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University of Southampton

Faculty of Environmental and Life Sciences

School of Biological Sciences

The Potential Impacts of Climate Change on the Extent, Distribution and Functional Diversity of the Montane-Specialist Tree Community in Mesoamerica

by

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Thesis for the degree of Doctor of Philosophy

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University of Southampton

Abstract

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Tropical montane forests (TMFs) are ecosystems that, despite their small global area, have rich biodiversity, provide essential ecosystem services, and are of cultural significance. Their restricted distribution makes them highly vulnerable to anthropogenic pressures, including climate change. Their high ecological variability in remote areas with complex terrain makes their study challenging and costly, which may impede the design and implementation of conservation measures to preserve their biota and functions. In Chapter 2, I systematically review and critically assess the research on global TMFs under ongoing climate change, revealing some important methodological, geographical, and thematic biases: trees are the most studied group, and the Neotropics is the most studied region. Although these biases should be overcome, they also constitute an opportunity to direct efforts within well-studied areas that could serve as proxies for analogous tropical montane regions while local research is underway. One such area of opportunity is the montane-specialist tree community in Mesoamerica. The Neotropics are a hotspot of montane biota and of rare and range-restricted species, yet there is a dearth of information on the impacts on the montane-specialist tree subcommunity of its forests. Given the disproportionate role that rare and range-restricted species play in terms of richness, functional diversity, and support of vulnerable ecosystem functions, it is critical to forecast their potential responses to climate change. In Chapter 3, I use species distribution modelling to project the range and distribution of 272 Mesoamerican montane-specialist tree species under current and future climatic conditions by the end of the century, showing that this subcommunity will undergo significant losses of suitable habitat, but with some relicts remaining even under a severe climate change scenario. In Chapter 4, I incorporate the modelling results into a functional trait analysis to identify spatial patterns of functional diversity throughout the Mesoamerican region, their potential carbon stock capacity in aboveground biomass, and how these are predicted to shift in response to climate change. I found that despite the projected losses in suitable habitat, the functional diversity and aboveground biomass spatial patterns will persist, although they will be less conspicuous. These findings highlight the contribution of the montane-specialist trees' role in providing functional redundancy and stability to their communities and call for urgent action to complement existing conservation measures with active efforts such as seed banks and assisted migration programmes for montane-specialist trees globally. Overall, this thesis establishes a framework for future research and policy to protect montane-specialist trees in Mesoamerica, highlighting the need for integrated evidence, cross-disciplinary methods, and international collaboration to address climate change challenges.

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Research Thesis: Declaration of Authorship

Erik Omar Mata Guel

The Potential Impacts of Climate Change on the Extent, Distribution and Functional Diversity of the Montane-Specialist Tree Community in Mesoamerica.

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Part of this work have been published as:

Mata-Guel, E.O., Soh, M.C., Butler, C.W., Morris, R.J., Razgour, O. and Peh, K.S.H., 2023. Impacts of anthropogenic climate change on tropical montane forests: an appraisal of the evidence. *Biological Reviews*, 98(4), pp.1200-1224.

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Author contributions

The first data chapter (Chapter 2) was prepared as a manuscript and has been published under the title:

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Chapter 1: I compiled, synthesised and structured the information to write this chapter with guidance and feedback from my supervisors Dr Kelvin Peh, Dr Orly Razgour and Dr Rebecca J Morris.

Chapter 2: I conceptualised this chapter and study design with guidance of my supervisors Dr Kelvin Peh, Dr Orly Razgour and Dr Rebecca j. Morris. A pilot literature search was done by Connor W. Butler, and subsequently, I carried out the bulk of the literature review, its processing and data analysis. All listed co-authors contributed with the revisions that led to the publication.

Chapter 3: this chapter was conceptualised jointly by me and my supervisors Dr Kelvin Peh and Dr Orly Razgour. I carried out the data collection, data processing and data analysis, with major guidance from Dr Orly Razgour, who helped me with the development of the modelling protocol. I received help from Dr Roberto Novella with the automation process for large data analysis and from PhD candidate Penelope Fialas with beta-diversity calculations. The final version was revised by my three supervisors Dr Kelvin Peh, Dr Orly Razgour and Dr Rebecca j. Morris.

Chapter 4: I conceptualised this chapter jointly with my supervisor Dr Kelvin Peh, and received major support and feedback from him and my supervisors Dr Orly Razgour and Dr Rebecca J Morris. I carried out all the data collection, processing, analysis and writing up. I also received help from PhD candidate Penelope Fialas with the calculation of functional diversity indices and community-weighted means.

Chapter 5: I carried out the synthesis of the findings of the other chapters to elaborate upon their significance in the wider ecological context to write up this chapter, with feedback from my supervisors Dr Kelvin Peh, Dr Orly Razgour and Dr Rebecca J Morris.

I carried out the final revision and corrections, as instructed by my examiners Dr Patrick Doncaster and Dr Aida Cuni-Sánchez.

During the execution of this PhD, I contributed with revisions to another project independent from this thesis, which led to the following publication:

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Definitions and Abbreviations

AGB: Aboveground biomass

ANN: Artificial neural networks

BIEN: Botanical Information and Ecological Network; <https://bien.nceas.ucsb.edu/bien/>

CWM: Community-weighted mean

DBH: Diameter at breast height

FD: Functional diversity

FDis: Functional dispersion

GAM: Generalised additive models

GBIF: Global Biodiversity Information Facility; <https://www.gbif.org/>

GBM: Generalised boosted models

IUCN: International Union for Conservation of Nature; <https://iucn.org/>

LMA: Leaf mass per area

MaxEnt: Maximum entropy

PC: Principal component

PCA: Principal component analysis

SDM: Species Distribution Models

TMCF: Tropical montane cloud forest

TMF: Tropical montane forest

TRY: Plant Trait Database; <https://www.try-db.org/TryWeb/Home.php>

WD: Wood density

Chapter 1. General Introduction

1.1 Overview of Tropical Montane Forests

1.1.1 Definition and Global Extent

Tropical montane forests (TMF) are an ecosystem type that occurs within the tropical (0° to 23.4° N and S) and subtropical (23.4° to 30° N and S) latitudinal boundaries (Corlett, 2013). They are often constrained to narrow altitudinal belts enveloped by trade-wind orographic clouds that result in a typically uneven canopy persistently exposed to mist or fog, and with an extraordinary abundance and diversity of epiphytes (Comarazamy and González, 2011; Foster, 2001; Hamilton, 1995; Loope and Giambelluca, 1998; Richter, 2008; Still et al., 1999). It is due to these defining features that TMF is commonly used as a synonym of cloud forests, mist forests, mossy forests, among many more alternative names, especially in Latin America (Brown and Kappelle, 2001), where most studies have been conducted (Laurance et al., 2011; Soh et al., 2019).

It should thus be noted that the nomenclature of TMFs is ambiguous (Bruijnzeel, 2001; Shi and Zhu, 2009). A clear distinction of tropical montane cloud forests (TMCf) as a subcategory of TMFs has been proposed (Bruijnzeel et al., 2011a) and a classification of TMFs based on elevation, fog incidence and canopy structure has existed for over two decades (Bruijnzeel and Hamilton, 2000). However, Bruijnzeel et al. (2011b) posit that TMCfs constitute a small fraction (6.6%) of the total TMF global area, without clarifying what vegetation type or types constitute the remaining area. More recent reviews on the environmental determinants of these forests' traits and distribution use TMF, TMCf, montane forest and cloud forest interchangeably (e.g. Dalling et al., 2016; Fahey et al., 2016; Oliveira et al., 2014). For the sake of consistency, henceforth TMF will be the preferred term in this document, encompassing all the alternative names and subtypes encountered in previous publications.

In addition to the ambiguity in the definition of TMFs, efforts to accurately quantify their extent and map their distribution have resulted in wildly varying estimates. A quantitative “hydro-climatic” definition of TMFs or “cloud-affected forests,” estimated 2.21 M km² of TMF globally (Mulligan, 2010), and a pantropical land cover classification based on topographic and satellite vegetation data estimated 2.12 M km² of TMF (Los et al., 2021). These studies are

an order of magnitude greater than the previously estimated 380,000 km² of ‘potential area’ and 215,000 km² of ‘actual’ TMF area worldwide that were based on an elevation approach rather than a hydro-climatic one (Bruijnzeel et al., 2010; Oliveira et al., 2014). Similarly, a study using a combination of distribution modelling, cloud cover metrics and climatic variables estimated ~624, 200 km² of TMCF in 2001 with an average annual rate of loss of ~2.4%, i.e., ~612,000 km² left by 2018 (Karger et al., 2021). At a more regional scale, Helmer et al. (2019) used cloud immersion and frost frequency metrics to calculate 401,370 km² of TMCF in the Neotropics, which is consistent with global estimates of ~2 M km² (Los et al., 2021; Mulligan, 2010).

The comparatively smaller estimations are often the result of a very restrictive TMF definition, but many tropical mountains in fact support forests that do not fit into the narrow definition of ‘cloud-affected’ systems (Martin and Bellingham, 2016). For example, Mexico, which harbours the most intensively studied TMFs globally (Soh et al., 2019), has historically employed in its national inventories the highly restrictive “mountain mesophyll forest” category (INEGI, 2024; www.inegi.org.mx/temas/usosuelo/#mapas). This category covers 1% (~18,500 km²) of the country, and only 0.4% if only primary vegetation is considered (Gual-Díaz and Rendón-Correa, 2014). However, employing a the broader “mountain humid forest” category (Villaseñor, 2010), the estimate increases to ~139,400 km² (7% of Mexico’s territory) (Cruz-Cárdenas et al., 2012), with the aim of informing conservation efforts that would otherwise overlook areas with potential high diversity and endemism.

1.1.2 General characteristics of TMFs and vulnerability

TMFs typically occur at altitudes from 1,000 to 3,500 m asl (Scatena et al., 2010). With topography being a defining feature, the general characteristics of TMFs are as variable as the land on which they grow. The presence and characteristics of arboreal vegetation on tropical mountains responds to the physical terrain (i.e., size of the mountain, distance to the ocean, slope, aspect and ruggedness) and the associated environmental conditions, such as temperature, precipitation, solar irradiance, cloud cover, among others. The gradual change in environmental conditions along mountain slopes influences the type of vegetation that grows at different elevations (Bruijnzeel and Hamilton, 2000; Scatena et al., 2010). The combination of lapse rate (the rate at which atmospheric temperature decreases with an increase in altitude) with humidity (including precipitation and ground-level clouds) generally allows

distinguishing three or four distinct TMFs subtypes, albeit with a high degree of variation between montane regions (Bruijnzeel et al., 2011a; Scatena et al., 2010):

- *Lower montane forest*: from ~1,000 (usually starting where average temperature drops below 18 °C) to ~1,500 m asl; multilayered canopy of 15–30 m with emergent individuals up to 37 m.
- *Upper montane forest*: from ~1,500–2,000 to ~2,800–3,000 m asl with mean temperatures ~14–17 °C; multilayered canopy of 1.5–18 m with rare emergent individuals up to 26 m.
- *Sub-alpine forest*: from ~2,800–3,000 (usually where mean temperature drops below 10 °C) to ~3,200 m asl, usually limited by the frostline; single or two-layered canopy of 1.5–9 m and very rare emergent individuals of up to 15 m.
- *Elfin forest*: on some montane regions, the high exposure to wind-driven fog and rain promotes the formation of a dense mass of gnarled, tangled stems, generally associated with upper altitudes, but without clear boundaries. The constant presence of ground-level clouds allows the establishment of mosses and vascular epiphytes, giving these assemblages an eerie appearance, for which they are commonly referred to as “elfin,” “fairy” or “mossy” forests.

One of the most common environmental characteristics of TMFs is the presence of frequent and persistent cloud immersion, which represents a constant input of water in addition to precipitation (Bruijnzeel et al., 2011a; Mulligan, 2010), often referred to as ‘horizontal precipitation.’ This continuous source of water combined with the multi-storeyed and complex structure of TMFs’ canopies translates into high microclimatic variability, and thus high levels of diversity and endemism (Oliveira et al., 2014), especially of bryophytes and vascular epiphytes, birds, amphibians and invertebrates (Berrios et al., 2022; Gotsch et al., 2015; Jankowski and Rabenold, 2007; Tobar-Suárez et al., 2022).

Montane forests had historically been shielded from direct human impact because they often occur in remote, difficult-to-access areas. Unfortunately, the same environmental conditions that shape these extraordinary biological communities in TMFs make them highly vulnerable to indirect anthropogenic pressure in the form of climate change. Their distribution on mountain slopes, naturally separated by lowland areas, results in small, discontinuous (or ‘archipelagic’) communities that are often isolated from each other. Aside from a constant

influx of water, ground-level clouds have the effect of shielding the canopy from strong solar irradiance and maintaining vapour pressure deficit low, which has resulted in the selection over evolutionary time of species that have poor water use efficiency and low resistance to water stress (Esperón-Rodríguez and Barradas, 2014, 2015a). Thus, changing climatic patterns accelerated by human emissions of greenhouse gases can severely jeopardise the environmental conditions that support montane communities. As a result, climate change, in combination with accelerating rates of human encroachment (Bruijnzeel and Hamilton, 2000), has made these ecosystems some of the most endangered on Earth (Soh et al., 2019), but also of major interest for thorough research aimed at informing urgent conservation and restoration efforts (Christmann and Menor, 2021; Peh et al., 2011).

1.2 Introduction to climate change

1.2.1 Definition and magnitude

The United Nations Framework Convention on Climate Change (UNFCCC) in its Article 1 (Sands, 1992), defines *anthropogenic* climate change as “a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods.” The main driver of anthropogenic climate change is human activities that emit large amounts of greenhouse gases to the atmosphere, increasing mean global surface temperature by as much as 1.1 °C from 2011 to 2020 above the 1850-1900 average (Lee et al., 2024). According to the most recent update from the Intergovernmental Panel on Climate Change, the observed human-induced warming during the last decade (2014-2023) was 1.19 [1.0 to 1.4] °C (Forster et al., 2024). In 2023, human-induced warming reached a record of 1.43 [1.32 to 1.53] °C, with an increase rate of 0.26 [0.2–0.4] °C per decade over 2014–2023 (Forster et al., 2024).

1.2.2 General impacts of climate change on biodiversity

Human-induced increases in global temperatures provoke rapid changes in the atmosphere, ocean, cryosphere and biosphere (Lee et al., 2024). Besides temperature, measures of climate change on a global scale including changes in precipitation patterns, snow cover, sea and river ice, glaciers, sea level, climate variability and extreme climatic events affect weather and climate extremes (Gitay et al., 2002). These measures in turn lead to widespread feedback

loops, generally with negative impacts to natural systems and human populations (Lee et al., 2024).

In the case of biodiversity, modelling and empirical evidence indicate that climate change may induce significant widespread changes in global ecosystems in terms of their distribution, composition, physical and trophic structure, successional and community dynamics, functioning and productivity (Campbell et al., 2009). These impacts are evident at all levels of ecological organisation, from genes to populations, to whole biomes (McCarty, 2001; Pauls et al., 2013; Peñuelas et al., 2013), and are often aggravated by other human activities, such as habitat destruction, resource extraction, pollution and introduction of invasive species.

1.2.3 Plants and forests in relation to climate change

Plants are a relatively well-studied taxonomic group in relation to climate change. A review conducted in 2015 found that plants were the focus of ~42% of studies on species' responses to changing climate (Parmesan and Hanley, 2015). Plants respond to climate change through phenological shifts (e.g., germination, leaf emergence and senescence, flowering and fruiting times, and greening-up events), distributional changes (e.g., latitudinal and altitudinal range shifts, range contractions and expansions, local extirpations and colonisation of novel areas), plasticity, adaptation, evolution and biotic interactions (Parmesan and Hanley, 2015).

Forests cover ~42M km² (~30%) of the Earth's land surface, providing invaluable ecological economic, sociocultural, and aesthetic services to human populations, as well as having a key biological role as major hubs of biodiversity (Bonan, 2008; Sanquetta et al., 2011). In the context of climate change, forests are widely regarded as both major players in the efforts to combat its adverse effects by helping with mitigation and adaptation efforts, and as a source of major concern due to their potential negative responses to shifting climatic patterns (Keenan, 2016).

Forests are a major player in the global carbon cycle, representing ~45% of terrestrial carbon, and ~50% of terrestrial net primary production (Bonan, 2008). Through photosynthesis, forests sequester carbon from the atmosphere, and lock it in their living biomass; they can also store carbon in their soils through leaf litter, woody debris, and roots. Some of that carbon is returned to the atmosphere as CO₂ through respiration and degradation of organic matter. Although the estimates of carbon stores in global forests vary between ~650 and

~1,100 metric gigatonnes and their rates of carbon sequestration vary across world regions, forests are widely seen as net carbon sinks and thus play a major role in climate change mitigation (Brack, 2019).

However, climate change threatens forests by increasing the intensity and frequency of natural disturbances, including fires, droughts, storms, snow, and ice, as well as subjecting them to physiological stress and altered biotic interactions that can make them vulnerable to pests and diseases. There are major concerns that physiological stress, heightened mortality, and increased decomposition rates due to climate change – often compounded with other human impacts such as deforestation – global forests can transform into net carbon emitters (Tubiello et al., 2021). It is thus crucial to expand our understanding of the potential impacts of climate change on forests across all world regions and scales to help with the design and implementation of effective policies aimed at preserving forests, their biodiversity, and the invaluable services they provide.

1.3 Tropical Montane Forests in Face of Climate Change

As temperature rises around the globe, rainfall patterns and overall water regimes shift unevenly at both spatial and temporal scales (Murugan et al., 2009). That heterogeneity is influenced by topography. There is abundant evidence that mountainous regions tend to warm up faster than surrounding lowland areas and enhance the effects of increasing temperatures on upper communities in the long term (Aiba and Kitayama, 2002; Karmalkar et al., 2008; Loarie et al., 2009; Torres et al., 2008; Williams et al., 2018). Raising levels of cloud formation and decreased or steady water regimes (i.e. rainfall, humidity and fog incidence) in mountainous regions have indeed been observed in association with higher mean annual temperatures in mountainous regions over the past decades (e.g. Crausbay and Hotchkiss, 2010; Murugan et al., 2009; Sperling et al., 2004).

1.3.1 General impacts on tropical montane flora

For more than two decades, it has been recognised that the particular climatic and topographic features of TMFs (i.e., their steep environmental gradients and their naturally discontinuous distribution on mountainous regions) make them especially susceptible to environmental change (Loope and Giambelluca, 1998). During that same decade, it was

suggested that they could serve as early warning systems, as some of their biotic components were expected to respond quickly to shifting environmental patterns (Hamilton, 1995).

Thus, the assumption that montane communities will migrate following their suitable climatic thresholds is the basis for most predictive ecological distribution models, although it is acknowledged that plants may also be able to acclimate or adapt to new climatic conditions (Heilmeier, 2019). A pioneering ecological niche modelling study (Still et al., 1999) projected that as cloud base levels rise due to global warming, whole ecological communities would be forced to migrate upslope in order to persist.

Since then, it has been observed that most montane communities migrate at a much slower rate than that of ongoing climate change (Bergamin et al., 2024; Feeley et al., 2011; Lutz et al., 2013). Moreover, unlike their temperate counterparts, a recent review found no evidence that tropical communities are successfully migrating latitudinally (Colwell and Feeley, 2024). This increases the risk of running out of available space in the mountaintops (Freeman et al., 2018; Jankowski et al., 2010; but see Elsen and Tingley, 2015).

Even where physical space is not a limiting factor, temperature rises and seasonal shifts in water regime can severely impact upper plant communities (Hiltner et al., 2016; Ortega et al., 2024) by making them more likely to be outcompeted by invasive lowland species (Loope and Giambelluca, 1998; Mamantov et al., 2021; Oliveira et al., 2014). The gradual upward displacement of species may thus lead to ‘thermophilisation’ at mid and high elevations, i.e., a replacement of a community by another one adapted to warmer regimes (Duque et al., 2015), and biotic attrition at lower elevations (Colwell et al., 2008).

Since plants can only migrate at a population level, individuals already established will experience continuous stressful ambient conditions. Trees, despite having access to ground water, are subjected to hydric stress as vapour pressure deficit increases due to a combination of higher air temperature and constant or decreased humidity (Esperón-Rodríguez and Barradas, 2014, 2015b). That stress could have possibly led to the widespread browning trend noticeable since the mid-1990s over large areas (Krishnaswamy et al., 2014).

The situation might be more severe for epiphytic communities that cannot access ground moisture. Despite showing some plasticity, field and laboratory experiments with bryophytes have found increased respiration and mortality rates under warmer, dryer air conditions

(Bader et al., 2013; Metcalfe and Ahlstrand, 2019; Wagner et al., 2014). Similarly, studies on vascular epiphytes have recorded decreases in growth rates, leaf production and reproductive success, as well as increased mortality (Crain and Tremblay, 2017; Nadkarni and Solano, 2002; Song et al., 2012; Zotz et al., 2010).

1.3.2 The significance of rare and montane-specialist species in Mesoamerica

Globally, species richness increases from the poles towards the equator. The proportion of rare species follows the same latitudinal pattern, but with precipitation acting as a major promoter of rarity at regional and local scales (Hordijk et al., 2024). Hence, even in boreal regions, rare species are important contributors to local richness (Heegaard et al., 2013). Although there are several approaches to measure rarity, including low local abundance, restricted distributional range and habitat breadth (Leitão et al., 2016), montane regions are known to have a high proportion of rare species (Mouillot et al., 2013).

The Neotropics host the highest number of plant species on Earth and also have a higher proportion of montane communities than other world regions (Laurance et al., 2011). It has also been noted that Neotropical montane regions concentrate most collections of rare species, including Central America (Zizka et al., 2018). A study in Panama found that the proportion of rare species peaked at the highest elevations (~2,000 m asl), which compounded with decreasing species richness with elevation, meant that the highest number of rare species was concentrated between 750 and 1,000 m asl (Tokarz and Condit, 2021). This pattern was especially noticeable in the western part of the country bordering Costa Rica. Therefore, it is reasonable to expect a similar pattern in the rest of Mesoamerica.

It has been recognised that rare species play a disproportionate role in expanding the functional and environmental niche space of their community (Mi et al., 2021). By presenting some of the most original (i.e., less redundant) combinations of traits, rare species often support the most vulnerable functions of their ecosystems (Mouillot et al., 2013), especially within species that have large-sized individuals (Kearsley et al., 2019). A study along an altitudinal gradient from 0 to 2,000 m asl in Mexico found that the high functional diversity and redundancy of montane communities made them resilient to disturbances, especially at mid elevations (Monge-González et al., 2021). In contrast, a simulation study found that extirpating rare species resulted in a disproportionately larger impact on levels of functional

richness, specialisation and originality than if species disappeared randomly (Leitão et al., 2016).

Three main points can be derived from this knowledge: 1) Mesoamerica is a global hotspot of montane flora, 2) montane regions harbour a high proportion of rare species, and 3) rare species contribute disproportionately to their communities' diversity, functional niche and resilience in face of disturbance. However, despite having some of the most intensely studied tropical montane forests (Soh et al., 2019), to my knowledge, no studies focusing specifically on the montane-specialist tree community of Mesoamerica have been conducted. With the threat of on-going climate change, it is thus crucial to characterise the montane-specialist tree community of Mesoamerica and predict the potential impacts that changing climatic regimes could have on their extent, distribution, community composition and functional diversity.

1.4 Overview of the Thesis

1.4.1 General Aim and Objectives

This project's aim was to produce a comprehensive picture of the state of knowledge of tropical montane forests globally with utility for future action and improved protection of these ecosystems. Subsequently, it focused on the Mesoamerican region as a case study, seeking to create a species-level characterisation of its montane-specialist tree community along latitudinal and altitudinal gradients. This characterisation served as the foundation to project the potential impacts of climate change on their extent, distribution, and community composition by the end of the century. Furthermore, to get a more in-depth understanding of the significance of those impacts, I described the spatial patterns of functional diversity of the Mesoamerican montane-specialist community and test the potential effects of climate change and its significance in terms of carbon storage capacity in aboveground biomass.

1.4.2 Structure of the thesis

The structure of the research chapters with their aims, objectives and main methodological approaches are presented in the Logical Framework (Table 1.1). A brief description of each chapter is presented below.

Chapter 2 consists of systematic review complemented with an evidence-based assessment that sought to compile and rank studies of the effects of climate change on TMFs based on the

quality of their evidence. With this information, I built a consistent and comprehensive narrative of the effects of climate change on global TMFs prioritising the strongest available evidence.

In Chapter 3, I compiled tree species from national inventories of countries in Mesoamerica characterised the montane-specialist community based on those with $\geq 75\%$ (upper 3 quartiles) of their occurrence records inside tropical montane areas. I then used an ensemble Species Distribution Modelling approach to estimate their current extent and distribution and forecast the potential impacts in terms of species richness and community composition of a severe climate change scenario (RCP8.5) by the end of the century.

In Chapter 4, I build upon the distribution models of Chapter 3 to describe the Mesoamerican montane-specialist tree community in terms of its functional diversity throughout space and phylogeny. Then, I predict the potential impacts of climate change on the montane-specialist tree community's functional diversity by the end of the century, and how it might affect its carbon storage capacity in terms of aboveground biomass.

Finally, Chapter 5 integrates the general findings of the whole thesis, discusses its relevance and contribution in the context of wider global science, and outlines the possible direction of further research.

Table 1.1 Logical Framework of the project “The potential impacts of Climate Change on the Extent, Distribution and Functional Diversity of the Montane-Specialist Tree Community in Mesoamerica”.

| Chapters | Aims | Objectives | Main analytical method |
|--|---|--|--|
| Chapter 2. Impacts of anthropogenic climate change on tropical montane forests: an appraisal of the evidence | Identify and critically assess the available knowledge of the impacts of climate change on global TMFs. | <ol style="list-style-type: none"> 1. Identify the general thematic and methodological trends in research on the impacts of climate change on TMFs. 2. Determine the implications of those trends in terms of our understanding and application of the current knowledge. 3. Rank the existing knowledge in terms of the quality of the evidence it provides. 4. Synthesise the general forecasts for TMFs globally based on the most reliable evidence. | <p>Systematic search of primary research.</p> <p>Ranking of evidence quality.</p> |
| Chapter 3. Distributional Responses of the Montane-Specialist Tree Community in Mesoamerica under Climate Change | Determine the current and future extent of the montane-specialist tree community in Mesoamerica under current and future climatic conditions. | <ol style="list-style-type: none"> 1. Characterise the MST community of Mesoamerica beyond political boundaries (including establishing whether its southern limit extends to the Panama-Colombia border, or it is truncated by Lake Cocibolca). 2. Estimate the spatial extent and distribution of Mesoamerican MSTs. 3. Assess the potential impacts of projected climate change on Mesoamerican MSTs in terms of extent, distribution, and species richness by the end of the century. | <p>Species Distribution Modelling under current and future climatic conditions.</p> <p>Post-SDM analysis, including estimations of richness, turnover and relation to latitudinal and elevational gradients.</p> |
| Chapter 4. Functional Traits of the Montane-Specialist Tree Community of Mesoamerica in the Present and under a Changing Climate | Understand the components and spatial patterns of the functional diversity of montane-specialist tree communities throughout Mesoamerica and investigate how it will be impacted by climate change. | <ol style="list-style-type: none"> 1. Assess the functional trait diversity of the montane-specialist tree community in Mesoamerica in terms of PCA axes and spatial patterns. 2. Project how functional trait diversity of those tree communities will change under climate change by the end of the century. 3. Evaluate how functional diversity translates into potential aboveground biomass of the montane-specialist tree community in Mesoamerica and how it might change under climate change by the end of the century. | Functional traits analysis, including community-weighted means, PCA of functional diversity, and functional dispersion. |
| Chapter 5. Synthesis and Conclusions | | | |

Chapter 2. Impacts of anthropogenic climate change on tropical montane forests: an appraisal of the evidence

2.1 Abstract

In spite of their small global area and restricted distributions, tropical montane forests (TMFs) are biodiversity hotspots and important ecosystem services providers, but are also highly vulnerable to climate change. To protect and preserve these ecosystems better, it is crucial to inform the design and implementation of conservation policies with the best available scientific evidence, and to identify knowledge gaps and future research needs. We conducted a systematic review and an appraisal of evidence quality to assess the impacts of climate change on TMFs. We identified several skews and shortcomings. Experimental study designs with controls and long-term (≥ 10 years) data sets provide the most reliable evidence, but were rare and gave an incomplete understanding of climate change impacts on TMFs. Most studies were based on predictive modelling approaches, short-term (< 10 years) and cross-sectional study designs. Although these methods provide moderate to circumstantial evidence, they can advance our understanding on climate change effects. Current evidence suggests that increasing temperatures and rising cloud levels have caused distributional shifts (mainly upslope) of montane biota, leading to alterations in biodiversity and ecological functions. Neotropical TMFs were the best studied, thus the knowledge derived there can serve as a proxy for climate change responses in under-studied regions elsewhere. Most studies focused on vascular plants, birds, amphibians and insects, with other taxonomic groups poorly represented. Most ecological studies were conducted at species or community levels, with a marked paucity of genetic studies, limiting understanding of the adaptive capacity of TMF biota. We thus highlight the long-term need to widen the methodological, thematic and geographical scope of studies on TMFs under climate change to address these uncertainties. In the short term, however, in-depth research in well-studied regions and advances in computer modelling approaches offer the most reliable sources of information for expeditious conservation action for these threatened forests.

Key words: biodiversity, cloud forests, conservation, ecological levels, ecosystem functions, evidence quality, global warming, research rigour, systematic review, tropical mountains.

2.2 Introduction

Tropical montane forests (TMFs) are typically an evergreen ecosystem constrained to a narrow altitudinal belt, with an uneven canopy layer frequently enveloped by orographic clouds (Foster, 2001; Hamilton, 1995; Loope and Giambelluca, 1998; Richter, 2008; Still et al., 1999). These forests often harbour high abundance and diversity of epiphytes (Collin, 2001; Foster, 2001; Loope and Giambelluca, 1998). TMFs are thus commonly referred to as cloud forests, mist forests or mossy forests, as well as numerous names in other languages, especially in Latin America (Brown & Kappelle, 2001) where most studies of this ecosystem have been conducted (Laurance et al., 2011; Soh et al., 2019).

Unlike other vegetation types defined by their taxonomic affiliation (e.g. coniferous forest, oak forest, etc.) or their phenological structure (e.g. deciduous forest, xerophilous shrubland, etc.), TMFs are characterised by the intersection of an atmospheric phenomenon (fog incidence) and a topographic feature (mountain slopes). Such restrictive features highlight the potential vulnerability of TMFs in the face of climate change (Hamilton, 1995), but also make impacts difficult to isolate from these ecosystems' intrinsic climatic variability (Vuille et al., 2003). In this study, we focus on *anthropogenic* climate change, as defined by the United Nations Framework Convention on Climate Change (UNFCCC) in its Article 1 (Sands, 1992): a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods.

There is abundant evidence that mountainous regions tend to warm up faster than their surrounding lowland areas and thus amplify the effects of increasing temperatures on upland plant communities in the long term (Aiba & Kitayama, 2002; Karmalkar, Bradley & Diaz, 2008; Loarie *et al.*, 2009; Nyongesa *et al.*, 2019; Ohmura, 2012; Torres, González & Comarazamy, *et al.*, 2008; Williams *et al.*, 2018; but see Pepin *et al.*, 2022). Rising altitude of cloud formation, and decreased water availability have been observed in response to higher mean annual air temperatures in tropical mountainous regions over recent decades (e.g. Crausbay & Hotchkiss, 2010; Murugan *et al.*, 2009; Sperling, Washington & Whittaker, 2004; but see Cuervo-Robayo *et al.*, 2020). Even if average annual changes in precipitation are small, marked seasonal shifts in water regime could severely impact upper montane communities (Hiltner et al., 2016) that already live near their physiological limits (e.g. Catenazzi, Lehr &

Vredenburg, 2014; Crausbay *et al.*, 2014; Muñoz *et al.*, 2016) and with little space to expand their ranges (the “escalator to extinction”; Freeman *et al.*, 2021, p. 1,706). These combined pressures could make them more likely to be outcompeted by climate-driven upwardly migrating species from nearby lowland areas (Loope and Giambelluca, 1998; Oliveira *et al.*, 2014; Sukumar *et al.*, 1995).

Despite recent advances in our understanding of the impacts of ongoing anthropogenic climate change on TMFs, concrete empirical evidence (i.e. compelling proof of climate change-driven impacts occurring in real time) remains scarce, partly because such assessments require long-term data that are difficult to collect and analyse (Wauchope *et al.*, 2021). For instance, it has been observed that plant communities can shift their distributions, but these movements lag behind the velocity of climate change (Corlett and Westcott, 2013; Feeley *et al.*, 2011; Sáenz-Romero *et al.*, 2016). Therefore, key ecosystems like TMFs help advance our knowledge of climate-driven distributional change because the microclimatic variability and island-like distribution of mountainous biomes not only results in high levels of endemism, but also high extinction vulnerability (Freeman *et al.*, 2018), making them natural laboratories for climate change (Silveira *et al.*, 2019; Tito *et al.*, 2020).

Numerous literature reviews on TMF research have been conducted, focusing on various aspects, including environmental determinants (Fahey *et al.*, 2016; Oliveira *et al.*, 2014), ecosystem functions (Dalling *et al.*, 2016), ecosystem services (Buytaert *et al.*, 2011), habitat degradation (Soh *et al.*, 2019), conservation (Peh *et al.*, 2011) and restoration strategies (Christmann and Menor, 2021), specific geographical regions (Rosas Rangel *et al.*, 2019; Sáenz-Romero *et al.*, 2020a; Tovar *et al.*, 2022) or taxonomic groups (Gotsch, Nadkarni & Amici, 2016; He, He & Hyvönen, 2016), and use of remote sensing technologies (Altarex *et al.*, 2022). Our study goes beyond a systematic review on the effects of climate change on TMFs by critically evaluating the quality of the available evidence. We applied a replicable evidence-appraisal methodology to synthesise the current knowledge of the impacts of climate change on TMFs, with a focus on the published studies yielding the strongest evidence. This will serve as a guide to identify knowledge gaps and inform future research on this highly threatened biome.

Specifically, our research questions are: (1) what are the general thematic and methodological trends in the published studies investigating the impacts of climate change on TMFs? (2) What

are the implications of those trends in terms of our understanding and application of the current knowledge? (3) How reliable is the literature in terms of the quality of the evidence it provides? (4) What are the general forecasts for TMFs globally based on the most reliable evidence and the direction of future research?

2.3 Methods

2.3.1 Systematic Review

We carried out a literature search on the effects of climate change on TMFs following a standard systematic review protocol (PRISMA-P; Shamseer *et al.*, 2015). The search terms were based on the most common names of TMFs and terms associated with long-term changes in the climate. The final search terms used were “(trop* monta* forest* OR cloud forest* OR trop* high* elevation* forest* OR trop* mid* elevation* forest* OR trop* mount* forest*) AND (climat* chang* OR glob* warm* OR temperature ris* OR clima* vari*).

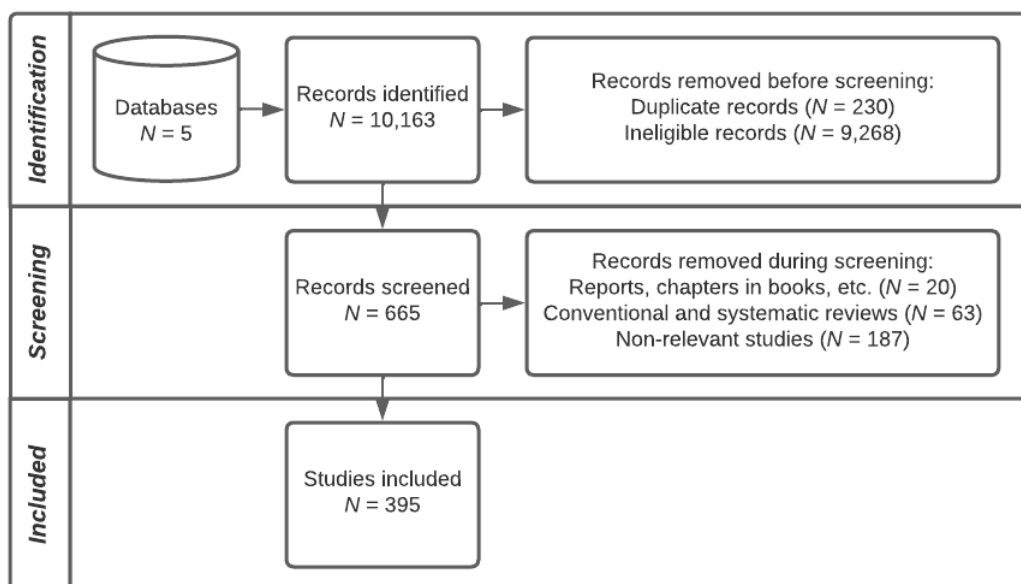


Figure 2.1 Systematic search protocol. The final count includes all relevant studies from 1994 to 2021.

We conducted the literature search in July 2022 using four academic databases (*Web of Science*, *Scopus*, *ScienceDirect* and *Google Scholar*) and the *Google* search engine for the period 1994–2021. Relevant studies published during 2022 were omitted from the statistical analysis but are included in the discussion. The search string was run choosing the ‘all fields’

option if available, hits were sorted alphabetically, and relevant publications – i.e. studies that explicitly reported observed or projected effects of anthropogenic climate change on TMFs (or any component thereof) – were chosen based on title and abstract. Duplicated records were removed, and studies that mentioned climate change only as a potential future threat but did not investigate its effects on TMFs were excluded. Likewise, studies that described diversity patterns along elevational gradients but did not link them to environmental factors to allow inferences of potential future shifts were also discarded (Figure 2.1). For *Google* searches, only the first 100 hits were reviewed to ensure that no relevant studies had been missed. A search in Spanish was conducted in the *Redalyc* database (www.redalyc.org), which did not yield any relevant studies, however, publications in Spanish and French listed under an English title, and thus captured by the search string, were retained. Since we aimed to rank the quality of the available scientific evidence, only peer-reviewed primary research articles were retained (see Section 2.3.2). However, we checked reviews for ‘snowballing’ purposes (i.e. pursuing references of references; see Greenhalgh & Peacock, 2005). We excluded book chapters, reports and other grey literature. Palaeoclimatic and palaeoecological studies were excluded because our focus was on current anthropogenic climate change only.

We extracted from individual studies information on study region, country, methodology, study duration, publication date, ecological level, taxonomic group, research topic, as well as measures of climate change and their observed effects in TMFs. We considered patterns of changing climate (rising temperature and increased or reduced precipitation) as binary variables (i.e. whether these measures were reported or tested in the study or not), and the observed impacts as categorical variables: occurrence of extreme events [strong El Niño Southern Oscillation (ENSO), cyclones, fires, frost, landslides], species’ distributional changes [habitat losses (range contractions or fragmentations), and upslope or downslope shifts], impacts on biodiversity (increased vulnerability, population decline, extinctions, reduced genetic diversity, invasion of neighbouring communities and lowland biotic attrition), and other local-scale effects (alterations to carbon and other nutrient fluxes and stocks, soil functions, and phenological/physiological patterns).

To elucidate general trends in TMF research related to climate change, we investigated if studies were skewed towards a particular geographical region, taxonomic group, ecological level, or research topic; and if there were any associations between these parameters. We also

investigated if studies reporting or testing an impact on TMFs tend to look at a particular measure of climate change or taxonomic group in their research. Only categories represented by at least 10 studies were analysed using chi-squared tests to avoid inferring spurious associations. These associations should be interpreted with caution because they are based solely on what individual studies reported (observations or historic records) or tested (experimentally or through modelling). Statistical tests were carried out in R 4.1.1, using *ggplot2* v.3.3.5 (Wickham, 2011) and *corrplot* v.0.90 (Wei et al., 2017) packages.

2.3.2 Evaluation of evidence quality

The evidence assessment tool devised by Mupepele *et al.* (2016) is designed to rank the quality of evidence provided by individual reviews and studies based primarily on their study designs. Studies that are poorly conducted (e.g. unclear research questions, inadequate sample sizes, lack of controls, etc.) are downgraded in the evidence hierarchy. The discrete categories of evidence quality and assessment criteria of the evidence assessment tool were specifically designed for conservation studies, but can be adapted for other fields of research. Our evidence assessment was an adaptation of Mupepele *et al.* (2016). We removed the ‘review’ (systematic and conventional) category, ranked highest by Mupepele *et al.* (2016), as its inclusion would result in double-counting of studies (i.e. studies captured by our search string are likely to occur in other reviews; Figure 2.2). In addition, we carried out a methodological appraisal of each study. Studies with flaws and biases identified in terms of data collection and analyses or that employed outdated methodologies (mainly applicable to modelling studies) were downgraded to a lower level in the evidence hierarchy. Studies that combined multiple methodological approaches were classified according to their highest level in the evidence hierarchy [e.g. a study with both *ex-situ* experiments and modelling would be ranked as Level of Evidence 1b (LoE1b); Figure 2.2, Table 2.1].

To define the hierarchical LoEs, we considered the following features: use of references and controls, execution of the study in the field (i.e. *in-situ*), long-term collection of data, high regularity of survey, and corroboration of findings derived from models with empirical observations (Table 1). Experimental study designs with a control carried out in the field provide very strong evidence (LoE1a). Experiments conducted *ex situ* yield only strong evidence (LoE1b) because artificial environments introduce potential biases to the study (Tito et al., 2020). Observational studies spanning a minimum of 10 years with observations at

regular intervals (weekly, monthly, etc.) also provide strong evidence by accounting for the long-term nature of climate patterns (Bruijnzeel, 2004; Chapman et al., 2018), and are included in LoE1b. We prioritised the highest-ranked study design in studies that had employed both an *ex-situ* experiment and a modelling approach and therefore assigned these to LoE1b. None of the studies captured by our search string had conducted both field experiments and modelling.

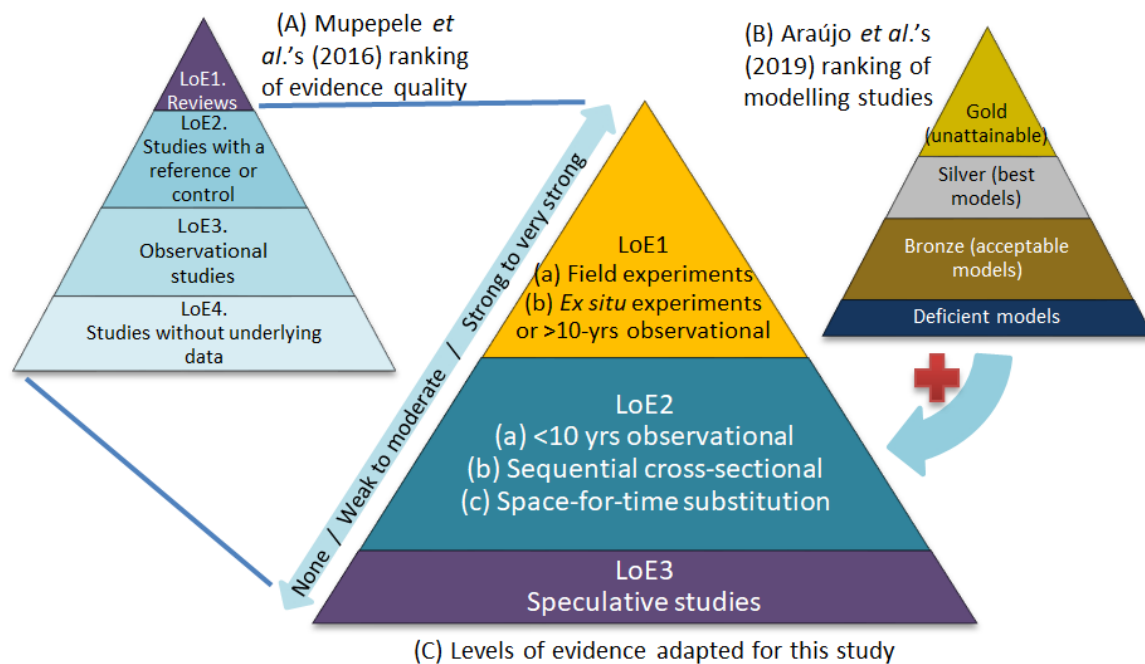


Figure 2.2 Schematic representation of the adapted and combined evidence assessment used in this study.

LoE2 comprises short (<10 years) longitudinal and all cross-sectional observational studies, as well as the bulk of studies that relied on computer-based simulations (hereafter ‘modelling’), i.e. projections of future climate conditions and especially ecological niche models, which include species distributions, life zones and relative abundance projections. Non-modelling studies are subdivided into <10-year long longitudinal studies (LoE2a, moderate evidence), sequential cross-sectional studies, i.e. resurveys (LoE2b, inconclusive evidence), and all other cross-sectional studies (LoE2c, circumstantial evidence), including comparative surveys (between different sites) and along altitudinal or latitudinal gradients (space-for-time substitution approach).

Table 2.1 Classification of studies according to Level of Evidence adapted from Mupepele et al. (2016). Modelling studies included in LoE2a-c correspond roughly to the silver, bronze and deficient levels proposed by Araújo et al. (2019), since their *gold standard* is unattainable for TMFs studies in relation to climate change.

| Level of Evidence (LoE) | Main study design | Explanation |
|--|-------------------|--|
| * Reviews are not included in this classification. | | |
| 1. Very strong to strong evidence of climate change effects. | 1a | Field experiments. Experimental studies that had a controlled design and were carried out in the field provide the strongest and most direct evidence. |
| | 1b | Ex situ experiments OR time-series studies (≥ 10 years of regular –yearly, monthly, etc.– observations). Long-term datasets provide strong evidence. Experiments carried out in artificial conditions may introduce uncertainty. (Studies that employed both an <i>ex situ</i> experiment and a modelling approach belong to this level.) |
| 2. Moderate, inconclusive and circumstantial evidence of climate change effects, including observational and modelling studies. | 2a | Time-series studies (< 10 years of regular –yearly, monthly, etc.– observations) OR modelling studies verified with empirical evidence. Short-term datasets provide evidence of changes taking place over time, but they may not be long enough to confidently attribute observed changes to shifting climatic patterns. Similarly, models that have been corroborated with field observations provide moderate evidence of changes that might occur in the future (comparable to the <i>silver standard</i> in Araújo et al., 2019). |
| | 2b | Sequential cross-sectional studies OR modelling studies not verified by empirical evidence. Cross-sectional studies that provide two or more snapshots of a system but lack regular/continuous data (resurveys), can inform of changes in a system. However, they do not allow an adequate analysis of the environmental influence on the observed changes. Similarly, models that have not been verified with field observations provide inconclusive evidence of the effects of climate change (comparable to the <i>bronze standard</i> in Araújo et al., 2019). |
| | 2c | Cross-sectional and comparative surveys, space-for-time substitution approaches OR non-forecasting modelling studies. Descriptive studies of conditions at a certain moment provide circumstantial evidence of environmental determinants of observed patterns. These include the use of spatial comparisons as a surrogate for temporal data, i.e., comparative surveys (e.g., temperate vs. tropical sites) or altitudinal/ latitudinal gradients as proxies for changes over time (space-for-time substitution). Modelling studies making inferences about future changes even though they are not designed to make forecasts or predictions are included in this level (comparable to the <i>deficient category</i> in Araújo et al., 2019). |
| 3. Studies without underlying data (no evidence). | 3 | Speculative studies OR data-deficient modelling-based inferences. Experts' educated guesses of expected future changes, usually based on past observed changes in analogous systems, are not considered as evidence. Modelling studies based on the knowledge from other systems are also included in this level. |

Given the requirement for long-term data in climate change research and the urgency to implement well-informed policies to preserve ecosystems from anthropogenic threats,

modelling is widely used to forecast outcomes both in the near and distant future. Our scoring of evidence strength for modelling studies (LoE2a–c and LoE3) was based on the model's function and whether their conclusions were validated by field observations, and corresponds loosely to the silver, bronze and deficient standards for models proposed by Araújo *et al.* (2019) (Table 1, Figure 2.2). In principle, modelling approaches using ideal data and next-generation tools that are still under development (the 'aspirational' gold standard) is unattainable for predictive climate change studies and is therefore not considered in our evidence quality scale. The silver standard corresponds to best modelling practices, i.e. a combination of the best-available data and tools to account for or quantify bias and uncertainty (LoE2a). The bronze standard implies limited acceptable practices that allow inferring implications from their results (LoE2b,c). Lastly, the deficient category corresponds to insufficiently robust data or modelling practices (LoE3), and this level also comprises all speculative studies, i.e., not supported by empirical data. These include expert opinions and speculations based on knowledge of other regions or ecosystem types.

2.4 Results

2.4.1 Distribution of studies

Our initial search string retrieved 10,163 studies. After successive elimination stages, the final data set included 395 studies (see Appendix A. Supplementary Information for Chapter 2, Table S1 for full list), published between 1994 and 2021 (Figure 2.1). The number of publications increased from less than ten annually before 2006 to an average of 30 from 2013 onwards, potentially reflecting an increased interest in TMFs.

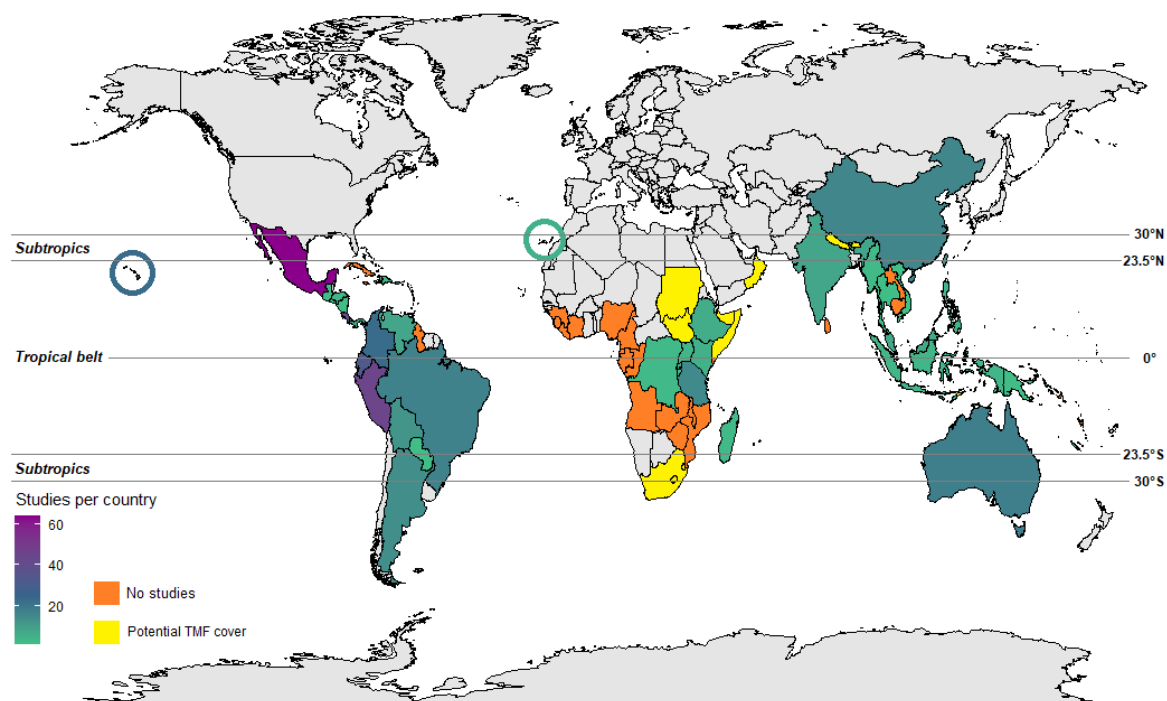


Figure 2.3 Geographical distribution of retrieved studies by country or territory. The number of studies is indicated by the colour scale from light blue to purple. In orange: countries with TMF cover for which no relevant studies were found. In yellow: countries with contested TMF cover (see Karger et al., 2021; Los et al., 2019; Mulligan, 2010).

Inconsistent definitions of TMFs, ambiguous latitudinal limits and different mapping methods have resulted in estimates of their global distribution and extent that vary by as much as an order of magnitude. However, an estimate of $\sim 2\text{M km}^2$ globally (Los et al., 2019; Mulligan, 2010) has been reported relatively consistently, and is compatible with other recent regional estimates (e.g. $\sim 401,300\text{ km}^2$ TMF cover in the Neotropics; Helmer *et al.*, 2019). Around 75 nations are thought to have some TMF cover, however, there is no consensus regarding many countries such as Bhutan, East Timor, Eritrea, Eswatini, Lesotho, Nepal, Oman, Somalia, South

Africa, South Sudan and Sudan (Figure 2.3), and some authors count subnational territories separately, e.g. New Caledonia, Tahiti and La Réunion Island (see Karger *et al.*, 2021; Mulligan, 2010).

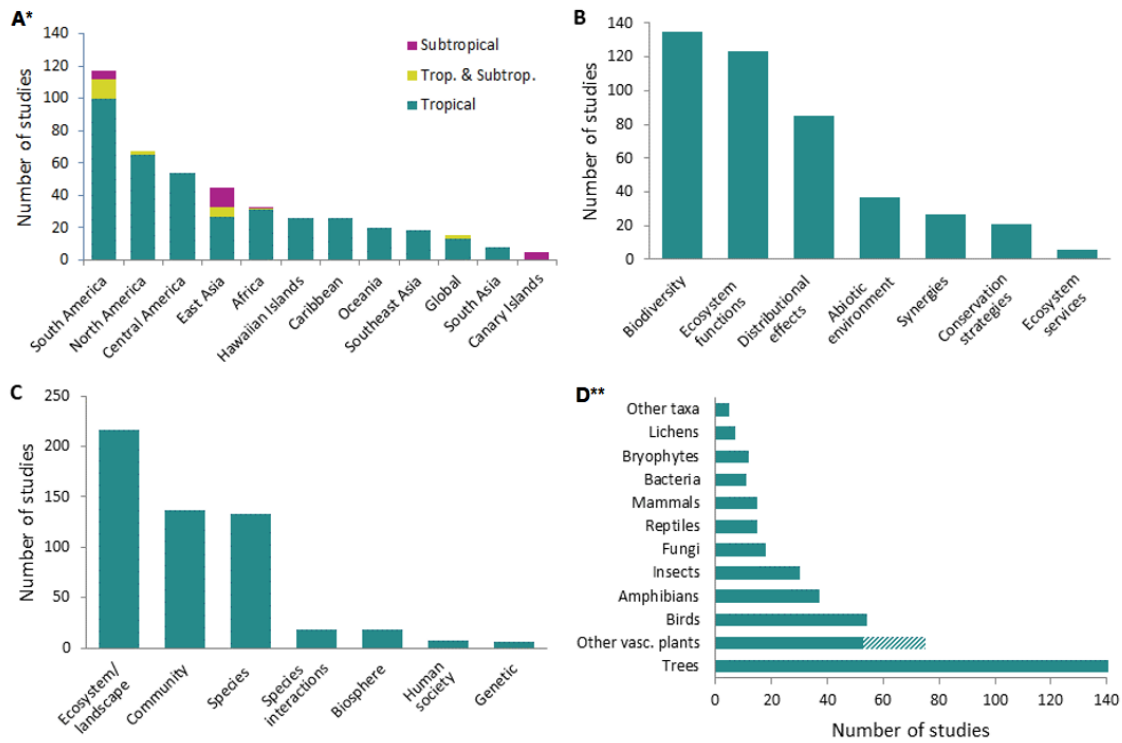


Figure 2.4 Number of studies published from 1994 to 2021 on the effects of climate change on tropical and subtropical montane forests for different (A) geographic regions, (B) effect types, (C) ecological levels, and (D) taxonomic groups.

* Oceania comprises Australia, Papua New Guinea and other islands of the South Pacific; the Hawaiian Islands are shown separately.

** The striped portion of the “other vascular plants” group corresponds to epiphytes.

Of the 395 reviewed studies, 66.8% (264) were carried out in the Neotropics. South America had the highest number of studies (117, 29.6%), followed by North America (Mexico) with 67 (17.0%) and Central America with 54 (13.7%). Only 26 studies (6.6%) focused on the Caribbean (Figure 2.3 and Figure 2.4A). Elsewhere, we found 71 (18.0%) studies in total for Asia; and there were 33 (8.4%) studies in Africa, 20 (5.1%) in Oceania (Australia, Papua New Guinea, and Melanesian islands), and 31 (7.8%) in other oceanic regions (Hawaii and Canary Islands). Relatively few studies examined TMFs in relation to climate change at a global scale (15, 3.8%; Figure 2.4A). The vast majority of studies took place in tropical regions (0° to 23.5° N and S), whereas exclusively subtropical (23.5° to 30° N and S; *sensu* Corlett, 2013) studies

were only those conducted in the Canary Islands (Figure 2.4A). Some studies included tropical–subtropical overlapping regions, mainly in Taiwan, Argentina and Brazil.

We found studies conducted in 32 countries and six subnational territories (Figure 2.3). The most studied TMFs were those in the Neotropics, namely Mexico (64 studies, 16.2%), Peru (45, 11.4%), Costa Rica (42, 10.6%), Ecuador (32, 8.1%), Colombia (23, 5.8%), Brazil (17, 4.3%), Argentina (14, 3.5%) and Bolivia (12, 3.0%). In other regions, only Australia (18, 4.6%), Tanzania (15, 3.8%) and Taiwan (12, 3.0%) stood out. Well-represented subnational territories were the Hawaiian Islands (24, 6.1%) and Puerto Rico (20, 5.1%). We found less than 10 studies each for other countries and territories. Countries with potential areas of TMF (Karger et al., 2021; Mulligan, 2010), for which we did not find any relevant studies include Angola, Cambodia, Cameroon, Comoros, Cuba, Equatorial Guinea, Gabon, Guinea, Guyana, Ivory Coast, Jamaica, Laos, Liberia, Malawi, Mauritius, Mozambique, Myanmar, Nigeria, Republic of the Congo, Sierra Leone, São Tomé and Príncipe, Saint Kitts and Nevis, Saint Vincent and the Grenadines, Solomon Islands, Sri Lanka, Vanuatu, Zambia and Zimbabwe.

Concerning the impacts of climate change on TMF components (Figure 2.4B), most studies examined the effects on biodiversity (135, 34.2%), ecosystem functions (123, 31.1%) and distributional effects (85, 21.5%). Abiotic environment, synergies with other drivers of change and conservation strategies were the focus of 37 (9.4%), 27 (6.8%) and 21 (5.3%) studies, respectively, and despite the recognition of TMFs as important provider of ecosystem services, these were the focus of only six (1.5%) studies. Research effort at different ecological levels was also noticeably imbalanced (Figure 2.4C). Most studies focused on the ecosystem or landscape (216, 54.7%), community (137, 34.7%) and species (132, 33.4%) levels. Considerably fewer studies investigated species interactions and biosphere (18, 4.6% each), human societal (7, 1.8%) and genetic (6, 1.5%) levels.

Taxonomically, vascular plants were the most researched taxonomic group (Figure 2.4D), with trees alone considered in 141 (35.7%) studies, followed by other vascular plants (75, 19.0%), of which 22 (5.6%) studies corresponded to epiphytes. The next best studied taxonomic groups were birds (54, 13.7%), amphibians (37, 9.4%), insects (30, 7.6%), fungi (18, 4.6%), mammals (15, 3.8%), reptiles (15, 3.8%), bryophytes (12, 3.0%) and bacteria (11, 2.8%), while other groups were the focus of less than ten studies each.

2.4.2 Trends in the literature

We found that research from certain regions tended to focus on a particular taxonomic group (chi-squared = 129.77, df = 81, $p < 0.001$). Research efforts in North America (i.e. Mexico) were skewed towards trees; in Oceania (mainly in the Wet Tropics Bioregion, northeastern Australia) were skewed towards insects; and in Central America (mainly in Costa Rica and Panama) towards both bryophytes and fungi. Conversely, studies on trees were scarce in Oceania, with only one study from Papua New Guinea (Venter et al., 2017).

Some research topics were associated with certain geographic regions (chi-squared = 104.25, df = 45, $p < 0.001$). For example, studies in the Caribbean tended to focus on the effects of changing abiotic conditions, such as changes in fog immersion, air temperature and streamflow. We also found an association between research topics and taxonomic groups (chi-squared = 268.83, df = 45, $p < 0.001$). This was mainly driven by studies on ecosystem functions whose focus was on trees and bacteria. Tree studies focused on large-scale processes such as primary productivity, carbon sequestration and distributional shifts, whereas bacteria studies mainly examined soil functions, such as nutrient cycling and decomposition. There was also a dearth of diversity (e.g. abundances and community composition) studies on trees, compared to other taxa, such as birds and insects.

We did not find evidence that studies reporting or testing climate change impacts tend to use a particular measure of climate change or consider a particular taxonomic group in their research (i.e. no association between focus on climate change measures and on taxonomic groups). Studies reporting habitat losses (range contractions or fragmentations) focused more frequently on mammals (chi-squared = 41.07, df = 10, $p < 0.001$), and were also more likely to report biodiversity losses in terms of abundances, species richness or species turnover, and extinctions (chi-squared = 10.32, df = 4, $p = 0.035$).

2.4.3 Assessment of the evidence on the impacts of climate change in TMFs

We found 30 (7.6%) field experimental studies (Figure 2.5A), i.e. providing a 'very strong' LoE (LoE1a). They reflected the general geographical trend described in Section 2.4.1, with five studies from Mexico, although four of these were conducted by one research team (García-Hernández et al., 2019; García-Hernández and Toledo-Aceves, 2020; Toledo-Aceves et al., 2019; Toledo-Aceves and del-Val, 2021a). Four LoE1a studies were from Peru, followed by

three each from China, Costa Rica and Hawaii, two each from Puerto Rico, Taiwan and Tanzania, and one study for Colombia, Ecuador, India, Panama, the Philippines and Rwanda. The scarcity of field experimental studies could be due to the relative inaccessibility of tropical montane regions, often in poorly connected rural areas of low-income countries, which makes field experiments impractical and costly in the absence of well-established research groups. By contrast, strong evidence (LoE1b; *ex-situ* experiments and long-term data sets), was found in 94 studies (23.8%). Around 13% of these studies (12, 3% of total) included the use of modelling methods. Studies that scored as moderate evidence (LoE2a) accounted for 58 studies (14.7%), including mainly <10 year data sets and a small contribution of modelling studies (6, 1% of total) that supported their forecasts with field observations. A third of the reviewed studies provided inconclusive evidence (LoE2b; 132 studies). The reliance of climate change studies on modelling methods was evident: modelling studies accounted for 81.8% (108, 27.3% of total) of studies in this level. The remaining studies in LoE2b were non-longitudinal observational resurveys that provided two or more snapshots suggesting temporal changes but did not allow identification of trends. Studies yielding circumstantial evidence (LoE2c) were common (73, 18.5%), mostly consisting of cross-sectional observational studies, and a small contribution from modelling approaches (11, 2.8% of total). Finally, speculative studies (LoE3a) were the least frequent (8, 2.0%).

Modelling methods were used by 144 (36.5%) studies in total. Climatic envelope models [mainly species distribution models (SDMs), as well as projections of species' population decline, extirpation or extinction under climate change] comprised over two thirds (102, 70.8%) of these; 20 (13.8%) were future climate projections (mainly estimations of future temperature and precipitation regimes), and the remainder (22, 15.3%) were a diverse array of computer-based simulations of changes in biomass, evapotranspiration, albedo, erosion, water runoff, etc. From 1994 to 2005, we found 14 studies that employed modelling methods, with no more than three studies annually, and zero modelling studies for some years, including 2005. Of these, only two were SDMs (Miles et al., 2004; Williams et al., 2003). From 2006 onwards, the use of modelling methods increased to an average of seven studies per year until 2018, and over 10 per year after 2019. Of the 130 modelling studies retrieved after 2006, 96 (73.8%) were SDMs. This trend coincides with the development of the modelling algorithm Maximum Entropy (MaxEnt; Elith *et al.*, 2006), which was employed by 58.5% of

SDM studies, either on its own or in combination with other algorithms [e.g. Random Forests, Genetic Algorithm for Rule-Set Production (GARP), etc.].

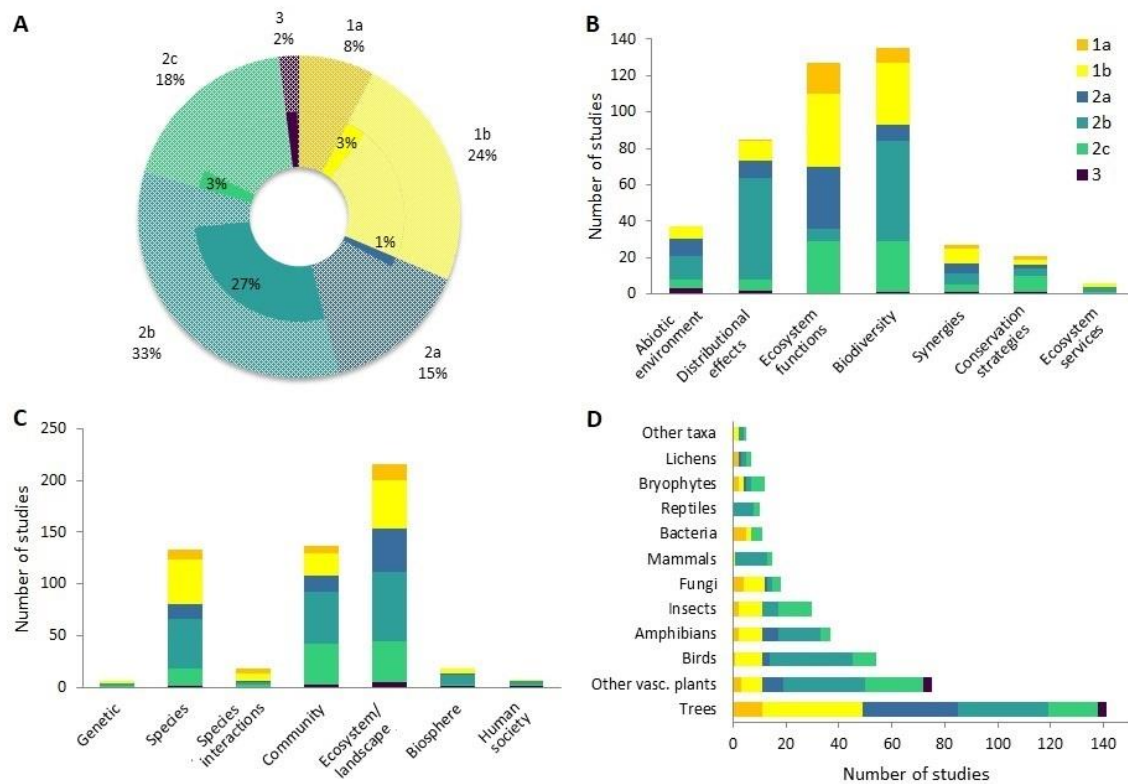


Figure 2.5 Distribution of reviewed studies according to levels of evidence hierarchy. (A) Percentage of studies by level of evidence, with solid-coloured portions indicating the frequency of modelling studies within each level; and levels of evidence of reviewed studies by (B) research topic, (C) ecological level, and (D) taxonomic group.

An association between the LoE strength and research topics (chi-squared = 116.11, $df = 20$, $p < 0.001$; Figure 2.5B) revealed some methodological trends. This association partly was an artefact of the ranking of most modelling studies in LoE2b (i.e. distributional shifts as a main research topic was strongly associated with LoE2b). However, the association persisted after removing distributional studies (chi-squared = 68.45, $df = 16$, $p < 0.001$) because studies on biodiversity also relied more on LoE2b approaches that yield inconclusive evidence (modelling and resurveys). Conversely, studies on ecosystem functions contained the most study designs providing strong evidence (LoE1b, experiments and long-term dendrochronological records).

Considering only the studies at species, community, and ecosystem or landscape levels (i.e. ecological levels with >100 studies each; Figure 2.5C), we found an association of these studies with certain LoE strength (chi-squared = 23.44, df = 10, $p = 0.009$). Whilst provision of inconclusive evidence (LoE2b) was most frequent in studies at these three ecological levels, the species and ecosystem or landscape levels also included a non-negligible proportion of studies yielding strong evidence (LoE1b). For the species level, these corresponded mainly to *ex-situ* experiments (e.g. thermal and drought tolerance experiments). For the ecosystem or landscape level, these were based on long-term data sets.

Regarding taxonomic groups, trees and other vascular plants, birds, amphibians, and insects were the only taxa represented in more than 20 studies each (Figure 2.5D). By retaining only these groups and grouping together the remaining taxa, we found that studies of some taxonomic groups were associated with certain LoE strength (chi-squared = 79.49, df = 20, $p < 0.001$). Studies of trees commonly provided evidence ranging from strong (LoE1b) to inconclusive (LoE2b), whereas studies of birds were associated more often with inconclusive evidence (LoE2b, modelling studies) and those of insects more with circumstantial evidence (LoE2c, comparative cross-sectional surveys). Very strong evidence (LoE1a) was provided most often in studies of other taxa (i.e. fungi, mammals, bacteria, reptiles, bryophytes, lichens, and others), driven by the use of field transplant experiments in studies of fungi, bryophytes, lichens, and bacterial (soil) communities.

2.4.4 Evidence-based synthesis of impacts of climate change on TMFs

Ranking the published studies according to LoE strength allows us to outline better the current state of knowledge on the present or expected future impacts of climate change on TMFs. In this section, we summarise the findings on climate change impacts on the abiotic environment, biodiversity and ecosystem functions of TMFs, focusing primarily on the studies ranked highest in our evidence hierarchy in each case.

a) Changes in atmospheric conditions

None of the published studies on atmospheric conditions employed field experiments (i.e. no LoE1a studies). Albeit scarce (7, 1.8%), evidence based on long-term studies (≥ 10 -year observations; LoE1b) suggested that atmospheric changes in TMFs were a local or regional effect, rather than a global trend. A study analysing 100 years of meteorological data in

Mexico showed that the subtropical (Nearctic) northern mountainous regions have experienced more consistent increments of both atmospheric temperature and precipitation since 1970 than the (Neo)tropical southern mountainous areas (Cuervo-Robayo *et al.*, 2020). Elsewhere, significant reductions in precipitation have been reported over recent decades (e.g. the Indian Western Ghats region; Murugan *et al.*, 2009). However, a decrease in rainfall does not necessarily affect the capacity of TMFs to intercept water from the atmosphere (e.g. La Hispaniola; Comarazamy *et al.*, 2015). TMFs in Puerto Rico had a higher likelihood of fog immersion during the dry periods of the year compared to the rainy season (Van Beusekom, González & Scholl, 2017). In addition, over 40 years of observations in Puerto Rico revealed no significant change of cloud base levels in the mountains (Miller *et al.*, 2018). Therefore, these data suggest that water availability within TMFs may not be adversely affected by reductions in precipitation.

Climatic trends can be confounded by large-scale factors such as topography (Aiba & Kitayama, 2002; Van Beusekom, González & Rivera, 2015; but see Loarie *et al.*, 2009) and global atmospheric patterns, including the ENSO cycle (Crausbay *et al.*, 2014), as well as by regional-scale phenomena like cyclones and fires. There is evidence of a feedback mechanism between defoliation caused by strong hurricanes and rising cloud levels (Scholl *et al.*, 2021), and accelerated thermophilisation (i.e. intrusion of lowland species adapted to warmer climates into cooler communities; Duque, Stevenson & Feeley, 2015; Fadrique *et al.*, 2018) of montane forests in the Caribbean region (Tanner *et al.*, 2022). Increased fire incidence linked to dryer atmospheric conditions could facilitate the expansion of fire-resistant species (Grau and Veblen, 2000), for instance, serotinous pine trees (Climent *et al.*, 2004; Rodríguez-Trejo and Fulé, 2003). In some regions (e.g. Mexico), however, fire incidence has declined over recent decades because of human management, which could negatively affect the regeneration of fire-adapted arboreal species (Cerano-Paredes *et al.*, 2021; Yocom and Fulé, 2012).

b) General decline of TMFs

Most models (LoE2b) predict substantial losses of TMF area and biodiversity in the coming decades. Mexico is projected to suffer important reductions in TMF area, population declines and even extinctions by the end of the century, either due directly to climate change or in combination with other drivers of change, notably land-use change (e.g. Correa Ayram *et al.*,

2017; Golicher *et al.*, 2008; Ponce-Reyes *et al.*, 2017, 2013). Similar outcomes have been forecast for other montane regions, including Costa Rica (Colwell *et al.*, 2008), the tropical Andes (Godoy-Bürki, 2016; Ledo *et al.*, 2009; Tejedor-Garavito *et al.*, 2015), the ‘campos rupestres’ (Bitencourt *et al.*, 2016) and the Atlantic forest biomes in Brazil (Castro *et al.*, 2020), the Neotropical realm as a whole (Helmer *et al.*, 2019), the Western Ghats region in India (Chakraborty *et al.*, 2013), China’s *Abies* forests (Liao *et al.*, 2020), Myanmar’s natural protected areas (Nwe *et al.*, 2020), and the Australian Wet Tropics (Costion *et al.*, 2015).

c) Distributional effects on flora

Atmospheric variables play a key role in shaping the distributions of species and whole communities, thus shifts in species’ ranges are one of the expected consequences of climate change. The presence of clear boundaries between forests and other vegetation types (treelines) is primarily defined by temperature, precipitation and fog incidence, and has been confirmed in various tropical montane regions, including the Cordillera Central in the Dominican Republic (Martin *et al.*, 2007; Martin and Fahey, 2014), the Afromontane forests in Ethiopia (Schmitt *et al.*, 2013), and in Hawaii (Crausbay and Hotchkiss, 2010). Upslope displacements of treelines have been observed over periods of 10 years or more (LoE1b) in Mexico (Jiménez-García *et al.*, 2021), protected areas in the tropical Andes (Lutz *et al.*, 2013), Taiwan (Greenwood *et al.*, 2014), Hawaii (Koide *et al.*, 2017) and Mount Kilimanjaro (Shugart *et al.*, 2001), as well as changes in community composition that reflect upslope migrations of lowland plant species in Costa Rica (Feeley *et al.*, 2013).

Yet, many species’ responses to spatial changes in temperature and precipitation may not be occurring at a sufficiently fast pace to keep up with the rate of climate change (Feeley *et al.*, 2013, 2011; Lutz *et al.*, 2013; but see Lu *et al.*, 2020). An analysis on avian seed dispersal in the Peruvian Andes concluded that several long-distance dispersal events would be necessary for the treeline to keep up with warming rates (Nowak *et al.*, 2022). And even if that dispersal occurs, experimental studies have found that species-specific thermal and drought tolerances might influence seedling recruitment rates at higher altitudes (Esperón-Rodríguez and Barradas, 2014; Fadrique *et al.*, 2018; Rehm and Feeley, 2016), potentially stymieing treeline expansion. However, an analysis of historic data of Taiwanese montane trees showed dissimilar responses at both intra- and interspecific levels; species already adapted to higher

elevations moved upslope at higher rates, but these responses varied among life stages (O'Sullivan *et al.*, 2021).

The main bulk of evidence of distributional changes comes from forecasting modelling studies (LoE2b), which overwhelmingly project range contractions, population declines, local extinctions or a combination of these in TMF tree communities (e.g. John *et al.*, 2020; Neto dos Santos, Silva & Higuchi, 2020; Rojas Briceño *et al.*, 2020) and herbaceous plants (Setyawan *et al.*, 2020). These predicted range contractions are partially explained by the topography of mountains themselves because as species migrate upwards, the available area decreases. However, upward area reduction does not happen monotonically in over half of the world's mountainous regions (Elsen and Tingley, 2015), and the influence of topography is complex, in some cases potentially leading to horizontal rather than vertical displacements (Lippok *et al.*, 2014).

Several studies have looked at the potential limiting factors for treelines to track new climatically suitable areas. These factors include frost (Joshi *et al.*, 2020; Rehm *et al.*, 2021; Rehm and Feeley, 2015), hydraulic stress (Song *et al.*, 2016b), fruit or seed production (Chapman *et al.*, 2018), seed dispersal (Hillyer and Silman, 2010; Nowak *et al.*, 2022; Rehm and Feeley, 2013), germination rates (Center *et al.*, 2016), and even the absence of nurse plants (Soto-Correa *et al.*, 2013). By contrast, a field transplant experiment carried out in the Peruvian Andes concluded that soil was not a limiting factor for the establishment of trees at higher elevations (Tito *et al.*, 2021). It has been suggested that plants that have evolved in nutrient-poor soils might be 'pre-adapted' to cope with other environmental stressors (Whitman *et al.*, 2021). Thus, intra- and interspecific differential migration rates, in combination with other processes such as higher mortality of cold-resistant species and intrusion of lowland species into montane areas (e.g. de Gasper *et al.*, 2021), may lead to the formation of new communities adapted to warmer regimes (Wright *et al.*, 2009), i.e. thermophilisation (Duque *et al.*, 2015; Fadrique *et al.*, 2018).

While experimental studies to test responses of tree species to climate change rarely went beyond seed dispersal and seedling establishment, another defining component of the TMF flora, epiphytes, has been researched more often through experimental manipulations (LoE1a and LoE1b). Field transplant experiments to different elevations to simulate changing climatic regimes on bryophytes (Nadkarni and Solano, 2002; Song *et al.*, 2012; Wagner *et al.*, 2014)

and ferns (Hsu et al., 2014) consistently found slower rates of growth and leaf production, and higher mortality, even if some species or individuals displayed some plasticity. Similar results were obtained from *ex-situ* experiments with both bryophytes and vascular epiphytes (Gotsch et al., 2015; Zotz et al., 2010). Epiphytes' reliance on different water sources seems to be linked to their taxonomic affiliation; Liu *et al.* (2021) found that in a Chinese subtropical montane forest, bryophytes and ferns obtained water both from humus and fog, whereas lichens and seed plants relied almost exclusively on fog. Although significant tolerance to desiccation (Bader et al., 2013) and temperature rise (up to an average of 3 °C) has been observed for some epiphytic species (Müller et al., 2017), their ability to track new climatically suitable areas was not experimentally tested.

d) Effects on fauna

Birds were the best-studied taxonomic group after all vascular plants (Figure 2.4D). There was some empirical evidence (LoE1a and LoE1b) for the effects of climate change on avian species, such as recorded cases of upslope migrations in Honduras (Neate-Clegg et al., 2018), the tropical Andes (Forero-Medina et al., 2011; Freeman et al., 2018; Hayes et al., 2018; Hermes et al., 2018), Tanzania (Neate-Clegg *et al.*, 2021b) and New Guinea (Freeman, 2016). Elevational shifts have also been reported for moth assemblages on Mount Kinabalu, Malaysia (Chen et al., 2009), and bats in Costa Rica (LaVal, 2004). However, these responses might be species specific (Anderson et al., 2013) and not all species can successfully expand their ranges (Campos-Cerqueira and Aide, 2017; Neate-Clegg et al., 2020). Even if elevational shifts do occur, they may result in intense competition for space and resources near mountaintops, triggering aggressive behaviours (Jankowski et al., 2010), or leading to higher morbidity (Freed and Cann, 2013) and mortality rates (Shiao et al., 2020).

Modelling studies (LoE2b) outline similar trends, overwhelmingly predicting range contractions, population declines, local extinctions or a combination of these in TMF birds (Colyn et al., 2020), mammals (Ramírez-Bautista *et al.*, 2020; Raman *et al.*, 2020b,a), amphibians (Cordier et al., 2020; Cruz-Elizalde et al., 2020) and scorpions (de Araujo-Lira et al., 2020). However, the influence of climate change on upslope migrations could be challenging to distinguish from that of land-use change (see Jacob *et al.*, 2015b,a).

The prospect for ectotherms is a matter of much concern. Thermal tolerance experiments (LoE1b) conducted with amphibians (González-del-Pliego *et al.*, 2020; Rueda-Solano *et al.*, 2016; von May *et al.*, 2017), reptiles (Muñoz *et al.*, 2016; Piantoni, Navas & Ibargüengoytía, 2016; Strangas *et al.*, 2019; but see Tao *et al.*, 2021) and insects (e.g. Montejo-Kovacevich *et al.*, 2020; Polato *et al.*, 2018; Shah *et al.*, 2017b) showed that tropical montane species are more susceptible to changes in temperature regimes relative to their lowland or temperate counterparts. However, some level of adaptive capacity was observed in some frog (von May *et al.*, 2017) and ant (Nowrouzi *et al.*, 2018) species, and in some cases, upslope migrations might be favoured by a relief from cold stress at higher elevations (Muñoz *et al.*, 2022). Many tropical montane amphibians have also been severely impacted by the compounding effect of pathogens (e.g. Anchukaitis & Evans, 2010; Catenazzi *et al.*, 2014, 2010; Neely *et al.*, 2020), with long-term studies confirming substantial population declines and even extinctions in recent decades (e.g. Barker & Ríos-Franceschi, 2015; Campos-Cerqueira & Aide, 2017; Pounds, Fogden & Campbell, 1999). Amphibian microhabitats can offer some buffering from impacts of climate change, especially for arboreal species (Scheffers *et al.*, 2013a,b, 2014), yet the overall expected outcome is loss of amphibian diversity at a global scale. Assemblages are projected to become much more homogenous due to selective extinctions of specialists (Menéndez-Guerrero *et al.*, 2020) and the intrusion of invasive lowland generalists (Rödger, 2009).

Empirical evidence showing effects of climate change on other major animal taxa, such as mammals, reptiles and most invertebrates, is too limited to identify any clear patterns. For instance, a resurvey of tropical montane ants in Costa Rica concluded that over a decade, the community became less diverse, with upland areas becoming more similar to lowland ones (Warne *et al.*, 2020) – suggesting that thermophilisation of communities is not limited to flora –, however, this finding was promptly contested (Klimes *et al.*, 2021).

e) Effects on ecosystem functions

Ecosystem functions are commonly studied through experimental manipulation in the field (LoE1a) or laboratory (LoE1b). Multiple soil transplant and litter decomposition experiments have found that increasing temperatures, altered water status or both can change decomposition rates and have a negative influence on the capacity of TMF soils to retain organic matter, potentially turning the systems into carbon emitters (e.g. Becker & Kuzyakov,

2018; Looby & Treseder, 2018; Nottingham *et al.*, 2019b, 2016). Higher temperatures also make nutrients more readily available, with potential cascading effects on vegetation and other soil properties (Dantas de Paula *et al.*, 2021). Some studies, however, have reached opposite conclusions or found no clear relationship between temperature or hydric regime and soil properties (e.g. He *et al.*, 2010; Scowcroft, Turner & Vitousek, 2000). Such equivocal conclusions could be due to the heterogeneity and localised nature of soil properties.

Montane trees are also expected to experience thermal and hydraulic stress under climate change. This may lead to increased respiration and reduced growth rates that translate into diminished carbon sequestration (e.g. Esperón-Rodríguez & Barradas, 2015b; Feeley *et al.*, 2020; Gutiérrez-García & Ricker, 2019). This vulnerability is partly due to the reliance of TMF plant communities on atmospheric water and the shielding effect of fog from direct solar radiation; both climatic factors at present attenuate vapour pressure deficit, to which TMF species are particularly responsive (e.g. Correa-Díaz *et al.*, 2020; Gotsch *et al.*, 2014b,a; Rodríguez-Ramírez *et al.*, 2020). These climatic factors also influence the growth rates of TMF trees ; but see Camarero *et al.*, 2021), seed production (Pau *et al.*, 2020; Rodríguez-Ramírez *et al.*, 2019), establishment (Chirino *et al.*, 2017; Toledo-Aceves *et al.*, 2019), and even plant–herbivore interactions (Bendix *et al.*, 2021; Toledo-Aceves and del-Val, 2021a). The generalised persistent stress caused by climate change could explain high tree mortality events at a global scale (Allen *et al.*, 2010). It could also be linked to a browning trend observed in pantropical forests since the mid-1990s (Krishnaswamy *et al.*, 2014), or the contrasting greening trend during the past 20 years in central Mexico (Correa-Díaz *et al.*, 2021). Such large-scale vegetation changes can further boost rising temperatures by altering the forests' albedo effect (Doughty *et al.*, 2018) and render plant communities more susceptible to droughts.

2.5 Discussion

This review of the literature on impacts of climate change on TMFs shows that: (1) the rates of climate change are generally intensified rather than attenuated by elevation, making montane communities more susceptible to their effects; (2) tropical montane communities might be able to respond by shifting their distributions primarily upslope, but (3) not all species seem able to shift their distributions and the factors preventing them from tracking or establishing in new climatically suitable areas are unknown or not well understood; (4) even if montane

species are able to track suitable conditions fast enough, they risk running out of physical space; (5) the impacts of climate change on genetic diversity and species interactions within tropical montane ecosystems remain largely unknown; and (6) the loss of biodiversity and functions of TMFs could result in the loss of valuable ecosystem services for human populations living close to tropical montane regions, with repercussions at a broader scale.

Additionally, this study revealed some significant knowledge gaps in several aspects (i.e. methodological approaches, geographical and taxonomic skews, and research topics) that need to be addressed, but also shows that there are some areas of opportunity, either expanding on the available knowledge, or by employing methodologies and data sources that have not been properly explored.

2.5.1 Methodological gaps and opportunities

The nature of climate change as a global and long-term phenomenon limits our ability to produce in the short term abundant empirical evidence of its effects in real time on particular ecosystem types or any of their functions and biotic components. Instead, our assessment of evidence strength showed that there has been greater reliance on study designs that yield moderate, inconclusive and circumstantial evidence. Given that conventional study designs that yield strong evidence tend to be time-consuming, effort-intensive and costly in remote mountainous regions, a practical strategy is to accumulate independent lines of moderate, inconclusive or circumstantial, yet coherent evidence that build up the same narrative. Thus, greater effort is needed to reconcile contradicting findings across different study sites and spatiotemporal scales, as well as attempts to disentangle the synergistic influences of multiple environmental factors on the diversity and functions of TMFs. Albeit likely geographically biased and difficult to interpret, long-term data sets are becoming increasingly abundant and accessible (Wauchope et al., 2021).

Additionally, environmental gradients along mountain slopes make TMFs ideal locations to conduct field manipulation experiments (e.g. transplant experiments along temperature gradients). Field transplant experiments are recognised as a powerful tool capable of yielding robust evidence by replicating complex projected environmental conditions more accurately than laboratory trials (Nooten and Andrew, 2016; Silveira et al., 2019; Tito et al., 2020). These types of experiments are useful to inform assisted migration programmes (e.g. Castellanos-

Acuña, Lindig-Cisneros & Sáenz-Romero, 2015; Sáenz-Romero *et al.*, 2020b), changes in ecological networks (e.g. Maunsell *et al.*, 2015), adaptation to urbanisation (e.g. Martin *et al.*, 2021), among others. Alternative methods to produce strong evidence in the short term include analysis of historical remote sensing data (e.g. aerial photography and satellite imagery to detect changes in ecosystem boundaries and canopy spectral changes over time), as well as ‘natural’ long-term records (e.g. dendrochronological studies; Rodríguez-Ramírez *et al.*, 2022).

Even though our review focuses exclusively on anthropogenic climate change, the potential value of palaeoclimatic and palaeoecological studies cannot be disregarded. In principle, studies of Quaternary-time and deep-time face similar challenges as long-term future-modelling studies, namely: “the impossibility of distinguishing between true and false” (Biondi, 2014, p. 1), and their findings should be interpreted cautiously. For instance, Fitzpatrick *et al.* (2018) projected that by 2090 (i.e. seven decades), climates in North America will have shifted by as much as they did during the past 13,000 years. Hence, it seems unreasonable to expect that species will be able to replicate in just a few decades past migrations spanning millennia. Conversely, a few decades might simply be too little time to detect distributional changes, especially for long-living, slow-growing organisms such as trees than can live for centuries. In fact, a common criticism of ecological niche modelling approaches is their underlying assumption that present distributions reflect the whole set of conditions in which a species can persist (Feeley & Silman, 2010a; Sax, Early & Bellemare, 2013), which is not necessarily true and needs to be accounted for. Some studies warn that relying exclusively on ‘realised distributions’ as input for predictive distributional studies could overly restrict potential future suitable habitats and overestimate risks of extinction and extirpation (Sax *et al.*, 2013; Veloz *et al.*, 2012). However, we argue that given the current rate of anthropogenic climate change, it is preferable to avoid overly optimistic assumptions that may lead to inaction, especially for montane ecosystems globally. Moreover, sets of good practices have been suggested to improve the accuracy of palaeoecological reconstructions (e.g. Nogués-Bravo, 2009) and a combination of short-term ecological studies with long-term palaeoecological evidence can help us to understand the impacts of climate change better (Lamentowicz *et al.*, 2016). These research strategies would help resolve conflicting lines of evidence to enable rapid preventive and adaptive responses to climate change impacts on TMFs.

2.5.2 Geographical and taxonomic gaps and opportunities

Studies have been heavily concentrated in the Mesoamerican and Andean regions, both part of the Neotropical biogeographic realm. The fragmented evidence from other world regions suggests that other tropical montane regions may share similar climate change-induced impacts, albeit with some degree of local variation. Research efforts should be refocused on understudied regions to find out if there are any major discrepancies among them.

Nonetheless, a few intensively researched areas, such as TMFs in Mexico, Costa Rica and Peru – representative of subtropical, mid-latitude tropical and high-equatorial TMFs, respectively – can be considered suitable proxies for environmental management while local studies elsewhere are in progress.

Most research on TMFs focuses on only a few taxa, yet these ecosystems are considered hotspots of biodiversity, much of which remains undescribed. For example, a recent survey of rove beetles (Staphylinidae), one of the largest families of organisms in the world, along an elevational gradient in Honduras found that they reached peak diversity precisely in the highly vulnerable TMF altitudinal belt (Dolson et al., 2021). Such lack of knowledge on biotic components of TMFs obscures our understanding of their ecological networks, ecosystem functions, and the magnitude of potential losses if cascading extinctions occur. Fortunately, surveys of soil, understorey and canopy biota can be carried out relatively quickly and are less costly and effort intensive than long-term monitoring or manipulative study designs. Additionally, knowledge biases towards charismatic taxa can be exploited to set up ‘umbrella species’ conservation schemes.

2.5.3 Thematic gaps and opportunities

Many studies support the notion that climate change will result in physiological pressures and distributional shifts of tropical montane communities, but assumptions of general climate-driven range shifts should be avoided (Rubenstein et al., 2020). Empirical evidence also shows that climatic conditions can impede the effective establishment of tree communities (Joshi et al., 2020; Rehm and Feeley, 2013; Song et al., 2016b) and likely other components of tropical montane biota. In fact, species’ ability to persist or migrate is influenced by their interactions with other ecosystem components, both biotic and abiotic (Jankowski et al., 2010; Joshi et al., 2020; Quiroga et al., 2018; Ramirez-Villegas et al., 2014), but few studies have looked at

ecological networks in TMFs (Benning et al., 2002; Hillyer and Silman, 2010; Jankowski et al., 2010; Ornelas et al., 2018; Tito et al., 2021). Improving our understanding of these interactions would help improve the accuracy of forecasts both in terms of distributional responses and potential future assemblages. Although field studies are needed to elucidate how tropical montane networks respond to climate change and other disturbances, existing databases can be used to construct and conduct robust analyses on ecological networks (e.g. de Almeida & Mikich, 2018; Fricke & Svenning, 2020), and project their responses under climate change scenarios.

More concerning is the paucity of studies at the genetic level in TMF research in relation to climate change, which has been previously acknowledged (Pauls et al., 2013). For example, tropical tree populations are experiencing genetic bottlenecks following intense disturbance events, but tropical montane regions are understudied (Pautasso, 2009). For mountainous regions, this might be crucial because microevolutionary processes operate differently within a population along an elevational gradient, i.e. the leading edge, the central population and the rear edge (Kremer et al., 2014). Sudden disturbance-induced migrations may lead to decreased phenotypic variability, further jeopardising the plasticity and ability of trees both to reach and to establish populations in new areas (Pertoldi et al., 2007). Also, highly variable conditions may not result in an adaptive response because selection processes are multi-directional and the existing genetic variation in a population might be insufficient to generate the genotypic combinations required for it to persist under new environmental conditions (Alfaro et al., 2014). As the most conspicuous biotic component of forests, declines of trees could trigger negative cascading effects (Bawa and Dayanandan, 1998; Nagel et al., 2019). Thus, the genetic status of trees is a factor that ought to be taken into account for assisted migration programmes (Alfaro et al., 2014), and all these considerations are equally valid for other taxa. Unlike other knowledge gaps, the scarcity of studies at the genetic level is difficult to overcome though indirect and remote methods, however, the increasing accessibility and affordability of sequencing methods should facilitate extensive genetic surveys of tropical montane populations in the short term.

2.6 Recent work

There have been recent developments since our systematic review was carried out. For example, Rico *et al.* (2023) reported that the genetic health of a tropical montane tree species in Mexico is threatened by human activity and climate change.

Research on treeline expansion has also shown that dry conditions in the boundary between TMF and *páramo* in the Venezuelan Andes support a seedling bank, but with slow growth (Ramírez *et al.*, 2022); and some species may need treatment, such as scarification, to increase germination rates (Liyanage *et al.*, 2022).

Thus, understanding the genetic adaptations and environmental influence of seeds and seedlings is crucial for conservation efforts. However, long-term monitoring is also necessary as some abiotic effects, such as soil properties, may not be noticeable for years (Martínez-Ramos *et al.*, 2022).

Lastly, new knowledge of diversity patterns and spatial partitioning in various regions (Berrios *et al.*, 2022; Morton *et al.*, 2022) emphasise the importance of traditional biodiversity surveys in TMFs, especially in understudied regions.

2.7 Conclusions

(1) We highlight the long-term need to widen the methodological, thematic, taxonomic and geographical scope of studies on TMFs under climate change. In the short term, however, the accumulation of moderate to circumstantial evidence constitutes the most accessible and reliable tool to address uncertainties and gaps in current knowledge. As such, in-depth research in well-studied regions, use of alternative data sources (remote sensing and ‘natural’ long-term records), palaeoecological supporting evidence and advances and refinements of forecasting modelling techniques offer the most reliable and immediate sources of information for expeditious conservation action for these threatened forests.

(2) Natural variability within TMF regions represents a challenge for the generalisation of the findings of individual studies, but it simultaneously represents an exceptional opportunity to generate high-quality evidence of the impacts of climate change for both tropical montane species and lowland species. Environmental gradients along mountain slopes have been identified as natural laboratories, where field manipulation experiments (e.g. field transplant

experiments, rain exclusion experiments, etc.) can be conducted in the short term to simulate complex projected environmental conditions with greater accuracy than can be achieved *ex situ*.

(3) We highlight the importance of modelling approaches in TMF research and encourage further refinement and development of these methods. To enhance their effectiveness, novel, more robust forecasting algorithms should be developed to account for uncertainties and sampling biases. Additionally, incorporating ecological information, such as species dispersal limitations, biotic interactions, and analyses of ecological networks, can make commonly used modelling approaches more informative. Optimizing these approaches with more ecological information is crucial for the success of conservation strategies, such as the design of protected areas that consider future suitable habitats for whole biotic communities, and minimizing losses of biodiversity and ecosystem functions.

(4) Despite the undeniable importance of trees in forests, the responses of other taxonomic groups to climate change should not be overlooked, as intraspecific interactions could prove decisive for the success of conservation measures. Similarly, the impacts of climate change at the genetic level remain largely unknown and the loss of genetic diversity can threaten the long-term viability of TMF populations.

(5) We urge scientists to conduct similar evidence quality assessments in their respective fields. Experts in each area of research should critically ponder what study designs and data sources yield the most robust body of evidence and take them into consideration when carrying out reviews and planning future research.

Chapter 3. Distributional Responses of Mesoamerican Tropical Montane Tree Communities under Climate Change

3.1 Abstract

Tropical Montane Forests are an ecosystem type with high ecological and cultural significance for their biodiversity and ecosystem services but that is threatened by climate change. In Mesoamerica, Tropical Montane Forests extend from the central mountain ranges parallel to the east and west coasts of Mexico, southwards into Central America, with a wide latitudinal discontinuity created by Lake Cocibolca in Nicaragua, and a smaller one at the Isthmus of Tehuantepec. I provide a latitudinal and altitudinal characterisation of the montane-specialist tree community from Mexico to Panama, based on the occurrence records of 272 species, that will serve as a baseline for conservation efforts of this biome. Furthermore, I employ ensemble Species Distribution Models to predict climatically suitable areas for this montane-specialist community under current (1981–2010 baseline) and future conditions by the end of the century (2071–2100) under a severe emissions scenario (RCP8.5). Areas with suitable climatic conditions for a high number (≥ 50) of montane-specialist species currently occupy $\sim 136,000$ km² out of $\sim 1,236$ M km² of aggregated suitable areas for the 272 species. Climatically suitable areas could be reduced by $>60\%$ by the end of the century due to severe climate change. Species turnover will also be affected, being more pronounced at low ($<1,000$ m asl) and mid elevations ($<1,500$ m asl), indicating species migrating upslope, and the highest communities remaining largely unchanged. The potential impacts on montane-specialist tree species were mainly driven by latitude, with greater losses in the northern part of the study area, with a compounding effect of increasing elevation. The severity of suitable habitat loss will be proportionately greater for already restricted species, which highlights the patchy nature of montane communities and the likely inefficacy of passive conservation policies, such as protected areas. I thus call for those policies to be reinforced and supplemented with active conservation efforts such as seed banks and assisted migration programmes.

3.2 Introduction

Tropical montane forests (TMF) are highly vulnerable to environmental changes because their extent and distribution are constrained by topographic boundaries (Salinas et al., 2021).

In addition to threats common to most terrestrial ecosystems, such as agricultural expansion and urban encroachment, TMF communities face unique stressors for mountainous areas, such as fog cover reductions and subsequent increases of solar radiation and vapour pressure deficit (Christmann and Menor, 2021). Not even remote mountainous areas free from direct human disturbance are spared, as there is little evidence that undisturbed vegetation provides additional mitigation to global warming (Trew et al., 2024). Within the tropics, Latin America, and especially Mesoamerica, have been identified as highly vulnerable regions to environmental change (Pacifiçi et al., 2015; Trew et al., 2024).

Mesoamerica, extending from the northern mountains of Mexico through Central America, is a bio-cultural region that hosts remarkably high biological diversity, the product of its recent geological history (Cody et al., 2010). TMFs are found in Mexico and Central America, and cover ~56,000 km² out of ~401,300 km² in the Neotropics (Helmer et al., 2019). Despite their smaller size compared to South American TMFs, Mesoamerican montane regions are critical for their unique biodiversity and as a convergent zone between Nearctic and Neotropical biotas (Corral-Rosas and Morrone, 2016). This region is also of great cultural and agroecological importance because it is inhabited by ethno-linguistically diverse indigenous groups and is centre of diversity and domestication of several world staple crops (Boege et al., 2008).

Mesoamerica is projected to be severely impacted by climate change by the end of the century (Williams et al., 2018), leading to 60% or more habitat losses (Altamirano-León et al., 2022; Ortega et al., 2024; Ramírez-Amezcuca et al., 2016) that could threaten key natural protected areas (Esperón-Rodríguez et al., 2019). Furthermore, large climatically suitable areas for TMF species do not fall within current protected area schemes (Jiménez-García and Peterson, 2019; Rojas-Soto et al., 2012; Sierra-Morales et al., 2021). Understanding how Mesoamerican TMFs will respond to climatic stressors is complex due to variations in species sensitivity (Esperón-Rodríguez and Barradas, 2014) and varying quality of the research evidence (Mata-Guel et al., 2023).

The high heterogeneity of montane regions in Mesoamerica has led to inconsistent classifications of its vegetation. For example, the Mexican government conflates TMFs with the highly restricted ‘mountain mesophyll forest’ (INEGI, 2024; <https://www.inegi.org.mx/temas/usosuelo/#mapas>), although mountainous regions in

Mesoamerica harbour a wider variety of assemblages, including pine, oak, mixed-broadleaf, seasonally-dry, among other forest types (Gual-Díaz and Rendón-Correa, 2014). Additionally, in its southern part, it is not clear whether Mesoamerican TMFs form one continuous community or are disrupted by Lake Cocibolca in Nicaragua (Morrone, 2020).

Mapping TMFs' extent and distribution has been equally challenging. Species Distribution Models (SDM) are an essential tool for projecting current areas of TMFs and predicting possible future changes in response to environmental changes (Araújo and Peterson, 2012; Elith and Leathwick, 2009; Pacifici et al., 2015). However, varying methodological choices, data availability, assumptions of species' representativeness of the whole biome, among other biases, have resulted in inconsistent estimates of Mesoamerican TMFs extent and distribution (Alfonso-Corrado et al., 2017; Gómez-Pineda et al., 2020; López-Arce et al., 2019; Rojas-Soto et al., 2012).

To address these challenges, I propose a novel and easily replicable and expandable methodology to assess the extent and distribution of TMFs under current and future climatic conditions, using the montane-specialist tree subset of Mesoamerican TMFs as a case study. By characterising the montane-specialist tree community without *a priori* assumptions of their representativeness of TMFs, this approach allows to forecast changes and make inferences related to community composition in addition to distributional shifts and allows to easily expand the approach to incorporate more community elements and taxa.

Thus, my study aims to contribute to a wider understanding of Mesoamerican montane-specialist trees and their responses to global change by estimating their current and future extent and distribution in Mesoamerica using ensemble SDMs with straightforward reproducibility in other communities and world regions. The specific objectives are to: (1) characterise the montane-specialist tree community beyond political boundaries with Mesoamerica as a case study; which includes determining whether its southern limit extends to the Panama-Colombia border or is cut off by Lake Cocibolca; (2) estimate the spatial extent and distribution of montane-specialist trees in Mesoamerica; and (3) assess the potential impacts of projected climate change on that montane-specialist tree community in terms of extent, distribution, and species richness by the end of the century.

3.3 Methods

3.3.1 Study area and data sources

I focused on the Mesoamerican region, covering the portion of Mexico below 25° N and Central America, and combined the tropical montane region estimates by Villaseñor (2010) and Los et al. (2021), allowing some buffer area north and south into the USA and Colombia, respectively (Figure 3.1) to capture potential unoccupied climatically suitable areas.

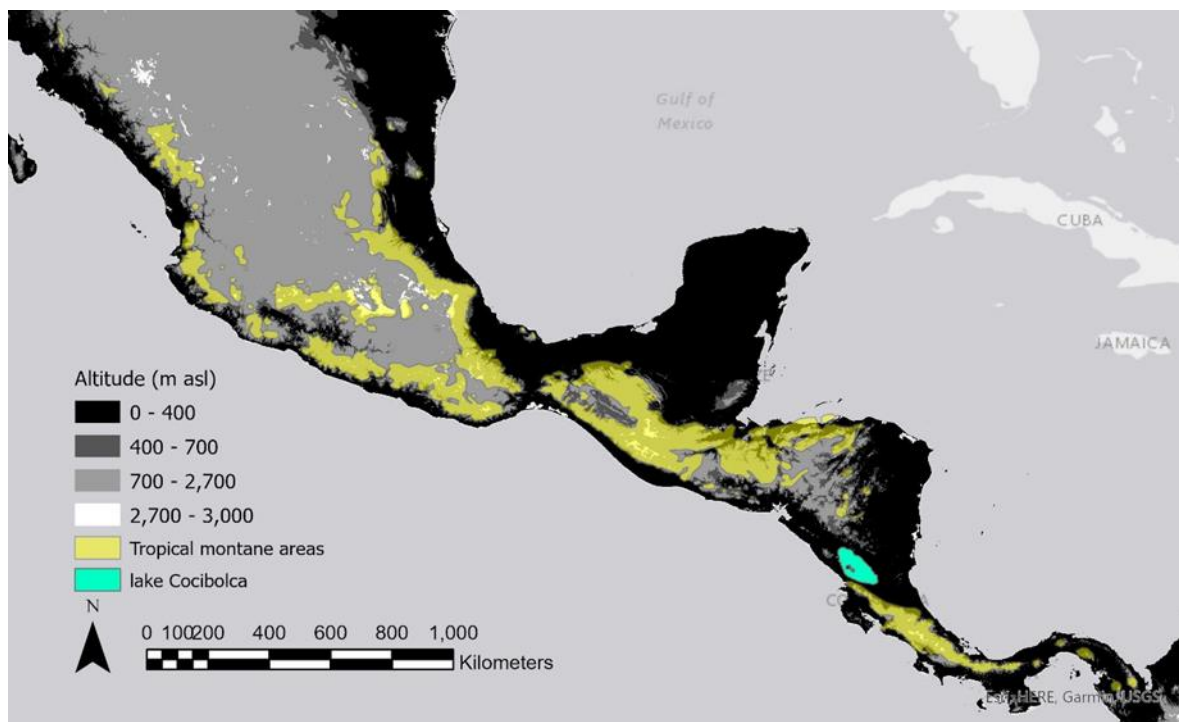


Figure 3.1 The study area. The altitude categories are based on historically reported elevational limits of TMFs in Mesoamerica, typically located between 700 and 2,700 m asl, with rare occurrences as low as 700 m asl, and as high as 3000 m asl (Ressl and Morales, 2008). The distribution of tropical montane forests is shown in yellow, based on the combined estimates by Villaseñor (2010) and Los et al. (2021). Lake Cocibolca (in light blue) creates a latitudinal discontinuity for montane habitats, but Costa Rica and Panama are included nonetheless as part of the Mesoamerican bioregion.

Occurrence records. I compiled a harmonised list of tree species from national catalogues and inventories from Mexico and Central America ($n = 5,307$ species) (Table S2), excluding Belize, whose territory falls entirely outside of our tropical montane polygons (Figure 3.1). I downloaded the species ($n = 4,342$) occurrence records from GBIF (www.gbif.org; 21st June 2022, <https://doi.org/10.15468/dl.dsbdhrh>) with filters for accepted names and exact matches, and intertropical latitudinal limits of 30°N and 30°S (*rgbif* R package; Chamberlain et al., 2017). To keep montane-specialist species only, I filtered the occurrence records in

ArcMap 10.8 by the tropical montane polygons in Figure 3.1, retaining species with $\geq 75\%$ (upper quartile) of records inside the polygons. I thinned occurrence points to 1 km² using the *spThin* package (Aiello-Lammens et al., 2019), and discarded species with < 20 usable occurrence records (Table S3). Finally, I verified the growth forms of the remaining species from digitised herbarium specimens available in GBIF to keep only tree species, although some can also occur as shrubs. The final dataset included 272 montane-specialist tree species and 15,555 occurrence records (Tables Table S4 and Table S5).

To test whether there is one continuous montane-specialist tree community along the whole latitudinal range or if Lake Cocibolca imposes a barrier, I used the Bray-Curtis dissimilarity index above and below the 12° N parallel (approximate mid-section of the lake). I also tested the second widest topographic discontinuity (terrain < 400 m asl) in the Isthmus of Tehuantepec ($\sim 16.5^\circ$ N; Figure 3.1), even though it occurs on a longitudinal axis and, to my knowledge, does not represent a significant dispersal barrier.

Environmental layers. I downloaded baseline (1981–2010) climatic variables from CHELSA v 2.1 (<http://chelsa-climate.org/bioclim/>, Karger et al., 2017), since it has been reported to perform slightly better than other sources in mountainous regions (Bobrowski et al., 2021; Noce et al., 2020). I initially retrieved 19 bioclimatic layers plus frost change frequency and net primary productivity, which could have biological significance for TMFs. I downloaded WorldClim’s digital elevation model (www.worldclim.org/data/worldclim21.html, Fick and Hijmans, 2017) and used it to derive aspect, slope, and ruggedness in ArcMap 10.8. I obtained soil types from the FAO’s Harmonized World Soil Database v 1.2 (Fischer et al., 2008). All environmental layers had a 30-sec resolution and WGS84 projection.

Variable selection. I clipped all layers and occurrences to the study area and used the Spearman test for raster objects using the *Correlation* function in *ENMTools* (Warren et al., 2019) to check for collinearity. For variable selection, I then ran pilot tests using MaxEnt (Phillips et al., 2006) with combinations of non-correlated environmental variables on the 20 species with most records, the 20 with fewest records, and 20 random species to ensure good representation of the community. After removing low-contributing and highly correlated variables ($> |0.75|$), the retained explanatory variables were slope, ruggedness, soil type, temperature seasonality (BIO4), mean temperature of the wettest quarter (BIO8), mean

temperature of the driest quarter (BIO9), precipitation of the driest month (BIO14), precipitation of the wettest quarter (BIO16) and precipitation of the coldest quarter (BIO19).

Future climate change scenarios. To forecast the effects of climate change on the distributions of the tropical montane trees, I employed the RCP8.5 scenario (rising radiative pathway leading to 8.5 W m^{-2} [$\sim 1,370 \text{ ppm CO}_2 \text{ eq}$] and $3.7 \pm 1.1^\circ\text{C}$ temperature rise by 2100; Leggett, 2021) by the end of the century (2071–2100). I chose the long-term severe pathway because observed emissions and existing global fossil fuel infrastructures already surpass emission thresholds of moderate pathways (Dhakal et al., 2022), and tropical montane trees have been reported to migrate more slowly than observed rates of climate change (Alexander et al., 2018; Corlett, 2015; Corlett and Westcott, 2013). I downloaded the projections for the six selected bioclimatic variables from CHELSA under the and the upgraded versions of three General Circulation Models recommended by the Mexican government (<https://www.gob.mx/inecc/acciones-y-programas/escenarios-de-cambio-climatico-80126>) or previously used for the Mesoamerican region (e.g., Esperón-Rodríguez et al., 2019; Helmer et al., 2019; Ramírez-Bautista et al., 2020; Williams et al., 2018): GFDL-ESM4 (Dunne et al., 2020), MPI-ESM-HR (Müller et al., 2018) and UK-ESM1 (Sellar et al., 2019).

3.3.2 Species distribution modelling

I generated SDMs under baseline (henceforth ‘current’) and future conditions for the 272 tropical montane tree species, using an ensemble of four complementary algorithms (GAM, ANN, GBM and MaxEnt; Guisan et al., 2017) in the *biomod2* package (Thuiller et al., 2016). I kept the spatial resolution at 30-arc seconds because coarser resolutions could miss important details in narrow TMF areas.

Due to the size of the study area and the number of species, I used the default parameters of the algorithms, whilst relying on the high number of species to dilute potential biases of any individual tree species. Therefore, the robustness of this models is based on the number of species used to model the Mesoamerican tropical montane tree community.

I parallelised the process on the Iridis5 High Performance Computing Facility of the University of Southampton, using the *foreach* (Weston, 2019) and *doParallel* (Calaway et al., 2015) packages (scripts available in SI). I divided the species into those with <50 occurrences ($n =$

168) and ≥ 50 occurrences ($n = 106$), and then into 11 batches of ~ 30 species. Each batch took ~ 20 processing hours.

For each species, I created 1,000 random background (pseudoabsences) points. To validate models, I used 5 cross-validation replications for species with < 50 records and 10 for species with ≥ 50 records. I combined the model outputs of the repetitions (5 or 10) and four algorithms and three GCMs for every species (*biomod2* 'PA+run' assembly rule), using a TSS > 0.5 (true skill statistic, Allouche et al., 2006) threshold for model inclusion. I overlapped the final ensemble present and future maps to analyse shifts in climatic suitability between present and future conditions. I generated categorical maps for each species with four possible values: -2 predicted to be lost, -1 predicted to remain occupied, 0 predicted to remain unoccupied, and 1 predicted to be gained (Thuiller et al., 2023).

3.3.3 Post-SDM Analysis

I imported each species' ensemble map under current and future conditions to R v4.1.1, using the *raster* package (Hijmans, 2020), and stacked them to generate current and future species richness maps and calculate predicted changes in richness between the two time periods. I converted the current and future richness maps to a projected coordinate system to estimate their extent in km^2 . To estimate turnover per pixel (i.e., each pixel as a site), we generated binary presence matrices, with species arranged in columns and pixels in rows. I used the *betapart* package (Baselga et al., 2018) to estimate the Jaccard dissimilarity index for each pixel, excluding those with incomplete data, i.e., pixels not containing any species in one of the two time periods to compare. I converted the turnover matrix into a map using the *raster* package.

To test whether projected distributions were associated with phylogenetic affiliation, I ran correlation tests between projected extent under current and future conditions and taxonomic groups at the family and order levels. Since Conifers and Angiosperms tend to form distinct communities that are often listed as separate assemblages in national inventories (e.g., pine forests distinct from oak forests, broadleaf forests, etc.), I tested differences between both clades per species (i.e., not aggregated) in terms of projected current and future extent, as well as percent range change, using the non-parametric Kruskal-Wallis test.

To characterise the Mesoamerican TMF tree communities throughout the study area and assess the changes in their suitable range sizes, I classified species based on their projected current latitudinal and altitudinal ranges. For the latitudinal range, I used 17.5° N (approximate northern limit of the Isthmus of Tehuantepec, where mountainous regions extend longitudinally rather than latitudinally) and 12.5° N (north of lake Cocibolca) as dividers for 'northern' (N), 'central' (C), and 'southern' (S) species. I labelled species spanning two contiguous areas 'northern-central' (N – C) or 'central-southern' (C – S), and 'widespread' (W) those with even broader ranges. The boundaries between altitudinal subtypes of TMFs (i.e., lower montane, upper montane and alpine) vary from 1,200–1,500 m asl (lower boundary) to 2,000–3,000 m asl (upper boundary), and are influenced by the height of the mountains and distance from the sea (Scatena et al., 2010). Thus, for altitudinal range, I based the classes on interquartile ranges into 'very low' (VL), 'low' (L), 'mid-low' (ML), 'middle' (M), 'mid-high' (MH), 'high' (H), and 'very high' (VH) (detailed criteria in Table S6). I used these classes to generate a species-level characterisation of the montane tree community in Mesoamerica.

To test an interactive effect of latitude and altitude on forecast climatic suitability changes, I simplified the classes above to ensure every class had enough species to compare and eliminate overlapping classes. Latitude classes were thus reclassified as 'northern' ('N' \cup 'N – C'), 'centred' ('C' \cup 'W') and 'southern' ('C – S' \cup 'S'), and altitudinal classes as 'low' ('VL' \cup 'L'), 'mid' ('ML' \cup 'M' \cup 'MH') and 'high' ('H' \cup 'VH'). I ran GLMs with these broad classes on percentage loss and log-transformed absolute loss in suitable range size, using the Gamma family with a log function for positive continuous data and to account for overdispersion of the data. Finally, I ran a linear regression of percent losses in response to log-transformed current projected size of suitable areas to test whether more restricted species will be more severely impacted than widespread ones. I report range sizes in km² but used current and future projections in their original 30 arc-seconds projections (i.e., pixels) for statistical tests to avoid errors caused by rounding while reprojecting to a 1 km² grid. All stats were done in R v.4.1.1 and the scripts are available in SI.

3.4 Results

3.4.1 Characterisation of the Mesoamerican TMF tree communities

Costa Rica had the highest number of TMF tree species (192) and almost as many occurrence records (6,180) as Mexico (155; 6,523) despite its considerably smaller size (Table S5). The distance between the southernmost TMF regions in Nicaragua and the northernmost TMF areas in Costa Rica is approximately 200 km. The Bray-Curtis index ($BC = 0.799$) indicated that there are two distinct montane-specialist tree communities separated by Lake Cocibolca. This is also evident in the number of occurrence records exclusive to Costa Rica and Panama, with 89 species of my dataset recorded in one or both countries and only four species shared between Costa Rica and Nicaragua. In contrast, the Bray-Curtis index seems to indicate another latitudinal discontinuity at the Isthmus of Tehuantepec ($BC = 0.690$), however, the subcommunity south of the isthmus harboured 264 out of the 272 species, whereas north of the isthmus there were 151 species, only 8 of which were exclusive (Table S7). Therefore, the dissimilarity index in this case showed that the subcommunity south of the isthmus was nearly twice as diverse as the northern one.

Based on the projected suitable habitats of 272 species under current conditions, I characterised the Mesoamerican montane-specialist tree community along altitudinal and latitudinal gradients (Figure 3.2). I grouped the projected suitable areas for the species by elevation and latitude, with a separate category for widespread species. Most species (darker classes in Figure 3.2) concentrated at low and mid elevations in the central and southern parts of the study area, indicating higher richness at lower latitudes. Few species fell neatly into the middle categories (mid elevation and central part of the range) and tended to skew instead into lower or upper elevations and northern or southern areas. There were suitable conditions spanning the whole latitudinal range for 51 species. Note that in Mexico, the northern montane areas are divided into two ranges along its east and west coasts, separated by the central highlands. Therefore, species categorised as northern might not necessarily co-occur longitudinally.

| | N | N - C | C | C - S | S | W | | |
|----|--|--|---|--|---|---|---|--|
| VH | | Comarostaphylis longifolia | | Clethra gelida | Maytenus woodsonii Prumnopitys standleyi | Abies hickelii | | |
| H | | Meliosma dentata Parathesis villosa Phymosia rosea Pinus ayacahuite Pinus hartwegii | Quercus affinis Quercus martinensis Stevia microchaeta Viburnum elatum Viburnum jucundum | Quercus crispipilis | Buddleja nitida Buddleja skutchii Piper irazuanum | Ardisia pleurobotrya Axinaea costaricensis Miconia biperulifera Myrcianthes storkii | | |
| MH | Meliosma alba Viburnum microcarpum | Chiranthodendron pentadactylon Clethra hartwegii Cleyera integrifolia Cornus excelsa Freziera guatemalensis Hedyosmum mexicanum Ilex discolor Lyonia squamulosa Miconia oligotricha Ostrya virginiana Parathesis leptota Parathesis melanosticta Pinus lawsonii Pinus pringlei Pinus pseudostrobus | Pinus strobus Prunus tetradenia Quercus candicans Quercus scytophylla Quercus xalapensis Roldana lanicaulis Saurauia oreophila Styrax ramirezii Symplocos citrea Telanthophora uspananensis Ternstroemia lineata Verbesina apleura Viburnum acutifolium | Ardisia verapazensis Glossostipula concinna Symplocos pycnantha Telanthophora cobanensis Zinowiewia rubra | Duranta costaricensis Frangula pendula Hypericum irazuense Ilex pallida Jessea multivenia Palicourea adusta Parathesis glabra Quercus costaricensis Styrax warszewiczii | Aegiphila odontophylla Ardisia glandulosomarginata Brunellia costaricensis Bunchosia ternata Cestrum poasanum Hoffmannia amplexifolia Meriania philomoides Miconia pittieri Miconia schnellii Ocotea mollicella | Ocotea praetermissa Oreopanax pycnocarpus Palicourea lasiorrhachis Palicourea purpurea Palicourea salicifolia Prunus fortuneensis Solanum storkii Tournefortia johnstonii Viburnum venustum Wercklea woodsonii | |
| M | | Verbesina perymenioides | Lepidaploa polypleura | Frangula oreodendron Magnolia poasana | | Frangula discolor Solanum nigricans | | |
| ML | Ocotea psychotrioides Perrottetia ovata Picramnia xalapensis | Clethra macrophylla Clethra pringlei Clethra suaveolens Daphnopsis mollis Juglans pyriformis Magnolia schiedeana Ocotea acuminatissima Persea liebmannii | Podocarpus matudae Quercus germana Rogiera cordata Saurauia scabrata Saurauia serrata Senna multifoliolata Sommeria arborescens Styrax radians | Dendropanax leptopodus Ocotea purpurea Oreopanax sanderianus Parathesis chiapensis | Alfaroa costaricensis Beilschmiedia ovalis Blakea storkii Cedrela tonduzii Cosmibuena valerii Dendropanax capillaris Dendropanax globosus Dichapetalum brenesii Eugenia austini-smithii Faramea ovalis Gonzalagunia rosea Guatteria oliviformis Guatteria verrucosa Hasseltia guatemalensis Ilex lamprophylla Ladenbergia brenesii Magnolia sororum Miconia tonduzii | Montanoa guatemalensis Oreopanax oerstedianus Panopsis costaricensis Persea veraguensis Piper maxonii Psychotria nubiphila Quercus benthamii Rauvolfia aphlebia Saurauia pittieri Saurauia rubiformis Schefflera rodriguesiana Sloanea ampla Symplocos costaricana Symplocos serrulata Ticodendron incognitum Viburnum costaricanum Weinmannia burserifolia | Aiuea brenesii Aiuea hammeliana Arachnothyrs aspera Ardisia palmata Cestrum rugulosum Chrysoclamys allenii Citharexylum macradenium Citronella costaricensis Clusia palmana Clusia torresii Coccoloba lipotizii Cajoba costaricensis Dendropanax querceti | Eugenia cartagensis Euonymus costaricensis Gonzalagunia stenostachya Guatteria costaricensis Hoffmannia arborescens Ilex maxima Inga longispica Ocotea brenesii Oreopanax vestitus Passiflora tica Perrottetia multiflora Psychotria orosiana Weinmannia wercklei Wercklea insignis |
| L | | Inga xalapensis Oecopetalum mexicanum | | Amphitecna sessilifolia Chrysoclamys psychotriifolia Clibadium leiocarpum Damburneya salicina Dendropanax gonatopodus Guatteria dolichopoda | Macrohasseltia macroterantha Meliosma idiopoda Ocotea austinii Saurauia montana Sommeria donnell-smithii | Amaloua pedicellata Arachnothyrs brenesii Arachnothyrs montevidensis Beilschmiedia brenesii Clusia croatii Coussarea caroliniana Eugenia siggersii Guatteria slateri Inga exalata Inga leonis Inga mortoniana Inga sierrae Inga tonduzii Malvaviscus palmanus | Meliosma brenesii Miconia albertobrenesii Miconia brenesii Mollinedia costaricensis Monteverdia recondita Ocotea endresiana Ocotea gomezii Palicourea alajuelensis Peltostigma guatemalense Pouteria exfoliata Psychotria jimenezii Tabernaemontana alfaroi Zygia palmana | |
| VL | | | | Arachnothyrs costaricensis Lacmellea zamorae | Palicourea eurycarpa Pimenta guatemalensis Rudgea reducticalyx Stenanona costaricensis | Croton megistocarpus Mollinedia viridiflora Persea schiedeana Picramnia teapensis Stauranthus perforatus | | |

Figure 3.2 Characterisation of Mesoamerican montane-specialist tree subcommunity (N = 272) by latitudinal (N = north, N - C = north-central, C = central, C - S = central-south, S = south, and W = widespread) and altitudinal (VH = very high, H = high, MH = mid-high, M = mid, ML = mid-low, L = low, and VL = very low; see Table S6) classes. Darker colour indicates projected suitable climatic conditions for higher number of montane-specialist tree species.

3.4.2 Suitable area projection of the Mesoamerican montane-specialist tree community and predicted impacts of climate change

The aggregated extent of suitable conditions for Mesoamerican montane-specialist tree species was projected to decrease under future conditions from ~1,236M km² suitable for the 272 species included in the analysis, to ~970,000 km², equating to a loss of 21.5% (Figure 3.3 and Table S8). The extent of losses of climatically suitable areas would likely be greater because many areas predicted to become suitable for a few montane-specialist tree species are in low-elevation coastal regions and the Yucatán Peninsula (Figure 3.4A and B), which do not qualify as TMFs. Future projections forecast an increase in low-diversity areas, with areas predicted to have suitable conditions for 1–5 tree species increasing from 548,061 km² currently to 648,145 km² (+18.3%) by the end of the century (Figure 3.3). This represents a projected expansion of a handful of species into lower elevations and a wider latitudinal range, rather than of the whole or even partial tree community. In contrast, areas with higher diversity (predicted to be suitable for >5 tree species) show consistent declines in suitable range (Figure 3.3; Figure 3.4A and B).

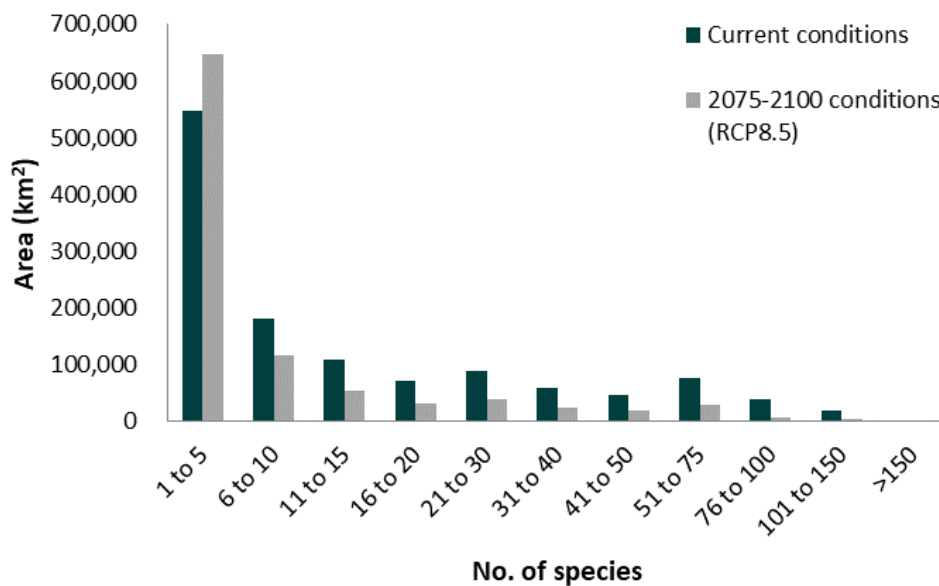


Figure 3.3 Projected climatically suitable habitat extent for the 272 montane-specialist trees by number of species under current (1981–2010 baseline) and future (2071–2100) conditions under a severe climate change scenario RCP8.5.

With few exceptions, montane-specialist tree species richness is predicted to decline under future conditions in almost all the TMF area in Mesoamerica (Figure 3.4C), being more severe at higher montane elevations, with some high-altitude areas projected to become unsuitable for >50 species. In contrast, most areas predicted to gain in suitability for some species are lowland regions where there is no TMF, but that could allow for the establishment of a handful of

species. In these cases, the expected gains in climatic suitability are for <5 species. Some small TMF areas that could see an increase in suitability for montane-specialist species are in the southernmost parts of the Mesoamerican bioregion, mainly Costa Rica and Panama, and even into the Andean region of South America, as shown by the southern buffer area in Figure 3.4A.

The composition of the montane-specialist community was also predicted to change. The beta diversity analysis (Jaccard turnover index; Figure 3.4D) showed that for most low- and mid-elevation TMF areas, the degree of dissimilarity between current and future conditions was higher than at the highest elevations, indicating that species currently at lower altitudes would experience proportionally larger (likely upslope) distributional shifts, changing the species assemblages along the way. The montane-specialist tree community compositions at the highest elevations were projected to remain relatively unchanged.

I did not find significant associations between taxonomic groups at the family and order levels with current distributional extent nor projected changes. I found that under current conditions and on a species-by-species basis (i.e., not aggregated), Conifers had on average larger areas with suitable climatic conditions than Angiosperms (Kruskal-Wallis chi-squared = 5.1306, d.f. = 1, $p = 0.0235$). However, I did not find any difference in habitat suitability between these groups under future conditions (chi-squared = 2.6709, d.f. = 1, $p = 0.1022$). There were no differences in the predicted percent losses in range suitability between groups ($p = 0.8473$).

I found moderate evidence that both elevation and latitude could jointly influence the magnitude of losses in climatically suitable areas (Figure 3.5). 'Southern' (i.e., <12.2 °N) montane-specialist tree species were projected to experience the smallest losses, especially at higher elevations. Losses were greatest among species with predominantly suitable areas at mid latitudes ('centred', i.e., 12.5 °N to 17.5°N) and intermediate among 'northern' species (>17.5 °N). There was a strong interaction between the linear components of both latitude and altitude ($t = -3.94$, $p = <0.001$) on log-transformed absolute losses; however, I found no effect of other combinations of the linear and quadratic components of latitude and altitude. Both the linear ($t = -5.60$, $p = <0.0001$) and the quadratic ($t = -6.13$, $p = <0.0001$) components of latitude had a strong effect on predicted range losses, while only the quadratic component of altitude had a moderate decelerating effect on range losses ($t = -3.01$, $p = <0.002$), except for the 'northern-low' species. This suggests that latitude will have a more pronounced effect on range shifts than elevation, as shown with the elevation classes 'following' an arched pattern along the latitudinal axis of Figure 3.5.

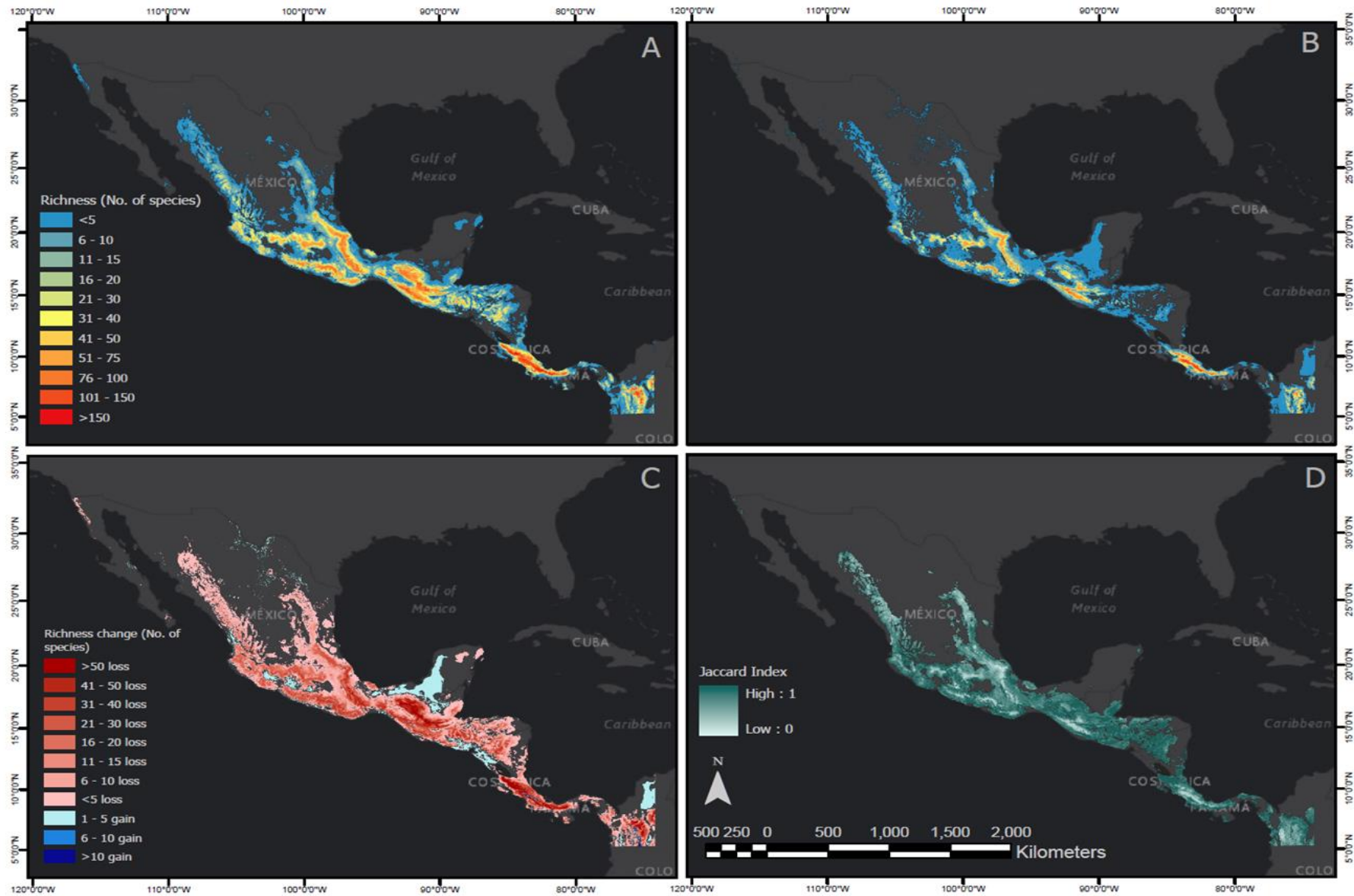


Figure 3.4 Number of montane-specialist tree species (richness) projected to have suitable habitat with current (A) and future (2071–2100) climatic conditions under RCP8.5 (B); change in climatic suitability from current to future conditions (C); and species turnover estimated with the Jaccard similarity index from current to future conditions (D).

The percent loss in predicted climatically suitable areas was negatively influenced by the projected range of the species. I found moderate evidence that the magnitude of projected percent losses of suitable area decreased with projected extent under current conditions ($\alpha = 136.2, p < 0.001$; $\beta = -5.85, p < 0.001$; $F_{1,265} = 81.35, p < 0.001$; $R^2 = 0.23$; Shapiro-Wilk's $W = 0.992, p = 0.173$; Fig. S1). This means that species with currently restricted distribution are more likely to experience the greatest proportional suitable habitat losses under future climate conditions, although the high variability in my models suggests that other factors could drive changes in range suitability in relation to the size of current suitable areas.

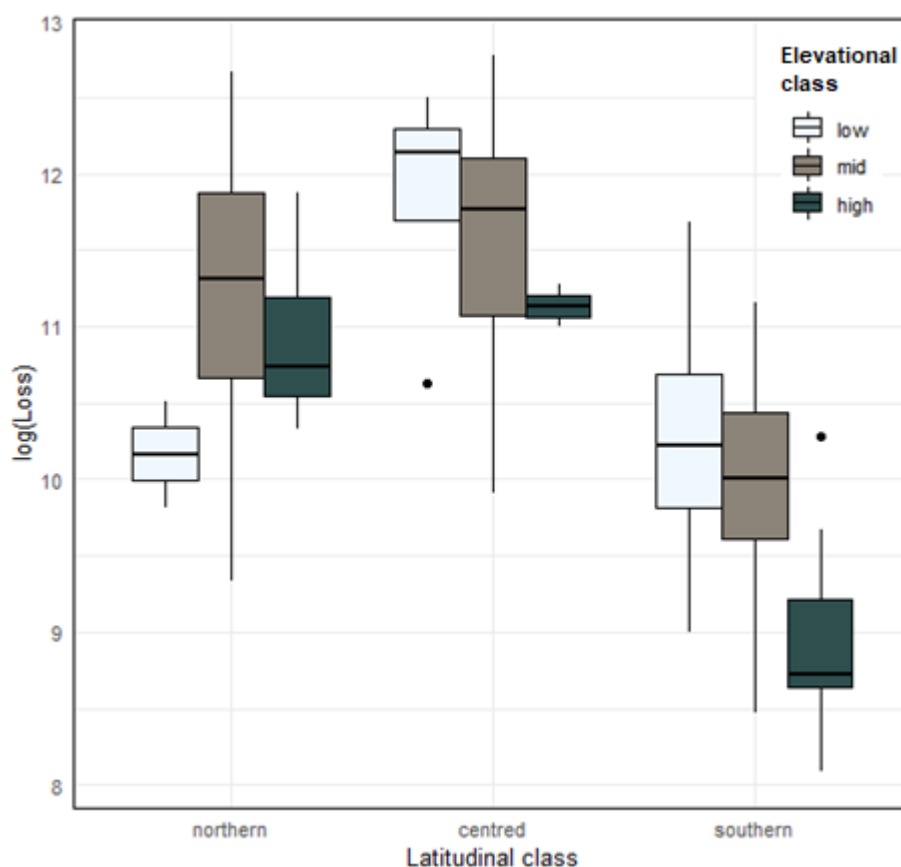


Figure 3.5 Interaction of latitudinal and altitudinal classes of Mesoamerican MST species on projected range losses by the end of the century under RCP8.5. Boxes indicate the interquartile range (25th and 75th percentiles) and the whiskers extend to the 10th and 90th percentiles.

3.5 Discussion

I conducted an assessment of the distribution of montane-specialist tree species in Mesoamerica based on climatic suitability with a transparent, replicable, and transferable methodology for other biological communities, world regions and ecosystems. The results

indicate that Lake Cocibolca splits the Mesoamerican montane-specialist tree community into two distinct subcommunities, while species richness significantly decreases north of the Isthmus of Tehuantepec. Additionally, I characterised the montane-specialist tree community at the species level across latitudinal and altitudinal gradients in Mesoamerican montane areas, which is lacking from national inventories and could serve as a baseline for further research and conservation policy of these key ecosystems. Finally, my models predicted that climate change will lead to loss of suitable area and high species turnover at low and mid elevations of Mesoamerican montane-specialist tree species by the end of the century.

3.5.1 The Mesoamerican montane-specialist tree community

My estimate of the current extent of Mesoamerican TMFs of $\sim 1.236\text{M km}^2$ based on the combined suitable areas of 272 montane-specialist tree species is higher than previous estimates. These range between $\sim 627\text{K km}^2$ (Karger et al., 2021) and $\sim 2\text{M km}^2$ (Los et al., 2019; Mulligan, 2010) globally for the most restrictive and broadest definitions, respectively. The discrepancies with previous estimates arise from aggregating the predicted suitable areas of the 272 species, as some of those areas are suitable for only a handful of species and cannot confidently represent a TMF community. By increasing the threshold of species considered as indicative of TMF presence – i.e., the number of montane-specialist species with projected suitable climatic conditions per site (pixel) –, my estimates align more closely with previous studies. For example, areas suitable for ≥ 15 montane-specialist tree species amount to $400,021\text{ km}^2$, and for ≥ 50 species to $136,199\text{ km}^2$. These estimates, although based on a reduced number of montane-specialist tree species, are more consistent with regional estimates for the biome, e.g., $\sim 401,300\text{ km}^2$ of TMF cover for the entire Neotropics (Helmer et al., 2019) and $\sim 139,400\text{ km}^2$ for Mexico (Cruz-Cárdenas et al., 2012). The remaining differences between estimates are due to varying definitions of TMFs and the use of different methodologies (Mata-Guel et al., 2023), as my study does not restrict TMFs to areas frequently covered by ground-level clouds (i.e., cloud forests).

The high dissimilarity between montane-specialist tree communities north and south of 12° N suggest that Lake Cocibolca acts as a topographic obstacle for dispersal, marking the southern boundary of the montane-specialist component of Mesoamerican TMFs. In contrast, studies that focus on conservation policies, such as the Mesoamerican Biological Corridor (a chain of natural protected areas covering mainly lowland tropical forests), extend the Mesoamerican

bioregion to Costa Rica and Panama (e.g., Ankersen, 2005; Barquet, 2015; Dettman, 2006). Additionally, the stark reduction in species richness north of the Isthmus of Tehuantepec may suggest another barrier for dispersal. However, a phylogeographic study on 16 populations of *Podocarpus matudae* (an endemic tree of Mesoamerican cloud forests) found that the greatest population divergence for this species could not be attributed to the formation of the Isthmus. Alternatively, the lower species richness north of the Isthmus may reflect the general global trend of lower species richness linked to lower productivity at higher latitudes (Gillman et al., 2015).

Regardless of the degree to which topographic discontinuities hinder dispersal, evidence of unambiguous latitudinal shifts in response to climate change within the tropics remains scant (Colwell and Feeley, 2024). Thus, although the lake may not constitute a dispersal barrier for lowland species and more motile animal taxa, my study provides evidence that the main portion of the Mesoamerican montane-specialist tree community ends at the mountainous regions of northern Nicaragua. Rising temperatures that push tree species upslope would further isolate already fragmented populations (Colwell and Feeley, 2024), and thus passive policies such as chains of protected areas, would need to be complemented with active conservation efforts specific for montane biota.

To my knowledge, this is the first study that provides a species-based characterisation of the Mesoamerican montane-specialist tree community, quantitatively separating montane species into altitudinal and latitudinal classes. The overlap between classes could be indicative of a gradual change in species composition along the altitudinal and latitudinal axes of the study area, except for the discontinuities at Lake Cocibolca and the Isthmus of Tehuantepec. However, since these altitudinal and latitudinal classes are based on model predictions, this characterisation should be corroborated with field surveys to confirm presence and co-occurrence of the listed species. This is particularly important at the northern end of the study area due to its funnel shape, as I do not make a longitudinal classification, and the Sierra Madre Occidental and Sierra Madre Oriental mountain ranges, extending along the Pacific and Atlantic coasts of Mexico, are separated by the Mexican central highlands. An additional consideration is that the species list is not exhaustive. Many tree species were excluded from the analysis because they did not meet the montane-specialist threshold ($\geq 75\%$ of records inside the TMF polygons), or due having insufficient usable records (< 20) to generate SDMs.

Despite increasing availability of global occurrence data, important sampling biases persist even between contiguous regions, such as in Nicaragua compared to Costa Rica and Guatemala compared to Mexico (Ramírez-Barahona et al., 2023).

3.5.2 Impacts of climate change on Mesoamerican montane-specialist trees

The predicted percent reductions of suitable range are consistent with previous studies that have predicted losses of 50% or more of TMFs in the coming decades due to climate change alone or in combination with land use change in Mesoamerica (Ortega et al., 2024), Mexico (Ponce-Reyes et al., 2013, 2012; Rojas-Soto et al., 2012) and at local scales (Altamirano-León et al., 2022; Correa Ayram et al., 2017; Estrada-Contreras et al., 2015). Globally, TMFs have declined at a rate of 0.14% per year between 2001 and 2018, with Guatemala being one of the most severely affected countries (Karger et al., 2021). For the Mesoamerican bioregion, my results suggest that the loss rate could accelerate to as much as 0.24% per year under a high emissions scenario, resulting in a 21.5% loss of suitable areas for the montane-specialist tree community by the end of the century.

This estimate could be worsened by direct anthropogenic impacts, such as land use change, illegal logging, and forest fires. Climate change is pushing agriculture to higher elevations, especially crops typically grown in tropical montane regions, such as coffee (Ovalle-Rivera et al., 2015). When fire is used to open areas for cultivation, recovery is slow due to altered microenvironments, even if seed dispersal is not directly impacted (Lippok et al., 2013). A study on African montane forests found that deforestation enhances air temperature and cloud base height increases beyond what would be expected by climate change alone and even offsetting the buffering effect of the elevational gradient (Abera et al., 2024). Large infrastructure projects, such as the “Corredor Interoceánico del Istmo de Tehuantepec,” consisting of a railway communicating Mexico’s Atlantic and Pacific ports (Thierry-Aguilera et al., 2021), could further disrupt connectivity between montane regions. Fragmentation of TMFs increases the edge effect, which favours the proliferation of pioneer plant species (Lippok et al., 2014), while also decreasing albedo, thus enhancing warming at high elevations (Zeng et al., 2021). Hence, climate change in combination with other direct anthropogenic pressures can generate feedback loops that could push TMFs to a tipping point.

A modest, albeit clear, trend I found is that proportional losses of suitable areas will be more severe for species with restricted range, which has been identified as a factor that increases vulnerability (Pacifi et al., 2015). This is expected due to the already small surface potentially occupied by these species, and because the orographic discontinuity of the suitable areas along mountain ranges might impede effective dispersal and genetic flows. None of the 272 species in my study are categorised by the IUCN (International Union for Conservation of Nature) as critically endangered (CR); only five are endangered (EN), 18 are vulnerable (VU) and 33 are near threatened (NT), two are data deficient (DD) and 12 are not even registered in the IUCN website (NA) (Table S4). With the exception of *Magnolia schiedeana* (see below), all vulnerable species risk losing 60–90% of their climatically suitable habitat by the end of the century. Moreover, the estimated losses of suitable areas by latitudinal and altitudinal classes under the high emissions scenario were predominantly >60%, except for the northern, low-elevation class. Losses were also higher for species with narrow latitudinal ranges (central and southern), and for those at the highest elevations (>2,000 m asl).

Similar trends in latitude and elevation as determining factors of distributional patterns have been reported for other taxa. Epiphytes, a defining feature of TMFs, show increased richness at mid- and high elevations (Krömer et al., 2013; Pouteau et al., 2016), and high levels of vulnerability to climate changes (Hsu et al., 2012; Reyes-Chávez et al., 2021). A study of climate change-driven community disassembly (defined as loss of co-occurrences) along altitudinal gradients comparing ectotherms and endotherms found positive relationships between elevational range and latitude for all included taxa (Sheldon et al., 2011). Moreover, tropical communities are consistently more sensitive than temperate ones to disassembly with increasing temperature (Sheldon et al., 2011), possibly because temperate communities are more successful in tracking suitable climatic conditions latitudinally (Colwell and Feeley, 2024). Greater projected losses at higher elevations could result from the boosting effect of altitude on rising temperatures (Loarie et al., 2009; Williams et al., 2018), combined with highland communities living closer to their physiological limits (Crausbay et al., 2014; Esperón-Rodríguez and Barradas, 2015; but see Mamantov et al., 2021) and limitations to dispersion (Chapman et al., 2016; Nowak et al., 2022) and establishment (e.g., Joshi et al., 2020; Song et al., 2016b, 2016a). These losses are particularly concerning because Neotropical TMFs have a high number of taxa, including birds, mammals, amphibians, and

tree ferns, that are strictly associated with them (Karger et al., 2021), i.e., higher proportion of montane-specialist taxa.

Montane oaks (*Quercus* spp.) are of special concern. A study of 12 endangered and range-restricted Mexican cloud forest trees projected severe habitat losses by 2050 under mid and high emissions scenarios, with the genus *Quercus* (*Q. germana*, *Q. sartorii* and *Q. xalapensis*) displaying the highest sensitivity (Jiménez-García and Peterson, 2019). Similarly, my models predicted that two oaks would experience the second largest losses in total potential suitable area (*Q. salicifolia*, -282,762 km², -74.4%) and percent of potential suitable area (*Q. crispipillis*, -18,173 km², -94.7%), whereas *Q. costaricensis* is categorised as vulnerable by the IUCN (Table S4). Conversely, my models predicted that *M. schiedeana* and *Lacmellea zamorae* will experience gains in suitable range of 185.9% and 27.4%, respectively. For *M. schiedeana*, most of the gains were projected to occur along lowland coastal areas, including the Yucatán peninsula. Previous studies of this species have also reported moderate habitat losses and some expansions to lower elevations (Altamirano-León et al., 2022; Vásquez-Morales et al., 2014). However, such large suitable range gains seem implausible, especially when other limiting factors, such as compromised genetic connectivity are considered (Rico et al., 2023). The projected changes for *L. zamorae* are likely an artefact of scale because it had the second smallest potential suitable range under current conditions (3,977 km²), which means that small changes in predicted suitable area translate into large percent changes.

3.5.3 Conservation management under global change

TMFs are important contributors to global biodiversity and key ecosystem services, such as atmospheric water interception, landslide prevention, and carbon storage (Tognetti et al., 2010); thus, the projected losses are concerning. However, this study shows that even under the severe climate change scenario, there are large areas that could be placed under protection or restoration schemes (e.g., along the Sierra Madre Oriental, the range along the Chiapas-Guatemalan Pacific coast and Costa Rica-western Panama). Due to TMF communities' low ability to track new climatically suitable areas (e.g., Bergamin et al., 2024; Colwell and Feeley, 2024), protected areas schemes might need to be accompanied by active conservation strategies, such as seed banks and assisted migration. Although these strategies have not been widely tested, a transplant experiment of 12 cloud forest tree species (30 seedlings per species) to higher elevations in southern Mexico recorded >90% survival rates after two

years, with canopy and herbaceous cover acting as the main promoters of establishment, and no effect from humidity (García-Hernández et al., 2019). Another transplant experiment of six TMF tree species (3 to 5 individuals per species) also found high establishment rates (>75%) at higher elevations, and detected moderate herbivory in all of them after four years, indicating that some trophic relationships can form or persist post-assisted migration (Toledo-Aceves and del-Val, 2021b).

Additionally, raising both public and academic awareness on the importance of montane flora and the threats it faces may be crucial for conservation efforts, especially for the most vulnerable species (Fišer et al., 2021). An analysis of publication trends on endangered plant species in Brazil found that their inclusion in its national Red List resulted in increased focus on those species, especially ones that are of no commercial interest (Andrade and Freitas, 2021). In that sense, the fact that none of the species in my study are categorised as endangered nor critically endangered by the IUCN might be counterproductive, and even deceptive if they have not been assessed adequately or recently, if at all (2 species are data deficient and 12 are absent [NA] from the IUCN's database; Table S4). For the species facing severe extinction risk, passive protection schemes are unlikely to be successful and may require complementary strategies, such as *ex situ* conservation, as well as population management to promote recovery within their historical range, and reintroduction in target areas (Heywood, 2019). These actions could be focused on species already identified as endangered and which are known to be indicative of TMF, such as the Conifers *Abies guatemalensis*, *A. hickelii* and *Podocarpus matudae*, and broadleaved Angiosperms like *Juglans pyriformis*, *Magnolia schiedeana*, *Persea schiedeana* and *Quercus costaricensis*. To increase success rate of those actions, it should also be a priority to deepen our knowledge of those species at the genetic, physiological and ecological levels.

Thus, a species-level characterisation of the biome throughout its latitudinal and altitudinal ranges is a crucial first step for designing effective conservation strategies for TMFs. Monitoring and taking measures to preserve the co-occurrence of the species that constitute the Mesoamerican TMF tree community would minimise the risk of community disassembly and loss of ecosystem functions and services. TMFs in Latin America have been the most intensively studied globally (Mata-Guel et al., 2023), especially with regard to ecological restoration after disturbances (Christmann and Menor, 2021), but have also been identified as

the region with the fastest climatic shifts (Trew et al., 2024). Cloud-base height/fog cover was not included in this study to avoid overly restricting the montane-specialist community to the narrow definition of tropical montane cloud forest (See Chapter 1.1.1). However, my approach is complementary to a study on cloud immersion declines of montane cloud forests and *páramos* throughout the Neotropics, which projected 60–90% cloud cover declines even under moderate scenarios, and also identified key areas for protection (Helmer et al., 2019). Overall, data availability was the main limitation of this study, leading to the exclusion of a large number of montane-specialist species (Table S3) and the omission of potentially relevant environmental and ecological factors, e.g., lack of data on co-occurrence and interactions with other taxa (herbivores, pollinators, seed dispersers, etc.), especially for rare, range-restricted taxa.

Nonetheless, this study introduces a clear methodology that estimates habitat suitability using species occurrence records instead of non-specific remote sensing data for the montane-specialist component of TMF communities, and projects their risk under climate change. This is particularly relevant for other parts of the world where baseline information on TMF biological communities is lacking, such as central Africa and southeast Asia. Although my methodology is intended to be easily transferable, its application in other regions or ecosystem types, especially those with significantly different dynamics compared to tropical montane regions, would require *ad hoc* variable selection and calibration (Qiao et al., 2019). Several good-practices guides have been published to help researchers increase the accuracy and usefulness of species distribution models (Araújo et al., 2019; Soley-Guardia et al., 2024). Still, with increasing availability of large occurrence databases for species across the globe (Ivanova and Shashkov, 2021), and global climatic models, my approach remains valid for other ecosystem types and taxa, especially if it is complemented with field surveys and experiments.

3.6 Conclusions

In the Mesoamerican bioregion, this study projects 400,021 km² of potential suitable area for >15 species, and 136,199 km² for >50 species out of 272 montane-specialist tree species, which is consistent with estimates based on alternative approaches, such as remote sensing and cloud-base level measurements. The southern limit of the Mesoamerican bioregion may extend to the Panama–Colombia border for lowland species, but Lake Cocibolca in southern

Nicaragua imposes a latitudinal discontinuity around 12° N for montane-specialist tree communities, indicating limited dispersal across lowland regions. Also, the species richness of the montane-specialist tree community halves north of the Isthmus of Tehuantepec, in accordance with global patterns of decreasing richness at higher latitudes. I provide a species-specific characterisation of the Mesoamerican montane-specialist tree community across latitude and altitude, based on predictions of range suitability. Although it necessitates further refinement with field surveys, it should serve as a foundational framework for policy design to monitor and preserve species co-occurrences under climate change.

The power of my estimates comes from the aggregated forecasts for the species included in the models, focusing on the overall habitat suitability of Mesoamerican TMF tree communities, rather than on highly specific parameters for individual species, and the broad extent of the study throughout the Mesoamerican bioregion, ignoring political boundaries. I provide a broad definition of the biome based on habitat suitability of predominantly montane tree species, rather than on topographic features and ground-level clouds that provide little information about species composition. This methodology can thus be easily adapted to other regions, ecosystems, and taxa, providing baseline data to inform the design of conservation policies in poorly studied regions.

Out of the 272 modelled species, 270 were predicted to experience substantial losses of climatically suitable area, in most cases >50%, and with increasing severity at higher elevations, at lower latitudes and for range-restricted species. However, I showed that even under the more severe climate change scenario, some portions of the biome are predicted to remain suitable for a high number of species. This calls for immediate and more effective inclusions of those areas under transnational protection schemes to shield them from other anthropogenic disturbances and ensure connectivity, complemented with active conservation measures to preserve this biologically and culturally crucial biome that extends over seven sovereign countries.

Chapter 4. Functional Traits of the Montane-Specialist Tree Community of Mesoamerica in the Present and under a Changing Climate

4.1 Abstract

Global forests are key ecosystems in the face of climate change. Assessing their functional diversity can aid in predicting how plant communities will respond to shifting environmental conditions and in estimating their potential contribution to mitigating climate change. This study describes the functional diversity of 272 montane-specialist tree species in Mesoamerica based on five functional traits – tree height, diameter at breast height (DBH), wood density (WD), leaf area and leaf mass per area (LMA) – and explores their latitudinal and altitudinal patterns and their phylogenetic influences. It also estimates the carbon storage potential in aboveground biomass (AGB) for the 272 montane-specialist species and possible responses under future climate scenarios. The montane-specialist tree community's functional diversity is adequately described along two axes, corresponding to (1) plant size (tree height and DBH) and (2) leaf and nutrient economics. Tree height and leaf area were correlated positively and negatively, respectively, with latitude. Tree height had the greatest influence on projected potential AGB, whereas I found no influence from WD and DBH. The observed spatial patterns in tree height and leaf area might be associated with the distribution of Conifers that generally reach larger sizes and have smaller leaves, but whose functional space forms a continuum with that of oaks (*Quercus* spp.), whereas other clades form a clearly separate functional cluster. Predicted distributional changes under climate change resulted in the attenuation of the observed latitudinal patterns, but these did not translate into similar losses of potential AGB nor functional diversity. The predicted stability of the functional diversity and spatial patterns of the montane-specialist tree community in Mesoamerica may allow the persistence of these valuable forests and their ecosystem services if adequate conservation measures are implemented to safeguard their remaining suitable habitats.

4.2 Introduction

In light of the impending predicted impacts of climate change, understanding how organisms are able to cope with and adapt to shifting environmental conditions is crucial to preserve biodiversity and ecosystem services. Those mechanisms are largely dictated by the spatial distribution of organisms' functional traits (Violle et al., 2014). Functional traits are the morphological, physiological or phenological characteristics of an organism that determine its fitness in and interactions with other elements of its environment (Violle et al., 2007). The value, range and relative abundance of functional traits in a community or ecosystem constitute its functional diversity (Apaza-Quevedo et al., 2015).

Functional trait analysis is a crucial ecological tool to understand the mechanisms that make organisms resilient or vulnerable to environmental factors (Sodhi et al., 2008). A wide variety of functional trait sets and metrics have been proposed to describe functional diversity, such as functional richness, divergence and evenness (Laliberté and Legendre, 2010), trait probability density (Carmona et al., 2016), hypervolumes (Blonder, 2018), among others. These approaches seek to use functional diversity as a link between environmental factors and plant communities' responses to them (Adler et al., 2013; Li et al., 2020).

To simplify and describe the complexity of functional diversity, a common approach is hypervolumes, which are conceptually similar to an environmental niche in that they represent biological diversity as an n-dimensional hyperspace (Blonder, 2018; Blonder et al., 2018). For functional diversity, each axis represents the possible range of values for each trait. However, there is no consensus on the exact number and identity of those traits. For example, the “global spectrum of plant form and function” (Díaz et al., 2016) posits that most of the variability determinant for plants' survival and reproduction is captured by six aboveground traits distributed along two main axes: (1) plant size (adult plant height, specific stem density and seed mass), and (2) leaf economics spectrum (leaf area, leaf mass per area and leaf nitrogen content per mass unit). Nevertheless, other functional traits such as root traits – often ignored due to the technical and financial difficulties associated with their measurement – can provide key complementary information (Carmona et al., 2021).

Besides the complex nature of functional diversity, a challenge in functional traits analysis is data availability. The development of open access databases, such as TRY (Kattge et al., 2020) and BIEN (Maitner et al., 2018), has recently made global quantitative studies possible. However, with the exception of plant height and wood density, there is a stark mismatch between the most influential traits and those most widely available in global databases (Kühn et al., 2021). There is also an overrepresentation of studies focusing on leaf traits relative to traits that promote plants' positive responses to environmental changes, such as water use efficiency, resprouting ability, growth rate and clonality (Kühn et al., 2021). Some additional shortcomings of functional trait analysis are the difficulty in detecting and explaining ‘holes’ in hypervolumes, i.e., unrealised combinations of traits that hint at non-considered ecological or evolutionary processes (Blonder, 2016), and the prevalent neglect of intraspecific trait variation, in favour of average values at species level (Heilmeier, 2019).

Despite the limitations and challenges of functional trait analysis, some consistent trends have been identified in global functional diversity and in relation to plants' resilience or vulnerability

in face of environmental change. Firstly, it has been shown that taxonomic diversity is not directly linked to functional diversity (Hernández-Vargas et al., 2019). Functional traits have varying degrees of inheritability reflected in clustering at the family level (Ahrens et al., 2020), which allows for the use of phylogeny as a proxy for missing data imputation (Flores and Coomes, 2011; Joswig et al., 2023). However, at small scales, functional diversity tends to show higher dispersion than phylogeny (Swenson and Enquist, 2009). This is likely an effect of competition, resulting in niche partitioning of the habitat (Adler et al., 2013) along multiple axes that enable coexistence (Kraft et al., 2015), albeit to a degree. Somewhat counterintuitively, interspecific variation can increase competition (Blonder, 2018) in the absence of temporal variation or due to dearth of resources (Adler et al., 2013), which may lead to functional convergence (Hernández-Vargas et al., 2019). Thus, diverse ecosystems maintain some degree of functional redundancy that makes the loss of some components without an immediate disruption of ecological functions possible (Aguirre-Gutiérrez et al., 2022; Carmona et al., 2016).

Secondly, functional diversity follows some identifiable geographical patterns, which are sometimes non-causally correlated to phylogenetic ones. Globally, functional diversity changes along latitudinal and altitudinal gradients, with the former having a stronger influence (Wieczynski et al., 2019). However, the mechanisms that drive these spatial patterns are highly disputed and are likely case-specific. Some studies have identified temperature as the single main driver of functional diversity (Moles et al., 2014) or in combination with other factors like nutrient availability (Apaza-Quevedo et al., 2015) or disturbances (van der Sande et al., 2023). Other studies have found water availability variables to be much more important than temperature (e.g., Álvarez-Dávila et al., 2017; Li et al., 2020). The actual mechanisms are likely more nuanced, with both energy and water-related variables playing compounding, and sometimes offsetting roles, depending on the site and the temporal scale. For instance, Wieczynski et al. (2019) found that while hydric pressure promotes functional diversity, high temperature variability is a limiting factor; in contrast, Wang and Ali (2021) concluded that high temperature and low aridity are positively correlated with functional diversity. Although the combination of temperature and water availability might explain up to 90% of local environmental variability (Vilanova et al., 2018), other factors such as nutrient availability, soil conditions, spatial and temporal heterogeneity and the presence of natural enemies can also shape a community's functional diversity (Adler et al., 2013; Apaza-Quevedo et al., 2015; Báez and Homeier, 2018). Furthermore, no two functional traits respond to the same set of environmental variables, leading to varying rates of trait divergence and evolution (Ahrens et al., 2020).

A third trend is the role that rare and range-restricted species have on functional diversity. It has been reported that despite their low abundance and narrow habitat breadths, rare species contribute disproportionately to their communities' functional diversity by occupying unique – i.e. non-redundant – functional spaces, which in turn support vulnerable ecosystem functions (Leitão et al., 2016; Mi et al., 2021; Mouillot et al., 2013). In the Neotropics, montane communities are larger than those of other tropical regions due to the presence of large and continuous mountain ranges (Laurance et al., 2011), and are thus a hotspot of rare species (Zizka et al., 2018). As climate change progresses pushing montane species to higher elevations, they are projected to run out of suitable areas faster than lowland and temperate communities (Freeman et al., 2021). Well-established mature communities (e.g., tropical montane forests) have developed over evolutionary time high phylogenetic and functional diversity that allow coexisting species to exploit many specialised microhabitats (Sodhi et al., 2008). They also sustain key ecosystem services, such as water interception (Ah-Peng et al., 2017; Holwerda et al., 2010) and carbon sequestration in standing biomass and soils (Augusto and Boča, 2022). In fact, there is evidence that carbon stocks in Neotropical montane regions have been underestimated (Álvarez-Dávila et al., 2017), highlighting the pertinence of characterising the functional diversity of its montane-specialist community along its geographical range and how it may respond to anthropogenic climate change.

In this chapter, I build upon the Species Distribution Models of Chapter 3 to characterise the montane-specialist subset of tree communities in Mesoamerica in terms of aboveground functional diversity. Firstly, I assess how the functional traits of the Mesoamerican montane-specialist trees are distributed throughout the latitudinal and elevational gradients of the study area and if their variation can be described along general PCA axes, such as tree size and leaf economics. Secondly, I explore how the functional diversity will be altered by climate change based on the projected suitable areas under current and future climatic conditions by the end of the century and if the projected changes can be explained by the montane-specialist trees' functional traits. Finally, I test the montane-specialist tree subcommunity's potential carbon storage capacity in the form of aboveground biomass under future compared to current climatic conditions. Even though this analysis could benefit significantly from abundance data, mainly to improve the accuracy of estimates locally, this study can still provide valuable insights. Examining the diversity, range and spatial distributions of functional traits within these montane subcommunity can shed light on their ecological roles, functional redundancy and potential resilience to environmental changes.

4.3 Methods

4.3.1 Study area, data sources and missing data imputation

Species Distribution Models. This study covered the montane-specialist community of the Mesoamerican montane forest region, as defined in Chapter 3.3.1. The community extends from the portion of Mexico below $\sim 25^\circ$ N throughout Central America to the Panama-Colombia border, and is based on the combined polygons of the tropical montane forest (TMF) area from Villaseñor (2010) and Los et al. (2021). The species list was built from the harmonised national inventories from Mexico and all Central American countries except Belize (whose territory lies entirely outside of my TMF polygons). I downloaded their occurrence records from GBIF (www.gbif.org; 21st June 2022, <https://doi.org/10.15468/dl.dsbdhrh>) and used the combined TMF polygon to retain montane specialists, i.e., species with $\geq 75\%$ of their occurrence records inside the TMF areas. I thinned the records to a 1 km² grid and discarded species with < 20 occurrences, resulting in 272 montane-specialist species (Table S4). As static variables, I derived aspect, slope and ruggedness from WorldClim's digital elevation model (www.worldclim.org/data/worldclim21.html, Fick and Hijmans, 2017) and obtained soil type from the FAO's Harmonized World Soil Database v 1.2 (Fischer et al., 2008). I downloaded all bioclimatic variables from CHELSA v2.1 (<http://chelsa-climate.org/bioclim/>, Karger et al., 2017) under current (1981–2010 baseline) and future conditions by the end of the century (2071–2100) with the severe climate change scenario RCP8.5. After testing for collinearity, I retained the following six: temperature seasonality (BIO4), mean temperature of the wettest quarter (BIO8), mean temperature of the driest quarter (BIO9), precipitation of the driest month (BIO14), precipitation of the wettest quarter (BIO16) and precipitation of the coldest quarter (BIO19). I generated the Species Distribution Models with the *biomod2* R package (Thuiller et al., 2016) using the ten environmental variables and four complementary algorithms (GAM, ANN, GBM and MaxEnt; Guisan et al., 2017). See Chapter 3.3.2 for full details.

Functional Traits Analysis. For the 272 tree species, I obtained four out of the six key functional traits according to the “global spectrum of plant form and function” (Díaz et al., 2016): adult plant height, stem specific density (henceforth wood density, WD), leaf area (LA), leaf mass per area (LMA), because these were the only traits available for most (60.2%) of the genera. I included an additional trait – diameter at breast height (DBH) – that allowed estimating standing biomass, using the equation $AGB = 0.0673 \cdot (WD \cdot DBH^2 \cdot H)^{0.976}$ (best-fit pantropical model; Chave et al., 2014; Cuni-Sanchez et al., 2021). I used the averages of the tree size variables (H and DBH), so the standing biomass represents potential mean AGB, henceforth AGB_P. I downloaded the functional traits from the TRY (Kattge et al., 2020) and BIEN v4.2

databases (Maitner et al., 2018). To build the most complete pre-imputation functional traits dataset possible (Table S9), I prioritised values at the species level, otherwise I used the average at the genus level if available, or calculated the average from other available species of the same genus, since functional traits tend to be conservative within lineages (Flores and Coomes, 2011; Joswig et al., 2023). I complemented average height and DBH with records from scanned herbaria specimens available in GBIF (www.gbif.org; consulted March-April 2024), and WD with the Global Wood Density Database (Zanne, 2009) and Ordóñez Díaz et al. (2015). When specific leaf area ($\text{mm}^2 \text{mg}^{-1}$) was reported, I calculated the inverse to obtain LMA. I harmonised all the variables to standard units (tree height in m, DBH in cm, WD in g cm^3 , LA in mm^2 , and LMA in mg mm^{-2}). For missing data, I used the data imputation process described in (Carmona et al., 2024) with the *V.PhyloMaker* package (Jin and Qian, 2022), which uses phylogenetic relationships as proxy to fill in missing values (Table S10).

4.3.2 Analysis of spatial patterns of functional traits and their influence on species' distributional changes under climate change

To examine the spatial patterns of the functional traits across the study area, I added the imputed functional traits data to species richness matrices derived from the distribution models under current (1981-2010 baseline) and future (2071-2100, RCP8.5) climatic conditions generated in Chapter 3.3.3. These matrices contain predicted climatic suitability data for each of the 272 tree species per pixel at 30 arc-seconds resolution. I calculated the community-weighted mean (CWM) for each functional trait and AGB_p per pixel based on the frequency of species present in all pixels (Lavorel et al., 2008). Additionally, I calculated functional dispersion (FDis) using the four available traits (tree height, wood density, leaf area and LMA) out six listed by Díaz et al. (2016). FDis measures the spread of species traits relative to the centroid of their multidimensional trait space, reflecting the breadth of ecological strategies within the community (Laliberté and Legendre, 2010). I chose FDis because, unlike other functional diversity metrics, it emphasises trait spread, and it is not dependant on species abundance, although it can incorporate abundance data when available (Laliberté and Legendre, 2010). All CWM and FDis calculations were performed using the *FD* R package (Laliberté et al., 2009). I converted the resulting CWM and FDis matrices back into georeferenced raster layers using the *raster* R package (Hijmans, 2020) and estimated the changes in each trait by the end of the century by subtracting each current raster layer from its corresponding future one.

To determine whether each of the functional traits was associated with elevation and latitude, as has been shown globally (Wieczynski et al., 2019), I transformed the rasters into *SpatRaster* objects and loaded an elevation layer using the *terra* package (Hijmans et al., 2022). To account

for spatial autocorrelation, I used the *spdep* package (Bivand et al., 2017) to estimate each functional trait layer's Moran's I coefficient (Table S11). I extracted the trait value and ran Pearson correlation tests between each trait and the associated elevation (m asl) and latitude per pixel. Since most montane-specialist tree species were projected to lose a large part of their suitable range (>60%), resulting in high species turnover at mid-elevations throughout the whole range (see Chapter 3.4.2), I expected these shifts to translate into significant changes in the spatial distribution of each functional trait by the end of the century.

To investigate whether the functional traits of the tree species have an influence on the predicted suitable areas under current and future climatic conditions, I ran linear regression models using each of the five functional traits for the species as explanatory variables for the predicted estimates of climatically suitable areas (in km²) under current and future conditions, and on projected total losses and percent losses. To explore how well the variation of the tree species is captured by the set of five functional traits, I ran a PCA using the *ade4* package (Dray and Siberchicot, 2017) and estimated the proportion of variation explained by each axis and their level of significance using Monte-Carlo simulations (Díaz et al., 2016). To identify variation patterns in my data, I plotted the PCA by taxonomic group, latitudinal and altitudinal classes (see Chapter 3.3.3). To handle collinearity between explanatory variables, I ran pairwise Pearson correlation tests, using the *rcorr()* function of the *Hmisc* R package (Harrell Jr, 2019). To standardise the data (reduce the influence of extreme values and varying degrees of magnitude between variables), I log10-transformed and scaled the dataset (Carmona et al., 2024; Díaz et al., 2016) and ran a bidirectional stepwise regression using the *stepAIC()* function of the *MASS* R package (Ripley et al., 2013) to identify the best performing linear model for each response variable, based on the Akaike Information Criterion. I thus reduced the number of explanatory variables to include only those with a significant effect on range sizes and changes. I tested the models' assumptions with the Shapiro-Wilk and Breusch-Pagan tests. All calculations were done in R v4.4.0.

4.4 Results

4.4.1 Current functional diversity patterns

Using the distribution models of 272 Mesoamerican montane-specialist tree species developed in Chapter 3, I calculated the community-weighted mean of each functional trait (tree height, DBH, WD, leaf area and LMA) and AGB_P, based on species projected to have suitable areas under current and future climatic conditions (RCP8.5 scenario).

Among the traits, WD ($0.54 \pm 0.03 \text{ g cm}^{-3}$) and LMA ($0.08 \pm 0.01 \text{ mg mm}^{-2}$) exhibited the least variation, whereas leaf area ($5,514.9 \pm 2,035.6 \text{ mm}^2$) varied by several orders of magnitude (Table 4.1), likely due to differences between scale- or needle-like leaves of Conifers and broadleaved Angiosperms. The mean sizes of the species were $15.28 (\pm 4.28) \text{ m}$ in height and $30.98 (\pm 14.88) \text{ cm}$ in DBH under current conditions (Table 4.1). The varying height-to-DBH ratios translated into highly variable AGB_P ($1,784.0 \pm 1,978.7 \text{ kg}$).

Table 4.1 Summary statistics of the community-weighted means of functional traits and aboveground biomass of the montane-specialist tree species throughout the study area on a pixel-by-pixel basis, under current (1981–2010 baseline) and future (2071–2100) climate conditions under RCP8.5. Change refers to the average difference per site (pixel) between current and future raster layers, so they do not correspond to a simple subtraction of the bulk current and future values.

| Trait | Time frame | mean | sd | min | 1st q | median | 3rd q | max |
|---------------------------------|------------|---------|---------|-----------|---------|---------|---------|----------|
| H (m) | current | 15.28 | 4.28 | 3.33 | 11.94 | 15.30 | 17.72 | 40.00 |
| | future | 16.02 | 4.36 | 3.83 | 12.72 | 15.88 | 18.75 | 38.17 |
| | change | 0.13 | 3.79 | -23.25 | -1.97 | 0.20 | 1.83 | 24.75 |
| DBH (cm) | current | 30.98 | 14.88 | 1.33 | 20.83 | 28.72 | 37.81 | 153.33 |
| | future | 33.94 | 16.29 | 1.90 | 22.28 | 31.37 | 40.61 | 140.00 |
| | change | 1.50 | 14.00 | -79.50 | -5.06 | 0.66 | 6.91 | 107.65 |
| WD (g cm⁻³) | current | 0.54 | 0.03 | 0.40 | 0.53 | 0.54 | 0.55 | 0.76 |
| | future | 0.53 | 0.03 | 0.40 | 0.52 | 0.53 | 0.55 | 0.70 |
| | change | -0.01 | 0.03 | -0.19 | -0.02 | 0.00 | 0.01 | 0.18 |
| LA (mm²) | current | 5,514.9 | 2,035.6 | 673.8 | 4,234.1 | 5,351.2 | 6,606.2 | 21,551.3 |
| | future | 5,724.7 | 2,310.1 | 789.1 | 4,212.4 | 5,444.5 | 7,025.5 | 21,551.3 |
| | change | 69.5 | 1,394.1 | -9,542.2 | -601.2 | 31.1 | 681.7 | 11,070.9 |
| LMA (mg mm⁻²) | current | 0.08 | 0.01 | 0.03 | 0.08 | 0.08 | 0.09 | 0.19 |
| | future | 0.09 | 0.01 | 0.03 | 0.08 | 0.08 | 0.09 | 0.18 |
| | change | 0.00 | 0.01 | -0.11 | -0.01 | 0.00 | 0.01 | 0.10 |
| AGB_P (kg) | current | 1,784.0 | 1,978.7 | 0.2 | 397.6 | 1,207.6 | 2,401.4 | 23,191.4 |
| | future | 1,868.2 | 1,836.2 | 1.2 | 421.7 | 1,334.8 | 2,666.3 | 15,420.9 |
| | change | -80.9 | 1,843.2 | -18,181.3 | -656.1 | -13.4 | 506.5 | 12,668.5 |

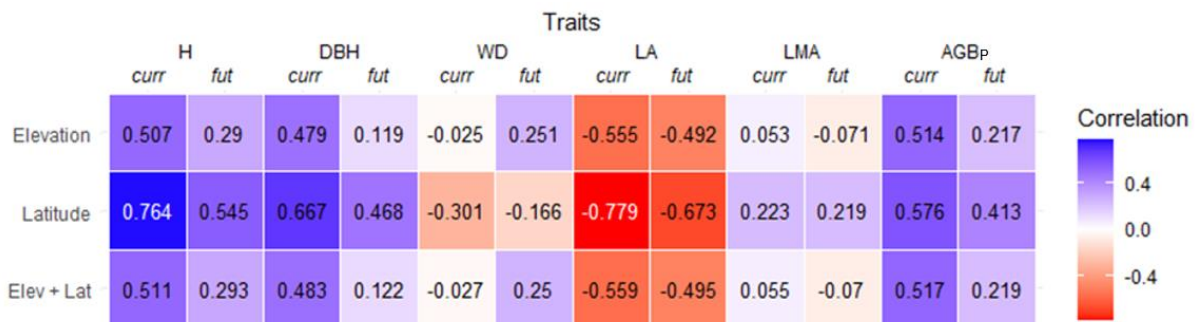


Figure 4.1 Heatmap of Pearson correlation coefficients of the elevational and latitudinal gradients and the CWMs of functional traits (H, DBH, WD, LA and LMA) and AGB_P of the species projected to have suitable area per pixel under current (1981–2010 baseline) and future (2071–2100) climate conditions (RCP8.5 scenario). Darker colours indicate stronger correlations. p-values < 0.0001 in all cases.

Out of the five traits and potential AGB_P , tree height and leaf area had the strongest correlations with elevation and especially latitude (Figure 4.1). Suitable areas for taller tree species tended to concentrate in higher latitudes ($r = 0.76$, $p < 0.0001$; Figure 4.2A) and elevations ($r = 0.51$, $p <$

0.0001), whereas areas suitable for species with large leaves were more common at lower latitudes ($r = -0.78$, $p < 0.0001$; Figure 4.2C) and lower elevation ($r = -0.56$, $p < 0.0001$), both under current conditions. Taller tree species were projected to have more suitable conditions on the inland-facing edges of the Sierra Madre Oriental and Sierra Madre Occidental ranges, flanked by slightly shorter species at similar latitudes and a shortening height pattern further into Central America. Leaf area also had a clear north-south gradient, with big-leaved species being more common at lower latitudes, especially into southern Central America and into Colombia (southern buffer area), and a pattern on the northern part of the range of larger leaves on the ocean-facing slopes and smaller leaves on the slopes facing inland.

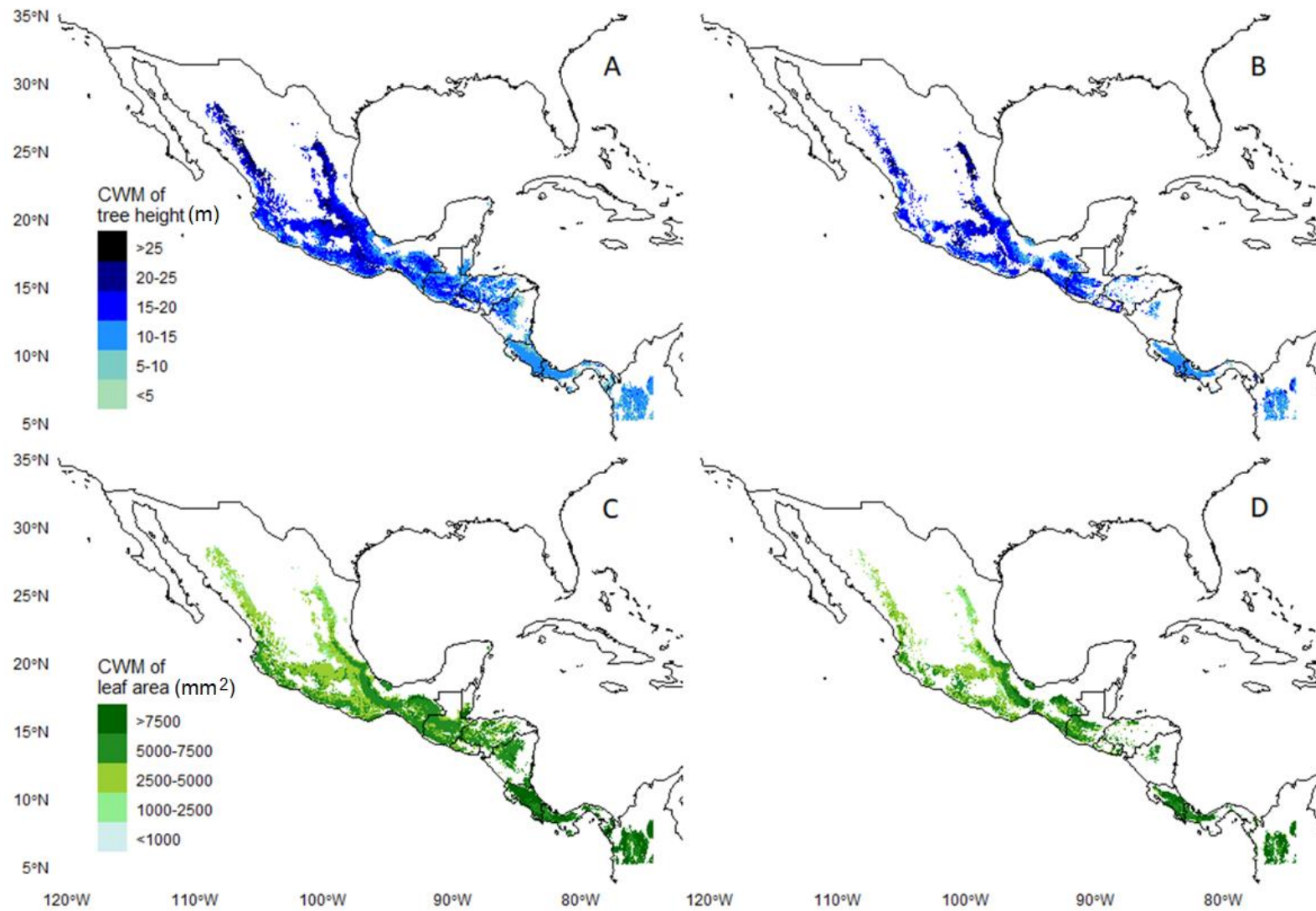


Figure 4.2 Community-weighted means of tree height (A and B) and leaf area (C and D) of the montane-specialist tree species projected to be present under current (A and C) and future (B and D) climatic conditions.

4.4.1 PCA of the montane-specialist trees functional traits

Out of the five functional traits, only height and DBH were moderately correlated ($r = 0.632$, $p < 0.0001$), which suggests varying ratios of height to stem width of tropical montane-specialist trees. The association between the two adult tree size-related traits was also apparent in the PCA, with tree height and DBH varying along the PC1 axis (Figure 4.3). The variation of the functional traits was captured by five components, with plant size-related traits (PC1) and leaf and biomass traits (PC2) explaining an accumulated 62.63% of the total variation (Table S12).

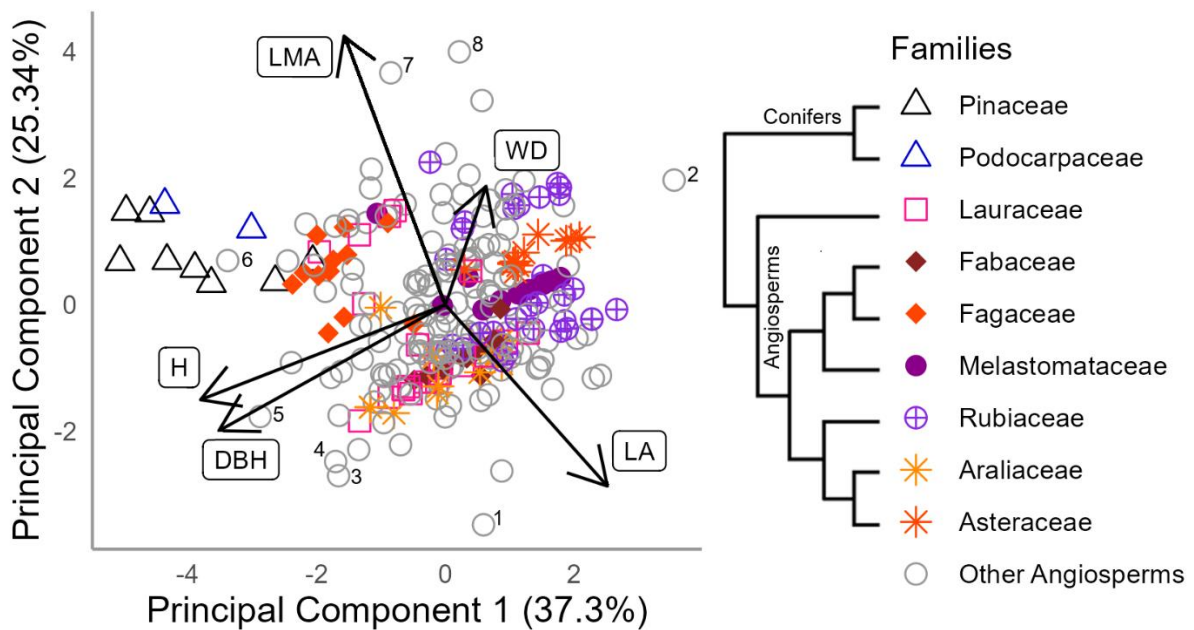


Figure 4.3 PCA of five functional traits of montane-specialist tree species by most frequent taxonomic groups. The directions and lengths of the loadings indicate that most of the variation in PC1 aligns with adult tree size-related variables (tree height and DBH), whereas PC2 is more aligned with leaf traits and biomass (leaf area, LMA and to a lesser extent WD). Height and DBH remain closely aligned when plotting other components. Most Conifers are outliers, occupying a distinct functional space along the PC1 separated from most Angiosperm families. Other outliers, belonging to various Angiosperm lineages (see Table S4), are shown with numbers:

- (1) *Meliosma alba* [Clade Basal Eudicots, Proteales, Sabiaceae],
- (2) *Hypericum irazuense* [Clade Rosid I/Fabids, Malpighiales, Hypericaceae],
- (3) *Juglans pyriformis* [N-fixing Clade, Fagales, Juglandaceae],
- (4) *Ulmus Mexicana* [N-fixing Clade, Rosales, Ulmaceae],
- (5) *Chiranthodendron pentadactylon* [Clade Rosid II/Malvids, Malvales, Malvaceae],
- (6) *Clethra suaveolens* [Clade Basal Asterids, Ericales, Clethraceae],
- (7) *Comarostaphylis arbutoides* and (8) *C. longifolia* [Clade Basal Asterids, Ericales, Ericaceae], and
- (9) *Buddleja nitida* [Clade Asterid I/Lamids, Lamiales, Scrophulariaceae].

The PCA also revealed some important taxonomic trends (Figure 4.3). Most Conifers were outliers and formed a clearly distinct group separated from the rest of the community along PC1, but they also seemed to form a continuous functional space with Fagaceae (*Quercus* spp.). Most species belonging to the remaining most abundant families formed another cluster separated from the Conifers-Fagaceae continuum along PC2. Only Lauraceae straddled these

two distinct clusters, with some species intermixed with Fagaceae, and the rest with the bulk of other frequent Angiosperms. Additionally, the most closely related families do not form continuous clusters. Such is the case of Fabaceae and Fagaceae within the N-fixing clade (Rosid I *sensu* APW v14, 2017; Stevens, P.F. (2001 onwards) Angiosperm Phylogeny Website, www.mobot.org/MOBOT/research/APweb/), and of Araliaceae and Asteraceae within the Asterid II clade (*IDEM*), but that form distinct clusters separated from each other. The remaining families (Other Angiosperms) had fewer than 5 representatives each to confidently describe any patterns. Aside from Conifers, nine other species were outliers in the PCA, which did not belong to closely related Angiosperm lineages.

4.4.2 Future functional diversity patterns

Under the RCP8.5 scenario, the community-weighted means of all traits remained relatively stable by the end of the century (Table 4.1). Except for wood density, most functional traits were projected to maintain their current distributional patterns throughout the study area, although correlations with latitude and elevation were noticeably less strong (Figure 4.1). Changes in species composition per site (pixel) might also lead to a slight decrease in the potential community average biomass under future climatic conditions (-80.9 kg difference in potential community-weighted mean AGB_P of species with predicted suitable conditions across all sites; Table 4.1).

The trends of higher community-weighted mean tree height at higher latitudes ($r = 0.55$, $p < 0.0001$; Figure 4.2B) and elevations ($r = 0.29$, $p < 0.0001$), and of greater leaf area at lower latitudes ($r = -0.67$, $p < 0.001$; Figure 4.2D) and elevations ($r = -0.49$, $p < 0.0001$) were attenuated, although they were still present. The functional traits maps under future conditions also reflect the predicted size reduction of climatically suitable areas due to climate change. Out of the remaining traits, only DBH (Fig. S2) showed a similar albeit less strong trend to tree height; there were no clear geographical patterns for WD (Fig. S3) and LMA (Fig. S4).

The latitudinal pattern of tree height (and correlated DBH) resulted in an estimated community-weighted mean AGB_P with the same latitudinal pattern. Since the community-weighted tree height was inversely correlated with latitude, the average AGB_P also decreased southwards, where there is projected climatically suitable habitat for a higher proportion of short-statured tree species (Figure 4.4A), some of which can occur as shrubs. When plotting the projected differences in potential community-weighted mean AGB_P between current and future conditions, there is a patchwork of areas projected to experience small potential gains and, to a lesser degree, losses in potential AGB_P throughout the study area (Figure 4.4B). Note that the

spatial AGB_p distribution is an estimate of the potential carbon stored by montane-specialist species under current or future climatic conditions in each site (pixel) within the study area. It should be taken as an indicator of where suitable conditions for montane-specialist species with high carbon storage capacity occur, rather than the actual amount of carbon in these ecosystems.

Functional dispersion (FDis) did not show a clear latitudinal pattern, but it seemed higher at higher elevations (centres of polygons) and decreased near the edges (Figure 4.4C), coinciding with areas projected to have high species richness (see Chapter 3). When subtracting projected future FDis from current FDis, it seemed to remain largely stable, except for some small gains at the highest elevations and small losses at low elevations (Figure 4.4D).

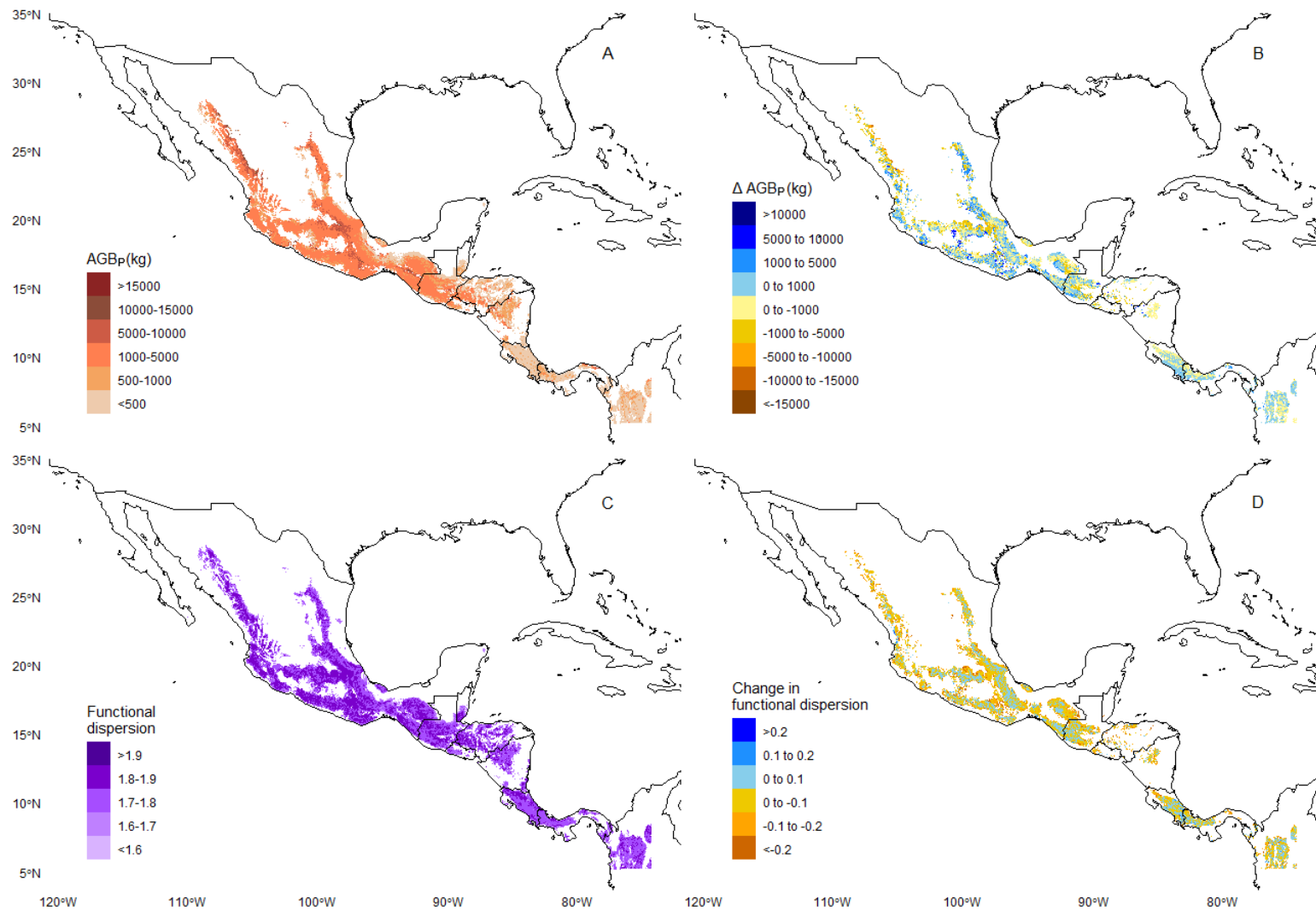


Figure 4.4 Community-weighted mean (CWM) of potential aboveground biomass (AGBP) based on the species projected to have suitable conditions under current climate conditions (A), projected changes in CWM AGBP under future with respect to current climatic conditions (B), functional dispersion of the 272 montane-specialist tree species under current conditions (C) and projected changes in functional dispersion under future with respect to future climatic conditions (D).

4.4.3 Functional traits' influence on projected habitat suitability loss under climate change

The stepwise regression showed that the combination of tree height and leaf area were the best predictors for both the current and future size of suitable ranges for the ensemble of species (best model in each case; **current** $\text{lm} = 4.96 + 0.45H - 0.19LA$; $F_{2, 269} = 21.92$; $p < 0.0001$; $R^2 = 0.13$; Shapiro-Wilk $W = 0.99$, $p = 0.225$; Breusch-Pagan $BP = 2.08$, $p = 0.353$; **future** $\text{lm} = 4.17 + 0.52H - 0.13LA$; $F_{2, 269} = 13.9$, $p < 0.0001$; $R^2 = 0.09$; $W = 0.99$, $p = 0.321$; $BP = 3.26$, $p = 0.195$). For both time frames, tree height and leaf area were the only variables with a significant effect on the size of the suitable area. Similarly, there was a small influence of height and leaf area on the total losses of predicted suitable areas under future with respect to present climatic conditions (Gamma $\text{glm} = 1.62 + 0.08H - 0.05LA$; $W = 0.99$, $p = 0.063$; $BP = 0.16$, $p = 0.923$). The taller species, which were predominantly distributed in the central and northern-central areas throughout the study region, and other widespread species were predicted to experience the largest losses in suitable area (Figure 4.5), in line with the total predicted area losses being associated with current range size (see Chapter 3.4.2). However, neither tree height, nor any other functional traits, on their own or in combination, were correlated with predicted percent range losses under future conditions.

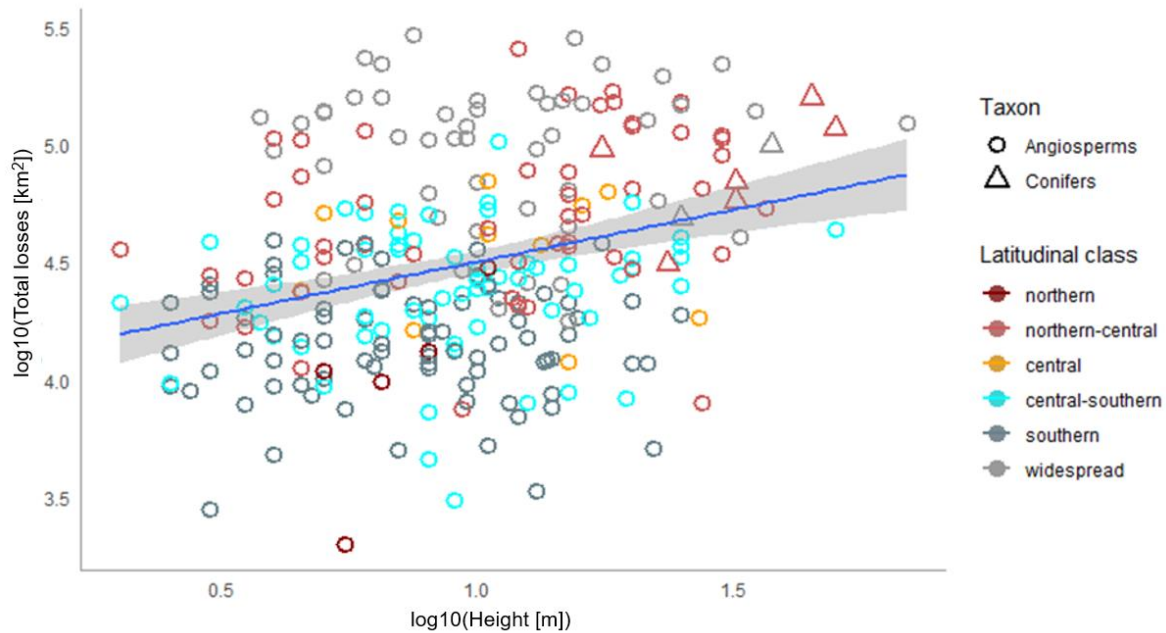


Figure 4.5 Relationship between adult tree height and log-transformed total losses projected suitable extent under future climate conditions relative to current conditions by taxonomic group and latitudinal class.

4.5 Discussion

I analysed five aboveground functional traits (tree height, DBH, WD, leaf area and LMA) of 272 montane-specialist tree species in Mesoamerica. The main drivers of functional diversity were tree height and leaf area. I also investigated how these traits translate into carbon storage capacity in the form of potential aboveground biomass (AGB_p) and estimated the functional dispersion of the montane-specialist community. AGB_p followed a similar pattern to tree height, with higher values at higher latitudes, whereas functional dispersion was more positively related to elevation. Under future conditions, both potential AGB_p and functional dispersion were projected to remain largely stable throughout the whole study area, but with marked local variation.

4.5.1 Current distributional patterns of functional diversity

The five functional traits included in this analysis revealed some significant trends. Within the range where tropical montane specialists are projected to occur currently, adult plant size tends to be larger, and leaf area tends to be smaller at higher latitudes. The greater variability in DBH compared to height is expected for montane communities, which either comprise several strata or transition from tall to short vegetation types within short distances along

mountain slopes (Scatena et al., 2010). This variability is reflected in varying height-DBH ratios. The wide standard error in DBH could also be attributable to a few very large species, including the Mexican elm (*Ulmus mexicana*), Mexican white pine (*Pinus ayacahuite*) and the cloud forest oak *Quercus benthamii*.

The absence of clear geographical patterns for the other traits aligns with previous studies, which have shown that height and leaf area are more responsive to environmental factors than, for instance, wood density and seed mass (van der Sande et al., 2023). Wood density is more commonly linked to successional stages and their growth strategies than directly to environmental drivers. Early successional species with a high resource acquisition strategy typically have low wood density, while late successional species have higher wood density (Castillo-Figueroa et al., 2023). Similarly, leaf mass per area indicates a resource acquisition strategy (Díaz et al., 2016), so the lack of a clear spatial pattern across a large, rugged area with microhabitat variation could be expected.

Similar observations for other traits such as deciduousness have been made, showing a stronger association with growth strategy rather than environmental factors. For example, a study of two subcommunities (deciduous and evergreen) in a karst forest in southern China found that deciduous species are linked to a high resource acquisition strategy, whereas evergreen species favour resource conservation by investing in long-lasting, high-quality tissues (Wang et al., 2023). Regarding functional traits that influence water use, high wood density is associated with greater drought tolerance, but this relationship is context-dependent (Ahrens et al., 2020). Stomatal control, a key functional trait for hydraulic failure prevention, does not always correlate with the water gradient either (Sterck et al., 2011).

The community-weighted mean AGB_p of the montane-specialist tree community followed a similar latitudinal gradient to tree height under current climatic conditions. Wood density, one of the least variable traits, had a lesser influence on AGB_p . These findings provide additional evidence that tree size (i.e. height) and AGB are strongly correlated (Wang and Ali, 2021) whereas AGB has weak or no relation with wood density (Álvarez-Dávila et al., 2017).

4.5.2 Phylogenetic divergence of functional diversity

The distribution of the analysed functional traits along two main PCA axes – with PC1 associated with plant size (height and DBH), and PC2 related to leaf economics and nutrient

acquisition strategy (wood density, leaf area, and leaf mass per area) – aligned with the "global spectrum of plant form and function" framework (Carmona et al., 2021; Díaz et al., 2016). The PCA also revealed some phylogenetic patterns. Firstly, the functional space of Conifers was clearly separated from the rest of the species along PC1 (tree size), indicating that Conifers tend to reach larger sizes than Angiosperms. This contributed to the larger community-weighted mean sizes in the less diverse northern parts of the study area. Secondly, the proximity of the functional trait spaces of Conifers and Fagaceae (*Quercus* spp.) suggests a functional gradient due to their similar roles as keystone species in montane regions, where they often form distinct pine- and oak-dominated communities with transitional mixed pine-oak forests between them (Alfaro et al., 2014). Thirdly, species within the same family tended to cluster in close functional spaces, reflecting a trend of trait conservatism within lineages at lower taxonomic levels. However, at higher taxonomic levels, closely related families tended to avoid each other's functional spaces. This pattern could be due to competitive pressures within lineages leading to niche partitioning, while environmental constraints push unrelated clades into narrower functional trait spaces.

These patterns match those observed in an Amazon-to-Andes altitudinal gradient, where closely related lineages were found to remain within similar elevations, whereas higher clades preferred different altitudes (Griffiths et al., 2021). Asterids were more dominant at higher elevations, Rosids at lower elevations and Podocarpaceae (Conifers) at mid elevations, whereas Magnoliids were split between mid and low elevations. Families within the Asterids and Rosids clades did not have such clearly split functional spaces, except for Fagaceae (Rosids) by forming a continuum with Conifers. Lauraceae straddled both functional space clusters, which could be related to the broader altitudinal range of the Magnoliid clade described by Griffiths et al. (2021). Additionally, other species with trait combinations that situate them on the edges of the functional trait space (outliers) belong to families spread across the whole Angiosperm cladogram, which might indicate non-redundant niches that, if lost, could result in a net reduction of the of the community's functional diversity. Among these, there are other large-statured Angiosperm species, such as *Chiranthodendron pentadactylon*, *Juglans pyriformis* and *Ulmus mexicana*.

While phylogenetic affiliation is generally a good proxy for ecological similarity, enabling missing data imputation (Jin and Qian, 2022; Joswig et al., 2023), co-occurring species face

pressures that promote both functional differentiation (e.g., competition) and convergence (e.g., limiting factors) (Swenson and Enquist, 2009). Given that this database relied on phylogeny to fill data gaps, the observed family-clustering pattern could partly result from the data imputation method. Nevertheless, the greater differentiation at higher taxonomic levels (between families) compared to lower levels (within families) may reflect evolutionary timescales, as some functional trait changes in response to environmental factors have been detected over periods of 10,000 years (van der Sande et al., 2023). This suggests that families have had more evolutionary time to develop distinct functional spaces than the genera within each family.

4.5.3 Predicted effects on functional traits and aboveground biomass under climate change

The latitudinal trends of tree height and, to a lesser extent, that of leaf area were less apparent under projected future climatic conditions. The higher proportion of big-leaved species predicted to remain constant was especially marked in the central part of the study area, in the Mexican states of Oaxaca and Chiapas flanking the Isthmus of Tehuantepec, and southern Central America, especially in Costa Rica, which also correspond to the areas with the highest species richness (see Chapter 3.4.2). Thus, even if proportionally similar richness losses occurred throughout the whole latitudinal range, the relative proportion of tall, small-leaved species would remain more noticeable in the northern parts of the study area.

The attenuations of latitudinal trends of functional traits are likely due to a reduction in the size of climatically suitable areas for the ensemble of tree species, rather than the northward migration of shorter, big-leaved species from more southern areas. A recent review of distributional changes in response to climate change did not find evidence of tropical communities successfully migrating latitudinally, as opposed to their temperate counterparts (Colwell and Feeley, 2024). Additionally, a study in the Brazilian Atlantic Forest biome found that half of the surveyed montane communities have not migrated in response to changing climate (Bergamin et al., 2024). Of the remaining communities, those at higher altitudes tended to migrate upward, whereas lowland communities migrated downward.

As the main driver of functional diversity of the montane-specialist tree community, tree height seemed to have an inverse relationship with the magnitude of suitable area losses, but

that did not translate into a positive association between tree height and percent losses of suitable habitat. Likewise, tree height drove the latitudinal pattern of AGB_P under current conditions, but that did not translate into a similar pattern of projected losses in AGB_P under future climatic conditions. It has been noted that several auxiliary factors can have a greater influence than commonly expected on AGB, such as dominant tree species, herbaceous cover, canopy closure, among others (Su et al., 2024).

Functional dispersion did not have a clear latitudinal pattern either, although it seemed to increase at higher elevations. Under future climatic conditions, functional dispersion was projected to remain largely stable, but with slight increases at higher elevations and slight declines at lower elevations. This could be further indication of upland species predicted to migrate upslope, and of lowland species to migrate downslope (Bergamin et al., 2024). Alternatively, the loss of functional diversity at lower elevations could be an indication of lowland attrition, in which there are no extant communities adapted to warmer regimes to replace those migrating upslope (Colwell et al., 2008).

Taken together, my AGB_P and functional dispersion findings could be attributed to some rare, but resilient and influential large tree species. A study in tropical Africa found that rare tree species with large individuals display the highest functional specialisation – thus the lowest functional redundancy – and can sometimes be ‘hyperdominant’ in terms of carbon storage (Kearsley et al., 2019). If the latitudinal pattern of tree height – and AGB_P – is preserved under future climatic conditions, it could be a reflection of the persistence of large-sized species at the northern parts of the range, and simultaneously, the relative stability of functional dispersion due to the preservation of rare species with the most specialised functional niches (Mi et al., 2021). However, conservation and recovery measures should be taken to preserve population of these very large species, as three of them (*Abies guatemalensis*, *A. hickelii* and *Juglans pyriformis*) are considered as endangered (EN) and one (*Podocarpus matudae*) as vulnerable (VU) by the IUCN (Table S4).

It has been reported that functional traits are not always clearly correlated to environmental variables (Heilmeyer, 2019). For instance, a study conducted on a dominant canopy species in Western Australia found significant correlations between functional traits and their responses to climate change, but with low explanatory power, which was attributed to high intra-functional trait variation and differential evolutionary rates (Ahrens et al., 2020).

4.5.4 Caveats and limitations

This study found some clear trends that were consistent with previous research. However, there are some limitations that call for a careful interpretation of the results: (1) they are not based on field measurements, (2) they are not weighted by abundance or basal area data, and (3) the traits included in the models were limited by data availability. Furthermore, potential carbon storage capacity (AGB_p) omits abundant species that did not meet the threshold to be considered montane specialists.

Thus, the low explanatory power of my models is likely due to the limited number of functional traits available for this set of montane-specialist species. For example, only two out of the 23 species listed as vulnerable or endangered by the IUCN had complete data for all the traits included in this study, whereas the rest only had data available at genus level or had to be imputed based on their phylogeny. Otherwise, the inclusion of water-use efficiency or root traits, among others, would likely improve the accuracy of current habitat suitability estimates and resilience to changing climatic patterns (Kühn et al., 2021). Additionally, the restrictive species selection process meant omitting the functional diversity context found in other growth forms, such as herbs, shrubs. Potentially, if other biomes or growth forms were included, more obvious trends would become detectable. Moreover, this study relies on species' average values of each functional trait, whereas other significant trends might arise by including intraspecific variation to make comparisons between locations and lineages (Heilmeyer, 2019).

Although beyond the scope of this study, the importance of dominant species cannot be overlooked. A study of pantropical lowland forests found that only 2.2–2.3% of 'hyperdominant' species make up half of all trees in Amazonia, Africa, and Southeast Asia (Cooper et al., 2024). Despite the absence of abundance data in this study, my dataset includes 19 tree genera featured in the list of 'hyperdominant' species (Cooper et al., 2024), 12 of which are found in the Neotropics (Amazonia): *Amaioua*, *Coccoloba*, *Croton*, *Eugenia*, *Guatteria*, *Inga*, *Lacmellea*, *Miconia*, *Ocotea*, *Pouteria*, *Sloanea*, and *Zygia*. Oaks only had representatives in southeast Asia, whereas pines were not included because the study did not cover montane regions.

Nonetheless, Mesoamerica has been reported to have a higher proportion than the global average of elevational specialist species (Laurance et al., 2011) and its mountainous regions are diversity hotspots for both pines (Farjon, 1996) and oaks (Valencia-A., 2004). Thus, it is possible that some species in this study's dataset could be abundant, if not 'hyperdominant,' and may have a significant influence on the functional traits of the montane-specialist tree community. Therefore, it seems likely that the conclusions of this study would hold up if corroborated by the addition of abundance data and field observations.

4.6 Conclusions

The combination of five aboveground functional traits produced a reasonable description of the functional diversity of the Mesoamerican montane-specialist tree community. Under current climatic conditions, tree height and leaf area were correlated positively and negatively, respectively, with latitude. However, a clear unidirectional relationship between each functional trait and the projected changes in suitable area under climate change was not accomplished.

This study showed that functional trait analysis without abundance data can still provide valuable insights into the functional traits present in an ecosystem. However, it should be emphasised that this study analysed the functional traits that are less likely to be influenced by abundance, which can nevertheless help in understanding the general drivers of functional diversity within the community.

Similarly, the estimate of aboveground biomass can be taken as indication of the areas with the greatest potential carbon sequestration capacity, rather than accurate estimates of current carbon stocks. Calculating actual standing biomass would require complementary abundance, basal area or population structure to both generate precise carbon stocks estimates and pinpoint at a fine scale key conservation areas for carbon sequestration, in addition to those for biological diversity (de Albuquerque et al., 2015).

Finally, the inclusion of more functional traits, intraspecific variation and abundance data could help establish clearer relationships between functional diversity and environmental factors, and potentially identify traits or combinations of traits that can make tree species more resilient or vulnerable to the projected effects of climate change in the Mesoamerican biodiversity hotspot.

Chapter 5. General Discussion

5.1 Significance of biases in existing research on impacts of climate change on tropical montane forests

The systematic search of the literature on the impacts of climate change on global tropical montane forests (TMF) conducted in Chapter 2 revealed important methodological, geographical and thematic trends. The most evident one is the disparity between world regions, with the Neotropics concentrating by far the majority of studies. Not only do vast regions with known presence of TMFs, such as Southeast Asia and Africa, have been less studied, but there were more than 20 countries for which not a single study meeting the inclusion criteria was found. Such a dearth of knowledge represents a serious obstacle in our ability to link ecological science with environmental policy during the present time of accelerated climatic change.

The observed geographic research bias might even call into question some basic notions that seem well established. For example, it is generally agreed that the Neotropics have the largest areas of TMF globally (Los et al., 2021; Mulligan, 2010), although conflicting definitions and detection methods lead to inconsistencies (e.g., Scatena et al. (2010) report a larger area in Southeast Asia). Compounded with the ambiguity in the definition of what constitutes a TMF (see Chapter 1.1), the neglect of vast world regions leaves open the debate on whether some countries have TMFs. Similarly, the Neotropics are claimed to have the highest plant diversity on Earth (Zizka et al., 2018) and also the greatest diversity of montane specialists thanks to its large and continuous mountain ranges (Laurance et al., 2011). However, African montane regions have been reported to have the highest degree of dissimilarity (i.e., uniqueness) among world regions for amphibians, birds, mammals and tree ferns (Karger et al., 2021).

The geographic trend persists at regional scales. With only five countries in the Neotropics (Colombia, Costa Rica, Ecuador, Mexico and Peru) having more than 5% of the 395 reviewed studies each, the stark contrast with some countries in the region is clear. This is also reflected in the limited data availability in global repositories for many countries in the region, such as Guatemala, Nicaragua and Panama (Ramírez-Barahona et al., 2023), despite neighbouring the most intensely studied ones. Such obvious sampling biases introduce

uncertainties that have to be accounted for by studies that rely on such databases (Hughes et al., 2021).

Unfortunately, there is no easy or short-term way to overcome the observed geographic bias. By looking at the global distribution of studies, it is reasonable to assume that it largely responds to socioeconomic or even geopolitical factors. Impoverished regions and countries by definition allocate fewer resources to science and environmental policies. Thus, research in those places often relies on foreign scientists and institutions conducting research sporadically, rather than knowledge being generated locally and continuously (Nuñez et al., 2021).

Thematically and taxonomically, the state of research is not balanced either. Research on vascular plants, especially trees, represents the majority of studies by a wide margin; in contrast, studies at the genetic or species interactions levels are particularly scarce (see Chapter 2.4.1). Thus, a high number of studies on a particular taxonomic group (or growth form in the case of trees) does not necessarily mean their biology and interaction with their environment are well understood. The accumulation of studies on TMF trees allowed for the construction of a somewhat consistent narrative of both observed and predicted significant range losses or due to climate change, but with high local and species-specific variability that remains hard to explain. Novel research looking at genetic diversity and interspecific interactions of TMF biota could shed light on the underlying mechanisms that drive their distributional responses to environmental stressors.

In the short term, it is important to make use of the available data and ecological tools to inform conservation in light of current accelerating climate change (Forster et al., 2024). Therefore, analyses of the literature, such as the one presented in Chapter 2, are useful to identify areas of opportunity to direct research, such as the absence of a species level characterisation of the montane-specialist tree community in Mesoamerica addressed in this thesis.

5.2 Significance of the predicted distributional changes of Mesoamerican montane-specialist trees in response to climate change

Species Distribution Models (SDM) are a crucial tool in conservation biology (Galbraith and Christoffersen, 2015) and their increasing accessibility has made them very popular in TMF

research (see Chapter 2). In addition to following as much as possible the best modelling practices (Araújo et al., 2019), it is also important to keep in mind assumptions that are independent of the input data and the choice of parameters for the correct interpretation of their outputs (Soley-Guardia et al., 2024).

The limitations of SDMs are well exemplified by the characterisation of the Mesoamerican montane-specialist tree community presented in Chapter 3. The Bray-Curtis indices, based on the occurrence data of 272 montane-specialist tree species indicated that the community is split latitudinally by the Lake Cocibolca, and is significantly less diverse north of the Isthmus of Tehuantepec. When modelling suitable areas under current climatic conditions, however, 51 species were projected to have climatically suitable areas spanning the most of the study area's latitudinal range. It can thus be inferred that most species are far from occupying their whole potential niche. Although SDM's have been employed specifically to predict the presence of rare species (e.g., Volis and Tojibaev, 2021; Williams et al., 2009), 'stacked' models – i.e., aggregated models of individual species as representatives of a whole community – are known to overestimate potential suitable habitat (Pottier et al., 2013). It is also possible that other non-considered factors (e.g., species interactions, fire dynamics, dispersal barriers, etc.) or simply random chance limit species' realised ranges.

Another caveat is that SDMs seldom incorporate information on the underlying mechanisms that drive plants' distributional changes in response to environmental conditions. By merely correlating recorded or projected environmental conditions to presence (and sometimes absence) records of target species, the predicted influence of each environmental factor is very unidirectional. For instance, a vast majority of modelling studies conclude that species will follow their preferred temperature regimes toward higher latitudes and elevations, but empirical evidence does not support these predictions. There is no evidence of tropical communities successfully tracking changing climatic conditions latitudinally (Colwell and Feeley, 2024). And although upslope migrations have been reported in many montane regions, plant migration significantly lagging behind the rate of change is the norm (Alexander et al., 2018; Corlett, 2015; Corlett and Westcott, 2013). Moreover, contrary to predictions, a global survey of 987 montane animal and plant species found that 28% actually moved downslope (Mamantov et al., 2021).

All these uncertainties call for a rethinking of the aims and utility of modelling studies, which in some instances might even make some modelling steps redundant. For example, it is common practice in modelling studies to compare multiple dispersal assumptions (Corlett, 2015). However, a recent modelling study in a montane region in eastern Mexico found negligible differences between the limited and unlimited dispersal assumptions, except for the most critically endangered species (Ortega et al., 2024), i.e., precisely for the subset of species for which natural dispersion is most unlikely. Therefore, I believe that given the rate of anthropogenic climate change (Forster et al., 2024), modellers should work under the default assumption that montane, rare and range-restricted species will not migrate on their own. This does not mean that the no-dispersal scenario should become the default, but rather that it might be redundant. Instead, SDMs should be seen as indicators of the most suitable areas for complementary active conservation schemes, such as managed recovery and reintroductions (Heywood, 2019) or assisted migration (Sáenz-Romero et al., 2020b, 2016).

Doubts on the efficacy of assisted migration programmes and ethical concerns about the intentional relocation of species in general have been raised (Corlett, 2015), for instance, the potential that some species might become invasive. However, the same characteristics that make a species vulnerable in the first place make this risk highly unlikely, including limited dispersal abilities, slow reproductive rates, specialised habitat and nutritional requirements, narrow physiological tolerances, among others (Pacifi et al., 2015). There is promising evidence that species can successfully establish at higher elevations (García-Hernández et al., 2019; Toledo-Aceves and del-Val, 2021a), where natural seed dispersion rarely reaches (Corlett and Westcott, 2013). Thus, the pertinence and necessity of active conservation measures, such as *ex situ* cultivation, targeted reintroduction and assisted migration, are increasingly acknowledged (Hällfors et al., 2016; Heywood, 2019; Sáenz-Romero et al., 2020b, 2016), prioritising species that have already been identified as endangered or vulnerable, e.g., *Abies guatemalensis*, *A. hickelii*, *Juglans pyriformis*, *Magnolia schiedeana*, *Podocarpus matudae* and *Quercus constaricensis*. Other relevant factors, such as limited pollination (Li et al., 2016) and decline of nurse shrubs (Soto-Correa et al., 2013) have also been explored, although addressing them might be more challenging and effort-intensive.

5.3 Significance of the predicted functional diversity shifts of Mesoamerican montane-specialist trees in response to climate change

The observed spatial patterns of five individual functional traits described in Chapter 4 performed well in describing the functional diversity within the montane-specialist tree community of Mesoamerica. Despite the lack of abundance data to generate accurate site-specific estimates per species, the general latitudinal trends of tree height and leaf area coincide with floristic trends described for the region. For example, the increasing dominance of pines toward the northern part of the study area and their functional space overlap with oaks (Corlett and Hughes, 2015).

More remarkable is the projected relative stability of the spatial patterns throughout the study area, despite the worrying magnitude of suitable area losses projected for most species under future climatic conditions. The fact that merely 272 species (out of the >32,000 plant species estimated for Mesoamerica including all growth forms and elevations; Ramírez-Barahona et al., 2023) exhibit such resilient functional diversity under a severe climate change scenario, suggests a high degree of functional redundancy (Monge-González et al., 2021). This is indicative of the significant contribution of rare and range-restricted species to functional diversity (Leitão et al., 2016; Mi et al., 2021), as well as to vulnerable ecosystem functions (Mouillot et al., 2013) and ecosystem services, such as carbon storage (Kearsley et al., 2019).

Therefore, further research on TMF functional diversity is not only important to better understand the mechanisms that make their communities resilient to environmental change (Ahrens et al., 2020; Kühn et al., 2021), but also to ponder their value as key ecosystems to mitigate the drivers of climate change. It is generally assumed that the carbon storage capacity of TMFs is tiny compared to lowland and temperate forests. However, carbon dynamics in many tropical regions are still not well understood (Cuni-Sanchez et al., 2021) and there is evidence that it has been underestimated (Álvarez-Dávila et al., 2017). Large-sized montane tree species have high carbon storage capacity (Kearsley et al., 2019; Venter et al., 2017), and trees' functional traits also influence other carbon sinks, such as soil organic content (Augusto and Boča, 2022; Iwashita et al., 2013).

Similarly, the observed variability in the height-to-diameter ratio is indicative of the uneven canopy structure characteristic of montane forests (Scatena et al., 2010). Maintaining a complex canopy structure is important, as it is the support of the epiphytic communities that are typical of TMFs and contribute to their water interception capacity (Ah-Peng et al., 2017; Gotsch et al., 2016), but are simultaneously highly threatened by hydric stress caused by rising temperatures and cloud base levels (Gotsch et al., 2018; He et al., 2016; Wagner et al., 2014; Zuleta et al., 2016). The reduction of functional complexity would result in the loss of key microhabitat for montane fauna (Scheffers et al., 2014, 2013a, 2013b) and in decreased water flows on which human populations rely (Viviroli et al., 2011; Zhou et al., 2017).

The lack of obvious spatial patterns for the other traits of the montane-specialist community can in itself be informative. For example, wood density was the least variable trait among the 272 montane-specialist species. The low variation in wood density is indicative of a late successional assemblage (Castillo-Figueroa et al., 2023), possibly indicating that co-occurrence of these montane specialists signals areas with low disturbance. Conversely, high wood density is generally associated with higher resistance to cavitation (Ahrens et al., 2020; Kühn et al., 2021). Thus, the relatively low average wood density of these montane specialists could make them vulnerable to increased vapour pressure deficit (Esperón-Rodríguez and Barradas, 2015b).

The influence of other functional traits cannot be overstated. The functional trait analysis in Chapter 4 was largely constrained by data availability, so some important level of detail is likely missing. For instance, traits that regulate water-use efficiency (e.g., stomatal control) or that influence reproduction (e.g., pollination and seed dispersal syndrome) and establishment (e.g. seed mass, growth rate, etc.) would greatly improve our predictions of which combinations of traits make species more or less likely to successfully cope with the current rates of climate change.

5.4 Implications for the direction of future research

Research on the impacts of climate change on TMFs is far from complete, as shown in Chapter 2, and the single gravest obstacle for this thesis was data availability, yet the resources and time to act are limited. Therefore, our first instinct might be to devote the bulk of research

towards the most neglected world regions and thematic gaps. However, it might be more efficient to instead focus on tackling the discrepancies in the existing literature.

Mismatches between theory, prediction and observations are not that uncommon. A clear example is the relatively high and unexpected proportion of montane species that are migrating downslope in response to climate change (Mamantov et al., 2021). What underlying mechanisms cause some species to move in the opposite direction of environmental shifts? What are the implications of these counterintuitive migrations in terms of community composition and interspecific interactions? Which is a better descriptor of the distribution and functional diversity of montane flora: temperature or water availability? Or in which cases one is more determinant than the other, or is it another factor altogether?

Uncertainties like these have been identified in relation to other widespread notions about the effects of climate change on global flora. A review devoted to unexpected or counterintuitive responses of plants to climate change (Parmesan and Hanley, 2015) listed some notable examples, such as (1) erroneous assumptions about plants' phenological responses to changing temperatures in autumn that were assumed to work the same as in spring; (2) negligible physiological responses of plants to increases in eCO_2 , despite a widespread notion that it would enhance productivity; and (3) difficulties in establishing a clear link between any one functional trait or combination of traits and responses to climatic shifts. Yet rather than portraying those complex responses as an obstacle, the authors point out that they are testament to plants' inherent adaptability and urge designing research in ways that allow disentangling inconsistent findings, for example, by coordinating manipulation experiments across networks of field sites.

By refining our knowledge of forest dynamics in well-understood proxy regions, the expansion of research into understudied regions would be better informed to specifically identify cases where the same diversity patterns are not applicable and understand why. The accuracy and utility of SDMs could thus be improved to forecast distributional changes and predict functional, ecological, and even genetic-level impacts in response to environmental stressors of tropical montane flora. This consideration is also applicable to other taxa and ecosystem types.

In conservation, a key underrepresented aspect is the link between climate and genetic diversity. Studies on intraspecific responses to environmental stressors are a lot less common than those at the species level (Carvalho et al., 2019). However, the relevance of genetic studies for conservation is increasingly recognised, by improving our understanding of species' demographic histories, population structure and connectivity, adaptive potential, and deleterious variation, among others (Hohenlohe et al., 2021).

More specifically for this thesis, immediate efforts would be to use field surveys to corroborate the characterization of montane-specialist tree communities across the study area. Abundance and population structure could be obtained simultaneously, which in turn could refine the functional trait analysis and allow, for example, for the precise estimation of the aboveground biomass of these species. And additionally, genetic studies of rare montane specialist species could reveal their life histories, connectivity, and adaptive potential amid environmental changes.

5.5 Conclusions

The overarching goal of this thesis was to widen our understanding of the likely impacts of climate change on the montane-specialist tree community in Mesoamerica. My findings highlight the need to broaden the methodological, thematic, taxonomic, and geographical scope of research on tropical montane forests globally, while also emphasising the importance of refining existing approaches to provide immediate and reliable conservation insights. By leveraging moderate to circumstantial evidence, such as remote sensing, palaeoecological data, and advanced forecasting models, we could better address current uncertainties and knowledge gaps, particularly in well-studied regions. Additionally, natural variability along TMFs' altitudinal gradients allows conducting field manipulation experiments to simulate complex environmental conditions more accurately than *ex situ* studies.

This thesis further emphasises the critical role of robust modelling approaches, calling for the development of novel forecasting algorithms that account for ecological factors like species dispersal limitations and biotic interactions. Such enhancements are vital for designing protected areas that accommodate future habitats for entire biotic communities, thus minimising biodiversity loss and preserving ecosystem functions. While trees are central to forest ecosystems, it is also crucial to consider the responses of other taxonomic groups and

genetic diversity to climate change, as these factors are key for the long-term viability of TMF populations. In the Mesoamerican bioregion, findings indicate significant reductions in climatically suitable areas for montane-specialist tree species, yet some regions may remain refuges for biodiversity at the highest elevations under a severe climate change scenario. These findings advocate for stringent protection measures, active conservation, reintroduction and assisted migration programmes for key vulnerable species, and immediate transnational collaboration to shield and connect these critical habitats that do not rely on unrealistic assumptions of natural dispersal.

The research also highlights the potential of functional trait analysis, which can provide valuable insights into ecosystem functioning and carbon sequestration potential, even with absence of abundance data. However, to achieve more accurate estimates of carbon stocks and identify key areas for conservation, additional data on abundance, basal area, and phenology are necessary. Incorporating more functional traits, intraspecific variation, genetic and abundance data could further clarify the relationships between functional diversity and environmental factors, helping to identify traits that may confer resilience or vulnerability to climate change and increase the success rate of active conservation strategies.

Overall, this thesis provides a foundational framework for future research and policy design aimed at safeguarding the ecological and biological integrity of montane-specialist trees in Mesoamerica, emphasising the importance of integrating multiple lines of evidence, cross-disciplinary approaches, and international cooperation in addressing the complex challenges posed by climate change.

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Appendix A. Supplementary Information for Chapter 2

Table S1. Details of 395 studies published between 1994 and 2021 included in the assessment of evidence strength.

LoE, Level of Evidence (see Table 2.1 and Figure 2.2 for definitions of categories); N/A, not available; SDM, species distribution model.

Research topic: AE = abiotic environment; BD = biodiversity; CS = conservation strategies; DE = distributional effects; EF = ecosystem functions; ES, ecosystem services; S = synergies.

Ecological level: bi = biosphere; co = community; ec = ecosystem or landscape; ge = genetic; hu = human society; si = species interactions; sp = species.

Taxa: amp = amphibians; bac = bacteria; bir = birds; bry = bryophytes; fun = fungi; ins = insects; lic = lichens; mam = mammals; oar = non-insect arthropods; oin = non-arthropod invertebrates; oth = other taxa; rep = reptiles; vpe = vascular plants (epiphytes); vpl = vascular plants (general); vpt = vascular plants (trees).

| Authors | Year | Region | Country | Study type | Research topic | Ecological level | Taxa | LoE |
|-----------------------------------|------|---------------------------------|---|---|----------------|------------------|---------------|-----|
| Aiba & Kitayama | 2002 | Southeast Asia | Malaysia | Survey (longitudinal) | AE | co, ec | vpt | 2a |
| Ainsworth & Drake | 2020 | Pacific Ocean | Hawaii | Survey (cross-sectional) | CS | co | vpl | 2c |
| Alfonso-Corradó <i>et al.</i> | 2017 | North America | Mexico | Modelling (SDM) | DE | sp | vpt | 2b |
| Altamirano-León <i>et al.</i> | 2022 | North America | Mexico | Modelling (SDM) | DE | sp, ec | vpt | 2b |
| Alvarado-Barrientos <i>et al.</i> | 2015 | North America | Mexico | Survey (longitudinal) | EF | ec | vpt | 2a |
| Alvarado-Barrientos <i>et al.</i> | 2014 | North America | Mexico | Survey (longitudinal) | EF | ec | vpt | 2a |
| Amici <i>et al.</i> | 2020 | Central America | Costa Rica | Survey (cross-sectional) | BD | co, ec | vpe | 2c |
| Anchukaitis & Evans | 2010 | Central America | Costa Rica | Historic data analysis | S | sp, si, ec | vpt, fun, amp | 1b |
| Anderson <i>et al.</i> | 2013 | Oceania | Australia | Survey (longitudinal) | BD | co | bir | 1b |
| Anderson <i>et al.</i> | 2012 | Oceania | Australia | Modelling (SDM) | BD | co, ec | bir | 2b |
| Arias-Aguilar <i>et al.</i> | 2020 | Central America | Costa Rica | Survey (cross-sectional) | BD | sp | mam | 2c |
| Arzac <i>et al.</i> | 2019 | South America | Venezuela | Modelling (SDM) | DE | co | vpl | 2b |
| Ashton <i>et al.</i> | 2011 | Oceania | Australia | Survey (cross-sectional) | BD | sp, co | ins | 2c |
| Bach <i>et al.</i> | 2007 | South America | Bolivia | Survey (cross-sectional), modelling (SDM) | BD | co | vpe | 3 |
| Bader <i>et al.</i> | 2013 | Central America | Panama | Experiment (<i>ex situ</i>) | BD | sp, ec | bry | 1b |
| Barker & Ríos-Franceschi | 2015 | Caribbean | Puerto Rico | Survey (longitudinal) | BD | sp | amp | 2a |
| Barnes <i>et al.</i> | 2017 | Pacific Ocean | Hawaii | Survey (cross-sectional) | EF | ec | vpl | 2c |
| Batumike <i>et al.</i> | 2022 | Africa | DRC | Survey (cross-sectional) | AE, ES | ec, hu | vpl | 2b |
| Baumbach <i>et al.</i> | 2021 | North America, Central America, | Mexico, Guatemala, Belize, El Salvador, | Modelling (SDM) | DE | ec | vpt | 2b |

| | | South America | Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela | | | | | |
|------------------------------------|------|--------------------------------|--|---|----|--------|---------------|----|
| Bax <i>et al.</i> | 2021 | South America | Peru | Modelling (SDM) | DE | ec | vpt | 2b |
| Becker & Kuzyakov | 2018 | Africa | Tanzania | Experiment (field) | EF | ec | bac, vpl, fun | 1a |
| Becker <i>et al.</i> | 2015 | Africa | Tanzania | Survey (longitudinal) | EF | ec | vpt | 2a |
| Bender <i>et al.</i> | 2019 | South America | Peru | Modelling (SDM, other) | BD | co | bir | 2b |
| Bendix <i>et al.</i> | 2021 | South America | Ecuador | Survey (cross-sectional) | EF | ec | vpt | 2c |
| Benning <i>et al.</i> | 2002 | Pacific Ocean | Hawaii | Modelling (other) | S | co | bir | 2b |
| Berriozabal-Islas <i>et al.</i> | 2018 | North America, Central America | Mexico, Guatemala | Modelling (SDM) | BD | sp | rep | 2b |
| Berry <i>et al.</i> | 2016 | North America | Mexico | Survey (cross-sectional) | EF | sp, ec | vpt | 2c |
| Bertoncello <i>et al.</i> | 2011 | South America | Brazil | Survey (cross-sectional) | BD | co | vpt | 2c |
| Bitencourt <i>et al.</i> | 2016 | South America | Brazil | Modelling (SDM) | DE | ec | vpl | 2b |
| Blundo <i>et al.</i> | 2012 | South America | Argentina | Survey (longitudinal) | DE | ec | vpt | 2a |
| Bogawski <i>et al.</i> | 2019 | Africa | Ethiopia, Tanzania, Kenya, DRC, Burundi, Rwanda | Modelling (SDM) | DE | sp | vpl | 2b |
| Borchert <i>et al.</i> | 2005 | North America, Central America | Mexico, Costa Rica | Survey (longitudinal) | EF | sp | vpt | 2a |
| Bothwell <i>et al.</i> | 2014 | Pacific Ocean | Hawaii | Experiment (field) | EF | ec | N/A | 1a |
| Bouskill <i>et al.</i> | 2013 | Caribbean | Puerto Rico | Experiment (field) | EF | co, ec | bac | 1a |
| Caballero-Villalobos <i>et al.</i> | 2021 | South America | Colombia | Modelling (SDM) | DE | ec | vpt | 2b |
| Camarero <i>et al.</i> | 2021 | Global | Peru | Historic data analysis, modelling (climate) | EF | bi | vpt | 1b |
| Campos | 2014 | North America | Mexico | Survey (longitudinal) | EF | ec | N/A | 2a |
| Campos-Cerqueira & Aide | 2017 | Caribbean | Puerto Rico | Survey (longitudinal) | BD | sp, co | amp | 1b |
| Campos-Cerqueira & Aide | 2021 | Caribbean | Puerto Rico | Survey (longitudinal) | DE | co | amp, bir | 2a |
| Campos-Cerqueira <i>et al.</i> | 2017 | Caribbean | Puerto Rico | Surveys (sequential) | BD | co | bir | 2b |

| | | | | | | | | |
|------------------------------|------|-----------------|-----------------------------|--|--------|------------|---------------|----|
| Cárdenas | 2016 | South America | Ecuador | Survey (cross-sectional) | BD | co | ins | 2c |
| Castro <i>et al.</i> | 2020 | South America | Brazil, Argentina, Paraguay | Modelling (SDM) | DE | sp | vpt | 2b |
| Catenazzi <i>et al.</i> | 2014 | South America | Peru | Experiment (<i>ex situ</i>) | BD | co | amp | 1b |
| Catenazzi <i>et al.</i> | 2010 | South America | Peru | Surveys (sequential) | S | co | amp | 2b |
| Ceballos <i>et al.</i> | 2021 | South America | Argentina | Survey (longitudinal) | EF | co | vpt | 1b |
| Center <i>et al.</i> | 2016 | Central America | Costa Rica | Experiment (<i>ex situ</i>) | EF | sp | vpt | 1b |
| Cerano-Paredes <i>et al.</i> | 2021 | North America | Mexico | Historic data analysis | S | ec | vpt | 1b |
| Chakraborty <i>et al.</i> | 2013 | South Asia | India | Modelling (life zones) | DE | bi | N/A | 2c |
| Chang <i>et al.</i> | 2008 | East Asia | Taiwan | Survey (longitudinal), experiment (field) | EF | ec | N/A | 1a |
| Chapman <i>et al.</i> | 2018 | Africa | Uganda | Survey (longitudinal) | EF | sp, si, co | vpt | 1b |
| Chen <i>et al.</i> | 2017 | Caribbean | Puerto Rico | Experiment (field) | EF | ec | N/A | 1a |
| Chen <i>et al.</i> | 2009 | Southeast Asia | Malaysia | Surveys (sequential) | DE | co | ins | 1b |
| Chen <i>et al.</i> | 2011 | Southeast Asia | Malaysia | Surveys (sequential) | BD | co | ins | 2b |
| Chirino <i>et al.</i> | 2017 | South America | Ecuador | Experiment (<i>ex situ</i>) | EF | sp | vpt | 1b |
| Chu <i>et al.</i> | 2014 | East Asia | Taiwan | Survey (longitudinal) | EF | sp, ec | vpt | 2a |
| Colares <i>et al.</i> | 2021 | South America | Brazil | Survey (cross-sectional) | BD | co | ins | 2c |
| Colwell <i>et al.</i> | 2008 | Central America | Costa Rica | Survey (cross-sectional), modelling (SDM) | BD | ec, bi | vpl, vpe, ins | 2c |
| Colyn <i>et al.</i> | 2020 | Africa | South Africa | Modelling (SDM) | BD, CS | co, ec | bir | 2b |
| Comarazamy & González | 2011 | Caribbean | Puerto Rico | Modelling (climate) | AE | ec | N/A | 2c |
| Comarazamy <i>et al.</i> | 2015 | Caribbean | Haiti, Dominican Republic | Historic data analysis, survey (longitudinal), modelling (other) | AE | ec | N/A | 1b |
| Cordier <i>et al.</i> | 2020 | South America | Argentina | Modelling (SDM) | DE, BD | sp, co | amp | 2b |
| Correa-Ayram <i>et al.</i> | 2017 | North America | Mexico | Modelling (SDM) | DE | ec | vpt | 2b |
| Correa-Díaz <i>et al.</i> | 2021 | North America | Mexico | Historic data analysis | EF | sp, ec | vpt | 1b |
| Correa-Díaz <i>et al.</i> | 2020 | North America | Mexico | Historic data analysis | EF | sp | vpt | 1b |
| Costion <i>et al.</i> | 2015 | Oceania | Australia | Modelling (SDM) | BD | sp | vpl | 2b |

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| Crain & Tremblay | 2017 | Caribbean | Puerto Rico | Experiment (<i>ex situ</i>) | EF | sp | vpe | 1b |
| Crausbay & Hotchkiss | 2010 | Pacific Ocean | Hawaii | Survey (cross-sectional) | AE | co, ec | bry, vpe, lic | 2c |
| Crausbay <i>et al.</i> | 2014 | Pacific Ocean | Hawaii | Survey (longitudinal) | AE | co, ec | vpt | 2a |
| Cruz-Elizalde <i>et al.</i> | 2020 | North America | Mexico | Survey (cross-sectional), modelling (SDM) | BD | sp | amp | 2b |
| Cuervo-Robayo <i>et al.</i> | 2020 | North America | Mexico | Historic data analysis, modelling (climate) | AE | bi | N/A | 1b |
| Cuesta <i>et al.</i> | 2020 | South America | N/A | Survey (longitudinal), climate projection | DE | co, ec | vpl | 2a |
| Cuni-Sanchez <i>et al.</i> | 2019 | Africa | Kenya | Survey (longitudinal), historic data analysis | ES | ec, hu | N/A | 1b |
| Cusack <i>et al.</i> | 2010 | Caribbean | Puerto Rico | Experiment (<i>ex situ</i>) | EF | ec | N/A | 1b |
| Dangles <i>et al.</i> | 2008 | South America | Ecuador | Survey (cross-sectional) | S | si, ec | ins | 2c |
| Dantas de Paula <i>et al.</i> | 2021 | South America | Ecuador | Survey (longitudinal), modelling (other) | EF | ec | vpt, fun | 1b |
| de Araujo-Lira <i>et al.</i> | 2020 | South America | Brazil | Modelling (SDM) | BD, DE | sp | oar | 2b |
| de la Cruz-Amo <i>et al.</i> | 2020 | South America | Ecuador, Peru | Survey (cross-sectional) | EF | ec | vpl | 2c |
| del Castillo <i>et al.</i> | 2009 | North America, Central America | Mexico, Guatemala | Survey (cross-sectional), modelling (climate, other) | CS | sp, co, ec | vpt | 2c |
| de Gasper <i>et al.</i> | 2021 | South America | Brazil | Modelling (SDM) | DE, BD | sp, ec | vpl | 2b |
| Delsinne <i>et al.</i> | 2013 | South America | Ecuador | Experiment (field) | BD | co | ins | 1a |
| Dialynas & Bras | 2019 | Caribbean | Puerto Rico | Modelling (climate, other) | EF | ec | N/A | 2b |
| Dolson <i>et al.</i> | 2021 | Central America | Costa Rica | Survey (cross-sectional) | BD | ge, co | ins | 2c |
| Doughty <i>et al.</i> | 2018 | South America | Peru | Survey (cross-sectional), modelling (climate, other) | EF | ec | vpt | 2b |
| Dulle <i>et al.</i> | 2016 | Africa | Tanzania | Survey (cross-sectional) | BD | co | bir | 2b |
| Duque <i>et al.</i> | 2015 | South America | Colombia | Historic data analysis | BD | co, ec | vpt | 1b |
| Dusenge <i>et al.</i> | 2021 | Africa | Rwanda | Experiment (field) | EF | sp | vpt | 1a |

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| Eaton <i>et al.</i> | 2012 | Central America | Costa Rica | Survey (cross-sectional) | EF | ec | bac, fun | 2c |
| Eguiguren-Velepucha <i>et al.</i> | 2016 | South America | Ecuador | Survey (cross-sectional), modelling (climate, other) | AE | ec | N/A | 2b |
| Eller <i>et al.</i> | 2016 | South America | Brazil | Experiment (<i>ex situ</i>) | EF | ec | vpt | 1b |
| Elsen & Tingley | 2015 | Global | N/A | Modelling (other) | AE | bi | N/A | 2a |
| Enquist | 2002 | Central America | Costa Rica | Modelling (life zones) | DE | ec | vpl (mainly) | 2b |
| Enquist & Enquist | 2011 | Central America | Costa Rica | Surveys (sequential) | EF | co, ec | vpl | 2b |
| Esperón-Rodríguez & Barradas | 2015 ^b | North America | Mexico | Experiment (<i>ex situ</i>), modelling (SDM) | EF | ec | vpt | 1b |
| Esperón-Rodríguez & Barradas | 2014 | North America | Mexico | Experiment (<i>ex situ</i>), modelling (SDM) | DE | co, ec | vpt | 1b |
| Esperón-Rodríguez & Barradas | 2015 ^a | North America | Mexico | Survey (cross-sectional) | EF | co, ec | vpt | 2c |
| Esperón-Rodríguez <i>et al.</i> | 2019 | North America | Mexico | Modelling (other) | AE | ec | N/A | 2b |
| Estrada-Contreras <i>et al.</i> | 2015 | North America | Mexico | Modelling (SDM) | DE | co, ec | vpt | 2b |
| Fadrique <i>et al.</i> | 2018 | South America | Colombia, Ecuador, Peru, Argentina | Survey (longitudinal) (meta-analysis?) | DE | co, ec | vpt | 1b |
| Feeley & Silman | 2010 ^c | South America | N/A | Modelling (SDM) | DE | ec | vpl | 2c |
| Feeley & Silman | 2010 ^b | South America | Colombia, Ecuador, Peru, Bolivia | Modelling (SDM) | DE | ec | vpl | 2b |
| Feeley <i>et al.</i> | 2020 | South America | Colombia | Experiment (<i>ex situ</i>) | EF | sp | vpt | 1b |
| Feeley <i>et al.</i> | 2013 | Central America | Costa Rica | Survey (longitudinal) | DE | co, ec | vpt | 2a |
| Feeley <i>et al.</i> | 2011 | South America | Peru | Surveys (sequential) | DE | co | vpt | 2b |
| Forero-Medina <i>et al.</i> | 2011 ^a | South America | Colombia | Modelling (SDM) | DE, BD | sp | amp | 2b |
| Forero-Medina <i>et al.</i> | 2011 ^b | South America | Peru | Surveys (sequential) | BD | co | bir | 2b |
| Franklin <i>et al.</i> | 2019 | Caribbean | Dominican Republic | Survey (cross-sectional) | DE | co | vpl, bir | 2c |
| Freed & Cann | 2013 | Pacific Ocean | Hawaii | Survey (longitudinal) | S | sp, si | bir, oth | 1b |
| Freeman & Class Freeman | 2014 | Oceania | Papua New Guinea | Surveys (sequential) | BD | co | bir | 2b |
| Freeman <i>et al.</i> | 2018 | South America | Peru | Survey (cross-sectional) | BD | co | bir | 2c |
| García-Hernández & Toledo-Aceves | 2020 | North America | Mexico | Experiment (field) | CS | sp | vpt | 1a |

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| García-Hernández <i>et al.</i> | 2019 | North America | Mexico | Experiment (field) | CS | sp, si, co | vpt | 1a |
| García-Robledo <i>et al.</i> | 2018 | Central America | Costa Rica | Experiment (<i>ex situ</i>) | BD | sp | ins | 1b |
| Gasner <i>et al.</i> | 2010 | Central America | Costa Rica | Surveys (sequential), modelling (other) | BD | sp, co | bir | 2b |
| Gavrutenko <i>et al.</i> | 2021 | Africa | Madagascar | Modelling (SDM) | DE | sp | mam | 2b |
| Geml <i>et al.</i> | 2014 | South America | Argentina | Survey (cross-sectional) | AE | co, ec | fun | 2c |
| Gerold <i>et al.</i> | 2008 | South America | Bolivia | Survey (longitudinal) | EF | ec | vpt | 2a |
| Giamminola | 2020 | South America | Argentina | Modelling (SDM) | DE | sp | vpt | 3 |
| Giardina <i>et al.</i> | 2014 | Pacific Ocean | Hawaii | Survey (longitudinal) | EF | ec | N/A | 2a |
| Girardin <i>et al.</i> | 2014 | South America | Ecuador, Peru, Bolivia | Survey (cross-sectional) | EF | co, ec | vpt | 2c |
| Godoy-Bürki | 2016 | South America | Argentina | Modelling (SDM) | BD | ec | vpl (?) | 2b |
| Goldsmith <i>et al.</i> | 2013 | Central America | Costa Rica | Survey (longitudinal), experiment (field) | EF | sp, ec | vpt | 2a |
| Golicher <i>et al.</i> | 2008 | North America | Mexico | Modelling (SDM) | DE | co, ec | vpt | 2a |
| Golicher <i>et al.</i> | 2012 | North America, Central America | Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama | Modelling (SDM) | BD | ec | vpt | 2b |
| Gómez-Pineda <i>et al.</i> | 2020 | North America | Mexico | Modelling (SDM) | DE | sp, ec | vpt | 2b |
| Gontijo <i>et al.</i> | 2018 | South America | Brazil | Survey (cross-sectional) | BD | sp | rep | 2c |
| González-del-Pliego <i>et al.</i> | 2020 | South America | Colombia | Experiment (<i>ex situ</i>) | BD | sp, ec | amp | 1b |
| González-Fernández <i>et al.</i> | 2018 | North America | Mexico | Modelling (SDM) | BD | sp | rep | 2b |
| Gotsch <i>et al.</i> | 2014a | North America | Mexico | Survey (longitudinal), experiment (field) | EF | sp, ec | lic | 1a |
| Gotsch <i>et al.</i> | 2014b | Pacific Ocean | Hawaii | Survey (longitudinal) | EF | sp, ec | vpt | 2a |
| Gotsch <i>et al.</i> | 2015 | Central America | Costa Rica | Experiment (<i>ex situ</i>) | EF, BD | sp, ec | vpe | 1b |
| Gotsch <i>et al.</i> | 2018 | Central America | Costa Rica | Survey (longitudinal) | BD | sp, co | vpe | 2a |
| Gotsch <i>et al.</i> | 2017 | Central America | Costa Rica | Survey (cross-sectional) | BD | co | bry, vpe | 2c |
| Grau & Veblen | 2000 | South America | Argentina | Survey (longitudinal) | DE | co, ec | vpt | 1b |

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| Gray <i>et al.</i> | 2017 | Southeast Asia | Malaysia, Brunei, Indonesia | Modelling (SDM) | DE | sp | vpl | 2b |
| Greenwood <i>et al.</i> | 2014 | East Asia | Taiwan | Historic data analysis, Survey (longitudinal) | DE | ec | vpt | 1b |
| Gu <i>et al.</i> | 2021 | East Asia | Taiwan | Surveys (comparative, longitudinal), modelling (other) | EF | ec | vpt | 2c |
| Guillaumet <i>et al.</i> | 2017 | Pacific Ocean | Hawaii | Modelling (SDM, other) | S | sp, si | vpt, bir, oth | 2b |
| Güizado-Rodríguez <i>et al.</i> | 2012 | North America | Mexico | Modelling (SDM) | BD | sp | rep | 2b |
| Gurdak <i>et al.</i> | 2014 | South America | Peru | Survey (cross-sectional) | EF | ec | vpt | 2c |
| Gutiérrez-García & Ricker | 2019 | North America | Mexico | Historic data analysis | EF | sp, ec | vpt | 1b |
| Gütlein <i>et al.</i> | 2018 | Africa | Tanzania | Survey (longitudinal), experiment (<i>ex situ</i> , field) | S | ec | N/A | 1a |
| Harris <i>et al.</i> | 2014 | Southeast Asia | Indonesia | Survey (longitudinal), modelling (climate, other) | BD | co | bir | 2b |
| Hayes <i>et al.</i> | 2018 | South America | Colombia, Ecuador, Peru, Bolivia, Brazil, Argentina, Paraguay | Historic data analysis | BD | sp | bir | 1b |
| He <i>et al.</i> | 2009 | East Asia | China | Experiment (field) | EF | ec | bac, fun | 1a |
| He <i>et al.</i> | 2010 | East Asia | China | Experiment (<i>ex situ</i>) | EF | ec | fun | 1b |
| Helmer <i>et al.</i> | 2019 | North America, Central America, South America, Caribbean | N/A | Modelling (SDM) | DE | bi | N/A | 2b |
| Hemp | 2009 | Africa | Tanzania | Survey (longitudinal) | S | ec | vpt | 1b |
| Hemp | 2005 | Africa | Tanzania | Survey (longitudinal) | S | co, ec | vpt | 2a |
| Henareh-Khalyani <i>et al.</i> | 2019 | Caribbean | Puerto Rico | Modelling (SDM) | DE | sp, si, ec | vpl | 2b |
| Hermes <i>et al.</i> | 2018a | South America | Ecuador | Modelling (SDM) | BD | sp | bir | 1b |
| Hermes <i>et al.</i> | 2018b | South America | Ecuador | Modelling (SDM, other) | CS | ec | bir | 2c |
| Hernández-Calderón <i>et al.</i> | 2013 | North America | Mexico | Survey (longitudinal) | EF | sp, ec | vpt | 2a |
| Hernández-Gordillo <i>et al.</i> | 2021 | Central America | Costa Rica | Survey (longitudinal) | EF | ec | vpt | 2a |

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| Hillyer & Silman | 2010 | South America | Peru | Experiment (field) | EF | si | vpt | 1a |
| Hiltner <i>et al.</i> | 2016 | Africa | Ethiopia | Modelling (other) | AE | ec | vpt | 2b |
| Horwath <i>et al.</i> | 2019 | South America | Peru | Survey (cross-sectional) | BD | ec | bry | 2c |
| Hsu <i>et al.</i> | 2014 | East Asia | Taiwan | Experiment (field) | BD | sp | vpe | 1a |
| Hsu <i>et al.</i> | 2012 | East Asia | Taiwan | Modelling (SDM) | BD | co, ec | vpe | 2b |
| Iturraide-Pólit <i>et al.</i> | 2017 | South America | Ecuador | Modelling (SDM) | BD | sp, ec | mam | 2b |
| Iwashita <i>et al.</i> | 2013 | Pacific Ocean | Hawaii | Survey (cross-sectional) | EF | ec | vpt | 2c |
| Jacob <i>et al.</i> | 2015b | Africa | Ethiopia | Historic data analysis, Surveys (sequential) | DE | ec | vpt | 1b |
| Jankowski & Rabenold | 2007 | Central America | Costa Rica | Surveys (sequential) | BD | co | bir | 2b |
| Jankowski <i>et al.</i> | 2010 | Central America | Costa Rica | Experiment (field) | BD | si | bir | 1a |
| Jankowski <i>et al.</i> | 2013 | South America | Peru | Survey (longitudinal) | BD | sp, co | vpt, bir | 2a |
| Jankowski <i>et al.</i> | 2009 | Central America | Costa Rica | Survey (cross-sectional) | BD | co, ec | bir | 2c |
| Jasso-Flores <i>et al.</i> | 2020 | North America | Mexico | Survey (cross-sectional) | EF | ec | vpt | 2c |
| Jiménez-García & Peterson | 2019 | North America | Mexico | Modelling (SDM) | DE | sp, ec | vpt | 2b |
| Jiménez-García <i>et al.</i> | 2021 | North America | Mexico | Historic data analysis | DE | ec | vpt | 1b |
| Jiménez-López <i>et al.</i> | 2020 | North America | Mexico | Survey (cross-sectional) | BD | co | vpe | 2c |
| Jiménez-Rodríguez <i>et al.</i> | 2015 | Central America | Costa Rica | Survey (longitudinal), modelling (other) | ES | ec | N/A | 2c |
| Jin <i>et al.</i> | 2012 | Southeast Asia | Malaysia | Survey (cross-sectional) | S | co | vpe | 2c |
| Johansson <i>et al.</i> | 2018 | Africa | Ethiopia | Survey (cross-sectional) | CS | co, ec | vpl | 2c |
| John <i>et al.</i> | 2020 | Africa | Tanzania | Modelling (SDM) | DE | ec | vpl | 2b |
| Jones <i>et al.</i> | 2008 | North America | Mexico | Survey (cross-sectional) | BD | co | ins | 2c |
| Joshi <i>et al.</i> | 2020 | South Asia | India | Experiment (field) | S | si, co | vpt | 1a |
| Karger <i>et al.</i> | 2021 | Global | N/A | Modelling (SDM) | DE, BD | bi | vpl, amp, bir, mam | 2b |
| Karmalkar <i>et al.</i> | 2008 | Central America | Costa Rica | Modelling (climate) | AE | ec | N/A | 2c |
| Keyimu <i>et al.</i> | 2020 | East Asia | China | Historic data analysis | EF | sp | vpt | 1b |
| Klauke <i>et al.</i> | 2016 | South America | Ecuador | Survey (cross-sectional) | BD | ge, sp | bir | 2c |
| Klorvuttimontara <i>et al.</i> | 2011 | Southeast Asia | Thailand | Modelling (SDM) | BD | co, bi | ins | 2b |

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| Koide <i>et al.</i> | 2017 | Pacific Ocean | Hawaii | Surveys (sequential) | DE | co | vpl | 2b |
| Kreyling <i>et al.</i> | 2010 | Africa | Ethiopia | Modelling (SDM) | DE | co, ec | vpl | 2b |
| Krishnaswamy <i>et al.</i> | 2014 | Global | N/A | Historic data analysis, modelling (other) | EF | bi | vpl | 1b |
| Krömer <i>et al.</i> | 2013 | North America | Mexico | Survey (cross-sectional) | DE | co | vpl, vpe | 2c |
| Kuo <i>et al.</i> | 2021 | East Asia | Taiwan | Surveys (sequential) | AE, BD | co, ec | vpl | 2b |
| La Marca <i>et al.</i> | 2005 | Central America, South America | Costa Rica, Ecuador, Venezuela | Surveys (sequential) | BD | sp | amp | 2c |
| La Sorte <i>et al.</i> | 2014 | Global | N/A | Modelling (climate, SDM) | BD | bi | bir | 2b |
| Larsen | 2012 | South America | Peru | Survey (cross-sectional) | S | co, ec | ins | 2c |
| Latta <i>et al.</i> | 2011 | South America | Ecuador | Surveys (sequential) | BD | co | bir | 2b |
| LaVal | 2004 | Central America | Costa Rica | Survey (longitudinal) | BD | co | mam | 1b |
| Lawton <i>et al.</i> | 2001 | Central America | Costa Rica | Modelling (climate) | S | ec | vpl | 2b |
| Ledo <i>et al.</i> | 2009 | South America | Peru | Modelling (SDM) | DE | co, ec | vpt | 2b |
| Li <i>et al.</i> | 2020 | East Asia | China | Experiment (field) | EF | sp | vpt | 1a |
| Li <i>et al.</i> | 2009 | Oceania | Australia | Survey (longitudinal), modelling (SDM) | BD | sp | bir | 2b |
| Liao <i>et al.</i> | 2020 | East Asia | China | Modelling (SDM) | DE | sp | vpt | 2b |
| Lippok <i>et al.</i> | 2014 | South America | Bolivia | Modelling (SDM) | DE | co, ec | vpt | 2c |
| Lips | 1998 | Central America | Costa Rica | Survey (longitudinal) | BD | co | amp | 2a |
| Liptzin <i>et al.</i> | 2011 | Caribbean | Puerto Rico | Survey (longitudinal) | EF | ec | N/A | 2a |
| Litton <i>et al.</i> | 2011 | Pacific Ocean | Hawaii | Survey (longitudinal) | EF | ec | vpt, fun | 2a |
| Litton <i>et al.</i> | 2020 | Pacific Ocean | Hawaii | Survey (longitudinal) | EF | ec | vpt | 2c |
| Liu <i>et al.</i> | 2021 | East Asia | China | Survey (cross-sectional) | EF | sp, ec | bry, vpe, lic | 2c |
| Lloret & González-Mancebo | 2011 | Macaronesia | Canary Islands | Modelling (SDM) | BD | co, ec | bry | 2b |
| Loarie <i>et al.</i> | 2009 | Global | Global | Modelling (climate) | AE | bi | N/A | 2b |
| Looby & Treseder | 2018 | Central America | Costa Rica | Experiment (field) | EF | ec | fun | 1a |
| Looby <i>et al.</i> | 2016 | Central America | Costa Rica | Surveys (sequential) | EF | co, ec | lic, fun | 2b |
| Loope & Giambelluca | 1998 | Pacific Ocean | Hawaii | Modelling (climate) | AE | co, ec | | 2b |

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| López-Arce <i>et al.</i> | 2019 | North America | Mexico | Modelling (SDM) | CS | sp, ec | vpl | 2b |
| Los <i>et al.</i> | 2021 | Global | N/A | Historic data analysis, modelling (SDM) | AE, DE | bi | N/A | 1b |
| Lutz <i>et al.</i> | 2013 | South America | Peru | Survey (longitudinal) | DE | ec | vpt | 1b |
| Lyu <i>et al.</i> | 2021 | Pacific Ocean | Hawaii | Survey (longitudinal) | EF, EF | ec | vpt | 2a |
| Macedo <i>et al.</i> | 2018 | South America | Brazil | Survey (cross-sectional) | BD | co | ins | 2c |
| Martin & Fahey | 2014 | Caribbean | Dominican Republic | Survey (longitudinal) | EF | co, ec | vpt | 1b |
| Martin <i>et al.</i> | 2007 | Caribbean | Dominican Republic | Survey (longitudinal) | AE | ec | vpt | 2a |
| Maul <i>et al.</i> | 2020 | Africa | Uganda | Survey (cross-sectional) | BD | co | bry | 2c |
| Menéndez-Guerrero <i>et al.</i> | 2020 | North America, Central America, South America | N/A | Modelling (SDM) | BD | bi | amp | 2b |
| Metcalfe & Ahlstrand | 2019 | South America | Peru | Experiment (<i>ex situ</i>) | EF | sp, ec | bry | 1b |
| Miles <i>et al.</i> | 2004 | South America | Bolivia, Brazil, Colombia, Ecuador, Peru | Modelling (SDM) | DE | sp,ec | vpl | 3 |
| Miller <i>et al.</i> | 2018 | Caribbean | Puerto Rico | Survey (longitudinal), historic data analysis | AE | ec | N/A | 1b |
| Molina-Venegas <i>et al.</i> | 2020 | Africa | Tanzania | Survey (cross-sectional) | DE | ec | vpl | 2c |
| Montejo-Kovacevich <i>et al.</i> | 2020 | South America | Ecuador | Surveys (comparative, longitudinal), experiment (<i>in situ</i>) | BD | sp | ins | 1b |
| Monterroso-Rivas <i>et al.</i> | 2016 | North America | Mexico | Modelling (other) | ES | ec, hu | vpt | 2b |
| Monterroso-Rivas <i>et al.</i> | 2013 | North America | Mexico | Modelling (SDM) | DE | co, ec | vpt | 2b |
| Morales <i>et al.</i> | 2004 | South America | Argentina | Historic data analysis | EF | sp | vpt | 1b |
| Mujawamariya <i>et al.</i> | 2018 | Africa | Rwanda | Survey (longitudinal) | EF | sp | vpt | 2a |
| Müller <i>et al.</i> | 2017 | Global | N/A | Experiment (<i>ex situ</i>) | BD | sp | vpe | 1b |
| Muñoz <i>et al.</i> | 2016 | Oceania | Australia | Survey (cross-sectional), experiment (<i>ex situ</i>) | BD | sp | rep | 1b |
| Murugan <i>et al.</i> | 2009 | South Asia | India | Survey (longitudinal) | AE | ec | N/A | 1b |
| Nadkarni & Solano | 2002 | Central America | Costa Rica | Experiment (field) | BD | co | vpe | 1a |

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| Navas <i>et al.</i> | 2013 | Central America, South America | Panama, Colombia | Surveys (sequential) | BD | sp, co | amp | 2b |
| Neate-Clegg <i>et al.</i> | 2021a | Africa | Tanzania | Survey (longitudinal) | BD | co | bir | 1b |
| Neate-Clegg <i>et al.</i> | 2020 | Africa | Rwanda | Survey (longitudinal) | BD | co | bir | 1b |
| Neate-Clegg <i>et al.</i> | 2018 | Central America | Honduras | Survey (longitudinal) | BD | co | bir | 1b |
| Neate-Clegg <i>et al.</i> | 2021b | Africa | Tanzania | Surveys (sequential) | DE | co | bir | 2b |
| Neely <i>et al.</i> | 2020 | South America | Brazil | Experiment (<i>ex situ</i>) | S | si | fun, amp | 1b |
| Neto dos Santos <i>et al.</i> | 2020 | South America | Brazil | Modelling (SDM) | DE | sp | vpt | 2b |
| Niessner <i>et al.</i> | 2020 | South America | Peru | Survey (longitudinal) | EF | sp | vpt | 2a |
| Notter <i>et al.</i> | 2007 | Africa | Kenya | Modelling (other) | S | ec | N/A | 2a |
| Nottingham <i>et al.</i> | 2019a | South America | Peru | Survey (cross-sectional), experiment (<i>ex situ</i>) | EF | ec | bac, fun | 1b |
| Nottingham <i>et al.</i> | 2019b | South America | Peru | Experiment (field) | EF | ec | bac, fun | 1a |
| Nottingham <i>et al.</i> | 2016 | South America | Peru | Experiment (<i>ex situ</i>) | EF | ec | N/A | 1b |
| Nowrouzi <i>et al.</i> | 2018 | Oceania | Australia | Survey (cross-sectional), experiment (<i>ex situ</i>) | BD | sp, co | ins | 1b |
| Nowrouzi <i>et al.</i> | 2016 | Oceania | Australia | Survey (cross-sectional) | BD | sp, co | ins | 2c |
| Nwe at al. | 2020 | Southeast Asia | Myanmar | Modelling (SDM) | DE | ec | N/A | 2b |
| O'Donnell & Kumar | 2006 | Central America | Costa Rica | Survey (cross-sectional) | BD | co, ec | ins | 2c |
| Odell <i>et al.</i> | 2016 | Oceania | Australia | Surveys (sequential) | BD | co | ins | 2b |
| Ornelas <i>et al.</i> | 2018 | North America | Mexico | Modelling (SDM) | S | sp, si | vpl, vpe | 2a |
| Ortega-Andrade <i>et al.</i> | 2015 | South America | Ecuador, Colombia, Peru | Modelling (SDM) | BD | sp | mam | 2b |
| O'Sullivan <i>et al.</i> | 2021 | East Asia | Taiwan | Historic data analysis | DE, EF | sp, ec | vpt | 2a |
| Pau <i>et al.</i> | 2020 | Pacific Ocean | Hawaii | Survey (longitudinal) | EF | sp | vpt | 1b |
| Phillips | 1996 | Global | N/A | Survey (longitudinal) | BD | ec, bi | vpt | 2a |
| Piantoni <i>et al.</i> | 2016 | North America, South America, Caribbean | N/A | Experiment (<i>ex situ</i>) | BD | co, ec | rep | 1b |
| Platts <i>et al.</i> | 2013 | Africa | Kenya, Tanzania | Modelling (SDM) | DE | co, ec | vpl | 2b |
| Polato <i>et al.</i> | 2018 | South America | Ecuador | Experiment (<i>ex situ</i>) | BD | ge, sp, ec | ins | 1b |

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|--------------------------------|-------|--------------------------------|---|---|----|------------|-------------------------|----|
| Ponce-Reyes <i>et al.</i> | 2017 | Africa | Uganda, Rwanda, Burundi, Tanzania, DRC | Modelling (SDM) | DE | ec | N/A | 2b |
| Ponce-Reyes <i>et al.</i> | 2013 | North America | Mexico | Modelling (SDM) | DE | sp, co, ec | vpl, amp, bir, mam | 2b |
| Ponce-Reyes <i>et al.</i> | 2012 | North America | Mexico | Modelling (SDM) | DE | ec | vpl, amp, rep, bir, mam | 2b |
| Ponette-González <i>et al.</i> | 2010 | North America | Mexico | Survey (longitudinal) | S | ec | vpt | 2a |
| Pounds & Crump | 1994 | Central America | Costa Rica | Survey (longitudinal) | BD | sp | amp | 2c |
| Pounds <i>et al.</i> | 2006 | Central America, South America | Costa Rica, Colombia, Venezuela | Survey (longitudinal) | S | si | fun, amp | 1b |
| Pounds <i>et al.</i> | 1999 | Central America | Costa Rica | Survey (longitudinal) | BD | co | amp, rep, bir | 1b |
| Pouteau & Birnbaum | 2016 | Pacific Ocean | New Caledonia | Modelling (SDM) | BD | co, ec | vpt | 2b |
| Pouteau <i>et al.</i> | 2016 | Pacific Ocean | Tahiti | Modelling (SDM) | BD | co, ec | vpl, vpe | 2b |
| Puschendorf <i>et al.</i> | 2009 | Central America | Costa Rica | Modelling (SDM) | S | ec | amp | 2b |
| Quadri <i>et al.</i> | 2021 | North America | Mexico | Historic data analysis | EF | sp, ec | vpt | 1b |
| Quiroga <i>et al.</i> | 2018 | South America | Bolivia, Argentina | Modelling (SDM) | DE | sp, ec | vpt | 2b |
| Raman <i>et al.</i> | 2020a | South Asia | India | Survey (cross-sectional), modelling (SDM) | DE | sp | mam | 2b |
| Raman <i>et al.</i> | 2020b | South Asia | India | Survey (cross-sectional), modelling (SDM) | DE | sp | mam | 2b |
| Rambal <i>et al.</i> | 2020 | Central America | Costa Rica, Honduras | Survey (cross-sectional), modelling (other) | EF | sp, ec | vpt | 2b |
| Ramírez-Amezcu <i>et al.</i> | 2016 | North America | Mexico | Modelling (SDM) | DE | sp, ec | vpl | 2b |
| Ramírez-Bautista <i>et al.</i> | 2020 | North America | Mexico | Modelling (other) | BD | sp, co | mam | 2b |
| Ramírez-Villegas <i>et al.</i> | 2014 | South America | Venezuela, Colombia, Ecuador, Peru, Bolivia | Modelling (SDM) | DE | sp, co, ec | vpl, bir | 2b |
| Rapp <i>et al.</i> | 2012 | South America | Peru | Survey (cross-sectional) | EF | sp, co | vpt | 2c |
| Ravindranath & Sukumar | 1998 | South Asia | India | Modelling (climate) | AE | co, ec | N/A | 3 |
| Raxworthy <i>et al.</i> | 2008 | Africa | Madagascar | Surveys (sequential), | BD | sp, co | amp, rep | 2b |

| | | | | | | | | |
|---------------------------------|------|-----------------------|----------------|---|--------|--------|---------------|----|
| | | | | historic data analysis | | | | |
| Regalado & Ritter | 2021 | Macaronesia | Canary Islands | Survey (longitudinal) | AE, EF | sp, ec | vpt | 2c |
| Rehm & Feeley | 2016 | South America | Peru | Experiment (field) | DE | ec | vpt | 1b |
| Rehm & Feeley | 2015 | South America | Peru | Survey (longitudinal), experiment (<i>ex situ</i>) | DE | ec | vpt | 1b |
| Rehm & Feeley | 2013 | South America | Peru | Survey (longitudinal) | DE | co | vpt | 2a |
| Rehm <i>et al.</i> | 2021 | Pacific Ocean | Hawaii | Experiment (<i>ex situ</i>), historic data analysis | AE, CS | sp, ec | vpl | 1b |
| Reyes-Chávez <i>et al.</i> | 2021 | Central America | Honduras | Survey (cross-sectional) | BD | co | vpl, vpe | 2c |
| Richards | 2021 | Central America | Nicaragua | Surveys (comparative, cross-sectional), modelling (other) | BD | co | bry, vpl, lic | 2b |
| Ricker <i>et al.</i> | 2007 | North America | Mexico | Modelling (other) | EF | sp | vpt | 2b |
| Ritter <i>et al.</i> | 2019 | Macaronesia | Canary Islands | Survey (longitudinal), modelling (climate) | EF | ec | vpt | 2a |
| Ritter <i>et al.</i> | 2009 | Macaronesia | Canary Islands | Survey (longitudinal) | EF | ec | vpt | 2a |
| Robertson <i>et al.</i> | 2010 | South America | Peru | Survey (cross-sectional) | EF | sp | vpl | 2c |
| Rödder | 2009 | Global, Pacific Ocean | Hawaii | Modelling (SDM) | S | sp | amp | 2b |
| Rodríguez-Quiel <i>et al.</i> | 2019 | Central America | Panama | Survey (longitudinal) | BD | co | bry, lic | 2a |
| Rodríguez-Ramírez <i>et al.</i> | 2020 | North America | Mexico | Historic data analysis | EF | sp | vpt | 1b |
| Rodríguez-Ramírez <i>et al.</i> | 2018 | North America | Mexico | Historic data analysis | EF | sp | vpt | 1b |
| Rodríguez-Ramírez <i>et al.</i> | 2019 | North America | Mexico | Historic data analysis | EF | sp | vpt | 1b |
| Rojas-Briceño <i>et al.</i> | 2020 | South America | Peru | Modelling (SDM) | DE | co | vpt | 2b |
| Rojas-Soto <i>et al.</i> | 2012 | North America | Mexico | Modelling (SDM) | DE | ec | vpl, bir | 2b |
| Román-Cuesta <i>et al.</i> | 2011 | South America | Peru | Historic data analysis, Survey (cross-sectional) | S | ec | vpt | 2a |
| Rosselli <i>et al.</i> | 2017 | South America | Colombia | Surveys (sequential) | BD | co | bir | 2b |
| Round & Gale | 2008 | Southeast Asia | Thailand | Survey (longitudinal) | BD | sp | bir | 1b |
| Rueda-Solano <i>et al.</i> | 2016 | South America | Colombia | Experiment (field) | BD | sp | amp | 1a |
| Ruiz-Benito <i>et al.</i> | 2015 | East Asia | Taiwan | Historic data analysis | EF | sp, ec | vpt | 1b |

| | | | | | | | | |
|------------------------------|-------|---------------------------------|------------------------------------|--|--------|------------|-------------------------|----|
| Salinas <i>et al.</i> | 2011 | South America | Peru | Experiment (field) | EF | ec | vpt | 1b |
| Santillán <i>et al.</i> | 2020 | South America | Ecuador | Survey (cross-sectional) | BD | co | bir | 2c |
| Sarmiento & Kooperman | 2019 | South America | N/A | Modelling (climate) | AE | ec, hu | N/A | 2b |
| Scheffers & Williams | 2018 | Africa, Southeast Asia, Oceania | Madagascar, Philippines, Australia | Surveys (comparative, cross-sectional) | BD | co, ec | ins, amp, rep, bir, mam | 2c |
| Scheffers <i>et al.</i> | 2013a | Southeast Asia | Philippines | Experiment (field) | BD | sp | amp | 1a |
| Scheffers <i>et al.</i> | 2013b | Southeast Asia | Philippines | Survey (cross-sectional) | BD | sp, co | amp | 2c |
| Scheffers <i>et al.</i> | 2014 | Southeast Asia | Philippines | Survey (longitudinal) | BD | ec | amp | 2a |
| Schmitt <i>et al.</i> | 2013 | Africa | Ethiopia | Survey (longitudinal) | AE | co | vpl | 2a |
| Scholl <i>et al.</i> | 2021 | Caribbean | Puerto Rico | Survey (longitudinal) | AE | ec | vpl | 2a |
| Schuur | 2001 | Pacific Ocean | Hawaii | Experiment (field) | EF | ec | vpt | 1a |
| Scowcroft <i>et al.</i> | 2000 | Pacific Ocean | Hawaii | Experiment (field) | EF | ec | vpt | 1a |
| Şekercioğlu <i>et al.</i> | 2008 | Global | N/A | Modelling (SDM) | BD | bi | bir | 2b |
| Selmants <i>et al.</i> | 2014 | Pacific Ocean | Hawaii | Survey (longitudinal) | EF | ec | vpl | 1b |
| Selmants <i>et al.</i> | 2016 | Pacific ocean | Hawaii | Survey (cross-sectional) | EF | co | bac | 2c |
| Setyawan <i>et al.</i> | 2020 | Southeast Asia | Indonesia | Modelling (SDM) | DE, BD | sp | vpl | 2b |
| Shah <i>et al.</i> | 2017a | South America | Ecuador | Experiment (<i>ex situ</i>) | BD | sp, ec | ins | 1b |
| Shah <i>et al.</i> | 2017b | South America | Ecuador | Experiment (<i>ex situ</i>) | BD | sp, ec | ins | 1b |
| Sheldon <i>et al.</i> | 2011 | Global | N/A | Modelling (SDM) | DE | co, ec, bi | ins, amp, rep, bir, mam | 2b |
| Shi & Zhu | 2009 | East Asia | China | Survey (cross-sectional) | BD | co, ec | vpt | 2c |
| Shiao <i>et al.</i> | 2020 | East Asia | Taiwan | Survey (longitudinal), modelling (SDM) | BD | sp | bir | 1b |
| Shiao <i>et al.</i> | 2015 | East Asia | Taiwan | Survey (longitudinal) | BD | sp | bir | 2a |
| Shoo <i>et al.</i> | 2010 | Oceania | Australia | Survey (longitudinal) | S | ec | amp | 2a |
| Shoo <i>et al.</i> | 2011 | Oceania | Australia | Modelling (SDM) | CS | ec | amp, rep, bir, mam | 2b |
| Shugart <i>et al.</i> | 2001 | Africa | Kenya, Tanzania | Survey (longitudinal) | DE | co, ec | vpl | 2a |
| Sierra-Morales <i>et al.</i> | 2021 | North America | Mexico | Modelling (SDM) | BD, DE | sp, ec | bir | 2b |
| Silva <i>et al.</i> | 2020 | South America | Brazil | Survey (longitudinal), | BD | ge, sp, co | ins | 1b |

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|--------------------------------|-------|----------------|--|--|--------|--------|----------|----|
| | | | | experiment (<i>ex situ</i>) | | | | |
| Singh <i>et al.</i> | 2021 | Southeast Asia | Malaysia, Brunei, Indonesia | Modelling (SDM) | BD | ec | bir | 2b |
| Song <i>et al.</i> | 2012 | East Asia | China | Experiment (field) | BD | co, ec | bry, lic | 1a |
| Song <i>et al.</i> | 2016a | East Asia | China | Survey (longitudinal) | EF | co | vpt | 2a |
| Song <i>et al.</i> | 2016b | East Asia | China | Survey (longitudinal) | DE | co | vpt | 2a |
| Song <i>et al.</i> | 2019 | Southeast Asia | China, Vietnam | Modelling (SDM) | DE | sp | vpt | 2b |
| Soto-Correa <i>et al.</i> | 2013 | North America | Mexico | Experiment (<i>ex situ</i>), modelling (climate) | BD | sp | vpt | 1b |
| Sperling <i>et al.</i> | 2004 | Macaronesia | Canary Islands | Modelling (future climate) | AE | ec | vpt | 3 |
| Sreekumar & Nameer | 2021 | South Asia | India | Modelling (SDM) | DE, BD | sp | bir | 2b |
| Staunton <i>et al.</i> | 2016 | Oceania | Australia | Survey (cross-sectional) | BD | sp, co | ins | 2c |
| Still <i>et al.</i> | 1999 | Global | Costa Rica, Colombia, Malaysia and Rwanda | Modelling (climate) | AE | co | vpl | 3 |
| Strangas <i>et al.</i> | 2019 | South America | Brazil | Experiment (<i>ex situ</i>), modelling (SDM) | BD | sp, si | rep | 1b |
| Strauch <i>et al.</i> | 2017 | Pacific Ocean | Hawaii | Modelling (other) | ES | ec | vpt | 2b |
| Sukumar <i>et al.</i> | 1995 | South Asia | India | Modelling (climate) | AE | co | | 2b |
| Sun <i>et al.</i> | 2020 | East Asia | China | Survey (cross-sectional) | EF | co | bac, vpl | 2c |
| Tagliari <i>et al.</i> | 2021 | South America | Brazil | Modelling (SDM) | DE | ec | vpt | 2b |
| Tao <i>et al.</i> | 2021 | East Asia | China | Experiment (<i>ex situ</i>) | BD | sp | rep | 1b |
| Tejedor-Garavito <i>et al.</i> | 2015 | South America | Argentina, Bolivia, Colombia, Ecuador, Peru, Venezuela | Modelling (SDM) | BD | ec | vpt | 2b |
| Téllez-Valdés <i>et al.</i> | 2006 | North America | Mexico | Modelling (SDM) | DE | sp, ec | vpt | 2b |
| Thang & Thu | 2021 | Southeast Asia | Myanmar | Survey (cross-sectional) | EF | so, co | vpt | 2c |
| Thang <i>et al.</i> | 2020 | Southeast Asia | Myanmar | Survey (cross-sectional), modelling (SDM) | EF | sp, co | vpt | 2c |
| Tito <i>et al.</i> | 2021 | South America | Peru | Experiment (field) | DE | sp, ec | vpt | 1a |
| Toledo-Aceves & del Val | 2021 | North America | Mexico | Experiment (field) | EF | si | vpt, ins | 1a |

| | | | | | | | | |
|----------------------------------|------|-----------------------|--|--|----|--------|----------|----|
| Toledo-Aceves <i>et al.</i> | 2019 | North America | Mexico | Experiment (field) | EF | ec | vpt | 1a |
| Toledo-Aceves <i>et al.</i> | 2011 | North America | Mexico | Survey (cross-sectional) | CS | ec, hu | N/A | 2c |
| Torres <i>et al.</i> | 2008 | Caribbean | Puerto Rico | Modelling (climate) | AE | ec | N/A | 2b |
| Tovar <i>et al.</i> | 2013 | South America | Venezuela, Colombia, Ecuador, Peru and Bolivia | Modelling (SDM) | DE | ec | N/A | 2b |
| Townsend & Masters | 2015 | Central America | Costa Rica | Conservation strategy proposal | CS | ec, hu | N/A | 3 |
| Tsai <i>et al.</i> | 2015 | East Asia | Taiwan | Surveys (sequential) | BD | sp, co | bir | 2b |
| Urrutia & Vuille | 2009 | South America | N/A | Modelling (climate) | AE | ec | N/A | 2b |
| Valtonen <i>et al.</i> | 2013 | Africa | Uganda | Survey (longitudinal) | BD | co, ec | ins | 1b |
| Van Beusekom <i>et al.</i> | 2017 | Caribbean | Puerto Rico | Survey (longitudinal) | AE | ec | N/A | 1b |
| Van Beusekom <i>et al.</i> | 2015 | Caribbean | Puerto Rico | Survey (longitudinal) | AE | ec | N/A | 2a |
| Vasquez-Morales <i>et al.</i> | 2014 | North America | Mexico | Modelling (SDM) | DE | sp | vpt | 2b |
| Velásquez-Restrepo <i>et al.</i> | 2012 | South America | Colombia | Survey (longitudinal) | AE | ec | vpt | 2a |
| Velásquez-Tibatá <i>et al.</i> | 2013 | South America | Colombia | Modelling (SDM) | BD | co | bir | 2b |
| Velo-Antón <i>et al.</i> | 2013 | North America | Mexico | Modelling (SDM) | BD | ge, sp | amp | 2b |
| Venter <i>et al.</i> | 2017 | Oceania | Papua New Guinea | Survey (cross-sectional) | EF | ec | vpt | 2c |
| Vieira <i>et al.</i> | 2011 | South America | Brazil | Survey (cross-sectional) | EF | ec | vpl | 2c |
| Villa <i>et al.</i> | 2019 | South America | Venezuela | Survey (longitudinal) | BD | sp, ec | amp | 2a |
| Villers-Ruiz & Trejo-Vásquez | 1998 | North America | Mexico | Modelling (climate, life zones) | DE | ec | vpt | 2b |
| Vollstädt <i>et al.</i> | 2020 | South America, Africa | Ecuador, Tanzania | Surveys (comparative, cross-sectional) | EF | si | vpt, bir | 2c |
| von May <i>et al.</i> | 2017 | South America | Peru | Experiment (<i>ex situ</i>) | BD | sp | amp | 1b |
| Wagner <i>et al.</i> | 2014 | Central America | Panama | Experiment (field) | BD | sp, co | bry | 1a |
| Wallace & McJannet | 2013 | Oceania | Australia | Survey (longitudinal) | AE | ec | vpl | 2a |
| Wang <i>et al.</i> | 2003 | Caribbean | Puerto Rico | Modelling (climate) | EF | ec | vpt | 2a |
| Wang <i>et al.</i> | 2002 | Caribbean | Puerto Rico | Modelling (other) | EF | ec | N/A | 2b |
| Warne <i>et al.</i> | 2020 | Central America | Costa Rica | Surveys (sequential) | BD | ge, co | ins | 2b |
| Weintraub <i>et al.</i> | 2016 | Central America | Costa Rica, Panama | Survey (cross-sectional) | EF | ec | bac, fun | 2c |
| Whitaker <i>et al.</i> | 2014 | South America | Peru | Survey (cross-sectional), | EF | ec | bac, fun | 1b |

| | | | | experiment (<i>ex situ</i>) | | | | |
|------------------------------|------|--------------------------------|--------------------|-------------------------------------|--------|--------|--------------------|----|
| Wicaksono <i>et al.</i> | 2017 | South America | Bolivia, Argentina | Modelling (SDM) | DE | sp, co | vpt, fun | 2b |
| Wilcke <i>et al.</i> | 2020 | South America | Ecuador | Survey (longitudinal) | EF, EF | ec | N/A | 1b |
| Wilcke <i>et al.</i> | 2013 | South America | Ecuador | Survey (longitudinal) | EF | ec | N/A | 2a |
| Williams <i>et al.</i> | 2020 | Central America | Costa Rica | Experiment (<i>ex situ</i>) | BD, EF | sp | vpe | 1b |
| Williams <i>et al.</i> | 2018 | North America | Mexico | Modelling (climate, other) | AE | ec | N/A | 2b |
| Williams <i>et al.</i> | 2003 | Oceania | Australia | Modelling (SDM) | BD | ec | amp, rep, bir, mam | 2b |
| Willig <i>et al.</i> | 2021 | Caribbean | Puerto Rico | Survey (longitudinal) | BD | co | oin | 1b |
| Wilson <i>et al.</i> | 2007 | Oceania | Australia | Surveys (sequential) | BD | sp, co | ins | 2b |
| Woodhams <i>et al.</i> | 2008 | Oceania | Australia | Experiment (<i>ex situ</i>) | S | sp, si | fun, amp | 1b |
| Wright <i>et al.</i> | 2009 | Global | N/A | Modelling (climate, other) | BD | bi | N/A | 2b |
| Yocom & Fulé | 2012 | North America | Mexico | Survey (longitudinal) | S | ec | vpt | 1b |
| Young & Lipton | 2006 | South America | Peru | Survey (cross-sectional) | CS | ec, hu | N/A | 2c |
| Young <i>et al.</i> | 2017 | South America | Peru | Historic data analysis | AE | ec | vpt | 2b |
| Yuste <i>et al.</i> | 2017 | South America | Colombia | Experiment (<i>ex situ</i>) | EF | ec | N/A | 1b |
| Zach <i>et al.</i> | 2010 | South America | Ecuador | Survey (longitudinal) | EF | sp | vpt | 2a |
| Zamora-Vilchis <i>et al.</i> | 2012 | Oceania | Australia | Survey (cross-sectional) | S | si, co | bir, oth | 2c |
| Zhang | 2010 | East Asia | China | Surveys (comparative, longitudinal) | EF | ec | vpt | 2a |
| Zhang <i>et al.</i> | 1996 | Global | N/A | Modelling (climate) | S | ec, bi | vpt | 3 |
| Zhou <i>et al.</i> | 2017 | East Asia | China | Historic data analysis | ES | ec | vpt | 1b |
| Zhou <i>et al.</i> | 2013 | East Asia | China | Survey (longitudinal) | EF | ec | vpt | 2a |
| Zimmermann <i>et al.</i> | 2010 | South America | Peru | Experiment (field) | EF | ec | bac | 1a |
| Zotz <i>et al.</i> | 2010 | North America, Central America | Mexico, Panama | Experiment (<i>ex situ</i>) | BD | co | vpe | 1b |
| Zuleta <i>et al.</i> | 2016 | South America | Colombia | Surveys (sequential) | BD | co, ec | vpe | 2b |

Appendix B. Supplementary Information for Chapter 3

Table S2. National inventories used to build the list of tropical montane tree in this study.

| Country* | Authors and year | Title | Description |
|--------------------|--|--|--|
| Mexico | González-Espinosa, 2011 | Red List of Mexican Cloud Forest Trees | List of 962 plant species recorded in Mexican TMFs, of which 754 are trees, and includes their description, common names and conservation status. |
| Guatemala | Véliz et al., 2000 | La Vegetación Montana de Guatemala | Inventory of montane flora of Guatemala, listing 608 plant species and their habit, of which 62 are trees. |
| Honduras | Zea Ramírez, 2006 | Resultados del inventario de bosques y árboles 2005-2006. Evaluación Nacional Forestal (No. Nc.860). SAG, COHDEFOR | Report on the conservation status of Honduran forests, listing 314 species, distinguishing only those recorded in forested and non-forested areas. |
| El Salvador | Ministerio de Medio Ambiente y Recursos Naturales (MARN), 2018 | Inventario nacional de bosques de El Salvador | Forest inventory which lists a 140 tree species in the country, without distinction of forest types. |
| Nicaragua | Williams, 2009 | Resultados del Inventario Nacional Forestal 2007-2008 | National inventory listing 370 tree species without distinction of forest types. |
| Costa Rica | Sistema Nacional de Áreas de Conservación (Sinac), 2014 | Protocolo de campo para la identificación de especies arbóreas: Información taxonómica y dendrológica de las especies arbóreas de Costa Rica. Volumen 3. | Master list of tree species for the country, containing 2,032 species without distinction of forest types. |
| Panama | Condit et al., 2020 | Trees of Panama: A complete checklist with every geographic range | Natonal inventory of trees, listing 3,035 species without forest type distinction. |

* Of the seven countries, only the inventories from Mexico and Guatemala listed montane species separately, and despite their focus on arboreal species, some of these sources included other life forms, such as ferns, climbers, epiphytes, etc.

Table S3. Species omitted ($N = 1,212$) due to low number (<20) of usable records (shown in brackets). This step was carried out before verifying growth habit and taxonomy, so this list may contain non-arboreal forms and lineages that do not occur as trees (e.g., pteridophytes or monocots).

| | | |
|--|--|--|
| <i>Abarema racemiflora</i> (17) | <i>Ardisia cartagoana</i> (5) | <i>Beilschmiedia sulcata</i> (17) |
| <i>Abarema zolleriana</i> (16) | <i>Ardisia colombiana</i> (6) | <i>Beilschmiedia tilaranensis</i> (9) |
| <i>Acanthocladus dukei</i> (1) | <i>Ardisia coloradoana</i> (3) | <i>Bernardia fonsecae</i> (1) |
| <i>Actinostemon caribaeus</i> (17) | <i>Ardisia conglomerata</i> (2) | <i>Bernardia macrocarpa</i> (4) |
| <i>Aegiphila hirsutissima</i> (12) | <i>Ardisia crassipes</i> (4) | <i>Bernardia macrophylla</i> (8) |
| <i>Aegiphila valerii</i> (14) | <i>Ardisia crassiramea</i> (19) | <i>Bernardia mollis</i> (8) |
| <i>Agave hurteri</i> (11) | <i>Ardisia darienensis</i> (3) | <i>Bernardia oblanceolata</i> (7) |
| <i>Ageratina ovilla</i> (12) | <i>Ardisia dodgei</i> (17) | <i>Besleria arborescens</i> (12) |
| <i>Agrostis exserta</i> (6) | <i>Ardisia dukei</i> (1) | <i>Bidens chrysanthemifolia</i> (13) |
| <i>Agrostis laxissima</i> (8) | <i>Ardisia dwyeri</i> (6) | <i>Bidens holwayi</i> (2) |
| <i>Aiouea obscura</i> (17) | <i>Ardisia folsomii</i> (7) | <i>Blakea crinita</i> (11) |
| <i>Aiouea vexatrix</i> (2) | <i>Ardisia fruticosa</i> (10) | <i>Blakea darcyana</i> (1) |
| <i>Alchornea guatemalensis</i> (6) | <i>Ardisia furfuracea</i> (11) | <i>Blakea fragrantissima</i> (9) |
| <i>Alfaroa manningii</i> (8) | <i>Ardisia furfuracella</i> (16) | <i>Blakea gregii</i> (6) |
| <i>Alibertia utleyorum</i> (17) | <i>Ardisia geniculata</i> (4) | <i>Blakea hammelii</i> (5) |
| <i>Allophylus gentryi</i> (11) | <i>Ardisia glomerata</i> (3) | <i>Blakea parvifolia</i> (8) |
| <i>Amaioua magnicarpa</i> (8) | <i>Ardisia gordonii</i> (1) | <i>Blakea pluvialis</i> (4) |
| <i>Amphitecna gentryi</i> (14) | <i>Ardisia granatensis</i> (9) | <i>Blakea purpusii</i> (12) |
| <i>Amphitecna haberi</i> (3) | <i>Ardisia hagenii</i> (9) | <i>Blakea wilsoniorum</i> (16) |
| <i>Amphitecna macrophylla</i> (12) | <i>Ardisia hammelii</i> (1) | <i>Bocconia glaucifolia</i> (14) |
| <i>Amphitecna parviflora</i> (5) | <i>Ardisia herrerana</i> (1) | <i>Bocconia vulcanica</i> (19) |
| <i>Amphitecna spathicalyx</i> (3) | <i>Ardisia jefeana</i> (12) | <i>Bourreria grandicalyx</i> (11) |
| <i>Amphitecna steyermarkii</i> (11) | <i>Ardisia knappiae</i> (4) | <i>Bourreria grayumii</i> (11) |
| <i>Anaxagorea panamensis</i> (10) | <i>Ardisia liesneri</i> (16) | <i>Bourreria rinconensis</i> (5) |
| <i>Aniba bracteata</i> (4) | <i>Ardisia maxonii</i> (9) | <i>Brachistus knappiae</i> (5) |
| <i>Annona caesia</i> (6) | <i>Ardisia megistophylla</i> (16) | <i>Brownea leucantha</i> (6) |
| <i>Annona danforthii</i> (8) | <i>Ardisia mexicana</i> (11) | <i>Browneopsis excelsa</i> (19) |
| <i>Annona hayesii</i> (4) | <i>Ardisia nervosissima</i> (9) | <i>Brunellia hygrophorica</i> (13) |
| <i>Annona inconformis</i> (3) | <i>Ardisia opaca</i> (2) | <i>Brunellia morii</i> (3) |
| <i>Annona pruinosa</i> (18) | <i>Ardisia perinsignis</i> (6) | <i>Brunellia standleyana</i> (15) |
| <i>Aphelandra laxa</i> (3) | <i>Ardisia pseudocuspidata</i> (1) | <i>Brunfelsia chocoensis</i> (12) |
| <i>Aphelandra leonardii</i> (5) | <i>Ardisia pulverulenta</i> (2) | <i>Brunfelsia dwyeri</i> (12) |
| <i>Aphelandra micans</i> (7) | <i>Ardisia rigidifolia</i> (7) | <i>Buddleja megaloccephala</i> (17) |
| <i>Aphelandra panamensis</i> (2) | <i>Ardisia scheryi</i> (16) | <i>Bunchosia brevisurcularis</i> (7) |
| <i>Aphelandra scolnikiae</i> (5) | <i>Ardisia storkii</i> (1) | <i>Bunchosia grayumii</i> (12) |
| <i>Arachnothryx calycosa</i> (15) | <i>Ardisia subsessilifolia</i> (10) | <i>Bunchosia stipulacea</i> (2) |
| <i>Arachnothryx chaconii</i> (6) | <i>Ardisia tenuis</i> (3) | <i>Bunchosia tutensis</i> (1) |
| <i>Arachnothryx chiriquiana</i> (6) | <i>Ardisia tysonii</i> (7) | <i>Bunchosia veluticarpa</i> (17) |
| <i>Arachnothryx darienensis</i> (1) | <i>Ardisia unguensis</i> (4) | <i>Bunchosia vulcanica</i> (8) |
| <i>Arachnothryx dwyeri</i> (8) | <i>Ardisia ursina</i> (7) | <i>Bursera glabra</i> (18) |
| <i>Arachnothryx guerrenensis</i> (5) | <i>Ardisia vesca</i> (1) | <i>Bursera inversa</i> (7) |
| <i>Arachnothryx manantlanensis</i> (8) | <i>Arthrostemma primaevum</i> (13) | <i>Buxus moctezumae</i> (10) |
| <i>Arachnothryx monticola</i> (2) | <i>Aspidosperma crypticum</i> (5) | <i>Byrsonima herrerae</i> (11) |
| <i>Arachnothryx purpurea</i> (4) | <i>Astrocaryum confertum</i> (5) | <i>Calamagrostis guatemalensis</i> (6) |
| <i>Arachnothryx secunda</i> (5) | <i>Bactris caudata</i> (11) | <i>Calamagrostis vulcanica</i> (8) |
| <i>Arachnothryx tayloriae</i> (5) | <i>Bactris charnleyae</i> (5) | <i>Calliandra erythrocephala</i> (14) |
| <i>Arachnothryx tuxtlensis</i> (19) | <i>Bactris kunorum</i> (5) | <i>Calophyllum nubicola</i> (5) |
| <i>Arawakia caputmonsia</i> (4) | <i>Bactris panamensis</i> (8) | <i>Calyptanthus chytraculia</i> (3) |
| <i>Arawakia panamaea</i> (2) | <i>Balmea stormae</i> (3) | <i>Calyptrogyne tutensis</i> (12) |
| <i>Archibaccharis corymbosa</i> (8) | <i>Bartlettina maxonii</i> (6) | <i>Campnosperma panamense</i> (18) |
| <i>Ardisia albispala</i> (1) | <i>Bartlettina prionophylla</i> (4) | <i>Canavalia dura</i> (17) |
| <i>Ardisia amanuensis</i> (9) | <i>Bauhinia chapulhuacana</i> (19) | <i>Caphexandra heydeana</i> (19) |
| <i>Ardisia atropurpurea</i> (1) | <i>Bauhinia proboscidea</i> (6) | <i>Cardamine eremita</i> (1) |
| <i>Ardisia blepharodes</i> (10) | <i>Beilschmiedia angustieliptica</i> (3) | <i>Carex cuchumatanaensis</i> (4) |
| <i>Ardisia breedlovei</i> (6) | <i>Beilschmiedia immersinervis</i> (11) | <i>Carex tojiquianensis</i> (4) |
| <i>Ardisia brevis</i> (10) | <i>Beilschmiedia manantlanensis</i> (7) | <i>Caryodendron angustifolium</i> (3) |
| <i>Ardisia capitellata</i> (18) | <i>Beilschmiedia ovalioides</i> (9) | <i>Casearia atlantica</i> (7) |

- Casearia cajambrensis* (17)
Casearia standleyana (16)
Castilleja tapeinoclada (9)
Cavendishia panamensis (8)
Cavendishia revoluta (4)
Cavendishia subfasciculata (15)
Cavendishia tenella (12)
Ceanothus coeruleus (10)
Cecropia garciae (17)
Cecropia heterochroma (16)
Cecropia longipes (18)
Cecropia pittieri (6)
Cecropia virgusa (15)
Cedrela monroensis (1)
Centrolobium yavizanum (9)
Cerastium guatemalense (12)
Cerastium juniperorum (3)
Ceratozamia matudae (19)
Cestrum acuminatum (12)
Cestrum dasyanthum (5)
Cestrum formosum (3)
Cestrum knappiae (10)
Cestrum langeanum (9)
Cestrum pacayense (4)
Chamaedorea alternans (19)
Chamaedorea anemophila (11)
Chamaedorea guntheriana (3)
Chamaedorea ponderosa (7)
Chamaedorea subjectifolia (10)
Chomelia grandicarpa (2)
Chomelia rubra (1)
Chrysochlamys angustifolia (14)
Chrysochlamys membrillensis (5)
Chrysophyllum striatum (1)
Cirsium nigriceps (9)
Cirsium skutchii (4)
Citharexylum bourgeauianum (7)
Citharexylum gentryi (6)
Citharexylum hintonii (8)
Citharexylum steyermarkii (7)
Clavija fusca (8)
Clethra chiapensis (5)
Clethra consimilis (13)
Clethra formosa (18)
Clethra fragrans (8)
Clethra gelida (17)
Clethra licanioides (7)
Clethra luzmariae (5)
Clethra pachecoana (14)
Clethra purpusii (7)
Clethra pyrogena (15)
Clethra tutensis (1)
Clethra tuxtensis (5)
Cleyera cernua (5)
Cleyera velutina (13)
Clibadium sessile (2)
Clitoria glaberrima (14)
Clusia pentandra (12)
Clusia talamancana (7)
Clusia veneralensis (7)
Coaxana purpurea (9)
Cobaea pachysepalala (18)
Coccoloba darienensis (5)
Coccoloba gentryi (19)
Coccoloba johnstonii (7)
Coccoloba lasseri (10)
Colpothrinax aphanopetala (10)
Colpothrinax cookii (11)
Conceveiba parvifolia (14)
Conchocarpus toxicarius (16)
Connarus silvanensis (7)
Connarus williamsii (13)
Copaifera panamensis (19)
Cordia anisophylla (14)
Cordia correae (2)
Cordia croatii (18)
Cordia lasiocalyx (14)
Cordia leslieae (4)
Cordia nitida (1)
Cordia tacarcunensis (1)
Couepia janzenii (3)
Couepia scottmorii (3)
Coussapoa glaberrima (11)
Coussapoa macerrima (16)
Coussarea brevipedunculata (3)
Coussarea curvigemmia (7)
Coussarea durifolia (3)
Coussarea garciae (13)
Coussarea veraguensis (8)
Crematosperma westrae (4)
Croizatia panamensis (12)
Crossopetalum gomezii (14)
Croton jimenezii (13)
Croton rosarianus (3)
Croton speciosus (12)
Croton tonduzii (7)
Crudia acuminata (18)
Cryosophila cookii (2)
Cryosophila grayumii (15)
Cryosophila guagara (13)
Cryptocarya panamensis (1)
Cuatresia amistadensis (12)
Cuatresia morii (12)
Cuchumatanea steyermarkii (1)
Cupania grandiflora (6)
Cupania largifolia (6)
Cuphea schumannii (9)
Cyathea cervantesiana (4)
Cyathea conformis (2)
Cyathea darienensis (1)
Cyathea impar (8)
Cyathea povedae (17)
Cyathea rojasiana (2)
Cybianthus montanus (16)
Cyclanthera steyermarkii (9)
Cymbopetalum rugulosum (9)
Dacryodes patrona (4)
Dahlstedtia calcarata (12)
Dalbergia tilarana (9)
Damburneya bicolor (6)
Daphnopsis correae (4)
Daphnopsis flavida (10)
Daphnopsis folsomii (8)
Daphnopsis hammelii (14)
Daphnopsis mexiae (16)
Daphnopsis morii (9)
Daphnopsis tuerckheimiana (12)
Decazyx macrophyllus (16)
Dendropanax alberti-smithii (8)
Dendropanax bracteatus (3)
Dendropanax hondurensis (14)
Dendropanax pachypedunculatus (1)
Dendropanax pallidus (15)
Dendropanax praestans (13)
Dendropanax punctatus (14)
Deppea guerrerensis (11)
Desmopsis biseriata (3)
Desmopsis brachypoda (5)
Desmopsis confusa (14)
Desmopsis dukei (10)
Desmopsis oerstedii (10)
Desmotes incomparabilis (5)
Dichapetalum gentryi (3)
Dichapetalum nevermannianum (8)
Disocactus phyllanthoides (6)
Disterigma trimerum (11)
Drymaria hypericifolia (5)
Duguetia gentryi (5)
Duguetia tuberculata (4)
Duguetia vallicola (9)
Dussia martinicensis (1)
Echeveria nuda (8)
Elaeagia glossostipula (4)
Elaeagia nitidifolia (11)
Elaphoglossum leporinum (16)
Elaphoglossum tenuifolium (12)
Endlicheria jefensis (1)
Endlicheria tschudiana (11)
Epidendrum microcharis (12)
Erisma blancoa (4)
Erythrina chiriquensis (15)
Erythrina cochleata (11)
Erythrina florenciae (11)
Erythrina globocalyx (13)
Erythrina hondurensis (11)
Erythroxylum brennae (10)
Erythroxylum oxycarpum (16)
Eschweilera biflora (17)
Eschweilera correae (18)
Eschweilera jacquelyniae (16)
Eschweilera jefensis (9)
Eschweilera longipedicellata (10)
Eschweilera pachyderma (10)
Esenbeckia panamensis (14)
Eugenia arrhaphocalyx (4)
Eugenia basilaris (2)
Eugenia belloii (4)
Eugenia brachyblastiflora (1)
Eugenia cerrocacaensis (7)
Eugenia chavarriae (5)
Eugenia chepensis (18)
Eugenia chiapensis (4)
Eugenia citroides (13)
Eugenia cocosensis (1)
Eugenia coibensis (12)
Eugenia coloradoensis (15)
Eugenia corusca (9)
Eugenia cricamolensis (11)
Eugenia darcyi (12)
Eugenia earthiana (5)
Eugenia glandulosopunctata (19)
Eugenia grayumii (3)
Eugenia haberi (4)
Eugenia hammelii (7)
Eugenia hartshornii (16)
Eugenia herrerae (4)
Eugenia jambos (3)
Eugenia lepidota (12)

- Eugenia letreroana* (5)
Eugenia leucadendron (2)
Eugenia lithosperma (6)
Eugenia magniflora (1)
Eugenia mcphersonii (5)
Eugenia monteверdensis (14)
Eugenia nesiotica (6)
Eugenia ovandensis (1)
Eugenia pacifica (9)
Eugenia paloverdensis (4)
Eugenia ravenii (10)
Eugenia riosiae (10)
Eugenia roseola (1)
Eugenia roseopetala (2)
Eugenia sancarlosensis (4)
Eugenia sanjuanensis (7)
Eugenia sarapiquensis (7)
Eugenia selvana (8)
Eugenia skutchii (4)
Eugenia teresae (15)
Eugenia tilarana (5)
Eugenia tonii (1)
Eugenia trunciflora (15)
Eugenia veraguensis (1)
Eugenia verruculata (4)
Eugenia zuchowskiae (7)
Euphorbia macropodoides (9)
Euphorbia zieroides (3)
Faramea accumulans (2)
Faramea areolata (15)
Faramea capulifolia (13)
Faramea cobana (6)
Faramea correae (3)
Faramea lehmannii (8)
Faramea liesneri (10)
Faramea macrura (6)
Faramea papillata (4)
Faramea papirifolia (11)
Faramea permagnifolia (10)
Faramea scalaris (3)
Festuca amplissima (10)
Ficus carchiana (6)
Ficus davidsoniae (13)
Ficus francoae (2)
Ficus osensis (2)
Ficus richteri (3)
Forchhammeria iltisii (9)
Frangula darienensis (1)
Freziera forerorum (1)
Furcraea quicheensis (17)
Galipea panamensis (5)
Garrya corvorum (3)
Gaultheria odorata (2)
Geissanthus perpuncticulosus (11)
Geonoma mooreana (17)
Geonoma triandra (13)
Gibsoniothamnus truncatus (5)
Gloeospermum blakeanum (1)
Gloeospermum dichotomum (8)
Gloeospermum pauciflorum (8)
Gloeospermum portobelense (5)
Gonzalagunia longithyrsa (17)
Graffenrieda jefensis (1)
Gratiola oresbia (5)
Guapira standleyana (9)
Guarea adenophylla (13)
Guarea aguilarii (5)
Guarea caulobotrys (11)
Guarea constricta (3)
Guarea corticosa (5)
Guarea donnell-smithii (7)
Guarea gentryi (16)
Guarea inesiana (3)
Guarea macrocalyx (2)
Guarea montana (16)
Guarea pilosa (12)
Guarea pyriformis (17)
Guarea subsessilifolia (5)
Guarea tafae-malekui (1)
Guarea talamancana (1)
Guarea zarceroensis (9)
Guatteria aberrans (10)
Guatteria acrantha (1)
Guatteria allenii (10)
Guatteria jefensis (13)
Guatteria panamensis (2)
Guatteria rostrata (19)
Guatteria rotundata (9)
Guatteria rubiginosa (7)
Guatteria sessilicarpa (13)
Guatteria tacarcunae (1)
Guatteria zamorae (6)
Guettarda brenesii (8)
Guettarda ramuliflora (15)
Gustavia fosteri (2)
Gustavia monocaulis (4)
Gymnanthes dressleri (2)
Gyranthera darienensis (8)
Hackelia skutchii (9)
Halenia alata (9)
Halenia schiedeana (17)
Hamelia barbata (9)
Hamelia sanguinea (16)
Hampea albipetala (11)
Hampea longipes (18)
Hampea micrantha (19)
Hampea montebellensis (10)
Hampea punctulata (16)
Hasseltia allenii (1)
Hedyosmum burgerianum (3)
Hedyosmum correaanum (5)
Hedyosmum gentryi (16)
Heisteria skutchii (2)
Helenium integrifolium (1)
Heliopsis buphthalmoides (16)
Henriettea strigosa (3)
Herrania pulcherrima (7)
Hibiscus spathulatus (3)
Hieracium guatemalense (1)
Hippotis stellata (3)
Hirtella papillata (11)
Hirtella trichotoma (4)
Hoffmannia hondurensis (6)
Hoffmannia manussatani (2)
Hordeum guatemalense (2)
Huberodendron allenii (18)
Huetea cubensis (15)
Hymenandra crosbyi (4)
Hymenopus costaricensis (9)
Hyperbaena allenii (1)
Hyperbaena eladioana (18)
Hypericum calcicola (7)
Hypericum epigeium (4)
Ilex condensata (18)
Ilex dugesii (6)
Ilex haberi (19)
Ilex mexicana (1)
Ilex servinii (3)
Ilex stellata (1)
Ilex tectonica (7)
Inga bracteifera (4)
Inga cabreriae (1)
Inga calderonii (18)
Inga canonegrensis (4)
Inga colimana (3)
Inga cuspidata (2)
Inga dasycarpa (7)
Inga dwyeri (3)
Inga filiformis (16)
Inga golfodulcensis (17)
Inga herrerae (9)
Inga huastecana (6)
Inga involucreta (2)
Inga jefensis (19)
Inga latipes (10)
Inga portobellensis (5)
Inga pseudoinvolucreta (1)
Inga saffordiana (6)
Inga spiralis (7)
Inga stenophylla (19)
Inga tenuiloba (4)
Inga urceolata (6)
Isertia scorpioides (6)
Ixchelia uxpanapana (4)
Ixora knappiae (4)
Jaltomata confinis (3)
Juglans boliviana (19)
Juniperus standleyi (15)
Karwinskia pluvialis (3)
Klarobelia stipitata (17)
Koanophyllon panamense (11)
Koanophyllon wetmorei (6)
Krugiodendron acuminatum (5)
Ladenbergia dwyeri (14)
Ladenbergia laurifolia (4)
Leptobalanus morii (1)
Leucaena salvadorensis (16)
Licania cruegeriana (7)
Licaria brenesii (9)
Licaria caribaea (3)
Licaria chinanteca (11)
Licaria cogolloi (3)
Licaria glaberrima (19)
Licaria mexicana (3)
Licaria multinervis (13)
Licaria nitida (10)
Licaria pergamentacea (12)
Licaria phymatosa (7)
Licaria sarapiquensis (11)
Licaria siphonantha (1)
Licaria velutina (17)
Liparis fantastica (5)
Lisianthus aurantiacus (13)
Lisianthus habuensis (2)
Lithospermum mediale (5)
Lobelia stolonifera (9)
Lobelia umbellifera (9)
Lonchocarpus hidalgensis (14)

- Lonchocarpus lasiotropis* (6)
Lonchocarpus megacarpus (1)
Lonchocarpus nebularis (2)
Lonchocarpus purpureus (8)
Lonicera guatemalensis (1)
Lopezia lopeziioides (10)
Lubaria aroensis (9)
Lycianthes howardiana (3)
Lycianthes rzedowskii (17)
Lycoseris crocata (18)
Lysimachia steyermarkii (4)
Mabea tenorioi (7)
Macoubea mesoamericana (8)
Macrolobium dressleri (19)
Macrolobium herrerae (11)
Macrolobium modicopetalum (13)
Macrolobium pittieri (16)
Magnolia chiriquiensis (1)
Magnolia guerrerensis (4)
Magnolia krusei (10)
Magnolia morii (3)
Magnolia panamensis (2)
Magnolia sambuensis (8)
Magnolia vazquezii (2)
Magnolia yoroconte (12)
Malmea dimera (11)
Malpighia verruculosa (14)
Mammea immansueta (3)
Manilkara spectabilis (1)
Mappia multiflora (19)
Mappia racemosa (19)
Marila domingensis (4)
Marila lactogena (12)
Matisia arteagensis (16)
Matisia dolichopoda (17)
Matisia dolichosiphon (1)
Matisia exalata (11)
Matisia jefensis (11)
Matisia pacifica (6)
Matisia sanblasensis (12)
Matisia tinamastiana (6)
Maytenus grisea (4)
Meliosma chiriquensis (2)
Meliosma clandestina (18)
Meliosma cordata (1)
Meliosma isthmensis (9)
Meliosma linearifolia (4)
Meliosma mexicana (3)
Meliosma nesites (6)
Meliosma oligantha (3)
Meliosma schlimii (12)
Meliosma subcordata (12)
Meriania odorata (6)
Meriania panamensis (15)
Miconia aurantiaca (19)
Miconia calocoma (9)
Miconia cionotricha (13)
Miconia colliculosa (2)
Miconia commutata (13)
Miconia coriacea (14)
Miconia crocata (13)
Miconia cuspidatissima (16)
Miconia dissita (15)
Miconia gentryi (3)
Miconia heterothrix (9)
Miconia hildeana (3)
Miconia incurva (18)
Miconia latidecurrans (16)
Miconia mcphersonii (2)
Miconia morii (5)
Miconia nutans (10)
Miconia quadridomius (12)
Miconia santaritensis (7)
Miconia saxicola (16)
Miconia sparrei (13)
Miconia talamancensis (12)
Miconia teotepecensis (8)
Miconia umbriensis (7)
Monnina crepinii (1)
Monnina sylvicola (10)
Monochaetum alpestre (18)
Monochaetum cordatum (18)
Monochaetum exaltatum (12)
Montanoa echinacea (4)
Montanoa pteropoda (13)
Monteverdia jefeana (5)
Monteverdia sieberiana (17)
Montia calcicola (2)
Moquilea chiriquiensis (2)
Moquilea dodsonii (6)
Moquilea fasciculata (3)
Mortoniendendron apetalum (12)
Mortoniendendron hirsutum (16)
Mortoniendendron ruizii (2)
Mosannonna costaricensis (13)
Mosannonna hypoglaucia (8)
Mosannonna maculata (5)
Mouriri completens (13)
Mouriri osaensis (14)
Mouriri panamensis (5)
Mouriri tuberculata (15)
Muehlenbeckia vulcanica (5)
Muhlenbergia breviculmis (5)
Muhlenbergia orophila (7)
Myosotis scorpioides (16)
Myrcia concinna (4)
Myrcia fosteri (17)
Myrcia fusca (5)
Myrcia grandis (2)
Myrcia lapidulosa (4)
Myrcia panamensis (2)
Myrcia zetekiiana (10)
Myrrhidendron maxonii (10)
Naucleopsis straminea (4)
Nectandra belizensis (11)
Nectandra hypoleuca (19)
Nectandra longipetiolata (5)
Nectandra ramonensis (11)
Neea amplexicaulis (9)
Neea darienensis (13)
Neomirandea burgeri (5)
Neomirandea folsomiana (4)
Neomirandea homogama (16)
Neosprucea wilburiana (10)
Neurolaena oaxacana (7)
Nyssa talamancana (9)
Ocotea adela (8)
Ocotea arcuata (6)
Ocotea atata (1)
Ocotea atlantica (11)
Ocotea candidovillosa (7)
Ocotea darcy (4)
Ocotea disjuncta (6)
Ocotea fendleri (7)
Ocotea glaucosericea (18)
Ocotea gordonii (7)
Ocotea guatemalensis (10)
Ocotea haberi (11)
Ocotea hartshorniana (14)
Ocotea holdridgeana (14)
Ocotea iridescens (6)
Ocotea jefensis (2)
Ocotea jorge-escobarii (14)
Ocotea lentii (13)
Ocotea matudae (3)
Ocotea monteverdensis (19)
Ocotea multiflora (15)
Ocotea parvula (7)
Ocotea patula (6)
Ocotea pausiaca (3)
Ocotea pentagona (7)
Ocotea pharomachrosorum (6)
Ocotea pittieri (10)
Ocotea platyphylla (12)
Ocotea producta (4)
Ocotea rivularis (18)
Ocotea rubrinervis (14)
Ocotea rufescens (5)
Ocotea salvinii (14)
Ocotea sarcodes (2)
Ocotea sauroderma (6)
Ocotea standleyi (10)
Ocotea subalata (3)
Ocotea tonduzii (12)
Ocotea tonii (6)
Ocotea truncata (11)
Ocotea valeriodides (18)
Ocotea viridiflora (10)
Ocotea wedeliana (2)
Onoseris silvatica (19)
Oreomunnea pterocarpa (17)
Oreopanax arcanus (10)
Oreopanax compactus (4)
Oreopanax costaricensis (16)
Oreopanax flaccidus (12)
Oreopanax nubigenus (19)
Oreopanax paramicola (13)
Oreopanax platyphyllus (7)
Oreopanax spatulatus (1)
Oreopanax striatus (10)
Oreopanax superoerstedianus (11)
Ormosia cruenta (15)
Ormosia intermedia (2)
Ormosia panamensis (7)
Ormosia tovarensis (13)
Ormosia velutina (8)
Osa pulchra (6)
Osmanthus americanus (17)
Ouratea darienensis (1)
Ouratea flexipedicellata (1)
Ouratea jefensis (10)
Ouratea knappiae (9)
Ouratea oblita (2)
Ouratea stenobasis (4)
Ouratea sulcatinervia (6)
Ouratea tristis (1)
Oxalis calcicola (2)
Oxylobus glandulifer (2)

- PRESERVED_SPECIMEN* (1)
Palicourea bella (6)
Palicourea boraginoides (12)
Palicourea chiriquina (14)
Palicourea discolor (9)
Palicourea hammelii (11)
Palicourea macrantha (18)
Palicourea montensis (10)
Palicourea ochroides (6)
Palicourea orosiana (12)
Palicourea pereziana (6)
Palicourea roseocremea (12)
Palicourea roseofaucis (5)
Palicourea tubuliflora (7)
Palicourea tumidonodosa (1)
Palicourea tutensis (1)
Palicourea vestita (13)
Panopsis cinnamomea (4)
Paramachaerium gruberi (7)
Parathesis acostensis (9)
Parathesis cartagoana (3)
Parathesis cintalapana (3)
Parathesis columnaris (17)
Parathesis crassiramea (9)
Parathesis croatii (1)
Parathesis fusca (17)
Parathesis glaberrima (1)
Parathesis glendae (2)
Parathesis lanceolata (6)
Parathesis leptopa (19)
Parathesis montana (2)
Parathesis panamensis (3)
Parathesis seibertii (10)
Parathesis subcoriacea (3)
Parathesis subulata (8)
Parietaria macrophylla (11)
Parinari chocoensis (7)
Parinari parvifolia (15)
Parmentiera cereifera (12)
Parmentiera dressleri (1)
Passiflora podadenia (16)
Patinoa almirajo (9)
Peltogyne mexicana (15)
Pentagonia angustifolia (6)
Pentagonia dwyeriana (1)
Pentagonia gymnopoda (11)
Pentagonia lobata (14)
Pentagonia nuciformis (15)
Pentagonia osaensis (9)
Pentagonia parvifolia (10)
Pentagonia sanblasensis (4)
Pentaplaris doroteae (9)
Peperomia cuchumatana (4)
Peperomia donaguiana (15)
Pera aperta (2)
Pera oppositifolia (2)
Perrottetia excelsa (1)
Persea albida (15)
Persea albiramea (2)
Persea brenesii (6)
Persea chrysanthra (1)
Persea laevifolia (3)
Persea obscura (2)
Persea obtusifolia (13)
Persea pallescens (13)
Persea rufescens (9)
Persea silvatica (3)
Perymenium gracile (6)
Phanerophlebia pumila (8)
Phaseolus chiapasanus (15)
Pholidostachys pulchra (12)
Photinia mexicana (16)
Phyllanthus gentryi (3)
Phyllanthus purpusii (9)
Phyllanthus tuerckheimii (6)
Phytelphas seemannii (17)
Picramnia guerrerensis (8)
Pilea quercifolia (13)
Pinus rudis (3)
Piper affectans (5)
Piper albopunctulatum (4)
Piper asymmetricum (1)
Piper auritifolium (17)
Piper cativalense (2)
Piper chiriquinum (17)
Piper clavuligerum (7)
Piper corozalanum (14)
Piper daguanum (19)
Piper decurrens (19)
Piper dunlapii (5)
Piper euryphyllum (18)
Piper gibbosum (9)
Piper gonocarpum (2)
Piper hartwegianum (5)
Piper hirtellipetiolum (10)
Piper melastomoides (16)
Piper paulowniifolium (1)
Piper pinoganense (16)
Piper sanctum (16)
Piper subnudispicum (18)
Piper xanthostachyum (18)
Pisonia silvatica (14)
Pithecellobium bipinnatum (6)
Pithecellobium furcatum (18)
Pithecellobium johansenii (14)
Platymiscium curuense (13)
Platymiscium darienense (14)
Pleurothyrium glabritepalum (13)
Pleurothyrium guindonii (8)
Pleurothyrium hexaglandulosum (4)
Pleurothyrium immersum (3)
Pleurothyrium oblongum (3)
Pleurothyrium pauciflorum (5)
Pleurothyrium racemosum (1)
Pleurothyrium triflorum (6)
Plinia cerrocampaensis (3)
Plinia coclensis (5)
Plinia cuspidata (4)
Plinia darienensis (3)
Plinia gentryi (3)
Plinia guanacastensis (5)
Plinia moralesii (2)
Plinia panamensis (7)
Plinia povedae (11)
Plinia puriscalensis (8)
Plinia salamancana (4)
Poa seleri (8)
Podocarpus costaricensis (5)
Podocarpus magnifolius (12)
Polystichum furfuraceum (1)
Polystichum ordinatum (10)
Porcelia magnifruta (6)
Posoqueria chocoana (12)
Posoqueria correana (6)
Posoqueria costaricensis (6)
Posoqueria grandifructa (19)
Posoqueria laevis (15)
Posoqueria robusta (14)
Potalia turbinata (14)
Potentilla goldmanii (2)
Potentilla heterosepala (13)
Pouteria austin-smithii (14)
Pouteria belizensis (16)
Pouteria bulliformis (13)
Pouteria calistophylla (18)
Pouteria chiricana (11)
Pouteria filiformis (9)
Pouteria foveolata (19)
Pouteria lecythidicarpa (9)
Pouteria sclerocarpa (5)
Pouteria silvestris (10)
Pouteria simulans (19)
Pouteria stipitata (13)
Pouteria triplarifolia (2)
Preslianthus panamensis (4)
Prestoea pubens (7)
Prockia costaricensis (8)
Prunus annularis (11)
Prunus guatemalensis (1)
Prunus lundelliana (10)
Pseudomalmea darienensis (1)
Psychotria cascajalensis (2)
Psychotria convergens (19)
Psychotria durilancifolia (6)
Psychotria insignis (1)
Psychotria jefensis (4)
Psychotria liesneri (2)
Psychotria olgae (5)
Psychotria pacorensis (2)
Psychotria philacra (2)
Psychotria sixaolensis (10)
Pterandra isthmica (2)
Pterandra mcphersonii (1)
Pterocarpus michelianus (18)
Pterygota excelsa (13)
Pyrola angustifolia (13)
Quadrella antonensis (17)
Quadrella dressleri (1)
Quadrella mirifica (4)
Quadrella morenoi (6)
Qualea cymulosa (4)
Qualea panamensis (3)
Quararibea ciroana (2)
Quararibea gomeziana (13)
Quararibea parviflora (1)
Quararibea pendula (7)
Quararibea platyphylla (18)
Quararibea pumila (7)
Quararibea santaritensis (1)
Quararibea tulekunae (3)
Quercus acuta (1)
Quercus brenesii (7)
Quercus delgadoana (2)
Quercus hirtifolia (3)
Quercus macdougallii (4)
Quercus nixoniana (2)
Quercus sarahmariae (5)
Quetzalia contracta (10)

- Quetzalia guatemalensis* (16)
Randia cookii (17)
Randia genipoides (19)
Randia grayumii (12)
Randia lasiantha (11)
Randia mira (13)
Randia tomatillo (15)
Raphia taedigera (15)
Raputiarana subsigmoidea (11)
Rauvolfia purpurascens (19)
Rhamnus serrata (19)
Rhynchosia amabilis (11)
Rhynchosia ehrenbergii (14)
Rinorea brachythrix (1)
Rinorea hirsuta (10)
Rinorea zygomorpha (10)
Rojasianthe superba (14)
Roldana anisophylla (5)
Roldana robinsoniana (11)
Romanschulzia alpina (1)
Romanschulzia guatemalensis (2)
Rondeletia hameliifolia (18)
Rondeletia panamensis (19)
Roupala percoriacea (7)
Rubus cymosus (18)
Rubus hadrocarpus (16)
Rubus phillyrophyllus (5)
Rudgea hemisphaerica (7)
Rudgea isthmensis (2)
Rudgea laevis (9)
Rudgea mcphersonii (5)
Rudgea panamensis (2)
Rudgea sanblasensis (2)
Rudgea trifurcata (18)
Russelia syringifolia (8)
Rustia costaricensis (15)
Rustia dressleri (3)
Sabazia pinetorum (1)
Sabinaria magnifica (1)
Sacoglottis holdridgei (9)
Salacia macrocremastra (2)
Salacia panamensis (11)
Salix aeruginosa (15)
Salvia atropaenulata (11)
Salvia disjuncta (16)
Salvia langlassei (18)
Salvia sanctae-luciae (12)
Salvia tonalensis (16)
Sapium allenii (4)
Sarcomphalus strychnifolius (6)
Saurauia conzattii (19)
Saurauia matudae (9)
Saurauia pustulata (10)
Saurauia seibertii (7)
Saurauia waldheimia (2)
Saurauia zahlbruckneri (4)
Schefflera albocapitata (1)
Schefflera aquaverensis (2)
Schefflera cartagoensis (2)
Schefflera cicatricata (3)
Schefflera instita (4)
Schefflera jefensis (6)
Schefflera macphersonii (4)
Schefflera panamensis (12)
Schefflera pubens (4)
Schefflera seibertii (5)
Schefflera whitefoordiae (1)
Schistocarpha liebmanni (12)
Schizocalyx veraguensis (15)
Schizocarpum dieterleae (8)
Schoepfia macrophylla (8)
Schradera neeoides (2)
Schradera rotundata (14)
Schultesianthus crosbyanus (11)
Sebastiania jaliscensis (10)
Sedum australe (10)
Sedum guatemalense (13)
Senecio godmanii (13)
Senna cajamarcae (6)
Senna caudata (18)
Sigesbeckia nudicaulis (1)
Simira klugei (10)
Simira panamensis (3)
Sisyrinchium johnstonii (13)
Sloanea brenesii (18)
Sloanea garcia-cossioi (9)
Sloanea geniculata (8)
Sloanea guapilensis (4)
Sloanea laevigata (8)
Sloanea ligulata (2)
Sloanea longipes (10)
Sloanea megaphylla (1)
Sloanea paucinervia (3)
Sloanea rugosa (14)
Smallanthus mcvaughii (10)
Sobralia galeottiana (17)
Solanum agrimoniifolium (2)
Solanum armentalis (12)
Solanum dimorphandrum (8)
Solanum fortuneense (17)
Solanum fosbergianum (10)
Solanum incomptum (12)
Solanum muenschleri (5)
Solanum narcoticosmum (11)
Solanum pastillum (15)
Solanum pluviale (8)
Solanum roblense (19)
Solanum sotobosquense (9)
Sommeria chiapensis (8)
Sorocea ruminata (14)
Spathacanthus parviflorus (15)
Sphaeropteris brunei (19)
Stachyarrhena heterochroa (14)
Stachys calcicola (13)
Stachys nubilorum (6)
Stanmarkia medialis (2)
Stelis oaxacana (6)
Stellaria irazuensis (14)
Stenanona panamensis (6)
Stenanona tubiflora (1)
Stenostomum turrialbanum (14)
Stephanopodium gentryi (7)
Sterculia allenii (4)
Steriphoma paradoxum (9)
Strychnos croatii (17)
Stylogyne hayesii (7)
Styphnolobium montevidensis (5)
Styphnolobium parviflorum (5)
Styphnolobium sporadicum (8)
Styrax austromexicanus (17)
Styrax conterminus (13)
Styrax magnus (18)
Styrax peruvianus (9)
Swartzia maquenqueana (5)
Swartzia nuda (6)
Swartzia picramnioides (13)
Swartzia robinifolia (13)
Swartzia zeledonensis (10)
Symphoricarpos guatemalensis (2)
Symplocos elliptica (7)
Symplocos excelsa (10)
Symplocos morii (4)
Symplocos naniflora (16)
Symplocos oreophila (1)
Symplocos panamensis (11)
Symplocos povedae (18)
Symplocos retusa (5)
Symplocos sousae (14)
Symplocos striata (6)
Symplocos tacanensis (3)
Tabebuia impetiginosa (14)
Tabebuia striata (7)
Tacarcuna gentryi (2)
Tachigali panamensis (12)
Talisia equatoriensis (10)
Talisia morii (1)
Talisia princeps (14)
Tapirira rubrinervis (12)
Tapura colombiana (10)
Tapura cubensis (6)
Tapura panamensis (2)
Tauschia steyermarkii (3)
Telanthophora liebmanni (18)
Telanthophora standleyi (19)
Ternstroemia sylvatica (9)
Tessmannianthus cereifolius (2)
Tessmannianthus gordonii (2)
Tetrorchidium costaricense (18)
Tetrorchidium robledoanum (15)
Tetrorchidium trichotocarpum (16)
Theobroma mammosum (16)
Tigridia immaculata (11)
Tournefortia multiflora (5)
Tournefortia ramonensis (11)
Tovomita morii (3)
Trichilia pittieri (19)
Trisetum rosei (13)
Trisetum tonduzii (8)
Triumfetta arborescens (1)
Trophis noraminervae (14)
Unonopsis bullata (18)
Unonopsis costaricensis (9)
Unonopsis darienensis (15)
Unonopsis hammelii (4)
Unonopsis longipes (13)
Unonopsis macrocarpa (2)
Unonopsis megalosperma (1)
Unonopsis osae (15)
Unonopsis penduliflora (7)
Unonopsis stevensii (6)
Urera martiniana (5)
Vaccinium luteyneri (5)
Vaccinium santafeense (2)
Vachellia melanoceras (15)
Vachellia ruddiae (16)
Valeriana deltoidea (18)
Valeriana scandens (16)
Vallesia spectabilis (1)

| | | |
|-----------------------------------|------------------------------------|-----------------------------------|
| <i>Vantanea barbourii</i> (13) | <i>Virola megacarpa</i> (10) | <i>Wercklea cocleana</i> (10) |
| <i>Vantanea occidentalis</i> (6) | <i>Virola montana</i> (15) | <i>Wercklea grandiflora</i> (2) |
| <i>Vatairea lundellii</i> (12) | <i>Virola otobifolia</i> (7) | <i>Wercklea lutea</i> (12) |
| <i>Verbesina baruensis</i> (2) | <i>Vismia jefensis</i> (19) | <i>Wercklea woodsonii</i> (19) |
| <i>Verbesina calciphila</i> (5) | <i>Vismia latisepala</i> (14) | <i>Wettinia donosoensis</i> (1) |
| <i>Verbesina fuscasiccans</i> (7) | <i>Vitex floridula</i> (5) | <i>Wimmeria montana</i> (16) |
| <i>Verbesina hidalgoana</i> (6) | <i>Vitex masoniana</i> (13) | <i>Wimmeria sternii</i> (14) |
| <i>Verbesina oerstediana</i> (3) | <i>Vochysia allenii</i> (13) | <i>Xylopia panamensis</i> (6) |
| <i>Verbesina tapantiana</i> (3) | <i>Vochysia gentryi</i> (8) | <i>Zanthoxylum apiculatum</i> (8) |
| <i>Viburnum discolor</i> (11) | <i>Vochysia jefensis</i> (13) | <i>Zanthoxylum harmsianum</i> (8) |
| <i>Viburnum disjunctum</i> (13) | <i>Volkameria pittieri</i> (13) | <i>Zanthoxylum pucro</i> (8) |
| <i>Viburnum euryphyllum</i> (1) | <i>Votomita cupuliformis</i> (2) | <i>Zapoteca mollis</i> (9) |
| <i>Viburnum obtusatum</i> (12) | <i>Votschia nemophila</i> (1) | <i>Ziziphus chloroxylon</i> (4) |
| <i>Virola albidiflora</i> (13) | <i>Weinmannia horrida</i> (4) | <i>Zygia biflora</i> (6) |
| <i>Virola amistadensis</i> (6) | <i>Weinmannia karsteniana</i> (14) | <i>Zygia brenesii</i> (19) |
| <i>Virola chrysocarpa</i> (14) | <i>Weinmannia trianae</i> (2) | <i>Zygia confusa</i> (9) |
| <i>Virola fosteri</i> (7) | <i>Weinmannia vulcanicola</i> (12) | <i>Zygia rubiginosa</i> (7) |

Table S4. List of the 272 species included in the study and number of records per species. Classification according to the Angiosperm Phylogeny Website, URL www.mobot.org/MOBOT/research/APweb/), and current IUCN status (URL <https://iconicspecies.iucnredlist.org/>).

| Order | Family | Species | Records | IUCN Status* |
|--------------------------|----------------|--------------------------------|---------|--------------|
| Clade: Conifers | | | | |
| Pinales | Pinaceae | <i>Abies guatemalensis</i> | 81 | EN |
| | | <i>Abies hickelii</i> | 27 | EN |
| | | <i>Pinus ayacahuite</i> | 104 | LC |
| | | <i>Pinus hartwegii</i> | 160 | LC |
| | | <i>Pinus lawsonii</i> | 48 | LC |
| | | <i>Pinus pringlei</i> | 52 | LC |
| | | <i>Pinus pseudostrobus</i> | 355 | LC |
| | | <i>Pinus strobus</i> | 51 | LC |
| | Podocarpaceae | <i>Podocarpus matudae</i> | 106 | VU |
| | | <i>Prumnopitys standleyi</i> | 20 | EN |
| Clade: Basal Angiosperms | | | | |
| Chloranthales | Chloranthaceae | <i>Hedyosmum mexicanum</i> | 106 | LC |
| Clade: Magnoliids | | | | |
| Laurales | Lauraceae | <i>Aiouea brenesii</i> | 23 | NT |
| | | <i>Aiouea hammeliana</i> | 29 | LC |
| | | <i>Beilschmiedia brenesii</i> | 32 | NA |
| | | <i>Beilschmiedia mexicana</i> | 21 | LC |
| | | <i>Beilschmiedia ovalis</i> | 23 | NT |
| | | <i>Damburneya cufodontisii</i> | 60 | LC |
| | | <i>Damburneya salicina</i> | 41 | LC |
| | | <i>Ocotea acuminatissima</i> | 41 | VU |
| | | <i>Ocotea austinii</i> | 39 | LC |
| | | <i>Ocotea brenesii</i> | 26 | LC |
| | | <i>Ocotea endresiana</i> | 35 | LC |
| | | <i>Ocotea gomezii</i> | 20 | LC |
| | | <i>Ocotea helicterifolia</i> | 98 | NA |
| | | <i>Ocotea mollicella</i> | 23 | NT |
| | | <i>Ocotea praetermissa</i> | 33 | LC |
| | | <i>Ocotea psychotrioides</i> | 33 | VU |
| | | <i>Ocotea purpurea</i> | 37 | LC |
| | | <i>Persea donnell-smithii</i> | 33 | VU |
| | | <i>Persea liebmannii</i> | 70 | LC |
| | | <i>Persea schiedeana</i> | 82 | EN |

| | | | | |
|--------------------------------|-----------------|--------------------------------------|-----|----|
| | | <i>Persea veraguasensis</i> | 23 | DD |
| | Monimiaceae | <i>Mollinedia costaricensis</i> | 61 | LC |
| | | <i>Mollinedia viridiflora</i> | 236 | LC |
| Magnoliales | Annonaceae | <i>Guatteria costaricensis</i> | 42 | LC |
| | | <i>Guatteria dolichopoda</i> | 77 | LC |
| | | <i>Guatteria oliviformis</i> | 52 | LC |
| | | <i>Guatteria slateri</i> | 22 | LC |
| | | <i>Guatteria verrucosa</i> | 36 | LC |
| | | <i>Stenanona costaricensis</i> | 31 | LC |
| | Magnoliaceae | <i>Magnolia poasana</i> | 36 | NT |
| | | <i>Magnolia schiedeana</i> | 36 | VU |
| | | <i>Magnolia sororum</i> | 29 | NT |
| Piperales | Piperaceae | <i>Piper irazuanum</i> | 47 | NA |
| | | <i>Piper maxonii</i> | 20 | NT |
| Clade: Basal Eudicots | | | | |
| Proteales | Proteaceae | <i>Panopsis costaricensis</i> | 46 | LC |
| | Sabiaceae | <i>Meliosma alba</i> | 29 | LC |
| | | <i>Meliosma brenesii</i> | 32 | LC |
| | | <i>Meliosma dentata</i> | 67 | LC |
| | | <i>Meliosma idiopoda</i> | 89 | LC |
| Clade: Pentapetalae | | | | |
| Saxifragales | Hamamelidaceae | <i>Matudaea trinervia</i> | 47 | LC |
| Clade: Rosid I / Fabids | | | | |
| Celastrales | Celastraceae | <i>Euonymus costaricensis</i> | 50 | LC |
| | | <i>Maytenus woodsonii</i> | 24 | NT |
| | | <i>Monteverdia recondita</i> | 26 | NT |
| | | <i>Zinowiewia integerrima</i> | 115 | LC |
| | | <i>Zinowiewia rubra</i> | 21 | VU |
| Malpighiales | Clusiaceae | <i>Chrysochlamys allenii</i> | 40 | LC |
| | | <i>Chrysochlamys psychotriifolia</i> | 45 | LC |
| | | <i>Clusia croatii</i> | 88 | LC |
| | | <i>Clusia palmana</i> | 46 | LC |
| | | <i>Clusia salvinii</i> | 121 | LC |
| | | <i>Clusia torresii</i> | 40 | LC |
| | Dichapetalaceae | <i>Dichapetalum brenesii</i> | 26 | LC |
| | Euphorbiaceae | <i>Croton megistocarpus</i> | 30 | LC |
| | Hypericaceae | <i>Hypericum irazuense</i> | 36 | NT |
| | Malpighiaceae | <i>Bunchosia ternata</i> | 25 | NT |
| | Passifloraceae | <i>Passiflora tica</i> | 30 | LC |
| | Salicaceae | <i>Hasseltia guatemalensis</i> | 38 | LC |
| | | <i>Hasseltiopsis dioica</i> | 24 | NT |

| | | | | | |
|-----------------------|------------------------|------------------------------|-----------------------|-------------------|-----|
| Oxalidales | Brunelliaceae | Macrohasseltia macroterantha | 41 | LC | |
| | | Brunellia costaricensis | 45 | VU | |
| | | Brunellia mexicana | 66 | LC | |
| | Cunoniaceae | Weinmannia burserifolia | 35 | LC | |
| | | Weinmannia wercklei | 35 | LC | |
| Sapindales | Elaeocarpaceae | Sloanea ampla | 27 | LC | |
| | Meliaceae | Cedrela tonduzii | 41 | LC | |
| | Rutaceae | Peltostigma guatemalense | 32 | LC | |
| | | Peltostigma pteleoides | 30 | LC | |
| | | Stauranthus perforatus | 24 | NT | |
| Clade: N-fixing clade | | | | | |
| Fabales | Fabaceae | Cojoba costaricensis | 49 | NT | |
| | | Inga exalata | 21 | LC | |
| | | Inga flexuosa | 67 | LC | |
| | | Inga leonis | 32 | LC | |
| | | Inga longispica | 24 | LC | |
| | | Inga mortoniana | 44 | LC | |
| | | Inga sierrae | 29 | LC | |
| | | Inga tonduzii | 32 | LC | |
| | | Inga xalapensis | 27 | LC | |
| | | Senna multifoliolata | 38 | VU | |
| | | Zygia palmana | 37 | NA | |
| | | Fagales | Betulaceae | Ostrya virginiana | 156 |
| Fagaceae | Quercus affinis | | 53 | LC | |
| | Quercus benthamii | | 64 | NT | |
| | Quercus candicans | | 158 | NA | |
| | Quercus costaricensis | | 61 | VU | |
| | Quercus crispipilis | | 36 | NT | |
| | Quercus germana | | 36 | LC | |
| | Quercus lancifolia | | 109 | LC | |
| | Quercus martinezii | | 21 | LC | |
| | Quercus salicifolia | | 82 | LC | |
| | Quercus scytophylla | | 77 | LC | |
| | Quercus seemannii | | 72 | LC | |
| | Quercus xalapensis | | 124 | LC | |
| Juglandaceae | Alfaroa costaricensis | | 47 | LC | |
| | Juglans pyriformis | | 29 | EN | |
| | Oreomunnea mexicana | | 44 | LC | |
| Ticodendraceae | Ticodendron incognitum | | 66 | NT | |
| Myrtales | Melastomataceae | | Axinaea costaricensis | 36 | LC |
| | | | Blakea storkii | 54 | LC |

| | | | | |
|----------------------------------|------------------|---------------------------------------|-----|----|
| | | <i>Meriania phlomoides</i> | 38 | LC |
| | | <i>Miconia albertobrenesii</i> | 60 | LC |
| | | <i>Miconia biperulifera</i> | 21 | LC |
| | | <i>Miconia brenesii</i> | 42 | LC |
| | | <i>Miconia hemenostigma</i> | 33 | VU |
| | | <i>Miconia oligotricha</i> | 31 | LC |
| | | <i>Miconia pittieri</i> | 27 | LC |
| | | <i>Miconia schnellii</i> | 30 | LC |
| | | <i>Miconia tonduzii</i> | 138 | LC |
| | Myrtaceae | <i>Eugenia austin-smithii</i> | 51 | LC |
| | | <i>Eugenia cartagensis</i> | 34 | DD |
| | | <i>Eugenia siggersii</i> | 47 | LC |
| | | <i>Myrcianthes storkii</i> | 21 | LC |
| | | <i>Pimenta guatemalensis</i> | 21 | LC |
| | Onagraceae | <i>Fuchsia paniculata</i> | 343 | LC |
| Rosales | Cannabaceae | <i>Lozanella enantiophylla</i> | 93 | LC |
| | Rhamnaceae | <i>Frangula discolor</i> | 128 | LC |
| | | <i>Frangula oreodendron</i> | 72 | LC |
| | | <i>Frangula pendula</i> | 40 | LC |
| | Rosaceae | <i>Prunus brachybotrya</i> | 126 | LC |
| | | <i>Prunus fortunensis</i> | 27 | VU |
| | | <i>Prunus rhamnoides</i> | 72 | LC |
| | | <i>Prunus tetradenia</i> | 25 | LC |
| | Ulmaceae | <i>Ulmus mexicana</i> | 79 | LC |
| Clade: Rosid II / Malvids | | | | |
| Caryophyllales | Polygonaceae | <i>Coccoloba liportizii</i> | 24 | NT |
| Huerteales | Dipentodontaceae | <i>Perrottetia longistylis</i> | 74 | LC |
| | | <i>Perrottetia multiflora</i> | 53 | LC |
| | | <i>Perrottetia ovata</i> | 34 | LC |
| Malvales | Malvaceae | <i>Chiranthodendron pentadactylon</i> | 63 | LC |
| | | <i>Malvaviscus palmanus</i> | 25 | LC |
| | | <i>Phymosia rosea</i> | 25 | LC |
| | | <i>Wercklea insignis</i> | 26 | LC |
| | | <i>Wercklea woodsonii</i> | 20 | LC |
| | Thymelaeaceae | <i>Daphnopsis mollis</i> | 22 | VU |
| Picramniales | Picramniaceae | <i>Picramnia teapensis</i> | 94 | LC |
| | | <i>Picramnia xalapensis</i> | 22 | VU |
| Clade: Basal Asterids | | | | |
| Cornales | Cornaceae | <i>Cornus disciflora</i> | 259 | LC |
| | | <i>Cornus excelsa</i> | 125 | LC |
| Ericales | Actinidiaceae | <i>Saurauia leucocarpa</i> | 28 | VU |

| | | | |
|------------------|------------------------------------|-----|----|
| | <i>Saurauia montana</i> | 134 | LC |
| | <i>Saurauia oreophila</i> | 25 | LC |
| | <i>Saurauia pittieri</i> | 46 | LC |
| | <i>Saurauia rubiformis</i> | 49 | LC |
| | <i>Saurauia scabrida</i> | 93 | NT |
| | <i>Saurauia serrata</i> | 44 | NT |
| | <i>Saurauia villosa</i> | 27 | VU |
| Clethraceae | <i>Clethra gelida</i> | 20 | LC |
| | <i>Clethra hartwegii</i> | 37 | LC |
| | <i>Clethra macrophylla</i> | 45 | LC |
| | <i>Clethra pringlei</i> | 28 | LC |
| | <i>Clethra suaveolens</i> | 60 | LC |
| Ericaceae | <i>Comarostaphylis arbutoides</i> | 88 | LC |
| | <i>Comarostaphylis longifolia</i> | 26 | NT |
| | <i>Gaultheria acuminata</i> | 88 | LC |
| | <i>Lyonia squamulosa</i> | 59 | LC |
| | <i>Vaccinium leucanthum</i> | 96 | LC |
| Pentaphylacaceae | <i>Cleyera integrifolia</i> | 70 | LC |
| | <i>Cleyera theaeoides</i> | 145 | LC |
| | <i>Freziera guatemalensis</i> | 22 | LC |
| | <i>Symplocarpon purpusii</i> | 89 | LC |
| | <i>Ternstroemia lineata</i> | 120 | LC |
| Primulaceae | <i>Ardisia glandulosomarginata</i> | 71 | LC |
| | <i>Ardisia palmana</i> | 59 | LC |
| | <i>Ardisia pleurobotrya</i> | 30 | VU |
| | <i>Ardisia verapazensis</i> | 30 | LC |
| | <i>Parathesis chiapensis</i> | 31 | LC |
| | <i>Parathesis glabra</i> | 40 | LC |
| | <i>Parathesis leptopa</i> | 22 | LC |
| | <i>Parathesis melanosticta</i> | 44 | LC |
| | <i>Parathesis villosa</i> | 26 | LC |
| Sapotaceae | <i>Pouteria exfoliata</i> | 20 | NT |
| Styracaceae | <i>Styrax glabrescens</i> | 145 | LC |
| | <i>Styrax radians</i> | 24 | NT |
| | <i>Styrax ramirezii</i> | 74 | NA |
| | <i>Styrax warscewiczii</i> | 74 | LC |
| Symplocaceae | <i>Symplocos citrea</i> | 72 | LC |
| | <i>Symplocos costaricana</i> | 33 | LC |
| | <i>Symplocos limoncillo</i> | 77 | LC |
| | <i>Symplocos pycnantha</i> | 58 | LC |
| | <i>Symplocos serrulata</i> | 60 | LC |

| Clade: Asterid I / Lamids | | | | |
|---------------------------|-----------------|------------------------------------|-----|----|
| Aquifoliales | Aquifoliaceae | <i>Ilex discolor</i> | 117 | LC |
| | | <i>Ilex lamprophylla</i> | 65 | LC |
| | | <i>Ilex maxima</i> | 24 | LC |
| | | <i>Ilex pallida</i> | 60 | LC |
| | Phyllonomaceae | <i>Phyllonoma laticuspis</i> | 105 | LC |
| Boraginales | Heliotropiaceae | <i>Tournefortia johnstonii</i> | 30 | LC |
| Gentianales | Apocynaceae | <i>Lacmellea zamorae</i> | 20 | NT |
| | | <i>Rauvolfia aphlebia</i> | 42 | LC |
| | | <i>Tabernaemontana alfaroi</i> | 66 | LC |
| | | <i>Vallesia aurantiaca</i> | 31 | LC |
| | Rubiaceae | <i>Amaioua pedicellata</i> | 29 | NT |
| | | <i>Arachnothryx aspera</i> | 20 | NT |
| | | <i>Arachnothryx brenesii</i> | 20 | NT |
| | | <i>Arachnothryx costaricensis</i> | 30 | NT |
| | | <i>Arachnothryx laniflora</i> | 28 | LC |
| | | <i>Arachnothryx monteverdensis</i> | 27 | NT |
| | | <i>Chiococca phaenostemon</i> | 70 | LC |
| | | <i>Cosmibuena valerii</i> | 48 | LC |
| | | <i>Coussarea caroliana</i> | 66 | LC |
| | | <i>Deppea grandiflora</i> | 101 | LC |
| | | <i>Faramea ovalis</i> | 29 | LC |
| | | <i>Glossostipula concinna</i> | 58 | LC |
| | | <i>Gonzalagunia rosea</i> | 103 | LC |
| | | <i>Gonzalagunia stenostachya</i> | 32 | LC |
| | | <i>Hoffmannia amplexifolia</i> | 27 | NA |
| | | <i>Hoffmannia arborescens</i> | 65 | LC |
| | | <i>Ladenbergia brenesii</i> | 51 | LC |
| | | <i>Palicourea adusta</i> | 55 | NA |
| | | <i>Palicourea alajuelensis</i> | 28 | LC |
| | | <i>Palicourea eurycarpa</i> | 37 | LC |
| | | <i>Palicourea galeottiana</i> | 145 | LC |
| | | <i>Palicourea lasiorrhachis</i> | 136 | LC |
| | | <i>Palicourea purpurea</i> | 70 | LC |
| | | <i>Palicourea salicifolia</i> | 34 | VU |
| | | <i>Psychotria jimenezii</i> | 31 | LC |
| | | <i>Psychotria nubiphila</i> | 60 | LC |
| | | <i>Psychotria orosiana</i> | 41 | LC |
| | | <i>Rogiera amoena</i> | 152 | LC |
| | | <i>Rogiera cordata</i> | 54 | LC |
| | | <i>Rudgea reducticalyx</i> | 45 | LC |

| | | | | |
|--|-------------------|------------------------------------|-----|----|
| | | <i>Sommera arborescens</i> | 61 | LC |
| | | <i>Sommera donnell-smithii</i> | 108 | LC |
| Lamiales | Bignoniaceae | <i>Amphitecna sessilifolia</i> | 41 | LC |
| | Lamiaceae | <i>Aegiphila odontophylla</i> | 56 | LC |
| | Scrophulariaceae | <i>Buddleja nitida</i> | 70 | LC |
| | | <i>Buddleja skutchii</i> | 44 | LC |
| | Verbenaceae | <i>Citharexylum macradenium</i> | 31 | LC |
| | | <i>Duranta costaricensis</i> | 30 | LC |
| Metteniusales | Metteniusaceae | <i>Oecopetalum mexicanum</i> | 25 | LC |
| Solanales | Solanaceae | <i>Cestrum poasanum</i> | 40 | NT |
| | | <i>Cestrum rugulosum</i> | 47 | LC |
| | | <i>Solanum nigricans</i> | 158 | LC |
| | | <i>Solanum storkii</i> | 39 | NA |
| Clade: Asterid II / Campanulids | | | | |
| Apiales | Araliaceae | <i>Dendropanax capillaris</i> | 26 | LC |
| | | <i>Dendropanax globosus</i> | 23 | LC |
| | | <i>Dendropanax gonatopodus</i> | 41 | LC |
| | | <i>Dendropanax leptopodus</i> | 24 | LC |
| | | <i>Dendropanax querceti</i> | 67 | LC |
| | | <i>Oreopanax echinops</i> | 47 | LC |
| | | <i>Oreopanax oerstedianus</i> | 61 | LC |
| | | <i>Oreopanax pycnocarpus</i> | 23 | NT |
| | | <i>Oreopanax sanderianus</i> | 31 | LC |
| | | <i>Oreopanax vestitus</i> | 32 | LC |
| | | <i>Oreopanax xalapensis</i> | 304 | LC |
| | | <i>Schefflera rodriguesiana</i> | 50 | LC |
| Asterales | Asteraceae | <i>Clibadium leiocarpum</i> | 96 | NA |
| | | <i>Jesseea multivenia</i> | 50 | LC |
| | | <i>Lepidaploa polypleura</i> | 31 | NT |
| | | <i>Montanoa guatemalensis</i> | 34 | LC |
| | | <i>Roldana lanicaulis</i> | 30 | NA |
| | | <i>Stevia microchaeta</i> | 43 | NA |
| | | <i>Telanthophora cobanensis</i> | 35 | NT |
| | | <i>Telanthophora grandifolia</i> | 188 | LC |
| | | <i>Telanthophora uspantanensis</i> | 37 | NT |
| | | <i>Verbesina apleura</i> | 29 | LC |
| | | <i>Verbesina perymenioides</i> | 57 | LC |
| Cardiopteridales | Cardiopteridaceae | <i>Citronella costaricensis</i> | 28 | LC |
| Dipsacales | Viburnaceae | <i>Viburnum acutifolium</i> | 69 | LC |
| | | <i>Viburnum costaricanum</i> | 179 | LC |
| | | <i>Viburnum elatum</i> | 42 | LC |

| | | |
|-----------------------------|----|----|
| <i>Viburnum jucundum</i> | 27 | VU |
| <i>Viburnum microcarpum</i> | 20 | LC |
| <i>Viburnum venustum</i> | 42 | LC |

* Applicable IUCN categories: DD (data deficient), LC (least concern), NT (near threatened), VU (vulnerable) and EN (endangered). The conservation status was not available (NA) for 12 species.

Table S5. Number of species and records per country and subnational division. Most species extent over more than one jurisdiction, thus the total number of species does not correspond to the addition of species per country. 37 records extended beyond our study region into Colombia, which we retained to avoid creating an artificial boundary along political lines.

| Country | State | No. spp. | No. records |
|--------------------------|---------------------------|----------|-------------|
| Costa Rica | N/A | 193 | 6235 |
| El Salvador | N/A | 48 | 125 |
| Guatemala | N/A | 97 | 469 |
| Honduras | N/A | 82 | 343 |
| Nicaragua | N/A | 69 | 423 |
| Panama | N/A | 164 | 1400 |
| Mexico | ALL STATES | 155 | 6523 |
| | <i>Ciudad de México</i> | 15 | 37 |
| | <i>Chiapas</i> | 132 | 1834 |
| | <i>Durango</i> | 13 | 32 |
| | <i>(Estado de) México</i> | 44 | 307 |
| | <i>Guerrero</i> | 68 | 304 |
| | <i>Guanajuato</i> | 6 | 9 |
| | <i>Hidalgo</i> | 54 | 332 |
| | <i>Jalisco</i> | 49 | 245 |
| | <i>Michoacán</i> | 43 | 424 |
| | <i>Morelos</i> | 15 | 22 |
| | <i>Nayarit</i> | 22 | 76 |
| | <i>Nuevo León</i> | 12 | 65 |
| | <i>Oaxaca</i> | 120 | 1215 |
| | <i>Puebla</i> | 72 | 362 |
| | <i>Queretaro</i> | 24 | 56 |
| | <i>Sinaloa</i> | 19 | 40 |
| | <i>San Luis Potosí</i> | 26 | 78 |
| | <i>Sonora</i> | 7 | 38 |
| | <i>Tamaulipas</i> | 26 | 98 |
| | <i>Tlaxcala</i> | 5 | 16 |
| | <i>Veracruz</i> | 92 | 795 |
| | <i>Other states</i> | 60 | 138 |
| Other (Colombia)* | N/A | N/A | 37 |
| TOTAL | N/A | 272 | 15,555 |

* Colombia is not included in our study, but records that fell within the southern buffer of my study area on montane areas in its territory were kept to avoid introducing unnatural political barriers to our analysis.

Table S6. Post-SDM Analysis – Species Classification

| <i>Broad altitudinal classes</i> | | |
|----------------------------------|------------|--|
| Class name | Class code | Altitudinal criteria |
| Very low | VL | <1,000 m asl |
| Low | L | median <1,000 m asl, but interquartile range extending above 1,000 m asl |
| Mid-low | ML | 1,000–1,500 m asl |
| Middle* | M | 1,000–2,000 m asl |
| Mid-high | MH | 1,500–2,000 m asl |
| High | H | median >2,000 m asl, but interquartile range extending below 2,000 m asl |
| Very high | VH | >2,000 m asl |

* Only 6 species had projected suitable habitat neatly within the 1,000–2,000 m asl; most species in the mid-elevation categories were skewed toward lower or upper elevations.

Table S7. Bray-Curtis indices at the topographic discontinuities of the Isthmus of Tehuantepec and Lake Cocibolca.

| Discontinuity | Isthmus of Tehuantepec | | Lake Cocibolca | |
|--------------------------------|-------------------------------|-------|-----------------------|-------|
| Latitudinal break (° N) | >16.5 | <16.5 | >12 | <12 |
| Number of records | 5,581 | 9,974 | 7,880 | 7,675 |
| Total No. of species | 151 | 264 | 178 | 199 |
| Exclusive species | 8 | 121 | 73 | 94 |
| <i>Bray-Curtis index</i> | <i>0.690</i> | | <i>0.799</i> | |

Table S8. SDM current and future projections in pixels and km². Projected number of pixels (30 arc-seconds resolution) and equivalent area (km²) suitable for TMF tree species under current (1981–2010 baseline) and future (2071–2100) climate conditions under RCP8.5.

| Number of species | Number of pixels | | | Area (km ²) | | |
|-------------------|--------------------|----------------------------|------------|-------------------------|----------------------------|------------|
| | Current projection | Future projection (RCP8.5) | Change (%) | Current projection | Future projection (RCP8.5) | Change (%) |
| 1 to 5 | 654,024 | 768,470 | 17.5 | 548,061 | 648,145 | 18.3 |
| 6 to 10 | 214,302 | 136,563 | -36.3 | 180,001 | 115,277 | -36.0 |
| 11 to 15 | 127,403 | 65,227 | -48.8 | 107,675 | 54,626 | -49.3 |
| 16 to 20 | 84,506 | 36,508 | -56.8 | 71,095 | 30,695 | -56.8 |
| 21 to 30 | 105,358 | 45,299 | -57.0 | 88,590 | 38,299 | -56.8 |
| 31 to 40 | 70,293 | 28,349 | -59.7 | 58,884 | 24,094 | -59.1 |
| 41 to 50 | 53,737 | 21,166 | -60.6 | 45,253 | 17,695 | -60.9 |
| 51 to 75 | 91,030 | 35,479 | -61.0 | 76,179 | 29,650 | -61.1 |
| 76 to 100 | 48,281 | 8,489 | -82.4 | 39,960 | 6,963 | -82.6 |
| 101 to 150 | 21,140 | 5,170 | -75.5 | 18,217 | 4,420 | -75.7 |
| >150 | 2,264 | 252 | -88.9 | 1,843 | 177 | -90.4 |
| Total | 1,472,338 | 1,150,972 | -21.8 | 1,235,758 | 970,041 | -21.5 |

Post-SDM Analysis - Results

1. GLM: Percent losses ('PercLoss') by latitude ('Dist2') and elevation ('Elev2'), Gamma family. Outliers removed $n = 8$.

Call:
`glm(formula = PercLoss ~ Dist2 + Elev2 + Dist2:Elev2, family = Gamma(link = "log"),
 data = postSDM[-c(77, 105, 108, 115, 146, 148, 227, 256),])`

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|----------|----------|---------|---------|---------|
| -0.60927 | -0.09119 | 0.01589 | 0.10303 | 0.32660 |

Coefficients: (1 not defined because of singularities)

| | Estimate | Std. Error | t value | Pr(> t) |
|-----------------|-----------|------------|---------|------------|
| (Intercept) | 4.364864 | 0.045592 | 95.737 | <2e-16 *** |
| Dist2.L | -0.027952 | 0.072496 | -0.386 | 0.7001 |
| Dist2.Q | -0.021375 | 0.021128 | -1.012 | 0.3126 |
| Elev2.L | 0.006898 | 0.069539 | 0.099 | 0.9211 |
| Elev2.Q | 0.146779 | 0.056745 | 2.587 | 0.0102 * |
| Dist2.L:Elev2.L | 0.229374 | 0.151534 | 1.514 | 0.1313 |
| Dist2.Q:Elev2.L | -0.165785 | 0.138158 | -1.200 | 0.2313 |
| Dist2.L:Elev2.Q | -0.153452 | 0.088436 | -1.735 | 0.0839 . |
| Dist2.Q:Elev2.Q | NA | NA | NA | NA |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

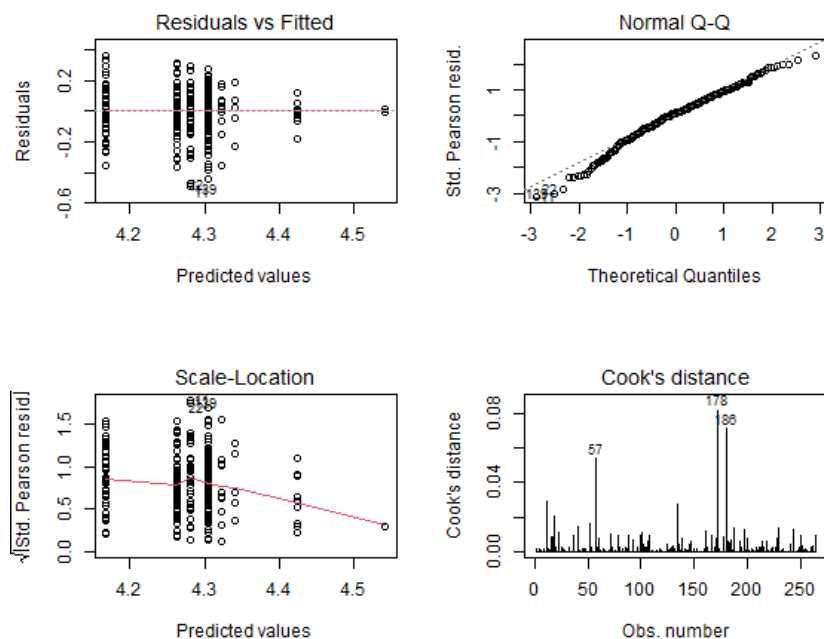
(Dispersion parameter for Gamma family taken to be 0.02491416)

Null deviance: 8.0871 on 263 degrees of freedom
 Residual deviance: 7.0322 on 256 degrees of freedom
 AIC: 2061.8

Number of Fisher Scoring iterations: 4

Bartlett test of homogeneity of variances

data: residuals(model.glm) by fitted(model.glm)
 Bartlett's K-squared = 12.201, df = 7, p-value = 0.09413



2. GLM: Absolute losses ('log(Loss)') by latitude ('Dist2') and elevation ('Elev2'), Gamma family. Outliers removed $n = 7$.

```
Call:
glm(formula = log(Loss) ~ Dist2 + Elev2 + Dist2:Dist2 + Dist2:Elev2,
     family = Gamma(link = "log"), data = postSDM[-c(25, 57, 108, 115, 146, 207, 271),])
```

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|-----------|-----------|----------|----------|----------|
| -0.176540 | -0.043774 | 0.002867 | 0.042320 | 0.136304 |

Coefficients:

| | Estimate | Std. Error | t value | Pr(> t) |
|-----------------|-----------|------------|---------|--------------|
| (Intercept) | 2.365127 | 0.008197 | 288.542 | < 2e-16 *** |
| Dist2.L | -0.068581 | 0.012247 | -5.600 | 5.52e-08 *** |
| Dist2.Q | -0.097465 | 0.015910 | -6.126 | 3.38e-09 *** |
| Elev2.L | -0.029808 | 0.017098 | -1.743 | 0.082477 . |
| Elev2.Q | -0.031700 | 0.010525 | -3.012 | 0.002857 ** |
| Dist2.L:Elev2.L | -0.100109 | 0.025431 | -3.936 | 0.000107 *** |
| Dist2.Q:Elev2.L | 0.017574 | 0.033276 | 0.528 | 0.597865 |
| Dist2.L:Elev2.Q | 0.011787 | 0.015910 | 0.741 | 0.459463 |
| Dist2.Q:Elev2.Q | -0.028316 | 0.020286 | -1.396 | 0.163986 |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

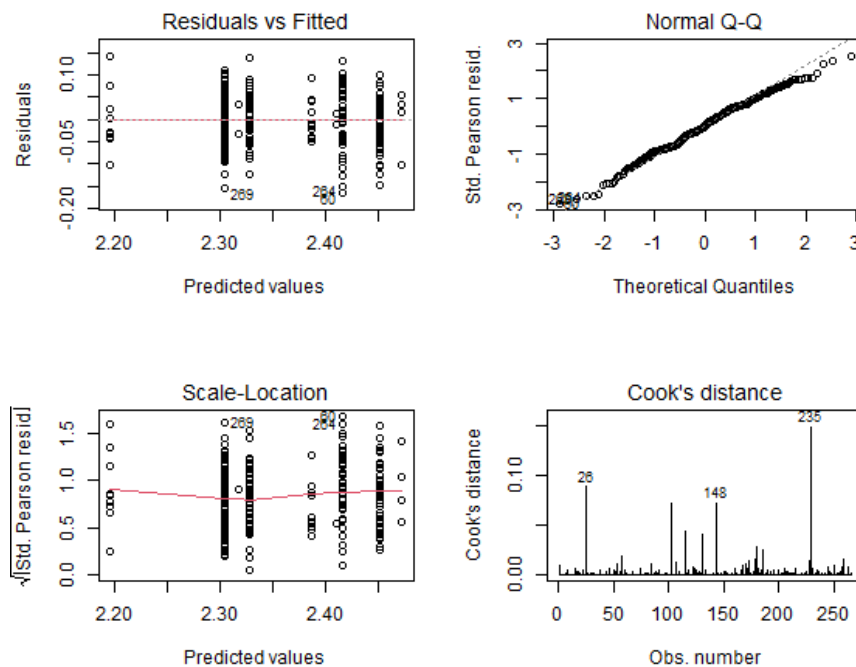
(Dispersion parameter for Gamma family taken to be 0.003566953)

Null deviance: 2.14678 on 264 degrees of freedom
 Residual deviance: 0.92643 on 256 degrees of freedom
 AIC: 524

Number of Fisher Scoring iterations: 3

Bartlett test of homogeneity of variances

data: residuals(model.gm2) by fitted(model.gm2)
 Bartlett's K-squared = 10.387, df = 8, p-value = 0.2389



3. Linear regression: Percent loss ('PercLoss') by projected current suitable areas ('log(CurrentSize)'). Outliers removed $n = 5$.

Call:

```
lm(formula = PercLoss ~ log(CurrentSize), data = postSDM[-c(22, 105, 108, 115, 146), ])
```

Residuals:

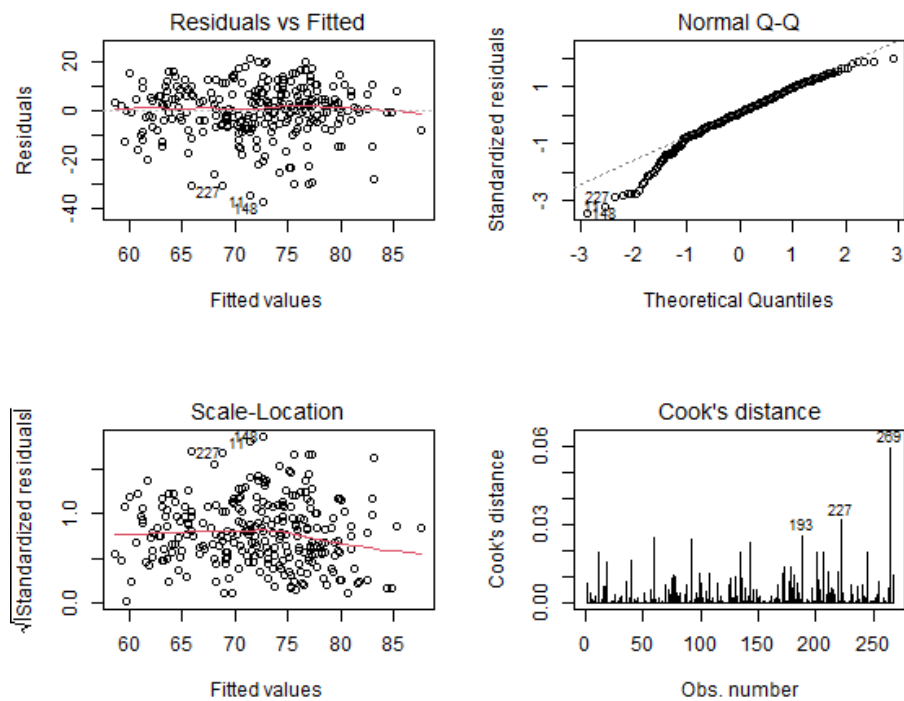
| | Min | 1Q | Median | 3Q | Max |
|--|---------|--------|--------|-------|--------|
| | -37.480 | -5.052 | 0.793 | 7.167 | 21.569 |

Coefficients:

| | Estimate | Std. Error | t value | Pr(> t) |
|------------------|----------|------------|---------|------------|
| (Intercept) | 136.2097 | 7.1485 | 19.054 | <2e-16 *** |
| log(CurrentSize) | -5.8485 | 0.6484 | -9.019 | <2e-16 *** |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 10.8 on 265 degrees of freedom
Multiple R-squared: 0.2349, Adjusted R-squared: 0.232
F-statistic: 81.35 on 1 and 265 DF, p-value: < 2.2e-16



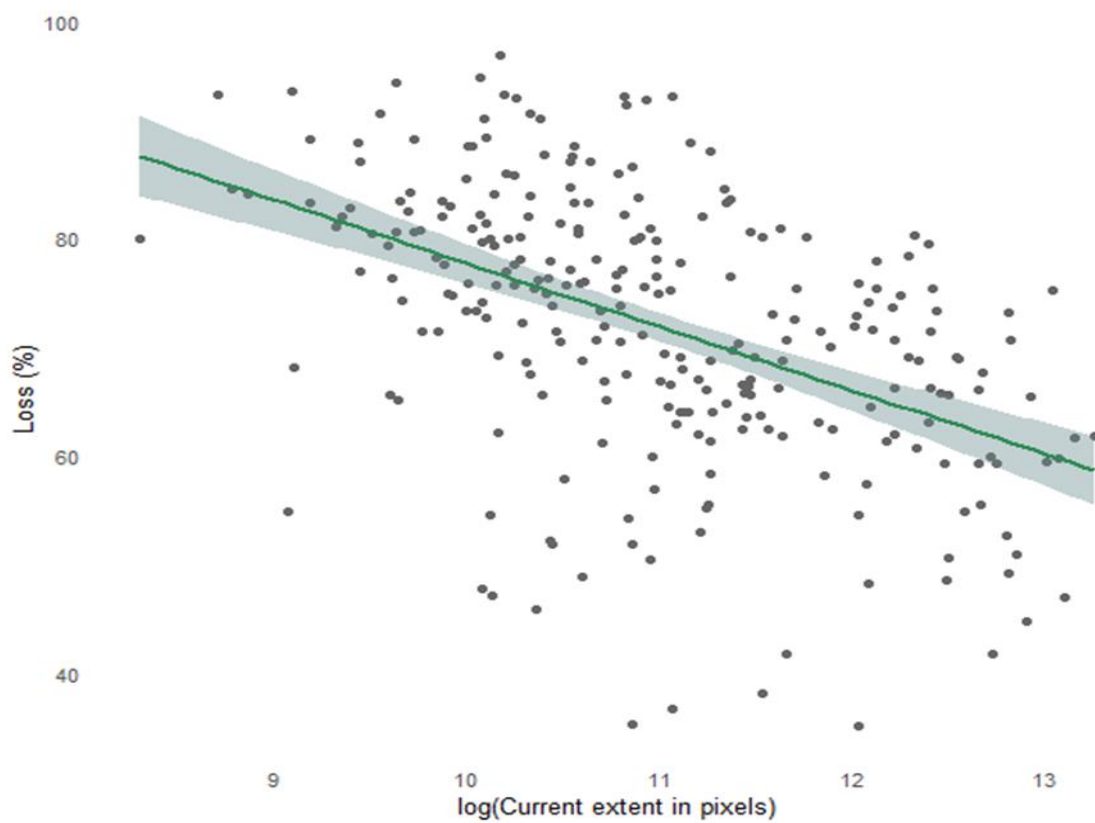


Fig. S1. Linear regression of projected range losses (%) in response to current extent by the end of the century under RCP8.5.

Appendix C. Supplementary Information for Chapter 4

Table S9. Functional trait data for the 272 species included in the analysis before imputation. Height, maximum height, diameter at breast height (DBH), leaf area (LA) and specific leaf area (SLA) were obtained from the TRY (Kattge et al., 2020) and BIEN v4.2 databases (Maitner et al., 2018). Data for height and DBH were complemented with records from scanned herbaria specimens available in GBIF (www.gbif.org; consulted March-April 2024). Wood density (WD) data was obtained from the Global Wood Density Database (Zanne, 2009) and Ordóñez Díaz et al. (2015). For LA, SLA and WD, species-specific data is shown in black, whereas data available at genus level is shown in red; this approach was necessary before imputation to reduce the number of genera without a single datum for any of those traits.

| Species | Height (m) | Max. height (m) | DBH (cm) | LA (mm ²) | SLA (mm ² mg ⁻¹) | Wood density (g cm ⁻³) |
|---------------------------------------|------------|-----------------|------------|-----------------------|---|------------------------------------|
| <i>Abies guatemalensis</i> | 30 to 45 | 45 | 100 to 150 | 59.3 | 8.4 | 0.43 |
| <i>Abies hickelii</i> | 20 to 30 | 30 | 100 to 130 | 59.3 | 8.4 | 0.38 |
| <i>Aegiphila odontophylla</i> | 8 | 8 | 20 | 8,645.4 | 22.6 | 0.66 |
| <i>Aiouea brenesii</i> | 8 | 20 | 30 | 10,661.7 | 13.6 | 0.37 |
| <i>Aiouea hammeliana</i> | 12 to 15 | 15 | 45 | 10,661.7 | 13.6 | 0.37 |
| <i>Alfaroa costaricensis</i> | 12 to 27 | 27 | 77 | NA | NA | 0.51 |
| <i>Amaioua pedicellata</i> | 10 to 12 | 12 | 22 | NA | NA | 0.62 |
| <i>Amphitecna sessilifolia</i> | 9 to 12 | 12 | 20 | 6,200.4 | 10.8 | 0.43 |
| <i>Arachnothryx aspera</i> | 3 to 8 | 8 | NA | NA | NA | 0.56 |
| <i>Arachnothryx brenesii</i> | 4 to 6 | 18 | 12 | NA | NA | 0.56 |
| <i>Arachnothryx costaricensis</i> | 10 to 15 | 15 | NA | NA | NA | 0.56 |
| <i>Arachnothryx laniflora</i> | 2 to 8 | 8 | NA | NA | NA | 0.56 |
| <i>Arachnothryx montevertensis</i> | 5 | 5 | NA | NA | NA | 0.56 |
| <i>Ardisia glandulosomarginata</i> | 4 to 8 | 8 | NA | 4,651.8 | 15.1 | 0.565 |
| <i>Ardisia palmana</i> | 5 to 15 | 15 | NA | 4,651.8 | 15.1 | 0.565 |
| <i>Ardisia pleurobotrya</i> | 6 to 8 | 8 | 20 to 35 | 4,651.8 | 15.1 | 0.565 |
| <i>Ardisia verapazensis</i> | 5 to 15 | 20 | NA | 4,651.8 | 15.1 | 0.565 |
| <i>Axinaea costaricensis</i> | 9 to 12 | 12 | 15 | NA | 13.0 | 0.53 |
| <i>Beilschmiedia brenesii</i> | 18 to 25 | 25 | 100 | 13,773.4 | 17.1 | 0.54 |
| <i>Beilschmiedia mexicana</i> | 10 to 20 | 20 | 20 to 30 | 13,773.4 | 17.1 | 0.54 |
| <i>Beilschmiedia ovalis</i> | 8 to 30 | 30 | 25 to 50 | 8,560.0 | 8.6 | 0.54 |
| <i>Blakea storkii</i> | 9 | 9 | 15 | 7,263.0 | 12.8 | 0.71 |
| <i>Brunellia costaricensis</i> | 6 to 10 | 10 | 35 to 47 | NA | NA | 0.32 |
| <i>Brunellia mexicana</i> | 20 to 25 | 25 | 40 | NA | NA | 0.32 |
| <i>Buddleja nitida</i> | 4.5 | 4.5 | NA | 1,067.1 | 5.7 | 0.52 |
| <i>Buddleja skutchii</i> | 3 to 10 | 15 | 30 | 1,951.7 | 7.4 | 0.52 |
| <i>Bunchosia ternata</i> | 2.5 to 7 | 7 | NA | 11,549.9 | 15.9 | 0.65 |
| <i>Cedrela tonduzii</i> | 6 to 8 | 8 | 16 to 25 | 2,443.0 | 28.5 | 0.36 |
| <i>Cestrum poasanum</i> | 2 to 5 | 5 | NA | 4,511.0 | 27.5 | 0.5 |
| <i>Cestrum rugulosum</i> | 3 | 3 | NA | 4,511.0 | 27.5 | 0.5 |
| <i>Chiococca phaenostemon</i> | 5 to 8 | 8 | NA | NA | NA | NA |
| <i>Chiranthodendron pentadactylon</i> | 30 | 30 | 200 | NA | NA | 0.44 |
| <i>Chrysochlamys allenii</i> | 10 to 12 | 12 | 20 | 13,397.1 | 17.0 | 0.43 |
| <i>Chrysochlamys psychotriifolia</i> | 5 to 10 | 10 | NA | 13,397.1 | 17.0 | 0.43 |

| | | | | | | |
|-----------------------------------|----------|----|----------|----------|------|-------|
| <i>Citharexylum macradenium</i> | 9 to 15 | 15 | NA | 4,700.0 | 9.6 | 0.645 |
| <i>Citronella costaricensis</i> | 9 to 18 | 18 | 40 to 50 | NA | 5.6 | 0.49 |
| <i>Clethra gelida</i> | 6 to 10 | 10 | 25 | 2,453.1 | 4.7 | 0.53 |
| <i>Clethra hartwegii</i> | 10 | 30 | 30 to 80 | 4,535.0 | 8.3 | 0.53 |
| <i>Clethra macrophylla</i> | 12 to 25 | 25 | NA | 1,805.8 | 6.4 | 0.53 |
| <i>Clethra pringlei</i> | 15 to 22 | 22 | 30 to 50 | 1,805.8 | 6.4 | 0.53 |
| <i>Clethra suaveolens</i> | 20 to 30 | 30 | 100 | 1,805.8 | 6.4 | 0.53 |
| <i>Cleyera integrifolia</i> | 15 | 15 | NA | 1,992.5 | 8.9 | 0.64 |
| <i>Cleyera theaeoides</i> | 6 to 12 | 12 | NA | 2,746.2 | 8.2 | 0.63 |
| <i>Clibadium leiocarpum</i> | 6 | 12 | NA | NA | NA | NA |
| <i>Clusia croatii</i> | 5 to 25 | 25 | NA | 6,681.3 | 11.1 | 0.65 |
| <i>Clusia palmana</i> | 10 | 10 | NA | 8,615.0 | 9.2 | 0.65 |
| <i>Clusia salvinii</i> | 3 to 12 | 12 | NA | 6,681.3 | 4.6 | 0.65 |
| <i>Clusia torresii</i> | 8 to 12 | 12 | NA | 6,681.3 | 11.1 | 0.65 |
| <i>Coccoloba liportizii</i> | 4 to 6 | 6 | 15 | 16,040.9 | 21.3 | 0.62 |
| <i>Cojoba costaricensis</i> | 15 to 20 | 20 | 15 | NA | 23.5 | NA |
| <i>Comarostaphylis arbutoides</i> | 1 to 4 | 20 | NA | 1,040.7 | 3.3 | NA |
| <i>Comarostaphylis longifolia</i> | 1 to 5 | 5 | NA | NA | 3.4 | NA |
| <i>Cornus disciflora</i> | 23 | 23 | 25 to 50 | 2,722.0 | 28.8 | 0.58 |
| <i>Cornus excelsa</i> | 12 | 12 | 15 | 2,722.0 | 28.8 | 0.57 |
| <i>Cosmibuena valerii</i> | 5 to 6 | 6 | 15 | NA | 4.8 | NA |
| <i>Coussarea caroliniana</i> | 3 to 5 | 5 | NA | 4,645.0 | 18.0 | 0.66 |
| <i>Croton megistocarpus</i> | 11 to 18 | 18 | 25 to 45 | 5,570.4 | 20.3 | 0.76 |
| <i>Damburneya cufodontisii</i> | 10 to 15 | 15 | NA | NA | NA | NA |
| <i>Damburneya salicina</i> | 7 | 7 | 38 | NA | NA | NA |
| <i>Daphnopsis mollis</i> | 5 to 8 | 15 | 15 | NA | 17.8 | 0.52 |
| <i>Dendropanax capillaris</i> | 4 to 8 | 30 | NA | 10,004.6 | 17.4 | 0.41 |
| <i>Dendropanax globosus</i> | 7 to 13 | 13 | 10 | 10,004.6 | 17.4 | 0.41 |
| <i>Dendropanax gonatopodus</i> | 10 to 30 | 30 | 12 to 58 | 10,004.6 | 17.4 | 0.41 |
| <i>Dendropanax leptopodus</i> | 5 to 9 | 9 | 10 | 10,004.6 | 17.4 | 0.41 |
| <i>Dendropanax querceti</i> | 5 to 8 | 8 | 10 | 3,166.0 | 19.3 | 0.41 |
| <i>Deppea grandiflora</i> | 3 to 5 | 5 | NA | NA | NA | NA |
| <i>Dichapetalum brenesii</i> | 4 to 9 | 9 | 20 | 3,573.0 | 18.3 | 0.761 |
| <i>Duranta costaricensis</i> | 3 to 4 | 4 | NA | NA | 11.7 | 0.56 |
| <i>Eugenia austin-smithii</i> | 8 | 8 | 12 | 4,545.8 | 14.4 | 0.86 |
| <i>Eugenia cartagensis</i> | 6 to 7 | 7 | 25 | 4,545.8 | 14.4 | 0.86 |
| <i>Eugenia siggersii</i> | 4 to 12 | 12 | 25 | 4,545.8 | 14.4 | 0.86 |
| <i>Euonymus costaricensis</i> | 3 to 10 | 10 | NA | 1,103.6 | 13.4 | 0.521 |
| <i>Faramea ovalis</i> | 6 | 6 | NA | 13,284.0 | 17.7 | 0.62 |
| <i>Frangula discolor</i> | 4 to 15 | 15 | NA | 4,157.2 | 26.1 | NA |
| <i>Frangula oreodendron</i> | 3 to 6 | 6 | NA | 2,759.2 | 11.0 | NA |
| <i>Frangula pendula</i> | 6 to 10 | 10 | NA | 4,157.2 | 26.1 | NA |
| <i>Freziera guatemalensis</i> | 12 | 12 | NA | NA | NA | 0.58 |
| <i>Fuchsia paniculata</i> | 10 | 10 | NA | NA | 21.6 | 0.56 |
| <i>Gaultheria acuminata</i> | 0.5 to 7 | 7 | NA | 2,877.5 | 6.9 | NA |
| <i>Glossostipula concinna</i> | 3 to 15 | 30 | NA | NA | NA | NA |
| <i>Gonzalagunia rosea</i> | 2 to 4 | 4 | 3 | NA | NA | NA |
| <i>Gonzalagunia stenostachya</i> | 2 to 3 | 9 | NA | NA | NA | NA |
| <i>Guatteria costaricensis</i> | 6 to 10 | 10 | 20 | 10,538.1 | 13.4 | 0.495 |
| <i>Guatteria dolichopoda</i> | 5 to 15 | 15 | 10 | 10,538.1 | 13.4 | 0.495 |
| <i>Guatteria oliviformis</i> | 9 | 9 | 15 | 10,538.1 | 13.4 | 0.495 |
| <i>Guatteria slateri</i> | 12 | 12 | 30 | 10,538.1 | 13.4 | 0.495 |
| <i>Guatteria verrucosa</i> | 8 to 12 | 12 | 16 to 35 | 10,538.1 | 13.4 | 0.495 |

| | | | | | | |
|-------------------------------------|----------|-----|----------|----------|------|-------|
| <i>Hasseltia guatemalensis</i> | 20 | 20 | NA | 6,880.7 | 14.2 | 0.575 |
| <i>Hasseltiopsis dioica</i> | 10 | 10 | NA | NA | NA | NA |
| <i>Hedyosmum mexicanum</i> | 20 | 20 | 9 | 5,753.0 | 21.6 | 0.45 |
| <i>Hoffmannia amplexifolia</i> | 1.5 to 4 | 4 | NA | NA | NA | NA |
| <i>Hoffmannia arborescens</i> | 4 | 4 | NA | NA | NA | NA |
| <i>Hypericum irazuense</i> | 2.5 | 2.5 | NA | 6,580.5 | 16.7 | 0.98 |
| <i>Ilex discolor</i> | 2 to 20 | 30 | NA | 5,096.9 | 11.2 | 0.575 |
| <i>Ilex lamprophylla</i> | 25 | 25 | 16 to 25 | 5,096.9 | 11.2 | 0.575 |
| <i>Ilex maxima</i> | 5 to 12 | 12 | NA | 5,096.9 | 11.2 | 0.575 |
| <i>Ilex pallida</i> | 6 to 10 | 10 | NA | 5,096.9 | 11.2 | 0.575 |
| <i>Inga exalata</i> | 9 to 12 | 12 | 10 | 19,076.2 | 14.7 | 0.58 |
| <i>Inga flexuosa</i> | 6 to 20 | 20 | 12 to 25 | 19,076.2 | 14.7 | 0.58 |
| <i>Inga leonis</i> | 10 | 10 | 25 | 19,076.2 | 14.7 | 0.58 |
| <i>Inga longispica</i> | 10 to 20 | 20 | 20 to 53 | 19,076.2 | 14.7 | 0.58 |
| <i>Inga mortoniana</i> | 7 to 15 | 15 | 10 to 25 | 19,076.2 | 14.7 | 0.58 |
| <i>Inga sierrae</i> | 20 | 20 | NA | 19,076.2 | 14.7 | 0.58 |
| <i>Inga tonduzii</i> | 8 | 8 | 20 | 19,076.2 | 14.7 | 0.58 |
| <i>Inga xalapensis</i> | 5 to 20 | 20 | NA | 19,076.2 | 14.7 | 0.58 |
| <i>Jessia multivenia</i> | 2.5 to 5 | 5 | NA | NA | NA | NA |
| <i>Juglans pyriformis</i> | 25 to 30 | 30 | 90 | 3,147.1 | 37.5 | 0.5 |
| <i>Lacmellea zamorae</i> | 3 to 8 | 8 | 25 | 1,968.3 | 19.7 | 0.5 |
| <i>Ladenbergia brenesii</i> | 6 to 12 | 12 | 8 to 28 | NA | NA | 0.49 |
| <i>Lepidaploa polyploea</i> | 5 to 10 | 10 | NA | NA | NA | NA |
| <i>Lozanella enantiophylla</i> | 6 to 10 | 10 | 12 | NA | NA | NA |
| <i>Lyonia squamulosa</i> | 3 to 6 | 6 | NA | 1,014.4 | 11.4 | NA |
| <i>Macrohasseltia macroterantha</i> | 13 to 37 | 37 | 70 to 90 | NA | NA | NA |
| <i>Magnolia poasana</i> | 7 to 15 | 15 | 20 | 6,040.4 | 10.6 | 0.45 |
| <i>Magnolia schiedeana</i> | 15 to 20 | 20 | 35 to 55 | 7,010.0 | 10.2 | 0.505 |
| <i>Magnolia sororum</i> | 6 to 20 | 20 | 25 | 6,040.4 | 10.6 | 0.47 |
| <i>Malvaviscus palmanus</i> | 4 to 20 | 20 | NA | NA | NA | NA |
| <i>Matudaea trinervia</i> | 8 to 35 | 35 | 5 to 40 | NA | NA | NA |
| <i>Maytenus woodsonii</i> | 2 to 4 | 4 | NA | 2,260.7 | 11.0 | 0.72 |
| <i>Meliosma alba</i> | 6 to 15 | 15 | 50 | 25,729.5 | 42.8 | 0.48 |
| <i>Meliosma brenesii</i> | 8 to 10 | 10 | 10 to 40 | 25,729.5 | 16.9 | 0.48 |
| <i>Meliosma dentata</i> | 8 to 22 | 22 | NA | 3,860.0 | 8.6 | 0.48 |
| <i>Meliosma idiopoda</i> | 5 to 20 | 20 | NA | 25,729.5 | 16.9 | 0.48 |
| <i>Meriania phlomoides</i> | 6 to 10 | 10 | NA | NA | NA | 0.49 |
| <i>Miconia albertobrenesii</i> | 3 to 5 | 5 | NA | 14,599.9 | 12.9 | 0.655 |
| <i>Miconia biperulifera</i> | 4 | 4 | NA | 14,599.9 | 12.9 | 0.655 |
| <i>Miconia brenesii</i> | 6 to 10 | 10 | NA | 14,599.9 | 12.9 | 0.655 |
| <i>Miconia hemenostigma</i> | 1 to 9 | 9 | NA | 14,599.9 | 12.9 | 0.655 |
| <i>Miconia oligotricha</i> | 2 to 4 | 4 | NA | 14,599.9 | 12.9 | 0.655 |
| <i>Miconia pittieri</i> | 2 to 5 | 5 | NA | 14,599.9 | 12.9 | 0.655 |
| <i>Miconia schnellii</i> | 4 to 15 | 15 | 32 | 2,022.5 | 8.2 | 0.655 |
| <i>Miconia tonduzii</i> | 2 to 10 | 10 | NA | 14,599.9 | 12.9 | 0.655 |
| <i>Mollinedia costaricensis</i> | 3 to 8 | 8 | NA | 12,269.6 | 18.3 | NA |
| <i>Mollinedia viridiflora</i> | 3 to 10 | 10 | NA | 4,711.9 | 21.5 | NA |
| <i>Montanoa guatemalensis</i> | 6 to 15 | 15 | NA | NA | NA | NA |
| <i>Monteverdia recondita</i> | 7 to 15 | 25 | 5 to 20 | NA | NA | NA |
| <i>Myrcianthes storkii</i> | 3 to 25 | 25 | NA | 640.0 | 14.2 | 0.76 |
| <i>Ocotea acuminatissima</i> | 5 to 10 | 20 | NA | 19,848.2 | 13.8 | 0.52 |
| <i>Ocotea austinii</i> | 15 to 16 | 16 | 35 to 49 | 19,848.2 | 13.8 | 0.48 |
| <i>Ocotea brenesii</i> | 4 to 8 | 8 | 10 | 19,848.2 | 13.8 | 0.51 |

| | | | | | | |
|---------------------------------|----------|----|-----------|----------|------|------|
| <i>Ocotea endresiana</i> | 12 to 23 | 23 | 10 to 80 | 19,848.2 | 13.8 | 0.52 |
| <i>Ocotea gomezii</i> | 7 to 8 | 8 | 5 to 20 | 19,848.2 | 13.8 | 0.52 |
| <i>Ocotea helicterifolia</i> | 3 to 8 | 15 | 8 | 5,470.0 | 11.2 | 0.52 |
| <i>Ocotea mollicella</i> | 3 to 20 | 20 | 50 | 19,848.2 | 13.8 | 0.52 |
| <i>Ocotea praetermissa</i> | 4 to 15 | 15 | 30 | 2,804.6 | 19.6 | 0.52 |
| <i>Ocotea psychotrioides</i> | 3 to 8 | 8 | NA | 19,848.2 | 13.8 | 0.52 |
| <i>Ocotea purpurea</i> | 18 | 18 | 38 | 19,848.2 | 13.8 | 0.52 |
| <i>Oecopetalum mexicanum</i> | 25 to 30 | 30 | 30 | NA | NA | 0.7 |
| <i>Oreomunnea mexicana</i> | 25 to 40 | 40 | 40 to 75 | 1,090.0 | 20.2 | NA |
| <i>Oreopanax echinops</i> | 15 | 15 | 17 | 6,150.7 | 22.3 | 0.5 |
| <i>Oreopanax oerstedianus</i> | 20 | 20 | 70 | 6,150.7 | 22.3 | 0.59 |
| <i>Oreopanax pycnocarpus</i> | 2 to 6 | 6 | 10 to 60 | 6,150.7 | 22.3 | 0.59 |
| <i>Oreopanax sanderianus</i> | 3 to 18 | 18 | NA | 6,150.7 | 22.3 | 0.59 |
| <i>Oreopanax vestitus</i> | 20 | 20 | 70 | 6,150.7 | 22.3 | 0.59 |
| <i>Oreopanax xalapensis</i> | 30 | 30 | NA | 6,050.9 | 20.8 | 0.59 |
| <i>Ostrya virginiana</i> | 25 | 25 | 50 | 2,311.1 | 37.1 | 0.5 |
| <i>Palicourea adusta</i> | 2 | 2 | NA | 11,245.8 | 19.5 | 0.55 |
| <i>Palicourea alajuelensis</i> | 5 to 8 | 8 | 10 to 25 | 11,245.8 | 19.5 | 0.55 |
| <i>Palicourea eurycarpa</i> | 6 to 7 | 7 | 15 | 10,756.0 | 19.2 | 0.55 |
| <i>Palicourea galeottiana</i> | 1 to 8 | 8 | NA | 11,245.8 | 19.5 | 0.55 |
| <i>Palicourea lasiorrhachis</i> | 2 to 4 | 4 | NA | 11,245.8 | 19.5 | 0.55 |
| <i>Palicourea purpurea</i> | 2 to 8 | 8 | NA | 11,245.8 | 19.5 | 0.55 |
| <i>Palicourea salicifolia</i> | 2 to 4 | 4 | NA | 11,245.8 | 19.5 | 0.55 |
| <i>Panopsis costaricensis</i> | 15 | 15 | 40 | NA | NA | 0.51 |
| <i>Parathesis chiapensis</i> | 3 to 6 | 6 | NA | NA | NA | 0.61 |
| <i>Parathesis glabra</i> | 3 to 5 | 5 | NA | NA | NA | 0.61 |
| <i>Parathesis leptopa</i> | 6 to 9 | 9 | NA | NA | NA | 0.61 |
| <i>Parathesis melanosticta</i> | 1 to 7 | 7 | NA | NA | NA | 0.61 |
| <i>Parathesis villosa</i> | 4 to 8 | 8 | NA | NA | NA | 0.61 |
| <i>Passiflora tica</i> | 2 to 6 | 6 | NA | NA | NA | NA |
| <i>Peltostigma guatemalense</i> | 4 to 6 | 6 | 8 | NA | NA | NA |
| <i>Peltostigma pteleoides</i> | 3 to 10 | 20 | NA | NA | NA | NA |
| <i>Perrottetia longistylis</i> | 5 to 15 | 15 | NA | NA | 17.6 | 0.71 |
| <i>Perrottetia multiflora</i> | 5 to 8 | 8 | NA | NA | 17.6 | 0.71 |
| <i>Perrottetia ovata</i> | 6 to 10 | 10 | 15 | NA | 17.6 | 0.71 |
| <i>Persea donnell-smithii</i> | 6 to 15 | 20 | NA | 1,856.7 | 8.0 | 0.52 |
| <i>Persea liebmannii</i> | 3 to 15 | 27 | 50 | 1,856.7 | 8.0 | 0.52 |
| <i>Persea schiedeana</i> | 4 to 15 | 25 | NA | 1,856.7 | 8.0 | 0.5 |
| <i>Persea veraguasensis</i> | 3 to 15 | 15 | 40 | 1,856.7 | 8.0 | 0.52 |
| <i>Phyllonoma laticuspis</i> | 4 to 15 | 15 | NA | NA | NA | NA |
| <i>Phymosia rosea</i> | 4 to 10 | 10 | NA | NA | NA | NA |
| <i>Picramnia teapensis</i> | 3 to 7 | 7 | 15 | 10,223.5 | 17.3 | NA |
| <i>Picramnia xalapensis</i> | 3 to 10 | 10 | NA | 10,223.5 | 17.3 | NA |
| <i>Pimenta guatemalensis</i> | 9 to 12 | 12 | 15 to 20 | NA | NA | 0.82 |
| <i>Pinus ayacahuite</i> | 50 | 50 | 200 | NA | NA | 0.45 |
| <i>Pinus hartwegii</i> | 32 | 32 | 145 | NA | NA | 0.44 |
| <i>Pinus lawsonii</i> | 10 to 25 | 25 | 25 to 40 | NA | NA | 0.48 |
| <i>Pinus pringlei</i> | 20 to 27 | 27 | 45 to 54 | NA | NA | 0.46 |
| <i>Pinus pseudostrabus</i> | 45 | 45 | 100 | NA | NA | 0.55 |
| <i>Pinus strobus</i> | 18 to 46 | 46 | 20 to 102 | 227.5 | 11.6 | 0.38 |
| <i>Piper irazuianum</i> | 2 to 7 | 7 | NA | 15,477.8 | 22.6 | 0.39 |
| <i>Piper maxonii</i> | 3 to 5 | 5 | NA | 15,477.8 | 22.6 | 0.39 |
| <i>Podocarpus matudae</i> | 30 | 30 | 150 | NA | 5.6 | 0.48 |

| | | | | | | |
|---------------------------------|-----------|-----|-----------|----------|------|-------|
| <i>Pouteria exfoliata</i> | 15 to 35 | 35 | 70 to 80 | 23,814.5 | 14.0 | 0.78 |
| <i>Prumnopitys standleyi</i> | 22 | 22 | 80 | NA | 6.8 | 0.53 |
| <i>Prunus brachybotrya</i> | 35 | 35 | 40 | 2,650.0 | 8.2 | 0.665 |
| <i>Prunus fortunensis</i> | 14 | 14 | NA | 5,700.8 | 12.6 | 0.665 |
| <i>Prunus rhamnoides</i> | 8 to 20 | 20 | 14 | 5,700.8 | 23.3 | 0.665 |
| <i>Prunus tetradenia</i> | 3 to 15 | 25 | NA | 5,700.8 | 12.6 | 0.665 |
| <i>Psychotria jimenezii</i> | 2 to 7 | 7 | NA | 7,368.2 | 16.2 | 0.53 |
| <i>Psychotria nubiphila</i> | 2 to 8 | 8 | NA | 7,368.2 | 16.2 | 0.53 |
| <i>Psychotria orosiana</i> | 2 to 3 | 3 | NA | 7,368.2 | 16.2 | 0.53 |
| <i>Quercus affinis</i> | 16 | 16 | NA | 1,312.5 | 8.9 | 0.58 |
| <i>Quercus benthamii</i> | 50 | 50 | NA | 2,045.5 | 10.2 | 0.575 |
| <i>Quercus candicans</i> | 25 | 25 | NA | 1,360.8 | 11.8 | 0.64 |
| <i>Quercus costaricensis</i> | 10 to 20 | 20 | 35 to 100 | 2,749.9 | 6.8 | 0.61 |
| <i>Quercus crispipilis</i> | 27 | 27 | 30 to 60 | 1,360.8 | 11.8 | 0.66 |
| <i>Quercus germana</i> | 12 | 12 | NA | 3,509.0 | 16.4 | 0.56 |
| <i>Quercus lancifolia</i> | 25 | 25 | NA | 1,360.8 | 11.8 | 0.575 |
| <i>Quercus martinezii</i> | 30 | 30 | NA | 1,360.8 | 11.8 | 0.575 |
| <i>Quercus salicifolia</i> | 6 to 25 | 25 | 100 | 1,360.8 | 19.4 | 0.67 |
| <i>Quercus scytophylla</i> | 20 | 20 | NA | 1,360.8 | 11.8 | 0.64 |
| <i>Quercus seemannii</i> | 10 to 15 | 15 | 12 to 18 | 1,990.0 | 8.7 | 0.575 |
| <i>Quercus xalapensis</i> | 30 | 30 | NA | 2,525.0 | 14.3 | 0.575 |
| <i>Rauvolfia aphlebia</i> | 5 to 9 | 9 | NA | 6,245.0 | 48.9 | 0.48 |
| <i>Rogiera amoena</i> | 1.5 to 10 | 10 | 18 to 20 | NA | NA | NA |
| <i>Rogiera cordata</i> | 2 to 10 | 10 | NA | NA | NA | NA |
| <i>Roldana lanicaulis</i> | 3 | 3 | NA | NA | NA | NA |
| <i>Rudgea reducticalyx</i> | 2.5 | 2.5 | NA | 7,099.0 | 20.9 | 0.57 |
| <i>Saurauia leucocarpa</i> | 10 | 10 | NA | NA | NA | 0.435 |
| <i>Saurauia montana</i> | 4 to 17 | 17 | 15 | 6,875.0 | 17.5 | 0.435 |
| <i>Saurauia oreophila</i> | 15 | 15 | 25 | NA | 17.5 | 0.435 |
| <i>Saurauia pittieri</i> | 5 to 15 | 15 | NA | NA | 17.5 | 0.435 |
| <i>Saurauia rubiformis</i> | 3 to 9 | 9 | NA | NA | 17.5 | 0.435 |
| <i>Saurauia scabrida</i> | 5 to 20 | 20 | NA | NA | 17.5 | 0.435 |
| <i>Saurauia serrata</i> | 6 to 15 | 15 | NA | NA | 17.5 | 0.435 |
| <i>Saurauia villosa</i> | 15 | 15 | NA | NA | NA | 0.435 |
| <i>Schefflera rodriguesiana</i> | 8 to 12 | 12 | 30 | 2,037.2 | 12.8 | 0.43 |
| <i>Senna multifoliolata</i> | 2 to 8 | 8 | NA | 4,050.5 | 22.7 | 0.56 |
| <i>Sloanea ampla</i> | 15 to 18 | 18 | NA | 18,590.5 | 13.4 | 0.81 |
| <i>Solanum nigricans</i> | 1 to 7 | 10 | NA | 10,224.4 | 20.7 | 0.42 |
| <i>Solanum storkii</i> | 2.5 to 10 | 10 | NA | 10,224.4 | 20.7 | 0.42 |
| <i>Sommera arborescens</i> | 2 to 10 | 10 | NA | NA | NA | NA |
| <i>Sommera donnell-smithii</i> | 7 to 15 | 15 | 10 | NA | NA | NA |
| <i>Stauranthus perforatus</i> | 5 to 6.5 | 6.5 | NA | NA | NA | NA |
| <i>Stenanona costaricensis</i> | 5 to 7 | 7 | 5 to 8 | NA | NA | NA |
| <i>Stevia microchaeta</i> | 3 to 4 | 4 | NA | NA | NA | 0.59 |
| <i>Styrax glabrescens</i> | 7 | 7 | NA | 9,218.0 | 13.7 | 0.44 |
| <i>Styrax radians</i> | 20 | 20 | 30 | 9,218.0 | 13.7 | 0.44 |
| <i>Styrax ramirezii</i> | 20 to 27 | 27 | NA | 9,218.0 | 13.7 | 0.44 |
| <i>Styrax warscewiczii</i> | 20 to 30 | 30 | 25 | NA | NA | 0.44 |
| <i>Symplocarpon purpusii</i> | 10 to 25 | 25 | 35 to 75 | NA | 20.1 | NA |
| <i>Symplocos citrea</i> | 15 | 15 | NA | 2,892.0 | 14.4 | 0.64 |
| <i>Symplocos costaricana</i> | 3 to 12 | 12 | 15 to 20 | 2,892.0 | 14.4 | 0.64 |
| <i>Symplocos limoncillo</i> | 12 to 20 | 20 | NA | 2,892.0 | 14.4 | 0.64 |
| <i>Symplocos pycnantha</i> | 9 to 12 | 12 | 10 to 35 | 2,892.0 | 14.4 | 0.64 |

| | | | | | | |
|-----------------------------------|----------|----|----------|----------|------|-------|
| <i>Symplocos serrulata</i> | 7 to 10 | 10 | 39 | 4,184.2 | 6.7 | 0.64 |
| <i>Tabernaemontana alfaroi</i> | 2 to 5 | 5 | NA | 6,544.8 | 34.1 | 0.56 |
| <i>Telanthophora cobanensis</i> | 1 to 9 | 9 | NA | NA | NA | NA |
| <i>Telanthophora grandifolia</i> | 3 to 7 | 7 | NA | NA | NA | NA |
| <i>Telanthophora uspananensis</i> | 2 to 5 | 5 | 10 | NA | NA | NA |
| <i>Ternstroemia lineata</i> | 10 to 20 | 20 | NA | NA | NA | 0.62 |
| <i>Ticodendron incognitum</i> | 25 | 25 | 35 | 2,230.0 | 8.8 | NA |
| <i>Tournefortia johnstonii</i> | 3 to 5 | 5 | NA | NA | NA | 0.47 |
| <i>Ulmus mexicana</i> | 50 to 70 | 80 | NA | 4,216.2 | 27.4 | 0.38 |
| <i>Vaccinium leucanthum</i> | 4 to 12 | 12 | NA | 456.6 | 14.9 | 0.291 |
| <i>Vallesia aurantiaca</i> | 2 to 6 | 20 | NA | NA | NA | NA |
| <i>Verbesina apleura</i> | 3 to 6 | 6 | NA | NA | NA | 0.437 |
| <i>Verbesina perymenoides</i> | 1 to 7 | 7 | NA | NA | NA | 0.437 |
| <i>Viburnum acutifolium</i> | 3 to 6 | 6 | NA | 2,485.4 | 13.3 | 0.54 |
| <i>Viburnum costaricanum</i> | 7 | 7 | NA | 1,133.7 | 11.4 | 0.54 |
| <i>Viburnum elatum</i> | 2 to 8 | 8 | NA | 2,485.4 | 17.5 | 0.54 |
| <i>Viburnum jucundum</i> | 3 to 6 | 6 | NA | 2,485.4 | 17.5 | 0.54 |
| <i>Viburnum microcarpum</i> | 3 to 7 | 7 | NA | 2,485.4 | 17.5 | 0.54 |
| <i>Viburnum venustum</i> | 2 to 7 | 7 | 8 to 10 | 2,002.0 | 16.0 | 0.54 |
| <i>Weinmannia burserifolia</i> | 12 | 12 | 60 | NA | 9.5 | 0.615 |
| <i>Weinmannia wercklei</i> | 10 to 15 | 15 | NA | NA | NA | 0.49 |
| <i>Wercklea insignis</i> | 10 | 10 | 30 to 40 | NA | NA | 0.24 |
| <i>Wercklea woodsonii</i> | 6 to 20 | 20 | NA | NA | NA | 0.24 |
| <i>Zinowiewia integerrima</i> | 13 | 13 | 40 | 1,525.0 | 9.1 | 0.71 |
| <i>Zinowiewia rubra</i> | 10 to 20 | 20 | 30 to 60 | 1,525.0 | 9.1 | 0.71 |
| <i>Zygia palmana</i> | 8 | 8 | 20 | 17,707.0 | 14.9 | 0.83 |

Table S10. Imputed functional traits for 272 species included in the analysis, following the data imputation process described in (Carmona et al., 2024) with the *V.PhyloMaker* package (Jin and Qian, 2022). Leaf mass per area (LMA) was obtained as the inverse of specific leaf area (SLA).

| Species | Mean height (m) | DBH (cm) | LA (mm ²) | LMA (mg ¹ mm ²) | Wood density (g cm ⁻³) |
|---------------------------------------|-----------------|----------|-----------------------|--|------------------------------------|
| <i>Abies guatemalensis</i> | 37.5 | 125 | 59.26 | 0.12 | 0.43 |
| <i>Abies hickelii</i> | 25.0 | 115 | 59.26 | 0.12 | 0.38 |
| <i>Aegiphila odontophylla</i> | 8.0 | 20 | 8,645.43 | 0.04 | 0.66 |
| <i>Aiouea brenesii</i> | 14.0 | 30 | 10,661.67 | 0.07 | 0.37 |
| <i>Aiouea hammeliana</i> | 13.5 | 45 | 10,661.67 | 0.07 | 0.37 |
| <i>Alfaroa costaricensis</i> | 19.5 | 77 | 3,222.43 | 0.05 | 0.51 |
| <i>Amaioua pedicellata</i> | 11.0 | 22 | 8,596.68 | 0.06 | 0.62 |
| <i>Amphitecna sessilifolia</i> | 10.5 | 20 | 6,200.40 | 0.09 | 0.43 |
| <i>Arachnothryx aspera</i> | 5.5 | 4 | 6,731.03 | 0.14 | 0.56 |
| <i>Arachnothryx brenesii</i> | 9.3 | 12 | 6,945.85 | 0.14 | 0.56 |
| <i>Arachnothryx costaricensis</i> | 12.5 | 4 | 6,786.89 | 0.14 | 0.56 |
| <i>Arachnothryx laniflora</i> | 5.0 | 4 | 6,731.03 | 0.14 | 0.56 |
| <i>Arachnothryx montevertensis</i> | 5.0 | 4 | 6,731.03 | 0.14 | 0.56 |
| <i>Ardisia glandulosomarginata</i> | 6.0 | 12 | 4,651.78 | 0.07 | 0.57 |
| <i>Ardisia palmana</i> | 10.0 | 12 | 4,651.78 | 0.07 | 0.57 |
| <i>Ardisia pleurobotrya</i> | 7.0 | 27.5 | 4,651.78 | 0.07 | 0.57 |
| <i>Ardisia verapazensis</i> | 13.3 | 12 | 4,651.78 | 0.07 | 0.57 |
| <i>Axinaea costaricensis</i> | 10.5 | 15 | 8,930.29 | 0.08 | 0.53 |
| <i>Beilschmiedia brenesii</i> | 21.5 | 100 | 13,773.42 | 0.06 | 0.54 |
| <i>Beilschmiedia mexicana</i> | 15.0 | 25 | 13,773.42 | 0.06 | 0.54 |
| <i>Beilschmiedia ovalis</i> | 19.0 | 37.5 | 8,560.00 | 0.12 | 0.54 |
| <i>Blakea storkii</i> | 9.0 | 15 | 7,263.00 | 0.08 | 0.71 |
| <i>Brunellia costaricensis</i> | 8.0 | 41 | 5,825.59 | 0.07 | 0.32 |
| <i>Brunellia mexicana</i> | 22.5 | 40 | 6,176.70 | 0.07 | 0.32 |
| <i>Buddleja nitida</i> | 4.5 | 2.5 | 1,067.13 | 0.18 | 0.52 |
| <i>Buddleja skutchii</i> | 9.3 | 30 | 1,951.69 | 0.13 | 0.52 |
| <i>Bunchosia ternata</i> | 4.8 | 8.5 | 11,549.92 | 0.06 | 0.65 |
| <i>Cedrela tonduzii</i> | 7.0 | 20.5 | 2,443.00 | 0.04 | 0.36 |
| <i>Cestrum poasanum</i> | 3.5 | 4.9 | 4,511.00 | 0.04 | 0.50 |
| <i>Cestrum rugulosum</i> | 3.0 | 4.9 | 4,511.00 | 0.04 | 0.50 |
| <i>Chiococca phaenostemon</i> | 6.5 | 3.7 | 6,960.95 | 0.09 | 0.54 |
| <i>Chiranthodendron pentadactylon</i> | 30.0 | 200 | 7,630.41 | 0.08 | 0.44 |
| <i>Chrysochlamys allenii</i> | 15.0 | 20 | 13,397.11 | 0.06 | 0.43 |
| <i>Chrysochlamys psychotriifolia</i> | 7.5 | 11.4 | 13,397.11 | 0.06 | 0.43 |
| <i>Citharexylum macradenium</i> | 12.0 | 11.8 | 4,700.00 | 0.10 | 0.65 |
| <i>Citronella costaricensis</i> | 13.5 | 30 | 4,441.09 | 0.18 | 0.49 |
| <i>Clethra gelida</i> | 8.0 | 25 | 2,453.06 | 0.21 | 0.53 |
| <i>Clethra hartwegii</i> | 20.0 | 55 | 4,535.00 | 0.12 | 0.53 |
| <i>Clethra macrophylla</i> | 18.5 | 7.9 | 1,805.79 | 0.16 | 0.53 |
| <i>Clethra pringlei</i> | 18.5 | 40 | 1,805.79 | 0.16 | 0.53 |
| <i>Clethra suaveolens</i> | 36.7 | 100 | 1,805.79 | 0.16 | 0.53 |
| <i>Cleyera integrifolia</i> | 15.0 | 8.2 | 1,992.50 | 0.11 | 0.64 |
| <i>Cleyera theaeoides</i> | 9.0 | 8.2 | 2,746.23 | 0.12 | 0.63 |
| <i>Clibadium leiocarpum</i> | 6.0 | 4.5 | 4,213.99 | 0.07 | 0.53 |
| <i>Clusia croatii</i> | 15.0 | 10 | 6,681.26 | 0.09 | 0.65 |
| <i>Clusia palmana</i> | 10.0 | 10 | 8,614.99 | 0.11 | 0.65 |

| | | | | | |
|-----------------------------------|------|------|-----------|------|------|
| <i>Clusia salvinii</i> | 7.5 | 10 | 6,681.26 | 0.22 | 0.65 |
| <i>Clusia torresii</i> | 10.0 | 10 | 6,681.26 | 0.09 | 0.65 |
| <i>Coccoloba liportizii</i> | 5.0 | 15 | 16,040.85 | 0.05 | 0.62 |
| <i>Cojoba costaricensis</i> | 13.7 | 15 | 15,355.66 | 0.04 | 0.68 |
| <i>Comarostaphylis arbutoides</i> | 8.3 | 6.1 | 1,040.74 | 0.30 | 0.55 |
| <i>Comarostaphylis longifolia</i> | 3.0 | 6.1 | 1,639.02 | 0.30 | 0.58 |
| <i>Cornus disciflora</i> | 23.0 | 37.5 | 2,722.00 | 0.03 | 0.58 |
| <i>Cornus excelsa</i> | 12.0 | 15 | 2,722.00 | 0.03 | 0.57 |
| <i>Cosmibuena valerii</i> | 5.5 | 15 | 6,857.29 | 0.21 | 0.55 |
| <i>Coussarea caroliana</i> | 4.0 | 7.8 | 4,644.98 | 0.06 | 0.66 |
| <i>Croton megistocarpus</i> | 14.5 | 35 | 5,570.43 | 0.05 | 0.76 |
| <i>Damburneya cufodontisii</i> | 12.5 | 33.8 | 19,166.46 | 0.07 | 0.50 |
| <i>Damburneya salicina</i> | 7.0 | 38 | 19,008.31 | 0.07 | 0.51 |
| <i>Daphnopsis mollis</i> | 9.3 | 15 | 8,036.85 | 0.06 | 0.52 |
| <i>Dendropanax capillaris</i> | 14.0 | 17.5 | 10,004.58 | 0.06 | 0.41 |
| <i>Dendropanax globosus</i> | 10.0 | 10 | 10,004.58 | 0.06 | 0.41 |
| <i>Dendropanax gonatopodus</i> | 20.0 | 30 | 10,004.58 | 0.06 | 0.41 |
| <i>Dendropanax leptopodus</i> | 7.0 | 10 | 10,004.58 | 0.06 | 0.41 |
| <i>Dendropanax querceti</i> | 6.5 | 10 | 3,166.00 | 0.05 | 0.41 |
| <i>Deppea grandiflora</i> | 4.0 | 17.5 | 6,846.48 | 0.15 | 0.55 |
| <i>Dichapetalum brenesii</i> | 6.5 | 20 | 3,573.04 | 0.05 | 0.76 |
| <i>Duranta costaricensis</i> | 3.5 | 2.5 | 3,507.17 | 0.09 | 0.56 |
| <i>Eugenia austin-smithii</i> | 8.0 | 12 | 4,545.76 | 0.07 | 0.86 |
| <i>Eugenia cartagensis</i> | 6.5 | 25 | 4,545.76 | 0.07 | 0.86 |
| <i>Eugenia siggersii</i> | 8.0 | 25 | 4,545.76 | 0.07 | 0.86 |
| <i>Euonymus costaricensis</i> | 6.5 | 3.6 | 1,103.63 | 0.07 | 0.52 |
| <i>Faramea ovalis</i> | 6.0 | 10.3 | 13,283.96 | 0.06 | 0.62 |
| <i>Frangula discolor</i> | 9.5 | 4.9 | 4,157.23 | 0.04 | 0.48 |
| <i>Frangula oreodendron</i> | 4.5 | 4.9 | 2,759.24 | 0.09 | 0.48 |
| <i>Frangula pendula</i> | 8.0 | 4.9 | 4,157.23 | 0.04 | 0.48 |
| <i>Freziera guatemalensis</i> | 12.0 | 21 | 6,050.55 | 0.06 | 0.58 |
| <i>Fuchsia paniculata</i> | 10.0 | 3.6 | 4,159.47 | 0.05 | 0.56 |
| <i>Gaultheria acuminata</i> | 3.8 | 3 | 2,877.49 | 0.14 | 0.55 |
| <i>Glossostipula concinna</i> | 16.0 | 21.7 | 7,986.22 | 0.06 | 0.58 |
| <i>Gonzalagunia rosea</i> | 3.0 | 3 | 6,723.28 | 0.14 | 0.55 |
| <i>Gonzalagunia stenostachya</i> | 2.5 | 4.2 | 6,705.24 | 0.14 | 0.56 |
| <i>Guatteria costaricensis</i> | 8.0 | 20 | 10,538.08 | 0.07 | 0.50 |
| <i>Guatteria dolichopoda</i> | 10.0 | 10 | 10,538.08 | 0.07 | 0.50 |
| <i>Guatteria oliviformis</i> | 9.0 | 15 | 10,538.08 | 0.07 | 0.50 |
| <i>Guatteria slateri</i> | 12.0 | 30 | 10,538.08 | 0.07 | 0.50 |
| <i>Guatteria verrucosa</i> | 10.0 | 25.5 | 10,538.08 | 0.07 | 0.50 |
| <i>Hasseltia guatemalensis</i> | 20.0 | 19 | 6,880.67 | 0.07 | 0.58 |
| <i>Hasseltiopsis dioica</i> | 10.0 | 23.7 | 7,444.00 | 0.07 | 0.61 |
| <i>Hedyosmum mexicanum</i> | 20.0 | 9 | 5,753.00 | 0.05 | 0.45 |
| <i>Hoffmannia amplexifolia</i> | 2.8 | 3.3 | 6,679.12 | 0.15 | 0.55 |
| <i>Hoffmannia arborescens</i> | 4.0 | 3.3 | 6,723.28 | 0.15 | 0.55 |
| <i>Hypericum irazuense</i> | 2.5 | 1 | 6,580.50 | 0.06 | 0.98 |
| <i>Ilex discolor</i> | 17.3 | 8.8 | 5,096.95 | 0.09 | 0.58 |
| <i>Ilex lamprophylla</i> | 25.0 | 20.5 | 5,096.95 | 0.09 | 0.58 |
| <i>Ilex maxima</i> | 8.5 | 8.8 | 5,096.95 | 0.09 | 0.58 |
| <i>Ilex pallida</i> | 8.0 | 8.8 | 5,096.95 | 0.09 | 0.58 |
| <i>Inga exalata</i> | 10.5 | 10 | 19,076.18 | 0.07 | 0.58 |
| <i>Inga flexuosa</i> | 13.0 | 18.5 | 19,076.18 | 0.07 | 0.58 |

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|-------------------------------------|------|------|-----------|------|------|
| <i>Inga leonis</i> | 10.0 | 25 | 19,076.18 | 0.07 | 0.58 |
| <i>Inga longispica</i> | 15.0 | 36.5 | 19,076.18 | 0.07 | 0.58 |
| <i>Inga mortoniana</i> | 11.0 | 17.5 | 19,076.18 | 0.07 | 0.58 |
| <i>Inga sierrae</i> | 20.0 | 32.5 | 19,076.18 | 0.07 | 0.58 |
| <i>Inga tonduzii</i> | 8.0 | 20 | 19,076.18 | 0.07 | 0.58 |
| <i>Inga xalapensis</i> | 12.5 | 32.5 | 19,076.18 | 0.07 | 0.58 |
| <i>Jessia multivenia</i> | 3.8 | 8.5 | 4,500.82 | 0.07 | 0.55 |
| <i>Juglans pyriformis</i> | 27.5 | 90 | 3,147.10 | 0.03 | 0.50 |
| <i>Lacmellea zamorae</i> | 5.5 | 25 | 1,968.27 | 0.05 | 0.50 |
| <i>Ladenbergia brenesii</i> | 9.0 | 18 | 8,646.89 | 0.08 | 0.49 |
| <i>Lepidaploa polypleura</i> | 7.5 | 2.8 | 3,506.38 | 0.08 | 0.50 |
| <i>Lozanella enantiophylla</i> | 8.0 | 12 | 4,950.97 | 0.05 | 0.48 |
| <i>Lyonia squamulosa</i> | 4.5 | 1.6 | 1,014.40 | 0.09 | 0.48 |
| <i>Macrohasseltia macroterantha</i> | 25.0 | 80 | 8,049.67 | 0.07 | 0.60 |
| <i>Magnolia poasana</i> | 11.0 | 20 | 6,040.43 | 0.09 | 0.45 |
| <i>Magnolia schiedeana</i> | 17.5 | 45 | 7,010.00 | 0.10 | 0.51 |
| <i>Magnolia sororum</i> | 13.0 | 25 | 6,040.43 | 0.09 | 0.47 |
| <i>Malvaviscus palmanus</i> | 12.0 | 3.2 | 8,889.88 | 0.06 | 0.40 |
| <i>Matudaea trinervia</i> | 21.5 | 22.5 | 8,071.52 | 0.05 | 0.50 |
| <i>Maytenus woodsonii</i> | 3.0 | 17.9 | 2,260.73 | 0.09 | 0.72 |
| <i>Meliosma alba</i> | 10.5 | 50 | 25,729.50 | 0.02 | 0.48 |
| <i>Meliosma brenesii</i> | 9.0 | 25 | 25,729.50 | 0.06 | 0.48 |
| <i>Meliosma dentata</i> | 15.0 | 37 | 3,860.00 | 0.12 | 0.48 |
| <i>Meliosma idiopoda</i> | 12.5 | 37 | 25,729.50 | 0.06 | 0.48 |
| <i>Meriania phlomoides</i> | 8.0 | 9.8 | 9,080.68 | 0.08 | 0.49 |
| <i>Miconia albertobrenesii</i> | 4.0 | 12.1 | 14,599.93 | 0.08 | 0.66 |
| <i>Miconia biperulifera</i> | 4.0 | 12.1 | 14,599.93 | 0.08 | 0.66 |
| <i>Miconia brenesii</i> | 8.0 | 12.1 | 14,599.93 | 0.08 | 0.66 |
| <i>Miconia hemenostigma</i> | 5.0 | 12.1 | 14,599.93 | 0.08 | 0.66 |
| <i>Miconia oligotricha</i> | 3.0 | 12.1 | 14,599.93 | 0.08 | 0.66 |
| <i>Miconia pittieri</i> | 3.5 | 12.1 | 14,599.93 | 0.08 | 0.66 |
| <i>Miconia schnellii</i> | 9.5 | 32 | 2,022.48 | 0.12 | 0.66 |
| <i>Miconia tonduzii</i> | 6.0 | 12.1 | 14,599.93 | 0.08 | 0.66 |
| <i>Mollinedia costaricensis</i> | 5.5 | 6.7 | 12,269.60 | 0.05 | 0.49 |
| <i>Mollinedia viridiflora</i> | 6.5 | 6.7 | 4,711.93 | 0.05 | 0.52 |
| <i>Montanoa guatemalensis</i> | 10.5 | 6.5 | 3,032.46 | 0.08 | 0.49 |
| <i>Monteverdia recondita</i> | 15.7 | 12.5 | 5,877.14 | 0.07 | 0.57 |
| <i>Myrcianthes storkii</i> | 14.0 | 11.2 | 640.00 | 0.07 | 0.76 |
| <i>Ocotea acuminatissima</i> | 11.7 | 33.7 | 19,848.21 | 0.07 | 0.52 |
| <i>Ocotea austinii</i> | 15.5 | 42 | 19,848.21 | 0.07 | 0.48 |
| <i>Ocotea brenesii</i> | 6.0 | 10 | 19,848.21 | 0.07 | 0.51 |
| <i>Ocotea endresiana</i> | 17.5 | 45 | 19,848.21 | 0.07 | 0.52 |
| <i>Ocotea gomezii</i> | 7.5 | 12.5 | 19,848.21 | 0.07 | 0.52 |
| <i>Ocotea helicterifolia</i> | 8.7 | 8 | 5,470.00 | 0.09 | 0.52 |
| <i>Ocotea mollicella</i> | 11.5 | 50 | 19,848.21 | 0.07 | 0.52 |
| <i>Ocotea praetermissa</i> | 9.5 | 30 | 2,804.58 | 0.05 | 0.52 |
| <i>Ocotea psychotrioides</i> | 5.5 | 33.7 | 19,848.21 | 0.07 | 0.52 |
| <i>Ocotea purpurea</i> | 18.0 | 38 | 19,848.21 | 0.07 | 0.52 |
| <i>Oecopetalum mexicanum</i> | 27.5 | 30 | 4,515.08 | 0.08 | 0.70 |
| <i>Oreomunnea mexicana</i> | 32.5 | 57.5 | 1,090.00 | 0.05 | 0.53 |
| <i>Oreopanax echinops</i> | 15.0 | 17 | 6,150.70 | 0.04 | 0.50 |
| <i>Oreopanax oerstedianus</i> | 20.0 | 70 | 6,150.70 | 0.04 | 0.59 |
| <i>Oreopanax pycnocarpus</i> | 4.0 | 35 | 6,150.70 | 0.04 | 0.59 |

| | | | | | |
|---------------------------------|------|-------|-----------|------|------|
| <i>Oreopanax sanderianus</i> | 10.5 | 7 | 6,150.70 | 0.04 | 0.59 |
| <i>Oreopanax vestitus</i> | 20.0 | 70 | 6,150.70 | 0.04 | 0.59 |
| <i>Oreopanax xalapensis</i> | 30.0 | 7 | 6,050.94 | 0.05 | 0.59 |
| <i>Ostrya virginiana</i> | 25.0 | 50 | 2,311.05 | 0.03 | 0.50 |
| <i>Palicourea adusta</i> | 2.0 | 6.1 | 11,245.83 | 0.05 | 0.55 |
| <i>Palicourea alajuelensis</i> | 6.5 | 17.5 | 11,245.83 | 0.05 | 0.55 |
| <i>Palicourea eurycarpa</i> | 6.5 | 15 | 10,756.00 | 0.05 | 0.55 |
| <i>Palicourea galeottiana</i> | 4.5 | 6.1 | 11,245.83 | 0.05 | 0.55 |
| <i>Palicourea lasiorrhachis</i> | 3.0 | 6.1 | 11,245.83 | 0.05 | 0.55 |
| <i>Palicourea purpurea</i> | 5.0 | 6.1 | 11,245.83 | 0.05 | 0.55 |
| <i>Palicourea salicifolia</i> | 3.0 | 6.1 | 11,245.83 | 0.05 | 0.55 |
| <i>Panopsis costaricensis</i> | 15.0 | 40 | 13,779.23 | 0.06 | 0.51 |
| <i>Parathesis chiapensis</i> | 4.5 | 6.2 | 2,526.22 | 0.11 | 0.61 |
| <i>Parathesis glabra</i> | 4.0 | 6.2 | 2,553.43 | 0.11 | 0.61 |
| <i>Parathesis leptopa</i> | 7.5 | 6.2 | 2,633.46 | 0.12 | 0.61 |
| <i>Parathesis melanosticta</i> | 4.0 | 6.2 | 2,553.43 | 0.11 | 0.61 |
| <i>Parathesis villosa</i> | 6.0 | 6.2 | 2,519.32 | 0.11 | 0.61 |
| <i>Passiflora tica</i> | 4.0 | 4.8 | 10,345.29 | 0.06 | 0.64 |
| <i>Peltostigma guatemalense</i> | 5.0 | 8 | 6,458.64 | 0.05 | 0.49 |
| <i>Peltostigma pteleoides</i> | 11.0 | 15.8 | 6,221.35 | 0.05 | 0.49 |
| <i>Perrottetia longistylis</i> | 10.0 | 8.22 | 7,303.01 | 0.06 | 0.71 |
| <i>Perrottetia multiflora</i> | 6.5 | 18 | 6,929.39 | 0.06 | 0.71 |
| <i>Perrottetia ovata</i> | 8.0 | 11.61 | 7,125.74 | 0.06 | 0.71 |
| <i>Persea donnell-smithii</i> | 13.7 | 8.6 | 1,856.67 | 0.13 | 0.52 |
| <i>Persea liebmannii</i> | 15.0 | 50 | 1,856.67 | 0.13 | 0.52 |
| <i>Persea schiedeana</i> | 14.7 | 8.6 | 1,856.67 | 0.13 | 0.50 |
| <i>Persea veraguasensis</i> | 9.0 | 40 | 1,856.67 | 0.13 | 0.52 |
| <i>Phyllonoma laticuspidis</i> | 9.5 | 3.3 | 3,952.23 | 0.10 | 0.54 |
| <i>Phymosia rosea</i> | 7.0 | 19.9 | 7,869.87 | 0.06 | 0.45 |
| <i>Picramnia teapensis</i> | 5.0 | 15 | 10,223.50 | 0.06 | 0.48 |
| <i>Picramnia xalapensis</i> | 6.5 | 14.6 | 10,223.50 | 0.06 | 0.48 |
| <i>Pimenta guatemalensis</i> | 10.5 | 17.5 | 3,812.80 | 0.07 | 0.82 |
| <i>Pinus ayacahuite</i> | 50.0 | 200 | 742.70 | 0.11 | 0.45 |
| <i>Pinus hartwegii</i> | 32.0 | 145 | 763.04 | 0.11 | 0.44 |
| <i>Pinus lawsonii</i> | 17.5 | 32.5 | 1,965.85 | 0.10 | 0.48 |
| <i>Pinus pringlei</i> | 23.5 | 49.5 | 1,192.47 | 0.10 | 0.46 |
| <i>Pinus pseudostrobus</i> | 45.0 | 100 | 1,263.16 | 0.10 | 0.55 |
| <i>Pinus strobus</i> | 32.0 | 61 | 227.45 | 0.09 | 0.38 |
| <i>Piper irazuatum</i> | 4.5 | 3.4 | 15,477.80 | 0.04 | 0.39 |
| <i>Piper maxonii</i> | 4.0 | 3.4 | 15,477.80 | 0.04 | 0.39 |
| <i>Podocarpus matudae</i> | 30.0 | 150 | 2,403.39 | 0.18 | 0.48 |
| <i>Pouteria exfoliata</i> | 25.0 | 75 | 23,814.47 | 0.07 | 0.78 |
| <i>Prumnopitys standleyi</i> | 22.0 | 80 | 3,314.63 | 0.15 | 0.53 |
| <i>Prunus brachybotrya</i> | 35.0 | 50 | 2,650.00 | 0.12 | 0.67 |
| <i>Prunus fortunensis</i> | 14.0 | 15.4 | 5,700.80 | 0.08 | 0.67 |
| <i>Prunus rhamnoides</i> | 14.0 | 14 | 5,700.80 | 0.04 | 0.67 |
| <i>Prunus tetradenia</i> | 14.3 | 15.4 | 5,700.80 | 0.08 | 0.67 |
| <i>Psychotria jimenezii</i> | 4.5 | 7.6 | 7,368.21 | 0.06 | 0.53 |
| <i>Psychotria nubiphila</i> | 5.0 | 7.6 | 7,368.21 | 0.06 | 0.53 |
| <i>Psychotria orosiana</i> | 2.5 | 7.6 | 7,368.21 | 0.06 | 0.53 |
| <i>Quercus affinis</i> | 16.0 | 23.7 | 1,312.49 | 0.11 | 0.58 |
| <i>Quercus benthamii</i> | 50.0 | 23.7 | 2,045.53 | 0.10 | 0.58 |
| <i>Quercus candicans</i> | 25.0 | 23.7 | 1,360.77 | 0.09 | 0.64 |

| | | | | | |
|-----------------------------------|------|------|-----------|------|------|
| <i>Quercus costaricensis</i> | 15.0 | 67.5 | 2,749.95 | 0.15 | 0.61 |
| <i>Quercus crispipilis</i> | 27.0 | 45 | 1,360.77 | 0.09 | 0.66 |
| <i>Quercus germana</i> | 12.0 | 23.7 | 3,508.97 | 0.06 | 0.56 |
| <i>Quercus lancifolia</i> | 25.0 | 23.7 | 1,360.77 | 0.09 | 0.58 |
| <i>Quercus martinezii</i> | 30.0 | 23.7 | 1,360.77 | 0.09 | 0.58 |
| <i>Quercus salicifolia</i> | 15.5 | 100 | 1,360.77 | 0.05 | 0.67 |
| <i>Quercus scytophylla</i> | 20.0 | 23.7 | 1,360.77 | 0.09 | 0.64 |
| <i>Quercus seemannii</i> | 12.5 | 15 | 1,990.00 | 0.11 | 0.58 |
| <i>Quercus xalapensis</i> | 30.0 | 23.7 | 2,525.00 | 0.07 | 0.58 |
| <i>Rauvolfia aphlebia</i> | 7.0 | 25.2 | 6,245.00 | 0.02 | 0.48 |
| <i>Rogiera amoena</i> | 5.8 | 19 | 7,878.25 | 0.06 | 0.59 |
| <i>Rogiera cordata</i> | 6.0 | 16 | 8,520.34 | 0.06 | 0.60 |
| <i>Roldana lanicaulis</i> | 2.0 | 7.7 | 4,469.11 | 0.07 | 0.55 |
| <i>Rudgea reducticalyx</i> | 2.5 | 12.8 | 7,099.00 | 0.05 | 0.57 |
| <i>Saurauia leucocarpa</i> | 10.0 | 16.5 | 5,876.19 | 0.06 | 0.44 |
| <i>Saurauia montana</i> | 10.5 | 15 | 6,875.00 | 0.06 | 0.44 |
| <i>Saurauia oreophila</i> | 15.0 | 25 | 5,937.58 | 0.06 | 0.44 |
| <i>Saurauia pittieri</i> | 10.0 | 16.5 | 6,086.54 | 0.06 | 0.44 |
| <i>Saurauia rubiformis</i> | 6.0 | 16.5 | 5,763.32 | 0.06 | 0.44 |
| <i>Saurauia scabrida</i> | 12.5 | 16.5 | 6,056.42 | 0.06 | 0.44 |
| <i>Saurauia serrata</i> | 10.5 | 16.5 | 5,870.07 | 0.06 | 0.44 |
| <i>Saurauia villosa</i> | 15.0 | 16.5 | 5,803.90 | 0.06 | 0.44 |
| <i>Schefflera rodriguesiana</i> | 10.0 | 30 | 2,037.18 | 0.08 | 0.43 |
| <i>Senna multifoliolata</i> | 5.0 | 19 | 4,050.54 | 0.04 | 0.56 |
| <i>Sloanea ampla</i> | 16.5 | 41 | 18,590.50 | 0.07 | 0.81 |
| <i>Solanum nigricans</i> | 6.0 | 6.1 | 10,224.40 | 0.05 | 0.42 |
| <i>Solanum storkii</i> | 6.3 | 6.1 | 10,224.40 | 0.05 | 0.42 |
| <i>Sommeria arborescens</i> | 6.0 | 3 | 8,053.96 | 0.06 | 0.57 |
| <i>Sommeria donnell-smithii</i> | 11.0 | 10 | 8,132.56 | 0.06 | 0.58 |
| <i>Stauranthus perforatus</i> | 5.8 | 12.8 | 6,424.79 | 0.05 | 0.47 |
| <i>Stenanona costaricensis</i> | 6.0 | 6.5 | 11,290.29 | 0.08 | 0.48 |
| <i>Stevia microchaeta</i> | 3.5 | 7.8 | 4,751.05 | 0.07 | 0.59 |
| <i>Styrax glabrescens</i> | 7.0 | 29.9 | 9,218.00 | 0.07 | 0.44 |
| <i>Styrax radians</i> | 20.0 | 30 | 9,218.00 | 0.07 | 0.44 |
| <i>Styrax ramirezii</i> | 18.3 | 29.9 | 9,218.00 | 0.07 | 0.44 |
| <i>Styrax warscewiczii</i> | 25.0 | 25 | 8,276.31 | 0.07 | 0.44 |
| <i>Symplocarpon purpusii</i> | 17.5 | 55 | 6,255.43 | 0.05 | 0.60 |
| <i>Symplocos citrea</i> | 15.0 | 12.8 | 2,892.00 | 0.07 | 0.64 |
| <i>Symplocos costaricana</i> | 7.5 | 17.5 | 2,892.00 | 0.07 | 0.64 |
| <i>Symplocos limoncillo</i> | 16.0 | 12.8 | 2,892.00 | 0.07 | 0.64 |
| <i>Symplocos pycnantha</i> | 10.5 | 22.5 | 2,892.00 | 0.07 | 0.64 |
| <i>Symplocos serrulata</i> | 8.5 | 39 | 4,184.22 | 0.15 | 0.64 |
| <i>Tabernaemontana alfaroi</i> | 3.5 | 16.4 | 6,544.75 | 0.03 | 0.56 |
| <i>Telanthophora cobanensis</i> | 5.0 | 8.7 | 4,468.32 | 0.07 | 0.54 |
| <i>Telanthophora grandifolia</i> | 5.0 | 8.7 | 4,468.32 | 0.07 | 0.54 |
| <i>Telanthophora usantanensis</i> | 3.5 | 10 | 4,574.59 | 0.07 | 0.55 |
| <i>Ternstroemia lineata</i> | 15.0 | 52.7 | 7,272.23 | 0.07 | 0.62 |
| <i>Ticodendron incognitum</i> | 25.0 | 35 | 2,230.00 | 0.11 | 0.55 |
| <i>Tournefortia johnstonii</i> | 4.0 | 4.2 | 7,330.52 | 0.06 | 0.47 |
| <i>Ulmus mexicana</i> | 69.0 | 16.2 | 4,216.22 | 0.04 | 0.38 |
| <i>Vaccinium leucanthum</i> | 8.0 | 2.2 | 456.58 | 0.07 | 0.29 |
| <i>Vallesia aurantiaca</i> | 9.3 | 19.9 | 5,697.34 | 0.04 | 0.52 |
| <i>Verbesina apleura</i> | 4.5 | 1.2 | 3,740.19 | 0.08 | 0.44 |

| | | | | | |
|--------------------------------|------|------|-----------|------|------|
| <i>Verbesina perymenioides</i> | 4.0 | 1.2 | 3,758.55 | 0.08 | 0.44 |
| <i>Viburnum acutifolium</i> | 4.5 | 7.6 | 2,485.44 | 0.08 | 0.54 |
| <i>Viburnum costaricanum</i> | 7.0 | 7.6 | 1,133.67 | 0.09 | 0.54 |
| <i>Viburnum elatum</i> | 5.0 | 7.6 | 2,485.44 | 0.06 | 0.54 |
| <i>Viburnum jucundum</i> | 4.5 | 7.6 | 2,485.44 | 0.06 | 0.54 |
| <i>Viburnum microcarpum</i> | 5.0 | 7.6 | 2,485.44 | 0.06 | 0.54 |
| <i>Viburnum venustum</i> | 4.5 | 9 | 2,001.98 | 0.06 | 0.54 |
| <i>Weinmannia burserifolia</i> | 12.0 | 60 | 2,787.48 | 0.10 | 0.62 |
| <i>Weinmannia wercklei</i> | 12.5 | 22.4 | 5,522.80 | 0.07 | 0.49 |
| <i>Wercklea insignis</i> | 10.0 | 35 | 8,089.06 | 0.06 | 0.24 |
| <i>Wercklea woodsonii</i> | 13.0 | 42.7 | 8,664.04 | 0.07 | 0.24 |
| <i>Zinowiewia integerrima</i> | 13.0 | 40 | 1,525.00 | 0.11 | 0.71 |
| <i>Zinowiewia rubra</i> | 15.0 | 45 | 1,525.00 | 0.11 | 0.71 |
| <i>Zygia palmana</i> | 8.0 | 20 | 17,707.00 | 0.07 | 0.83 |

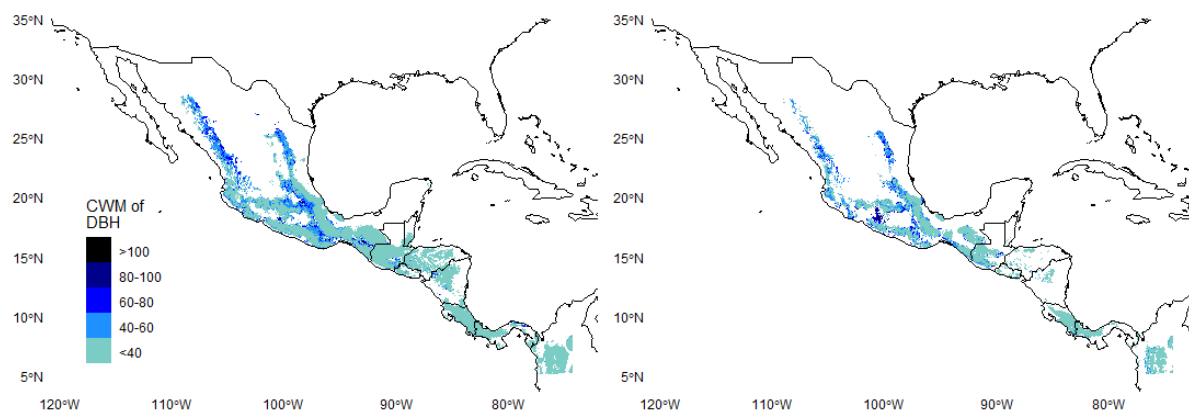


Fig. S2. Community-weighted means of diameter at breast height (cm) under current (1981-2010; left) and future (2071-2100; right) climatic conditions.

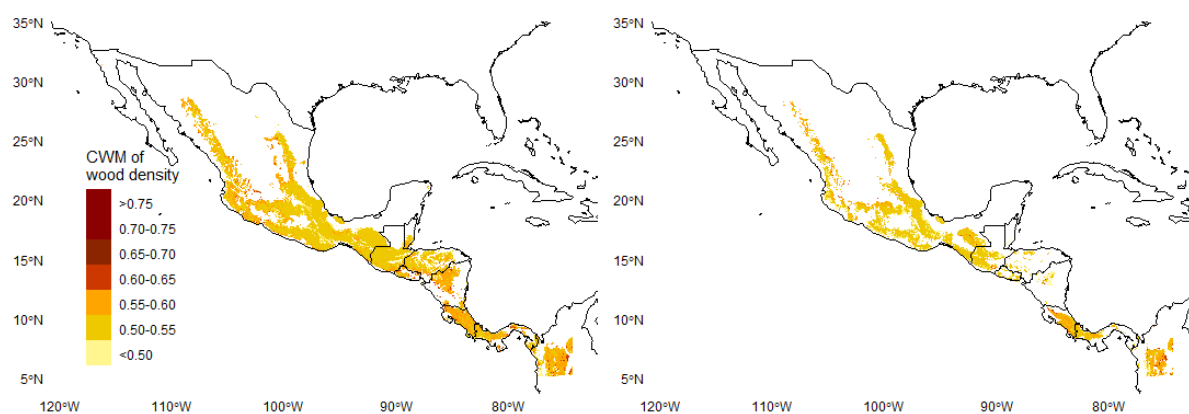


Fig. S3. Community-weighted means of wood density (g cm^{-3}) under current (1981-2010; left) and future (2071-2100; right) climatic conditions.

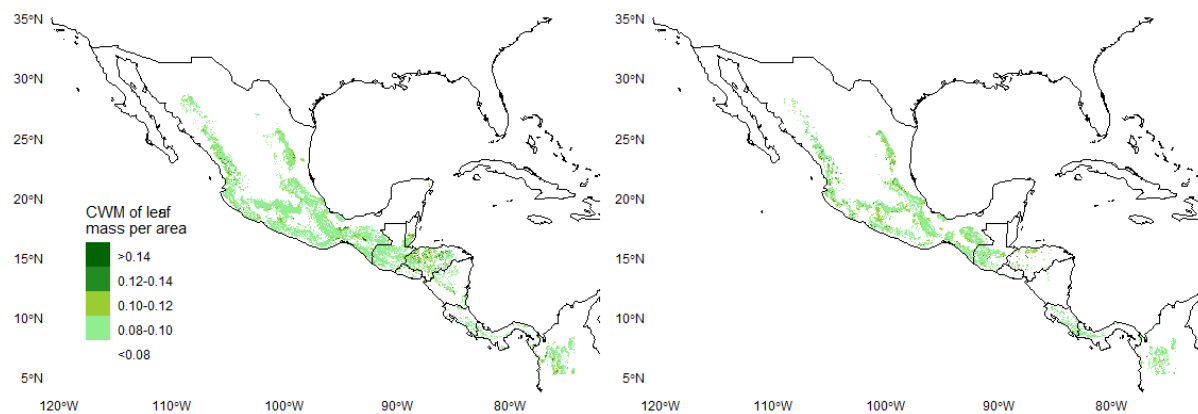


Fig. S4. Community-weighted means of leaf mass per area (g cm^{-2}) under current (1981-2010; left) and future (2071-2100; right) climatic conditions.

Table S11. Moran's I coefficients of five functional traits (H, DBH, WD, LA and LMA) and AGB throughout the study area.

| Variable | Time | Moran I Statistic | p-value |
|------------|---------|-------------------|---------|
| H | Current | 0.606 | <0.0001 |
| | Future | 0.407 | <0.0001 |
| DBH | Current | 0.493 | <0.0001 |
| | Future | 0.347 | <0.0001 |
| WD | Current | 0.330 | <0.0001 |
| | Future | 0.371 | <0.0001 |
| LA | Current | 0.670 | <0.0001 |
| | Future | 0.520 | <0.0001 |
| LMA | Current | 0.277 | <0.0001 |
| | Future | 0.258 | <0.0001 |
| AGB | Current | 0.476 | <0.0001 |
| | Future | 0.343 | <0.0001 |

Table S12. PCA stats of five functional traits (H, DBH, WD, LA and LA) of 272 montane-specialist tree species. Significance of the PCA axes calculated with Monte-Carlo tests, number of repetitions = 999, number of tests = 6.

| PC | Eigenvalue | Proportion of Variance | Cumulative proportion | Obs. | Std. Obs. | Alternative | P-value |
|----------|------------|------------------------|-----------------------|-------|-----------|-------------|---------|
| 1 | 1.86 | 37.30 | 37.30 | 0.682 | 11.134 | greater | 0.001 |
| 2 | 1.27 | 25.34 | 62.63 | 0.631 | 2.866 | greater | 0.009 |
| 3 | 1.02 | 20.38 | 83.01 | 0.673 | -2.761 | greater | 1 |
| 4 | 0.55 | 11.00 | 94.01 | 0.843 | 22.482 | greater | 0.001 |
| 5 | 0.30 | 5.99 | 100.00 | 0.876 | 14.028 | greater | 0.001 |

GAM model outputs

```

$H_current

Family: gaussian
Link function: identity

Formula:
H_current ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) 15.51398    0.04904   316.4   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Ref.df    F p-value
s(lat)       7.903  8.643 285.77 <2e-16 ***
s(elev)      7.239  8.258  95.16 <2e-16 ***
ti(lat,elev) 9.812 11.560  22.36 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.555   Deviance explained = 55.7%
-REML = 12672   Scale est. = 9.1674    n = 5000

```

```

$H_future

Family: gaussian
Link function: identity

Formula:
H_future ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
      Estimate Std. Error t value Pr(>|t|)
(Intercept) 15.46532    0.09072   170.5  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
      edf Ref.df    F p-value
s(lat)    8.565  8.933 49.19  <2e-16 ***
s(elev)    6.148  7.343 10.14  <2e-16 ***
ti(lat,elev) 12.198 13.399 41.36  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.214  Deviance explained = 21.9%
-REML = 15657  Scale est. = 30.165    n = 5000

$DBH_current

Family: gaussian
Link function: identity

Formula:
DBH_current ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
      Estimate Std. Error t value Pr(>|t|)
(Intercept) 31.9306    0.2236   142.8  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
      edf Ref.df    F p-value
s(lat)    8.125  8.756 116.60  <2e-16 ***
s(elev)    7.842  8.648  22.79  <2e-16 ***
ti(lat,elev) 9.521 11.209   7.93  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.309  Deviance explained = 31.3%
-REML = 20270  Scale est. = 191.72    n = 5000

$DBH_future

Family: gaussian
Link function: identity

Formula:
DBH_future ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
      Estimate Std. Error t value Pr(>|t|)
(Intercept) 34.3664    0.3604   95.36  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
      edf Ref.df    F p-value
s(lat)    8.228  8.812 48.56  <2e-16 ***
s(elev)    7.215  8.240 10.34  <2e-16 ***
ti(lat,elev) 10.301 11.963 17.23  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.159  Deviance explained = 16.4%
-REML = 22622  Scale est. = 491.46    n = 5000

```

```

$WD_current

Family: gaussian
Link function: identity

Formula:
WD_current ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.5370691  0.0004425   1214   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Ref.df      F p-value
s(lat)        8.256  8.830 43.30  <2e-16 ***
s(elev)        6.619  7.774 11.48  <2e-16 ***
ti(lat,elev) 13.132 14.061 26.75  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.178   Deviance explained = 18.3%
-REML = -10979   Scale est. = 0.00070472   n = 5000

$WD_future

Family: gaussian
Link function: identity

Formula:
WD_future ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.5244384  0.0006344   826.7   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Ref.df      F p-value
s(lat)        8.510  8.909 75.867  < 2e-16 ***
s(elev)        7.456  8.410 32.701  < 2e-16 ***
ti(lat,elev)  9.403 11.244  4.308 3.89e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.18   Deviance explained = 18.5%
-REML = -9047.7   Scale est. = 0.001533   n = 5000

$LA_current

Family: gaussian
Link function: identity

Formula:
LA_current ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) 5382.42      26.25   205.1   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Ref.df      F p-value
s(lat)        8.611  8.943 342.37  <2e-16 ***
s(elev)        5.775  6.969  37.38  <2e-16 ***
ti(lat,elev) 10.192 11.869  18.30  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.524   Deviance explained = 52.6%
-REML =  44040   Scale est. = 2.602e+06   n = 5000

$LA_future

```

```

Family: gaussian
Link function: identity

Formula:
LA_future ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  5498.24      37.43   146.9  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Ref.df      F p-value
s(lat)        8.585  8.935 152.87 <2e-16 ***
s(elev)        3.711  4.661  47.87 <2e-16 ***
ti(lat,elev)   9.962 11.670   10.74 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.354  Deviance explained = 35.7%
-REML = 45826  Scale est. = 5.3293e+06  n = 5000

$LMA_current

Family: gaussian
Link function: identity

Formula:
LMA_current ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.0843336  0.0002619    322  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Ref.df      F p-value
s(lat)        8.684  8.962 13.80 <2e-16 ***
s(elev)        6.229  7.421 10.26 <2e-16 ***
ti(lat,elev)  12.694 13.684 25.46 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.119  Deviance explained = 12.4%
-REML = -13597  Scale est. = 0.00024689  n = 5000

$LMA_future

Family: gaussian
Link function: identity

Formula:
LMA_future ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.0865418  0.0003499   247.3  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Ref.df      F p-value
s(lat)        8.676  8.962 13.42 <2e-16 ***
s(elev)        7.139  8.192 30.52 <2e-16 ***
ti(lat,elev)  12.925 13.935 19.70 <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.133  Deviance explained = 13.8%
-REML = -12150  Scale est. = 0.00044024  n = 5000

$AGB_current

```

```

Family: gaussian
Link function: identity

Formula:
AGB_current ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
      Estimate Std. Error t value Pr(>|t|)
(Intercept) 1796.51      28.88  62.21  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
      edf Ref.df    F p-value
s(lat)    8.532  8.915 81.92  <2e-16 ***
s(elev)    8.385  8.891 54.46  <2e-16 ***
ti(lat,elev) 9.732 11.323 24.95  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.345  Deviance explained = 34.8%
-REML = 44552  Scale est. = 3.1836e+06  n = 5000

$AGB_future

Family: gaussian
Link function: identity

Formula:
AGB_future ~ s(lat) + s(elev) + ti(lat, elev)

Parametric coefficients:
      Estimate Std. Error t value Pr(>|t|)
(Intercept) 1779.55      40.34  44.12  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
      edf Ref.df    F p-value
s(lat)    8.651  8.947 45.263  <2e-16 ***
s(elev)    5.804  6.995 20.900  <2e-16 ***
ti(lat,elev) 7.819  9.836  9.452  <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.129  Deviance explained = 13.3%
-REML = 46252  Scale est. = 6.3221e+06  n = 5000

```