

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

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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.

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I. 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 (Hamilton, 1995; Loope & Giambelluca, 1998; Still, Foster & Schneider, 1999; Foster, 2001; Richter, 2008). These forests often harbour high abundance and diversity of epiphytes (Loope & Giambelluca, 1998; Foster, 2001; Collin, 2001). 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; Ohmura, 2012; Torres, González & Comarazamy, 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. 1706). These combined pressures could make them more likely to be outcompeted by climate-driven upwardly migrating species from nearby lowland areas (Sukumar, Suresh & Ramesh, 1995; Loope & Giambelluca, 1998; Oliveira *et al.*, 2014).

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 (Feeley *et al.*, 2011; Corlett & Westcott, 2013; 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, Vasconcelos & Feeley, 2020).

Numerous literature reviews on TMF research have been conducted, focusing on various aspects, including environmental determinants (Oliveira *et al.*, 2014; Fahey, Sherman & Tanner, 2016), ecosystem functions (Dalling *et al.*, 2016), ecosystem services (Buytaert, Cuesta-Camacho & Tobón, 2011), habitat degradation (Soh *et al.*, 2019),

conservation (Peh *et al.*, 2011) and restoration strategies (Christmann & 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 (Alvarez, Apan & Maraseni, 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: (i) what are the general thematic and methodological trends in the published studies investigating the impacts of climate change on TMFs? (ii) What are the implications of those trends in terms of our understanding and application of the current knowledge? (iii) How reliable is the literature in terms of the quality of the evidence it provides? (iv) What are the general forecasts for TMFs globally based on the most reliable evidence and the direction of future research?

II. METHODS

(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*).'

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 (Fig. 1). For *Google* searches,

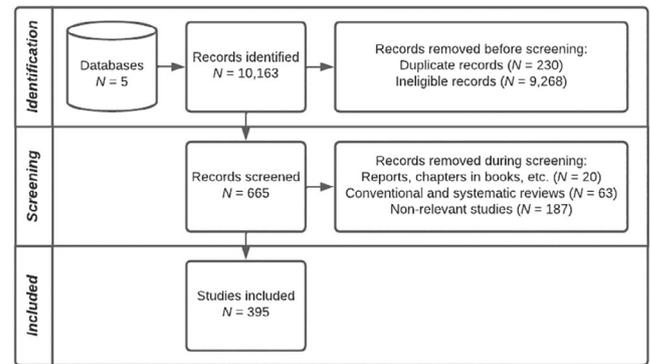


Fig. 1. Systematic search protocol. The final count includes all relevant studies from 1994 to 2021.

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 II.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) 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; Fig. 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); Fig. 2, Table 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 (Brujnzeel, 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.

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).

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

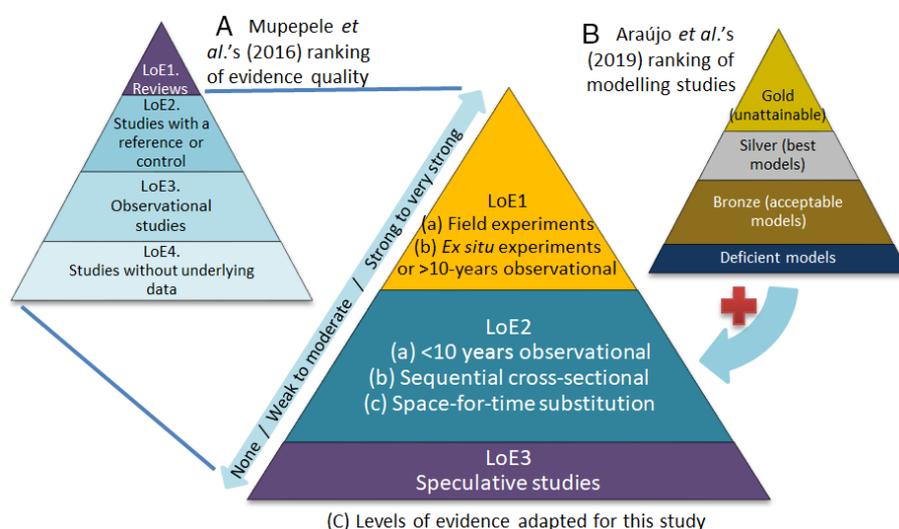


Fig. 2. Schematic representation of the adapted classification of studies according to (A) Level of Evidence (LoE) from Mupepele *et al.* (2016) and (B) assessment of modelling studies from Araujo *et al.* (2019). (C) The combined evidence assessment used in this review. See Table 1 for detailed explanation of levels.

Table 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 tropical montane forest (TMF) 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	<i>Ex situ</i> experiments OR time-series studies (≥ 10 years of regular – yearly, monthly, etc. – observations)	Long-term data sets 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 data sets provide evidence of changes taking place over time, but they may not be long enough to attribute observed changes confidently 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 silver standard in Araújo <i>et al.</i> , 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 on 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 bronze standard in Araújo <i>et al.</i> , 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 <i>versus</i> 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 deficient category in Araújo <i>et al.</i> , 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 knowledge from other systems are also included in this level.

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, Fig. 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.

III. RESULTS

(1) Distribution of studies

Our initial search string retrieved 10,163 studies. After successive elimination stages (Fig. 1), the final data set included 395 studies (see online Supporting Information, Table S1 for full list), published between 1994 and 2021 (Fig. 1). The number of publications increased from less than 10 annually before 2006 to an average of 30 from 2013 onwards, potentially reflecting an increased interest in TMFs.

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 (Mulligan, 2010; Los *et al.*, 2019) 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 (Fig. 3), and some authors count subnational territories separately, e.g. New Caledonia, Tahiti and La Réunion Island (see Karger *et al.*, 2021; Mulligan, 2010).

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 (Figs 3 and 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%; Fig. 4A).

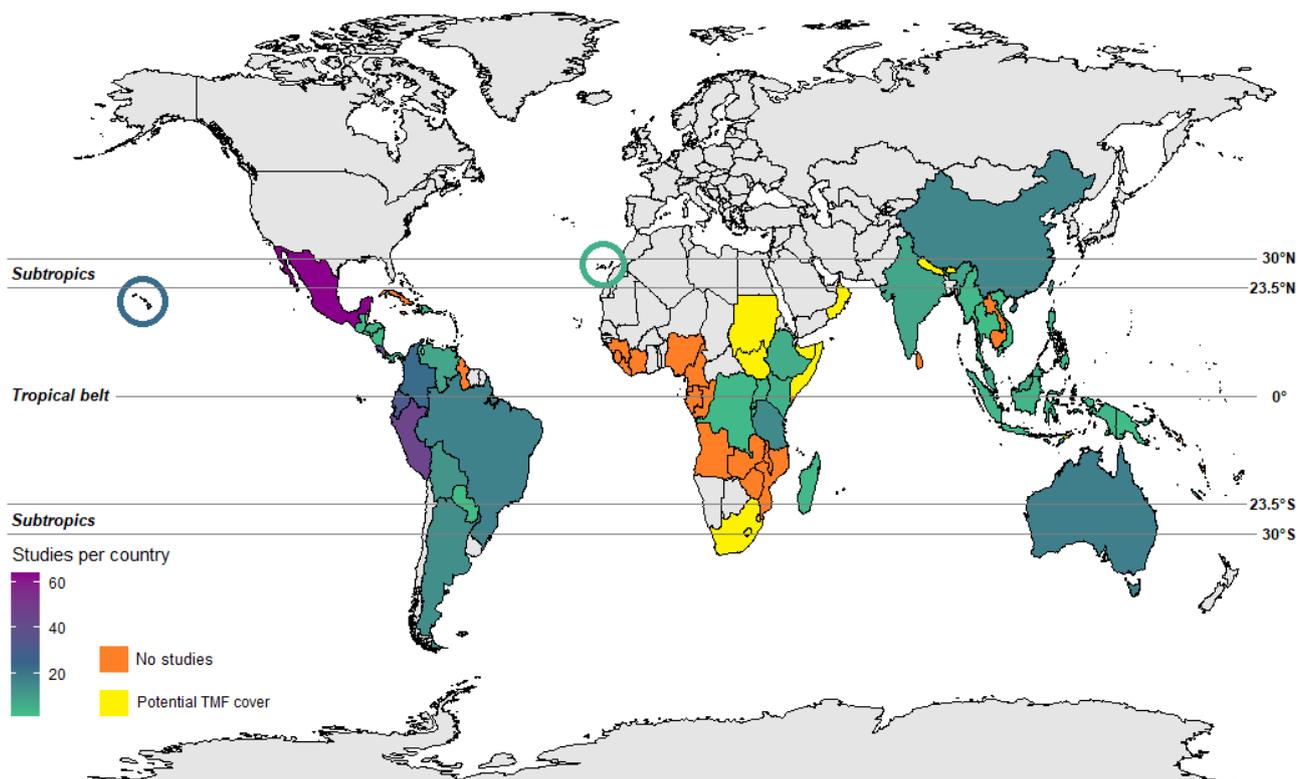


Fig. 3. Geographical distribution of retrieved studies by country or territory. The number of studies is indicated by the colour scale shown on the bottom left. Orange indicates countries with tropical montane forest (TMF) cover for which no relevant studies were found. Yellow indicates countries with contested TMF cover (see Karger *et al.*, 2021; Los *et al.*, 2019; Mulligan, 2010).

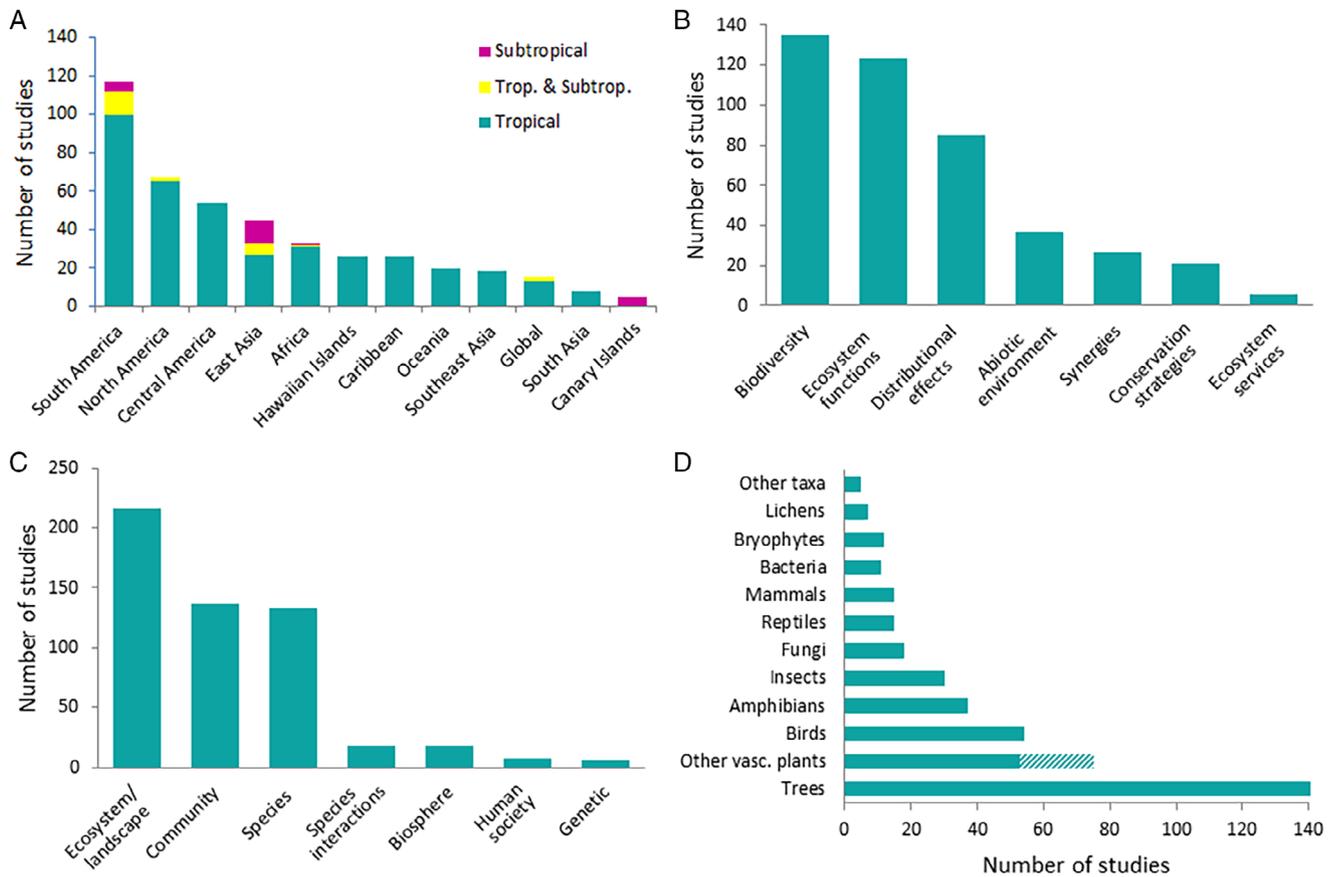


Fig. 4. Number of studies published from 1994 to 2021 on the effects of climate change on tropical and subtropical montane forests for different (A) geographic regions, (B) research topic, (C) ecological levels, and (D) taxonomic groups. In A, Oceania comprises Australia, Papua New Guinea and other islands of the South Pacific; the Hawaiian Islands are shown separately. In D, the striped portion of the ‘other vascular plants’ group corresponds to epiphytes.

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 (Fig. 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 (Fig. 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 fewer than 10 studies each for other countries and territories. Countries with potential areas of TMF (Mulligan, 2010; Karger *et al.*, 2021), 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 (Fig. 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 (Fig. 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 (Fig. 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 10 studies each.

(2) Trends in the literature

We found that research from certain regions tended to focus on a particular taxonomic group ($\chi^2 = 129.77$, $df = 81$, $P < 0.001$). 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 ($\chi^2 = 104.25$, $df = 45$, $P < 0.001$). 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 ($\chi^2 = 268.83$, $df = 45$, $P < 0.001$). 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 ($\chi^2 = 41.07$, $df = 10$, $P < 0.001$), and were also more likely to report biodiversity losses in terms of abundances, species richness or species turnover, and extinctions ($\chi^2 = 10.32$, $df = 4$, $P = 0.035$).

(3) Assessment of the evidence on the impacts of climate change in TMFs

We found 30 (7.6%) field experimental studies (Fig. 5A), i.e. providing a 'very strong' LoE (LoE1a). They reflected the general geographical trend described in Section III.1, with five studies from Mexico, although four of these were conducted by one research team (García-Hernández *et al.*, 2019; Toledo-Aceves, García-Hernández & Paz, 2019; García-Hernández & Toledo-Aceves, 2020; Toledo-Aceves & del-Val, 2021). 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 (Williams, Bolitho & Fox, 2003; Miles, Grainger & Phillips, 2004). 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.].

An association between the LoE strength and research topics ($\chi^2 = 116.11$, $df = 20$, $P < 0.001$; Fig. 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 ($\chi^2 = 68.45$, $df = 16$, $P < 0.001$) because studies on biodiversity also relied more

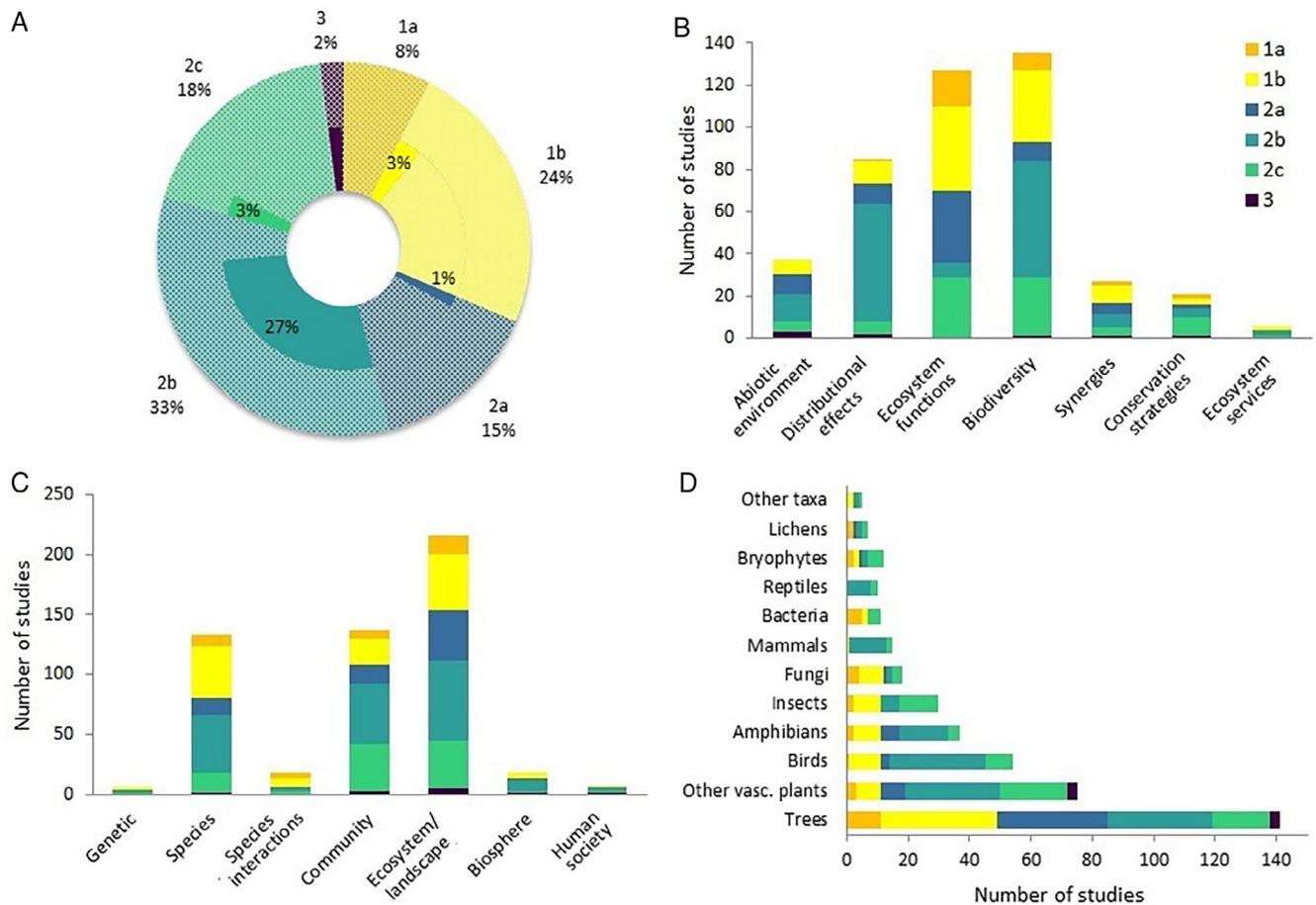


Fig. 5. Distribution of reviewed studies according to levels of evidence (LoE) category (see Table 1 and Fig. 2 for definitions of LoE categories). (A) Percentage of studies by LoE. Solid-coloured portions indicate the frequency of modelling studies within each level. (B–D) LoE of reviewed studies by (B) research topic, (C) ecological level, and (D) taxonomic group. In D, vascular epiphytes are included in the ‘other vasc. plants’ category.

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; Fig. 5C), we found an association of these studies with certain LoE strength ($\chi^2 = 23.44$, $df = 10$, $P = 0.009$). 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 (Fig. 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 ($\chi^2 = 79.49$, $df = 20$, $P < 0.001$). 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.

(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, Bassiouni & Torres-Sánchez, 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 & Veblen, 2000), for instance, serotinous pine trees (Rodríguez-Trejo & Fulé, 2003; Climent *et al.*, 2004). 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 (Yocom & Fulé, 2012; Cerano-Paredes *et al.*, 2021).

(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 (Ledo, Montes & Condes, 2009; Tejedor-Garavito *et al.*, 2015; Godoy-Bürki, 2016), 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, Zomer & Corlett, 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, Sherman & Fahey, 2007; Martin & Fahey, 2014), the Afro-montane forests in Ethiopia (Schmitt *et al.*, 2013), and in Hawaii (Crausbay & 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, Powell & Silman, 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 & Barradas, 2014; Rehm & Feeley, 2016; Fadrique *et al.*, 2018), 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 & 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 (Rehm & Feeley, 2015; Joshi, Ratnam & Sankaran, 2020; Rehm, Yelenik & D'Antonio, 2021), hydraulic stress (Song *et al.*, 2016b), fruit or seed production (Chapman *et al.*, 2018), seed dispersal (Hillyer & Silman, 2010; Rehm & Feeley, 2013; Nowak *et al.*, 2022), germination rates (Centre *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, Vasconcelos & Feeley, 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, Muller-Landau & Schipper, 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 & Solano, 2002; Song, Liu & Nadkarni, 2012; Wagner, Zotz & Bader, 2014) and ferns (Hsu, Oostermeijer & Wolf, 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 (Zotz *et al.*, 2010; Gotsch *et al.*, 2015). 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, Albach & Zotz, 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 (Fig. 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.*, 2011b; Hermes *et al.*, 2018a; Hayes, Lecourt & del Castillo, 2018; Freeman *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 & 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, Robinson & Levey, 2010), or leading to higher morbidity (Freed & 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.*, 2020a,b), amphibians (Cruz-Elizalde *et al.*, 2020; Cordier *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.*, 2015a,b).

The prospect for ectotherms is a matter of much concern. Thermal tolerance experiments (LoE1b) conducted with amphibians (Rueda-Solano *et al.*, 2016; von May *et al.*, 2017; González-del-Piego *et al.*, 2020), reptiles (Muñoz *et al.*, 2016; Piantoni, Navas & Ibargiengoytia, 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.*, 2013*a,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, Green & Davies, 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.*, 2019*b*, 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, 2015*b*; 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.*, 2014*a,b*; Rodríguez-Ramírez *et al.*, 2020). These climatic factors also influence the growth rates of TMF trees (Keyimu *et al.*, 2020; Li *et al.*, 2020; Niessner *et al.*, 2020; Quadri, Silva & Zavaleta, 2021; Ricker, Gutiérrez-García & Daly, 2007; Rodríguez-Ramírez, Luna-Vega & Rozas, 2018; but see Camarero *et al.*, 2021), seed production (Rodríguez-Ramírez, Terrazas & Luna-Vega, 2019; Pau *et al.*, 2020), establishment (Chirino *et al.*, 2017; Toledo-Aceves *et al.*, 2019), and even plant–herbivore interactions (Bendix *et al.*, 2021; Toledo-Aceves & del-Val, 2021). 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 pan-tropical forests since the mid-1990s (Krishnaswamy, John & Joseph, 2014), or the contrasting greening trend during the past 20 years in central Mexico (Correa-Díaz, Romero-Sánchez & Villanueva-Díaz, 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.

IV. DISCUSSION

This review of the literature on impacts of climate change on TMFs shows that: (i) the rates of climate change are generally intensified rather than attenuated by elevation, making montane communities more susceptible to their effects; (ii) tropical montane communities might be able to respond by shifting their distributions primarily upslope, but (iii) 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; (iv) even if montane species are able to track suitable conditions fast enough, they risk running out of physical space; (v) the impacts of climate change on genetic diversity and species interactions within tropical montane ecosystems remain largely unknown; and (vi) 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.

(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 & 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. Martín *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 (Veloz *et al.*, 2012; Sax *et al.*, 2013). 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, Słowińska & Słowiński, 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) 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.

(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 (Rehm & Feeley, 2013; Song *et al.*, 2016b; Joshi *et al.*, 2020) 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; Ramirez-Villegas *et al.*, 2014; Quiroga, Premoli & Kitzberger, 2018; Joshi *et al.*, 2020), but few studies have looked at ecological networks in TMFs (Benning *et al.*, 2002; Jankowski *et al.*, 2010; Hillyer & Silman, 2010; Ornelas, Licona-Vera & Ortiz-Rodriguez, 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 micro-evolutionary processes operate differently within a population along an elevational gradient, i.e. the leading edge, the central population and the rear edge (Kremer, Potts & Delzon, 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, Bijlsma & Loeschcke, 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 & 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 through 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.

V. 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, Coronado & Marsico, 2022; Morton *et al.*, 2022) emphasises the importance of traditional biodiversity surveys in TMFs, especially in understudied regions.

VI. 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. Optimising 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 minimising 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.

VII. ACKNOWLEDGEMENTS

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Details of 395 studies published between 1994 and 2021 included in the assessment of evidence strength for impacts of anthropogenic climate change on tropical montane forests.

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