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Towards integrated ecological research in tropical montane cloud forests

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Abstract: Tropical tropical montane cloud forests (TMCFs) cover a small portion of the Earth, yet they are significant biodiversity hotspots and centres of endemism, and they provide important hydrological and biogeochemical functions that affect human livelihoods. Given their fundamental sensitivity to climate, TMCFs also serve as an early warning system for climate change impacts. This paper outlines a new international initiative, CloudNet, that aims to promote integrated research across TMCFs, and introduces a special issue that reviews emerging themes and topics in the ecology of TMCFs, highlighting knowledge gaps and suggesting new directions for research. CloudNet is helping coordinate several new research projects and protocols: (1) a global repository of TMCF data and meta-analyses across multiple sites; (2) a multi-site study of plant functional traits across TMCFs; (3) a multi-site study of decomposition processes across TMCFs; (4) a protocol for standardizing climate data collection across TMCFs. These studies are intended to evaluate the extent to which general patterns emerge, accounting for biogeographic, phylogenetic and environmental differences among sites. Common data collection across TMCFs should also allow better integration across disciplines, such as linking nutrient limitation, seed production and propagule recruitment, and enable cross-site comparisons of how TMCFs respond to drivers of global change, including rising cloud bases, increasing temperatures, altered disturbance regimes, biological invasions and extinction, and changing human land use.

Key Words: biodiversity, cloud forest, climate change, disturbance, epiphytes, metacommunities, nutrient limitation, productivity, seed dispersal ecology, tropical montane cloud forest

INTRODUCTION

On tropical mountains, forests ecosystems of complexity, beauty and value have evolved under the influence of distinctive climatic conditions and biogeographic assemblages. Over small distances, tropical mountains experience steep and compressed gradients in temperature and moisture (Lomolino 2001), especially in patterns of cloud formation (Bruijnzeel *et al*. 2011a). Tropical montane cloud forests (TMCFs) are further shaped by geographic isolation at high altitudes and summits (La Sorte & Jetz 2010), mountain-mass (Massenerhebung) effects (Grubb 1971) and Hadley cell synoptic climate influences of the trade wind inversion (Giambelluca & Nullet 1991, Martin & Fahey 2014). In this setting, TMCFs house a species-rich and biogeographically diverse assembly of flora and fauna, with affinities spanning pantropical to Holarctic (Ashton 2003, Myers *et al*. 2000, Ohsawa 1990, 1995; Troll 1968, Willig & Presley 2016), with especially high levels of beta diversity and endemism (Gentry 1995, Kier & Barthlott 2001). In the cloudiest areas, the trees are frequently short-statured with small diameters (Fahey *et al*. 2016), and are characteristically covered with abundant and species-rich epiphytic vegetation (Gotsch *et al*. 2016b). A marked increase in the intensity and scale of study in TMCFs in the past 15–20 y has greatly expanded our knowledge of these threatened ecosystems.

A key challenge addressed in recent years has been the mapping, cataloguing and classification of TMCFs (Mulligan 2011a), in conjunction with an improved conceptualization of the key drivers of spatial patterns along the altitudinal gradient (Bruijnzeel *et al*. 2011a). Efforts with remote sensing and models of cloud immersion have also improved our knowledge of cloud occurrence patterns on large scales (Mulligan 2011a, Nair *et al*. 2008, Welch *et al*. 2008), and a

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better biophysical model of how cloud immersion affects hydrology and ecology has been developed, though more testing and calibration are needed (Mulligan *et al.* 2011b). Work has expanded on traditional classifications that were based on altitude alone (Hamilton *et al.* 1995), to incorporate the 'context sensitivity' of TMCFs to local and regional factors – today we have an improved understanding of how local factors such as geology and topography, wind, natural disturbance agents (e.g. fire, landslides, tropical cyclones) and biogeographic histories interact with higher-level macroclimatic drivers to create the complex mosaic characteristic of TMCF landscapes (Asbjornsen & Wickel 2009, La Torre-Cuadros *et al.* 2007, Martin & Fahey 2006, Martin *et al.* 2007, 2011).

Ecological research in TMCFs continues to expand into new areas, conceptually and geographically. Yet increased coordination among TMCFs investigators is needed, as research remains spread widely across numerous political jurisdictions and geographic boundaries, hindering opportunities for coordinated study. In particular, new and updated reviews and syntheses are needed to help identify the next important themes and gaps in TMCF ecology research. This is an urgent matter from both ecological and conservation standpoints, as TMCFs provide key ecosystem services (e.g. carbon storage, water flow regimes, slope stability, biodiversity maintenance, landscape connectivity; Spracklen & Righelato 2014), yet are regionally threatened by deforestation and degradation (Armenteras *et al.* 2003, Bruijnzeel *et al.* 2011a, Bubb *et al.* 2004, Cayuela *et al.* 2006, FAO 1993, Hansen *et al.* 2013, Peh *et al.* 2011) and globally by climate change (Bruijnzeel *et al.* 2011a, Lawton *et al.* 2001). In this introduction, we emphasize the ecological study and importance of tropical montane cloud forests, yet tropical mountains often support forests which do not fit into a narrow definition of cloud-affected systems – notwithstanding, we consider forests in drier and less cloudy areas of tropical mountains a key part of these ecosystems, and their role in these systems is included throughout this special issue.

Research Coordination Network – CloudNet

CloudNet (http://cloudnet.agsci.colostate.edu/) was started in 2013, with support from the US National Science Foundation, to foster a collaborative network for the advance of study in tropical montane forests and tropical montane cloud forests. CloudNet began with the premise that the effectiveness of ongoing ecological research in TMCFs is constrained by: limited cross-site study and methodological compatibility, limited integration of studies and discourse across disciplinary boundaries, and limited synthesis of current research. A primary source of these constraints is the insularity of research and collaboration in TMCFs due to the wide dispersion of research sites across the tropics and the scarcity of large-scale, comparative and multi-site studies. Hence, the central objectives of CloudNet are to foster research efforts in TMCFs across regions and investigators, to facilitate the formulation of standardized methods, cross-cutting hypotheses and broad-scale synthesis, and to initiate replicated studies of environmental and biological patterns and processes across sites. These objectives necessitate an international effort, as the key variables in TMCF ecology – climate, physiography, biogeography and ecological isolation – vary over large distances (e.g. islands vs. continental, equatorial vs. subtropics, isolated vs. clustered mountains).

Special issue

The themes and gaps in this special issue were first identified and outlined at a CloudNet-sponsored meeting 'Tropical montane cloud forest ecology: key gaps and priorities in research and coordination', held at the Colorado State University on 11–14 October 2013. During the meeting, a consensus was reached that to set the stage for future research an updated effort at synthesis was needed, and this special issue was planned to present reviews of emerging themes and topics, to highlight knowledge and research gaps, and identify the next frontiers in ecological research in TMCFs. Here, we summarize the key findings of the reviews in this special issue, place them in the wider context of TMCFs and global change, and conclude by highlighting some themes and challenges for future research and coordination.

Contributions to the special issue

In the first contribution to this special issue, Fahey *et al.* (2016) provide an assessment of the environmental drivers that make tropical montane cloud forests distinctive. At and above the altitude at which regular cloud formations occur on mountains in the humid tropics, forest canopy height and above-ground net primary productivity are much reduced from the lowlands, root-to-shoot ratio increases, leaves becomes smaller and thicker, alpha diversity drops (for most taxa), some types of epiphytes peak in abundance and diversity, and dead organic matter accumulates in the canopy, forest floor and soils (Grubb 1977, Fahey *et al.* 2016). As Fahey *et al.* (2016) note: 'the overriding role of cloud immersion in shaping this vegetation's physiognomy is emphasized by its recurrence across sites for which other environmental factors (e.g. temperature, precipitation, altitude, wind, slope, soils) exhibit wide variation; and in tropical regions with different biogeographic affinities'.

Depending on the biogeographic and climatic setting, the altitude of this vegetation pattern and its specific expression vary from mountain to mountain.

Although Fahey *et al*. (2016) emphasize the similar features of TMCFs worldwide, there is still considerable variation within and among them. Dalling *et al*. (2016) review some of the probable causes of this variation, which include parent material, substrate age, disturbance history and the species pool. Nitrogen limits growth across most TMCFs (Grubb 1977, Tanner *et al*. 1998), but Dalling *et al*. (2016) emphasize that many TMCFs are likely to be limited by multiple nutrients, and that nutrient limitation can vary over short distances in topographically diverse mountainous regions (Werner & Homeier 2015). In addition to biogeochemistry, Dalling *et al*. (2016) point to a need for a greater emphasis on understanding how soil microbial communities (especially mycorrhizas) and plant–soil feedbacks (including contributions of epiphytes) contribute to the heterogeneity and ecosystem functions of TMCFs.

Disturbance regimes are another major source of heterogeneity within and between TMCFs. Crausbay & Martin (2016) review the major natural disturbances in TMCFs, noting that some of them, such as landslides, affect TMCFs more than lowland forests. The importance of disturbances in tropical mountains is well appreciated by geomorphologists (Strecker *et al*. 2007) but, as Crausbay & Martin (2016) point out, many syntheses of the ecology and function of TMCFs have given scant attention to their disturbance regimes, even though there have been numerous studies of individual disturbances in TMCFs. Integrating an understanding of disturbance in the ecology of TMCFs will not only yield a more dynamic interpretation of them, but also will advance understanding of their resilience to human disturbance, and altered disturbance regimes resulting from climate change (e.g. fire, drought, cyclones).

Gotsch *et al*. (2016a) emphasize that the ecophysiological processes of photosynthesis and respiration are quite different in TMCFs than in lowland tropical forests, resulting in an overall lower rate of NPP in tropical mountains. The authors confirm earlier research (Shreve 1914, Gates 1969) that low NPP of TMCFs is most likely due to their distinctive environments of cooler temperatures, reduced solar radiation from persistent cloud cover and lower evaporative demand. This review shows why ecophysiological studies from tropical lowland forests are unlikely to apply in TMCFs, and that more studies across the altitudinal and biogeographic ranges are needed to understand variation among TMCFs.

Willig & Presley (2016) synthesize the concepts and evidence on the pattern of biodiversity and metacommunity structure along altitudinal gradients in TMCFs. They demonstrate that tropical mountains are notably high in diversity and endemism, have high species turnover along altitudinal gradients, and altitudinal increases in richness are restricted to amphibians while all other taxa decline. Despite variation across sites, the ecotone between lower-altitude rain forest and TMCF is always associated with changes in faunal composition, regardless of taxa. The authors conclude that an effort to collect replicated environmental and species data within and between altitudinal gradients on TMCFs is needed to enhance our mechanistic understanding of biodiversity and metacommunity structure patterns.

The contribution by Chapman *et al*. (2016) shows that seed-dispersal ecology in TMCFs differs in predictable ways from tropical lowland forests. In particular, there are strong patterns with increasing altitude; as diaspore size decreases, fleshy fruits remain the most common fruit type in TMCFs, but the quantity of wind-dispersed diaspores increases, and avian dispersers increase in importance in TMCFs compared with the role of mammalian dispersers in tropical lowland forests. Seed rain may be less diverse and density-dependent mortality may decline with increasing altitude, with implications for seedling establishment, forest structure and tree species coexistence. Small mammals tend to be most abundant at approximately middle altitudes on tropical mountains, while both birds and volant mammals may migrate annually along altitudinal gradients following food resources. The abundance of small mammals in TMCFs could shift the dispersal–predation balance in plant–rodent mutualisms, where small mammal seed predation becomes more prevalent over dispersal functions in TMCFs compared with tropical lowland forests.

Gotsch *et al*. (2016b) show how epiphytes and associated arboreal soils are ubiquitous and emergent features of TMCFs, and that they play a major role in ecosystem function. Epiphytes intercept water and nutrients from the atmosphere and can contribute significant inputs of these resources to the forest floor. The range of epiphytic biomass and associated function (e.g. water storage) in TMCFs varies greatly across sites, however, depending primarily on stand age and microclimate. Given that many epiphytes are more sensitive than trees to the limits of the cloud belt and its associated moisture (Sugden 1981), projected shifts in cloud-base heights or precipitation are likely to have a large impact on the epiphytic community, with cascading impacts on the ecosystem function of the TMCF.

Research initiatives in tropical montane cloud forests

RCN participants promulgated four new research efforts at an international, CloudNet-sponsored meeting held on 31 May–5 June 2015 in Gamboa, Panama. For interested parties, more details on how to participate can be found at http://cloudnet.agsci.colostate.edu or by contacting the leader of each initiative:

(1) CloudNet global database and meta-analysis, a global data repository for tropical montane forests. The CloudNet RCN database is a data repository of researchers, sites and studies conducted in tropical montane forests. This database is intended to facilitate cross-site comparisons and meta-analyses. Researchers who contribute published and unpublished data can access the database for meta-analyses and research. The database will archive data on forest structure, plant species composition, plant traits, soil chemistry, ecology, hydrology and climate of tropical montane forests, along with select data from lowland tropical sites that are part of large altitudinal gradients in tropical mountains. Many researchers from the TMCF community have already contributed data: currently the CloudNet database has over 170 000 measurements from individual trees sampled from over 2000 vegetation plots in 41 sites across 21 countries, and a preliminary meta-analysis is underway. If you are interested in contributing data and using the database, use the link on the CloudNet website or contact Dr Katherine Heineman (katie.heineman1@gmail.com).

(2) Plant functional traits multi-site study. We have initiated a global, multi-site study to assess variation in plant functional traits across different TMCFs, with an emphasis on cloud-affected forests. We are interested in examining trait variation across large geographic scales (i.e. Hawaiʻi vs. Peru), as well as within sites along environmental gradients (climate, land use, soil fertility, etc.). This study will address whether TMCFs are globally characterized by a similar trait composition and if the biogeographic and phylogenetic constraints that structure assemblages in TMCFs also result in important differences in ecosystem function. For example, some functional types are rare or absent in isolated TMCFs, such as those on islands where ectomycorrhizal tree species are few (e.g. oaks are prevalent in TMCFs in Mexico and Central America but are absent from TMCFs in the Greater Antilles). Absences of functional groups could render some TMCFs less resilient to global change, and possibly more susceptible to invasion (Denslow 2003). We are collating published data and collecting new data for traits that are inexpensive and easy to measure: (a) specific leaf area, (b) leaf carbon, nitrogen and phosphorus concentrations, (c) stomatal density, (d) wood density, (e) seed dispersal mode, (f) seed mass, (g) cuticular conductance following standard protocols (Pérez-Harguindeguy *et al.* 2013). This study began in 2015 and will end in 2017. If you are interested in participating in this study, contact Dr Sybil Gotsch at Franklin and Marshall College (sybil.gotsch@fandm.edu).

(3) Decomposition patterns across TMCFs. This protocol will initiate a standardized effort to evaluate decomposition rates across as many TMCFs as possible. Prior decomposition studies have been conducted in individual sites, and do not encompass the wide range in climate, soil saturation and soil fertility found across TMCFs. The protocol will allow us to greatly expand the environmental variation sampled in determining how these factors influence decomposition and detrital fluxes in TMCFs. The objectives are to: (a) determine how rates of leaf and wood decomposition vary in TMCFs with altitude, temperature, precipitation, soil nutrient availability, soil saturation and faunal access; (b) evaluate whether there is an interaction between above- vs. below-ground decomposition rates and environmental characteristics; and (c) correlate wood and foliar decomposition rates. The decomposition protocol is based on Powers *et al.* (2009), in which above- and below-ground decomposition was compared across sites, but only three sites in that study were at >1000 m asl and these were relatively dry, so much remains unknown about decomposition processes in TMCFs. TMCFs may be significantly different than other tropical forests in their decomposition and nutrient dynamics, given frequent soil saturation and high fog water inputs in these systems. This study will begin in early 2017. If you are interested in learning more and participating, email Dr Jim Dalling at the University of Illinois at Urbana–Champaign (dallingj@life.illinois.edu).

(4) Climate characterization protocol. Obtaining accurate, comparable and comprehensive climate measurements is challenging in TMCFs due to the complexity of climate in these systems and the technical challenges of measuring non-standard climate variables that are especially important in TMCFs (e.g. wind-driven rain, fog water inputs). To help characterize and determine the importance of various climate variables across TMCFs, this protocol promulgates standard methods and instruments for maximizing coverage and comparability of climate data. If you are interested in learning more and participating, email Dr Mark Mulligan at King's College London (mark.mulligan@kcl.ac.uk) and Dr Tom Giambelluca at the University of Hawaiʻi at Mānoa (thomas@hawaii.edu).

Themes for future research

Like other mountainous biomes (Sundqvist *et al.* 2013), the prospects for TMCFs to contribute to an improved understanding of community organization and patterns of biodiversity are strong, particularly patterns under pronounced climate variation. Altitudinal gradients in general are model systems to study a number of macro-ecological hypotheses ranging from the spatial structure of biodiversity (Crist *et al.* 2003, Gering *et al.* 2003, Presley & Willig 2009), patterns of species richness and range size (Rowe & Lidgard 2008, Willig *et al.* 2009), and the organization of metacommunities (Presley *et al.* 2011). Strong vertical connections develop across montane landscapes as a result of the lift of air masses and the downhill flow of water, solutes and sediments. Many ecosystem functions are affected by these connections, including biogeochemistry, hydrology, energetics, and biotic pathways and interactions. The cloud zone is well known as a hot-spot of ecosystem function – in this zone, high beta diversity and species turnover are commonly encountered (Martin *et al.* 2007), biogeochemical cycles exhibit non-linear changes (Schuur & Matson 2001), cloud stripping provides important moisture inputs during the dry season (Bruijnzeel & Proctor 1995), and total carbon storage increases as soil carbon peaks (Schuur *et al.* 2001). TMCF sensitivity to climate also makes them sentinels of climate change (Pounds *et al.* 1999).

A particular challenge to our understanding of TMCF ecology is their wide geographic distribution, and site-level variation in environment and geographic context: climate and hydrology, geology and soils, the geographic setting (e.g. distance from coast, size of mountains), biogeographic lineages of the biota, and natural and anthropogenic disturbance regimes all can generate substantial variation between TMCFs. To address these sources of variation, we propose a series of research priorities for future TMCF research: (1) atmospheric humidity and cloud immersion frequency are clearly crucial to TMCF dynamics, yet the availability of quantitative data on cloud immersion, cloud-stripping and horizontal and wind-driven precipitation is highly limited; (2) the geophysical template supporting and regulating TMCF ecosystem dynamics is inadequately characterized at most sites, especially lithological patterns, soil catenas, hydrologic flowpaths, mesotopography and mesoclimate; (3) accurate measurements of soil wetness, saturation and soil oxygen – potentially central in biogeochemical and hydrologic behaviour, and forest structure and productivity – are needed; (4) patterns of forest below-ground carbon allocation undoubtedly contribute to the TMCF forest structure patterns and processes, yet few measurements are available; (5) the profusion of epiphytes so characteristic of TMCFs has only rarely been quantified in terms of biomass, biodiversity and ecophysiology (Darby *et al.* 2016, Gotsch *et al.* 2015, Nadkarni *et al.* 2004). Given the importance of epiphytes in the composition and function of TMCFs, and in particular the critical role some types of epiphytic vegetation play in cloud-stripping (Mulligan *et al.* 2011b), improved study is needed; and (6) while surveys of biota are available for many TMCFs, more quantitative information on abundance and dynamics of key taxa, including altitudinal distributions, are needed (Safont *et al.* 2014). Key taxa could be defined according to biomass, functional distinctiveness and major radiations that are especially well represented in TMCFs with high local endemism (e.g. Cyatheaceae tree ferns; Kluge & Kessler 2006).

Future synthesis and reviews could also prioritize better integration across the research areas in this special issue. For example, it is striking that the TMCFs in which seed dispersal have been best studied (Chapman *et al.* 2016) have not been the focus of plant–soil studies (Dalling *et al.* 2016) and vice versa. Future studies in TMCFs could address the extent to which nutrient limitation of the forests at a range of scales (Dalling *et al.* 2016) determines seed size, seed crops from individual trees (Abe *et al.* 2016), and how these influence composition of the disperser communities. They could also focus on how disturbances common in TMCFs (Crausbay & Martin 2016) affect seed production and disperser communities, with subsequent feedbacks on post-disturbance forest regrowth and dynamics. For example, 4 mo after a major hurricane affected Jamaican TMCFs, bird abundance and species richness were 30% and 22% lower respectively than before the hurricane (Wunderle *et al.* 1992), but the consequences of these depletions of disperser communities for seed dispersal are unknown. Likewise, the effects of other long-term disturbances and perturbations in TMCFs, such as El Niño Southern Oscillation (ENSO) droughts, on seed production and disperser communities merit investigation.

Global change

As summarized in the Fifth Assessment Report of the IPCC (Stocker *et al.* 2013), global climatic changes – such as increasing temperatures, heat extremes, droughts, heavy precipitation events and altered precipitation patterns – are likely to become more prevalent in the coming decades. These changes will have substantial impact on TMCFs, possibly pushing forest ecosystems towards tipping points and into alternate states of vegetation cover (Field *et al.* 2014). The dynamics of TMCF ecosystems are connected to drivers at multiple scales and global change promises profound alterations of those dynamics (Bruijnzeel *et al.* 2011a, Martin *et al.* 2011). Even small changes in climatic drivers, especially those related to patterns of cloud formation (e.g. ocean circulation and temperature, regional atmospheric circulation of the Intertropical Convergence Zone (ITCZ), the trade wind inversion, and wind intensities), may have cascading ramifications for TMCFs (Foster 2001, Loope & Giambelluca 1998).

An analysis of six different general circulation models highlighted TMCFs as exceptionally vulnerable to global warming (Malcolm *et al.* 2006). There is already evidence that increased temperatures in TMCFs in the northern Andes have resulted in thermophilization of the vegetation, i.e. the colonization upslope of tree species with ranges previously centred at lower, hotter altitudes along with concurrent mortality of the resident TMCF trees, suggesting fundamental shifts in the compositional of TMCF tree communities over the long term (Duque *et al.* 2015). Pressing questions about climate change and TMCFs remain, such as how increased temperatures will alter the feedbacks between fog interception, epiphytes and soil saturation (Gotsch *et al.* 2016b).

Palaeoecological studies provide some of the best indication of how TMCFs may respond to climate change. These studies have found that, as temperatures shift, simple upslope and downslope migrations of vegetation belts have not occurred in TMCFs (Willis & Birks 2006), and that non-linear ecological responses to climate change may be common, as observed in Bolivian TMCFs (Bush *et al.* 2010). Rising cloud levels and increasing temperatures are likely to compress the areas currently occupied by TMCFs, especially where they extend to the summits of mountains. Even on tropical mountains with grasslands and alpine areas at higher altitudes into which TMCF could potentially expand, many TMCF trees seem to be unable to colonize these habitats, as found in the alpine grasslands of the Andes (Rehm & Feeley 2015). In contrast, there is palaeoecological evidence that African TMCF taxa expanded into the lowlands several times, suggesting a possible tolerance to warm temperatures (Ivory *et al.* 2016). Likewise, low plant endemism in isolated TMCFs above dry forests on the Caribbean coast of Colombia suggests that these are resilient ecosystems, colonized by long-distance dispersal from distant seed sources when climatic conditions are suitable for their formation (Sugden 1982). A 6000-y palaeoecological study in the mountains of the Dominican Republic found that shifts in the altitude of orographic cloud formation caused strong and occasionally rapid vegetation movements both up and down slope, including the disappearance and long absence of the TMCF forest type from high altitudes, pointing to the close link of TMCF distributions to regional-scale climate drivers (Crausbay *et al.* 2015).

Rising temperatures and cloud bases are just one manifestation of global climate change. Climate models also predict that tropical cyclones may become less frequent but much more intense in a warmer climate (Sobel *et al.* 2016), causing greater disturbance in TMCFs within the cyclone belts. In other tropical regions outside the cyclone belts, general increases in storm intensity could lead to altered dynamics, such as more frequent landslides. Climate change could also result in altered and more intense ENSO events that could cause soil water deficits and drought-induced diebacks in TMCFs that seldom experience them, if at all (Bruijnzeel *et al.* 1993, Kapos & Tanner 1985). More broadly, global change effects in TMCFs could include increasing numbers of biological invasions. There are invasive plants in some TMCFs currently (Bellingham *et al.* 2005, Binggeli & Hamilton 1993, Martin *et al.* 2004, Meyer 1996), but their effects on ecological processes (such as whether invasive trees support epiphyte biomass) are often unknown. The effects of invasive animals in TMCFs have received especially scant attention (but see Shiels 2011). Defaunation and extinctions in some TMCFs are also a pressing concern (Maisels *et al.* 2001), and the consequences of these for ecosystem functioning and maintenance merit more attention.

In summary, climate change and other facets of global change are likely to affect TMCFs differently worldwide, underscoring the need for a worldwide network of study sites and for the consistent measurement of variables likely to respond across them, particularly components likely to be sensitive to climate change: epiphyte biomass, composition and function (Gotsch *et al.* 2016b) and intra-seasonal variation in $\delta^{13}C$ and $\delta^{18}O$ in tree cellulose along altitudinal gradients, as was recently proposed (Hu & Riveros-Iregui 2016).

In many tropical regions (though not all, e.g. the Andes, New Guinea), mountains were the last ecosystems to be deforested for agriculture because of their infertile soils while inaccessibility provided some protection from logging. As a consequence, tropical mountains are often the best refugia of regional biodiversity and are disproportionately well represented in the tropical protected areas. Population and development pressure, however, are changing and worldwide the most direct pressure on TMCFs and the broader tropical montane ecosystem is human deforestation and fragmentation. Studies of forest fragmentation are a major focus in the lowland tropics (Laurance *et al.* 2011) and have been conducted in some TMCFs (Tabarelli *et al.* 1999, Williams-Linera *et al.* 1995); more will be needed to understand the consequences as deforestation continues. Conversely, secondary succession after previous clearance in some tropical montane regions provides new forest cover (Aide *et al.* 2013, Chai & Tanner 2011, Martin *et al.* 2004) and we need more study to understand the extent to which these secondary TMCFs provide valuable habitat and ecosystem services (Chazdon 2014) or are severely impoverished compared with original forests (Barlow *et al.* 2016).

Conclusion

In response to these and other issues in the lowland tropics, the past few decades have seen significant investment in permanent plots and research sites in lowland tropical forests (e.g. the CTFS plot network, www.ctfs.si.edu). Yet, only two sites in TMCFs (Ngel Nyaki in Nigeria and Laupāhoehoe in Hawai'i) are so far included in the CTFS network. More are needed, spread across the biogeographic range of TMCFs. The very factors – remoteness, inaccessibility by roads, and steep topography – that have protected many TMCFs make establishment of permanent plots and some experimental investigations in them logistically challenging and expensive, making organized support and guidance all the more essential.

As direct and indirect human pressure on the integrity of tropical montane ecosystems continues to increase, the urgency of efforts to characterize, understand and protect TMCFs grows apace (Bruijnzeel *et al*. 2011b). The study of tropical montane ecosystems has come a long way since its first international meeting in 1993 and today there is momentum to build on this progress. CloudNet provides an opportunity to improve collaboration between investigators across biogeographic and environmental gradients, and to provide a focus for ongoing, empirically driven research of tropical montane ecosystems.

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IN MEMORIAM: FREDERICK SCATENA 1954–2013

This special issue is dedicated to the memory of Fred Scatena, a founder of the Luquillo Long-Term Ecological Research Program and a leader in ecological research in tropical montane cloud forests. His many contributions included an ability for synthesis and generating new ideas to solve challenges, but his greatest gift was his generosity. Fred was the consummate collaborator and mentor. All who knew him were impressed by his graciousness and passion for working with others to advance the ecology and conservation of tropical forests.

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