DOI: 10.1111/jbi.13228

RESEARCH PAPER

WILEY Journal of Biogeography

Will climate change shift the lower ecotone of tropical montane cloud forests upwards on islands?

Robin Pouteau[1] | Thomas W. Giambelluca[2] | Claudine Ah-Peng[3] | Jean-Yves Meyer[4]

[1]Institut Agronomique néo-Calédonien, Nouméa, New Caledonia

[2]University of Hawai'i at Mānoa, Honolulu, HI, USA

[3]UMR PVBMT, Université de La Réunion, Saint-Denis, La Réunion, France

[4]Délégation à la Recherche, Government of French Polynesia, Papeete, French Polynesia

Correspondence
Robin Pouteau, Institut Agronomique néo-Calédonien, Centre IRD de Nouméa, Nouméa, New Caledonia.
Email: robin.pouteau@ird.fr

Editor: Matt McGlone

Abstract

Aim: Island tropical montane cloud forests (TMCFs) host a disproportionally high share of the global biodiversity and provide critical ecosystem services to vulnerable insular societies. However, this ecosystem is imperilled by anthropogenic impacts including climate change that might push TMCFs towards higher elevations. The elevation at which TMCFs start varies greatly among islands and may depend on topographically driven local climate, which may in turn be influenced by large-scale climate. Thus, a necessary prerequisite to assessing the vulnerability of island TMCFs to climate change is to determine the role of island features versus regional climate in influencing local climate at the lower TMCF ecotone.

Location: Tropical islands.

Methods: An extensive literature review of the elevation at which island TMCFs start was undertaken. This elevation was modelled as a function of the altitude of the lifting condensation level (LCL) imposed by regional climate, island maximum elevation and upwind forest loss over the past 15 years.

Results: The elevation of the lower TMCF boundary was found to have been reported for 93 islands worldwide. TMCFs starts from as low as 300 m on the small islands of Kosrae (Micronesia; maximum elevation = 628 m) and Aneityum (Vanuatu; 852 m) to a maximum of 1,600 m on the large islands of Cuba (1,974 m) and Hispaniola (3,175 m), providing a spectacular example of the 'Massenerhebung effect'. Both regional climate (LCL altitude) and island features (maximum elevation) influenced the elevation of the lower TMCF boundary, and these variables together accounted for 79% of the variance.

Main conclusions: On islands, climate change is likely to cause significant but small upslope shifts of the LCL and subsequently of TMCF lower boundary elevation in the future (+4.4 m for each 1°C increase in temperature). TMCF clearing and biological invasions might appear to be more pressing threats.

KEYWORDS

Climate change, environmental correlates, island biogeography, island conservation, Massenerhebung effect, montane ecosystems, mountain mass elevation effect, telescoping effect

1 | INTRODUCTION

Tropical montane "cloud forests" (TMCFs) sensu Hamilton, Juvik, and Scatena (1995), also called "elfin woodlands" (Beard, 1949), "mossy forests" (Gleason & Cook, 1927) or "upper montane and subalpine forest" (Richards, 1952) are forest ecosystems of tropical mountains (Hamilton et al., 1995). Despite their relatively small spatial extent worldwide (1.4% of global tropical forest area; Bruijnzeel, Mulligan, & Scatena, 2011), TMCFs provide critical benefits to human society by capturing, storing and transporting water, protecting soils against erosion and acting as biodiversity reservoirs (Doumenge, Gilmour, Pérez, & Blockhus, 1995). TMCFs found on islands are of critical importance as they host a disproportionally high share of the global biodiversity (Irl et al., 2017), and provide vital ecosystem services to highly vulnerable insular populations (one-third of the world's population) (Ah-Peng et al., 2017).

Tropical montane "cloud forests" are globally under an increasing threat from human population pressures associated with deforestation, resource overexploitation and biological invasions, which push the lower TMCF boundary upward (Aldrich, Billington, Edwards, & Laidlaw, 1997; Doumenge et al., 1995). TMCFs, especially those on islands (Loope & Giambelluca, 1998), may also be among the most sensitive of the world's ecosystems to climate change (Foster, 2001; Hu & Riveros-Iregui, 2016; Oliveira, Eller, Bittencourt, & Mulligan, 2014; Still, Foster, & Schneider, 1999). Islands are expected to experience, on average, an increase in mean annual temperature ranging from 1.3 to 2.8°C by the end of the century (Harter et al., 2015), which may favour the "invasion" of island TMCFs by better competitors from lower elevation with higher leaf area index and higher optimum temperature for photosynthesis (Allen & Ort, 2001; Bruijnzeel et al., 2011). Despite severe threats to island TMCFs, little is known about this critical ecosystem. Thus, a better knowledge of their ecology would facilitate better conservation and maintenance of the benefits provided by this ecosystem to island societies (Hu & Riveros-Iregui, 2016).

Island TMCFs provide a spectacular example of the "Massenerhebung", "telescoping" or "mountain mass elevation" effect. This phenomenon refers to the occurrence of physiognomically and floristically similar vegetation types at higher elevations on large mountains compared with those on small outlying mountains (Grubb, 1971; Richards, 1952). The Massenerhebung effect remains poorly understood, but some explanations of the phenomenon have involved: (1) cloud formation on isolated peaks that increases humidity and reduces insolation (Bruijnzeel, Waterloo, Proctor, Kuiters, & Kotterink, 1993); (2) lower diurnal and annual temperature amplitudes on islands compared to continents because of the buffering effect of the ocean (Leuschner, 1996); and (3) steeper lapse rates over lowlands than over large mountain masses (Forster, 1982). Although the Massenerhebung effect has become a paradigm in biogeography (Bruijnzeel et al., 1993; Flenley, 1995; Grubb, 1971), no quantitative assessments have been undertaken until lately (Irl et al., 2016; Zhao et al., 2015), and a quantitative assessment focusing on island TMCFs remains missing.

Land use in lowlands is also thought to influence cloudiness and thus TMCFs in adjacent mountains (Nair et al., 2003). It has been shown from satellite imagery that deforested areas of Costa Rica's Caribbean lowlands remain more frequently cloud-free than forested regions, which have well-developed dry season cumulus cloud fields (Lawton, Nair, Pielke, & Welch, 2001). Furthermore, regional atmospheric simulations showed that the lifting condensation level (LCL, the level where rising air cools to the dew point temperature) is higher over pasture than over tropical forest areas. Despite evidence that clearing tropical forest can alter the climate of downwind areas, interactions of land cover change with local and regional circulation in shaping favourable climatic conditions for TMCFs remain poorly understood.

In addition to their effects on the lower TMCF boundary, island characteristics might also play a role in determining the tree line elevation on tropical islands. Recently, a global survey suggested that, in addition to local influences, tree line would also be shaped by large-scale thermal limitation as tree lines occur at lower elevations poleward (Irl et al., 2016). However, the relationship between temperature and tree line elevation is not significant within the tropics, perhaps because of low seasonal variation of temperature (Körner, 1998). Rainfall has also been shown to have a negative effect on tree line elevation with the highest tree lines occurring in relatively dry regions (Paulsen & Körner, 2014). On the other hand, tree lines may sometimes not be actual thermal ecotones, rather their elevation may be restricted by decreased moisture availability due to the presence of the trade wind inversion layer (Leuschner, 1996). In contrast, relatively high humidity and cloud immersion are recognized to have a positive effect on trees within TMCFs (Cavelier, Tanner, & Santamaría, 2000; Crausbay, Frazier, Giambelluca, Longman, & Hotchkiss, 2014; Fahey et al., 2015; Hu & Riveros-Iregui, 2016). As a result, tree line research provides only inconclusive and conflicting inferences on how regional climate and the local Massenerhebung effect drive the elevational distribution of island TMCFs. Although the lower TMCF ecotone is known to be gradual across space compared to tree line and, therefore, not as clear as a bio-indicator, research on the lower TMCF boundary remains needed because it is highly imperilled by anthropization, invasive species and climate change.

Islands offer a well-suited natural laboratory for such a biogeographical study because they are "discrete, internally quantifiable, numerous and varied entities" with different surface area, isolation, height, etc. (Whittaker & Fernández-Palacios, 2007). In order to assess the vulnerability of island TMCFs to climate change, the environmental correlates for TMCF distribution should be determined (Morelli et al., 2016). Local climate conditions are certainly playing some role in determining the elevation of the lower TMCF boundary. For instance, the frequent cloud immersion, which is a prerequisite to support TMCFs, is climatically determined (Hu & Riveros-Iregui, 2016). The zone of frequent cloud contact on a mountain slope is delimited by the LCL on the lower end and, for some tropical islands, the trade wind inversion on the upper end (Oliveira et al., 2014; Still et al., 1999). The question then arises as to how island features affect the local elevational gradients of relevant climate variables. This is a critical question to address in order to determine whether climate change threatens island TMCFs and, if so, how. If the elevation of the lower TMCF boundary can be predicted on the sole basis of "static" island features (e.g. as expected by the Massenerhebung effect), climate change is unlikely to cause major distributional shifts of TMCFs in the future. In contrast, if the elevation of the lower TMCF boundary is mostly driven by already changing global climatic conditions, appropriate adaptation and mitigation strategies should be adopted rapidly.

2 | MATERIALS AND METHODS

2.1 | Response variable

An extensive literature review of the lower TMCF ecotone on all oceanic and continental islands (>1 km² and <800,000 km²) situated between the tropics (23°26′ north and south of the equator) was undertaken. The reported elevation of the same lower TMCF ecotone was sometimes found to vary between references (e.g. on Aneityum (Vanuatu), 300 m according to Mueller-Dombois and Fosberg, 1998 vs. 500 m according to Schmid, 1975). When reported limits did not match among several references, the reference or alternatively the author (of several references) referring to the highest number of islands was given preference in order to promote between-islands consistency. Mueller-Dombois and Fosberg (1998) was the most exhaustive reference with mention of 23 islands followed distantly by Meyer (2010) and Bruijnzeel et al. (2011) with mention of seven and six islands, respectively. If several references provided different values and referred to the same number of islands, the reference providing the lowest value of TMCF elevation was preferred as we assumed that the other author(s) may have missed lower elevation TMCF sites (usually on an island's windward side). When the ecotone was given as a range (e.g. "the vegetation graded abruptly into a Metrosideros–Weinmannia–Kermadecia (Proteaceae) cloud forest at 400–500 m altitude"; Mueller-Dombois & Fosberg, 1998), the mid-range (450 m in this example) was used. When different lower TMCF elevations were given for leeward and windward slopes of an island, the mid-range was also used.

2.2 | Explanatory variables

The predictive power of three island attributes was tested: (1) mean LCL altitude imposed by regional climate; (2) maximum elevation, considered to be a proxy of the local Massenerhebung effect (Irl et al., 2016); and (3) forest loss between 2000 and 2014 as the lower TMCF ecotone might be shaped by direct deforestation or might at least be locally affected by upwind deforestation through an increase of the orographic cloud bank altitude (Lawton et al., 2001; Nair et al., 2003) (Table 1). Mean LCL altitude was calculated through the Lawrence's formula $H_{LCL} = (20 + 0.2 * T).(100\text{-RH})$ where H_{LCL} is the LCL altitude in metres, T the sea-level air temperature in degrees Celsius and RH the sea-level relative humidity in per cent (Lawrence, 2005). Mean annual temperature was based on the WorldClim dataset (BIO1; Hijmans et al., 2005) and taken from the comprehensive global environmental characterization of the world's islands published by Weigelt, Jetz, and Kreft (2013). Mean annual relative humidity was extracted from the global map published by the Climate Research Unit of the University of East Anglia (available at https://nelson.wisc.edu/sage/data-and-models/atlas/data.php?incdataset=Average%20Annual%20Relative%20Humidity). Island boundaries were derived from the shapefile of the Global Administrative Areas database (available at http://www.gadm.org/version1). Maximum island elevation was extracted from the Island Directory of the United Nations Environment Programme (available at http://islands.unep.ch/isldir.htm; Dahl, 1991). The forest cover loss in the period 2000–2014 was extracted for each island from a global diachronic analysis of Landsat satellite imagery based on decisions trees (available at https://storage.googleapis.com/earthenginepartners-hansen/GFC2015/loss.txt; Hansen et al., 2013). This map with an initial resolution of 30 m at the equator has been resampled to 300 m using a majority resampling to facilitate computation. Finally, as TMCFs may have changed between publication of the oldest references used to estimate the elevation of the lower TMCF boundary (as early as 1945) and today, publication date was added as an additional variable in the model (Table 1).

2.3 | Statistical analyses

Island attributes were tested for multicollinearity by computing a correlation matrix based on Pearson's r. Cross-correlations did not exceed $|r| = .45$ (between LCL altitude and maximum elevation), which is below the threshold of $|r| = .70$ from which collinearity begins to severely distort model estimations (Dormann et al., 2013). Square root and logarithmic transformations were applied if transformed variables performed better at fitting TMCF elevation in pairwise correlations than original variables. Then, the lower limit of TMCFs was modelled as a function of the four independent variables (LCL altitude, maximum elevation, forest cover loss and publication date). Linear mixed-effect models were used to account for the fact that, in the absence of clearly defined bio-indicator, the lower TMCF ecotone remains author-specific and to control for any bias due to the unbalanced number of islands, an author referred to (authors were included as the random effect) using the 'lmerTest' package (Kuznetsova, Brockhoff, & Christensen, 2017) developed in R (R Development Core Team, 2017). The level of significance of each significant predictor in the full model was examined. The relative importance of each significant predictor was measured with the sum of Akaike weights of all possible combinations of variables using the R package 'MuMIn' (Bartoń, 2018). The performance of the full model (r^2) was evaluated using the 'sjstats' package (Lüdecke, 2017). Analyses were performed for all islands together, then on oceanic (i.e. not connected to mainland during the Last Glacial Maximum)

TABLE 1 Summary of the independent variables used to explain the elevation of the lower tropical montane cloud forest ecotone on 93 oceanic and continental islands. Transformations (Transf.) used for improving model fitting on the basis of the highest explanatory power in an a priori univariate test are given: no transformation (None), logarithmic (Log) or square root (√). We set significance levels of variables in the linear mixed-effect model with .050 > p ≥ .010*, .010 > p ≥ .001**, P < .001***

Variable	Unit	Min. value	Max. value	Transf.	*p*-value	Importance
Oceanic and continental islands						
LCL altitude	m	324	841	None	*	0.65
Max. elevation	m	417	5,030	√	***	1.00
Forest loss	ha	0	108,499	√	.39	—
Publication date	—	1945	2015	None	.48	—
Oceanic islands						
LCL altitude	m	324	815	None	.14	—
Max. elevation	m	417	4,169	√	***	1.00
Forest loss	ha	0	23,630	√	.41	—
Publication date	—	1945	2015	None	.38	—
Continental islands						
LCL altitude	m	377	841	Log	.28	—
Max. elevation	m	940	5,030	None	.23	—
Forest loss	ha	47	108,499	Log	.27	—
Publication date	—	1949	2015	None	.65	—

and continental islands (i.e. connected) separately. Geological history was taken from Weigelt et al. (2013) who assumed a sea level at 18,000 year BP of 122 m below the present level.

3 | RESULTS

A total of 47 references reporting the elevation of the lower TMCF boundary for 93 islands, including 84 oceanic islands and 9 continental islands, were considered. Sampled islands included 44 islands situated in the Pacific Ocean, 18 in the Atlantic Ocean, 10 in the Indian Ocean, and 21 in-between the Pacific and Indian Oceans (Bismark and Malay archipelagos) (Figure 1; see Appendix S1 in Supporting Information). The most studied archipelagos comprised the Malay archipelago (17 islands) followed by the Caribbean (15), and the Hawaiian and Marquesas Islands (6). The lower boundary of TMCFs was reported from as low as 300 m, on the islands of Kosrae, Federated States of Micronesia (culminating at 628 m) and Aneityum, Vanuatu (852 m) to as high as 1,600 m on the islands of Cuba (1,974 m) and Hispaniola (shared by the Dominican Republic and Haiti, 3,175 m). Oceanic and continental islands were found to exhibit similar maximum elevation (Wilcoxon test; p = 1.00) and similar TMCF lower elevation (p = .45).

When considering oceanic and continental islands together, the lower TMCF ecotone was found to be primarily influenced by maximum island elevation then by LCL altitude imposed by regional climate (Table 1). Together, these two variables explained 79% of the variance in the elevation at which TMCFs start. By contrast, forest loss and publication dates were found to have no significant effect on the lower elevation of TMCF reported by the authors (Table 1). When oceanic islands were taken separately, maximum elevation remained highly significant but not LCL altitude (Table 1), while no variables were found to be significant with regard to the nine continental islands taken separately (Table 1).

The square root relationship found between the lower TMCF elevation and the maximum island elevation means that the increase in lower TMCF elevation will be steeper on low-elevation islands than on high-elevation islands. As a result, the variation in lower TMCF elevation will be similar (*c.* 100 m) between two islands below 1,000 m with an elevation difference of 250 m and two islands beyond 4,000 m high with an elevation difference of 500 m (Figure 2). In contrast, the elevation of the lower TMCF boundary was linearly and positively correlated with LCL altitude. According to Lawrence's equation linking LCL altitude with sea-level air temperature and sea-level air relative humidity (assumed constant), the upward migration of the lower TMCF ecotone will be, on average, 4.4 ± 0.8 m/°C on the 93 tropical islands.

4 | DISCUSSION

4.1 | Effect of regional LCL altitude on TMCFs

Tropical islands feature a diversity of geographic, topographic and climatic characteristics that provided the opportunity to disentangle the drivers of the elevation at which TMCF lower boundaries occur. This response variable was found to be significantly related to the LCL, or at least to the level where fog presence meets or exceeds some critical frequency of occurrence, which would in turn be related to air temperature and relative humidity (Oliveira et al., 2014; Still et al., 1999). On Taiwan, the elevational pattern of montane plant species even appears primarily determined by interaction between the northeast monsoon and topography, rather than by the Massenerhebung effect (Chiou et al., 2010). The need for further research to address the influence of LCL seasonality and periodic drying events such as those induced by El Niño remains as TMCFs are recognized to be particularly responsive to such climate extrema (Crausbay et al., 2014).

4.2 | The Massenerhebung effect on TMCFs

Maximum island elevation also largely explains the variation in the tropics-wide pattern of the lower TMCF elevation on islands, and this is particularly apparent on oceanic islands. With increasing island elevation, the 3D land area increases due to the cone-shaped geometry of most oceanic islands. Thus, large land areas warm more intensely with solar radiation than surrounding air masses, leading to local

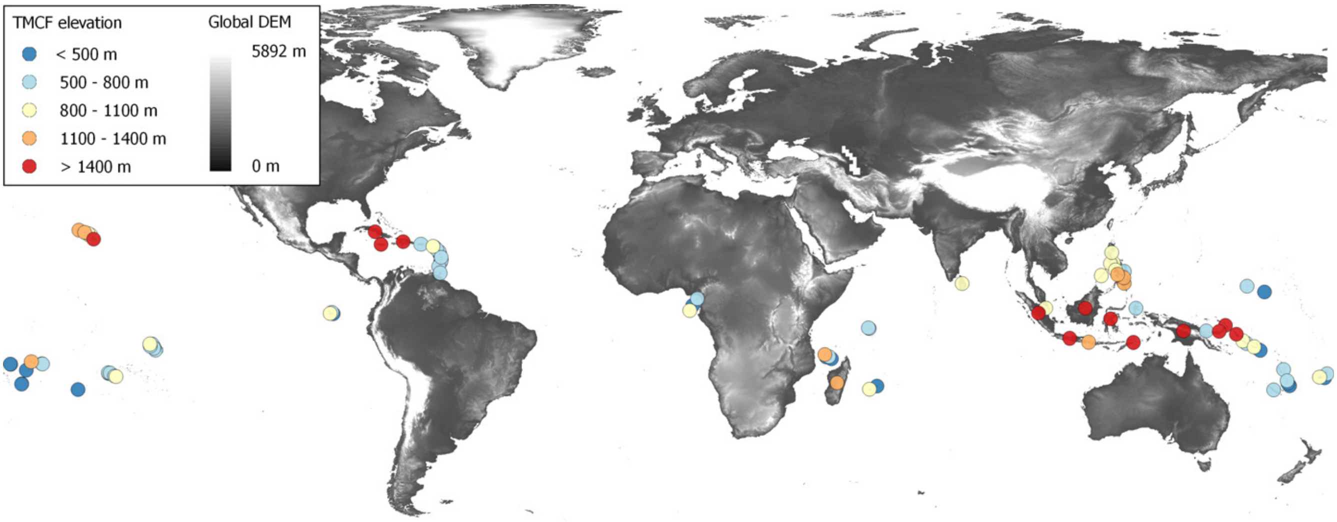

FIGURE 1 Distribution of 93 tropical islands on which the lower elevational limit of montane cloud forest has been found to be reported in the literature

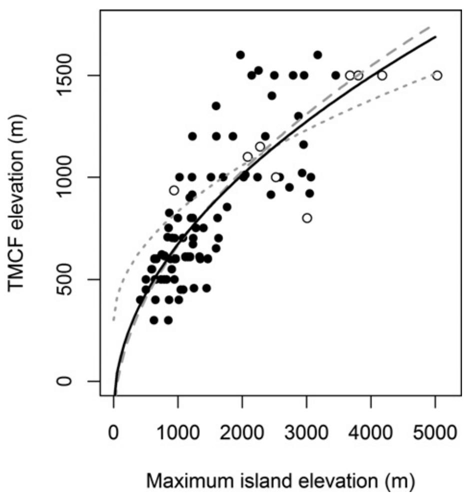

FIGURE 2 The lower elevational limit at which tropical montane cloud forest (TMCF) occurs as a function of maximum island elevation of 84 oceanic islands (black points) and 9 continental islands (white points). Lines are univariate square root models based on all 93 oceanic and continental islands together (solid black line), on oceanic islands only (dashed grey line) and on continental islands only (dotted grey line)

climatic conditions favourable for a higher elevation TMCF (Körner, 2012). This first quantitative assessment of the Massenerhebung effect using TMCF as a model system provides evidence that the lower TMCF boundary elevation does not rise linearly with maximum island elevation, but increases more rapidly on low-elevation islands than on high-elevation islands. This is consistent with results from Irl et al. (2016), who also found the square root transformation was the best-fitting transformation for tree line elevation on tropical islands.

Warming of the air over land causes the LCL to shift higher, because the warmer air does not necessarily have compensating higher water vapour content (Körner, 2012). Such a warming can, therefore, cause the relative humidity of air approaching a mountain slope to be lower, hence, requiring more lifting to cool it to the dew point temperature. The differences in the lower TMCF elevation related to temperature at sea level might reflect some effect of heating of the rising air by the land, especially for islands (during the day, air warms up more and more as it passes over land). This would cause the LCL to be higher on larger mountains, on which air would travel farther over land to get to a given elevation. Island to island variation in this effect could be explained by differences in lowland moisture availability, for example, because of land cover effects, which are thought to affect LCL elevation in tropical mountains (Lawton et al., 2001; Nair et al., 2003).

4.3 | Effect of deforestation on TMCFs

Previous studies have indeed shown that lowland forest loss can alter cloudiness on nearby mountains and thus the elevation at which TMCFs start (Lawton et al., 2001; Nair et al., 2003). Here, deforestation estimated from detection of change in satellite imagery within the period 2000–2014 was used to measure this phenomenon. Surprisingly, the variable did not have a significant effect on the elevation of the lower TMCF ecotone in any multivariate models. At least three assumptions can be made to explain this result: (1) elevations reported in the literature arise from natural rather than anthropogenic processes on a majority of islands; (2) the published information about TMCF elevation often have been based on observations made prior to the clearing; or (3) the data source we selected offered a unique opportunity to measure forest loss at a tropics-wide scale based on a single standardized metric, but there is a temporal mismatch between upwind forest loss and its effect on the elevation at which TMCF starts. Even though the considered time lapse (2000–2014) covers the publication date of many studies reporting TMCF limits (38% and 72% being 5 years on either side of the period), the time required for the effects of clearing to become apparent is probably of several decades or longer.

4.4 | Possible climate change implications

Ice core records have provided evidence of vertical migration of montane vegetation of hundreds of metres since the late glacial stage in South America (Thompson et al., 1995, 1998). General circulation models (GCMs) also project an increase in LCL altitude of hundreds of metres in Central America as a consequence of increasing global temperatures over the next decades, and such changes would result in a shift of the same order of magnitude of the current elevation at which TMCFs start (Still et al., 1999). In our study, we demonstrated that, across tropical islands, this elevation will only shift about 4.4 m higher for each 1°C increase in air temperature. Over large land areas, relative humidity can decrease with warming and, hence, larger increases in LCL height are possible. In contrast, over relatively small islands presumably with no significant change in relative humidity, the rise in LCL with warming will be much smaller.

Assuming that air temperature decreases by *c.* 0.6°C per 100 m increase in elevation on tropical islands, the lower TMCF elevation would have been expected to occur 167 m higher in a +1°C scenario if we considered temperature as the sole driving force (Baruch & Goldstein, 1999; Loope & Giambelluca, 1998). This great difference (+4.4 m vs. + 167 m) demonstrates the importance of identifying the appropriate drivers of TMCF elevation (LCL) rather than proxies of them (air temperature), which do not necessarily covary linearly to produce realistic scenarios. Our upward shift of 4.4 m/°C is an order of magnitude smaller than upward shifts observed in continental tropical areas: e.g. 50 to 83 m/°C estimated for 38 Andean tree genera based on forest plots re-censused after an average of 4 years (Feeley et al., 2011), or in subtropical islands: e.g. 360 m/°C measured for 24 montane plant species on the subtropical island of Taiwan based on century-old occurrence records (Jump et al., 2012).

But vulnerability of TMCFs cannot be fully evaluated without considering direct causes of habitat alteration: if imminent threats to TMCFs are not correctly managed, longer term climate change adaptation strategies will inevitably be useless. It was estimated that forests on the Comoro Islands were lost at a rate of 9.3% per year during 2000–2010, one of the world's highest rate of deforestation (FAO, 2010). There, resilience to climate change is perhaps not the most extremely pressing issue, but rather a "second ranking priority", behind the cutting of trees for construction wood and the extension of the agricultural frontier, driven by unproductive agricultural systems, a high population growth rate, poverty, a lack of economic alternatives and uncertain land tenure (Bourgoin, Parker, Martínez-Valle, Mwongera, & Läderach, 2016).

Moreover, Invasive alien species are one of the main drivers of biodiversity loss on islands, with dramatic impacts on certain TMCF endemic biota (Kueffer et al., 2010; Russell, Meyer, Holmes, & Pagad, 2017; Tershy, Shen, Newton, Holmes, & Croll, 2015; Vitousek, 1988). Invasive species often benefit from competitive advantages and the lack of natural predators on islands, while many island endemic species show lower competitive capabilities and lower growth plasticity (Loope & Mueller-Dombois, 1989). As a result, inherent characteristics of island ecosystems such as low species richness and low number of species in certain taxonomic lineages or with certain functional traits in comparison with continents provide opportunity for invasive species to take advantage of vacant niches and unused resources (Denslow, 2003).

5 | CONCLUSION

On tropical islands, the elevation at which TMCFs start is determined by both static island features (the Massenerhebung effect) and regional climate (the temperature-dependent LCL altitude). We have demonstrated that climate change is likely to cause significant but small upslope shifts of the LCL and subsequently of TMCF lower boundary elevation in the future (+4.4 m for each 1°C increase in temperature). This finding suggests that, on islands, climate change might not represent the most significant risk to TMCFs in the short-to mid-term, and that other issues like TMCF clearing and biological invasions perhaps are more pressing. However, notwithstanding the seemingly small upward shift in the TMCF lower boundary with projected warming, significant losses of rare endemic plants and animals are likely to occur in TMCFs currently surviving on isolated peaks with limited vertical range. In this context, it is urgently needed to reinforce and better orchestrate research on the biota, the functioning and the threats to island TMCFs and their interactions as well as to develop innovative solutions in cooperation with local governments and NGOs.

ACKNOWLEDGEMENTS

We thank Christopher J. Still (Oregon State University, USA), Valentin Duflot (LACy lab, University of La Réunion) and three anonymous referees for their insightful comments and suggestions on an earlier version of the manuscript. We also acknowledge ENVRI+ and OMNCG (Clever 2) for support to Thomas W. Giambelluca for a multidisciplinary access to La Réunion platform (OSU-R).

ORCID

Robin Pouteau http://orcid.org/0000-0003-3090-6551

REFERENCES

Ah-Peng, C., Cardoso, A. W., Flores, O., West, A., Wilding, N., Strasberg, D., & Hedderson, T. A. (2017). The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. *Journal of Hydrology*, *548*, 665–673. https://doi.org/10.1016/j.jhydrol.2017.03.043

Aldrich, M., Billington, C., Edwards, M., & Laidlaw, R. (1997). Tropical montane cloud forests: an urgent priority for conservation. *WCMC Biodiversity Bulletin*, *2*, 1–14.

Allen, D. J., & Ort, D. R. (2001). Impacts of chilling temperatures on photosynthesis in warm-climate plants. *Trends in Plant Science*, *6*, 36–42. https://doi.org/10.1016/S1360-1385(00)01808-2

Bartoń, K. (2018). Multi-model inference. Retrieved from: https://cran.r-project.org/web/packages/MuMIn/index.html

Baruch, Z., & Goldstein, G. (1999). Leaf construction cost, nutrient concentration, and net CO2 assimilation of native and invasive species in Hawaii. *Oecologia*, *121*, 183–192. https://doi.org/10.1007/s004420050920

Beard, J. S. (1949). *The natural vegetation of the Windward and Leeward Islands*. London: Oxford University Press.

Bourgoin, C., Parker, L., Martínez-Valle, A., Mwongera, C., & Läderach, P. (2016). A spatially explicit assessment of climate change vulnerability in the agricultural sector of the Union of the Comoros. Working Paper No. 186. Copenhagen, Denmark: CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS).

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

Bruijnzeel, L. A., Waterloo, M. J., Proctor, J. K. A. T., Kuiters, A. T., & Kotterink, B. (1993). Hydrological observations in montane forests on Gunung Silam, Sabah, Malaysia, with special reference to the "Massenerhebung" effect. *Journal of Ecology*, *81*, 145–167. https://doi.org/10.2307/2261231

Cavelier, J., Tanner, E., & Santamaría, J. (2000). Effect of water, temperature and fertilizer on soil nitrogen net transformations and tree growth in an elfin cloud forest of Colombia. *Journal of Tropical Ecology*, *16*, 83–99. https://doi.org/10.1017/S0266467400001280

Chiou, C. R., Song, G. Z. M., Chien, J. H., Hsieh, C. F., Wang, J. C., Chen, M. Y., … Chen, T. Y. (2010). Altitudinal distribution patterns of plant species in Taiwan are mainly determined by the northeast monsoon rather than the heat retention mechanism of Massenerhebung. *Botanical Studies*, *51*, 89–97.

Crausbay, S. D., Frazier, A. G., Giambelluca, T. W., Longman, R. J., & Hotchkiss, S. C. (2014). Moisture status during a strong El Niño explains a tropical montane cloud forest's upper limit. *Oecologia*, *175*, 273–284. https://doi.org/10.1007/s00442-014-2888-8

Dahl, A. L. (1991). Island directory – UNEP Regional Seas Directories and Bibliographies 35, Nairobi.

Denslow, J. S. (2003). Weeds in paradise: thoughts on the invasibility of tropical islands. *Missouri Botanical Garden Press*, *90*, 119–127. https://doi.org/10.2307/3298531

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Münkemüller, T. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Doumenge, C., Gilmour, D., Pérez, M. R., & Blockhus, J. (1995). Tropical montane cloud forests: conservation status and management issues. In: L. S. Hamilton, J. O. Juvik & F. N. Scatena (Eds.), *Tropical montane cloud forests* (pp. 24–37). New York, NY: Springer.

Fahey, T. J., Sherman, R. E., & Tanner, E. V. (2015). Tropical montane cloud forest: environmental drivers of vegetation structure and ecosystem function. *Journal of Tropical Ecology*, *32*, 355–367.

FAO. (2010) *Évaluation des Ressources Forestières Mondiales 2010. Rapport National : Comores*. Report #FRA2010/044. Food and Agriculture Organization of the United Nations, Rome, Italy.

Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., … Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography*, *38*, 783–791. https://doi.org/10.1111/j.1365-2699.2010.02444.x

Flenley, J. R. (1995). Cloud forest, the Massenerhebung effect, and ultraviolet insolation. In: L. S. Hamilton, J. O. Juvik & F. N. Scatena (Eds.), *Tropical montane cloud forests* (pp. 150–155). New York, NY: Springer.

Forster, R. M. (1982) A study of the spatial distribution of bryophytes on Rakata. In: The Krakatoa Centenary Expedition. University of Hull, Geography Department, Miscellaneous Series No. 25, pp. 103-126.

Foster, P. (2001). The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews*, *55*, 73–106. https://doi.org/10.1016/S0012-8252(01)00056-3

Gleason, H. A., & Cook, M. T. (1927). Plant Ecology of Porto Rico. Vol. 7 of Scientific Survey of Porto Rico and the Virgin Islands (N. Y. Acad. Sci.).

Grubb, P. J. (1971). Interpretation of the Massenerhebung effect on tropical mountains. *Nature*, *229*, 44–45. https://doi.org/10.1038/229044a0

Hamilton, L. S., Juvik, J. O., & Scatena, F. N. (Eds.) (1995). *Tropical montane cloud forests*. New York: Springer.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., … Kommareddy, A. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*, 850–853. https://doi.org/10.1126/science.1244693

Harter, D. E., Irl, S. D., Seo, B., Steinbauer, M. J., Gillespie, R., Triantis, K. A., … Beierkuhnlein, C. (2015). Impacts of global climate change on the floras of oceanic islands – projections, implications and current knowledge. *Perspectives in Plant Ecology, Evolution and Systematics*, *17*, 160–183. https://doi.org/10.1016/j.ppees.2015.01.003

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/(ISSN)1097-0088

Hu, J., & Riveros-Iregui, D. A. (2016). Life in the clouds: are tropical montane cloud forests responding to changes in climate? *Oecologia*, *180*, 1061–1073. https://doi.org/10.1007/s00442-015-3533-x

Irl, S. D., Anthelme, F., Harter, D. E., Jentsch, A., Lotter, E., Steinbauer, M. J., & Beierkuhnlein, C. (2016). Patterns of island treeline elevation – a global perspective. *Ecography*, *39*, 427–436. https://doi.org/10.1111/ecog.01266

Irl, S. D., Schweiger, A. H., Medina, F. M., Fernández-Palacios, J. M., Harter, D. E., Jentsch, A., … Beierkuhnlein, C. (2017). An island view of endemic rarity – Environmental drivers and consequences for nature conservation. *Diversity and Distributions*, *23*, 1132–1142. https://doi.org/10.1111/ddi.12605

Jump, A. S., Huang, T. J., & Chou, C. H. (2012). Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. *Ecography*, *35*, 204–210. https://doi.org/10.1111/j.1600-0587.2011.06984.x

Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, *115*, 445–459.

Körner, C. (2012). *Alpine treelines: functional ecology of the global high elevation tree limits*. Basel: Springer. https://doi.org/10.1007/978-3-0348-0396-0

Kueffer, C., Daehler, C. C., Torres-Santana, C. W., Lavergne, C., Meyer, J. Y., Otto, R., & Silva, L. (2010). A global comparison of plant invasions on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics*, *12*, 145–161. https://doi.org/10.1016/j.ppees.2009.06.002

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. (2017). lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of the lme4 package). Retrieved from: https://cran.r-project.org/web/packages/lmerTest/index.html

Lawrence, M. G. (2005). The relationship between relative humidity and the dew point temperature in moist air: a simple conversion and applications. *Bulletin of the American Meteorological Society*, *86*, 225–233. https://doi.org/10.1175/BAMS-86-2-225

Lawton, R. O., Nair, U. S., Pielke, R. A., & Welch, R. M. (2001). Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science*, *294*, 584–587.

Leuschner, C. (1996). Timberline and alpine vegetation on the tropical and warm-temperate oceanic islands of the world: elevation, structure and floristics. *Vegetatio*, *123*, 193–206. https://doi.org/10.1007/BF00118271

Loope, L. L., & Giambelluca, T. W. (1998). Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. *Climatic Change*, *39*, 503–517. https://doi.org/10.1023/A:1005372118420

Loope, L. L., & Mueller-Dombois, D. (1989). Characteristics of invaded Islands, with special reference to Hawaii. In J. A. Drake, & H. A. Mooney (Eds.), *Biological invasions: a global perspective* (pp. 258–280). New York: John Wiley & Sons Ltd.

Lüdecke, D. (2017) Collection of convenient functions for common statistical computations. Available at: ftp://cran.r-project.org/pub/R/web/packages/sjstats/index.html

Meyer, J. Y. (2010). Montane cloud forests on remote islands of Oceania: the example of French Polynesia (South Pacific Ocean). In L. A. Bruijnzeel, F. N. Scatena, & L. S. Hamilton (Eds.), *Tropical montane cloud forests: Science for conservation and management* (pp. 121–129). Cambridge: Cambridge University Press.

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., … Nydick, K. R. (2016). Managing climate change refugia for climate adaptation. *PLoS ONE*, *11*, e0159909. https://doi.org/10.1371/journal.pone.0159909

Mueller-Dombois, D., & Fosberg, F. R. (1998). *Vegetation of the tropical Pacific islands*. New York: Springer-Verlag. https://doi.org/10.1007/978-1-4419-8686-3

Nair, U. S., Lawton, R. O., Welch, R. M., & Pielke, R. A. (2003). Impact of land use on Costa Rican tropical montane cloud forests: sensitivity of cumulus cloud field characteristics to lowland deforestation. *Journal of Geophysical Research*, *108*, 4206. https://doi.org/10.1029/2001JD001135

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

Paulsen, J., & Körner, C. (2014). A climate-based model to predict potential treeline position around the globe. *Alpine Botany*, *124*, 1–12. https://doi.org/10.1007/s00035-014-0124-0

R Development Core Team. (2017). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Richards, P. W. (1952). *The tropical rain forest: An ecological study*. Cambridge: Cambridge University Press.

Russell, J. C., Meyer, J. Y., Holmes, N. D., & Pagad, S. (2017). Invasive alien species on islands: impacts, distribution, interactions and management. *Environmental Conservation*, *44*, 359–370. https://doi.org/10.1017/S0376892917000297

Schmid, M. (1975). La flore et la vegetation de la partie méridionale de l'Archipel des Nouvelles Hébrides. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *272*, 329–342. https://doi.org/10.1098/rstb.1975.0091

Still, C. J., Foster, P. N., & Schneider, S. H. (1999). Simulating the effects of climate change on tropical montane cloud forests. *Nature*, *398*, 608–610. https://doi.org/10.1038/19293

Tershy, B. R., Shen, K. W., Newton, K. M., Holmes, N. D., & Croll, D. A. (2015). The importance of islands for the protection of biological and linguistic diversity. *BioScience*, *65*, 592–597. https://doi.org/10.1093/biosci/biv031

Thompson, L. G., Davis, M. E., Mosley-Thompson, E., Sowers, T. A., Henderson, K. A., Zagorodnov, V. S., … Cole-Dai, J. (1998). A 25,000-year tropical climate history from Bolivian ice cores. *Science*, *269*, 1858–1864. https://doi.org/10.1126/science.282.5395.1858

Thompson, L. G., Mosley-Thompson, E., Davis, M. E., Lin, P. N., Henderson, K. A., Cole-Dai, J., … Liu, K. B. (1995). Late glacial stage and Holocene tropical ice core records from Huascarán, Peru. *Science*, *269*, 46–50. https://doi.org/10.1126/science.269.5220.46

Vitousek, P. M. (1988). Diversity and biological invasions. In E. O. Wilson, & F. M. Peter (Eds.), *Biodiversity* (pp. 181–189). Washington DC: National Academy Press.

Weigelt, P., Jetz, W., & Kreft, H. (2013). Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences*, *17*, 15307–15312. https://doi.org/10.1073/pnas.1306309110

Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: Ecology, evolution, and conservation*. Oxford: Oxford University Press.

Zhao, F., Zhang, B. P., Zhang, S., Qi, W. W., He, W. H., Wang, J., & Yao, Y. H. (2015). Contribution of mass elevation effect to the altitudinal distribution of global treelines. *Journal of Mountain Science*, *12*, 289–297. https://doi.org/10.1007/s11629-014-3223-x

BIOSKETCH

Robin Pouteau is a post-doctoral fellow at Institut Agronomique néo-Calédonien (IAC) interested in island biogeography and conservation. He worked in several island countries including French Polynesia (University of French Polynesia, Punaauia), New Zealand (Lincoln University, Christchurch) and New Caledonia (French National Research Institute for Sustainable Development, Koné and IAC, Nouméa).

Author contributions: R.P. conceived the idea, collected and analysed the data, and drafted the paper. All authors contributed to the writing of the paper.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Pouteau R, Giambelluca TW, Ah-Peng C, Meyer J-Y. Will climate change shift the lower ecotone of tropical montane cloud forests upwards on islands? . *J Biogeogr*. 2018;00:1–8. https://doi.org/10.1111/jbi.13228