

Identifying indicator species of elevation: Comparing the utility of woody plants, ants and moths for long-term monitoring

AKIHIRO NAKAMURA,^{1,2,3*} CHRIS J. BURWELL,^{2,3} LOUISE A. ASHTON,² MELINDA J. LAIDLAW,⁴ MASATOSHI KATABUCHI^{1,5} AND ROGER L. KITCHING^{1,2}

¹Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China (Email: a.nakamura@xtbg.ac.cn);

²Environmental Futures Research Institute, Griffith University, ³Natural Environments Program, Queensland Museum and ⁴Department of Science, Information Technology and Innovation, Queensland Herbarium, Brisbane, Queensland, Australia; and ⁵Department of Biology, University of Florida, Gainesville, Florida, USA

Abstract Ecologists have found the distributions of many groups of organisms to be elevationally stratified. Consequently, various taxa (or species) have been proposed as indicators for inclusion within long-term monitoring programmes to quantify the ecological impacts of future climatic change. Ideal indicators should be restricted to a particular elevational range (i.e. have high specificity) and be readily detectable across space and time (i.e. have high fidelity). This, however, has not been rigorously tested for elevational studies. We employed a spatially and temporally replicated sampling design to test the utility of tree, ant, and canopy and understorey moth species as indicators of elevation within continuous subtropical rainforest of eastern Australia. Using the classical indicator value protocol, we tested (i) whether the number of indicator species (all taxa) found in the observed data was significantly greater than the number obtained by chance; (ii) whether the indicator species (ants and moths) identified from one sampling season responded to elevation in a similar way in samples obtained from other seasons; and (iii) whether the indicator species (ants) identified from one elevational transect responded to elevation in a similar way in a nearby transect that incorporated similar elevational ranges. All groups had significantly greater numbers of indicator species than expected by chance. Temporal fidelity of moth indicator species was lower than that of ants as the suite of moth indicator species showed high seasonal variation. In contrast, ants showed high spatial and temporal fidelity. Most ant indicator species were, however, indicative of low and mid-elevations, and only one species was indicative of the highest elevation, suggesting their relatively low conservation significance in relation to climate warming in this region. It is essential that we understand how spatial and temporal variation affects the distributions of different taxonomic groups when incorporating multiple taxa for long-term monitoring programmes.

Key words: biodiversity, elevational stratification, Formicidae, IBISCA, indicator value, Lepidoptera.

INTRODUCTION

Humans are modifying environments at an unprecedented rate at both local (e.g. deforestation, pollution) and global scales (e.g. atmospheric CO₂ releases) (Hansen *et al.* 2013; Laurance *et al.* 2014). It is becoming ever more crucial to understand how biodiversity responds to altered habitat conditions. To this end, ecologists often focus upon environmental gradients that provide a useful framework to understand how species (or whole communities) respond to progressive changes in environmental conditions (Liow

et al. 2001; Sanford *et al.* 2009). An increasingly well-studied environmental gradient is that of elevation up mountain slopes, which are often used as a surrogate for changes in temperature and other climatic conditions (Egger & Hoinka 1992; Hodkinson 2005). Increases in elevation are accompanied by adiabatic decreases in temperature (0.4–0.8°C per 100 m increase in elevation, Strong *et al.* 2011) and changes in humidity near peak elevations (such as cloud forest in Australian tropical and subtropical forests, Hutley *et al.* 1997). Elevational gradients provide strong environmental gradients within short geographical distances, offering opportunities to study the influence of climatic variation and potential impacts of future climate changes on species distribution patterns (Körner 2007).

*Corresponding author.

Accepted for publication May 2015.

Many species are known to be restricted to certain elevational ranges (Pyrz & Wojtusiak 2002; Chatzaki *et al.* 2005; Botes *et al.* 2006), and some are only found at the upper limits of elevational gradients (Wilson *et al.* 2007). Species showing elevationally restricted distributions are considered to have narrow 'bioclimatic envelopes' (note that 'bioclimatic envelope' also refers to latitudinally restricted species distributions, e.g. Berry *et al.* 2002). Many predictive models have suggested that the climatic envelopes (and hence the distributions) of elevationally restricted organisms will shift in response to future climate changes, and that changes in distributions along elevational gradients will occur over shorter distances than would be needed along latitudinal gradients for the same temperature change (Chen *et al.* 2011). The concept of bioclimatic envelopes, however, has been heavily criticized as it is fundamentally based upon the premise that climate is the dominant driver of species distributions (Pearson & Dawson 2003), without sufficiently addressing other important aspects such as ecological interactions (competition, mutualism and trophic interactions, Davis *et al.* 1998; Gilman *et al.* 2010), behavioural adaptation (Sunday *et al.* 2014), rapid evolutionary adaptations (Hoffmann & Sgro 2011) and dispersal ability (Pearson & Dawson 2003). Indeed, meta-analysis of distribution changes has found that latitudinal and elevational shifts of some species were unrelated to recent climatic changes (Chen *et al.* 2011). Despite these anomalies, range shifts in a majority of species have tended to follow predictions based on climatic variation, suggesting that assemblages *as a whole* will respond to climatic variation (Parmesan & Yohe 2003; Thomas 2010; Chen *et al.* 2011).

Previous elevational studies have identified species or sets of species with restricted elevational distributions and suggest these as focal groups to effectively monitor and predict the ecological impacts of climate change on biodiversity (e.g. Wilson *et al.* 2005; Wilson *et al.* 2007; Maunsell *et al.* 2013). These focal groups are defined as ecological indicators (*sensu* McGeoch 1998) whose distributions are restricted to certain habitats or a range of environmental gradients (in our case, elevation), and possibly represent the characteristics of the whole assemblages ('predictor sets', Kitching & Ashton 2013). The choice of ecological indicators is, however, often biased towards certain groups of organisms based on the taxonomic expertise of researchers, with little attention given to cross-taxon assessment of their usefulness as indicator species (Andersen 1999).

Ideal ecological indicators should exhibit not only high habitat specificity (i.e. exclusive occurrence within particular elevations) but also temporal and spatial fidelity without being substantially influenced by background 'noise', such as seasonal variations and

other habitat heterogeneities (Dufrêne & Legendre 1997). Species with high temporal fidelity should consistently be recorded from particular habitats (or elevations) regardless of seasonal and/or annual fluctuations in environmental conditions, such as temperature and precipitation. Nevertheless, species with low temporal fidelity may still be good indicators if their elevational shifts are predictable (e.g. elevational migration in response to seasonal changes in food resources and predation regimes, McGuire & Boyle 2013). Species with high spatial fidelity should occur ubiquitously within a given habitat without being influenced by small-scale within-habitat heterogeneity (e.g. geology, aspects and other changes in microhabitat conditions).

For logistical reasons, many elevational studies spatially aggregate replicate sites of the same (or similar) elevations (e.g. Brehm & Fiedler 2003; Kitching *et al.* 2011; Sam *et al.* 2015). Indicator species of very narrow elevational ranges should therefore be treated with caveats as their distribution may not necessarily be driven solely by climatic factors, but influenced by other local habitat conditions. Alternatively, species whose elevational distributions encompass the lowest and/or highest elevations may not be good indicator species as the trailing (lower) or leading (upper) edge of their elevational distribution may lie beyond elevations of the mountain slopes under consideration, making it difficult to predict or quantify the impacts of climate change.

One of the best studied groups within elevational gradients are trees (e.g. Swenson *et al.* 2010; Tang *et al.* 2012). Trees are structurally dominant components of many plant communities and play essential roles in many aspects of ecosystem functioning (e.g. carbon sequestration). Invertebrates are also proposed as potential candidates for monitoring climate change impacts as many species are known to have limited elevational distributions due to restricted thermal tolerances (Hodkinson 2005; Sunday *et al.* 2014). Although vertebrate and plant species are often suggested as ecological indicators of elevational changes, the shorter lifespan of invertebrates may allow them to track future climate change more closely (Wilson *et al.* 2007). Invertebrates, however, may be more susceptible to influence by seasonal fluctuations in temperature and resource availability (Levings 1983). Understanding the usefulness of different taxonomic groups as ecological indicators of elevational ranges may have important implications for monitoring the biodiversity responses to future climate changes.

Here we compared trees and three arthropod groups (ants, and canopy and understorey moths) for their use as ecological indicators of elevational ranges. We aimed to investigate the following: (i) whether the number of indicator species (trees, ants, and canopy and understorey moths) found in the observed data

was greater than the number obtained by chance using a null model, and if so by how much; (ii) whether the indicator species (ants, and canopy and understorey moths) identified from one sampling season responded to elevation in a similar way in samples obtained from other seasons; and (iii) whether the indicator species (ants only) identified from one elevational transect responded to elevation in a similar way in a nearby transect that incorporated similar elevational ranges, but different soil types and aspects.

METHODS

Survey areas

Our study was conducted in Lamington National Park in eastern Australia (28° 13'S, 153° 08' E), located just north of the state border between Queensland and New South Wales. This park comprises 23 000 ha of broad-leaved subtropical rainforest, spanning the Lamington Plateau, which forms the northern flanks of the Mt Warning erosion caldera (Strong *et al.* 2011). The park is divided into two sections, the Green Mountains section to the west and the Binna Burra section to the east (Fig. 1). Annual average rainfall varies with elevation, with areas at higher elevation receiving more rainfall. At the Green Mountains National Park headquarters (about 940 m a.s.l.), annual average rainfall is 1827 mm, 21% more rainfall than a nearby weather station at 100 m a.s.l. (Canungra Finch Road meteorological station). Precipitation at higher elevations (≥ 900 m) is supplemented by moisture inputs from frequent low cloud and fog. Average temperature decreased by 1.5°C per 200 m at Green Mountains (based on hourly temperature recordings from July 2007 to June 2008 measured from 300 m to 1100 m a.s.l., Strong *et al.* 2011). Soil is generally derived from tertiary basaltic rocks, forming loam to silty clay loam. Lower elevations of the Binna Burra section are characterized by the presence of rhyolite (Strong *et al.* 2011). Vegetation types vary with elevation, with low elevations (about 300 m) characterized by *Araucarian* notophyll vine forest, mid-elevations (about 500–900 m) by complex notophyll vine forest, and high elevations (≥ 1000 m) by microphyll fern forest dominated by Antarctic beech, *Nothofagus moorei* (Laidlaw *et al.* 2011).

Sampling

We established one elevational transect within the Green Mountains section to sample trees, moths and ants, and another transect within the Binna Burra section to sample ants (Fig. 1). At Green Mountains, the elevational transect was subdivided into five elevational zones (*viz.* 300, 500, 700, 900 and 1100 m a.s.l.). Four survey plots were established at similar elevations at each of the elevational zones (actual elevation of the plots were within a mean of 37 m of each elevational zone, Kitching *et al.* 2011). Likewise, the elevational transect at Binna Burra was subdivided into seven elevational zones (450, 600, 750, 850, 950, 1000, 1100 m a.s.l.), and two plots were established per elevational zone,

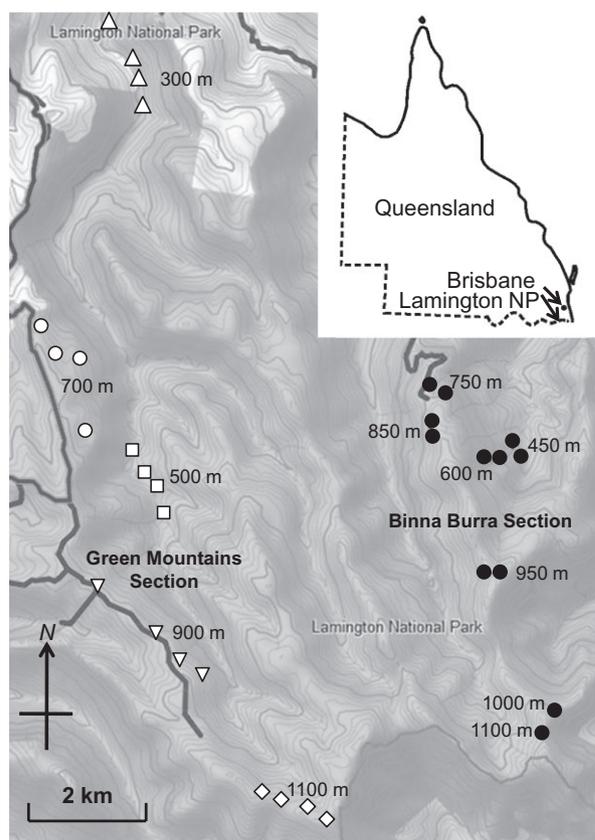


Fig. 1. Map of Lamington National Park, showing Green Mountains and Binna Burra sections (grey lines represent roads or paved walking tracks). At Green Mountains, survey plots were elevationally stratified into 300 m (triangle), 500 m (square), 700 m (circle), 900 m (inverted triangle) and 1100 m a.s.l. (diamond). Additional plots were established at Binna Burra to sample ants at elevations similar to those at Green Mountains.

with the exception of 1000 and 1100 m where only one plot each was established. All plots at Green Mountains were established at approximately the same north-easterly aspect to minimize temperature variation due to varying degrees of insolation. At Binna Burra, however, aspects varied substantially from westerly to north-easterly. Survey plots at Green Mountains were separated by at least 400 m, but plots at Binna Burra at the same elevational zone were as close as 100 m.

At each of the Green Mountains survey plots, a permanent 20 m \times 20 m marked quadrat was established. In August 2006, all trees greater than 5-cm diameter at breast height (d.b.h., measured at 1.3 m above the ground) were numbered and identified to species within each quadrat (see Laidlaw *et al.* 2011 for more details). Within, or in the immediate vicinity of, each quadrat, moths were sampled in October 2006 (austral spring) and March 2007 (early autumn) using two Pennsylvania style light traps, one in the understorey and one at the canopy level. Canopy traps were suspended by ropes approximately 35 m from the ground, just below the canopy crown, and understorey traps were suspended approximately 2 m above the ground. The two

traps at each plot were set simultaneously for three nights. Traps were emptied daily, and moths with a wing length greater than 1 cm (plus smaller Pyraloidea) were sorted to families and species or morphospecies (see Ashton *et al.* 2011 for more details). Samples collected from three trapping nights were pooled for each trap. Canopy and understorey moths were analysed separately as assemblages were clearly compartmentalized between these two strata (L. A. Ashton *et al.*, unpubl. data, 2015). Due to logistical problems, we did not collect canopy moths from all four plots at 300 m in October 2006, or canopy and understorey moths at two of the four plots at 500 m in March 2007.

Ants were collected in three seasons (October 2006, March 2007 and January 2008) using three different sampling techniques. Just outside each survey quadrat, we collected two sets of litter samples to extract litter-dwelling ants. Each litter sample was derived from 1 m² of leaf litter collected as four 50 cm × 50 cm squares at least 5 m away from each other. We selected sampling areas that had relatively uniform litter coverage and avoided rain-washed areas. All litter and loose surface soil within the squares were collected by hand, sieved with a litter sifter and ants were extracted using Tullgren funnels for 24–36 h. Ants inhabiting living tree trunks were collected by spraying 10 tree trunks greater than 30 cm d.b.h. within and outside each quadrat with pyrethroid insecticide. Falling arthropods were collected on a rectangular sheet (160 cm × 105 cm) placed at the base of each tree for approximately 15 min after spraying. Ants were also hand-collected for 60 min per plot within a 50-m radius from the centre of each quadrat between 09.00 and 17.00 hours. Foraging worker ants on the ground, logs, foliage and tree trunks, as well as nests located within various types of microhabitats (including epiphytes), were collected by hand. We employed these three sampling techniques in order to maximize the number of ant species living in various microhabitats (as opposed to using the Ants of the Leaf Litter (ALL) Protocol developed by Agosti *et al.* (2000), which targets ground-dwelling ants only). Additional ant samples were collected from the Binna Burra transect using the same three sampling techniques in February 2008. All worker ants were identified to genus and species or morphospecies (see Burwell & Nakamura 2011 for more details).

Data analyses

We generated a single dataset for trees (surveyed in August 2006), two datasets for each of canopy and understorey moths (October 2006 and March 2007), and four datasets for ants (October 2006, March 2007 and January 2008, and Binna Burra samples). Tree and moth datasets were based on square root-transformed abundance of species per survey plot, but the ant dataset was based on incidences of species due to their eusocial nature.

We first generated coverage-based rarefaction curves to compare sampling sufficiency among the four groups of datasets (Chao & Jost 2012). Coverage-based rarefaction curves plot sample completeness, expressed as a proportion, against a given number of individuals (for trees, and canopy and understorey moths) or samples (for ants), suggesting what proportion of the community is represented by those samples. Rarefaction curves were drawn and sample com-

pleteness calculated using the *iNEXT* package ver. 1.0 available in *R* statistical software ver. 3.1.0 (Hsieh 2013).

Effectiveness of tree, ant, and canopy and understorey moth species as indicators of elevational changes was assessed using the classical indicator value protocol developed by Dufrêne and Legendre (1997). For this analysis, we used trees surveyed in August 2006, ants, and canopy and understorey moths collected at the same time in March 2007. March samples were selected because these were more species-rich (105, 447 and 467 species of ants, canopy moths and understorey moths, respectively) compared with October 2006 (104, 353 and 385 species). The indicator value protocol assesses individual species as indicators of certain habitat types (in our case, elevations) by quantifying species habitat specificity and fidelity to a given habitat, expressed as a percentage. A maximum indicator value of 1.0 (or 100%) is given to a species if it achieves maximum specificity (it occurs only within the habitat of interest) and fidelity (it occurs in all sampling plots within that habitat).

We calculated the indicator values of all species for each individual elevational zone (e.g. 300 m, 500 m) and all possible ranges of sequential elevations (e.g. 300–500 m, 500–900 m, 500–1100 m), excluding the entire range of the transect (300–1100 m), giving a total of 14 indicator values per species. A species was deemed indicative of the elevational zone or range where the highest indicator value was attained for that species. The significance of this indicator value was then tested by permuting the samples 999 times, so that species with patchy distributions (e.g. singletons and doubletons) were not selected as indicator species. We summed the number of significant indicator species for each of the four groups. The total number of significant indicator species, however, cannot be compared directly because species richness varied greatly among the groups (i.e. a dataset with more species is likely to yield a greater number of significant indicator species). The usefulness of individual groups was therefore compared by measuring the departure of the number of observed indicator species from those based on the null model. A total of 999 permuted datasets were generated by shuffling the samples (note that we did not shuffle individuals so that ecological integration of species was maintained within each plot). We calculated the effect size of the four taxonomic groups by calculating the differences in the numbers of significant indicator species between the observed and the mean of the null data divided by the standard deviation of the null data. *R* code to conduct these analyses was written by MK and AN using the *labdsv* package ver. 1.6-1 (code is available upon request from the corresponding author).

We tested the temporal and spatial fidelity of ant and moth indicator species by examining whether these species consistently occurred at similar elevations when sampled in different seasons and locations. We employed canonical analysis of principal coordinates (CAP) to model how the assemblage composition of ant and moth indicator species changed with elevation. Unlike unconstrained ordination methods (e.g. non-metric multidimensional scaling ordination), CAP generates canonical axes that best separate *a priori* groups (elevations in our study) through the multivariate points of a given similarity matrix (Anderson 2005). We then incorporated new data (collected from different seasons or location) to test whether the model could predict the actual elevations at

which the new samples had been collected. If the indicator species respond to elevational variation in a similar way between samples collected in different seasons or locations, then the model should give a good fit between predicted and actual elevations. The model was generated using significant indicator species based on March samples, and the new data consisted of October samples for moths, and October and January samples for ants, and only of species that were found to be significant indicator species based on March samples (this allowed us to test the predictive power of indicator species found in one season). Ants were also tested using data collected from the Binna Burra transect (again only using indicator species based on March samples from Green Mountains) as the new data to test the spatial fidelity of indicator species. We used CAP available within the *PERMANOVA* + add-on package in *PRIMER6* statistical software (Clarke & Gorley 2006). Similarity matrices were calculated using Bray–Curtis (for square root abundance of moths) and Sørensen (for ant incidence data) indices.

RESULTS

We sampled a total of 114 tree, 147 ant, 624 canopy moth and 643 understorey moth species from the entire surveys (i.e. all datasets). Despite large numbers of moth species, over half were either singletons (256 and 245 species of canopy and understorey moths with one individual, respectively) or doubletons (82 and 85 species with two individuals), whereas only 35% of tree species were either singletons or doubletons (20 species each). We recorded plot-level incidence data for ants with 28 uniques and 11 duplicates (i.e. those that occurred at one or two plots from the entire survey). Although ants were intensively surveyed (three seasons and two transects), a relatively small number of species was collected due to their low spatial and temporal turnover between surveys (104, 105, 123 and 82 species from October, March, January and Binna Burra surveys, respectively, comprising a total of 147 ant species).

Coverage-based rarefaction curves showed over 85% sample coverage for all datasets, suggesting that the actual communities along the elevational transects were well represented by our samples. Relatively low sample coverage was obtained from canopy and understorey moths collected in October (88% and 91%, respectively) and ants collected from the Binna Burra transect (93%) compared with at least 95% coverage for all other datasets.

The indicator value protocol identified 36 tree, 33 ant, 56 canopy moth and 75 understorey moth species as being significant indicator species. Most species of trees and ants were indicative of a range of elevations, with only 33% (12 indicator species) of tree and 18% (6 indicator species) of ant species indicative of a single elevational zone, whereas 69% (38 indicator

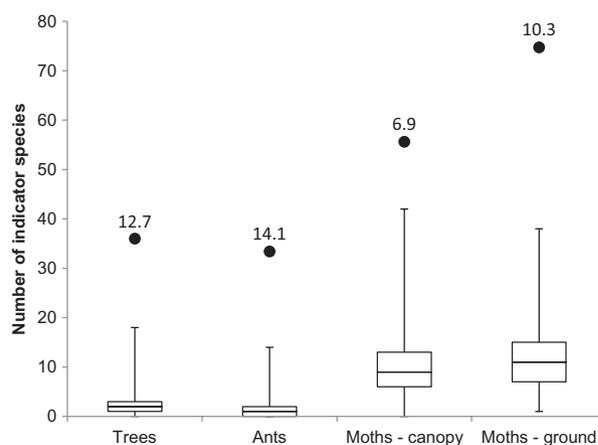


Fig. 2. Number of indicator species found from the observed datasets (black dots) and 999 permuted null data shown as box plots from the first to third quartiles with whiskers from maximum to minimum. Effect size of the four groups is also shown above the observed number of indicator species.

species) and 45% (34) of canopy and understorey moth species, respectively, were indicative of a single elevational zone.

Observed numbers of indicator species for all four groups were substantially larger than the number of indicator species obtained from any of the 999 null data (Fig. 2). It is not surprising that we found more indicator species of moths due to the large number of species investigated. However, when we compared the effect sizes (standardized differences in the number of indicator species between observed and null data), ants showed the largest effect size (14.1), followed by trees (12.7), understorey (10.3) and canopy moths (6.9). Omitting ‘uniques’ (i.e. those that occurred only at one plot) from the same analysis generated essentially the same effect sizes (13.3, 12.3, 9.8, 7.4 for ants, trees, understorey and canopy moths, respectively). As we employed three different sampling techniques to sample ants (as opposed to only one sampling technique to capture moths), we reran the indicator value protocol on ants collected by a single trapping technique (litter extraction) in March. Although we found only 12 significant indicator species out of a total of 51 litter ant species, the effect size (11.2) was still larger than those of canopy and understorey moths but lower than that for trees.

Elevational distributions of ant indicator species were concentrated around low to mid-elevations (300–700 m), and few species were indicative of high elevations (Fig. 3). In fact, only one ant species (*Monomorium* IBISCA2) was indicative of the highest elevational zone of 1100 m a.s.l., as opposed to 4 trees, 7 canopy and 14 understorey species of moths restricted to 1100 m.

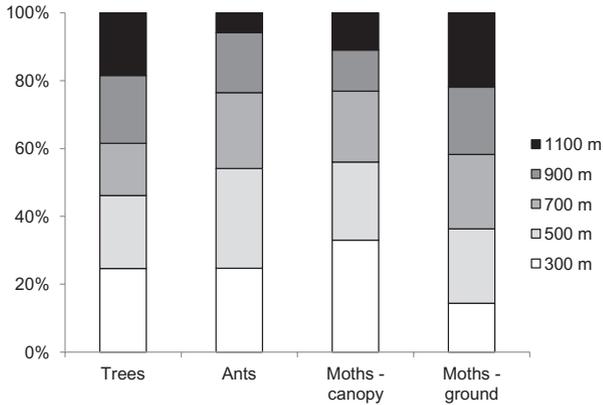


Fig. 3. Proportions of the number of indicator species indicative of different elevational zones, based on trees, ants, and canopy and understorey moths.

Using indicator species of ants and moths collected in March, we generated CAP models and assessed whether these models could predict the actual elevations at which samples comprising the additional datasets were collected. For ant indicator species, we found very high levels of correlation (correlation coefficient = 0.98) with an almost 1:1 relationship between predicted and actual elevations of samples collected from October surveys (Fig. 4). The same near 1:1 relationship was found for January data (correlation coefficient = 0.99, Appendix S1). Good predictive power was also found for ants collected from the Binna Burra transect with a correlation coefficient of 0.97 (Fig. 4). The predictive power of the CAP model based on both canopy and understorey moth datasets was inferior to that of ants. Correlation coefficients between predicted and actual elevations of both canopy and understorey moth assemblages (0.59 and 0.89, respectively) were lower than that of ants. Predicted elevations for both canopy and understorey moths were higher at lower elevation plots and lower at higher elevation plots, resulting in more horizontal relationships between predicted and actual elevations (Fig. 5). Further investigation of data revealed that there were many moth indicator species that occurred outside their indicative elevational ranges (based on March samples) or were simply absent in October samples, whereas ant indicator species showed good spatial and temporal fidelity (Appendices S2 and S3).

DISCUSSION

Elevational indicator species

All four groups of organisms were elevationally stratified (see Ashton *et al.* 2011; Burwell & Nakamura 2011; Laidlaw *et al.* 2011 for more details), and our

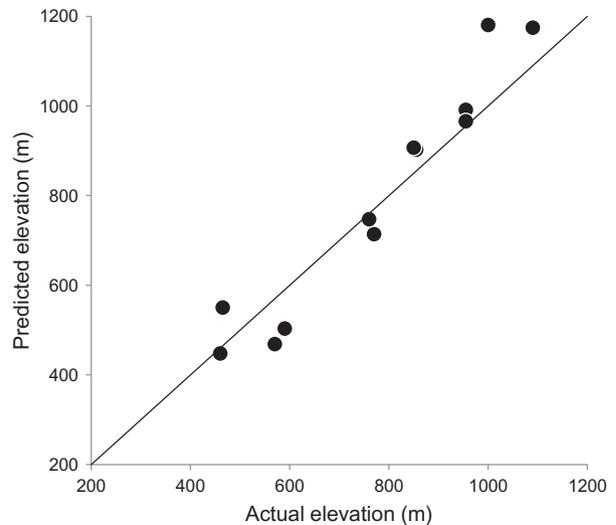
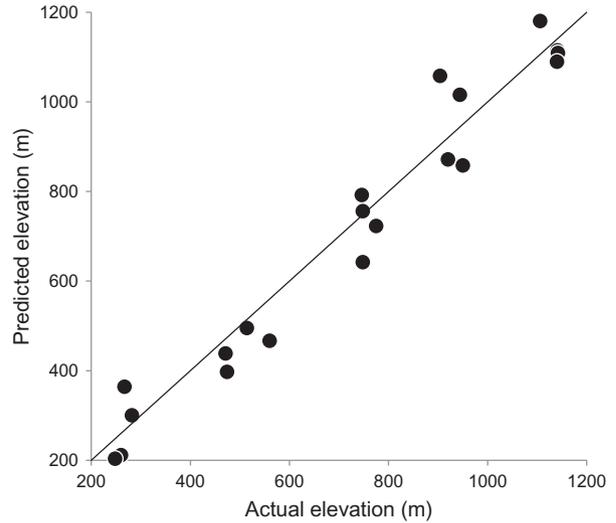


Fig. 4. Correlation between actual and predicted elevations of ant assemblages from samples collected in October from Green Mountains (top) and in February from Binna Burra (bottom). Predicted elevations were calculated based on a CAP model derived from the ant indicator species collected in March from Green Mountains and using only the occurrences of these species in the October and Binna Burra samples. Line of equality is also shown.

results show that numerous species were significantly restricted to certain elevational ranges. This is in concordance with other elevational studies claiming that their target organisms are good for long-term monitoring of global-scale climate change as their species had elevationally restricted distributions (e.g. Maunsell *et al.* 2013; Smith *et al.* 2014; Hall *et al.* 2015). Here we shed light on the *relative differences* in the usefulness of different groups of organisms for monitoring along elevational gradients.

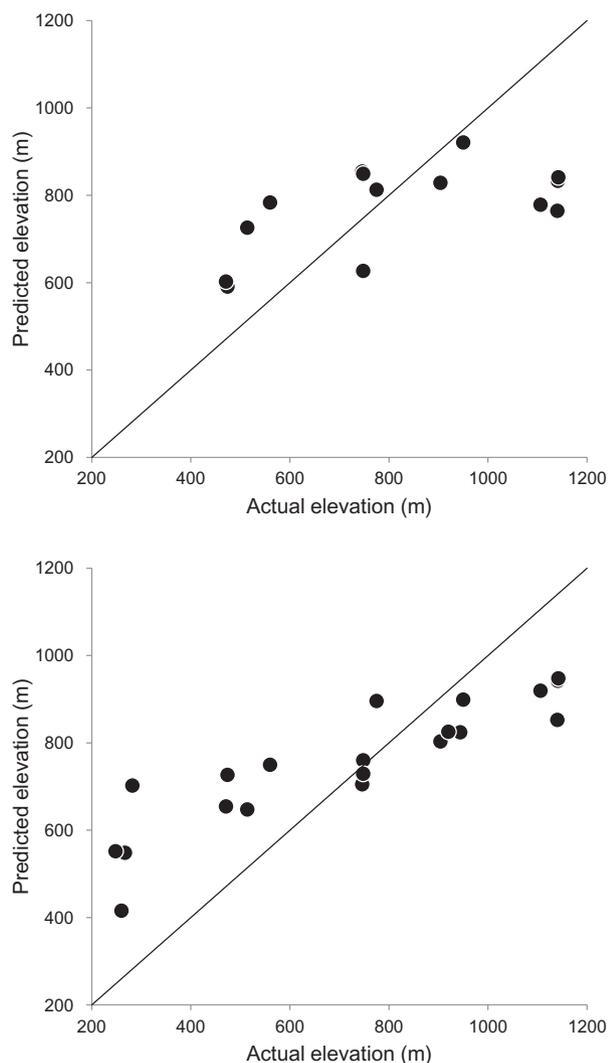


Fig. 5. Correlation between actual and predicted elevations of canopy (top) and understorey (bottom) moth samples collected in October. Predicted elevations were calculated based on CAP models derived from the moth indicator species collected in March, and using only the abundance of these species in October samples. Line of equality is also shown. Note that lower number of points for canopy moths is because moths from all four 300-m plots were not sampled from the canopy in October, and two of the 900-m plots were not included as no indicator species were collected.

Compared with trees and ants, we found larger numbers of both canopy and understorey moth species that had elevationally restricted distributions. However, the effect sizes of canopy and understorey moths were surprisingly smaller than trees and ants as the elevational distributions of moth species were patchier than those of ants and trees. Furthermore, our study design spatially aggregated replicated plots within each elevational zone (which is a common problem in other elevational studies). Many moth species were indicative of a single elevational zone;

hence, it is unclear whether those species are elevationally restricted due to climatic variation or other local habitat conditions (e.g. distribution of larval host plants).

Despite smaller numbers of indicator species, ants and trees exhibited larger effect sizes than those of moths. As opposed to moths, many indicator species of ants and trees showed less patchy occurrences and distributions extending over more than one elevational zone. The use of ants as indicator species for monitoring, however, requires a caveat from an ecological and conservation point of view as they were restricted largely to low and mid-elevational zones. It is a well-known phenomenon that the upper elevations of mountain ranges are often characterized by high levels of endemism as they provide climatically stable refugial habitat in the face of historical climate change allowing the *in situ* speciation of relictual taxa (Yeates *et al.* 2002). In Lamington National Park, there are many regional and local endemic species that are restricted to the 1100-m elevational zone, including plant (e.g. *Parsonia tenuis*) and moth species (*Lychnographa heroica* and *Middletonia hemichroma*) (Kitching *et al.* 2013a). Despite intensive surveys, we found only a single species of ant to be a significant indicator of the peak elevation at 1100 m. The lack of high elevation specialist species suggests that the conservation implications of climate change for ants may be relatively low, provided that species of lower elevations can shift their distributions upslope. The paucity of high elevation specialist species is probably universal for tropical and subtropical ants, as the ant species richness in these regions generally declines with increasing elevation (e.g. Bruhl *et al.* 1999; Longino *et al.* 2014). In contrast, the role of ants as predators may have strong ecological implications. Predation pressure exerted from ants was observed to decline with increasing elevation within our study location (Bito *et al.* 2011) and elsewhere (Sam *et al.* 2015) due to decline not only in species richness but total abundance of ants at high elevations. If climate change causes upslope shifts of ant species, and thus an increase in ant abundance, increased predation pressure at high elevations may cause reduction or local extinction of endemic species within this region.

Like ants, tree species showed a high effect size, but in contrast many species were indicative of the highest (as well as mid and low) elevations. Their use for monitoring, however, may be limited as their lifespan is generally much longer than that of vertebrates and invertebrates; hence, their response may lag behind the actual velocity of climate change. Indeed, Feeley *et al.* (2011) found that the rate of upslope migration of tree species lags behind recent temperature increase for the same region. The use of seedling and understorey plant species may be more useful. Lenoir *et al.* (2009) compared elevational distributions of seedlings with

those of adult trees, and found that average elevational distributions at the seedling life stage were higher upslope than those at the adult life stage probably due to recent increase in temperature. Elevational distributions of seedlings are currently being surveyed in our study location and will also be used to monitor the impacts of climate change (M. J. Laidlaw *et al.*, unpubl. data, 2015).

Due to the small elevational range encompassed by our study transect, most species were indicative of elevations that included the lowest (300 m) or highest (1100 m) elevational bands. These indicator species are less than ideal as the upper or lower limits of their potential elevational distributions in the region cannot be determined. Other elevational studies, such as those conducted on Andean mountain slopes (which can encompass elevational ranges up to 4000 m a.s.l.), found many species restricted to mid-elevations (e.g. Escobar *et al.* 2005; Herzog *et al.* 2013). Elevational ranges of Australian studies are limited by the availability of high mountains (the highest mountain in Australia is Mt Kosciuszko at 2228 m). In addition, the presence of human disturbance at lower elevations further limits available elevational ranges, making it difficult to detect species with mid-elevational ranges.

Spatial and temporal fidelity

Despite the large number of moth indicator species, the CAP model did not predict the correct elevations of new samples collected in the austral spring (October). The CAP model was calculated using indicator species collected in late summer (March); hence, we expected that the same indicator species may have been absent or shifted their elevational distribution downslope in response to the cooler and drier conditions in October (detailed seasonal climatic conditions for each elevational bands available from Strong *et al.* 2011). The response patterns of moth indicator species were, however, rather random, and many low and high elevation indicators were absent or very rare from October samples (Appendix S3). Furthermore, some species indicative of mid-elevations actually shifted upslope despite the cooler climatic conditions in October. The seasonal phenology of moths can be highly variable, and mass emergence of moths occurs in response to leaf flushing and rain, making seasonal and inter-annual fluctuations of moth species rather unpredictable (Intachat *et al.* 2001). Indeed, Kitching *et al.* (2013b) collected moths at the same time of year in two consecutive years from the same areas of Bornean tropical rainforest and found significant differences in moth assemblage between years. The use of plurivoltine moth species may reveal more consistent patterns throughout the year; however, we know little

about the biologies of moth species in subtropical (let alone tropical) rainforests. More intensive sampling investigating both inter- and intra-annual fluctuations of moths may be required to reveal their phenological patterns along the elevation gradient, and thus the effectiveness of individual species as elevational indicators.

Unlike moths, we observed high seasonal fidelity of ant indicator species with the CAP model correctly predicting actual elevations of both October and January samples. Although a few species showed inconsistent patterns, the overall fidelity of most species was very high (Appendix S2). This high temporal fidelity is probably attributable to the eusocial nature of ants: their nests within soil, forest litter or tree cavities are generally perennial, persisting for more than a year. Furthermore, unspecialized food resources of many ant species (they are primarily scavengers) may not be substantially influenced by seasonal availabilities of food resources.

To our surprise, the elevational distributions of ant indicator species were consistent between the Green Mountains and Binna Burra sections where aspects and soil types were different. At both large and small spatial scales, changes in average temperature are known to strongly influence ant community composition, and other factors such as net primary productivity and geometry (i.e. mid-domain effect) play relatively minor roles (Sanders *et al.* 2007; Longino & Colwell 2011). Elevation is a good surrogate for temperature at our study location (Strong *et al.* 2011) and elsewhere (Körner 2007); consequently, ant assemblages showed progressive and consistent changes with elevation (Burwell & Nakamura 2011). One exception lies at the peak elevation (>1000 m a.s.l.) where high moisture levels are maintained throughout the year due to cloud stripping (Strong *et al.* 2011). As a result, ants (and other organisms including trees and moths) had substantially different assemblage composition at this elevation. Our results suggest that elevational distributions of ant species are likely to be determined by temperature (and moisture at the peak elevations), while other factors such as aspect and soil type do not significantly influence ant species that have elevationally restricted distributions.

One may argue that if an elevational study involves transects that are separated by tens of kilometres (if not hundreds or thousands), indicators at this taxonomic resolution (i.e. species) may no longer be useful. A survey that encompasses both latitudinal and elevational differences (e.g. elevational transects across different latitudes) inevitably incorporates biogeographical complexities whereby latitudinally distant transects may have functionally similar, yet entirely different suites of species (Kitching *et al.* 2004). For studies at much larger spatial scales than the current study, taxonomic resolution may need to be 'diluted'

(to genus, family or above), or indicator species may need to be identified for individual elevational transects.

Here we have demonstrated that despite the assemblage composition of all four groups of organisms being elevationally stratified, the relative usefulness of their species as indicators of elevation, as well as the conservation and ecological implications, differ among these groups. Our aim here was not to choose the best groups for monitoring climate change impacts, but to stress the importance of a multi-taxon approach as different taxonomic groups with different biologies often show different biodiversity patterns along the same environmental gradient.

ACKNOWLEDGEMENTS

Fieldwork was conducted during the IBISCA-Queensland project, funded by the Queensland Government Smart State Initiative, Queensland Museum, Queensland Herbarium, SEQ Catchments, the Global Canopy Program and the Queensland National Parks Association. The research included in this paper was supported by the Griffith School of Environment and the Environmental Futures Research Institute, Griffith University, Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, and Queensland-Chinese Academy of Sciences Biotechnology Fund (GJHZ1130). We thank Min Cao, Xiaoyang Song and Shuyin Huang for their kind assistance and advice.

REFERENCES

- Agosti D., Majer J., Alonso L. & Schultz T. (2000) *Sampling Ground-Dwelling Ants: Case Studies from the World's Rain Forests*. Curtin University of Technology, Perth.
- Andersen A. N. (1999) My bioindicator or yours? Making the selection. *J. Insect Conserv.* **3**, 61–4.
- Anderson M. J. (2005) *PERMANOVA: a FORTRAN Computer Program for Permutational Multivariate Analysis of Variance*. Department of Statistics, University of Auckland, Auckland.
- Ashton L. A., Kitching R. L., Maunsell S. C., Bito D. & Putland D. A. (2011) Macrolepidopteran assemblages along an altitudinal gradient in subtropical rainforest—exploring indicators of climate change. *Mem. Queensl. Mus. Nat.* **55**, 375–89.
- Berry P. M., Dawson T. P., Harrison P. A. & Pearson R. G. (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Glob. Ecol. Biogeogr.* **11**, 453–62.
- Bito D., Novotny V., Burwell C. J., Nakamura A., Kitching R. L. & Ødegaard F. (2011) Predator pressure, herbivore abundance and plant damage along a subtropical altitudinal gradient. *Mem. Queensl. Mus. Nat.* **55**, 451–61.
- Botes A., McGeoch M. A., Robertson H. G., Niekerk A., Davids H. P. & Chown S. L. (2006) Ants, altitude and change in the northern Cape Floristic Region. *J. Biogeogr.* **33**, 71–90.
- Brehm G. & Fiedler K. (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *J. Biogeogr.* **30**, 431–40.
- Bruhl C. A., Mohamed V. & Linsenmair K. E. (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *J. Trop. Ecol.* **15**, 265–77.
- Burwell C. J. & Nakamura A. (2011) Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Mem. Queensl. Mus. Nat.* **55**, 391–411.
- Chao A. & Jost L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**, 2533–47.
- Chatzaki M., Lymberakis P., Markakis G. & Mylonas M. (2005) The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. *J. Biogeogr.* **32**, 813–31.
- Chen I.-C., Hill J. K., Ohlemüller R., Roy D. B. & Thomas C. D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–6.
- Clarke K. R. & Gorley R. N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E Ltd, Plymouth.
- Davis A. J., Jenkinson L. S., Lawton J. H., Shorrocks B. & Wood S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783–6.
- Dufrène M. & Legendre P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* **67**, 345–66.
- Egger J. & Hoinka K. P. (1992) Fronts and orography. *Meteorol. Atmos. Phys.* **48**, 3–36.
- Escobar F., Lobo J. M. & Halffter G. (2005) Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in the Colombian Andes. *Glob. Ecol. Biogeogr.* **14**, 327–37.
- Feeley K. J., Silman M. R., Bush M. B. *et al.* (2011) Upslope migration of Andean trees. *J. Biogeogr.* **38**, 783–91.
- Gilman S. E., Urban M. C., Tewksbury J., Gilchrist G. W. & Holt R. D. (2010) A framework for community interactions under climate change. *Trends Ecol. Evol.* **25**, 325–31.
- Hall C. R., Burwell C. J., Nakamura A. & Kitching R. L. (2015) Altitudinal variation of parasitic Hymenoptera assemblages in Australian subtropical rainforest. *Aust. Entomol.* DOI: 10.1111/aen.12114. in press.
- Hansen M. C., Potapov P. V., Moore R. *et al.* (2013) High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–3.
- Herzog S. K., Hamel-Leigue A. C., Larsen T. H. *et al.* (2013) Elevational distribution and conservation biogeography of Phanaeine dung beetles (Coleoptera: Scarabaeinae) in Bolivia. *PLoS ONE* **8**, e64963.
- Hodkinson I. D. (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biol. Rev.* **80**, 489–513.
- Hoffmann A. A. & Sgro C. M. (2011) Climate change and evolutionary adaptation. *Nature* **470**, 479–85.
- Hsieh T. C. (2013) *iNEXT: iNterpolation and EXTrapolation for Species Diversity*. R package version 1.0. [Cited 15 Feb 2015.] Available from URL: <http://chao.stat.nthu.edu.tw/blog/software-download/>
- Hutley L. B., Doley D., Yates D. J. & Boonsaner A. (1997) Water balance of an Australian subtropical rainforest at altitude: the ecological and physiological significance of intercepted cloud and fog. *Aust. J. Bot.* **45**, 311–29.
- Intachat J., Holloway J. D. & Staines H. (2001) Effects of weather and phenology on the abundance and diversity of

- geometroid moths in a natural Malaysian tropical rain forest. *J. Trop. Ecol.* **17**, 411–29.
- Kitching R. L. & Ashton L. A. (2013) Predictor sets and biodiversity assessment: the evolution and application of an idea. *Pac. Conserv. Biol.* **19**, 418–26.
- Kitching R. L., Ashton L. A., Burwell C. J. *et al.* (2013a) Sensitivity and threat in high-elevation rainforests: outcomes and consequences of the IBISCA-Queensland project. In: *Trees at Risk: Challenges of Global Canopy Ecology and Conservation* (eds M. Lowman, S. Devy & T. Ganesh) pp. 131–9. Springer, New York.
- Kitching R. L., Ashton L. A., Nakamura A., Whitaker T. & Khen C. V. (2013b) Distance-driven species turnover in Bornean rainforests: homogeneity and heterogeneity in primary and post-logging forests. *Ecography* **36**, 675–82.
- Kitching R. L., Bickel D., Creagh A. C., Hurley K. & Symonds C. (2004) The biodiversity of Diptera in Old World rainforest surveys: a comparative faunistic analysis. *J. Biogeogr.* **31**, 1185–200.
- Kitching R. L., Putland D., Ashton L. A. *et al.* (2011) Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Mem. Queensl. Mus. Nat.* **55**, 235–50.
- Körner C. (2007) The use of ‘altitude’ in ecological research. *Trends Ecol. Evol.* **22**, 569–74.
- Laidlaw M. J., McDonald W. J. F., Hunter R. J. & Kitching R. L. (2011) Subtropical rainforest turnover along an altitudinal gradient. *Mem. Queensl. Mus. Nat.* **55**, 271–90.
- Laurance W. F., Sayer J. & Cassman K. G. (2014) Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* **29**, 107–16.
- Lenoir J., Gégout J.-C., Pierrat J.-C., Bontemps J.-D. & Dhôte J.-F. (2009) Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography* **32**, 765–77.
- Levings S. C. (1983) Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecol. Monogr.* **53**, 435–55.
- Liow L. H., Sodhi N. S. & Elmqvist T. (2001) Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *J. Appl. Ecol.* **38**, 180–92.
- Longino J. T., Branstetter M. G. & Colwell R. K. (2014) How ants drop out: ant abundance on tropical mountains. *PLoS ONE* **9**, e104030.
- Longino J. T. & Colwell R. K. (2011) Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere* **2**, art29.
- McGeoch M. A. (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biol. Rev.* **73**, 181–201.
- McGuire L. P. & Boyle W. A. (2013) Altitudinal migration in bats: evidence, patterns, and drivers. *Biol. Rev.* **88**, 767–86.
- Maunsell S. C., Kitching R. L., Greenslade P., Nakamura A. & Burwell C. J. (2013) Springtail (Collembola) assemblages along an elevational gradient in Australian subtropical rainforest. *Aust. J. Entomol.* **52**, 114–24.
- Parmesan C. & Yohe G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- Pearson R. G. & Dawson T. P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **12**, 361–71.
- Pyrz T. W. & Wojtusiak J. (2002) The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zepa (Cordillera de Merida, Venezuela) with remarks on their diversity and parapatric distribution. *Glob. Ecol. Biogeogr.* **11**, 211–21.
- Sam K., Koane B. & Novotny V. (2015) Herbivore damage increases avian and ant predation of caterpillars on trees along a complete elevational forest gradient in Papua New Guinea. *Ecography* **38**, 293–300.
- Sanders N. J., Lessard J.-P., Fitzpatrick M. C. & Dunn R. R. (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Glob. Ecol. Biogeogr.* **16**, 640–9.
- Sanford M. P., Manley P. N. & Murphy D. D. (2009) Effects of urban development on ant communities: implications for ecosystem services and management. *Conserv. Biol.* **23**, 131–41.
- Smith M. A., Hallwachs W. & Janzen D. H. (2014) Diversity and phylogenetic community structure of ants along a Costa Rican elevational gradient. *Ecography* **37**, 720–31.
- Strong C., Boulter S., Laidlaw M. J., Maunsell S. C., Putland D. & Kitching R. (2011) The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Mem. Queensl. Mus. Nat.* **55**, 251–70.
- Sunday J. M., Bates A. E., Kearney M. R. *et al.* (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *PNAS* **111**, 5610–15.
- Swenson N. G., Anglada-Cordero P. & Barone J. A. (2010) Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. *Proc. Biol. Sci.* **278**, 877–84.
- Tang Z., Fang J., Chi X. *et al.* (2012) Patterns of plant beta-diversity along elevational and latitudinal gradients in mountain forests of China. *Ecography* **35**, 1083–91.
- Thomas C. D. (2010) Climate, climate change and range boundaries. *Divers. Distrib.* **16**, 488–95.
- Wilson R. J., Gutierrez D., Gutierrez J., Martinez D., Agudo R. & Monserrat V. J. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* **8**, 1138–46.
- Wilson R., Trueman J., Williams S. & Yeates D. (2007) Altitudinally restricted communities of Schizophoran flies in Queensland’s Wet Tropics: vulnerability to climate change. *Biodivers. Conserv.* **16**, 3163–77.
- Yeates D. K., Bouchard P. & Monteith G. B. (2002) Patterns and levels of endemism in the Australian Wet Tropics rainforest: evidence from flightless insects. *Invertebr. Syst.* **16**, 605–19.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site.

Appendix S1. Correlation between actual and predicted elevations of ant samples collected in January from Green Mountains.

Appendix S2. Ant indicator species and their proportional indicator values.

Appendix S3. Canopy and understorey moth indicator species and their proportional indicator values.