IMPACTS OF CLIMATE WARMING ON RANGE SHIFTS WITH EMPHASIS ON TROPICAL MOUNTAINS

Thesis submitted by

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ABSTRACT

Climate warming induced range shifts are evident globally for a wide range of taxonomic groups. However, whether such responses have taken place in tropical insect species is unclear. I provided the first such evidence that tropical insects have moved uphill over four decades of climate warming. I repeated a historical moth transect on Mount Kinabalu in Borneo in 2007, 42-years after the original survey in 1965. I duplicated the 1965 sampling strategy in 2007, and excluded sites where habitat changes were evident. I estimated that the average elevation of 102 montane moth species, in the family Geometridae, increased by a mean of 67 m. A sub-group of species retreated their upper boundaries, which may be associated with cloud cover changes and the presence of geological / vegetation transitions. Without these constraints, most species expanded their upper boundaries upwards (by an average of 152 m) more than they retreated at their lower boundaries (77 m), indicating that different ecological mechanisms may predominate in leading and trailing edge populations. Declines of local endemic species, ecological barriers constraining uphill movements, disappearing climate types and a decreasing area of land at higher elevations are the major concerns for conservation. Research of biodiversity risk under warming is urgently required in Southeast Asia. I conducted a meta-analysis of range shifts representing ~1700 species worldwide. The average rate of elevational range shift was 12.2 m/decade uphill, and latitudinal shifts averaged 17.6 km/decade poleward. These rates are faster than previously reported. Latitudinal range shifts responded to the rates of regional warming, but these were not the cases for elevational range shifts. Poikilotherms shifted their distributions faster than homeotherms. The original data and meta-analysis presented in this thesis indicate that climate change is having a pervasive impact on the distributions of species, including in the tropics.

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I declared that the thesis is my own work and was written by myself, except where specific references have been given to the work of others.

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The data were gathered from the Mount Kinabalu moth transect resurvey project, in which, I, Jeremy Holloway, Henry Barlow, Jane Hill and Chris Thomas designed the research; Jane and Henry guided the field sampling; I and Hau Jie Shiu collected moths from 7 of the 10 sites and Suzan Benedick collected 4 of the 10 sites; I and Suzan sorted our specimens respectively, with laboratory support from Vun Khen Chey and identification advice from Jeremy; I identified a subset of Suzan’s specimens and dissected moth genitalia to identify all ambiguous specimens; I compiled the dataset, performed the statistical analysis and produced the figures and tables; Hau Jie assisted in GIS techniques, produced the study area maps and extracted the land area data of the 100-m elevation band in Mount Kinabalu; randomization was conducted by Hau Jie (using COMPAQ VISUAL FORTRAN) and myself (using R); I, Chris and Jane wrote the papers.

CHAPTER 1

GENERAL INTRODUCTION

The Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment (2007b) found that the global surface temperature has warmed by *ca* 0.74°C for the past 100-years, at a rate about twice the average for the later half of the 20th century and concluded that the current warming is "very likely due to the observed increase in anthropogenic greenhouse gas concentrations", including carbon dioxide, methane and nitrous oxide from various human activities. With very high confidence, the IPCC (2007a) indicated that the climate change, particularly the regional temperature increase has affected natural systems throughout all continents and most oceans; the discernable physical impacts were widespread, with regard to changes in snow, ice and frozen ground globally. The biological effects were evident for a wide spectrum of species, showing that species adjusted their distribution polewards or upwards and showed changes in their phenologies (earlier in spring, later in autumn) (Parmesan & Yohe, 2003; Root *et al.*, 2003; IPCC, 2007a), with directional demographic changes and evolutionary adaptations, and changes to the synchrony of species and ecosystem functions (Parmesan, 2006; Traill *et al.*, 2010).

Warming-related range shifts and the biodiversity risks that may arise from those shifts are the primary concerns of this thesis, with a particular focus on a tropical mountain in Borneo. Along with global climate changes, elevated sea level, doubled atmospheric CO_2, altered precipitation patterns and extreme climate events etc. will have important biological consequences (IPCC, 2007a; Thibault & Brown, 2008; Tylianakis *et al.*, 2008; Serreze, 2010) but are beyond the scope of the thesis.

1.1 Warming related range shifts and biodiversity risks

1.1.1 Range and range dynamics

Species distributions hold ecological and evolutionary significances because the global distributions of different environmental (including biotic) conditions support the existence of a diversity of species (Lavergne *et al.*, 2010). These patterns have long been the major concern from autecology to macroecology. Range dynamics help reveal the underlying mechanisms that species depend on / interact with and that determine their distributions (Helmuth *et al.*, 2005; Sexton *et al.*, 2009). Temperature gradients contribute strongly to species' distribution as directional range shifts under warming have observed across a wide range of taxa (Parmesan & Yohe, 2003; Root *et al.*, 2003; Hickling *et al.*, 2006; Rosenzweig *et al.*, 2007). The patterns and processes with which species track rapid warming through range shifts attracts multidisciplinary research (Gaston, 2009b; Hill *et al.*, 2011), and evaluation of the current and future distributions and survival of species and biodiversity has implications for conservation (Thomas *et al.*, 2004; Guisan & Thuiller, 2005; Thuiller *et al.*, 2008; Wiens *et al.*, 2009).

1.1.2 Biodiversity risks concerning range shifts

Species undertake behavioural and evolutionary adaptations, and shift their ranges, in response to climate change (Thomas *et al.*, 2001; Kearney *et al.*, 2009; Hill *et al.*, 2011), and although projections of future ranges vary, the biological impacts are generally consistent; indicating reductions in global biodiversity and disruption to some ecosystems. This is because, firstly, species responses are lagging behind the warming. While paleoecological records indicate that species may survive climate changes by range shifts (e.g. Graham *et al.*, 1996; Bush, 2002; Hofreiter & Stewart, 2009; Lyons *et al.*, 2010), current migrations are slower than the rates required to track the rapid contemporary warming (Davis & Shaw, 2001). Lags are evident in terms of both distribution shifts and community changes (Menéndez *et al.*, 2006; Devictor *et al.*, 2008; review in Chapter 4). Second, small range species are especially vulnerable (Thomas *et al.*, 2004; Schwartz *et al.*, 2006; Ohlemüller *et al.*, 2008), including numerous endemic species (Midgley *et al.*, 2002; Malcolm *et al.*, 2006), habitat specialists (Warren *et al.*, 2001; Bale *et al.*, 2002), and montane species (Williams *et al.*, 2003; Colwell *et al.*, 2008). Relatively speaking, this favours species with opposite sets of characteristics (e.g. generalists). The third issue is that individualistic responses disrupt species interactions, and lead to novel communities (González-Megías *et al.*, 2008) and great uncertainty about the functioning of novel ecosystems (see Introduction of Chapter 4). Finally, the interplay between climate change and other drivers of biodiversity change, particularly habitat fragmentation, further imperil biodiversity (Warren *et al.*, 2001; Travis, 2003; Jetz *et al.*, 2007; Malhi *et al.*, 2008)

1.2 Knowledge gap in the tropics

1.2.1 Uncertainty of biological impacts in the tropics

Regional warming varies. Considering the current phase of global warming (from the 1970s to the present), the temperature increase is strongest in the northern hemisphere extra-tropics. For example, Europe has warmed at rate of 0.41°C per decade but Southeast Asia warmed between 0.1°C and 0.3°C per decade (IPCC, 2007a). Pre- and post- IPCC 2007 reports of climate-relevant range shifts have predominantly summarized the data available for temperate taxa (e.g. Rosenzweig *et al.*, 2007; Lenoir *et al.*, 2008; Moritz *et al.*, 2008; Myers *et al.*, 2009; Tingley *et al.*, 2009; Zuckerberg *et al.*, 2009; Forister *et al.*, 2010). Whether tropical species have also undergone temperature-driven range shifts is open to debate because the observed warming at low latitudes was much less pronounced (Root *et al.*, 2003; Rosenzweig *et al.*, 2008) and the empirical data to evaluate tropical species responses was generally lacking (but see Pounds *et al.*, 1999; Raxworthy *et al.*, 2008). Data from tropical regions is urgently required to test whether such responses are taking place; given that the largest number of climate-change caused extinctions is likely to take place in the tropics (Thomas *et al.*, 2004; Jetz *et al.*, 2007).

1.2.2 Vulnerable tropic species

Tropic biota could be highly vulnerable to climate change considering their physiological characteristics (Tewksbury *et al.*, 2008). Annual variation of temperature is smaller in the tropics than that of higher latitude (Janzen, 1967; Ghalambor *et al.*, 2006) which is thought to drive tropic biota to evolve narrow thermal ranges / tolerances (van Berkum, 1988; Addo-Bediako *et al.*, 2000; Deutsch *et al.*, 2008; McCain, 2009). For species that are specialized to aseasonal tropical environments, in particular, a modest temperature increase may have profound ecophysiological consequences – if these species have limited acclimatation capacities (Tewksbury *et al.*, 2008; Wake & Vredenburg, 2008; Kingsolver, 2009). Many tropical ectotherms live close to their thermal optima (Deutsch *et al.*, 2008) and with the high baseline temperature, climate warming may result in non-linear increases of metabolic rates, higher energy consumptions and negative demographic impacts (Dillon *et al.*, 2010). The magnitudes of impacts amplify in tropical regions that are global centers of biodiversity and endemism (Myers *et al.*, 2000; Sala *et al.*, 2000; Orme *et al.*, 2005; Brooks *et al.*, 2006). However, thermal tolerances and physiological flexibility are largely unstudied in montane faunas, which may contain the species that are most at risk from climate warming.

1.2.3 Mountain systems

Mountains are important biologically systems to consider under climate warming. Steep thermal (elevation) gradients facilitate range shifts within short distances, allowing species to shift their distributions upwards, as the climate warms (Colwell *et al.*, 2008). The heterogeneous topography also provides microclimate refugia to sustain local populations (Bush, 2002; Hardy *et al.*, 2010; Illán *et al.*, 2010). Elevational and microclimatic refugia are crucial if species are to survive climate warming, particularly in the tropics where the latitudinal thermal gradients are shallow (Wright *et al.*, 2009). Tropical mountains also harbor many ecological (e.g. host, habitat, climate) specialists (Williams *et al.*, 2003; Rodríguez-Castañeda *et al.*, 2010; Laurance *et al.*, 2011). Habitat specialists and species with narrow altitudinal ranges are particularly likely to experience range-shift gaps, i.e., a lack of overlap between the current distribution and potentially suitable future conditions; temperature-sensitive lowland biodiversity may show range attrition and mountaintop species may be at risk of extinction, with higher elevations not available to them (Colwell *et al.*, 2008). The threats to biodiversity differ among taxonomic groups. Homeotherms (birds, mammals) will experience changes in basal energy requirements as well as changes in resource availability, many poikilothermic insects may become extinct by virtue of their diversity, and plants are vulnerable if their distribution changes lag behind climate change (Miles *et al.*, 2004; Lenoir *et al.*, 2008; Laurance *et al.*, 2011).

The rate of warming in the mountains may accelerate in the future and is likely to be important to the distributions of species (Nogués-Bravo *et al.*, 2007). However, cloud cover and precipitation may be equally important. Cloud uplifts are expected to take place, resulting in changes to annual and seasonal precipitation, and hence to the hydrological cycles of tropical mountains (Still *et al.*, 1999; Foster, 2001; Bush, 2002;

Fischlin *et al.*, 2007; Karmalkar *et al.*, 2008). In particular, certain types of existing climate regime (combinations of temperature and precipitation, and their seasonality) are predicted to disappear, threatening biodiversity that is endemic to such climatic conditions (Williams *et al.*, 2007). Mountains are socially and economically significant as they provide wide range of ecosystem services, such as regulating regional water supply, and supporting unique agriculture and tourism (Bradley *et al.*, 2006; Nogués-Bravo *et al.*, 2007; Peh *et al.*, 2011). Hence, mountain systems will continue to be among the top concerns in global change ecology (Williams *et al.*, 2003; Fischlin *et al.*, 2007).

1.2.4 Mount Kinabalu moth resurvey

Resurvey is an ideal approach to detect biological fingerprints (Moritz *et al.*, 2008; Tingley & Beissinger, 2009) but requires high quality baseline data. To investigate biological impacts in the tropics, particularly in the mountains, I surveyed references to identify historical transects with the feasibility to carry out repeat census work. The studies examined were those: (1) conducted in mountains that fell between the Tropic of Cancer and the Tropic of Capricorn; (2) carried out within the last *ca* 30-40 years to represent current warming (longer time spans might include the consequences of environmental changes in the pre-warming period, while shorter spans may not capture species responses); (3) where there were no major land-use changes or other drivers to compound climate effects; (4) with enough sampling sites and appropriate gaps in between to detect species range shifts along elevational gradients; (5) sufficient numbers of species / abundances to be able to carry out robust statistical analyses; and (6) most importantly, repeatable, in terms of accessibility, ability to locate historical sites, availability of field notes making it possible to repeat the protocol exactly, and clear taxonomy to ensure that comparisons were of the same species. Most studies that were located failed several of these criteria.

The moth transect on Mount Kinabalu, Sabah, Malaysia was established by J. D. Holloway, H. S. Barlow and H. J. Bank in 1965 (Holloway, 1970; Holloway, 1976), and met almost all criteria. The 1965 survey covered a wide elevation range, a large number of moth species, and the transect ran alongside the major (then and now) route that ascends Mount Kinabalu, facilitating access. The original collection contributed many specimens to the “Moths of Borneo” series, in which the author J. D. Holloway established a stable foundation for the taxonomy of Indo-Australian macrolepidoptera, facilitating the identification of new specimens. Mount Kinabalu was declared as a national park in 1964, so the potentially confounding effects of habitat disturbance were substantially reduced (entirely so for a subset of sites). In 2007, we were able to conduct the resurvey with the participation of two of the original researchers (J.D.H. and H.S.B.), which greatly increased the comparability of the two surveys, considering locating the sites, repeating the field work and specimen identification (see Methods in Chapters 2 and 3 for detail). With approapriate control for variation in recorder efforts, in Chapter 2, I tested whether moth assemblages have shifted their range uphill, in line with biological fingerprints expected under global warming.

1.2.5 Testing asymmetric boundary shifts

Anthropogenic warming of the global climate provides for “natural” experimental tests of macroecological and biogeographical hypothesis (Thomas, 2010); for instance, whether the margins of species’ distribution depend on abiotic conditions or other factors. Range boundaries reflect physiological requirements within which species can thrive. Temperature is thought to be a major determinant of species distributions (Grinnell, 1917). If temperature is the ultimate determinant of range borders, and if niche conservation (Wiens *et al.*, 2010) maintains thermal limits of a species over the time scale considered, one would expect symmetric extinction events in the trailing edge (e.g. Franco *et al.*, 2006) as well as colonization in the leading edge, as species track their favorable climate surfaces (Tingley *et al.*, 2009). In fact, the rate of colonization seems to exceed that of retraction (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Brommer, 2004), which raises debate about the underlying mechanistic processes, particularly at trailing range edges. Theoretical and empirical studies indicate that biotic interactions also affect where a species reaches its limits (e.g. Hutchinson, 1957; Davis *et al.*, 1998; Harrington *et al.*, 1999; Brooker *et al.*, 2007; Schweiger *et al.*, 2008; Berggren *et al.*, 2009). Moreover, demographic parameters and capacities of local populations to persist may vary between leading and trailing edges (Gaston, 2009a; Thomas, 2010). Climate induced range shifts provide a valuable opportunity to examine possible differences between the leading / cool boundaries and trailing / warm boundaries of species' distributions.

Ideally, one would examine changes to the entire distributions of species, including both their leading and trailing edges, but data are often lacking; most research on the impacts of climate change on species' distribution margins have only examined a small portion of the range, usually a single boundary (Parmesan, 2007; Jump *et al.*, 2009). In Chapter 3, I used the data from Mount Kinabalu to compare the leading and trailing edges of the same species and evaluate whether asymmetric boundary shifts are occurring, and consider possible explanations for differences in the boundary responses of different groups of species.

1.3 Global meta-analysis of range shifts

The previous, key meta-analysis of distribution responses to climate change was based on data for three temperate zone taxonomic groups, and this study estimated that species shifted at a rate of 6.1 km/m per decade; movements in kilometres towards the poles and metres uphill were equated in this analysis (Parmesan & Yohe, 2003). Considerably more data have accumulated since that time, including more tropical studies, and information on a much wider range of taxonomic groups. Hence, it is appropriate to carry out an updated meta-analysis. In Chapter 4, I compiled a dataset of range shifts of various taxa / locations, and related these to the amount of regional warming that had taken place. The new meta-analysis helps me to address the fundamental question of whether range shifts are keeping pace with climate warming－at a global scale. The new analysis is also a development since Parmesan & Yohe (2003) because there are now sufficient data to analyze elevational (mountain) and latitudinal (lowland) range shifts separately. To the best of my knowledge, this is the first attempt to compare elevational and latitudinal warming-induced range shifts at a global scale.

There is interest in attempting to identify differences in the responses rates of different species, based on their ecological traits and the taxonomic groups to which they belong, e.g., Perry *et al.* (2005), Buckley (2008), Kadlec *et al.*(2009), Pöyry *et al* (2009), an important approach to identify vulnerable subgroups and to prioritize conservation activities (Koh *et al.*, 2004; Mattila *et al.*, 2008; Jiguet *et al.*, 2010). In the meta-analysis, I assess whether rates of range shifting vary with species' mobility, thermal strategy, trophic position, and taxonomic group (see Introduction in Chapter 4).

1.4 Conserving biodiversity in Southeast Asia

The vulnerabilities to climate changes vary between the three major tropical regions. For example, tropical Africa seems to be the most susceptible to declines in precipitation and increased droughts; while the El Niño Southern Oscillation affects inter-annual climate variability strongly in the tropical Americas and Southeast Asia (Malhi & Wright, 2004). The Amazon Basin and Congo River Basin lack significant elevation gradients to provide cool refugia (Wright *et al.*, 2009) while the fragmented topography in Southeast Asia restricts large scale range shifts for species that cannot cross the sea. Moreover, the different histories of biogeography (Bush, 2002; Woodruff, 2010) and patterns of human activities (Asner *et al.*, 2009; Laurance & Useche, 2009) result in different environmental synergies and conservation priorities in the three regions. Peer-reviewed articles addressing conservation issues under climate changes are scarce for Southeast Asia and Africa, yet their biodiversity and ecosystem services are likely to be strongly affected, and potentially threatened. In the final chapter, I consider the ecological significance of findings in the thesis and suggested future research priorities for Southeast Asia.

CHAPTER 2

ELEVATION INCREASES IN MOTH ASSEMBLAGES OVER 42 YEARS ON A TROPICAL MOUNTAIN

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2.1 Abstract

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 1885 and 3675 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.

Key words: biodiversity, climate change, Lepidoptera, tropical ecology

2.2 Introduction

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 (Janzen, 1967; Addo-Bediako *et al.*, 2000; Deutsch *et al.*, 2008). However, there is no empirical evidence showing whether or not tropical insects are responding to climate change. The Intergovernmental Panel on Climate Change (Rosenzweig *et al.*, 2007) found 28,586 cases of significant biological trends on land between 1970 and 2004, of which only seven were tropical, and none concerned tropical insects – which of course dominate multicellular terrestrial biodiversity (Øegaard, 2000; Novotny *et al.*, 2002). Extinctions of species from climate change are projected to be most numerous in the tropics (Thomas *et al.*, 2004; Malcolm *et al.*, 2006; Jetz *et al.*, 2007; Wilson *et al.*, 2007; Colwell *et al.*, 2008), and so data on observed responses to climate warming are urgently required in order 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 (Pounds *et al.*, 1999; Peh, 2007; Seimon *et al.*, 2007; Raxworthy *et al.*, 2008); 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 (Wilson *et al.*, 2005; Franco *et al.*, 2006; Hickling *et al.*, 2006), 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 (Wilson et al., 2005; Raxworthy et al., 2008) and other taxa (Moritz et al., 2008) 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 (Raxworthy *et al.*, 2008).

We were able to repeat an elevation transect survey of moths on Mt. Kinabalu (Holloway, 1970) in Borneo (Sabah, Malaysia; 6º4' N, 116 º33' E), after an interval of 42 years. Mt. Kinabalu represents a centre of endemism, and it is the highest mountain within the Sundaland global biodiversity hotspot (Myers *et al.*, 2000). 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 (Holloway, 1970). We repeated the elevational-transect survey in 2007, at 6 sites between 1,885 and 3,675 m elevation (Fig. 2.1), 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 1.1), replicating 1965 protocols and catch effort (Holloway, 1970). 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. 2.1). 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.

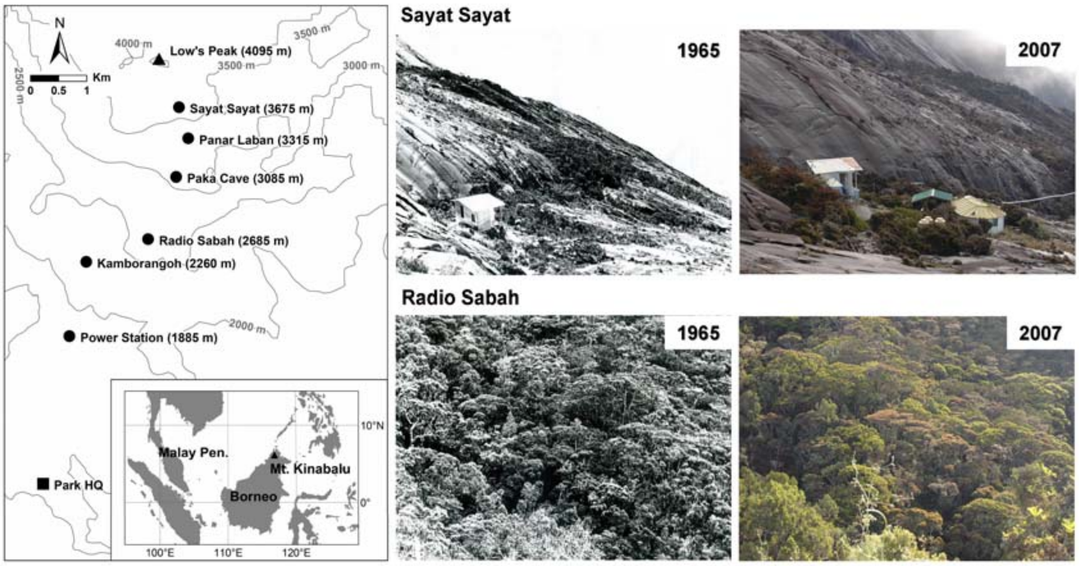


Figure 2.1 Locations of the 6 sample sites on mount Kinabalu, Borneo, and photographs of 2 sites in 1965 and 2007. Sites were included only if the vegetation remained similar. Sayat Sayat, at 3,675 m, is the highest site considered. It is set in a rocky landscape, with only small pockets of vegetation 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.

2.3 Methods

2.3.1 Species included

For taxonomic and logistic reasons, we restricted analysis to the family Geometridae (Holloway, 1994 [dated 1993], 1996, 1997). We captured 3,283 geometrid individuals from 216 species in 2007, comparable to 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 (Holloway, 1997).

Table 2.1 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 vapour light trap, modified from the Robinson trap.

2.3.2 Elevation calculations

Catch differed somewhat between years at each elevation, despite repeating the 1965 sampling protocol in 2007 (Table 1.1). 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 data sets 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 three methods, estimates of elevation change per species were compared between years.

2.3.3 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 (http://www.ncdc.noaa.gov/oa/climate/research/ghcn/ghcngrid.html#top) for the 5º cell that contains Mt. Kinabalu to estimate climate change over the study period.

2.4 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 (below) because somewhat different numbers of individuals were caught at each site in 1965 and 2007 (Table 1.1). 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 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, non-endemic 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. 2.*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. 2.*2A*).

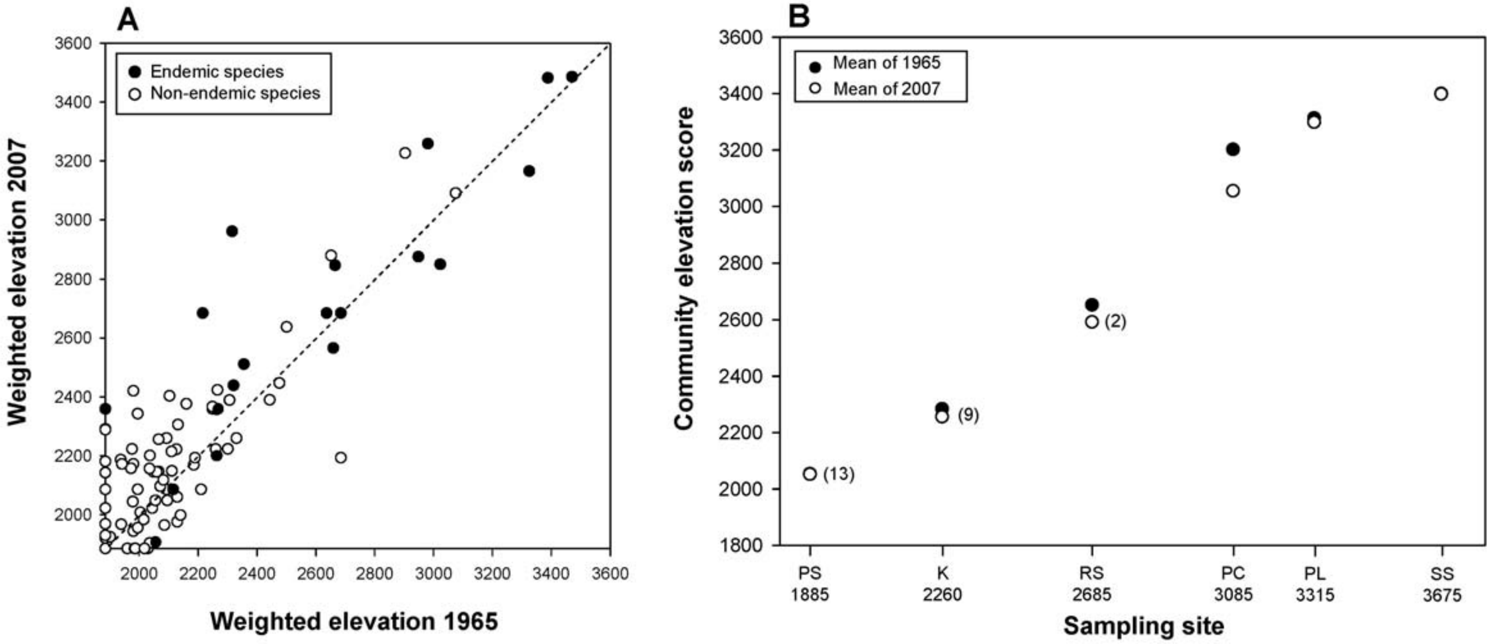


Figure 2.2 Elevation changes of moths on Mount Kinabalu between 1965 and 2007. (A) Species elevations (m). Species above the equal-elevation diagonal represent those estimated to have increased in elevation, using Elevation Calculation method *Bi*. (B) Community elevation scores (m). Where open circles fall below filled circles, the community in 2007 has an increased representation of previously-lower elevation species. Abbreviations relate to sites in Table 1.1. Values in brackets are numbers of species recorded only at <1885 m in 1965, but found higher in 2007.

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, 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 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 six 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. 2.2*B*).

2.5 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 1965 and 2007. 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. 2.2*B*). These species were not included in the community elevation scores, so the upwards shifts reported for the lowest three sites are under-estimated. A lack of suitable vegetation for most moth species at our highest site, where the ground is mainly bare rock (Sayat Sayat, Fig. 2.1), is the probable main reason for the limited community response seen at this site.

Regional warming for the 5º cell in which Mt. Kinabalu lies (*Methods*) was ≈0.7ºC over the 42-year period. Mean annual temperature anomalies (compared to 1961-1990 mean) for the decades before the two surveys (1956-1965 & 1998-2007) were -0.202ºC and +0.478 ºC respectively, showing a warming of 0.68ºC in 42 years. We also regressed annual temperature anomalies against year for the period 1965 to 2007 (coefficient = 0.017, r^2 = 0.55), which gave an estimate of 0.71ºC over 42 years. Lapse rates for the moist tropics are likely to be ≈0.55ºC reduction in temperature per 100-m increase in altitude (Gaffen *et al.*, 2000). At this lapse rate, 0.7ºC 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 5º×5º 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 (Beckage *et al.*, 2008; Lenoir *et al.*, 2008; Parolo & Rossi, 2008), 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 (Wilson *et al.*, 2005; Franco *et al.*, 2006; Hickling *et al.*, 2006) 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 (Still *et al.*, 1999; Williams *et al.*, 2003; Thomas *et al.*, 2004; Wilson *et al.*, 2007; Ohlemüller *et al.*, 2008; Raxworthy *et al.*, 2008; Sekercioglu *et al.*, 2008); 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 (Janzen, 1967; Addo-Bediako *et al.*, 2000; Deutsch *et al.*, 2008) 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 (Øegaard, 2000; Novotny *et al.*, 2002). Despite these risks, Mt. Kinabalu and other tropical mountains (Colwell *et al.*, 2008) 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 (http://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 (Pielke *et al.*, 2007; Pyke & Andelman, 2007). 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 (Colwell *et al.*, 2008; Ohlemüller *et al.*, 2008).

2.6 Acknowledgements

We thank Sabah Parks, Nasir Majid (Royal Society SE Asia Rainforest Research Programme & Universiti Malaysia, Sabah), Richard Lusi Ansis (Forest Research Centre, Sabah) and Dr. Shen-Horn Yen and lab members (National Sun Yat-sen University, Taiwan) for assistance with field work, specimen sorting, facilities and identification, including genitalia dissection. Two anonymous referees made helpful suggestions. This project was funded by the U.K. Darwin Initiative (Defra), the Ministry of Education in Taiwan, and a U.K. Overseas Research Students Award.

2.7 Supplementary Material

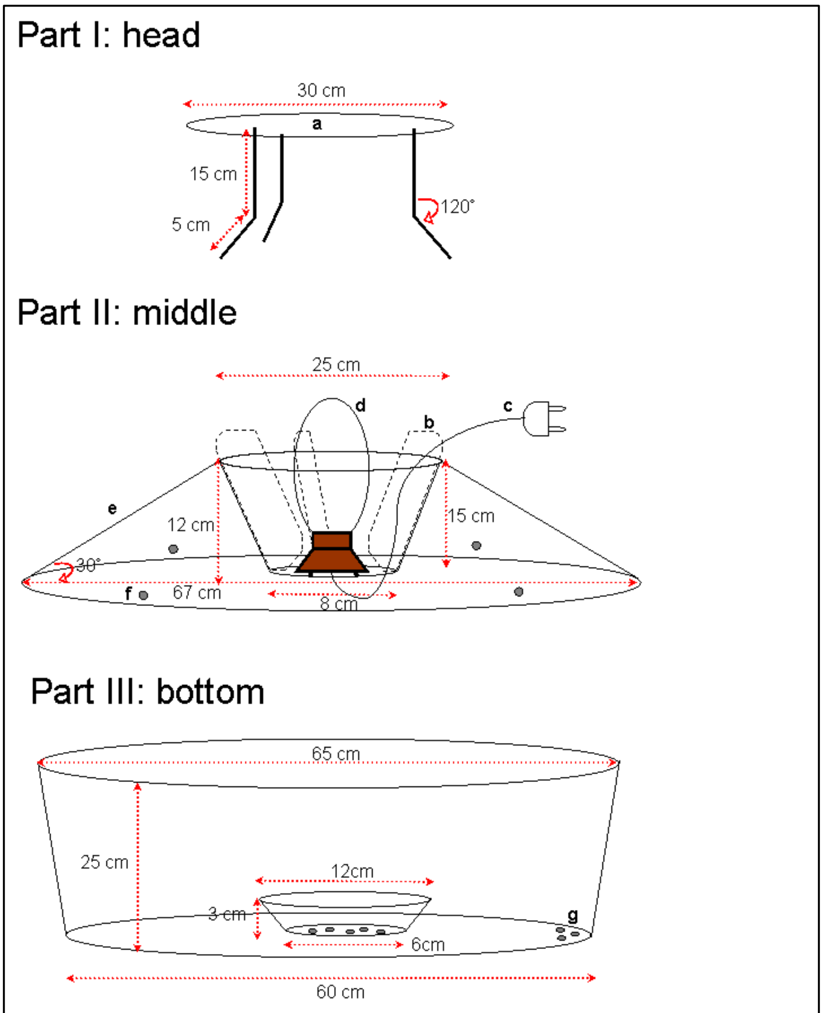
Appendix S 2.1 Additional information of field sampling

I conducted pilot studies in Taiwan and Park Headquarters of Mount Kinabalu to ensure the formal study going smoothly. In Taiwan (14 June-26 July 2007), I participated in several field trips of moth light trapping, and learned the general skills of trap setting, moth collection, preservation and specimen preparation. I prepared most of the equipment required for field sampling in Taiwan, including materials to make the trap, which were not all available in Sabah. At 26 July 2007, the field team (including myself, Dr. Hau Jie Shiu, Dr. Suzan Benedick and Nair Majid) met in Kota Kinabalu, Sabah, where we purchased supplies, Tilley lamps and chemicals (ethyl acetate). We visited several hardware stores and supermarkets to find components to make two mercury vapour light traps and one trap to fit the Tilley lamps (see below for the design). In early August, we paid a visit to Dr. Vun Khen Chey in Forest Research Centre of Sabah in Sepilok to make sure the lab support of sorting after the field collection and then set up our base in Park Headquarters of Mount Kinabalu. Prof. Jane Hill and Henry Barlow joint us on 5 August in Park Headquarters. We ran the traps together to ensure the consistency between two surveys and two sampling teams in 2007. We decided on the sampling and storage process and also sorted part of our pilot collection. We identified original sampling sites and excluded those with major vegetation changes (see below).

Trap design and setting

(A) Mercury vapour light trap

The 1965 survey used either a mercury vapour light trap (M.V. trap) or a Tilley lamp trap (T.L. lamp), depending on the availability of electricity. The M.V. trap used a 125W mercury vapor lamp and was modified from the Robinson trap (Fig. S 2.1).


Part I: head

Part II: middle

Part III: bottom

a.e. transparent plastic **b.** white plastic cone with three vanes **c.** electric wire and plug (3 m), apply a ballast if necessary **d.** 125W mercury bulb with seat; fixed to the bottom of the funnel or the vanes, but make sure the base with enough space for moth to enter the trap **f.** four little holes (within 0.2cm) 1 cm to the margin **g.** Three draining holes (0.5cm) 1 cm to the margin and five draining holes (0.5cm) in the central funnel

Figure S2.1 Design of mercury vapour light trap in 2007.

The M.V. trap was designed with enhanced waterproof structures to prevent the collections from being damped and with large container to allow huge catch in a short time. Heavy rainfall was quite often in Mount Kinabalu during August and September. The catch per night may exceed two thousands if the weather permitted. The trap contains three parts (Fig. S2.1). Part I was fixed to the top of the part II. The realized size depended on the materials acquired locally. The base of the funnel in the middle (Part II) was reduced to 4 cm. The bottom of the trap (Part III) was replaced and modified using the largest bucket available from the local store.

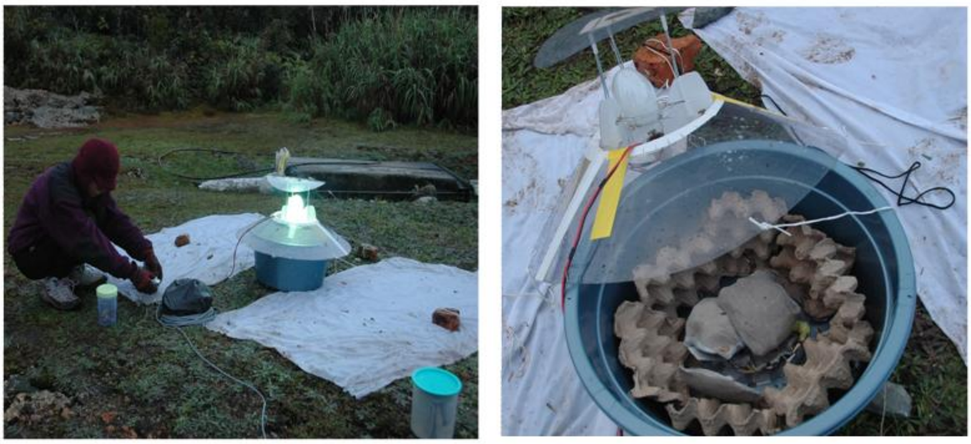


Figure S2.2 Setting of Mercury vapour light trap (in Kamborangoh).

When running the M.V. trap, we applied white sheets on the ground to enhance the reflection (Fig. S2.2, left). This also facilitated the collection of moths setting around the trap. We tied up the trap by nylon ropes, through the holes in the margin of the lid to some heavy objects around the trap (Fig. S2.2, left). Within the trap, we added egg shells for moths to settle inside the trap (Fig. S2.2, right). We added ethyl acetate, the killing agent to cotton wool and wrapped it in craft paper and wire meshes. The design allowed the chemical to release slowly and last longer. The trap was lighted up at 18:00. We applied the wrapped cotton wool to the trap at 23:00, collected the moths, emptied and set up the light trap again. The trap worked over night and was collected again at dawn. Several jars were prepared for hand-collecting of moths settling on the surrounding vegetation. We fixed the wrapped cotton wool with killing agent in the bottom of the jar. Geometrid moths were collected separately from other families, which facilitated the sorting afterwards. We had to prevent beetles from going into the light trap. They may do great damage to the specimens. Bats, birds and rats were also attracted by the moths but it was difficult to keep all of them away from the collections.

(B) Tilley lamp trap

The T.L. trap contained two sets of Tilley lamps in the middle and a handmade trap to fit the lamps (Fig. S2.3, left). The design and the size of the trap were available in Holloway (1970). We made the trap by flexible plastic plates, with a separate frame made out of water pipes to support the trap. The trap was foldable and the frame was detachable. We also added egg shells and killing agent (in wrapped cotton wool) within the trap. A mosquito net was prepared under the trap. The trap went with the T.L. lamps at lower sites (Park Headquarters, Lycaenid Cut and Kiau Gap, included in the analysis of Chapter 3) but not in the higher sites (Paka Cave, Panar Laban, and Sayat Sayat), where we used white sheet or reflection from the hut to enhance collections (Fig. S2.3 right).

Figure S2.3 Setting of Tilley lamp trap in Park Headquarters (left) and Panar Laban (right).

Preliminary sorting and specimen preparation

When conducting the pilot study in Park Headquarters, we sorted part of our collection to learn more tips of identifying geometrid moths, layering and pinning small specimens. Layering was an efficient method to preserve and store large amount of specimens in the field for sorting afterward (Fig. S2.4). Plastic containers (about the size of lunch box), tissues and loose silica were prepared for layering. We put several layers of tissue as cushion in the bottom of the container. We arranged a layer of specimens carefully in a piece of tissue and then folded the tissue to cover the specimens (Fig. S2.4, left). The process kept going until the container was almost full. We put notes of time, method, location, amount, collectors of the collection, on the top of layers or in the middle, if the sources differed. Several layers of tissue and a pack of loose Silica, the desiccating agent were added before fixing the lid. Descriptions of collections needed to be added again outside the containers (Fig. S2.4, right). Geometrid moths were layered separately from other families.

Layering can be done after the specimens were air-dry. The boxes of specimens were brought back from the mountains to the lab in the Park Headquarters, dried again in the oven and stored in the refrigerator.

Figure S2.4 Layering and storage of specimens

Site identification

The pair-photo of sampling sites at 1965 and 2007 were illustrated below. The 1965 photos were taken by Dr. Jeremy Holloway.

Sayat Sayat (3675m)

This was the highest site characterized by granodiorite rock with poor soil formation and stunt summit vegetation. The plants rooted in limited clefts with soils. The Tilley lamps were set outside the hut. (photos in the main text, Fig. 2.1)

Panar Laban (3315m)

Panar Laban was characterized by granodiorite rock and subalpine vegetation. The site was largely exposed to the south. Two Tilley lamps were set up against the aluminum wall of the tourist hut.

Paka Cave (3085m)

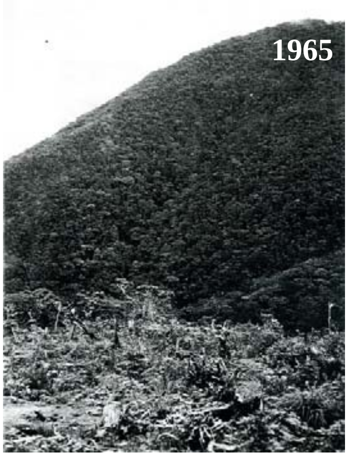
This site was away from the main footpath, nearby the Paka river and sheltered by a vast rock. Tilley lamps were set nearby the camp or on the valley when it was dry (no photo available in 1965).

Radio Sabah (2685m)

This site was within the upper montane forest (i.e. cloud forest, *c*. 2000 to 2800 m), abundant in epiphytes and often bathed in dense mist in the afternoon. The light trap was powered by the radio station and set in a helicopter apron, with good view to surrounding forest (photos in the main text, Fig. 2.1).

Kamborangoh (2260m)

Part of the vegetation was cleared 4 decades ago and now remained bald for the microwave radio repeater of Telecom Malaysia. The light trap was powered by Telecom Malaysia.



1965

2007

Power Station (1885m)

The site was in the lower montane forest (1200 to 2000/2350 m), with a good view on the mountain edge. The light trap was powered by the station.

Kiau Gap (1775m)

The site was nearby the driveway to the climbing path, with view to the west and attracted many moths from the valley. Nearby vegetation was more developed in 2007 than in the early period.

Lycaenid Cut (1650m)

The site was nearby the driveway to the climbing path, but surrounding forest was much more closed than in KG.

Park Headquarters (1440m)

The sampling site 40 years ago was located in the entrance of the park, which had been converted to driveway (as the photo of 2007). We moved the trapping site to a temporary car park surrounded by primary forest. The elevation was 50 m lower than the original site.


1965


2007

Bunda Tuhan (1265m)

The site was surrounded by primary forest, secondary forests and agricultural area 40 years ago. The primary forests were reduced in 2007.


1965


2007

CHAPTER 3

ASYMMETRIC BOUNDARY SHIFTS OF TROPICAL MONTANE LEPIDOPTERA OVER FOUR DECADES OF CLIMATE WARMING

This chapter has published as:
Chen, I.C., Hill, J.K., Shiu, H.J., Holloway, J.D., Benedick, S., Chey, V.K., Barlow, H.S. & Thomas, C.D. (2011) Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography*, **20**, 34-45.

3.1 Abstract

Aim

To estimate whether species have shifted at equal rates at their leading edges (cool boundaries) and trailing edges (warm boundaries) in response to climate change. We provide the first such evidence for tropical insects, here examining elevation shifts for the upper and lower boundaries shifts of montane moths. Threats to species on tropical mountains are considered.

Location

Mount Kinabalu, Sabah, Malaysia.

Methods

We surveyed Lepidoptera (Geometridae) on Mount Kinabalu in 2007, 42 years after the previous surveys in 1965. Changes in species' upper and lower boundaries, elevational extents and range areas were assessed. We randomly sub-sampled the data to ensure comparable datasets between years. Estimated shifts were compared for endemic versus more widespread species, and for species that reached their range limits at different elevations.

Results

Species that reached their upper limits at 2500–2700 m (n = 28 species, 20% of those considered) retreated at both their lower and upper boundaries, and hence showed substantial average range contractions (-300 m in elevational extent and -45 km^2 in estimated range area). These declines may be associated with cloud cover changes and the presence of ecological barriers (geological and vegetation transitions) which impede uphill movement. Other than this group, most species (n = 109, 80% of the species considered) expanded their upper boundaries upwards (by an average of 152 m) more than they retreated at their lower boundaries (77 m).

Main conclusions

Without constraints, leading margins shifted uphill faster than trailing margins retreated, such that many species increased their elevational extents. However, this did not result in range area increases because the area of land available declines with increasing elevation. Species close to a major ecological / geological transition zone on the mountain flank declined in their range areas. Extinction risk may increase long before species reach the summit, even when undisturbed habitats are available.

Keywords: climate change, cloud, ecological barrier, endemic species, geology, Geometridae, leading edge, Malaysia, range shift, trailing edge.

3.2 Introduction

Anthropogenic climate warming is driving the geographic distributions of most species towards higher latitudes and elevations (e.g. Parmesan, 2006; Thomas, 2010). Changes of range boundaries reflect species responses to climate change. However, it remains unclear whether retreat and expansion rates are comparable, and there are very few studies that consider *both* the cool (leading) and warm (trailing) edges of species distributions. Range retreats have been observed at warm range boundaries (Parmesan, 1996; Wilson *et al.*, 2005; Franco *et al.*, 2006; Zuckerberg *et al.*, 2009), where conditions are potentially becoming too hot for survival. However, there is a much larger body of evidence reporting range expansions at species cold margins, and some evidence that cool margins may be expanding faster than warm margins are retreating (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Brommer, 2004; Hitch & Leberg, 2007; Peh, 2007; Reif *et al.*, 2008). It has been hypothesized that this asymmetry might arise from a greater importance of biotic interactions than physical variables in determining species limits at warm margins, whereas physical constraints might predominate at cool margins (Davis *et al.*, 1998; Araújo & Luoto, 2007); although there is little convincing evidence in the literature that directly tests this hypothesis. Secondly, moisture availability may be a more important constraint than temperature at low latitude or low elevation boundaries (Engelbrecht *et al.*, 2007; Svenning & Condit, 2008). In addition, lags between climate warming and range changes may be greater for population declines and extinctions than for colonisations (Easterling *et al.*, 2000). Finally, heterogeneous topography may provide temporary population refuges (Parmesan *et al.*, 1999; Hampe & Petit, 2005), and may also make the initial stages of decline difficult to detect (Thomas *et al.*, 2006). However, many of these studies compared the cool and warm margins of different species, so it would be useful to assess both boundaries of the same species (Parmesan *et al.*, 1999) to clarify whether range changes at leading and trailing boundaries differ.

The lack of studies that encompass both the leading and trailing edges of ranges also makes it very difficult to evaluate whether projections of extinction risk from climate change (Thomas *et al.*, 2004; Fischlin *et al.*, 2007) are realistic. Species are particularly threatened on tropical mountains, where there is high endemism (e.g. Pounds *et al.*, 1999;

Williams *et al.*, 2003; Colwell *et al.*, 2008; Raxworthy *et al.*, 2008) and where climate change (Fischlin *et al.*, 2007; Nogués-Bravo *et al.*, 2007) and local human perturbations are both altering ecosystems. If, however, leading range boundaries are generally expanding faster than trailing edges are retreating, projected extinctions may not be imminent, providing some time to mitigate climate change and develop biodiversity adaptation strategies. The absence of published data on recent changes to the leading and trailing edges of species range boundaries for any group of tropical insects is a concern because tropical insects may experience the largest number of extinctions from climate change, given their diversity (Deutsch *et al.*, 2008; Fonseca, 2009). Here we extend the work of Chen *et al.* (2009), who documented upwards shifts in the average elevations of species of geometrid moths on Mount Kinabalu in Borneo, associated with regional warming of *c.* 0.7°C, to: (1) examine upper and lower boundary shifts and the corresponding changes in the land areas available to each species, (2) evaluate the extent to which responses vary among species that were historically found at different elevations on the mountain, and (3) consider whether any such changes represent potential risks to biodiversity.

3.3 Materials and methods

3.3.1 Study area

Mount Kinabalu, Sabah, Malaysia, lies in the north of Borneo. The summit, Low’s Peak (4095m, 6º4' N, 116 º33' E), is the highest peak in Southeast Asia between the Himalaya and New Guinea. Mount Kinabalu is within the Sundaland global biodiversity hotspot and is notable for its endemic species (Myers *et al.*, 2000). The geology along the mountain trail where moths were sampled changes from sandstone (lower montane areas) to ultrabasic rock at *c.* 2700 m, and from ultrabasic to granodiorite at *c.* 3000 m, with granodiorite forming the summit (Collenette, 1964; Lee Tain Choi, 1996).

The climate is typical of the humid tropics. The mean annual temperature at sea level is *c.* 27.5°C with estimated lapse rates on the mountain of 0.0055°C m^{-1} (Kitayama, 1992). Mean annual temperature has estimated to increase at a rate of *c.* 0.017°C per year or *c.* 0.7°C for the past four decades (Chen *et al.*, 2009). Annual precipitation is > 2500 mm in the lowlands, increases with elevation up to *c.* 2800 m and then decreases above that. Clouds form daily and envelop the forest at 2000 to 2800 m (Kitayama, 1995). Lower montane forest occurs from 1200 to 2000/2350 m, upper montane forest (i.e. cloud forest) from *c.* 2000 to 2800 m, and subalpine forest from 2800 to 3400 m (Kitayama, 1992). Closed forest occurs up to 3400 m, above which the terrain is mainly rocky, with a scattering of scrubby trees and shrubs. Upwards shifts of species above 3400 m may be limited by the need for primary succession to take place.

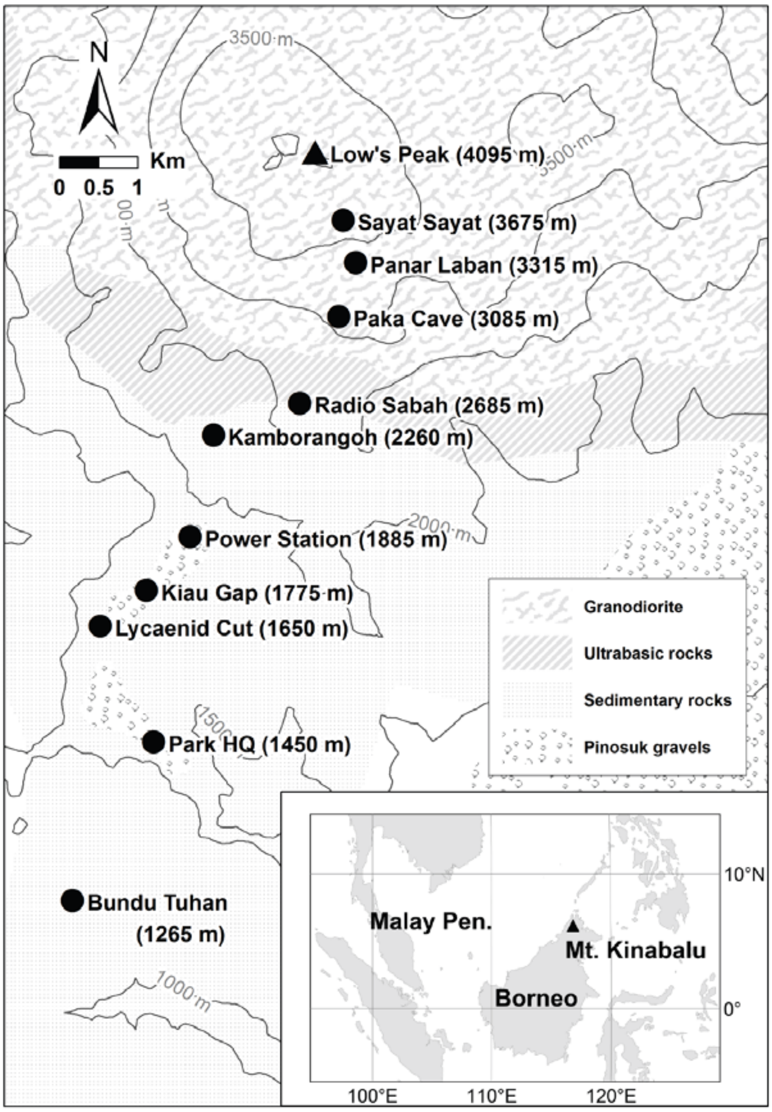


Figure 3.1 Study transect on Mount Kinabalu, Sabah, Malaysia; geology modified from Lee Tain Choi (1996).

3.3.2 Moth transect resurvey

The study is based on a moth transect survey on Mount Kinanbalu that was first carried out in 1965 (Holloway, 1970), and then repeated in 2007 (Chen *et al*. 2009). Two of the authors (JDH, HSB) who were involved in the 1965 study contributed to the 2007 resurvey, enabling us to locate the same sampling sites and replicate field protocols. Ten of the original 12 sites were resurveyed (Fig. 3.1), omitting the two (lowest) sites that had experienced major land-use change since 1965. All sites except Bundu Tuhan (Table 3.1) are within Mount Kinabalu National Park, established in 1964, a year before the original study; hence they are fully protected.

In 2007, we resurveyed moths using the same techniques (Tilley lamps, Mercury Vapour traps), during the same months (August, September), and during similar moon phases and at a similar stage of the El Niño–Southern Oscillation (ENSO) cycle as in 1965. Sampling nights and trap types differed among sites, as in 1965 (Table 3.1), and occurred mainly from 18:00 (just after sunset) until 23:00. Mercury Vapour traps worked overnight and were collected at dawn. As in 1965, moths that settled on the vegetation by traps were collected by hand (except at sites 1 and 3, see below; Table 3.1).

The 2007 resurvey was designed to repeat the same number of trapping nights at all sites. However, numbers of individuals caught per night at sites 5, 6, 7 and 9 were so high that we sampled fewer nights to ensure that specimen sorting and identification would be feasible (trapping stopped once the number of specimens obtained was comparable to the numbers caught in 1965). We sampled for eight nights at site 2 in 2007 rather than for 25 nights as in 1965. We collected all moths that came to light traps, but for logistic and taxonomic reasons we restricted our analyses to the Geometridae. Specimens were sorted to species level wherever possible, cross-checked by assistants associated with the Royal Society Southeast Asia Rainforest Research Program and Forest Research Centre in Sepilok, Sabah, Malaysia (see Acknowledgements). Ambiguous specimens were dissected and identified by genitalia (396 specimens were dissected; *c*. 10% of geometrids caught); lab work was supported by Dr Shen-Horn Yen at National Sun Yat-sen University in Taiwan. Specimens will ultimately be deposited at the Forest Research Centre in Sepilok.

Table 3.1 Sample sites and catch summary from 1965 and 2007.

	Sampling sites	Elevation (m)	Vegetation	Trap	Trap nights		Geometridae moth individuals (species)		Total individuals of all moths	
					1965	2007	1965	2007	1965	2007
1	Bundu Tuhan	1265	Lower montane	MV †	8	8	448 (129)	132 (55)	1473	1779
2	Park Headquarters	1450	Lower montane	TL	25	8	1999 (212)	225 (91)	4480	799
3	Lycaenid Cut	1650	Lower montane	TL †	4	4	174 (66)	60 (30)	658	152
4	Kiau Gap	1775	Lower montane	TL	4	4	463 (131)	256 (61)	1045	505
5	Power Station	1885	Lower montane	MV	8	4	2549 (220)	1398 (172)	6064	6488+
6	Kamborangoh	2260	Upper montane	MV	14	4	663 (103)	582 (103)	1620	2000+
7	Radio Sabah	2685	Upper montane	MV	10	5	898 (65)	940 (69)	2060	2572+
8	Paka Cave	3085	Subalpine	TL	4	4	70 (9)	39 (8)	78	95
9	Panar Laban	3315	Subalpine	TL	6	4	81 (7)	264 (10)	129	471
10	Sayat Sayat	3675	Rock face	TL	4	4	100 (5)	60 (5)	137	85

Vegetation zonation follows Kitayama (1992).

†Catch by trap only, without hand collections from the surrounding vegetation.

TL, Tilley Lamp trap; MV, Mercury Vapour light trap.

3.3.3 Controlling for sampling

Catch numbers of specimens at each site in 2007 and 1965 inevitably had some differences because catch sizes varied with the weather, and the proportion of geometrids amongst the total catches varied between sites and years. Thus, we carried out analyses in a number of ways to ensure that our conclusions are robust. The 1965 and 2007 data are most equivalent for sites 5 to 10 (1885 m upwards, Table 3.1), where total sampling effort was most comparable between the years; the first analysis considered only these six sites. Our second analysis included these six sites plus sites 2 and 4, where many fewer individuals were caught in 2007 than in 1965 but where, otherwise, data collection was comparable between 1965 and 2007. Our third analysis also included data from sites 1 and 3, although no hand collecting of moths took place from the vegetation surrounding the light traps in 2007. Thus, the three combinations of sites analysed were: (1) the six sites from site 5 upwards, providing direct comparability with Chen *et al.* (2009); (2) eight sites, adding sites 2 and 4 to the previous six sites; and (3) all 10 sites shown in Table 3.1.

We randomly subsampled 1965 and 2007 survey data to obtain the same number of individuals between years at each site. For each site, we randomly selected individuals (using COMPAQ VISUAL FORTRAN 6.6 and R 2.10.1) based on whichever year had the larger number of geometrids. For example, to generate the first resampled dataset for 1965, we randomly selected 132 individuals (the number caught in 2007) from the 448 geometrids at site 1 (Table 3.1), selected 225 from the 1999 individuals at site 2 and so forth for all other sites in which more geometrid individuals had been caught in 1965 than in 2007 (sites 1–6, 8, 10) and retained all individuals in site 7 and site 9. To generate the first resampled 2007 dataset, we randomly selected 898 individuals from the 940 geometrids in site 7, 81 individuals from the 264 geometrids in site 9, and retained all individuals in other sites. We then determined a species' upper and lower boundary by identifying the highest and lowest records at 1965 and 2007, respectively, and boundary changes were the differences between years. The subsampling and above calculations were repeated 500 times to obtain means (and variations) of the upper / lower boundary changes of each species. Upper boundaries were excluded if they occurred at the highest sites in both years, and lower boundaries were excluded if they reached the lowest site in both years. The lowest sites were site 5 for the analyses of six sites, site 2 for eight sites, and site 1 for the 10-site analyses.

To test whether boundary responses were asymmetrical, we calculated for each species the difference in the observed change at the upper and lower boundaries. We also estimated the potential land areas (subsequently termed “range area”, see below) available between the upper and lower boundaries. Responses were compared for endemic (to Mount Kinabalu) versus more widespread species, and for species that reached their range limits at different elevations. To ensure that our conclusions were robust, we carried out our analyses including the whole dataset for each of the three combinations of sites analysed, and again excluding singleton records at the margins, which were particularly susceptible to random sampling.

Chen *et al*. (2009) estimated the mean elevation shifts of Mount Kinabalu moths from the highest six sites. We compared and extended the same calculation to the three combinations of sites analysed here (six, eight and ten sites). All comparisons were based on the random sub-sampling described above.

3.3.4 Range area

The available land area usually decreases when ascending a mountain. Hence, similar elevational extents on higher parts of the mountain provide smaller areas available to species than at lower elevations. We estimated the areas of land on Mount Kinabalu that fall between the lower and upper limits of a given species. We obtained topographical data for Mount Kinabalu from a 90-m grid resolution digital elevation model (http://srtm.csi.cgiar.org/Index.asp) and calculated (ARCGIS software) the areas of each 100-m elevation band from 1200 m to the top of Mount Kinabalu. The land area in each 100-m band decreases with elevation (filled circles; Fig. 3.2). To estimate the area potentially occupied by each species, given its upper and lower boundaries, we applied the Michaelis-Menten model (Soberon & Llorente, 1993) to fit the observed accumulated area with elevation. Using this model, a species’ range area was obtained by calculating the accumulated area below its mean upper limit minus the accumulated area below its mean lower limits (see Fig. 3.2). We then calculated the 1965 to 2007 change in range area for each species.

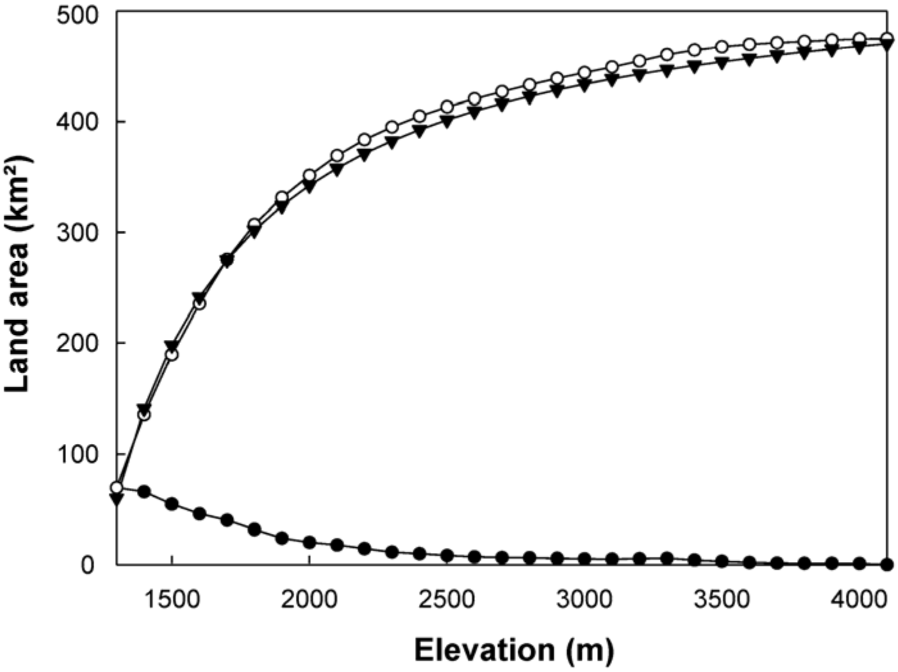


Figure 3.2 Land area in 100-m elevation bands (filled circles) and cumulative land area above 1300 m (observed, open circles; modelled, filled triangles) with increasing elevation on Mount Kinabalu.

3.4 Results

The 2007 survey captured >15,000 moth individuals, of which 3956 were geometrids, representing 271 species. These compared with 17,744 moths in total in 1965, including 7,445 geometrid individuals from 335 species (Table 3.1). Elevation changes could only be compared for species caught in both years, providing up to 208 species for analysis (depending on which sites and species constraints were applied; see Appendix S 3.1 in Supporting Information). Elevational extents and mean elevations are illustrated in Fig. 3.3 for endemic species restricted to Mount Kinabalu (Holloway, 1997).

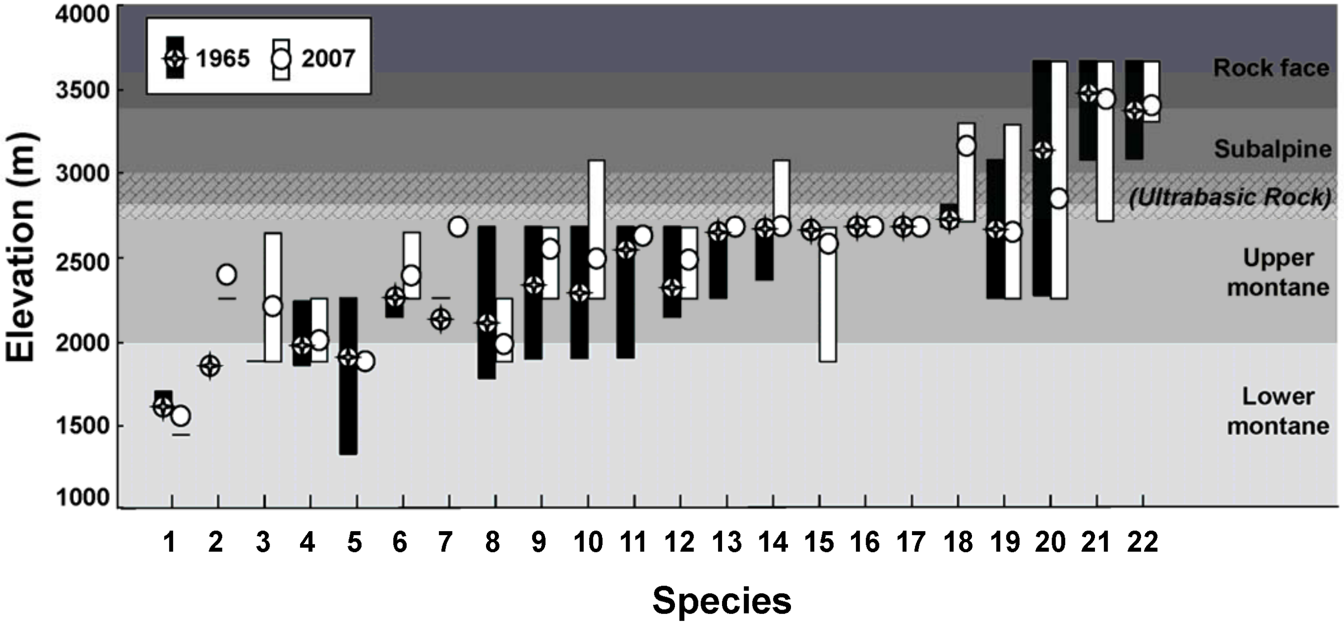


Figure 3.3 Elevational extents (bars) and weighted average elevations (circles) of Mount Kinabalu endemic geometrids in 1965 and 2007; estimates were calculated from random subsampling using data from 10 sites, excluding marginal singletons, and are arranged in the order of their 1965 upper boundaries. The average elevation of species 3 in 1965 is missing because only two individuals were caught and it failed to meet the criteria for calculating average elevations (see methods). Species code: 1, *Myrioblephara geniculata*; 2, *Catoria proicyrta*; 3, *Xanthorhoe liwagu*; 4, *Axinoptera penataran*; 5, *Ozola submontana*; 6, *Dysstroma pendleburyi*; 7, *Idiochlora stictogramma*; 8, *Ecliptopera furvoides*; 9, *Syncosmia discisuffusa*; 10, *Pasiphila luteata*; 11, *Phthonoloba altissima*; 12, *Phthonoloba stigmatephora*; 13, *Synegia punctinervis*; 14, *Syncosmia layanga*; 15, *Garaeus altapicata*; 16, *Apophyga altapona*; 17, *Papuarisme lagadani*; 18, *Pasiphila coelica*; 19, *Bornealcis versicolo*r; 20, *Hypocometa titanis*; 21, *Poecilasthena nubivaga*; 22, *Pasiphila sayata*.

3.4.1 Average elevation changes

Species shifted their average elevations uphill significantly over the 42-yr period (Table 3.2; one-sample *t*-test, H_0: $\mu = 0$ m, $P < 0.01$ in all cases). Estimated shifts varied between 52.3 m upwards to 67.7 m upwards, and were quite similar regardless of whether six, eight or all ten sites were analysed, and whether all species were analysed or just those with three or more individuals in both years. The more comparable the sampling effort between surveys (i.e. analysing six sites) and reliable the data (i.e. excluding rare species), the greater the estimated elevation increase (Table 3.2), but the absolute difference among estimates was small (15.4 m).

Table 3.2 Shifts of average elevations of geometrid moth distributions (in metres) between 1965 and 2007, weighted by abundances.

Sites included	All species		Species with ≥ 3 individuals in each year	
	n	Mean (SE)	*n*	Mean (SE)
6[†]	157	55.6 (16.2) ***	102	67.7 (16.2) ***
8	189	57.1 (15.9) ***	121	59.5 (15.1) ***
10	208	52.3 (18.0) **	130	58.9 (15.1) ***

Results are based on different numbers of study sites being included.

Significance levels are based on one-sample *t*-tests: ** $P < 0.01$; *** $P < 0.001$.

[†] Six-site analysis from Chen *et al*. (2009).

n, number of species included in the analysis.

3.4.2 Boundary shifts

Species upper boundaries shifted significantly upwards, by 52.8 m to 61.1 m over the 42-yr period (one-sample *t*-test, $H_0 : \mu = 0$ m, $P < 0.05$ in all cases; Table 3.3, whole dataset), comparable to average elevation shifts. Excluding singleton records at boundaries produced slightly higher estimates; 67.8 m to 82.7 m shifts upslope.

Lower boundaries also shifted significantly upwards, but in these comparisons the estimated elevation shift was more sensitive to the analysis (from 53.2 m to 109.5 m increases; Table 3.3, whole dataset). The analysis of six sites produced the largest shift, but was based on data from only the higher sites, and hence missed the lower boundaries of many species: i.e. of the 157 species in six-site dataset, only 66 species reached their lower boundaries within that elevation range. Excluding singleton records at the boundaries resulted in slightly larger estimates. As with the average elevation analysis, the more consistent the data (six sites) and the less susceptible the analysis to sampling error (i.e. excluding singleton margins), the higher were the estimated elevation increases. Because both upper and lower boundaries shifted upwards to a comparable extent, when averaged across all species, the elevational extent of species' ranges did not change significantly over time for any analysis (Table 3.3).

The mean changes in range areas of species might be expected to decline over time as both elevational boundaries shift uphill and less land is available at higher elevations. Overall (based on ten sampling sites and excluding margin singletons), however, the range areas of species remained quite stable overtime (a slight decrease, median = -1.49 km^2; Fig. 3.4). Nonetheless, 23 more species showed estimated declines in available areas from 1965 to 2007 than showed increases (69 reduced, 46 increased; $\chi^2 = 4.6$, d.f. = 1, $P = 0.032$).

Table 3.3 Shifts of upper and lower boundaries and elevational extents between 1965 and 2007 (in metres).

Sites included	Whole dataset						Excluding singleton boundaries					
	Upper boundary		Lower boundary		Elevational extents		Upper Boundary		Lower Boundary		Elevational Extents	
	n	Mean (SE)	*n*	Mean (SE)	*n*	Mean (SE)	*n*	Mean (SE)	*n*	Mean (SE)	*n*	Mean (SE)
6	154	52.8 (27.4)*	66	109.5 (42.3)**	157	5.8 (29.4)	118	67.8 (30.3)*	43	126.6 (45.5)**	121	21.2 (29.9)
8	186	61.1 (26.7)*	179	57.8 (21.0)**	189	5.4 (29.8)	132	76.8 (28.4)**	126	82.7 (22.8)***	135	-2.0 (33.7)
10	205	55.7 (26.9)**	203	53.2 (22.5)**	208	3.0 (29.1)	134	82.7 (28.2)**	136	86.0 (23.5)***	137	-4.5 (35.1)

Significance levels are based on one-sample *t*-tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

n, number of species included in the analysis.

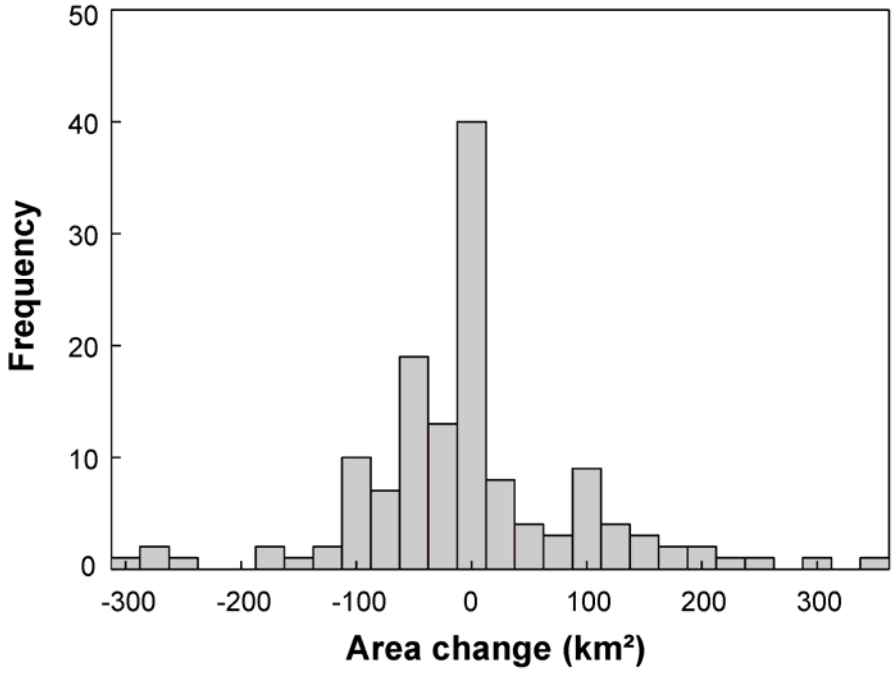


Figure 3.4 Frequency distribution of changes in species range area between 1965 and 2007 (*n* = 137 species) on Mount Kinabalu. Data are based on 10 sampling sites and exclude margins estimated from singletons. The median change in range area is a reduction of 1.49 km^2.

3.4.3 Responses of endemic species

We define endemic species in this paper as entirely restricted to Mount Kinabalu (Holloway, 1997). Of 30 Mount Kinabalu endemic geometrids recorded in 2007, 22 species could be compared with 1965 data (based on 10 site data, excluding marginal singletons), and were considered in the following analyses. According to their upper boundaries, the percentage of geometrids classed as endemic increased with elevation: 3 out of 71 species (4%) that reached their limits below 2000 m (lower montane forest) were endemic; as were 14 out of 58 species (24%) with upper limits between 2000 m and 2800 m (upper montane forest); 2 out of 4 (50%) species with limits between 2800 m and 3400 m (subalpine forest); and 3 out of 4 (75 %) species with upper boundaries above 3400 m.

Endemic species showed significant average elevation increases (88.5 m), and both upper and lower boundaries shifted upwards by >125 m (Table 3.4). The upwards shifts of endemic species were not significantly different from those of non-endemic species (two-sample t-test comparing average elevation shifts: $t = -0.858$, d.f. = 128, $P = 0.393$; comparing upper boundary shifts: $t = -0.647$, d.f. = 132, $P = 0.519$; comparing lower boundary shifts: $t = -0.869$, d.f. = 134, $P = 0.386$). There were also no significant differences between endemic and non-endemic species in changes in their elevational extents over time ($t = 0.220$, d.f. = 135, $P = 0.826$) or in range areas over time ($t = 0.763$, d.f. = 135, $P = 0.447$). Comparable results were obtained for analyses in which six or eight sites were included, and when marginal singletons were included (not shown).

Table 3.4 Shifts of average elevations, boundaries, elevational extents and range areas of endemic species (restricted to Mount Kinabalu) and non-endemic species, estimations were based on data from 10 sites, excluding marginal singletons.

	Endemic species		Non-endemic species	
	n	Mean (SE)	*n*	Mean (SE)
Average elevation (m)	21	88.5 (45.9)*	109	53.2 (15.8)**
Upper boundary (m)	19	127.7 (71.4)*	115	75.3 (30.7)**
Lower boundary (m)	22	132.5 (70.5)*	114	77.0 (24.5)**
Elevational extent (m)	22	-22.2 (90.9)	115	-1.1 (38.2)
Range area (km^2)	22	-17.2 (15.8)	115	0.22 (9.5)

Significance levels are based on one-sample *t*-tests: * P <0.05; ** P < 0.01.

3.4.4 Elevation-specific analyses

Boundary shifts over the 42-yr study period differed among species in relation to where species reached their elevation boundaries in 1965 (Fig. 3.5). For these analyses, we used all 10 sites and excluded singleton margins. Species were grouped into 200-m elevational bands according to their 1965 limits. Not all bands contained range boundaries, and several contained data for only one species (open circles in Fig. 3.5) and were excluded from the following analysis. The shifts of upper boundaries differed significantly between elevation bands (ANOVA: $F_{5,124} = 6.08$, $P < 0.001$). *Post-hoc* tests indicated that species reaching their upper boundary in the 2500–2700 m band were responsible for this significance; they showed a significant downhill shift over time ($n = 28$ species, mean = -178.8 m; Fig. 3.5a). Lower boundary shifts were also significantly different among elevation bands ($F_{7,125} = 3.297$, $P = 0.003$). The same elevation band (2500–2700 m) was responsible for the difference. However, because only five species reached their lower boundaries here, we remain cautious about this conclusion (Fig. 3.5b).

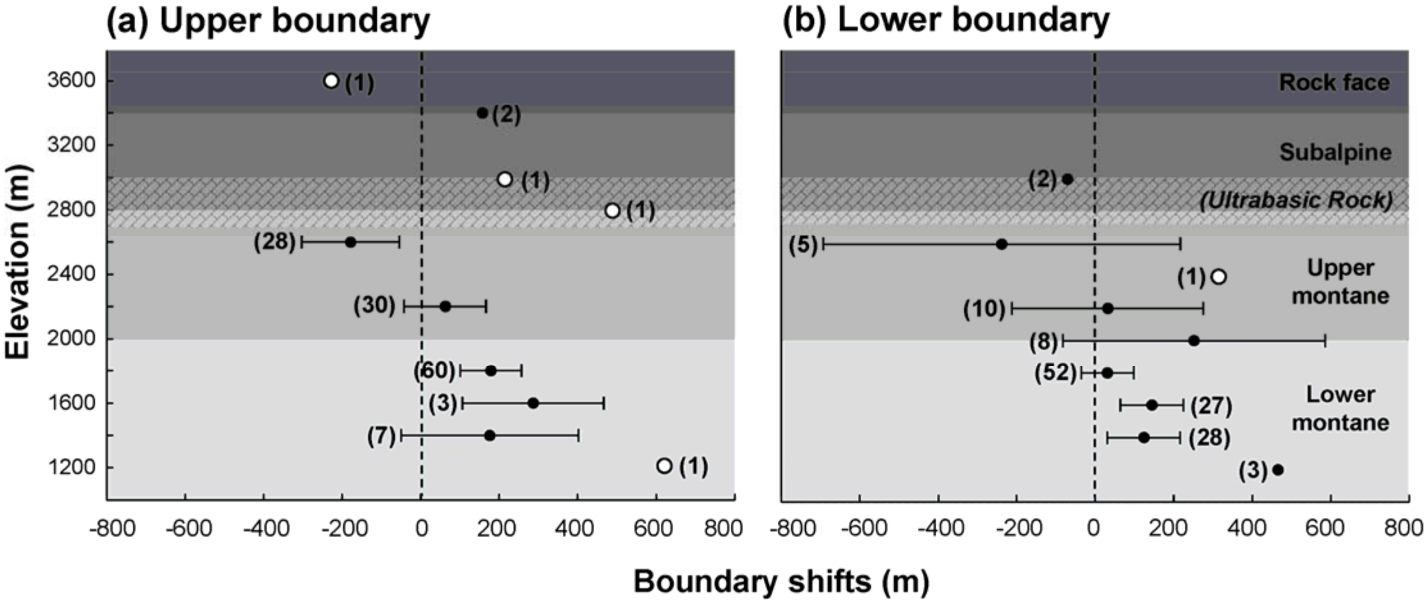


Figure 3.5 Shifts of species upper (a) and lower (b) boundaries, relative to 1965 distributions. The vertical dotted line represents no change in range boundary locations; positive values indicate uphill shifts, negative values represent downhill shifts. Range boundary data are presented as means (error bars = 95% confidence intervals of the means) for 200-m wide elevation bands. Data are based on 10 sampling sites and exclude margins estimated from singletons. Numbers of species are in parenthesis (data for single species reaching boundaries in particular elevation bands are shown as open circles). Ultrabasic rock occurs from *c*. 2700 m to 3000 m.

Species with their upper boundaries at 2500–2700 m in 1965 behaved differently from those in other elevation groups. However, different trap types (which differ in catch efficiency) and uneven gaps between sampling sites (which may affect the likelihood of detecting a shift) could be sources of error and could have given rise to the appearance of variation in response rates at different locations even if there was no underlying variation. Therefore, we carried out GLM analyses of upper boundary shifts that included the effects of elevation gaps between sites and trap types (and their interactions). Trap types and gaps were not significant in this analysis; whereas the comparison between species that reached their upper boundaries at 2500–2700 and the other species remained significant (see Appendix S 3.2).

In light of these findings, we compared species with their upper boundaries in the 2500–2700 m elevation band (subsequently termed Group A; Table 3.5) with species reaching their upper boundaries in other bands (Group B; Table 3.5). The 28 Group A species represented 20% of the species considered; 10 were endemic, representing 45% of the endemic species for which we had data. The upper boundaries of Group A species shifted downwards between 1965 and 2007, by an average of 178.8 m, and, whilst not statistically significant, their lower boundaries showed a mean upwards shift of 121.4 m. Asymmetry in the responses of the two boundaries is shown by the substantial and significant decrease in the elevational extents of the Group A species over time (average reduction of 300.1 m), which represents a 40% reduction in elevational extent. These changes convert into estimated range area decreases, by 44.5 km^2 or 39% on average (Table 3.5). Amongst these 28 species, the upper boundaries of 13 species remained within the same elevation range, 13 retreated downwards, and only two species (*Pasiphila luteata, Syncosmia layanga*) moved upwards into the subalpine vegetation. These patterns remained similar if we included boundaries represented by single individuals (49 species), with the observed 33.6 km^2 decline in range areas corresponding to a loss of 20% of the 1965 range areas (Table 3.5). For these, the upper boundaries of 21 species remained in the same elevation band, 26 retreated downwards, and the same two species colonised upwards.

In contrast, Group B species that have their upper boundaries outside the 2500–2700 m zone (Table 3.5) showed substantial elevation increases at their upper boundaries (mean = 151.8 m, or 133.5 m including marginal singletons) and weaker upwards retreats at their lower boundaries (mean = 76.8 m, or 41.6 m with marginal singletons; Table 3.5). This suggests possible asymmetric boundary responses by the Group B species. However, the uneven gaps between sampling sites are again a cause for potential concern when considering whether the shifts are asymmetric. Most species reached their lower boundaries at relatively low elevations, where the gaps between sampling sites are relatively small (sites 1–5, within 200 m differences), whereas most species reached their upper boundaries at higher elevations, where the gaps between sampling sites are larger (sites 6–10, 230 to 425 m apart). Because larger gaps tend to underestimate upward expansions, it is very unlikely that that cool edge increases have been exaggerated, relative to lower boundary retreats. The asymmetric upper and lower boundary shifts were supported by paired comparisons within each species (paired-*t* test, H_1: $\mu > 0$ m, $t = 1.91$, d.f. = 104, $P = 0.03$). Asymmetry in boundary responses is demonstrated by the significant increases in elevational extents (by 71.5 m, or 90.7 m including singleton margins; Table 3.5). However, range areas remained stable (a non-significant +8.2 km^2), despite the increases elevational extents, reflecting the reduction in areas available at higher elevations (Table 3.5). Hence, the 28 Group A species that had their upper elevation boundaries at 2500–2700 m experienced substantial average declines since 1965, whereas the Group B species that reached their elevational boundaries elsewhere on the mountain have expanded their elevational extents and, in many cases, maintained their range areas.

Table 3.5 Shifts of boundaries, elevational extents and range areas between 1965 and 2007, for two groups of species.

	All species dataset				Excluding singleton boundaries			
	Group A		Group B		Group A		Group B	
	n	Mean (SE)	*n*	Mean (SE)	*n*	Mean (SE)	*n*	Mean (SE)
Upper boundary (m)	49	-192.0 (44.6)***	156	133.5 (29.9)***	28	-178.8 (60.8)**	106	151.8 (28.3)***
Lower boundary (m)	49	89.7 (50.9)	154	41.6 (24.8)	28	121.4 (66.8)	108	76.8 (24.0)**
Elevational extent (m)	49	-281.7 (63.9)***	159	90.7 (29.4)*	28	-300.1 (83.7)*	109	71.5 (35.3)*
Range area (km^2)	49	-33.6 (14.5)*	159	17.7 (8.3)*	28	-44.5 (17.0)*	109	8.2 (9.3)

Significance levels are based on one-sample *t*-tests: * P <0.05; ** P < 0.01; *** P < 0.001.

Group A represents species with their upper boundaries between 2500 and 2700 m in 1965; Group B represents all other species.

3.5 Discussion

Our results indicate that the upper- and lower-elevation boundaries of geometrid moths on Mount Kinabalu shifted uphill between 1965 and 2007, during a period of regional and global warming. Our results were robust to the type of analysis we performed, and the expansion of upper boundaries and retreat of lower boundaries were significant regardless of how many sites were included and whether boundaries were defined by locations where more than one individual was observed, or by all data available. Given that our findings were broadly similar in all analyses, we are confident in our general conclusions concerning uphill range shifts by these tropical moths. If we consider findings from analyses of data from all 10 sites (to reflect the full extent of the transect) and exclude single captures at the distribution margins (which appear particularly susceptible to sampling error), we estimate the upper and lower boundaries of moth species to have shifted uphill by an average of 83 m and 86 m, respectively. Across all species, the elevational extents of species and the range areas available to them remained stable. Endemic and non-endemic species showed similar responses in this respect.

However, the overall stability of average elevational extents and range areas masked considerable variation. One group of species, which reached their upper boundaries at 2500–2700 m in 1965, experienced contractions at both their upper and lower boundaries. Meanwhile, most other species expanded their cool boundaries upwards significantly more than their warm boundaries retreated. This finding supports the hypothesis that, without other constraints, species may shift their leading edges faster than they retreat at their trailing edges.

3.5.1 Geological and ecological barriers to uphill movement

The failure of most species with upper boundaries at 2500–2700 m to shift upwards may be partly attributable to geological and other constraints. Above this elevation, the geology changes from sandstone to ultrabasic rock, the latter forming an outcrop from 2700–3000 m (Collenette, 1964; Lee Tain Choi, 1996). The vegetation associated with ultrabasic rock is distinct in physiognomy and plant species composition (i.e. host plants for insect herbivores) (Aiba & Kitayama, 1999). The soil here supports only a low diversity of soil invertebrates (Ito et al., 2002; Hasegawa et al., 2006), and may also support low herbivore diversity due to the accumulation of toxic heavy metals within plant tissues (Proctor, 2003) as has been suggested for the moth fauna of ultrabasic vegetation in New Caledonia (Holloway, 1993). The vegetation also changed from upper montane to subalpine forest around 2800 m, and the geology further changes from ultrabasic to granodiorite around 3000 m. The complex environmental transitions above 2700 m may hinder the capacity of plants and their herbivores to shift their ranges in response to higher temperature.

3.5.2 Possible cloud changes

Downwards range shifts of around half of the species that originally exhibited upper boundaries at 2500–2700 m may be associated with changes in cloud cover; the upper levels (ceiling) of persistent cloud cover reach *c.* 2800 m on Mount Kinabalu (Kitayama, 1995). Warming-induced lifting of the cloud base has been related to amphibian declines in Neotropical mountains (Pounds et al., 1999; Still et al., 1999) but much less is known about corresponding cloud ceiling changes and the possible impacts on associated species. Warmer and drier climate conditions (and resultant fires) surrounding Mount Kilimanjaro in Africa forced the tree line downwards (Hemp, 2009). Lowland deforestation, as well as climate change, has the potential to reduce cloud cover on adjacent mountains, as a result of reduced air humidity (Lawton et al., 2001). Borneo has experienced 0.7°C warming, and increased periods of drought and deforestation (McMorrow & Talip, 2001), including in the foothills surrounding Mount Kinabalu. If reduced cloud cover has led to a downwards shift in the cloud ceiling, species that require the thermal or moisture regimes associated with cloud forest are likely to have retreated downhill. A combination of global climate warming and regional deforestation may provide high risks to cloud forest biotas in many parts of the tropics.

3.5.3 Asymmetrical elevation boundary shifts

Other than these declining cloud-forest species, with their upper boundaries at

2500–2700 m in 1965, the remaining species (109 species, 80% of those considered) have moved their upper boundaries upwards (by 152 m) more than their lower boundaries have retreated (by 77 m). This supports the hypothesis that, in the absence of other constraints to expansion, cool, leading-edge range margins may expand faster than warm, trailing-edge boundaries retreat. These upper boundary shifts are comparable to those expected under 0.7°C of regional warming (127 m thermal isotherm uplift; Chen *et al.*, 2009) whereas the lower boundaries appear to be lagging behind the rate of warming. The asymmetric boundary shifts indicate that different ecological and physiological mechanisms may predominate in leading and trailing edge populations.

There is no particular biological reason why we would expect symmetrical population or distributional responses, given that population growth and colonisation predominate at leading edges, whereas decline and extinction predominate at trailing range boundaries (Wilson *et al.*, 2004). For example, heterogeneous environments potentially allow populations to survive for longer than might otherwise be expected in areas of decline (Parmesan et al., 1999; Hampe & Petit, 2005), whereas environmental heterogeneity may represent barriers to dispersal at leading edges, and have the potential to restrict expansion. It is also questionable whether climatic versus biotic constraints (e.g. Case *et al.*, 2005; Araújo & Luoto, 2007) or whether the same abiotic factors (e.g., temperature, moisture gradients) are equally important at leading and trailing edges (Engelbrecht *et al.*, 2007; Svenning & Condit, 2008).

3.5.4 Biodiversity risks

Climate warming on Mount Kinabalu will potentially prove hazardous to many species because: (1) there are many narrowly distributed endemic species which can only be expected to survive in this one location; (2) elevational shifts of many species are likely to be constrained by geological and ecological barriers (e.g. lack of appropriate host plants on ultrabasic rocks and granodiorite); (3) decoupled environmental changes may cause some types of environment to decline, rather than shift uphill—in particular, if the interaction between global warming and local human activities result in reduced cloud cover, there may be a substantial loss of species from the endemic-rich cloud forest biota; and (4), as species move upwards, a smaller land area is available at higher elevation (Wilson *et al.*, 2005).

In particular, the group of species with their upper range boundaries at 2500–2700 m, and which face both geological and climatic (cloud cover) constraints, contained a disproportionate number of species endemic to Mount Kinabalu (45% of all endemic species encountered). This suggests that some entire species may be at risk of extinction. The moth species under greatest threat on Mount Kinabalu appear not to be those inhabiting the very top of the mountain but those associated with cloud-forest habitats and sandstone substrates on the mountain flanks, more than 1,500 m below the highest point of the mountain. The habitat area available to them is being compressed. As yet, the species that inhabit the lower montane forest, which harbours the majority of moth diversity, have not come up against these constraints, but they may eventually also do so.

Tropical mountains support many endemic species and are clearly important for conservation (Brooks et al., 2006). These localised species, as well as many other thermally sensitive species, are likely to survive climate warming if they are able to undertake range shifts and reach cooler conditions. However, the distances involved may be prohibitively far for many tropical species, except where they are able to survive at higher elevations, more locally (Wright et al., 2009). For the species that occur on Mount Kinabalu, and presumably on other mountains, temperature is not necessarily the only driver of range shifts. Temperature and moisture gradient changes are likely to interact with other (e.g. geological) constraints, and could lead to extinctions much sooner than would be expected were one to make projections based on temperature alone.

3.6 Acknowledgements

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3.7 Supplementary Material

Appendix S 3.1 Species-site matrix for geometrids on Mount Kinabalu

Geometrids caught in both 1965 (Holloway, 1976) and 2007 are listed, with nomenclature following Holloway (1994, 1996, 1997); 208 species are included, summarized from the 10 site, original data (O, observed in 1965; X, observed in 2007, * endemic species).

Subfamily	**Species**		**Sites**									
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Oenochrominae	*Sarcinodes reductatus*		O	OX		O	OX		O			
Desmobathrinae	*Ozola falcipennis*		O	O			OX					
	Ozola apparata		O	OX			OX					
	Ozola submontana	*	O	OX	O	O	OX	OX				
	Noreia anacardium		O	OX	OX		O					
Geometrinae	*Herochroma urapteraria*		O	OX	O	X	OX					
	Pingasa lariaria						OX	O				
	Pingasa rubimontana		OX		O	O	X					
	Pingasa tapungkanana		O	O			OX					
	Pingasa ruginaria		X				O	O				
	lophophelma luteipes		OX	O		X	OX	O				
	lophophelma erionoma		OX	O	O		X					
	lophophelma vigens			O	O	O	OX	X				
	lophophelma rubroviridata		O	O			OX					
	Dindica alaopis		OX	OX		O	OX	X	O			
	Tanaorhinus rafflesii		OX	O		O	OX	X	O			
	Mixochlora vittata			O		O	OX	X				
	Paramaxates posterecta		X				O					
	Dooabia plana			O		O	OX		O			
	Dooabia lunifera			O			OX					
	Dooabia puncticostata						X	O				
	Agathia succedanea		O			OX	O					
	Ornithospila submonstrans			O			O	X				
	Ornithospila succincta			O		O	OX					
	Eucyclodes discata			X	O	OX	O	OX				
	Spaniocentra apatelloides		O	O	X	X	OX					
	Comibaena albimarginata			OX		O	OX	X	X			
	Thalassodes curiosa			OX		X	OX	X				
	Pelagodes falsaria		OX	O	O	O	OX	O				
	Idiochlora berwicki	*					O	X				
	Idiochlora stictogramma	*					O	O	X			
	Maxates waterstradti		X	O								
	Maxates thetydaria					O	X					
	Berta anteplaga		X	O			O					
	Comostola turgescens		OX	X		O						
	Comostola orestias		O	OX			O					

Appendix S 3.1 (continued) Species-site matrix for geometrids on Mount Kinabalu

Subfamily	Species	Sites									
		1	2	3	4	5	6	7	8	9	10
Sterrhinae	*Timandra punctinervis*		O	O	OX	O					
	Synegiodes diffusifascia				O		X				
	Cyclophora hirtipalpis	O	O		O	OX	OX	OX			
	Cyclophora lowi		O		OX	OX	OX	O			
	Cyclophora carsoni	O	OX			O	O	O			
	Cyclophora dimerites		O	X	O						
	Perixera absconditaria		OX		O	O	OX	X			
	Organopoda cnecosticta				O	OX	OX	X			
	Problepsis borneamagna	O	O	O	O	OX	X	X			
	Problepsis plenorbis	OX									
	Scopula voluptaria		O		O	X					
	Scopula leucopis		O		X	OX					
	Scopula pauperata	X				O					
	Idaea themeropis				X	X	X	O			
Larentiinae	*Trichopterigia sanguinipunctata*					OX	O	X			
	Brabira emerita		O	OX	O	OX	OX	O			
	Tristeirometa bathylima *		O			O	X				
	Tristeirometa bostryx		O	OX	O	OX					
	Hypocometa clauda		O		O	OX					
	Hypocometa leptomita		O		O	OX	OX	X			
	Hypocometa titanis *					O	OX	OX	OX	OX	OX
	Phthonoloba stigmatephora *					O	OX	OX			
	Phthonoloba caliginosa *							OX			
	Phthonoloba lutosa	X	O			OX	OX	OX			
	Phthonoloba altissima *					O	X	OX	O	X	O
	Tympanota arfakensis	O	OX	O	O	OX	OX	OX	O	X	
	Tympanota erecta						OX	OX	OX	OX	O
	Tympanota ceramica	O	O		O	OX	OX	OX			
	Episteira vacuefacta		O		O	O	OX	O			
	Sauris usta		O		O	OX	X	O			
	Sauris denigrata					OX					
	Collix mesopora		O			OX	X	X			
	Collix blosyra		O			X	X	X			
	Collix intrepida		O		O	O	OX	O			
	Pseudocollix hyperythra				O	OX	O				
	Carbia calefacta			O	X	O	X				
	Pomasia salutaris	OX	OX	OX	OX	OX	OX				
	Eupithecia costalis	OX									
	Eupithecia kamburonga	X			OX	X	OX	X			
	Eupithecia melanolopha		O			OX	OX				
	Eupithecia mundiscripta	OX	OX		OX	OX	O	X			
	Chloroclystis obturgescens		O	O	O	OX	OX	O			
	Pasiphila chlorocampsis						OX	OX	O	OX	X
	Pasiphila coelica *							OX	OX	X	X

Appendix S 3.1 (continued) Species-site matrix for geometrids on Mount Kinabalu

Subfamily	**Species**		**Sites**									
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Larentiinae	*Pasiphila eurystalides*	*						OX	OX			
	Pasiphila luteata	*					OX	OX	OX	X		
	Pasiphila palpata						O	OX	OX	X	OX	
	Pasiphila rubrifusa						O	OX	OX			
	Pasiphila rufogrisea			OX	O	O	O	OX	X			
	Pasiphila sayata	*							OX	O	OX	OX
	Pasiphila subpalpata		O			O	O	X				
	Tripteridia dinosia				O	O		X	O			
	Tripteridia latistriga						OX	O				
	Tripteridia subcomosa			O			OX					
	Syncosmia discisuffusa	*		O	O		O	OX	OX			
	Syncosmia eurymesa		O	OX	O	OX	OX	OX	OX			
	Syncosmia layanga	*						OX	OX	X		
	Syncosmia xanthocomes			OX		O	OX	X	X			
	Axinoptera penataran	*	O	O		O	OX	OX				
	Eriopithex lanaris		OX	X								
	Gymnoscelis fasciata		O	X								
	Onagrodes oosyndica		X	O		O						
	Antimimistis attenuata		OX				X	X				
	Poecilasthena character			O		O	O	OX	OX			
	Poecilasthena nubivaga	*						X	X	OX	OX	OX
	Xanthorhoe liwagu	*					OX	X	X			
	Xanthorhoe mesilauensis	*			X	X	O	O	X			
	Ecliptopera furvoides	*		OX	X	O	OX	OX	OX			
	Dysstroma pendleburyi	*					O	OX	OX			
	Papuarisme lagadani	*							OX			
	Papuarisme murudensis					O	OX	OX	X			
	Papuarisme submontana			O			X					
	Acolutha albipunctata						O	OX	O			
	Acolutha flavivitta			OX			O					
Ennominae	*Hypochrosis albodecorata*			OX	OX	OX	O					
	Hypochrosis binexata		OX	OX	O	OX	OX					
	Hypochrosis cryptopyrrhata			OX			X					
	Hypochrosis hyadaria		OX	OX	X	OX	OX	OX				
	Hypochrosis sternaria		O				X					
	Hypochrosis waterstradti		OX	O		X	OX					
	Omiza herois		O	OX	OX	OX	OX					
	Omiza lycoraria		O	OX			X					
	Achrosis lithosiaria			OX	O	O	X					
	Achrosis recitata		O			O	OX					
	Achrosis rigorata			OX		X	OX					
	Pseudeuchromia maculifera		O	OX			OX					
	Heterolocha polymorphoides		O	OX	O	O	OX	X				
	Garaeus altapicata	*					X	OX	OX			

Appendix S 3.1 (continued) Species-site matrix for geometrids on Mount Kinabalu

Subfamily	**Species**		**Sites**									
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Ennominae	*Garaeus apicata*		O	OX	O	OX	OX	OX				
	Garaeus u-lucens			X		O	OX	OX				
	Fascellina albicordis			OX		OX	OX		X			
	Fascellina altiplagiata			OX		X	OX	OX	O			
	Fascellina plagiata		OX	OX		X	OX					
	Ourapteryx claretta		O	OX		OX	OX	OX				
	Ourapteryx incaudata		X	OX	OX	O	OX					
	Ourapteryx picticaudata		OX	O								
	Lomographa luciferata			O	O		OX					
	Tasta elliptica			O			X					
	Tasta montana		O	OX	X	O	OX	X				
	Synegia decolorata		O	O	O	O	O	O	OX			
	Synegia obscura		O	OX	O	O	OX	X	O			
	Synegia ocellata			O	O		OX	OX	X			
	Synegia punctinervis	*					O	O	OX			
	Platycerota balia			O		X	O	O				
	Platycerota percrinita		O	O			OX	OX	OX			
	Borbacha altipardaria		O	O			OX					
	Plutodes flavescens		O	O		O	OX					
	Nadagara synocha			O			OX					
	Petelia delostigma		O	OX	X	O	OX	O	X			
	Petelia medardaria		OX			O	X					
	Astygisa waterstradti	*	X			O	O					
	Abraxas intervacuata		O	O		O	OX	X				
	Abraxas invasata		O	O		O	OX	O				
	Peratophyga sobrina			OX		O	O	O				
	Peratophyga trigonata			OX								
	Zamarada baliata		X	O			O					
	Orthocabera similaria			OX	O	O	OX	O				
	Calletaera subexpressa			O			OX	O				
	Calletaera subgravata		O	OX	O	OX	OX					
	Luxiaria amasa		O	O		O	OX					
	Luxiaria emphatica		OX	OX	O	X	O		OX			
	Luxiaria hyalodela		O	OX	O	O	OX	O	O			
	Luxiaria mitorrhaphes		OX	O	O	OX	OX	OX	OX			
	Luxiaria subrasata		O				X					
	Luxiaria tephrosaria		O	O	O	O	OX	OX	OX			
	Oxymacaria temeraria		O				X					
	Godonela avitusaria		O	O			OX					
	Godonela nora		O	O			O		X			
	Milionia fulgida						OX	X				
	Milionia pendleburyi	*				O	X					
	Bracca maculosa		O	O			X					
	Pogonopygia nigralbata			OX			X		OX			

Appendix S 3.1 (continued) Species-site matrix for geometrids on Mount Kinabalu

Subfamily	Species		Sites									
			1	2	3	4	5	6	7	8	9	10
Ennominae	*Pogonopygia xanthura*		O	OX	O	O	OX	OX	OX			
	Dalima mjoebergi			O		OX	OX	X				
	Dalima patularia		OX	OX		O	OX	OX				
	Apophyga altapona	*							OX			
	Apophyga apona			OX								
	Dasyboarmia delineata		OX	OX	O	X	OX	O				
	Dasyboarmia isorropha			OX	O	OX	OX	OX	O			
	Krananda semihyalina		O	O			OX	X				
	Racotis boarmiaria		O	OX	OX	OX	OX	OX	X			
	Xerodes ypsaria		OX	OX			OX					
	Xandrames latiferaria			OX	O	OX	OX	X				
	Chorodna pseudobolima			OX	OX	X	OX	O				
	Lassaba vinacea		O	OX	O	OX	OX	OX	O			
	Amblychia cavimargo			OX	O	O	OX					
	Amblychia infoveata			OX	O		X					
	Cleora mjoebergi			O	OX	OX	OX	OX	OX			
	Cleora pendleburyi		O	OX		OX	OX		OX			
	Cleora tenebrata		OX	O			X					
	Ectropis longiscapia		O	OX	O	O	OX	OX	X			
	Ectropis pais		O	OX	OX	OX	OX	OX	X			
	Gasterocome pannosaria		OX	O	O	OX	OX	OX	OX			
	Catoria proicyrta	*		O		O	O	X	X			
	Psilalcis bisinuata		X	OX		O	X					
	Alcis maculata			O		OX	O	OX	X			
	Alcis praevariegata		OX	OX	OX	OX	OX	OX	OX			
	Bornealcis expleta		OX	OX	OX	OX	OX	OX				
	Bornealcis versicolor	*						OX	OX	OX	OX	
	Hypomecis glochinophora			O			OX					
	Hypomecis lioptilaria		O	OX			X					
	Abaciscus tristis			OX	O	O	OX					
	Lophobates mesotoechia		X	OX		O	O					
	Myrioblephara bifida		X	O		O	OX	OX	X			
	Myrioblephara geniculata	*	O	OX	O	O	OX					
	Myrioblephara simplaria		O	OX	O	OX	OX	OX	X			
	Necyopa chloana						O	OX	OX			
	Necyopa subtriangula			OX	X	OX	OX	OX				
	Diplurodes submontana		OX	OX		OX	OX	X				
	Diplurodes sugillata		O	O	O		OX	O				
	Prochasma dentilinea			O	OX	OX	X	X				
	Fritillerinnys clathraria		O	X								

Appendix S 3.2 General linear model predicting upper boundary shifts.

The arrangement of traps and sampling elevations were uneven along the transect, and this could be a source of error when considering boundary shifts. These differences arose for practical reasons (electricity supplies) in 1965. It was essential to replicate the same pattern in 2007, but the implications of this variation require consideration.

Because Tilley lamp traps are less effective than Mercury Vapour traps and give rise to smaller catches, this may result in “apparent” variation on the levels of elevation shift at different points along the transect (e.g., a Tilley lamp at the next site above an MV lamp may decrease the probability of detecting an upward shifts, relative to the chances of doing so if both traps were MV type).

In addition, there are smaller elevational gaps between sites in the lower half of the transect (sites 1 to 5, 110 m to 200 m apart) and larger gaps in the higher half (sites 6 to 10, 230 m to 425 m apart). It could be argued that we are more likely to record uphill movements where the next higher site is close by (in elevation); in the lower part of the transect. Equally, recorded retreats of upper boundaries could be overestimated if the next lower site is far below; in the upper part of the transect. Because the “aberrant” 2500–2700 m group was from sites that coincided with trap changes, and was from a part of the transect where there were large sampling gaps both upwards (400 m) and downwards (425 m), we need further analyses to ensure that our conclusions were not compounded by trap changes and elevation gaps.

Methods

We concentrated our analysis on the upper boundary because this was the type of range limit that showed the greatest anomaly in the 2500–2700 m, and which drives the conclusion that species in this region of the mountain behaved unusually. We ran a general linear model using the following variables to predict upper boundary shifts: (i) elevation gap to the next higher site, (ii) elevation gap to the next lower site, (iii) trap type at the next higher site, (iv) trap type at the next lower site, and (v) the interactions among these variables. We also included (vi) a categorical variable representing species that reached their 1965 upper boundaries at 2500–2700 m, versus those with their upper boundaries elsewhere on the mountain. This analysis allowed us to assess whether the apparently aberrant behaviour of this species group can be accounted for by the spatial allocation of traps and sites, or whether the categorical elevation group effect is independently significant.

The elevation gaps to the next higher/lower sites were calculated as follows. For each species, the upper boundary was obtained by averaging across 500 outcomes of sub-sampling, which produced a weighted mean elevation (which sometimes fell between recorded sites). For each upper boundary, we then "rounded" the distribution margin to the nearest actual sample site. We then calculated the distances (in metres of elevation) to the nearest upper and lower sites to which they could have expanded or retreated.

Results and discussion

The general linear model showed that species category was the only significant variable explaining variation in upper boundary shifts. This indicates that the boundary shifts of species reaching their upper boundaries at 2500–2700 m are indeed different from those at other elevations, even when controlling for trap type and elevation gaps between sample locations. Thus, the conclusion remained robust.

Table 1 General linear model predicting upper boundary shifts.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	*P*
Gap (m) to higher site	4055	1	4055	0.046	0.830
Gap (m) to lower site	18488	1	18488	0.210	0.647
Trap type at higher site*	175962	1	175962	2.001	0.160
Trap type at lower site*	248543	1	248543	2.826	0.095
Interaction of gap and trap type at higher site	28041	1	28041	0.319	0.573
Interaction of gap and trap type at lower site	154911	1	154911	1.761	0.187
Species category*	421531	1	421531	4.793	0.030
Error	1.08171E+07	123	87944		

* indicates categorical variables

CHAPTER 4

META ANALYSIS OF RANGE SHIFTS UNDER GLOBAL WARMING－CAN SPECIES RESPONSES KEEP PACE WITH WARMING AND CAN FUNCTIONAL TRAITS PREDICT RANGE SHIFTS?

4.1 Abstract

Aim

To assess rates of elevational and latitudinal range shifts under climate change. To evaluate whether species responses are correlated / keep pace with rates of regional warming, and whether response rates vary among different taxonomic and functional groups.

Location

Global; terrestrial, freshwater and marine.

Methods

I conduct a meta-analysis of rates of range shifts along elevational and latitudinal gradients. Only multi-species studies were included, to avoid publication bias. I took the average range shift for a given taxonomic group in a specified region to represent a data point. I analysed range shifts in relation to the magnitude and rate of temperature increase in the region / period considered. I assessed whether range shifts differed between major taxonomic groups, and with mobility, thermal strategy, and trophic level.

Results

Twenty-five studies met our criteria, representing ~1700 species worldwide. Species shifted significantly upwards and to higher latitudes. The average rate of elevational range shift was 12.2 m uphill per decade, and latitudinal shifts averaged 17.6 km poleward per decade. Latitudinal range shifts were significantly greater in regions where the speed of warming was faster. Rates of elevational range shift were not significantly associated with levels of regional warming. Poikilotherms responded faster than homeotherms, and arthropods faster than birds, but other taxonomic and functional traits were not consistently associated with rates of distribution change.

Main conclusion

Our meta-analysis showed substantially higher rates of mean range shifts than did a previous study (Parmesan & Yohe, 2003). Latitudinal range shifts responded to regional

warming regardless of taxonomic or functional groups and shifted polewards at a rate similar to that of climate warming. Rates of range shifts were variable but not closely associated with the particular types of organism; other than that poikilotherms shifted their distributions faster than homeotherms.

4.2 Introduction

Anthropogenic climate change is affecting species in many ways (Parmesan, 2006). An important response is that species potentially track their climate-envelope, altering their distributions or abundances to meet their ecophysiological requirements, e.g., Devictor *et al.* (2008), Tingley *et al.* (2009). Given the large-scale thermal gradients on earth, the shifts are generally pole-wards in latitude and upwards in elevation (Walther *et al.*, 2002; Parmesan, 2006; IPCC, 2007a). Whilst observations of distribution changes are ubiquitous, individual species responses vary. Species differ in the timing and rate of dispersal according to ecological or life-history traits, their physiological tolerances, and their means of perceiving environmental changes (Helmuth *et al.*, 2005). For example, herbivores that are generalists and mobile species have been observed to expand their distribution more than specialists due to the interplay of food availability and habitat changes (Hill *et al.*, 1999; Warren *et al.*, 2001; Bale *et al.*, 2002; Menéndez *et al.*, 2006; Pöyry *et al.*, 2009). For birds, higher natal dispersal may allow species to track climate change better than other species (Jiguet *et al.*, 2007). As species vary their responses to rapid global warming, the disassociation of recently-observed distribution and abundance patterns will result in major changes to the interactions between species and to the formation of novel communities (Tylianakis *et al.*, 2008; Berggren *et al.*, 2009; Berg *et al.*, 2010; Montoya & Raffaelli, 2010). Even though such changes might be expected to underpin major ecosystem changes associated with climate warming (Petchey *et al.*, 1999; Montoya & Raffaelli, 2010; Walther, 2010), little empirical evidence is available to assess how different taxonomic group vary in their rates of range shifts (Harrington *et al.*,(1999) but see Kinlan & Gaines (2003), Schweiger *et al.*(2008), Berg *et al.* (2010), Kissling *et al.* (2010)). More broadly are different functional or trophic groups responding at different rates, and hence changing the functional composition of communities?

The attributes of different taxonomic groups might be expected to affect their responses to climate change. In particular, poikilotherms and homeotherms may show very different response rates, or at least mechanisms underlying their responses (Deutsch *et al.*, 2008; Huey *et al.*, 2009). Poikilothermal species regulate their activities according to environmental conditions and their body temperatures vary greatly. This may make them particularly sensitive to warming. Alternatively, homeotherms allocate a larger percentage of their energy consumption to thermal maintenance and these costs may be unsustainable under some climatic conditions (Helmuth *et al.*, 2005; Aragón *et al.*, 2010). The differences are particularly pronounced in the early stages of the life cycle (Aragón *et al.*, 2010). An empirical assessment of whether homeotherms and poikilotherms differ in their response rates is needed.

Taxa also differ in their mobility. Mobile species are expected to track the climate better than more sedentary species (Pearson & Dawson, 2003). Therefore, mode of dispersal, such as active flight versus non-flying, should be important determinants of rates of range shifting (Araújo & Pearson, 2005; Guisan & Thuiller, 2005; Brooker *et al.*, 2007).

Biological interactions mediate species' responses under climate warming (Davis *et al.*, 1998; Petchey *et al.*, 1999; Voigt *et al.*, 2003; Suttle *et al.*, 2007); here I consider different trophic levels. From bottom-up perspective, species can not move more than their basal resources, i.e. lower trophic groups (Gilman *et al.*, 2010). On the other hand, species at higher trophic level have observed to be better dispersers (Kinlan & Gaines, 2003; Berg *et al.*, 2010) and have larger home ranges (Holt, 1996; Tscharntke & Brandl, 2004). Investigating rates of change for primary producers, herbivores and carnivoreas has the potential to reveal whether the trophic composition is changing in a consistent manner.

Empirical studies of distribution change usually focus on either mountain or lowland systems (Jump *et al.*, 2009). A few studies compared these two systems simultaneously (e.g. Franco *et al.*, 2006; Hickling *et al.*, 2006; Zuckerberg *et al.*, 2009), but it is not yet clear whether there are consistent differences in vertical and horizontal range shifts. Warming differs regionally (Core Writing Team *et al.*, 2007), it remains an open question whether shifts in elevation and latitude correlate / keep pace with climate changes.

A previous global meta-analysis showed that species on average shifted 6.1 km/m per decade (Parmesan & Yohe, 2003). This excellent study was, nonetheless, based on a limited range of taxonomic groups (59 United Kingdom birds, 31 Swedish butterflies, 9 Swiss herbs). With the data available at that time, species and location effects could not be separated, and latitudinal and elevational shifts were combined into a single estimate of the average rate of change. Since then, more studies have been published and are available to include in an updated meta-analysis. The updated meta-analysis presented here aims to (1) quantify the magnitude of species distribution changes in response to climate warming; (2) investigate whether range shifts correlate / keep pace with regional warming; (3) investigate whether different levels of response are associated with taxonomic group, thermal biology, mobility and trophic level; and (4) consider latitudinal and elevational responses separately.

4.3 Methods

4.3.1 Criteria to include literatures

I used key words and citation maps in ISI Web of Knowledge to find peer-reviewed literature on (potentially) warming-associated range shifts. Key words “climate change or climate warming” and “range or distribution” were applied. Citation maps were checked for highly relevant articles. Only papers that gave estimates of distribution changes were included; diversity, proportion or abundance changes were not considered. Only multiple species research without biased selection for / against highly responsive species were included in the meta-analysis. Single species studies could potentially suffer from publication bias (Parmesan & Yohe, 2003; Parmesan, 2007) and were not considered here. Groups represented by a small number of species could be included, provided that all species that met specified data quality criteria were considered for analysis.

4.3.2 Defining data points

For the purposes of this meta-analysis, I treated the mean distribution change of a taxonomic group in a region as an independent data point (e.g., mean latitudinal shift for spiders in Britain, mean elevational shift for plants in Switzerland). Parmesan and Yohe (2003) treated individual species as separate data points because there were so few multi-species studies available at that time. However, species of a given taxonomic group, studied in the same way and for the same duration in a particular region (with a given topography and climatic gradients), may not provide genuinely independent estimates of movement.

In practice, the distribution of taxa and regions available for analysis is still far from ideal. If a paper reported responses of multiple taxonomic groups in a region (a number of different taxonomic groups within the same region, e.g., Hickling *et al.*(2006)) it contributed multiple data points to the meta-analysis. If two or more papers analysed range shifts of the same taxonomic group in a region, I retained the most recent and removed the duplications. For example, I included Hickling *et al.*(2006) to represent changes for British butterflies, dragonflies and birds; replacing Hill *et al.*(2002), Hickling *et al.*(2005) and Thomas & Lennon (1999) respectively. Franco *et al.*(2006) and Hickling *et al.*(2006) both reported range shifts for British butterflies, but for non-overlapping sets of species (northern and southern species, respectively), so both studies were included. Bird responses in North America have been reported at more than one spatial scale, so I selected combinations of studies that were most inclusive (and contained fewest confounding factors). I included Hitch & Leberg (2007) in the meta-analysis for latitudinal range shifts (rather than La Sorte & Thompson(2007)) because the former excluded mountain areas (a confounding effect). I also included Peterson (2003) and Zuckerberg *et al.*(2009). Peterson (2003) reported average bird range shifts in the Great Plains and has only one species (*Tyrannus forficatus*) overlap with Hitch & Leberg (2007). Zuckerberg *et al.*(2009) has 34 species overlap with Hitch & Leberg (2007) but was at a different spatial scale, focusing only on the New York State; Zuckerberg *et al.* was the only one of the three used in the analysis of elevation changes. These three bird studies in the North America were brought into the analysis without excluding duplicating species since I used the average for a taxonomic group in a region as a separate data point, not individual species.

I consider latitudinal (in km) and elevational (in meter) range shifts separately throughout the analysis. Different studies have focused differently on cold (upper or leading) margins, warm (lower or trailing) margins or average distribution changes. Although changes regarding cold and warm margins are significantly different within some studies, no significant trend was found across all studies considered here (Wilcoxon signed rank test, elevational shifts, $n = 8$, $p > 0.05$; latitudinal shifts, $n = 6$, $p > 0.05$). Some papers reported separately the shifts at warm and cold margins of a given taxonomic group in the same region. These were unlikely to be independent, so I either included the author-reported average or derived a weighted mean of the warm and cold margin averages, based on the number of species in each group (see Appendix S 4.1 for the recalculation of each study). These means were treated as independent data points in the meta-analysis (and the separate estimates for the two margins were excluded).

4.3.3 Obtaining temperature change of each data point

Wherever available, I used author reported temperature changes for the regions and time periods considered. To enhance comparability between studies, I adopted mean annual temperatures; or took the equivalent by averaging minimum and maximum temperature changes. Durations of studies were defined as differences between the years that were compared. Most studies compared the differences in species' distributions between two blocks of time (see Tables 4.1, 4.2), but authors often provided temperature changes from the first year of the first period to the last year of the second period. To calculate the temperature change between the two time periods, I assumed linear warming through time, with the temperature change (and study duration) defined as the difference between the mid point of the first period and the mid point of the second period. If such information was not available from the original paper, I estimated temperature changes from CRU_TS2.0, a global annually temperature database at 0.5 degree resolution (Mitchell *et al.*, 2004). For each study location, I averaged across grids to obtain yearly temperature and ran least square regression over the entire study period. Temperature changes for each data point were the product of the coefficeint and the duration of study (Appendix S 4.1).

Table 4.1 Literatures included for meta-analysis for altitudinal range shifts, listed as separated data points.

No	Reference	Margin	Species	Number of Species	Location	Duration	Range shifts (m)	Temperature change (℃)	Rate of Shift (m/decade)	Rate of Temperature change (℃/decade)	Time span
1	Archaux 2004	Average	bird	29	Alps/France	25	-19.3	1.3	-7.70	0.52	1973-1980,2000-2002
2	Beckage et al. 2008	Average†	plant	6	Green Mountains/ Vermont,US	43	69.0	1.2	16.05	0.28	1962-2005
3	Bergamini et al. 2009	Average	bryophytes	61	Switzerland	92	89.0	1.3	9.67	0.14	1880-1920,1980-2005
4	Chen et al. 2011	Average	moth	130	Mt Kinabalu/ Malaysia	42	58.9	0.7	14.02	0.17	1965-2007
5	Franco et al. 2006	Trailing	butterfly	4	Britain	19	44.8	0.6	23.58	0.31	1970-1999,2004-2005
6	Hickling et al. 2006	Leading	aquatic bugs	14	Britain	20	19.2	0.5	9.60	0.27	1970-1980,1990-2000
7	Hickling et al. 2006	Leading	bird	22	Britain	20	-2.1	0.2	-1.05	0.12	1968-1972,1988-1991
8	Hickling et al. 2006	Leading	butterfly	29	Britain	25	11.1	0.7	4.44	0.26	1970-1982,1995-1999
9	Hickling et al. 2006	Leading	dragonflies and damselflies	20	Britain	25	61.9	0.5	24.76	0.18	1960-1970,1985-1995
10	Hickling et al. 2006	Leading	fish	15	Britain	25	32.7	0.7	13.08	0.26	1965-1975,1990-2000
11	Hickling et al. 2006	Leading	grasshopper and allies	22	Britain	25	30.5	0.5	12.20	0.18	1960-1970,1985-1995
12	Hickling et al. 2006	Leading	ground beetle	59	Britain	25	12.7	0.7	5.08	0.26	1965-1975,1990-2000
13	Hickling et al. 2006	Leading	harvestmen	4	Britain	20	35.8	0.4	17.90	0.19	1965-1975,1985-1995
14	Hickling et al. 2006	Leading	herptile	3	Britain	25	-33.0	0.5	-13.20	0.18	1960-1970,1985-1995
15	Hickling et al. 2006	Leading	lacewings	6	Britain	25	7.4	0.7	2.96	0.26	1965-1975,1990-2000
16	Hickling et al. 2006	Leading	longhorn beetle	11	Britain	25	39.3	0.5	15.72	0.18	1960-1970,1985-1995
17	Hickling et al. 2006	Leading	mammal	9	Britain	25	31.0	0.5	12.40	0.18	1960-1970,1985-1995

Table 4.1 (continued) Literatures included for meta-analysis for altitudinal range shifts, listed as separated data points.

No	Reference	Margin	Species	Number of Species	Location	Duration	Range shifts (m)	Temperature change (℃)	Rate of Shift (m/decade)	Rate of Temperature change (℃/decade)	Time span
18	Hickling et al. 2006	Leading	millipede	6	Britain	25	24.0	0.7	9.60	0.26	1965-1975,1990-2000
19	Hickling et al. 2006	Leading	soldier beetle and allies	16	Britain	25	62.1	0.7	24.84	0.26	1965-1975,1990-2000
20	Hickling et al. 2006	Leading	spider	85	Britain	25	24.3	0.7	9.72	0.26	1965-1975,1990-2000
21	Hickling et al. 2006	Leading	woodlice	8	Britain	25	55.3	0.5	22.12	0.18	1960-1970,1985-1995
22	Holzinger and Hülber 2008	Leading	plant	140	Switzerland	94	20.7	0.5	2.20	0.05	1910-2004
23	Kelly and Goulden 2008	Average	plant	10	Santa Rosa Mountains/ CA,US	30	64.9	0.4	21.63	0.14	1977,2006-2007
24	Klanderud and Birks 2003	Average	plant	-	Jotunheimen/ central Norway	68	81.6	-0.1	12.00	-0.02	1930-1931,1998
25	Konvicka et al. 2003	Average	butterfly	117	Czech Republic	33	7.8	0.6	2.36	0.17	1951-1980,1995-2001
26	le Roux and McGeoch 2008	Leading	plant	14	Marion Island	40	55.0	1.2	13.75	0.30	1965-1966,2005-2007
27	Lenoir et al. 2008	Average	plant	171	West Europe	22	64.8	0.8	29.45	0.35	1905-1985,1986-2005
28	Moritz et al. 2008	Average†	mammal	28	Yosemite NP/ US	88	69.0	2.6	7.84	0.30	1914-1920,2003-2006
29	Parolo and Rossi 2008	Leading	plant	93	Rhaetian Alps/ North Italy	48	88.6	1.5	18.46	0.31	1954-1958,2003-2005
30	Popy et al. 2010	Average	bird	56	Alta Valsessera/ North Italy	11	7.6	1.0	6.91	0.91	1992-1994,2003-2005
31	Raxworthy et al. 2008	Average	herptile	30	Tsaratanana Massif/ Northern Madagascar	10	65.3	0.2	65.30	0.24	1993-2003
32	Wilson et al. 2005	Average	butterfly	23	Spain	34	108.6	1.5	31.94	0.43	1967-1973,2004
33	Zuckerberg et al. 2009	Average	bird	129	New York State/ US	20	-5.2	0.6	-2.60	0.30	1980-1985,2000-2005

[†] Average of range shifts were estimated from mean of leading and trialing margins.

Table 4.2 Literatures included for meta-analysis for latitudinal range shifts, listed as separated data points.

No	Reference	Margin	Species	Number of Species	Location	Duration	Range shifts (km)	Temperature change (℃)	Rate of Shift (km/decade)	Rate of Temperature change (℃/decade)	Time span
1	Brommer 2004	Average†	bird	150	Finland	12	9.3	-0.2	7.76	-0.18	1974-1979,1986-1989
2	Franco et al. 2006	Trailing	butterfly	4	Britain	19	40.9	0.6	21.53	0.31	1970-1999,2004-2005
3	Hickling et al. 2006	Leading	aquatic bugs	14	Britain	20	64.0	0.5	32.00	0.27	1970-1980,1990-2000
4	Hickling et al. 2006	Leading	bird	22	Britain	20	29.0	0.2	14.50	0.12	1968-1972,1988-1991
5	Hickling et al. 2006	Leading	butterfly	29	Britain	25	37.0	0.7	14.80	0.26	1970-1982,1995-1999
6	Hickling et al. 2006	Leading	dragonflies and damselflies	20	Britain	25	104.0	0.5	41.60	0.18	1960-1970,1985-1995
7	Hickling et al. 2006	Leading	fish	15	Britain	25	47.0	0.7	18.80	0.26	1965-1975,1990-2000
8	Hickling et al. 2006	Leading	grasshopper and allies	22	Britain	25	34.0	0.5	13.60	0.18	1960-1970,1985-1995
9	Hickling et al. 2006	Leading	ground beetle	59	Britain	25	55.0	0.7	22.00	0.26	1965-1975,1990-2000
10	Hickling et al. 2006	Leading	harvestmen	4	Britain	20	8.0	0.4	4.00	0.19	1965-1975,1985-1995
11	Hickling et al. 2006	Leading	herptile	3	Britain	25	-83.0	0.5	-33.20	0.18	1960-1970,1985-1995
12	Hickling et al. 2006	Leading	lacewings	6	Britain	25	44.0	0.7	17.60	0.26	1965-1975,1990-2000
13	Hickling et al. 2006	Leading	longhorn beetle	11	Britain	25	40.0	0.5	16.00	0.18	1960-1970,1985-1995
14	Hickling et al. 2006	Leading	mammal	9	Britain	25	22.0	0.5	8.80	0.18	1960-1970,1985-1995
15	Hickling et al. 2006	Leading	millipede	6	Britain	25	74.0	0.7	29.60	0.26	1965-1975,1990-2000
16	Hickling et al. 2006	Leading	soldier beetle and allies	16	Britain	25	91.0	0.7	36.40	0.26	1965-1975,1990-2000
17	Hickling et al. 2006	Leading	spider	85	Britain	25	84.0	0.7	33.60	0.26	1965-1975,1990-2000
18	Hickling et al. 2006	Leading	woodlice	8	Britain	25	79.0	0.5	31.60	0.18	1960-1970,1985-1995
19	Hitch & Leberg 2007	Average†	bird	55	North America	31	33.4	0.6	10.78	0.20	1967-1971,1998-2002
20	Lima et al. 2007	Average†	algae	37	Portugal	50	61.4	0.7	12.27	0.15	1950-1960,2001-2006
21	Perry et al. 2005	Average†	fish	20	North Sea	25	55.4	1.1	22.16	0.42	1997-2001
22	Peterson 2003	Average	bird	5	Great Plains/US	25	46.0	0.5	18.40	0.19	1971-1995
23	Pöyry et al. 2009	Leading	butterfly	48	Finland	8	72.9	1.1	91.13	1.41	1992-1996,2000-2004
24	Rivadeneira and Fernandez 2005	Leading	intertidal sp.	10	Chilean coast	39	-75.5	0.0	-19.36	0.00	1947-1975,1998-2000
25	Zuckerberg et al. 2009	Average	bird	129	New York State/US	20	3.6	0.6	1.79	0.30	1980-1985,2000-2005

† Average of range shifts were estimated from mean of leading and trialing margins.

4.3.4 Obtaining observed and expected range shifts of each data point

To represent an overall range shift of a taxonomic group in a region, authors must have reported pole-ward, stable and equator-ward distribution changes in latitude or reported upward, stable and downward shifts in elevation, regardless of the significance. If the literature focused only on a subset of movements, e.g., only those species showing individually significant shifts, I recalculated the mean range shifts across all species. For example, Moritz *et al.* (2008) reported an ~500m upward shift of lower limits of small mammals in Yosemite National Park, US; considering upward, stable and downward shifts, the mean shift was recalculated as 119.0 m (Appendix S 4.1). I could not include Walther *et al.*(2005) or Kullman (2002) because only the upward shifts of plants were reported. Most papers compared the “raw” distribution changes while some studies adjusted the observed shifts by changes in occupied areas, to control for effects of overall range expansion or compression. To enhance comparability between studies, I adopted unadjusted estimates, most of them available from the raw data (Appendix S 4.1). Pole-ward or upward range shifts were in accord with expectations under climate warming and were denoted as positive. Equator-ward or downward range shifts were denoted as negative.

For each study, I obtained an “expected” latitudinal or elevational range shift, based on movement of thermal isotherms over the relevant period of warming, in the region considered. For elevational range shifts, I used the author-reported lapse rate at each study location. Lapse rates are stated as the temperature decrease (°C) for every metre increase in elevation. I divided the overall temperature increase by the lapse rate to calculate the thermal isotherm shift, as an estimate of the elevation increase that a species would need to undertake to remain within the same temperature regime; 26 of the 33-case studies provided lapse rates, enabling us to compare the differences between expected and observed range shifts.

To obtain expected latitudinal range shifts, I calculated a temperature-distance transfer rate (T_D rate) as temperate change per unit distance in a poleward direction. I use an annual temperature dataset on global 10' grid (average from 1961-2000). Within each study region, I calculated the nearest distances that a species would need to move from a source grid cell so as to locate the nearest target cell that was 0.5°C cooler. These distances were then averaged across all grid cells in a region. To ensure relevance to observed latitudinal shifts, source and target cells were constrained to be within ± 1 degree of longitude of one another, and within 50 m elevation of each other. The T_D rates were temperature decreases (°C) per km north. Expected latitudinal range shifts were the overall regional temperature change divided by the T_D rates. Calculations were possible for 22 out of the 25 cases.

4.3.5 Range shifts against temperature changes

I compared distribution changes with the corresponding temperature changes in terms of the absolute changes (total changes over the duration of study) and the decadal rates of changes; using least square regressions for statistical analysis. I compared observed against the expected range shifts to evaluate whether species have kept pace with climate warming.

Variation in range shifts were analyzed in relation to the: rates of temperature changes, mean latitude of each study location, duration of study, last year of study, major taxonomic groups, mobility, thermoregulation types, and trophic levels. The major taxonomic groups were plants (i.e. vascular plants, bryophytes, algae), birds, fish, herptiles, mammals, molluscs and arthropods. I define mobility coarsely as flying or non-flying depending on whether they possess active or passive flight behavior. If a group of species contained both, they were classified as “partly flying”; e.g. 6 out of 9 mammal species in Britain in Hickling *et al.*(2006) were bats and hence classified as partly flying for this data point. Plants, bryophytes, and spiders are mainly passively wind-dispersal and were classified as non-flying. Thermoregulation types were poikilothermic or homeothermic; plants were not included in this analysis. Trophic levels were producer, herbivore, carnivore, and omnivore. If an animal group contained species with different diets, omnivore was applied to this category; e.g. birds in French Alps (Archaux, 2004). I conducted analysis of covariance in an univariate manner to evaluate whether these categorical variables were associated with observed range shifts, using rates of temperature change as the covariate.

4.4 Results

Twenty-five studies met our criteria and entered the meta-analysis, of which 18 reported altitudinal range shifts and 10 reported latitudinal shifts; contributing 33 (Table 4.1) and 25 (Table 4.2) data points respectively. The studies encompassed plants, arthropods, fish, herptiles, birds, mammals and marine taxa, and included around 1700 species. Studies ranged from the tropics to sub-arctic zones. Most studies were from northern hemisphere (6°N to 65°N) and 3 were from the southern hemisphere (14°S, 30°S and 46° S). Studies varied from 8 to 94 years duration, with a mean of 30 ± 2 SE years. Temperatures increased at a mean of 0.6 ± 0.06 SE °C per decade, but with a few studies show little or no warming (Tables 4.1, 4.2).

I estimated a median elevational range shift of 12.2 m upward per decade (mean = 13.2, n = 33; 4 decreases and 29 increases, Wilcoxon signed-rank test of zero changes, $P < 0.01$), and a median latitudinal shift of 17.6 km poleward per decade (mean = 18.7, n = 25; 2 decreases and 23 increases, Wilcoxon signed-rank test of zero changes, $P < 0.01$) (Fig. 4.1).

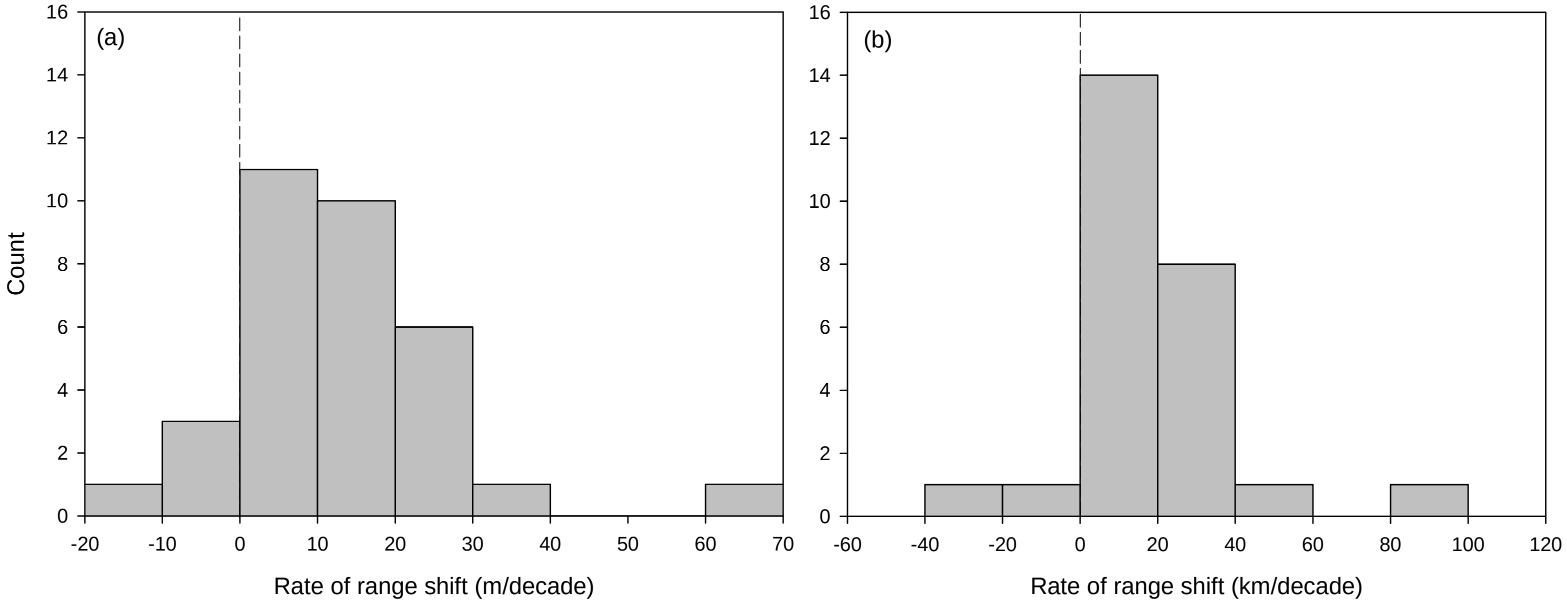

Figure 4.1 Histograms of (a) elevational range shifts (b) latitudinal range shifts.

Total elevational shifts were not significantly related to the total increase in temperature (Pearson $R^2 = 0.09$, $F_{1, 31} = 2.9$, $P = 0.10$, Fig. 4.2 (a)); nor were the decadal rates of elevation shifts and warming significantly correlated ($R^2 = 0.00$, $F_{1, 31} = 0.01$, $P = 0.94$, Table 4.3 (a), Fig. 4.2 (b)). Latitudinal range shifts were significantly related to temperature change; for both overall shifts ($R^2 = 0.25$, slope = 80.1, $F_{1, 23} = 7.50$, P = 0.01, Fig. 4.3 (a)) and decadal rates of change ($R^2 = 0.54$, slope = 61.2, $F_{1, 23} = 26.57$, $P < 0.001$, Table 4.3 (b), Fig. 4.3 (b)). These trends remained similar when excluding outliers ($|$studentized residual$| > 3$).

Table 4.3 Pearson correlation matrix of numeric variables concerning (a) elevational range shifts (b) latitudinal range shifts

(a)

	Study location[a] (latitude)	Duration (year)	Rate of shift (km/decade)	Rate of temperature change (˚C per decade)
Duration	-0.09	-		
Rate of shift	-0.41	-0.18	-	
Rate of temperature change	-0.09	-0.36	-0.01	-
Last year of study	-0.56*	0.34	0.18	0.35

(b)

	Study location[a] (latitude)	Duration (year)	Rate of shift (km/decade)	Rate of temperature change (˚C per decade)
Duration	-0.76***	-		
Rate of shift	0.49	-0.42	-	
Rate of temperature change	0.36	-0.41	0.73***	-
Last year of study	-0.28	0.29	0.25	0.48

Significance levels: * *P* <0.05; *** *P* < 0.001.

[a] North or south latitudes are not separate here. The latitudes represent the relative location in the pole-equator gradient.

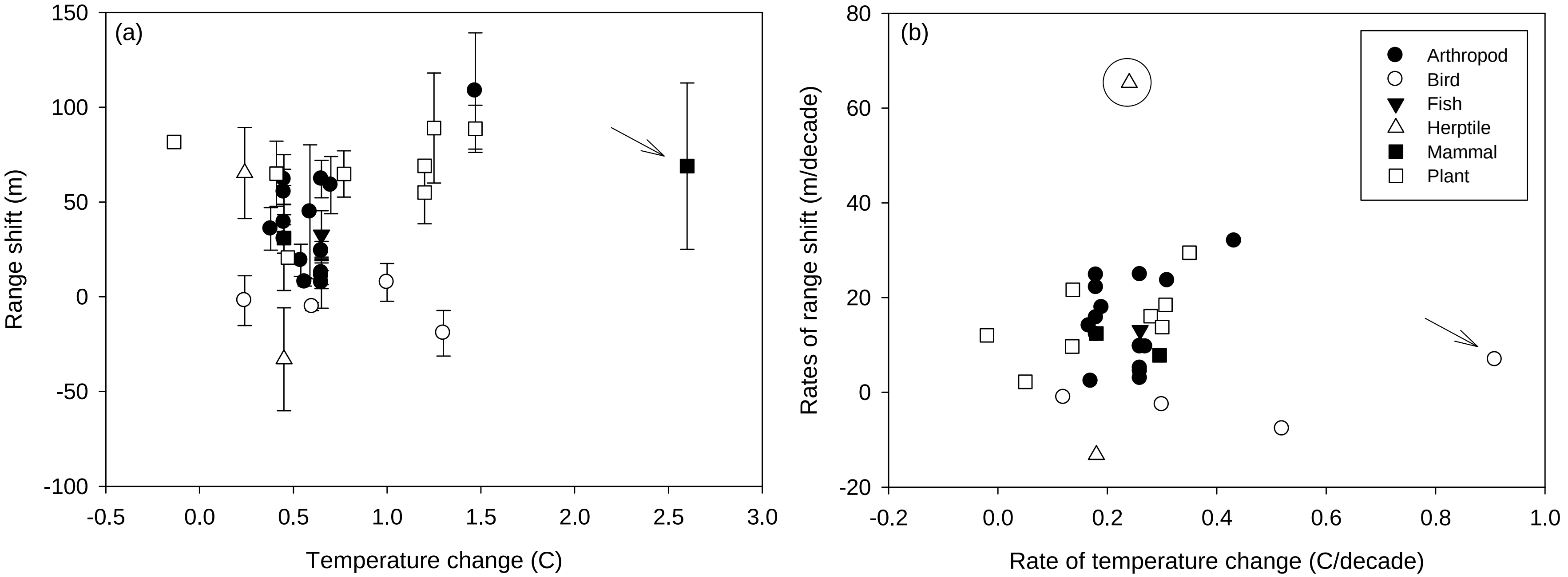

Figure 4.2 Relationship of elevational range shifts and temperature changes. (a) Overall range shift against overall temperature change for each data point. Regression was conducted using mean range shifts. Error bars represent the SE of each mean shift. Arrow indicated data point of higher influence: case 28, mammals in Yosemite NP, US. (b) Rates of range shifts against rates of temperature changes in decade scale. Data point of higher influence: case 30, birds in north Italy. Circle indicated outlier: case 32, reptiles in Madagascar.

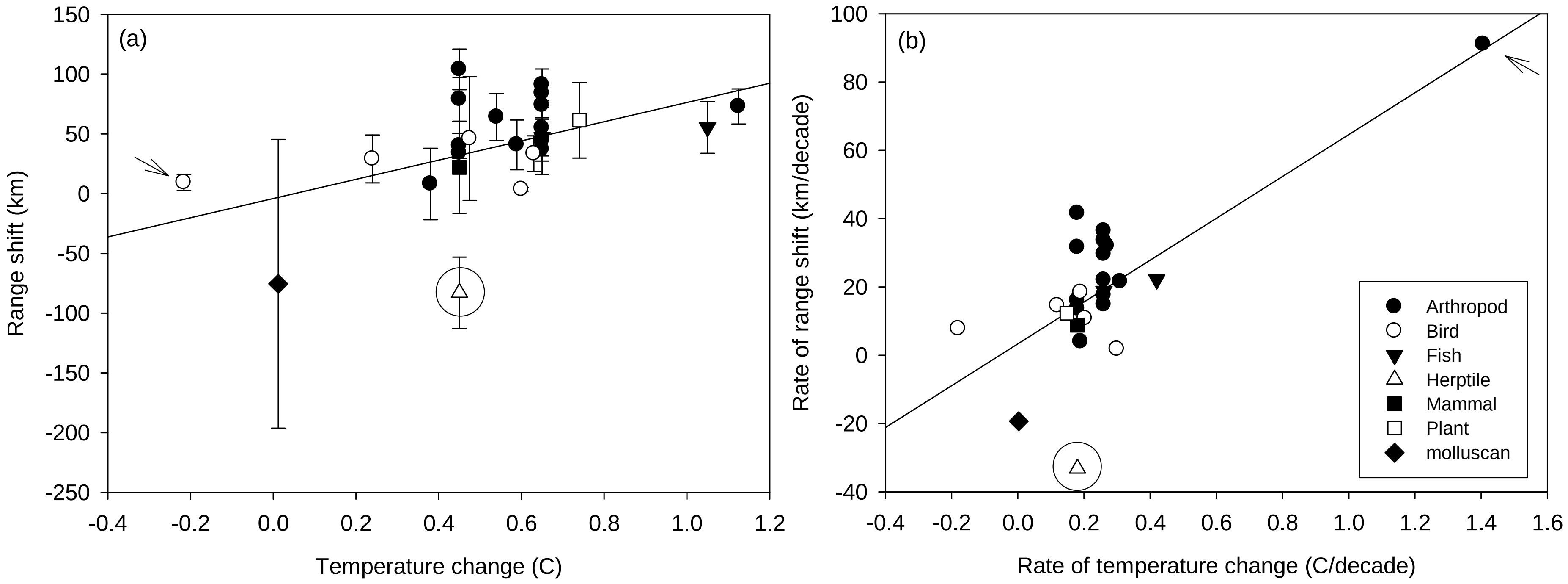

Figure 4.3 Relationship of latitudinal range shifts and temperature changes. (a) Overall range shifts against overall temperature change for each data point. Regression was conducted using mean range shifts. Error bars represent the SE of each mean shift. Arrow represented data point of higher influence: case 1, birds in Finland. Outlier was marked in circle: case11, herptiles in Britain. (b) Rates of range shifts against rates of temperature changes in decade scale. Data point of high influence: case 23, butterflies in Finland. Outlier: case 11, herptiles in Britain.

Elevational range shifts generally lagged behind the change expected based on regional warming (Fig. 4.4), with most of the data points located below the diagonal 1:1 line; only two cases exceeding the expected shifts (plants in the Santa Rosa Mountains, California, US and herptiles in Madagascar). The mean ratio of observed to expected range shift was 0.39, indicating that elevations increased by less than half of that expected from the thermal isotherm uplift. In contrast, the latitudinal range shifts tracked warming better as most data points were around the diagonal line. The mean ratio of observed to expected range shift was 0.7 (excluding an obvious outlier of -25.2 for intertidal sp. on the Chilean coast).

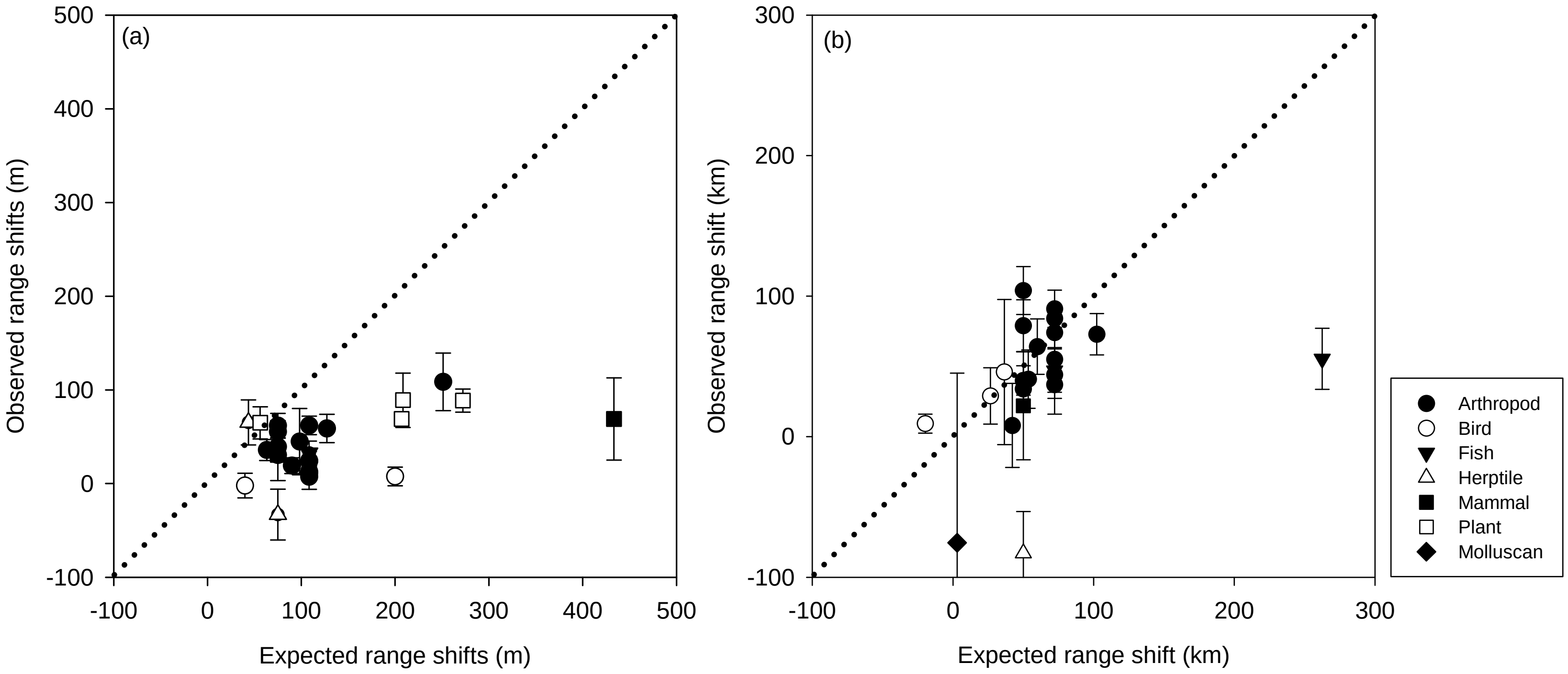

Figure 4.4 Expected and observed (a) elevational and (b) latitudinal range shifts.

Cross correlations of rates of range shifts with other study attributes did not reveal other or major confounding effects. The earlier studies of elevation changes came from relatively high latitudes, and short-term studies of latitudinal range shifts have been commonly published at high latitudes (Table 4.3). Because rates of range shifts are not correlated with these variables, these correlations between independent variable are unlikely to alter the main conclusions.

Whilst taking into account the effects of regional warming, I found that major species groups differed in their rates of elevational range shifts; plants and arthropods moved faster than birds (ANCOVA $F_{2, 24} = 8.5$, $P < 0.05$, pairwise comparison by Tukey's HSD tests; Table 4.4, Fig. 4.5 (a)). Species group differences were not significant for latitudinal range shifts (ANCOVA $F_{1, 16} = 1.97$, $P = 0.18$; Table 4.5, Fig. 4.5 (e)).

Poikilothermic species responded more than homeothermic species, significantly so for elevational range shifts ($F_{1, 21} = 4.7$, $P < 0.05$; pairwise comparison by Tukey's HSD tests; Table 4.4). There was no significant effect of dispersal mode on response rates (Table 4.4, Table 4.5, Fig. 4.5(b),(f)).

Trophic levels were ambiguous in regard to relating to the range shifts. Latitudinal range shifts increased with trophic level (Table 4.5; Fig. 4.5(h)) but the non-significant trend was reversed when considering elevational shifts (Table 4.4; Fig. 4.5(d)).

Table 4.4 Relationships between rates of elevational range shifts and species categories using analysis of covariance

Effect	N	Coefficient (SE)	Least square means (SE)	*F* value	Model R^2	Model *F* value
Group[a]				8.5**[d]	0.41	5.7**
Arthropod	16	6.1 (2.2)*	14.8 (2.0)			
Bird	4	-14.1 (3.4)***	-5.4 (4.6)			
Plant[b]	8	-	16.8 (2.9)			
Covariate	28	20.8 (10.9)	0.3 (0.2)	3.6		
Mobility[c]				0.2	0.01	0.1
Non-flying	15	1.6 (2.8)	12.7 (2.8)			
Flying	13	-0.4 (3.0)	10.7 (3.1)			
Partly-flying[b]	4	-	9.9 (5.4)			
Covariate	32	1.4 (13.0)	0.3 (0.2)	0.0		
Thermoregulation[c]				4.7*	0.19	2.4
Poikilotherm	18	5.7 (2.6)*	13.1 (2.5)			
Homeotherm[b]	6	-	1.7 (4.5)			
Covariate	24	8.6 (14.5)	0.3 (0.2)	1.5		
Trophic level[c]				1.3	0.13	1.0
Carnivore	6	-2.1 (3.5)	9.9 (4.2)			
Herbivore	7	3.0 (3.3)	15.0 (3.9)			
Omnivore	11	-4.8 (3.0)	7.2 (3.2)			
Producer[b]	8	-	15.8 (3.7)			
Covariate	32	6.5 (12.5)	0.3 (0.2)	0.3		

Rates of temperature changes were entered each univariate analysis as covariate. Significance levels: * P <0.05, ** P <0.01, *** P < 0.001.[a] Herptile, mammal and fish were excluded from the analysis for less than 3 cases were available to test the homogeneity of coefficients for the covariate across the levels of the effect.

[b] Redundant variable. [c] Herptile in Madacascar was excluded as outlier in all analysis (│ studentized residual │ > 3). [d] Mean shifts of birds were significantly differed from that of arthropods and plants (P < 0.01). [e] Mean shifts of homeotherm were significantly differed from that of poikilotherm and plants (P < 0.05).

Table 4.5 Relationships between rates of latitudinal range shifts and species categories using analysis of covariance

Efffect	N	Coefficient (SE)	Least square means (SE)	*F* value	Model R^2	Model *F* value
Group[a]				2.0	0.72	20.4***
Bird	5	-4.2 (3.0)	17.9 (5.1)			
Arthropod[b]	14	-	26.4 (3.0)			
Covariate	19	51.3 (9.3)***	0.3 (0.3)	30.7***		
Mobility[c]				0.2	0.66	12.8***
Flying	12	1.5 (3.5)	22.2 (3.6)			
Partly-flying	4	0.3 (4.6)	21.0 (6.2)			
Non-flying[b]	8	-	18.9 (4.4)			
Covariate	24	58.5 (9.7)***	0.3 (0.3)	36.5***		
Thermoregulation[c]				0.8	0.66	19.7***
Homeotherm	6	-2.7 (3.0)	17.3 (5.2)			
Poikilotherm[b]	17	-	22.7 (3.0)			
Covariate	23	56.7 (9.9)***	0.3 (0.3)	32.9***		
Trophic level[c]				2.5	0.72	16.6***
Omnivore	11	-1.4 (3.3)	20.2 (3.5)			
Herbivore	6	-6.6 (3.8)	15.0 (4.8)			
Carnivore[b]	6	-	29.6 (4.7)			
Covariate	23	60.9 (9.3)***	0.3 (0.3)	42.6***		

Rates of temperature changes were entered each univariate analysis as covariate. Significance levels: *** $P < 0.001$.
[a] Herptile, mammal, molluscan and plant were excluded from the analysis for less than 3 cases were available to test the homogeneity of coefficients for the covariate across the levels of the effect. [b] Redundant variable. [c] The only plant case were excluded for not being able to test the assumption of ANCOVA. Herptile in Britain was excluded as outlier in all analysis (│ studentized residual │ > 3).

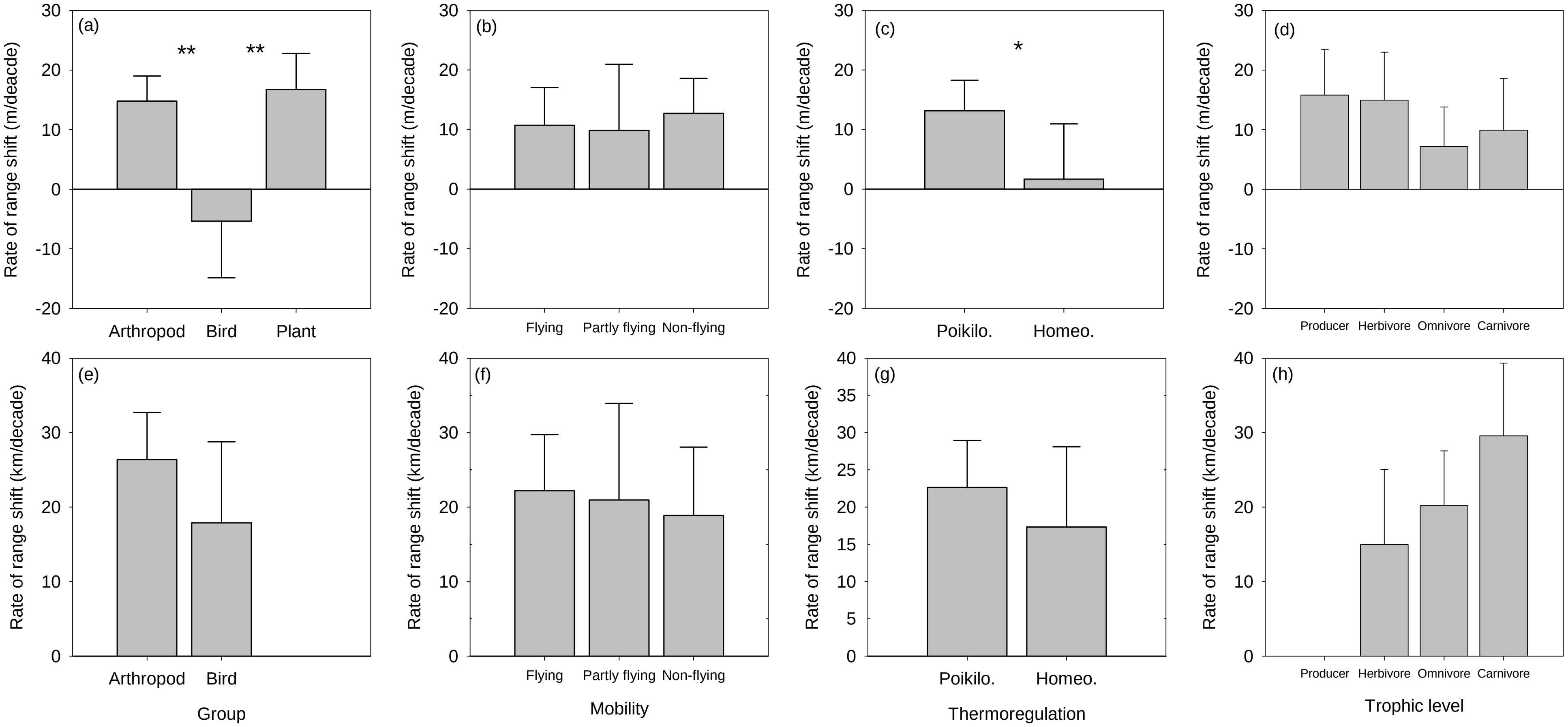

Figure 4.5 Least squares means and their 95% confidence intervals of rates of (a)-(d) elevational range shifts and (e)-(h) latitudinal range shifts according to major species groups: (a) and (e), mobility: (b) and (f), thermoregulation: (c) and (g) and trophic level: (d) and (h). Start sing indicates significant level of differences: * $P < 0.05$, ** $P < 0.01$.

4.5 Discussion

Our meta-analysis suggest that rates of range shifts are two- to three- times higher (for elevational and latitude respectively) than those reported in a previous analysis (Parmesan & Yohe, 2003). The substantially increased recent literature concentrates on the recent period of anthropogenic warming; largely avoiding underestimates associated with century-long studies that covered long pre-warming periods (i.e. Grabherr *et al.*, 1994; Parmesan *et al.*, 1999). This study confirms high frequencies and rates of distribution changes in response to recent climate change.

4.5.1 Comparing the elevational and latitudinal range shifts

Latitudinal shifts were correlated with the magnitude and rate of regional warming. About half ($R^2 = 0.54$) of the variation in the rate of latitudinal change can be explained by the rate of warming, which I consider to be very strong given that (a) a wide range of taxonomic and functional groups was considered, (b) latitude and climate are not perfectly correlated, (c) species groups may respond to somewhat different sets of climate variables (I only considered average temperature), and (d) species may have considerable difficulty shifting their distributions across human-dominated landscapes.

In contrast, although species shifted their elevations significantly upwards, and faster than previously reported (Parmesan and Yohe), absolute shifts and rates of shift were not correlated with the level of regional warming. Given that the absolute geographic distances required to track climate change are smaller for elevation shifts than for latitude (Colwell *et al.*, 2008), it may imply other constraints. Some species may be reaching limits at the tops of mountains, for example retreating at their lower boundaries but failing to expand upwards (Wilson *et al.*, 2005) reaching geological or vegetation changes that impede movement, or be limited by moisture availability, which may not be shifting upwards in the same manner as temperature (Pounds *et al.*, 1999; Still *et al.*, 1999; Bush, 2002; Körner, 2007; Chen *et al.*, 2011). Alternatively, the resolution of analysis may remain too coarse to record within grid / gap elevational shifts adequately (Thomas *et al.*, 2006).

Both latitudinal and elevational range shifts appeared to lag behind the observed regional climate change but the lag was much greater for elevational shifts. The constrains discussed above may contribute to the lagging elevational shifts so that whather the lagging is pronounced in elevation requires further investigation. Nevertheless, the tardy range shifts raise concerns of biodiversity risks if keeping pace with suitable climate regimes is difficult.

4.5.2 Species categories in explaining the range shifts

The analyses of the attributes of species-groups associated with distribution changes were mixed. A number of significant results were obtained, but they often differed between the elevational and latitudinal analyses, suggesting that a larger number of studies may be required before consistent patterns emerge. The overall impression is that species type is not a strong predictor of the rate of response.

The only result that was consistent for latitude and elevation was an increased rate of response for poikilotherms than for homeotherms (and for poikilothermic arthropods than for homeothermic birds). Poikilothermic invertebrates react directly to the physical environment, and have short generation times, facilitating rapid responses (Bradshaw & Holzapfel, 2006, 2010). Birds and mammals have generally been found to be lagging behind or even static in their distributions, despite shifts of temperatures (Devictor *et al.*, 2008; Sekercioglu *et al.*, 2008 and reference in this study). In addition to their thermal biology, these taxa also differ in a number of additional life history traits, e.g., generation time, life span (Morris *et al.*, 2008; Aragón *et al.*, 2010; Bradshaw & Holzapfel, 2010), so I remain circumspect about the interpretation of this slow response.

Mobility and trophic levels did not predict range shifts, or were inconsistent between elevation and latitude analyses. The failure of mobility to predict changes may partly be due to the coarse manner in which it was measured.

Finally, herptiles (Hickling *et al.*, 2006; Raxworthy *et al.*, 2008) often represented as outliers due to the high dependence on moisture availability to complete their life cycle (Araújo *et al.*, 2006; Aragón *et al.*, 2010), and the threat posed by invasive pathogens (Pounds *et al.*, 2006).

4.5.3 Conclusion

This updated meta-analysis covered a wide range of taxonomic groups and geographic locations; giving estimated range shifts of 12.2 m uphill per decade and 17.6 km poleward per decade. Latitudinal changes tracked variation in regional warming (both magnitude and rate), despite the wide variety of taxa and locations considered; elevational shifts appeared to lag behind regional warming to a greater extent, but further work is required to confirm this. The slow responses raise concern of biodiversity risk as species have difficulty keep pace with climate warming (Devictor *et al.*, 2008; González-Megías *et al.*, 2008). The data available to date also suggest that response rates are not easily predicted by the traits of a given taxonomic group. On the basis of current evidence, I would tentatively conclude that poikilotherms are responding faster than homeotherms. Quantity of research skews to the northern high latitude, and knowledge gap occurs in the tropical and sub-tropical regions, where keep the majority of global biodiversity.

4.6 Acknowledgements

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4.7 Supplementary Material

Appendix S 4.1 Recalculations of range shifts and temperature changes for literatures included

No.	Reference	Recalculation of range shifts	Recalculation of temperature changes
1	Archaux (2004)	Bird censuses were carried out on two sites in different periods: Mont Ventoux massif in 1973/74 and 2000/01; the upper Giffre valley in 1978/80 and 2001/02. Rates of range shifts (m per decade) of each species were the mean of those at two sites. I then averaged across all species to get the mean rate of range shift for the meta-analysis. Duration (25 years) was the mean of study periods of two sites (23 and 27 years respectively). I multiplied the mean shift rate by the mean duration to obtain overall range shifts.	Author reported a mean annual temperatures increase of 1.3 °C for 25 years.
2	Beckage *et al.* (2008)	Ecotone shifts were estimated from remotely sensed data for Camels Hump and Mount Abraham. I took mean of them as the observed range shifts.	Author reported 1.13°C increase between 1963 and 2003; I multiply the yearly increase (0.028) by duration (43) to get the temperature change.
3	Bergamini *et al.* (2009)	Compared bryophyte altitudinal data between the two periods 1880–1920 and 1980–2005. Duration is the difference between two mid points (1900,1992). Changes in upper and lower elevations obtained from the author.	Author reported 1.25°C increase between 1990 and 1992.
4	Chen *et al.* (2011)	Obtained average elevation changes from 10 site data with ≥ 3 catches in each year; obtained upper and lower boundary shifts from “Group B” species, excluding singleton boundaries, for the shifts of Group A species might be impeded by non-climate barriers.	Author reported 0.7°C increase between 1965 and 2007 and lapse rate equals to 0.55°C per 100 m.
5	Franco *et al.* (2006)	Included all four species	Author reported temperature increased in a rate of 0.031°C per year and lapse rate equals to 0.6°C per 100 m.
6	Hickling *et al.* (2006)	I adopted data from “recorded squares” into the meta-analysis to represent all taxonomic groups.	Corresponding temperature changes for each taxonomic group were extracted from CRU_TS2; range restricted to Britain England. The periods on which temperature regressed against the years were depended on the time span of each group.
7	Holzinger and Hülber (2008)	Migration rates for each species were the mean of four mountains with historical surveys in 1910, 1910, 1920 and 1902 respectively. I use the mean year (1910) as the beginning year, duration as 94 years (1910~2004). I multiplied the mean migration	Author reported mean summer temperature increased by at least 0.6 K fro the past 120 years; I proportioned this to the duration of 94 year, hence a 0.47°C in temperature increase.

		rate (2.2±0.3m per decade) by 9.4 to get overall range shifts.	
8	Kelly and Goulden (2008)	I recalculated the mean and SE as 64.9 m and 54.4 m from Table 1 in the paper.	Author reported the mean temperature has increased 0.41 for the 30 years and lapse rate as 0.73°C per 100 m.
9	Klanderud and Birks (2003)	I multiplied the rate of elevational advance (1.2m per year) by duration (68 years) to obtain overall range shifts. Bound set as average.	Corresponding temperature changes for the region was extracted from CRU_TS2; range restricted to: central south Norway (61°N-62°N;7°30'E9°30'E)
10	Konvicka *et al.* (2003)	Author reported range shifts of 15 significantly ascended butterfly species out of total 117 species, of which none descended. I applied 0 m shift to the 102 insignificantly changed species and recalculated the mean and SE of the overall range shifts.	Corresponding temperature changes for the region was extracted from CRU_TS2; range restricted to: Czech Republic
11	le Roux and McGeoch (2008)	Within three sets of data published, I adapt "broad scale analysis" (14 species) into the meta-analysis. The estimates acquired from resurvey and values fell between the other two sets, the "fine-scale analysis" (5 common species) and "island scale analysis" (with *ad hoc* observation reference data, 21 species).	Author reported a mean temperature increase of 1.2°C for the 40 years
12	Lenoir *et al.* (2008)	Obtained SE from the 95% confidence interval.	Although the author reported 0.9°C warming of the entire study period (the 20th cnetury), the mid points at which comparisons based on were actually 1971 and 1993. Proportioning the 20th century warming to the 22-year study duration will largely underestimate the real warming that most of the species encountered in the late half of the century. I extracted temperature change at west Europe from 1971 to 1993 from CRU_TS2, range restricted to France (42°30'N-50°30'N;2°E-9°30'E). I use the product of the slope (0.035°C/year) and 22-year duration as the corresponding temperature increase (0.77°C).
13	Moritz *et al.* (2008)	For the transect had represented the full elevational gradient in the Yosemite valley, species reported as "no changes" or insignificant in their upper or lower limits were treated as 0 m shifts. Upper and lower limit shifts were recalculated by including all 28 species. Study period set as 88 years, i.e. mid points between Grinnell survey (1914-1920, using 1917) and resurvey (2003-2006, using 2005)	Author reported an observed ~3°C increase in minimum temperatures. I adopted a mean slope of temperature change against years (0.0295, including minimum and maximum temperatures in January and July, see their appendix Figure S1), multiplied by study duration to obtain the average temperature change.
14	Parolo and Rossi (2008)	I recalculated species range shifts by including all 93 species, of which 37 without range shifts were assigned 0 m shift.	Author reported summer and winter temperature increases as 1.6°C and 1.1°C respectively from 1959 to 2003. I adopted the mean temperature increase (1.35°C) and proportioned the change to study duration to obtain corresponding warming.
15	Popy *et al.*	Adopted Appendix S2 to recalculate overall	Author reported a corresponding

	(2010)	range shift; number of species were those with data available (56 instead of author reported 61).	temperature increase of 1°C
16	Raxworthy *et al* .(2008)	Combined reptiles and amphibians as herptile, producing one data point, to be comparable to Hicklings *et al.* (2006).	Author reported northern Madagascar temperature increased from 0.10°C to 0.37°C between 1984–1993 and 1994–2003. I adopted mean of them as overall temperature increases.
17	Wilson *et al.* (2005)	Author provided the raw data of range shifts, without adjusting of changes of occupancies, including minimum, maximum and average elevations of each butterfly species.	Author reported 1.3°C temperature increase for 30 years from 1967-1973 to 1997-2003. I proportioned the amount of increase to the 34-year study.
18	Zuckerberg *et al.* (2009)	Range shifts were recalculated using raw data from the author; occupancy changes were not considered here.	Author reported a rate of increase at 0.3°C per decade in northeastern United States. I set the overall temperature warming in the region for the 20-year study as 0.6°C.
19	Brommer (2004)		No corresponding temperature information provided in the paper. I extracted annually temperature (1974-1989) from CRU_TS2 and regress against years. The slope was then multiplied by duration to obtain overall temperature change.
20	Hitch & Leberg (2007)	I followed our definition of duration, i.e. mid points between two study periods (31 years), rather than author reported 26 years.	Author reported 1.1°C increase in spring maximum temperatures between 1950 and 2004 in the northern hemisphere. I proportioned this to the temperature change of study duration.
21	Lima (2007)	Excluded two cold water species whose distribution changes were “not applicable”. Apply 0 m to species of “no change” recalculated the mean shifts.	Author reported 0.74°C temperature increase for the study period.
22	Perry (2005)	Northern and southern boundary shifts for each species were obtained from the author. Species not shifting with climate were assigned 0 m changes.	Author reported 1.05°C increase from 1977 to 2001 in the North Sea.
23	Peterson (2003)	Author ran regression of mean latitudes against 5-year intervals. I multiplied the slope by 110 km and 5 intervals to obtain overall shifts in km for the 25 year study.	Corresponding temperature changes for the region was extracted from CRU_TS2; range restricted to: great plains in US (95°W-105°W,30°N-49°N)
24	Pöyry *et al.* (2009)		I took mean of author reported 0.45°C–1.8°C of warming in the summer months (June–August)
25	Rivadeneira and Fernandez, (2005)	Distribution changes (in degree latitude) of species had come from different study periods. I multiplied the mean rate (converted to km per year) by the mean duration to obtain overall range shifts.	Author reported warming rates for the last half-century varied between -0.0079 and 0.0085 C per year. I took mean as rate of warming.

CHAPTER 5

CONSERVATION IMPLICATIONS AND FUTURE RESEARCH: ADDRESSING BIODIVERSITY RISKS IN SOUTHEAST ASIA

5.1 Biological impacts of climate warming in Southeast Asia

The findings of the thesis, concerning the tropics—particularly Southeast Asia—reveal the complexity and urgency of conservation in this region. Southeast Asia has warmed for 0.2°C-1.0°C since 1970 (Corlett, 2009), and at least a further 2.5°C increase is expected before the end of this century (Cruz *et al.*, 2007). The species are likely to have reacted through phenotypic plasticity, such as changes in behaviour or physiology, or even to have adapted evolutionarily (Bradshaw & Holzapfel, 2006), even though the empirical evidence is scarce. I have shown the moth assemblages moved uphill over four decades of climate warming (Chen *et al.*, 2009; Chen *et al.*, 2011). Peh (2007) compared elevational changes of 94 common residential birds in Southeast Asia and found that they have expanded the lower and / or upper boundaries uphill regardless of habitat preference. In a montane national park in Thailand, Round and Gale (2008) found that a lowland pheasant *Lophura diardi* increased in abundance relative to their highland counterpart and argued that climate change was a plausible explanation. For herpetofauna, despite limited field observations, the trends of climate changes are likely to decrease overall fitness, owing to the disruption of development, increased metabolic rates, desiccation stress, susceptibility to diseases, range shifts and associated competition (Bickford *et al.*, 2010).

Although species show some plasticity to cope with climate changes, whether responses are fast enough to survive climate change in the long run is questionable. The average uphill movements of Mount Kinabalu moths was lagging behind the thermal isotherm uplift of 127 m. In addition to the shrinking land area uphill, the Kinabalu resurvey showed that many species are likely to face risks because ecological and geological barriers may impede upward movements. The interaction between global warming and local deforestation may exacerbate the problem, both because of a reduction in total forest area and the impact of deforestation on the climate; even fully protected national parks cannot fully safeguard species when they move upward to find cooler refugia. Williams *et al.* (2007) warned that the disappearance of particular types of climate from tropical mountains will eventually decrease the value of nature reserves, if climate warming continues.

5.2 Biogeography and the risks to biodiversity in Southeast Asia

The geography and biogeography in Southeast Asia could result in particularly high levels of risk from climate warming in this region. Southeast Asia comprises four global biodiversity hotspots, namely Sundaland, Wallacea, Philippines, and Indo-Burma; regions that contain high concentrations of endemic species and that are also experiencing rapid habitat loss (Myers *et al.*, 2000). These regions comprise only 4% of the global land area, but contain 9.7% of the global total of endemic vascular plants and 8.3% of endemic vertebrates, including mammals, birds, reptiles and amphibians are confined to these four bioregions (Myers *et al.*, 2000; Corlett, 2009; Sodhi *et al.*, 2010a). Latitudinal temperature gradients are generally very weak within the tropics, making it challenging (in terms of dispersal) for species to undertake latitudinal range shifts to find cooler refugia (Wright *et al.*, 2009). Thus, mountain ranges within the islands of Southeast Asia represent more likely climatic refugia for species that cannot survive hotter conditions. In Southeast Asia, however, terrestrial range shifts are further constrained by marine barriers. Current sea-level separate this region into several tens of thousands of islands. Such high sea-levels have characterized only ~ 2% for the past million years of glacial cycles, and hence the current geography and distribution of the biota can be considered atypical, on this time scale (Woodruff, 2010). During the last million years, the sea-level was on average 62 m lower, such that the Sunda plains emerged and connected most of the major islands, and connected the islands to continental Asia. During warm but short interglacial episodes, plants and animals retreated to isolated islands and peninsulas (Corlett, 2009; Woodruff, 2010). In other words, today’s biota can be regarded as the refugial-phase of Southeast Asia biodiversity (Cannon *et al.*, 2009; Woodruff, 2010). The sea-level is expected to continue rise with further warming (Hansen, 2007), which will compress the current land area slightly more. Marine barriers will remain, impeding latitudinal (and longitudinal) distribution changes, and hence reinforcing the conclusion that the survival of heat-sensitive species will depend on their capacity to retreat to relatively cool, montane areas.

5.3 Drivers of biodiversity loss and research priorities

Biodiversity in Southeast Asia is seriously threatened by multiple stressors including habitat loss, overexploitation and invasion (Bradshaw *et al.*, 2009; Nijman, 2010; Peh, 2010; Sodhi *et al.*, 2010a). Increasing demand for agriculture products (e.g. oil palm) and timber has led to rapid rates of forest conversion, with the annual forest loss faster than in any other tropical regions (Sodhi *et al.*, 2004; Sodhi *et al.*, 2010a; Wilcove & Koh, 2010). More than half of the primary forests have already been destroyed and no more than a quarter will be left by the end of this century (Achard *et al.*, 2002), threatening 13-85% of species (Sodhi *et al.*, 2010a). Protected areas cover only 13.4% of the land area in the region (Sodhi *et al.*, 2004). On top of that, climate warming emerges as a new driver that will further imperil the biodiversity (Brook *et al.*, 2008). As shown in this thesis, even species that are well-represented in protected areas may be at risk from climate change. However, very limited information is available to assess these risks, with Chen *et al.* (2009) representing, it seems, the first such study for any group of tropical insects. To establish the nature of the threat and what conservation actions might be needed, I highlight three areas of research to prioritize: (1) integration and reusing of museum / herbarium collections to evaluate range shifts (2) species distribution modeling to investigate range shifts, impediments due to fragmentation and to assess the effectiveness of the current protect area system, and (3) using tropical montane cloud forests as exemplars to study ecosystem services and degradation under climate warming

5.3.1 Reusing museum / herbarium collections

Distribution data are required to develop effective conservation strategies, including the evaluation and mitigation of the biological impacts under climate changes. To document range shifts, resurveys of historical sites / transects (e.g. Wilson *et al.*, 2005; Kelly & Goulden, 2008; Moritz *et al.*, 2008; Parolo & Rossi, 2008; Chen *et al.*, 2009) and the analysis of systematic biodiversity inventories (e.g. Konvicka *et al.*, 2003; Hickling *et al.*, 2006; La Sorte & Thompson, 2007) are the best approaches (Tingley & Beissinger, 2009). However, historical data are needed for such analyses, and they need to be of a sufficient standard / repeatable that it is possible to confirm that distribution changes have taken place, or what environmental drivers are most likely to be responsible for such changes; historical, baseline data are scarce in Southeast Asia and the original Mount Kinabalu moth transect may be a rare exception. In the absence of many formal historical transects, an alternative to detect species distributions changes through time is to make greater use of museum / herbarium collections (Graham *et al.*, 2004). Accuracy is the major concern using museum collections, particularly ensuring taxonomic consistency across specimens and georeferencing (Graham *et al.*, 2004). These data normally represent presence-only data; apparent absences will be a mixture of true absence and locations where a species is, or was, present, but where it has not been recorded (Graham *et al.*, 2004; Tingley & Beissinger, 2009). Nevertheless, if data can be obtained in sufficient quantity and over a sufficient time span, and appropriate statistical designs implemented, it should be possible to analyze distribution changes (e.g. Lenoir *et al.*, 2008; Bergamini *et al.*, 2009). The magnitudes of carried-out range shifts provide insights into meaningful future projections. Such research is at its early stages in Southeast Asia and deserves much more attention, particularly taking advantage of web networking and preferably, encouraging formal resurveys (Webb *et al.*, 2010).

5.3.2 Modeling species distribution changes in fragmented landscapes

Vertical migration will be the most likely response of species to survive global warming in Southeast Asia; however, there is no evaluation whether distribution shifts are practicable in areas where dramatic habitat losses have taken place. Lowland fragmentation hinders their connectivity to highland habitats and between reserve networks. Despite mounting evidence of monoculture plantations and other land-use changes altering species composition (e.g. Sodhi *et al.*, 2009; Wanger *et al.*, 2010), there is no empirical or modeling work addressing the capacity that species could “percolate” through mosaic landscapes in the region to find their way uphill (but see Koh *et al.* (2009) for sustainable design of oil palm plantation; Barlow *et al.* (2007), Berry *et al.* (2010) for conservation value of logged forest; Benedick *et al.* (2006), Sodhi *et al.* (2010b) for conserving heterogeneous landscape). Thus, it is urgently required that species distribution modeling evaluates range shifts in fragmented habitats, using methods that combine bioclimate models with population dynamics, that consider different dispersal abilities.

Protecting elevation gradients has suggested to be effective conservation approach (Bush, 2002; Killeen & Solórzano, 2008), even though some unexpected threats may still occur (Chen *et al.*, 2011). This work programme would need to assess whether current configuration of protected areas supports uphill movements and their future success of maintaining biodiversity under rapid climate regime shifts (Malcolm *et al.*, 2006; Williams & Jackson, 2007; Lee & Jetz, 2008; Klorvuttimontara, 2010). Moreover, large scale range shifts may involve species crossing boundaries between countries, and so require multi-government conservation actions (Hannah, 2010). The "Heart of Borneo" initiative is a multi-country protected area scheme, which would benefit from a sound scientific basis to assess how it will (and could with modification) accommodate range shifts and compensate for extinction risks outside protected areas (Rautner *et al.*, 2005; Struebig *et al.*, 2010).

5.3.3 Cloud forest degradation and ecosystem service changes

Tropical montane cloud forests (TMCF) are distinct forests on tropical mountain slopes that only exist where there is frequent cloud or fog immersion (Bubb *et al.*, 2004). TMCF are important systems considering their ecosystem functions. Provisioning and regulating services that TMCF provide are vital to regional livelihoods as they intercept cloud moisture and help regulate dry-wet season water supplies (van Dijk & Bruijnzeel, 2001; Bruijnzeel, 2004; Ponette-González *et al.*, 2010). From the biodiversity point of view, they are rare habitats occur approximately 0.26 percent of the Earth's land surface (Bubb *et al.*, 2004) but harbor disproportionally high numbers of endemic species (Leo, 1995; Long, 1995; Anderson & Ashe, 2000; Pineda & Halffter, 2004). In Borneo, more than half of the endemic birds and mammals are confined to montane cloud forests (Peh *et al.*, 2011).

The dynamic hydro-climate system renders the TMCF sensitive to climate change and other human activities (Foster, 2001; Bush, 2002; Anchukaitis & Evans, 2010; Figueroa-Rangel *et al.*, 2010). In Costa Rica, biodiversity loss and invasion by lowland species have been observed and related to the elevated cloud base, which itself has been linked to global warming (Pounds et al., 1999; Still et al., 1999; Pounds et al., 2006). Nevertheless, lowland deforestation and agriculture land-use may well contribute to cloud decreases through changes to the hydrological balance (Lawton *et al.*, 2001; Nair *et al.*, 2003; Ponette-González *et al.*, 2010). The preliminary reported in this thesis, that moth populations have disproportionately declined in the cloud forest zone of Mount

Kinabalu, indicates that the degradation of cloud forest ecosystem are not restricted to the Neotropics. This is a particular concern for conservation because both the Mount Kinabalu and Monteverde (in Costa Rica) cloud forests are entirely contained within protected areas; but their regional climatic conditions are likely being compromised by the dual impacts of global climate change and downslope deforestation affecting the regional climate.

Southeast Asia contains 60% of global TMCF (Bubb 2004) but is losing it at alarming rates across the region; however, there is insufficient research of its impacts on ecosystem funtions and services. For example, Malaysia has lost 23% of its cloud forest due to agriculture expansion, logging, road construction and tourism (Peh *et al.*, 2011). The direction and magnitude of future changes to TMCF are uncertain under all of these anthropogenic drivers, as are the impacts on the ecological and economic services they provide. With its environmental significance, TMCF should serve as excellent model systems to understand the combined impacts of climate warming and other drivers of environmental change on ecosystems (Brook *et al.*, 2008; Laurance & Useche, 2009; Gasner *et al.*, 2010; Montoya & Raffaelli, 2010) and ultimately their effects on human life (Guariguata & Balvanera, 2009; Lele, 2009).

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