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## **The IBISCA-Queensland Project**

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PO Box 3300, South Brisbane 4101, Australia  
Phone 06 7 3840 7555  
Fax 06 7 3846 1226  
Email [qmlib@qm.qld.gov.au](mailto:qmlib@qm.qld.gov.au)  
Website [www.qm.qld.gov.au](http://www.qm.qld.gov.au)

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# Macrolepidopteran assemblages along an altitudinal gradient in subtropical rainforest - exploring indicators of climate change

Louise A. ASHTON

Roger L. KITCHING

Sarah C. MAUNSELL

Darren BITO

Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan Qld 4111, Australia. Email: l.ashton@griffith.edu.au

David A. PUTLAND

Growcom, PO Box 202, Fortitude Valley Qld 4006, Australia.

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## ABSTRACT

Moth assemblages have been widely used to estimate patterns of beta-diversity in forest ecosystems. As part of the IBISCA-Queensland project we examined patterns of diversity in a large subset of night-flying moths along an altitudinal gradient in subtropical rainforest. The permanent IBISCA-Queensland transect located in Lamington National Park, south-east Queensland, Australia, spans altitudes from 300 metres (m) to 1100 m above sea level (a.s.l.) within continuous, undisturbed rainforest. We sampled four replicate plots at each of five altitudes (300, 500, 700, 900, 1100 m a.s.l.). A total of 11 379 individual moths were sampled, belonging to approximately 865 morphospecies. Moth assemblages displayed a strong altitudinal signal at each of two sampling periods (October 2006 and March 2007). The results show that cloud forest above 900 m a.s.l. where *Nothofagus moorei* becomes dominant, contains a number of moth species that are restricted to the high elevation forest and these species may be most threatened by climatic change. The analyses presented here suggest a set of 18 moth species which may be useful as part of a multi-taxon predictor set for future monitoring of the impact of global warming on forest biodiversity. □ *climate change, subtropical, rainforest, IBISCA, Lepidoptera.*

Climate change is having a marked effect on terrestrial ecosystems, as evidenced by poleward and elevational shifts in the distributions of many species of plants and animals (Bale *et al.* 2002; Grabherr *et al.* 1994; Hickling *et al.* 2006; IPCC 2007; Parmesan 1996). The IBISCA-Queensland project aimed to quantify the relationship between climate and biodiversity along an altitudinal gradient

in subtropical rainforest and, by so doing, develop robust measures for future monitoring of climate change impacts (Kitching *et al.*, 2011). This paper investigates moth assemblages along this altitudinal gradient, and suggests a group of moth species that may be used to monitor altitudinal shifts in distributions.

It has been predicted that climatic warming over the course of the next century will cause an increase in global average temperature of between 1.4°C and 5.8°C (IPCC 2007). Changes to climatic conditions are likely to result in increased weather variability and extreme weather events (Easterling *et al.* 2000), leading to dramatic changes in ecosystem dynamics (Weltzin *et al.* 2003). The responses of ecosystems to climate change are wide and varied, and are confounded by species interactions and feedback relationships. Species interactions may enable some groups to adapt to new conditions, for example, through shifts in community composition and simplification of food webs (Suttle *et al.* 2007). However, changed conditions may exceed the environmental thresholds for many species leading to changes in distribution or, if this is not possible, local or even global extinction (Pounds *et al.* 1999; Thomas *et al.* 2004). Biological responses due to climate change, such as distribution shifts and phenological changes, have already been measured in a variety of taxa and ecosystems (Parmesan & Yohe 2003; Walther *et al.* 2002).

Studies of altitudinal gradients are an effective method of investigating and monitoring the impacts of climate change because they allow for a wide range of changing environmental variables to be observed over small geographical areas. They provide ideal situations to explore how species distributions may be associated with, and limited by, climatic factors, while minimising confounding historical factors that influence species distributions over latitudinal gradients (Fiedler & Beck 2008; Shoo *et al.* 2006). Altitudinal gradients potentially provide insight into climate change impacts, because they encompass steep temperature and moisture gradients, leading to stratified environmental parameters and faunal assemblages (Hodkinson 2005; Shoo *et al.* 2006). Many studies have shown that montane cloud forests are highly sensitive to, and threatened by, climate change (Foster 2001; Nadkarni & Solano 2002; Pounds *et al.* 1999; Still *et al.* 1999; Williams *et al.* 2003).

A medium-range climate change scenario predicts an average global temperature increase of 4°C over the next 100 years, which would push current climate envelopes around 800 m upwards in altitude (Malhi & Phillips 2004). Even an optimistic climate change scenario predicts upward shifts in climatic envelopes of up to 450 m (Loope & Giambelluca 1998). However, these estimates are likely to vary regionally and will also depend on local conditions. Despite this, the estimates are of particular concern because cloud forest ecosystems often encompass rare and endemic species with limited altitudinal ranges (Foster 2001). Some plant species in tropical montane forests, for example, display ranges of less than 300 m (Loope & Giambelluca 1998).

IBISCA-Queensland was a collaborative, international investigation of patterns of diversity and ecosystem processes along an altitudinal gradient. This study investigated which species are sensitive to climatic variability associated with increasing altitude and therefore most likely to be sensitive to climate change and, by doing so, sought to establish current baseline information, laying the foundation for longer-term monitoring programs. Study sites for this project are located in the UNESCO World Heritage listed Lamington National Park, noted for its isolated patches of montane, Antarctic Beech (*Nothofagus moorei*) dominated, 'cool temperate' rainforest.

The collaborative approach of the IBISCA-Queensland project involved a broad range of taxonomic and ecological specialists each working to a fixed experimental design. This helped ensure that a wide range of taxa were studied, producing a multi-faceted baseline dataset describing a range of invertebrate and plant assemblages. The culmination of the study will be a powerful 'predictor set' (Kitching 1993) that can be re-sampled in the future in order to monitor impacts of climate change. In this paper we examine the potential of moths for inclusion in this predictor set. Monitoring protocols such as those which will be created by this study

will provide important tools for understanding biotic responses to climate change, subsequently facilitating adaptive management strategies that encompass such responses. Moths are potentially particularly useful in this regard because they are diverse, relatively well-known taxonomically and, as herbivores, reflect closely the vegetational health of the forest (Kitching *et al.* 2000; Scoble 1995). They are also sensitive to environmental variables, being strongly affected by temperature and precipitation and resource limiting factors such as food availability (Holloway *et al.* 1992). Moths have been used as indicators of environmental change and the success of restoration in a variety of different terrestrial ecosystems, such as rainforests, temperate forests and agro-ecosystems (Beccaloni & Gaston 1994; Brown & Freitas 2000, New 1997; Ricketts *et al.* 2001).

The current study posed the following two questions by sampling moth assemblages along an altitudinal transect within the subtropical forest of Lamington National Park.

- (1) Do moth assemblages change with altitude?
- (2) If so, which moth species show the strongest altitudinal signal thus making them potentially appropriate indicators of future climate change within Lamington National Park?

## METHODS

### Study site

Lamington National Park is a protected area of forests covering 206 km<sup>2</sup> and includes the Lamington Plateau, which is located across the Queensland-New South Wales border, a part of the larger Tweed Caldera region (Willmont 2004). Lamington National Park is part of the Gondwana Rainforests of Australia, a group of eight national parks in south-east Queensland and north-east New South Wales, and has been World Heritage listed since 1994. The area mainly lies upon Cainozoic igneous rock, derived from volcanic eruptions. Lamington Plateau

was formed by a now extinct shield volcano, centred at Mount Warning, in north-eastern New South Wales (Stevens 1997).

The altitudinal transect that is the basis of the IBISCA-Queensland project was established in continuous rainforest within the Green Mountains section of Lamington National Park and encompasses a steep temperature and moisture gradient (Strong *et al.* 2011). The transect encompasses altitudes between 300 and 1100 m a.s.l. with four replicate plots located within coarse elevational bands centred upon altitudes of 300, 500, 700, 900 and 1100 m a.s.l. Lower elevation plots (300 and 500 m a.s.l.) are located within the valley of West Canungra Creek. Middle and high elevation plots (700 m a.s.l. and above) are located along the western slopes of the same valley, along the access road to Green Mountains, O'Reilly's Guesthouse and the Border Track leading to Mount Bithongabel. Low altitude plots are characterised by dryer, hotter conditions and the high altitude sites experience lower temperatures and higher moisture levels (Strong *et al.* 2011). The cloud cap, the lower limit of which sits between 800 and 900 m a.s.l. depending on season and weather conditions, is likely to have a strong influence on local climate.

The rationale for the overall project and the locations of study plots are presented by Kitching *et al.* (2011). Strong *et al.* (2011) describe the climate and soil conditions prevailing across the selected altitudes. Laidlaw *et al.* (2011) describe vegetation changes along the transect. The low elevation plots at 300 m a.s.l. are classified as complex notophyll vine forest (*sensu* Webb and Tracey 1978) dominated by Hoop Pine (*Araucaria cunninghamii*). The mid-elevation plots, 500, 700 and 900 m a.s.l., are also complex notophyll vine forest (McDonald & Hunter 2008). The highest altitude plots at 1100 m a.s.l. are simple microphyll fern forest dominated by Antarctic Beech (*Nothofagus moorei*).

## Moth collection and identification

**Trap design.** Moths were sampled using modified Pennsylvania light traps (Frost 1957; Kitching *et al.* 2005) fitted with 12 volt gel-cell batteries. Traps employed a vertical actinic tube, producing short wavelength blue light. This tube was surrounded by three transparent vanes that intercepted and knocked down insects attracted to the light into a bucket below. The bucket contained a Sureguard® resin strip impregnated with Dicholorvos™ insecticide which killed moths *in situ*. Traps were set daily and ran for 12 hours from 6 pm to 6 am.

Two Pennsylvania light traps were run simultaneously on a plot on each trapping night, with one trap at ground level and one in the forest canopy. Canopy traps were raised to a height of approximately 35 metres, depending on the height of the canopy, and ground traps were raised a few metres above the ground and hung from a low branch. The light traps were placed at both ground and canopy level to ensure a broader sampling of moth diversity (Brehm 2007; Beck *et al.* 2002; Schulze *et al.* 2001).

**Sampling regime.** Sampling took place in October 2006 and March 2007. Two traps (ground and canopy) were set simultaneously for three nights at each plot. Traps were emptied daily and all arthropods caught were transferred to sample containers and taken to a field laboratory. In total, 120 samples were collected in the first sampling period, from 14<sup>th</sup> to 31<sup>st</sup> October 2006, and 108 samples were collected in the second sampling period, from 10<sup>th</sup> March to 2<sup>nd</sup> April 2007. Two of the four 500 m a.s.l. plots were not sampled in March 2007 due to time constraints. In order to minimise the negative effect of moonlight on catches (Muirhead-Thomson 1991; Yela & Holyoak 1997; Nowinszky 2004) no trapping was carried out five days either side of the full moon.

**Processing catches.** Moths with a wing length of 1 cm or more were processed, thus representing the macrolepidoptera. In addition, all moths belonging to the superfamily Pyraloidea (i.e. the families Crambidae and Pyralidae), regardless of their size, were also processed. This group was

targeted in addition to the macrolepidoptera because of the relatively good resources available for the identification of many subgroups within the Pyraloidea (Common 1990).

Based on external characteristics, moths were sorted to species, hereafter referred to as 'morphospecies' and each morphospecies was assigned a unique code number. As sorting proceeded, a reference collection including at least one representative of each morphospecies was assembled. Individuals in a given sample that could be readily identified as belonging to an existing, numbered morphospecies were recorded and discarded. Identification to generic and species level was carried out principally by comparison with the reference collections available in the Queensland Museum, Brisbane, Australia. Identified material from previous surveys in the Lamington region held by the Arthropod Biodiversity Laboratory at Griffith University was also used in addition to printed and electronic resources (Common 1990; [www.ento.csiro.au/anic/moths.html](http://www.ento.csiro.au/anic/moths.html)).

## ANALYSIS.

Data from the paired canopy and ground-level traps across three trap nights were pooled into one dataset for each plot. Quantitative samples of insects are often characterised by zero-inflated data with a small number of very abundant species and this was found to be the case in our samples. Multivariate analyses were based on the proportion of species within samples and these were log transformed in order to reduce the impact of highly dominant species. The multivariate analysis package Plymouth Routines in Multivariate Ecological Research [PRIMER 6™] (Clarke & Gorley 2006) was used to investigate patterns of moth assemblages across altitudinal zones.

Permutational multivariate analysis of variance (PERMANOVA) was conducted in PRIMER 6 with PERMANOVA+ add-on software (Anderson *et al.* 2008), testing for significant differences in the moth assemblage composition among a number of *a priori* groups, in this case the five

altitudinal bands. This analysis was run with 9999 permutations, using the Bray-Curtis dissimilarity measure (Bray & Curtis 1957). The pair-wise post-hoc comparisons of each altitudinal group were used here to explore differences between altitudinal bands. Owing to time constraints, in the October 2006 sampling session, only three of the 300 m a.s.l. sites were sampled, and in March 2007 only two of the 500 m a.s.l. sites were sampled. Because of this discrepancy pair-wise comparisons between altitudes for the 500 m sites in the March 2007 have been excluded to avoid unbalanced replication.

The Bray-Curtis dissimilarity measure (Bray & Curtis 1957) was also used to create a distance matrix. From this matrix, non-metric multi-dimensional scaling (NMDS), set to 100 random starts, was used to produce ordination plots illustrating the relationship of moth assemblages among sampling sites. The NMDS approach to analysis has been adopted successfully in similar studies of moths, and is useful in detecting patterns in assemblages that tend toward high diversity and low evenness (Beck & Chey 2008; Brehm & Fiedler 2004; Fielder *et al.* 2008).

Relationships between environmental variables and overall moth assemblage composition were investigated using the Distance-based Linear Model (DistLM) function in PERMANOVA+. Marginal tests available within the DistLM procedure investigate which environmental variables are significantly correlated to the variation in moth assemblage composition. The vectors of significant environmental variables were then superimposed on NMDS ordinations of moth assemblages. The length of vectors indicates the strength of the correlation and their direction indicates whether the environmental variables were positively or negatively correlated with the observed patterns of assemblage composition. Environmental vectors which were measured as part of the IBISCA-Qld project included soil moisture, soil organics, tree species richness and median temperature. The methods of collection

of this environmental data are summarised by Strong *et al.* and Laidlaw *et al.* (2011). A metric called 'fog events' was also used, indicating days when weather data recorders showed periods of 100% atmospheric humidity, thought to reflect fog events, although some inaccurate readings may result from the data loggers being wet from rainfall.

We also investigated the extent of variation in moth assemblage explained by spatial-auto correlation, in comparison to altitudinal differences. To this end, latitudes and longitudes of the site locations were first centred and rotated using PCA ordination with PRIMER 6, and the resultant x and y coordinates were used to generate a between-site distance matrix based on Euclidean distance measures. Similarly, another distance matrix (based on Euclidean distance measures) was generated using altitudinal differences between sites. Two separate Mantel tests (available from the RELATE routine within PRIMER 6) were conducted to calculate correlation coefficients and associated *P* values between distance matrices of moth assemblages and site locations, and moth assemblages and altitudinal differences.

## RESULTS

A total of 11 379 moths belonging to 865 morphospecies was sampled in this study; 3490 individuals in October 2006 and 7889 in March 2007. Samples collected in October 2006 showed a mid-elevation peak in species richness which was highest at 500 m a.s.l. No such peak was apparent in the March 2007 data, although it should be noted that sampling effort at 500 m a.s.l. in March 2007 was restricted to two sites.

Ordination plots of moth assemblages sampled in October 2006 (Fig. 2a) and March 2007 (Fig. 2b) show a clear altitudinal signal in assemblage structure between 300 and 1100 m a.s.l. The PERMANOVA analysis indicated a highly significant relationship between altitude and moth assemblages for both the October 2006 (pseudo-*F*

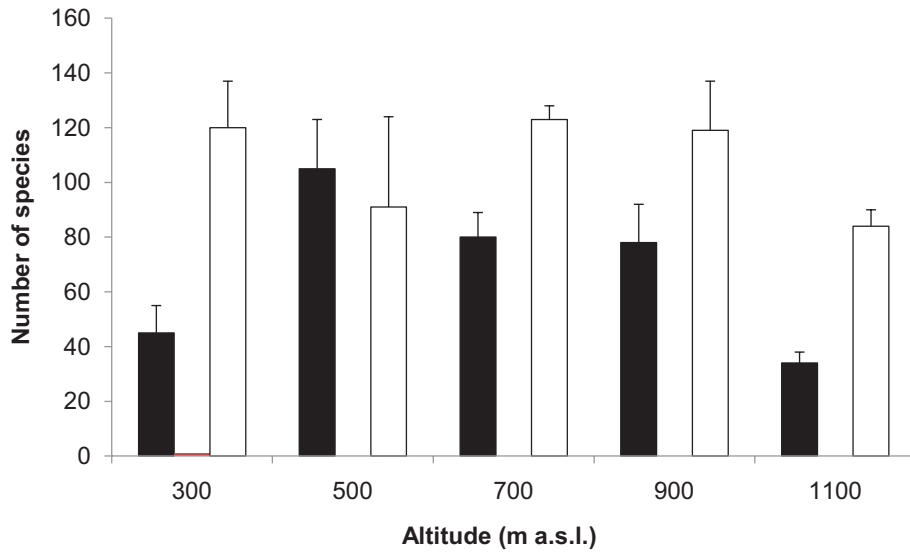


FIG. 1. Mean moth species richness (+ 1 x standard deviation) at each sampled elevation in October 2006 (black bars) and March 2007 (open bars). In March 2007, only two of the four 500 m a.s.l plots were sampled, therefore the complete range is shown for this sampling occasion.

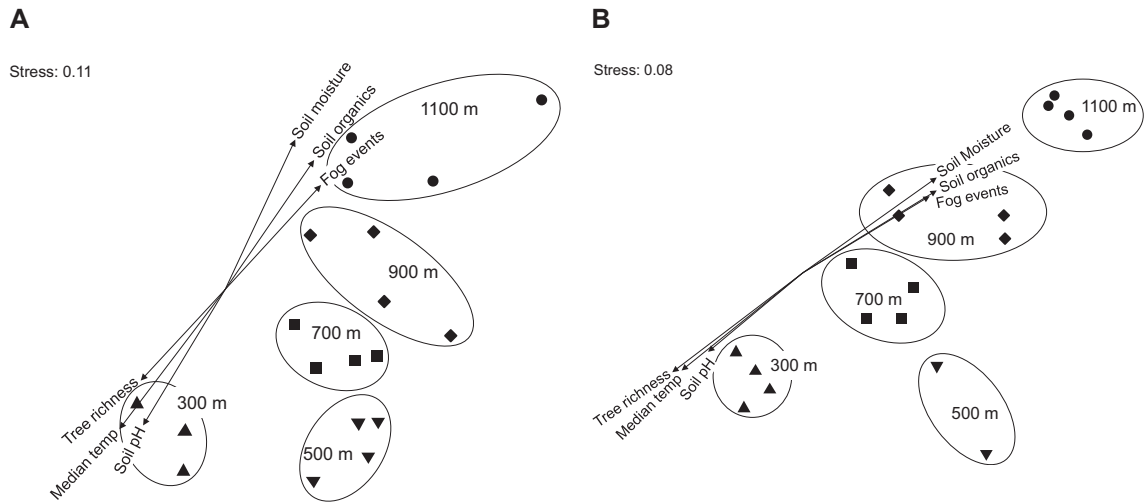


FIG. 2. NMDS ordination plots of moth assemblages, based on log transformed proportion of morpho-species, collected in (a) October 2006 and (b) March 2007. Only three of the 300 m a.s.l. plots were sampled in October 2006, and only two of the 500 m a.s.l. plots during March due to time constraints. Superimposed vectors are environmental parameters significantly correlated to the assemblage composition.

## Macrolepidopteran assemblages along an altitudinal gradient

TABLE 1. Results of pair-wise post-hoc comparisons of moth assemblages between altitudinal (m a.s.l.) groups for October 2006 and March 2007 (500 m sites have been excluded from March 2007 analysis due to low replication), showing degrees of freedom (df), *t* and *P* values. Analyses were based on log transformed proportions of morphospecies.

Comparison	October 2006			March 2007		
	df	<i>t</i>	<i>P</i>	df	<i>t</i>	<i>P</i>
300 and 500 m	5	1.85	0.030	-	-	-
300 and 700 m	5	1.83	0.029	6	2.32	0.028
300 and 900 m	5	2.02	0.028	6	2.35	0.029
300 and 1100 m	5	2.02	0.026	6	3.55	0.031
500 and 700 m	6	1.28	0.057	-	-	-
500 and 900 m	6	1.69	0.030	-	-	-
500 and 1100 m	6	2.02	0.029	-	-	-
700 and 900 m	6	1.26	0.062	6	1.60	0.028
700 and 1100 m	6	1.69	0.030	6	2.86	0.028
900 and 1100 m	6	1.39	0.025	6	2.05	0.026

TABLE 2. Average similarities between and within altitudinal (m a.s.l.) groups, based on log transformed proportions of morphospecies, from four plots at each altitudinal band collected in (a) October 2006 and (b) March 2007.

a) Collection from October 2006					
	300 m	500 m	700 m	900 m	1100 m
300 m	44.89				
500 m	24.23	40.16			
700 m	21.89	33.36	36.34		
900 m	16.18	25.60	32.24	37.27	
1100 m	12.96	14.45	19.95	27.23	32.03

b) Collection from March 2007					
	300 m	500 m	700 m	900 m	1100 m
300 m	50.83				
500 m	20.14	38.30			
700 m	22.12	27.79	42.23		
900 m	16.43	23.01	28.12	36.03	
1100 m	07.73	11.77	14.06	26.44	56.23

= 2.95,  $P = 0.001$ ) and March 2007 datasets (pseudo- $F = 5.13$ ,  $P = 0.0001$ ). Pair-wise post-hoc comparisons, testing between each of the altitudinal groups (Table 1), showed that most altitudinal groups were significantly different from each other, with the exception of 500 and 700 m, and 700 and 900 m, but only in the October 2006 results, when fewer moths were collected.

Marginal tests within the DistLM routine showed the same six environmental variables significantly correlated with moth assemblages collected in both October 2006 and March 2007. Changes in moth assemblages with increasing altitude were positively correlated to soil moisture (October,  $F = 3.6$ ,  $P = 0.0001$ ; March,  $F = 6.4$ ,  $P = 0.0001$ ), soil organic content (October,  $F = 3.2$ ,  $P = 0.0001$ ; March,  $F = 5.5$ ,  $P = 0.0001$ ) (presumably reflecting slower breakdown processes induced by lower temperatures) as well as fog events (October,  $F = 2.6$ ,  $P = 0.0004$ ; March,  $F = 5.2$ ,  $P = 0.0001$ ) (100% atmospheric humidity, from which we may infer a higher frequency of fog events and rainfall), whereas reverse trends were found for median temperature (October,  $F = 3.7$ ,  $P = 0.0001$ ; March,  $F = 6.5$ ,  $P = 0.0001$ ), soil pH



TABLE 3. Altitudinally restricted moth species collected along the IBISCA-Queensland transect in Lamington National Park based on combined data from samples taken in October 2006 and March 2007. Only species that were represented by 30 or more individuals included. The black bars indicate the altitude or range of altitudes at which at least 80% of the total number of individuals were restricted.

Species	Family	Subfamily	Fig.	Altitude (m a.s.l.)				
				300	500	700	900	1100
<i>Termessa gratiosa</i>	Arctiidae	Lithosiinae	3A	■				
<i>Rhimphalea sceletalis</i>	Crambidae	Pyraustinae	3B	■				
<i>Lyclene structa</i>	Arctiidae	Lithosiinae	3C	■				
<i>Asura cervicalis</i>	Arctiidae	Lithosiinae	3D	■	■	■		
<i>Eustixis laetifera</i>	Lacturidae		3E			■		
<i>Palaeosia bicosta</i>	Arctiidae	Lithosiinae	3F			■	■	
<i>Ectropis bispinaria</i>	Geometridae	Ennominae	3G			■	■	■
<i>Hesychocha chionora</i>	Arctiidae	Lithosiinae	3H			■	■	■
<i>Xylodryas leptoxantha</i>	Geometridae	Ennominae	3I				■	■
<i>Aboetheta pteridonoma</i>	Crambidae	Pyraustinae	3J				■	■
<i>Eurychoria fictilis</i>	Geometridae	Ennominae	3K				■	■
<i>Lyelliana dryophila</i>	Geometridae	Ennominae	3L				■	■
<i>Larophylla animeta</i>	Geometridae	Ennominae	3M				■	■
<i>'Dyscheralcis' crimnodes</i>	Geometridae	Ennominae	3N					■
<i>Heterochasta conglobata</i>	Geometridae	Larentiinae	3O					■
<i>Lychnographa heroica</i>	Geometridae	Ennominae	3P					■
<i>Thalatha trichroma</i>	Noctuidae	Amphipyrrinae	3Q					■
<i>Middletonia hemichroma</i>	Geometridae	Ennominae	3R					■

(October,  $F = 3.4$ ,  $P = 0.0001$ ; March,  $F = 5.0$ ,  $P = 0.0001$ ) and tree species richness (October,  $F = 1.7$ ,  $P = 0.027$ ; March,  $F = 2.8$ ,  $P = 0.007$ ) (Figures 2a and 2b).

Mantel tests showed a high correlation between moth assemblages and altitude (correlation coefficient (Rho) of 0.84,  $P < 0.002$  in March, and  $Rho = 0.73$ ,  $P < 0.001$  in October). However, moth assemblages were also equally highly correlated with the geographic arrangement of the sites ( $Rho = 0.85$ ,  $P < 0.001$  in March, and  $Rho = 0.728$ ,  $P < 0.001$  in October).

The moth assemblages of plots at 1100 m a.s.l. were clearly differentiated from those at other elevations, particularly in the March sample (Fig. 2b), and featured a number of moth species not found at lower elevations. The average similarity between altitudinal groups, summarised in Table

2, demonstrates decreasing assemblage similarity with increasing distance between altitudinal groups, indicating strong altitudinal turnover of moth assemblages with altitude.

### Species with altitude-restricted distributions

As a first step towards nominating which species might be useful as indicators of climate change at particular elevations, or ranges of elevations, and hence promising candidates for future monitoring, we identified species with restricted altitudinal distributions (Table 3). For this we selected species represented by at least 30 specimens with at least 80% of the catch restricted to one or a small range of altitudes. In total there were 28 such taxa, 18 of which we have thus far been able to identify with confidence to species level. Of these 18 species (and using the 80% criterion mentioned above) nine were

Macrolepidopteran assemblages along an altitudinal gradient

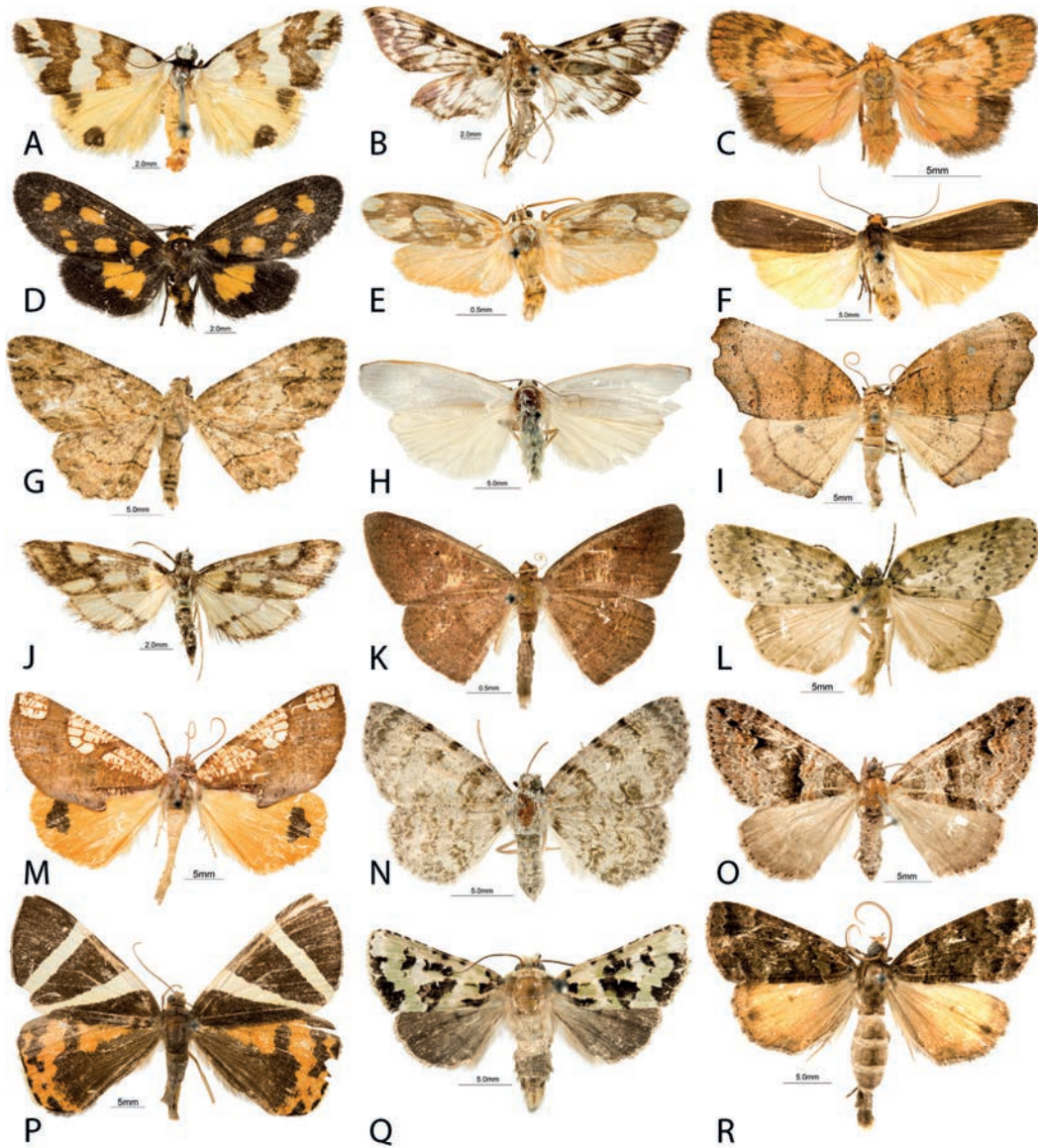


FIG. 3. Altitudinally restricted moth species collected along the IBISCA-Queensland transect in Lamington National Park (see Table 3 for family and subfamily placements). A, *Termessa gratiosa* (Walker); B, *Rhimphalea sceletalis* Lederer; C, *Lyclene structa* (Walker); D, *Asura cervicalis* Walker; E, *Eustixis laetifera* (Walker); F, *Palaeosia bicosta* (Walker); G, *Ectropis bispinaria* (Guenée); H, *Hesychopa chionora* (Meyrick); I, *Xylodryas leptoxantha* (Turner); J, *Aboetheta pteridonoma* Turner; K, *Eurychoria fictilis* (Turner); L, *Lyelliana dryophila* Turner; M, *Larophylla amimeta* Turner; N, '*Dyscheralcis*' *crimnodes* (Turner); O, *Heterochasta conglobata* (Walker); P, *Lychmographa heroica* Turner; Q, *Thalatha trichroma* (Meyrick); R, *Middletonia hemichroma*. (Turner).

characteristic of a single altitude; three to 300 m, one to 700 m and five to 1100 m a.s.l. A further six species were commonly spread over two altitudes; one from 700 – 900 m and five from 900 – 1100 m a.s.l. Finally, three species occupied less restricted altitude ranges; one from 300 – 700 m and two from 700 – 1100 m a.s.l. These altitudinally restricted species represented five families. The ‘lower elevation species’, those characteristic of plots from 300 to 700 m a.s.l., comprised three lithosiine arctiids and a single pyraustine crambid. In contrast, species characteristic of higher elevations (900–1100 m a.s.l.) were principally geometrids (nine ennomines and one larentiine) with one amphipyridine noctuid and a pyraustine crambid. Species restricted to mid-elevations (500–700 m a.s.l.) were, in general, scarce. The two species we identified in this category comprised a lithosiine arctiid and the lacturid, *Eustixis laetifera*.

## DISCUSSION

The main objective of this study was to document changes in moth assemblages along an altitudinal gradient within continuous rainforest. We have demonstrated that there are characteristic assemblages of species at each elevation in two seasons and have identified particular species with indicator potential. In this discussion we examine potential explanations for these patterns and the potential impacts of climate change upon them. We discuss the likely generality of our results and avenues for further research.

The occurrence of a species in a particular sample results from a multiplicity of factors. These may be methodological or biological. Methodologically we acknowledge that we are sampling only night-flying, light-attracted moths. This is a subset of all moths but, nevertheless, is sufficiently large to provide a degree of confidence to identify community patterns from which usable management tools can be derived. Light traps are relatively easy to use and produce large samples. Poor catches can result from their use on cold and/or windy nights and bright

moonlight undoubtedly adversely affects catches on clear nights (Nowinszky 2004). Any moth trapping programme must be flexible enough to substitute additional sampling nights in response to the occasionally unsuccessful trap night. A more serious issue concerning the repeatability and representativeness of light-trap samples is that of seasonality. There are undoubtedly different assemblages of moth species flying at different times of the year. Further, even for a particular species, there will be a peak time of flight activity and the first emergents or last survivors of a species, appearing in trap catches, may give a false impression of rarity. We have partly addressed this problem by sampling on two different occasions (and a third not reported on here). Nevertheless, any comparisons using results of the kind we have reported must aim to target a comparable season. Of course, year-long sequences of catches would be useful in resolving the issue of seasonality across species. There are, however, no such datasets available for any subtropical Australian location. Even where such datasets available, the highly variable Australian climate would, quite possibly, prevent the drawing of general conclusions concerning species diversity from a single year’s data. We suggest the large sample sizes and the fact that rather similar patterns emerged from two quite different sampling periods lends a good deal of credibility to the conclusions. We note also that singletons or doubletons (i.e. species that appear only once or twice within our samples) had little impact on the results of multivariate ordinations (results not presented here).

Ecologically, the presence or absence of a particular species at a particular elevation will be determined by the limiting dimensions of the niche of each species. These may be physico-chemical dimensions such as temperature, moisture and soil chemistry, or biological variables based on interactions with food-plants, competitors and natural predators. The physico-chemical variables are dimensions of the fundamental niche of the species and reflect the evolved physiological tolerances of the species concerned. Biological

interactions add dimensions to the niche space which define the realised niche of the species and usually define a hypervolume nested within that circumscribed by the fundamental niche dimensions (Hutchinson 1957). We say 'usually' because, in rare instances, mutualistic interactions may expand the niche of a species beyond the volume defined by its physiological tolerances to physio-chemical factors. It would be in line with general niche theory (see for example Dobzhansky 1950; McCoy 1990) to suppose that species restricted to altitudes presenting more extreme and challenging microclimates, would be more likely to be restricted by their physiological tolerances of climatic extremes, whereas those species spread across altitudes, presumably comfortably within their physiological envelopes, are more likely to be restricted by biological interactions. Biological interactions that may restrict the spatial distribution of moths are likely to include the presence or absence of acceptable food-plants and the suite of predators and parasitoids co-occurring with them.

Our nomination of moth species which may be useful as indicators is preliminary. As other species are firmly identified, so additional, usable, range-restricted species can be added to the list. Further statistical characterisation of the 'attachment' of these species to particular altitudinal ranges is in progress. Of course, one set of information that would assist in explaining these patterns are lists of the larval food plants of these species. Very little published information is available on this subject ([www-staff.it.uts.edu.au/~don/larvae](http://www-staff.it.uts.edu.au/~don/larvae)). There is general agreement that larvae of many lithosiines feed on lichens and this has been confirmed for *Termessa gratiosa* and *Palaeosia bicosta*. Given that montane and boreal lichen distributions are predicted to shift under climate change (Ellis *et al* 2007), these species feeding on lichens may be of conservation concern.

There is published food-plant data available for only one of the remaining species, *Ectropis bispinaria* (Geometridae: Ennominae), which

is highly polyphagous, being recorded from species of Rutaceae, Lauraceae, Rosaceae and Proteaceae with all families being well represented in the flora of the Lamington rain-forest. Larval rearing by one of us (D. Bito) adds Monimiaceae (*Daphnandra micrantha*) and Sapindaceae (*Arytera divaricata* and *A. dystilis*) to this list. Other species within the lacturid genus *Eustixis* have been reared from *Ficus* spp. and this association might reasonably be expected for *E. laetifera*. Unpublished rearing records provide a few additions. Among the ennomines, *Middletonia hemichroma* has been reared from *Nothofagus moorei* (Nothofagaceae), *Quintinia verdonii* (Quintiniaceae) and *Syzygium crebrinerve* (Myrtaceae); and *Dyscheralcis crimnodes* has been reared from *Neolitsea australiensis* (Lauraceae) and *Pentaceras australis* (Rutaceae) (D. Bito, unpub. data).

Testing these explanatory hypotheses related to the altitudinal distributions of species is restricted by insufficient data on both host plants and natural enemies. We have some, albeit sparse, data on food-plants but we have virtually no information on parasitoid loads. Both deficiencies point to likely rewarding future areas of investigation. The IBISCA-Qld Project has generated substantial samples of micro-Hymenoptera through Malaise trapping (see Boulter *et al.*, this issue) and further analysis of these samples may provide more insight into their likely significance in structuring moth assemblages.

The existence of clear cut patterns of altitudinally delimited moth assemblages, with particular species having clearly restricted altitudinal distributions, suggests that selected moth taxa will be useful in tracking any upward shifts in distribution and invasions of higher altitudes - a likely consequence of global warming. It also suggests that the highly distinctive upper elevation assemblage must be regarded as vulnerable and of conservation concern. The patterns we have identified are concordant with studies of other taxa that formed part of

the IBISCA-Qld Project and with other studies of moths on altitudinal gradients elsewhere (Fiedler *et al.* 2008; Brehm & Fiedler 2003). Our results suggest that the most sensitive altitudes to target for monitoring in the relatively short-term (say over 20-30 years) will be those at 700 m a.s.l. and above, where cloud base fluctuations are predicted to alter ecosystem structure and dynamics (Laidlaw *et al.* this issue). This conforms with the opinions of earlier authors who have suggested that such ecotones are the areas that will show the strongest signals of climate change (Parmesan & Yohe 2003).

The selection of suitable indicator species depends on several criteria. An effective indicator needs to be present in large numbers, be easily recognisable, as well as being sensitive to environmental variables (Holloway 1998; Scoble 1995). Moth groups that are sensitive to floristic change and which have low vagility, such as the Geometridae and some Pyralidae, fulfil these criteria and have been demonstrated to be good indicators across a variety of ecological investigations (Beck *et al.* 2002; Holloway 1985; Kitching *et al.* 2000; Scoble 1995).

The set of moth species identified will be usefully incorporated as part of a 'predictor set' of arthropod and plant species, reflecting different trophic levels and guilds within the rainforest community. This will be significant for the ecological monitoring of future changes in ecosystem composition and function (Kitching 1993; McGeogh 1998).

The generality of our results is inevitably a potential point of contention. Firstly, we have examined only a single gradient within a single biome and a single catchment at one latitude. Although it is likely, as a general principal, that the higher taxa we have identified are likely to be useful generators of indicator species at other rainforest locations, no claims for generality of our results beyond the target locations can be (or is) made. Wider distribution records (as well as altitudinal information) for the indicator

species are being collected from the Australian National Insect Collection, Canberra, and other museums. Future research will target additional rainforest transects within Australia at a range of scales. In particular, the local role of aspect and the continental role of latitude require investigation. This work is in progress.

Clearly, because of the way sites are necessarily distributed across the altitudinal gradient, geographic distances between sites will be correlated with moth assemblages. It is impossible to separate how much of this correlation is driven by inter-site distances and how much by the effects of altitude *per se*. However, the most parsimonious and most ecologically sensible explanation is that moth assemblages are more highly influenced by altitude (and the suite of environmental variables that are associated with altitude). Further work at additional altitudinal gradients, such as at Border Ranges National Park, will help test this hypothesis.

The analyses we have presented here are the first, necessarily, preliminary results of the Lepidoptera studies within the IBISCA-Queensland project. Further analyses examining responses on a family by family basis, formal quantification of 'indicator values' (Dufrene & Legendre; 1997), and comparisons of the ground-zone catches with those from the canopy, will probably also be informative.

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