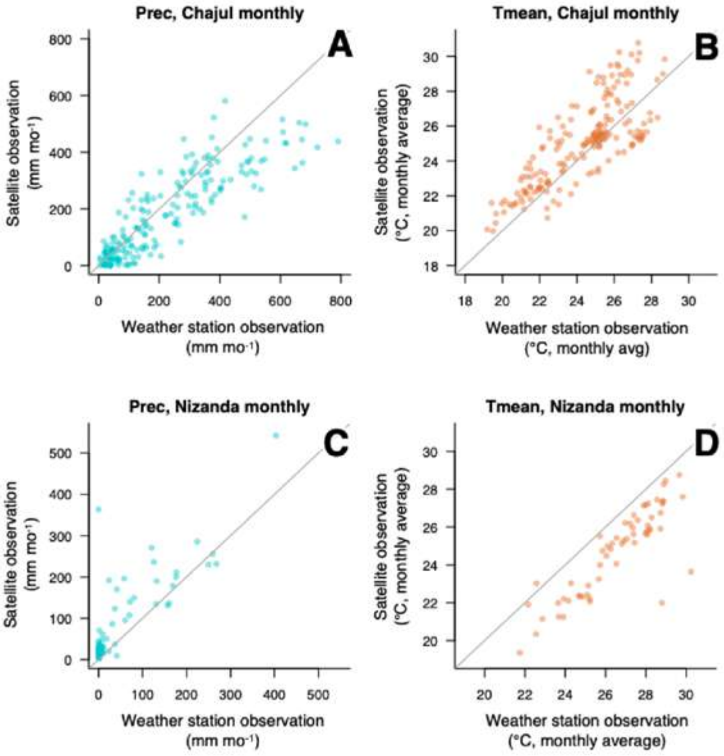


Figure 3.EM2

Correlation between satellite- and ground-based observations at monthly time resolution for precipitation and mean temperature for Chajul (wet forest) and Nizanda (dry forest). Climate variable and site are indicated on the header of each panel. Observations in this figure are not corrected for monthly bias.

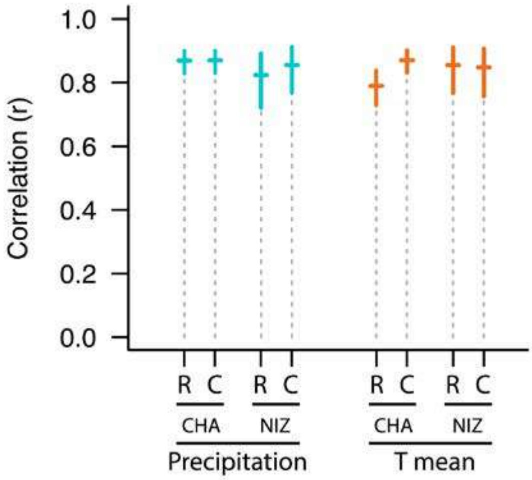


Figure 3.EM3

Correlation coefficients (*r*) for field and satellite observations monthly, with and without bias correction for precipitation and mean temperature for the wet and dry forest sites. 'R' indicates raw satellite data without bias correction, and 'C' indicates corrected satellite data.

CHAPTER 4

Lithological substrates influence tropical dry forest structure, diversity, and composition, but not its dynamics

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SUMMARY

Tropical dry forests (TDF) are not only the most widespread tropical forest type but also the most threatened forest ecosystem worldwide. Yet, because their dynamics have been insufficiently studied, our knowledge about the factors responsible for the spatial and temporal variability in TDF dynamics remains very limited. In this study, we aimed (1) to assess the effect of two lithological substrates on TDF structure, diversity, and species composition, and (2) to determine whether and how these substrates affects temporal dynamics on TDF attributes. We used information gathered through a 12-yr long annual monitoring of 14 old-growth TDF permanent plots in southern Mexico, seven of which were established on limestone and seven on phyllite. Previous work shows that limestone-derived soils have higher humidity, conductivity, and phosphorous and calcium contents, but lower nitrogen content. Our results showed that TDF structure and diversity attributes were consistently higher on limestone TDF, while canopy height was higher on phyllite TDF. By contrast, temporal variation in TDF attributes, demographic rates (recruitment, growth, and mortality) and attribute residence times were indistinguishable between substrates. We also found a strong differentiation of species composition between substrates, yet substrates did not influence the temporal behavior of composition. Our results suggest that limestone is a more favorable environment for TDF development (soil-effects mechanism), but the flora of the forest on phyllite seems to be better adapted to cope with harsher environmental conditions (composition-effects mechanism), which counterbalances the environmental advantage of limestone, ultimately resulting in spatially-homogeneous TDF dynamics at the landscape level. Future studies should examine the role of functional attributes on old-growth TDF dynamics, as this will allow a better understanding of the impacts of extreme climatic events on forest attributes and their dynamics, as well as to foresee potential ecosystem state shifts and tipping points.

1 INTRODUCTION

Tropical forests cover nearly 18.3 million km^2 across five continents (FAO, 2020). Considering this immense area, it is natural that the regions where they occur encompass an huge variety of climates, topographies, and geologies, which results in an outstanding heterogeneity in tropical forest features, including their physiognomy, structure, biodiversity, and ecosystem functioning (Walter, 1973; ter Steege et al., 2006). Such a colossal variety of tropical forests is amazing and intriguing. Yet, at the same time it complicates their understanding, so that after several decades of study we have only attained the still limited knowledge that we currently have on their structure, diversity, and functioning.

One of the least understood tropical forests properties is their dynamics. Forest dynamics can be defined as the set of changes in stand structure, species composition and biotic interactions that forests experience over time (Frelich, 2016; McDowell et al., 2020). Forest dynamics arises from the complex interaction between the inherent demographic processes that plants undergo through their life cycles (recruitment, growth, reproduction and dead) and the external factors that determine resources and conditions for plant development (*e.g.*, climate and soil) (McDowell et al., 2020). External factors also include disturbances, which are sudden changes in environmental conditions resulting in the removal of biomass and individuals from the forest community. Good knowledge on tropical forest dynamics is essential for several purposes, ranging from the design of sound forest management practices to anticipating their responses to climatic changes (McDowell et al., 2020). At present, there is a sizeable number of studies on tropical moist and rain forest dynamics (Grubb, 1996; Sheil et al., 2000; Condit et al., 2004; Lewis et al., 2004; Laurance et al., 2009), but our understanding of tropical dry forest (TDF) dynamics lags considerably behind (Siyum, 2020; Muñoz et al., 2021). This is unfortunate, as TDFs account for more than half of the forest cover across the tropics and represent the tropical ecosystem most threatened by human activities (Janzen, 1988; Miles et al., 2006; Chaturvedi et al., 2017; Hasnat and Hossain, 2020).

Lithological substrates, hereafter referred only as substrates, are a key factor explaining tropical forest heterogeneity within landscapes (Durán et al., 2006; Fayolle et al., 2012). Lithological substrates are the main prime material that soils are made of, and thus they largely determine soil physical attributes and chemical composition (Searcy et al., 2003). Substrates may potentially influence tropical forest attributes either (1) directly, through their impact on soil properties, mainly nutrient composition, texture, and water retention capacity (Peña-Claros et al., 2012; Hahm et al., 2014; Callahan et al., 2022), or (2) indirectly, through their influence on forest species composition (Searcy et al., 2003; Ribeiro et al., 2007). These two mechanisms will ultimately determine how substrates impact forest structure, diversity, and their temporal dynamics.

This study focuses on the TDF region of Nizanda, a climatically homogeneous area located in southern Mexico (Pérez-García et al., 2010). TDF in this region grows on soils derived from bedrocks of limestone (carbonate sedimentary rock) and siliciclastic phyllite (foliated metamorphic rock, hereafter phyllite) (Pérez-Gutiérrez et al., 2009). Lithology-driven differences in structure and physiognomy have been observed between the two communities. Forest growing on limestone tends to be better developed (*i.e.*, bigger trees, more biomass) and richer in tree species compared to its counterpart on phyllite (Muñoz, 2015), apparently due to higher soil water content and nutrient availability in limestone-derived soils (Sandoval Granillo, 2020). However, these differences in forest attributes have not been formally assessed, and it is unclear whether they are associated with different dynamic behaviors.

The objectives of this study were (1) to assess substrate effects on TDF structure, diversity, and species composition, and (2) to determine whether and how substrates affect temporal dynamics on these TDF attributes. Regarding (1), we hypothesized that more benign environmental conditions in limestone TDF (higher soil water content and nutrient availability) lead to higher vegetation development and diversity, while also contributing to a distinct species composition compared to TDF growing on phyllite, which offers harsher or more restrictive conditions for plant growth. Regarding (2), we hypothesized three alternative scenarios based on the two mechanisms of geological effects advanced earlier, *i.e.*, direct effects on forest dynamics through soil conditions differentially affecting the same set of species (soil-effects mechanism) against indirect effects on forest dynamics through species composition, where different species respond differently to environmental factors (composition-effects mechanism). If phyllite represents a harsher environment for TDF growth than limestone, it is likely that trees growing on this substrate are better adapted to cope with water and nutrient limitations (Scholz et al., 2014; Díaz-Castellanos et al., 2022). In this case, the soil-effects mechanism would result in increased stability of limestone TDF by providing higher and more stable soil water content, regardless of interannual variation in precipitation. Conversely, based on the composition-effects mechanism, it is reasonable to expect higher forest stability on phyllite TDF because this community hosts an array of species furnished with more conservative functional traits, enabling them to better resist the impacts of climate-harsh (dry and hot) years at the cost of growing slower in climate-benign (wet and cool) years, in line with the fast-slow continuum hypothesis (Reich, 2014; Oliveira et al., 2021). Therefore, depending on the relative importance of each mechanism for TDF dynamics, these forests may be (1) more stable on limestone if the soil-effects mechanism acts with higher intensity, (2) more stable on phyllite if the composition-effects mechanism acts with higher intensity, or (3) equally stable across bedrocks if the two mechanisms act with similar intensity.

We examined the effects of two lithological substrates on TDF attributes and their dynamics by using annual information gathered on the vegetation of both substrates over 12 years. The results of this study will provide new insights into the role of lithology on tropical forest development potential and its responses to environmental and climate changes. Given the large extent of TDF across the tropics (Murphy and Lugo, 1986; Hasnat and Hossain, 2020) and the variety of lithologies characterizing the landscapes where it occurs (Mooney et al., 1995), the results of this study will advance the understanding of TDF dynamics at landscape and regional scales.

2 METHODS

2.1 Study site and vegetation monitoring

We conducted our study in the region of Nizanda, southern Mexico (16.66° N, 95.01° W). The region has a mean annual temperature of 27.7 °C and a mean annual precipitation of 902 mm yr^{-1}, with a marked rainy season spanning from mid-May to mid-October (precipitation > 50 mm mo^{-1}). Tropical dry forest (TDF) is the dominant vegetation type in the region and large undisturbed forest patches are still present in the landscape, alongside areas devoted to food production (mechanized and shifting agriculture, and cattle ranching) and extensive patches of secondary vegetation in different stages of succession. TDF in this region occurs on limestone and siliciclastic phyllite, two contrasting parental materials whose weathering results in different soil types. Limestone outcrops are associated with major faults in the terrain and can reach elevations of ca. 500 m above mean sea level (amsl). By contrast, the terrain on phyllite is hilly with much lower elevations (ca. 280 m amsl at most). These two substrates represent the main parental material of the most common soil types (Cambisols, Leptosols

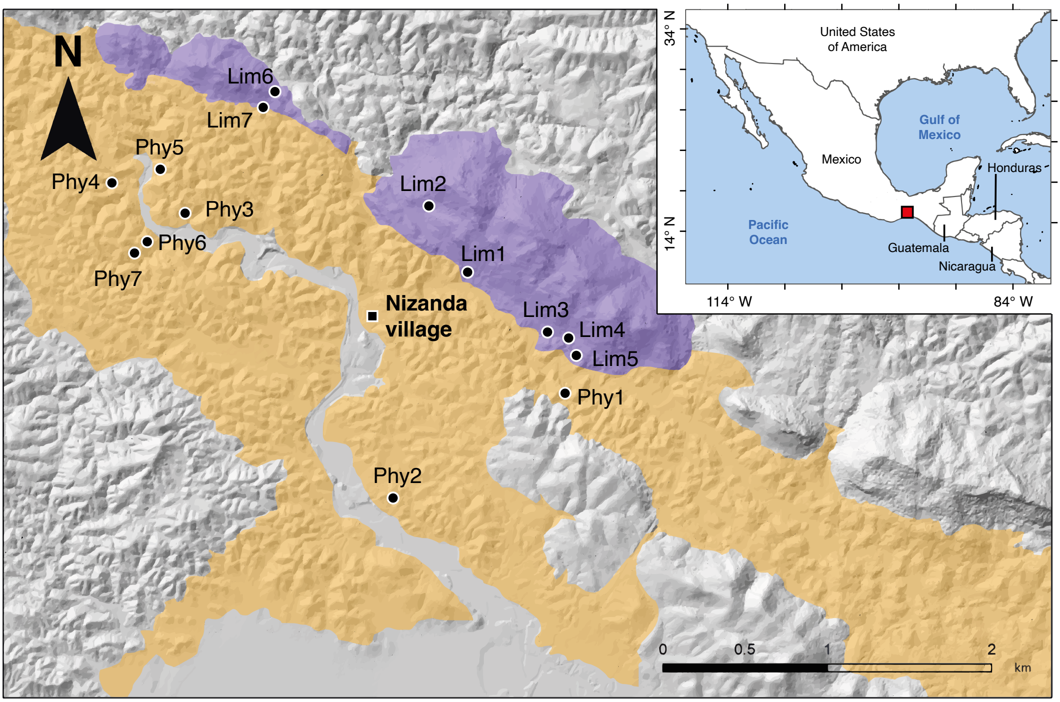

Figure 4.1

Map of the study area in the tropical dry forest (TDF) region of Nizanda, Mexico. Locations of the permanent old-growth TDF plots on soils derived from limestone bedrock (purple shading) and siliciclastic phyllite bedrock (yellow shading) are shown. Grey shading represents other parental materials occurring in the area (see Pérez-Gutiérrez et al. 2009). **(Inset)** Location of the Nizanda region in Mexico.

and Regosols) on which the tropical dry forest develops (C. Miguel-Talonia, unpublished data). The physical characteristics of these soils such as color (an organic matter content indicator) and texture differ notably between the two substrates. Overall, limestone-derived soils are darker and have higher clay contents, and in some places of the limestone mountains the high clay content results in shrink-swell cracks during the dry season; consequently, water availability for plants is higher in limestone- than in phyllite-derived soils. Therefore, soil water content emerges as one of the major factors potentially driving differences for TDF development on these substrates (Covelo et al., 2017). In Nizanda, physiognomic differences between TDF developing on the two substrates are evident, and these seem to be linked to variations in structure and diversity between the two TDF subtypes.

In 2008 we established seven 500 m^2 permanent forest plots in each forest subtype (14 permanent plots in total). At present, we continue monitoring these plots but for this study we used data for the 2008-2020 period. The plots are subdivided in five 100-m^2 transects, each of which is further subdivided into four 25 m^2 quadrats. We used a stratified, nested sampling design for measuring trees in the plots. Stems with a diameter at breast height (DBH) ≥ 5 cm were measured in the whole 500 m^2 plot area, medium-sized stems with a DBH ≥ 2.5 cm were measured in a 375 m^2 plot subarea, while small stems with a DBH ≥ 1 cm were only measured in a 125 m^2 plot subarea. In each transect, 25 m^2 quadrats were randomly assigned a minimum DBH criterion (5, 2.5 or 1 cm). All trees meeting the inclusion criterion were tagged, identified to species (96.1 % of all trees), and their DBH and height were measured. At each annual census, survival, DBH, and height were recorded, as well as new recruits meeting the inclusion criteria.

2.2 Data analysis

Based on the annual vegetation censuses of permanent plots, we estimated four forest structure variables (basal area, aboveground biomass [AGB], tree density, and canopy height), and three community diversity variables (species richness [^0D], common species [^1D], and dominant species [^2D]). Aboveground biomass (AGB) was estimated by using a broadly used allometric equation (Chave et al., 2014) that integrates DBH, height, and species-specific wood density measurements. Canopy height was calculated as the average height of trees on the top canopy layer (details for canopy height estimation are provided in the **Extended methods** section of Supp. mat.). Community diversity values (^0D, ^1D, and ^2D) correspond to Hill numbers of order q = 0 (total species richness), q = 1 (typical species), and q = 2 (dominant species), which represent the effective number of species in the community when the weight given to rare species is gradually reduced (Chao et al., 2014). These diversity metrics were estimated with the `vegan` package (Oksanen, 2007) in *R* by using species abundances. All community variables were estimated on an annual basis per plot.

To assess substrate effects on TDF structure and diversity, we estimated the mean value for the seven response attributes per substrate on an annual basis. Next, 95 % confidence intervals around these means were constructed through bootstrapping with 1,000 iterations per estimation. Mean values and their confidence intervals were plotted against time to illustrate the temporal trajectories of structure and diversity attributes on both substrates.

To compare the dynamics in TDF attributes between substrates, we calculated a mean value per TDF attribute per substrate (including all plot-year combinations over the study period). Then, we standardized individual plot-year estimates by dividing these values by their substrate mean. This allowed us to express plot variability relative to their substrate mean, a procedure that controlled for larger variation caused by larger absolute values in forest attributes. Next, we estimated again substrate mean values with 95 % bootstrapped confidence intervals on an annual basis. Standardized TDF attributes were plotted against time to visualize the temporal trajectories of the TDFs growing on the two substrates. For all forest attributes, a value of 1 represented the substrate average value for the entire study period.

Next, we assessed quantitative differences in TDF dynamics between substrates by comparing plot deviations from their substrate mean using linear mixed-effects models (LMM). For each standardized TDF attribute, we computed the absolute deviations between individual plot values and their entire-period substrate mean on an annual basis (*i.e.*, |1 – standardized plot value|). We then fitted a LMM of individual plot-year deviations as a function of substrate, adjusting a random intercept for each permanent plot. By including a plot-dependent intercept, we controlled for the pseudo-replication arising from repeatedly measuring the same plots over time. To assess whether variation in TDF dynamics is determined by substrates, we extracted the substrate coefficient from the previously fitted LMMs and then estimated their 95 % bootstrapped confidence intervals with 1,000 iterations. Coefficient estimates and their confidence intervals were plotted separately for each forest attribute to show whether TDF dynamics was more intense either on limestone or on phyllite.

We also compared differences in demographic rates (net rate of change, recruitment, growth, mortality, and residence time) between substrates for basal area, AGB, tree density, and species richness (^{0}D). These four variables are, to some extent, additive forest attributes which can be decomposed into their gain and loss demographic components. To this end, we analyzed the individual tree trajectories over time (2008-2020) and determined, on an annual basis, what demographic process a given individual was undergoing: either recruitment, survival, or death. Based on these demographic classification, we determined the contribution of an individual towards a specific state variable (positive, negative, or null), and then added those change rates per demographic process, year, and plot (Muñoz et al., 2021). We performed this procedure for all four state variables analyzed. Later, we computed residence times per state variable as in Galbraith et al. (2013) by using Equation 1.

$$\tau_Y = \frac{\bar{M}_Y}{\bar{Y}_P} \tag{1}$$

Where τ_y is the residence time of a unit of the state variable Y, $\bar{M}_Y$ is the average value for Y during a yearly period, and $\bar{Y}_P$ is the productivity in Y during the yearly period resulting from the addition of recruitment and growth. We did not differentiate between biomass and density formulas as in Galbraith et al. (2013) to enable direct comparisons between the residence times of the four attributes analyzed. Annual demographic rates were averaged per plot and then per substrate to obtain substrate-level estimates. Bootstrapped confidence intervals (95 %, 1,000 iterations) were computed to compare demographic rates between substrates.

To assess whether sudden decreases and increases in TDF attributes were associated to El Niño and La Niña events (which are known to promote dry and rainy weather conditions, respectively), we ran non-parametric (Spearman) correlations between the Oceanic El Niño Index (ONI, referred to as NINO3.4 in van Oldenborgh et al. (2021)) and the net rates of change in all seven forest attributes. ONI values were retrieved from the National Oceanic and Atmospheric Administration historical El Niño/La Niña episodes (NOAA, 2022). Net rates of change were retrieved from the analysis of demographic rates for basal area, AGB, tree density and species richness; for canopy height and diversity metrics ^{1}D and ^{2}D, rates of change were simply computed as $(Y_{t+1} - Y_t) / Y_t$. Correlation coefficients and their respective *P*-value were reported per substrate. Although this analysis was not essential to test the core hypotheses of this work, we considered it would be appropriate to explain notorious tendencies on the dynamics of TDF attributes.

To visualize differences in species composition between TDF substrates, as well as their differences in dynamics, we used a non-parametric multidimensional scaling ordination (NDMS) of species composition and abundance data for all plots and years. Species were considered as variables and plot-year combinations were considered as observations. We used Bray-Curtis distance to estimate the dissimilarity matrices for the analysis, and projected the NMDS scores into a bidimensional scatterplot. Permanent plots from the same substrate were enclosed into an ellipse to show the ordination space occupied by each substrate based on its species composition. The NMDS ordination was performed using the `vegan` package in *R* (Oksanen, 2007).

To quantify differences in species composition dynamics between substrates, we computed three metrics of composition dynamics: annual mean distance, dispersion from centroid, and distance from initial to final point. Annual mean distance quantified the distance that any plot moved on average on the ordination space during an annual period. Dispersion from centroid quantified how broadly or tightly spread all datapoints belonging to each plot were on the ordination space. Distance from initial to final point, as its name implies, quantifies the distance between the 2008 and 2020 datapoints on the ordination space, and represents a proxy of circularity (*i.e.*, floristic stability) in individual plot trajectories. To assess differences in these three metrics between substrates, we performed a LMM for annual mean distance and dispersion from centroid, and a standard linear regression for distance from initial to final point. In the three models, substrate was set as the fixed factor. For the LLMs, a plot-dependent random intercept was adjusted to account for the temporal autocorrelation

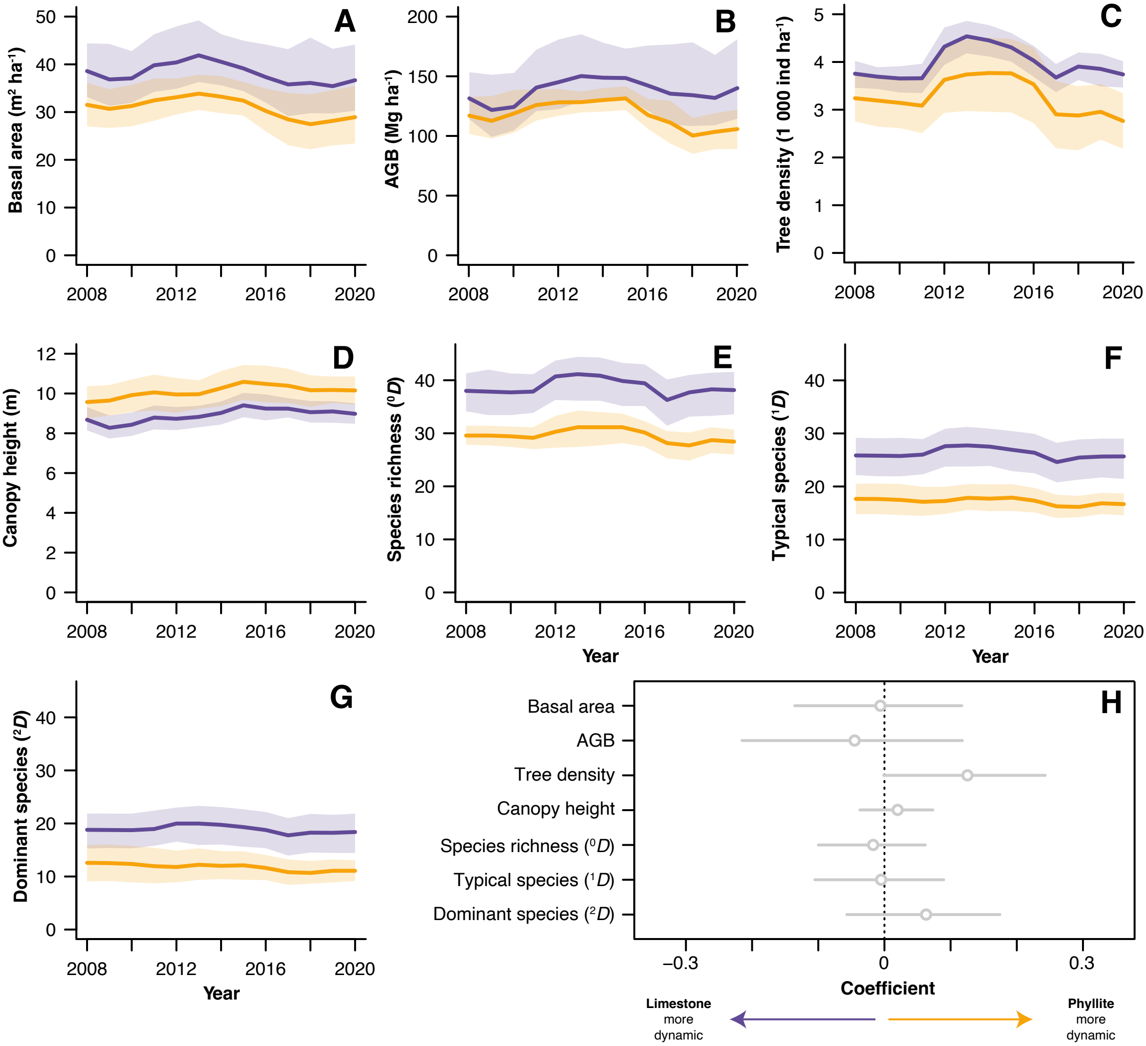

Figure 4.2

Dynamics of tropical dry forest attributes in limestone (purple) and siliciclastic phyllite (yellow) substrates. Panels show the dynamics of **(A)** basal area, **(B)** aboveground biomass [AGB], **(C)** tree density, **(D)** canopy height, **(E)** species richness [^0D], **(F)** number of common species [^1D], **(G)** number of dominant species [^2D], **(H)** and the substrate-wise comparison of the dynamics of all seven TDF attributes analyzed. For panels A-G, the thick lines represent substrate mean values (n = 7) and the shading around them represents 95 % confidence intervals. For panel H, the substrate-wise comparison of dynamics was done by regressing the deviations of each plot from its substrate mean value as a function of forest substrate (standardized dynamics shown in **Figu-**

re 4.S1 in Supp. mat.). Linear mixed-effects models were used to control for temporal autocorrelation due to repeated measurements, including plots as a random effect. Coefficients = 0 represent identical attribute dynamics between the two substrates, coefficients > 0 represent more intense dynamics in phyllite TDF, and coefficients < 0 represent more intense dynamics in limestone TDF. Mean coefficients and their 95 % confidence intervals are shown for each attribute; coefficients significantly different from 0 are indicated in color (yellow for phyllite, purple for limestone).

between datapoints. Coefficients were extracted from the three models, and their 95 % bootstrapped confidence intervals were computed. The coefficients along with their confidence intervals were plotted to show differences in composition dynamics between substrates.

3 RESULTS

3.1 Comparison of TDF attributes between substrates

The TDF on limestone had consistently higher values for almost all forest attributes than the TDF on phyllite except for canopy height. The largest differences between substrates were observed for diversity variables, with limestone TDF displaying higher diversity, while differences in structure attributes were less pronounced (**Figure 4.2 A-G**).

3.2 Forest dynamics between substrates

The dynamic behavior of all TDF attributes was remarkably similar over time in terms of direction at both substrates, with limestone and phyllite TDF following nearly parallel trajectories (**Figure 4.2 A-G**, **Figure 4.S1** in Supp. mat.). This weak differentiation between substrates was particularly evident for the standardized TDF attributes, which followed almost identical patterns over time on limestone and phyllite, both in terms of direction and magnitude of the variation on their dynamics (**Figure 4.S1**). Similarly, LMM modeling did not reveal a significant role of parental bedrock on the variability of TDF dynamics; the analysis of plot deviations in standardized TDF attributes showed that substrates did not yield large differences in dynamics of any of the attributes analyzed (**Figure 4.2 H**).

3.3 Analysis of demographic rates

Temporal trends in net change, recruitment, growth, and mortality were remarkably similar between substrates over time (**Figure 4.3 A-D**). Also, the analysis of mean demographic rates did not reveal any differences between demographic rates for any of the four TDF attributes analyzed from this demographic perspective (basal area, AGB, tree density, and species rich-

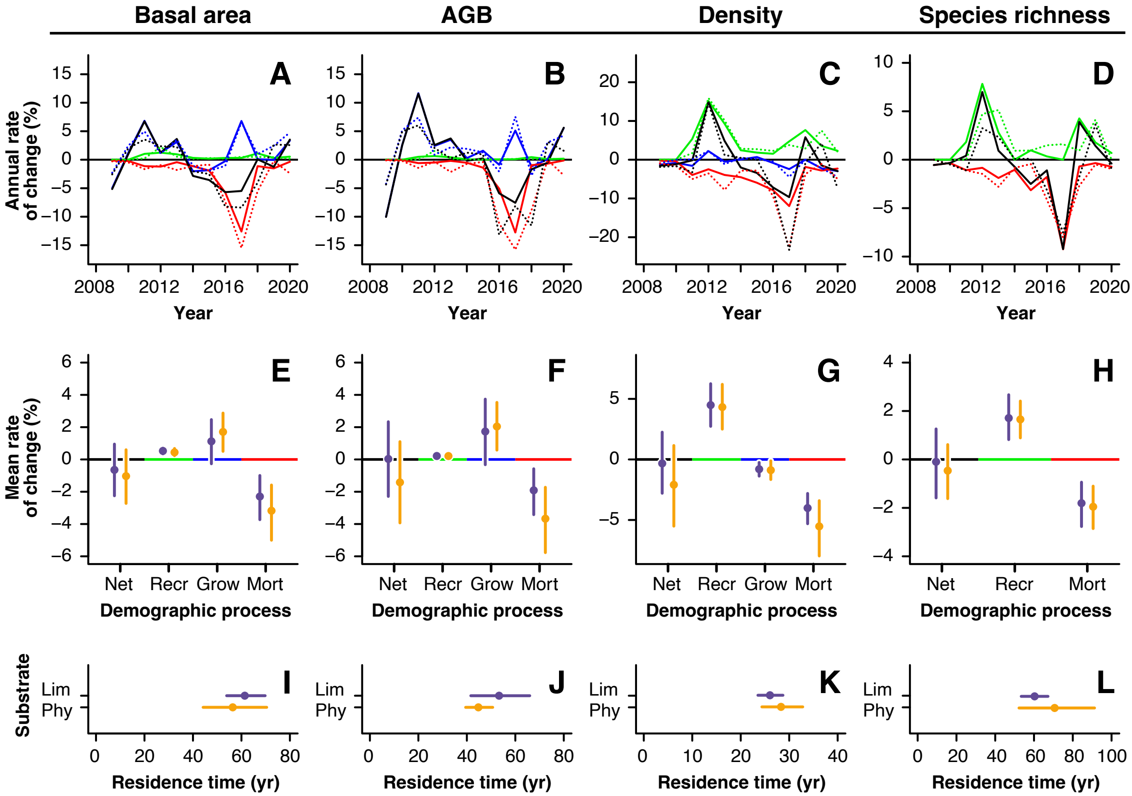

Figure 4.3

Demographic rates for basal area, aboveground biomass (AGB), tree density and species richness (^{0}D) in a tropical dry forest established over limestone and phyllite substrates. **(A-D)** Temporal behavior of net change (black), recruitment (green), growth (blue), and mortality (red) rates on an annual resolution for limestone (continuous) and phyllite (dotted lines) permanent plots. **(E-H)** Mean demographic rates per substrate (dots) with 84 % confidence intervals (whiskers); overlapping whiskers from the mean estimates for limestone (purple) and phyllite (yellow) indicate non-significant mean differences with 95 % confidence level (Goldstein and Healy, 1995). **(I-L)** Mean residence time for the four forest attributes on limestone and phyllite TDF plots, including mean estimates (dots) and their 84 % confidence intervals (whiskers). Forest attributes represented in each panel are indicated above the panel.

ness; **Figure 4.3 E-F**). Similarly, residence times, which were estimated from recruitment, growth, and attribute values, did not show differences for any of the four TDF attributes analyzed.

3.4 Species composition dynamics

The NMDS analysis based on the floristic species composition recorded over the study period confirmed a clear segregation of the plots from the two forest types on the ordination space (**Figure 4.4 A**). The overlap of the ordination spaces corresponding to the forests on limestone and phyllite was relatively small, pointing to large differences in the presence and abundance of species between substrates. Interestingly, however, the dynamics of floristic composition did not show such a between-substrate differentiation: all three NMDS-based metrics (annual mean distance, dispersion from centroid, and distance between initial and final points) were indistinguishable between substrates (**Figure 4.4 B**). Therefore, despite clear differences in species composition between the two substrates, there is no evidence of differences in composition dynamics over time.

3.5 General patterns in TDF dynamic

In the two forest subtypes, structure and diversity attributes increased around 2010-2011, remained high for several years, and then showed a sudden decrease around 2015-2016 (**Figure 4.2 A-G**, **Figure 4.S1** in Supp. mat.). These generalized increases and decreases in vegetation development show some degree of association with both the rainy years produced by La Niña event of 2010-2012 and the drought years arising from El Niño event of 2015-2016 recorded in the region (**Figure 4.S2** in Supp. mat.).

4 DISCUSSION

4.1 Vegetation development and diversity were higher on limestone

Our results confirmed previous observations that structure and diversity attributes were generally higher in limestone than in phyllite old-growth TDF. The only exception to this pattern was canopy height that showed higher values in phyllite (**Figure 4.2**), probably suggesting different tree architectures and allometric relationships across communities, given that trees in the forest on limestone are taller. The fact that structure and diversity differences were consistent over the entire study period (2008-2020) suggests that this is a permanent pattern rather than a peculiarity of exceptionally dry or wet years. More importantly, these results provide strong support to our first hypothesis, which states that limestone represents a more

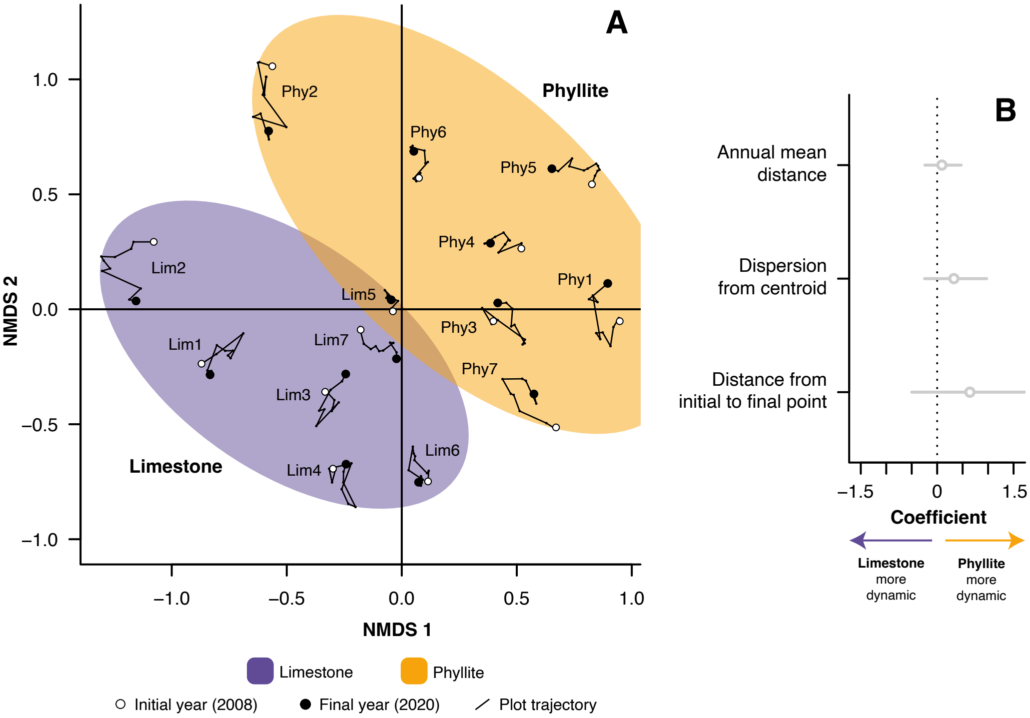

Figure 4.4

Temporal trajectories of tropical dry forest (TDF) species composition recorded in permanent plots established on limestone and siliciclastic phyllite. **(A)** NMDS ordination based on species abundance of all annual plot observations. For each plot, lines and dots depict its 12-yr long compositional trajectory; open dots represent the initial year of the trajectory (2008), and closed dots represent the endpoint (2020). Purple and yellow ellipses depict the ordination space occupied by limestone and phyllite plots, respectively. **(B)** Quantitative comparison of three NMDS-based metrics: 'Annual mean distance' was calculated as the arithmetic average of all distances between two annual measurements in the NMDS ordination space (i.e., mean length of line segments in panel A) for each substrate; 'Dispersion from centroid' was calculated as the bidimensional dispersion from a plot's centroid in the ordination space; 'Distance from initial to final point' reflects the floristic difference in each plot between the initial (2008) and final (2020) points, as represented by the distance between them in the ordination space. Coefficients and their 95 % confidence intervals show the lack of significant substrate effects on the three NMDS-based metrics.

favorable environment for plant growth and thus for TDF development due to higher water content and nutrient availability, because lime materials enhance the availability and plant uptake of elements such as molybdenum, phosphorus, calcium, and magnesium (Brady, 1984).

TDFs are typically water limited, as they grow in areas with high temperatures and relatively little annual precipitation and long dry seasons (≥ 3 months, but often up to 6 months) (Sánchez-Azofeifa et al., 2005; Allen et al., 2017). Therefore, they should benefit from a substrate characterized by higher soil water content to maximize water uptake periods. Limestone seems to provide such an environment. Preliminary analyses showed that soils derived from limestone have higher clay and lower sand contents that soils derived from phyllite, with a gravimetric humidity 37 % higher in limestone soils (Sandoval Granillo, 2020). Therefore, water limitation should be weaker on limestone than on phyllite, consequently yielding a greater potential for vegetation development (Terra et al., 2018). Our observations for four out of the five forest structure variables analyzed here (basal area, AGB, tree density and canopy height) support this idea.

The higher diversity at all levels analyzed (Hill numbers of order q = 0, 1, and 2) in limestone TDF can also arise from weaker limitations related to soil water content and fertility in this substrate. Limestone-derived soils have a higher conductivity, Ca, and P concentrations, while phyllite-derived soils have a higher concentration of total N, nitrates, and ammonia (Sandoval Granillo, 2020). Given the high proportion of legume species in TDFs and their frequent symbioses with nitrogen-fixing *Rhizobium* bacteria (Gei et al., 2018), nitrogen limitations are probably unimportant for these forests. Therefore, the higher diversity documented here for limestone might be, at least partially, related to higher soil water content but also to higher P availability, an element known to limit vegetation development on TDFs (Campo and Vázquez-Yanes, 2004) and other forest ecosystems (Hahm et al., 2014). Empirical observations from sites on the two substrates also suggest that limestone environments are rockier and highly heterogeneous, with many small and irregular patches of developed soils, shallow soils, and bare rock (C. Miguel-Talonia, unpublished data). Thus, limestone environments may provide a wider variety of microhabitats than phyllite, thus allowing more species to establish on this TDF community (Ribeiro et al., 2007; Díaz-Castellanos et al., 2022).

4.2 Structure and diversity dynamics were similar between substrates

Unexpectedly, the dynamic behavior of TDF attributes was very similar between the two substrates, not only in terms of direction (increases and decreases in value) but also regarding its variability (magnitude of changes). In other words, changes in forest attributes over time were parallel in both forest types (**Figure 4.S1** in Supp. mat.), with all attributes showing non-significant differences in variation (**Figure 4.2 H**). The finding of similar dynamics between limestone and phyllite TDF plots was also supported by the analysis of demographic rates. Rates of net change, recruitment, growth, mortality, and residence time were similar between substrates for the four forest attributes analyzed from a demographic perspective (basal area, AGB, density and ^{0}D). These results coincide with our third predicted scenario for TDF dynamics, which anticipated equally stable dynamics between substrates due to the soil-effects mechanism acting with a similar intensity as the composition-effects mechanism. This is the most intriguing finding of this study, as it suggests that, at least for our studied landscape, forest composition adapts to local environmental conditions (composition-effects mechanism) while ecosystem functioning remains spatially homogeneous even in patches with harsher environmental conditions (soil-effects mechanism).

The conclusion that soil- and composition-effects offset each other should be treated with care, as it relies on the assumption that species on phyllite TDF have rather conservative traits. However, the strong differences in structure and diversity, together with the soil differences observed by Sandoval Granillo (2020), point to clearly different environmental conditions between substrates, as discussed earlier. As soils derived from phyllite seem drier and less fertile, one may reasonably assume that species in this substrate are better adapted to harsher environmental conditions (Díaz-Castellanos et al., 2022). For instance, communities in which conservative traits are prevalent in a Brazilian TDF showed higher productivity and biomass stocks than their counterparts with more acquisitive traits (Prado-Junior et al., 2016), which provides support to our hypothesis. Further research on the functional differences between the species occurring on limestone and phyllite TDF is needed to clarify if and how substrates influence forest functional profiles.

The result that in this region limestone TDF achieves an overall higher vegetation development without significant differences in dynamics is somewhat puzzling. Higher values in TDF attributes should arise with differing residence times, allowing limestone forests to keep a unit of a given attribute for a longer period in order to build higher attribute stocks. It should be noted that mortality was higher (more negative) for the variables analyzed on the demographic analysis; however, due to large within-substrate variation, results from the substrate-wise mortality comparison were not significant. Previous studies have shown that variation in attributes and rates increases with smaller samples (Galbraith et al., 2013). In this study, we used a surface area of 500 m^{2} for the 14 permanent TDF plots. While this sampling area might be enough to obtain a reliable estimate for some TDF attributes, demographic rates may require larger samples (larger areas, longer study periods, and/or more sampling units) to be fully representative of the vegetation type they represent. Still, probably the differences in dynamics and demographic rates are small, and thus the noise-to-signal ratio does not allow to detect potential differences in dynamics between substrates. Therefore, for this site, it is essential to continue the monitoring for a longer period of time, as this would be the most feasible way of increasing the reliability of the estimations arising from this set of permanent plots.

4.3 Species composition differs between substrates, but compositional dynamics is similar

In line with the results for TDF attributes, the NMDS demonstrated that species composition differed between substrates, with the respective floristic sets showing a relatively minor overlap on the ordination space (**Figure 4.4 A**). Since the NMDS ordination was based on species abundances, year-to-year plot trajectories not only reflect differences in species presence/ absence but also is species abundances between plots and substrates. Geology has been shown to affect species composition and abundance in other TDF sites (Durán et al., 2006), probably by differentially affecting soil fertility, soil water content and environmental physical heterogeneity. Soil fertility, which is largely dependent on parent material (Scholes, 1990; Augusto et al., 2016), has been shown to positively affect species dominance in TDFs (Peña-Claros et al., 2012) and to influence species and functional composition in tropical forests in general (Fayolle et al., 2012; Terra et al., 2018). Moreover, increasing soil water availability over time increased species richness and functional diversity in TDFs (Raymundo et al., 2019), and these results can be also extrapolated to a spatial dimension. Hence, lithological substrates, which determine soil spatial variability in TDFs (Pulla et al., 2016), can influence forest floristics through various mechanisms; thus, the finding of large differences in species composition and abundance is not surprising in these contrasting environments.

Contrary to the notorious compositional differences between the two forest subtypes, the NMDS ordination also revealed virtually identical dynamics regarding floristics in limestone and phyllite TDFs. The similarity in forest dynamics held regardless of the metric used to assess floristic dynamics (*i.e.*, annual mean distance, dispersion from plot centroid, or the distance from initial and final points). In fact, the latter metric suggests a nearly circular pattern in the trajectories of most plots in the ordination space, irrespective of substrate. This observation implies a highly stable floristic composition, as is usually expected in old-growth forests under stable climatic regimes (Muñoz et al., 2021). The lack of differences in forest dynamics, even on these substrates associated with clearly dissimilar abiotic environments, is difficult to explain. Unfortunately, predicting species composition and its changes over time is extremely difficult, as the process of species assemblage in communities depends on too many biotic and abiotic factors and is of course species-specific (*e.g.*, propagule and microhabitat availability, priority effects, nutrient limitations). Using a functional trait approach would likely be useful to understand floristic changes, as functional ecology links plant traits to plant responses to environmental stimuli. By doing so, changes in species composition and abundance could be framed in the context of the environments that these forests experience.

4.4 Conclusions

Lithological substrates had a strong effect on TDF structure, diversity, and species composition, with the TDF on limestone showing better vegetation development and higher diversity than its counterpart on phyllite. Nevertheless, the temporal dynamics and demographic rates of these forest attributes did not differ between substrates, suggesting that the harsher environmental conditions associated with the phyllite substrate are buffered by means of a species composition that is better adapted to cope with those conditions. The net result of this balance seems to be a relatively spatially-homogenous dynamics across this geologically complex TDF landscape, implying that future analyses of the responses of these forests to novel climatic conditions need not pay attention to substrate heterogeneity.

However, a word of caution is important with regard to this conclusion, as it is based on results obtained over a 12-yr period for the climatic conditions experienced by our study forests during this time. Extreme events (intense or prolonged drought and heat waves) could push one of these TDF subtypes beyond its eco-physiological threshold, thus decoupling their dynamics. We hypothesize that this is more likely to be the case for the TDF on limestone, as its species assemblage is adapted to more mesic conditions (Romero et al., 2019; Romero et al., 2022), which could potentially cause massive diebacks once their climatic tipping points are surpassed (Brodribb et al., 2020; Powers et al., 2020). Ecologists need to continue their great efforts to keep and expand the long-term monitoring of these ecosystems. Perhaps in the future we will be able to remove the infamous tag of the ‘most threatened and vulnerable forest type in the world’ from these fascinating tropical ecosystems (Hasnat and Hossain, 2020).

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AUTHORS' CONTRIBUTIONS

R.M. and J.A.M. conceptualized the study and led manuscript writing. J.A.M. and F.B. led permanent plot establishment and secured project continuity and funding. R.M. and M.E. conducted data analyses. R.D.L.-M. coordinated field campaigns (2015 onwards). C.M.-T provided advice related to the geological aspects of the study. All authors gathered field data, discussed results, commented on the manuscript, and approved its submission.

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DATA AVAILABILITY STATEMENT

The original contributions presented in the study are publicly available. These data can be found here: https://doi.org/10.5281/zenodo.7680666 (Muñoz et al., 2023).

CHAPTER 4

Supplementary material

Extended methods – Estimation of canopy height

Figure 4.S1 – Standardized dynamics of TDF attributes in limestone and phyllite plots

Figure 4.S2 – TDF dynamics and El Niño/La Niña occurrence

Table 4.S1 – Importance Value Index (IVI) for tropical dry forest species occurring in two lithological substrates

EXTENDED METHODS
ESTIMATION OF CANOPY HEIGHT

Canopy height was estimated as the average height of the trees on the top canopy layer of a plot. We estimated the number of trees composing the top canopy layer inspired by the Perfect Plasticity Approximation (PPA) (Strigul et al., 2008). PPA considers that competition for light on closed-canopy forests is strong, and thus the canopies of trees will try to reach the upper canopy layer to get a competitive advantage over lower-statured trees. Usually, the trees with the largest canopies are also the tallest trees composing the top canopy layer.

Crown cover area for every tree was recorded from 2008 to 2018 by measuring the longest axis on the crown and its orthogonal axis, estimating the area as an ellipse. Then, trees were sorted by crown cover area (from largest to smallest) and the height of the top largest trees accounting for 500 m^2 of total crown area (100 % of plot surface) was averaged. These trees would, in principle, cover the top canopy layer and account for the tallest and most dominant trees within a plot. However, because crown cover area was only measured from 2008 to 2018 but height data is available up to 2020, we conducted the top canopy height estimation for all plots annually for the 2008-2018 period, and then retrieved the average number of trees needed to fill the top canopy layer per plot (as species composition and species architecture on each plot may largely influence this relationship). Lastly, we computed canopy height as the average height of the trees that (in average) are needed to fill the top canopy layer at each plot.

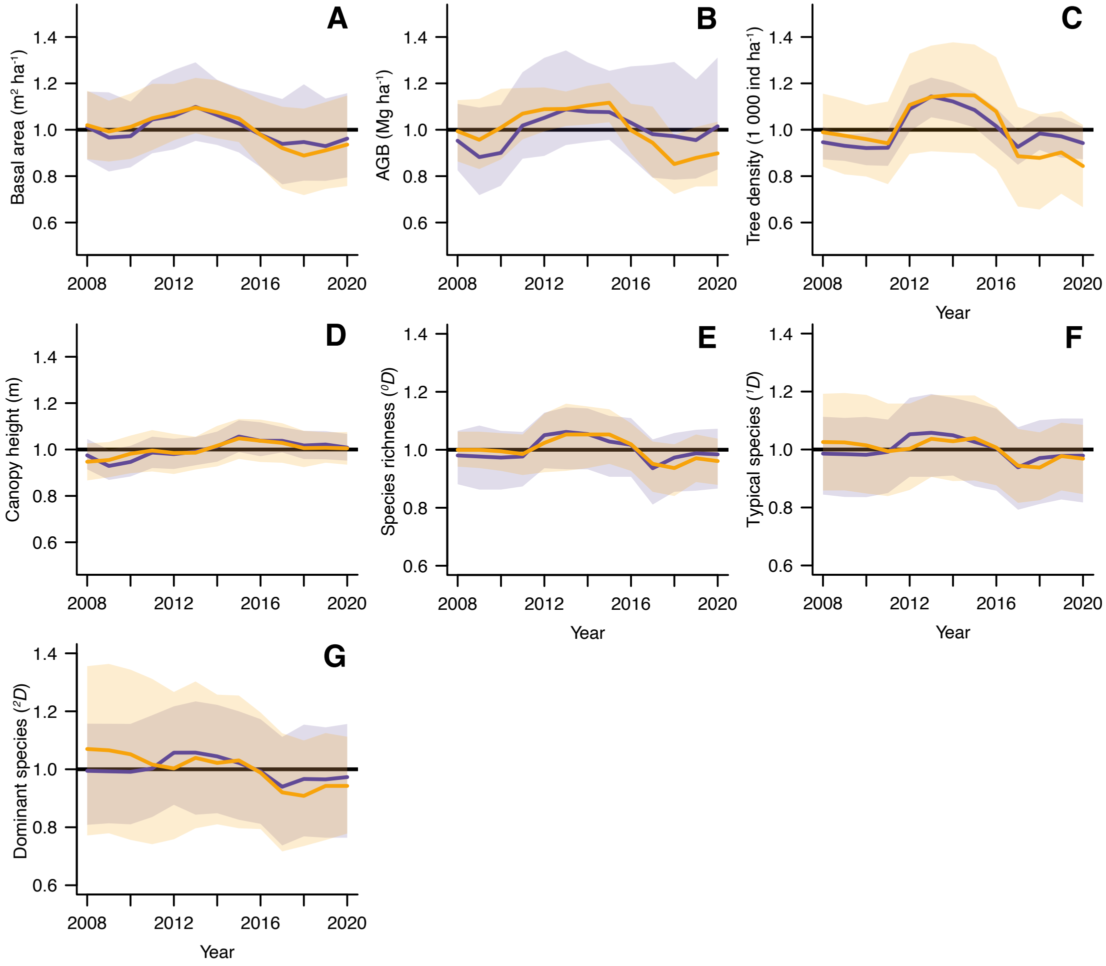

Figure 4.S1

Standardized dynamics of tropical dry forest (TDF) structure and diversity attributes in permanent plots established on soils derived from limestone (purple) and siliciclastic phyllite (yellow) for the 2008-2020 period. Standardization was done by dividing observed values in individual plots by the mean attribute value in each substrate. (A) Basal area, (B) above ground biomass (AGB), (C) tree density, (D) canopy height, (E) species richness [0D], (F) number of common species [1D], and (G) number of dominant species [2D]. Thick lines represent mean values by substrate (n = 7) and the shading around them are 95 % confidence intervals.

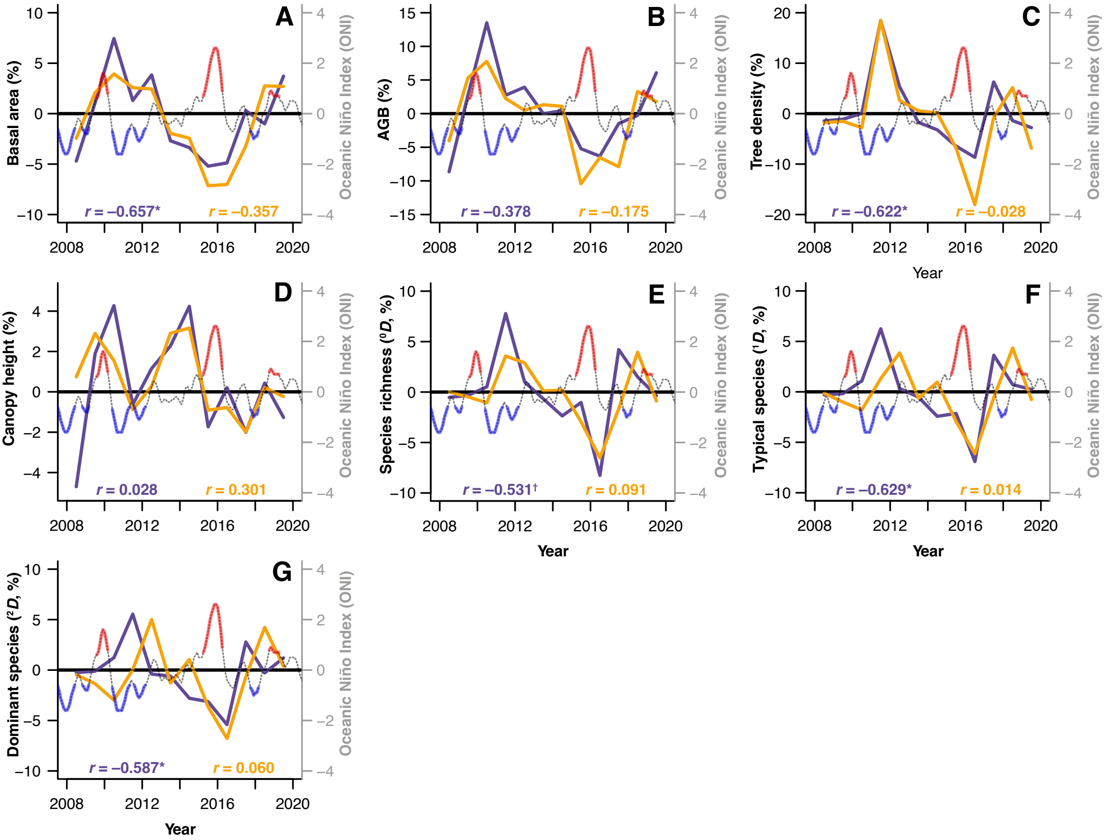

Figure 4.S2

Comparison of the rate of change (%) for structure and diversity attributes against the Oceanic El Niño Index (ONI). Colored lines depict temporal trends for limestone (purple) and phyllite (yellow) plots. The dotted gray line depicts the Oceanic El Niño Index temporal behavior on an monthly resolution (NOAA, 2022). Correlation coefficients at the bottom of each panel represent the association between ONI and limestone (purple text) and phyllite (yellow text) TDF dynamics. ONI is the three-month rolling average of the sea-surface temperature anomalies on the NINO 3-4 region of the Pacific Ocean. ONI is a commonly used predictor for the occurrence of El Niño and La Niña events (van Oldenborgh et al., 2021).

Table 4.S1

Importance Value Index (IVI) for the species occurring in limestone and phyllite tropical dry forest plots. IVI (%) was estimated as the addition of the relative basal area and relative density of each species on each substrate. Every individual IVI value is accompanied by a colored rectangle which intensity indicates the relative importance of each species (more important in intense purple/yellow, less important in white). Taxonomic family for all species is also indicated in the table.

	Species	*Limestone IVI (%)*		*Phyllite IVI (%)*	
Acanthaceae	*Aphelandra scabra*	---	---	0.50	
Amaranthaceae	*Iresine diffusa*	0.23		---	---
	Iresine sp.	2.50		2.82	
	Lagrezia monosperma	0.38		0.18	
Anacardiaceae	*Amphipterygium simplicifolium*	0.02		---	---
	Astronium graveolens	---	---	1.15	
	Pseudosmodingium multifolium	0.03		---	---
Annonaceae	*Annona squamosa*	1.99		0.57	
	Annonaceae sp.	---	---	0.19	
Apocynaceae	Apocynaceae sp.	0.20		---	---
	Cascabela ovata	0.16		---	---
	Plumeria rubra	1.84		1.71	
	Tabernaemontana odontadeniiflora	0.08		0.26	
Asteraceae	Asteraceae sp.	0.10		0.14	
Bignoniaceae	*Arrabidaea floribunda*	0.69		---	---
	Handroanthus impetiginosus	3.48		10.46	
Bixaceae	*Cochlospermum vitifolium*	---	---	2.70	
Boraginaceae	*Bourreria purpusii*	0.09		---	---
	Cordia alliodora	0.63		0.10	
	Cordia dentata	3.31		0.85	
	Cordia gerascanthus	0.18		---	---
	Cordia sp.	0.18		---	---
	Cordia truncatifolia	---	---	0.24	

	Species	*Limestone IVI (%)*		*Phyllite IVI (%)*	
Acanthaceae	*Aphelandra scabra*	---	---	0.50	
Amaranthaceae	*Iresine diffusa*	0.23		---	---
	Iresine sp.	2.50		2.82	
	Lagrezia monosperma	0.38		0.18	
Anacardiaceae	*Amphipterygium simplicifolium*	0.02		---	---
	Astronium graveolens	---	---	1.15	
	Pseudosmodingium multifolium	0.03		---	---
Annonaceae	*Annona squamosa*	1.99		0.57	
	Annonaceae sp.	---	---	0.19	
Apocynaceae	Apocynaceae sp.	0.20		---	---
	Cascabela ovata	0.16		---	---
	Plumeria rubra	1.84		1.71	
	Tabernaemontana odontadeniiflora	0.08		0.26	
Asteraceae	Asteraceae sp.	0.10		0.14	
Bignoniaceae	*Arrabidaea floribunda*	0.69		---	---
	Handroanthus impetiginosus	3.48		10.46	
Bixaceae	*Cochlospermum vitifolium*	---	---	2.70	
Boraginaceae	*Bourreria purpusii*	0.09		---	---
	Cordia alliodora	0.63		0.10	
	Cordia dentata	3.31		0.85	
	Cordia gerascanthus	0.18		---	---
	Cordia sp.	0.18		---	---
	Cordia truncatifolia	---	---	0.24	
Burseraceae	*Bursera excelsa*	---	---	0.25	
	Bursera ovalifolia	0.23		---	---
	Bursera simaruba	8.50		9.31	
	Bursera sp.	0.45		---	---
Cactaceae	*Neobuxbaumia scoparia*	1.59		---	---
	Opuntia sp.	---	---	0.08	
	Pachycereus pecten-aboriginum	6.98		1.43	
	Pilosocereus collinsii	7.88		6.42	
Capparaceae	*Capparis verrucosa*	2.25		---	---
	Forchhammeria pallida	2.64		0.69	
	Morisonia americana	0.54		---	---

	Species	*Limestone IVI (%)*		*Phyllite IVI (%)*	
	Quadrella incana	9.30		11.71	
	Quadrella indica	0.34		0.60	
	Quadrella lundellii	0.11		---	---
Caricaceae	*Jacaratia mexicana*	12.79		22.13	
Celastraceae	*Schaefferia frutescens*	0.14		---	---
Combretaceae	*Bucida macrostachya*	1.62		5.49	
Erythroxylaceae	*Erythroxylum havanense*	1.20		3.77	
Euphorbiaceae	*Bernardia aff. mexicana*	0.59		0.14	
	Bernardia sp.	0.15		---	---
	Cnidoscolus megacanthus	2.89		3.45	
	Croton fragilis	0.18		---	---
	Croton morifolius	0.11		---	---
	Croton niveus	2.78		1.29	
	Euphorbia schlechtendalii	1.46		3.79	
	Hippomane mancinella	0.10		---	---
	Jatropha alamanii	0.53		0.44	
	Manihot oaxacana	0.07		0.09	
Fabaceae	*Acacia picachensis*	5.12		2.33	
	Aeschynomene compacta	3.98		0.16	
	Apoplanesia paniculata	10.77		8.46	
	Bauhinia ungulata	0.02		1.17	
	Caesalpinia eriostachys	0.00		1.02	
	Caesalpinia platyloba	1.33		0.18	
	Caesalpinia sp. 1	0.26		---	---
	Caesalpinia sp. 2	---	---	1.49	
	Erythrina lanata	0.43		0.73	
	Havardia campylacantha	13.30		5.02	
	Leucaena lanceolata	0.25		0.00	
	Lonchocarpus emarginatus	0.97		0.88	
	Lonchocarpus lanceolatus	2.32		---	---
	Lonchocarpus lineatus	0.23		---	---
	Lonchocarpus torresiorum	4.04		8.06	
	Lysiloma divaricatum	5.62		20.10	
	Lysiloma microphyllum	6.16		1.31	

	Species	*Limestone IVI (%)*		*Phyllite IVI (%)*	
	Mimosa eurycarpa	---	---	0.28	
	Myrospermum frutescens	---	---	0.71	
	Piptadenia flava	---	---	0.38	
	Piptadenia obliqua	0.07		0.24	
	Pterocarpus rohrii	0.05		0.32	
	Zapoteca formosa	0.14		---	---
Hernandiaceae	*Gyrocarpus mocinoi*	1.26		1.47	
Malpighiaceae	*Bunchosia strigosa*	2.07		0.39	
	Lasiocarpus salicifolius	0.20		0.19	
	Malpighia emarginata	8.14		3.37	
	Malpighia mexicana	5.04		2.03	
Malvaceae	*Bakeridesia gaumeri*	0.17		---	---
	Ceiba aesculifolia	0.23		0.13	
	Heliocarpus pallidus	1.33		---	---
	Hibiscus kochii	0.73		0.08	
	Luehea candida	---	---	0.50	
	Pseudobombax ellipticum	---	---	0.72	
Myrtaceae	*Eugenia* aff. *Salamensis*	---	---	0.14	
	Myrtaceae sp.	0.07		---	---
Nyctaginaceae	*Pisonia aculeata*	1.37		---	---
Opiliaceae	*Agonandra obtusifolia*	---	---	0.08	
	Agonandra sp. 1	---	---	0.18	
Polygonaceae	*Coccoloba liebmannii*	0.16		1.04	
	Coccoloba sp.	---	---	0.49	
	Ruprechtia pallida	1.00		2.06	
Primulaceae	*Bonellia macrocarpa*	3.30		1.68	
Rhamnaceae	*Colubrina elliptica*	0.44		---	---
	Krugiodendron ferreum	0.95		---	---
	Ziziphus amole	0.09		---	---
Rubiaceae	Rubiaceae sp.	0.11		---	---
	Exostema caribaeum	0.20		0.37	
	Hintonia latiflora	0.11		0.13	
	Randia obcordata	0.69		---	---
	Randia sp.	0.39		0.56	

	Species	*Limestone IVI (%)*		*Phyllite IVI (%)*	
	Randia thurberi	0.35		0.35	
Rutaceae	*Amyris jorgemeavei*	1.29		0.29	
	Esenbeckia berlandieri	0.61		2.08	
	Esenbeckia collina	0.12		0.03	
	Pilocarpus goudotianus	---	---	2.32	
	Zanthoxylum arborescens	0.11		0.25	
	Zanthoxylum caribaeum	0.05		0.43	
	Zanthoxylum sp.	0.00		0.14	
Salicaceae	*Casearia tremula*	2.24		1.26	
Sapindaceae	*Thouinia villosa*	11.99		20.11	
	Thouinidium decandrum	0.31		---	---
Sapotaceae	*Sideroxylon celastrinum*	1.87		0.26	
	Sideroxylon obtusifolium	0.26		0.03	
	Sideroxylon sp.	0.06		0.22	
Schoepfiaceae	*Schoepfia* sp.	0.25		---	---
Simaroubaceae	*Castela retusa*	0.14		---	---
Solanaceae	*Physalis arborescens*	---	---	0.11	
	Physalis campechiana	---	---	0.11	
	Solanum diphyllum	0.06		---	---
Surianaceae	*Recchia connaroides*	1.32		---	---
Ulmaceae	*Phyllostylon rhamnoides*	8.04		9.57	
Unknown	Unknown	1.14		1.09	
Urticaceae	*Myriocarpa* sp.	0.11		---	---
Zygophillaceae	*Guaiacum coulteri*	5.06		---	---

CHAPTER 5

General discussion

Rodrigo Muñoz

SUMMARY

The last chapter of this thesis engages in a comprehensive discussion of the research findings presented in the previous chapters. It begins by summarizing the main research questions posed in the **General Introduction (Chapter 1)**, which revolve around the roles of autogenic regulation, climatic conditions, and substrate heterogeneity in shaping dry (TDF) and wet (TWF) tropical forest dynamics.

The key messages of this **General Discussion** are:

1. *Autogenic regulation.* Autogenic regulation plays a pivotal role in forest dynamics, with its strength varying in relation to a forest's proximity to its stable state. This is illustrated by the relationships observed between state variables (e.g., basal area, tree density, species richness) and their rates of change. The discussion underscores the differences in autogenic regulation between TDFs and TWFs, with TWFs exhibiting stronger autogenic regulation, likely due to higher species richness and more favorable environmental conditions.

2. *Climatic conditions.* The results indicate that changes in temperature negatively affect aboveground net primary productivity (ANPP) in both forest types, but TDFs show higher sensitivity to climate variations. Seasonality plays a crucial role in mediating these effects, with differing responses to temperature during the rainy and dry seasons. The El Niño–Southern Oscillation (ENSO) phenomenon also significantly impacts old-growth TDFs, with La Niña and El Niño events acting as stabilizing factors.

3. *Substrate heterogeneity.* While substrates (limestone and siliciclastic phyllite) do not directly influence old-growth forest dynamics, they lead to clear contrasts in forest structure, diversity, and composition. The contrasting species composition between substrates suggests that forests may respond differently to environmental stimuli due to variations in functional composition.

4.*The future of tropical forests.* The chapter concludes by emphasizing the vulnerability of TDFs to climate change, with potential state shifts and biomass losses predicted under rising temperatures. This section stresses the need for further research, particularly across broad climatic gradients, to understand the impacts of climate change on various types of tropical forests.

In summary, **Chapter 5** provides a comprehensive synthesis of the thesis's findings, offering insights into the complex interplay of factors influencing the dynamics of tropical forests and highlighting the importance of continued research to address the challenges posed by climate change and forest conservation.

In this thesis, I examined the dynamics of secondary and old-growth tropical dry forests (TDFs) and tropical wet forests (TWFs), focusing on the role of external factors and autogenic regulation. To conduct this research, I used two extensive datasets from southern Mexico. The first dataset belongs to the Nizanda region in Oaxaca state, which features a TDF with a six-month dry season. The average annual precipitation (MAP) is 900 mm and the mean annual temperature (MAT) is 27.7 °C. This area has well-preserved forest cover, and the TDF grows on limestone- and siliciclastic phyllite-derived substrates. The second dataset belongs to the Marqués de Comillas region in Chiapas state, which is a TWF with a mild three-month dry season. The MAP for this area is 3,000 mm and the MAT is 24.4 °C. The region experiences moderate forest fragmentation. At both sites, permanent plots were established to monitor changes in the structure and diversity of the tropical forests. These valuable datasets were utilized to investigate how do tropical forest dynamics is influenced by:

- Autogenic regulation (**Chapter 2**)
- Variation in climatic conditions (**Chapter 3**)
- Substrate heterogeneity across the landscape (**Chapter 4**)

In this general discussion, I will address the role of each of these factors by confronting the results from **Chapters 2-4** with other studies and the conceptual framework I posed in the General Introduction of this thesis (**Chapter 1**, **Figure 1.1**).

1 HOW DOES AUTOGENIC REGULATION INFLUENCE TROPICAL FOREST DYNAMICS?

1.1 Autogenic regulation within a single forest type

Autogenic regulation is an important property of ecosystems because it allows them to remain stable over time and respond and adjust to new environmental conditions. Changes in the state of forests or their environment modify resource availability, triggering responses in recruitment, growth, and mortality rates. When a forest state variable is below its average stable state, which is in equilibrium with the long-term environment, then recruitment and growth rates increase and outbalance mortality, resulting in a net positive change. The opposite takes place when a forest state variable is above its stable state (**Figure 2.1**, **Figure 2.5**). Thus, the effect of autogenic regulation depends on the current state of the community relative to its stable state. As shown in **Chapter 2**, autogenic regulation can be assessed by simply regressing rates of change (ΔY) on their state variables (Y).

Autogenic regulation appears to be stronger as the community gets farther away from its stable state. This may be the reason why asymptotic trajectories are observed in the recovery of multiple forest attributes in secondary tropical forests (Poorter et al., 2021): young secondary forests are farther from equilibrium than old ones, thus the rates of change are higher in young forests. In **Chapter 2**, I found that basal area, tree density and species richness (state variables, Y) had significant negative relationships with their respective rates of change (ΔY; **Figure 2.5**). Each state variable has a different mechanistic explanation for the autogenic regulation observed. Basal area is a good indicator of biomass; thus, with low biomass there is ample availability of space and resources (light, water, nutrients) to be exploited, but resource exploitation becomes slower as biomass increases until achieving stable values (which are capped by abiotic constrains) (Odum, 1969). In contrast, tree density is poorly correlated with biomass. During the early stages of succession, density and biomass are typically minimal, which enables copious recruitment, often overshooting density's stable state (Lebrija-Trejos et al., 2010). As stems grow a process of negative density-dependence is triggered, driving the community back to its stable state (Courchamp et al., 1999; Pillet et al., 2018). Similarly, autogenic regulation in species richness arises from multiple factors, yet density-dependence appears to be the ultimate driver of species stability and maintenance in ecosystems (Comita et al., 2014). Rare species have shown higher offspring survival rates than common species within a patch (Wills et al., 2006). From a deterministic perspective, this would promote the increase of rare species, as their individuals have better chances of surviving than those of dominant species. However, stochastic fluctuations in population sizes make rare species more susceptible to become locally extinct (Lande et al., 2003). The balance between density-dependence and stochasticity in the population dynamics of tropical forests generates a stabilizing effect on the number of species in tropical forests (Wills et al., 2006).

1.2 Contrasts in the autogenic regulation of TDF and TWF

The strength of autogenic regulation showed clear differences between vegetation types. In **Chapter 3**, I found that changes in productivity were better explained by successional age (a good proxy of forest state) (van Breugel et al., 2006; Lebrija-Trejos et al., 2010) in TWFs than in TDFs (27 % vs. 4 % variation explained; **Figure 3.2**). Autogenic regulation was also stronger in TWFs compared to TDFs for basal area, density, and species richness (the same analysis performed for the net rates of change in TDF in **Chapter 2**, now also applied to the TWF dataset). I used two metrics to quantify the strength of autogenic regulation: slopes and R^2 values. Slopes were steeper (*i.e.*, more negative) for all three variables and R^2 values (both marginal and conditional) were higher for the TWF (**Table 1**), likely due to three reasons. First, higher species richness at the wet site can result in higher functional diversity (Cadotte et al., 2011), which in turn can lead to more efficient exploitation of resources whenever they become available (Peterson et al.,1998; but see Hordijk et al., 2023). Second, the environmental conditions at the wet site are less limiting in general for forest development (*cf.* Poorter et al., 2016), thus boosting plant growth and helping the community return to its stable state quickly. Third, the environmental conditions at the wet site enable plants with rather acquisitive traits to thrive (Lohbeck et al., 2013), possibly making all ecological processes –including autogenic regulation– happen faster in the TWF. These results are also consistent with the faster recovery rates (which arise from autogenic regulation; **Chapter 1**) observed in moist and wet tropical forests for biomass and species diversity (Poorter et al., 2016; Rozendaal et al., 2016; Rozendaal et al., 2019).

2 HOW DOES VARIATION IN CLIMATIC CONDITIONS INFLUENCE TROPICAL FORESTS DYNAMICS?

2.1 Comparing wet and dry secondary tropical forests

Climatic conditions are a major driver of forest dynamics, given their strong influence on temperature, water availability and solar radiation (Schuur, 2003; Sullivan et al., 2020). In this

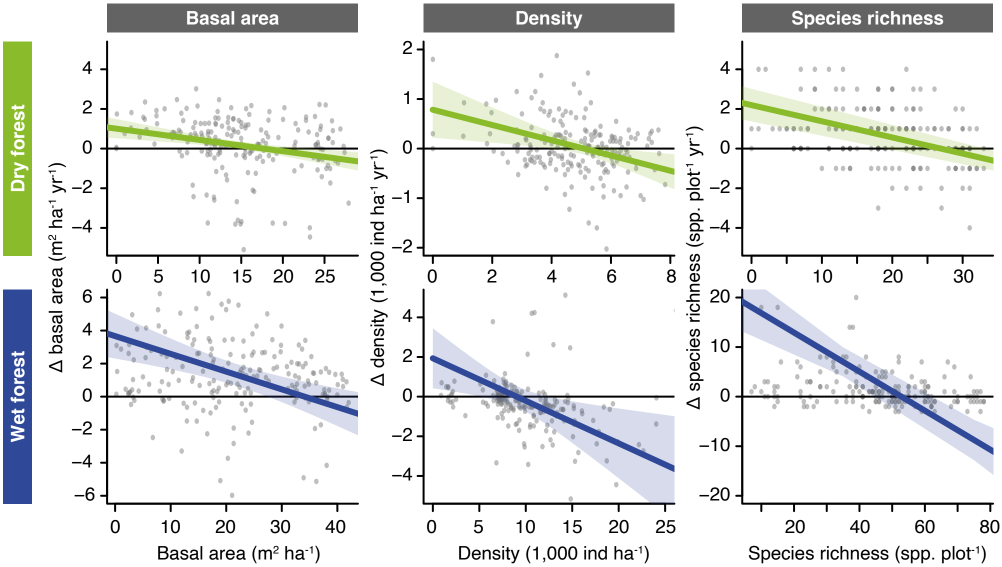

Figure 5.1

Autogenic regulation in dry and wet tropical forests. Basal area, density and species richness are shown for each study site. Only data from secondary forests were included in the analysis. Lines depict linear mixed-effects models of state variables regressed on the rates of change of the same state variable [variable ~ Δ variable + (1 + Δ variable | Plot)], no random effects included (for further details see **Chapter 2**); confidence intervals (95 %) are shown in light color; gray dots represent all plot-year combinations. Summary statistics for these regressions are shown in **Table 5.1**.

Table 5.1

Summary statistics for autogenic regulation regressions shown in **Figure 5.1**. including marginal R^2 values (R^2_{marg}, *i.e.*, without random effects) and conditional R^2 values (R^2_{cond}, *i.e.*, with plot introducing a random effect in regression slopes and intercepts). β values represent the slope of the regression; more negative slopes indicate faster return to the stable state and thus stronger autogenic regulation.

Forest type	*Statistic*	*Basal area*	*Density*	*Richness*
DRY	R^2_{marg}	6.5 %	12.3 %	16.0 %
	R^2_{cond}	6.5 %	32.5 %	20.1 %
	β	−0.057	−0.154	−0.082
WET	R^2_{marg}	17.7 %	18.9 %	49.4 %
	R^2_{cond}	41.2 %	61.2 %	94.9 %
	β	−0.108	−0.215	−0.394

thesis, I found that the effects of climatic conditions on old-growth and secondary forests were similar in direction but stronger in TDFs. Increases in temperature have a negative effect on aboveground net primary productivity (ANPP) for secondary TDFs and TWFs. Yet, climatic sensitivity is ecosystem-specific: half of the variation in ANPP of secondary TDFs was driven by climatic conditions (47 %), while secondary TWFs were only marginally influenced by them (3 %; **Figure 3.2**). Temperature negatively influenced ANPP by reducing growth and enhancing mortality in TDFs (**Figure 3.3**). Seasonality influenced this response as well, as growth was driven by climatic conditions during the rainy season, and mortality was driven by climatic conditions during the dry season (**Chapter 3**).

Counterintuitively, precipitation in the previous dry season had a negative impact on TDF's ANPP (**Figure 3.3, Chapter 3**), which contrasts with the findings of other studies (Brando et al., 2008; Martínez-Ramos et al., 2018; Becknell et al., 2021) and the hypothesis of this chapter itself about the positive effects of precipitation on biomass productivity. Yet, a recent study on experimental throughfall reduction in a TDF plantation found that soil moisture reductions led to slight increases in ANPP, although possible mechanisms are not discussed because of the small differences with the control treatment (Condit et al., 2004; Vargas Gutiérrez et al., 2023). A possible explanation is that biomass increases during rainy years, which usually display cool temperatures as well (correlation of annual precipitation and mean temperature: $r = -0.44$, $P = 0.003$, data from **Figure 5.2 A**). Reduced growth and/or increased mortality can be a consequence of higher competition for space and resources because of the increase in biomass in the previous year (**Chapter 2**). Further investigation is required to unravel whether it is an actual pattern or a statistical artifact.

The findings from **Chapter 3** indicate that dissecting ANPP into its demographic components (recruitment, growth, and mortality) provides a more comprehensive understanding of productivity variation (**Figure 3.2**). The demographic analysis highlights the role of seasonality in mediating the effect of climatic conditions on growth and mortality (Saenz-Pedroza et al., 2020) with differing responses to temperatures during the rainy and dry seasons attributed to distinct physiological processes (McDowell et al., 2008). Growth primarily relies on photosynthetically active periods occurring in the rainy season, where temperature and cell turgor significantly impact growth rates (Nonami, 1998). Conversely, mortality in TDFs is driven by conditions in the dry season (Saenz-Pedroza et al., 2020) when most trees lack foliage and depend on stored nutrients for basal metabolism maintenance (McDowell et al., 2019). Since respiration increases with temperature but photosynthesis is not occurring (except for a few species with inverse phenology or photosynthetic bark), depletion of nutrient reserves under warmer conditions may result in carbon starvation and tree death (**Chapter 3**) (McDowell et al., 2008).

In summary, secondary TDFs exhibit higher sensitivity to climatic conditions compared to tropical wet forests, with seasonality playing a crucial role in determining how these conditions, particularly temperature, affect the various demographic processes that shape forest dynamics.

2.2 The case of old-growth tropical dry forests

The El Niño–Southern Oscillation (ENSO) macroclimatic phenomenon also affected old-growth forests at the dry site (**Figure 4.S2**) by producing dry and hot conditions during El Niño phase and cool and wet conditions during La Niña phase (**Figure 5.2**; **Chapter 4**). La Niña event of 2010 resulted in a sharp increase in the development of the structure and diversity of old-growth TDFs while El Niño resulted in sharp decreases, offsetting each other over time and creating a zero-sum situation (**Figure 4.3 E-H**). Old-growth forest trajectories for the whole study period (2008-2020) therefore suggest that gains made during La Niña events are lost during subsequent El Niño events. In fact, the trajectories of these plots resemble the classical depiction of stability, with fluctuations within a wide but constrained dynamic regime. Although the study period for old-growth forests was rather short (compared to the lifespan of tropical trees), it suggests that these systems are stable over time. Yet, their stability can arise from climatic stability (as suggested by a remarkable climatic sensitivity of TDFs in **Chapter 3**). If true, the higher climatic variability and increasing temperatures expected in coming years arising from global warming (Timmermann et al., 1999; Cai et al., 2014; Diffenbaugh et al., 2015) will produce more variable forest dynamics, with consequences for the ecosystem services they provide, such as carbon sequestration (Balvanera et al., 2021).

During the El Niño event of 2015-2016, massive mortality caused big losses in basal area and aboveground biomass (AGB), which were partially compensated by a surprising increase in growth rates (**Chapter 4**) (*cf.* Condit et al., 2004). The high growth rates observed (for basal area, as high as those observed during La Niña 2010 event) are likely caused by plant expansion into the space left by trees dying during the dry season, when mortality is high (**Chapter 3**) (Saenz-Pedroza et al., 2020).

In summary, both old-growth and secondary TDFs show high climatic sensitivity. The dynamics of these forests are influenced by the ENSO phenomenon, with the alternating El Niño and La Niña events acting as stabilizing factors. However, increasing variation in climatic conditions and temperatures may reduce forest stability and structural development on the long term.

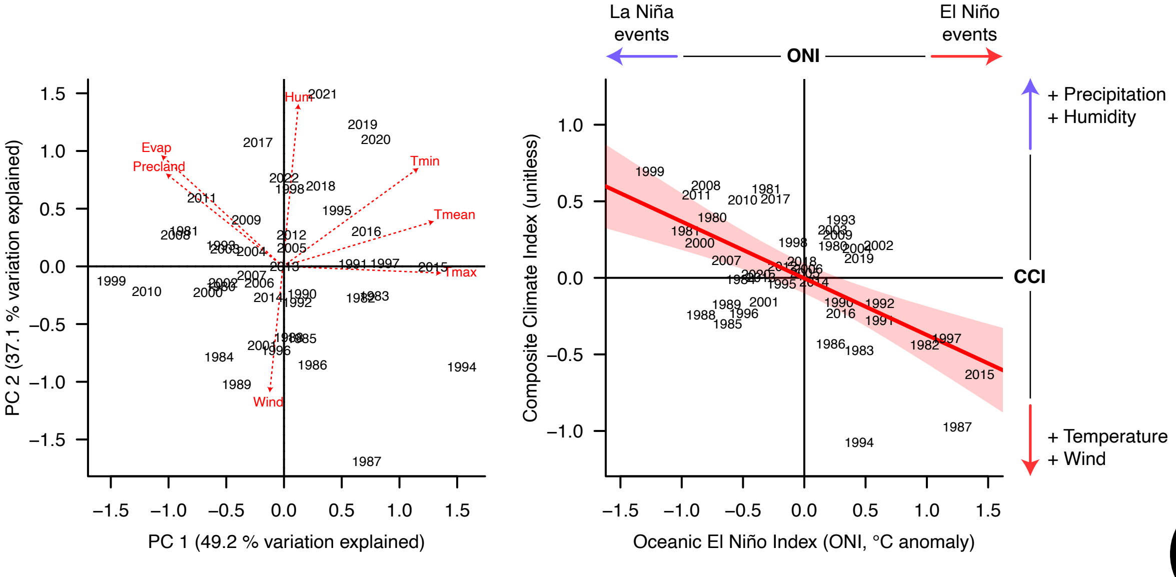

Figure 5.2

Influence of El Niño–Southern Oscillation (ENSO) on the climatic conditions of Nizanda's TDF. **(A)** Principal component analysis of annual climatic conditions at the site. Climatic information was retrieved from NASA's MERRA-2 product (for further details see *Extended methods* in **Chapter 3**). *Years* were treated as observations. **(B)** ENSO effects on local climatic conditions. The Oceanic El Niño Index (ONI) represents the oceanic temperature anomaly on the mid-eastern section of the Pacific Ocean and is one of the most widespread indicators of El Niño (positive anomalies) and La Niña (negative anomalies) events (van Oldenborgh et al., 2021). The Composite Climate Index (CCI) is an index based on the principal components 1 and 2 of the PCA analysis in panel A (CCI = –0.492*PC1 + 0.371*PC2); positive CCI values indicate high precipitation and air humidity, while negative CCI values indicate high temperatures and wind speeds. The red line represents the linear regression between the two variables, and the red envelope represents its 95 % confidence interval ($R^2 = 0.35$, $P < 0.001$).

3 HOW DOES SUBSTRATE HETEROGENEITY ACROSS THE LANDSCAPE INFLUENCE TROPICAL FOREST DYNAMICS?

Substrates provide mechanical support, water, and nutrients to plants, affecting therefore plant performance and forest dynamics. Limestone and siliciclastic phyllite, the two substrates on which TDF occurs in Nizanda, did not directly influence the dynamics of old-growth forest stands. Yet, they brought about strong contrasts in structure, species diversity and composition (**Figure 4.2**, **Figure 4.3**, **Figure 4.4**), and they showed a different behavior regarding the Oceanic El Niño Index (ONI, metric broadly used to identify El Niño and La Niña occurrences; **Figure 4.S2**).

Although it was initially hypothesized that siliciclastic phyllite, with its lower soil water content and fertility, represented a harsher environment for plant development compared to limestone, strong evidence supporting this hypothesis was not found in **Chapter 4**. However, there was a clear differentiation in species composition between the two substrates (**Figure 4.4**). This contrasting species composition suggests that forests may respond differently to environmental stimuli, possibly due to variations in functional composition (Cadotte et al., 2011; Díaz-Castellanos et al., 2022). Given that TDFs experience highly seasonal and harsh dry seasons (Allen et al., 2017), plant traits related to drought tolerance and nutrient storage are crucial for the ecological performance of species in this ecosystem (Pineda-Garcia et al., 2013; Powers et al., 2020; Romero et al., 2022).

To gain a deeper understanding of the dynamics of this TDF, future research could focus on quantifying functional differences between plots and substrates and examining their relationship with forest's responses to environmental changes (*e.g.*, Prado-Junior et al., 2016; van der Sande et al., 2017; Powers et al., 2020). The alternation of La Niña and El Niño years offers a unique opportunity to test species' abilities to cope with extreme conditions. In principle, plots with acquisitive functional profiles may have an advantage during rainy and cool La Niña years, while plots with conservative profiles may better withstand the effects of hot and dry El Niño years (Poorter et al., 2008; Aleixo et al., 2019; Powers et al., 2020).

Substrates effects on forest dynamics are particularly relevant for secondary forests, as forest recovery rates are influenced by the value of their stable state (**Chapter 2**, **Figure 5.1**), which is related to substrate properties (Durán et al., 2006; Peña-Claros et al., 2012; Terra et al., 2018). At the TDF site, old-growth forests in phyllite, where secondary plots are located, exhibit a wide range of AGB values (70 – 170 Mg ha^{-1}). The stable state of secondary forest plots may also vary within this range, thus impacting recovery rates especially in early successional stages when recovery occurs more rapidly (Holl et al., 2018).

Some studies have quantified the impact of vegetation dynamics on substrates (*e.g.*, Gei et al., 2018; van der Sande et al., 2023b), but the opposite relationship (*i.e.*, studies on the impact of substrates on dynamics) requires further examination (but see van der Sande et al., 2017 for a compehensive evaluation of soil effects on dynamics). Understanding the substrate-vegetation relationship can provide useful information to foresee how tropical forests will recover after land abandonment, and what the impacts of agricultural intensification might be for the forests in the future (Kopittke et al., 2019; Jakovac et al., 2021).

4 INTERPLAY BETWEEN AUTOGENIC REGULATION AND CLIMATIC CONDITIONS

The drivers of forest dynamics showed substantial differences between dry and wet systems. In the secondary TDF, autogenic regulation was the most relevant driver of forest dynamics in young secondary stands, which are father away from their stable state. This was indicated by the results from **Chapter 2**, that showed positive rates of change for very low values in state variables. Strong autogenic regulation was also evidenced by the high recovery rates in productivity in secondary stands ranging 0-10 years after abandonment in **Chapter 3**, period after which the ANPP-productivity relationship becomes negligible (**Figure 3.1 B**). Additionally, old-growth TDF was very sensitive to climatic conditions arising from the ENSO phenomenon (**Chapter 4**). These results suggest that there is a shift in the dominance of forest dynamics drivers along secondary succession and state variable gradients, from autogenic regulation in early successional stages with low state variable values, to climatic conditions in later successional stages with higher state variable values (> 10 years after abandonment).

The TWF showed high and constant productivity regardless of successional age (**Figure 3.1 A**), suggesting that autogenic regulation is the dominant driver of dynamics in the first 35 years of secondary succession analyzed. Unfortunately, because of the recent colonization history at the TWF site (**Chapter 1**; Berget et al., 2021), the oldest successional stands are maximum 50 years old, impeding the analysis of the drivers of dynamics on old-successional fields. Information on old-growth forests was also not available at the TWF. However, it is possible that autogenic regulation has a more important role in TWF dynamics overall (secondary and old-growth), given that density-dependance shows to be more intense in wet tropical forests (Comita et al., 2014), and recovery rates (driven by autogenic regulation) are also higher for wetter forests (Poorter et al., 2016). Future research can explore how autogenic regulation and climatic conditions drive TWF dynamics in longer successional gradients by including old-growth TWF dynamics in successional analyses.

5 THE FUTURE OF TROPICAL FORESTS IN A WARMER, MORE FRAGMENTED WORLD

TDFs are in greater peril of undergoing state shifts under changing climate conditions compared to TWFs. In secondary TDFs, an increase of 1 °C in mean temperature may result in yearly losses of 3.7 Mg ha^{-1} of AGB (3.1 % of average AGB in old-growth forests) compared to 1.9 Mg ha^{-1} in secondary TWFs (unknown old-growth forest reference) (**Chapter 3)**. La Niña and El Niño events are major drivers of the dynamics of old-growth TDFs (*cf*. Calvo-Rodriguez et al., 2021), and the alternation of wet and dry years (climatic stability) generates compensating fluctuations in tropical forest dynamics over time (*i.e.*, vegetation stability) (**Chapter 4)**. Therefore, TDFs are more likely to undergo state shifts under climate change, particularly because of their sensitivity to rising temperatures and the strong coupling of their dynamics to climatic conditions (Allen et al., 2017).

Plants may track short-term changes in environmental conditions through plastic acclimation responses of their traits (Díaz-Castellanos et al., 2022; Romero et al., 2022). However, in the long term, climate change will produce significant changes in the species and functional composition of forest communities (Phillips et al., 2010). The findings of this thesis and other studies quantifying climate effects over longer timeframes (Sakschewski et al., 2016; van der Sande et al., 2023a) suggest that increases in temperature, more erratic precipitation, and new disturbance regimes (*e.g.*, hurricane occurrence in places that did not previously experience them) will reduce the biomass and productivity of these tropical forests (Brienen et al., 2010; Phillips et al., 2010; McDowell et al., 2020).

While our understanding of tropical forest dynamics still has gaps, the current body of knowledge is robust enough to anticipate the obvious impacts of climate change on various types of tropical forests, including TDF and TWF, secondary and old-growth forests (Sakschewski et al., 2016; Sullivan et al., 2020). This thesis provides evidence that the overall response of secondary forests to climatic variations is similar to that of old-growth forests, at least in terms of the direction of change caused by climate shifts. However, the major differences are determined by the climatic contexts of tropical forests (TDF vs. TWF). I suggest conducting comparative studies that explore the effects of climatic variations along broad climatic gradients (from dry to moist to wet tropical forests) with substantial sample sizes. The availability of forest dynamics datasets and the presence of international research networks such as 2ndFOR, RAINFOR, AfriTRON, ForestPlots.net, ForestGEO, and ITFS offer promising opportunities for such research endeavors. These networks have played a vital role in generating fundamental research, and their significance will likely increase as the impacts of climate change become more evident. They can serve as a "thermometer" for monitoring the actual effects of climate change on our tropical forests. Access to high-quality information is crucial for making informed decisions, whether to stimulate under-researched areas of study, implement effective conservation and management strategies, or advocate for appropriate policies to safeguard and restore tropical forests.

6 CONCLUSIONS

In this thesis, I investigated the effects of autogenic regulation and allogenic factors on the dynamics of old-growth and secondary tropical forests. The research findings led to the following conclusions:

1. Autogenic regulation serves as the primary driver of dynamics in secondary TWFs and young secondary TDFs, while climate exerts the most significant influence on older secondary and old-growth TDFs, showing that autogenic regulation becomes stronger as the community gets farther away from its stable state.
2. Biomass dynamics in secondary TDFs and TWFs is negatively affected by temperature. In TDFs, precipitation had a surprisingly marginal effect.
3. Secondary TDFs are more sensitive to changes in climatic conditions than secondary TWFs.
4. The occurrence of El Niño events, leading to dry and hot years, reduce structural development and species diversity in TDFs. La Niña events, leading to wet and cool years, show the opposite consequences.
5. Substrates do not exhibit significant effects on the dynamics of old-growth TDFs. Yet, their indirect influence on forest dynamics via floristic and functional composition needs further examination.

The balance between the importance of autogenic regulation and the impact of allogenic factors on forest dynamics requires broad comparisons along the major environmental gradients. Together, these co-determine our potential to interfere ecosystem management, use and conservation of tropical forests.

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If I have seen further, it is by standing on the shoulders of giants
Isaac Newton

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SUMMARY

Tropical forests face continuous exposure to environmental changes due to external factors such as climate variability, land use change, soil degradation, and human-induced climate change. These factors disrupt the state of tropical forests, triggering a process called autogenic regulation, where forests adjust their demographic properties to maintain stability. The interaction between external factors and autogenic regulation determines the temporal behavior of tropical forests, known as forest dynamics.

This thesis aimed to investigate the role of external factors and autogenic regulation in the dynamics of secondary and old-growth tropical dry forests (TDF) and tropical wet forests (TWF). To achieve this aim, three research questions were addressed in three chapters that assess, regarding tropical forests dynamics:

- The influence of autogenic regulation (**Chapter 2**)
- The impact of climatic conditions (**Chapter 3**)
- The effects of substrate heterogeneity across the landscape (**Chapter 4**)

In **Chapter 2**, the autogenic regulation of old-growth forests (OGF) and secondary forests (SF) was analyzed by studying important state variables such as basal area, tree density, and species richness, along with their rates of change. The study tested the hypothesis that demographic rates in forests respond to disturbances to reestablish a stable state, thereby demonstrating autogenic regulation. Data from 17 SF plots (16 years) and 7 OGF plots (11 years) were used. The results confirmed that demographic rates responded as expected to disturbances: recruitment and growth increased when plots were below their stable state, while mortality decreased. The study concluded that autogenic regulation, achieved through the balance of recruitment, growth, and mortality, is a crucial mechanism for tropical forest resilience.

In **Chapter 3**, I focused on the influence of climatic conditions on biomass productivity in wet and dry tropical secondary forests. The study used data from secondary vegetation in a TDF (16 plots, 15 years) and a TWF (20 plots, 18 years), coupled with satellite-based climatic records. The effects of precipitation, temperature, and photosynthetically active radiation (PAR) on forest dynamics were assessed. The findings revealed that climatic conditions

predominantly drove forest dynamics in TDF, while autogenic regulation played a major role in TWF. Temperature was identified as the primary influencer of aboveground net primary productivity (ANPP). Surprisingly, precipitation had only a marginal, negative effect on ANPP in TDF, and PAR had no significant effects. The study predicted that a 1°C increase in temperature would lead to a biomass loss of 3.65 Mg ha-1 per year in TDFs and 1.94 Mg ha-1 per year in TWFs. These findings suggest that global warming will diminish the carbon mitigation potential and long-term productivity of secondary tropical forests, particularly in TDFs.

In **Chapter 4**, the dynamics of forest structure, diversity, and composition were compared between two substrates in an old-growth TDF landscape. A 12-year dataset from 7 plots on limestone (high soil water content and fertility) and 7 plots on siliciclastic phyllite (low soil water content and fertility) was utilized. The study revealed that TDF on limestone exhibited higher structural development, greater diversity, and distinct floristic composition compared to TDF on phyllite. However, the dynamics of structure, diversity, and floristic composition did not differ significantly between substrates. These findings indicate that limestone provides a more favorable environment for TDF development, while phyllite supports a flora better adapted to harsh conditions, resulting in opposing effects that balance out in old-growth TDF dynamics. The study emphasized the importance of considering functional attributes and extreme climatic events when studying TDF dynamics.

In conclusion, autogenic regulation is the primary driver of dynamics in secondary TWFs and early successional TDFs, whereas climate exerts the most significant influence on the dynamics of old-growth TDFs. Temperature was identified as the key driver of biomass dynamics in TDFs, while precipitation had a surprisingly marginal effect. Furthermore, El Niño events lead to dry and hot years with negative consequences for forest structure and diversity at the TDF site, while La Niña events result in wet and cool years with opposing consequences. Although substrates did not exhibit significant effects on the dynamics of old-growth TDFs, further research is required to better understand their influence on floristic and functional composition. The results of this thesis suggest that global warming, leading to warmer and more variable climatic conditions, will decrease the structural development and stability of TDFs.

RESUMEN

Los bosques tropicales se encuentran continuamente expuestos a cambios ambientales provocados por factores externos como la variabilidad climática, el cambio de uso de la tierra, la degradación del suelo y el cambio climático. Estos factores modifican el estado de los bosques tropicales, desencadenando así un proceso llamado regulación autogénica, en el cual los bosques ajustan sus tasas demográficas para recuperar su estado estable. La interacción entre los factores externos y la regulación autogénica determina el comportamiento temporal de los bosques tropicales, mejor conocido como dinámica forestal.

Esta tesis tuvo como objetivo examinar el papel de los factores externos y la regulación autogénica en la dinámica de los bosques tropicales secos (BTS) y húmedos (BTH), tanto secundarios como maduros. Para lograr este objetivo, se abordaron tres preguntas de investigación en tres capítulos que evaluaron:

- La influencia de la regulación autogénica (**Capítulo 2**)
- El impacto de las condiciones climáticas (**Capítulo 3**)
- Los efectos de la heterogeneidad del sustrato a nivel de paisaje (**Capítulo 4**)

En el **Capítulo 2**, se analizó la regulación autogénica de los bosques maduros (BM) y los bosques secundarios (BS) estudiando el área basal, la densidad de árboles y la riqueza de especies, junto con sus tasas de cambio. El estudio puso a prueba la hipótesis de que las tasas demográficas en los bosques tropicales responden a perturbaciones en su estado para restablecer así el estado estable, demostrando así la regulación autogénica. Se utilizaron datos de 17 parcelas de BS (16 años) y 7 parcelas de BM (11 años). Los resultados confirmaron que las tasas demográficas respondieron a las perturbaciones según lo esperado: el reclutamiento y el crecimiento aumentaron cuando las parcelas se encontraban por debajo de su estado estable, mientras que la mortalidad disminuyó. El estudio concluyó que la regulación autogénica, lograda mediante el equilibrio entre el reclutamiento, el crecimiento y la mortalidad, es un mecanismo crucial para la resiliencia de los bosques tropicales.

En el **Capítulo 3**, se investigó la influencia de las condiciones climáticas en la productividad primaria aérea neta (PPAN) de BTS y BTH secundarios. El estudio utilizó datos de vegetación secundaria de un BTS (16 parcelas, 15 años) y de un BTH (20 parcelas, 18 años), junto con sus respectivos registros climáticos derivados de información satelital. Se evaluaron los efectos de la precipitación, la temperatura y la radiación fotosintéticamente activa (RFA) en la dinámica forestal. Los hallazgos de este estudio revelaron que las condiciones climáticas afectaron principalmente la dinámica forestal en los BTS, mientras que la dinámica de los BTH fue dirigida principalmente por regulación autogénica, siendo los BTH sólo marginalmente afectados por las condiciones climáticas. De las tres variables climáticas analizadas, la temperatura fue el factor influyendo la PPAN. Sorprendentemente, la precipitación mostró un efecto marginal y negativo sobre la PPAN en los BTS, y la RFA no tuvo un efecto significativo. Los datos de este estudio muestran que un aumento de 1°C en la temperatura media de los sitios de estudio conduciría a una pérdida de biomasa de 3.65 Mg ha-1 por año en el BTS y de 1.94 Mg ha-1 por año en el BTH. Estos hallazgos sugieren que el calentamiento global disminuirá el potencial de secuestro de carbono y la productividad a largo plazo de los bosques tropicales secundarios, especialmente en sistemas relativamente secos.

En el **Capítulo 4**, se compararon las dinámicas de la estructura del bosque, la diversidad y la composición entre dos sustratos en un paisaje de BTS maduro. Se utilizó un conjunto de datos con 12 años de observaciones provenientes de 7 parcelas establecidas sobre roca caliza (con alto contenido de agua y fertilidad del suelo) y 7 parcelas establecidas en roca filita siliciclástica (con bajo contenido de agua y fertilidad del suelo). El estudio reveló que el BTS sobre caliza mostraba un mayor desarrollo estructural, mayor diversidad y una composición florística distinta en comparación con el BTS sobre filita. Sin embargo, las dinámicas de la estructura, la diversidad y la composición florística no difirieron significativamente entre sustratos. Estos hallazgos indican que la caliza proporciona un entorno más favorable para el desarrollo del BTS, mientras que la filita posee una flora mejor adaptada a condiciones ambientales adversas, lo que resulta en efectos opuestos que se contrarrestan en la dinámica de los BTS maduros. Este estudio enfatizó la importancia de considerar atributos funcionales y eventos climáticos extremos al estudiar la dinámica de los BTS.

En conclusión, la regulación autogénica es el principal motor de la dinámica en BTH secundarios y en la sucesión temprana de BTS, mientras que el clima ejerce la influencia más importante en la dinámica de los BTS maduros. La temperatura mostró ser la principal causa de la dinámica de la biomasa aérea en los BTS, mientras que la precipitación tuvo un efecto sorprendentemente marginal. Además, los eventos climáticos extremos producidos por El Niño conducen a años secos y cálidos con consecuencias negativas para la estructura y diversidad del bosque en el sitio de BTS, mientras que los eventos de La Niña resultan en años húmedos y frescos con consecuencias positivas. Aunque los sustratos no mostraron efectos significativos en la dinámica de los BTS maduros, se requiere más investigación para comprender mejor su influencia en la composición florística y funcional. Los resultados de esta tesis sugieren que el calentamiento global, que provoca condiciones climáticas más cálidas y variables, disminuirá el desarrollo estructural y la estabilidad de los BTS.

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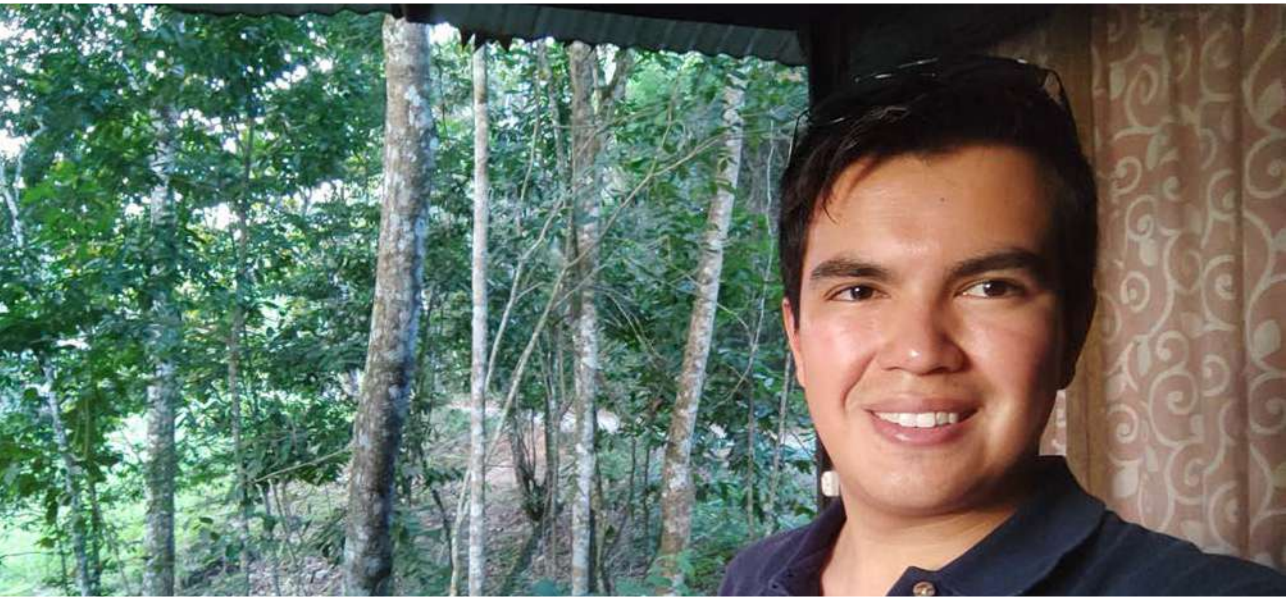
SEMBRANDO VIDA
EL MEJOR
MOMENTO PARA
PLANTAR UN ÁRBOL
ES HOY.



ABOUT THE AUTHOR

Rodrigo Muñoz is a Mexican ecologist specializing in the study of tropical forests and their drivers of change. His research interests encompass a wide range, from tree physiology and anatomy to comprehensive comparisons of forest ecosystems across the tropics. He actively participates in the 2ndFOR network, dedicated to studying tropical forest recovery, and is part of the iDIV sUCCESS group, focusing on synthesizing forest succession research. He has authored and coauthored over twenty scientific papers and a book chapter. Additionally, he has presented his research at numerous international academic conferences, being awarded twice as best conference presenter.

One of Rodrigo's most significant career achievements is his contribution to creating the Nizanda Tropical Dry Forest dataset. This dataset, compiled over two decades, meticulously documents the dynamics of secondary and old-growth tropical dry forests in the Nizanda region of southern Mexico. It stands as one of the most extensive and detailed surveys of tropical dry forest recovery and dynamics worldwide.

▲ **Top**

"The best moment to plant a tree is today." PhD project's fieldwork in Chiapas. *Motozintla, Chiapas state, Mexico. March 2022.*

▼ **Middle**

Fieldwork campaing for functional trait measurement in the tropical wet forest site. *Chajul, Chiapas state, Mexico. February 2022.*

◀ **Bottom**

Fieldwork campaign for species identification in old-growth forest plots, holding plant press, pole prunner and a big smile. *Nizanda, Oaxaca state, Mexico. September 2013.*

EARLY LIFE

Rodrigo was born in Mexico City in the early 1990s. After some family relocations, he settled in Oaxaca. This significant period in his life introduced him to the majestic landscapes of the region, which were intertwined with persistent social conflicts stemming from poverty and marginalization. These encounters ignited his interest and dedication to environmental research and a profound awareness of the social challenges encountered in one of Mexico's most economically disadvantaged areas, factors that would go on to profoundly influence his career.

ACADEMIC TRAJECTORY

His academic journey started with a bachelor's degree in biology at the National Autonomous University of Mexico (UNAM) in Mexico City from 2010 to 2015. During this period, he delved into various facets of the life sciences, from fundamental concepts in physics and chemistry to the intricacies of organismal diversity, ecology, and evolution. He followed the Ecology course with Prof. Jorge A. Meave, who later advised his bachelor's thesis and who would become Rodrigo's mentor and friend. Rodrigo's undergraduate thesis –centered on the dynamics of old-growth tropical dry forests– ignited his interest in studying forest dynamics at a landscape scale, laying the foundation for his subsequent work, including Chapter 4 of his thesis as well as his significant involvement in the Nizanda project.

Continuing his academic journey, Rodrigo pursued a research master's in Biological Sciences at UNAM. Here, he deepened his exploration of ecological stability mechanisms in tropical dry forests, employing the Nizanda forests as a case study. As part of this program, he embarked on a three-month exchange program at Wageningen University & Research in 2017 under the guidance of Prof. Frans Bongers and Dr. Danaë Rozendaal. This experience broadened Rodrigo's horizons and set the stage for his doctoral studies.

Rodrigo commenced his Ph.D. at Wageningen in 2019, guided by Profs. Frans Bongers, Lourens Poorter, Jorge A. Meave, and Miguel Martínez-Ramos. His research focused on comprehending the dynamics of dry and wet tropical forests in southern Mexico. The dual experience of living between two worlds - The Netherlands and Mexico - profoundly impacted Rodrigo. It provided him with a better understanding of social inequalities and their underlying causes. Moreover, his fieldwork in rural and marginalized areas of Mexico heightened his awareness that ecological degradation often stems from poverty and limited opportunities for human development, igniting his passion for sustainable development as a means to combat these challenges.

Looking ahead, Rodrigo aspires to pursue a career in the broad world of sustainable development. He envisions leveraging his diverse experiences, from interacting with subsistence farmers to collaborating with international experts, to create programs and policies that alleviate poverty, mitigate ecological degradation, and promote fairness among all stakeholders.

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Tree demographic strategies largely overlap across succession in Neotropical wet and dry forest communities

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Global Ecology and Biogeography. DOI: https://doi.org/10.1111/geb.12364

PE&RC TRAINING AND EDUCATION STATEMENT

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review/project proposal (9 ECTS)

- Demographic drivers of tropical dry forest resilience
- Structure, biodiversity and ecosystem functioning of secondary tropical forests (S-BEF)

Post-graduate courses (7.2 ECTS)

- Linear models; PE&RC (2020)
- Generalized linear models; PE&RC (2020)
- Mixed linear models; PE&RC (2020)
- Meta-analysis; PE&RC (2020)
- Dynamic models in R; PE&RC, SENSE (2021)
- AlterNet summer school biodiversity, ecosystem services: science and its impact on policy and society; AlterNet (2021)

Invited review of (unpublished) journal manuscripts (3.6 ECTS)

- Ecology and Evolution: abiotic and biotic drivers of forest productivity in temperate forests (2020)
- Journal of Vegetation Science: microclimatic drivers of shrubland structure (2020)
- Journal of Ecology: edaphic and climatic drivers of tropical forest productivity (2020/2021)
- Botanical Sciences: environmental factors of species establishment (2021)
- Botanical Sciences: structure, diversity, and floristics of a tropical dry forest (2021)
- Environmental Research Lett.: drought resilience in deciduous forests (2021)
- Applied Vegetation Science: landscape effects on tropical dry forest recovery (2022)
- Journal of Ecology: drought impacts on a tropical forest’s biomass (2022)

Deficiency, refresh, brush-up courses (0.8 ECTS)

- Swiss climate summer school; ETH Zurich (2021)

Competence strengthening/skills courses (2.9 ECTS)

- Wilderness first aid; SENSE (2019)
- Competence assessment; PE&RC (2020)
- Ethics in plant sciences; WGS (2021)
- Proposition writing; WGS (2022)
- Career perspectives; WGS (2022)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC First years weekend (2019)
- PE&RC Last years weekend (2022)

Discussion groups/local seminars or scientific meetings (7.6 ECTS)

- Plant ecology and diversity group seminar; UNAM, Mexico (2019-2022)
- Journal club; FEM, Wageningen (2019-2023)
- R Club; FEM, Wageningen (2020-2023)
- Successional theories discussion group; FEM, Wageningen (2022)

International symposia, workshops and conferences (6.6 ECTS)

- VII Mexican meeting of ecology; Mexico (2019)
- VII Mexican meeting of ecology; Mexico (2022)
- Association for tropical Biology and conservation meeting; Colombia (2022)

Societally relevant exposure (2 ECTS)

- EU ERC PANTROP social media (2021-2023)
- Workshop to communicate research outcomes to rural communities (2023)

Lecturing/Supervision of practicals/tutorials (6.3 ECTS)

- Forest ecology and management (2019-2023)
- Resource dynamics (2020-2022)

BSc/MSc thesis supervision (6.9 ECTS)

- Climate drivers of biomass-related demographic processes
- Changes in hydraulic functional changes along secondary succession in a tropical wet forest
- Drought resilience in old/growth and secondary tropical dry forests

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