

Changes in climate and vegetation with altitude on Mount Batilamu, Viti Levu, Fiji

Jacynta Anderson^{1,§}, Gunnar Keppel^{1,2,3,§,*}, Sophie-Min Thomson¹, Anthony Randell¹, Jone Raituva⁴, Iliesa Koroi⁴, Ramokasa Anisi⁴, Tanya Charlson¹, Hans Juergen Boehmer⁵ and Sonia Kleindorfer⁶

¹ Natural and Built Environments Research Centre, School of Natural and Built Environments, University of South Australia, GPO Box 2471, Adelaide, South Australia 5001, Australia

² Future Industries Institute, University of South Australia, Mawson Lakes Campus, GPO Box 2471, Adelaide, South Australia 5001, Australia

³ Biodiversity, Macroecology & Biogeography, Faculty of Forest Sciences, University of Goettingen, Büsgenweg 1, 37077 Göttingen, Germany

⁴ South Pacific Regional Herbarium, Faculty of Science, Technology and Environment, University of the South Pacific, Suva, Fiji

⁵ School of Geography, Earth Science and Environment, Faculty of Science, Technology and Environment, University of the South Pacific, Suva, Fiji

⁶ College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide 5001, Australia

(Received 20 September 2017; revised 6 August 2018; accepted 6 August 2018)

Abstract: To investigate changes in vegetation and climate with altitude, we established forest plots and recorded climatic data at 100-m intervals between 550–1100 m asl on the western slopes of Mount Batilamu, Mount Koroyanitu range, Viti Levu, Fiji. Trees with a dbh ≥ 10 cm were identified and measured in 21 10 × 10-m plots, starting at 750 m altitude. Temperature and relative humidity sensors were deployed in two habitats, leaf litter and 50 cm above the ground, and two vegetation types, grasslands and forest, at six altitudes over a 48-h period. Two significantly distinct forest types, lowland and montane, were present. Montane forest was found at higher elevations (>950 m asl) and had significantly higher stem density. Mean temperature decreased significantly with altitude and was strongly moderated by vegetation type (lower average and less variation in forest). While average relative humidity significantly increased with altitude, it was strongly moderated by both habitat and vegetation type (higher average and less variation in leaf litter and forest). The lapse rate varied with time of day (higher during the day) and vegetation type (higher in grasslands). Therefore, vegetation and microhabitats create unique microclimates, and this should be considered when investigating current or future climatic patterns along altitudinal gradients on forested mountains.

Key Words: altitudinal gradient, endemism, lowland rain forest, microclimate, montane forest, Mount Koroyanitu National Heritage Park, relative humidity, South Pacific, temperature, tropical oceanic island

INTRODUCTION

As altitude increases, changes in temperature, rainfall, humidity, solar radiation and evapotranspiration occur (Strong *et al.* 2011). Temperature decreases and humidity increases with altitude (Brehm *et al.* 2007, McVicar *et al.* 2007, Shanks 1954). The rate of temperature decline (the lapse rate) is usually about 0.5–0.6°C per 100 m (Osborne 2012). The lapse rate is influenced by season (McVicar *et al.* 2007), time of the day (steeper during daytime; Pepin 2001), and topography (e.g. effects of relative solar radiation, slope and proximity to streams; Lookingbill & Urban 2003). Different microhabitats may

also modify temperature and humidity (Keppel *et al.* 2017a, Scheffers *et al.* 2014).

Altitudinal gradients in environmental parameters impact species distributions (Körner 2007, McCain & Grytnes 2010, Strong *et al.* 2011). As a result, the composition and structure of vegetation change along altitudinal gradients in response to climatic and environmental variables (McCain & Grytnes 2010). These changes may be manifested in distinct vegetation zones at different altitudes, which have been variously classified (Ashton 2003, Boehmer 2011, Richards 1996). An important transition between lowland and montane rain forest generally occurs between 800–1200 m asl (occasionally lower on islands), with montane forest being characterized by lower numbers of woody climbers, and a greater abundance of ground ferns, herbaceous

* Corresponding author. Email: gunnar.keppel@unisa.edu.au

§ Authors contributed equally to this paper.

angiosperms and epiphytes (Ashton 2003, Boehmer 2011).

In addition to species composition, diversity and forest structure tend to change with altitude (Moser *et al.* 2008, Richards 1996, Slik *et al.* 2010, Steinbauer *et al.* 2016). Plant diversity usually decreases or displays a hump-shaped pattern with increasing altitude (Clark *et al.* 2015, McCain & Grytnes 2010, Rahbek 1995). Conversely, the proportion of endemic species increases with altitude, a trend believed to be caused by increased isolation promoting speciation (Steinbauer *et al.* 2016, Trigas *et al.* 2013). Stem density generally increases, canopy height decreases and basal area displays varying patterns with increasing altitude (Ibanez *et al.* 2014, Moser *et al.* 2008, Slik *et al.* 2010). Similarly, lower tree height and higher stem densities at higher elevations are commonly observed in the Pacific (Ash 1987, Ibanez *et al.* 2014, Kirkpatrick & Hassall 1985).

Plant communities along mountain slopes are changing rapidly in response to anthropogenic climate change (Pauli *et al.* 2012, Penuelas & Boada 2003). Increased global temperatures are causing plant species to move upslope as they track suitable environmental conditions (Gottfried *et al.* 2012, Parmesan 2006, Penuelas & Boada 2003). Mountaintop species are thought to be particularly vulnerable to the effects of climate change due to their limited range (Boehmer 2011, Costion *et al.* 2015, Keppel *et al.* 2017b, Parmesan 2006). However, we lack fine-scale climatic data on forest-covered tropical mountains, as most of our climatic data are derived from meteorological stations that are not shaded by vegetation (De Frenne & Verheyen 2016). In the Pacific, basic ecological data, such as vegetation changes with altitude, are very limited (Keppel *et al.* 2011).

Here we investigate the changes in climate and vegetation along an altitudinal gradient (500–1100 m asl) along the western slopes of Mount Batilamu in the Mount Koroyanitu Range, western Viti Levu, Fiji. Specifically, we predicted based on literature that with altitude, species composition would change; species richness, canopy height, tree volume and temperature would decrease; and endemism, stem density and relative humidity would increase.

STUDY SITE

Fiji originated through volcanic activity 30–40 million y ago (Neall & Trewick 2008). It consists of about 330 islands and is located in the seasonal tropics of the Pacific Ocean on the Australian and Pacific plate convergence boundary (Mueller-Dombois & Fosberg 1998). Fiji has a tropical climate with annual temperatures averaging 20–27°C, with a warmer wet season from November to April and a cooler dry season from May to October (Mataki *et al.*

2006). Precipitation ranges from c. 1800 mm y⁻¹ in the drier western part to about 3000 mm y⁻¹ on the wetter eastern part of the archipelago, with ridges exposed to the south-east tradewinds receiving up to 10 000 mm y⁻¹ (Keppel & Tuiwawa 2007, Mataki *et al.* 2006).

Fiji's vascular flora mostly originated from the Indo-Malesian and Australian regions (Keppel *et al.* 2009) and has c. 1315 native species (Heads 2006). The key natural vegetation types are lowland, lower montane and upper montane rain forests, mesic forest, tropical dry forest, mangroves, coastal forest and wetlands (Keppel & Tuiwawa 2007, Mueller-Dombois & Fosberg 1998). On the drier, western parts of the archipelago, grassland- and savanna-like talasiga (meaning 'sunburnt') vegetation has become dominant due to increased fire frequency since human settlement 3000–4000 BP (Ash 1992, Mueller-Dombois & Fosberg 1998).

Mount Batilamu reaches about 1110 m asl in altitude and is located within the Koroyanitu National Heritage Park, which is a 25 000-ha, community-managed protected area of conservation, ecotourism and experimental significance (Olson *et al.* 2010, Smith 1948, Thaman 1996). The park includes Mount Koroyanitu (formerly Mount Evans), which, at 1195 m asl, is Viti Levu's third tallest peak (Smith 1948). Many of its over 700 plant species are culturally important and 11 species are endemic to the park, which includes lowland, lower and upper montane rain forests, talasiga and secondary vegetation (Thaman 1996).

METHODS

Vegetation sampling and analyses

In July 2016, vegetation was sampled along a trail ascending the western slopes of Mount Batilamu (Figure 1), which was forested from ~700 m asl. Plots were established at ~750, 800, 900, 1000 and 1100 m asl, each measuring 10 × 10 m. Because the tree flora of Fijian rain forests can be diverse (Keppel *et al.* 2010), we established five plots at each altitudinal band except at 750 and 800 m, where only three plots could be established due to very steep (>60° slopes) terrain. This resulted in a total of 21 plots, ranging in altitude from 751 to 1096 m asl (Figure 2). The four corners of each plot were permanently marked with 50-cm-long PVC pipes. Altitude and plot location were recorded with a Garmin *GPSmap* 62 GPS.

In each plot, the following data were collected: the identity (name), dbh measured at 1.3 m above the ground, and height of each individual tree with a dbh ≥10 cm. For trees of unknown identity, herbarium-type specimens were collected, preserved in a 70% alcohol solution, pressed, transported to the South Pacific

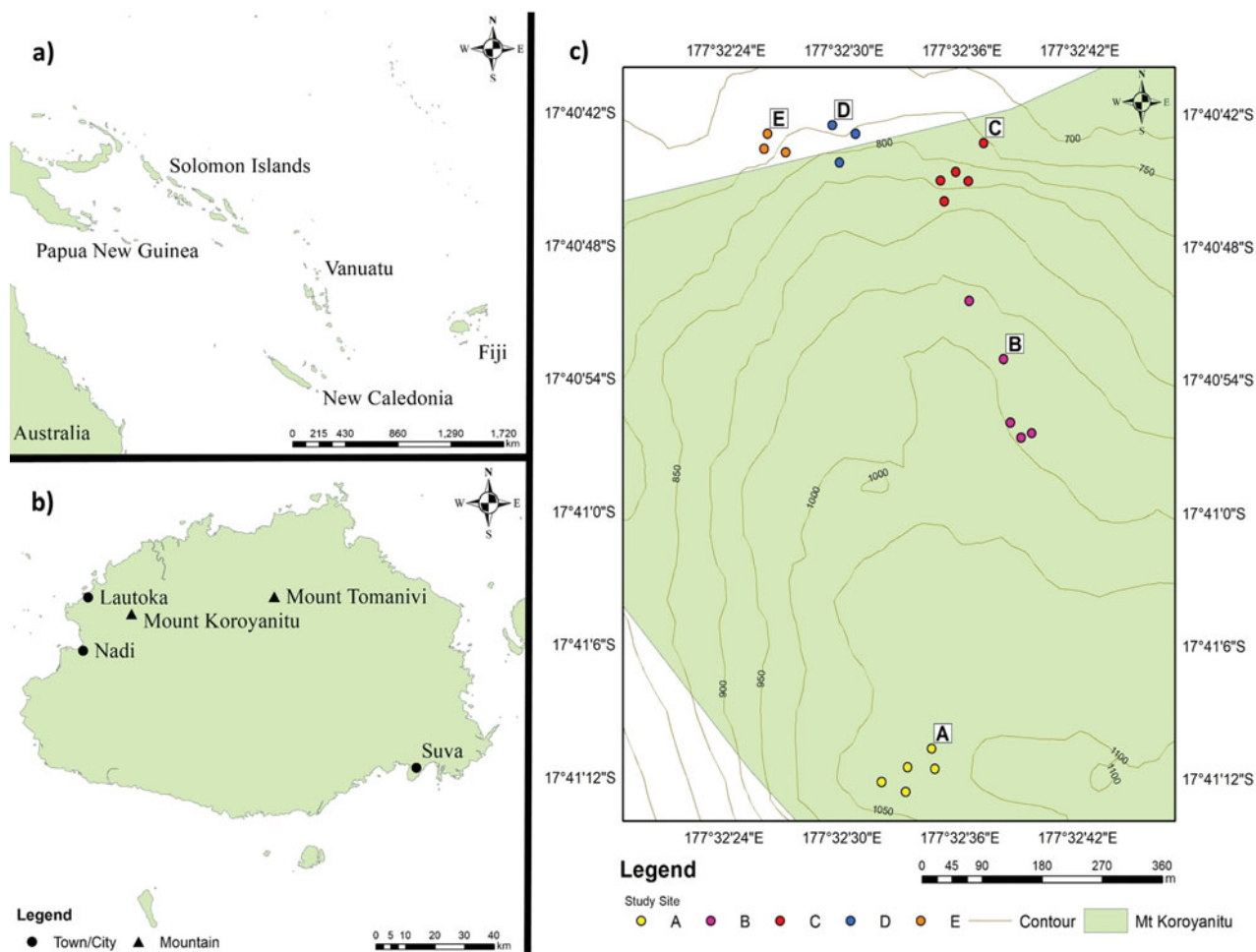


Figure 1. Location of Fiji in the South-west Pacific (a), Mount Koroyanitu on Viti Levu Island in Fiji (b), and the study plots along the western slopes of Mount Batilamu in Mount Koroyanitu National Park (c).

Regional Herbarium (SUVA) at the University of the South Pacific (USP), and dried at 50°C. Specimens were identified using the Flora Vitiensis Nova (Smith 1979–1991) and herbarium collections at SUVA.

All analyses were undertaken in the R version 3.4.2 statistical computing environment (<https://www.r-project.org/>) using 'ggplot', 'ggpubr', 'lme4', 'MASS', 'MuMin' and 'vegan' packages. To investigate the species composition of the plots, non-metric multidimensional scaling (nMDS) was performed using the Jaccard similarity index to test for distinct forest types. A one-way Analysis of Similarity (ANOSIM; Clarke 1993) using 95% ($\alpha = 0.05$) confidence intervals was used to test for significant differences between forest types identified.

For each plot the following variables were measured or calculated: species richness (number of species per stem, to account for differences in stem density), endemism (proportion of species endemic to Fiji), stem density (total number of stems per plot), height (average of

the five tallest trees) and volume. Tree volume was calculated assuming a conical tree shape: $\text{volume} = [(dbh \div 2)^2 \times \pi \times \text{tree height}] \div 3$. A conical shape was assumed because it provides more conservative volume estimates than assuming a cylindrical shape, and because there were no local or regional equations for estimating volume (Magnussen & Reed 2015).

In addition, the relative density (number of individuals of a species \div total number of individuals \times 100), dominance (volume of a species \div total volume \times 100) and frequency (number of plots a species occurs in \div sum of frequency for all species \times 100) were calculated for each species in each of two forest types. The sum of the relative density, dominance and frequency constitutes the importance value of a species (Mueller-Dombois & Ellenberg 2002), which was converted to relative importance (sum of all importance values \div 3).

Based on visual data inspection and the small sample sizes employed, we assumed that the data collected were not normally distributed. Therefore, non-parametric tests

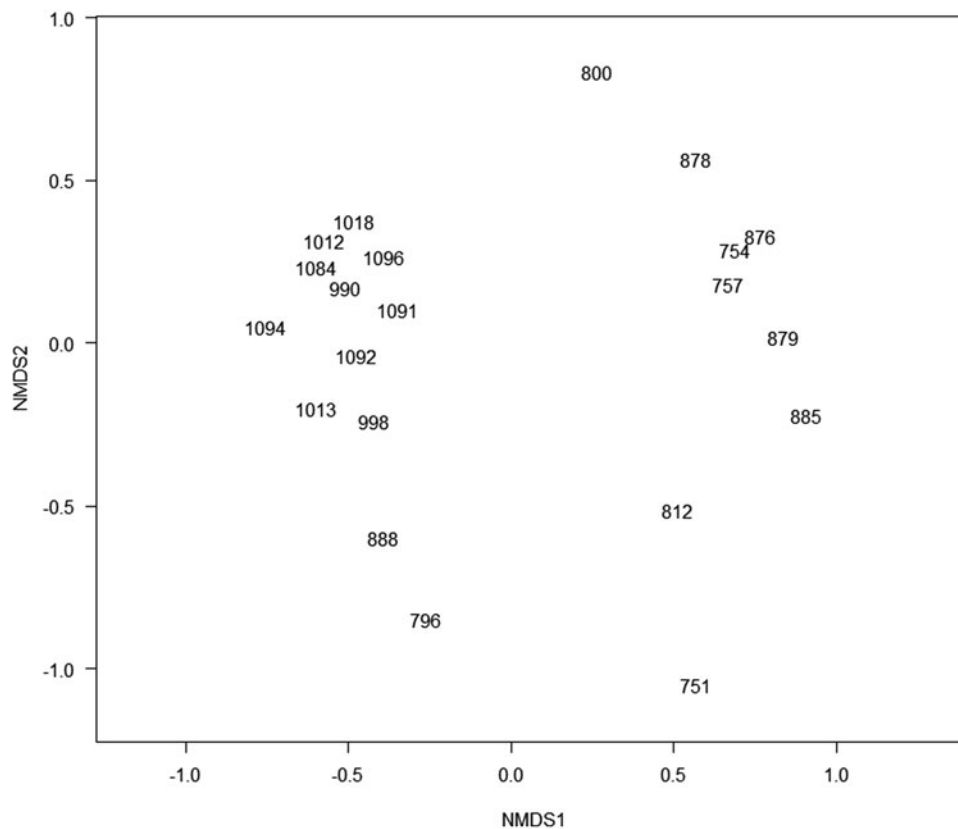


Figure 2. Non-metric MDS using the Jaccard similarity index, 21 plots along an altitudinal transect on Mount Batilamu, Viti Levu, Fiji. The plots are labelled with the altitude at which they are located.

were used; Kruskal–Wallis tests to determine significance differences between variables at the various altitudes, a Wilcoxon test to determine which altitudes or forest types differed significantly, and a Spearman r_s test to identify correlations between the various variables and altitude.

Microclimate sampling and analysis

Paired Maxim iButtons (DS1923) were placed at altitudinal intervals of about 100 m, recording instantaneous readings of temperature and relative humidity every 20 min. One sensor was suspended 50 cm above the ground on bamboo sticks on the inside of inverted, white plastic cups, which were covered with white duct tape on the upper half. The other sensor was positioned inside leaf litter by placing it inside a metal tea strainer, which was covered with white duct tape on the upper (and upward-facing) half and left uncovered in the lower half (Keppel *et al.* 2017a). Where feasible the paired iButtons were placed in both forested and grassland vegetation at each altitude in close proximity, resulting in four iButtons per altitude; one each in the air in grasslands, leaf litter in grasslands, air in forest, and leaf litter in forest. The

iButtons were mostly placed close to the plots, but we also placed a quadruplet of sensors in grassland and a forested gully at ~550 m asl.

A 48-h data window (07h00 on 19 July–06h40 on 21 July, sunshine with little cloud cover was observed during this period) was used for analyses. For this time period we calculated the average, standard deviation, maximum and minimum values of temperature and humidity for each iButton, separately for day and night time. Day and night time periods were determined by using sunrise and sunset data from timeanddate.com for the nearby city of Lautoka. The hour prior to and after sunrise and sunset were removed in order to allow a settling period between the two phases.

For both temperature and humidity, we calculated the mean, standard deviation, maximum and minimum values, separately for day- and night-time. We then used these as response variables in generalized linear mixed-effect models, with altitude as the sole fixed effect and vegetation type (open grasslands versus forest), habitat type (air versus leaf litter) and time of the day (day versus night) as random effects. We extracted the slope of the fixed effect (i.e. the lapse rate) and the percentage variance explained by each random effect

Table 1. Importance values of the 10 tree species with the highest importance value in either lowland or montane forest along an altitudinal transect on Mount Batilamu, Fiji. RDe = relative density (%), RDo = relative dominance (%), RF = relative frequency (%), IV = importance value (%).

Species	Lowland				Montane			
	RDe	RDo	RF	IV (rank)	RDe	RDo	RF	IV (rank)
<i>Agathis macrophylla</i> Mast.	Not present				12.1	47.3	10.1	23.2 (1)
<i>Bischofia javanica</i> Blume	8.3	21.1	6.9	12.1 (3)	Not present			
<i>Celtis vitiensis</i> A.C.Sm.	3.6	0.5	3.4	2.7 (10)	5.5	2.0	5.1	4.2 (7)
<i>Cryptocarya parinarioides</i> A.C.Sm.	3.6	1.0	3.4	3.1 (9)	3.6	1.1	2.0	2.2 (16)
<i>Degeneria</i> sp.	Not present				3.6	4.3	5.1	4.32 (3)
<i>Dendrocnide harveyi</i> (Seem.) Chew	15.5	14.3	8.6	12.8 (2)	Not present			
<i>Dysoxylum aliquantulum</i> A.C.Sm.	10.7	31.4	6.9	16.3 (1)	4.8	2.2	3.0	3.3 (9)
<i>Dysoxylum lenticellare</i> Gillespie & A.C.Sm.	Not present				4.8	5.7	4.0	4.9 (2)
<i>Dysoxylum richii</i> C.DC.	6.0	20.7	6.9	7.1 (5)	0.6	0.9	1.0	0.6 (44)
<i>Elattostachys falcata</i> (A.Gray) Radlk.	2.4	0.5	3.4	2.1 (12)	4.2	4.5	4.0	4.3 (6)
<i>Hedyocarya dorstenioides</i> A.Gray	6.0	1.4	3.4	3.6 (7)	Not present			
<i>Litsea pickeringii</i> Benth. & Hook.f. ex Drake	3.5	0.8	5.2	3.2 (8)	Not present			
<i>Meliccytus fasciger</i> Gillespie	Not present				3.6	2.8	3.0	3.1 (10)
<i>Metrosideros collina</i> (J.R.Forst. & G.Forst.) A.Gray	Not present				2.4	7.4	3.0	4.3 (5)
<i>Podocarpus nerifolius</i> D.Don.	6.0	0.4	6.9	4.4 (6)	6.6	2.2	4.0	4.3 (4)
<i>Vavaea amicomum</i> Benth.	Not present				4.2	2.3	4.0	3.5 (8)
<i>Viticipremna vitilevuensis</i> Munir	4.8	11.8	5.2	7.2 (4)	Not present			

from this model. We determined the significance of the fixed effect by comparing the performance of the model with and without altitude using a chi-squared test. The explanatory power of selected models was assessed using a pseudo- r^2 -value (Nakagawa & Schielzeth 2013), which calculates the marginal (variation explained by fixed effects) and conditional r^2 (variation explained by fixed and random effects).

RESULTS

Vegetation

Overall, there were 292 stems belonging to 71 species (in 37 families) of trees with a dbh ≥ 10 cm in the 21 plots. Of these, 43 species (60.56%) were endemic to Fiji. Two seemingly distinct plot clusters were produced by non-metric multidimensional scaling (nMDS; Figure 2). One group (montane plots) consisted of 10 plots at higher (>950 m) altitudes. The other group (lowland plots) consisted of plots at lower (<885 m) altitudes. The plots at 888 and 795 m had intermediate species composition, including taxa otherwise associated with higher altitudes (e.g. *Podocarpus nerifolius*, Podocarpaceae). The plot at 751 m was dominated by *Pterocymbium oceanicum* (Sterculiaceae) and was the only plot with this species. The one-way analysis of similarity (ANOSIM) supported montane and lowland plots to be significantly different ($P = 0.001$, $r = 0.622$).

The lowland plots were dominated by *Dendrocnide harveyi* (Urticaceae), *Dysoxylum aliquantulum* (Meliaceae) and *Bischofia javanica* (Euphorbiaceae). Together, these

species accounted for more than a third of all stems and more than 60% of the total basal area, while also having the highest importance values (Table 1). The montane plots were dominated by *Agathis macrophylla* (Araucariaceae), which accounted for more than 10% of all stems and almost 50% of the total tree volume. Of the 17 most important species in this study (based on being among the 10 most important species in either the lowland or montane plots), only six species occurred in both forest types (Table 1).

Measures of species diversity (richness, endemism) and forest structure (density, height, volume) did not differ significantly among altitudes, except for volume (Kruskal–Wallis, $P = 0.027$). Tree volume at 1000 m asl was significantly smaller than at 750 m ($P = 0.037$), 900 m ($P = 0.012$) and 1100 m ($P = 0.012$). Only canopy height had a significant, linear correlation with altitude (Spearman r_s , $\rho = -0.9$, $P = 0.017$). The measures of species diversity and forest structure generally displayed predicted differences between the two forest types, i.e. higher species richness and greater canopy height and tree volume in lowland forest, and higher endemism and stem density in montane forest. However, those differences were only significant for stem density ($P = 0.0048$).

Climate

Models consisting of altitude, vegetation type, habitat and time were good predictors of the temperature and humidity variables investigated, explaining 62–85% of the total variation (conditional r^2). Altitude was a

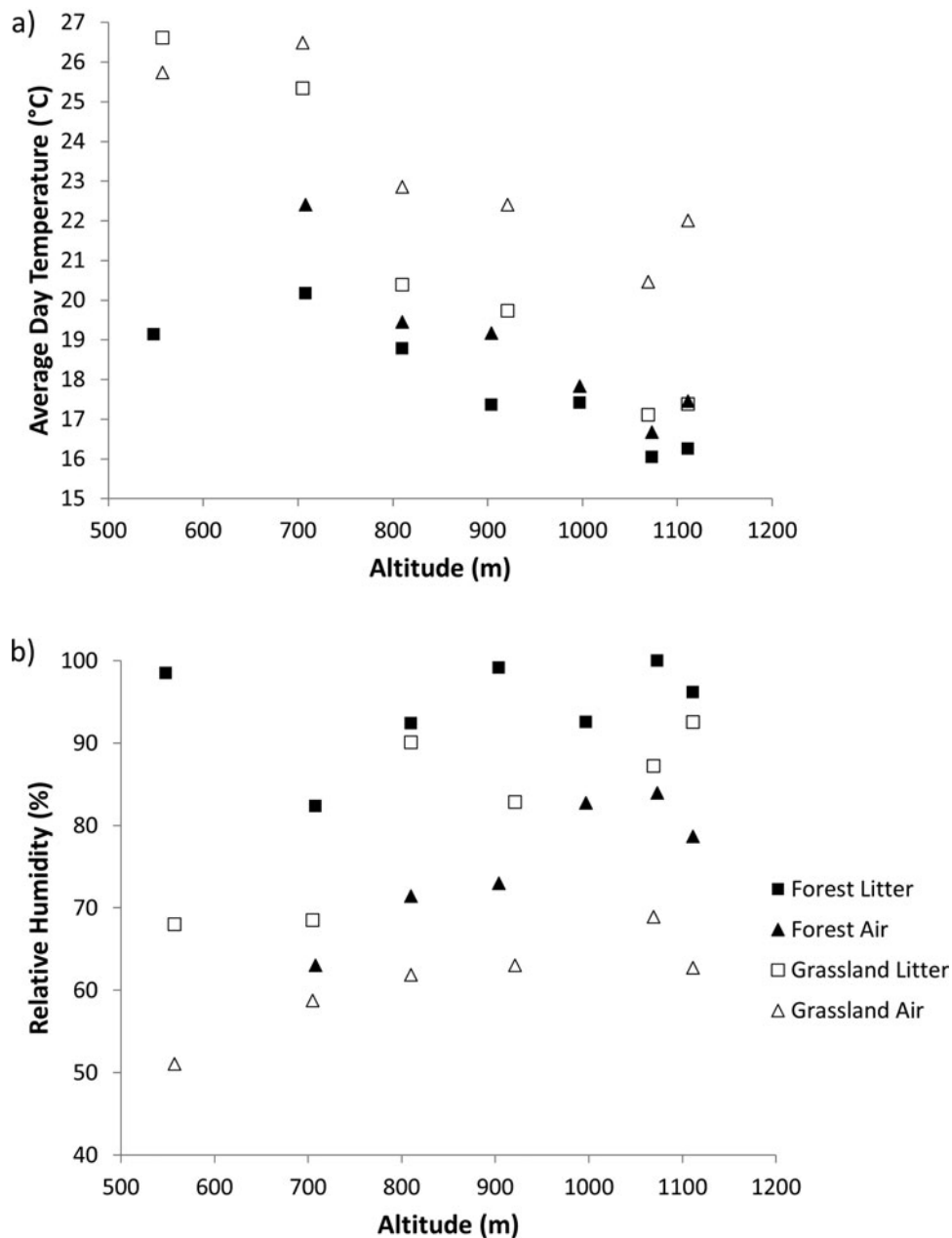


Figure 3. Variation of average (19–20 July 2016) daytime temperature (a) and relative humidity (b) along an altitudinal gradient on Mount Batilamu, Fiji.

significant predictor of the average, maximum and minimum temperature, explaining about 15%, 8% and 30% of the variation in these variables, respectively (marginal r^2). Time of day and vegetation type were other important predictors of these variables. Daytime temperature was generally lower in forests than in grasslands (black versus white shapes, Figure 3). The variation (standard deviation) in temperature was mostly driven by time of day (lower variation at night) and vegetation type (lower variation in forests).

The average lapse rate was *c.* -0.9°C per 100 m, being higher during the day (-1.1°C per 100 m) than at night (-0.6°C per 100 m). Comparing the different microhabitats, the lapse rate was higher in grasslands (-1.15°C per 100 m in the leaf litter and -0.88°C per 100 m in the open) than in the forest (-0.86°C per 100 m in the open air and -0.64°C per 100 m in leaf litter). From about 900 m (the break between the two forest types), the average temperature did not exceed 19°C and the average relative humidity did not drop below 75%.

Altitude was a significant predictor of the average and minimum humidity (though considerably less so than for temperature), explaining about 4% and 3% of the variation in these variables, respectively (marginal r^2). Habitat type, time of the day and, to a lesser extent, vegetation type were other important predictors of these variables. Daytime humidity indeed tended to be higher in leaf litter (squares) than in the air (50 cm above the ground; triangles; Figure 3). The variation (standard deviation) in humidity was mostly driven by time of day (lower variation at night), with habitat type (lower variation in leaf litter) and vegetation type (lower variation in forests) also being important. Only habitat type was a good predictor (explaining almost 60% of the total variation in this variable) of maximum humidity, with leaf litter having consistently higher maximum humidity.

DISCUSSION

The two major forest types identified along the altitudinal transect on the western slopes of Mount Batilamu correspond to lowland and montane rain forest, with the transition occurring between 800–900 m asl and corresponding with the altitude suggested for the break between these forest types (Ashton 2003). The montane forest appears to be the *Agathis–Podocarpus* type described by Mueller-Dombois & Fosberg (1998; as upland rain forest), with the conifer *Agathis macrophylla* as the dominant element. The montane forest is lower montane forest *sensu* Hamilton *et al.* (1995) and Ashton (2003), as it is different from cloud forest, lacking trees with stunted growth and twisted trunks. The lowland rain forest has common lowland rain-forest elements, such as *Dysoxylum* spp., *Bischofia javanica*, *Hedyocarya dorstenioides* and *Viticipremna vitilevuensis* (Keppel *et al.* 2011). Other altitudinal transects in Fiji have similarly found turnover of dominant species with altitude (Ash 1987, Kirkpatrick & Hassall 1985).

Although the variables related to rain-forest diversity and structure tended to differ between lowland and montane forest as expected based on literature, the differences were more subdued than expected – with only those in stem density being significant. The limited sample size and altitudinal range of this study may have limited our ability to detect differences. Furthermore, we used the number of species endemic to Fiji (as there were no species endemic to the Mount Koroyanitu Range in our plots) and this may not respond strongly to altitude, as the percentage of endemic tree species in Fiji's lowland rain forests exceeds 50% (Keppel *et al.* 2010).

Decreasing temperature and increasing relative humidity with altitude are well documented (Grubb &

Whitmore 1966, Pepin & Losleben 2002, Shanks 1954). Our lapse rates are higher than the usual average of about 0.5–0.6°C per 100 m (Osborne 2012). However, the altitudinal range that we used to calculate lapse rates was comparatively small, which can affect results (Pepin & Losleben 2002). Furthermore, lapse rates are generally calculated as the average over an entire year and our data are based on a relatively short time period during which there was little cloud cover. Lapse rates are known to differ among seasons and with cloud cover (McVicar *et al.* 2007, Pepin 2001, Pepin & Losleben 2002) and we here show that they also differ among vegetation types and in different microhabitats.

Both canopy cover and microhabitats are known to moderate microclimate (Keppel *et al.* 2017a, Scheffers *et al.* 2014). In our study, the absence of canopy cover strongly increased temperature and decreased relative humidity. These microclimatic differences between forests and more open vegetation, such as grasslands, savannas and canopy gaps, are well documented (Grubb & Whitmore 1966, Holl 1999, Ibanez *et al.* 2013, Turton & Sexton 1996). The leaf-litter microhabitat strongly moderated climatic variables, especially relative humidity. In addition, topographic variation can strongly affect microclimate measurements (Lookingbill & Urban 2003). While we minimized the effects of aspect, which can be significant, we could not include other important effects, such as solar radiation and distance to a stream (Lookingbill & Urban 2003), as fine-scale digital elevation models (DEMs) are not available for the area.

Only recently has the ability of microhabitats to retain microclimates that are more stable than external conditions been quantified and its potential importance under anthropogenic climate change been realized (Keppel *et al.* 2017a, Scheffers *et al.* 2014). As such microhabitats can maintain more consistent and favourable climates and, therefore, they are likely to be important in facilitating the persistence of biota as regional environmental conditions change (Lenoir *et al.* 2017, Scheffers *et al.* 2014). Our study shows that vegetation and microhabitats interact to create a patchwork of microclimates (Keppel *et al.* 2017a), which is important for facilitating the persistence of species under forecast anthropogenic climate change, as species respond to this fine-scale interplay of abiotic and biotic factors (Keppel *et al.* 2017b, Oorebeek & Kleindorfer 2008).

Our findings therefore highlight the importance of including the moderating effects of vegetation and microhabitats on climatic conditions when forecasting future changes in climate and species distributions. This even holds true for the tropical South-West Pacific islands, which are experiencing milder climate change than higher latitudes (IPCC 2014). However, climatic data are currently mostly derived from meteorological stations in open areas without tall vegetation and

we therefore cannot currently quantify the effects of canopy cover on microclimate (De Frenne & Verheyen 2016).

ACKNOWLEDGEMENTS

We would like to thank Abaca Village, Vuda District, Ba Province, for kindly giving us permission for, and providing assistance, during the fieldwork. Geon C. Hanson and Leomar Longworth assisted with data collection. This research was undertaken as part of a joint undergraduate student project between Flinders University, the University of South Australia and the University of the South Pacific, and funded through the Department of Foreign Affairs and Trade of the Australian Government as part of the New Colombo Plan initiative. During part of the analyses and writing GK was supported by an Alexander von Humboldt fellowship. A study tour travel grant by the University of South Australia assisted JA, SMT, AR and TC.

LITERATURE CITED

- ASH, J. 1987. Stunted cloud-forest in Taveuni, Fiji. *Pacific Science* 41:191–199.
- ASH, J. 1992. Vegetation ecology of Fiji: past, present, and future perspectives. *Pacific Science* 46:111–127.
- ASHTON, P. S. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspectives in Plant Ecology, Evolution and Systematics* 6:87–104.
- BOEHMER, H. J. 2011. Vulnerability of tropical montane rain forest ecosystems due to climate change. Pp. 789–802 in Brauch, H. G., Oswald Spring, Ú., Mesjasz, C., Grin, J., Kameri-Mbote, P., Chourou, B., Dunay, P. & Birkmann, J. (eds). *Coping with global environmental change, disasters and security – threats, challenges, vulnerabilities and risks*. Springer, Berlin.
- BREHM, G., COLWELL, R. K. & KLUGE, J. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography* 16: 205–219.
- CLARK, D. B., HURTADO, J. & SAATCHI, S. S. 2015. Tropical rain forest structure, tree growth and dynamics along a 2700-m elevational transect in Costa Rica. *PLoS ONE* 10:e0122905.
- CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Journal of Ecology* 18:117–143.
- COSTION, C. M., SIMPSON, L., PERT, P. L., CARLSEN, M. M., JOHN, K. W. & CRAYN, D. 2015. Will tropical mountaintop plant species survive climate change? Identifying key knowledge gaps using species distribution modelling in Australia. *Biological Conservation* 191:322–330.
- DEFRENNE, P. & VERHEYEN, K. 2016. Weather stations lack forest data. *Science* 351:234.
- GOTTFRIED, M., PAULI, H., FUTSCHIK, A., AKHALKATSI, M., BARANCOK, P., BENITO ALONSO, J. L., COLDEA, G., DICK, J., ERSCHBAMER, B., FERNANDEZ CALZADO, M. R., KAZAKIS, G., KRAJCI, J., LARSSON, P., MALLAUN, M., MICHELSEN, O., MOISEEV, D., MOISEEV, P., MOLAU, U., MERZOUKI, A., NAGY, L., NAKHUTSRISHVILI, G., PEDERSEN, B., PELINO, G., PUSCAS, M., ROSSI, G., STANISCI, A., THEURILLAT, J.-P., TOMASELLI, M., VILLAR, L., VITTOZ, P., VOGIATZAKIS, I. & GRABHERR, G. 2012. Continent-wide response of mountain vegetation to climate change. *Nature Climate Change* 2:111–115.
- GRUBB, P. J. & WHITMORE, T. C. 1966. A comparison of montane and lowland rain forest in Ecuador: II. The climate and its effects on the distribution and physiognomy of the Forests. *Journal of Ecology* 54:303–333.
- HEADS, M. 2006. Seed plants of Fiji: an ecological analysis. *Biological Journal of the Linnean Society* 89:407–431.
- HAMILTON, L. S., JUVIK, J. O. & SCATENA, F. N. (eds). 1995. *Tropical montane cloud forests*. Springer, Berlin.
- HOLL, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica* 31:229–242.
- IBANEZ, T., HELY, C. & GAUCHEREL, C. 2013. Sharp transitions in microclimatic conditions between savanna and forest in New Caledonia: insights into the vulnerability of forest edges to fire. *Austral Ecology* 38:680–687.
- IBANEZ, T., MUNZINGER, J., DAGOSTINI, G., HEQUET, V., RIGAUT, E., JAFFRÉ, T. & BIRNBAUM, P. 2014. Structural and floristic diversity of mixed tropical rain forest in New Caledonia: new data from the New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN). *Applied Vegetation Science* 17:386–397.
- IPCC. 2014. *Climate Change 2014: Synthesis Report*. Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva.
- KEPPEL, G. & TUIWAWA, M. V. 2007. Dry zone forests of Fiji: species composition, life history traits, and conservation. *New Zealand Journal of Botany* 45:545–563.
- KEPPEL, G., LOWE, A. J. & POSSINGHAM, H. P. 2009. Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. *Journal of Biogeography* 36:1035–1054.
- KEPPEL, G., BUCKLEY, Y. M. & POSSINGHAM, H. P. 2010. Drivers of lowland rain forest community assembly, species diversity and forest structure on islands in the tropical South Pacific. *Journal of Ecology* 98:87–95.
- KEPPEL, G., TUIWAWA, M. V., NAIKATINI, A. & ROUNDS, I. A. 2011. Microhabitat specialization of tropical rain-forest canopy trees in the Sovi Basin, Viti Levu, Fiji Islands. *Journal of Tropical Ecology* 27:491–501.
- KEPPEL, G., ANDERSON, S., WILLIAMS, C., KLEINDORFER, S. & O'CONNELL, C. 2017a. Microhabitats and canopy cover moderate high summer temperatures in a fragmented Mediterranean landscape. *PLoS ONE* 12:e0183106.
- KEPPEL, G., ROBINSON, T. P., WARDELL-JOHNSON, G. W., YATES, C. J., VAN NIEL, K. P., BYRNE, M. & SCHUT, A. G. T. 2017b. A low-altitude mountain range as an important refugium for two narrow endemics

- in the Southwest Australian Floristic Region biodiversity hotspot. *Annals of Botany* 119:289–300.
- KIRKPATRICK, J. B. & HASSALL, D. C. 1985. The vegetation and flora along an altitudinal transect through tropical forest at Mount Korobaba, Fiji. *New Zealand Journal of Botany* 23: 33–46.
- KÖRNER, C. 2007. The use of 'altitude' in ecological research. *Trends in Ecology and Evolution* 22:569.
- LENOIR, J., HATTAB, T. & PIERRE, G. 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography* 40:253–266.
- LOOKINGBILL, T. R. & URBAN, D. L. 2003. Spatial estimation of air temperature differences for landscape-scale studies in montane environments. *Agricultural and Forest Meteorology* 114: 141–151.
- MAGNUSSEN, S. & REED, D. 2015. Modelling for estimation and monitoring. Pp. 111–136 in *Knowledge reference for national forest assessments*. Food and Agriculture Organisation of the United Nations, Rome.
- MATAKI, M., KOSHY, K. C. & LAL, M. 2006. Baseline climatology of Viti Levu (Fiji) and current climatic trends. *Pacific Science* 60: 49–68.
- MCCAIN, C. M. & GRYTNES, J.-A. 2010. Elevational gradients in species richness. Pp. 1–10 in *Encyclopedia of life sciences*. John Wiley & Sons, Chichester.
- MCVICAR, T. R., VAN NIEL, T. G., LI, L., HUTCHINSON, M. F., MU, X. & LIU, Z. 2007. Spatially distributing monthly reference evapotranspiration and pan evaporation considering topographic influences. *Journal of Hydrology* 338:196–220.
- MOSER, G., RÖDERSTEIN, M., SOETHE, N., HERTEL, D. & LEUSCHNER, C. 2008. Altitudinal changes in stand structure and biomass allocation of tropical mountain forests in relation to microclimate and soil chemistry. Pp. 229–242 in Caldwell, M. M., Heldmaier, G., Jackson, R. B., Lange, O. L., Mooney, H. A., Schulze, E. D. & Soomer, U. (eds). *Gradients in a tropical mountain ecosystem of Ecuador*. Springer, Berlin.
- MUELLER-DOMBOIS, D. & ELLENBERG, H. 2002. *Aims and methods of vegetation ecology*. Blackburn Press, Caldwell. 547 pp.
- MUELLER-DOMBOIS, D. & FOSBERG, F. R. 1998. *Vegetation of the Tropical Pacific Islands*. Springer, New York. 733 pp.
- NAKAGAWA, S. & SCHIELZETH, H. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- NEALL, V. E. & TREWICK, S. A. 2008. The age and origin of the Pacific islands: a geological overview. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 363: 3293–3308.
- OOREBEEK, M. & KLEINDORFER, S. 2008. Understorey predicts the spatial distribution of *Ixodes hirsti* in South Australia. *Australian Journal of Zoology* 56:123–127.
- OLSON, D., FARLEY, L., PATRICK, A., WATLING, D., TUIWAWA, M., MASIBALAVU, V., LENOA, L., BOGIVA, A., QAUQUAU, I., ATHERTON, J., CAGINITOBA, A., TOKOTA'A, M., PRASAD, S., NAISILISILI, W., RAIKABULA, A., MAILAUTOKA, K., MORLEY, C. & ALLNUTT, T. 2010. Priority forests for conservation in Fiji: landscapes, hotspots and ecological processes. *Oryx* 44:57–70.
- OSBORNE, P. L. 2012. *Tropical ecosystems and ecological concepts*. (Second edition). Cambridge University Press, Cambridge.
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- PAULI, H., GOTTFRIED, M., DULLINGER, S., ABDALADZE, O., AKHALKATSI, M., ALONSO, J. L. B., COLDEA, G., DICK, J., ERSCHBAMER, B., CALZADO, R. F., GHOSN, D., HOLTEN, J. I., KANKA, R., KAZAKIS, G., KOLLÁR, J., LARSSON, P., MOISEEV, P., MOISEEV, D., MOLAU, U., MESA, J. M., NAGY, L., PELINO, G., PUŞÇAŞ, M., ROSSI, G., STANISCI, A., SYVERHUSET, A. O., THEURILLAT, J.-P., TOMASELLI, M., UNTERLUGGAUER, P., VILLAR, L., VITTOZ, P. & GRABHERR, G. 2012. Recent plant diversity changes on Europe's mountain summits. *Science* 336: 353–355.
- PENUELAS, J. & BOADA, M. 2003. A global change-induced biome shift in the Montseny Mountains (NE Spain). *Global Change Biology* 9:131–131.
- PEPIN, N. 2001. Lapse rate changes in northern England. *Theoretical and Applied Climatology* 68:1–16.
- PEPIN, N. & LOSLEBEN, M. 2002. Climate change in the Colorado Rocky Mountains: free air versus surface temperature trends. *International Journal of Climatology* 22:311–329.
- RAHBEK, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18:200–205.
- RICHARDS, P. W. 1996. *The tropical rain forest. An ecological study*. Cambridge University Press, Cambridge.
- SCHEFFERS, B. R., EVANS, T. A., WILLIAMS, S. E. & EDWARDS, D. P. 2014. Microhabitats in the tropics buffer temperature in a globally coherent manner. *Biology Letters* 10:20140819.
- SHANKS, R. E. 1954. Climates of the Great Smoky Mountains. *Ecology* 35:354–361.
- SLIK, W. F., AIBA, S., BREARLEY, F. Q., CANNON, C. H., FORSHED, O., KITAYAMA, K., NAGAMASU, H., NILUS, R., PAYNE, J., PAOLI, G., POULSEN, A. D., RAES, N., SHEIL, D., SIDIYASA, K., SUZUKI, E. & VAN VALKENBURG, J. L. C. H. 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography* 19:50–60.
- SMITH, A. C. 1948. An ascent of Koroyanitu. *Proceedings of the National Academy of Sciences USA* 34:579–585.
- SMITH, A. C. 1979–1991. *Flora Vitiensis nova: a new flora of Fiji (spermatophytes only)*. Volumes 1–5. Pacific Tropical Botanical Garden, Lawai, Hawai'i.
- STEINBAUER, M. J., FIELD, R., GRYTNES, J. A., TRIGAS, P., AH-PENG, C., ATTORRE, F., BIRKS, H. J. B., BORGES, P. A. V., CARDOSO, P., CHOU, C. H., DE SANCTIS, M., DE SEQUEIRA, M. M., DUARTE, M. C., ELIAS, R. B., FERNÁNDEZ-PALACIOS, J. M., GABRIEL, R., GEREAU, R. E., GILLESPIE, R. G., GREIMLER, J., HARTER, D. E. V., HUANG, T. J., IRL, S. D. H., JEANMONOD, D., JENTSCH, A., JUMP, A. S., KUEFFER, C., NOGUÉ, S., OTTO, R., PRICE, J., ROMEIRAS, M. M., STRASBERG, D., STUESSY, T., SVENNING, J. C., VETAAS, O. R. & BEIERKUHNLIN, C. 2016. Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography* 25:1097–1107.

- STRONG, C. L., BOULTER, S. L., LAIDLAW, M. J., MAUNSELL, S. C., PUTLAND, D. & KITCHING, R. L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum* 55:251–270.
- THAMAN, R. 1996. The biodiversity of Koroyanitu National Park. *Domodomo* 10:28–51.
- TRIGAS, P., PANITSA, M., TSIFTISIS, S. & MOREAU, C. S. 2013. Elevational gradient of vascular plant species richness and endemism in Crete – the effect of post-isolation mountain uplift on a continental island system. *PLoS ONE* 8:e59425.
- TURTON, S. M. & SEXTON, G. J. 1996. Environmental gradients across four rainforest-open forest boundaries in northeastern Queensland. *Austral Ecology* 21:245–254.