Nicola Clerici *Editor*

Conservation of Andean Forests

Conservation of Andean Forests

Nicola Clerici
Editor

Conservation of Andean Forests

Springer

Editor
Nicola Clerici
Faculty of Natural Sciences
Universidad del Rosario
Bogota, Colombia

ISBN 978-3-031-80804-3 ISBN 978-3-031-80805-0 (eBook)
https://doi.org/10.1007/978-3-031-80805-0

© The Editor(s) (if applicable) and The Author(s), under exclusive license to Springer Nature Switzerland AG 2025

This work is subject to copyright. All rights are solely and exclusively licensed by the Publisher, whether the whole or part of the material is concerned, specifically the rights of reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

If disposing of this product, please recycle the paper.

Foreword

Stretching from Venezuela to Chile, Andean forests are crucial ecosystems, representing outstanding reservoirs of biodiversity and habitats of unique endemic species. These forests provide vital services to society, by regulating global and regional climates, providing water, maintaining biodiversity, and supporting the well-being of millions of people and countless species. Yet, Andean forests are experiencing unprecedented threats in the face of the rapidly growing human population in the region. Increasing land use demands drive deforestation and habitat fragmentation, which is further exacerbated by agricultural expansion, mining, and illegal cropping. Furthermore, the converging effects of climate change and the spread of non-native plant species magnify the pressures on these fragile ecosystems. In light of these pressing challenges, it is imperative to recognize the urgent need for conservation efforts to protect Andean forests and their unique socio-ecological heritage.

This book provides an understanding of the ecological functioning of Andean forests, spacing from community to landscape ecology studies. It discusses the regional and global threats affecting them, and gives multidisciplinary reflections on their unique socio-ecological dynamics. *Conservation of Andean Forests* presents a synthesis of recent and relevant research on these key ecosystems, discussing in detail methodological approaches, and providing the complex background on Andean forest systems functioning.

The book is organized into 11 chapters, presenting research results and future implications, discussing case studies and research methods, and novel geospatial approaches. It is the goal of this book to stimulate new ideas for future work and help managers to take decisions, as well as to becoming a critical resource for students, new and experienced researchers, academics, and professionals working with forest ecosystems.

As Editor, I am indebted to all the recognized researchers who have contributed to this work, scientific reviewers, and Springer-Nature for agreeing to publish this book. Further, I thank Universidad del Rosario (Colombia) for supporting the Editor in realizing this initiative.

Faculty of Natural Sciences
Universidad del Rosario, Bogota, Colombia

Nicola Clerici

A Multi-Scale Ecological Approach for the Conservation and Restoration of Venezuelan Andean Cloud Forests

Carlos García-Núñez, Fermin Rada, Ana Quevedo-Rojas, Mauricio Jerez-Rico, Luis D. Llambí, Carlos E. Pacheco-Angulo, Luis E. Gámez, and Emilio Vilanova

1 Introduction

The Andean eco-region of South America is one of the most prominent biodiversity hotspots in the world (Myers et al., 2000). This can be attributed to the existence of contrasting environments that are largely linked to complex latitudinal and altitudinal gradients from tropical to sub-tropical and temperate regions and from the foothills to the snow-capped peaks. This together with the presence on both flanks of the mountain range of extensive depositional plains, make the Andean landscape a mosaic of strongly interlocked ecosystems. The different precipitation patterns, both in amount and temporal distribution (i.e., seasonality) also contribute to generating favorable conditions for high biodiversity in which we can often find at the same elevation ecosystems as contrasting as montane forests, dry thorny shrublands or paramos depending on whether it is a humid slope or an arid pocket (Ataroff & Sarmiento, 2003).

C. García-Núñez (✉)
Instituto de Ciencias Ambientales y Ecológicas (ICAE), Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela

Center for Urban and Global Studies (CUGS), Trinity College, Hartford, CT, USA

F. Rada
Instituto de Ciencias Ambientales y Ecológicas (ICAE), Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela

Laboratorio de Ecología y Fisiología Vegetal, Universidad de Los Andes (UniAndes), Bogotá, Colombia

A. Quevedo-Rojas
Facultad de Ciencias Forestales y Ambientales, Escuela Técnica Superior Forestal (ETSUFOR), Universidad de Los Andes, Mérida, Venezuela

M. Jerez-Rico · C. E. Pacheco-Angulo
Facultad de Ciencias Forestales y Ambientales, Centro de Estudios Forestales y Ambientales de Postgrado (CEFAP), Universidad de Los Andes, Mérida, Venezuela

© The Author(s), under exclusive license to Springer Nature Switzerland AG 2025

N. Clerici (ed.), *Conservation of Andean Forests*,
https://doi.org/10.1007/978-3-031-80805-0_6

An important feature of the Andean Mountain landscape is the presence of diverse and structurally complex forests, which are fundamental in the provision of ecosystem services mainly linked to water provision and regulation and protection against erosion, ability to absorb and store a substantial amount of carbon in the form of soil organic matter (SOM) and plant biomass, and high levels of biodiversity and endemism (Hostettler, 2002; Raich et al., 2006; Bruijnzeel et al., 2010). Among these, tropical mountain cloud forests (TMCFs) occur in the cloud immersion zone which encompasses a lower limit between 1500 and 2750 m asl and an upper limit from 2400 to 3300 m asl depending on latitude (Stadtmüller, 1987). The presence of frequent and persistent cloud immersion and/or fog, results in a distinct environment which influences the structure and function of the vegetation (Fahey et al., 2016). The global extension of TMCFs is about 215,000 km^2 which represents 1.4% of the total area of global tropical forests (Oliveira et al., 2014).

In Venezuela, the Andean ecoregion is geographically located in the western-central zone, covering approximately 10% of the land area of the country. The section of the Andean Cordillera in Venezuela is located from 7° 30′ to 10° 10′ N and 69° 20′ to 72° 50′ W. It extends for about 450 km in a northeast direction, from the Colombian border to the central-western region of Venezuela. As a part of the Andes, the "Cordillera de Mérida" constitutes the longest continuous mountain range in the country and includes the highest elevations (i.e., maximum summit is the "Pico Bolivar" at 4978 m asl) (Ataroff, 2001). The main ecological units that have been defined are submontane forests, semi-deciduous forests, cloud forests, dry evergreen forests, thorny shrublands and páramos (Ataroff & Sarmiento, 2003).

In the "Cordillera de Mérida", cloud forests represent about 20–30% of the vegetation formations and have been classified by its elevation range into lower montane (between 1700 and 2200 m asl) and upper montane (between 2200 and 3000 m asl). Overall, species richness is lower in the upper montane forest (ca. 1.7 times) and there is an increase in epiphyte cover and decrease in tree height, canopy stratification and leaf area index with increasing elevation (Ataroff, 2001) (Fig. 1).

In Venezuela, the studies of mountain forests date back to the beginning of the nineteenth century following the work of naturalists such as Alexander Von Humboldt and Aimé Bonpland, who explored the different altitudinal levels of vegetation on the mountains of the American tropics. Since then, there has been an

L. D. Llambí
Instituto de Ciencias Ambientales y Ecológicas (ICAE), Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela

Consorcio para el Desarrollo Sostenible de la Ecoregión Andina-CONDESAN, Quito, Ecuador

L. E. Gámez
Laboratorio de Dendrología, Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes, Mérida, Venezuela

E. Vilanova
Wildlife Conservation Society (WCS), Bronx, NY, USA

Fig. 1 Left panel: Approximate distribution of cloud forests in the Venezuelan Andes for the year 2020. Map elaborated using the Hansen et al. (2013) product of global forest cover including the gains and losses of cover since the year 2000; Right panel: a typical image of Venezuelan Andean cloud forests, taken at La Carbonera. (Photo: Emilio Vilanova)

increasing number of studies that have contributed to the understanding of cloud forests focusing on aspects related to species richness (i.e., floristic inventories), and different environmental aspects (geology, geomorphology, soils and climate). Systematic studies in the cloud forests of Venezuela, mainly in the Coastal Cordillera (e.g., ecological studies at the Rancho Grande biological station, Henri Pittier National Park, Aragua State) started in the 1950s, with the arrival of the Austrian botanist Volkmar Vareschi, who contributed to the creation of the School of Biology of the Central University of Venezuela (UCV), and its program of Plant Ecology largely with a floristic and functional focus (Lindorf, 2013).

At the same time, the first phytosociological studies of the Andean cloud forests began, mainly in La Mucuy (LM) and La Carbonera (LC), in the Cordillera de Mérida, and was led by two Swiss botanists, Hans Lamprecht and Jean Pierre Veillon, hired by the School of Forestry Sciences of the Universidad de Los Andes (ULA). Since the 1980s, with the consolidation of the different research groups and graduate programs in Venezuela, the scientific knowledge of our mountain forests covered different aspects, from its structure and floristic composition to its functional ecology (i.e., eco-hydrology, productivity and ecophysiological aspects related to carbon, water and nutrient relations at plant scale level). For example, detailed information is available on their distribution, structure and floristic composition (Lamprecht, 1954; Veillon, 1965, 1985, 1989; Huber, 1986a, b; Medina, 1986;

Vareschi, 1992; Bono, 1996; Michelangeli, 1998; Ataroff, 2001, 2003; Ataroff & García-Núñez, 2013). Ecological studies on the functioning of these forests are more limited and concentrated in specific localities of the Cordillera de La Costa (Altos de Pipe and Rancho Grande) and in the Cordillera de Mérida, particularly in La Mucuy (LM) and La Carbonera (LC) (Huber, 1986a, b; Medina, 1986; Ataroff & García-Núñez, 2013).

Studies on ecosystem productivity and nutrient cycling (Fassbender & Grimm, 1981a, b; Grimm & Fassbender, 1981a, b; Delaney et al., 1997; Vilanova et al., 2018) and ecohydrology (Steinhardt, 1979; Ataroff & Rada, 2000) have also been carried out in LM and LC. These studies show a relatively high accumulation of carbon in the aboveground biomass and in the superficial soil, as well as its regulating role of the water balance when compared to pastures as the main replacement system. Likewise, for these localities (mainly for LC) there is information at the community level related to forest structure and species composition associated with environmental factors (e.g., soil water conditions; contrasting environments along gradients determined by tree fall gaps considering relative humidity, temperature and light availability) (Hetsch & Hoheisel, 1976; García Núñez et al., 1995; Acevedo et al., 2001, 2003; Dávila, 2009; Quiroz, 2010; Schwarzkopf et al., 2011; Naranjo, 2013; Quevedo et al., 2015, 2016, 2018).

For many tropical mountain forests there is limited evaluation of the impacts of habitat fragmentation at all ecological levels (Soh et al., 2019), and this is particularly evident in the case of the Andean region, including Venezuela. There is a great value from many of the aforementioned studies in that they could serve as the basis for planning conservation and restoration programs, particularly important for Andean cloud forests (ACFs), which have been subjected to severe deforestation and fragmentation processes in the last 70 years (Rodríguez-Morales et al., 2009). Yet, both theoretical and applied studies in ecological restoration are incipient. For example, ecological restoration studies based on ecophysiological characteristics of shade tolerance of cloud forest native species have been conducted in LC, illustrating the usefulness of this functional approach for restoration planning (Quevedo-Rojas & Jerez-Rico, 2020). Furthermore, this approach is useful for the development and implementation of mechanistic and process-based models to improve our understanding and prediction of ecosystem function under future scenarios of land use and climate change (see Nagy et al., 2023).

In this chapter, we present a review of ecological studies conducted at different spatial scales, from the landscape to plant levels, to describe the main structural and functional characteristics of the Andean cloud forests in Venezuela. In doing so, we place special emphasis on the research carried out at *La Carbonera* (LC) and *La Mucuy* (LM) in the Mérida Cordillera, two of the most intensively studied sites in the Venezuelan Andes, which also include long-term monitoring plots part of the Andean Forest Network (https://redbosques.condesan.org). While reviewing an important research base about how these ecosystems function and their current state, we also explore how this cumulative body of knowledge may provide guidelines for conservation, restoration and adaptation planning. We conclude with a discussion of the main challenges for future research towards an understanding and

better prediction of the dynamics of Venezuelan Andean forests under scenarios of global change. We specifically address the following questions:

1. What are the main environmental characteristics of the Andean cloud forests in Venezuela?
2. How forest cover has changed across Venezuelan Andean cloud forests in the last two decades and what are the main drivers of change?
3. How the ecohydrology of Andean cloud forests in Venezuela respond to changes from intact forest stands to pastures?
4. How forest structure in Andean cloud forests respond to light and soil-water gradients, and changes due to fragmentation processes?
5. What are the recent trends in the long-term dynamics of tree turnover and productivity in Venezuelan cloud forests?
6. How an ecophysiological approach could be used as a tool for ecological restoration of Andean cloud forests?

2 Environmental Characteristics of the Andean Forests of Venezuela

Most of the cloud forests in the Venezuelan Andes are composed by mosaics of evergreen forests, with their structure and composition varying depending on abiotic (e.g., elevation, temperature, soil, etc.) and biotic elements (e.g., disturbance regime), and the history of land use and anthropogenic disturbances. Josee et al. (2009) indicate that there are four main types of forests ecosystems in this region, where the Humid Montane Forest and the Seasonal Montane Forest of the Northern Andes are the most prominent and are characterized by a great natural variability and biological diversity (Rodríguez & Rojas-Sánchez, 1999; Hokche et al., 2008; Huérfano et al., 2020). In the case of vascular plants, from the approximately 7500 species that have been identified broadly for the Venezuelan Andes (Huérfano et al., 2020), there are more than 4100 species specifically associated to forests, which in many cases lack in-depth ecological studies. In fact, in the latest version of the Red Book of the Flora of Venezuela (Huérfano et al., 2020), only 196 Andean Forest species are reported with information about their Conservation Status, with the rest categorized as Data Deficient.

2.1 Site Description: Location, Climate, and Soils

Because of their ecological representativeness of the wider montane cloud forest ecosystem of the Venezuelan Andes, we use La Carbonera (LC) and La Mucuy (LM) sites as models to describe the environmental characteristics of these ecosystems (Fig. 2). Both sites represent the most intensive studied locations of the cloud

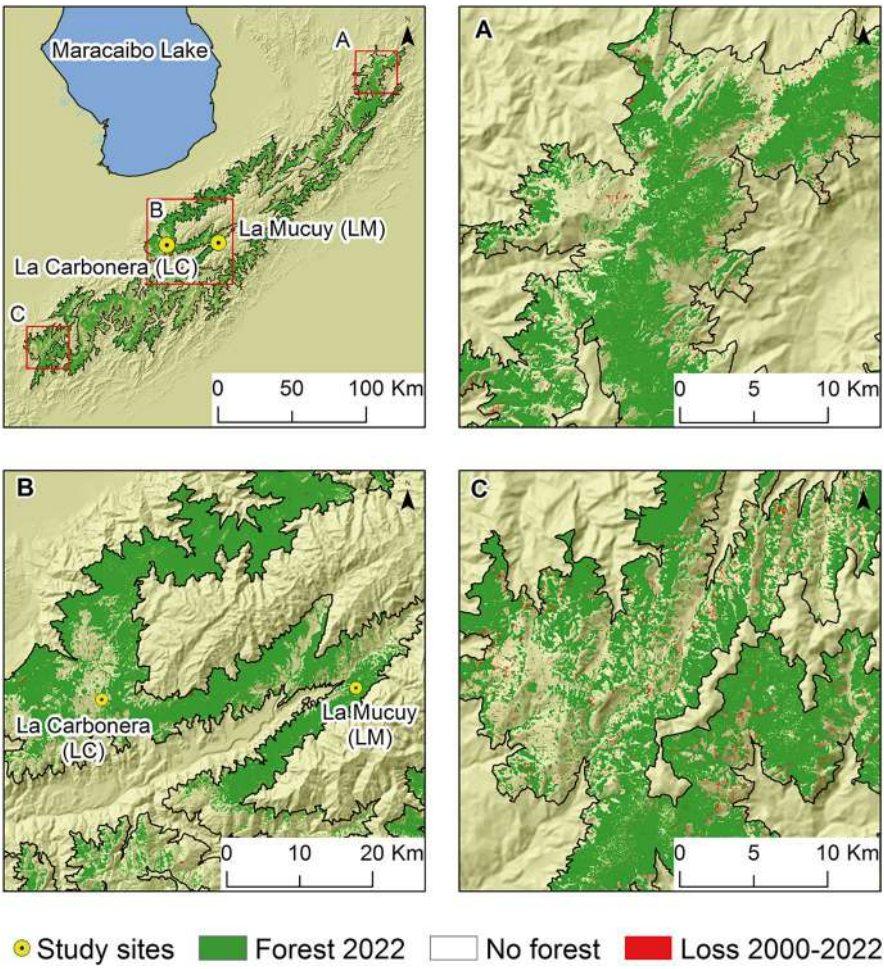

Fig. 2 Dynamics of forest cover in the Venezuelan cloud forests between 2000 and 2022. The different map insets in A, B and C show how cover has changed or remained stable in three locations. In B, the location of LC and LM is included for reference

forests in the Andes of Venezuela and encapsulate the rich biodiversity, soils, and environmental dynamics of the wider region. First, LC (8° 37′ 00″ N, 71° 21′ 00″ W) includes the San Eusebio University Forest (SEUF), the experimental station of the University of Los Andes established in 1950 for silvicultural and ecological research. The elevation ranges from 2200 to 2500 m, and the site receives an annual precipitation between 1400 and 1560 mm with a short dry season (December–February). The annual average temperature is 14.9 °C with little variation throughout the year. The soils are derived from the Colón Cretacean formation, characterized by stratified, massive, black, non-calcareous (i.e., argillaceous) shales with conchoidal fractures. The landscape consists of rounded hills, with mild to steep slopes

(Marquez, 1988). Overall, soils are mainly silty-clay, greatly variable in depth, structure and drainage condition, highly acidic (pH 4.2–5) and with high levels of exchangeable aluminum, low in base saturation, and cation exchange capacity (12–18 meq/100 g soil), high organic matter in the A1 layer (5–8% C content) of a depth of 26–33 cm; presenting an udic moisture regime (Grimm & Fassbender, 1981a; Marquez, 1988).

La Mucuy (LM) (08° 38′ N, 71° 02′ W) is located in the Sierra Nevada National Park. The vegetation extends from the lower limit of the upper montane cloud forest (2200 m asl) to the limit of the forest-paramo line (3065 m asl). Mean annual temperature at the lower limit of the cloud forest is 14 °C, with little variation throughout the year, while at the upper limit is 11 °C. Mean annual precipitation at 2300 m ranges between 2800 and 3400 mm. The precipitation pattern shows two annual peaks, one between April and May, and the other between October and November. Low clouds and fog are the main ecological factor acting on these forests most of the year, producing a limited radiation (4–7 hours of insolation) and very humid climate, with relative humidity between 80% and 100% throughout the day (Ataroff 2003; Linares, 2008). This forest presents a very rugged relief with slopes from medium to very strong (40–80%) and a NW orientation. The geology is complex and diverse, dominated by the "Iglesias Complex", characterized by pre-Cambrian igneous and metamorphic rocks. Soils are entisols (Psamments udipsamments) with loamy, sandy loam and/or clay loam textures, acid (pH 3.5–4.5), with good drainage and high stone content; surface soil has dark colors (brown to black) and high organic matter content 6.6–35.5%; average depth of the soil organic layer is 34 cm (Lamprecht, 1954) (Table 1).

2.2 General Characteristics of the Vegetation

La Carbonera and La Mucuy are both broadly classified as upper montane cloud forest sites. Early studies on the structure and floristic composition of these sites started in the 1950s (Lamprecht, 1954; Veillon, 1965), including subsequent floristic inventories (total cormophytes species, including spermatophytes and pteridophytes) in LC (Vareschi, 1992; Engwald, 1999), and in LM (Linares, 2008). In LM, above 2900 m, canopy height declines (up to 10–15 m in height), with low stem density and with characteristics of a stumpy forest with abundant bamboo species (*Chusquea spencei* Ernst) (Lamprecht, 1954). In general, both study sites share structural features in relation to the number of tree species, tree density and basal area. However, LC displays a taller canopy and higher LAI values (Table 2). Overall, at elevations of 2200–2500 m, the forest communities are characterized by a high diversity of epiphytes, mosses and lichens, structurally composed by two to three layers with irregular open canopies at 20–30 m, a medium stratum (trees 6–15 m in height), and a low stratum of small trees and shrubs (1–6 m in height). The families with the highest number of tree species reported in the Andean forests of Venezuela are:

Table 1 Geographic location and environmental characteristics of two representative Andean cloud forests locations in Venezuela

Localities	Geographic location	Altitude (m asl)	Rainfall (mm)	Temperature (°C)	Radiation/ Insolation (cal cm^{-2}) [h]	Soil characteristics
La Carbonera	8° 37′ N,[b] 71° 21′ W	2200–2500[b]	1400–1560[b]	14.9[b]	296[a] (247–350) [7.2][a]	Mainly silty-clay, greatly variable in depth, structure and drainage condition; highly acidic, low in base saturation and cation exchange capacity, high organic matter.[b]
La Mucuy	8° 38′ N,[c] 71° 02′ W	2200–3000[c]	2800–3400[c]	14.0[c]	300[a] (200–400) [7.2][a]	Loamy, sandy loam and/or clay loam, acids, with good drainage and high stone content and high organic matter content.[c]

Altitudinal range, mean annual rainfall range, mean annual temperature, mean daily solar radiation (range in parenthesis), mean daily solar insolation [in brackets]
Source:
[a]Veillon (1989)
[b]Vareschi (1992)
[c]Ataroff (2001)

Lauraceae, Rubiaceae, Melastomataceae, Myrtaceae, Euphorbiaceae, Piperaceae and Solanaceae (Lamprecht, 1954; Gentry, 1993; Ataroff, 2001; Estrada, 2003; Schneider et al., 2003; Hokche et al., 2008; Linares, 2008; Gutiérrez et al., 2012). In relation to this, Gentry (1993) mentions that the composition of Andean forests is determined by a set of families and genera predominantly of Laurasic origin, which explains the existence of several of these families at elevations above 1500 meters. The most common genera in these cloud forests include: *Alchornea, Axinaea, Billia, Beilschmiedia, Centronia, Cestrum, Clusia, Cyathea, Eugenia, Ficus, Hedyosmum, Miconia, Myrcia, Nectandra, Ocotea, Oreopanax, Palicourea, Psychotria, Solanum, Tetrorchidium* and *Piper* (Estrada, 2003), including some species of palms (e.g., *Chamaedorea pinnatifrons* (Jacq.) Oerst.), shrubs and herbs (Linares, 2008; Quevedo et al., 2015).

Table 2 General characteristics of the vegetation for La Carbonera and La Mucuy in the Venezuelan Andes

Site	N° total spp/families of pteridophytes and spermatophyta	N° tree spp ha^{-1} (≥10 cm dbh)	N° ind. trees ha^{-1} (≥10 cm dbh)	Basal area (m^2 ha^{-1})	Canopy height (m)	Leaf Area Index (LAI)
La Carbonera	369/77[d]	40[a, b]	400–850[a, b]	30–69[h]	20–30[a, b]	4.4–5.4[j]
La Mucuy	208/71[g]	35–48[b, c]	272–723[b, c]	32–61[b, c]	20–25[i]	1.6–2.3[c, f]

Source:
[a]Lamprecht (1954)
[b]Veillon (1965)
[c]Lamprecht, 1980
[d]Engwald (1999)
[e]Ataroff and Rada (2000)
[f]Acevedo et al. (2001)
[g]Linares (2008)
[h]Quiroz (2010)
[i]Schwarzkopf et al. (2011)
[j]Quevedo et al. (2016)

2.3 *The Light Environment and Its Relationship with Forest Structure*

For both study sites, investigations focusing on the light conditions and the relation with forest structure include measurements of global radiation through standard meteorological stations (open field) (Veillon, 1989), and measurements of the light conditions of the forest floor under undisturbed forest, canopy gaps (gap area of 100 and 200 m^2 for LC and LM, respectively) and open field using data loggers with quantum sensors (photosynthetic photon flux density (PPFD), and pyranometers (global solar radiation) (García Núñez et al., 1995; Vilanova, 1996; Cabrera, 1999; Quevedo et al., 2018). Hemispherical photographs have also been used to derive different parameters of the forest floor light environment (e.g., the percentage of Canopy Openness (%CO), a Light Index (LI) calculated from the relative proportions of direct and diffuse light transmitted to the understory, and the Leaf Area Index - LAI) (Acevedo et al., 2001, 2003; Schwarzkopf et al., 2011; Quevedo et al., 2015, 2016, 2018).

In general, these sites are characterized by a daily insolation pattern in which the maximum radiation values are reached between mid-morning and noon, being the forest profusely covered by low clouds and fog from about 14:00 h in the afternoon onwards. Daily measurements showed that an open field site and the center of a canopy gap site (gap area = 200 m^2) received mean maximum values of PPFD between 1561 and 1800 μmol m^{-2} s^{-1} for LC and LM, respectively. In both sites, mean PPFD in the forest understory ranged between 15 and 26 μmol m^{-2} s^{-1} (≅

1–2% of the radiation measured in the open field) with mean maximum values between 214 and 240 μmol m^{-2} s^{-1} during brief sun flecks (García Núñez et al., 1995; Vilanova, 1996; Cabrera, 1999).

The studies on the quantity and quality of the understory light environment have shown that these forests have relatively low canopy openness (% CO ≤ 5%) (Acevedo et al., 2001, 2003; Quevedo et al., 2016). Higher LAI values were measured in LC (5.4 and 4.4 for undisturbed forest and gaps, respectively) compared to LM (1.6 and 2.3) (Table 2). For LC, Quevedo et al. (2016) showed that significant differences were found between seasons, as well as when comparing different gap sizes and under closed canopy conditions (Table 3) (Ataroff & Rada, 2000; Acevedo et al., 2001; Schwarzkopf et al., 2011; Quevedo et al., 2016). Studies carried out in Venezuelan Andean cloud forests show lower LAI values (1.6–5.9; Ataroff & Rada, 2000; Quevedo et al., 2016; Schwarzkopf et al., 2011) when compared to lowland humid forests (6.9–12.0; Grubb, 1977). Low LAI has been attributed to low light input, and as a response to increasing slope angle and elevation (Kitayam & Aiba, 2002; Leuschner et al., 2007; Moser et al., 2007). For example, structural comparisons between cloud forest sites in the "Cordillera de Merida" indicate that LAI is correlated with slope orientation (i.e., LAI showed higher values at south facing plots) (Schwarzkopf et al., 2011).

Table 3 Estimates of the light and canopy structure variables for undisturbed forest (UF) and gaps in San Eusebio University Forest (n = 288, UF = 120, gaps = 168) in each season

Variables	Season	Undisturbed forest	Gaps	P-value
LAI	Dry	5.2 (0.1)[b]	4.0 (0.1)[b]	<0.01
	Wet	5.6 (0.1)[a]	4.4 (0.1)[a]	0.01
%CO	Dry	2.3 (0.1)[a]	4.9 (0.2)[a]	<0.01
	Wet	1.5 (0.1)[b]	4.1 (0.2)[b]	<0.01
%TDIR	Dry	4.0 (0.2)[a]	9.1 (0.5)[a]	0.04
	Wet	3.1 (0.2)[a]	6.5 (0.4)[b]	<0.01
%TDIF	Dry	3.2 (0.1)[a]	8.0 (0.4)[a]	<0.01
	Wet	2.5 (0.2)[a]	6.6 (3.3)[b]	<0.01
SFD	Dry	15.7 (1.0)[a]	34.6 (2.9)[a]	<0.01
	Wet	13.9 (0.9)[a]	34.1 (2.6)[a]	<0.01
SFF	Dry	12.3 (0.7)[a]	21.5 (1.2)[a]	<0.01
	Wet	4.9 (0.3)[b]	7.9 (0.5)[b]	0.12

Table from Quevedo et al. (2016) (CC By Open Access license)
Standard errors in parenthesis. Small letters indicate statistically significant differences
LAI: Leaf area index; %CO: percentage of canopy openness; %TDIR: percentage of transmitted direct light; %TDIF: percentage of transmitted diffuse light; SFD: average duration in minutes of sun-flecks; SFF: sun-fleck frequencies. Different letters in the cells indicate statistically significant differences between seasons ($P < 0.05$). The P-value corresponds to the signification level for the comparisons between UF and gaps

3 Dynamics of Forest Cover in the Cloud Forests of the Venezuelan Andes

As defined earlier, the Andean cloud forests located in western Venezuela are inserted in a high and narrow mountain range (1800–3000 m asl) that extends from northeast to southwest over about 450 km, and from northwest to southeast over a distance of 66 km, covering an area of ~800,000 ha within two long mountain ranges and two long intermontane valleys (Chacón-Moreno et al., 2021) (Fig. 1).

Using information for the year 2000 from the Global Forest Change (GFC) product in its version 1.10 (Hansen et al., 2013), the cloud forest ecosystem covered about 53.6% (429,777 ha) of their potential range in the Venezuelan Andes. Between 2000 and 2022, about 1.1%, equivalent to 8112 ha of cover were lost over this 22-year period, with an annual average of −369 ha (−0.1% per year). As of 2022, the cloud forests covered ~421,666 ha. Annual losses between 2000 and 2022 ranged from as low as 80 ha (2014–2015) to as high as 973 ha (2011–2012). 71.4% (5792 ha) of these losses were concentrated between 1800 and 2200 meters, 20.6% (1674 ha) between 2200 and 2600 meters above sea level, and 8.0% (646 ha) between 2600 and 3000 meters above sea level (Fig. 2).

To understand the main drivers of deforestation in this ecosystem, the criteria proposed by Geist and Lambin (2002) for tropical countries and Pacheco et al. (2011) for Venezuela were considered. With these criteria, a causal model of deforestation was generated to characterize and group deforestation drivers into five major classes: agropastoral expansion, infrastructure extension, logging, mining exploitation, and the presence of social conflicts. These drivers were identified in the literature review and subsequently analyzed and quantified based on the frequency of occurrence in the various sources analyzed and within each study period. This allowed for an analysis of each group of main drivers to determine, based on their percentage, their specific influence on deforestation. This analysis revealed a complex interaction between the primary and underlying causes acting independently or via different combinations varying in frequency and magnitude depending on historical and spatial contexts to drive the observed decline of forest cover in the Venezuelan Andes. Nevertheless, the primary cause with the greatest influence on deforestation has been the expansion of agricultural and cattle raising activities (37.3%,) followed by infrastructure development (29.4%), and logging (23.5%). The most common interaction pattern between primary and underlying causes in the last 20 years stemmed from the occupation of private and public lands for agriculture. This occupation process has been further incentivized by political and institutional factors through agricultural instruments, benefits, and inputs provided by national agricultural institutions, thereby increasing demographic pressure to achieve better economic benefits.

An additional but often overlooked process of change is related to forest degradation, which refers to the gradual deterioration of forest's health, structure, or functioning, often resulting from human activities such as logging, unsustainable land use, or the impacts of climate change, but that does not involve a total loss of cover.

These activities are responsible for the reduction of ecological integrity (Grantham et al., 2020), which ultimately results in a decline of important ecosystem services. Anthropogenic pressures that have contributed to forest degradation, many of which are also responsible for the loss of forest cover, include forest encroachment and fragmentation for agricultural and cattle expansion. In this regard, using the definition of forest degradation proposed by Vancutsem et al. (2021), degraded cloud forests in Venezuelan Andes covered close to 58,000 ha or 13% of the total area up to 2022, an area significantly higher than the reported for deforestation, which highlights the importance of considering degradation as a major process of change in the Venezuelan Andes.

4 Ecohydrological Effects of the Loss of Intact Cloud Forests in the Venezuelan Andes

Cloud forests are of special importance as water collectors and reservoirs, and for the maintenance of stable hydrological systems (Stadtmüller, 1987; Bruijnzeel et al., 2011). An important aspect which differentiates cloud forests from other lower elevation montane forests is the persistent presence of fog and low clouds which supply an additional input of water to the vegetation. This "extra" water varies considerably between different tropical mountain regions (0.2–4.0 mm day^{-1}) (Bruijnzeel et al., 2011).

In the Cordillera de Mérida, research has focused on the main water fluxes in the cloud forests and the impact that deforestation can have when these intact ecosystems are replaced by pastures, mostly of *Pennisetum clandestinum* (Hochst. *ex* Chiov.) Morrone, and *Melinis minutiflora* P. Beauv. (Ataroff & Rada, 2000). In LM for example, measured cloud water interception (309 mm) under intact conditions is equivalent to an extra month of rain (mean annual precipitation of 3124 mm) (Ataroff & Rada, 2000). In relation to rainfall interception, LM presents higher values (49–51% of total input) (Ataroff & Rada, 2000), compared to LC (2300 m asl), with a lower rainfall input (1400–1600 mm), where interception ranges between 20 and 35% (Steinhardt, 1979; Montilla, 2009). These values of water interception represent a very wide range reflecting the differences found in these forests in both rainfall patterns and the structure of the vegetation.

Calculated evapotranspiration (Steinhardt, 1979) accounts for almost 62% of rainfall in LC, while in LM, Ataroff and Rada (2000) estimated this to be ~73% of rainfall partitioned as: 16% transpiration, 51% foliage evaporation and 6% evaporation from the soil. Overall, of the infiltrated fraction, 26% in LM and 37% in LC becomes subsurface runoff, eventually contributing to the maintenance of streams and rivers (Ataroff and Rada 2000). Additionally, the lower proportion in the case of surface runoff (1%) throughout the year reduces the risks of flooding in streams of forested areas. Water budget studies of *P. clandestinum* pastures in LM indicate that as much as 91% of incoming water reaches the soil's upper surface (about

2843 mm yr^{-1}). Compared to the forest, surface runoff in the pasture was slightly higher, showing an average value of 2% while transpiration represented 66% of the incoming water (2070 mm yr^{-1}), a high value compared to the intact forest. The different components of the water dynamics of both cloud forests are shown in Fig. 3 (Grimm & Fassbender, 1981b; Ataroff & Rada, 2000).

Given these marked differences between intact forests and pastures, it is important to highlight that the increased pressure to convert forests into pasture for cattle grazing in the high Andean basins in Venezuela (Rodríguez-Morales et al., 2009) under drier/warmer climate scenarios, would potentially lead to lower soil storage capacity and rainfall interception, and higher transpiration rates in pastures compared to intact forests (Ataroff & Rada, 2000). These transformations may increase soil erosion, lower streamflow, and increase fires due to added flammable material (i.e., dry pastures) with the consequent losses of SOM, increased CO_2 emissions, and higher risks of tree mortality at the edges of forest patches (Bonnesoeur et al., 2019; Breshears et al., 2013; Brodribb et al., 2020; Choat et al., 2018; Dávila, 2009; Herold et al., 2011; Roman-Cuesta et al., 2014; Oliveras et al., 2017; Soh et al., 2019).

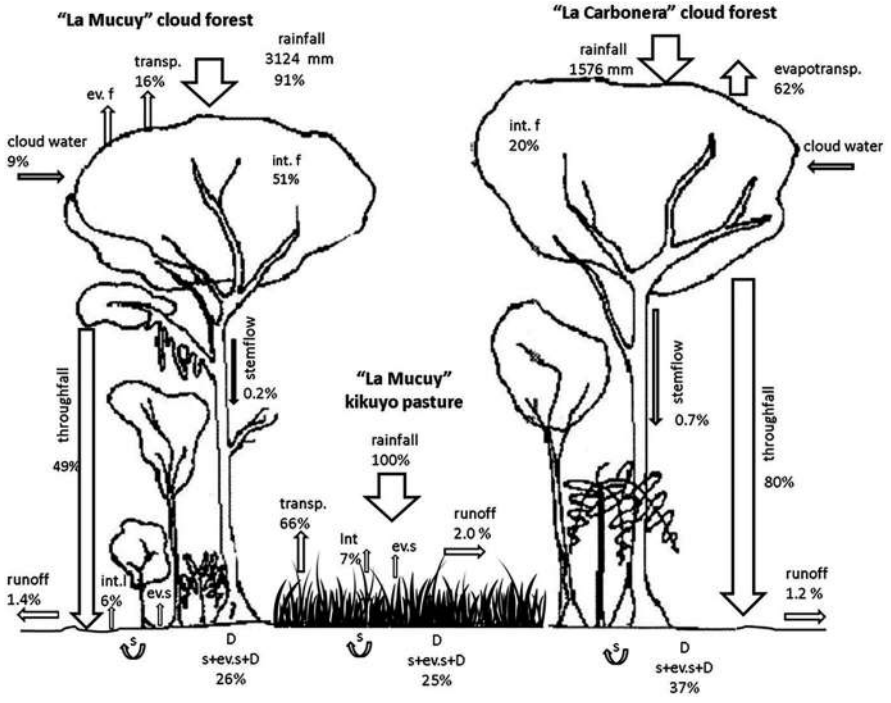

Fig. 3 Water dynamics for undisturbed upper montane cloud forests (La Mucuy and La Carbonera), and a kikuyu pasture at the Cordillera de Merida, Venezuela. Abbreviations: transp. = transpiration rate; ev.f = foliage evaporation; int.f = foliar interception; int.l = litter interception; ev.s = soil evaporation; s = soil storage; D = drainage by throughflow

5 The Effects of Light and Soil-Water Gradients on Forest Structure

5.1 Structure of Juvenile Tree Communities in Relation to the Understory Light Environment

The light-limited environment of the wet tropical forest understory is very heterogeneous at different spatial and temporal scales (Chazdon & Fetcher, 1984; Endler, 1993). In the case of tropical montane cloud forests, the frequent cloudiness together with high topographic variations accentuate this heterogeneity, which imposes energetic limitations and affects other factors such as evapotranspiration, temperature and humidity (Hogan & Machado, 2002; Schwarzkopf et al., 2011).

Understanding the factors that drive regeneration and species composition of these forests, and in particular how light availability affects the patterns of juvenile tree distribution in the understory, is critical for informing conservation and restoration programs. Since light is a limiting factor for plants in these ecosystems, regeneration and subsequent growth is largely limited in the understory, where most juveniles of tree species often must take advantage of small canopy openings (Chazdon et al., 1996). This light gradient partitioning therefore plays a major role in determining the tree community structure (Quevedo et al., 2015). In a study conducted in LC, the average range size of the cumulative distribution of the abundance of juveniles of the most important species was analyzed along the light gradient represented by the percentage of canopy openness (%CO), and the average pairwise overlap of these ranges was estimated (Quevedo et al., 2015). Figure 4 shows the range size distributions and the degree of overlap of 20 juvenile tree species along a gradient of canopy openness (%CO). More than 75% of the plots studied showed a %CO $\leq$ 4.5% and 50% had a %CO $\leq$ 2.2%; maximum %CO was 12.6% (Quevedo et al., 2015). In general, the abundance-based distribution of tree species was non-random in relation to the light environment, but with a high overlap within the interquartile range of %CO. In fact, depending on the tree species, juveniles growing in this usually low light environment show a differential distribution along the light gradient, which allows them to be categorized into functional groups according to their light requirements using evidence from physiological and morphological features measured in a shade house experimental study (Quevedo et al., 2015, 2016, 2018; Quevedo-Rojas & Jerez-Rico, 2020).

Although 15 of the 20 studied species showed a non-random distribution along the canopy openness gradient, suggesting some degree of light partitioning, the test based on the bounded null model indicates that the community fits within the confidence interval for the null model, meaning that species' range overlap did not deviate significantly from a random pattern (Fig. 5). This species distribution pattern indicate that low canopy openness is the rule in these forests, despite the scattered tree-fall gaps, and suggests that light partitioning does not determine the tree community structure at the juvenile stage, but rather there is a strong niche overlap in relation to light availability (Lieberman et al., 1995; Lusk et al., 2006; Quevedo et al., 2015).

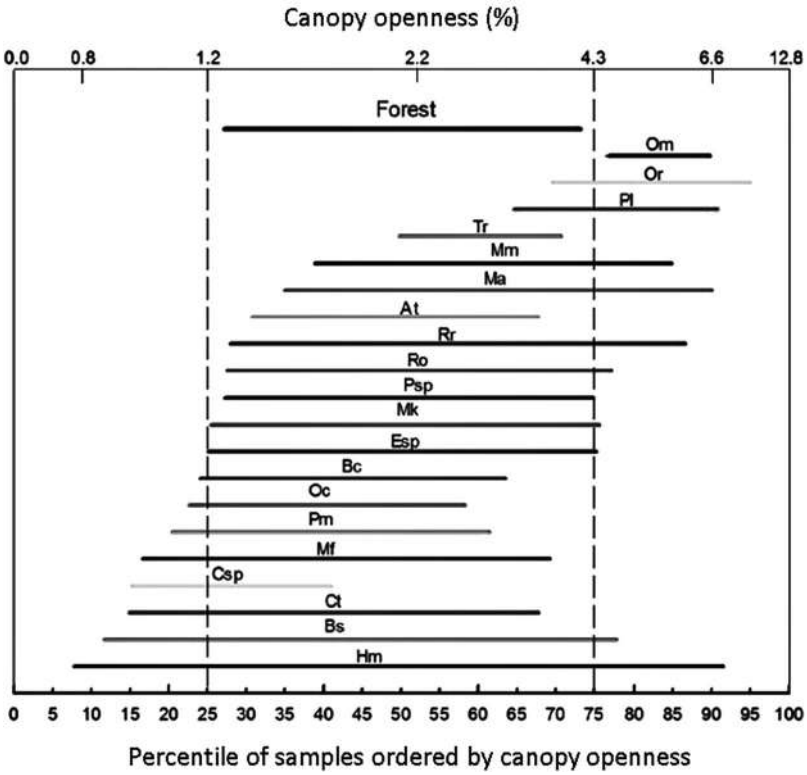

Fig. 4 Interquartile ranges of juvenile tree species' distribution on the rank transformed gradient of percentage of canopy openness (280 plots, 1975 individuals), in high dense forest plots of the San Eusebio University Forest in LC. Letters identifying species abbreviations and their position corresponds to median (midpoint) of the abundance distribution of juvenile trees. Figure from Quevedo et al. (2015) (CC by NC-4.0). Species are: Hm *Hyeronima moritziana* (Euphorbiaceae); Om *Ocotea macropoda* (Laureaceae); Bs *Beilshmiedia sulcata* (Laureaceae); Tr *Tetrorchidium rubrivenium* (Euphorbiaceae); Rr *Retrophyllum rospigliosii* (Podocarpaceae); Ma *Myrcia acuminata* (Myrtaceae); Oc *Oreopanax capitatus* (Araliaceae); Bc *Billia colombiana* (Hippocastanaceae); Csp *Cyathea spp* (Cyatheaceae); Or *Oreopanax reticulatus* (Araliaceae); Pl *Passiflora lindeniana* (Passifloraceae); Mm *Miconia meridensis* (Melastomataceae); Ct *Casearia tachirensis* (Flacourtiaceae); Pm *Prunus moritziana* (Rosaceae); Esp *Eugenia sp*. (Myrtaceae); Mf *Myrcia fallax* (Myrtaceae); Ro *Roupala obovata* (Proteaceae); Mk *Myrcianthes karsteniana* (Myrtaceae); Psp *Psicotria spp*. (Rubiaceae); At *Aegiphila terniflora* (Verbenaceae).

5.2 Characteristics of Forest Structure in Small Fragments and at the Treeline Ecotone

Forest fragmentation in the Andean basins of Venezuela have resulted in a mosaic of small fragments (often <10 ha) with strong edge effects from the surrounding grassland matrix (Dávila, 2009; Rodríguez-Morales et al., 2009). An evaluation of the Capaz River watershed (where LC site is located), showed that since the 1950s the

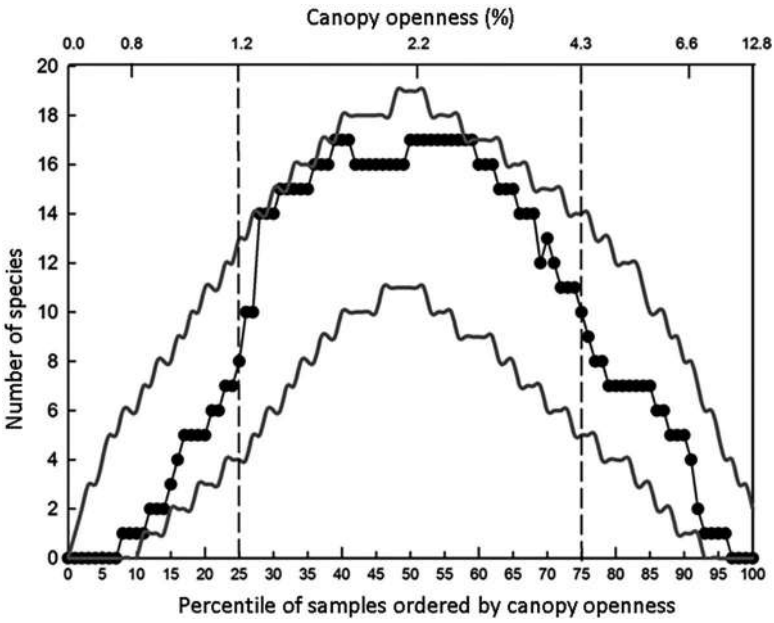

Fig. 5 Empirical distribution of species richness along the canopy openness gradient (dotted line) and 95% confidence limits for the average distribution predicted by the bounded null model (continuous lines) in La Carbonera cloud forests, Venezuelan Andes. Figure from Quevedo et al. (2015) (CC by NC-4.0))

landscape has been fragmented into small forest patches (fragments ranging from 356 ha in 1952 to 80 ha in 1997), with most of these patches surrounded by a matrix of grasslands and crops (Rodríguez-Morales et al., 2009). Edge effects produce distinct changes in biotic and microclimatic conditions between forest borders and the interior, with these changes being more severe as the forest fragments become smaller (Hansen et al., 2020).

The brighter and drier conditions of the forest edges in small fragments are a strong selective pressure for the dominance of gap-specialist tree species (Laurance, 2000). In general, the small forest patches studied in the Capaz River watershed (2228–2336 m asl), although floristically diverse and with a composition relatively similar to the undisturbed forest (Dávila, 2009; Naranjo, 2013), tend to be dominated by species described as early successional colonizers of gaps (e.g., *Myrcia acuminata* DC., *Alchornea triplinervia* (Spreng.) Müll.Arg., *Clusia multiflora* Kunth, *Tetrorchidium rubrivenium* Poepp. & Endl.) (García Núñez et al., 1995; Jaimes, 2015; Quevedo et al., 2018). The small fragments are characterized by a higher tree density (>2.5 cm diameter) and recruitment rates comparable to forests stands in undisturbed areas (Naranjo, 2013). These results suggest that protecting multiple cloud forest patches is essential to conserve landscape-level tree diversity, and even small forest reserves can contribute significantly to biodiversity conservation (Wilson & Rhemtulla, 2018). Ultimately, this means that actions are needed to

enhance connectivity to favor dispersal and establishment, hence increasing the likelihood of forest recovery.

Similar edge effects have been observed in the upper limit of continuous forests in the treeline ecotone (3000–3400 m of elevation). In these areas, small forest fragments/islands occur naturally above the forest line, and they are dominated, specially at their edges, by small pioneer tress (e.g., *Diplostephium venezuelense*, *Vallea stipularis*), which sometimes are also able to colonize the open páramo grasslands of the lower alpine páramo belt (Ramirez et al., 2009; Llambí et al., 2013). In turn, when these treeline forests are cleared for agriculture or cattle grazing, trees face severe limitations for establishment, generating open patches dominated by páramo grassland species (González et al., 2011). Edge effects are also key in these successional areas, with most forest regeneration occurring near the borders of these open grassland patches within the forest matrix (Bueno & Llambí, 2015).

5.3 *The Effects of Soil Water Content on Forest Structure*

Hetsch and Hoheisel (1976) described vegetation communities at LC based on slope and soil characteristics, primarily physical features related to soil water content, proposing the hydro-sequence concept as the main ecological gradient which may explain the differences in forest structure, productivity and reserves of organic and inorganic soil matter. The soil - hydric sequences consisted of seven site-types according to soil water tension measurements along the year at 25 and 80 cm in soil depth (Table 4). These authors indicated that the accumulation of organic matter in

Table 4 Site characteristics of the San Eusebio University Forest in LC from the hydro-sequence proposed by Hetsch and Hoheisel (1976)

Site	Slope (%)	[a]Soil water tension (cm)	[b]Soil types	Limitations	Average Wood volume (m^3/ha)
1–2	>25	101–1000	troperthents, dystropepts, humitropepts	Frequently saturated from 90 cm in depth	490
3–4	10–25	11–100	humitropepts, troperthents, dystropepts	Saturation starting at 60 cm in depth	530
5–6	5–10	≅0	tropaquepts, haplaquepts, dystropets	Saturation starting at 30 cm in depth	170
7	0–5	≅0	tropaquepts, haplaquepts	Frequently saturated from the soil surface	_

[a]Tensions close to 0 cm indicate water saturation; between 100 and 330 cm, field capacity; 1000 cm, drying levels for sensitive species to water deficit
[b]Valcarcel (1982)

above-ground biomass (AGB) and mineral soil reserves (e.g., mineral nitrogen) are strikingly reduced in soils with slight slopes with marked hydromorphism. Sites at LC have been mapped according to topography and water saturation (Valcarcel, 1982), where less sloped sites (0–10%) were classified as: tropaquepts, haplaquepts, dystropets; the more inclined sites (>10%) as: troperthents, dystropepts, humitropepts. The highest basal area (m^2 ha^{-1}) and trunk biomass volume (m^3 ha^{-1}) were found on well drained sites (medium slopes) and the lowest in valley bottoms (Hetsch & Hoheisel, 1976; Quiroz, 2010). In this regard, Quiroz (2010) found a mean tree density (tree species ≥5 cm DBH) between 1050 ind ha^{-1} in valley bottom sites, and 2140 ind ha^{-1} for top of hills; mean basal area ranged between 29.5 and 68.5 m^2 ha^{-1} (medium slopes with 23–47% of inclination, respectively).

In spatially heterogeneous environments, like the mountain forests of the Andes, topography and the competitive environment can influence the severity of water stress experienced by individual trees, leading to individual-level variation in drought impacts (Schwartz et al., 2020).

These studies underline the variability of factors that control stand structure and species composition in montane forests (e.g., hydro-sequence and/or nutrient gradients) and, at the same time, the need to further understand the ecosystem functional and structural responses in the face of a changing climate (Bellingham & Tanner, 2000; Bruijnzeel et al., 2010; Homeier et al., 2010; Werner & Homeier, 2015).

6 The Long-Term Dynamics of Tree Turnover and Productivity in Venezuelan Cloud Forests

Several studies over the last three decades have shown that mature tropical forests have experienced changes in stand structure, species composition, and species interactions with disturbance and the environment. Some of these changes include tree growth exceeding losses from tree death, thus increasing productivity and the overall aboveground biomass both in the Amazon (Phillips et al., 2004) and African forests (Lewis et al., 2009). The interpretations of the potential causes behind these long-term demographic processes have been diverse. Increased resource availability and improved conditions for growth (i.e., increase in CO_2 levels and higher temperatures) have been argued as a possibility for increasing levels of dynamism (Lewis et al., 2009; Phillips & Lewis, 2014). Yet, some forests might be responding to past natural or anthropogenic disturbances (Wright, 2005; Muller-Landau, 2009; McMichael et al., 2017), thus stand development and maturation processes (i.e., competition followed by gap-replacement dynamics) could also be driving these changes. In a study based on data collected from permanent plots across multiple forest-types in Venezuela, including the cloud forests of La Carbonera, Vilanova et al. (2018) demonstrated how elevation and low temperatures are key drivers of a 'slow dynamics' in which the turnover rate (calculated as the mean between recruitment and mortality) of these Andean cloud forests (mean of 1.61 ± 0.09% y^{-1}) is

significantly lower than the case of more dynamic and productive sites of the Western lowland plains (mean of 2.74 ± 0.17% y^{-1}). This difference has important implications on how turnover and stem dynamics can drive biomass accumulation, and how different demographic mechanisms, especially tree mortality may affect forest structure, which in turn may affect forest biomass, with cloud forests attaining higher biomass stocks comparable to those observed in other carbon-rich regions of the tropics such as the Guiana Shield (Baker et al., 2004).

On the temporal trends, Vilanova (2019) reported for multiple intact forest sites in Venezuela that between 1960 and 2012 overall stem recruitment (r) and mortality (m) rates both showed significantly increasing trends, simultaneously showing a positive net change in aboveground biomass of 0.71 ± 0.24 Mg C ha^{-1} y^{-1}, with 80% of the plots analyzed nationally gaining biomass through time (mean relative change in AGB = 0.39% $year^{-1}$), thus acting as a net carbon sink. Along these lines, in a recent analysis comparing the forest dynamics between 2016 and 2022 in permanent monitoring plots in San Eusebio and La Mucuy, both part of the Andean Forest Network, a general increase in tree density, basal area and AGB in all plots was found. However, it is possible that different patterns may emerge as we continue the monitoring of these sites in the future.

7 An Ecophysiological Approach as a Tool for Ecological Restoration of Andean Cloud Forests

For tropical cloud forests in the Venezuelan Andes, ecophysiological studies on photosynthetic response to light environment (i.e., light gradients determined by canopy structure and gap openings) or edge-to-interior conditions in small forest fragments (<1 ha), and studies on the ability to acclimate to sudden changes in light intensity (García Núñez et al., 1995; Vilanova, 1996; Cabrera, 1999; Dulhoste, 2002; Bracho, 2014; Jaimes, 2015; Quevedo et al., 2018), show that species that dominate in gaps and small forest patches have relatively high maximum photosynthetic rates, comparable to sun leaves and pioneer species in lowland tropical moist forests (Strauss-Debenedetti & Bazzaz, 1996). On the contrary, shade-tolerant species have low photosynthetic rates, with lower foliar nitrogen content. Species with an acquisitive strategy have high assimilation rates and fast growth, related to larger and thinner leaves with a high specific leaf area (SLA), as well as low wood density. Conversely, resource investments of conservative species are directed primarily toward building perennial tissues that allow for longevity and resistance to biological and abiotic stress (e.g., low SLA and high wood density) (Wright et al., 2004, 2010; Chave et al., 2009; Reich, 2014; Díaz et al., 2016).

The study of the community structure of juvenile trees conducted in LC helped identify representative species from different shade tolerance groups along wide light gradients in the understory (Quevedo et al., 2015). This approach shed light on the physiological tolerance limits of species, revealing where they lie along

successional gradients determined by the dynamics of natural disturbances (e.g., falling trees creating gaps in the canopy). The functional characteristics of shade tolerance (i.e., plant functional traits) are linked to life history traits related to the regeneration process, including relationships with the germination processes over time and space (e.g., seed size, reserve capacity, dispersal type, light responses, dormancy, etc.), water relations (e.g., hydraulic conductivity, water potentials at turgor loss) and nutritional status (e.g., leaf nitrogen content which correlates with photosynthetic capacity and relative growth rate). In turn, these characteristics are linked with morpho-anatomical features of the species (e.g., shoot/root ratio, leaf area ratio, specific leaf area, stomatal density, wood density, etc.) that can explain biotic interactions (e.g., leaf nitrogen content correlates with specific leaf area and its palatability). In summary, these traits indicate how plants use and acquire resources, signaling a compromise between growth and mortality (Kitajima, 1994; Lohbeck et al., 2013), and involve a spectrum of life history strategies from acquisitive to conservative species (Reich, 2014).

This combined understanding of the community and the ecophysiological processes can inform the development of restoration strategies for degraded or deforested areas by directly answering a key question such as which and where to introduce a particular species during restoration. A pioneering study for the Venezuelan Andean cloud forest that focused on the application of knowledge derived from research at the community and ecophysiological levels is the work of Quevedo-Rojas and Jerez-Rico (2020) who studied the establishment of mixed plantations for ecological restoration purposes in LC. This is a clear example of an assisted restoration approach aiming at facilitating the process of community recovery (Chazdon, 2008; Chazdon et al., 2021; Christmann & Oliveras, 2021; Christmann et al., 2023; Chua & Potts, 2018; Werden et al., 2022). As Quevedo-Rojas and Jerez-Rico (2020) pointed out, mixed plantations could be successful as a restoration option for creating a forest cover under certain conditions, where forests cannot regenerate by natural successional mechanisms as is the case in many degraded pasturelands.

In mixed plantations, two or more species are established in the same stand, which may vary in their functional characteristics (i.e., conservative vs. acquisitive species) according to their growth habits (i.e., shade tolerance, succession stage), tree architecture and potential use. Species arrangements can vary from monospecific patches, rows or intimate assemblages with several species of the same age or at different times to create uneven-aged stands. Silviculture and management of mixed species with native tropical cloud forests species is complex because the lack of knowledge on growing these species (e.g., most tree species seedlings are characterized by slow growth and low tolerance to direct sunlight), plant availability, production in nurseries, plantation establishment, and complex silvicultural management, particularly in species mixtures.

In the study of Quevedo-Rojas and Jerez-Rico (2020) twenty-five native tree species with different shade tolerance conditions were planted. This was done in mixed assemblages (excluded from cattle) on degraded areas originally covered by exotic pastures, including planting some isolated trees (sites at 2250 to 2300 m asl., slope

30–80%, with soils poor in organic matter and nutrients). Species were selected initially based on the findings from Quevedo et al. (2015, 2016) (about the distribution of juveniles along light gradients see Sect. 5.1 and Figs. 4 and 5) and landowner's preferences. The species were categorized in functional groups based on shade tolerance and fitted into three categories: (a) shade intolerant (SI), (b) partially shade tolerant (PT), and (c) shade tolerant (ST) (Table 5). Planting areas were subdivided into plots (~200 m^2 each, ~100 trees per plot). Plots were assigned to levels of light intensity (LI) based on %CO (measured with hemispherical photographs) at planting time. Three levels of LI were differentiated: (a) High light (HL, above 50% CO); (b) Medium light-(ML, 40–50% CO); and (c) Low light intensity (LL <40% CO). Overall, survival was high for all categories of shade tolerance

Table 5 List of species used for restoration in LC cloud forest in the Venezuelan Andes according to their shade tolerance and potential uses

Scientific name	Family	Shade Tolerance[a]	Uses[b]
Tetrorchidium rubrivenium	Euphorbiaceae	SI	WDF, FD, FA
Alchornea grandiflora	Euphorbiaceae	SI	WDF, MTB, FA
Montanoa quadrangularis	Asteraceae	SI	WDF, FD; FA
Ruagea pubescens	Meliaceae	SI	MTB; OR, FA
Cedrela montana	Meliaceae	SI	MTB, OR, FA
Inga oerstediana	Leguminosae	SI	MTB; FA, NF
Ocotea macropoda	Laureaceae	SI	MTB; FA
Miconia meridensis	Melastomataceae	SI	MTB, FA
Cecropia telenitida	Urticaceae	SI	MTB; OR
Hieronyma moritziana	Euphorbiaceae	PT	MTB, FA
Billia columbiana	Hippocastanaceae	PT	MD, MTB, FA
Casearia tachirensis	Flacourtiaceae	PT	HWR, MTB, FA
Beilschmiedia sulcata	Laureaceae	PT	HWR, FA
Nectadra laurel	Laureaceae	PT	MTB, FA
Prunus moritziana	Rosaceae	PT	MTB, OR, FA
Retrophyllum rospigliosii	Podocarpaceae	PT	MTB, OR, FA
Myrcia acuminata	Myrtaceae	PT	TB, FW, FA
Vochysia meridensis	Vochysiaceae	PT	MTB, OR, FA
Eugenia tamaensis	Myrtaceae	ST	MWR; FA
Myrcianthes karsteniana	Myrtaceae	ST	HWR, OR, MD, FA
Miconia resimoides	Melastomataceae	ST	MTB; OR
Podocarpus oleifolius	Podocarpaceae	ST	MTB, OR
Myrcia fallax	Myrtaceae	ST	MTB; MD
Aegiphila terniflora	Verbenaceae	ST	MTB, HWR, FA
Eschweilera tenax	Lecytidaceae	ST	HWR, FA

From: Quevedo-Rojas and Jerez-Rico (2020) (CC By Open Access license)
[a]Species shade tolerance group: *SI* shade intolerant, *PT* partially tolerant, *ST* shade tolerant
[b]Species uses: *FD* fodder, *FA* fauna attraction, *MD* medicinal, *FW* firewood, *NF* nitrogen fixing, *OR* ornamental, *MTB* multipurpose timber, *HWR* hardwood for building roofs, *WDF* wooden fences

within different levels of light intensity, averaging over 70% for all plots after 4.5 years. The high survival rates for most species were attributed to a relatively intense monitoring and maintenance within the first two years after planting, with cattle exclusion, irrigation during the first dry season after planting and the control of aggressive weeds and grasses at least for two years, being highly significant factors for survival. As expected, shade-intolerant species displayed faster height and root-collar diameter growth.

Shade-tolerant species had larger crown ratios due to persistence of lower branches, whereas shade-intolerant showed signs of crown recession at age 7. The positive results of the restoration project carried out in LC by Quevedo-Rojas and Jerez-Rico (2020) have motivated landowners to establish plantations of native species in critical areas with their support. Tree planting with native species is an attractive approach to integrate the ecological knowledge generated as a product of many years of research of the Venezuelan Andean Cloud Forests for testing predictions of performance at the species level. Successful trials based on a scientific foundation with the participation of local communities during their establishment and management provide strong evidence of the feasibility of using such method at small-medium scale to solve tangible and current environmental problems, which is evidence that ecological restoration projects are relevant, useful and desired by local communities (Quevedo-Rojas & Jerez-Rico, 2020).

8 Conclusions

The conservation efforts of Venezuelan ecosystems have largely focused on the creation of a system of extensive protected natural areas (Areas Under Special Administration - ABRAEs), covering approximately 46% of the territory with administrative figures such as national parks (14.8% of the territory), natural monuments, forest reserves, biosphere reserves (although none is located in the Andes), and other categories. About 72% of these areas are covered by forests (Gfw-Ven, 2002; Bevilacqua et al., 2006; Torres-Lezama et al., 2008). Among several challenges in forest conservation is maintaining and, when possible, improving the integrity, connectivity and long-term monitoring of these areas. In the Venezuelan Andes, there are several protected areas (e.g., National Parks: Sierra Nevada, Sierra La Culata, Tapo-Caparo, Paramos Batallon y La Negra, Chorro del Indio) that include a considerable area of the Andean cloud forest ecosystem. On the other hand, unprotected forest areas that are under public or private management could be integrated into special plans based on a multiple use approach (e.g., agriculture-forestry-livestock, eco-tourism, etc.), including ecological restoration projects.

This review shows that, although deforestation rates in the Andean zone seem to have stabilized and have been relatively low in recent years, fragmentation and forest degradation continue to be important threats. Thus, the long-term monitoring of the impacts that these anthropogenic forces have on the structure, dynamics and function is of primary importance. It is also important to highlight that the research

conducted in La Carbonera and La Mucuy over many years, emphasizes that deforestation and the replacement of intact forests by pastures limit the capacity of these landscapes to regulate water flows, fog catchment, soil water storage and deep drainage, putting at risk the water provision for many neighboring communities.

The use of an ecophysiological lens has also allowed us to improve our understanding of the functional characteristics of the most abundant species that compose these complex forests. This research has shown that at least in the seedling–sapling stage, many tree species comprise a broad functional group of shade-tolerant generalists and are characterized by a limited capacity of photosynthetic acclimation to high radiation conditions. This is important knowledge to better understand the dynamics of regeneration in undisturbed forests in favor of practices that can contribute to their recovery and restoration.

Long-term forest studies show that these low-temperature high elevation montane forests are characterized by a slow dynamics with low turnover rates and woody productivity having important implications on the carbon cycle of these forests. The studied plots in LC and LM are characterized by high biomass stocks comparable to those observed in other carbon-rich regions of the tropics. Moreover, recent results of forest dynamics in LC and LM have shown that Andean cloud forests are important hotspots for climate change mitigation acting as net carbon sinks. Nevertheless, projections of forest dynamics under warmer and drier climate scenarios forecast an increase in tree mortality rates and a potential shift in species range from lowland areas towards the Andes that could displace cloud forest species from their current altitudinal belt (i.e., "thermophilization") (Foster, 2001; Willis & MacDonald, 2011; Oliveira et al., 2014; Fadrique et al., 2018). This, in turn, could affect the current carbon sink provided by these forests. Therefore, to understand the dynamics of these ecosystems in climate change scenarios and derive adaptation strategies, it is necessary to continue monitoring the dynamics and ecology of these forests, including the collection of functional trait data that can serve to identify their potential for climate change mitigation. Finally, the positive results of the restoration project carried out in LC serves as a solid starting point that has motivated local landowners to establish plantations of native species in critical areas with their support. This bottom-up approach (from local ecological restoration to landscape restoration) constitutes a strong support to the incorporation of alternative restoration approaches such as assisted regeneration and passive restoration, which must be considered in forest landscape restoration plans.

As shown in this chapter, Andean cloud forests are ecosystems with a complex ecology and the evidence collected from two representative long-term research and monitoring sites, although limited in geographical scale, can help understanding how tropical cloud forests may respond to climate change and how management activities can contribute to increase their resilience and adaptive capacity. This review was an attempt to consolidate a body of knowledge while highlighting the potential gaps and needs for future research.

Acknowledgments The different research projects analyzed in this review have been supported by the Institute of Environmental and Ecological Sciences (ICAE), Faculty of Sciences, and the

Faculty of Forestry and Environmental Sciences, Universidad de Los Andes, Mérida, Venezuela. CG-N thanks the Institute of International Education's Scholar Rescue Fund (IIE-SRF) and CUGS, Trinity College, for their academic and financial support. FR and LDLL respectively thank UniAndes-Colombia and CONDESAN for their academic and financial support (particularly within the Andean Forests Program and the Adaptation at Altitude project financed by SDC). We thank Jean Pierre Veillon, a true pioneer in the study of Venezuelan forests whose vision and energy led to the establishment and monitoring of a set of long-term plots nationwide. EV acknowledge funding from the Amazon Forest Inventory Network (RAINFOR) project for field work and data collection between 2004 and 2022 for San Eusebio plots. The RAINFOR forest monitoring network in Venezuela has been supported by the Natural Environment Research Council (http://www.nerc.ac.uk/) (grants NE/D005590/1andNE/ I028122/1), and the Gordon and Betty Moore Foundation (https://www.moore.org/).

References

Acevedo, M. F., Ataroff, M., Monteleone, S., & Estrada, C. (2001). Aberturas del dosel y espectro de la luz en el sotobosque de una selva nublada andina de Venezuela. *Universidad del Zulia, 9*(2), 165–183.

Acevedo, M. F., Ataroff, M., Monteleone, S., & Estrada, C. (2003). Heterogeneidad estructural y lumínica del sotobosque de una selva nublada andina de Venezuela. *Interciencia, 28*(7), 394–403.

Ataroff, M. (2001). Venezuela. In M. Kappelle & A. D. Brown (Eds.), *Bosques Nublados del Neotrópico. Domingo de Heredia* (pp. 397–442). Editorial IMBIO.

Ataroff, M. (2003). Selvas y bosques de montaña. In M. Aguilera, A. Azócar, & E. González-Jiménez (Eds.), *Biodiversidad en Venezuela* (pp. 762–810). Ediciones CONICIT-Fundación Polar.

Ataroff, M., & García-Núñez, C. (2013). Selvas y bosques nublados de Venezuela. In E. Medina, O. Huber, J. Nassar, & P. Navarro (Eds.), *Recorriendo el Paisaje Vegetal de Venezuela* (pp. 125–155). Ediciones Instituto Venezolano de Investigaciones Científicas (IVIC).

Ataroff, M., & Rada, F. (2000). Deforestation impact on water dynamics in a Venezuelan Andean cloud forest. *Ambio, 29*(7), 438–442. https://doi.org/10.1579/0044-7447-29.7.4400

Ataroff, M., & Sarmiento, L. (2003). Diversidad en los Andes de Venezuela. I. Mapa de unidades ecológicas del Estado Mérida. CD-ROM, ICAE, Mérida, Venezuela.

Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Monteagudo, A., Neill, D. A., Núñez Vargas, P., Pitman, N. C. A., Silva, J. N. M., & Vásquez Martínez, R. (2004). Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society B: Biological Sciences, 359*, 353–365.

Bellingham, P. J., & Tanner, E. V. J. (2000). The influence of topography on tree growth, mortality, and recruitment in a tropical montane forest. *Biotropica, 32*, 378–384. https://doi.org/10.1111/j.1744-7429.2000.tb00484.x

Bevilacqua, M., Cárdenas, L., & Medina, D. (2006). *Las áreas protegidas en Venezuela: diagnóstico de su condición 1993–2004* (p. 163). Fundación Empresas Polar.

Bonnesoeur, V., Locatelli, B., Guariguata, M., Ochoa-Tocachi, B. F., Vanacker, V., Mao, Z., Stokes, A., & Mathez-Stiefel, S. L. (2019). Impacts of forests and forestation on hydrological services in the Andes: A systematic review. *Forest Ecology and Management, 433*(15), 569–584. https://doi.org/10.1016/j.foreco.2018.11.033

Bono, G. (1996). Flora y Vegetación del Estado Táchira, Venezuela. Museo Reg. Scienze Naturali, Torino. Monografie XX. p. 951.

Bracho, J. (2014). *Respuestas ecofisiológicas de tres especies arbóreas a diferentes regímenes de luz en el bosque nublado San Eusebio* [Undergraduate Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p.52.

Breshears, D. D., Adams, H. D., Eamus, D., McDowell, N. G., Law, D. J., Will, R. E., Williams, A. P., & Zou, C. B. (2013). The critical amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional die-off. *Frontiers in Plant Science, 4*(266), 1–4. https://doi.org/10.3389/fpls.2013.00266

Brodribb, T. J., Powers, J., Cochard, H., & Choat, B. (2020). Hanging by a thread? Forests and drought. *Science, 368*, 261–266.

Bruijnzeel, L. A., Scatena, F. N., & Hamilton, L. S. (Eds.). (2010). *Tropical montane cloud forests. Science for conservation and management*. Cambridge University Press.

Bruijnzeel, L. A., Mulligan, M., & Scatena, F. N. (2011). Hydrometeorology of tropical montane cloud forests: Emerging patterns. *Hydrological Processes, 25*(3), 465–498. https://doi.org/10.1002/hyp.7974

Bueno, A., & Llambí, L. D. (2015). Facilitation and edge effects influence vegetation regeneration in old-fields at the tropical Andean forest-line. *Applied Vegetation Science, 18*(4), 613–623.

Cabrera, H. M. (1999). *Mecanismos de aclimatación a la luz en especies de la sucesión de bosques tropicales montanos* [Doctorate Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 171.

Chacón-Moreno, E., Rodríguez-Morales, M., Paredes, D., Suárez del Moral, P., & Albarrán, A. (2021). Impacts of global change on the spatial dynamics of treeline in Venezuelan Andes. *Frontiers in Ecology and Evolution, 9*, 615223. https://doi.org/10.3389/fevo.2021.615223

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters, 12*, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chazdon, R. L. (2008). Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science, 320*, 1458–1460.

Chazdon, R. L., & Fetcher, N. (1984). Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology, 72*, 553–564. https://doi.org/10.2307/2260066

Chazdon, R., Pearcy, R., Lee, D., & Fetcher, N. (1996). Photosynthetic responses of tropical forest plants to contrasting light environments. In S. S. Mulkey, R. L. Chazdon, & A. P. Smith (Eds.), *Tropical forest plant ecophysiology* (pp. 5–55). Chapman & Hall.

Chazdon, R. L., Falk, D. A., Banin, L. F., Wagner, M., Wilson, S., Grabowski, R. C., et al. (2021). The intervention continuum in restoration ecology: Rethinking the active–passive dichotomy. *Restoration Ecology*, e13535. https://doi.org/10.1111/rec.13535

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., Lopez, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature, 558*, 531–539. https://doi.org/10.1038/s41586-018-0240-x

Christmann, T., & Oliveras, M. I. (2021). A synthesis and future research directions for tropical mountain ecosystem restoration. *Scientific Reports, 11*, 23948. https://doi.org/10.1038/s41598-021-03205-y

Christmann, T., Palomeque, X., Armenteras, D., Wilson, S. J., Malhi, Y., & Oliveras, M. I. (2023). Disrupted montane forest recovery hinders biodiversity conservation in the tropical Andes. *Global Ecology and Biogeography, 32*, 793–808. https://doi.org/10.1111/geb.13666

Chua, S. C., & Potts, M. D. (2018). The role of plant functional traits in understanding forest recovery in wet tropical secondary forests. *Science of the Total Environment, 642*, 1252–1262. https://doi.org/10.1016/j.scitotenv.2018.05.397

Dávila, Y. (2009). *Efecto de borde y respuestas funcionales durante el establecimiento de Alchornea triplinervia y Myrcia acuminata en un fragmento de selva nublada andina* [Masters Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 80.

Delaney, M., Brown, S., Lugo, A. E., Torres-Lezama, A., & Bello, N. (1997). The distribution of organic carbon in major components of forests located in five life zones of Venezuela. *Journal of Tropical Ecology, 13*(5), 697–708. https://doi.org/10.1017/S0266467400010877

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., et al. (2016). The global spectrum of plant form and function. *Nature, 529*, 167–171. https://doi.org/10.1038/nature16489

Dulhoste, R. (2002). *Caracterización florístico-estructural y ecofisiologia de las especies dominantes de un bosque secundario en la Selva Nublada* [Masters Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 87.

Endler, J. A. (1993). The color of light in forests and its implications. *Ecological Monographs, 63*, 1–27. https://doi.org/10.2307/2937121

Engwald, S. (1999). *Diversitat und Okologie der vaskularen Epiphyten in einem Berg-und einem Tieflandergenwald in Venezuela* [Doctorate Thesis]. Bonn (Deutschland): Universität Bonn, p. 390.

Estrada, J. (2003). *Análisis multivariante de la variación altitudinal de la composición florística en la Cordillera de Mérida*. Trabajo de Ascenso. Universidad de Los Andes. Facultad de Ciencias, Centro Jardín Botánico. Mérida, Venezuela.

Fadrique, B., Báez, S., Duque, A., Malizia, A., Blundo, C., Carilla, J., Osinaga-Acosta, O., Malizia, L., Silman, M., Farfán-Ríos, W., et al. (2018). Widespread but heterogeneous responses of Andean forests to climate change. *Nature, 564*, 207–212. https://doi.org/10.1038/s41586-018-0715-9

Fahey, T., Sherman, R., & Tanner, E. (2016). Tropical montane cloud forest: Environmental drivers of vegetation structure and ecosystem function. *Journal of Tropical Ecology, 32*(5), 355–367. https://doi.org/10.1017/S0266467415000176

Fassbender, H., & Grimm, U. (1981a). Ciclos biogeoquímicos en un ecosistema forestal de Los Andes Occidentales de Venezuela. II. Producción y descomposición de los residuos vegetales. *Turrialba, 31*, 39–47.

Fassbender, H., & Grimm, U. (1981b). Ciclos biogeoquímicos en un ecosistema forestal de Los Andes Occidentales de Venezuela. IV. Modelos y conclusiones. *Turrialba, 31*, 101–108.

Foster, P. (2001). The potential negative impacts of global climate change on tropical montane cloud forests. *Earth Science Reviews, 55*, 73–106. https://doi.org/10.1016/s0012-8252(01)00056-3

García Núñez, C., Azócar, A., & Rada, F. (1995). Photosynthetic acclimation to light in juveniles of two cloud forest tree species. *Trees, 10*, 114–124. https://doi.org/10.1007/bf00192192

Geist, H., & Lambin, E. (2002). Proximate causes and underlying driving forces of tropical deforestation. *Bioscience, 52*(2), 143–150.

Gentry, A. (1993). *Biodiversity and conservation of neotropical montane forests*. The New York Botanical Garden.

GFW-VEN. (2002). *The state of Venezuela's forest: A case study of the Guayana region* (p. 132). Global Forest Watch, Venezuelan Chapter-WRI-Fundación Polar.

González, W., Llambí, L. D., & Smith, J. K. (2011). Dinámica sucesional del componente arbóreo en la zona de transición entre el bosque y el páramo en los Andes Tropicales. *Ecotropicos, 24*(1), 60–79.

Grantham, H. S., Duncan, A., Evans, T. D., et al. (2020). Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. *Nature Communications, 11*, 5978. https://doi.org/10.1038/s41467-020-19493-3

Grimm, U., & Fassbender, H. (1981a). Ciclos biogeoquímicos en un ecosistema forestal de Los Andes Occidentales de Venezuela. I. Inventario de las reservas orgánicas y minerales (N, P, K, Ca, Mg, Mn, Fe, Al, Na). *Turrialba, 31*, 27–37.

Grimm, U., & Fassbender, H. (1981b). Ciclos biogeoquímicos en un ecosistema forestal de Los Andes Occidentales de Venezuela. III. Ciclo hidrológico y translocación de elementos químicos con el agua. *Turrialba, 31*, 89–99.

Grubb, P. J. (1977). Control of forest growth and distribution on wet tropical mountains: With special reference to mineral nutrition. *Annual Review of Ecology and Systematics, 8*, 83–107. https://doi.org/10.1146/annurev.es.08.110177.000503

Gutiérrez, N., Gärtner, S., Gaviria, J., Meier, W., & Reif, A. (2012). Successional vegetation patterns in abandoned pastures of the lower montane cloud forest zone in the Venezuelan Andes. *Phytocoenologia, 42*(3–4), 101–132.

Hansen, M., Potapov, P., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T., et al. (2013). High-resolution global maps of 21st-century forest cover change. *Science, 2013*(342), 850–853.

Hansen, M. C., Wang, L., Song, X.-P., Tyukavina, A., Turubanova, S., Potapov, P. V., & Stehman, S. V. (2020). The fate of tropical forest fragments. *Science Advances, 6*(11), eaax8574. https://doi.org/10.1126/sciadv.aax857

Herold, M., Román-Cuesta, R. M., Mollicone, D., Hirata, Y., Van Laake, P., Asner, G. P., Souza, C., Skutsch, M., Avitabile, V., MacDicken, K., et al. (2011). Options for monitoring and estimating historical carbon emissions from forest degradation in the context of REDD+. *Carbon Balance and Management, 6*, 13. http://www.cbmjournal.com/content/6/1/13

Hetsch, W., & Hoheisel, H. (1976). Standorts –und Vegetationsgliederung in einem tropischen Nebelwald. *Allgemeine. Forst-und. Jagd-Zeitung, 147*, 200–209.

Hogan, K. P., & Machado, J. L. (2002). La luz solar: consecuencias biológicas y su medición. In G. Kattan & M. R. Guariguata (Eds.), *Ecología y Conservación de Bosques Neotropicales* (pp. 119–143). Libro Universitario Regional, EULAC-GTZ.

Hokche, O., Berry, P., & Huber, O. (2008). *Nuevo Catálogo de la Flora Vascular de Venezuela*. Fundación Instituto Botánico de Venezuela.

Homeier, J., Breckle, S. W., Gunter, S., Rollenbeck, R. T., & Leuschner, C. (2010). Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species rich Ecuadorian montane rain Forest. *Biotropica, 42*(2), 140–148. https://doi.org/10.1111/j.1744-7429.2009.00547.x

Hostettler, T. (2002). Tropical montane cloud forests: A challenge for conservation. *Bois et forêts des tropiques., 274*(4), 19–31.

Huber, O. (1986a). El clima. In O. Huber (Ed.), *La Selva Nublada de Rancho Grande, Parque Nacional Henri Pittier* (pp. 17–30). Fondo Editorial Acta Científica Venezolana.

Huber, O. (1986b). Las selvas nubladas de Rancho Grande: observaciones sobre su fisionomía, estructura y fenología. In O. Huber (Ed.), *La Selva Nublada de Rancho Grande, Parque Nacional Henri Pittier* (pp. 131–170). Caracas.

Huérfano, A., Fedón, I., & Julián, M. (2020). *Libro Rojo de la Flora Venezolana. Segunda edición*. Instituto Experimental Jardín Botánico Dr. Tobías Lasser. Universidad Central de Venezuela. Caracas, Venezuela.

Jaimes, J. C. (2015). *Dinámica de la aclimatación del aparato fotosintético a cambios en el ambiente de luz en individuos juveniles de especies arbóreas de la sucesión temprana en la Selva Nublada Andina* [Undergraduate Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 54.

Josee, C., Francisco, C., Navarro, G., Barrena, V., Cabrera, E., Chacón-Moreno, E., Ferreira, W., Peralvo, M., Saito, M., & Tovar, A. (2009). Ecosistemas de los Andes del Norte y Centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperación, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, RUMBOL SRL. Lima. ISBN: 978-9972-787-77-5.

Kitajima, K. (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia, 98*(3), 419–428.

Kitayam, K., & Aiba, S. I. (2002). Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology, 90*(1), 37–51. https://doi.org/10.1046/j.0022-0477.2001.00634.x

Lamprecht, H. (1954). *Estudios Selviculturales en los Bosques del Valle de La Mucuy, Cerca de Mérida*. Facultad de Ciencias Forestales, Universidad de Los Andes.

Lamprecht, H. (1980). Silvicultura en los Trópicos. Deutsche Gesellschat fur Technische Zusammenarbeit (GTZ) GmbH.

Laurance, W. (2000). Do edge effects occur over large spatial scales? *Trends in Ecology & Evolution, 15*(4), 134–135. https://doi.org/10.1016/s0169-5347(00)01838-3

Leuschner, C., Moser, G., Bertsch, C., Röderstein, M., & Hertel, D. (2007). Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology, 8*(3), 219–230. https://doi.org/10.1016/j.baae.2006.02.004

Lewis, S. L., Lloyd, J., Sitch, S., Mitchard, E. T. A., & Laurance, W. F. (2009). Changing ecology of tropical forests: Evidence and drivers. *Annual Review of Ecology, Evolution, and Systematics, 40*, 529–549.

Lieberman, M., Lieberman, D., Peralta, R., & Hartshorn, G. S. (1995). Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. *Journal of Tropical Ecology, 11*(2), 161–178. https://doi.org/10.1017/s0266467400008609

Linares, A. (2008). *Análisis florístico y estructural de la vegetación de una Selva Nublada Andina en un gradiente altitudinal en La Mucuy, Estado Mérida* [Doctorate Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 139.

Lindorf, H. (2013). Volkmar Vareschi como docente en la Escuela de Biología de la Universidad Central de Venezuela. In E. Medina, O. Huber, & J. M. Nassar (Eds.), *Recorriendo el Paisaje Vegetal de Venezuela* (pp. 21–42). Ediciones IVIC, IVIC.

Llambí, L. D., Puentes, J., & García-Núñez, C. (2013). Spatial relations and population structure of a dominant tree along a treeline ecotone in the tropical Andes: Interactions at gradient and plant neighbourhood scales. *Plant Ecology and Diversity, 6-7*, 343–353.

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J. A., Paz, H., et al. (2013). Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology, 94*, 1211–1216. https://doi.org/10.1890/12-1850.1

Lusk, C. H., Chazdon, R., & Hofmann, G. (2006). A bounded null model explains juvenile tree community structure along light availability gradients in a temperate rain forest. *Oikos, 112*(1), 131–137. https://doi.org/10.1111/j.0030-1299.2006.13922.x

Marquez, O. (1988). Génesis de una sequencia de suelos en el Bosque Experimental de San Eusebio, La Carbonera, Estado Mérida. *Rev Forest Venez., 32*, 133–150.

McMichael, C. N. H., Matthews-Bird, F., Farfan-Rios, W., & Feeley, K. J. (2017). Ancient human disturbances may be skewing our understanding of Amazonian forests. *Proceedings of the National Academy of Sciences, 114*, 522–527.

Medina, E. (1986). Aspectos ecofisiológicos de plantas de bosques nublados tropicales: el bosque nublado de Rancho Grande. In O. Huber (Ed.), *La Selva Nublada de Rancho Grande, Parque Nacional Henri Pittier* (pp. 189–196). Fondo Editorial Acta Científica Venezolana.

Michelangeli, F. (1998). *La Selva Nublada: Rancho Grande*. Armitano Editores.

Montilla, F. (2009). *La hojarasca y su papel en la erosión hídrica en tres ecosistemas y agroecosistemas de Los Andes venezolanos* [Masters Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 129.

Moser, G., Hertel, D., & Leuschner, C. (2007). Altitudinal change in LAI and stand leaf biomass in tropical montane forests: A transect study in Ecuador and a pan-tropical meta-analysis. *Ecosystems, 10*(6), 924–935. https://doi.org/10.1007/s10021-007-9063-6

Muller-Landau, H. C. (2009). Sink in the African jungle. *Nature, 457*, 969.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403*(24), 853–858.

Nagy, L., Eller, C. B., Mercado, L., Cuesta, F., Llambí, L. D., et al. (2023). South American mountain ecosystems and global change – a case study for integrating theory and field observations for land surface modelling and ecosystem management. *Plant Ecology & Diversity, 16*(1–2), 1–27. https://doi.org/10.1080/17550874.2023.2196966

Naranjo, M. E. (2013). *Impacto de la fragmentación de la selva nublada y su reemplazo por pasturas sobre su estructura y ecohidrología en los Andes Venezolanos* [Doctorate Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 276.

Oliveira, R. S., Eller, C. B., Bittencourt, P. R. L., & Mulligan, M. (2014). The hydroclimatic and ecophysiological basis of cloud forest distributions under current and projected climates. *Annals of Botany, 113*(6), 909–920. https://doi.org/10.1093/aob/mcu060

Oliveras, I., Roman-Cuesta, R. M., Urquiaga-Flores, E., Quintano-Loayza, J. A., Kala, J., Huaman, V., Lizarraga, N., Sans, G., Quispe, K., Lopez, E., et al. (2017). Fire effects and ecological recovery pathways of tropical montane cloud forests along a time chronosequence. *Global Change Biology, 24*(2), 758–772. https://doi.org/10.1111/gcb.13951

Pacheco, C., Aguado, I., & Mollicone, D. (2011). Las causas de la deforestación en Venezuela: un estudio retrospectivo. *Biollania, 10*, 281–292.

Phillips, O. L., & Lewis, S. L. (2014). Evaluating the tropical forest carbon sink. *Global Change Biology, 20*, 2039–2041. https://doi.org/10.1111/gcb.12423

Phillips, O. L., Baker, T. R., Arroyo, L., Higuchi, N., Killeen, T. J., Laurance, W. F., Lewis, S. L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D. A., Nüñez Vargas, P., Silva, J. N. M., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J. A., Czimczik, C. I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S. G., Nascimento, H. E. M., Olivier, J., Palacios, W., Patiño, S., Pitman, N. C. A., Quesada, C. A., Saldias, M., Torres Lezama, A., & Vinceti, B. (2004). Pattern and process in Amazon tree turnover, 1976-2001. *Philosophical Transactions of the Royal Society B: Biological Sciences, 359*, 381–407.

Quevedo, A. M., Jerez, M., Schwarzkopf, T., & García-Núñez, C. (2015). Distribution of juveniles of tree species along a canopy closure gradient in a tropical cloud forest of the Venezuelan Andes. *iForest, 9*, 363–369. https://doi.org/10.3832/ifor1568-008

Quevedo, A. M., Schwarzkopf, T., García, C., & Jerez, M. (2016). Ambiente de luz del sotobosque de una selva nublada andina: estructura del dosel y estacionalidad climática. *Revista de Biología Tropical, 64*(4), 1699–1707.

Quevedo, A. M., García-Núñez, C., Jerez, M., Jaimez, R., & Schwarzkopf, T. (2018). Leaf acclimation strategies to contrasting light conditions in saplings of different shade tolerance in a tropical cloud forest. *Functional Plant Biology, 45*(9), 968–982. https://doi.org/10.1071/FP17308

Quevedo-Rojas, A., & Jerez-Rico, M. (2020). Mixed forest plantations with native species for ecological restoration in cloud forests of the Venezuelan Andes. In A. C. Gonçalves (Ed.), *Silviculture*. https://doi.org/10.5772/intechopen.95006

Quiroz, L. (2010). *Definición de comunidades arbóreas asociadas a sitios específicos en una selva nublada de Los Andes venezolanos* [Masters Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 144.

Raich, J. W., Russell, A. E., Kitayama, K., Parton, W. J., & Vitousek, P. M. (2006). Temperature influences carbon accumulation in moist tropical forests. *Ecology, 87*(1), 76–87. https://doi.org/10.1890/05-0023

Ramirez, L., Llambí, L. D., Schwarzkopf, T., Gamez, L. E., & Marquez, N. J. (2009). Vegetation structure along the forest-páramo transition belt in the Sierra Nevada de Mérida: Implications for understanding treeline dynamics. *Ecotropicos, 22*(2), 83–98.

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology, 102*, 275–301. https://doi.org/10.1111/1365-2745.12211

Rodríguez, J. P., & Rojas-Sánchez, F. (1999). *Libro Rojo de la Fauna de Venezuela*. Provita y Fundación Empresas Polar, Caracas, Venezuela.

Rodríguez-Morales, M., Chacón-Moreno, E., & Ataroff, M. (2009). Transformación del paisaje de selvas de montaña en la Cuenca del río Capaz, Andes Venezolanos. *Ecotropicos, 22*, 64–82.

Roman-Cuesta, R. M., Carmona-Moreno, C., Lizcano, G., New, M., Silman, M., Knoke, T., Malhi, Y., Oliveras, I., Asbjornsen, H., & Vuille, M. (2014). Synchronous fire activity in the tropical high Andes: An indication of regional climate forcing. *Global Change Biology, 20*(6), 1929–1942. https://doi.org/10.1111/gcb.12538

Schneider, J., Gaviria, J., & Zizka, G. (2003). Inventario florístico de un bosque altimontano húmedo en el Valle de San Javier. Edo. Mérida, Venezuela. *Plántula, 3*(2), 65–81.

Schwartz, N. B., Feng, X., Muscarella, R., Swenson, N. G., Umaña, M. N., Zimmerman, J. K., & Uriarte, M. (2020). Topography and traits modulate tree performance and drought response in

a tropical forest. *Frontiers in Forests and Global Change, 3*, 596256. https://doi.org/10.3389/ffgc.2020.596256

Schwarzkopf, T., Susan, J. R., Fahey, T. J., & Degloria, S. (2011). Are cloud forest tree structure and environment related in the Venezuelan Andes? *Austral Ecology, 36*(3), 280–289. https://doi.org/10.1111/j.1442-9993.2010.02160.x

Soh, M. C. K., Mitchell, N. J., Ridley, A. R., Butler, C. W., Puan, C. L., & Peh, K. S.-H. (2019). Impacts of habitat degradation on tropical montane biodiversity and ecosystem services: A systematic map for identifying future research priorities. *Frontiers in Forests and Global Change, 2*, 83. https://doi.org/10.3389/ffgc.2019.00083

Stadtmüller, T. (1987). *Los Bosques Nublados en el Trópico Húmedo*. Centro Agronómico Tropical de Investigación y Enseñanza (CATIE).

Steinhardt, U. (1979). Untersuchungen uber den Wasser- und Nahrstoffhaushalt eines Andinen Wolkenwaldes in Venezuela. *Göttinger Bodenkundliche Berichte., 56*, 1–185.

Strauss-Debenedetti, S., & Bazzaz, F. (1996). Photosynthetic characteristics of tropical trees along successional gradients. In S. S. Mulkey, R. L. Chazdon, & A. P. Smith (Eds.), *Tropical forest plant ecophysiology* (pp. 162–186). Chapman & Hall.

Torres-Lezama, A., Ramírez-Angulo, H., Vilanova, E., & Barros, R. (2008). Forest resources in Venezuela: Current status and prospects for sustainable management. *Bois et forêts des tropiques., 295*(1), 21–33.

Valcarcel, R. (1982). *Clasificación y mapeo de sitios en la Estación Experimental de San Eusebio basada en criterios físicos-hidrológicos del suelo* [Masters Thesis]. Mérida (Venezuela): Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes, p. 153.

Vancutsem, C., Achard, F., Pekel, J.-F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Aragão, L. E. O. C., & Nasi, R. (2021). Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Science Advances, 7: eabe 16*, 1–21.

Vareschi, V. (1992). *Ecología de la Vegetación Tropical*. Sociedad Venezolana de Ciencias Naturales.

Veillon, J. P. (1965). Variación altitudinal de la masa forestal de los bosques primarios en la vertiente nor-occidental de la Cordillera de Los Andes, Venezuela. *Turrialba, 15*, 216–224.

Veillon, J. P. (1985). El crecimiento de algunos bosques naturales de Venezuela en relación con los parámetros del medio ambiente. *Rev Forest Venez, 29*, 1–122.

Veillon, J. P. (1989). *Los Bosques Naturales de Venezuela. Parte I: el Medio Ambiente*. Instituto de Silvicultura, Universidad de Los Andes.

Vilanova, I. (1996). *Intercambio de gases y relaciones hídricas en plantas del sotobosque de la selva nublada de La Mucuy, Estado Mérida, Venezuela* [Undergraduate Thesis]. Mérida (Venezuela): Facultad de Ciencias, Universidad de Los Andes, p. 117.

Vilanova, E. (2019). *Patterns and processes in tropical forests: an analysis of forest structure and function from long-term permanent plots in Venezuela, Northern South America*. PhD Dissertation, University of Washington, Seattle, USA.

Vilanova, E., Ramírez-Angulo, H., Torres-Lezama, A., Aymard, G., Gámez, L., Durán, C., Hernández, L., Herrera, R., van der Heijden, G., Phillips, O. L., et al. (2018). Environmental drivers of forest structure and stem turnover across Venezuelan tropical forests. *PLoS One, 13*(6), e0198489. https://doi.org/10.1371/journal.pone.0198489

Werden, L. K., Zarges, S., Holl, K. D., Oliver, C. L., Oviedo-Brenes, F., Rosales, J. A., & Zahawi, R. A. (2022). Assisted restoration interventions drive functional recovery of tropical wet forest tree communities. *Frontiers in Forests and Global Change, 5*, 935011. https://doi.org/10.3389/ffgc.2022.935011

Werner, F. A., & Homeier, J. (2015). Is tropical montane forest heterogeneity promoted by a resource-driven feedback cycle? Evidence from nutrient relations, herbivory and litter decomposition along a topographical gradient. *Functional Ecology, 29*(3), 430–440. https://doi.org/10.1111/1365-2435.12351

Willis, K. J., & MacDonald, G. M. (2011). Long-term ecological records and their relevance to climate change predictions. *Annual Review of Ecology, Evolution, and Systematics, 42*, 267–287. https://doi.org/10.1146/annurev-ecolsys-102209-144704

Wilson, S. J., & Rhemtulla, J. M. (2018). Small montane cloud forest fragments are important for conserving tree diversity in the Ecuadorian Andes. *Biotropica, 50*(4), 586–597. https://doi.org/10.1111/btp.12542

Wright, S. J. (2005). Tropical forests in a changing environment. *Trends in Ecology & Evolution, 20*, 553–560.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., et al. (2004). The worldwide leaf economics spectrum. *Nature, 428*, 821–827. https://doi.org/10.1038/nature02403

Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., et al. (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology, 91*(12), 3664–3674. https://doi.org/10.1890/09-2335.1