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Altitudinal patterns of moth diversity in tropical and subtropical Australian rainforests

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Abstract Altitudinal gradients are an excellent study tool to help understand the mechanisms shaping community assembly. We established a series of altitudinal gradients along the east coast of Australia to describe how the distribution of a hyper-diverse herbivore group (night-flying Lepidoptera) changes across an environmental gradient in subtropical and tropical rainforests. Two transects were in subtropical rainforest in the same bioregion, one in south-east Queensland (28.7°S) and one in north east New South Wales (29.7°S). Two were in tropical rainforest, one in mid-east Queensland (21.1°S) and one in the Wet Tropics of northern Queensland (17.5°S). Replicate plots were established in altitudinal bands separated by 200 m. Canopy and understorey moths were sampled at the beginning and end of the wet season using automatic Pennsylvania light traps. We sorted a total of 93 400 individuals, belonging to 3035 species. The two subtropical transects in the same region showed similar patterns of turnover across altitude, with the most distinctive assemblage occurring at the highest altitude. Moth assemblages in the tropical transects tended to show distinct 'lowland' and 'upland' communities. For species that were common across several of the transects, many were found at lower altitudes in the subtropics and higher altitudes in the tropics, suggesting they are sensitive to environmental conditions, and track their physiological envelopes across latitudes. These results suggest ubiquitous altitudinal stratification in tropical and subtropical Australian rainforests. The marked response of species to latitude and altitude demonstrates they are sensitive to climatic variables and can be used as indicators to understand future community responses to climate change.

Key words: altitude, beta diversity, climate change, elevation, latitude, tropical and subtropical rainforest.

INTRODUCTION

Altitudinal gradients are excellent study systems for ecology, encompassing steep shifts in biotic and abiotic factors in a small geographic area (Hodkinson 2005). They have been used to study the driving forces and mechanisms that underlie patterns in diversity and community structure (Gagne 1979; Hebert 1980; Bravo *et al.* 2008). Mountain ecosystems and altitudinal gradients are notable for their high level of diversity (Körner 2000) and have become an important tool for investigating the factors that shape the distributions of organisms, for observing shifts in altitudinal ranges and for predicting future responses to climate change (Shoo *et al.* 2006; Fischer *et al.* 2011).

Organisms may exhibit altitudinal stratification, with some species occupying very small altitudinal ranges, leading to a high turnover in assemblage structure across altitudes. On the other hand, species that are able to cope with a wide range of environmental conditions may occur across an entire altitudinal gradient. Generally, studies have found altitudinal stratification in assemblages, including in ants (Burwell & Nakamura 2011), moths (Brehm & Fiedler 2003; Ashton *et al.* 2011), beetles (Escobar *et al.* 2005), collembola (Maunsell *et al.* 2012), birds (Williams *et al.* 2010), mammals (Williams 1997) and vegetation (Hemp 2006). Different taxonomic groups may respond in distinctive ways to altitude (Stork & Brendell 1990). Many species may be restricted to only high altitudes and are often associated with high levels of endemism (Kessler 2002; Szumik *et al.* 2012).

The relationship between species richness and altitude can be variable. The two most commonly

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observed patterns are linear declines in richness with increasing altitude (Hebert 1980), or unimodal (humped) shaped patterns in species richness (Beck & Chey 2008). Several factors may influence observed species patterns, including the altitudinal range of the studied gradient which often reflects the degree of disturbance in lowland areas due to human impact (these disturbed areas are usually avoided by researchers). In such cases, it is not possible to incorporate the full altitudinal range within an ecosystem, and sampling points have to be placed in locations where intact forest is available. The scale or resolution at which altitudinal studies are conducted (i.e. the distance between altitudinal bands) may also impact observed patterns, and can, in fact, produce completely different patterns of species richness (hump shaped or linear) (Rahbek 2005; Nogués-Bravo *et al.* 2008).

Climate change is driving a range of responses in species, communities and ecosystems (Steffen *et al.* 2009) and is predicted to lead to a variety of severe impacts including species extinction, range contraction and mismatched phenologies of interacting species (Hughes 2000; Williams *et al.* 2003). Distribution shifts are predicted for terrestrial biota (Sekercioglu *et al.* 2008; Kreyling *et al.* 2010; Laurance *et al.* 2011). Such shifts may occur when species climatic envelopes (the limits of individual species tolerances of environmental variables such as precipitation and temperature) move as a result of changed environmental conditions (Kullman 2001; Walther *et al.* 2002; Battisti *et al.* 2006).

Tropical species may be particularity vulnerable to climate-driven distribution shifts, as they tend to exhibit low ranges of thermal tolerance, linked to warmer, more seasonally stable environments (Laurance *et al.* 2011; Cadena *et al.* 2012). High altitude species are also particularly at risk and may show early signs of climate driven responses (Dirnbock *et al.* 2011). Another sensitive area to monitor is the ecotone between cloud forest and lower altitude forest, as climate change-driven drying may also produce early climate change responses (Foster 2001). Although changes to rainfall under future climate change scenarios are hard to predict (Reisinger *et al.* 2014), the average level of the cloud base is predicted to rise, which is particularly important for rainforest in the dry season where cloud stripping maintains high moisture levels (Still *et al.* 1999). An average temperature increase of 4°C by 2100 (a scenario that is perceived as being increasingly likely (Sanford *et al.* 2014) would result in an 800 m upward altitudinal shift in climatic conditions (Malhi & Phillips 2004). More optimistic climate change scenarios still predict upwards shifts of 450 m (Loope & Giambelluca 1998).

Australian biota are predicted to display significant range shifts, population declines and contraction, and extinctions, especially in areas with large numbers of regionally endemic species such as the tropical rainforests of the Wet Tropics. In Australia, there are few data on the impacts of climate change on the biota, especially invertebrates (but see Beaumont and Hughes (2002)). In order to understand how species are responding to climate change, we need to generate baseline data on the current distributions of species. By examining species distributed across tropical and subtropical rainforests in Australia and investigating how their altitudinal ranges are driven by environmental variables at different latitudes, we will be better able to predict how these species may respond to further climate warming.

We sampled moths along altitudinal transects in Border Ranges (BR) and Lamington (LAM) National Parks, which are within the same bioregion, in order to compare assemblages essentially drawn from the same regional species pool but influenced by key environmental differences, principally, in this case, aspect. Aspect is an important factor determining the structure of plant communities, and by extension, their insect herbivores. It is particularly important for the subtropical rainforests of New South Wales (NSW) and south-east Queensland, especially in winter, where a south facing slope may receive less than 10 h of sunlight in a day (Laidlaw *et al.* 2011). The importance of aspect is reduced in tropical rainforests closer to the equator, where south and north facing slopes receive similar amounts of daily sunlight. Consequently, the comparison of these subtropical transects should provide insight into the influence of local environmental conditions on moth assemblages.

Tropical rainforest may present a different suite of environmental drivers compared to subtropical forests. Accordingly, we established altitudinal transects at different tropical latitudes in Queensland to assess patterns of altitudinal stratification in locations with different climates, weather patterns and biogeographical histories. Here, we investigate whether tropical rainforest moths respond to changes in environmental conditions across altitudes in a similar way to subtropical assemblages. Tropical species may be less able to cope with a wide range of temperature fluctuations (Janzen 1967; Addo-Bediako *et al.* 2000; Tewksbury *et al.* 2008). We therefore hypothesize that the altitudinal stratification of moth assemblages in tropical areas will show strong turnover across altitudinal zones, as environmental factors that shift with altitude may be a major constraining factor on the distributions of individual species. This is the first study of a key insect herbivore group across multiple altitudinal gradients in Australia. It demonstrates the insights that can be gained from spatially replicated studies across substantial geographical distances using standardized sampling methodologies.

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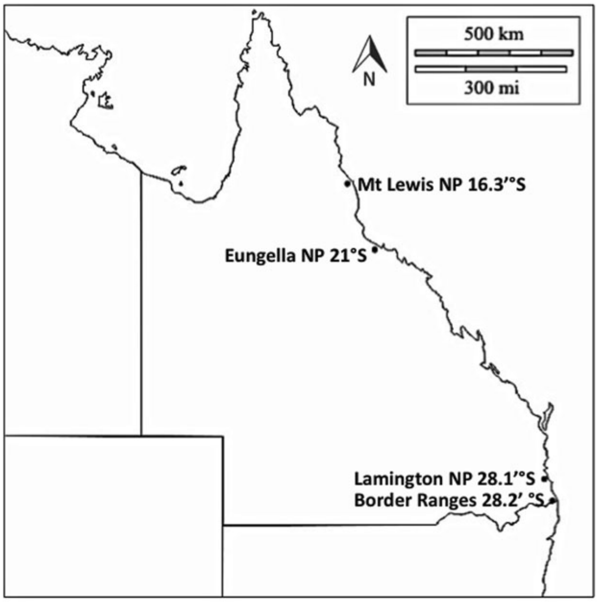

Fig. 1. Map of altitudinal gradient locations – Border Ranges National Park, northern Nsw, Lamington National Park, south-east Qld, Eungella National Park, Qld and Mt. Lewis National Park north Qld.

METHODS

At each of four locations (Fig. 1), we established an altitudinal transect, with four 20 × 20 m replicate plots within five or six altitudinal bands, separated by approximately 200 m of altitude. Within-band plots were placed at least 400 m apart and cool drainage areas associated with stream lines were avoided, however, at some locations this was not possible. At each plot, all woody stems with a diameter at breast height (dbh) greater than 5 cm were tagged and measured.

Lamington and Border Ranges National Parks

Lamington and BR National Parks are within the Gondwana Rainforests of Australia World Heritage Area, which contains one of the largest remaining areas of undisturbed subtropical rainforest in the world. The Investigating Biodiversity of Soil and Canopy Arthropods (IBISCA) Queensland Project, within which the moth data presented here were collected, was conducted in Lamington NP (latitude 28°1′S) between 2006 and 2010 (Ashton *et al.* 2011; Kitching *et al.* 2011). Four replicate plots were located within each of five elevational bands at 300, 500, 700, 900 and 1100 m a.s.l. We aimed to study assemblages across continuous rainforest gradients. The highest available altitude at Lamington is 1100 m a.s.l. and below 300 m much of the forest has been cleared with only remnant patches remaining. The vegetation across this transect is complex notophyll vine forest at the 300 m–900 m a.s.l. plots, and simple notophyll fern forest at the 1100 m a.s.l. plots, dominated *Nothofagus moorei* (Antarctic Beech) (Laidlaw *et al.* 2011). Where possible, plots were located on soils derived from Cainozoic igneous rock, with a north-easterly aspect (Strong *et al.* 2011). This region is subject to strong seasonality, with pronounced wet and dry seasons (Morand 1996). The base of the cloud cap sits between 800 m and 900 m a.s.l., which can provide 40% of total annual precipitation (Hutley *et al.* 1997).

Border Ranges National Park (latitude 28.2′°S), covers 318 km^2 and was logged between 1965 and 1975. Average annual rainfall in the region is 2500–4000 mm, and soils are kraznozems or ferrosols (Isbell 2002). As at Lamington, the base of the cloud cap sits between 800 m and 900 m a.s.l., and regulates moisture above this level. There is approximately 20 km of continuous subtropical rainforest between the Border Ranges and Lamington transects. At Border Ranges, the altitudinal extent is lower than at Lamington, therefore, four replicate plots were located at 300, 500, 700, 900 and 1010 m a.s.l. Border Ranges was slightly cooler than Lamington (see Appendix S1 for a description of temperature data collected during this study).

Eungella National Park (EU)

Eungella (EU) National Park is located approximately half way between the Wet Tropics of north Queensland and the subtropical rainforests of south-east Queensland (latitude 21°S). Some of the forest in this region has been subject to logging, mining and clearing for dairy farming. In 1941, the National Park was established and now conserves 300 km^2 of rainforest on primarily granitic soils (Graham 2006). Four replicate plots were located at 200, 400, 600, 800, 1000 and 1200 m a.s.l., encompassing the available altitudinal height at Mt. Dalrymple, Mt. Henry and Mt. William, down to 200 m a.s.l., below which most forest has been cleared. We collected soil samples and measured temperature using i-Buttons between 01.12.14 and 01.03.15. Mean temperatures decreased by 0.6°C per 100 m increase in altitude.

Mt. Lewis National Park

The Australian Wet Tropics World Heritage Area is the largest area of rainforest in Australia, covering 2 million hectares, in a series of fragmented patches. Mt. Lewis (ML) National Park (latitude 16.3°S) is located 80 km north-north-west of Cairns, and protects areas of both primary and logged upland rainforest, encompassing a total area of 229 km^2. Four replicate plots were located at 400, 600, 800, 1000 and 1200 m a.s.l. (the highest altitudinal extent at ML). Rainfall and temperature data were collected by researchers at James Cook University. Temperature data were collected at one plot per altitude between 01.01.2006 and 09.12.2008. Mean temperatures ranged between 21°C at 400 m a.s.l. to 16°C at 1200 m a.s.l., an average decrease of 0.5°C per 100 m. Daily rainfall data between 01.01.2006 and 01.01.2009 were collated from data from the Bureau of Meteorology's Australian Water Availability Project (http://www.bom.gov.au/jsp/awap/rain/index.jsp). Average annual rainfall ranged between 2140 mm at 400 m a.s.l. and 2924 mm at 1200 m a.s.l.

Sampling and light traps

Each altitudinal transect was sampled at the beginning and end of the wet season. Lamington was sampled from 14–30

October 2006 and 10 March–2 April 2007, as part of the IBISCA–Queensland project. Due to time constraints, two 300 m a.s.l. plots were not sampled in October 2006, and two 500 m a.s.l. plots were not sampled in March/April 2008. Border Ranges was sampled from 4–22 April 2011 and 27 October–12 November 2010, Mt. Lewis from 21 November–13 December 2009 and 1–18 April 2011, and Eungella from 4–30 November 2013 and 16 March–12 April 2014.

Moths were sampled using Pennsylvania light traps (Frost 1957), employing an 8-watt actinic UV bulb and run for three nights from dusk to dawn. We sampled both the canopy and understorey fauna, to account for vertical stratification (Schulze *et al.* 2001; Brehm 2007) and, therefore, get a better picture of the overall forest moth fauna (Beck *et al.* 2002). Understorey traps were situated approximately 2 m above the ground while those in the canopy were suspended in the upper half of the canopy approximately 20 to 35 m above the ground depending on the height of the forest. Canopy traps were located where canopy lines could be shot using a compound bow, understorey traps were placed within 10 m of the canopy lines. All moths with a forewing length greater than 1 cm and, in addition, all Pyraloidea (i.e. Crambidae and Pyralidae), were processed.

Analysis

Data from three nights of collection in the canopy and understory at each plot were pooled, and data collected at the beginning and end of the wet season were combined. We log transformed the data prior to multivariate analysis to overcome the influence of dominant species (Southwood & Henderson 2000). We constructed plot-based similarity matrices for each transect (LAM, BR, EU, ML) using the Bray–Curtis similarity measure (Bray and Curtis 1957). From these matrices non-metric multidimensional scaling was conducted, set to 1000 random starts, to produce ordination plots illustrating the relationships among assemblages of the plots. Using the same similarity matrices, we performed 'permutation-based analysis of variance' (PERMANOVA) (Anderson *et al.* 2008) using 1000 permutations to test for differences between *a priori* groups (i.e. adjacent altitudinal zones). Another plot-based Bray–Curtis similarity matrix for each transect (LAM, BR, EU, ML), was created, based on tree (dbh > 5 cm) assemblage data and a Mantel Test of correlation between the moth and tree assemblages performed using Spearman's rank correlation and 1000 permutations.

For each altitudinal transect, we used a distance-based linear model (DistLM) (Ardle & Anderson 2001) to identify plot-based environmental variables (biotic and abiotic) that were significantly correlated with moth assemblage structure. Across all transects, analysis incorporated data on altitude, tree species richness, air temperature (average, minimum and maximum). At Lamington, we also measured soil properties (moisture, pH, total organic content, potassium and carbon) and inferred fog events. At Eungella, we collected soil variables (sodium, nitrogen, calcium, clay and total organic content). The Mt. Lewis analysis incorporated rainfall, soil temperature, carbon, nitrogen and potassium. Many of these variables were highly correlated; the BEST procedure was used to run sequential tests to determine the combination of variables that had the best explanatory power (r^2). Significant variables ($P < 0.05$) were superimposed onto moth assemblage ordination plots.

As moth samples can be highly variable, and some sites were under-sampled, estimated moth richness is a more informative metric than observed species richness. We therefore present the total estimated species richness at each altitude which was estimated using sample-based rarefaction curves in EstimateS (Colwell 2013). We used the non-parametric Chao1 estimator, as this has been suggested for mobile organisms (Brose *et al.* 2003). We plotted the pairwise Bray–Curtis similarity of moth assemblages between plots against the altitudinal distance between plots in order to illustrate how the relationship between beta-turnover shifts across altitude. We also set out to establish indicator species which are altitudinally restricted in order to allow possible re-sampling in the future to monitor any climate change-driven shifts in altitudinal distributions. The indicator species presented here are those that are indicative of a single altitudinal band or of two or three altitudinal bands (e.g. found at 700 m, 900 m and 1100 m a.s.l.). IndVal (version 2.1; Dufrêne & Legendre 1997) analysis was conducted on all species represented by more than 35 individuals from a transect, as rare species are unlikely to be useful indicator species. This analysis was conducted in the R statistical environment (R Development Core Team 2010), using the IndVal procedure in the labdsv package (Roberts 2010). This method uses a randomization procedure to identify taxa that are indicative of *a priori* groups (i.e. altitudes). Based on the specificity (proportion of replicate plots, within groups, occupied by the species) and fidelity (proportion of the species within a group, across all replicates) of the species within a group, indicator values are calculated as a percentage. We selected species with an indicator value greater than 70%. Once this analysis had established statistically significant indictor species, those which were hard to identify, or had not yet been assigned a scientific name were removed from the final set of indicator species.

For the purposes of this paper, we only present those species that occurred across two or more of the four altitudinal gradients, as we were primarily interested in the altitudinal distribution of species at different latitudes. We also collated distributional data, which included altitude information, for the indicator species from specimens in the collections of the Queensland Museum, Brisbane, the Australian National Insect Collection, Canberra and the Australian Museum, Sydney. Although these specimen data do not encompass the entire ranges of these species, they provide some indication of the wider latitudinal and altitudinal distributions of the indicator species. We also note that a detailed analysis of canopy/understorey contrasts in moth assemblage composition will be the subject of a separate contribution.

RESULTS

Border Ranges National Park

Border Ranges sampling (November and April 2010) produced a total of 40 859 individuals belonging to

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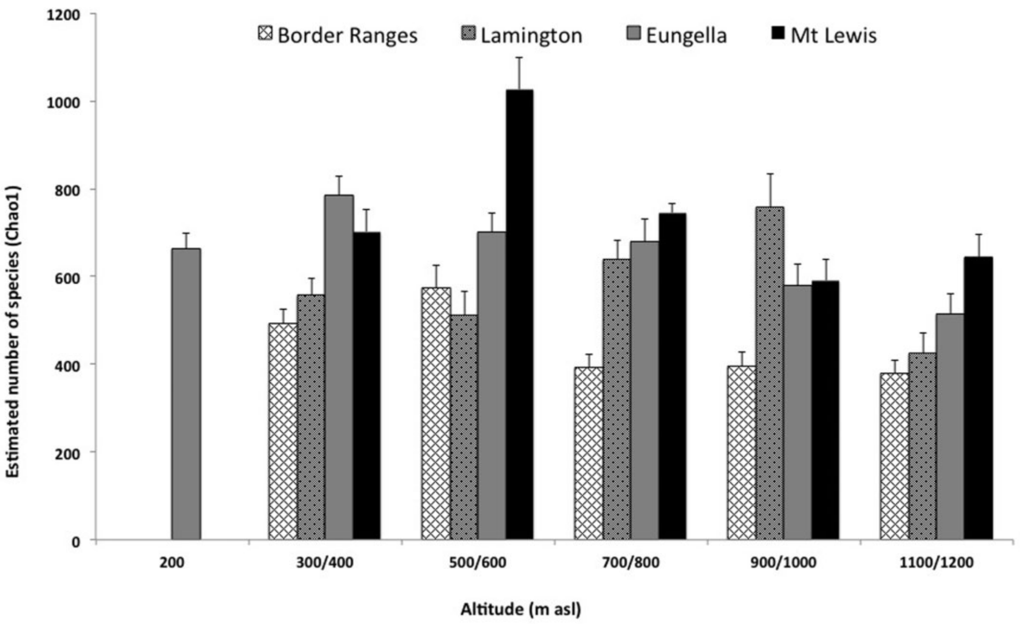

Fig. 2. Estimated mean moth species richness (Chao1 with standard deviation) across altitudinal gradients in two sampling occasions for Border Ranges, Lamington, Eungella and Mt. Lewis National Park.

612 species. Estimated species richness was highest at 500 m a.s.l. (Fig. 2). Minimum and median temperature and altitude were significantly correlated with the multivariate moth assemblage pattern (Fig. 3). A combination of minimum temperature and altitude explained most variation in moth assemblage composition (87%). Moth assemblages showed gradual turnover in composition across altitudes (Fig. 3). Pairwise comparisons of moth assemblages between adjacent altitudinal bands were all significantly different (Table 1). There was, however, no obvious change in the rate of turnover (beta diversity) with increasing altitude, as indicated by mean Bray–Curtis similarity of assemblages from adjacent altitudinal bands (Table 1). Moth and tree assemblages were significantly correlated (Rho = 0.55, $P = 0.001$).

Lamington NP

A total of 11 379 individuals belonging to 865 species were collected at Lamington National Park (October 2006 and March 2007). Estimated species richness peaked at 900 m a.s.l. (Fig. 2). There was strong turnover of moth assemblages with increasing altitude at Lamington (Fig. 3) with assemblages from adjacent altitudinal bands all significantly different (Table 1). There was no consistent pattern in the mean Bray–Curtis similarity of adjacent altitudes (Table 1). Environmental variables significantly correlated with moth assemblage structure at Lamington NP included altitude, number of fog events, minimum and average temperature and a suite of soil characteristics (Fig. 3; Appendix S2). A combination of altitude, minimum temperature and medium temperature best explained (83%) assemblage structure. Moth and tree assemblages were significantly correlated (Rho = 0.605, $P = 0.0010$).

Eungella NP

At Eungella National Park we sampled (November 2013 and March 2014) 23 906 individuals belonging to 1040 species. Species richness peaked at 400 m a.s.l. (Fig. 2). Moth assemblages showed a separation into 'lowland' (200, 400 and 600 m a.s.l.) and 'upland' (800 m, 1000 m and 1200 m a.s.l.) assemblages (Fig. 3), a pattern reflected in the results of PERMANOVA tests, which showed that the assemblages at 200 m and 400 m ($t = 1.3$, $P = 0.09$) and 400 m and 600 m ($t = 0.9$, $P = 0.5$) were not significantly different from each other. The average Bray–Curtis similarity of moth assemblages between pairs of altitudes was between 32.8 and 38.9 (Table 1), except between 600 m and 800 m a.s.l., which had an average Bray–Curtis similarity of 22.2, indicating higher turnover between these altitudes. Environmental factors significantly correlated with assemblage structure included maximum temperature, average temperature, soil organics and altitude (Fig. 3, Table 1). BEST analysis showed that the combination average temperature and altitude explained 78% of variation in moth assemblage structure. Moth and tree assemblages were significantly correlated (Rho = 0.436, $P = 0.001$).

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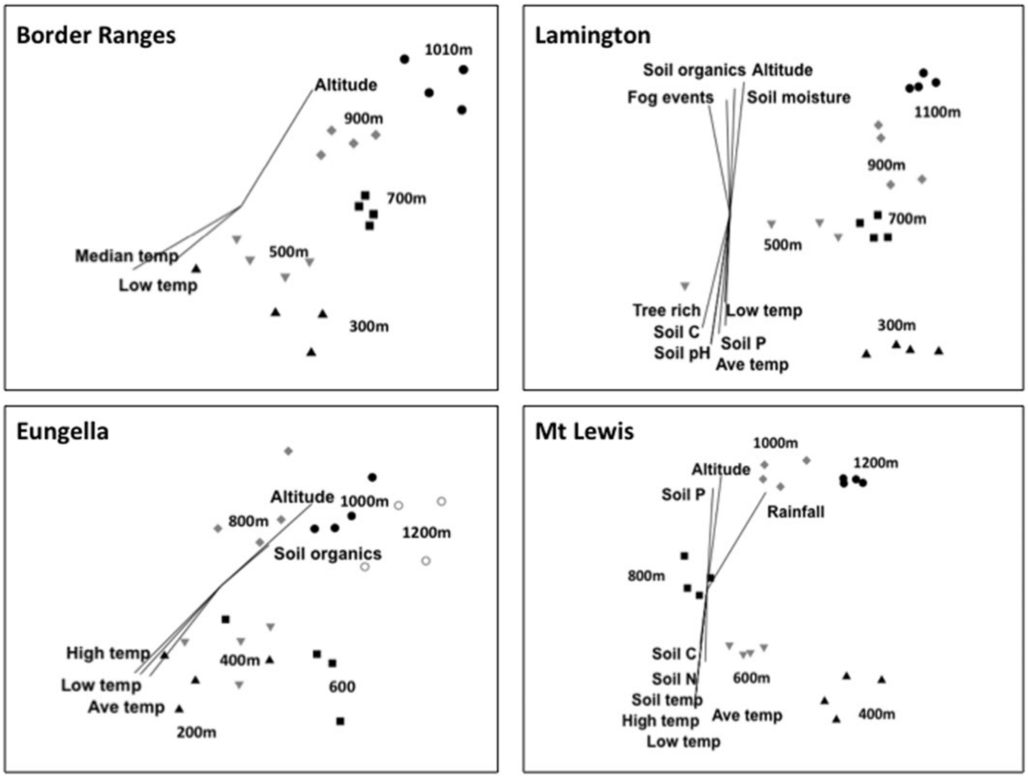

Fig. 3. Non-metric multidimensional scaling ordinations for (a) Border Ranges, (b) Lamington, (c) Eungella and (d) Mt. Lewis altitudinal transects with superimposed vectors. Only the significant variables were incorporated into this visual summary of variables that correlate with the observed moth assemblage pattern. The direction of each vector line indicates the positive or negative direction of the trend, and the length of each vector line indicates the strength of the relationship.

Mt. Lewis NP

Mt. Lewis sampling (November 2009 and April 2011) yielded a total of 17 258 individuals belonging to 1134 species, making it the most species-rich location examined in this study. Estimated species richness was highest at 600 m a.s.l. (Fig. 2). Moth assemblages at Mt. Lewis showed clear altitudinal stratification and several environmental and biotic variables correlated significantly with observed moth assemblage patterns (Fig. 3). The combination of maximum temperature, average temperature, soil temperature and altitude explained most variation in assemblage structure (92%). Moth and tree assemblages were significantly correlated (Rho = 0.548, $P = 0.001$).

Comparative analyses and indicator species

The relationship between beta diversity and altitude did not change across latitude, as illustrated by Fig. 4, which shows the pairwise similarity of plots plotted against altitudinal distance. IndVal analyses identified suites of altitudinally restricted species for each location: 26 species at Border Ranges, 15 at Lamington, 22 at Eungella and 9 at Mt. Lewis (see Appendix S3). Indicator species shared across two or more transects are presented in Table 2. Shared species, in general, occurred at higher altitudes in the tropical transects (EU and ML) and lower altitudes further south (BR and LAM). Collection data derived from museum specimens of species common to LAM and BR provide further evidence that the altitudes from which these species were collected is influenced by their latitude (Table 3).

DISCUSSION

Altitudinal and latitudinal patterns of diversity

We found that moth assemblages are sensitive to altitude, and are clearly altitudinally stratified in both tropical and subtropical rainforests. Altitudinal turnover has also been found elsewhere for moths, as well as beetles, frogs, mammals and plants (Brehm & Fiedler 2003; Escobar *et al.* 2005; Hemp 2006). Studies of Australian altitudinal gradients have shown altitudinal stratification in ants (Burwell & Nakamura 2011), Collembola (Greenslade & Kitching 2011; Maunsell

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Table 1. Metrics of pairwise comparisons between adjacent altitudinal bands, for Border Ranges, Lamington, Eungella and Mt. Lewis altitudinal gradients; permutational ANOVA results (*t* and *P* values), average Bray–Curtis similarity, and average distance among multivariate centroids. All altitudinal bands at Border Ranges, Lamington and Mt. Lewis are significantly different ($P > 0.05$). At Eungella, there was no significant difference between 200 and 400 m and 400 and 600 m at Eungella. There was no consistent pattern of increasing or decreasing similarity or distance among centroids across altitude

Location	Permanova		Average Bray–Curtis similarity
Border Ranges	*t*	*P*	
300 and 500	1.301	0.037	50.175
500 and 700	2.106	0.031	46.803
700 and 900	1.940	0.035	50.589
900 and 1100	2.012	0.027	45.949
Lamington	*t*	*P*	
300 and 500	1.801	0.036	25.976
500 and 700	1.439	0.026	35.029
700 and 900	1.577	0.028	38.236
900 and 1100	1.816	0.031	38.31
Eungella	*t*	*P*	
200 and 400	1.319	0.088	37.562
400 and 600	0.989	0.512	36.919
600 and 800	1.470	0.033	22.248
800 and 1000	1.280	0.049	32.746
1000 and 1200	1.284	0.032	38.957
Mt. Lewis	*t*	*P*	
400 and 600	1.712	0.033	31.099
600 and 800	1.664	0.025	34.075
800 and 1000	1.717	0.036	29.353
1000 and 1200	1.561	0.030	35.640

et al. 2012) and birds (E. Leach. pers. comm.). The altitudinally stratified moth assemblages at all four locations suggest that altitude (or some associated correlate) is important in structuring moth communities. As the vegetation assemblage structure also exhibited altitudinal turnover, and was significantly correlated with moth assemblages, it is difficult to untangle the relative importance of these abiotic and biotic drivers. We hypothesized that moth species in the tropics would be more sensitive to altitude than those in the subtropics; however, the rate of turnover did not shift with decreasing latitude. If tropical species were more altitudinally restricted, we would expect the beta-diversity turnover across altitudinal distance to be steeper in the tropical locations, and perhaps, more altitudinally restricted indicator species. What we found was a uniform relationship between beta-turnover and altitude across tropical and subtropical gradients and few altitudinally restricted indicator species in the tropical locations.

There was strong altitudinal turnover in moth assemblages in both subtropical and tropical transects but with some key differences. In the subtropical locations, we found stepwise turnover in assemblage composition and a unique moth assemblage at 1100 m a.s.l. associated with a change in the vegetation from complex notophyll vine forest to simple microphyll fern forest with a monodominant canopy of *Nothofagus moorei*. In the tropical transects, however, there was greater turnover at mid-altitudes separating moth assemblages into lowland and upland faunas. In the Wet Tropics, within which our Mt. Lewis transect is located, a similar division is found in vertebrate assemblages, including mammals (Williams 1997) and birds (Williams *et al.* 2010). These observed differences in turnover between tropical and subtropical transects are also apparent in the vegetation assemblages and may be largely driven by the warmer, wetter conditions in the tropics, influencing the height of the cloud cap and the stability of moisture through time. The subtropical higher altitudinal sites may exhibit more frequent drying, producing a gradual turnover in assemblage structure across altitude, driven primarily by the altitudinal shifting of environmental variables rather than by the presence of the cloud cap.

Although fewer species were collected from Border Ranges (612 spp.) than Lamington (865 spp.), both transects displayed stepwise turnover in moth assemblages with increasing altitude, thus their differing aspects did not dramatically influence the pattern of altitudinal stratification. We recorded a lower average temperature gradient at Border Ranges compared with Lamington, which may be due to microhabitat effects, different aspects or to high rainfall levels that occurred during the year temperature was recorded at Border Ranges. The temperature differences, between these locations, which are only 20 km apart, may influence the altitudinal ranges of species. Of the seven indicator species found at both locations, six had a distribution extending one altitudinal band lower at Border Ranges National Park. This suggests that these species are particularly sensitive to temperature. That the distributions of these shared indicator species are driven by temperature is supported by museum specimen data, which indicate they are generally found at higher altitudes at lower latitudes and at lower altitudes at higher latitudes. For example, *Xylodryas leptoxantha*, found at 900 m and 1100 m a.s.l. at Lamington, and 700 m, 900 m and 1100 m a.s.l. at Border Ranges, has been recorded as low as 245 m in Coffs Harbour, NSW (30°2 S). Three species collected at Lamington and Border Ranges, *Dyscheralcis crimnodes, Heterochasta conglobate* (Geometridae, Larentiinae) and *Eurychoria fictilis* also occur in warmer tropical forests, but have been only recorded at or above 1500 m a.s.l., suggesting that these species altitudinal distributions are restricted by temperature and/or other correlated factors that shift with altitude (all species mentioned above belong to Geometridae, Ennominae unless

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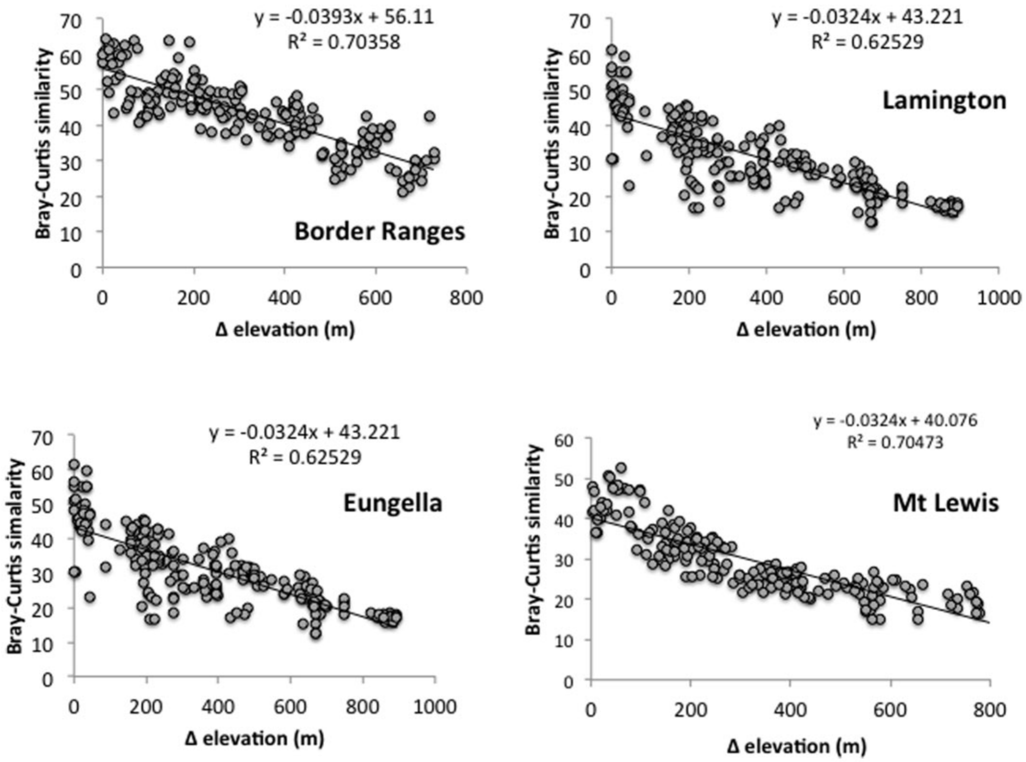

Fig. 4. Pairwise Bray–Curtis dissimilarity values of moth assemblages, plotted against the difference in actual altitude at Border Ranges, Lamington, Eungella and Mt. Lewis.

Table 2. Species of moth that are common across at least three of our four altitudinal gradients – Border Ranges, Lamington, Eungella and Mt. Lewis. Generally, species are found at higher altitudes in our tropical transects and lower altitudes further south

Species	BR	LAM	EU	ML
Larophylla amimeta	700–1100	900–1100		
Lyelliana dryophylla	700–1100	900–1100		
Eurychoria fictilis	700–1100	900–1100		
Heterochasta conglobata	700–1100	900–1100		
Dyscheralcis crimnodes	900–1100	700–1100		
Xylodras leptoxantha	700–1100	900–1100		
Middletonia hemichroma	900–1100	1100		
Conogethes punctiferalis		300	400–800	
Pleuropyta bateata		300	400	
Orthaga thyrusalis		300	400–600	
Taxeotis sp.		500–900	600–1000	
Prorodes mimica		300	400–800	600–1200
Taxeotis epigea		500–900	1000	1000
Endrotricha mesenterialis		1100	500–1000	1200
Agris convolvulii		1100	600–1000	
Prophanta caletoralis		400–600	400–600	
Paradromulia ambigua			800–1000	400–800
Parotis atlitalis			400–800	600
Maruca testulalis			400–600	600–1200
Calamidia hirta			800	800
Endrotricha dispergens			400	1200

Table 3. Indicator species common between Lamington (LAM)and Border Ranges (BR). In all but one case (*Dyscheralcis crimnodes*) the indicators at BR are present one altitudinal band below those at LAM. Museum records gathered for these species illustrate that indicators are found at higher altitudes in North Queensland and lower altitudes further south in NSW, supporting the hypothesis that these species distributions are primarily driven by temperature

Name	LAM (m a.s.l.)	BR (m a.s.l.)	Museum records location	Lat Ca (S)	Altitude (m a.s.l.)
Xylodryas leptoxantha	900, 1100	700, 900, 1100	Bunya Mountains, QLD	26°29	1065 m
			Gibraltar Range, QLD	29°28	950 m
			Acacia Plateau, NSW	28°19	915 m
			Clyde Mountain, NSW	35°24	730 m
			Cambewarra Mountain NSW	34°46	620 m
			Dorrigo NP, NSW	30°22	520 m
			Mt. Warning, NSW	28°24	500 m
			Up Allyn R, NSW	32°10	455 m
			Coffs Harbor	30°15	245 m
Dyscheralcis crimnodes	700, 900, 1100	900, 1100	Bellenden-Ker, north QLD	17°15	1560 m
			Paluma, QLD	19°1.7	900 m
Heterochasta conglobata	900, 1100	700, 900, 1100	Bellenden-Ker, QLD	19°0.6	1560 m, 1500 m
			Mt. Bartie Frere, QLD	17°23	1500 m
			Clyde Mt., NSW	35°24	731 m
Eurychoria fictilis	900, 1100	700, 900, 1100	Bellenden-Ker, QLD	19°0.6	1560 m
			Mt. Edith, QLD	17°4.5	1035 m
Lyelliana dryophylla	900, 1100	700, 900, 1100	Killarney, NSW	28°18	920 m
Larophylla amimeta	900, 1100	700, 900, 1100	New England, NSW	30°29	1585 m
			Coneac, NSW	31°51	900 m
			Killarney, NSW	28°18	920 m
			Cambewarra Mountain, NSW	34°46	620 m
Middletonia hemichroma	1100	900, 1100	Barrington Tops, NSW	31°56	1545 m
			New England, NSW	30°29	1615 m
			Springbrook, NSW	28°11	700 m

otherwise noted). In addition, indicator species that occurred at two or more of our latitudinal locations generally occurred at higher altitudes towards the tropics, likely tracking their physiological envelopes or that of their host plants.

Altitudinal patterns of diversity

Species richness generally showed a mid-altitude peak, similar to a number of previous altitudinal moth studies (Brehm *et al*. 2007; Choi & An 2010). Although there was variation in which particular altitude had the highest estimated richness at each location, it was generally between 400 and 600 m a.s.l. How do alternative explanations help interpretation of our data from the subtropical and tropical transects? The 'mid-domain effect' in which mid-altitude peaks are produced by the random overlap of species occurrences across altitudes which are postulated to represent homogenous habitats (Colwell & Lees 2000) is fundamentally a neutral explanation. Accordingly, unless host plant distributions form a mid-altitude peak, this explanation seems weak for moth distributions. There is, generally, no such peak in the plant data (see Appendix S4). Another explanation is that mid-altitude peaks are the result of overlapping ecotones from adjacent ecosystems (e.g. the coincidence of the upper bounds of low altitude ecosystems with the lower bounds of the upper altitudes ecosystems (Terborgh 1971)). Finally, species-area effects could produce a mid-altitude peak when lower altitudes have been substantially modified by human activities (McCoy 1990), a likely contributor to the patterns we observe simply because, for all of our transects, it was not possible to sample below around 300 m a.s.l. as most of the lower forest had been cleared. Our results, based on Australian altitudinal transects up to 1200 m a.s.l. (the highest available altitudinal extents) also may not reach high enough altitudes required in order to capture the high-altitude decline in species richness observed elsewhere (monotonic declines) or the more clearly defined mid-altitudinal peaks observed in some tropical locations.

Altitudinal gradients – indicators of climate change

High altitude communities are isolated from other mountain tops and accordingly, have lower rates of immigration and higher rates of extinction (Lomolino 2001). Mountain ecosystems today represent areas of high conservation concern (Foster 2001), containing

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high numbers of endemic, endangered and climate sensitive species, often with small altitudinal ranges (Loope & Giambelluca 1998; Williams *et al.* 2003). Mountain ecosystems are, by virtue of these features, also sensitive indicator systems, and may be used as early warning tools for the monitoring of climate change responses (Beniston *et al.* 1997). We have established four suites of altitudinally restricted moth indicator species in Australia and demonstrated (for the shared species) their altitudinal ranges shift upslope towards the tropics. These insects are suitable climate indicator species, as our analysis of their general distributions shows that they are highly sensitive to climate. They are easy to identify and readily collected (Kitching & Ashton 2014). The utility of these indicators in the tropics, where there can be large inter-annual fluctuations in insect populations, may require additional testing. It is also important to note that there are physical limits to further distribution shifts of species to higher altitudes and latitudes in Australia, as, in many cases, there are simply no higher altitudes or latitudes accessible with suitable habitat or host plants.

Our results show that the altitudinal stratification of moths is ubiquitous across different latitudes, forest types and biogeographic areas. This research has established baseline data which can be used to assess future impacts of climate change. These data, however, have value beyond simply setting baselines: they have added to our knowledge of how a hyper-diverse insect group is distributed across environmental gradients – altitudinally and latitudinally. An intrinsic quality of this type of extensive baseline research is the novel and comprehensive faunistic and biogeographical datasets that are generated concerning groups of organisms for which very little existing information has been available in Australia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. Temperature data from Lamington and Border Ranges.

Appendix S2. DISTLM analyses of correlations between environmental variables and moth assemblages.

Appendix S3. Moth species which met indicator species criteria.

Appendix S4. Tree species richness across altitude at four locations.

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