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SPECIAL
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The determinants of land snail diversity along a tropical elevational gradient: insularity, geometry and niches

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ABSTRACT

Aim We investigated the patterns of species richness in land snails and slugs along a tropical elevational gradient and whether these patterns correlate with area, elevation, geographic constraints, and productivity. We did so both at the scale at which land snail population processes take place and at the coarser scale of elevational zones.

Location Mount Kinabalu (4096 m) and the adjacent Mount Tambuyukon (2588 m) in Kinabalu Park, Sabah, Malaysian Borneo.

Methods We used an effort-controlled sampling protocol to determine land snail and slug species richness in 142 plots of 0.04 ha at elevations ranging from 570 to 4096 m. Extents of elevational ranges were determined by interpolation, extended where appropriate at the lower end with data from lowlands outside the study area. We used regression analysis to study the relationships between species density and richness on the one hand and elevation and area on the other. This was done for point data as well as for data combined into 300-m elevational intervals.

Results Species density (based on the individual samples) showed a decline with elevation. Elevational range length profiles revealed that range lengths are reduced at greater elevations and that a Rapoport effect is absent. Diversity showed a mild mid-domain effect on Kinabalu, but not on Tambuyukon. When the data were combined into 300-m elevational intervals, richness correlated more strongly with elevation than with area. Ecomorphospace was seen to shrink with increasing elevation.

Main conclusions The elevational species richness patterns show the combined effects of (1) reduced niche diversity at elevations with lower productivity and (2) historical events in which the upward migration of lowland species as well as the speciation of highland endemics took place.

Keywords

Biodiversity, Borneo, elevation, Gastropoda, Malaysia, mid-domain effect, Mollusca, range size, snails.

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INTRODUCTION

One of the most striking macroecological (Brown & Maurer, 1989) rules is the negative relationship between latitude and species richness. For most taxa, richness increases towards the equator and decreases towards the poles (Gaston, 2000).

This must mean that the balance between species appearance (speciation) and disappearance (extinction) shifts as one

moves along a latitudinal gradient. Over the years, more than 25 mechanisms have been proposed for why this shift in balance should occur. Many of these mechanisms emphasize either greater species origination in the tropics ('cradle' hypothesis) or reduced extinction in the tropics ('museum' hypothesis; Chown & Gaston, 2000).

Support for cradle effects exists in the form of evidence for greater speciation rates in the tropics owing to greater area

(hence, more opportunity for geographic isolation; Rosenzweig, 1995), higher mutation rates (hence, more opportunity for speciation triggered by evolutionary novelty; Rohde, 1992), or more available niches (hence, more opportunity for ecological speciation; Roy *et al.*, 1994). Support for museum effects also exists, namely as evidence for reduced extinction rates in the tropics owing to greater area (hence, larger populations, which are less prone to demographic collapse; Rosenzweig, 1995).

Several authors have argued, however, that the latitude–richness gradient could be explained only or chiefly by geometry. Such explanations are, to a greater or lesser degree, divorced from speciation and extinction processes, and hence could be considered ‘neutral’. One explanation, the mid-domain effect (MDE; Colwell & Hurtt, 1994; Grytnes *et al.*, 2008), stresses that ranges of random size, when constrained by boundaries on two sides (i.e. the poles), will always show the greatest degree of overlap in the mid-range (i.e. the equator). Rapoport’s rule, finally, states that species ranges tend to be smaller in the tropics, and hence are more packed, also leading to a latitudinal gradient in richness (Rapoport, 1982; Stevens, 1989).

With so many factors possibly involved, identifying the ones responsible is very difficult, especially because most factors that have been deemed to be relevant (e.g. area, temperature, productivity, seasonality, precipitation) all vary with latitude in a similar fashion (Willig *et al.*, 2003). Rahbek (1997, 2005) and Körner (2000), among others, suggested that studies of montane diversity may aid in bringing clarity. Elevational gradients in species richness are almost as well known as latitudinal ones (Gaston, 2000), and, assuming they have similar causes (McArthur, 1972; Brown, 1988), might suffer less from confounding factors than latitudinal richness gradients, especially in taxa for which both the elevational and latitudinal scales of analysis are greater than the spatial scale at which population processes occur. A given elevational gradient is subject to invariant solar influx, biogeographical history and evolutionary history, and, in some parts of the humid tropics, elevational gradients are not affected by seasonality. Area and temperature are the only factors that decline monotonically with elevation. However, the methodological issues relating to interpolating and extrapolating elevational distribution ranges from incomplete data can be problematic (Rahbek, 1997, 2005; Grytnes & Vetaas, 2002).

Here, we obtain detailed (142 sampling points) data on land snail species richness along a 3500-m-long elevational gradient in the tropics. For land snails, the characteristic dispersal distance tends to be of the order of metres (Schilthuizen & Lombaerts, 1994; Pfenninger *et al.*, 1996; Giokas & Mylonas, 2004), which means that the population processes responsible for what Rosenzweig (1995) terms ‘point diversity’ take place at a scale that is small relative to both elevational and latitudinal gradients. By choosing a grain size (Rahbek, 2005) that is of the same order of scale as land snail population processes, and then scaling up from there, we aim to identify the relative roles of area and productivity in producing

elevational (and perhaps also latitudinal) gradients in species richness.

MATERIALS AND METHODS

Kinabalu Park (6°10′ N, 116°39′ E) is located in the state of Sabah in Malaysian Borneo (Fig. 1). There is a single mountain system within this park, consisting of two main peaks, Mount Kinabalu (4095 m) and Mount Tambuyukon (2588 m), connected by a saddle at c. 2000 m. The two mountains include a number of major geological substrates, such as rock debris and alluvium, ultrabasic and basic rock, granodiorite, and sedimentary rock. Uplift occurred in several stages. Initially (11–17 Ma; Hall, 1998), ultrabasic rocks intruded, forming Mount Tambuyukon and the ultrabasic parts of Mount Kinabalu (Collenette, 1964). Then, beginning 9 Ma, the Kinabalu batholith intruded (Jacobson, 1970). Finally, 1.5 Ma, the Kinabalu granodiorite moved upwards, followed by a final uplift of the Kinabalu core, c. 1 Ma. Thus, the mountain reached its present height and shape relatively recently. Current vegetation comprises 21 types, which are mostly correlated with elevation and rock type (Kitayama, 1991). Mean air temperature declines by 0.55 °C with every 100 m increase in elevation, ranging from 28 °C at sea level to 8 °C at 3780 m (Kitayama *et al.*, 1999). Total yearly precipitation is constant (2600–2900 mm year^{−1}) from sea level to 2500 m, but then increases to 3600 mm year^{−1} at 3200 m and above (Kitayama, 1995). Net primary productivity data are not available for Kinabalu, but in general temperature combined with water availability correlate well with productivity (Zheng *et al.*, 2003). Because water availability is relatively constant on Kinabalu but temperature declines with elevation (see above), we assume elevation to be a good proxy for productivity [although Takyu *et al.* (2003) have pointed out that the type of bedrock can produce differences of a factor of 2.5 among productivities at the same elevation].

One hundred and forty-two 20 m × 20 m plots were set up in undisturbed forest along seven sampling transects. Each plot was at a distance of 100–250 m in elevation from adjacent ones along a given transect (Fig. 1). Sampling was performed from December 2004 to November 2005. Each plot was searched for both dead and living macrosnails for two person hours, and 2.5 L of soil and leaf litter was gathered. The soil was subsequently dried in an oven and disaggregated through a series of sieves (5.0, 2.0 and 0.5 mm). Microsnail shells were extracted by searching the dried and finely sieved samples under a dissection microscope. All specimens were identified to species level where possible. Identification and nomenclature follow J.J. Vermeulen, M. Schilthuizen & T.-S. Liew (unpublished manuscript) with reference to the *BORNEENSIS* mollusc collection at Universiti Malaysia Sabah. Species that have not yet been described are indicated by using provisional names in quotation marks (“ ”). All the specimens were deposited in *BORNEENSIS* and the Sabah Parks Zoological Museum.

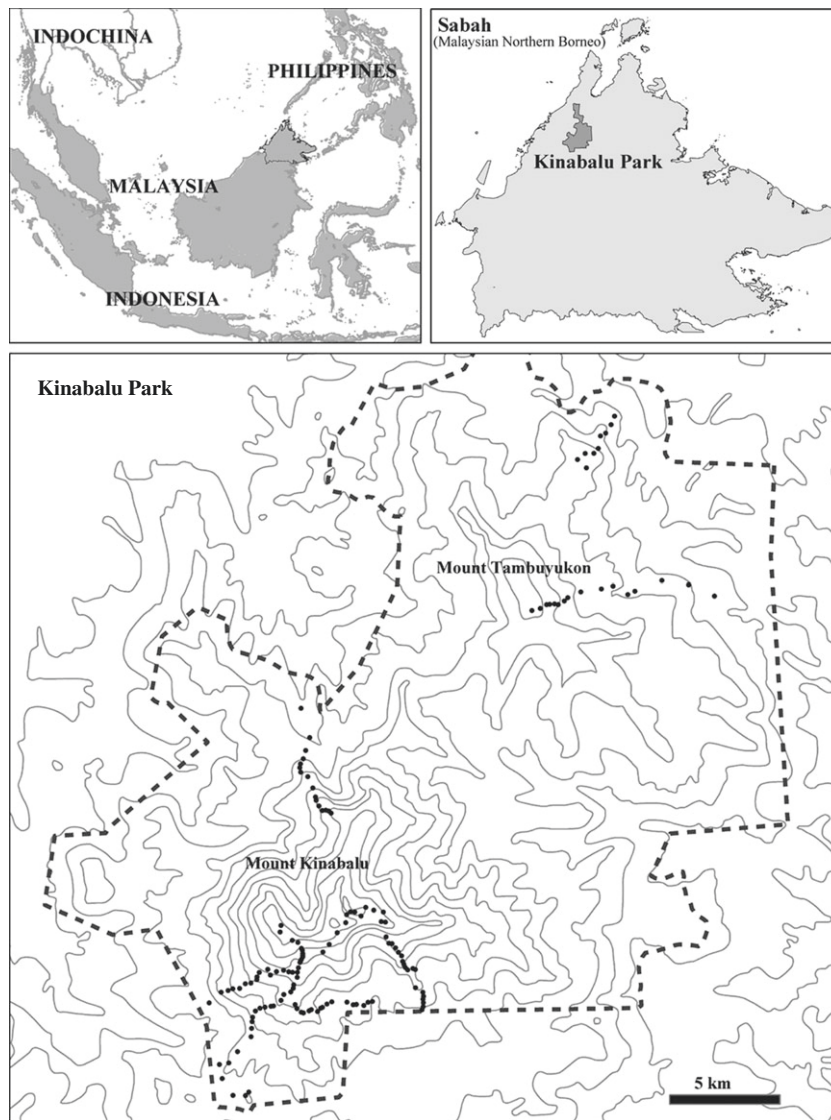


Figure 1 Map of Kinabalu Park, Sabah, Malaysia, with locations of the sampling points (solid circles) for land snails.

Species density was determined for each plot, and the relationship with the elevation of each plot was tested with Spearman's correlation and regression. In principle, the elevational range for each species was acquired from its recorded distribution at maximum and minimum elevations for each of the mountains. However, for common lowland species known to occur at lower elevations outside our transects, we determined the lowest extent based on previous intensive but non-standardized sampling in the vicinity of Kinabalu Park (M. Schilthuizen, T.-S. Liew & J.J. Vermeulen, unpublished data; Schilthuizen, 2004; Schilthuizen & Liew, 2009; Liew *et al.*, 2009). An elevational range profile (e.g. Patterson *et al.*, 1998) was produced by plotting the ranked elevational mid-points, minima and maxima of the elevational ranges of the species for each mountain.

To examine large-scale elevational patterns of richness, we used 300-m elevation intervals, which were determined for

both peaks separately. The species richness for each elevation interval was obtained from three methods: (1) observed number of species, (2) number of species estimated from each species' elevational range, and (3) rarefied number of species (calculated with ESTIMATES 7.5.1). For each elevation interval, area was calculated using 3D analyst tools in ARCGIS 9.2.

We then used regression analysis to examine the relationships among species richness, area and elevation. Because of the curvilinearity of the species–area relationships, area was log-transformed prior to the analysis (Conner & McCoy, 1979; McCain, 2007).

The observed patterns of species richness were further analysed to consider the MDE. The MDE null model was calculated with RANGEMODEL 4.0 (Colwell, 2005). Simulations were carried out by randomly placing the empirical elevational ranges and range mid-points (derived as above) between the two ends of the extent (Colwell & Lees, 2000). Five thousand

resamplings without replacement were performed. The effect of the MDE on species richness was estimated by regression analysis between simulated species richness and empirical species richness.

Microhabitat and resource use is unknown for the majority of Malaysian land snail species. However, many shell traits in land snails are known to correlate well with geometric, hydrological, thermal, nutritional, and other aspects of niche use. Based on generalizations in Cain (1977) and Goodfriend (1986), for each species (except for the five species of slug) we scored maximum values for four quantitative shell traits in which relevance for niche use has been demonstrated repeatedly, namely shell height, shell width, aperture height and aperture width. These variables were log-transformed and subjected to a principal components analysis in PC-ORD 4.14 (McCune & Mefford, 1999). The volume of morphospace occupied, which was interpreted as a proxy for niche-use diversity, was visualized for elevational intervals of 500 m.

Unless indicated otherwise, all statistics were carried out in SPSS (release 11.0.; SPSS, Chicago, IL, USA).

RESULTS

We found a total of 2832 individuals belonging to 109 species (82 species on Kinabalu, 66 species on Tambuyukon, 39 species shared by the two mountains). The full dataset is presented in Appendix S1 in the Supporting Information. Species density decreased significantly ($P < 0.001$) with increasing elevation (Fig. 2). The elevational patterns of species density were best described by cubic models. There was no relationship between abundance and elevation ($r_s = 0.012$, $P = 0.883$). The regression analyses showed (Table 1) that all richness measures displayed, on Kinabalu as well as on Tambuyukon, significant negative correlations with both elevation and area. The elevational range profiles for Mount

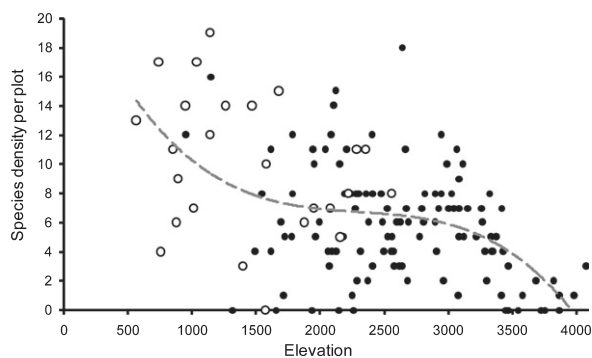


Figure 2 Elevational relationship for land snail species richness. Solid and open symbols represent data from transects along Mount Kinabalu and Mount Tambuyukon, respectively. Species density decreased significantly with increasing elevation ($r_s = -0.360$, $P < 0.001$). The dashed line indicates the cubic model that best describes the pattern: $y = -8 \times 10^{-10}x^3 + 5.8 \times 10^{-6}x^2 - 1.57 \times 10^{-2}x + 21.160$, $R^2 = 0.264$.

Table 1 Results for regression analyses between elevational interval and species richness for three species richness measures of land snails on Mount Kinabalu (number of elevational intervals = 10) and Mount Tambuyukon (number of elevational intervals = 7). The coefficients of determination (R^2) and significance value indicate the fit of the species richness to a quadratic model for Mount Kinabalu and to a linear model for Mount Tambuyukon, respectively (see text).

	Kinabalu		Tambuyukon	
	R^2	P -value	R^2	P -value
Richness versus elevation				
Observed	0.836	0.002	0.674	0.024
Estimated	0.875	0.001	0.959	0.000
Rarefied	0.875	0.022	0.832	0.005
Estimated richness versus				
Log(area)	0.540	0.024	0.697	0.019
Log(area) + elevation	0.795	0.009	0.965	0.001

Kinabalu and Mount Tambuyukon (Fig. 3) show that species occurring below 1600 m mostly have long elevational ranges: almost half of the lowland species ranges extend above 2000 m. In contrast, most species with elevational mid-points above 1600 m have much shorter ranges. In the MDE analysis, MDE

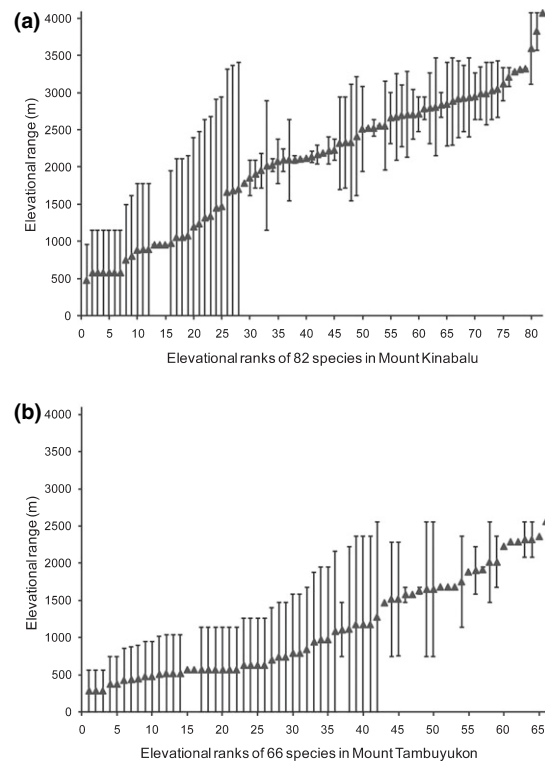


Figure 3 Elevational range profiles for land snails on (a) Mount Kinabalu and (b) Mount Tambuyukon. Bars indicate the maximum and minimum elevational limits for each species' range, and species are arranged along the horizontal axis by ranked elevational mid-points.

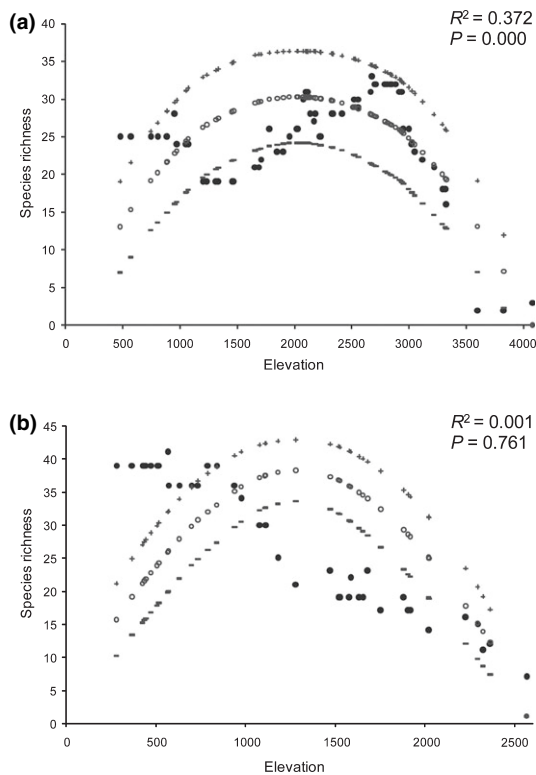


Figure 4 Mid-domain effect (MDE) analysis of land snails on Mount Kinabalu and Mount Tambuyukon. The solid circles represent empirical species richness, and the open circles are simulated species richness by random placement of empirical elevational ranges. The results for (a) Mount Kinabalu and (b) Mount Tambuyukon are shown separately. Plus and minus signs represent 95% simulation limits.

explained 37% of the variation of richness for Mount Kinabalu (Fig. 4a). On Mount Tambuyukon, the species richness patterns were not accounted for by the MDE (Fig. 4b). The analysis of ecomorphospace, finally, revealed that ecomorphospace occupied by the species assemblage at each elevational interval declined with elevation (Fig. 5).

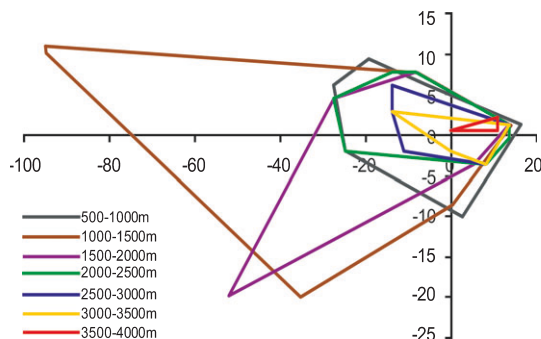


Figure 5 Ecomorphospace occupied by land snails at various 500-m elevational intervals, shown for Mount Kinabalu. The two axes represent 99% of the variation contained in four quantitative shell characters.

DISCUSSION

Temperature, productivity, area and MDEs have all been implicated in producing the observed macroecological patterns of increased richness with lower latitudes and lower elevations. However, although elevational and latitudinal gradients in species richness are often considered to mirror one another, Rahbek (2005), in a review of over 200 elevational gradient studies, pointed out that, in fact, decreases of richness with elevation are less common than hump-shaped patterns, especially in large-scale, properly controlled studies. In latitudinal gradients, on the other hand, mid-range peaks are extremely rare (Rosenzweig, 1995; Lyons & Willig, 1999). This might suggest that MDE is an important factor, because it is the only factor that would simultaneously produce a peak at low latitudes and at mid-elevations. However, Rahbek (1997, 2005) also pointed to the role of spatial scale. Processes responsible for producing the richness gradients are often implicitly considered to be scale-independent, which is why latitudinal and elevational gradients are often assumed to be directly comparable. This may be inappropriate, because Rahbek found a strong effect of the scale of the analysis. In elevational gradients, hump-shaped patterns are reported mostly when data points are pooled into elevational intervals, whereas when the individual data points are considered, the predominance of hump-shaped patterns disappears, especially when the basic unit of analysis (the 'grain size') is very small.

Rahbek's (2005) review highlights the necessity of considering spatial scale in analyses of elevational gradients of species richness, especially with reference to the spatial scale at which population processes take place in the taxon under consideration. Sessile animals with low dispersal and limited gene flow (such as land snails) might be a particularly fortuitous choice of organism, because their low vagility may cause determinants of richness to vary strongly with spatial scale. At the scale of land snail deme size (often no more than several tens of square metres; Schilthuizen & Lombaerts, 1994; Arnaud & Laval, 2004; Giokas & Mylonas, 2004), patterns of richness are likely to be strongly determined by population processes: dispersal, local extinction, and competition. At a greater spatial scale, the effects of historical biogeographical developments in range size and extent will probably become more important.

We find that these effects of the scale of analysis show up in our study. As in similar studies of malacofauna along elevational gradients (e.g. Tattersfield *et al.*, 2001; Aubry *et al.*, 2005), we found a decline of species richness with increasing elevation, when considering the smallest spatial scale, that of the 400-m² grain size (Fig. 2). Notably, we found that the decline is not linear, but conforms to a cubic curve, with much scatter about the curve and a lack of a distinct trend between 1800 and 2800 m. This is possibly associated with the fact that at mid-elevations variation in type of bedrock (and associated edaphic parameters) is greatest, leading to increased differentiation in vegetation type and productivity (Kitayama, 1991; Takyu *et al.*, 2003).

After interpolating the data from the sampling points to infer elevational species ranges, we found that the elevational range profiles for Kinabalu and on Tambuyukon are very similar, with longer ranges in the lowland and lower montane areas, and shorter ranges at higher elevations (Fig. 3). This similarity is particularly striking because the two mountains share only a small proportion of species assemblages, and thus the patterns are independent of species identities. Furthermore, the two peaks are different in elevation, which means that, if the profile shape were attributable to geometric constraints, the shift from long to short ranges would have happened at a lower elevation on Tambuyukon than on Kinabalu. The fact that this is not the case means that geometric constraints do not dictate these patterns. Moreover, the data do not conform to Rapoport's rule, because species at higher elevations appear to have shorter ranges, not longer ones. Many of these high-elevation short-range species are endemic: all 26 Kinabalu endemics have their range mid-points above 1600 m, and mostly have elevational ranges of 1000 m or less.

The non-randomness of range length also means that strong MDEs are not expected, because these require a relatively random distribution of long and short ranges between the elevational extremes. Correlating empirical species richness with simulated random placement of empirical range lengths indeed revealed relatively weak MDEs (Fig. 4). On Mount Kinabalu, the MDE explained 37% of the variation of richness. In fact, a bimodal richness pattern along the elevational gradient was found, with peaks at 1000 and 2600 m. On Tambuyukon, an MDE was not seen – rather, a monotonic decrease of richness. Colwell & Lees (2000) report that the magnitude and detectability of an MDE depend on the taxa involved, their range sizes, boundary constraints and sampling regions, and on underlying biological, climatic or historical determinants of species richness. The discrepancy in the effects of MDE on both mountains is thus most likely to result from the uplift of the Kinabalu pluton and the fact that glaciations have played a greater role on Kinabalu than on Tambuyukon (see below). Grytnes *et al.* (2008) tested for and found an MDE in vascular plant distribution data on Mount Kinabalu (which was best explained by a model in which all species were included that had their theoretical mid-point in the domain – a procedure similar to that followed by us).

Finally, we did not find a strong area effect. When we combined our data into 300-m elevational intervals, the estimated and observed species richness pattern was accounted for more strongly by elevation alone than by the surface area of the respective interval. Combining area and elevation effects did not improve the correlation that was found with elevation alone.

In summary, the richness patterns seen for land snails on Mount Kinabalu and the adjacent Mount Tambuyukon fall into two distinct categories. At the smallest spatial scale, that of individual 400-m² plots, species density falls with increasing elevation, presumably as a result of reduced productivity leading to fewer ways in which resources can be subdivided

into niches. This is reflected in the general trend for ecomorphospace to decline with elevation (but not in the numbers of individuals, which do not show an elevational trend; see above). At larger spatial scales, however, the richness patterns show a mixture of correlations, in which MDEs as well as direct effects of elevation and its ecological correlates play a role. In view of the low vagility of land snails and the high number of endemic species in the higher elevational zones of Kinabalu, we suggest that the following overall explanation of land snail diversity along this elevational gradient is realistic.

The uplift of Kinabalu has, in the lower elevational zones (up to c. 2500 m), mostly resulted in the differential upward range expansion of lowland and lower montane species. At the same time, adaptation to the more extreme elevational zones has led to frequent speciation in the higher elevational zones, possibly aided by the presence of nunataks among the glaciers that covered the summit of Kinabalu during the glaciations (Jacobson, 1970). This explains the elevational range profiles, which show a dichotomy of lowland species that have their lowest occurrence at sea level, and highland species that are restricted to a relatively short range at high elevation. This scenario produces the MDE signal on Kinabalu because of the mid-elevation overlap of upward-dispersing lowland species and their high-elevation-restricted endemic evolutionary descendants. Tambuyukon, which is much lower, has a relatively small number of high-elevation species, and no endemics, which explains the absence of an MDE there. Productivity declines with increasing elevation on both mountains, however, and the species density decreases in concert because of the lower number of available niches. This produces the elevational gradient in species density, and, at a larger scale, combines with the above-mentioned MDE to result in idiosyncratic patterns on the two mountains.

In conclusion, we do agree in principle with Körner (2000) that mountains hold the key to understanding macroevolutionary patterns of diversity. Mountains are somewhat less complex because fewer interrelated factors need to be accounted for than in latitudinal gradients. However, even in relatively small, insular and uniform mountains such as Kinabalu, differences in the spatial scale of analysis can produce very different interpretations (Rahbek, 2005).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Abundance of the land snail species that were found in the standard sampling.

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