Elevation increases in moth assemblages over 42 years on a tropical mountain

I-Ching Chen[a], Hau-Jie Shiu[b], Suzan Benedick[c], Jeremy D. Holloway[d], Vun Khen Chey[e], Henry S. Barlow[f], Jane K. Hill[a], and Chris D. Thomas[a,1]

[a]Department of Biology, University of York, P.O. Box 373, York YO10 5YW, United Kingdom; [b]Graduate Institute of Environmental Sciences and Ecology, National University of Tainan, 33 Su-Lin Street, Section 2, Tainan 700, Taiwan; [c]School of Sustainable Agriculture, Universiti Malaysia Sabah, Aras 2, Blok B, Bangunan Sekolah Sains and Teknologi, Locked Bag 2073, 88999 Kota Kinabalu, Sabah, Malaysia; [d]Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom; [e]Entomology Section, Forest Research Centre of Sabah, Sepilok, P.O. Box 1407, Postcode 90715, Sandakan, Malaysia; and [f]P.O. Box 10139, Postcode 50704, Kuala Lumpur, Malaysia

Physiological research suggests that tropical insects are particularly sensitive to temperature, but information on their responses to climate change has been lacking—even though the majority of all terrestrial species are insects and their diversity is concentrated in the tropics. Here, we provide evidence that tropical insect species have already undertaken altitude increases, confirming the global reach of climate change impacts on biodiversity. In 2007, we repeated a historical altitudinal transect, originally carried out in 1965 on Mount Kinabalu in Borneo, sampling 6 moth assemblages between 1,885 and 3,675 m elevation. We estimate that the average altitudes of individuals of 102 montane moth species, in the family Geometridae, increased by a mean of 67 m over the 42 years. Our findings indicate that tropical species are likely to be as sensitive as temperate species to climate warming, and we urge ecologists to seek other historic tropical samples to carry out similar repeat surveys. These observed changes, in combination with the high diversity and thermal sensitivity of insects, suggest that large numbers of tropical insect species could be affected by climate warming. As the highest mountain in one of the most biodiverse regions of the world, Mount Kinabalu is a globally important refuge for terrestrial species that become restricted to high altitudes by climate warming.

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The narrow physiological specialization of tropical insects may render them particularly sensitive to temperature changes, and it is possible that they may be even more sensitive to climate change than are their temperate-zone counterparts (1–3). However, there is no empirical evidence showing whether or not tropical insects are responding to climate change. The Intergovernmental Panel on Climate Change (4) found 28,586 cases of significant biological trends on land between 1970 and 2004, of which only 7 were tropical, and none concerned tropical insects—which of course dominate multicellular terrestrial biodiversity (5, 6). Extinctions of species from climate change are projected to be most numerous in the tropics (7–11), and so data on observed responses to climate warming are urgently required to develop strategies to minimize biodiversity losses.

Elevation increases are likely responses to climate warming in the tropics. Evidence that such changes are taking place is currently limited to tropical vertebrates (12–15); birds, reptiles, and amphibians are increasing their elevations on tropical mountains—although data are scarce, even for these taxa. For insects, multispecies analyses of elevation changes are limited to the temperate zone (16–18), where elevation increases appear to be proceeding in line with regional temperature increases. Until now, it has been considered difficult or impossible to obtain comparable evidence for tropical insects, given the dearth of long-term population and distribution datasets for tropical insects. However, perhaps the most convincing temperate-zone studies of elevation change in insects (15, 16) and other taxa (19) have involved repeat surveys, whereby researchers have revisited the specific locations of former records to identify possible changes. This strategy can potentially be applied in the tropics, just as it has been in a resurvey of amphibians and reptiles in Madagascar (15).

We were able to repeat an elevation transect survey of moths on Mt. Kinabalu (20) in Borneo (Sabah, Malaysia; 6°4′ N, 116°33′ E), after an interval of 42 years. Mt. Kinabalu represents a center of endemism, and it is the highest mountain within the Sundaland global biodiversity hotspot (21). The summit, Low's Peak at 4,095 m, is the highest point between the eastern Himalaya in Burma and the mountains of New Guinea. The original moth transect was carried out by 2 of the current authors, H.S.B. and J.D.H., and H. J. Banks between July and September, 1965 (20). We repeated the elevational-transect survey in 2007, at 6 sites between 1,885 and 3,675 m elevation (Fig. 1), with one of the 1965 surveyors (H.S.B.) visiting field sites in 2007. Our resurvey was conducted at the same sites and season, August to September 2007, with actual dates at each site following similar moon phases. We applied the original trap designs (Table 1), replicating 1965 protocols and catch effort (20). Twelve sites were surveyed in 1965, but major vegetation change associated with human activities occurred at 2 low-elevation sites, and sampling protocols differed at another 4. We excluded all data from these sites. Thus, we obtained comparable data for the 6 sites considered here, in habitats that are relatively unscathed by human influence (Fig. 1). If temperature increases had already affected these tropical moth assemblages, we predicted that, on average, moth species would be found at higher elevations in 2007 than in 1965.

Results

We calculated the elevational "center of gravity" of 102 geometrid moth species recorded in both years, using 3 different approaches. Each method was equivalent to calculating the average elevation of individuals of each species.

The first approach was to calculate the average elevation of individuals of each species in both years, by using the raw data (see elevation calculation A in *Methods*). These calculations are the simplest but subject to potential error (see below) because somewhat different numbers of individuals were caught at each site in 1965 and 2007 (Table 1). This analysis revealed a mean elevation increase across all species of 97 m (SD = 170 m, 1-sample $t = 5.79$, d.f. = 101, $P < 0.001$). Nearly twice as many species showed uphill trends as showed downhill trends in the
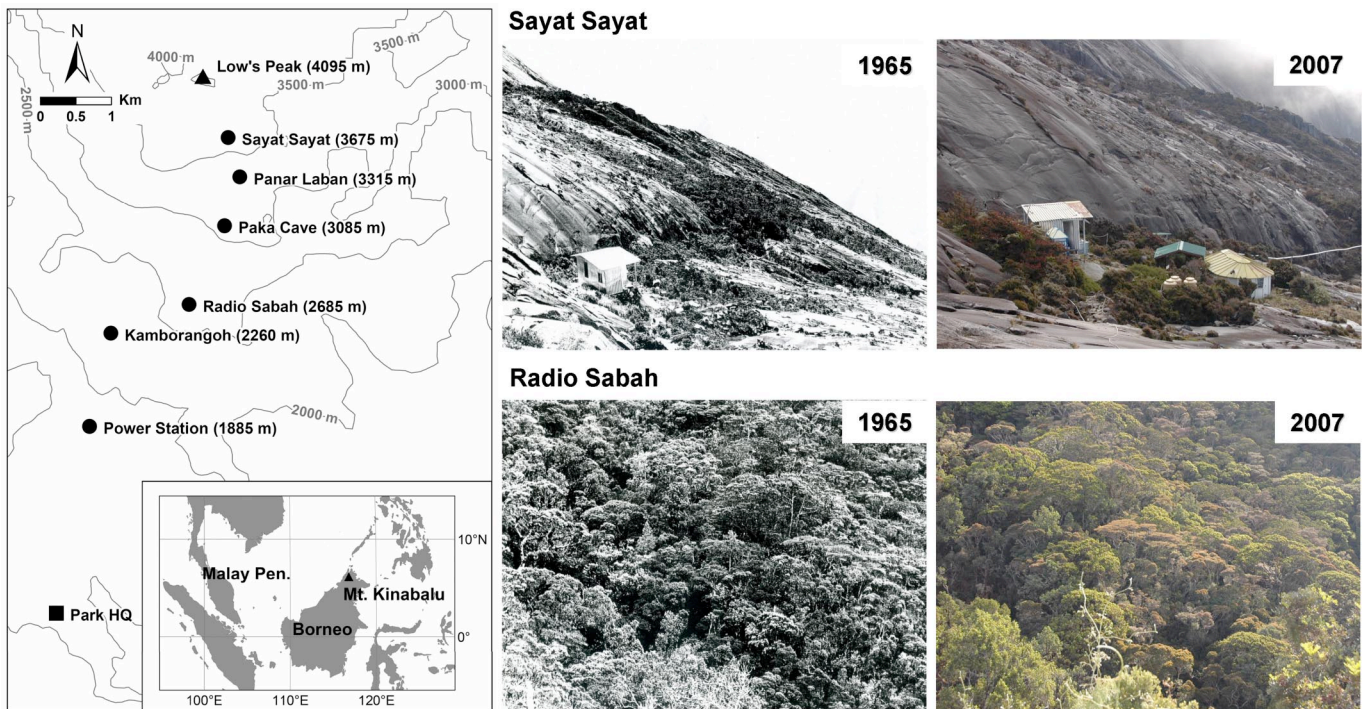
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Fig. 1. Locations of the 6 sample sites on Mount Kinabalu, Borneo, and photographs of 2 sites in 1965 and 2007. Sites were included only if the vegetation remained similar. Sayat Sayat, at 3,675 m, is the highest site considered. It is set in a rocky landscape, with only small pockets of vegetation present. Most of the higher ground on the mountain is dominated by bare rock. Radio Sabah, at 2,685 m, is densely forested, more representative of the lower mountain slopes.

raw data (58 uphill, 12 no change, 32 downhill; Wilcoxon signed-rank test for species showing uphill versus downhill movement, $P = 0.004$). Elevation increases were significant separately for endemic species that are restricted to Mt. Kinabalu ($n = 20$, mean = 113 m upwards, SD = 224 m, $t = 2.27$, $P < 0.05$) as well as for more geographically widespread, nonendemic species ($n = 82$, mean = 93 m upwards, SD = 155 m, $t = 5.44$, $P < 0.001$). Changes were not significantly different between endemic and wider-ranging species (2-sample t = 0.38, $P = 0.71$).

The second approach adjusted elevation estimates to take account of total numbers of moths (of all geometrid species) caught at each elevation in the 2 years (elevation calculation Bi in *Methods*). Elevations increased by an average of 67 m per species (SD = 166 m, 1-sample $t = 4.07$, d.f. = 101, $P < 0.001$; Fig. 2A). Over 3 times as many species showed uphill trends as showed downhill trends (69 uphill, 12 no change, 21 downhill; Wilcoxon signed-rank test, uphill versus downhill, $P < 0.001$). Uphill shifts were significant separately for endemic ($n = 20$,

mean = 91.8 m upwards, SD = 224 m, $t = 1.83$, $P < 0.05$) and nonendemic species ($n = 82$, mean = 61 m upwards, SD = 150 m, $t = 3.68$, $P < 0.001$). Changes were not significantly different between endemic and wider-ranging species (2-sample $t = 0.58$, $P = 0.57$; Fig. 2A).

The third method involved randomly subsampling (500 times) the data so that the same number of individuals was "sampled" in each year, with exactly the same altitudinal distribution of catch in both 1965 and 2007 (elevation calculation Bii in *Methods*). This gave 500 estimates per species of the difference in elevation between 1965 and 2007, the mean of which was used as the elevation change estimate for each species. Elevations increased by an average of 68 m per species (SD = 163 m, 1-sample $t = 4.18$, d.f. = 101, $P < 0.001$). The mean and standard deviation remain very similar to those estimated from the Bi analysis, above. Twice as many species showed uphill trends as showed downhill trends (60 uphill, 12 no change, 30 downhill; Wilcoxon signed-rank test, uphill versus downhill, $P = 0.001$). Uphill shifts were significant separately for endemic ($n = 20$,

Table 1. Sampling sites and catch summary

Site	Altitude, m	Trap	Geometridae moth individuals (species)		Total individuals of all moth families	
			1965	2007	1965	2007
Sayat Sayat	3,675	T.L.*	100 (5)	60 (5)	137	85
Panar Laban	3,315	T.L.	81 (7)	264 (10)	129	471
Paka Cave	3,085	T.L.	70 (9)	39 (8)	78	95
Radio Sabah	2,685	M.V. [†]	898 (65)	940 (69)	2,060	>2,572
Kamborangoh	2,260	M.V.	663 (103)	582 (103)	1,620	>2,000
Power Station	1,885	M.V.	2,549 (220)	1,398 (172)	6,064	>6,488

*Tilley lamp trap.
[†]Mercury vapor light trap, modified from the Robinson trap.
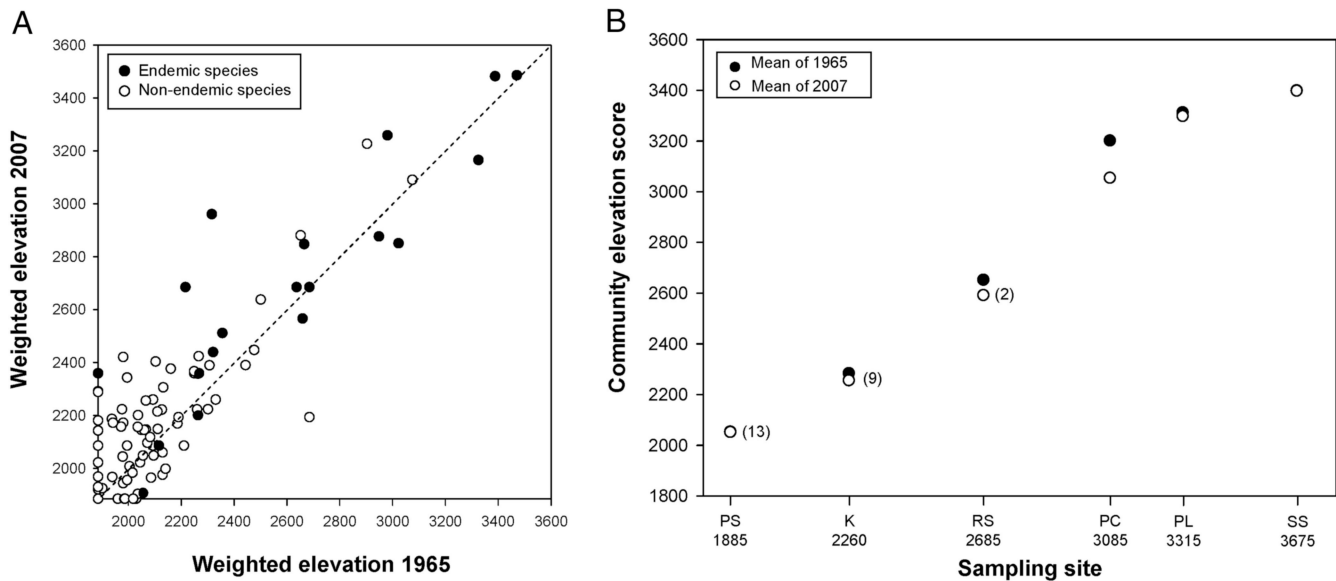
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Fig. 2. Elevation changes of moths on Mount Kinabalu between 1965 and 2007. (*A*) Species elevations (m). Species above the equal-elevation diagonal represent those estimated to have increased in elevation, by using elevation calculation method *Bi*. (*B*) Community elevation scores (m). Where open circles fall below filled circles, the community in 2007 has an increased representation of previously lower elevation species. Abbreviations relate to sites in Table 1. Values in brackets are numbers of species recorded only at <1,885 m in 1965 but found higher in 2007.

mean = 90 m upwards, SD = 212 m, t = 1.89, P < 0.05) and nonendemic species (n = 82, mean = 62 m upwards, SD = 150 m, t = 3.76, P < 0.001). As before, changes were not significantly different between endemic and wider-ranging species (2-sample t = 0.54, P = 0.59).

All of the previous analyses were calculated by using the subset of species recorded 3 or more times in both years. Using the randomization procedure, we also carried out a comparable analysis for a larger sample of all 157 species recorded in both years. Elevations increased by an average of 56 m per species (SD = 204 m, 1-sample t = 3.43, d.f. = 156, P < 0.001). Not surprisingly, including the rarest species increased the standard deviation somewhat, but otherwise the results remained similar.

We also calculated "community elevation scores," based on all species present at each site (using those for which ≥3 individuals were recorded in each year). For this analysis, each species was assigned its center of gravity based on the 1965 data alone (treating this as equivalent to a species' trait, indicating its 1965 "favored" elevation based on data from these 6 sites), and the mean elevation of species present at each site was calculated for both 1965 and 2007. The community elevation score decreased at all 6 sites (Wilcoxon signed-rank test, P = 0.028), revealing uphill shifts in the moth communities equivalent to 1.1 to 146.4 m (mean 41.9 m) (Fig. 2*B*).

Discussion

As predicted, the results showed a consistent increase in average elevation of moths over the 42-year period, in both species- and assemblage-level analyses. We consider that it is appropriate to adjust estimated elevations to take account of differences in sample sizes at each elevation between 1965 and 2007, and hence we estimate that the average elevations of moth species increased by 67 m, based on the "proportional" analysis and the randomization procedure (*Bi* and *Bii*). The assemblage-level analysis suggested a more modest 42 m increase, but this is almost certainly an underestimate of the true elevation shift because our analyses were based solely on species recorded within the 1,885 to 3,675 m elevation range in both years. Sampling in 1965 also took place at lower elevation than the 6 sites considered here; a number of species that were recorded only <1,885

m in 1965 moved upwards, colonizing the 3 lowest 2007 sites (Fig. 2*B*). These species were not included in the community elevation scores, so the upwards shifts reported for the lowest 3 sites are underestimated. A lack of suitable vegetation for most moth species at our highest site, where the ground is mainly bare rock (Sayat Sayat, Fig. 1), is the probable main reason for the limited community response seen at this site.

Regional warming for the 5° cell in which Mt. Kinabalu lies (*Methods*) was ≈0.7 °C over the 42-year period. Mean annual temperature anomalies (compared with 1961–1990 mean) for the decades before the 2 surveys (1956–1965 and 1998–2007) were −0.202 °C and +0.478 °C, respectively, showing a warming of 0.68 °C in 42 years. We also regressed annual temperature anomalies against year for the period 1956 to 2007 (coefficient = 0.017, r^2 = 0.55), which gave an estimate of 0.71 °C over 42 years. Lapse rates for the moist tropics are likely to be ≈0.55 °C reduction in temperature per 100-m increase in altitude (22). At this lapse rate, 0.7 °C regional warming would be equivalent to an upwards shift of 127 m. This is greater than the mean observed moth elevation increase of 67 m, although somewhat closer to the unadjusted estimate of 97 m. However, observed range changes may be truncated by the finite elevational range considered here and, hence, could be underestimated. We should also be cautious because specific lapse rates are not known between the transect locations we considered in Borneo, and warming at the transect sites on the mountain may differ from that estimated for the 5° × 5° cell; detailed meteorological measurements along the Kinabalu transect would be required to identify whether moth elevation changes are really lagging behind climate change.

We conclude that upwards elevation shifts of moth species on Mt. Kinabalu are consistent with being responses to the climate change observed in the region, either as a direct physiological response to climate or as a consequence of altered interactions with other species. For example, plant elevation increases have been observed recently on temperate-zone mountains (23–25), and if the same phenomenon is taking place on Mt. Kinabalu, this could be facilitating elevation increases by the insects that feed on them. It is too early to judge whether these responses differ from those of temperate-zone Lepidoptera; but on current

evidence (16–18) it would appear that the responses are fairly similar.

We suspect that data from other historic surveys of biodiversity must exist for other locations and taxa in the tropics. We suggest that it would be productive for ecologists to seek these out so that they can form the basis for further repeat surveys.

Tropical mountains, including Mt. Kinabalu, support endemic montane species that occur nowhere else in the world, some of which may become threatened with extinction if they are pushed to higher elevations (7, 10, 15, 26–29); especially if elevation increases are constrained by a lack of vegetation and slow succession on bare rock at high altitudes. The combination of thermal sensitivity of tropical insects (1–3) and the uphill shift reported here indicate that tropical insects could potentially come to dominate lists of species threatened with extinction from climate change, given their underlying diversity (5, 6). Despite these risks, Mt. Kinabalu and other tropical mountains (11) may become important climate-change refugia for lower-elevation species. Mt. Kinabalu is the highest mountain, and hence coolest location, within the Sundaland global biodiversity hotspot, to which ≈1,100 vertebrate species, 15,000 plant species and probably many times that number of insect species are endemic, mostly supported by the remaining 6.7% of native vegetation that remains intact in the region (www.biodiversityhotspots.org/). However, high mountains will only become important refugia for low-elevation species if surrounding lowland forests and other natural habitats are maintained. The conservation of lowland forest will permit lowland species to survive locally and so be available to colonize upwards while also minimizing additional regional impacts on climate change associated with lowland deforestation (30, 31). High tropical mountains and their surrounding lowland habitats represent some of the most important locations in the world to maintain biodiversity in the face of climate change (11, 29).

Methods

Species Included. For taxonomic and logistic reasons, we restricted analysis to the family Geometridae (32–34). We captured 3,283 geometrid individuals from 216 species in 2007, comparable with the 4,361 geometrid individuals and 241 species in 1965. We included only species for which ≥3 individuals were recorded in 1965 and ≥3 in 2007, giving 102 species for analysis (mean of 66 individuals per species, for species included in the analysis). Endemics were defined as species that have only ever been recorded from Mt. Kinabalu, Borneo (34).

Elevation Calculations. Catch differed somewhat between years at each elevation, despite repeating the 1965 sampling protocol in 2007 (Table 1). Changes in total moth numbers caught at each site might represent sampling error in each year or could alternatively reflect ''true'' shifts in relative abundance patterns (summed across all species) associated with climate change. Therefore, we carried out analyses based on these alternative assumptions, to ensure that the conclusions were robust.

(A) True shifts in total moth abundance. If climate change results in real changes numbers of moths at each elevation on the mountain, the appropriate analysis is simply to calculate the average elevation of individuals of each species in both years.

(B) Assuming random sample error. Based on the 6 sites sampled, we calculated an average weighted center of gravity elevation for each species that should be unbiased by differences in catch in 2 ways. (*Bi*) First, we calculated the proportion of individuals that belonged to a given species at each site/elevation. Then, we took the average of all elevations at which the species had been recorded, weighting each elevation by the proportion of the fauna that the species in question represented there. (*Bii*) We randomly selected subsamples of individuals to generate 500 comparable datasets for 1965 and 2007. Thus, 1,398 individuals (the smaller 2007 sample) were selected at random from the 2,549 individuals caught at Power Station in 1965 (Table 1). Similarly, 898 individuals (the smaller 1965 sample) were selected at random from the 940 individuals caught at Radio Sabah in 2007, and so on for the remaining 4 sites. For 1 randomization, this generated the same number of individuals in both 1965 and 2007, for each elevation. This was repeated, giving 500 estimates of the elevation change per species, the mean of which was used in subsequent analyses. For all 3 methods, estimates of elevation change per species were compared between years.

Temperature Change 1965 to 2007. In the absence of long-running weather station data from Mt. Kinabalu, we used data from the Global Historical Climatology Network (www.ncdc.noaa.gov/oa/climate/research/ghcn/ghcngrid.html#top) for the 5° cell that contains Mt. Kinabalu to estimate climate change over the study period.

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